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Contributors

Bennett, Alfred W. 1833-1902.
Thiselton-Dyer, William T. 1843-1928.
Sachs, Julius, 1832-1897.
Royal College of Physicians of Edinburgh

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TEXT-BOOK OF BOTANY

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Oxford

TEXT-BOOK

OF

BOTANY

MORPHOLOGICAL AND PHYSIOLOGICAL

BY

JULIUS SACHS

PROFESSOR OF BOTANY IN THE UNIVERSITY OF WÜRZBURG



TRANSLATED AND ANNOTATED

BY

ALFRED W. BENNETT, M.A., B.Sc., F.L.S.

LECTURER ON BOTANY AT ST. THOMAS'S HOSPITAL

ASSISTED BY

W. T. THISELTON DYER, M.A., B.Sc., F.L.S.

SOMETIME JUNIOR STUDENT OF CHRIST CHURCH, OXFORD

Oxford

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PREFACE.

This Text-book of Botany is intended to introduce the student to the present state of our knowledge of botanical science. Its purpose is not only to describe the phenomena of plant-life which are already accurately known, but also to indicate those theories and problems in which botanical research is at present especially engaged; the arrangement of the material and the mode of treatment of the separate subjects are adapted to this purpose. Detailed discussions of questions of minor importance have been avoided, as these would only mar clearness of outline in the design; critical remarks have been introduced occasionally where they seemed necessary, in order to determine facts, or to justify the views taken on matters of fundamental importance.

The historical development of botanical views and theories does not seem to come within the scope of a Text-book of Botany, and would only interfere with the unity of design of the work. It would therefore be superfluous to quote scientific works which have only a historical interest. In the references which will be found in the work the chief object has been to introduce the student to those writings in which he will find a fuller discussion of those parts of the subject which have been only touched on briefly. In some cases the writings of others have been quoted because they represent views different from those of the author, and because it is desirable to place the student in a position to form a judgment for himself. Others again of the references are simply for the purpose of citing the authorities on which reliance is placed for statements that have not come within the range of the author's own observation. The reader of this work will at least learn the names and standing of those workers who have in recent times contributed most essentially to the science of which it treats.

By far the greater number of the illustrations are original, many of them the result of laborious investigation. Where they have been copied the name of the author from whom they are borrowed is in each case given in the description; illustrations from other sources are used only when the objects themselves have not been accessible, or when it seemed impossible to obtain better ones.

The Table of Contents will give sufficient indication of the plan of the work; the Index should be consulted for references to other parts of the book where an explanation of technical terms will be found when their meaning does not appear in any particular passage.

TRANSLATOR'S PREFACE.

In introducing to the English public Sachs's 'Lehrbuch der Botanik' in an English form, the translator believes that he is supplying a want which has long been felt by English botanical students. Our own literature has not at present produced any work at once so comprehensive in its scope and so minute and accurate in its details,—qualities which have recommended the German work to every one familiar with that language.

In the notes the citations of authorities have been somewhat increased. It has also seemed desirable sometimes to depart from the author's rule of passing over authorities whose interest is now chiefly historical. References have been given to English and French translations of many of the papers and memoirs quoted, as these are at any rate often more accessible in this country than the originals.

On several points additional matter has been introduced into the footnotes. With respect to these the translator has to acknowledge the kind help of numerous scientific friends, amongst whom he may more especially mention Professor W. C. Williamson, Mr. H. C. Sorby, and Professor W. R. Mc Nab. In the selection of English expressions for German technical terms he has also in many instances had recourse to their advice. One case of great difficulty may be pointed to in 'Stoffwechsel'; as an equivalent to this the term 'Metastasis' has been used. It had already been employed in a more restricted although analogous way by Graham; speaking of the mutability of colloids due to internal molecular rearrangements, that distinguished chemist says, 'Their existence is a continued metastasis' (Journ. Chem. Soc. 1862, p. 217).

The fourth edition of the German work has been passing through the press concurrently with the printing of this edition. Where possible the new matter introduced into it, or the new views adopted by the author, are referred to in the footnotes to the present edition. The new classification of Cellular Cryptogams adopted by Sachs will be found at p. 847.

A. W. B.

LONDON, *February* 1875.

ERRATA.

P. 16, l. 10 *from bottom, and description to Fig.* 13; *for* antheridium *read* globule.
P. 25, l. 4 *from bottom; after* Bordered Pits *insert reference to footnote* 2.
P. 30, l. 18, *for* exospores *read* exospore.
P. 64, *first line of footnote; for* p. 254 *read* p. 252.
P. 65, l. 12 *from bottom; for* Salms-Laubach *read* Solms-Laubach.
P. 65, *last line; for* Gingko biloba *read* Salisburia adiantifolia.
P. 82, l. 2; *for* colourless *read* coloured.
P. 101, l. 5; *dele* previous.
P. 101, l. 6; *for* cannot be *read* has not been.
P. 106, l. 19; *for* bundle *read* bundles.
P. 112, l. 3; *for* Asclepiadæ *read* Asclepiadeæ.
P. 147, l. 40; *for* root-bearers *read* rhizophores.
P. 148, *footnote; for* Oaniopsis *read* Calliopsis.
P. 241; *omit* 3*rd footnote.*
P. 254, *footnote; for* Rees *read* Reess.
P. 279, l. 6 *from bottom*; *for* p. 287 *read* p. 291.
P. 287, *description to Fig.* 207; *for* antheridia *read* globules.
P. 288, *description to Fig.* 208; *for* antheridium *read* globule.
P. 296, l. 3 *of footnote; for* Synopsia *read* Synopsis.
P. 307, *first line of description to Fig.* 222; *for* its *read* a.
P. 327, l. 9 *from bottom; for* colourless cells elongated in a parenchymatous manner *read* elongated colourless parenchymatous cells.
P. 340; *the reference in footnote to Ray Society's publication should follow that to Hofmeister's papers.*
P. 361, l. 4 *from bottom; for* the single *read* a single.
P. 454, l. 11 *of footnote; dele* entire.
P. 456, l. 6 *from bottom; dele the first* archegonium.
P. 585, l. 14; *for* Balanophoræ *read* Balanophoreæ.
P. 647, l. 9 *from bottom; for* Sect. 8 *read* Sect. 7.
P. 770, *footnote; for* Ailanthus malabarica *read* Ailantus excelsa.

CONTENTS.

BOOK I.

GENERAL MORPHOLOGY.

CHAPTER I.

Morphology of the Cell.

PAGE

Sect. 1. Preliminary Inquiry into the Nature of the Cell 1
„ 2. Difference in the Forms of Cells 5
„ 3. Formation of Cells 7
„ 4. The Cell-Wall 19
„ 5. Protoplasm and Nucleus 37
„ 6. The Chlorophyll-Bodies and similar Protoplasmic Structures . . . 45
„ 7. Crystalloids 49
„ 8. Grains of Aleurone (Proteine-grains) 51
„ 9. Starch Grains 56
„ 10. The Cell-sap 62
„ 11. Crystals in the Cells of Plants 64

CHAPTER II.

Morphology of Tissues.

Sect. 12. Definition 68
„ 13. Formation of the Common Wall of Cells combined into a Tissue . . 70
„ 14. Forms and Systems of Tissues 77
„ 15. The Epidermal Tissue 79
„ 16. The Fibro-vascular Bundles 92
„ 17. The Fundamental Tissue 102
„ 18. Laticiferous and Vesicular Vessels; Sap-conducting Intercellular Spaces; Glands 109
„ 19. The Primary Meristem and the Apical Cell 117

CHAPTER III.

Morphology of the External Conformation of Plants.

PAGE

Sect. 20. Difference between Members and Organs. Metamorphosis . . . 128
„ 21. Leaves and Leaf-forming Axes 131
„ 22. Hairs (Trichomes) 138
„ 23. The Root 140
„ 24. Various Origin of Equivalent Members 148
„ 25. Different Capacity for Development of the Members of one Branch-system 155
„ 26. The Relative Positions of Lateral Members on a Common Axis . . 166
„ 27. Directions of Growth 182
„ 28. Characteristic Forms of Leaves and Shoots 190
„ 29. Alternation of Generations 202

BOOK II.

SPECIAL MORPHOLOGY

AND OUTLINES OF CLASSIFICATION.

Group I. **Thallophytes** 207
Class 1. Algæ 208
„ 2. Fungi 238
Group II. **Characeæ** 278
Class 3. Characeæ 278
Group III. **Muscineæ** 292
Class 4. Hepaticæ 296
„ 5. Mosses 311
Group IV. **Vascular Cryptogams** 335
Class 6. Ferns 340
„ 7. Equisetaceæ 362
„ 8. Ophioglossaceæ 378
„ 9. Rhizocarpeæ 383
„ 10. Lycopodiaceæ 400
Group V. **Phanerogams** 421
Class 11. Gymnosperms 433
Sub-group. Angiosperms 466
Class 12. Monocotyledons 541
„ 13. Dicotyledons 556

BOOK III.

PHYSIOLOGY.

CHAPTER I.

Molecular Forces in the Plant.

PAGE

Sect. 1. The Condition of Aggregation of Organised Structures 587
„ 2. Movement of Water in Plants 598
„ 3. Movements of Gases in Plants 614

CHAPTER II.

Chemical Processes in the Plant.

Sect. 4. The Elementary Constituents of the Food of Plants 618
„ 5. Assimilation and Metastasis 626
„ 6. The Respiration of Plants 644

CHAPTER III.

General Conditions of Plant-life.

Sect. 7. The Influence of Temperature on Vegetation 647
„ 8. Action of Light on Vegetation 659
„ 9. Electricity 687
„ 10. Action of Gravitation on the Processes of Vegetation 690

CHAPTER IV.

The Mechanical Laws of Growth.

Sect. 11. Definition 692
„ 12. Various Causes of Growth 695
„ 13. General Properties of the Growing Parts of Plants 697
„ 14. Causes of the Condition of Tension in Plants 708
„ 15. Phenomena due to the Tension of Tissues in the Growing Parts of Plants . 715
„ 16. Modification of Growth caused by Pressure and Traction 729
„ 17. Cause of the Growth in Length under constant External Conditions . . 735
„ 18. Periodicity of Growth in Length caused by the alternation of Day and Night 743

PAGE

Sect. 19. Effect of Temperature on Growth 748
„ 20. Action of Light on Growth.—Heliotropism 752
„ 21. Influence of Gravitation on Growth.—Geotropism 758
„ 22. Unequal Growth 765
„ 23. Torsion 770
„ 24. The Twining of Climbing Plants 772
„ 25. The Twining of Tendrils 775

CHAPTER V.

Periodic Movements of the Mature Parts of Plants and Movements dependent on Irritation.

Sect. 26. Definition 782
„ 27. Review of the Phenomena connected with Periodically Motile and Irritable Parts of Plants 783
„ 28. Mobile and Immobile Condition of the Motile Parts of Plants . . . 788
„ 29. Mechanism of the Movements 792

CHAPTER VI.

The Phenomena of Sexual Reproduction.

Sect. 30. The Essential Element in the process of Sexual Reproduction . . . 801
„ 31. Influence of the origin of the Reproductive Cells on the product of Fertilisation 807
„ 32. Hybridisation 816

CHAPTER VII.

The Origin of Species.

Sect. 33. Origin of Varieties 822
„ 34. Accumulation of new characters in the Reproduction of Varieties . . 826
„ 35. Causes of the Progressive Development of Varieties 830
„ 36. Relationship of the Morphological Nature of the Organ to its adaptation to the Conditions of Plant-life 835
„ 37. The Theory of Descent 842

APPENDIX 847

INDEX 849

BOOK I.

GENERAL MORPHOLOGY.

CHAPTER I.

MORPHOLOGY OF THE CELL.

Sect. 1. **Preliminary Inquiry into the Nature of the Cell.**—The substance of plants is not homogeneous, but is composed of small structures, generally indistinguishable by the naked eye; and each of these, at least for a time, is a whole complete in itself, being composed of solid, soft, and fluid layers, different in their chemical nature, and disposed concentrically from without inwards. These structures are termed Cells. For the most part, a group of them are in close contact and firmly united; they then form a Cell-tissue. But every plant which completes its term of life has at least one period in which certain cells separate themselves at definite points from the union, and, after isolation, each begins for itself a separate course of life (spores, pollen-grains, ovum-cells, gemmæ).

The shape and size of the whole plant, the form, structure, and volume of the cells are subject to regular changes, and their nature cannot therefore be inferred from the knowledge of one single phase, but rather from the sum of changes which may be called the life-history of the cell. And as, moreover, each cell fulfils its own definite part in the economy of the plant, *i. e.* is specially intended for certain chemical or mechanical purposes, so also cells show a variety in form, which corresponds to the different functions. These differences, however, do not usually arise until the cells have passed through their earlier stages; the youngest cells of a plant are only slightly distinguishable from one another.

The law of configuration that prevails in all cells is also more clearly evident in the young state; the more the developing cells assume the special purposes for which they exist, the more difficult it becomes to recognise this law. The morphological law of cells, thus briefly pointed out, we will now endeavour to expound more in detail.

By far the largest proportion of cells in the living succulent parts of plants, *e. g.* young roots, leaves, internodes, fruits, are seen to be made up of three

concentrically-disposed layers: firstly, an outer skin, firm and elastic, the Cell-membrane or Cell-wall, consisting of a substance peculiar to itself, which we call Cellulose (Fig. 1, *B*, *C*, *h*). Close up to the inner side of this entirely closed membrane is a second layer, also entirely closed, the substance of which is soft and inelastic, and always contains albuminous matter; H. v. Mohl, who first discovered this substance, has given it the very distinctive appellation of Protoplasm [1]. In the condition of cells now under consideration it forms a sac enclosed by the cell-wall, in which usually also other portions of protoplasm are present in the form of plates and threads (Fig. 1, *B*, *C*, *p*). Absent from some of the lowest organisms, but present in all the higher plants without exception, there lies imbedded in the protoplasm a roundish body, the substance of which is very similar to that of the protoplasm, the Nucleus (Fig. 1, *A*, *C*, *k*). The cavity enclosed by the protoplasm-sac is filled with a watery fluid, the Cell-sap (Fig. 1, *B*, *C*, *s*). And besides this, there are also very commonly found in the interior of the cell granular bodies, which however may be passed over for the moment.

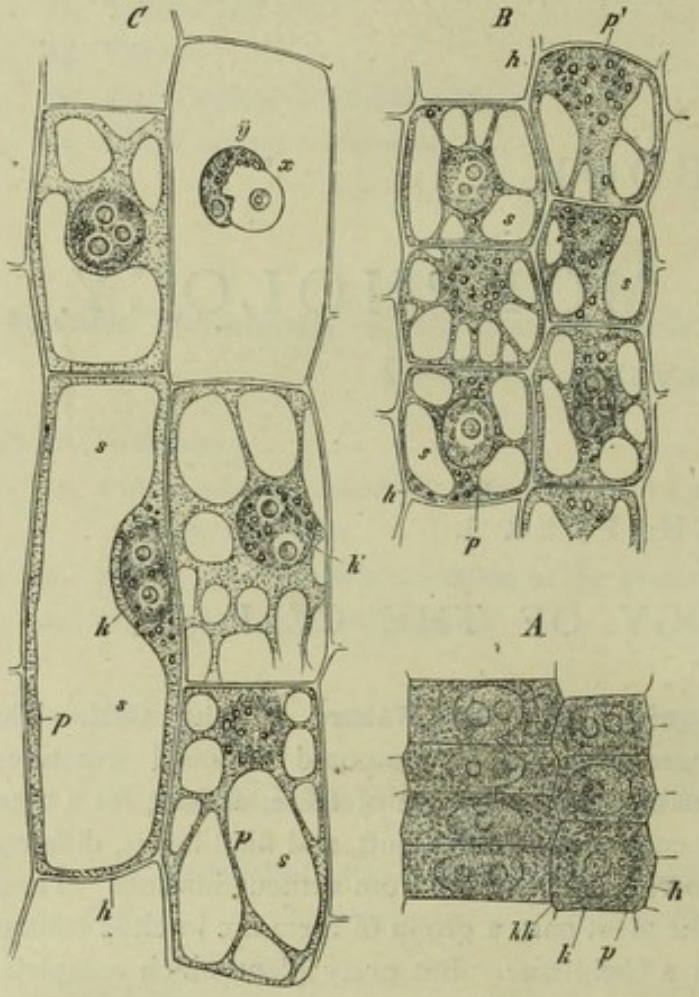

FIG. 1.—Parenchyma-cells from the central cortical layer of the root of *Fritillaria imperialis*; longitudinal sections (×550). *A* very young cells lying close above the apex of the root, still without cell-sap. *B* cells of the same description about 2 mm. above the apex of the root; the cell-sap *s* forms separate drops in the protoplasm *p*, behind which lie walls of protoplasm; *C* cells of the same description about 7—8 mm. above the apex of the root; the two cells to the right below are seen in a front view; the large cell to the left below is in section; the cell to the right above is opened by the section; the nucleus shows, under the influence of the penetrating water, a peculiar appearance of swelling (*x*, *y*).

Thus, then, cells in the stage of development now described consist of a firm membrane, soft protoplasm (including the nucleus), and fluid cell-sap. At first, however, the sap is wanting; if the same cells be examined in a very early state of their development they are smaller (Fig. 1, *A*), their cell-wall thinner, and the protoplasm forms a solid body in the middle of which lies the nucleus, at this time relatively very large (*k*). The cell-sap first appears when the whole cell is increasing quickly in volume (Fig. 1, *B*); it presents itself originally in the form of drops (vacuoli) in the interior of the protoplasmic body (Fig. 1, *B*, *s*); at a later period these usually coalesce, and form a single sap-cavity (Fig. 1, *C*, *s*) which is enclosed by the now sac-like hollow substance of the protoplasm.

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[1] H v. Mohl, Ueber die Saftbewegungen im Inneren der Zellen.—Bot. Zeitg. 1846, p. 73.

In their earliest state the cells of the wood and cork of trees show also conditions of development which correspond essentially to those represented in Fig. 1. In these cells, however, a new condition follows very soon after the appearance of the cell-sap; the protoplasm containing the nucleus disappears, leaving the cell-wall filled either with air or with water. Older wood and cork when completely formed thus consist of a mere framework of cell-walls.

But now arises an important difference between the behaviour of those cells which enclose a protoplasmic body, and of those from which it has already disappeared. The former only can grow, develop new chemical combinations, and, under certain conditions, form new cells. The latter are never capable of further development; if they are wood, they are of service to the plant only from their firmness, power of absorbing water, and from their peculiar form; if cork, they form protecting envelopes which surround the living succulent cellular tissue.

Since then no further process of development can take place in the cells which no longer contain protoplasm, it may be concluded that the latter is the proximate cause of growth. We shall see in a future paragraph that the development of each cell begins with the formation of a protoplasmic body, and that

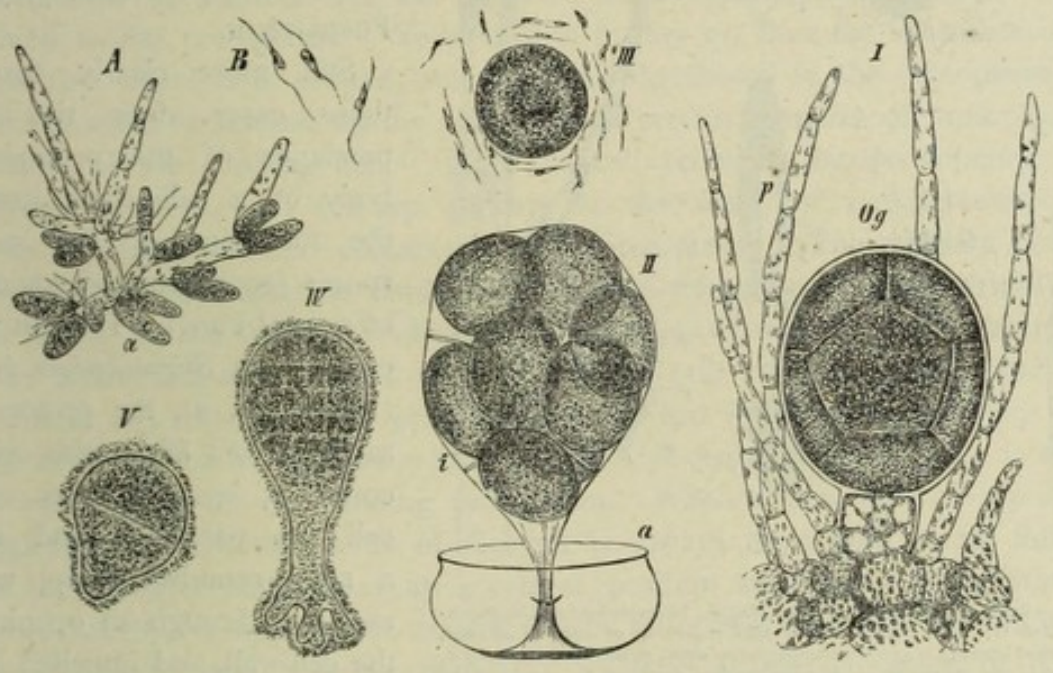

FIG. 2.—Sexual reproduction of *Fucus vesiculosus*; *A* cellular filaments bearing antheridia; *B* spermatozoids; *I* Oögonium, *Og* with paraphyses *p*; *II* the exterior membrane *a* of the oögonium is split, the inner *i* protrudes, containing the ova; *III* an escaped ovum, with spermatozoids swarming round it; *V* first division of the fertilised ovum: *IV* a young Fucus resulting from the growth of the fertilised ovum (after Thuret, Ann. des Sci. Nat. 1854, vol. ii). (*B* ×330; all the rest ×160.)

the cell-wall is also generated from it; but the relation of the protoplasm to cell-formation is still more strikingly conspicuous in those cases in which it continues its life for some time as a naked sharply-defined solid body, and only at a later period clothes itself again with a fresh cell-wall, and again takes up cell-sap within itself. We have an excellent example of this in the reproduction of the Fucaceæ. On the fertile branches of these great marine Algæ, of which we may take *Fucus vesiculosus* as an example, large cells are formed in peculiar receptacles, the Oögonia (Fig. 2, *I*, *Og*); the space enclosed by the cell-wall is densely filled with fine-grained protoplasm, which at first presents a homogeneous mass, but at last

falls into eight portions, and these, completely filling up the cell-cavity of the oögonium, press against one another, and become polygonal. The wall of the oögonium consists of two layers ; the outer one splits, and the inner one protrudes in the form of a sac, which distends by absorption of water ; in this enlarged sac the portions of protoplasm become globular (Fig. 2, *II*); then this also bursts, and the protoplasmic bodies, now completely spherical, escape. By the fertilising action of other smaller protoplasmic structures, the spermatozoids, these spherical bodies are excited to further development; out of the interior of the ball of protoplasm (the fertilised ovum) a colourless substance next makes its appearance, which hardens into a closed cell-wall. The newly-formed cell now grows in two different directions in different modes, and produces after further transformations (Fig. 2, *V* and *IV*) a young Fucus-plant.

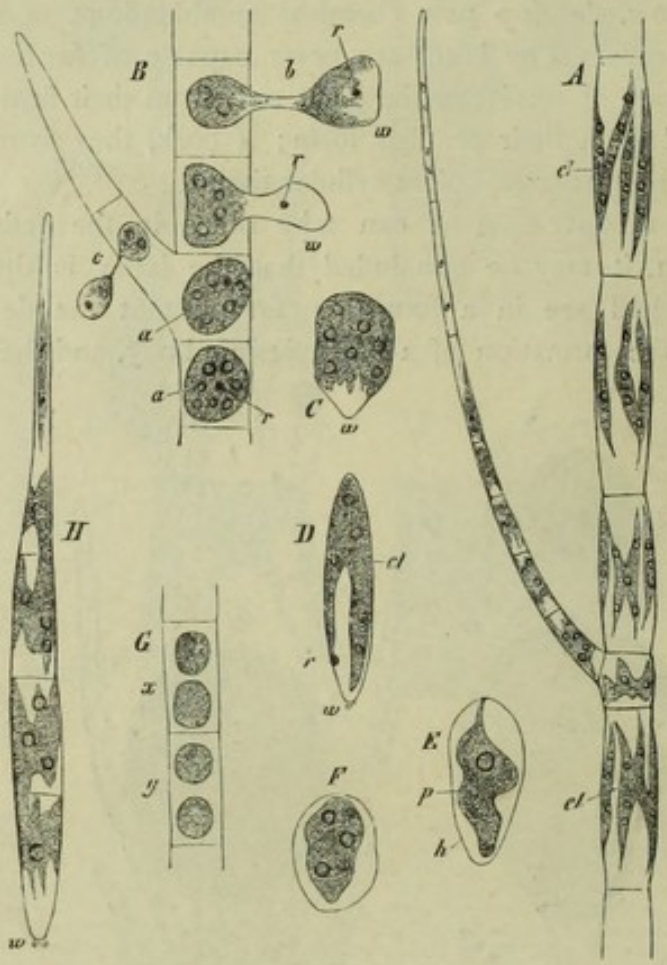

FIG. 3.—*Stigeoclonium insigne* (after Nägeli, Pflanzenphysiol. Untersuchungen, Heft 1); *A* a branch of the Alga consisting of one row of cells, with a lateral branch; *cl* green-coloured protoplasmic structures (chlorophyll), imbedded in the colourless sac of protoplasm of each cell not shown in the drawing; *B* the protoplasmic bodies of the cells contracting and protruding through openings in the cell-wall; *C* swarm-spores still without cell-wall; *D* one come to rest; at *E* and *F* killed; the protoplasm *p* contracts and allows the newly-formed cell-wall *h* to be recognised; *H* a young plant grown from the swarm-spore; *G* two cells of a filament in the act of dividing; the protoplasmic body of each cell (*x*, *y*) has temporarily split into two equal parts, and contracted by addition of a re-agent.

Still more clearly than in these cases does the independence of the protoplasmic body of a cell show itself in the formation of the swarm-spores (zoospores) of Algæ and of several Fungi. Here in many cases, as in *Stigeoclonium insigne* (Fig. 3; *B*, *a*), the protoplasm-sac of a cell filled with cell-sap contracts, lets the water of the cell-sap pass out, and forms a solid roundish lump, which, escaping through an opening in the cell-wall, and impelled by an internal force, swims about in the water (*C*). While it is passing out of the cell-wall, the protoplasmic body shows, by its motions and changes of form, that it is soft and extensible; but, once freed, it assumes a definite specific form, conditioned by an internal force. At last, usually after some hours, the swarm-spore comes to rest; if killed by the proper means, the protoplasmic body contracts (*E*, *F*, *p*), and a fine cell-wall may now be recognised, which it did not possess at the time of its exit, and at the beginning of its swarming. When once at rest, it also changes its form, and increases in volume, while fluid cell-sap collects in the interior. The cell formed in this way now grows in a manner dependent

on the specific nature of the plant;—in our example it specially elongates itself (Fig. 3, *D* and *H*),—whereon new changes (in this case, *e.g.*, cell-divisions) begin.

These examples, and many more might be added, show us that the protoplasmic body forms the cell; the cell, in the sense defined above, is evidently only a further form of development of it; the formative forces proceed from it. It has hence become usual even to consider a protoplasmic body of this kind as a cell, and to designate it as a naked membraneless cell or Primordial Cell; its relationship to a cell provided with membrane and cell-sap is somewhat like that of a larva to the perfect insect, which is developed from the larva into the more perfectly matured form.

The development of a swarm-spore, like that of a Fucus-ovum, shows,—as may also be proved in the case of every other cell,—that the substance out of which the cell-wall is formed was already contained in the protoplasm in some form or other which could not be recognised; and so the formation of the cell-wall must be regarded as a separation of matter hitherto contained in the protoplasm. In the same manner the water of the cell-sap, although taken up from without, must nevertheless pass in through the protoplasm; and, while it gathers inside as cell-sap, it takes up from it soluble substances; and so far the formation of the cell-sap also appears as a separation of matter hitherto contained in the protoplasm. We shall see, further on, that the substance of the nucleus also, where it is present, was originally distributed in the protoplasm, and that the nucleus is formed by the collection of certain particles of protoplasm at the centre of the growing cell. Thus the cell provided (by development) with membrane, nucleus, and cell-sap appears as the result of a differentiation of particles of matter hitherto contained in the protoplasm. The essential point is this,—that this differentiation always leads to the formation of concentrically disposed layers, the outermost of which, the cell-wall, is firm and elastic, the middle one, the protoplasm-sac, soft and inelastic. If the cell, as is usually the case, is at first without any sap-cavity, the protoplasm is the less firm and more watery in the middle, or a nucleus in this case is formed, which, at least in young cells, is always more watery than the surrounding protoplasm. When at last the cell-sap makes its appearance, the inner cavity of the cell is always filled with actual fluid, in which the nucleus often takes up a central position surrounded by protoplasm, or, more usually, it approaches, together with the protoplasm, the circumference of the sap-cavity, and becomes parietal. So long as that condition of cell-development in which the cell appears as a sap-cavity bounded by a membrane—certainly the one most commonly seen—had alone been observed, it was correct enough to define the cell as a vesicle; it is obvious, however, that this view does not apply to many true cells, *e.g.* to young tissue-cells (as Fig. 1, *A*), of the true nature of which we should get but a very ill-defined conception were we to regard them as vesicles. The term applies still less to the structure of swarm-spores and of the ova of Fuci.

Sect. 2. **Difference in the Forms of Cells.**—In the conformations described in the previous paragraphs, the development of the cells seldom remains stationary. Still further changes of form usually take place in the separate parts of the cell. The collective volume of the whole cell generally increases for a

considerable time with corresponding increase of the cell-sap; not unfrequently it mounts up to a hundred or even a thousandfold the volume of the cell at the time of its formation. During this increase, the contour—the collective form—of the whole cell, commonly undergoes a change; if it was at first roundish or polyhedral, it may afterwards become elongated, filiform, bag-like, prism-shaped in length or tabular in breadth, many-armed, or branched. The cell-wall may increase very considerably in thickness, and this thickening is usually not uniform; single spots remain thin, in others the thickened membrane becomes prominent without or within; strap-shaped prominences, spines, knobs, &c. appear. In the substance of the cell-wall itself, differences also manifest themselves, which result in imparting to it greater firmness, elasticity, or hardness, or, on the other hand, greater softness or pliancy. The protoplasm may, in these processes, decrease more and more in quantity, until at last it forms an extremely thin membrane, which lies so close to the cell-wall that it does not become visible till contraction takes place; after the completion of the growth of the cell-wall it may even entirely disappear. But in many other cases the protoplasm increases with the increase in volume of the cell; it forms a thick-walled sac, the substance of which is endowed with constant motion, while filiform or strap-shaped strings of protoplasm often pass through the sap-cavity of the cell. In those cells which appear externally green, certain portions of the protoplasm become separated, and assume a green colouring; these particles of chlorophyll may appear in the form of bands, stars, or irregular masses; but they usually form numerous roundish granules, and the particles of chlorophyll always appear as parts of the collective protoplasmic substance of a cell. Sometimes, mixed with the green colouring matter which tinges these portions of the protoplasm, are pigments of other colours, red, blue, or yellow (as in Florideæ, Oscillatorieæ, and Diatomaceæ); or the particles of chlorophyll assume, through changes in their colouring matter, other tints, mostly yellow or red. Colouring matters may also appear as dissolved in the cell-sap. The other chemical compounds which are formed in extremely large numbers in the cell, are mostly dissolved in the cell-sap; but many of them assume definite forms; thus arise granules of fat, drops of oil, and frequently true crystals or crystalline bodies. One of the commonest granular compounds present in almost all plants, with the exception of Fungi and some Algæ and Lichens, is Starch, the grains of which often accumulate in the cell in numbers greatly exceeding all other substances.

The most perfectly developed form of cells is found in certain families of Algæ, the Conjugatæ, Siphoneæ, and Diatomaceæ. Since in these cases one and the same cell unites in itself the organs for all vegetative functions, and at the same time a many-sidedness in the phenomena of life presents itself, the whole cell attains a high degree of differentiation; the separate parts,—the cell-wall, the protoplasmic body, and its contents,—show a variety of structure which does not occur elsewhere concurrently in the different parts of one and the same cell. Hence it happens that the same cell has in these cases often to go through the most diverse metamorphoses, so that besides its manifold development as to size, it also undergoes a series of temporary changes of form. Hence these forms of Algæ become of great importance for an accurate comprehension of the nature of the cell. (Book II. Algæ.) But above all, these cells are distinguished by this,—that, after they have attained the highest grade of development, they are in a condition to divide and to multiply, and at length, sooner or later, give up their

cell-wall, contract their protoplasmic body, together with all its serviceable contents (starch, oil, chlorophyll, &c.), expel the water of the cell-sap, and form a new cell.

We may pass over the innumerable intermediate forms, and turn our attention at once to the other extreme, namely those plants of which each usually consists of thousands or even millions of cells, as is the case with Vascular Cryptogams and Phanerogams; and in which at the same time the different parts of the plant undergo an entirely different morphological development, and are adapted to different functions for the support of the whole. Here then we find that certain cells never attain their full development, they remain constantly in the condition of youth which is represented in Fig. 1, *A*; these however assist the whole by continually giving rise to new cells by division, which then, on their part, undergo a further development. Such cells, which serve exclusively for the purpose of producing new ones, are found at the extremities of all roots and branches, and abundantly at the base of leaves. The cells produced in these positions undergo a different development according to their situation, and usually in such a way that whole aggregations of them into layers or strings follow the same course of development. Some grow quickly in all directions, their wall remains thin, the great bulk of their protoplasm becomes transformed into chlorophyll, they are rich in cell-sap, and serve, as we shall see hereafter, for assimilation, *i. e.* the production of new organic substance, which is formed out of the elements of the absorbed nutritive material; in other parts of the same plants the cells extend greatly in length, their diameter remains small, they form no chlorophyll; a certain number remain succulent and serve to conduct certain assimilated substances; other cells of the same string thicken their walls rapidly in many ways, their septa become absorbed, numerous cells in the same row join into a long tube (vessel), from which the protoplasm and the cell-sap disappear; they serve then as air-passages for the interior of the plant. In their neighbourhood are formed the wood-cells; they are mostly fibre-like, extended in length, their wall greatly thickened, and its substance chemically changed (lignified); they form collectively a firm frame-work which supports the remaining tissues, lends firmness and elasticity to the whole, and is especially adapted for the rapid conduction of water through the tissues of the plant. In the tissue of tubers, bulbs, and seeds, most of the cells remain thin-walled; they become filled in the interior with albuminous substances, starch, fat, inuline, &c., which afterwards, when new organs are being formed, serve as material for the construction of new cells. In the same manner a considerable series of other forms of tissue could be adduced, cork, the testa of seeds, the stone of stone-fruit, &c., which all alike attain the needful firmness and strength by a peculiar development of their cell-walls, in order to serve as protective envelopes for the other masses of cells which are still capable of further development; their contents disappear as soon as the cell-wall has assumed these properties, and their purpose has been fulfilled.

Each of the forms of cell hitherto spoken of, occurring in one and the same plant, thus serves especially or exclusively for one purpose only; in correlation with this, either the cell-wall, the protoplasmic body, the chlorophyll, the cell-sap, or its granular deposits, is specially developed. Very commonly these specialised cells lose the power of reproduction and of multiplying by division; when they have fulfilled their function, they disappear, or their woody frame-work, the cell-wall, alone remains. The whole plant, of which these cells form a part, continues to remain as such; at definite places it possesses cells, which, at the proper time, again produce new masses of cells, and these again are adapted to fulfil for the time all these functions.

Sect. 3. **Formation of Cells**[1]. — The formation of a new cell always commences with the re-arrangement of a protoplasmic body around a new centre;

[1] H. von Mohl, Vermischte Schriften botanischen Inhalts, Tübingen 1845, pp. 65, 84, 362.—Schleiden in Müller's Archiv, 1838, p. 137.—Unger, Botan. Zeitung, 1844, p. 489; H. v. Mohl,

the material required is always afforded by protoplasm already present; the newly constituted protoplasmic body clothes itself, sooner or later, with a new cell-wall. This is the only process common to all reconstruction of cells. A description which goes more into detail requires a distinction to be at once drawn between different cases, or we shall be led into erroneous generalizations, since there is great variety in the mode in which new cells are formed.

It appears to me convenient and natural to distinguish three principal types:—(1) The Renewal or Rejuvenescence of a Cell; *i. e.* the formation of one new cell from the whole of the protoplasm of a cell already in existence; (2) The Conjugation or Coalescence of two (or more) protoplasmic bodies in the formation of a Cell; (3) The Multiplication of a Cell by the formation of two or more protoplasmic bodies out of one. Each of these types shows a series of variations and transitions into the others. Great diversity arises, especially in the multiplication of cells. Two cases are here to be distinguished first of all, according as a part only of the protoplasm of the mother-cell is applied to the formation of the new cells (Free Cell-formation), or as the whole mass passes over into the daughter-cells (Division). The last, by far the most common case, again exhibits variations, according as the masses of protoplasm, which become separated and then collect around new centres, expel water and contract, and become globular, or not, and according as the cell-wall is secreted during the division or only after the complete formation of the new cell, and even after the appearance of cell-sap and nuclei.

In the course of the vegetation of a plant, different forms of cell-formation are brought into play. On Cell-division depends the formation of the vegetative parts of the plant, the production of the *Cell-tissue;* Free Cell-formation occurs in the production of the ascospores of Fungi and Lichens, and in the embryo-sac of Phanerogams; Cell-formation by Conjugation is limited, in its typical form, to single groups of Algæ and Fungi for the purpose of reproduction; the Renewal or Rejuvenescence of Cells is found in the formation of a single swarm-spore out of the whole contents of a vegetative cell in many Algæ; and analogous phenomena occur in the sexual reproduction of Cryptogams.

In what follows I purpose to give a summary of the different kinds of cell-formation according to the principles already indicated. The brevity required in an introductory treatise will be my excuse if I omit the details necessary for a more accurate knowledge.

A. Cell-formation by Renewal or Rejuvenescence of a Cell.—A good example is afforded in the formation of the swarm-spores of *Stigeoclonium insigne* (Fig. 3,

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Botan. Zeitung, 1844, p. 273.—Nägeli, Zeitschrift für wiss. Botanik, I. 1844, p. 34, III, IV, 1846, p. 50. —A. Braun, Verjüngung in der Natur, Freiburg 1850, p. 129 et seq.—Hofmeister, Vergleichende Unsersuchungen über die Embryobildung der Kryptog. u. Conif., Leipzig 1851.—De Bary, Untersuchungen über die Familie der Conjugaten, Leipzig 1858. — Nägeli, Pflanzenphys. Untersuchungen, Heft I.—Pringsheim, Jahrb. für wiss. Botanik, I. 1858, pp. 1, 284, II. p. 1.—Hofmeister, Lehre von der Pflanzenzelle, Leipzig 1867. [Schleiden's Contributions to Phytogenesis are in Taylor's Scient. Mem., vol. II. pp. 281–312, and Sydenham Society, 1847; Braun's Rejuvenescence was published by the Ray Society in Bot. and Phys. Mem. 1853; and Nägeli on Vegetable Cells by the same Society in their Reports and Papers on Botany, 1845 and 1849.]

page 4); the whole contents of a vegetative cell of a filament contracts, expels a portion of the water of the cell-sap; the arrangement of the differentiated protoplasmic body is changed, the bands of chlorophyll disappear; its form alters as it escapes from its cell-wall; from almost cylindrical, the protoplasmic body becomes ovoid, and shows a broad green and a narrower hyaline end; after the swarming is completed, the latter becomes the base, the green end alone grows at the apex as soon as the new cell clothes itself with a cell-wall. The observations of Pringsheim on Oedogonium also show that the direction of growth of the renewed cell is at right angles to the original direction of growth before the renewal; for the hyaline, or rooting-end of the swarm-spore, which afterwards attaches itself, is formed on the side (Fig. 4, *A*, *E*), not at the upper or lower end of the protoplasmic body. An essentially different arrangement in space of the entire protoplasmic body of the cell also takes place; the transverse becomes the longer diameter of the cell and of the plant arising from it. The material remains, as far as can be seen, the same, but its arrangement is different; this is morphologically determinate, and every new formation of cells depends essentially on a fresh arrangement of protoplasm already in existence; hence the rejuvenescence of a cell not only may but must be regarded morphologically as the formation of a new one.

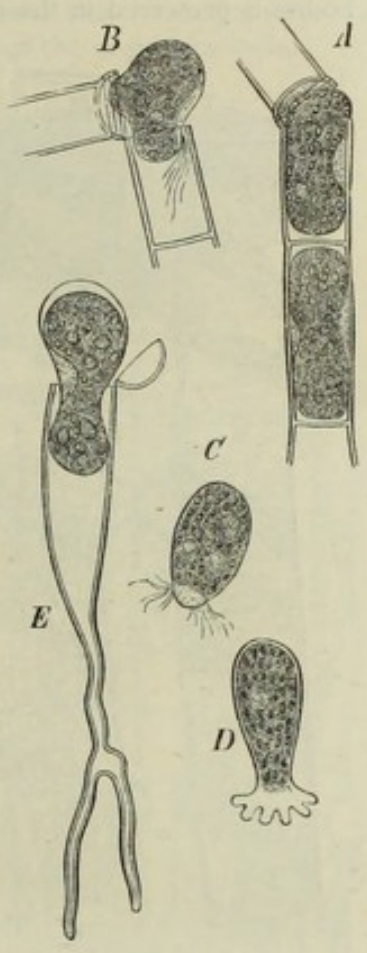
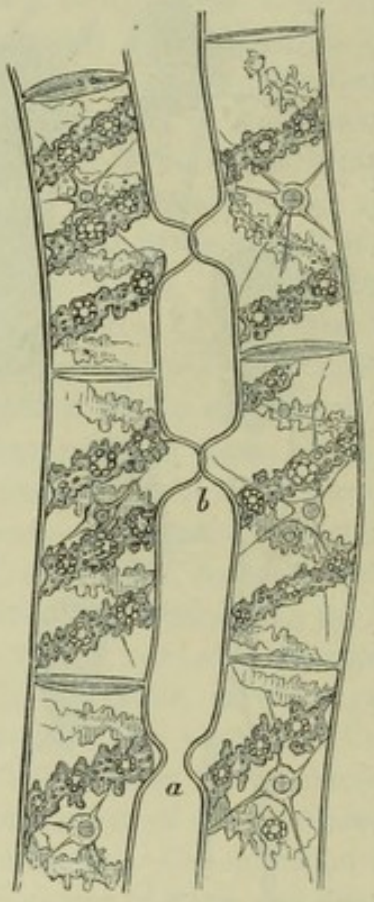


FIG. 4.—*A*, *B* escape of the swarm-spores of an Oedogonium; *C* one free in motion; *D* the same after it has become fixed and has formed the attaching disc; *E* escape of the whole protoplasm of a germ-plant of Oedogonium in the form of a swarm-spore (×350). (After Pringsheim, Jahrb. für wiss. Bot. I. pl. 1.)

B. Cell-formation by Conjugation.—The protoplasmic bodies of two or more cells coalesce to form one common protoplasmic body which surrounds itself with a cell-wall, and becomes endowed with the other properties of a cell. For the elucidation of this process, which presents many variations, we may observe the conjugation of one of our commonest filamentous Algæ, *Spirogyra longata* (Figs. 5, 6). Each filament (Fig. 5) consists of a row of similar cylindrical cells, each of which contains a protoplasm-sac; this encloses a relatively large quantity of cell-sap, in the midst of which hangs a nucleus, enveloped in a small mass of protoplasm, and attached to the sac by threads of the same substance; in the sac lies a band of chlorophyll, which is spirally coiled, and at definite places contains grains of starch. In this case the conjugation always takes place between the adjacent cells of two more or less parallel filaments. A preparation is made for it by the formation of lateral protuberances, as represented in Fig. 5, *a*; these continue to grow until they meet (*b*). The protoplasm-sac of each cell concerned then contracts; it detaches itself sharply from the surrounding cell-wall; rounds itself into an ellipsoidal form, and contracts still more by expulsion of the water of the cell-sap. This occurs simultaneously in the two conjugating cells. Next the cell-wall opens between the two protuberances (Fig. 6, *a*), and one of the two ellipsoidal protoplasmic bodies forces itself into the connecting channel thus formed; it glides slowly through it into the other cell-cavity, and as soon as it touches the protoplasmic body contained in it, they coalesce (Fig. 6, *a*). After complete union (Fig. 6, *b*) the united body is again ellipsoidal, and scarcely larger than one of the two which compose it; during the union a contraction has evidently taken place with expulsion of

water. The coalescence gives the impression of a union of two drops of fluid; but the protoplasm is never a fluid; and, independently of other circumstances, there is a fact that shows that altogether peculiar forces are here active which are absent from all fluids;—the spiral band of chlorophyll of each of the two conjugating protoplasmic bodies is preserved in the contraction; it only becomes closely drawn together; during



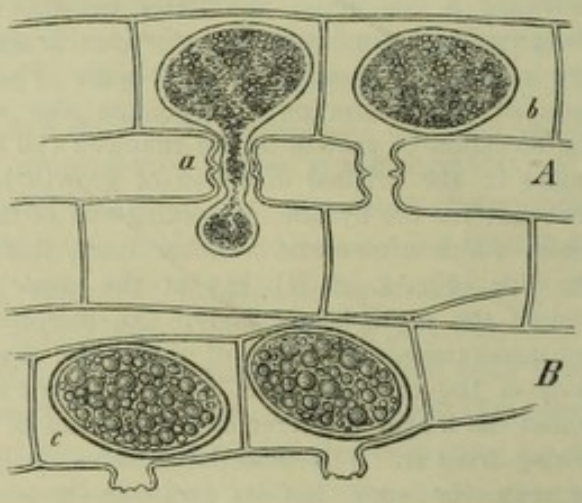


FIG. 5.—*Spirogyra longata*. Cells of two filaments preparing for conjugation, they show the spirally coiled bands of chlorophyll in which, at different places, lie wreath-like arrangements of starch-grains; small drops of oil are also distributed through them (cf. sect. 6); this is the behaviour of the chlorophyll after the action of strong sunlight; the nuclei are also to be seen in the cells, each surrounded by protoplasm, threads of which touch the cell-wall in different places; *a* and *b* are the protuberances preparing for conjugation (×550).

FIG. 6.—*Spirogyra longata*. *A* Cells in the act of conjugation; at *a* the protoplasmic body of one cell is passing over into the other; at *b* this has already taken place; the band of chlorophyll together with starch-grains is still partially recognisable. *B* the young zygospores surrounded by membrane; the protoplasmic body contains numerous drops of oil (×550).

the coalescence the ends of the two bands of chlorophyll place themselves together in such a manner as to form one band. The conjugated protoplasmic body clothes itself with a cell-wall, and forms the body called a Zygospore, which germinates after a period of repose of some months, and developes a new filament of cells. With greater or smaller deviations from this plan, conjugation takes place in a group of Algæ comprising a large number of species, the Conjugatæ, among which the Diatoms must be included, and in some Fungi. In the latter more considerable deviations occur (*e.g.* Syzygites, *Mucor stolonifer*). In *Spirogyra nitida* it also happens (according to De Bary, Conjugaten, p. 6) that one cell conjugates with two others, and takes up their masses of protoplasm; in these cases a Zygospore is the product of the contents of three cells. In the Myxomycetes the swarm-spores (Myxo-amœbæ), which are endowed with a peculiar motion, coalesce gradually in great numbers, and finally form large, motile, membraneless protoplasmic bodies, the Plasmodia, which only at a subsequent period are transformed into numerous cells.

In the cases hitherto considered, the uniting protoplasmic bodies are of equal size; the process of fertilisation in many Cryptogams differs only in the fact that the two protoplasmic bodies which coalesce are of unequal size, and otherwise of different properties. In Book II we shall treat in detail of the reproduction of Cryptogams; here we need only state that the male, motile fertilising bodies (Spermatozoids) of Cryptogams are naked protoplasmic bodies, which are considered to be primordial cells; in the female organ of these plants is a cell which opens outwardly, and contains a protoplasmic body which is fertilised by the spermatozoids. In cases which have been accurately observed (Oedogonium, Vaucheria), these coalesce

with the former; and from this the reconstruction of a cell results. Here, as with the conjugation of the Conjugatæ and some Fungi, the cell which results in this manner from the coalescence is always a reproductive cell; with it begins the formation of a new individual plant. In fertilisation one of the two bodies is evidently very different from the other; it may therefore be assumed that in conjugation also a difference exists, although at present undiscovered, between the coalescing cells.

C. Free Cell-formation.—In the protoplasmic body of a cell new centres of formation arise, around each of which a portion of the protoplasm gathers, and forms a cell. *Another portion of the protoplasm remains over*, and represents the still-persisting protoplasmic body of the mother-cell, which survives for a longer or shorter time. The new centres of formation may or may not be indicated by the previous appearance of nuclei. Generally, the number of daughter-cells which arise in this manner is considerable; as an instance may be mentioned the formation of spores in a small Ascomycete, a Peziza[1] (Fig. 7). The sac-like mother-cells of the spores (*a*) are at first densely filled with protoplasm, and contain only one small nucleus. This disappears; *i. e.* its substance becomes distributed through that of the protoplasm; this latter becomes frothy, and roundish drops of sap make their appearance in it (*b*, *c*). Preparation is made for the formation of spores by the condensation of the protoplasm in the upper part of the sac, while in the lower part it remains frothy (*e*, *f*). The formation of spores does not in this case precede the appearance of the nuclei; and the spores always remain devoid of a nucleus; and this is the more instructive as in other Pezizæ (*e. g. P. confluens*, according to De Bary) nuclei are formed in the first place, around each of which a lump of protoplasm collects[2], which then forms the spore. In this case eight spores are always formed in each sac within the upper dense protoplasm; *i. e.* around each of eight points a portion of the protoplasm collects in an ellipsoidal mass (*d*); each such collection consists at first of coarse-grained protoplasm surrounded by a clear space; a portion of

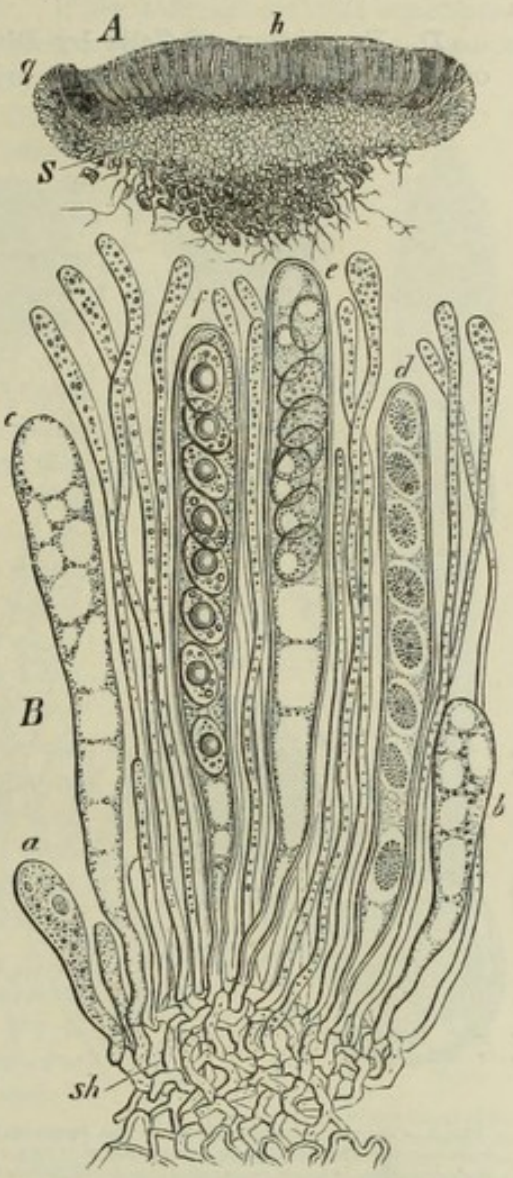


FIG. 7.—*Peziza convexula*. *A* vertical section of the whole plant (× about 20); *h* hymenium, *i. e.* the layer in which the spore-forming sacs lie; *S* the tissue of the Fungus enveloping the hymenium at its edge *q* in a cup-like manner; at the base of the tissue *S* fine threads arise, which grow between the particles of earth. *B* a smaller portion of the hymenium (× 550); *sh* sub-hymenial layer of densely interwoven cell-filaments (hyphæ); *a*—*f* spore-forming sacs; among them thinner sacs, the paraphyses, in which lie red granules.

[1] It appears in considerable quantity on the ground among Phascum along forest-paths in the neighbourhood of Bonn in the month of March. The cup is from ½–1 inch broad, brick-red, sessile, with slightly projecting rim. According to Rabenhorst, Deutschlands Kryptogamenflora, 1844, p. 368, it may be *P. convexula*.

[2] In the embryo-sac of Phanerogams fresh nuclei are formed in the protoplasm, and around each of these one cell. (Cf. Book II. Conifers, Monocotyledons, Dicotyledons.)

fine-grained protoplasm forms the ground, so to speak, in which the spores are imbedded. Afterwards each spore becomes more sharply defined, the clear space disappears (*e*), its substance becomes more fine-grained and clearer; and in one of its foci is formed a vacuole, *i. e.* a transparent drop of fluid. Finally, each spore surrounds itself with a firm membrane, the vacuole disappears, and in the centre is formed a large drop of a strongly refractive oil, as well as numerous smaller drops of oil.

D. Formation of Cells by Division of the Mother-Cell.—In the protoplasm of a cell new centres of formation arise; around each of these a portion of the protoplasm of the mother-cell gathers, in order to form a new cell; *in this manner the entire protoplasm of the mother-cell is completely used up;* its cell-wall alone remains, if it possess one, which is not always the case. If the mother-cell has a nucleus, this is usually dissolved in the protoplasm[1]; and as many new nuclei are produced[2] as daughter-cells originate; or the nucleus of the mother-cell *divides into two nuclei*, while the whole protoplasm separates *into two portions* (see Hanstein).

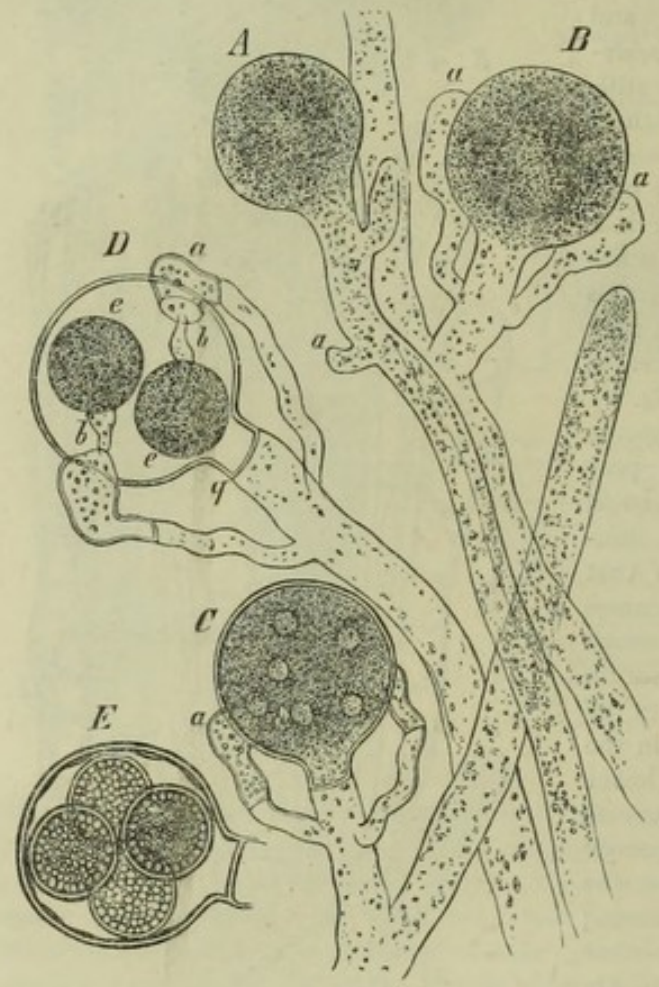


FIG. 8.—Oögonia and antheridia of *Achlya lignicola*, growing on wood in water; the course of development is indicated by the letters *A*—*F*. *a* the antheridium, *b* its sac penetrating into the oögonium (×550).

1st Case. *Cell-Division with Contraction and Rounding-off of the Daughter-cells.*

a. A Cell-wall is not secreted till daughter-cells, already isolated, have become completely separate. An example is afforded by the formation of the oöspores of Achlya (Fig. 8). At the end of a sac-shaped cell or of a branchlet of one, the protoplasm collects, the larger end itself swells up into a globular form (*A*, *B*), and, by the formation of a septum (*C*), becomes an independent cell (the oögonium). Nucleus-like structures sometimes, but not usually, form in the protoplasm (as in *C*). The whole protoplasmic body then breaks up into two, three, four, or more parts, which very quickly round themselves off into a perfectly spherical form; (in a large number of observations I have never seen an intermediate form between *C* and *D*.) The parts thus formed (*e*, *e* in *D*) contract violently during their separation; *i. e.*, their protoplasm becomes denser by expulsion of

[1] An exception occurs in the formation of spores of Anthoceros, where the nucleus of the mother-cell is not absorbed until four new nuclei are formed.

[2] In Spirogyra, Mougeotia, and Craterospermum, the new nuclei only arise *during* the progress of the division of the protoplasm (De Bary, Die Familie der Conjugaten, Leipzig 1858). In the formation of the stomata of *Hyacinthus orientalis*, I was unable either before, during, or immediately after the division of the mother-cell, to perceive a nucleus; it did not appear in any of the derivative cells until a considerable time after the division.

water; and only after they have become fertilised by the antheridium-tubes (*a*, *b* in *D*) do they surround themselves with a cell-wall.

This form of cell-division evidently bears, throughout its whole course, a close resemblance to Free Cell-formation; it is distinguished only by the circumstance, that here the whole protoplasm collects round several centres. If the whole protoplasmic body, in its contraction, were to form only *one* ball, which also happens, the case would be analogous to that of Renewal or Rejuvenescence. If the balls, *during* their separation, were to surround themselves with copiously secreted cellulose, the process would bear a strong similarity to the formation of pollen in many Dicotyledons [see below].

There occurs also in this same plant (Fig. 9) a variation of this process of division, when it forms its swarm-spores; here the protoplasm breaks up in the club-shaped swollen end of a sac into a large number of small portions (*A*), which become completely rounded off only (*a*) after their escape from the sporangium (*B*), and are then surrounded by a thin membrane which they shortly abandon (*b*) in the process of swarming (*e*).

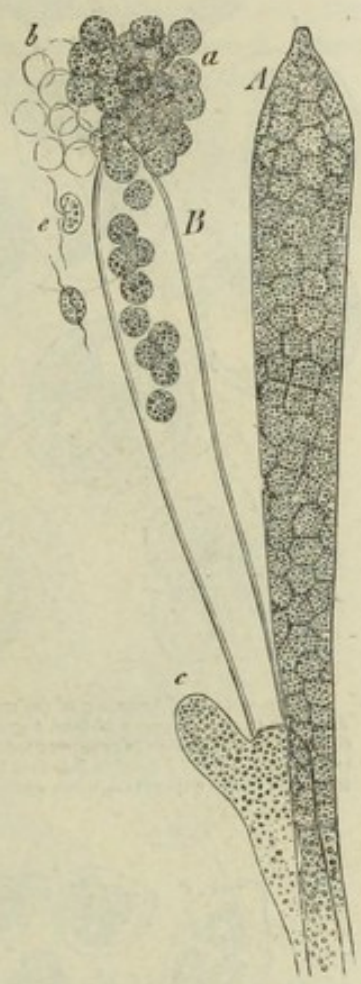


FIG. 9.—Zoosporangia of an Achlya (×550). *A* still closed, *B* allowing the zoospores to escape, beneath it a lateral shoot *c*; *a* the zoospores just escaped; *b* the abandoned membranes of the zoospores which have already swarmed; *c* swarming zoospores.

The formation of the spores of Mosses and Vascular Cryptogams, and of the pollen of Phanerogams, always takes place by the division of the mother-cell into four parts, either at once or by repeated bipartition. This is the common character of these formations, which are also otherwise morphologically related. In the special processes of formation, however, some deviations occur; with the Mosses (e. g. *Funaria hygrometrica*, see Book II) the formation of spores in the mother-cell follows essentially the plan we are here considering; the protoplasmic body of the mother-cell breaks up into four lumps, which quickly round themselves off and contract, and become enveloped by a cell-membrane only after complete separation; four small cells thus lie encased in the membrane of the mother-cell, just like the oöspores of Achlya in the oösporangium, but in this case the mother-cell becomes quickly absorbed.

The spores of Equisetaceæ are formed on the same type; only the four newly-formed sister-cells (in *E. limosum*) do not here lie in a mother-cell-membrane, since the mother-cell does not in general form a cell-membrane before the separation. This case may be examined somewhat more closely, since it brings before us very clearly the behaviour of the nucleus in the division; and since the behaviour of the other parts is remarkably clear here also. At a certain time the mother-cells of the spores swim in the fluid which fills the cavity of the sporangium; according to their mode of formation they form groups of two or four sister-cells (Fig. 10, *a*, *b*). Each mother-cell consists at first of a large spherical nucleus (including nucleoli), surrounded by fine-grained turbid protoplasm, which has a sharply defined contour, but is without a cell-wall. Dilute alcoholic solution of iodine, and other substances which cause contraction, show this very definitely; with the contraction of the protoplasmic body of the mother-cell not the very finest trace of membrane becomes visible in any state of division. The first preparation for the division of the mother-cell is manifested by the clarifying of the protoplasm (*b*), by the gathering of a group of greenish-yellow granules on the side of the nucleus which lies next the sister-cell; then the nucleus disappears, and the granules arrange themselves in the form of a disc, which passes through the centre of the

spherically-formed mother-cell (*c*); the protoplasm thus becomes perfectly free from granules, and as transparent as a drop of oil; but soon a turbidity again sets in to the right and left of the disc of granules; fine granules appear at both poles of the mother-cell, and spread further and further, until at last only a clear ellipsoidal space remains right and left (*e*); these spots free from granules are two nuclei; the disc of granules begins to shift its position; the two large ellipsoidal nuclei again disappear; and in their place appear four smaller ones (*f*), arranged in the angles of a tetrahedron, each of which is surrounded on the side facing its neighbours by a portion of the greenish-yellow granules which before formed the disc. The optical section soon shows lines which indicate the separation of the four portions of protoplasm (*f*), commencing internally; this advances towards the outside, while the daughter-cells become globular, and a nucleolus always appears in each of their nuclei. Finally the young spores become fully isolated (*i*), adhering only to one another. Here, as in very many other cases of the formation of tetrahedra, preparation is made by a bipartition which is at least indicated (*e*), but the mother-cell proceeds to a division into four, even before this first division is completed. The young spores, when first separated, are still naked, but they soon become surrounded by a cell-membrane, the peculiar history of whose development we shall investigate at the proper time (Book II. Equisetaceæ).

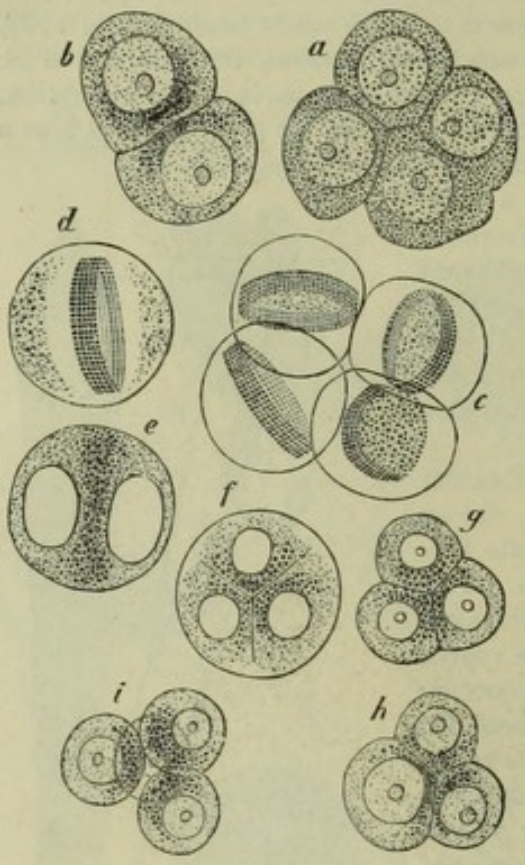


FIG. 10.—Mode of formation of the spores of *Equisetum limosum* (×550); *a* group of four, *b* group of two mother-cells; *c* and *d* mother-cells preparing for division; *e* one with two nuclei; *f*, *g* and *i* division into four spores; *h* abnormal formation of three spores from one mother-cell.

b. The contracting daughter-cells secrete cellulose even during their separation. Since in this case the mother-cell is already clothed with cellulose, the process often gives the impression that the cell-wall of the mother-cell forms at certain spots a projecting ridge on the inside, constricts the protoplasmic body, and at length severs it.

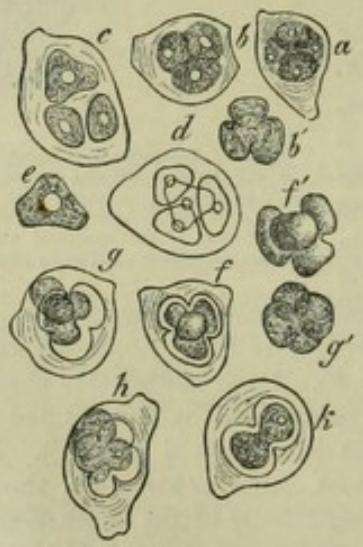


FIG. 11.—Mode of formation of the pollen of *Tropæolum minus* (×550) reduced.

The clearest examples of this case occur in the formation of the pollen of many Dicotyledons. Fig. 11 shows this process in *Tropæolum minus*. At *a* and *b* four nuclei have already appeared in the protoplasm of the mother-cells which are much thicker on two sides, arranged at the angles of a tetrahedron (this arrangement is common, though not without exception); the protoplasm gives, in fresh examples, the impression of being already divided into four roundish lumps; but by contraction in an alcoholic solution of iodine (*f*, *g*, *b*, *k*) it is seen that they are still connected, and that the cell-wall

projects inwards at the indentations in the form of acute-angled ridges. The division of the simultaneously contracting and rounding masses of protoplasm, proceeding from without inwards, now becomes more evident if they are freed by pressure (*b' f'*) or by solution of the cell-wall in sulphuric acid; they then have the appearance of four-lobed bodies. The separation at length proceeds so far that the four segments part from one another; but since the formation of the cell-wall proceeds simultaneously, each of these now lies in a chamber surrounded by a cell-wall (*c*). Later each protoplasmic body (young pollen-grain) forms a new wall around itself, the thick common cell-wall is dissolved, and thus the four pollen-grains become free.

2nd Case. *When there is no perceptible contraction of the dividing protoplasm*[1]; the cavity of the mother-cell remains completely filled by the daughter-cells; these therefore are not rounded off, the derivative cells appearing as segments of the mother-cell.

As in the preceding case, so here also we must distinguish, according as the cell-wall is formed only after the division, or advances during the division from without inwards. In both cases the newly formed cell-wall gives the impression of a lamella thrust in between the derivative cells, which becomes joined to the wall of the mother-cell; it is usually called a division-wall; its direction and position are of great importance in morphology; it always stands at right angles to the connecting line of the centres of the new cells. In this mode of cell-division, there is, with rare exceptions, a bipartition of the mother-cell[2]; it is the invariable process in the formation of tissues, but occurs also distinctly, though less conspicuously, in the formation of spores and pollen.

a. The protoplasm arranges itself in the interior of the mother-cell in two portions, the boundary-surface of which is already visible before the partition-wall of cellulose is formed; *this partition-wall arises simultaneously at all points of the boundary-surface as a thin membrane;* it is only when it afterwards increases in thickness that it sometimes splits into two lamellæ, one of which belongs to each of the sister-cells[3].

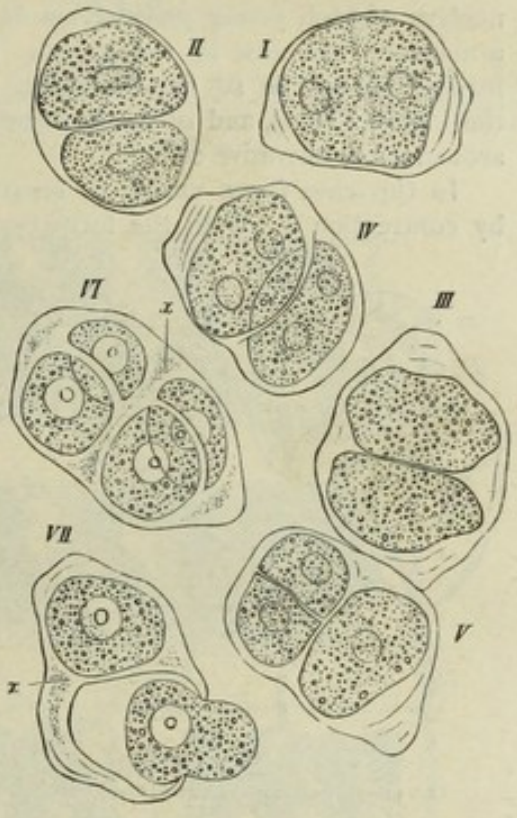


FIG. 12.—Mode of formation of the pollen of *Funkia ova* (×550). In *VII* the wall of the daughter-cell has absorbed wate till it burst; its protoplasmic body is forcing itself through the cleft, and is lying before it, assuming a spherical form.

This mode of Cell-formation may be very clearly observed in the formation of the pollen of some Monocotyledons. Fig. 12 shows the process in *Funkia ovata*. In *I* the

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[1] Hofmeister (Handbuch der physiol. Botanik, I. p. 86) supposes in this case also a contraction of the contents, in order to get room for the division-wall; since, at the time the molecules out of which it is formed are separated out of the protoplasm itself, a change in position takes place, by which the particles of protoplasm approach one another a little; though it is doubtful whether this is the necessary result of the plan indicated in Figs. 8 and 11.

[2] In many hairs (*e.g.* Tradescantia) a division into more than two daughter-cells placed in a row occurs simultaneously. (A. Weiss, 'Die Pflanzenhaare' in Karsten's Botan. Untersuchungen, p. 494.)

[3] It should be remarked at the outset that in tissue-cells the division-wall of two cells is a lamella common to both, the growth and interior differentiation of which usually proceeds equally on both sides. (Compare sect. 4 under *b*, and Formation of Tissue.)

protoplasmic contents of the mother-cell has already become divided after the disappearance of its nucleus ; the protoplasm has collected round two nuclei which lie in the foci of the nearly elliptical figure of the mother-cell in such a manner that a translucent plane at right angles to the line of union of the nuclei indicates the separation. The next condition to be observed is always that represented in *II*, where a lamella of cell-wall completely divides the mother-cell, lying in the translucent plane already indicated in *I*. The place where the wall of the mother-cell and the partition-wall meet soon becomes thicker, and the two daughter-cells here become rounded off. The two nuclei in *II* are elongated, corresponding to the form of their cells; they soon become absorbed (*III*), and in their place two new nuclei immediately arise in each half-cell (*IV*), whose position again corresponds to the foci of the elliptical daughter-cells. Sometimes this preparation for division remains uncompleted in one of the two cells (*V*). Between each pair of tertiary nuclei a division-wall now suddenly arises (*VI*). Now for the first time the nucleus of each young pollen-grain is further developed; it becomes transparent, and a nucleolus can now be recognised. In the formation of pollen of Dicotyledons the further process is so far the same, that the common cell-wall softens (at first on the inside, *VII*, *x*), and is at last absorbed, while a new and firmer membrane is formed around each derivative cell.

In this case I was unable to separate the two halves of the protoplasmic body (*I*) by contraction[1]. With the formation of the pollen of Canna I was successful, only however when the second division had already begun; four masses of protoplasm are then seen completely separated; they are not rounded, but formed as if the body of the mother-cell had been divided by two cuts; the division-walls then appear suddenly between these primordial cells. In a similar manner the attempt has also sometimes been successful, in the formation of tissue-cells, to separate the two daughter-cells completely by contractile reagents, before a division-wall has arisen between them : as also in the first divisions of the young antheridium of Characeæ (Fig. 43, *B*). But usually, especially in the formation of the tissues of the higher plants, the appearance of the division-wall follows so rapidly after that of the two nuclei, that it is seldom possible to catch the exact moment when the derivative cells are already parted, but are not yet separated by a partition-wall. In the examination of the *Punctum vegetationis* of roots and stems, one sees at a glance hundreds of cells which are in process of division at the same time; and yet it is seldom possible to see the condition in question. This however shows at the same time that the partition-wall always arises in these cases simultaneously over the whole surface; if it grew from without inwards, this would actually be seen, since

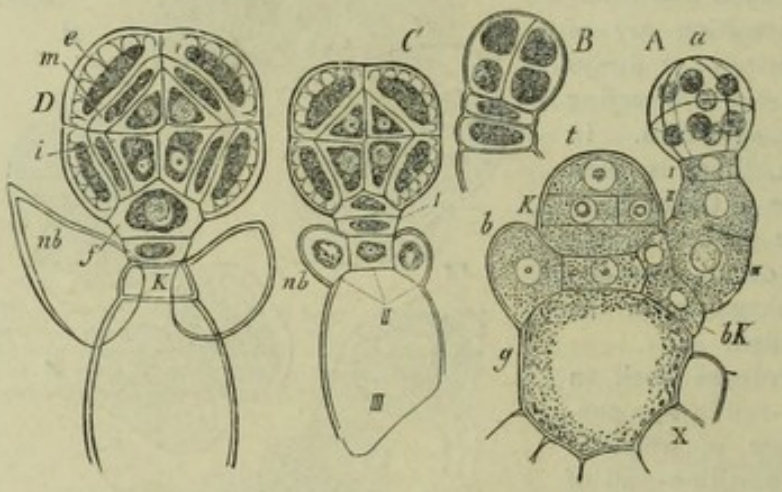

FIG. 13.—Formation of the antheridium of *Nitella flexilis* (cf. Book III).

[1] The firm connexion of the two daughter-cells before the formation of the partition-wall occurs also in a different manner, *e. g.* in Oedogonium (Hofmeister, *l. c.* pp. 84 and 162). The preliminary indication of the partition-wall by the appearance of a disc of granules in the boundary plane is not universal, as is shown in the formation of the pollen of Funkia and of the spores of Funaria. (Hofmeister, *l. c.* Fig. 20.)

all the steps of the development in this case come easily into view; here and there half-formed partition-walls would be found. So is it also with the first cell-divisions of the embryos in the embryo-sac; here the circumstances are peculiarly favourable; but here also the next stage which comes into view after the formation of two nuclei (Fig. 14, *I*) is usually the presence of a complete thin partition-wall (*II*). I was also successful in crushing an embryo of *Allium Cepa* (*III*) in iodine-solution in such a manner that it was evident that the younger derivative cells were not yet separated by a partition-wall, although sharply defined.

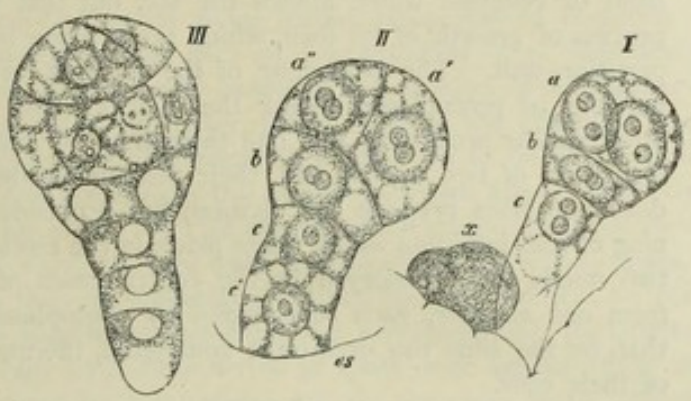

FIG. 14.—Embryos in the embryo-sac of *Allium Cepa*; the cells contain very large nuclei, each with two nucleoli. At *I* the spherical apical cell contains two nuclei (*a*); at *II* it has already divided (*a* has split up into *a'* and *a''*), and in the same manner the cell *c* (in *I*) has split up into *c* and *c'*.

b. While the division of the protoplasmic body is taking place from without inwards, cell-membrane is formed; a ridge of cellulose intrudes into the dividing fold which arises in the protoplasmic body[1].

A clear and well-studied example is afforded in the stouter forms of the genus Spirogyra. In order to observe the divisions here, it is necessary to place strongly vegetating filaments after midnight in very dilute alcohol, that they may be examined later, the divisions taking place only by night. Fig. 15 shows a living cell of a filament of *S. longata* by day; *B* to *E* the conditions of division at night; the protoplasm-sacs of the cells are contracted by the life-destroying reagent.

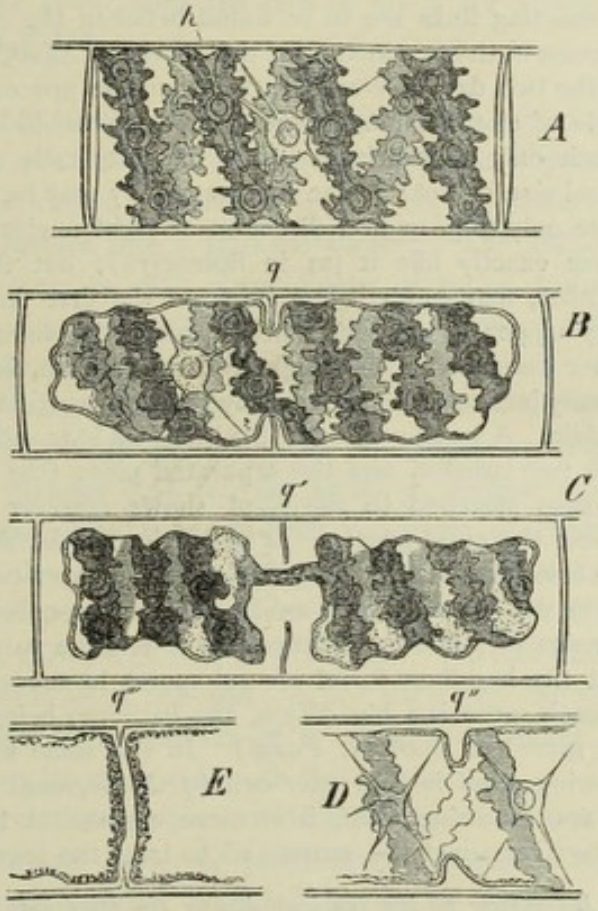

FIG. 15.—*Spirogyra longata* (×550). *A* a cell in the living state; *B*, *C* cells laid in dilute alcohol during the division by night; *D*, *E* central portion of cells in the act of division.

B and *C* (Fig. 15) show, at *q* and *q'* the folding-in of the protoplasm-sac, and the annular ridge of cellulose which is growing into it. While the folding-in advances further and further, the lamella of cellulose does the same; finally the channel closes, the annular lamella becomes a disc, and now lies between the two new completely closed sacs of protoplasm as a partition-wall. Sometimes the

[1] This case was the first of all processes of cell-formation that was accurately examined; H. von Mohl first described it in 1835 in *Conferva glomerata*. (Mohl: Vermischte Schriften bot. Inhalts. Tübingen 1845.)

folding-in of the protoplasmic body makes great progress, pushing on even to the separation into two sacs, before the partition-wall of cellulose begins to form (q'' and q''' in D and E); an abnormal condition which shows plainly that it is not the band of cellulose which infolds the sac, but that this latter becomes constricted by a process of growth of its own, which takes place independently of the formation of the partition-wall. The behaviour of the nucleus, and generally the arrangement of the portions of protoplasm during the division, here shows considerable deviation from other similar processes; this one thing however must be clearly borne in mind, that the formation of two nuclei, and their position in the middle of the newly-formed cells, does not here precede the division, but proceeds along with it. Not till the beginning of the infolding which takes place in the circumference of the central nucleus, are two nuclei to be observed in the central mass of protoplasm; these separate slowly from one another, each surrounded by protoplasm, while the folding-in proceeds, so that, by the time the division is completed, the nuclei have reached nearly the centres of their cells.

In some cases modes of division occur which appear, at the first glance, to differ essentially from any hitherto described; *e. g.* the production of the basidiospores of the Basidiomycetes (as Agaricus, Boletus). A closer study, however, shows that such processes follow more or less exactly one of the types described. Thus, for example, all possible connecting links are to be found between the usual mode of division and the peculiar process in the production of the spores of Agaricus and other Fungi. If the behaviour of the two daughter-cells, rather than the process of division itself, were made the principle of classification, many other cases would have to be considered. On this I will touch only very briefly. The daughter-cells resulting from the division may be of equal size or not; in the first case they may be so similar to the mother-cell that they have only to grow in a direction at right angles to that of the division in order to become exactly like it (as in Spirogyra); but the daughter-cells, even when like one another, may nevertheless be from the first different from the mother-cell; and this may happen in very different ways, and the difference may constantly increase. But, in other cases where the daughter-cells are from the commencement unlike, this difference usually increases later, especially in the formation of the spores of Fungi on the so-called basidia. A small portion of the end of a long cell becomes divided off; the septum splits into two lamellæ, and the separated piece (the basidiospore) falls off; the part which remains attached to the plant shows scarcely any change, and can again and again repeat the same process. The portion of the mother-cell which remains behind, called the basidium, has evidently become a daughter-cell as truly as the detached spore; but, while the spore is very unlike the mother-cell, the other daughter-cell, the basidium, remains very like it. Hence has arisen the pardonable, but very incorrect expression, that the basidium forms several spores in succession; whereas properly the formation of each spore is a bipartition, the basidium being always as much a daughter-cell as is the spore (cf. Book II. Fungi). In the same manner the apical cell at the end of a growing stem is the sister-cell to the segment last formed; but since the former is always renewing itself, it is more convenient to express oneself as if the apical cell always remained the same, and to treat the segments as its products.

Behaviour of the Nucleus during the Division. Where the cell-division is combined with contraction and rounding off of the newly-formed portions of protoplasm, as in the formation of spores and pollen-grains, it is the rule that the new nuclei become visible in the centres of the future daughter-cells, whether, as is usually the case, the nucleus of the mother-cell have previously disappeared, or whether it remain during the process, as in the formation of the spores of Anthoceros (pp. 14–16). From these cases, a clear observation of which was easy, the opinion has hitherto prevailed that in the bipartition of the tissue-cells of growing parts the nucleus of the mother-cell also becomes absorbed in the protoplasm, and that in this latter two new nuclei arise in the centres of the forming derivative-cells. But the bipartition of the cells of Spirogyra

(p. 17) does not justify this conclusion, in so far as it is only during the folding-in of the protoplasm-sac that the two new nuclei slowly separate from one another; whether they are formed afresh after the absorption of the mother-nucleus, or arise from its division, is still uncertain. According to the more recent researches of Hanstein[1], the bipartition of the parenchyma-cells of the pith of Dicotyledons (*e. g.* Sambucus, Helianthus, Lysimachia, Polygonum, Silene) really precedes the division of the mother-nucleus; a mass of protoplasm, enclosing the latter, places itself in the centre of the mother-cell. Even before the cell-division, two nucleoli at least are to be detected in the nucleus, and soon afterwards a fine line divides the nucleus into two halves; 'directly afterwards, or at the same time, the whole layer of plasma which surrounds it shows a free intersecting division surface, in which the new wall of cellulose then gradually arises.' The nuclei of the two sister-cells thus lie, immediately after their production, on the new division-wall: but they usually soon leave this situation; very commonly they move in opposite directions along the wall, until they arrive at spots over against those at which they arose, and there they come to (temporary) rest on the older septa. Since these parenchyma-cells usually divide in regular succession, two newly-formed nuclei of different origin thus lie opposite to one another on each side of all the older septa.

Whether these processes also take place in the primary parenchyma of the same plants, and whether possibly they occur in all plants the cells of which are united into tissues, Hanstein has not yet definitely stated.

Sect. 4. **The Cell-Wall**[2].—The substance of the cell-wall is secreted from the protoplasm. In what form it is contained in the protoplasm immediately before the secretion is not yet certainly known; it always appears as a solution, and then becomes first organised on the surface into a thin membrane. The substance capable of forming cell-wall always consists of a combination of water, cellulose, and incombustible materials (ash-constituents), but may afterwards undergo further chemical changes.

By the continual secretion of substance which forms cell-wall out of the protoplasm, and the deposition of this between the molecules of the membrane already formed, this latter grows in such a manner that on one hand its surface, and on the other hand its thickness, increases. The mode of both processes of growth is dependent on the specific nature of the cell, and on the function which it has to fulfil in the life of the plant; it therefore varies almost infinitely. Generally the growth in surface first preponderates, afterwards that in thickness. Neither the one nor the other is uniform over all points of a cell-wall; hence each cell, during its growth, also changes its form; moreover the growth of a cell-wall continues only so long as it is in immediate contact on its inner side with the protoplasm.

The want of uniformity of the growth in surface at different points causes cells which are at first, for example, spherical, ovoid, or polyhedral, to become subsequently cylindrical, conical, bag-shaped, tabular, bounded by waved surfaces, &c. The want of uniformity of the growth in thickness usually brings about sculpture of the surface, which is very characteristic. The thickened parts may project either

[1] Sitzungsberichte der niederrheinischen Gesellschaft in Bonn, Dec. 19, 1870, p. 230.

[2] H. von Mohl, Vermischte Schriften bot. Inhalts. Tübingen 1845 (numerous treatises).—Schacht, Lehrbuch der Anat. und Phys. der Gewächse, 1856.—Nägeli, Sitzungsberichte der Münch. Akademie, 1864, May and July.—Hofmeister, Die Lehre von der Pflanzenzelle, Leipzig 1867. Also numerous treatises in the Botanische Zeitung.

outwardly or inwardly. The former occurs commonly in the free-lying surface of cell-wall, the latter in the partition-walls of adjoining cells. The thickenings which project outwardly may appear in the form of knots, humps, spines, or ridges; but those which project on the inside are much more various. In this case peg-shaped protuberances occur but seldom; much more common are annular ridges or spirally-curved bands; these latter may be united in a reticulate manner, so that thin polygonal interstices remain; or the thicknesses may spread, and the thin parts then appear in the thick wall as fissures or roundish pits. If the wall is very thick, the latter become channels, which pass entirely or partially through the wall. Not unfrequently the thin portion of the wall, which at first closes such a channel on the outside, becomes absorbed, and the cell-wall is then perforated. But as, when contiguous cells are united into a tissue, the partition-wall usually becomes thickened in the same manner on both sides, the pits and pit-channels of both sides meet, and the intermediate thin portion of membrane becomes absorbed; a channel thus arises uniting two cell-spaces (Bordered Pits, perforated septum of vessels).

During the increase of the surface and of the thickness of the wall by deposition of new substance in both a tangential and radial direction between the molecules already formed, a finer internal structure usually becomes visible, which is termed Stratification and Striation. Both are the result of a different regularly alternating distribution of water and solid substance in the cell-wall; at every visible point water is combined with cellulose, but in different proportions; portions less and more watery, denser and less dense, alternate. Thus, in every cell-wall sufficiently thick, a system of concentric layers becomes visible, of which the outermost and innermost are always denser, while between them alternate more and less watery layers. The stratification is visible on the transverse and longitudinal sections of the cell-wall, the striation also on the surface being usually most evident there, but is in general less easily seen than the stratification; it consists in the presence of alternately more and less dense layers of cell-wall, cutting its surface at an angle. Mostly two such systems of lamellæ may be recognised mutually intersecting one another. There are thus altogether three kinds of stratification present in a cell-wall, one concentric with and two vertical or oblique to the surface, cutting one another or mutually intersecting, like the cleavage-plain of a crystal cleaving in three directions (Nägeli); and as this cleavage takes place in different directions, at one time the stratification, at another the striation is more evident.

Independently of this internal structure, chemical changes arise in the cell-wall which never affect the whole mass uniformly, but usually divide the thickened cell-wall into concentric layers which differ from one another chemically and physically. These chemical differentiations, which are always combined with an alteration of physical properties, show a great variety, but can conveniently be reduced to three categories;—Conversion into Cuticle or Cork (Verkorkung), Lignification (Verholzung), and Conversion into Mucilage (Verschleimung). The first consists in the change of the outer layers of the cell-wall into a plastic very elastic substance which water cannot at all, or scarcely penetrate or cause to swell (as the outer cell-wall-layer of the epidermis and of pollen-grains and spores and cork). Lignification occasions an increase in the hardness of the cell-wall, a decrease of its

plasticity, and easy permeability to water without any considerable swelling. The conversion into mucilage at length causes the cell-wall to become capable of absorbing great quantities of water, so as to increase its volume to a corresponding extent, and to assume a gelatinous consistence. In the dry state such cell-walls are hard, brittle, or flexible like horn (as the cell-walls of many Algæ, the so-called intercellular substance of the endosperm of *Ceratonia Siliqua*, of linseed, and quince-mucilage). Several of these changes may occur simultaneously in a cell-wall, so that, for instance, the outer layers become woody and the inner mucilaginous (*e. g.* wood-cells of the root of Phaseolus).

Besides these changes in the substance of the cell-wall, which are not unfrequently correlated with peculiar colourings, changes in its chemico-physical behaviour may also be induced by the interposition between its molecules of considerable quantities of incombustible substances, especially lime and silica. If the deposition of these substances take place in sufficient quantities, they remain behind, after destruction of the organic groundwork of the cell-wall, in the form of what is termed an ash-skeleton.

(a) *The Surface-growth* causes not only an increase of the size of the cell, but also changes of form, in proportion as it is wanting in uniformity at different parts of the circumference; hence cells of originally dissimilar form may become similar by unequal growth; but it is much more common for cells originally alike in form to become entirely unlike. This is most usually the case with the multicellular organs of the higher plants, leaves, stems, and roots; cells in their infancy can here often scarcely be distinguished from one another; whereas in the completely developed organ the most various forms are contiguous (Fig. 16). It is only rarely, as in the growth of some spores and pollen-grains, that the surface-growth is so uniform that the original form is nearly retained even after considerable increase in volume (*e. g.* pollen of Cucurbita and Althæa). But even in these cases the uniformity is only temporary, for the pollen-grains subsequently emit their pollen-tubes or the spores germinate, in both cases by the local growth of their inner layer of cell-wall. This also shows at the same time that the surface-growth of a cell-wall may be very different at different times; and this indeed is usually the case. From the infinite variety of the surface-growth of cell-walls, it is convenient, for the sake of arrangement, to reduce the different cases to classes, and to bestow names upon them[1]. Thus it is usual to distinguish between inter-

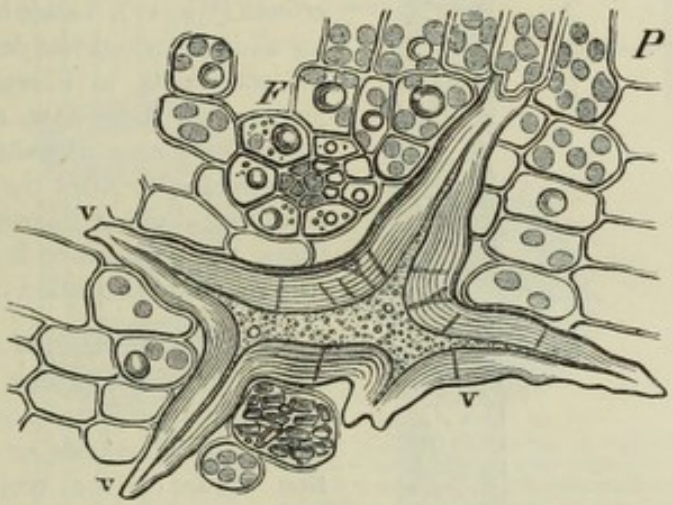

FIG. 16.—From the transverse section of a leaf of *Camellia japonica*; *P* parenchyma-cells with grains of chlorophyll and drops of oil; *F* a very thin fibro-vascular bundle; *v v* a large, branched, thick-walled cell, which intrudes its arms between the parenchyma-cells.

[1] A good classification of the processes of growth is, of course, still more important for the study of the mechanics of growth; but little has, however, yet been done in this direction, and we can only give a brief abstract.

calary and terminal growth of the cell-wall. Terminal growth takes place when the surface-growth attains a maximum at any one part of the circumference (by interposition of new particles of cell-wall), while the intensity of this process decreases on all sides of this point, and at a definite distance attains a minimum, so that this portion of the cell-wall projects as a point, or appears as the rounded end of a prominence, or of a cylindrical sac (*e. g.* hairs, filamentous Algæ). If several points of terminal growth occur in a cell which was originally round, it may become star-shaped; if new points of growth are formed beneath the continuously growing end of sac, the sac-like cell branches (as in many filamentous Algæ, hyphæ of Fungi, Vaucheria, Bryopsis). Hofmeister[1] distinguishes as a peculiar form of terminal growth the case in which, instead of a point, a line is rapidly raised on the cell-wall; this may occur as the terminal line or intersecting edge of two curved surfaces. Intercalary growth of the cell-wall occurs in a typical form in the case in which the deposition of new substance within a belt lying in the surface of a cell takes place in such a manner that this belt extends, and a fresh interposed piece of the cell-wall from time to time makes its appearance. To the last-named case may be referred the common phenomenon of the occurrence of growth in the whole of the side-wall of a cubical, tabular, or cylindrical cell, as, for example, in the cells of Spirogyra, and the parenchyma-cells of growing roots and stems of Phanerogams (cf. Fig. 1). Oedogonium presents a peculiar case of intercalary surface-growth (Fig. 17). Inside below the septum is formed a projecting annular cylindrical deposit of cellulose (*A*, *w*); there the cell-wall splits, as if separated by a circular cut, into two pieces; and these now, retreating from one another, remain united by a zone of cell-wall (*B*, *w'*) formed by extension of the cylinder *w*. After the interposition of this new cylindrical zone, cell-division follows; and, since this is repeated many times, the appearance is presented which is figured at *A*, *c* (the so-called formation of a cap[2]).

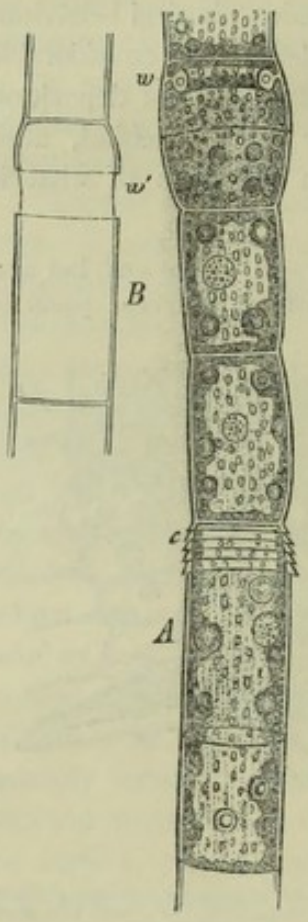

FIG. 17.—Intercalary surface-growth of Oedogonium.

(b) *The Growth in Thickness of a Cell-wall* is usually strictly localised, so that the thicker parts appear mostly as very abrupt projections on the thinner parts of the cell-wall, either on the outside or the inside. The collective impression made by the sculpture is especially dependent on whether the extension of surface is less on the thicker or on the thinner parts. If the thickening is especially strong on certain points, the structure takes the form outwardly (Fig. 19) or inwardly (Fig. 18, *C*, *D*) of projecting warts, pegs, or spines; if the thickening occurs most strongly in linear or strap-shaped spots of the cell-wall, projecting cylinders, ridges, bands, or combs are formed on the inner or outer side. These ridge-like projections may form reticulated figures on the inner or outer side (Fig. 18, *B*, Fig. 20, *l*), or rings, or spiral bands, a development especially frequent in those thickenings of certain tissue-cells which project from within. If the internally projecting rings or spiral bands are thick and firm, and the intermediate portions of cell-wall thin and easily destructible, these thickenings may become free even within the plant, and remain lying as isolated threads of cellulose in channels of

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[1] Handbuch der physiol. Botanik, I. p. 162.

[2] For further details of these somewhat complicated processes see Pringsheim, Jahrbuch für wissen. Bot. I; Hofmeister, Handbuch der phys. Bot. I. p. 154, and Nägeli und Schwendener, Mikroskop, II. p. 549.

the tissue (annular vessels in the fibro-vascular bundle of Equiseta, *Zea Mais*, &c.); but the thickenings formed like spiral bands may often be drawn out to considerable length as isolated fibres (very striking examples of these so-called untwisting spiral vessels are found in the rachis of the inflorescence of *Ricinus communis* and in the leaves of Agapanthus). If the thickening of the cell-wall takes place over more extended portions of the surface, and if only smaller portions remain thin, these latter appear as pits of very various outline, either roundish or like fissures, or, when the thickening of the cell-wall is very considerable, as channels, which perforate them. These kinds of thickening most frequently project on the inner side of the cell-wall; the channels therefore run from the

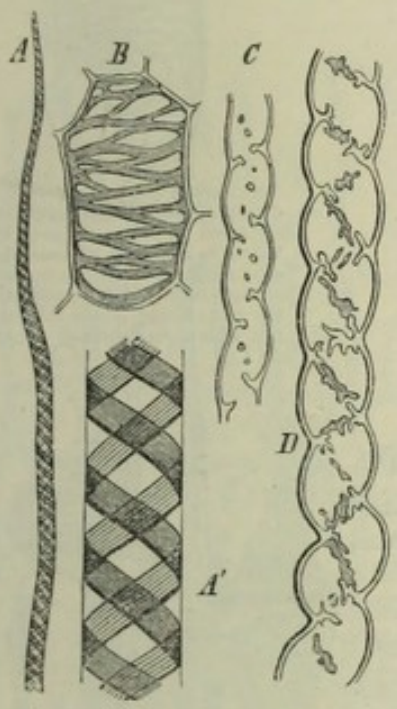
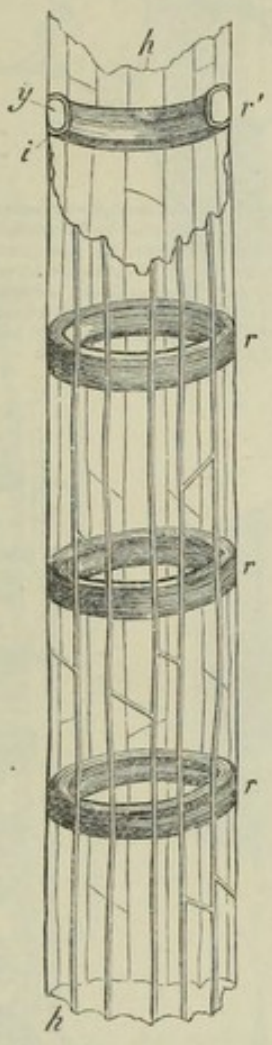


FIG. 18.—Cell-forms of *Marchantia polymorpha* with thickenings projecting inwards; *A* an elater (Schleuderzelle) (one-half) from the sporangium, with two spiral bands; *A'* a portion more strongly magnified; *B* a parenchyma-cell from the centre of the thallus, with thickenings projecting inwards in a reticulate manner; *C* a thin root-hair with thickenings projecting inwards, these are arranged on a spiral constriction of the cell-wall; at *D* a thicker root-hair, with projections thicker and branched, and spiral arrangement still clearer.



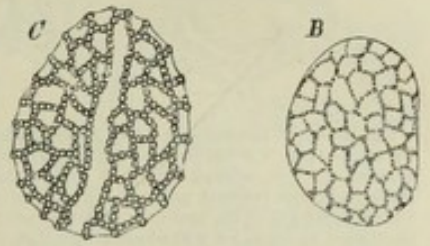


FIG. 19.—*B* a young pollen-cell of *Funkia ovata*; the knob-like thickenings projecting outwardly are still small; in the older pollen-cell *C* they are larger; they are arranged in lines united into a net-work.

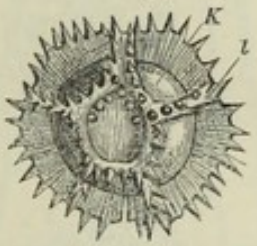


FIG. 20.—Ripe pollen-grain of *Cichorium Intybus*; the almost spherical substance of the cell-wall is furnished with ridge-like thickenings united into a net-work; each of these bears thickenings which project still more, in the form of spines arranged like a comb.

FIG. 18 *bis*.—Piece of an annular vessel from the fibro-vascular bundle of the stem of *Zea Mais* (×550). *h h* the thin cell-wall of the vessel, on which the boundary lines of the adjoining cells are clearly seen. *r r* the annular thickenings of the wall of the vessel; *y* the inner substance of one of the rings laid open; *i* the denser layer which extends over the inner side of the ring projecting into the cavity of the cell.

cavity of the cell outwards, and are there closed by a thin membrane[1]; when the cell loses its protoplasm and dies, the latter is in many cases destroyed, and the pit or the channel then becomes open (as, for instance, in Sphagnum and many wood-cells). The pits, especially in elongated cells, appear to be generally arranged in spiral rows, but in other cases are peculiarly grouped (Fig. 21, *A*). A remarkably striking form of this grouping is the Sieve-structure which occurs in the sieve-cells of the fibro-vascular bundles of vascular plants, generally in the septa, but also in the longitudinal walls. In

[1] Sometimes strongly thickened cell-walls with branched pit-channels show a very complicated structure, *e. g.* in the hard testa of Bertholletia. (Cf. Millardet in Ann. des Sciences Nat., fifth series, vol. vi. part 5.)

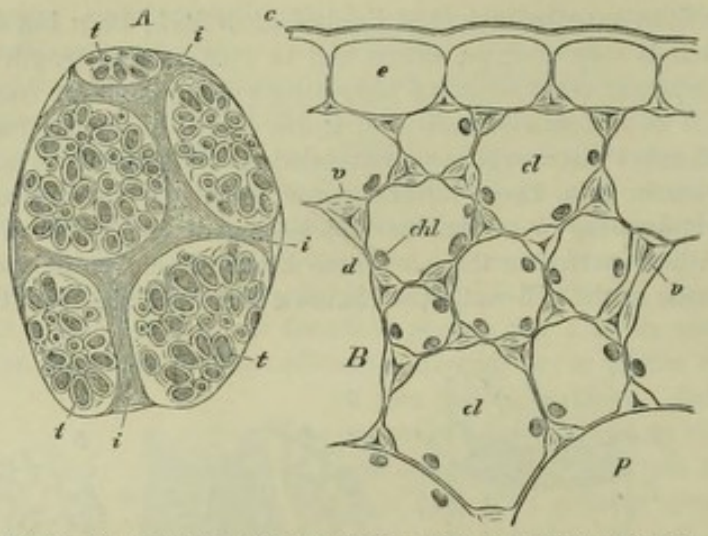


FIG. 21.—*A*, a parenchyma-cell of the cotyledon of *Phaseolus multiflorus* isolated by maceration; *i i* the parts of the cell-wall where it is bounded by intercellular spaces; *t*, *t* the cell-wall furnished with numerous simple pits, but not greatly thickened; the thinnest parts of the pits are drawn dark. *B* epidermis (*e*) and collenchyma (*cl*) of the leaf-stalk of a Begonia; the epidermis-cells are uniformly thickened on the outer wall where they adjoin the collenchyma, but are thickened like the collenchyma at the angles where three cells meet; these thickenings have great power of swelling; *chl* chlorophyll grains; *p* parenchyma-cell (×550).

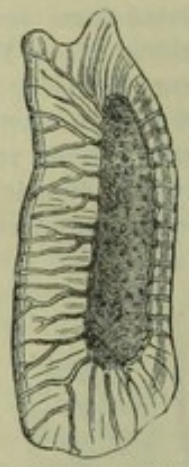
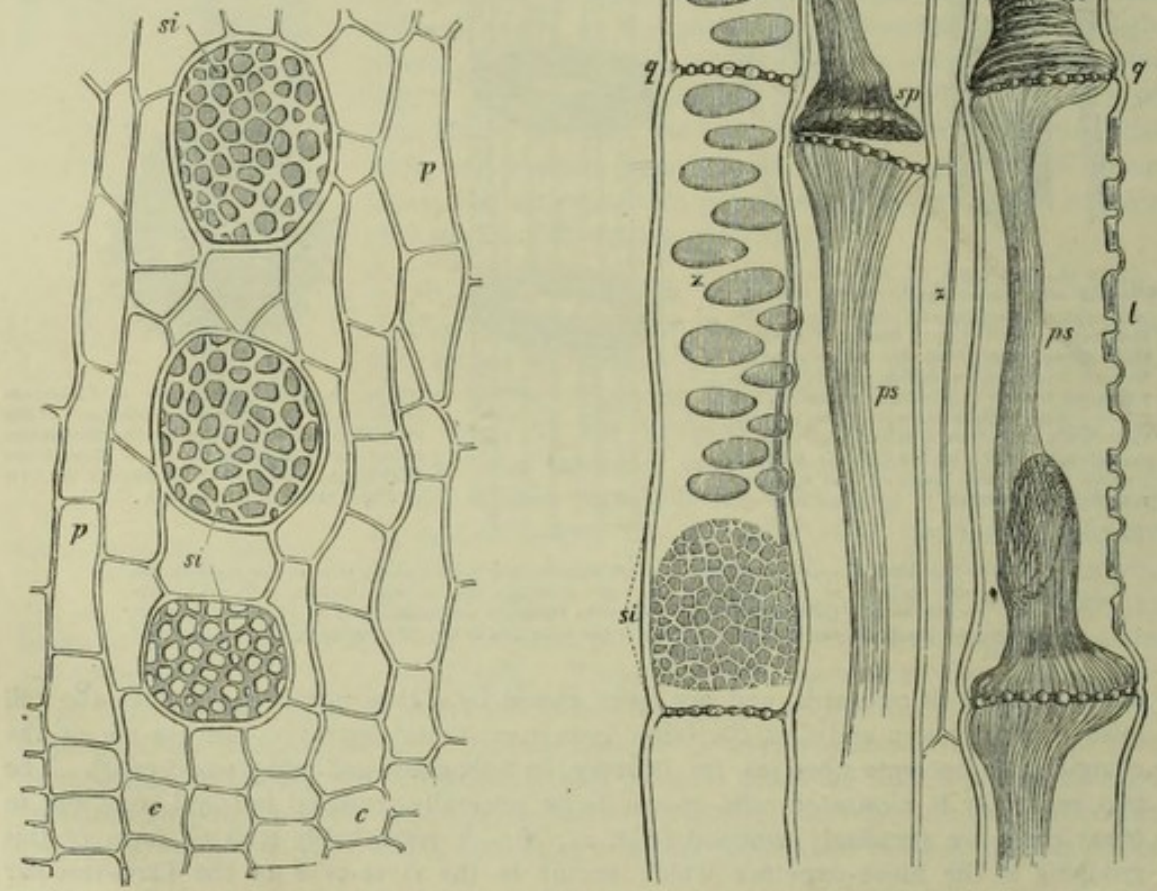


FIG. 22.—A cell beneath the epidermis of the underground stem of *Pteris aquilina*, isolated by boiling in a solution of potassium chlorate in nitric acid; it is more strongly thickened on the left side; the unthickened places here appear as branched channels (×550).



FIGS. 23, 24.—Young sieve-cells of *Cucurbita Pepo* (×550); the preparation has been taken from pieces of the stem which by having lain for a long time in absolute alcohol have allowed the production of extremely clear sections. The sieve-plates do not at present show anything of the subsequent more complicated structure, which may be examined in Nägeli, *l. c.*; the opening of the sieve-pores has not yet begun; they are as shown in Fig. 24, *sp*, still closed, their contents not yet combined. Fig. 23. Transverse section; *c c* cambium; *p* parenchyma; *si* the septa of the sieve-cells, developing into sieve-plates. Fig. 24. Longitudinal section; *q* the transverse view of the sieve-like septa; *si* a sieve-plate on the side-wall; *x* thinner parts of the longitudinal wall, seen at *l* in longitudinal section; in them are subsequently formed a number of small sieve-pores, at present they are still homogeneous; *ps* the contracted protoplasm-sac, lifted off at *sp* from the septum; *z* parenchyma-cells between the sieve-cells.

the simplest case the thin places (pits) are densely crowded, only separated by thicker ridges, and polygonal (Fig. 23, 24, *si*); they very often appear as sharply circumscribed groups of numerous points; the whole surface of such a group may then be thinner than the rest of the cell-wall. But in many cases the thin part of such a pit becomes absorbed, and the protoplasmic contents of adjoining cells enters into communication through these narrow channels. (Fig. 88.) Sometimes the structure of these sieve-plates (*e.g.* in *Cucurbita Pepo*) becomes, when old, very peculiar and complicated from further thickening and swelling of the thickened portions[1].

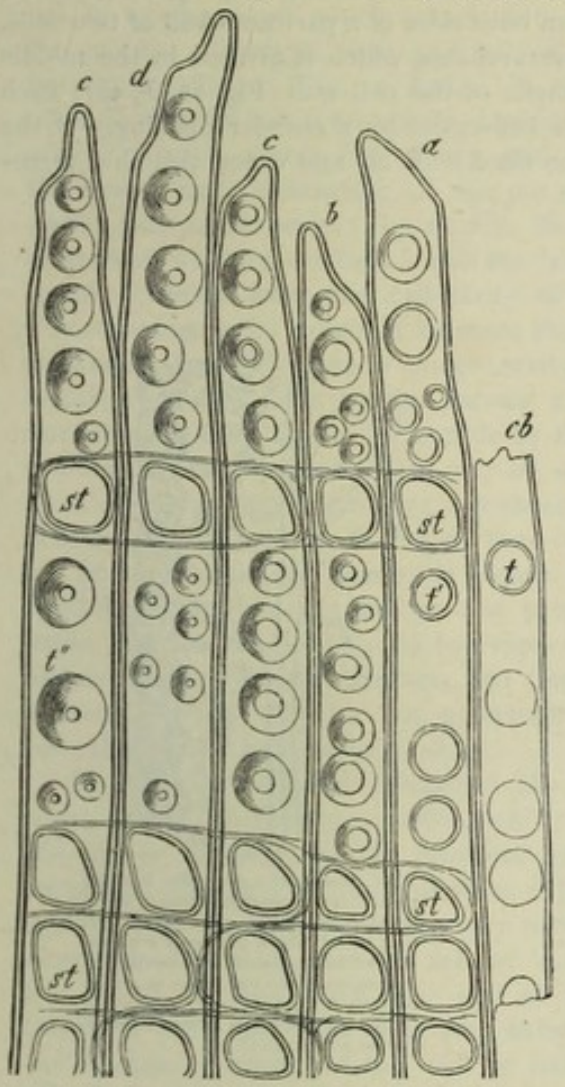


FIG. 25.—*Pinus sylvestris*; radial longitudinal section through the wood of a rapidly growing branch; *cb* cambial wood-cells; *a—c* older wood-cells; *t t' t''* bordered pits of the wood-cells, increasing in age; *st* large pits where cells of the medullary rays lie next the wood-cells (×550).

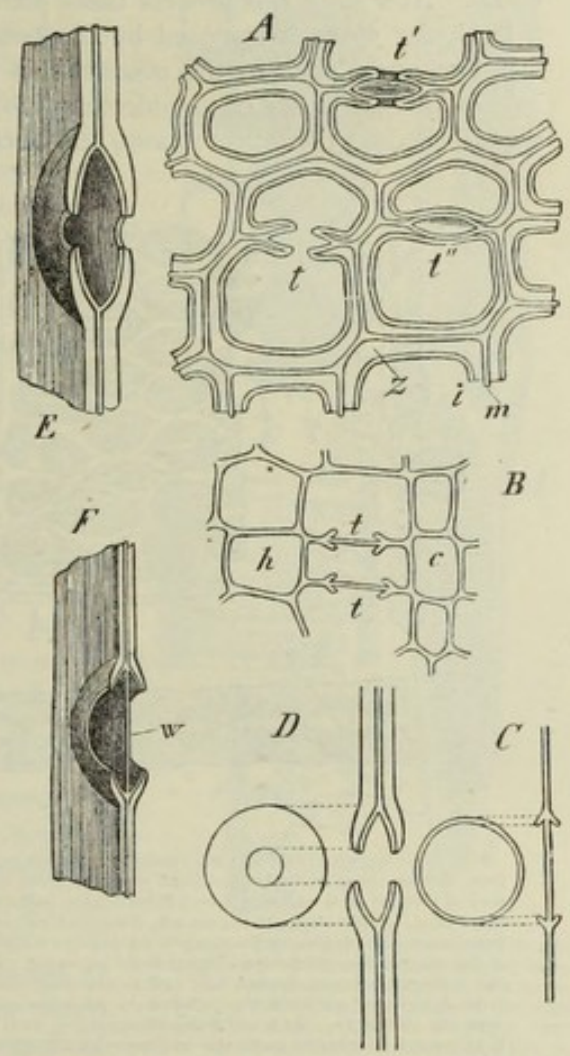


FIG. 26.—*Pinus sylvestris*; *A* transverse section of mature wood-cells (×800); *m* central layer of the common wall; *i* inner layer, clothing the cavity; *z* intermediate layer of the cell-wall; *t* a mature pit cut through the middle; *t'* the same, but at a thicker part of the section, the part of the cavity of the pit lying beneath is seen in perspective; *t''* a pit cut through beneath its inner opening; *B* transverse section through the cambium (×800); *c* cambium; *h* wood-cells still young; between them two very young wood-cells with the formation of pits beginning *t t*; *C—F* diagrams.

One form of the internally projecting thicknesses which is of extremely common occurrence in wood-cells and vessels, viz. the formation of Bordered Pits, deserves a fuller exposition at this place.

The formation of Bordered Pits arises thus: comparatively large spaces remain thin at the commencement of the thickening of the cell-wall (Fig. 25, *t*; Fig. 26, *B*, *t*); and

[1] Compare Nägeli, Ueber die Siebröhren von Cucurbita, in the Sitzungsberichte der k. bayerischen Akad. der Wissenschaften. München 1871; and Hanstein, Die Milchsaftgefässe. Berlin 1864.

[2] The development of these was first accurately recognised by Schacht, De maculis in plantarum vasis, &c. Bonn 1860.

after increased thickening, the thickening-mass which is always projecting inwardly, acquires a larger surface, and forms an arch over the thin part of the wall (Fig. 25, *a–e*; Fig. 26, *C–F*). The outline of the thin parts of the wall in the wood of *Pinus sylvestris* appears circular on a front view; the rim of the thickening-mass which becomes arched over it grows also in a circular manner, gradually contracting the opening; and thus the front view of such a pit appears in the form of two concentric circles, the larger of which represents the original dimensions of the thin parts of the cell-wall (Fig. 25, *cb*, *t*), and the inner one the gradually widening circular rim of the thickening (Fig. 25, *a–e*; Fig. 26, *C*, *D*). Now since this process takes place on both sides of a partition-wall of two cells, a lenticular space is enclosed by the two overarchings, which is divided in the middle into two equal parts by the original thin lamella of the cell-wall (Fig. 26, *F*, *w*); each half of this pit-cavity communicates with the cell-cavity by a circular opening. If the wood-cells lose their protoplasm, and become filled with air and water, this thin mem-

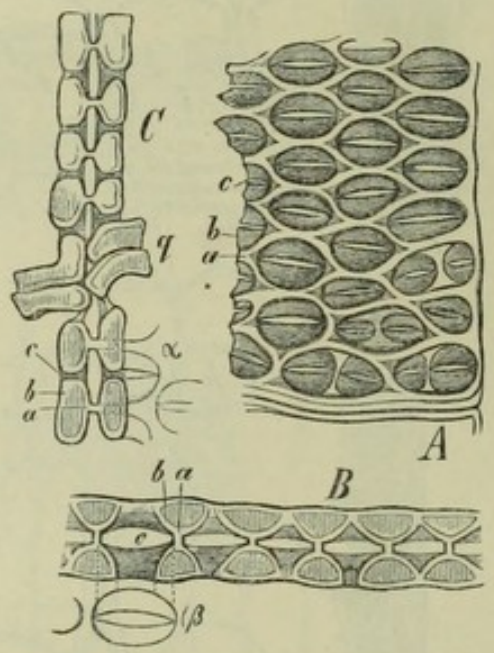


FIG. 27.—*Dahlia variabilis*; wall of a vessel with bordered pits from the succulent root-tuber; *A* front view of a piece of the wall of a vessel from without; *B* transverse section of the same (horizontal, at right angles to the paper); *C* longitudinal section (vertical, at right angles to the plane of the paper); *q* septum; *a* the original thin thickening-ridges; *b* the expanded part of the thickening-masses, formed later and over-arching the pit; *c* the fissure through which the cavity of the pit communicates with the cell-cavity. At α and β the corresponding front view is appended in order to make the transverse and longitudinal sections more clear (×800).

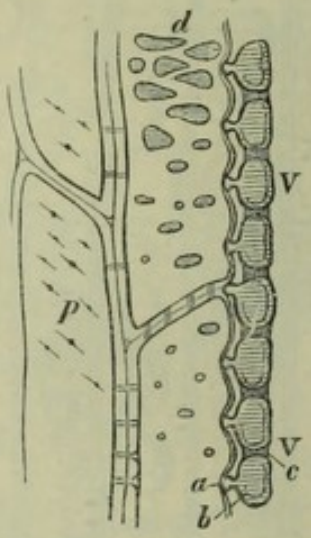


FIG. 28.—*Dahlia variabilis*, from the root-tuber; *P* parenchymatously developed wood-cells; *V* a piece of the wall of a vessel, where it adjoins a parenchymatous wood-cell; *a b* the thickening-masses of the wall of the vessel cut through at right angles; *c*, *t* fissure of the pit; *d* simple pits in the parenchymatous wood-cells (×800).

brane is destroyed (as in Fig. 26, *E*); the pit-space forms a single cavity, which is enclosed between the over-arching thickening-masses of the partition-wall, and is united, right and left, with the adjoining cell-cavities by a circular opening (Fig. 26, *A*, *D*, *E*). In *Pinus sylvestris* the pits are large and distant from one another, and the whole process may be easily traced step by step. The process appears somewhat different when pits lie very near to one another, as in Pitted Vessels. In this case the thickening first presents itself in the form of a net-work, which surrounds the thin parts of the cell-wall in the form of roundish polygonal meshes, as may be very easily recognised in young maize-roots, for instance. Fig. 27, *A*, represents a portion of the side-wall of an already mature vessel[1] of the root-tuber of Dahlia. The ridges which originally appear on the thin cell-wall are indicated by *a* and are left clear; they enclose elliptical meshes pointed at both ends. As the thickening continues, each ridge retains its

[1] On the idea of a vessel, see chap. ii.

original breadth, where it is raised on the thin cell-wall; but the free rim which grows further inwards, expands, and becomes arched over the thin parts of the cell-wall. But in this case the overarchings do not grow uniformly, but in such a manner that their rims form at least a fissure (*c*, in *A* and *B*). Here also, when two similar cells adjoin, the same process takes place on both sides of the partition-wall; and here also lenticular spaces are formed by the overarchings; these are at first bisected by the original thin lamella of the cell-wall, which afterwards disappears, and the two cell-cavities are placed in communication at each bordered pit; the channel or bordered pit which unites them is wide in the middle, and opens right and left into each cell by a narrow fissure (Fig. 27, *B*, *C*). If, on the other hand, a vessel of this kind adjoins a parenchyma-cell which remains always full of sap and closed, the thickening and overarching of the pit occurs only on the side of the vessel (Fig. 28, *V*); the thin parts of the cell-wall are retained [1], and the bordered pits remain closed; from the cell-cavity of the vessel a narrow fissure (*c*) proceeds between the expanded thickening-masses (*b*) to a wider cavity, which is bounded on the sides by the narrow part of the thickening-masses (*a*), on the outside by the primary cell-wall. These processes can only be seen in sections of extraordinary tenuity; but these are easily obtained if larger pieces of the parts to be observed are allowed to lie for months in plenty of absolute alcohol, then taken out before the preparation is made, and the alcohol allowed to evaporate: in this manner pieces of some hardness and toughness are obtained, which may be cut extremely well and smoothly if the knife is very sharp.

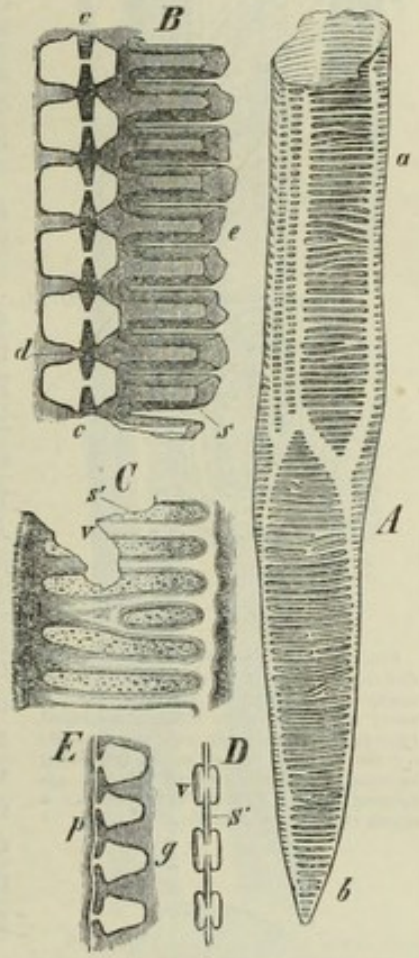


FIG. 29.—*Pteris aquilina*, vessel from the underground stem thickened in a scalariform manner; *A* a half-vessel, isolated by Schulze's maceration; *B*—*D* obtained from pieces of the stem hardened in absolute alcohol; *B* after a very clean section, represented half as a diagram; to the right, front view of the wall of the vessels from within; *c c* vertical section of the same; *C* front-view of the young wall of a vessel; *D* its vertical section; *E* place where a vessel adjoins a succulent cell, in section vertical to the thickening-ridges of the vessel (×800).

In the walls of vessels thickened like ladders or steps, which are developed with peculiar beauty in the higher Cryptogams, the bordered pits are fissure-like; they are often as broad as the partition-wall of two adjoining cells, but very narrow in the direction of the longitudinal axis of the cell. In Fig. 29, *A*, is shown the lower half of a vessel of this kind with the fissure-like pits, between which the thickening-masses of the wall lie like rungs of a ladder; the larger clear spaces are the angles of the contiguous cells. The formation of such a scalariform thickening begins by the growth, on the originally very thin wall which separates two vessels (*C*, *s'*), of transverse ridges of thickening (*v*), which pass over, right and left, into that thickening which always lies on the angle of a cell-wall. *C* shows this horizontally, *D* in vertical section. When completely developed, the thin lamella (*s'*) has disap-

[1] These thin pieces of cell-wall which close up bordered pits may, by rapid surface-growth, form bag-like prominences, which grow through the pores of the pits into the vessels, spread themselves out there, become separated by septa, and thus form a thin-walled tissue, which not unfrequently fills up the whole of the cavity. These formations were long known under the name of 'Tüllen'; they are abundantly and easily seen, for instance, in old roots of Cucurbita, and in the wood of *Robinia pseudacacia*, &c. [These cells contained in the ducts are, according to Mohl and Reess, really hernioid protrusions from adjacent cells; see Journ. of Bot. 1872, pp. 321–323, t. 126; and Reess, Bot. Zeitg. 1868, pp. 1–11, t. 1.]

peared (*c*, *c*, in *B*), the thickening-ridges have become overarched, growing inwards, so that now only a narrow fissure (*d*, *B*) remains between its margins; still further inwards the ridge again becomes narrower. The interior cavities of two adjoining vessels are thus united by a number of broad fissures (*B*, *s*); the frame-work of the ladder is formed of peculiarly-shaped rungs, which may be seen in *B* at *cc* in section, at *e* along the surface. Where the wall of a vessel bounds a parenchyma-cell (*E*), the scalariform thickening takes place only on the side towards the vessel (*g*), it is absent from the other side (*p*). In this case also the thin original wall remains; it closes the broader exterior space of the bordered fissure-shaped pit.

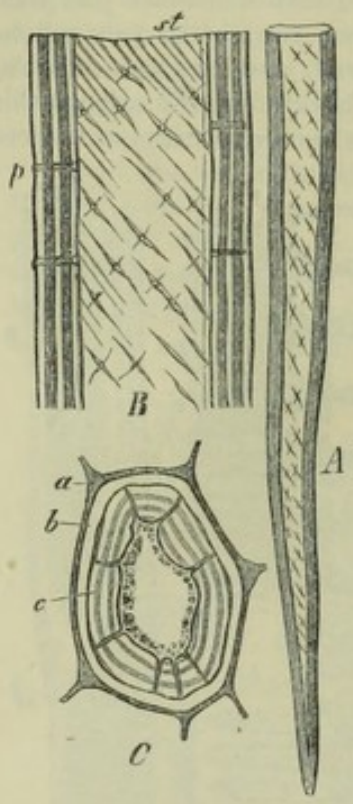


FIG. 30.—Brown-walled cells in the stem of *Pteris aquilina*; *A* a half-cell isolated and rendered colourless by Schulze's maceration; *B* a piece more strongly magnified (×550); the fissure-like pits are crossed; *i. e.* the fissure is twisted as the thickening increases; at *p* side-view of a fissure, appearing here as a simple channel, since it shows the narrow diameter.

The variety in the formation of pits is by no means exhausted by these examples; but all the processes cannot be described here; we can only indicate a few.

We saw in the formation of vessels in the Dahlia (Fig. 27) how the pit occupies at first a large round space, while the margins of the overarching thickening enclose a fissure. By a change in this process of growth, the fissure may attain a length much greater than the diameter of the exterior cavity of the pit; then the pit appears, on a front-view, as a roundish opening, crossed by a fissure (Fig. 28, *P*). It also sometimes happens that the pit-fissure changes its direction as the thickening increases, and in this case, on a front-view, two fissures crossing one another are perceived (Fig. 30, *A* and *B*, *st*). But in order to be certain that this takes place within the layers of the wall of one cell, the cells must be isolated by maceration. Similar appearances are also often presented on a front-view, if the whole partition-wall of two cells is observed from the front. If the fissure runs upwards to the left in the one cell, the corresponding fissure may run upwards to the right on the other side; on a front-view they then appear crossed[1].

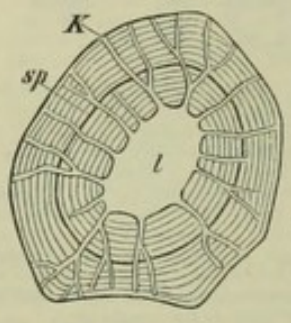


FIG. 31.—Transverse section of a bast-cell of the root-tuber of *Dahlia variabilis* (×800); *l* the cell-cavity; *K* pit-channels which penetrate the stratification; *sp* a crack by which an inner system of layers has become separated.

In cells of tissues the partition-wall is always at first a very thin simple lamella; as the thickness increases, the thickening-masses always project right and left into the adjoining cell-cavities. Generally the growths right and left of a partition-wall, as we have already seen, correspond; and this occurs most clearly in the formation of pits, as far as the pit-channels of adjoining cells meet one another. But since a cell often adjoins very different contiguous cells on different sides, different sides of the same cell may show different forms of thickening, and especially different formations of pits. The total growth in thickness may also be very different on different sides; thus, for instance, the epidermis-cells on the outer free wall are mostly very strongly thickened on the inner wall, where they adjoin parenchyma-cells, being either very thin or corresponding in form to the adjoining cells.

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[1] A very clear representation of a twisted pit-channel, whose outer and inner fissure (within the same cell-wall) cross, may be seen in Nägeli, Berichte der Münchener Akademie, 1867, vol. v. fig. 45.

The corresponding growth in thickness is less marked if the thickenings show a distinctly spiral structure, or if they arise in the form of strong spiral bands, as in spiral fibre-cells; if, in this case, in each pair of adjoining cells one or more spiral bands wind in the same direction, they must necessarily cross on the common partition-wall.

(c) *Stratification and Striation of the Cell-wall* [1]. When the cell-walls have attained a certain thickness and extent of surface, stratification and striation take place more or less clearly. In consequence of stratification the cell-wall appears composed of very thin membranes enclosed one within another and fitting very closely together; the stratification is seen both on the transverse and the longitudinal section of the cell-wall. The striation is generally to be seen most plainly from the front; it may be observed in the form of two systems of lines (sometimes apparently several) which are marked on the upper surface. The one system, consisting of parallel striæ, is always cut by the other system, which also consists of parallel striæ. A closer investigation shows that the structure which gives the appearance of striation does not belong merely to the upper surface or to one layer of the cell-wall; but that the striation rather penetrates the whole thickness of the cell-wall, and that the striæ are thus lamellæ which cut the upper surface, and are continued through all the concentric layers. If the striation is very clearly marked, and if it is nearly parallel to the longer axis of the cell, it may also be recognised under transverse section in the form of striæ, which penetrate the concentric layers; when the cell-wall is cut lengthwise only those systems of striation are to be clearly recognised which, seen from the surface, run almost diagonally round the cell.

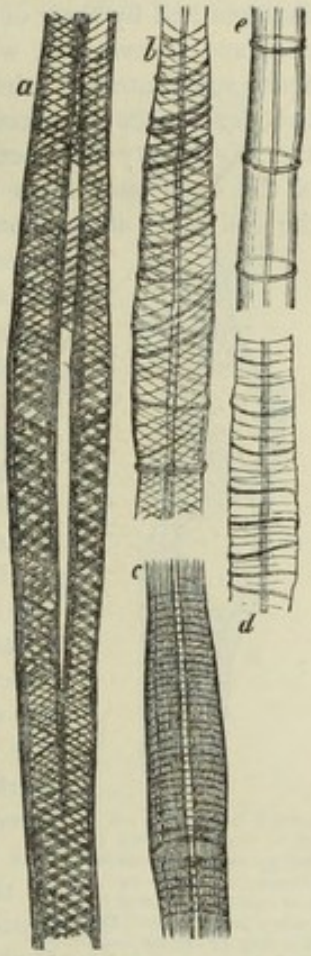

FIG. 32.—Bast-cells from the leaf of *Hoya carnosa* (×800), showing the striation. These are not nearly so strongly marked in nature, but are quite as plain; *a* optical longitudinal section of the crossed annular striation; *b* external view of the side where the annular striation cross; *c* external view of the side where they do not cross; *d* the same; *e* a piece of cell-wall, where only single annular striations can be seen.

Every system of stratification or striation consists of lamellæ of visible thickness and of different refractive powers, so that a more strongly refractive layer or stria always alternates with a less strongly refractive one. This difference of refraction results from a different distribution of water and of the solid particles in the cell-wall; the less strongly refractive lamellæ are more watery, poorer in cellulose, and thus less dense; the more strongly refractive and denser lamellæ contain less water and more cellulose. Hence stratification and striation of the cell-wall disappear when water is completely eliminated, as also when it swells violently, *i. e.* absorbs much water; because, in the first case, the more watery layers are reduced to the condition of the less watery ones, in the latter case the less watery, by plentiful absorption, become similar to the others. On the other hand stratification and striation become most conspicuous when for a given proportion of water in the cell-wall the difference between the dense and the soft layers is greatest. In many cases this may be brought about by addition of acids or alkalies which occasion a moderate swelling. But if the dense layers are very dense,

[1] H. von Mohl, Bot. Zeitg. 1858, pp. 1, 9.—Nägeli, Ueber den inneren Bau der vegetabilischen Zellenmembran, in the Sitzungsberichte der Münchener Akad. der Wissenschaften, 1864, May and July.—Hofmeister, Lehre von der Pflanzenzelle, p. 197.

and the less dense ones very watery, as is the case with some wood-cells (*e. g. Pinus sylvestris*), the striation becomes more evident through desiccation, because then the dense layers stand forwards, while the less dense ones give way.

The systems of striation and stratification of a cell-wall intersect one another, like the cleavage-planes of a crystal splitting in three directions. But since the striations and laminæ consist of lamellæ of a measurable thickness, composed of alternately denser and less dense substance, the cell-wall appears to be composed of parallelopipedal pieces, distinguished by their content of water. If we for a moment disregard the stratification, and assume that we have two intersecting systems of striation, then, where two dense striæ intersect, the densest or least watery places are always to be found; where two dense ones intersect, the least dense or most watery; and where places of greater and less density intersect, areolæ of intermediate density are formed. The intersections of the striæ must form prisms which stand vertically or obliquely upon the surface of the cell-wall; if the concentric stratification is very strongly developed, every one of these prisms must become decomposed into denser and less dense sections lying in radial order behind one another; if the concentric lamination is feebly developed, the prismatic structure may sometimes appear very clearly; the peculiar internal structure of the exospores of Rhizocarpeæ, and the yet more various structure of the extine of many pollen-grains, may be resolved into a further development of this kind of process; but our space does not permit us to pursue this in detail. The lamellæ which appear externally as striation may possess the form of closed rings; *i. e.* may be similar to thin sections of the cell, or may run in a spiral manner round the axis of the cell. A distinction must accordingly be drawn between annular and spiral striation; it is often, however, very difficult to decide which of the two is present; sometimes both are developed at different parts of the same cell-wall. Sometimes one system of striation is very obscure, the other more strongly marked; or one system may be the better developed in one layer of the cell-wall, the other system in another layer; and this is genetically connected with the above-mentioned twisting of the pit-fissures. The striation is mostly clearest in cells with broad uniform thickening-surfaces (as *Valonia utricularis*, hairs of Opuntia, pith-cells of the root-tubers of the Dahlia, in the latter case remarkably plain); but it may also be recognised when the sculpture of the cell-wall is complicated; *e. g.* in the walls of very wide vessels of *Cucurbita Pepo*, provided with densely crowded small bordered pits (after Schulze's maceration, especially in vessels of the root, very clear crossed spiral-striation). The striation may itself give occasion to differences of level; sometimes the denser lamellæ project a little on the inner side of the cell-wall (Fig. 34, *B*); or single denser lamellæ of one system of striation alone become prominent; thus, for instance, a fine spiral band makes its appearance on the inner sides of the wood-cells of the yew, which is not unfrequently crossed by one running in the opposite direction. When elongated fissure-like pits are arranged in a spiral line on the cell-wall, a system of striation is generally found in a corresponding direction.



FIG. 33.—A cell beneath the epidermis of the stem of *Pteris aquilina*, isolated by Schulze's maceration. The wall is seen in optical longitudinal section; it shows an innermost very dense layer, a central less dense layer (to the right below is the dark striation) enclosed by two denser layers; these layers are penetrated by pit-channels, which are seen on the hinder wall in transverse section.

This slight sketch must suffice to introduce the beginner to the nature of stratification and striation, and to their relation to the sculpture of the cell-wall; further detail would exceed the limits of this book [1].

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[1] The striation may easily be seen, even with slight magnifying power, in the large pith-cells of the root-tubers of Dahlia, in the hairs of Opuntia, in *Valonia utricularis*; but only by very high

(d) *Intussusception as a cause of the growth of the Cell-wall in surface and thickness.* The surface-growth of the cell-wall may now be regarded as an interposition, between its already existing particles, of new particles which force the old ones asunder. It is very probable that the striæ have a genetic connexion with this process, similar to that which Nägeli has shown to exist between the concentric stratification of starch-granules and their growth. It was long thought that the growth in thickness of the cell-wall arose from the repeated deposition of new concentric layers on the inner side of the cell-wall which was originally thin, so that the innermost layer must always be the youngest. This appeared to be an extremely simple explanation of the stratification of the cell-wall; and the chemical differentiation of thick cell-walls appeared entirely to support this idea. But the increased powers of new microscopes revealed a fact quite fatal to the theory of apposition; the stratification of thickened cells was shown, in short, as we have seen, to be not a separation of similar, but an alternation of dissimilar, layers. For reasons which cannot here be discussed, it must be concluded that these alternate deposits of more and less watery layers must, in general, be not the result of an apposition, but rather only of an internal differentiation of the cell-wall already formed. The fact is, however, decisive, that on the inner side of every cell-wall and on each side of dense ones lies a layer containing but little water; if growth in thickness took place by successive deposits of layers, the innermost and youngest layer must be alternately denser and less dense, which is not the case. The growth also of such thicknesses as project outwardly, like the combs and spines of pollen-grains, &c., can only be explained by intussusception, not by apposition.

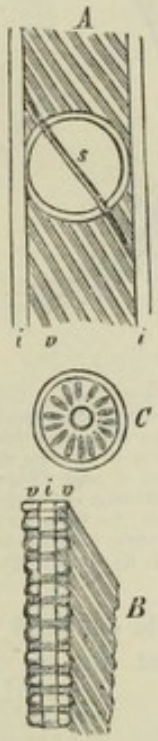

FIG. 34.—Striation of the wood-cells of *Pinus Strobus*; *A* front view of a young cell, a fissure runs across the still young bordered pit, corresponding to the spiral striation; *B* sectional view of the cell-wall with a part of the side-view; *i* the central lamella of the wall common to two cells; *v v* the thickening-layers in contact with them; these are striated, the striation may be recognised as a formation of lamellæ penetrating the whole thickness; the denser (clear) lamellæ project in the form of little knobs. *C* front view of a pit; the striation here appears as a star-like arrangement of less dense places (×800).

Growth by deposit can only be considered of this nature:—that an aqueous solution from the protoplasm penetrates, by diffusion, between the molecules of the cell-wall. What kind of solution this is, cannot at present be said with certainty; probably it contains some carbo-hydrate which is easily transformed into cellulose. This substance then forms between the molecules of the cell-wall new solid molecules of cellulose. The actual process of growth, as well as the internal structure of the cell-wall already described, and certain phenomena which polarised light induces in it, as well as the swelling of the cell-wall, lead to the conclusion that it consists of solid molecules of definite form, each of which is surrounded by an envelope of water, and separated from the adjoining molecules; the more watery a layer of cell-wall or a striæ is, the smaller, according to the principles laid down by Nägeli[1], are the solid molecules, the more numerous and the thicker their aqueous envelopes. From this it follows that a certain quantity of water is as indispensable to the growth and the internal organisation of the cell-wall as is cellulose itself; this water may be designated 'water of

magnifying power in isolated wood-cells of Pinus, in bast-fibres, &c.; one of the examples longest known is the bast-cells of Apocynaceæ provided with power of extension and contraction. (Mohl, Vegetabilische Zelle, Fig. 27.)

[1] The theory of the growth of the cell-wall (as of all organised structures) by intussusception was first originated by Nägeli in his great work on Starch-granules (1858). Compare also Sachs, Handbuch der Experimentalphysiologie der Pflanzen, § 114.

organisation' in the same sense we speak of as 'water of crystallisation;' and as the latter is indispensable to the formation of many crystals, so is the former to the structure of the cell-wall. It is moreover, as we shall see, a peculiarity of all organised structures, that they contain 'water of organisation,' at least as long as they grow, because they all alike grow by intussusception.

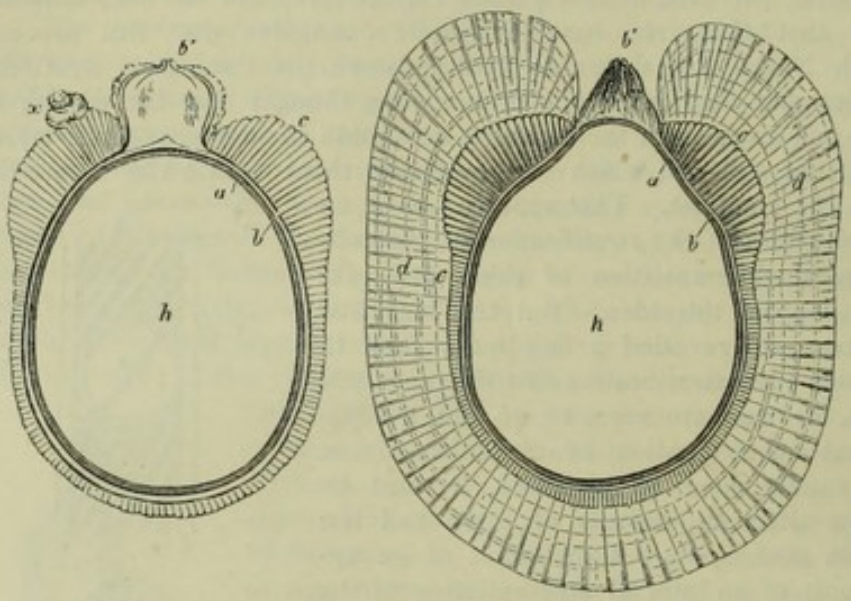

FIG. 35.—Macrospores of *Pilularia globulifera*, in optical longitudinal section; to the left a still unripe spore, in which the outermost gelatinous layer of the cell-wall is still wanting, which is present in the ripe spore to the right; the two outermost layers of the cell-wall of the latter (*c* and *d*) have assumed a prismatic structure, which is especially clearly manifest at *c*; at *d* stratification is feebly indicated at the same time. Seen from the surface the prisms appear like areolæ; the boundary surfaces of the prisms are, in the corresponding cell-wall-layer of *Marsilea salvatrix*, more solid and cuticularised, by which the appearance of a honey-comb is obtained. (Cf. J. Hanstein, Berliner Monatsbericht; Feb. 6, 1862, Fig. 17, and Book II. Rhizocarpeæ.)

From what has been said, it can easily be seen that the concentric formation of layers of a cell-wall growing by intussusception essentially differs from the repeated formation of cell-wall round one and the same protoplasmic body; cell-walls enclosed one within another may be produced in this manner; these, however, must not be considered as layers of one cell-wall. This process is very common in the formation of the pollen-grains of Phanerogams; within that mass of cell-wall-layers which forms what is usually designated the special mother-cells, each protoplasmic body forms round itself a new cell-wall, before the mother-cell-wall is destroyed (Fig. 36).

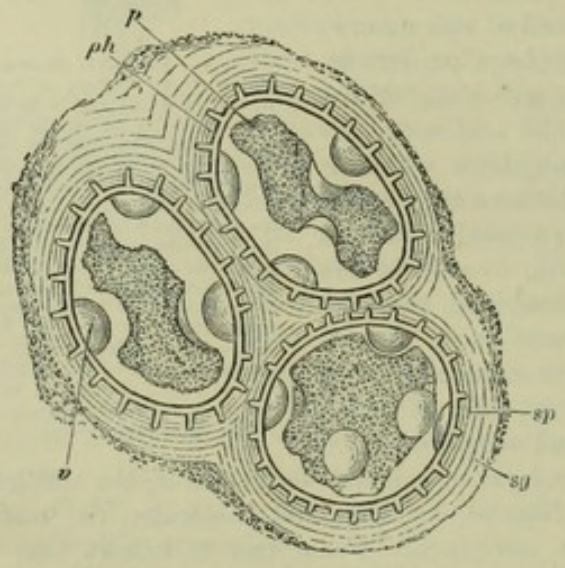

FIG. 36.—Pollen-mother-cell of *Cucurbita Pepo*; *sg* the externa common layers of the mother-cell in the act of absorption; *sp* the so-called special mother-cells, consisting of masses of layers of the mother-cell which surround the young pollen-cells; they also are afterwards absorbed; *ph* the wall of the pollen-cell; its spines grew outwards and penetrate the special mother-cell; *v* hemispherical deposition of cellulose on the pollen-cell-wall, from which the pollen-tubes are afterwards formed; *p* the contracted protoplasmic body of the pollen-cell (the preparation was obtained by dissection of an anther which had lain for some months in absolute alcohol (×550).

But the renewal of a cell-wall may also be brought about by the external mass of layers undergoing no further growth, while the internal layers of the same cell-wall increase by intussusception. Thus the cell-wall of spores and pollen-grains is originally a whole increasing by deposit; by subsequent internal differentiation masses of layers are formed differing in their chemical and physical properties; the outer firm cuticle (exospore, extine) remains subsequently unchanged: it is thrown off as an envelope, while an inner mass of layers (the endospore in one, the intine in the other case) begins a new growth with the germination of the spores and pollen-grains. A similar process occurs with many filamentous Algæ (Rivularieæ and Scytonemeæ), where a large number

of cell-walls enclosed within one another are gradually formed, while from time to time the older masses of layers cease growing, and are pierced by the growing filament, which now forms new layers of cell-wall (cf. Nägeli und Schwendener: Das Mikroskop, II. p. 551). It need scarcely be mentioned that tehse appearances do not contradict the theory of the growth of the cell-wall by intussusception, but only represent, in general, particular modifications of the life of the cell.

(e) *Differentiation of the Cell-wall into Systems of Layers (Shells) with different chemical and physical properties.*

Very young and thin cell-walls, while still in rapid growth, as also many older ones, are constituted throughout their whole thickness of what has been termed pure cellulose; *i. e.* they are easily permeable by water, only slightly extensible and capable of swelling, very elastic, colourless, soluble in sulphuric acid; with iodine and sulphuric acid they assume an intense blue colour, as also with Schultz's solution, rarely with solution of iodine alone (as the spore-sacs of Lichens). Together with these common properties, they may, according to the nature of the cell, show also many peculiar reactions. Among the older developed cells, the greater number of succulent thin-walled parenchyma-cells of the higher plants behave in this manner, many thick-walled cells of Algæ, and,—with the exception of the blue colour produced by iodine and sulphuric acid, and by Schultz's solution,—the greater number of filaments of Fungi and Lichens.

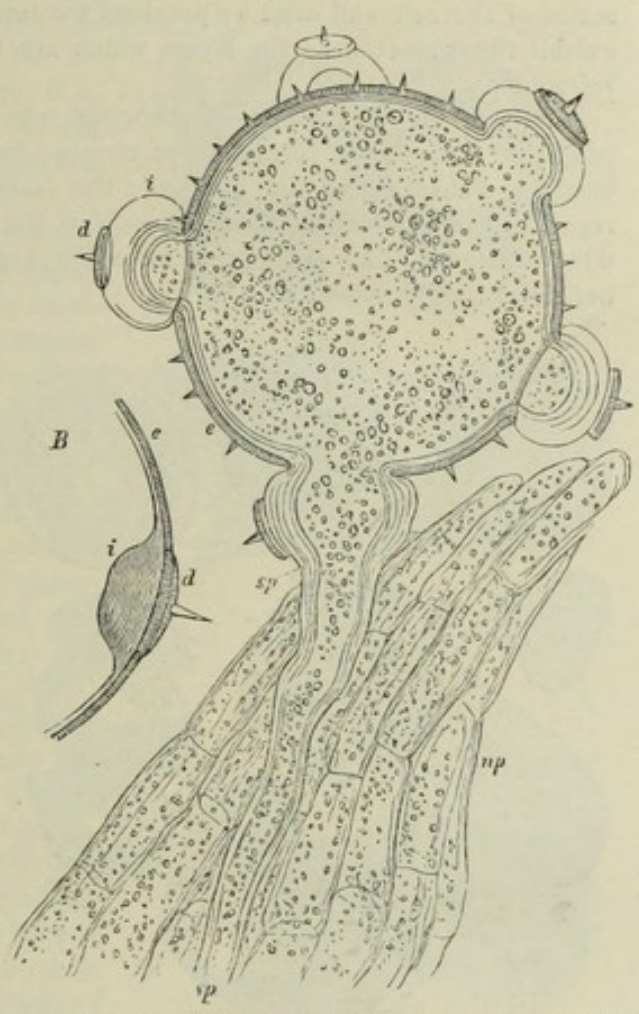

FIG. 37.—A germinating pollen-grain of *Cucurbita Pepo*, which has emitted a pollen-tube (*sp*) into a papilla of the stigma. The cell-wall of the pollen-grain consists of a cuticularised extine (*e*), and an intine capable of growth (*i*); the latter is greatly thickened at certain places (*B i*); on each thickening-mass the extine forms a roundish lid (*d*); when the pollen-grain is preparing for germination, the thick parts of the intine swell, and thus tilt up and lift off the lid of the extine; the pollen-tubes are formed of one or two of these thickening-masses (×550).

With more strongly thickened cells (rarely with moderately thin ones, *e. g.* some cork-cells), whole masses of layers behave in a different manner chemically and physically, so that the cell-wall appears split into two or more shells [1], each of which may again exhibit numerous layers and the striation already described. In the case of free-lying cells which require protection (as pollen or spores), or of those which themselves serve as a protection to other tissues (as cork), an outermost shell (of greater or less thickness) of each cell-wall is transformed into cork or cuticle; when the cells are destined to

[1] It is desirable to employ the expression layers (Schichten) only in the sense mentioned under (d), where it implies a regularly alternating difference in the proportion of water, as in the striæ; but in that case another term must be employed for the formations now under consideration; the expression 'shells' (Schalen) appears to me to answer the purpose.

form a firm framework, the outer masses of layers become lignified; in other cases, on the other hand, the outer, rarely the inner layers, are transformed into mucilage. Usually an inner layer of the cell-wall remains unchanged in all three cases, enabling the above-mentioned cellulose reactions to be recognised, while the corky and lignified scales of the cell-wall may, by previous treatment with alkalies or with nitric acid, also exhibit these reactions; the layers which are transformed into mucilage are the most refractory.

Some of the morphological processes here treated of find their explanation only when we observe the formation of tissues; but I cannot enter on an account of the chemical behaviour of the cell-wall; the reactions here mentioned must properly be regarded not as chemical tests, but only as the means of recognising the morphological differentiation. The description of some examples will be sufficient to direct the beginner.

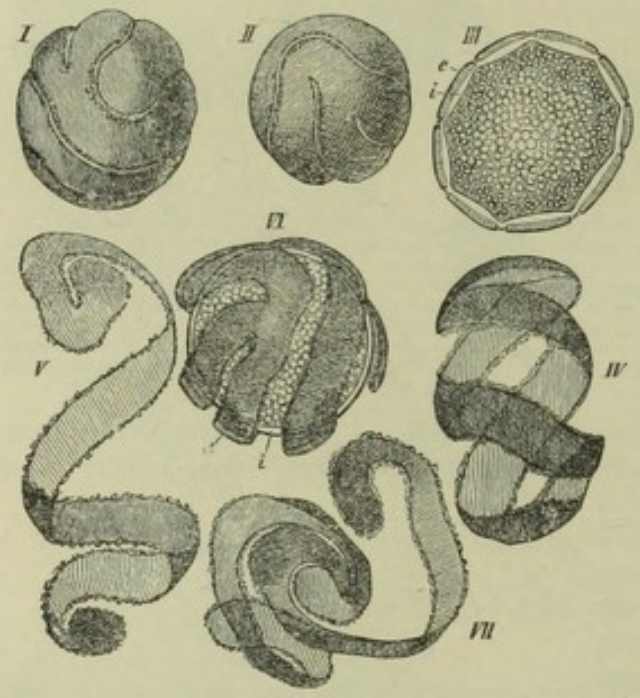

FIG. 38.—Pollen of *Thunbergia alata* (×550). *I* and *II* placed in concentrated sulphuric acid; *IV*, *V*, *VII* also after solution of the intine; sometimes the fissures of the extine run so that isolated pieces of it fall off, corresponding to the lids of the extine of other pollen-grains, *e.g.* of Cucurbita; *III* in Schultz's solution; *VI* in strong solution of potash, *e* extine, *i* intine. The fissures of the extine clearly arise by subsequent inner differentiation in the same manner as the elaters are formed from the so-called special mother-cell of the spores of Equisetum. (Cf. Book II. Equisetaceæ.)

The pollen of *Thunbergia alata* (Fig. 38) shows that the different development of two systems of layers of a cell-wall may go so far that the cuticularised layer (here called extine) becomes actually separated from the non-cuticularised shell (here designated intine) which still possesses the power of growth; and that by this means it becomes broken up by previously formed fissures in most cases into one or two spiral bands. This can be artificially induced by laying these pollen-grains in concentrated sulphuric acid or potash; the extine then assumes a very beautiful red colour, while the intine in the first case dissolves, in the second case swells a little and remains colourless. In the germination also of many spores (*e.g.* Spirogyra, Mosses, &c.) the cuticularised exospore becomes completely separated and stripped from the endospore, which still continues to develop; both shells, however, corresponding to the extine and intine of the pollen-grain, consist, in their actual development, of systems of layers of a single cell-wall possessing a different chemico-physical constitution.

In the epidermis-cells, the cuticularisation either affects a shell of the outer wall, or it attacks the side-walls, as may be seen, for instance, in a very exquisite manner on the under-side of the leaf-veins of the holly. If a very thin transverse section (Fig. 39, *A*) is treated with Schultz's solution, and submitted to a very high magnifying power (800), each cell-wall of the epidermis appears to be composed of two shells, of which the inner, softer, and more capable of swelling (*c*) becomes dark blue, while an outer shell does not assume this colour. But this latter shows itself even further to be composed of two chemically different layers, an inner (*b*), which assumes a yellow colour and penetrates laterally between the cells (*b'*), and an outer one which remains colourless (*a*), and extends continuously over the cells (the so-called true cuticle). Between these two may be observed yet another boundary zone, which, when the microscope is exactly focussed, passes over it like a shadow. The inner shell, which

assumes the blue colour, as well as the cuticularised substance, is formed of several layers in the sense indicated under (d); each is composed of a system of layers. In the latter moreover the radial lamellar structure (striation) is more evident, as is shown in Fig. 39, *A*, *a*, *b*; these radial lines are not, as was formerly thought, pores, but are the appearance presented transversely by the lamellæ; they are to be seen (in Fig. 39, *B*, *s*, a front view of the cuticle) as striæ, which, following the veins of the leaf lengthways, pass over the septa of the cells (*q*).

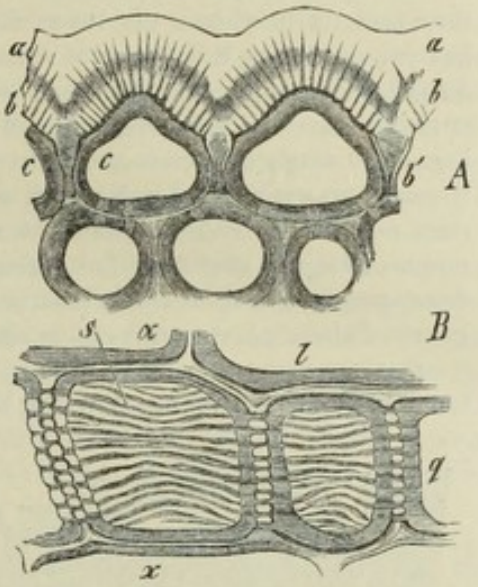

FIG. 39.—Epidermis of the central vein of the leaf of the holly; *A* transverse section; *B* superficial appearance.

An example of strongly *lignified* cell-walls, divided into three shells, occurs in the dark-brown-walled sclerenchyma-cells which compose the firm bands between the vascular bundles in the stem of *Pteris aquilina* (Fig. 40). The very thick wall between two cells contains an intermediate, hard, deep-brown lamella (*a*); this is followed on each side by a light-brown, more horny shell (*b*); and this encloses a third, likewise light-brown shell. By boiling in nitric acid with potassium chlorate the first (*a*) is dissolved, and the cells are thereby isolated (cf. Fig. 30); the two other shells of the cell-wall (*b* and *c*) remain unchanged by this maceration, except that they lose their colour; and hence the shell *c* is shown to be composed of some more and some less watery layers (Fig. 30, *C*, *c*). The three shells also show a different behaviour on treatment with concentrated sulphuric acid: *a* becomes a dark reddish brown, and does not swell, or only slightly; *b* swells in the radial direction and becomes thicker; while *c* swells in the radial, tangential, and longitudinal directions (cf. Fig. 40, *C*, *c*, and *D*, *c*); in transverse sections *c* breaks away from *b*, and curves spirally (*C*); in longitudinal sections it is bent in a wavy manner (*D*).

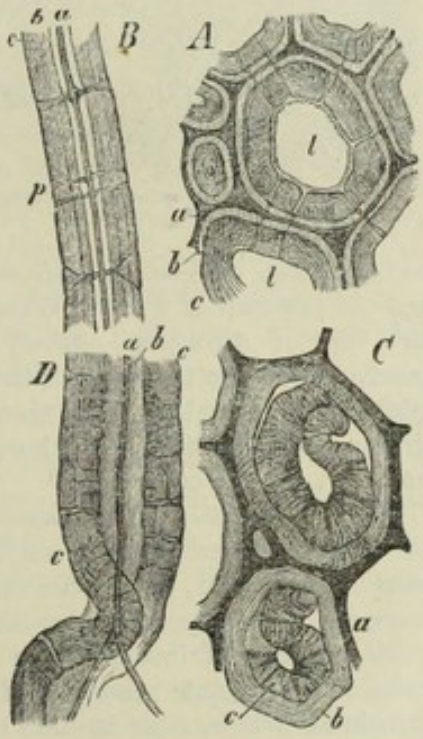

FIG. 40.—*Pteris aquilina*; structure of the brown-walled sclerenchyma in the stem (×550). *A* a fresh thin transverse section; *B* the longitudinal wall between two cells, fresh (a curved pit-channel at the lower end); *C* transverse section in concentrated sulphuric acid; *D* longitudinal section of the wall in sulphuric acid; *a* the central lamella of the wall; *b* second shell; *c* third, inner shell of the cell-wall; *p* pore-channels; *l* cavity of the cell.

In true wood-cells, *e. g.* in *Pinus sylvestris* (Fig. 26, *A*), three shells are likewise generally to be distinguished: a central one (Fig. 26, *A*, *m*), next a thicker one (*z*), and an inner (*i*); the two first turn yellow on treatment with solution of iodine or iodine and sulphuric acid, the innermost blue with the latter reagent; *z* and *i* are dissolved by concentrated sulphuric acid, and the central lamella *m* remains; here also the possibility of isolating the cell depends on the circumstance that the central lamella *m* may be dissolved by boiling in nitric acid with potassium chlorate; and thus the isolated cells consist only of the two inner shells. In many wood-cells (the 'Libriform Fibres' of Sanio) the inner thickening-layers form a shell of cartilaginous and gelatinous consistence (as in the wood of many Papilionaceæ).

When the outermost layers of cells which are combined into tissues become gelatinous or mucilaginous, the boundary-line readily disappears; and the appearance may then be presented as if the cells, enclosed by the inner shell, which is not mucilaginous, were imbedded in a homogeneous jelly as a ground-work; and this latter especially gave rise in time past to the theory of 'Intercellular Substance,' to which we shall recur. This behaviour occurs in the tissue of some Fucaceæ, and also in the endosperm of *Ceratonia Siliqua* (Fig. 41); *cc* are the outer layers of the wall of the cells *a*, which have become entirely converted into mucilage and rendered indistinguishable, their inner layer appearing as a strongly refractive shell. In the dry state the mucilaginous mass is almost horny; it swells up strongly in water with solution of potash; with iodine and sulphuric acid it does not become coloured, but the sharply defined layer turns blue. In free-lying cells numerous layers of cell-wall may also form a mucilaginous shell, which is most beautifully developed in the spores of Pilularia (Fig. 35) and Marsilea. In the spore-fruit (sporangium) of these plants are certain masses of parenchyma, the cell-walls of which become mucilaginous on the inner side; when dry the mucilaginous masses are firm and horny, but absorb so much water that they increase in bulk several hundred-fold, and burst the pericarp (Book II. Rhizocarpeæ). On a similar transformation into mucilage of inner layers of cell-wall, while an outer, thin, and cuticularised shell retains its power of resistance, depends also the formation of the mucilage of linseed and quince-seed. The inner thickening-masses of the epidermis of the seed, transformed into mucilage, absorb the surrounding water with great force, swell violently, and, bursting the cuticle which is incapable of swelling, appear, in the presence of a small quantity of water, as a hyaline layer enveloping the seed; and, with more copious addition of water, become more and more diluted into thin mucilage. A similar process occurs in some other seeds, such as those of *Teesdalia nudicaulis* and *Plantago Psyllium*, in the seed-hairs of Ruellia, and the pericarp of Salvia. Gum-tragacanth consists of the cells of the pith and medullary rays of *Astragalus creticus*, *A. Tragacantha*, and other species, transformed into mucilage. When the walls of these cells become mucilaginous, and swell up on copious addition of water, they force themselves through slits in the stem as viscid masses, and dry up on the outside into a horny mass capable of swelling. Vegetable mucilage can, however, arise in other ways [1].

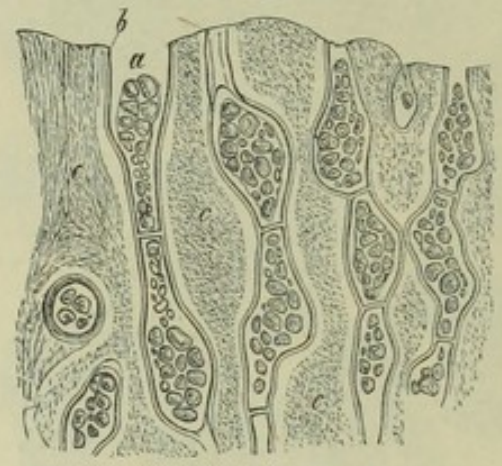

FIG. 41.—Section of the endosperm of *Ceratonia Siliqua*.

(f) *Incombustible Deposits* occur in every cell-wall. The presence of lime and silica can be directly proved; but it can scarcely be doubted that potash, soda, magnesia, iron, sulphuric acid, &c., also occur in small quantities. The deposit of lime-salts and silica increases with age. The deposit may take place in two ways; usually only extremely small particles of incombustible substance are deposited regularly between the molecules of the organic substance of the cell-wall; and this may be recognised by the ash remaining behind after ignition in the organised form of the cell-wall (as a skeleton); but lime salts may also be contained in the cell-wall in the form of numerous very small crystals; they then lie imbedded in the substance of the cell-wall itself, sometimes in the form of particular growths which project into the cell-cavity and are termed Cystoliths (cf. sect. 10).

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[1] Compare further, Frank: Ueber die anatomische Bedeutung und die Entstehung der veget. Schleime. (Jahrb. für wissen. Bot. V. 1866.)

Skeletons composed of a substance[1] soluble in weak acids (generally thought to be lime), are obtained by combustion of very thin layers of tissue on glass or platinum-foil; they occur so generally that it is unnecessary to adduce examples; from entire vessels, I obtained, in the case of *Cucurbita Pepo*, beautiful lime-skeletons. Silica-skeletons are obtained most abundantly from the epidermis-cells and from Diatoms; but silicified cell-walls occur also in the interior of tissues (as leaves of *Ficus Sycomorus*, *Fagus sylvatica*, *Quercus suber*, *Deutzia scabra*, *Phragmites communis*, *Ceratonia Siliqua*, *Magnolia grandiflora*, &c., according to Mohl[2]). The silicification does *not* generally affect the whole thickness of the cell-wall, but only an outer shell, as, for instance, in the case of epidermis-cells, the cuticularised portion only. In order to obtain fine skeletons, it is necessary previously to soak the removed epidermis or thin sections of it in nitric or muriatic acid, and then to burn them on platinum-foil. I have found another method much more convenient: I place larger pieces of the tissue (*e. g.* of leaves of grass, stems of Equisetum, &c.) on platinum-foil in a large drop of concentrated sulphuric acid, and heat over the flame; the acid immediately turns black, a violent formation of gas follows; the heat must be continued until only the pure white ash remains. This is soon effected by this means, whereas otherwise the reduction to ash is generally very tedious, and often does not afford an entirely colourless skeleton. (On the crystals sometimes deposited in the cell-wall, see infra sect. 11.)

Sect. 5. **Protoplasm and Nucleus**[3].—Now that the signification of the protoplasm as the peculiar living body of the cell has been sufficiently brought out, we need only add what is absolutely essential both as respects its chemical and physical nature, and its structure and movements. The protoplasm consists of a combination of (apparently different) albuminous substances with water and small quantities of incombustible materials (ashes). In most cases it also contains, as may be concluded on physiological grounds, considerable quantities of other organic compounds, belonging probably to the series of carbo-hydrates and fats. These admixtures are distributed through its mass in an invisible form; but it not unfrequently includes visible granular formations of starch and fats, which at a subsequent period may either entirely disappear or may increase in bulk. Very commonly the rapidly increasing protoplasm, in itself colourless and hyaline, is rendered turbid by numerous small granules, consisting, probably, of small drops of oil. The protoplasm, as it is generally met with, ought therefore to be considered as true protoplasm with varying admixtures of different formative materials (Metaplasm of Hanstein). The consistence of protoplasm varies greatly at different times and under different circumstances. It commonly appears as a soft, plastic, tough, inelastic, very extensible mass; in other cases it is more gelatinous, sometimes stiff, brittle (in the embryos of seeds before germination); but very commonly it gives outwardly the impression of being a fluid. All these conditions depend

[1] The salts found in the ashes are partly products of combustion. Carbonic-acid salts may arise by the combustion of salts of vegetable acids. Since a strong red heat is necessary, easily volatile chlorides (potassium chloride or common salt) may disappear from the ash, &c.

[2] H. von Mohl, Ueber das Kieselskelet lebender Pflanzenzellen, in Bot. Zeitg. 1861, no. 30 et seq.—Rosanoff, Bot. Zeitg. 1871, nos. 44, 45.

[3] H. von Mohl, Bot. Zeitg. p. 273, 1844, and p. 689, 1855.—Unger, Anatomie und Physiologie der Pflanzen, p. 274, 1855.—Nägeli, Pflanzenphysiol. Untersuchungen, Heft I. Zürich.—Brücke, Wiener akad. Berichte, p. 408 et seq. 1861.—Max Schultze, Ueber das Protoplasma der Rhizopoden und Pflanzenzellen, Leipzig 1863.—De Bary, Die Mycetozoen, Leipzig 1864.—Hofmeister, Die Lehre von der Pflanzenzelle, Leipzig 1867.—Hanstein, Sitzungsberichte der niederrheinischen Gesellschaft in Bonn, Dec. 19, 1870.

essentially on the quantity of water it has absorbed. But, however great may be the quantity of water, and its consequent similarity to a fluid, *the protoplasm is nevertheless never a fluid;* even the ordinary dough-like, mucilaginous, or gelatinous conditions of other bodies can only be very superficially compared with it. For the living and life-giving protoplasm is endowed with internal forces, and, as the result of this, with an internal and external variability which is wanting in every other known structure; its active molecular forces cannot, in short, be compared with those of any other substance[1]. The capacity which protoplasm has, in consequence of the forces which become manifested in it, of assuming definite external forms, and of varying these, as well as its capacity of secreting substances of different chemical and physical properties according to definite laws, is the immediate cause of cell-formation and of every process of organic life.

The protoplasm of plants in a state of vital activity is generally very watery, and shows on one side an internal differentiation of its substance into layers and portions differing in their consistence and chemical nature; on the other side it assumes definite outlines, and becomes bounded by surfaces of determinate, and mostly very variable, form.

The internal differentiation of protoplasm is most commonly manifested by an outer, hyaline, apparently firmer, but mostly very thin layer, enclosing the inner mass, but in such a manner that the two remain in the most intimate contact. Every portion of a protoplasmic body immediately surrounds itself, when it becomes isolated, with such a skin (Hautschicht). Also in the interior a quantity of fluid sap, which permeates its substance throughout, invariably becomes separated in the form of drops (vacuoli); when the protoplasm is contained in a growing cell, these vacuoli increase in proportion as the cell grows, and the protoplasmic body becomes a sac filled with watery sap. One of the most common internal differentiations of the young protoplasmic body, while constituting itself into a separate individual, is observable in the formation of the nucleus. The substance of the nucleus is at first indistinguishable from that of the rest of the protoplasm, and its formation is essentially nothing but the collection of certain particles of protoplasm round a centre, which is also usually the centre of the whole protoplasmic body. Once formed, the nucleus (whose chemical nature, as far as observation goes, is altogether very much like that of the protoplasm) may become more sharply defined; it may itself form a skin, and vacuoli and granular formations (the nucleoli) may become separated in it. But the nucleus always remains a part of the protoplasmic body; it is always imbedded in it; very commonly it becomes again dissolved, after a short existence, in the protoplasm, *i. e.* its substance combines with it (*e. g.* in cells which frequently divide, as on p. 14; in the sacs of the Characeæ the nucleus disappears altogether when the streaming (Strömung) of the protoplasm begins). Another very common differentiation of the substance of the protoplasm consists in single portions of it becoming separated in a definite form and assuming a green colour, thus forming chlorophyll structures, which, like the nucleus, not only arise out of the protoplasm, but always remain as portions of the protoplasmic body. But since these require

[1] For further details on this point, see Book III; also my Handbook of Experimental Physiology, § 116. Leipzig 1865.

a more minute investigation, they are only mentioned here; the next section will be specially devoted to them.

The external configuration of the protoplasm into a definitely formed body can be reduced to two cases: — either its single smallest particles are constantly grouping themselves concentrically around a common centre, or an internal motion takes place, which causes the protoplasmic body to become elongated in some one direction, and disturbs the centripetal arrangement. The former occurs commonly in the formation of new cells, the latter in their growth.

The movements of the smallest particles of protoplasm which bring about its grouping and configuration in the formation and growth of cells, are generally so slow as not to be visible even when the cells are very highly magnified. Much quicker movements, even appearing rapid under a very high magnifying power, occur in cells already formed, more or less independently of their growth, and either preceding it (as in swarm-spores) or following it. As to the external appearance, the following kinds of movements of this nature may be distinguished:—(A) Movements of naked, membraneless protoplasmic bodies. (1) *The swimming* of swarm-spores and spermatozoids; this is characterised by the naked protoplasmic body, swarm-spore or spermatozoid, not changing its external form, while motile vibratile cilia, themselves probably thin threads of protoplasm, cause rotation round the longer axis, and at the same time a progressive movement in the water. (2) *Amœba-movement;*—consisting of rapid changes of the external contour of naked protoplasmic structures, Myxoamœbæ and Plasmodia, which, supported under water or in the air on a firm moist body, creep about as if flowing, extending and contracting; while within both the principal mass and the appendages which proceed from it, 'streaming' motion occurs. (B) Movements of the protoplasm within the cell-wall; this occurs after the protoplasmic body of the cell has formed a larger sap-cavity, and continues commonly after the growth of the cell has ceased until the end of its life. (3) Those movements are distinguished as *Circulation* when strings and bands, proceeding from the parietal protoplasm, run to that portion which envelopes the nucleus, and often stretch completely across the sap-cavity. A distinction is drawn between mass-movements of larger portions of protoplasm, and streaming movement of the substance of which they are composed; the former consist in accumulation or diminution of the parietal layer, wanderings of the mass which contains the nucleus in different directions, and, dependent on this, of different groupings of the strings. Within these structures of the body of the cell itself streamings often occur, which are apparent from the movement of the enclosed granules, often in opposite directions within the same thin string. In the cells of lower and higher plants which are rich in protoplasm and sap but poor in granular contents, the circulation is a widely distributed phenomenon, especially visible in the hairs. (4) The term *Rotation* is applied to those movements where the whole mass of protoplasm enclosing a cell-cavity circulates on the cell-wall as a thick current complete in itself, and carries along with it the grains and granules contained in it. This occurs in some water-plants, Characeæ, Vallisneria, root-hairs of Hydrocharis, &c.

(a) The protoplasm shows two conditions, which may be distinguished as the living and the dead; the former passes over into the latter by the most various chemical

and mechanical processes; the reactions of living protoplasm towards chemical reagents are essentially different from those of dead protoplasm, but this of course can only be perceived when the reagents do not at the same moment cause death. Solutions of different colouring matters, as aqueous solutions of the colours of flowers and the juices of fruits, especially also weak acetic extract of cochineal, have no power of colouring living protoplasm[1]; but if it has previously been killed, or if it has been deprived of its life-giving condition by continual action of these reagents, it absorbs a proportionately larger quantity of colouring material as a solvent; the whole substance assumes a much more intense colour than the solution itself. Solutions of iodine in water, alcohol, potassium iodide and glycerine, act in a similar manner; they all cause a yellow or brown colouring of the protoplasm, which is more intense than that of the solution itself. If protoplasm is first heated with nitric acid, the excess of acid removed by water, and solution of potash added, it assumes a deep yellow colour; saturated with a solution of copper-sulphate and then treated with potash, it becomes of a beautiful dark violet. Protoplasm containing but little water treated with a large quantity of concentrated English sulphuric acid, assumes a beautiful rose-red colour, without at first changing its form; subsequently this colour and the form disappear together, the protoplasm dissolving. Dilute solution of potash (sometimes also liquid ammonia), dissolves protoplasm, or at least destroys its form, and makes it homogeneously transparent. If, on the other hand, cells with protoplasm of characteristic form are placed in a concentrated solution of potash, the form itself remains for weeks, but disappears immediately on addition of water. All these reactions are collectively characteristic of true albuminoids, as caseine, fibrine, albumen; and we are therefore justified in supposing that substances of this kind are always contained in protoplasm. If the protoplasm-sac in cells rich in sap is very thin, it acquires a greater power of resistance, and withstands the solvents mentioned for a longer or shorter time. In another respect also protoplasm behaves like albuminoids; by heating very watery protoplasm to above 50° C. it is killed, and becomes turbid and stiff, and gives the impression of coagulation; alcohol and dilute mineral acids act in the same manner. The nucleus behaves towards all colouring substances, solvents, and coagulating agents in the same manner as living watery protoplasm, or it shows itself even more sensitive, especially in young cells; in older cells however it may be less easily acted on.

At the base of all protoplasmic structures there probably lies a substance which is colourless, homogeneous, and not visibly granular, to it alone the name Protoplasm ought perhaps to be applied, or at all events it ought to be distinguished as the foundation of protoplasm. The fine granules which are so often mingled with it, and which some used to consider an essential ingredient, are probably finely divided assimilated food-materials, which undergo a further chemical metamorphosis into protoplasm; every intermediate form occurs from these more or less fine granules to the largest, which may be clearly recognised as fat and starch. Homogeneous protoplasm destitute of granules is found in the cotyledons of dormant embryos of Helianthus, and in the cotyledon-leaves of Phaseolus; out of it chlorophyll is subsequently formed, and here the protoplasm contains but very little water; but the extremely watery protoplasm which rotates in the cells of Vallisneria is also destitute of granules; nothing but nucleus and grains of chlorophyll can be recognised in it. In the development of the spores of Equisetum (Fig. 10) the finer granules separate repeatedly from the homogeneous protoplasm, and afterwards become again distributed through it. But in some cases the protoplasm is so loaded with granular and coloured materials, that the colourless hyaline original substance can no longer be distinguished, as, for instance, in the ova of Fucus (Fig. 2),

[1] In the same manner the protoplasm and nucleus in living cells with coloured sap are also colourless; in other cases, on the other hand, the protoplasm is tinged by a colouring matter soluble in water, which is not present in the cell-sap. (As in Florideæ and the flowers of Compositæ, the last according to Askenasy.)

the zygospores of Spirogyra (Fig. 6), and in many spores and pollen-grains[1]. In the food-reservoirs of dry seeds (*e.g.* the cotyledons of peas and beans), the protoplasm itself is often collected into small roundish grains, between which lie the grains of starch; this condition of protoplasm will be further touched on hereafter.

(b) *Skin, Vacuoli, Movement.* Naked protoplasmic bodies, as the plasmodia of the Myxomycetes, some swarm-spores, *e.g.* of Vaucheria, allow the skin to be recognised, under sufficient magnifying power, as a hyaline edging; in the swarm-spores of Vaucheria it is evidently striated radially in the optical section, just as some cell-walls are; Hofmeister (Handbuch, I. p. 25) found the same in the plasmodia of Æthalium. Probably this skin is nothing but the pure original substance

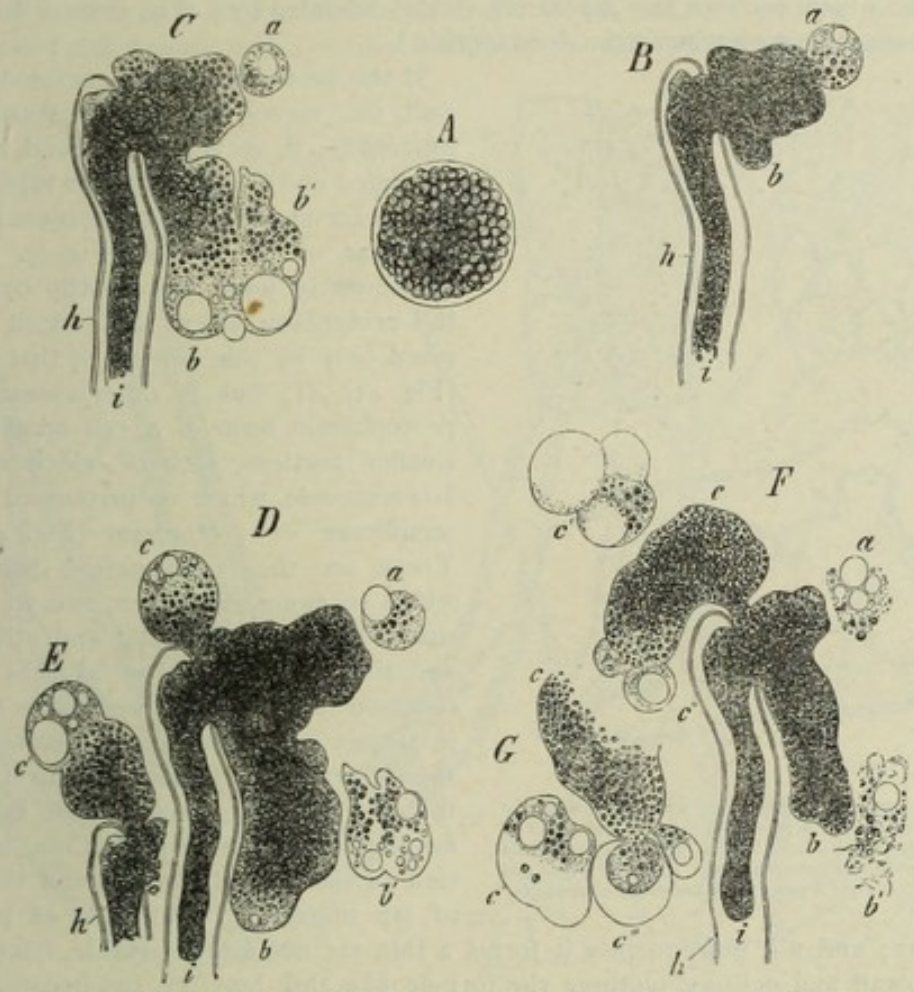

FIG. 42.—*B-G* protoplasm from an injured sac of *Vaucheria terrestris*, slowly emerging in water, in different successive conditions, at intervals of about five minutes; *h* the cell-wall of the ruptured sac; *i* the part of the protoplasm which still remains in the sac; *a* in *B*, *C*, *D*, and *F*, a ball of protoplasm detaching itself, forming vacuoli, then dissolving (in *F*); *b* a branchlet of the protoplasm from which the mass *b'* is detached, this mass isolated in *D*, dissolved in *F*; *c* and *c'* behave in a similar manner; *G* shows the further changes of the part *c''* in *F*. *A* a freshly escaped mass of protoplasm, rounded off into a sphere, the chlorophyll-grains lie all together in the inside; hyaline protoplasm envelopes the whole as a skin.

of the protoplasm itself free from granules, of which the whole body is formed; only the parts which lie most in the interior are permeated by grains and granules. It follows that in the amœba-like movements of the plasmodia the new processes are always at first formed of the skin alone; it is only when they increase in size that the interior granular substance makes its appearance in them. This is more clearly the case in the masses of protoplasm that escape into water from the injured sacs of Vaucheria, which often instantly become rounded into globular bodies, but not unfrequently show the amœba-like movement of plasmodia for as much as half-an-hour or an hour (Fig. 42). This interpretation of the skin is not at all opposed to the fact that

[1] J. Hanstein gives to the substances mingled with the true protoplasm and which undergo many transformations, the collective name of 'Metaplasm.' (Bot. Zeitg. p. 710, 1868.)

it is denser than the inner and more watery substance. That the cohesion in each protoplasmic body decreases from without inwards, follows from the easier mobility of the inner mass, which is especially the case with the plasmodia, and also from the formation of vacuoli, which clearly depends on the collection of a portion of the water present in the protoplasm round internal points, and the final formation of drops there, presupposing that the cohesion is overcome at these points. The view here presented that the hyaline homogeneous original substance itself is formed on each free surface of motion of the protoplasm as a skin destitute of granules, entirely agrees with the supposition that not only every vacuole in a solid protoplasmic body, but also every thread of protoplasm which penetrates the sap-cavity, and finally the inner side of the protoplasm-sac which encloses the sap-cavity, is also bounded by a skin, even if it be so thin that it cannot be seen when strongly magnified[1].

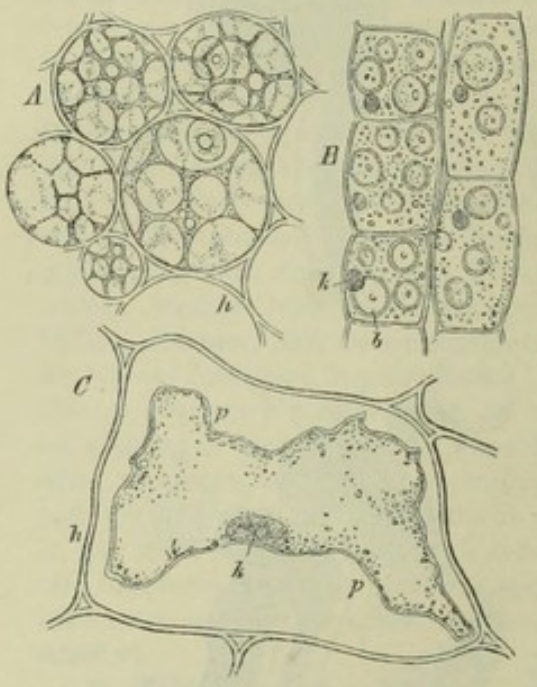

FIG. 43.—Forms of the protoplasm contained in cells. *A* and *B* of *Zea Mais*; *A* cells from the first leaf-sheath of a germinating plant; *B* from its first internode; *C* from the tuber of *Helianthus tuberosus*, after action of iodine and dilute sulphuric acid; *h* cell-wall; *k* nucleus; *p* protoplasm.

If the protoplasm is not enclosed in a cell-wall, the vacuoli are usually small and not numerous; if, on the other hand, a cell-wall is formed and if the cell grows rapidly, this is always accompanied by an increase in number and size of the vacuoli (Fig. 1). This not unfrequently leads to a frothy condition of the protoplasm where the vacuoli are separated only by thin lamellæ of that substance (Fig. 43, *A*); but in other cases the inner protoplasmic mass of a cell breaks up into smaller portions, each of which encloses a large vacuole, which is surrounded by a thin membrane of protoplasm (Fig. 43, *B*, *b*). These are the 'sap-vesicles' (Saftbläschen) which so commonly occur, and which sometimes enclose chlorophyll and other grains, and thus become similar to cells (not uncommon in the flesh of berry-like fruits, and in tissues with mucilaginous juices). If the rapidly growing cell does not form new protoplasm, *i.e.* if its protoplasmic body is not correspondingly nourished, then, in proportion as the size of the cell and the amount of sap increase, the quantity of protoplasm decreases; and not unfrequently it forms a thin sac not directly visible, lying between the cell-wall and cell-sap, clothing the former like thin tapestry, and becoming visible only by means of substances that remove the water, and loosen the protoplasm-sac (Primordial Utricle of Mohl) from the cell-wall by contraction (Fig. 43, *C*, *p*). The signification of this thin-walled protoplasm-sac, its production by increase in number and size of the vacuoli in an originally solid protoplasmic body, will no longer be doubtful to the reader after all that has been said in sects. 1, 2, and 3, and by comparison of Fig. 1 with Fig. 43.

In younger cells, where the protoplasm forms a still thicker layer, or where it presents a net-work permeated by vacuoli, its substance, with the exception perhaps of the outermost layer lying on the cell-wall, appears to be always engaged in a 'streaming' movement, which is however usually very slow. In many mature and large cells this condition is permanent, when they do *not* serve for the storing up of assimilated materials, and when the protoplasmic body is sufficiently nourished,

[1] Cf. Hanstein, Die Bewegungserscheinung des Zellkerns, u. s. w. Sitzungsberichte der niederrheinischen Gesellschaft zu Bonn, p. 224, 1870.

and does not, when the cell distends, contract to a mere thin membrane. If the whole mass of protoplasm withdraws to the cell-wall, enclosing a single large vacuole (the sap-cavity of the cell), all the particles of protoplasm, flowing in one direction, may form a continuous broad current encircling the cell (rotation), the direction of which is always such as to describe the longest course round the cell-cavity (Nägeli). Examples occur in Characeæ, in many other submerged water-plants, as Vallisneria, Ceratophyllum, Hydrilleæ, root-hairs of Hydrocharis; the globular nucleus, when present (in Characeæ it soon disappears), is carried along with the current. The protoplasmic body which encloses a large sap-cavity may, however, possess ridge-like prominences arranged in a net-work, the substance of which flows in different directions; by this means the nucleus may either, relatively, remain at rest, and, in a certain manner, form the centre of movement, or it is carried along with it. Cases of this kind occur tolerably

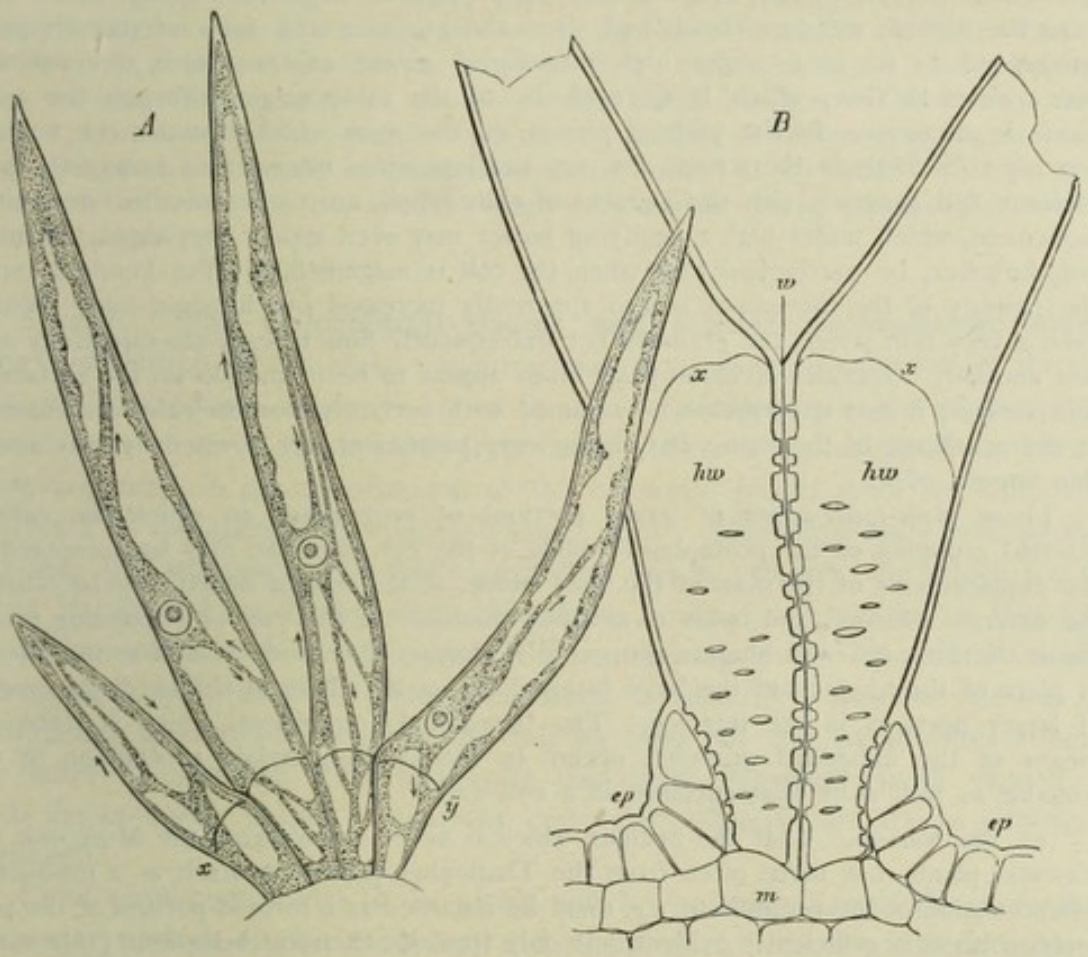

FIG. 44.—*A* stellate hair on the calyx of the young flower-bud of *Althæa rosea*; thicker portions of protoplasm lie on the protoplasm-sac of each cell; these are in the act of 'streaming' motion (indicated by the arrows). *B* epidermis (*ep*) with the basal portion of a mature stellate hair, showing the structure of the wall (×550).

frequently in the hairs of land-plants (as in the stinging hairs of *Urtica urens*, stellate hairs of *Althæa rosea*). But the strings of protoplasm which show these currents may also penetrate the sap-cavity of the cell; not unfrequently (*e.g.* Spirogyra, hairs of Cucurbita) the nucleus then lies in its centre, enveloped by a mass of protoplasm; the strings unite it with the protoplasm-sac which clothes the cell-wall. These strings or threads, stretching across the sap-current, may at first arise from the thin lamellæ of protoplasm which in younger quickly growing cells still separate adjoining vacuoli; when these finally flow together into a single sap-cavity, the thicker parts of these lamellæ (Fig. 1, *B*) may remain as strings, forming a more or less irregular net-work, which at first corresponds, in position and size, to the vacuoli that have now coalesced, but subsequently, as the cell continues to grow, and in consequence of the internal movements

of the whole protoplasmic body, undergoes further distortions and entire change of form. But new strings also make their appearance; ridge-like portions arise from the peripheral plasma, or even on the thicker strings, and finally become detached in such a way that the two ends of the new string remain united with the rest of the protoplasmic substance; they do not grow up as branches with one free extremity. (Hanstein, *l. c.* p. 221.) In the same manner threads disappear; both ends, remaining in connexion with the rest of the protoplasmic body, coalesce with it. The strings form, together with the central masses of protoplasm which contain the nucleus and those which clothe the cell-wall, a connected system, single portions of which may change their position with respect to one another.

Besides these displacements of large portions of the protoplasm of a cell endowed with circulation—in consequence of which the parietal protoplasm at any one spot accumulates or diminishes, and the mass of protoplasm in the cell-cavity which contains the nucleus wanders about, and alters the grouping and form of the strings to correspond to its own—under high magnifying power another form of movement then comes in view, which is undoubtedly of the same origin, although the exact mode is unknown. In the parietal plasma, in the mass which contains the nucleus, but most distinctly in the strings, the very small granules interspersed among the protoplasm, and generally also small grains of chlorophyll, are to be seen in 'streaming' movement, which under high magnifying power may even appear very rapid. It must not, however, be overlooked that when the cell is magnified, say five hundred times, the rapidity of the movement is also apparently increased five hundred-fold. Within even a very thin string, the granules not unfrequently flow in opposite directions near one another. Granules of chlorophyll often appear to be in motion on the surface of thin strings; it may nevertheless be assumed with certainty that they also are enclosed in the substance of the string, but, being very prominent, are covered by only a very thin lamella of it.

Those mass-movements of larger portions of protoplasm on which the various internal grouping of the protoplasmic body of the cell depends, may be compared to the displacements of the mass of the body which, in the case of naked Amœbæ, change the external contour, and cause its creeping motion; in the case of circulating protoplasm the firm cell-wall hinders the external change of contour as well as the change of place of the whole; but the large internal sap-cavity allows of similar displacements of larger portions in the interior. The 'streaming' movement, which is visible by means of the imbedded granules, occurs in the creeping naked protoplasm of the Amœbæ as well as in that enclosed in a cell-wall.

(c) *The Nucleus.* That the nucleus, which is never absent from the Muscineæ and Vascular plants, but more often from the Thallophytes, presents itself as a product of differentiation of the protoplasm, *i. e.* must be regarded as a formed portion of the protoplasm itself, is sufficiently evident, not only from its chemical behaviour (vide supra, under *a*), but also from its participation in the processes of cell-formation (cf. sect. 3); and this need not be further demonstrated. On the other hand, it must be made clear that, once formed, it constitutes a characteristically formed portion of the cell which, to a certain extent, has a mode of development of its own. At first the nucleus is always a homogeneous roundish body of protoplasmic substance; subsequently its surface becomes firmer without its taking the form of a special skin; in the interior arise usually two or three (sometimes more) larger granules, called Nucleoli, which, however, are often entirely wanting. The nucleus has, at the time of its origin in the young cell, usually already attained its permanent size, or nearly so; its growth is never proportional to that of the cell; in young tissue-cells (Fig. 1) it usually occupies a large portion of the cell-cavity; in fully grown cells its mass is increasingly small in proportion to that of the whole cell. Usually a further development remains also in the sharper bounding by a firmer outer layer and the formation of small vacuoli and nucleoli; only rarely does it grow for a longer time; more vacuole-fluid collects in the interior; its substance may

become frothy; and it is also sometimes the case that it moves in a 'streaming' manner, and in the interior of the firmer enveloping layer a circulation sets up, as in a cell[1]. The nucleus always remains enclosed in the substance of the protoplasm; if this latter forms vacuoli or assumes the condition of circulation already described, the nucleus remains enveloped in a coating or in a thicker mass of protoplasm, which is connected with the parietal protoplasm-sac by the lamellæ lying between the vacuoli as well as by the current-threads. The nucleus apparently follows passively the displacements and wanderings of the portion of protoplasm in which it is enveloped; it also undergoes changes of form under the pressure and progress of the moving mass, which proceed under the eye of the observer. 'During the movement,' says Hanstein (*l. c.* p. 226) admirably, 'the bands of protoplasm are and remain .... very tightly stretched, so that the envelope of the nucleus is drawn out by them into sharp angles. It looks as if the nucleus (together with its envelope) were towed about like a ferry-boat by ropes stretched across. But since during this towing the bands themselves alter their direction and form, it is self-evident that the envelope of the nucleus must also change its form. But not only the envelope, but also the nucleus itself, does this. This latter is never spherical or of any similarly regular form during the time of its wandering, but is irregularly elongated, and usually in the direction of its motion at the time.' This change in the form of the nucleus may also be recognised from the displacement of the nucleoli within its mass.

Sect. 6. **The Chlorophyll-Bodies and similar protoplasmic Structures**[2].—Chlorophyll, the green colouring matter so generally distributed through the vegetable kingdom, is always united to definitely formed portions of the protoplasmic body of the cells in which it is found; these green-coloured portions of protoplasm may, in contradistinction to the colouring matter itself by which they are tinged, be designated Chlorophyll-bodies. Every chlorophyll-body consists then of at least two substances, the colouring matter and its protoplasmic vehicle; if the former is removed by alcohol, ether, chloroform, benzine, or essential or fatty oils, the latter remains behind colourless. The colouring matter contained in each chlorophyll-body is itself only extremely small in quantity; after its removal the protoplasmic ground-work retains not only its form but also its previous volume. The latter is always a solid soft body containing extremely small vacuoli, in which the colouring matter is generally completely, though not always uniformly, distributed.

Chlorophyll-bodies arise in the young cells by the separation of the protoplasm into portions which remain colourless and others which become green and sharply defined. The process may be supposed to take place by very small particles of a somewhat different nature originally existing in or being distributed through the previously homogeneous protoplasm, then collecting at definite places and appearing as separated masses. The grains of chlorophyll which arise in this manner always remain imbedded in the colourless protoplasm in a similar manner to the nucleus; they

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[1] In young hairs of *Hyoscyamus niger*, according to A. Weiss in the Sitzungsberichte der kais. Akademie der Wissenschaften, Vol. LIV. Vienna, July 1866.

[2] H. von Mohl, Bot. Zeitg. nos. 6 and 7, 1855.—A. Gris, Ann. des Sci. Nat. Ser. IV. Part VII. p. 179, 1857.—Sachs, Flora, p. 129, 1862; p. 193, 1863.—Sachs, Handbuch der Exper. Physiol. der Pflanzen, § 87, Leipzig 1863.—Hofmeister, Die Lehre von der Pflanzenzelle, § 44, Leipzig 1867. —Kraus, Jahrb. für wissensch. Bot. VIII. p. 131, 1871.

are never in immediate contact with the cell-sap, but are enveloped on all sides by the colourless protoplasm. Their chemical and physical properties distinctly show that their colourless ground-work is a substance altogether similar to protoplasm. The chlorophyll-bodies consequently always behave as integral parts of the protoplasm; and this is especially evident in the division of cells containing chlorophyll, in conjugation, in the formation of swarm-spores, &c. But the chlorophyll-bodies, when once formed, grow, and if they possess roundish forms they may be increased by division. Both appear always to depend on the growth of the collective protoplasm-body in which they are deposited.

It is only in the Algæ that the forms of the chlorophyll-bodies show much variety; in them it is frequently the case that the whole protoplasmic body, with the exception of an outermost layer, or of a little more than this, either appears homogeneously green (*e. g.* many swarm-spores, Palmellaceæ, gonidia of Lichens) or the chlorophyll-grains assume stellate forms (*e. g. Zygnema cruciatum*, Fig. 45), or they form several lamellæ which have the appearance of a star when the cell is cut across (as in Closterium, &c.), or straight or spiral bands (*e. g.* Spirogyra). But in most Algæ and all Mosses and Vascular plants, the chlorophyll-bodies are rounded or polygonal masses collected around a centre, and are termed Grains of Chlorophyll. Generally a large number are contained in one cell, sometimes, however, only a few relatively large ones (*e. g.* Selaginella), and in one of the Hepaticæ of simplest structure (Anthoceros) only a single grain of chlorophyll is to be found, enclosing the nucleus; this therefore, when the cells divide, itself also divides in a corresponding manner.

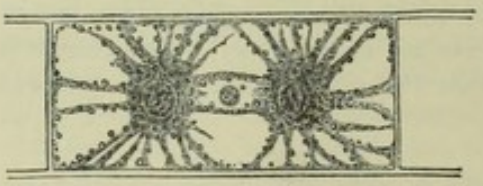

FIG. 45.—A cell of *Zygnema cruciatum*, with two stellate chlorophyll-bodies which are suspended in the interior of the cell; they are united by a colourless bridge of protoplasm in which lies a nucleus; the rays which form the union with the parietal sac are already nearly colourless in the middle. In each of the two chlorophyll-bodies lies a large grain of starch (×550).

With extremely few exceptions *Grains of Starch* arise in the homogeneous solid substance of the chlorophyll-bodies, and, where these have special forms, are distributed in definite places (cf. *e. g.* Fig. 5); in the ordinary chlorophyll-grains they arise in the interior in larger or smaller numbers. They are at first visible as points, gradually increase in size, and finally may so completely fill up the space of the chlorophyll-grain that the green substance is represented only by a fine coating on the mature starch-grain; even this coating may, under certain circumstances, disappear (as in old yellow leaves of *Pisum sativum*, Nicotiana), and the starch-contents then lie in the cell (destitute of protoplasm) in the place of the chlorophyll-grains. Sometimes drops of oil also form in the interior of the chlorophyll-substance (*e. g.* in the bands of Spirogyra); and here and there granular contents of an unknown nature are observed. All these structures which arise in the chlorophyll-bodies are, however, not constant portions of them; their appearance and disappearance depend entirely on the light, temperature, and on other circumstances; the appearance of the chlorophyll-bodies themselves is also bound up with these conditions of life, to a description of which we shall not recur till Book III, where it will be shown that chlorophyll is one of the most important elementary structures, and that its contents are especially its products of assimilation. The

consideration of these and of numerous other purely physiological properties of chlorophyll must be deferred till then. Sooner or later, in the normal course of things, the chlorophyll-bodies are again absorbed; this occurs in the most conspicuous manner at the time when the leaves of the higher plants are preparing for their fall; for instance, in the case of our native trees and shrubs, in the autumn. Here the whole mass of protoplasm,—and with it the chlorophyll-bodies from the cells of the leaves destined to fall,—is absorbed, and transferred to the perennial parts; the appearances which then present themselves are very different; but finally there

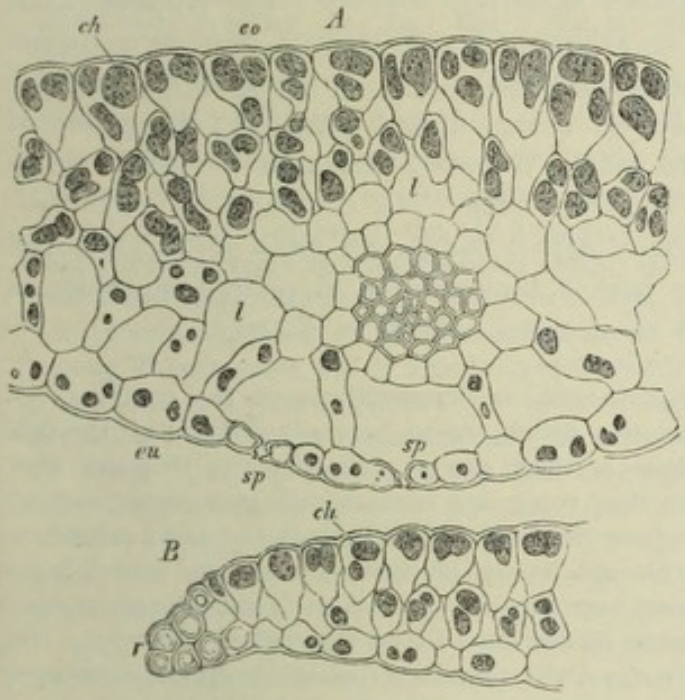

FIG. 46.—Transverse section through the leaf of *Selaginella inæqualifolia* (×550). *A* in the middle, *B* at the margin; *ch* the grains of chlorophyll; visible in them are points, the small granules of starch; *eu* the lower epidermis; *eo* the upper epidermis; *l* the air-conducting intercellular space; *sp* stomata.

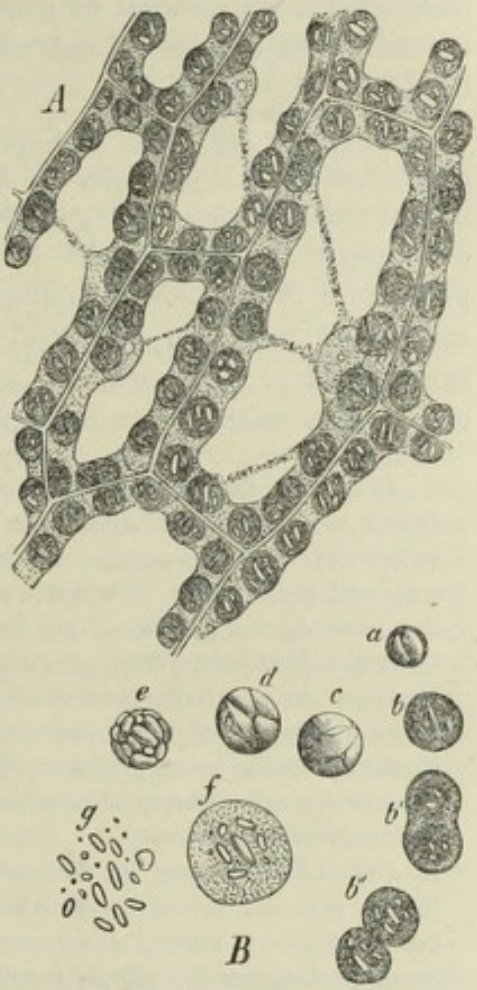

FIG. 47.—Chlorophyll-grains of *Funaria hygrometrica* (×550). *A* cell of a mature leaf, seen from the surface; the parietal chlorophyll-grains lie in a layer of protoplasm, in which the nucleus is also imbedded; the chlorophyll-grains contain starch grains (left white). *B* single grains of chlorophyll containing starch; *a* a young one, *b* an older one, *b'* and *b''* grains in the act of division; *c*, *d*, *e* old chlorophyll-grains, the starch granules of which take up the space of the chlorophyll; *f* a young chlorophyll-grain swollen up in water; *g* the same after longer action of the water; the chlorophyll is destroyed, the starch-granules remaining behind.

remain in the cells filled with water and often containing pointed crystals, a number of yellow glittering granules which have no similarity to chlorophyll; if the falling leaves are red, this depends on a substance dissolved in the sap; but in this case also the yellow granules are to be found.

The presence of chlorophyll in tissues is not always to be recognised by the naked eye in the colouring of the organs. Sometimes the cells that possess chlorophyll themselves contain a red sap; in other cases the green tissue of the leaves is covered by an epidermis provided with red sap (young plants of *Atriplex hortensis*); in this case, if the coloured epidermis be removed, the green tissue may be readily recognised. But in Algæ and Lichens we find that the chlorophyll-

body of the cell itself contains, in addition to the green colouring matter, a red, blue, or yellow substance soluble in water; the fresh chlorophyll-body appears then, by the admixture of the chlorophyll contained in it with these substances, verdigris-green (Oscillatoria, *Peltigera canina*, &c.), a fine red (Florideæ), or brown (Fucus, *Laminaria saccharina*), or buff (Diatomaceæ). (Cf. Book II. Algæ).

From this are to be distinguished those processes in which the originally green chlorophyll grains assume a red or yellow colour from transformation of their colouring material; these, in reference to their physiological bearings, I have designated a degradation of chlorophyll. Thus the green bodies in the walls of the antheridia of Mosses and Characeæ become, at the time of fertilisation, of a beautiful red; in ripening fruits (*Lycium barbarum*, *Solanum pseudo-capsicum*, &c.), the change of colour from green to yellow and red depends also on a similar loss of colour of the chlorophyll-grains, accompanied by a breaking up into angular forms with two or three points (Kraus, *l. c.*). Nearly related to the grains of chlorophyll are the vehicles of the yellow colouring materials to which many petals owe their yellow colouring (*e. g.* Cucurbita). The occasional blue (*Tillandsia amœna*) or brown and violet (*Orchis Morio*) bodies, are much further removed from this type, although they also have a basis similar to protoplasm which is tinged by a colouring material, in these cases soluble in water.

(a) The *Substance of the Chlorophyll-bodies* is, irrespectively of the contents referred to, destitute of those fine granules which are so generally distributed through colourless motile protoplasm; in spite of their sharply defined form, they are very soft, and greasy when crushed; when they come into contact with pure water, vacuoli are formed, which at last, from their great distension, burst through the green substance as hyaline bladders; young grains of chlorophyll may thus become converted into delicate bladders, in which the grains of starch remain; old grains have a greater consistence. After extraction of the green colouring matter out of true chlorophyll-bodies, *e. g.* the bands of Spirogyra or grains of *Allium Cepa*, the remaining colourless ground-substance possesses greater power of resistance, is coagulated, and shows all the reactions of protoplasm already mentioned.

(b) The *Origin of the Chlorophyll-bodies* has, at present, only been directly observed in the granular forms; it can to some extent be compared with the process of free cell-formation; around given centres of formation within the protoplasm extremely small portions of it collect, forming sharply defined masses; if the centres of formation are at a considerable distance from one another, the chlorophyll-grains become round (as in hairs of Cucurbita); but if they lie close to one another and the grains are large, they are at first polygonal, as if they had been flattened against one another by pressure. The process then gives somewhat the same impression as the formation of numerous small zoospores in a sporangium of Achlya (Fig. 9, *A*); only that in this latter case colourless protoplasm always continues to lie between the green portion (parietal chlorophyll-grains of the leaves of Phanerogams). If a mass of protoplasm collects around the central nucleus during the formation of chlorophyll, the grains are often formed in its neighbourhood; they may then revolve with the circulating protoplasm in the cell, or afterwards assume definite positions. In the filamentous Algæ with apical growth (*e. g.* Vaucheria, Bryopsis), they form in the colourless protoplasm-body of the growing end of the sac, and then remain applied to the wall. In ripe spores of *Osmunda regalis* the chlorophyll surrounds the nucleus in the form of amorphous cloudy masses, which, however, separate on germination as oval grains, at first weakly afterwards sharply defined (Kny). In the chlorophyll-forming cells of the embryo-leaves of Phanerogams (cotyledons of the sunflower, primordial leaves of

Phaseolus, buds of the tubers of *Helianthus tuberosus*, &c.) a definitely formed hyaline protoplasm devoid of granules is to be observed, close to the cell-wall, which, as it developes, forms the grains of chlorophyll; here the appearance is sometimes presented as if the mass were cut up into polyhedral pieces. The formation of the grains of chlorophyll is not always contemporaneous with that of its colouring matter; they may be at first colourless (as in Vaucheria or Bryopsis, according to Hofmeister) or yellow (in the case of leaves of Monocotyledons or Dicotyledons imperfectly exposed to light, or in the process of development), and may afterwards become green; in the cotyledons of Coniferæ the green colour appears contemporaneously with their origin even in the dark when the temperature is sufficiently high, as also in Ferns. The grains of chlorophyll, after assuming their green colour, grow by intussusception to many times their original size; if they are parietal, their growth in length and breadth is generally proportional to that of the corresponding piece of the cell-wall and of the protoplasm-body in which they lie. But if the growth of the cell is very considerable, the growing parietal chlorophyll-grains divide; this occurs by bipartition, a constriction arising which always penetrates more deeply in a direction vertical to the longest diameter, until the grain at length breaks up into two usually equal secondary grains. If it contained small grains of starch before the division, these arrange themselves round the centres of the newly formed grains. These processes are inferred from the increase of the number of grains on the one hand, and from the frequent occurrence of biscuit-shaped constricted forms on the other hand. After this bipartition of the chlorophyll-grains had been discovered by Nägeli in Nitella, Bryopsis, Valonia, and in prothallia, it was subsequently noticed in all the families of Cryptogams which form chlorophyll; among Phanerogams also it appears widely distributed; it was discovered by Sanio in Peperomia and Ficaria, subsequently by Kny in Ceratophyllum, Myriophyllum, Elodea, Utricularia, Sambucus, Impatiens, &c. In cells of the prothallium of Osmunda exposed to feeble light and containing but little chlorophyll, Kny states that moniliform rows of chlorophyll-grains arise by repeated bipartition, which, like the chains of cells of Nostoc, continue to elongate by intercalary divisions; a branching of the rows takes place here also, in a manner similar to that which occurs in Nostoc; single grains of chlorophyll increase in size transversely, and produce branch-rows by division.

(c) With reference to the *Internal Structure* of the chlorophyll-bodies, scarcely anything else can be said than that their outer layer often appears denser, and that the proportion of water in the substance increases towards the interior the cohesion decreasing, as is apparent from the formation of vacuoli. A perceptible differentiation into lamellæ of different density crossing one another has, at present, only been once observed in old chlorophyll-grains of *Bryopsis plumosa* (Rosanoff).

Sect. 7. **Crystalloids**[1].—A portion of the protoplasmic substance of the cells sometimes assumes crystalline forms; bodies are formed which, bounded by plane surfaces and sharp edges and angles, possess an illusory resemblance to true crystals, even in their behaviour to polarised light; on the other hand they are essentially distinguished from them by the action of external agents, and at the same time present significant resemblances to organised parts of cells. It is therefore legitimate to distinguish them by the term Crystalloids proposed by

[1] Hartig, Bot. Zeitg. p. 262, 1856.—Radlkofer, Ueber die Krystalle proteïnartiger Körper pflanzlichen und thierischen Ursprungs, Leipzig 1859.—Maschke, Bot. Zeitg. p. 409, 1859.—Cohn, Ueber Proteïnkrystalle in den Kartoffeln, in the thirty-seventh Jahresbericht der Schlesischen Gesellschaft für vaterländ. Cultur, 1858, Breslau.—Nägeli, Sitzungsberichte der k. bayer. Akademie der Wissenschaften, p. 283, 1862.—Cramer, Das Rhodospermin (in the seventh volume of the Vierteljahrsschrift der naturforsch. Gesellschaft in Zürich).—J. Klein, Flora, No. 11, 1871.

Nägeli. They are usually colourless, but sometimes act as vehicles of colouring matters (not green) which may be removed from them. Their collective mass shows all the essential reactions of protoplasm, its power of coagulation and of taking up colouring matters, the yellow reaction with potash after treatment by nitric acid, as well as that with iodine. The solubility of different crystalloids varies greatly, as is generally the case with albuminoids. They are capable of imbibing water, and swell up enormously under the influence of certain solutions; their outer layer possesses greater power of resistance than the inner more watery mass. Those crystalloids which have been most carefully examined consist of a mixture of two kinds of materials of different solubility; the two are so combined that when the more soluble is slowly removed, the less soluble remains as a skeleton (Nägeli).

Their form is very different in different plants; they appear as cubes, tetrahedra, octohedra, rhombohedra, and in other forms; usually, however, their crystallographic characters cannot be exactly defined, a consequence of their small size and of the inconstancy of their angles.

In quickly growing organs of phanerogamic plants they are known only in *Lathræa squamaria;* more commonly they form in cells where large quantities of reserve-materials are collected which are only turned to use at a later period; the crystalloids themselves appear to be a form of protoplasmic structure especially adapted for a dormant condition (as potato-tubers, many oily seeds); they are seldom found in cells which contain sap (potato-tubers), more often in sapless, and especially in oily seeds. Crystalloids containing colouring matters are found in the petals and fruits. Sometimes they are formed only after the action of alcohol or a solution of sodium-chloride on the plants externally or internally (Rhodospermine).

The crystalloids of potato-tubers are imbedded in the protoplasm; those that are widely distributed in the tissues of *Lathræa squamaria* are contained in great numbers in the interior of the nucleus; those found in oily seeds are generally enclosed in grains of aleurone.

The *Crystalloids* discovered by Cohn in the tubers of the potato are convenient for observation; they are found very abundantly in some kinds, in others less frequently, in the parenchyma-cells beneath the skin which contain but little starch, but tolerably deep in the tissue; they lie enclosed in the protoplasm. Generally they are in the form of cubes (less often of derivative forms, as tetrahedra) of the most perfect form. Those found by Radlkofer in the nuclei of *Lathræa squamaria* lie together in great quantities within each nucleus; they have the form of thin square rectangular plates; sometimes they appear to have rhombic or trapezoid forms; Radlkofer thinks it most probable that they belong to the rhombic system. These crystalloids present themselves immediately to observation, and their relation to their environment is at once clear. The case is different with the crystalloids of oily seeds enclosed in grains of aleurone; I shall recur to their properties, and will only mention here that the crystalloids of the brazil-nut are obtained in quantity by washing out the crushed oily parenchyma by oil or ether, the crystalloids settling down in the form of fine meal; in sections through the tissue but little can be clearly made out. They were carefully investigated in the isolated state by Nägeli; according to the manner in which they are seen they appear rhombohedral, octohedral, or tabular; but it is uncertain whether they belong to the hexagonal or the klino-rhombic system. Dry crystalloids placed in water alter their angles about 2° or 3°; in solution of potash they swell strongly and then alter their angles 15° or 16°. By weak acids and dilute glycerine a substance is extracted, and a

weak skeleton with firmer skin remains behind. The crystalloids in the endosperm-cells of *Ricinus communis* are, like all crystalloids, insoluble in water, and are very conspicuous when thin sections of the tissue are laid in water, which destroys the structures surrounding the crystalloid, and sets it free. They frequently take the form of octohedra or tetrahedra, less frequently of rhombohedra; but the system is not certainly determined. The crystalloids of colouring matter were first detected by Nägeli in an imperfect form in the petals of *Viola tricolor* and Orchis, better developed in the dried fruits of *Solanum americanum;* in the latter case they form in the large cells of the flesh of the fruit clusters of a deep violet colour; the separate crystalloids are thin plates, single regular rhombs, often with truncated angles, &c. According to Nägeli it does not admit of a doubt that the crystalline form is the rhombic prism in a very abbreviated tabular shape; the hexagonal tables are composed of six simple ones. In pure water they remain unchanged; alcohol extracts the colouring matter, as also do dilute acids; both leave, after long treatment, a very weak skeleton which is capable of swelling, while the whole crystal does not swell; Nägeli states that the crystalloid consists of a very small quantity of albuminous and a large quantity of another substance, with some colouring matter.

Crystalloids of albuminous substance have also been found in red marine Algæ (Florideæ) and in one Fungus. Cramer observed the first case of this kind; in specimens of the Floridea *Bornetia secundiflora* which had lain a long while in solution of sodium-chloride, as well as in specimens prepared in alcohol of *Callithamnion caudatum* and *seminudum* he found hexagonal plates and prisms with all the properties of crystalloids, and coloured red by the expelled colouring matters of the Algæ. They were found in the vegetative cells as well as in the spores. In sodium-chloride preparations of Bornetia octohedral crystalloids were found also, apparently belonging to the klino-rhombic system; they were colourless. In living plants of the same Alga, Cohn also dicovered colourless octohedral crystalloids which absorb the red colouring matter expelled from the pigment-grains. Within and without the cells of *Ceramium rubrum* preserved in sea-water with glycerine, klino-rhombic prisms formed, coloured red by the expelled pigment; they are clearly similar to the hexagonal crystalloids first observed by Cramer which appeared only after death, while the colourless octohedra are to be found in the living cells. Finally, in dried specimens of other Florideæ, *Griffithsia barbata*, *G. neapolitana*, *Gongoceros pellucidum*, *Callithamnion seminudum*, Klein observed colourless crystalloids of a different form. These formations may all be comprised in the name first given by Cramer,—Rhodospermine. In the sporangiferous filaments of Pilobolus, Klein found also colourless octohedra of tolerably regular structure with the properties of crystalloids described above.

Sect. 8. **Grains of Aleurone (Proteine-grains**[1]**).**—The reservoirs of ripe seeds, *i. e.* the endosperm and the cotyledons of the embryo, always contain

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[1] These structures were discovered by Hartig (Bot. Zeitg. p. 881, 1855), and described in detail but imperfectly (ibid. p. 257, 1856); further observations were furnished by Holle (Neues Jahrb. der Pharmacie, Bd. X, 1858) and Maschke (Bot. Zeitg. 1859). All these observations left undecided the relationship of the grains to the surrounding matrix; it appeared in particular to be assumed that in oily seeds the latter consists of oil only. In the first and second editions of this book I opposed this view, and pointed out that the matrix in the cells of oily seeds consists of a mixture of oil and albuminoids, or rather, of a very oily protoplasm; on the other hand I fell into the error, partly in consequence of the use of diluted ether, of considering the aleurone-grains themselves as a compound of albuminoids and oil. This error has been refuted by Dr. Pfeffer's recent researches. This very careful investigation was commenced in the Würzburg laboratory, where I had the opportunity of seeing numerous preparations which were decisive as to the principal question. Dr. Pfeffer had the kindness to communicate to me, before going to press, a detailed

considerable quantities of albuminoids together with starch and oily matter. If they contain much starch, as in the grasses, Phaseolus, Vicia, the oak, horse-chestnut, Spanish chestnut, &c., the albuminoid, which only contains very little oily matter, occupies the interstices; it consists of small or even minute granules, as shown in Fig. 48. In oily seeds, on the other hand, granular structures of roundish or angular form (Fig. 49) are found in place of the grains of starch, which also are sometimes not dissimilar to starch-grains in their appearance, surrounded by a more or less

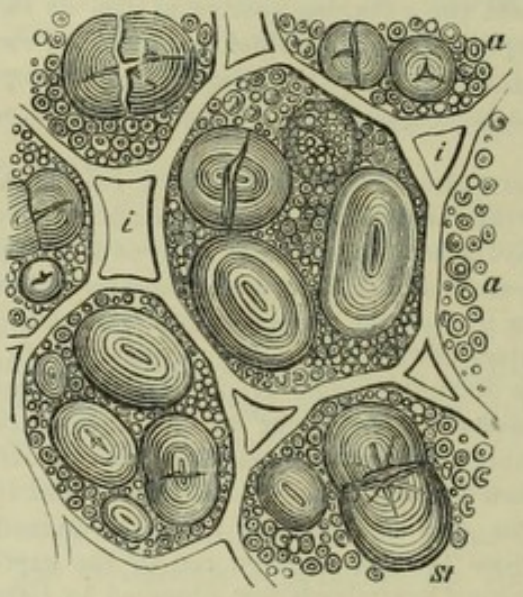

FIG. 48.—Cells of a very thin section through a cotyledon of the embryo in a ripe seed of *Pisum sativum*; the large concentrically stratified grains *st* are starch-grains (cut through); the small granules *a* are aleurone, consisting principally of legumine with a little oily matter; *i* the intercellular spaces.

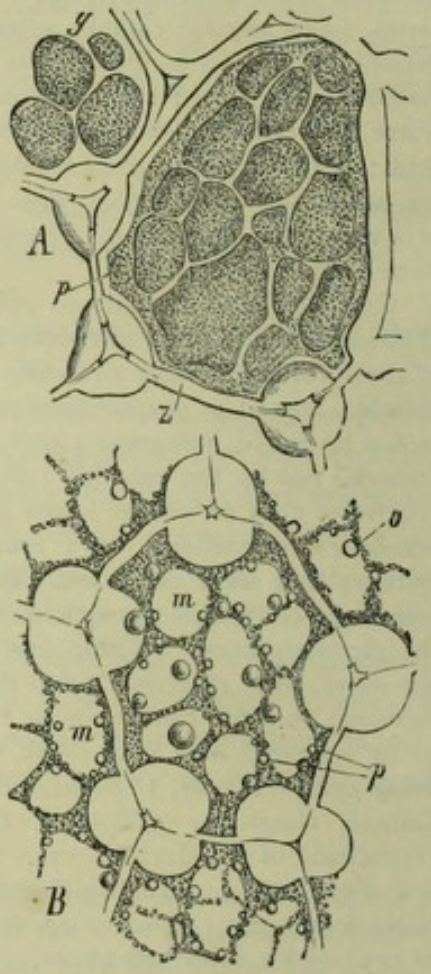

FIG. 49.—Cells from the cotyledon of the ripe seed of *Lupinus varius*; *A* in alcohol containing iodine; *B* after destruction of the grains by sulphuric acid; *z* the cell-wall; *β* the protoplasmic principal mass, containing but little oily matter; *y* the aleurone-grains; *a* drops of oil expelled from the principal mass by action of the sulphuric acid; *m* empty spaces from which the aleurone-grains have been dissolved (×800).

homogeneous matrix, which, as closer investigation shows, consists, according to the oiliness of the seed, of more or less oil combined with albuminoids. The grains themselves, on the other hand, consist, independently of certain enclosed matters, of albuminoids.

In the grains of aleurone the albuminoid must be distinguished from the enclosed substances. The latter are either crystals of calcium oxalate, or they are non-crystalline, roundish, or clustered granules, Globoids. These are a double calcium and magnesium phosphate, in which the latter is greatly in excess.

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account of his labours for my use here; what I have said above follows his views tolerably closely. There is, in fact, scarcely any one who combines, to the same extent as Dr. Pfeffer, the necessary skill in microscopic work with the chemical knowledge required in this excessively difficult work.

The whole albuminous mass (proteine) is now amorphous, and in that case not doubly refractive; or the greater part is developed into the shape of a crystalloid (sect. 7), which, together with the enclosed substances already named, is surrounded by a sparse amorphous envelope, constituting, together with the former, the grain of aleurone. (Fig. 50.)

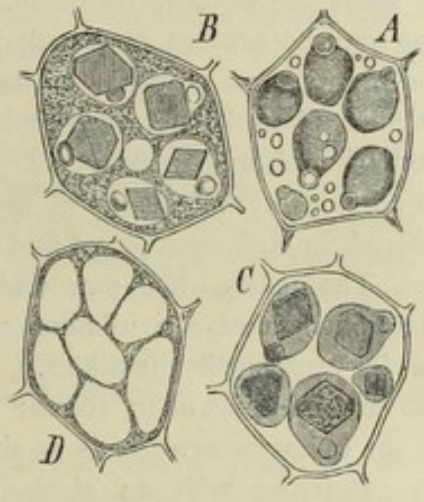

FIG. 50.—Cells from the endosperm of *Ricinus communis* (×800). *A* fresh, in thick glycerine, *B* in dilute glycerine, *C* warmed in glycerine, *D* after treatment with alcohol and iodine, the aleurone grains are destroyed by sulphuric acid, the albuminoid remaining behind as a net-work. In the aleurone-grains the globoid may be recognised, and in (*B*, *C*) the crystalloid.

The crystalloids are all insoluble in water; neither alcohol nor water extracts anything from them. The grains destitute of crystalloids dissolve in water entirely (as Pæonia), partially (as Lupinus), or not all (as Cynoglossum). But all dissolve completely in water containing only a trace of potash. With careful treatment there always remains behind a membrane surrounding the grain, which behaves like coagulated albumen; but it may be a yet unknown proteinaceous substance. With grains of aleurone containing crystalloids, there remains, after careful solution, a similar membrane, but the crystalloid itself also leaves behind a similar one; this occurs also in the solution of globoids in acetic or hydrochloric acid, and reminds one of the similar behaviour of true crystals of calcium oxalate.

The crystalline enclosures of calcium oxalate occur as clusters, clearly recognisable crystals, and needles, but are nevertheless not commonly met with. The globoids, on the other hand, are never absent from aleurone-grains; when they occur together with crystals, it is almost always the case that globoids only are enclosed in one cell, crystals in another (as in *Silybum marianum*, and in all Umbelliferæ that have been examined). There occur however exceptions; and in *Vitis vinifera* it is even the case that a globoid forms itself around a crystal or a cluster of crystals. The globoids are soluble in all inorganic acids, and in acetic, oxalic, and tartaric acid, but not in dilute potash.

The globoids, like the crystals, may occur in an aleurone-grain singly or in numbers; in the latter case they are small, and the globoid-grains even too minute to be measured, but are then present in enormous numbers in one grain (*e.g. Lupinus luteus*, *L. polyphyllus*, *Delphinium Requieni*, &c.). Large globoids around crystals occur singly, the largest in the grape-vine. Pfeffer found crystals accompanying crystalloids only in *Æthusa Cynapium*. The enclosed substances especially are most often absent from very small aleurone-grains.

In some seeds there is in each cell one aleurone-grain distinguished from the others by its size (Solitär of Hartig), both when crystalloids are present and when they are absent (Elaeis, Myristica, Vitis, *Lupinus luteus*); and a larger grain of this kind may also be distinguished by its enclosed substances. Thus in *Lupinus luteus* it possesses a tabular crystal; the others only small and numerous globoids. In Silybum a cluster of crystals lies in one large grain, in the others a number of needle-shaped crystals. In other cases the enclosed substances are also similar,

as is always the case with the globoids, which are especially larger in the large grain.

The crystalloids are tolerably widely distributed, although the greater number of seeds are destitute of them. They are not, however, characteristic of families, but may be present or absent in members of the same family; thus among palms, *Sabal Adansonii* is without, *Elaeis guineensis* provided with crystalloids; in the same manner all Umbelliferæ which have been investigated are deficient, with the exception of *Æthusa Cynapium*, &c. In other cases all seeds of the same family appear to contain crystalloids, as in the Euphorbiaceæ, among which in particular Ricinus offered the first example of fine crystalloids in the grains of aleurone.

The matrix which surrounds the grains of aleurone in oily seeds is, as has been mentioned, always a mixture of oily matter and albuminoids, but the latter may be in very small quantities. Thus even in Ricinus and the brazil-nut, where the matrix appears to consist entirely of oily matter, the albuminous constituent is yet quite discernible, as is shown in Fig. 50, *D*; Pfeffer succeeded most readily by extracting with an alcoholic solution of calomel, and then colouring with aniline-blue dissolved in water. The matrix may be considered as the protoplasmic mass of the cell, in which the water is replaced on drying by oil. But in addition it contains in the whole mass, not only insoluble albuminoids, but other substances also which are soluble in water containing potash in solution. This composition of the matrix, together with the solubility of the amorphous mass of the aleurone-grains in water, are the cause of the complete loss of form which the cell-contents of oily seeds immediately undergo in water (sections under the microscope). In order to recognise their structure it is necessary to place fresh sections in thick glycerine, or in alcoholic solution of calomel, in concentrated sulphuric acid, or in oil.

The oily matter may besides separate out of the matrix in crystals, as Pfeffer has observed in the brazil-nut, *Elaeis guineensis*, and the nutmeg.

To the above may be added from Pfeffer's communication some explanations concerning the more difficult points.

(a) *The Mass* of the grains of aleurone always consists to by far the greater extent of proteinaceous substances, with which only very small quantities of other vegetable substances are usually or always mixed; these, nevertheless, are difficult of detection. This conclusion rests essentially on the following grounds: — all aleurone-grains are absolutely insoluble in alcohol, ether, benzol, and chloroform (that I formerly considered them soluble in ether, was the result, as Pfeffer showed, of the ether containing a small quantity of water). All these reagents would dissolve oil (alcohol dissolves also glucose), if it were present, and would consequently also alter the appearance of the grain. There are grains insoluble in water (*e.g. Cynoglossum officinale*); those soluble in water[1] pass over, on digestion with absolute alcohol in which corrosive sublimate has been dissolved, into an insoluble mercury-compound, out of which water dissolves nothing worth notice. Gum, pectinaceous substances, cane-sugar, and dextrine, do not, under this treatment, yield an insoluble compound. Of all widely distributed vegetable substances, only a proteinaceous substance can be mentioned which behaves in this manner towards corrosive sublimate. This may be recognised by reactions, of

[1] On the causes of the solubility in water Pfeffer's exhaustive treatise which is immediately to appear must be referred to.

which the best in this case is boiling the mercury-compound with water. The modification of proteinaceous substance insoluble in dilute acids and alkalies is thus formed.

(b) In proving that the aleurone-grains of oily seeds contain no oil, we have already seen that it must be present in the matrix. The doubt which arises from the first glance at sections of oily seeds, whether the great mass of oily matter can find space in the interstices of the grains, can be settled by calculation; for if spheres (the grains may here be considered in this light) are so placed that they are enclosed in any number of equal cubes forming part of one great cube, 47·6 p. c. of the cavity remains; and if the spheres are distant from one another only about one-third of their radius, 69·7 p.c. of the cavity is left, and this is more than is sufficient in oily seeds to take up the oily matter.

Immediate proof can be given of the existence of the oil in seeds which contain a certain amount of it by the appearance presented by the observation of dry sections; if benzol is then added the intermediate masses are seen to disappear, while small quantities of albuminoids always remain. Treated with alcoholic tincture of alkanet the matrix becomes of a deep blood-red colour if it contains a considerable amount of oil; if the oily constituents of the seed are very small, the evidence cannot be obtained in this manner.

If the oil is extracted from the sections of seeds by alcohol, and the grains of proteine then removed by solution of potash, a net-work remains behind in which the grains are replaced by cavities; on addition of acetic acid and iodine the net-work assumes a yellow-brown colour (Fig. 49, *B*; 50, *D*). In most seeds this net-work is very beautiful, comparable, to a certain extent, to parenchymatous tissue; in extremely oily seeds it often breaks up into fragments, the nucleus lying in it like a shrivelled ball. The threads of the net-work are composed of the insoluble proteinaceous materials of the matrix and of the enveloping membranes of the grains of proteine; although a net-work may exist without the latter if grains have disappeared.

(c) *The Crystalloids* of the grains of aleurone are, as has been said, insoluble in water; they may therefore easily be isolated by treatment of fresh sections with water, the amorphous masses of aleurone dissolving, and the rest of the cell-contents being destroyed; they then show all the reactions and the different forms of the crystalloids mentioned in sect. 7. But that they consist of two proteinaceous substances, and grow from within by intussusception, Pfeffer thinks he has good grounds for doubting.

(d) If sections of the endosperm of the peony are treated with alcohol containing a small quantity of sulphuric acid, and if, after washing, they are placed in water, the substance of the grains of aleurone (not containing crystalloids) is seen to be distinctly stratified; but only a few firm and soft layers occur, the inner part of the mass is amorphous. Pfeffer's work should also be consulted here.

(e) *The Development* of the grains of aleurone is thus described by the investigator already so often named.—Their formation commences when the seeds attain the last condition of ripeness and the funiculus begins to become sapless; in the very turbid emulsion which now fills the cells, the enclosed substances, especially the globoids, are already formed; they are, even if not quite perfect, nearly fully developed. Then, as the seed loses its water, the formation of mucilaginous masses commences, consisting of proteinaceous substances, which mostly already surround enclosed substances; these mucilaginous bodies, usually nearly globular, continue to grow; their mutual distance thus decreases, and at last the separation is complete; the grains of proteine, still consisting of mucilaginous substance, are separated from the still turbid matrix, which becomes clearer and clearer, while the seed becomes drier. Thus the previously spherical or ellipsoidal grains become more or less polyhedral, especially, as may easily be observed, in a few oily seeds which have generally but little matrix (*e.g.* Lupinus).

While the formation of the grains of aleurone is beginning, the protoplasmic mass of the cell is only to be detected with difficulty in the turbid cell-contents; yet, on removing the oily matter by alcohol, it may be shown that it is present in the normal form; sometimes in the copious matrix of some seeds the dried strings of protoplasm may be

afterwards seen still extended. In *Lupinus luteus* the crystal of calcium oxalate, which is afterwards enclosed by the largest grain, is already present in the cell-sap before the formation of the grains of proteine. Pfeffer was able to follow the development of the grains with remarkable ease in the peony; in this case the seed is still, even when it has attained its full size, filled with large starch-grains, which become changed into oil only when fully ripe; or even when the seed has been removed from the carpel before the reserve-materials have been completely introduced. The starch is not always, however, completely changed into oily matter. If the starch-grains in the seeds of the peony are imagined to be not completely transformed, and the intermediate mass, almost devoid of oily matter but very rich in proteinaceous substances, forms very small grains of proteine, we have what does actually occur in Phaseolus and in other seeds extremely rich in starch. There are, however, also seeds in which proteine and starch-grains occur in nearly equal quantities, but then always associated with oily matter.

No argument can be founded on the turbid condition of the cell-contents and the softness of the growing grains of proteine, with respect to the manner of growth. Nevertheless it can mostly be affirmed with regard to ripe grains, that those situated farther towards the inside are softer, and that, consequently, on the application of very dilute reagents, they dissolve from within outwards. Different facts appear, nevertheless, to show that no growth takes place by intussusception, as with the grains of starch. The origin of the grains of aleurone is simply a dissociation, which arises from loss of water by the seed, and, on germination, the cell-contents first of all returns more or less completely to the condition of a union of the matrix with the substance of the grains of proteine.

Pfeffer followed out the formation of the crystalloids in Ricinus and *Euphorbia segetum;* they arise nearly simultaneously with the globoids, at a rather early period, and both grow gradually, while the turbidity of the cell-contents at first somewhat increases. They mostly lie, even at an early stage, quite close to one another, but completely surrounded by the turbid mass; the vacuoli which Gris (Recherches sur la germination, Pl. I, Figs. 10–13) figures are the result of the very slight commencement of disorganisation of the cell-contents. The crystalloids are from the first sharp-edged, and, as soon as their size permits their form to be recognised, it agrees with that of the mature crystalloids. The envelopment of crystalloid and globoid by amorphous coatings follows first, if the crystalloids are mature and the drying of the seed has commenced.

With germination the crystalloids dissolve as well from without as from within, even after the envelope has first disappeared; the enveloping membranes are for a time persistent, but gradually become invisible. The globoids also dissolve (no doubt in consequence of the acid reaction which the tissue assumes), and in the case of old seeds from the outside inwards. The grains of aleurone destitute of crystalloids next swell up and resume, on the germination of the seed, the form which they possessed in ripe but still watery seeds; they then begin to mix with the substance of the matrix; and thus sometimes a definite dissolution can be followed from without inwards; but they often coalesce as mucilaginous masses. These changes occur with the first signs of germination in the embryo; formation of starch then also takes place simultaneously in the contents of the cells.

Sect. 9. **Starch Grains**[1].—Plants which vegetate under favourable circumstances produce by assimilation a larger quantity of new formative organisable substance than they require or can employ at the time for the growth of the cells. These materials are stored up in some form or other in the cells them-

[1] Nägeli, Die Stärkekörner, in Pflanzenphys. Untersuchungen, Heft II, and Sitzungsber. der k. bayer. Akad. der Wissenschaften, 1863.—Sachs, Handbuch der Exp. Phys. Leipzig 1865, § 107. What I give here is essentially after Nägeli's work.

selves, and only undergo conversion later. It has already been shown in the preceding paragraphs how this happens with albuminous protoplasm-forming materials, and with oily matter. In far larger quantities another substance, in the most eminent sense organisable, *Starch*, is formed beforehand and stored up in an organised form in anticipation of future use. The starch always appears in an organised form as solid grains having a concentrically stratified structure, which arise at first as minute masses in the protoplasm, and continue to grow while lying in it; if at a subsequent period they reach the cell-sap and cease to remain in contact with the protoplasm which nourishes them, their growth stops[1]. Every grain of starch consists of starch, water, and of very small quantities of mineral substances (ash). The first is a carbo-hydrate of the same percentage composition as cellulose, to which it bears the greatest similarity of all known substances in chemical and morphological properties. The starch, however, occurs in each grain in two modifications: one more easily soluble, which assumes a beautiful blue colour with solution of iodine and addition of water (Granulose), and the other less easily soluble, which in its reactions comes nearer to cellulose (Starch-cellulose). At every point of a grain of starch both materials occur together; if the granulose is extracted, the cellulose remains behind as a skeleton; this skeleton shows the internal organisation of the whole grain, but is less dense or poorer in substance, and its weight amounts to only a small fraction of the whole grain (about 2–6 p. c.). Since, then, the granulose greatly preponderates, and is present at every point of the grain, the grain shows, in the reaction with iodine, the blue granulose-colouring throughout its whole extent.

The starch-grains have always rounded forms, and their internal organisation has reference to a centre of formation lying within themselves; the young small bodies appear to be always spherical; but since their growth is scarcely ever uniform, their form changes into ovoid, lenticular, rounded polyhedral, &c.

The internal organisation of the starch-grain is especially recognised by the different distribution of water in it (water of organisation). Every point of the grain contains water in addition to granulose and cellulose. Most usually the amount of water increases from without inwards, and attains its maximum at a fixed point in the interior. With the increase in the proportion of water, the cohesion and density decrease, as also the index of refraction, on which partly depends the power of perceiving these properties. This change in the proportion of water is not, however, constant, but intermittent. To the outermost least watery layer succeeds a sharply defined watery layer, to this again a less watery one, &c., until the innermost less watery denser layer surrounds finally a very watery part, the nucleus. All the layers of a grain are disposed around this nucleus as their common centre, but every layer is not continuously developed around the whole nucleus; in small spherical grains with few layers this is always the case, but when their number increases with growth, the number of layers increases most in

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[1] According to Hofmeister, the starch-grains in the milk-sap of Euphorbia appear to form an exception; nothing however is known about their development; the milk-sap (latex) always contains protoplasm-forming substances, albuminoids, which perhaps here also take part in the production of the starch-grains.

the direction of most vigorous growth, which is continuous in a straight or curved line with the direction of least vigorous growth; this line is called the axis of the grain; it always passes through the nucleus.

The growth of the grains of starch is accomplished exclusively by intussusception; new particles of the formative material become intercalated between those already existing both in a radial and tangential direction, by which means the proportion of water at particular places is at the same time changed. The youngest *visible* globular grains of starch consist of denser less watery substance; in this is formed subsequently the central watery nucleus; in the latter a central part may become denser, and in this, when the increase in size has advanced sufficiently, a softer nucleus may again arise. It may however also happen, after a softer nucleus has arisen surrounded by a dense layer by differentiation of the original dense nucleus, that in the dense layer a new soft one may arise, and thus become split into two dense layers, the inner of which encloses the soft nucleus. The layers increase by deposition in thickness and circumference. When a layer has attained a definite thickness, it becomes differentiated by further growth into three layers. If it is a dense layer, watery substance becomes deposited in its middle, and there arises in the dense layer, which now splits into two lamellæ, a less dense layer. But when a watery layer becomes sufficiently thick, its middle lamella may become denser, and a new dense layer is formed between two lamellæ of a less dense one. This process of splitting of the layers depends on their increase in thickness; and since this itself is the most vigorous where the layers are intersected by the longer branch of the axis of growth, the splittings, *i. e.* the new formations of layers, ensue there most abundantly, least often on the opposite side of the nucleus, and may even entirely cease there. The layers of the more quickly growing side of the grain become, from bending round on the slowly growing side, constantly thinner, and finally disappear. Lenticular grains (*e. g.* in the endosperm of wheat) have a lenticular nucleus; their layers grow most quickly in the direction of the radii of a great circle concentric with it, and here most commonly split, the nucleus remaining central. If, on the other hand, the growth takes place in one direction (*e. g.* in the ovoid grains of the potato-tuber) the nucleus becomes eccentric, is further and further removed from the centre of gravity of the grain, and is in this case globular. In some ellipsoidal (in the cotyledons of peas and beans) or elongated grains, the nucleus is extended in the direction of the longest axis.

It is very common for two nuclei to form in a small young grain; round each of them layers are formed, and the growth is strongest in the line of union. The distance of the nuclei from one another becomes continually greater; thus a tension arises in the few common layers which surround both; this leads to the formation of an inner fissure, which lies at right angles to the line of union of the two nuclei; it is continued towards the outside, and the grain breaks up into two half-grains which may nevertheless adhere to one another. If this division occurs more often, perfectly compound grains arise, consisting of numerous secondary grains, the number of which may amount even to thousands (*e. g.* in the endosperm of Spinacia and Avena).

Perfectly compound grains of from two to ten half-grains, with a mulberry-like

appearance, are extremely common in the parenchyma of quickly growing plants (*e.g.* seedlings of Phaseolus, stem of Cucurbita). Grains of this description are different in their origin from compound grains of the kind which occur in chlorophyll; in this latter case a number of small grains exist in the first place, which only touch and adhere to one another in consequence of increase of size. (Cf. Fig. 47, p. 47.)

Partially compound starch-grains result when new nuclei and surrounding masses of layers are formed in one grain after each one has already formed several layers. The secondary grains appear therefore to be imbedded in the mass of layers of the mother-grain. In this case also tension arises from the unequal growth of the common layers and of those belonging to each secondary grain, leading at length to the formation of fissures; but these do not usually extend to the outside; the secondary grains remain united.

(a) *The Growth* of grains of starch by intussusception must be inferred from the following considerations:—Supposing that the formation of layers occurs from without by deposition, grains would be found the outermost layer of which would be a watery one; this, however, never occurs; the outermost layer is always the densest and least watery. According to this supposition the nucleus would also possess the properties of the youngest grains, whereas the nucleus is always soft, the youngest grains dense. The theory of apposition could only be brought in to explain the formation of the partially compound grains; if we were to suppose that the common layers of a grain which is forming secondary grains had been subsequently deposited around two or more previously isolated grains, then the common layers would have a different form, and the fissures in the interior of such grains remain unexplained. The theory of apposition, finally, is incompetent to explain why, in secondary grains, the strongest growth always takes place in the line of union of their nuclei (Fig. 51). The possible hypothesis of a deposition of new layers from within would presuppose that the starch-grains were at least temporarily hollow bladders, which has never been observed; on this hypothesis, moreover, it cannot be explained how the phenomena arise which occur in the formation of half and secondary grains; and the only hypothesis which can be accepted is growth by intussusception, namely in the direction of the surfaces of the layers. The hypothesis of the growth of starch-grains by intussusception alone affords the simplest explanation of all phenomena; and, after Nägeli's researches, may be considered as a fully established fact. The formative material which penetrates from without into the grain once formed and there becomes deposited in the form of new particles of starch, is, of course, in solution; but its chemical nature is not yet certainly known; dissolved starch can never be found to exist in the plant, at least in those cells where active formation and growth of starch-grains has been observed. It is, however, probable that

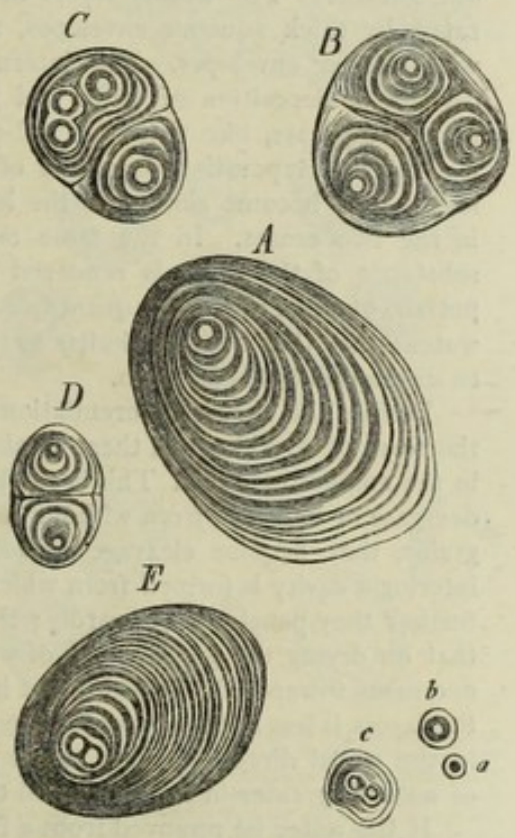

FIG. 51.—Starch-grains from the tuber of a potato (×800). *A* an older simple grain; *B* a partially compound grain; *C*, *D* perfectly compound grains; *E* an older grain, the nucleus of which has divided; *a* a very young grain, *b* an older grain; *c* a still older grain with divided nucleus.

a solution of sugar contained in the protoplasm is the material out of which particles of starch are formed by further chemical and physical changes. The starch is easily changed into sugar by different agencies. From various facts (*e. g.* the production of radial fissure-surfaces on drying), it must be concluded that the molecules of starch have not only a definite position in the direction of the radii, but are also arranged tangentially in a definite manner in each layer. A lamellar structure and the formation of areolæ corresponding to this, appearing as a radial striation, has, however, been observed only occasionally and doubtfully.

Growth by intussusception depends on the permeability of all parts of the grain to water and aqueous solutions. This again can only be explained by supposing that the substance of starch is not continuous, but consists of distinct invisibly minute particles, each of which possesses the power of attracting water, and surrounds itself with an aqueous envelope; the particles of starch (molecules) are separated from one another by these aqueous envelopes; the smaller the molecules in a given volume of a starch-grain, the more numerous are these envelopes, and the more watery the volume of starch under consideration. From this it results, on purely mechanical principles, that in this case the aqueous envelopes are thicker, that, on the other hand, as the molecules increase in size, they become thinner, and the molecules thus approach nearer one another. The watery layers therefore consist of small molecules which are separated by thick aqueous envelopes, the denser less watery layers of larger molecules with thinner envelopes. The internal organisation thus depends, in these cases, on a definite co-deposition of water and particles of starch; the stratification of a starch-grain disappears, like that of a cell-membrane, as soon as the water is removed from it (*e. g.* by evaporation or action of absolute alcohol, &c.), because the more watery layers then become similar to the less watery, and the difference of refractive power in the two ceases. In the same manner the stratification also disappears when the substance of the grain is rendered capable by chemical means (as weak solution of potash) of absorbing large quantities of water; the denser layers absorb relatively more water; they thus become similar to the more watery layers, and it is no longer possible to distinguish between them.

Besides the abrupt differentiation of the proportion of water which is recognised in the form of stratification, there is also in every grain an increase from without inwards in the amount of water. This is partly ascertained by the refraction, partly by the regular decrease of cohesion from without inwards. If the water is removed from fresh starch-grains, they acquire cleavage-surfaces which cross the layers at right angles; in the interior a cavity is formed from which the fissures radiate; these become narrower the further they penetrate outwardly; they are widest in the middle. From this it follows that on drying the greatest loss of water occurs in the interior, and that this regularly decreases towards the outside; but it also follows at the same time that the cohesion of the layers is less in the tangential direction (at right angles to the cleavage-surfaces) than in the radial direction; this points to the conclusion that within every layer the loss of water is greater in the tangential than in the radial direction.

If the water be removed from a fresh starch-grain or from one saturated with water, it contracts; the molecules contained in it approach one another when the layers of water between them become thinner. A similar change takes place if the granulose is removed from a grain; the cellulose-skeleton of the grain which remains is, although saturated with water, much smaller than the intact grain. This possibly results from the fact that the molecules, now consisting only of cellulose, possess less attraction for water, and, having thinner envelopes, approach nearer; the cause may however also be that the number of molecules has diminished.

(b) *The Extraction of the Granulose* of starch-grains, leaving behind a skeleton of cellulose, can be brought about in very different ways:—1. By maceration in saliva at an elevated temperature; in the starch of *Canna indica* the extraction, according to H. von Mohl, is slow at 35°–40° C., but is completed in a few hours at 50°–55° C.; a lower

temperature suffices for wheat-starch, a higher is required for that of the potato. Nägeli gives in general 40°–47° C. 2. According to Melsens a similar extraction may also be effected by organic acids, diastase, and pepsin. 3. According to Nägeli it can be accomplished also by very slow action of hydrochloric or sulphuric acid which has been so diluted with water that it does not cause the starch-grains to swell. 4. According to Franz Schulze, the granulose is extracted by a saturated solution of sodium chloride containing 1 p. c. of concentrated hydrochloric acid, at 60° C. in two to four days; the residuum, which does not perfectly show the organisation of the starch-grain, amounted, according to Dragendorff, to 5·7 p. c. in potato-starch, 2·3 p. c. in wheat-starch. These skeletons are not at all coloured by iodine (Nägeli's preparation with sulphuric acid after one and a quarter year's extraction), or they become copper-red, and in places where the extraction was not perfect, bluish. They do not swell in boiling water. At 70° C. the whole starch-grain, according to Mohl, is dissolved in saliva: the skeleton produced at 40°–55° C. is, however, not affected by saliva at 70°.

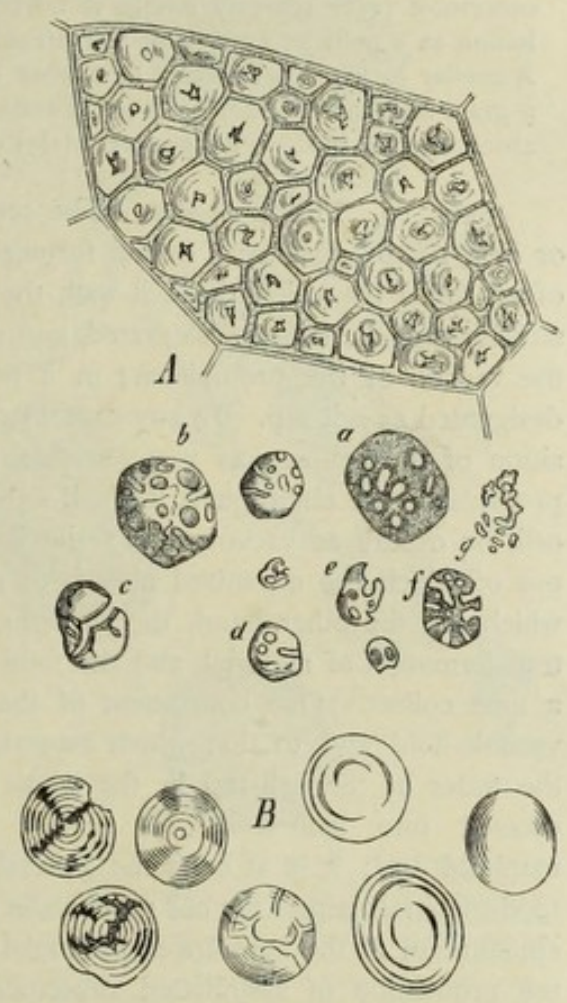

FIG. 52.—*A* a cell of the endosperm of *Zea Mais*, filled with crowded and therefore polygonal starch-grains: between the grains lie thin plates of dried fine-grained protoplasm; small cavities and fissures are formed in the interior of the grains by drying; *a*—*g* grains of starch from the endosperm of a germinating seed of maize; *B* grains of starch (lenticular) from the endosperm of a germinating seed of wheat; the commencement of the action of the solvent is shown by the more evident appearance of stratification (×800).

Within the living cell the starch may be dissolved in very different ways; probably solution occurs mostly under the influence of protoplasm or by the assistance of nitrogenous combinations in the cell-sap. Sometimes the solution begins, as in the extractions mentioned above, with the removal of the granulose, the cellulose remaining behind; but this often takes place only partially; the extraction proceeds in single places from without inwards; the extracted places are coloured copper-red by aqueous iodine, the remaining mass blue; then the grain breaks up into pieces, which finally are completely dissolved (as in the endosperm of germinating wheat, Fig. 52, *B*). In other cases the solution begins also in particular places of the circumference; the whole substance, however, gradually dissolves; holes are formed, and finally the grain in these cases also breaks up into pieces (*Zea Mais*, Fig. 52, *A*). In the cotyledons of germinating beans, the solution of the ellipsoidal grains begins from within; but before they break up into pieces the granulose is often so completely extracted that they assume with iodine a copper-red and in parts a bluish colour; afterwards the whole is dissolved. In germinating potatoes and the root-stock of *Canna lanuginosa*, on the other hand, the solution of the grains proceeds from without inwards, removing layer after layer. Probably the same takes place here as when saliva is employed, whether the solvent acting slowly first extracts the granulose, or attacking it energetically dissolves the whole substance. Observations on germinating plants of the same species, developed at different temperatures, would possibly show corresponding differences.

(c) *Solubility, Swelling.* If grains of starch are crushed in cold water, a small

portion of the granulose is dissolved; addition of iodine occasions precipitation of fine-grained blue pellicles[1]. Starch-grains ground with fine sand give up an actual solution of granulose to cold water. Other fluids, as dilute acids, do not cause a solution of the starch, but rather a transformation into other substances (dextrine, dextrose), which then dissolve.

Water of at least 55° C. causes swelling and formation of paste in the larger more watery starch-grains; in smaller denser ones this begins, according to Nägeli, at 65°. Heated in the dry state, at about 200° C. they are so changed that subsequent moistening causes swelling; but the substance is by this means chemically changed; it is transformed into dextrine. In the production of paste, the interior watery parts swell first, the outermost layer scarcely swells, it bursts and remains for a long time discernible by iodine as a pellicle, even after the breaking up of the inner parts into small particles. A similar action is occasioned by a weak cold solution of potash or soda; the volume of a grain may thus be increased one hundred and twenty-five fold, and so much fluid be absorbed that the swollen grain contains only 2–½ per cent. of solid starch.

Sect. 10. **The Cell-sap.**—The term Cell-sap may be understood in a wider or in a narrower sense. In the former sense it would express the collective mass of all fluids by which the cell-wall, the protoplasm-body, and all other organised structures of the cell are saturated, and would also embrace the fluids contained in the vacuoli of the protoplasm; in a narrower sense the latter only is ordinarily designated as cell-sap. In any case there are grounds for considering the composition of the cell-sap as very variable, according as it has been imbibed by the protoplasm, the chlorophyll, the cell-wall, or the starch-grains of one and the same cell, or occurs as vacuole-fluid; the latter may in general represent the reservoir out of which the organised absorbent parts of the cell supply their needs, but in which, on the other hand, the superfluous soluble products of assimilation and of transformation of material, and the food-materials that have been absorbed, also for a time collect. One constituent of the cell-sap, water, is always common to the vacuole-fluid and to that which saturates the organised structures. The share of the water of the cell-sap in the whole building-up of the cell has already been entered into sufficiently in detail. Its signification in the cell is a very manifold one; it is at once the general solvent and the agent of transport of the food-materials within the cell; the water itself enters in many ways into the chemical constitution of the substances produced in the plant; its elements are essential for the production of assimilated substances; for the formation of organised structures, the cell-wall, the protoplasm-structures, and the starch-grains, it is indispensable (water of organisation); the growth of the whole cell-body depends immediately on the absorption of water, and on the accumulation of the cell-sap as vacuole-fluid (cf. Figs. 1, 43, 44). The increase of size of rapidly growing cells is nearly proportional to the accumulation of the sap in them. The hydrostatic pressure which the vacuole-fluid exercises on the protoplasm-utricle and cell-wall co-operates in the conformation of the cell.

The substances dissolved in the water of the cell-sap, partly salts absorbed from without, partly compounds produced in the plant itself by assimilation and transformation of

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[1] On the actual solubility of starch, see my remarks in my Handbuch der Experimental Physiologie, p. 410.

material, are, as such, not immediately the subject of morphological observation, to which we are for the time confining ourselves. Inuline[1] only, which is precipitated by the action of cold and desiccating agents from its solution in cell-sap in definite forms, and becomes visible in the interior of cells, need here be particularly mentioned. In the cell-sap of certain Algæ (Acetabularia) and many Compositæ (perhaps also in many other plants), Inuline, a substance closely related to starch and sugar, occurs. In sap obtained by pressure or boiling, it precipitates spontaneously after some time in the form of a white fine-grained precipitate. From solutions it crystallises in the form of so-called sphere-crystals (Fig. 53, *A*), which consist of crystalline elements disposed in a radiate manner. Within the cells it may be made visible as a finely granular precipitate by drying or by rapid removal of water by means of alcohol (Fig. 53, *F*). It is abundantly precipitated in the cells in the form of smaller sphere-crystals on dipping thin sections of the tissue in alcohol, becoming immediately visible on addition of water (Fig. 53, *B*). They are obtained much larger by laying whole Acetabularias or large pieces of tissues containing inuline (tubers and stems of Dahlia and *Helianthus tuberosus*) for a longer time in alcohol or glycerine; in the latter case a sphere-crystal very commonly includes several cells of the tissue (Fig. 53, *E*), a proof that the crystalline arrangement is not necessarily destroyed by the cell-walls. Similar forms (as in Fig. 53, *B*) are formed when tissues containing inuline freeze, and they do not again become dissolved in the cell-sap on thawing. Since the sphere-crystals consist of doubly refractive crystalline elements arranged radially, they show, under polarised light, the cross which occurs under such circumstances. They are not capable of swelling, are slowly dissolved in a large quantity of cold water, and quickly in a small quantity of warm water of from 50°–55° C.; in solution of potash and nitric and hydrochloric acids they dissolve easily, the solution always commencing from without; by boiling in very dilute sulphuric or hydrochloric acid the inuline is immediately transformed into glucose. Solutions of iodine in alcohol or water penetrate into the fine crevices of the sphere-crystals, but occasion no special colour. Inuline-structures are easily and certainly recognised by these reactions, as

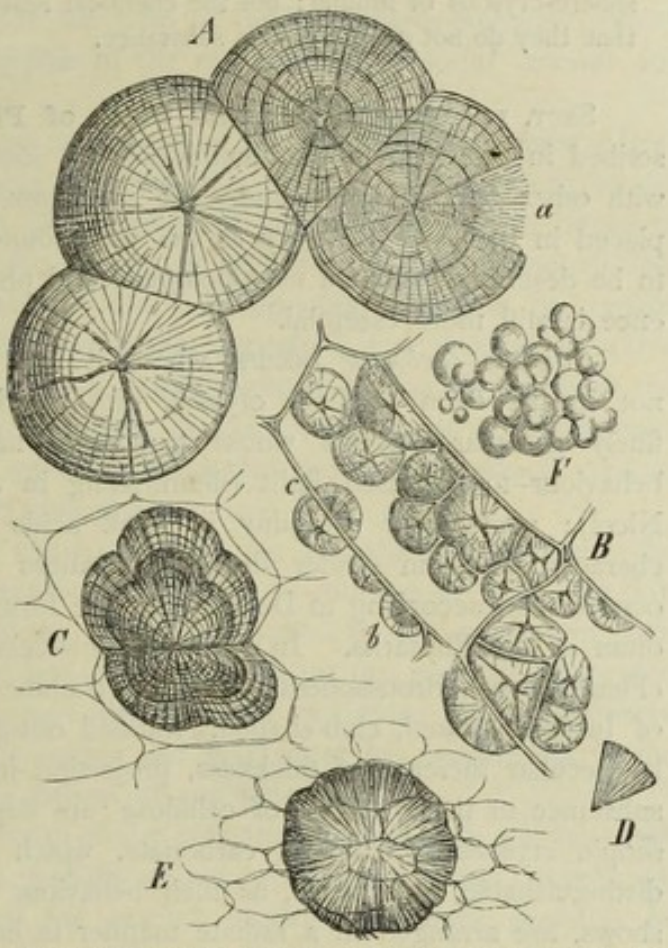

FIG. 53.—Sphere-crystals of Inuline. *A* from an aqueous solution laid aside for 2½ months; at *a* the action of nitric acid is commencing. *B* cells of the root-tuber of *Dahlia variabilis*; a thin section was placed for 24 hours in alcohol of 90 p.c., and was then dipped in water. *C* two cells with half sphere-crystals having their common centre in the middle of the separating cell-wall; from an internode 8 mm. thick at the apex of an older plant of *Helianthus tuberosus*, which had remained for some time in alcohol. *D* fragment of a sphere-crystal. *E* a large sphere-crystal including several cells, from a larger piece of the tuber of *Helianthus tuberosus*, after lying for a longer time in alcohol. *F* Inuline after evaporation of the water from a thin section from the tuber of *Helianthus tuberosus* (×500; *E* not so much).

[1] Sachs, Bot. Zeitg. p. 77, 1864.—Prantl, Das Inulin, ein Beitrag zur Pflanzen-Physiologie. Preisschrift. Munich 1870.—Dragendorff, Materialien zu einer Monographie des Inulins. Petersburg 1870.

well as by their appearance. If masses of tissue containing much inuline (tubers of *Inula Helenium* and *Helianthus tuberosus*, roots of dandelion and of other Compositæ) are examined in the dry state, the parenchyma-cells are found to be filled with angular, irregular, shining, colourless fragments, which are seen in polarised light to be crystalline, and may be recognised as inuline by the reactions above-named.

If the ovaries and unripe fruits of the orange or citron are laid for some time in alcohol, concretions are found in their tissues, which completely resemble in form the sphere-crystals of inuline; but the chemical reactions and the degree of solubility show that they do not consist of this substance.

Sect. 11. **Crystals in the Cells of Plants**[1]. — The crystalline forms described in sect. 7, in which albuminoids are sometimes found, though always mixed with other organic compounds, are not common phenomena, and must not be placed in the same category as the very abundant true crystals of lime salts now to be described; from a morphological and physiological point of view the difference is still more essential.

Calcium carbonate occurs, where it has hitherto been observed in plants, not in the form of large crystals with clearly defined surfaces, but in that of finely granular deposits whose crystalline nature is recognised only by their behaviour to polarised light (illuminating in a dark field of view by a crossed Nicol); while their solubility in weak acids with evolution of bubbles of gas, characterises them (under the circumstances named) as calcium carbonate. It occurs thus, according to De Bary, in the form of roundish grains in the plasmodium of the Physariæ. In the epidermis-cells of the leaves of many Urticaceæ (Ficus, Morus, Broussonetia, Humulus, Bœhmeria, &c.), and in the stem of species of Justicia, stalked, club-shaped, stratified out-growths of the cell-wall are formed, by peculiar increase of thickness, projecting into the cavity of the cells. In the substance of these masses of cellulose 'are deposited clusters of very small microscopic crystals of calcium carbonate, which singly are scarcely or not at all distinguishable, and which, as their behaviour on illuminating with polarised light shows, are arranged in a radiate manner in each single cluster (group of crystals) around its centre.' (Hofmeister, *l. c.*) These structures are known as Cystoliths. The lime deposited in the cell-walls of many marine Algæ appears to be still more finely divided; their structure becoming in consequence stony and brittle. (*Acetabularia*, *Corallina*, Melobesiaceæ, &c.)

All other crystals found in plants and hitherto accurately examined are shown, by their form where this is recognisable, and by their reactions, especially by their insolubility in acetic acid, and their solubility without evolution of bubbles in hydrochloric acid, to consist of *Calcium oxalate*. This salt is widely distributed, especially in the tissue of crustaceous Lichens, most Fungi and Phanerogams, and in the form of very small granules of crystalline structure, of clusters, of bundles of needles (Raphides), and often of large, beautiful individuals with perfectly formed crystalline surfaces.

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[1] Sanio, Monatsber. der Berl. Akad. p. 254, April 1857.—Hanstein, ibid. Nov. 17, 1859.—Gg. Holzner, Flora, pp. 273, 556, 1864, and p. 499, 1867.—G. Hilgers, Jahrbuch für wiss. Bot. VI, p. 285, 1867.—Rosanoff, Bot. Zeitg. 1865 and 1867.—Solms-Laubach, Bot. Zeitg. nos. 31–33, 1871.—Hofmeister, Lehre von der Pflanzenzelle, Leipzig 1867; cystoliths are treated of at p. 180.

In Fungi and Lichens the crystalline granules are commonly small and deposited not in the interior of the cells, but on the outside of the cell-walls, and frequently in such large numbers that the tissue of hyphæ becomes opaque and stiff in consequence. In some Lichens minute granules of calcium oxalate are deposited in the cell-walls of the dense cortical tissue (*Psorosma lentigerum*, De Bary). It is only exceptionally that crystalline deposits occur in the interior of the cells of Fungi, as, for example, in the form of radiate spheres (sphere-crystals) in the swellings of some of the hyphæ of the mycelium of *Phallus caninus* according to De Bary.

Little or nothing is known of the occurrence of calcium oxalate in most Algæ, in Muscineæ, and in Vascular Cryptogams; but it is found very abundantly in the tissues of most Phanerogams. In Dicotyledons it often occurs in the form of large beautifully perfect crystals in the cavities of cells (*e. g.* in the mesophyll and leaf-stalk of Begonia, and the stem and root of Phaseolus); clusters of crystals are, however, in this class much more commonly deposited in a nucleus of protoplasmic substance (*e. g.* in the cotyledons of *Cardiospermum Halicacabum*), where the separate crystals are completely formed only in the detached part. Sometimes also (as in the hairs of Cucurbita) small, beautiful, and perfectly developed crystals are seen enclosed in the circulating protoplasm.

In Monocotyledons, especially those allied to the Liliaceæ and Aroideæ, the crystals of calcium oxalate occur mostly in the form of bundles of long very thin needles, forming the so-called Raphides, which lie parallel to one another in such a manner that they usually more or less completely fill up the generally elongated cells. Needles of this kind are formed also in great quantities when the leaves of many woody plants change their colour and lose water by evaporation in the autumn, although absent during the period of vegetation.

Where the crystals lie in the cavity of the cell, and this is usually the case with Angiosperms, they are commonly, perhaps always, coated by a thin membrane, which remains after the solution of the calcium oxalate, and must probably be considered as a coating of protoplasm. This is also the case, according to the older statements of Payen, even with the raphides, and according to the accurate observations and statements of others, also in the larger single crystals and clusters.

In Dicotyledons calcium oxalate occurs apparently only rarely deposited in the substance of the cell-wall; Salms-Laubach (*l. c.*) names different species of Mesembryanthemum (*M. rhombeum, tigrinum, lacerum, stramineum, Lemanni*) and *Sempervivum calcareum*, in which fine granules or (in the case of *Sempervivum*) larger angular fragments of crystalline calcium oxalate are scattered through certain layers of the outer wall of the epidermis-cells of leaves.

The occurrence of crystals of calcium oxalate in the substance of the cell-walls is, on the other hand, according to the same observer, of common occurrence in Gymnosperms. They generally consist of numerous small granules of unrecognisable shape; not unfrequently, however, also of well-developed crystals. In the bast-tissue of all parts of the stem deposits of this kind are found in the Cupressineæ, Podocarpus, Taxus, Cephalotaxus, and Ephedra; they are absent, on the other hand, from *Phyllocladus trichomanoides, Gingko biloba, Dammara australis,*

and from all Abietineæ that have been examined. The small angular granules or larger individual crystals are usually deposited in the soft lamella between the elements of the bast-tissue. Much more widely distributed even than in their bast, calcium oxalate occurs deposited in the cell-wall of the primary cortical parenchyma of the branches and leaves of Gymnosperms, with the possible exception of some Abietineæ; here also the middle lamella of the common wall between each two cells is the place where the crystals are formed, as also in the bundles of thick-walled cells beneath the epidermis (*e. g.* Ephedra). The thick-walled often branched fibre-cells abundantly scattered through the parenchymatous tissues of Gymnosperms, the so-called 'spicular cells,' not unfrequently contain crystals deposited in their outer mass of layers; these occur in unusually large numbers and great perfection in *Welwitschia mirabilis*. If the crystals are dissolved in hydrochloric acid, the empty cavities in the substance of the cell-wall retain completely the form of the crystals, so that the unpractised observer thinks that he still sees them. Finally, fine granules are abundantly scattered through the thickened outer wall of the epidermis of Gymnosperms (Welwitschia, *Taxus baccata*, Ephedra, &c.) or, in other cases, well-developed small crystals (*Biota orientalis*, *Libocedrus Doniana*, *Cephalotaxus Fortunei*, &c.).

Connected with these deposits in the cell-wall itself are the clusters of crystals discovered by Rosanoff (Bot. Zeitg. 1865, 1867) in the pith of *Kerria japonica*, *Ricinus communis*, and in the leaf-stalk of different Aroideæ (Anthurium, Philodendron, and Pothos), which, lying in the cavity of the cell, are united with the cell-wall by simple or branched threads of cellulose, and are even covered with a membrane of cellulose.

The crystalline forms in which the calcium oxalate occurs in the cells of plants are extremely numerous, an immediate consequence of the circumstance that this salt crystallises in two different systems, according as it is combined with six or with two equivalents of water. The calcium oxalate containing six equivalents of water of crystallisation $\left(\begin{matrix}CaO\\CaO\end{matrix}\right\}C_4O_6+6\text{ aq.}\Big)$, crystallises in the quadratic system, the fundamental form is an obtuse quadrate-octahedron (envelope-shaped); combinations of the quadratic prism with the obtuse octahedron are met with in abundance. The raphides, however, belong, as respects their behaviour in polarised light, according to Holzner, to the klino-rhombic system, in which calcium oxalate crystallises with two equivalents of water of crystallisation $\left(\begin{matrix}CaO\\CaO\end{matrix}\right\}C_4O_6+2\text{ aq.}\Big)$. The fundamental form of the numerous combinations belonging to this class is a hendyohedron; it produces derivative forms which are very similar to calcspar (as, for instance, in the deposits in the cell-wall), and others very similar to calcium sulphate. The clusters of crystals may consist of individuals of one or the other system.

On the physiological signification of calcium oxalate what is necessary to be said will be found in Book III. ch. 2. Here however a few remarks may be made on the directly recognisable relation of the crystals to the cells which produce them.

When the crystals remain so small that their volume appears inconsiderable in relation to that of the cell itself, this latter retains its usual character; it may possess protoplasm, nucleus, chlorophyll, and starch (as in the case of the hairs of Cucurbita or

the mesophyll of Begonia); when, on the other hand, a crystal, or a cluster, or a bundle of raphides, or finally a mass of small crystals, nearly fills up a cell, no other constituent of definite form is usually present; it appears as if, in such cases, the cell is usually approaching a condition of rest or even of slow dissolution; if at an earlier stage a larger mass of crystals has been formed in a cell, it often remains smaller and with thinner walls than its neighbours. The cells which contain raphides show loosened walls which easily swell, and the bundles of raphides are generally surrounded by a thick gummy mucilage. A similar reason also explains why the granules and crystals deposited in the cell-wall of Gymnosperms usually lie in a softened mucilaginous middle lamella or in the cuticularised layers of the epidermis [1].

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[1] [Professor M^c^Nab gives (Journal of Botany, new series, vol. i. p. 33) for the composition of the potassium-chlorate solution: three grains of potassium-chlorate dissolved in two drachms of nitric acid of sp. gr. 1·10. The preparation of 'Schultz's solution' is thus described by Schacht (The Microscope and its application to vegetable anatomy and physiology, translated by F. Currey, p. 43): Zinc is dissolved in hydrochloric acid; the solution is allowed to evaporate under contact with metallic zinc, until it attains the thickness of a syrup; the syrup is then saturated with potassium iodide, the iodine added, and the solution, when necessary, diluted with water. For the 'iodine-solution' the same authority recommends one grain of iodine, and three grains of potassium iodide in one ounce of distilled water.—Ed.]

CHAPTER II.

MORPHOLOGY OF TISSUES.

Sect. 12. **Definition.** — In the widest sense every aggregate of cells which obeys a common law of growth (usually however not uniform in its action) may be termed a Tissue. Aggregates of this kind may originate in different ways. The cells concerned may be at first isolated, subsequently during their growth they may come into contact, and become so completely united at the surfaces of contact of their walls that the boundary surface between them becomes indistinguishable. This happens, *e.g.* in the sister-cells which have arisen by division in the mother-cells of Pediastrum, Cœlastrum, and Hydrodictyon; the sister-cells show in these cases within the mother-cell a 'creeping' motion which lasts for a considerable time before they become connected into a surface (Pediastrum), or in the form of a sac-like hollow net (Hydrodictyon), and form by their growth a tissue. In the same manner the sister-cells (endosperm) which arise in the embryo-sac of Phanerogams by free-cell-formation, unite with one another and with the wall of the embryo-sac itself, continuing then to develop as a continuous tissue and to increase by division.

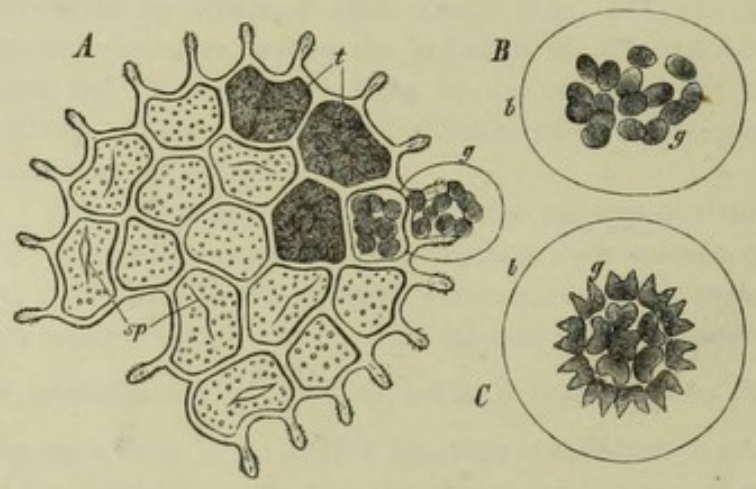

Fig. 54.—*Pediastrum granulatum* (after A. Braun) (×400). *A* a disc consisting of cells grown together; at *g* the innermost layer of a cell-wall is protruding; it contains the daughter-cells resulting from division of the green protoplasm; at *t* are various states of division of the cells; *sp* the fissures in the already empty cell-walls; *B* the inner lamella of the mother-cell-wall which has entirely escaped (greatly enlarged); *b* contains the daughter-cells (*g*), these are in active creeping motion; *C* the same family of cells 4½ hours after its birth, 4 hours after the small cells have come to rest; these have arranged themselves into a disc, which is already beginning to develop into one similar to *A*.

In Fungi and Lichens the formation of tissue originates by the apical growth of juxtaposed thin filaments consisting of rows of cells (the hyphæ), and different orders of branchlets of them; each filament grows by itself, increasing the number of its cells by division, and branches copiously; but this takes place in such a manner that the different hyphæ undergo a similar development at definite spots on the whole body of the Fungus or Lichen; thus arise surfaces, strings, hollow structures, &c.,

which show a common growth, and yet consist of single elementary structures developing individually (Fig. 55).

With the exception, however, of the instances named, and of some allied ones, the formation in the vegetable kingdom of many-celled bodies regulated by a common growth always arises from the tissue-cells which originate by the often repeated bipartition from common primary mother-cells, remaining from the very



FIG. 55.—Part of a longitudinal section of a Gastromycete (*Crucibulum vulgare*), showing the course of the hyphæ: their interstices are filled with a watery jelly, which has probably resulted from the conversion into mucilage of the outer cell-wall layers of the filaments. (For further details of the internal organisation, see Book II. Fungi. The drawing is partially diagrammatic, inasmuch as the hyphæ are too thick for the small magnifying of the whole (about 25), and not so numerous as in nature.)

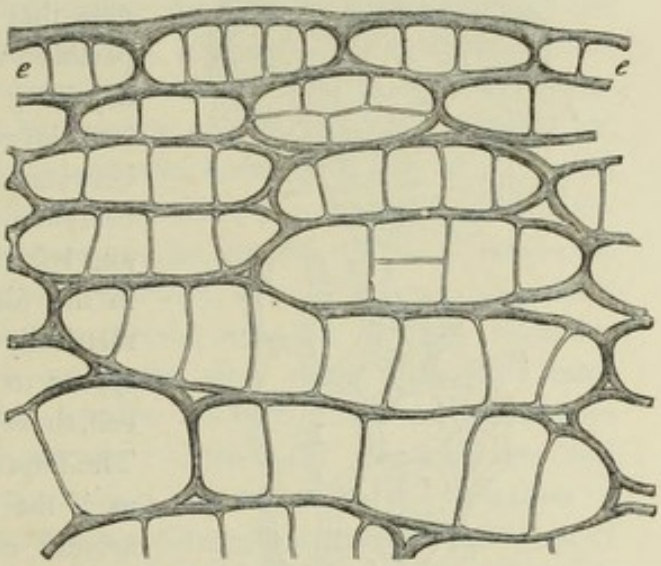

FIG. 56.—Epidermis (*e*) and subjacent cortical parenchyma of the hypocotyledonary segment of the sunflower, which thickens quickly after completion of the division; the darker, thicker cell-walls are the original ones, the thinner radial ones those most newly formed. The strong tangential growth even of the epidermis-cells together with their cuticle is of special interest in this process.

commencement in connexion, in consequence of the manner of formation of the partition-wall; the cells are in these cases, at least originally, so united that they appear at an earlier stage like chambers in a mass which continues to grow uniformly (Fig. 56).

The two first-named kinds of tissue-formation may be distinguished as *spurious* from the latter or genuine form; but there is no sharp boundary-line between them. In many cases, for example, the endosperm is only in its rudimentary state a spurious tissue, due to the amalgamation of originally isolated cells; in its further development by cell-division it becomes a true tissue (*e.g.* Ricinus, &c.). The formation of tissue-surfaces occurs in the formation of the cortex of many Algæ and of the genus Chara, by the development of single cell-filaments; but in such a manner that by these means combinations make their appearance which can no longer be distinguished from true tissues.

Nägeli and Schwendener (Das Mikroskop, II. 563 et seq.) may be consulted further on the growth of *Acrochæticum pulvereum*, *Stypopodium atomarium*, *Delesseria*, *Hypoglossum*, and the leaves of Mosses[1].

Sect. 13. **Formation of the common wall of Cells combined into a Tissue**[2]. — If the cell-wall between two adjoining cells is thin, it appears, even when very highly magnified, as a simple lamella; and sometimes this is also the case when it has already attained a considerable thickness (in succulent parenchyma-cells). Usually it is only when the wall has attained some thickness that it can be seen that the one side of the partition-wall belongs to one, the other to the other adjoining cell. If stratification and differentiation into layers occur in a sufficiently thickened wall between two tissue-cells, a middle lamella always becomes discernible (Fig. 57, *m*), on which, right and left, the remaining cell-substance is superposed in the form of layers and shells, generally symmetrically distributed, so that those on one side *appear* to belong exclusively to the one adjoining cell, those on the other side to the other (Fig. 57, *i*). The impression may thus be given to the observer as if the layers which are concentrically deposited around each cell-cavity formed the wall belonging to it alone, while the middle lamella belonged to a common matrix in which the cells are imbedded; or as if it were excreted from the neighbouring cells. Both views were actually held for a considerable time, and the middle lamella was then termed Intercellular Substance. If the older fragments of tissue represented in Fig. 57 are compared with the younger condition of the same, the thought at first suggests itself that the middle lamellæ may be the originally thin walls, on which the thickening-layers have been deposited on both sides inward by apposition; this view has also found its defenders, by whom the middle lamella is distinguished as the Primary Cell-wall. The remaining thickness is then correspondingly described as secondary; or if it is differentiated into two shells, as secondary and tertiary cell-wall.

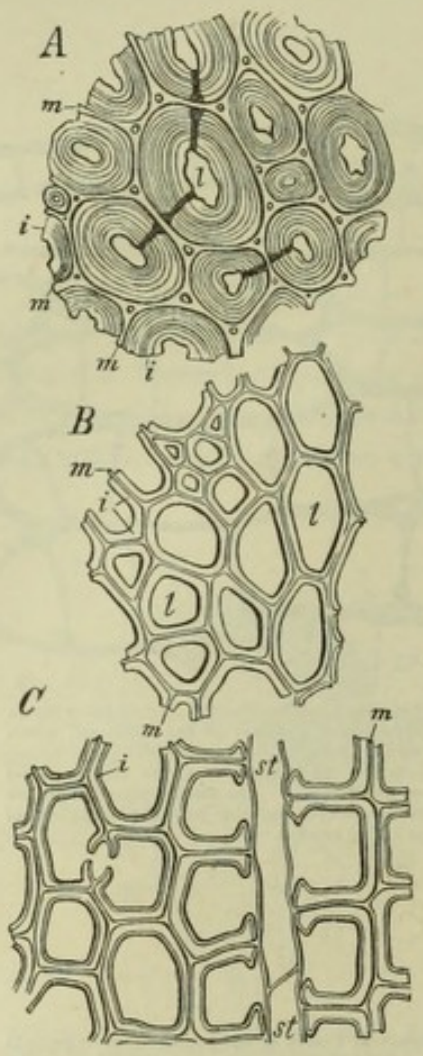

Fig. 57.—Transverse section through thickened cells with evident formation of central lamellæ (*m*); *i* is always the whole of the superposed cell-substance; *l* the cavity of the cell, from which the contents have been removed. *A* from the cortical tissue of the stem of *Lycopodium chamæcyparissus*; *B* wood-cells from the inner part of the wood of a young fibro-vascular bundle of the sunflower; *C* wood of *Pinus sylvestris*, *st* a medullary ray (×800).

[1] On the formation of the cortex of Ceramiaceæ, see Nägeli, Die neueren Algensysteme (Neuenburg 1847), and Nägeli und Cramer, Pflanzenphysiologische Untersuchungen.

[2] H. v. Mohl, Vermischte Schriften botanischen Inhalts. Tübingen 1845, p. 314 et seq.—H. v. Mohl, Die vegetabilische Zelle, p. 196.—Wigand, Intercellularsubstanz und Cuticula. Braunschweig 1850.—Schacht, Lehrbuch der Anatomie und Physiologie der Gewächse, I. p. 108, 1856.—Müller, Jahrb. für wiss. Bot. V. p. 387, 1867.—Hofmeister, Lehre von der Pflanzenzelle. Leipzig 1867, § 31.

The middle lamella is generally thin in lignified tissues, but strongly refractive, and formed of dense substance not capable of swelling; when the rest of the substance of the cell-wall has been dissolved in concentrated sulphuric acid, it remains (in fine transverse sections) as a delicate net-work; if, on the other hand, the cells are isolated by boiling in potash or nitric acid, solution of this middle lamella which resists sulphuric acid takes place, while in this case the rest of the cell-wall is preserved (as in all wood-cells and very many bast-cells). In other cases, as has already been mentioned in sect. 4, the middle layers of the partition-wall of adjoining cells are, on the contrary, converted into mucilage; the layer of cell-wall immediately surrounding each cell-cavity is dense, and appears like the entire cell-wall imbedded in a mucilaginous, swelling, weakly refractive matrix (the so-called intercellular substance); this occurs very commonly in many Fucaceæ and in the endosperm of *Ceratonia Siliqua* (Fig. 41, p. 36). On a fine transverse section through the cambium tissue of a branch of *Pinus sylvestris*, the two phenomena here described may be seen simultaneously; the wood-cells show the thin dense middle lamella, the young bast-cells appear deposited in a soft mucilaginous substance, which is especially thick between the radial rows of cells, and is interspersed with fine strongly refractive granules; but both forms of tissue arise out of the same young tissue (the cambium), the walls of which are simple thin lamellæ, between which the cell-cavities themselves appear as so many compartments. Objects of this kind are well adapted to prove the correctness of the supposition that in general the formation of denser or softer middle lamellæ depends only on a differentiation of the substance of the partition-walls during their thickening, a view which explains in a perfectly simple manner all the phenomena belonging to it, and agrees altogether with growth by intussusception.

The thin entirely homogeneous lamella of cellulose which bounds the young cells never allows a separation into two lamellæ to be recognised; the bounds of the two cells are never marked by a fissure dividing the partition-wall. Nevertheless such a splitting of the still very thin lamella often takes place later locally, when the surface grows more quickly, as in the formation of the intercellular space of the large-celled succulent tissue (parenchyma) of vascular plants, in the formation of stomata, &c. Fig. 58 shows some fully grown parenchyma-cells from the stem of *Zea Mais* in transverse section; the cells were at first bounded by perfectly flat walls, which met nearly at right angles. As the growth increased, a tendency towards the rounding off of the polyhedral forms arose; the unequal growth clearly leads to tensions which are compensated by the fact that on the line where one wall meets the other, the cohesion is destroyed in

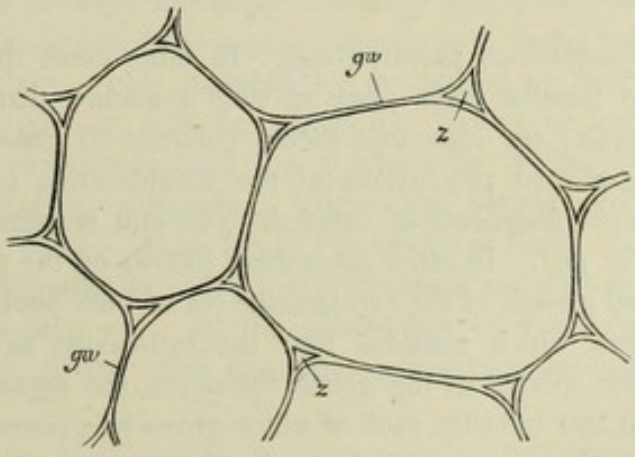

FIG. 58.—Transverse section through the succulent parenchyma of the stem of *Zea Mais*; *gw* common partition-wall of each pair of cells; *z* intercellular space caused by their splitting (×550).

the interior of the substance of the cell-wall. Thus a fissure arises which, corresponding to the relationship pointed out, assumes the form of a triangular prism with concave sides (Fig. 58, *z*). It becomes filled with air, and now becomes one of those intercellular spaces which very usually form in the parenchyma a continuous system of narrow channels. Not unfrequently the portions of the wall which confine the intercellular space grow rapidly, and thus it increases in width; the cells assume irregular outlines, or appear star-shaped in transverse section, touching one another only at small portions of the surface (as in the parenchyma on the under side of many leaves of Dicotyledons, and the stems of *Juncus effusus*). In the middle also of the faces of the cell, when no other wall intersects them, splittings of the homogeneous lamella may occur locally; sometimes these are limited to narrowly circumscribed places, which can then be recognised as shallow excavations in the otherwise

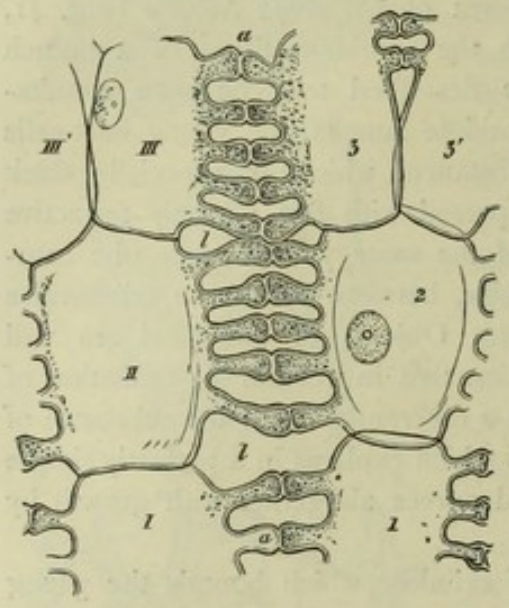

FIG. 59.—Two rows of cells running in a radial direction *I, II, III* and 1, 2, 3) of the cortical parenchyma of the root of *Sagittaria sagittaefolia* in transverse section; *a* the protrusions, *e* the cavities between them (× about 350).

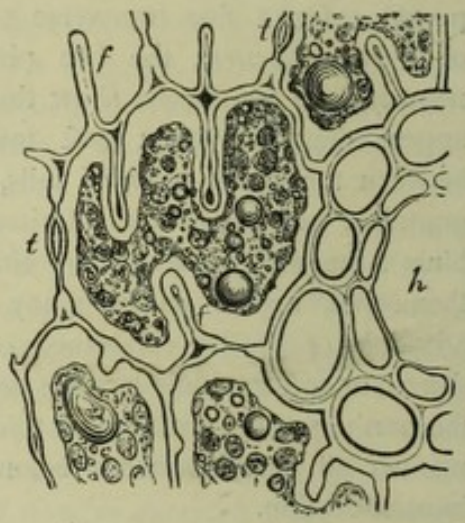

FIG. 60.—From a tranverse section of the leaf of *Pinus pinaster*; *h* half of a resin-passage, to the left parenchyma-cells containing chlorophyll with foldings-in (*f*) of the cell-wall; *t* pit-like formations (the contents of the cells contracted by glycerine, and containing drops of oil) (×800).

homogeneous partition-wall. In other cases the splitting of the partition-wall into two lamellæ takes place in such a manner that only single roundish places remain unsplit; the separated pieces continue to grow rapidly by intercalary growth, and bag-shaped protrusions of the neighbouring cells arise which allow the originally unsplit fragments of cell-wall to be still recognised between them as partition-walls (Fig. 59). In other cases there follows on the partial splitting of the partition-wall a local growth of the two lamellæ (or of only one) of such a character that a folding-in arises, which intrudes into the cell-cavity, as shown in Fig. 60, *f*. Finally, in some species of the genus Spirogyra, the septum between each pair of cells splits into two lamellæ, each of which grows in a peculiar manner; a protrusion is formed into the interior of the cell, which, when the adjoining cells separate, becomes turned inside out somewhat like the finger of a glove previously folded in. When the simple walls of cells united into a tissue split everywhere into two lamellæ (the separation proceeding always from the original intercellular spaces) and become rounded off, a complete dissolution of the tissue takes place in this manner, and the tissue becomes a mere mass of isolated cells. This occurs in the

flesh of many succulent fruits (*e. g.* in the snowberry in winter); and this separation can sometimes be artificially brought about by continued boiling in water (as in potato-tubers).

The origin of the partition-walls in tissue-cells which increase by bipartition by no means requires the supposition that they were originally composed of two lamellæ. In this case one would be led, by careful consideration of the properties of those tissues where numerous divisions follow one another and intercellular spaces afterwards arise, to extremely complicated hypotheses (which, moreover, also contradict growth by intussusception). Even in those cases where the union of the cells into a tissue arises from the amalgamation of originally separate cells (which are not sister-cells), the union of the cell-walls is so intimate that no boundary line can any longer be perceived; and the formation of a middle lamella proves also in such cases [1], as does the formation of a middle lamella generally, that the hypothetical boundary-surface does not exist, and that the splitting of the homogeneous lamella is a consequence of different growth on its two sides. Both the manner in which the splittings of the homogeneous thin partition-walls arise, and also the formation of the middle lamella of thick walls, oppose the supposition of an originally double partition-wall in tissue-cells [2].

The splitting of the partition-wall and the growth of its now separated lamellæ lead to a variety of configurations in the interior of tissues which may be collectively included in the conception of the Intercellular Space. To this belong especially the large air-conducting channels in the tissue of many water and marsh plants (Nymphæaceæ, Irideæ, Marsileaceæ, &c.), and the formation of the cavity between the wall of the capsule and the spore-sac in the fruit of Mosses [3]. Not unfrequently peculiar processes of growth of the adjoining cells unite in the origin of intercellular spaces. I will here only allude to three very different examples, the formation of stomata, the air-cavities of Marchantia, and resin and gum passages (*vide infra*).

But in quite a different manner the behaviour of the partition-wall of two cells contributes to the production of air- or sap-conducting channels, which, like the air- or sap-conducting intercellular spaces, may form a continuous system in the collective mass of the substance of a plant. This happens by the partial or entire absorption of the partition-walls of adjoining cells, by which the cavities of long rows of cells of a tissue become connected; and the single cells themselves become members of a bag-like or tubular structure. Unger has appropriately designated this Coalescence of Cells. Vessels of this kind (Tracheïdes of Sanio) are formed in the wood of fibro-vascular bundles, in which the protoplasm and cell-sap disappear, and they serve for conducting air. In the sieve-tubes in the bast-substance of the fibro-vascular bundles, on the other hand, the watery mucilaginous

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[1] For examples, see Hofmeister, Handbuch, I. pp. 262, 263.

[2] Further detail of this subject is not possible here. I may here remind the reader only of the cleavage of crystals as an analogous case; the cleavage surfaces are determined by the molecular structure, but there is a wide difference between them and true fissures, however fine.

[3] The wide air-canals in the stem of Equiseta, Grasses, species of Allium, Umbelliferæ, and Compositæ arise, on the other hand, from the cessation of the growth of inner masses of tissue and their drying and bursting, while the surrounding tissues continue to grow.

contents of the cells is not replaced by air; the communication established between the cells of one row serves rather for a quicker movement of the succulent contents over greater distances. The Laticiferous Vessels must also be regarded as composed of coalesced cells; they are the result of very early and complete absorption of the partition-walls of adjoining cells belonging to straight or much branched rows in the interior of different systems of tissues.

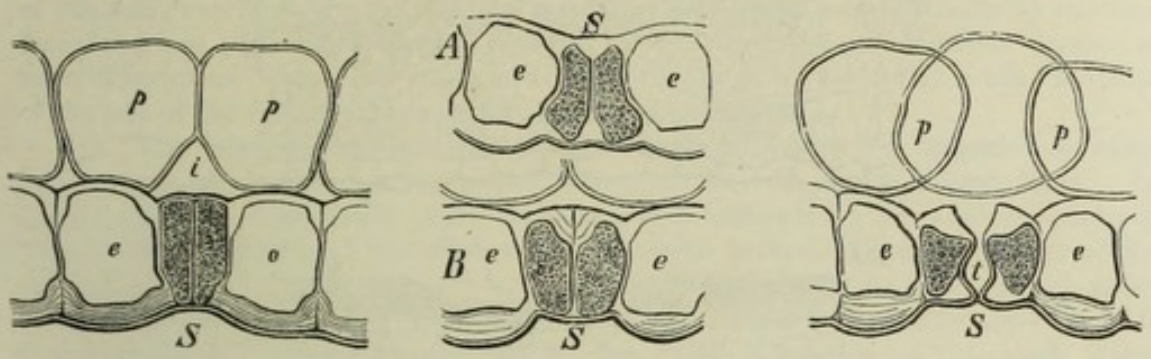
Here however tubes produced by the coalescence of cells need only be opposed to intercellular spaces for the sake of contrast; a more minute consideration will come better in connexion with the description of the systems of tissues.

(a) *'Intercellular Substance' and 'Primary Cell-wall.'* The hypotheses implied by these terms could only be entertained so long as it was supposed that the original thin lamellæ between two adjoining tissue-cells were double; and so long as it was believed that the stratification of the cell-wall was brought about by apposition of new layers. The expression that the original thin partition-wall between two tissue-cells is a double lamella can only be understood in two senses; either it means that the lamella consists of molecular layers, and that two of these contain between them the *ideal* boundary-surface of both lamellæ belonging to the adjoining cells, or that there is an actual interruption of the molecular connexion, and from the first an actual crevice. The last supposition is inadmissible, since it does not rest upon observation; it is besides contradicted by the detection of weak boundary lines between layers which nevertheless are molecularly united, and have no crevices between them. Thus in the layers of thick cell-walls and of starch-grains there are no crevices, and yet the bounds of the layers may be seen; why then should the assumed actual crevice not be visible in the original partition-wall? If now the first alternative is assumed to be correct, and the composition from two lamellæ considered as purely ideal, the question depends on a mere verbal controversy with reference to the intercellular substance; for if the original homogeneous partition-wall, although consisting of molecular layers, is yet held together everywhere by molecular forces, and the supposed boundary surface is no interruption of the molecular structure, then the deposition of a different substance (intercellular substance) at the same place appears only as a process of ordinary growth by intussusception. The fact that the boundary line between previously separated cells disappears by subsequent coalescence proves that the outer molecular layers of cell-walls already formed may yet enter into molecular union. If in such cases a differentiated middle lamella is afterwards formed, this is the most striking evidence against the explanation of it as primary cell-wall. If an attempt is made further to construe on paper step by step the behaviour of a developing woody tissue, for example, while retaining the theory of the primary cell-wall, one is immediately involved in difficulties which do not arise on the supposition that the middle lamella is simply the result of subsequent differentiation of the cell-wall.

(b) *Addition to the Intercellular Spaces.* With the origin of these spaces is very often connected, as has been mentioned, a peculiar development of separating cells, quite different from that of the rest of the tissue; so that the intercellular space, together with its environment, represents, in a certain sense, a peculiar form of tissue or an organ for a definite purpose. The observation of some cases of this kind is well calculated to show the beginner how, even in the domain of tissue-formation, morphologically similar or equivalent processes lead to entirely different results from a physiological point of view. This subject will be treated in a more general and detailed manner in the third chapter, and in Book III.

(1) The cleft of the stomata of the epidermis belongs also to the category of Intercellular Spaces, and its origin is peculiarly calculated to afford an insight into the mode of formation of an intercellular space. I have chosen the stomata on the leaves of

Hyacinthus orientalis as an example. Figs. 61–64 are transverse sections perpendicular to the upper surface of the leaf; *ee* in all of them are the epidermis-cells, *pp* the parenchyma of the leaf. The stoma (*S*) is formed of a smaller epidermis-cell which divides



FIGS. 61-63.—Development of the stomata of the leaf of *Hyacinthus orientalis*, seen in transverse section (×800).

into two equal sister-cells by a wall standing vertically to the surface of the leaf; in Fig. 61, *S*, this has just taken place; the partition-wall is formed[1] it appears as a very thin simple lamella, which soon attains greater thickness, and especially thickens more rapidly where it meets at right angles the wall of the mother-cell without and within (Fig. 62, *A*). The thickening mass appears at first quite homogeneous; afterwards an indication of stratification is to be observed, and the first trace of a separation of the still simple lamella into two lamellæ (Fig. 62, *B*). In Fig. 63, *t*, the splitting is already completed; the growth of the separated lamellæ now proceeds in a peculiar manner, so that a cleft arises narrower in the middle, wider without and within, which unites the intercellular space *i* (the air-cavity) with the external air (Fig. 64). It is worth mention that before the division of the mother-cell, an obvious not very thin cuticle has already overspread it together with the adjoining cells of the epidermis. This is especially to be recognised in the condition *B*, Fig. 62, while still continuous; by the splitting of the partition-wall into two lamellæ it finally becomes ruptured (Fig. 63); and by the cuticularising of the outermost layer of the now separated lamellæ the cuticle is afterwards continued over the surfaces of the cleft (Fig. 64). If the process of the formation of the stoma is followed up on a superficial view, it shows that the splitting of the partition-wall does not extend through its whole surface, but that a portion still remains above and below (taking the leaf in a vertical position) as a simple lamella (cf. sect. 15, Figs. 73–75). Both the Guard-cells (the cells which enclose the cleft) are not only distinguished from the other epidermis-cells by this peculiar mode of division and of growth; they also differ from them by containing chlorophyll and starch.

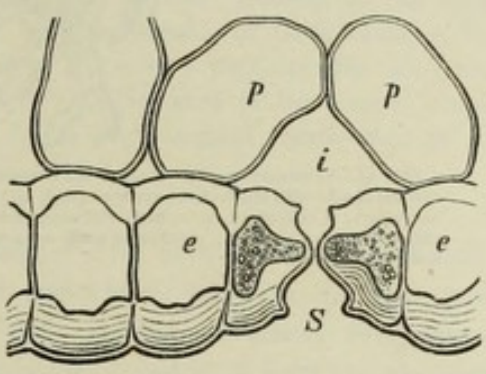


FIG. 64.

(2) In the family of Marchantieæ belonging to the Hepaticæ, the origin and structure of the stomata (Fig. 65, *B*, *sp*) is much more complicated; of this we must speak hereafter. Here it need only be pointed out that even before their formation the epidermis-cells have become detached from those lying beneath; and in such a manner that the separating surfaces (seen from above) represent rhomboidal plates beneath the epidermis, which are marked off from one another by the walls of unseparated cells

[1] I was unable to detect nuclei immediately before and for a considerable time after the division.

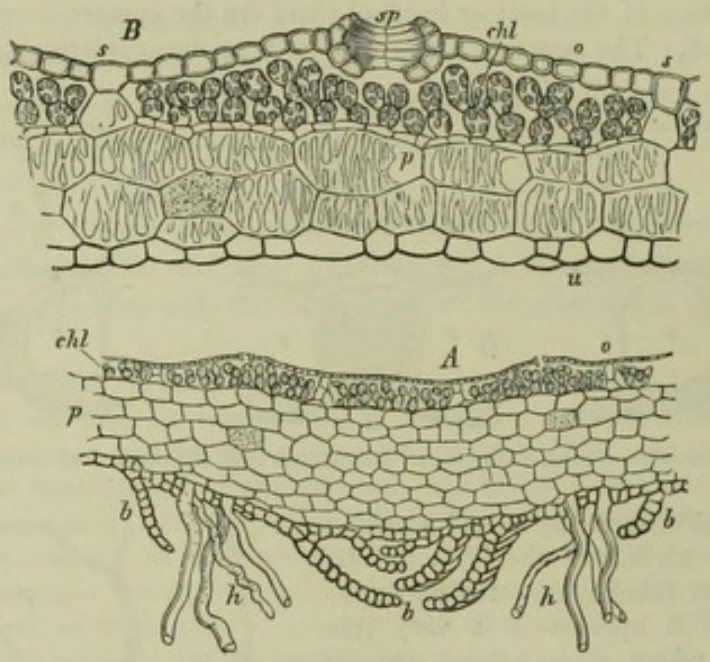


FIG. 65.—Transverse section through the horizontal thallus of *Marchantia polymorpha*; *A* central part, furnished on the under side with the leaf-like appendages *b*, and the root-hairs *h* (×30); *B* marginal part of the thallus, more highly magnified; *p* colourless, reticulately thickened parenchyma; *o* epidermis of the upper side; *chl* the cells containing chlorophyll; *sp* stomata; *s* partition-walls between the broad intercellular spaces; *u* lower epidermis with its cell-walls coloured dark.

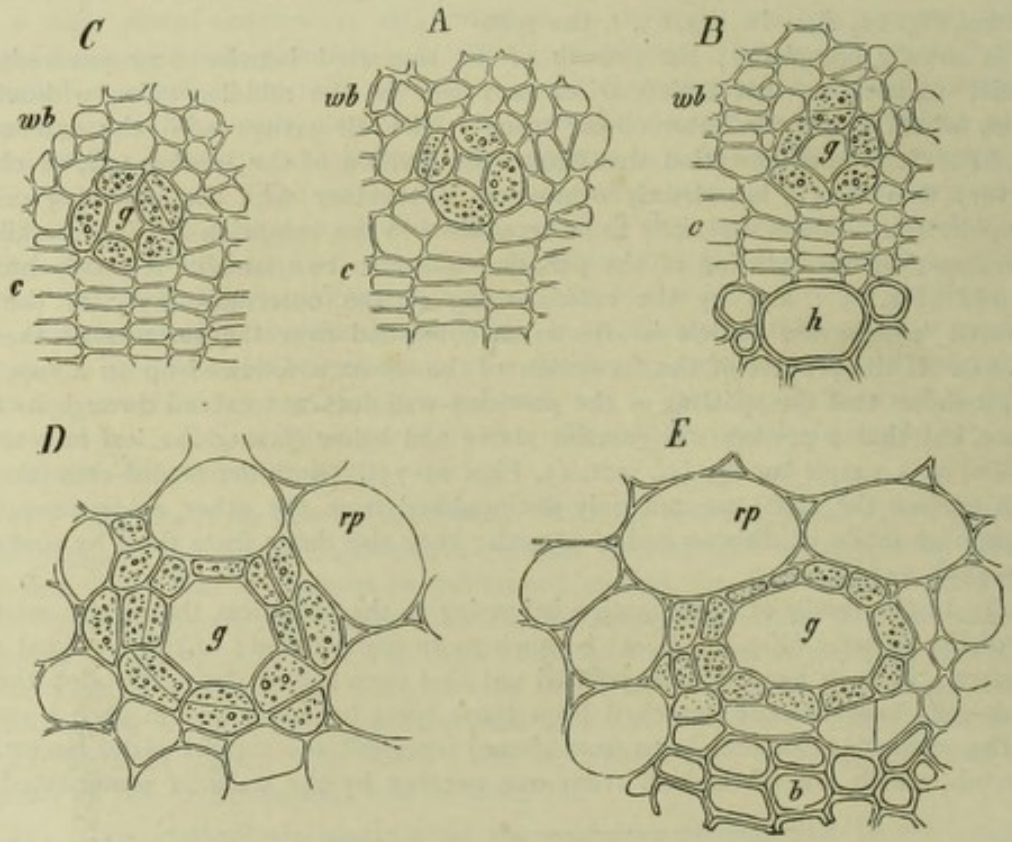


FIG. 66.—Sap-conducting intercellular passages in the young stem of ivy, in transverse section (×800); *A*, *B*, *C* show young passages at *g*, placed at the boundary of the cambium *c* and the soft bast *wb*; *h* the wood; *D* and *E*, at *g*, larger and older passages, lying at the boundary of the bast *b* and the cortical parenchyma (*rp*).

(Fig. 65, *B*, *ss*). These intercellular spaces, which separate whole layers of cells each opening to the outside in its middle by a stoma, are destined to enclose the chlorophyll-containing tissue of these plants. The layer of cells which forms the bottom of the flatly extended intercellular space, after repeated divisions vertically to the surface, sends out protrusions upwards into the cavity; these grow in a similar manner to many filamentous Algæ, divide and branch and form grains of chlorophyll, while the whole of the rest of the tissue of these plants produces no chlorophyll.

(3) The origin of resin and gum passages depends also on the formation of intercellular passages with a peculiar development of the cells which bound them. As I shall recur to other points in this structure, it is sufficient to refer to one example. Fig. 66 shows passages of this kind in the transverse section of young portions of the stem of the ivy. Conditions, such as *B*, *C*, show clearly that the intercellular space arises by the parting of four or five cells, and that these latter, distinguished by their turbid granular contents, increase by division. The formation of the much wider passages, *D*, *E*, is also to be referred to a similar subsequent increase and corresponding growth of the cells which surround the passage. By the growth of the cells which bound the intercellular passage, as well as by the manner of their division, by their contents, and by the circumstance that they excrete a peculiar sap into the passage, a structure of this kind appears as a differentiated part of the tissue, which is sharply marked off from its environment, and has a physiological significance of its own.

Sect. 14. **Forms and Systems of Tissues.**—The whole mass of the cell-tissue which forms the body of a plant may be uniform or not; in the first case the cells are all similar to one another, and their modes of union everywhere uniform. This case is rare in the vegetable kingdom; and it is only the simplest forms that are constructed in this manner. Since in a homogeneous not differentiated tissue all the cells are alike, their union into a whole is physiologically and morphologically of very subordinate importance, because each cell represents the character of the whole tissue; hence it not unfrequently happens in these cases that the cells become actually isolated and continue their life singly; and such individuals are termed Unicellular Plants. Only a little higher are those which consist of an unbranched row of perfectly uniform cells, or of an arrangement of such into a surface or mass. When numerous and densely crowded cells form a mass of tissue, then it is usually the case that different layers of tissue develop differently; the body of the plant consists then of a differentiated tissue, or of different forms of tissue. In general their arrangement is determined by the fact that the whole mass of tissue has a tendency to become definitely bounded on the outside, so that there arises a differentiation of outer layers of tissue from the inner mass. But in the interior of the body enclosed by the epidermal tissues, fresh differentiations arise in the higher plants; string-like arrangements of cells are formed, surrounded by fundamental tissue lying between them and the epidermis; these strings of tissue (vascular, fibrous or fibro-vascular bundles) usually follow in their longitudinal course the direction of the most vigorous growth which immediately precedes their differentiation. Not only the epidermal layer, but also the bundles and the fundamental tissue lying between them, are, however, usually not uniform among themselves; the epidermal tissue itself is often differentiated into layers of different nature; each bundle is also differentiated, but in a different manner and generally in a still higher degree. In this manner arise in the higher plants, in the place

of different layers of tissue, systems of tissue-forms, which may be designated simply as *Systems of Tissue*. We thus usually find an Epidermal System, a Fascicular System, and the system of the Fundamental Tissue between them (Fig. 67). But whenever a differentiation of tissues of this kind arises in a plant, it only takes place subsequently; originally the whole mass consists of a growing portion of the plant (stem, leaf, root), always of a uniform tissue, out of which by diverse development of its layers these tissue-systems have their origin; this tissue of the youngest parts of plants which is not yet differentiated may be termed, in opposition to the others, Primary Tissue[1].

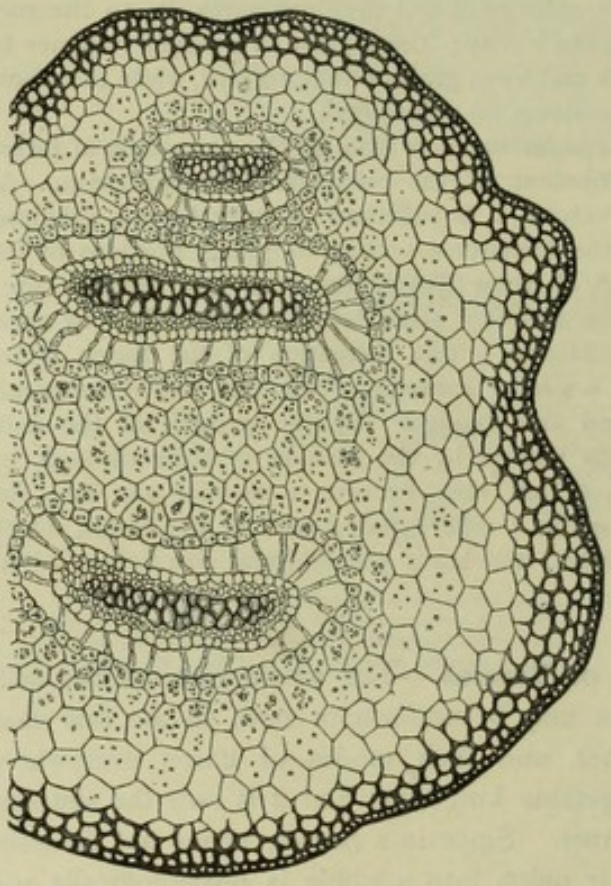


FIG. 67.—Transverse section of the stem of *Selaginella inaqualifolia*. The cell-tissue, consisting of several layers of cells, has dark thick cell-walls; the thinner-walled fundamental tissue envelopes three fibro-vascular bundles, separated from it by large intercellular spaces (*i*) (×800).

(a) Within each tissue-system the cells may be formed and arranged in very different ways; their contents and their cell-wall may be differently developed; in each system they may be capable or incapable of division[2]. If the cells are pointed at the ends, and much longer than they are broad, and at the same time their ends penetrate between one another so that no intercellular spaces occur, then the tissue is termed *Prosenchyma*. If, on the other hand, the cells are arranged in rows, bounding one another with broad surfaces, thin-walled, not much longer than broad, and forming intercellular spaces, they form a *Parenchyma*. The two forms of tissue pass over into one another in many ways, and in the use of the term Parenchyma a painful uncertainty prevails in vegetable anatomy. There are forms of tissue which cannot be included under either of these two terms, if they are made to possess any definite signification; as, *e.g.*, the tissue of Fungi and Lichens, and even of Fucaceæ. In parenchyma as well as in prosenchyma the cells may be thick or thin walled, lignified or not, the contents may be succulent or may consist of air. It would be convenient to generalise the term Sclerenchyma used by Mettenius,

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[1] It may not be superfluous to remark here, in the meantime, that pith and cortex are neither forms nor systems of tissue, but altogether indefinite and undefinable ideas; we speak, *e.g.*, of cortex in Thallophytes in quite a different sense to what we do in Vascular Plants; the cortex of Monocotyledons is something different from that of Conifers and Dicotyledons; in the latter the cortex has quite a different signification in young and in older parts of stems. The same is the case with the pith.

[2] An enumeration of the nomenclature of tissues would here be of no service. In elucidating the facts, as I do partly in the following paragraphs partly in Book II, I shall employ the technical terms as they are required by a consideration of the different objects and relationships. I keep, with a few deviations, to the terms and distinctions proposed by Nägeli (Beiträge zur wiss. Botanik, Heft I, 1858).

and to designate by it cells united in both a parenchymatous and prosenchymatous manner, when they are not only thickened, but also hard. We should then have Sclerenchyma in cork, in fundamental tissue (as the dark strings in the stem of *Pteris aquilina*, or the stone of stone-fruit), and in wood; the indurated cells in the flesh of pears would also come under this name. In one word, by this term would be designated not a tissue-system, but only a physiological property of particular cells of a tissue-system[1]. If the cells of a tissue are all or mostly capable of division, it is a Generating Tissue (Meristem of Nägeli); if they are not it is a Permanent Tissue. The primary tissue of the youngest parts of plants is always a Meristem, and may be distinguished as Primary Meristem. In the older parts of plants portions of the tissue also remain merismatic or become so subsequently; they may be designated Secondary Meristem. At one time this tissue was designated Cambium; but it is convenient to retain this word in its original signification for that merismatic layer in the tissue of older parts of plants by means of which the increase in thickness of Dicotyledons and Conifers is accomplished. The arrangement may produce a simple row or line of cells, in contrast to a cell-surface where the cells form a lamella consisting of a single layer. If the cells are united in all directions, we have a Tissue with dimensions in three directions. When the latter is greatly elongated in one direction, and its growth proceeds especially at one or both ends, and it lies inside another tissue, it is a Fascicular Tissue; the cells of such a tissue are usually elongated in the direction of its length, mostly prosenchymatous, and we then have Prosenchyma bundles. The most important form of these are the *Fibro-vascular Bundles* which are dispersed through the fundamental tissue of the higher Cryptogams and Phanerogams, whose cells are mostly elongated and partly prosenchymatous, and are thus formed into vessels, *i. e.* long rows of lignified cells, the septa of which have been broken through.

(b) The youngest parts of stems, extremities of roots, leaves, and other organs, consist almost entirely of Primary Meristem; as they become more perfectly developed a separation may be recognised into layers of tissue and bundles, which represent the commencement of the tissue-systems; within each system its different forms of tissue become gradually differentiated. When different tissue-systems in a mature condition are in contact, the history of development alone can often determine whether certain layers belong to one or the other system; especially also because similar cell-forms occur in different systems. Thus, for instance, parenchyma and prosenchyma, sclerenchyma and secondary meristem may arise both in the fundamental tissue and in the fibro-vascular bundles; in the layers lying beneath the epidermis it often cannot be determined whether they belong to the epidermal tissue or to the fundamental tissue which bounds it. In the same manner also different forms of glands, vesicular vessels, laticiferous ducts, resin and gum passages, occur in all three systems or in the fundamental tissue and the fibro-vascular bundles. The forms of cells and tissues here named cannot be considered equivalent to these three tissue-systems; they occur rather as constituents of different systems. Nevertheless, on account of their physiological peculiarities, I shall consider them together in a special paragraph, while the other more important forms of tissue will be treated of under the three systems.

Sect. 15. **The Epidermal Tissue**[2].—A differentiation into epidermal tissue and inner fundamental tissue can evidently only arise in plants and parts of plants

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[1] Cf. Otto Buch, Ueber Sclerenchymzellen. Breslau 1870.

[2] By the introduction of the idea of the Epidermal Tissue into general use, as I here employ it, a real want will, I think, be remedied in histology. In any case a series of histological facts, which have hitherto been treated of in a detached manner, will thus be brought under a common and higher point of view.

which consist of a thick mass of tissue. In general the contrast of the two is the plainer the more the part of the plant concerned is exposed to air and light, underground and submerged parts showing it in a smaller degree; in those destined to a longer term of life the formation of epidermis is usually also more perfect. The difference between epidermis and fundamental tissue can only be established by the outer layers of cells, whose morphological character is otherwise the same, becoming distinguished by the thickness and firmness of their cell-walls, and hence usually by being smaller than those which lie deeper inside. In this case a sharp boundary of the two tissues does not usually occur; the distinctions gradually increase the more nearly the cell-layers approach the upper surface. This is usually the case, among Algæ, with the Fucaceæ and larger Florideæ, with many Lichens and the fructification of Fungi; even in the stem of Mosses the formation of epidermis is often indicated only in this manner. A further development of the contrast between epidermal and inner tissue arises when not only a sharp boundary lies between the two, but when an essentially different morphological development also distinguishes the epidermal from the inner tissue. In many Mosses and all Vascular Plants at least one outer layer of cells is to be distinguished in this sense as epidermal structure, and is here termed Epidermis. In true roots and many root-like underground parts of stems, as also in many submerged plants, it is generally only slightly different from the tissue lying beneath; but in most parts of stems and leaves it shows an altogether peculiar development of its cells, giving rise to stomata and hair-formations of the most various kinds. In many leaves and parts of stems, the epidermis, after it has already become recognisable as a tissue of a peculiar kind (during or after the bud-condition of the organs concerned) undergoes cell-division tolerably late, by which it becomes divided into two or more layers. From this epidermis formed of several layers of cells (Pfitzer, *l. c.* p. 53) may be conveniently distinguished as Hypoderma[1] such layers of tissue as lie very commonly beneath the simple, rarely beneath the many-layered epidermis, and perform the physiological function of strengthening the epidermal tissue, without however belonging to it genetically; while they are strikingly distinct from the deeper lying fundamental tissue, although, according to their development, they are a part of it. This hypoderma consists chiefly of layers or bundles of thick-walled sclerenchyma-cells, sometimes even of bast-like fibres. In Phanerogams, especially Dicotyledons, the hypoderma is mostly developed as Collenchyma, the cell-walls of which are strongly thickened and in a high degree capable of swelling at the longitudinal angles where three or four of them meet (Fig. 21, *B*, p. 24).

In the parts of plants which live long and are endowed with vigorous growth in thickness, the epidermal system attains a further development in the production of *Cork;* this originates by subsequent cell-division in the epidermis itself or in the subjacent layers of tissue, occurring often very late, and by the transformation into cork of the newly-formed cells. The formation of cork is very frequently continuous, or is renewed with interruption; and when this occurs uniformly over the whole

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[1] I prefer the word Hypoderma proposed by Kraus and adopted by Pfitzer to the expression previously used by me 'sub-epidermal layers.' Cf. besides sect. 17 (c).

circumference, there arises a stratified cork-envelope, the Periderm, replacing the epidermis which is in the meantime generally destroyed, and surpassing it in efficiency as a means of protection. But not unfrequently the formation of cork penetrates much deeper; lamellæ of cork arise deep within the stem as it increases in thickness; parts of the fundamental tissue and of the fibro-vascular bundles, or of the masses of tissue which afterwards proceed from them, become, as it were, cut out by lamellæ of cork. Since everything which lies outside such a structure dies and dries up, a peripheral layer of dried masses of tissue collects, which are very different in form and origin; this structure, abundant in pines and in many dicotyledonous trees, is the *Bark*, the most complicated epidermal structure in the vegetable kingdom.

(a) *The Formation of the Epidermis of Thallophytes* is chiefly confined to this,—that the cells of the fundamental tissue become smaller and firmer the nearer they are to the surface; the cell-walls very generally become darker, as in the outer layers of

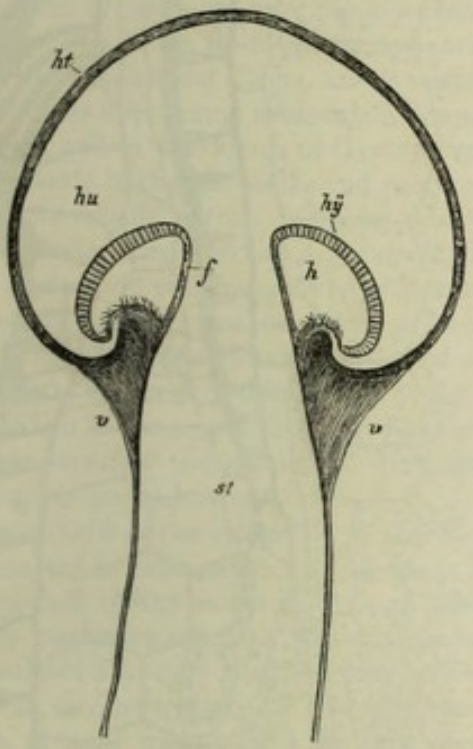

FIG. 68.—Receptacle of *Boletus flavidus* in longitudinal section slightly magnified; *st* stipes: *hu* pileus, *hy* hymenium; *v* velum; *h* cavity beneath the hymenium; *f* prolongation of the hymenial layer on the stipes; *ht* the separable yellow skin of the pileus.

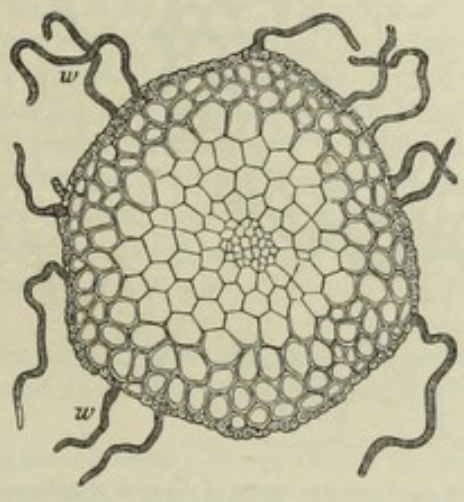

FIG. 69.—Transverse section of the stem of *Bryum roseum* (×90): *w* root-hairs formed by the development of single cells of the outermost cell-layer.

the cortical tissue of many Lichens, the outer layers of the peridia in Gastromycetes and Pyrenomycetes; in the pileus of many Hymenomycetes, the epidermal layer may be detached in large pieces (Fig. 68). From the small development of the difference between cortex and pith in these Thallophytes, it may appear doubtful whether the outer layer should be termed bark or epidermis; when the cortical tissue is thicker, the epidermis can usually be distinguished from it. With Thallophytes, as with higher plants, the outermost layer of cells displays a tendency to the formation of hairs.

The Muscineæ (Hepaticæ, Sphagnum, Mosses) exhibit a great variety with reference to the formation of epidermis. While in many other Hepaticæ we have scarcely any indications of one, in the group of Marchantieæ (Fig. 65) an epidermis perfectly developed with stomata suddenly makes its appearance. In the Mosses the formation of epidermis on the leafy stem is limited to this, that the cells towards the surface become narrower and thicker-walled, while their walls assume a deeper red colour; the outermost layer often produces numerous long root-hairs (Fig. 69). In the Bog-mosses (Sphagnum), on the

other hand, one outermost layer of cells of the stem, or 2–4 such, assume an entirely different character. These cells (Fig. 70, *e*) have thin coloured walls, they are much broader than those of the inner tissue; the walls sometimes show thin thickening-bands running in a spiral manner, and open externally by large orifices, being also in communication with one another by similar orifices (*l*). In the fully developed condition they contain only air or water, which rises in them as in an actual capillary apparatus. Within this epidermal tissue the stem is similar to that of Mosses; the cells become towards the surface gradually narrower, thicker-walled, and of a darker colour. A similar epidermal layer, and with similar hygroscopic properties, occurs in the aërial roots of Orchids and of some Aroideæ.

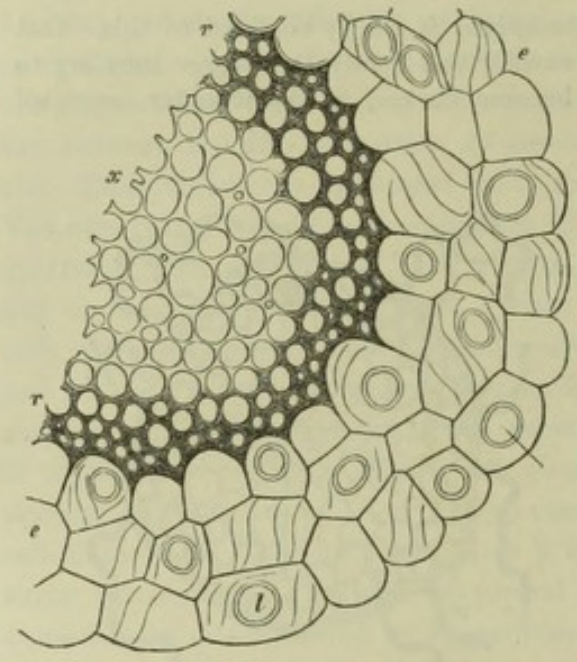

FIG. 70.—Transverse section of the stem of *Sphagnum cymbifolium* (×900); *x* inner cells with colourless soft walls; *r* cortical cells, becoming gradually narrower and thicker-walled towards the surface; *e e* the epidermal layer; *l* orifices through which the opposite cells communicate with one another.

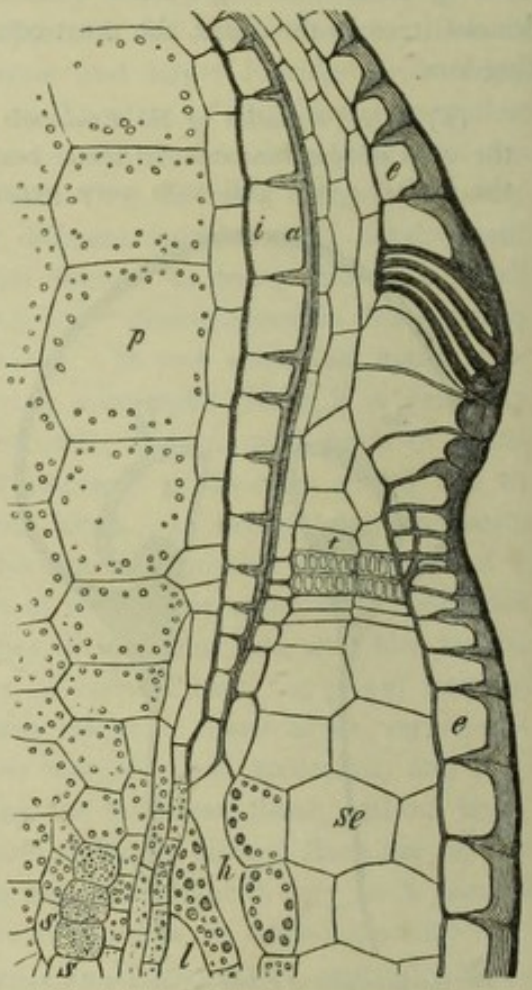

FIG. 71.—Piece of a radial transverse section through the sporangium of *Funaria hygrometrica* (×300); *e* epidermis; the thick black streak at its circumference is the cuticle. (For further explanation of the fig. see Book II.)

As in Mosses the formation of tissue attains especially a greater perfection in the sporangia, this is also the case in reference to the formation of epidermis; the variously differentiated internal tissue of the capsule is surrounded by a highly developed true epidermis (sometimes provided with stomata) (Fig. 71).

(b) *The Epidermis*[1]. In Vascular Plants the epidermal tissue consists usually only of a single superficial layer of cells, the Epidermis. In its origin it always consists of a single layer; but it sometimes becomes split into two or more layers by divisions

[1] H. von Mohl, Vermischte Schriften bot. Inhalts, p. 260. Tübingen 1845.—F. Cohn, De Cuticula. Vratislaviæ 1850.—Leitgeb, Denkschriften der Wiener Akad. XXIV, p. 253, 1865.—Nicolai, Schriften der phys.-ökonom. Gesells. Königsberg, p. 73, 1865.—Thomas, Jahrb. für wiss. Bot. IV, p. 33.—Kraus, ditto, IV, p. 305 and V, p. 83.—Pfitzer, ditto, VII, p. 561 and VIII, p. 17.—De Bary, Bot. Zeitg. nos. 9–11 and 34–37, 1871.

parallel to the surface which originate rather late during or after the bud-condition of the organs in question. In such cases the outermost may be distinguished, as the epidermis proper, from those which lie beneath, or the thickening-layers; these latter generally consist of large thin-walled cells with contents as clear as water, for which reason Pfitzer terms them Aqueous Tissue. Epidermis of this kind, consisting of several layers, occurs in the leaves of most species of Ficus, in the stems and leaves of many Piperaceæ, and in the leaves of Begonia. In the roots also of some species of Crinum, the epidermis, at first simple, splits into several layers; but this is much more striking in the aërial roots of Orchids and Aroideæ, where these cell-layers afterwards lose their succulent contents and surround the substance of the root as an air-containing root-envelope (velamen). The Hypoderma is distinct in its development from the strengthening-layers which result by division from the originally simple epidermal layer, since it arises from the layers of the fundamental tissue covered by the true and simple epidermis. The cells of the hypoderma may also become developed as aqueous tissue like that mentioned above, and often to an enormous thickness; this occurs in many Bromeliaceæ and some species of Tradescantia. The hypoderma more often exists in the form of layers of very thick-walled often sclerenchymatous cells, whose origin has been proved to be from the fundamental tissue, not from the epidermis, at least in the case of Ephedra and Elegia, and is very probably so in other cases. While this sclerenchymatous hypoderma is especially frequent in Vascular Cryptogams (*e. g.* Equisetum and Ferns), and in the leaves of Gymnosperms, a third form, the Collenchyma, occurs very abundantly in the leaf-stalks and succulent stems of Angiosperms, especially of Dicotyledons, its usually narrow but long cells being strikingly distinguished by the thickening-masses often deposited to a great extent in internally projecting longitudinal ridges at the angles, and swelling greatly with water or more powerful reagents (Fig. 21, *B*, p. 24). That the collenchyma originates from the fundamental tissue, and thus not from the epidermis, has been actually observed only in *Euonymus latifolius*, Peperomia, Nerium, and Ilex, but is probable also in other cases.

When in the sequel the term Epidermis is used without further remark, the ordinary simple layer, or the outermost when the epidermal tissue consists of several layers, is always to be understood.

The cells of the epidermis, as also those of the strengthening-layers and of the hypoderma, are in close contact on all sides; intercellular spaces are formed only between the guard-cells of the stomata, through which the intercellular spaces of the fundamental tissue communicate with the surrounding air. This connexion without interstices is sometimes the only distinguishing mark of the epidermis, as in the submerged Hydrilleæ, Ceratophyllum, &c.; in other cases the formation of hairs helps to distinguish it, as in most roots, where the cells of the epidermis are otherwise similar to those of the fundamental tissue in contents and in the nature of their wall. But usually in the stem and foliar organs the epidermis is destitute of chlorophyll, starch, and especially of granular contents, while in Ferns and in the water-plants mentioned above, as well as in other cases, the epidermis-cells contain grains of chlorophyll. Not unfrequently the otherwise colourless cell-sap is tinged by a red substance.

The form of the epidermis-cells in organs the development of which is chiefly in length, as roots, long internodes, and leaves of Monocotyledons, is usually elongated longitudinally; in leaves with a broad surface it is mostly broadly tabular; in both cases the side-walls are often curved in an undulating manner, so that the adjoining cells project into one another.

The outermost lamella of the epidermis-cells is always cuticularised, and usually to the extent that cellulose is either not at all, or only with difficulty, to be detected in it. This true cuticle extends uninterruptedly over the boundaries of the cells, and is strongly contrasted with the subjacent layers of the epidermis. With preparations of iodine, with or without addition of sulphuric acid, the cuticle is coloured yellow or yellow-brown; it is insoluble in concentrated sulphuric acid, but soluble in boiling caustic

potash. In submerged organs and roots it is very thin, difficult to be seen immediately, but rendered visible by iodine and sulphuric acid. The true cuticle is much thicker in aërial stems and leaves; it may be obtained in them even in large lamellæ by decay or solution of the subjacent cells in concentrated sulphuric acid. In many cases, and especially in stout leaves and internodes, the outer wall of the epidermis-cells lying beneath the cuticle is strongly often enormously thickened; while the inner-walls remain thin, the lateral walls are usually strongly thickened outwardly, becoming inwardly suddenly thinned. The thick portions of the wall are usually differentiated into at least two shells; — an inner thin shell, immediately surrounding the cell-cavity, shows the reactions of pure cellulose, while the epidermal layers lying between it and the cuticle are more or less cuticularised, and the more so the nearer they lie to the cuticle. Not unfrequently these layers of cuticle extend downwards in the thick part of the side-walls, in which case the middle lamella sometimes behaves like the true cuticle, with which it is in contact on the outside. Like the isolated cells of the cuticle (pollen-grains, spores), the epidermis has also a tendency to form projecting lumps, knots, ridges, &c., but they almost always remain very insignificant, and are best seen on a superficial view; as, for example, in many delicate petals (cf. sect. 4, (e)).

According to the recent researches of De Bary, particles of wax are deposited in the substance of the cuticular layers of the epidermis which cannot be seen on section, but separate in the form of drops when warmed to about 100° C. This deposit of wax (often combined with resin) is one of the causes which protect the aërial parts of plants from becoming moistened with water. But very frequently the wax extends in an unexplained manner over the cuticle, and becomes deposited there in different forms, forming the so-called bloom on fruits and some leaves, or as a continuous shining coating, which is reformed on young organs after being wiped off, and in ripe fruits of *Benincasa cerifera* (the wax-cucumber) appears again long after maturity. De Bary distinguishes four principal forms of this wax-coating. The bloom or gloss which is easily wiped off consists of small particles of two forms:—(1) of quantities of delicate minute rods or needles, *e. g.* the white-dusted Eucalypti, Acaciæ, many Grasses, &c.; or of granules collected into several layers, as in *Kleinia ficoides* and *Ricinus communis;* these are aggregated wax-coatings. (2) Simple granular coatings consist of grains isolated or touching one another in one layer; this is the most common form, *e. g.* in *Iris pallida*, *Allium Cepa*, *Brassica oleracea*, &c. (3) Coatings of minute rods consisting of thin, long, rod-shaped particles, bent above or even curl-shaped, and standing perpendicularly upon the cuticle, *e. g. Heliconia farinosa* and other Musaceæ, Cannaceæ, Saccharum, *Benincasa cerifera*, leaves of *Cotyledon orbicularis*. (4) Membrane-like layers of wax or incrustations; (a) as a gritty glazing in Sempervivum, *Euphorbia Caput-Medusæ*, *Thuja occidentalis;* (b) as thin scales, in *Cereus alatus*, Opuntia, *Portulaca oleracea*, *Taxus baccata;* (c) as thick connected incrustations of wax, which sometimes permit a finer internal structure to be recognised, similar to the striation and stratification of the cell-wall: *Euphorbia canariensis*, fruits of species of Myrica, stems of *Panicum turgidum*. On the stem of the Peruvian wax-palms, especially of *Ceroxylon andicola*, these incrustations attain a thickness of 5 mm.; those on the stem of *Chamædorea Schiedeana* are thinner, but of similar structure. According to Wiesner (Bot. Zeitg. p. 771, 1871), these flakes of wax consist of doubly refractive four-sided prisms standing perpendicularly close to one another.

Hairs[1] are products of the epidermis; they originate from the growth of single epidermis-cells, and are present in most plants in large numbers; when they are

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[1] A. Weiss, Die Pflanzenhaare, in vols. IV and V of the Bot. Untersuchungen aus dem phys. Laborat. by Karsten, 1867.—J. Hanstein, Bot. Zeitg. p. 697 et seq., 1868.—Rauter, Zur Entwickelungsgeschichte einiger Trichomgebilde. Wien 1871. [See also J. B. Martinet: Organes de sécrétion des végétaux. Ann. des Sci. Nat. Fifth series, vol. XIV, 1871.]

wanting in any part of a plant, it is termed glabrous. Their form is subject to extraordinary variation. The first indication of the formation of hairs occurs in the papillose protuberances of the epidermis of many petals, to which their velvety appearance is due. To the simplest forms belong also the root-hairs which grow from the epidermis of true roots or underground stems (*Pteris aquilina*, Equisetum, &c.); they are thin-walled bag-like protuberances of the epidermis-cells which lengthen by growth at the apex, or only branch exceptionally (as sometimes in *Brassica Napus*). In Vascular Cryptogams their wall readily acquires a brown-red colour; their length of life is usually short, and when they die all trace of them disappears. In a similar manner the woolly hairs behave which appear early on the leaves and internodes of vascular plants, while still in the bud, especially Dicotyledons. On the unfolding of these organs they commonly fall off and disappear, as in the horse-chestnut, Rhododendron, and *Aralia papyrifera*, where they form a felt easily wiped off from the freshly developed leaves; in other cases they remain as a woolly coating, especially on the under-sides of leaves. In prickles the wall is mostly thicker, silicified, and hard; they are shorter than the woolly hairs, pointed upwards, and a septum separates the prominence from the mother-cell. When two or more points endowed with a greater power of growth in their surface and apex arise on the free outer wall of unicellular hairs, branched forms result with continuous cavity. The papillose bulging of the epidermis-cells may become separated by a septum; the hair then consists of a basal cell fixed in the epidermis and of a free hair-cell (as in *Aneimia fraxinifolia*); but the separated papilla may also become segmented by the formation of more or less numerous septa, when the hair grows considerably in length, and thus arise segmented hairs (as *e.g.* on the filaments of Tradescantia). Sometimes the segments form lateral shoots; and thus arise tree-like branched structures with whorled or alternate branches (*e.g. Verbascum Thapsus*, *Nicandra physaloides*). If longitudinal divisions occur in the segment-cells of the hair, or if the hair continues to grow by an apical cell which forms segments on two sides, flatly expanded hairs are the result. To this form belong, for example, the so-called paleæ of Ferns which sometimes entirely cover the younger leaves. Finally the divisions in the young hair may be so arranged that it presents at length a tissue, which on its part may again assume different forms, *e.g.* the pappus-like hairs of *Hieracium aurantiacum* and *Azalea indica*, the capitate hairs of Korrea and *Ribes sanguineum*.

Very commonly the terminal cell of a segmented or the end of a solid hair (*i.e.* of one consisting of a mass of tissue), swells in a globular manner, and then usually forms a multicellular gland, while the cells of the head produce peculiar secretions. (On these Glandular Hairs cf. sect. 17, (b).) Not unfrequently the papilla which projects above the epidermis and is separated by a septum becomes divided by vertical and radial walls, expanding in a disc-like manner, so that the head consists of a radially arranged disc of numerous cells; thus arise the peltate hairs, *e.g.* of Eleagnus, Hippuris, and Pinguicula. Tufts of hairs arise when the mother-cell of the hair which belongs to the epidermis breaks up early into several cells lying close to one another; each of which then grows independently into a hair, as is shown in Fig. 72, which is completed by Fig. 44, p. 43.

Not unfrequently a luxuriant growth of the parenchyma takes place beneath the hair; and this is imitated also by the epidermis; the hair itself is then borne on a peg-shaped prominence or protuberance of the leaf or stem, and is often deeply implanted into it in its lower part; as, for instance, in the prickles (stinging hairs) of the stinging-nettle. Thus also the prickles (climbing hairs) on the six projecting angles of the stem of the hop grow into a large basal protuberant mass of tissue, while the hair-cell grows in opposite directions into two sharp points. Such double-pointed unicellular hairs occur also on the under-side of the leaf of *Malpighia urens*; they are 5–6 mm. long, fusiform, very thick-walled, and grow into the epidermis by their central part (without protuberance). In this case they easily become detached, and remain sticking in the

skin of the hand which touches the leaf. (For further details on the Morphology of Hairs cf. sect. 22.)

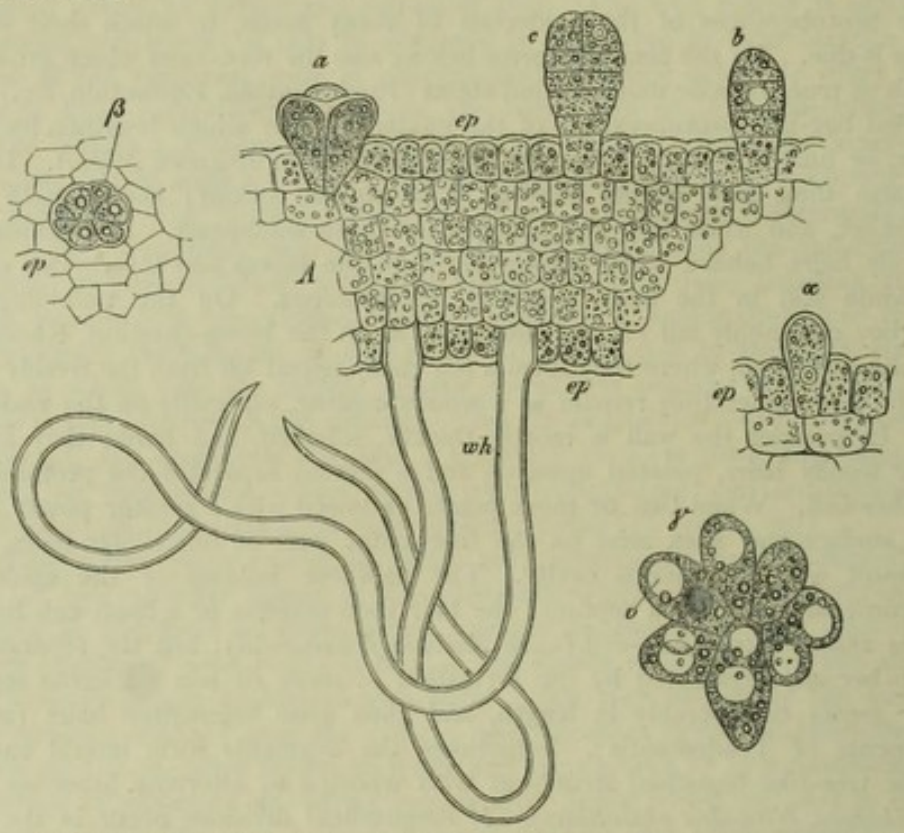
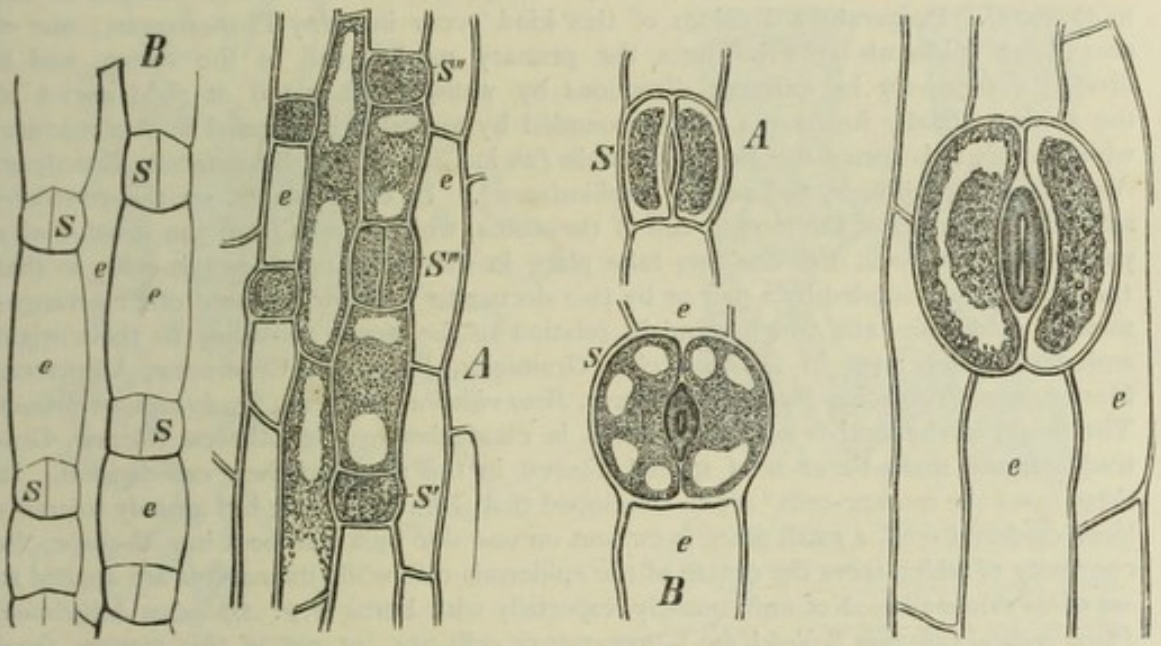


FIG. 72.—Development of the hairs on the calyx of a flower-bud of *Althaea rosea* (×300); *A wh* woolly-hairs of the inner side; *b* and *c* glandular hairs in different stages of development; at α (to the right) rudiment of a glandular hair; *ep* always signifies the (still young) epidermis. The figures α in *A*, β (to the left) and γ (to the right below) show the first stages of development of the stellate hairs (or rather tufts of hairs), the subsequent condition of which may be compared in Fig. 44 (p. 43); at *A a* is the hair in longitudinal section; β and γ show the appearance seen from above; the cells are rich in protoplasm; the formation of vacuoli (v) in the protoplasm is beginning in γ.

The Stomata[1] are always absent from the epidermis of true roots; on the other hand they are usually present on underground axial organs and leaves; even on submerged parts they are occasionally found (Borodin, *l. c.*); but they are formed in the largest numbers on the aërial internodes and leaves, but are not altogether absent from the petals and carpels; they are even formed in the interior of the cavity of the ovary (*e.g.* in Ricinus). They are most abundant where an active interchange of gases takes place between the plant and the surrounding air; for, considered physiologically, they are nothing more than the mouths of the intercellular spaces of the inner tissue which open in places externally between the epidermis-cells; this is however always preceded by a peculiar development in a young epidermis-cell. Since the stomata do not arise till rather late, that is during or after the expansion of the internodes and leaves, their arrangement is partially dependent on the already elongated form of the epidermis-cells; if these are greatly elongated in one direction and arranged in rows (as in Equisetum and the stem and leaves of many Monocotyledons, and Pinus), the stomata also appear arranged in longitudinal rows (the cleft lying in the direction of the axis of growth, the guard-cells right and left); if the epidermis-cells are irregular on a superficial view, curved, &c., the position of the stomata is more undefined and

[1] H. von Mohl, Verm. Schriften bot. Inhalts, pp. 245, 252. Tübingen 1845.—Ditto, Bot. Zeitg. p. 701, 1856.—A. Weiss, Jahrb. für wiss. Bot. IV, p. 125, 1865.—Czech, Bot. Zeitg. p. 101, 1865.—Strasburger, Jahrb. für wiss. Bot. V, p. 297, 1866.—E. Pfitzer, ditto, VII, p. 532, 1870.—J. Rauter, Mittheil. der naturwiss. Vereins für Steiermark, vol. II, Heft 2, 1870.—Borodin, Bot. Zeitg. p. 841, 1870.—Hildebrand, ditto, p. 1.—Ditto, Einige Beobachtungen aus dem Gebiete der Pflanzenanatomie. Bonn 1861.

apparently irregular. The number of the stomata is generally extraordinarily great in the epidermis of organs containing chlorophyll; A. Weiss counted on one square mm. in 54 species examined 1–100 stomata, in 38 species 100–200, in 39 species 200–300, in 9 species 400–500, and in 3 species 600–700 stomata. The origin of stomata is always the result of the formation of a mother-cell, first of all by division



FIGS. 73-75.—Formation of the stomata of the leaf of *Hyacinthus orientalis*, seen from the surface (×800); the preparations were made from leaves which were at first 3-4 cm. long; they were obtained simply by removing the epidermis; *e* always signifies the epidermis-cells, *S* the stoma. The order of development is Fig. 73, *A*, *S'*, *S''*, *S'''*; then Fig. 74, *A*, *B*, and finally Fig. 75. In Fig. 73, *B*, a piece of epidermis is represented with the mother-cells of the stomata already divided, after extraction of the protoplasm by solution of potash and acetic acid. Preparations of this kind show most distinctly that the partition-wall never grows from without inwards; it is either entirely absent or present along the whole surface. Fig. 75 shows the guard-cells after treatment with potassium odide; the protoplasm has contracted; the stoma is not yet perfectly developed.

of a young epidermis-cell, which is sometimes preceded by several preparatory divisions in it or in the adjoining epidermis-cells; and this mother-cell becomes more and more rounded off, and the guard-cells of the stoma are produced from it by division. The variety of these processes up to the point when the opening itself appears, can hardly be explained in a few words; I prefer therefore to describe some examples more minutely. One of the simplest is afforded by the development of the stomata on the leaf of *Hyacinthus orientalis*, which has already been depicted in transverse section in Figs. 61–64 (p. 75); these the reader must compare with Figs. 73–75, which represent the process seen from the surface. The preparation for the formation of the stoma is here very simple:—a nearly cubical piece of a long epidermis-cell (Fig. 73, *A*, *S*, *S'*) is separated by a septum, and this is the mother-cell of the stoma. It is divided by a longitudinal wall (*i. e.* by one lying in the direction of the axis of growth of the leaf, and standing at right angles to its surface) into two equal cells, which round themselves off as they grow. The manner in which the opening follows the partition-wall has already been described in Figs. 61–64, and can now easily be understood with help of the superficial view in Fig. 74. In *Equisetum limosum* a similar appearance to that represented in Fig. 73 shows itself immediately after the first formation of the mother-cells of the stomata; but the mother-cell undergoes in these cases three divisions, first one obliquely to the right, then one obliquely to the left; finally the *middle* one of the cells which originate in this manner is bisected by a wall standing at right angles to the surface. Four cells thus arise *in one plane*, of which the two outer ones grow more rapidly, while the inner are forced downwards and come to lie beneath them; the stoma then appears, when perfect, as if it had been formed according to the Hyacinthus type, in which each guard-cell has been again

divided into an upper and a lower cell. But, according to Strasburger, this is not the case, the two pairs of guard-cells lie originally in one plane, and, strictly speaking, it is only the middle cell,—which is divided by a perpendicular wall, and the splitting of which forms the cleft, — that is to be considered as the mother-cell of the stoma; the two oblique divisions by which the two lateral cells are formed that afterwards lie uppermost, must be regarded merely as a preparation for the formation of the mother-cell. Preparatory divisions of this kind occur in many Phanerogams; one of the young epidermis-cells becomes the primary mother-cell of the stoma, and is divided successively in different directions by walls, which stand at right angles to the surface; finally we have a cell surrounded by several cells formed in this manner, which afterwards forms the two guard-cells (as in Crassulaceæ, Begoniaceæ, Cruciferæ, Violarieæ, Asperifolieæ, Solanaceæ, Papilionaceæ). In other plants, on the contrary, after the formation of the mother-cell of the stoma, which results from the division of a young epidermis-cell, divisions also take place in the adjoining epidermis-cells, so that the stoma is surrounded by a pair or by two decussate pairs, or by some other arrangement of epidermis-cells, which stand in relation to the stoma according to their origin and development; (as in *Aloe socotrina*, Gramineæ, Juncaceæ, Cyperaceæ, Alismaceæ, Marantaceæ, Proteaceæ, *Pothos crassinervia*, *Ficus elastica*, Coniferæ, *Tradescantia zebrina*). The origin of the mother-cell of the stoma in Plantaginaceæ, Oenothereæ, Sileneæ, Centradenia, and many Ferns is of special interest in the mode of their cell-division. In these cases the mother-cells[1] are so developed that from the young but already tolerably large epidermis-cell, a small piece is cut out on one side by a wall bent in a U-shape, the convexity of which faces the centre of the epidermis-cell, while its margins are applied to *one* of its side-walls. Not unfrequently, especially with Ferns (*e.g. Asplenium bulbiferum*, *Pteris cretica*, *Cibotium Schiedei*, &c.), preparatory cells are cut out in this manner from the epidermis-cell before the period of the formation of the stoma-cell, out of which moreover the guard-cells are formed by simple longitudinal division.

In consequence of the U-shape of the division-wall which separates the mother-cell of the stoma from the epidermis-cell, the former is half, or more than half, enclosed by the latter, when the epidermis is looked at from above. In some Ferns (and Sileneæ) the wall of the mother-cell of the stoma is from the very commencement so strongly curved that it touches one side of the upper epidermis-cell only in one narrow band; in *Aneimia villosa* it touches it only at one point, the curved partition-wall as seen from above appearing annular. In *Aneimia densa* and *A. fraxinifolia* the side-wall of the upper epidermis-cell does not anywhere touch the wall of the mother-cell of the stoma[2]. At its commencement this cell has the form of a hollow cylinder, or, more exactly, of a truncated cone, the bases of which are portions of the upper and lower wall of the upper epidermis-cell; out of the latter a cell is thus cut out like a piece out of a cork by a corkborer; the piece thus cut out is the mother-cell of the stoma, and thus arises the remarkable arrangement represented in Fig. 76, where, as may be seen, the two guard-cells are enclosed by a single annular epidermis-cell. Similar, but more complicated, are, according to Rauter, the arrangements in *Nipholus Lingua*.

By further growth of the guard-cells and of the epidermis-cells which surround them, different relative positions of the former to the surface may be brought about; the guard-cells may, when mature, lie in one plane with those of the epidermis, or may be deeply pressed down and apparently belong to a deeper layer of cells; sometimes they are on the contrary elevated above the surface of the epidermis.

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[1] Strasburger calls them 'special mother-cells.' I think it, however, better entirely to abandon this expression, the more so as its first introduction in the formation of pollen depended on an obsolete view of the formation of the cell-wall (compare our description, pp. 32, 33).

[2] Strasburger, Jahrb. für wiss. Bot. VII, p. 393.

The stomata of Marchantia may shortly be mentioned here in connexion with what has already been said on Fig. 65. After the formation of the air-cavities which are filled with outgrowths containing chlorophyll, one cell of the epidermis lying above the

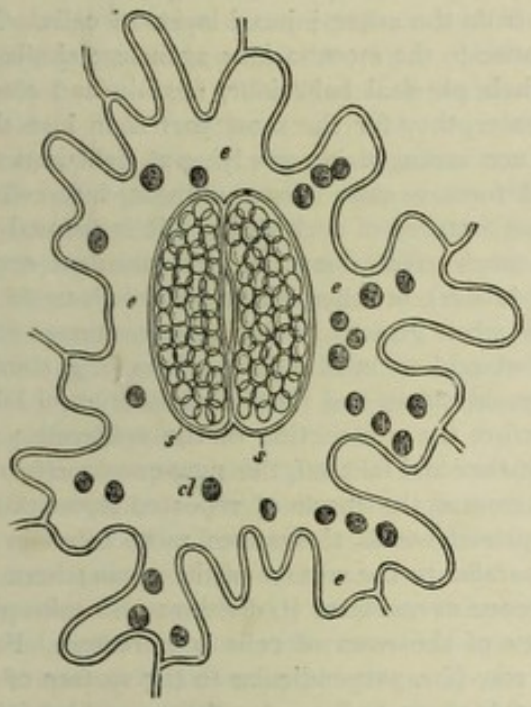

FIG. 76.—Superficial view of the stoma of *Anemia fraxinifolia* with the epidermis-cells surrounding it; *e* epidermis, *ss* guard-cells.

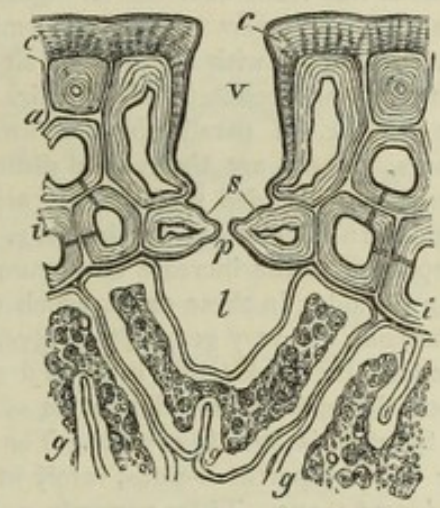

FIG. 77.—Transverse section through the leaf of *Pinus Pinaster* (×800); *s* guard-cells of the stoma; *p* its pore; *v* entrance; *l* air-cavity; *c* cuticularised layers of the epidermis; *a* middle lamella, *i* inner thickening layers of the cells beneath the epidermis; *g* parenchyma of the leaf containing chlorophyll.

centre is divided by several bipartitions into four, six (Marchantia, Fegatella) or several (Rebouillia) cells, which are arranged radially about a point where their walls unite; here the cells separate from one another, and the pore (*po*) originates surrounded by four, six, or more guard-cells (Fig. 78, *B* and *C*, *sl*). Each of these cells is finally divided

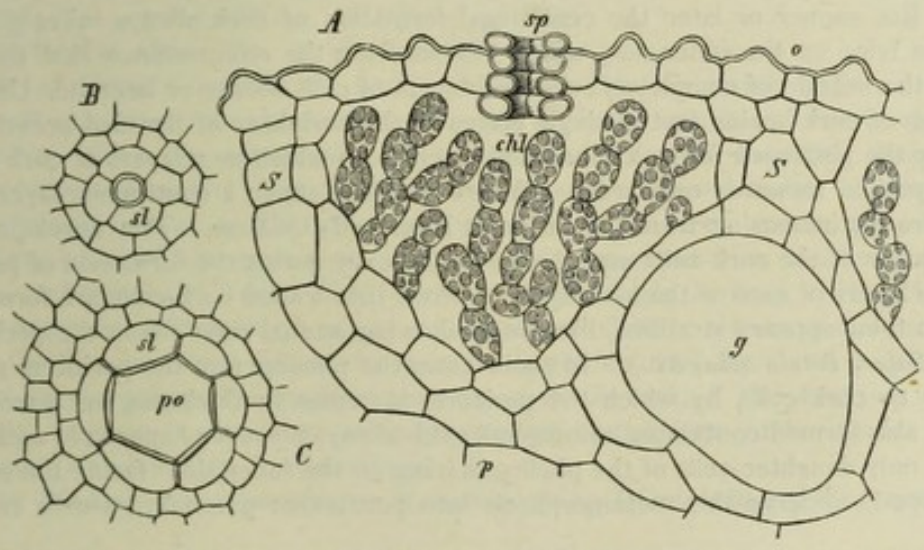

FIG. 78.—*Marchantia polymorpha*. Part of a young receptacle; *A* vertical section, *o* epidermis, *S* partition-wall between the air-cavities with their chlorophyll-cells *chl*; *g* large parenchyma-cell; *sp* stoma; *B* and *C* young stomata seen from above (×550).

by walls parallel to the epidermis-cell into 4–8 cells lying one above another, and the stoma becomes a channel surrounded by 4–8 or more rows of cells.

(c) *Cork, and Epidermal Formations produced by it*[1] (Periderm, Lenticels, Bark). When succulent organs of the higher plants, no longer in the bud-condition, are injured, the wound generally becomes closed up by cork-tissue; *i. e.* new cells arise near the wounded surface by repeated division of those which are yet sound, and these, forming a firm skin, separate the inner living tissue from the outer injured layers of cells. The walls of this tissue offer the strongest resistance to the most various agencies; similar to the cuticular layers of the epidermis in their physical behaviour, flexible and elastic, permeable only with difficulty by air and water, they for the most part soon lose their contents and become filled with air. They are arranged in rows lying at right angles to the surface, of parallelopipedal form, and form a close tissue without intercellular spaces. These are the general distinguishing features of cork-tissue. It is formed not merely on wounded surfaces, but arises in much greater mass where succulent organs require an effectual protection (*e. g.* potato-tubers), or where the epidermis is unable to keep up with the increase of circumference when growth in thickness continues for a long period. In these cases, which occur but seldom in Monocotyledons (*e. g.* stem of Dracæna), but very generally in several-year-old stems and roots of Conifers and Dicotyledons, the cork-tissue is formed even before the destruction of the epidermis; and when this splits under the action of the weather and falls off, the new envelope formed by the cork is already present. The cork-tissue is the result of repeated bipartition of the cells by partition-walls, rarely in the epidermis-cells themselves, more often in the subjacent tissue. These partition-walls lie parallel to the surface of the organ; here and there, where the increase of the circumference necessitates it, divisions also take place in a vertical direction, by which the number of the rows of cells is increased. From the two newly formed cells of each radial row (*i. e.* perpendicular to the surface of the organ) one remains thin-walled and rich in protoplasm, and in a condition capable of division; the other becomes transformed into a permanent cork-cell. Thus arises usually parallel to the surface of the organ a layer of cells capable of division, which continues to form new cork-cells, the *Cork-cambium* or layer of Phellogen. In general this is the innermost layer of the whole cork-tissue, so that the production of cork advances outwardly, and new layers of cork are constantly formed out of the phellogen on the inner surface of those already in existence. But, according to Sanio, it also happens *at the commencement* of the formation of cork that the formation of permanent cells proceeds centripetally, or an alternation of centripetal and centrifugal cell-formation takes place in the *young* cork-tissue. But sooner or later the centrifugal formation of cork always takes place with phellogen lying on the inner side, which follows from the circumstance that the tissues lying on the outside of completely suberised layers of cells sooner or later die. Usually the formation of cork begins first at single places of the periphery of lignified branches; but gradually the phellogen forms a connected layer, from which new layers of cork are continually pushed forwards outwardly. When in this manner a continuous layer of cork arises, steadily increasing from the inside, it is termed *Periderm*. The development and configuration of the cork-cells may change periodically during the formation of periderm; alternate layers of narrow thick-walled and broad thin-walled cork-cells are formed; the periderm then appears stratified, like wood showing annual rings (as in the periderm of *Quercus Suber*, *Betula alba*, &c.). In some cases the phellogen of the periderm gives rise not only to cork-cells, by which the periderm increases in thickness, but parenchyma-cells are also formed containing chlorophyll; this always however happens in such a manner that only daughter-cells of the phellogen lying on the inner side (facing the substance of the wood) undergo this metamorphosis into permanent parenchyma-cells containing

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[1] H. von Mohl, Vermischte Schriften bot. Inhalts, pp. 221-233. Tübingen 1845.—J. Hanstein, Untersuch. über den Bau u. die Entwickelung der Baumrinde. Berlin 1853.—Sanio, Jahrb. für wiss. Bot. II, p. 39.—Merklin, Mélanges biol. du Bulletin de l'Acad. Imp. des sciences de St. Pétersbourg, vol. IV, Feb. 26, 1864.

chlorophyll. In this manner the green cortical tissue of some dicotyledonous plants becomes thickened by the layers of tissue proceeding from the phellogen, which Sanio terms the suberous cortical layer (Phelloderm). This occurs, for example, in two year or older branches of *Salix purpurea* and *S. alba*, the beech, &c. In such cases the phellogen lies between the periderm and the phelloderm, the outer of its daughter-cells producing cork-cells, the inner phelloderm (Fig. 79). The layers of periderm which first undergo conversion into cork sometimes bear a very close resemblance to true epidermis, as, for instance, in first years' branches (August) of *Pinus sylvestris*, where, while the epidermis still remains, the cork-cambium is formed in the cortical parenchyma, and at first presents the appearance as if a second epidermis were formed with cells greatly thickened on the outside.

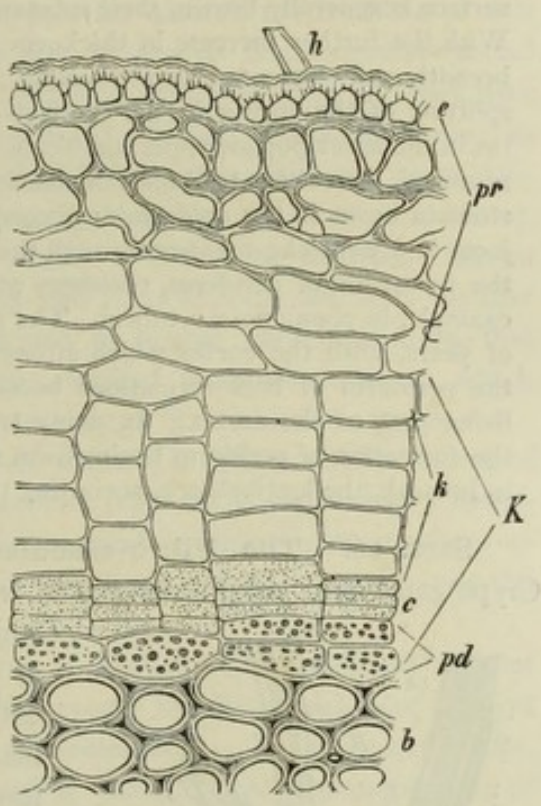

FIG. 79.—Formation of cork in a one-year old branch o *Ribes nigrum*; part of a transverse section; *e* epidermis, *h* hair, *b* bast-cells, *pr* cortical parenchyma distorted by the increase in thickness of the branch; *K* the total product of the phellogen *c*; *k* the cork-cells arranged radially in rows formed from *c* in centrifugal order, *pd* phelloderm (parenchyma containing chlorophyll formed from *c* in centripetal direction) (×550).

As the epidermis is at first replaced by the periderm, so the periderm is afterwards replaced by the formation of bark when the increase in thickness continues long and vigorous. In larger woody plants, as oaks and poplars, the surface of one-year-old boughs is covered with epidermis, that of several-year-old boughs with periderm, that of the older branches and of the stem with bark[1]. The formation of bark depends on the repeated production of new lamellæ of phellogen in the succulent cortical tissues of Conifers and Dicotyledons which continue to grow from within outwards. Layers of cells which can extend themselves through the most different tissues of the cortex, become changed into cork-cambium, which becomes torpid after the production of thicker or thinner lamellæ of cork, *i. e.* ceases to be active. These lamellæ of cork cut out, so to speak, from the cortex, scaly or annular pieces of the surface; everything which lies outside them becomes dried up; and since this process is constantly repeated on the outside of the stem, and the new lamellæ of cork continually intrench further on the growing cortical tissue, a layer, constantly increasing in thickness, of dried up masses of tissue becomes separated from the living part of the cortex, and this is the Bark. The process is very clear in the bark of the oriental plane which detaches itself in large scales; and almost as clear in old stems of *Pinus sylvestris*. Since the bark does not follow the increase in thickness of the stem, it splits in longitudinal crevices from the surface inwards, as in the oak, if the direction of weakest cohesion requires it; in other cases it peels off in the form of horizontal rings from the stem (ring-bark), as in the cherry.

The *Lenticels* are a peculiarity of cork-forming Dicotyledons; they appear before

[1] A considerable increase of thickness is not always combined with the formation of periderm, as, *e. g.* in the sunflower and other annual stems. In *Viscum*, the epidermis always remains capable of development, and its thick cuticular layers render the protection of periderm superfluous; the formation of cork is also not a *necessary* consequence of vigorous increase of thickness; the copper-beech and the cork-oak, for example, form only periderm.

the formation of periderm in one-year-old branches as long as the cortex is still covered with uninjured epidermis; and are visible as roundish flakes. At the end of the first or in the following summer, the epidermis splits above the lenticel in the direction of its length; it becomes changed into a more or less projecting wart, which is often divided by a central furrow into two lip-shaped rolls; their upper surface is generally brown, their substance to a certain depth dry, brittle, and cork-like. With the further increase in thickness of the branch, the lenticels become extended in breadth and present transverse striæ; when afterwards cork or bark is formed, the splitting of the cortex in the lenticels commences, and they become indistinguishable (as in the silver poplar, apple and birch); by the scaling off of the bark they are of course removed. According to Unger, the lenticels arise only at those places of the cortex where stomata occur in the epidermis; according to Mohl the inner cortical parenchyma projects in a wart-like manner through the outer, and forms there a cork-tissue, which, on the formation of periderm, coalesces with the cork of the periderm; as occurs also, for example, in young potato-tubers. The formation of cork on the lenticel lasts for a series of years, until the cortex which afterwards grows from within dies off on the outside, the periderm or bark-formations becoming interposed between the lenticels and the living part of the cortex. In many trees (as Cratægus, Pyrus, Salix, Populus), where the formation of periderm begins from single points, and then becomes further extended in breadth, the lenticels are, according to Mohl, the points of departure.

Sect. 16. **The Fibro-vascular Bundles**[1]. — The tissue of the higher Cryptogams and of Phanerogams is traversed by string-like masses of tissue, which in some cases develop by increase in thickness in such a manner that they lose externally the form of strings and present that of strong masses, retaining, however, internally the corresponding structure. These are the Fibro-vascular Bundles. Very often they can be completely isolated with ease from the rest of the tissue of the plant. If, for instance, the leaf-stalk of *Plantago major* is broken across, they hang out from the parenchyma as tolerably thick, flexible, elastic threads. In *Pteris aquilina* it is possible, by scraping off the mucilaginous parenchyma after removing the hard skin of the underground stem, to expose them as strap-shaped or filiform very firm light yellowish bands (Fig. 80). From older foliage-leaves of trees, dry pericarps (as Datura), stems of Cactus, &c., the fibro-vascular bundles are left, through the decay of the parenchyma which surrounds them, as a skeleton

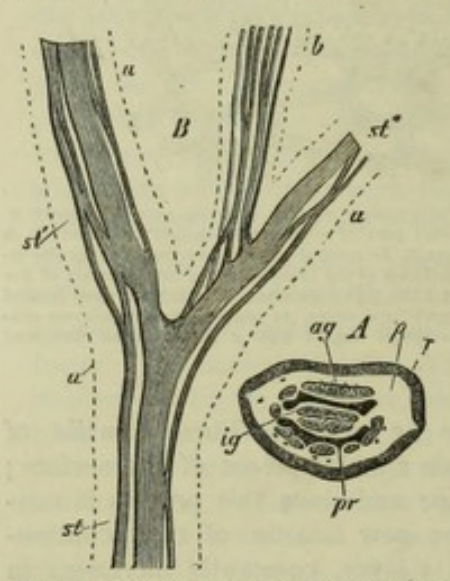

FIG. 80.—*Pteris aquilina*. *A* transverse section of the underground stem (natural size); *r* brown hard epidermal tissue; *p* soft mucilaginous parenchyma, rich in starch; *pr* dark-walled sclerenchyma, forming two broad bands penetrating the stem; *ag* fibro-vascular bundles running outside these bands of sclerenchyma; *ig* others running within them. *B* the fibro-vascular bundle represented in *A*, isolated by scraping off the parenchyma; it shows divisions and anastomoses; the dotted lines *u* show the outline of the stem *st*, its forked branches *st'* and *st''*, and a leaf-stalk *b*.

[1] H. von Mohl, Vermischte Schriften, pp. 108, 129, 195, 268, 272, 285, 1845.—Ditto, Bot. Zeitg. p. 873, 1855.—Schacht, Lehrb. der Anat. u. Phys. der Gewächse, pp. 216, 307–354, 1856.—Nägeli, Beiträge zur wiss. Bot. Leipzig 1858. Heft 1.—Sanio, Bot. Zeitg. no. 12 et seq. 1863.—Nägeli, Das Dickenwachsthum des Stammes u. die Anordnung der Gefässstränge bei den Sapindaceen, München 1864.—Rauwenhoff, Archives Néerlandaises, vol. V, 1870. (Caractère et formation du liège dans les dicotylédons.)

imitating more or less the form of the whole. Exceptionally beautiful and instructive skeletons of this nature are afforded by the stems of Tree-ferns, Dracæna, Yucca, Maize, &c., when their parenchyma is perfectly destroyed by long-continued decay, and only the epidermal tissue and the firm bundles in the interior remain. The beginner would do well in any case to prepare for himself preparations of this kind, or to examine them in collections; they are, at least at first, extremely useful for a right comprehension of their structure. This is, however, the case only with lignified fibro-vascular bundles when they run isolated between soft parenchyma; in some plants, on the contrary, the tissue of the bundles is even softer and more delicate than that of their environment (*e. g.* Ceratophyllum, Myriophyllum, Hydrilleæ, and other water-plants); in these cases they cannot of course be isolated. But in the older lignified stems and roots of Conifers and Dicotyledons, the fibro-vascular bundles are so densely crowded, and so developed by further tissue-formation, that at last very little or even nothing is left of the original fundamental tissue which separated them, and such stems consist almost entirely of fibro-vascular masses.

Each separate fibro-vascular bundle consists, when it is sufficiently developed, of several different forms of tissue, and must therefore itself be considered as a tissue-system; but different bundles, often in very large number, unite in most plants to form a system of a higher order. At present however we shall consider only the separate bundle.

The fibro-vascular bundle consists at first of similar cells combined without intercellular spaces[1]; this form of tissue of the young bundle, which has not yet undergone differentiation, may be termed *Procambium*[2]. As it grows older, single cells of the rows forming the young bundle change into permanent cells of definite form (vessels, bast, &c.); from these points of origin the transformation of the procambium-cells into permanent cells in the transverse section of the bundle advances until the cells are altogether changed into permanent cells; or an inner layer of the bundle remains in a condition capable of further development, and is then called *Cambium*. In advanced age there are thus bundles devoid of and bundles containing cambium; the former may be termed closed, the latter open[3]. As soon as a procambium bundle has become transformed into a closed fibro-vascular bundle, all further growth ceases, as in Cryptogams, Monocotyledons, and some Dicotyledons. The open fibro-vascular bundle, on the other hand, continues to produce new layers of permanent tissue on both sides of its cambium, and thus the portion of the stem or root concerned continually increases in thickness, as occurs in woody Dicotyledons and Conifers; the leaf-structures, however, of these

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[1] The young cells of the fibro-vascular masses are not always elongated and prosenchymatous; in the roots, *e. g.* of *Zea Mais*, the young tissue-cells which no longer divide and their neighbours are diagonally tabular or cubical.

[2] Nägeli calls the tissue of the young fibro-vascular bundles simply Cambium, and distinguishes by the same term the tissue, capable of further development, of the bundles which increase in thickness, which nevertheless ought to be distinguished from them.—Sanio terms the latter only Cambium, which I adopt. (Sanio in Bot. Zeitg. p. 362, 1863.)

[3] This distinction was first made by Schleiden, but he incorrectly ascribed to Dicotyledons in general only open bundles; his distinction of simultaneous and successive cannot be sustained; all bundles become differentiated successively in transverse section. Schleiden's simultaneous bundles of the higher Cryptogams belong to the closed description.

plants possess closed bundles, or, if they are open, the activity of their cambium soon ceases.

The different forms of tissue of a differentiated fibro-vascular bundle may be classified into two groups, which Nägeli calls the *Phloëm-* (Bast) and *Xylem-* (Wood) portion of the bundle. They are separated by the cambium if there is any. In many bundles the phloëm is formed on one, the xylem on the other side of the procambium, and the development of both advances towards the centre of the bundle, where at length they meet. The phloëm consists of succulent, generally thin-walled cells;

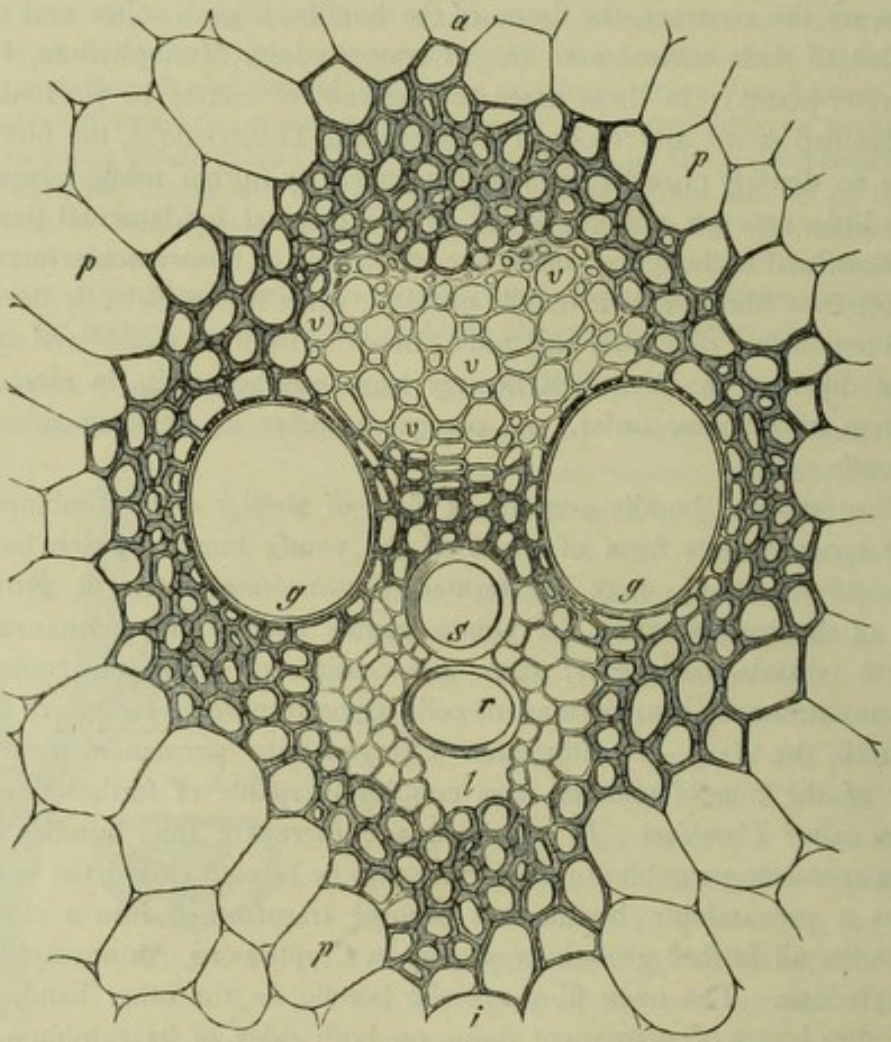

FIG. 81.—Transverse section of a closed fibro-vascular bundle in the stem of maize (×550); *p p* the surrounding thin-walled parenchyma; *a* outer side, *i* inner side (facing the axis of the stem); *g g* two large pitted vessels; *s* spirally thickened vessel; *r* isolated ring of an annular vessel; *l* air-containing cavity, from splitting caused by growth; *v v* the cambiform or latticed cell-tissue which has passed over last into permanent tissue; between it and the vessel *s* lie reticulately thickened and bordered pitted vessels; the periphery of the whole bundle forms a firm sheath of thick-walled lignified prosenchyma-cells.

only the bast-cells, which are often absent, but very often massively developed, are usually greatly thickened (mostly however not lignified but flexible). These thin-walled succulent cells are either parenchymatous, or they are cambiform or latticed-cells, or finally sieve-tubes. The xylem-portion of the fibro-vascular bundle has mostly a strong tendency to thicken its cell-forms; their walls become hard and woody; in vessels and the bordered pitted wood-cells the contents disappear, and they henceforth conduct air. Woody parenchyma is also abundant, but in some cases the lignifying does not take place; the whole bundle is then soft and succulent, sometimes traversed only by single thinner bundles of lignified vessels and wood-cells

(as in the roots of radish, tubers of the potato, &c.). The elements of the fibro-vascular bundles, as far as they consist exclusively of procambium, are prosenchymatous or at least elongated in the direction of the axis of growth of the bundle. In open bundles there arise also in the cambium, with the increase of their thickness, horizontally extended rows and layers of cells disposed radially, by which the later-formed xylem- and phloëm-layers of the bundle become arranged in a radial fan-like

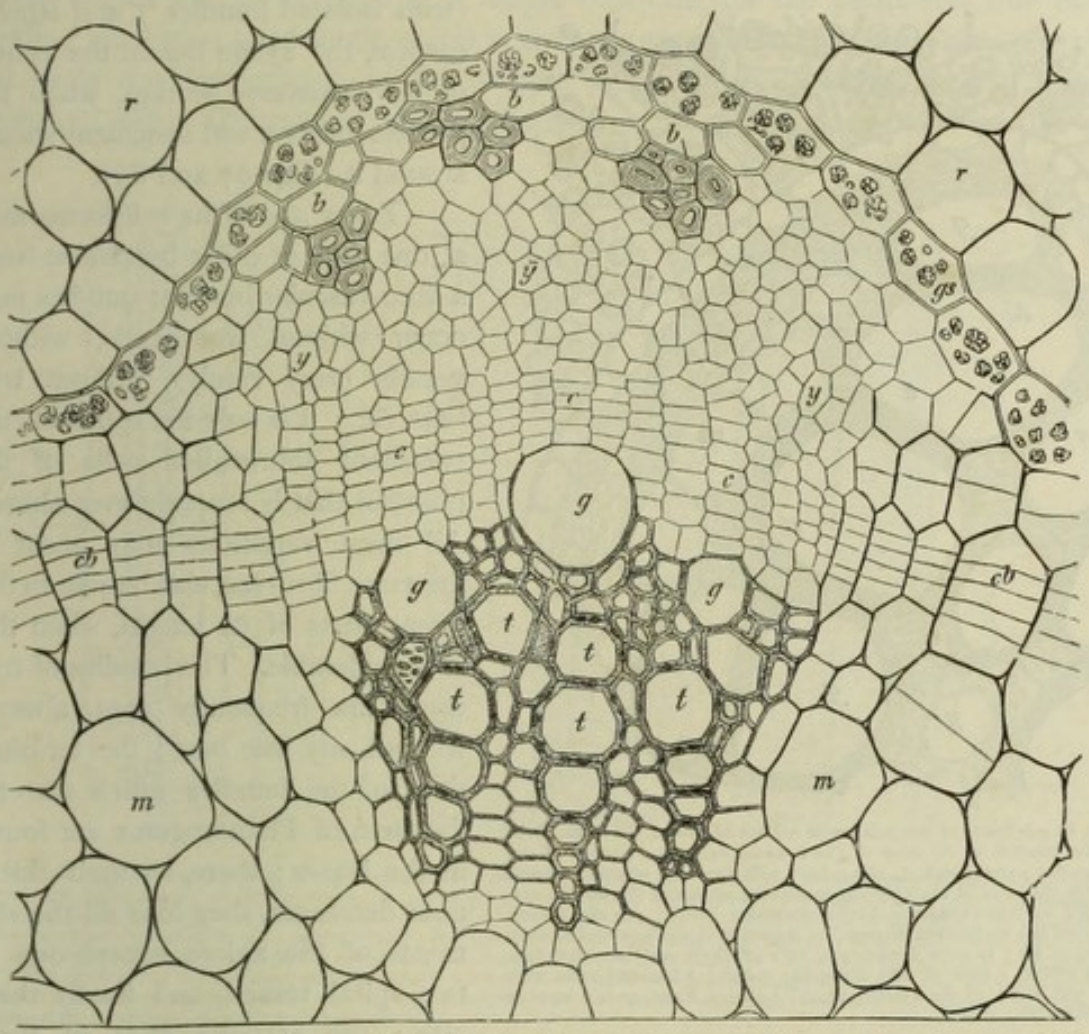

FIG. 82.—Transverse section of a fibro-vascular bundle in the mature elongated hypocotyledonary portion of the stem of *Ricinus communis*; *r* cortical parenchyma; *m* parenchyma of the pith; *b* bast; *y* phloëm portion with thin-walled cells; *c* cambium; *g g* large pitted vessels; *t t* smaller pitted vessels with wood-cells between them; *cb* continuation of the cambium into the parenchyma lying between the bundles; the parenchyma-cells are repeatedly divided by tangential walls. (Between the cortex (*r*) and the phloëm of the bundle lies a layer filled with compound starch-grains, the bundle-sheath, or starch-bearing layer.)

manner; these horizontal elements mostly assume the character of parenchymatous cells, and may be generally designated as rays; within the xylem they are called xylem-rays, within the phloëm, phloëm-rays.

The position of the layers of phloëm and xylem in the transverse section of a bundle varies according to the class to which the plant belongs and the organ in which they are found; in the open bundle in the stem of Dicotyledons and Conifers the former lies towards the circumference[1], the latter facing the axis of the organ; between the two lies the cambium-layer (Fig. 82). But it sometimes occurs that a

[1] In Dicotyledons bundles also occur exceptionally within the circle of wood proper (in the pith), where the phloëm portion is surrounded by wood as by a sheath (in the rachis of the inflorescence of *Ricinus*); in *Heterocentron roseum* the medullary bundles have, according to Sanio, their

layer of phloëm is found in addition on the axial side of the xylem, so that the bundle possesses two phloëm-layers, a peripheral, and an axial (*e. g.* in Cucurbitaceæ and Nicotiana). In the closed bundles there occur, among Dicotyledons, considerable deviations from the typical position of the tissues; among Monocotyledons these are still more conspicuous, especially if the sheath of lignified prosenchyma, which often occurs with them, is taken into account (see Fig. 81). Among Ferns, Lycopodiaceæ (with isolated bundles[1]), and Rhizocarpeæ, the xylem lies in the centre of the transverse section, while the phloëm forms a soft succulent sheath around it (Figs 67 and 83).

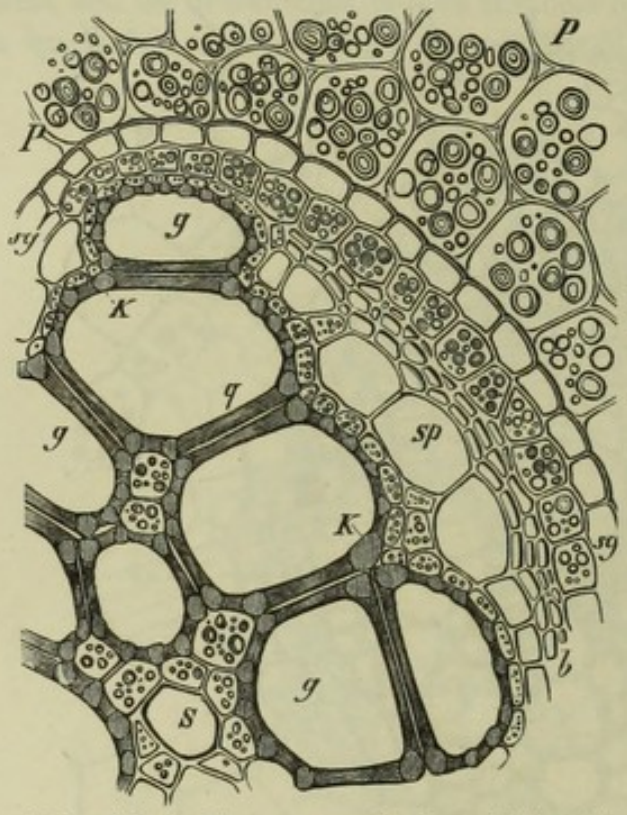

FIG. 83.—A fourth of the transverse section of one of the large fibro-vascular bundles in the stem of *Pteris aquilina*, with a portion of the surrounding parenchyma, *p*; this is filled with starch (in winter); *s* spiral vessel in the focus of the elliptical transverse section of the bundle, surrounded by thin-walled wood-cells containing starch; *g g* the vessels thickened in a scalariform manner, the structure of which is explained in Fig. 29 (p. 27); *sp* wide lattice-cells, between them and the xylem lies, in the winter, a layer of cells containing starch; *b* bast-like cells, with thick soft wall; *sg* the bundle-sheath; between *b* and *sg* is a layer of cells containing starch.

Every one of its cell-forms may at one time or other be absent from a fibro-vascular bundle; bundles may occur without wood-cells, without vessels (very rarely), without true bast, &c.; it is only the soft bast (the succulent thin-walled cells of the phloëm) that is scarcely ever absent. All these variations may occur in the same fibro-vascular bundle in different parts of its length, when this is considerable. The bundles of true roots are frequently (not always) without any true bast; the terminations of the bundles which traverse the stem of Phanerogams are found in the leaves; there, as their thickness decreases, they lose all the elements of the xylem except one or two spiral vessels, and finally these also; the extreme ends of these bundles which traverse the mesophyll of the leaves often consist only of long narrow thin-walled succulent or of cambiform cells (Fig. 16, *F*, p. 21).

If the fibro-vascular bundle is formed at the very earliest period within an organ which afterwards grows rapidly in length, then the elements which were formed before the increase in length (the innermost vessels and the outermost bast-cells) are the longest, since they participate in the whole increase of length of the organ; the elements developed later, during the elongation, are shorter; and those are shortest of all which arise after the increase of length of the whole organ has been

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vessels in the centre; they are completely surrounded by cambiform tissue; in *Campanula latifolia*, according to the same authority, the bundles of the inner circle behave in the same manner as in *Ricinus*. (Cf. Bot. Zeitg p. 179, 1865.)

[1] The bundle in the stem of *Lycopodium chamæcyparissus*, &c., is clearly a union of several fibro-vascular bundles.

completed; this occurs in particular with the open bundles of Dicotyledons and Conifers.

The development of the elements of a bundle always begins at single points in the transverse section, and extends from them in different directions; and thus the permanent cells which arise one after another acquire different mature forms. In the open bundles in the stem of Dicotyledons and Gymnosperms the development usually begins with the thickening of single bast-cells on the peripheral side of the bundle; somewhat later single spiral vessels (or annular-vessels) arise next the pith; and while the development of the phloëm proceeds centripetally, forming successively and often alternately bast-cells, latticed cells and parenchyma,—annular and

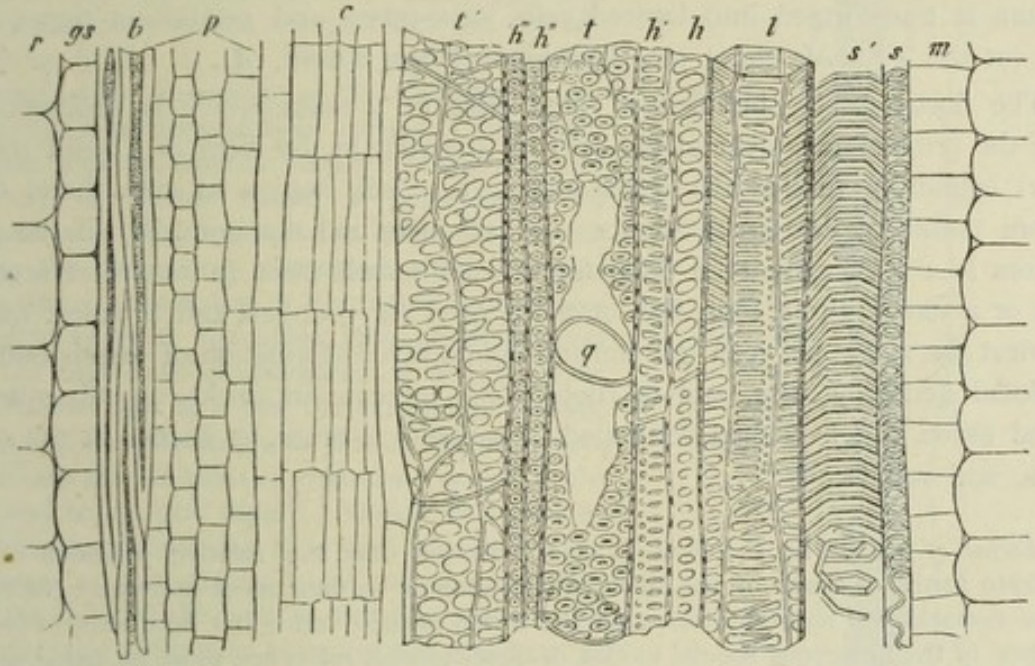

FIG. 84.—Longitudinal section of the fibro-vascular bundle of Ricinus, the transverse section being shown in Fig. 82; *r* cortical parenchyma; *gs* bundle-sheath; *m* parenchyma of the pith; *b* bast-fibres; *p* phloëm-parenchyma; *c* cambium, the row of cells between *c* and *p* is afterwards developed into a sieve-tube. In the xylem portion of the bundle the elements are developed beginning from *s* gradually to *t'*; *s* the first narrow and very long spiral vessel, *s'* wide spiral vessel, both with a spiral band which can be unrolled; *l* vessel thickened partly in a scalariform, partly in a reticulate manner; *h h'* wood-cells; *t* pitted vessel; at *q* the absorbed septum; *h'' h'''* wood-cells; *t'* pitted vessel, still young; the pits at first show the outer border; afterwards the formation of the inner pore commences; at *t t' t''* in the wall of the vessel are observed the boundary-lines of the adjoining cells which have been removed.

spiral vessels[1] either separately or together, or reticulated vessels and eventually pitted vessels often alternating with wood-cells, arise centrifugally in the xylem (Fig. 84). In Coniferæ only prosenchyma-cells with bordered pits (together with xylem-rays) are subsequently produced, so long as the stem or root grows. In Dicotyledons on the contrary, after the first year a combination of vessels and wood-prosenchyma, often mixed with wood-parenchyma, is annually formed. In trees with annual rings in the wood a periodicity may be remarked in the development of the xylem-cells; and on this depends the stratification of the xylem into annual layers. Not unfrequently the phloëm portion also shows a similar stratification. In the closed bundles of Monocotyledons the order of development in the first

[1] These are formed only before the completion of the increase in length of the organ, to which the bundle belongs.

year is similar to that already described. In Fig. 81, for example, the annular vessel *r* is first formed in the xylem portion, then the spiral vessel *s*, then advancing right and left the pitted vessels *g g*, and in the middle (advancing radially) the narrow pitted vessels. It sometimes occurs (*e. g.* in Calodracon, according to Nägeli) that the formation of vessels advancing right and left encloses the procambium, which afterwards passes over into latticed cells. In the leaf-stalk of *Pteris aquilina* the development of the xylem begins in the procambium bundles with an elliptical transverse section, by the formation of some narrow spiral vessels in the foci of the section; then, following the longer axis, scalariform vessels are formed, first centrifugally then centripetally, until a compact woody mass is produced, elongated in transverse section; around this the still remaining procambium is transformed into latticed cells, sieve-tubes, and cambiform tissue, and partly (at the circumference) into bast-fibres (Figs. 83, 87, *A*).

The fibro-vascular bundles of roots arise in a tissue which is differentiated out of the primary meristem of the apex of the root in the form of a solid (rarely hollow) cylinder. In this the development of vessels begins at two, three, four, or more points of the circumference, and advances radially inwards. If the procambium is a solid cylinder, a diametral row of vessels (seen in transverse section) arises, or a star of three, four, five, or more rays, the youngest and broadest vessels lying next the axis; between the starting-points of this formation of vessels bundles of phloëm generally arise, and in roots which increase in thickness subsequently cambial tissue, which is then developed in centrifugal order, as occurs in the stem, vessels, and wood-cells [1].

Forms of Cells. In the text I have indicated only the relative positions of the separate forms of tissue of the fibro-vascular bundle in their most important features; some remarks will naturally follow on the forms of their cells; but here also, in consequence of the numerous special modes of development, reference must be made to the special morphology of separate classes of plants in Book II. The cell-forms of the fibro-vascular bundles attain their most perfect and varied development in Dicotyledons; the forms which occur in them may therefore be employed as a basis for the critical examination of the corresponding phenomena in other classes of plants.

The Xylem-portion of the fibro-vascular bundle of Dicotyledons is composed of numerous cell-forms, which may be referred, according to Sanio's careful researches, to three types. He distinguishes (1) Vascular, (2) Fibrous, and (3) Parenchymatous.

To the *Vascular* forms belong the ducts and the vascular wood-cells or Tracheïdes. This group of forms is characterised by their walls forming open orifices where two cells of the same form meet, so that their cell-contents soon disappear and air takes their place; the thickenings show a tendency towards the formation of spiral bands, net-work, and bordered pits. True vessels (Figs. 27, 84) arise when the septa of cells whose form is similar, arranged in rows longitudinally over one another, are entirely or partially absorbed; and thus long air-conducting tubes originate, consisting of many cells, distinguished from the adjoining wood-cells principally by their greater breadth. The septa may be placed horizontally or more or less obliquely; and in general the mode of their perforation is directed accordingly; hori-

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[1] Cf. Van Tieghem, Recherches sur la symmetrie de structure des plantes vasculaires. Paris 1871.

zontal walls are often entirely absorbed, or they have large round cavities. The more oblique the septum, the more do the perforations take the form of narrow broad parallel fissures; and the thickening-bands of the septum which remain present more or less the appearance of rungs of a ladder, while reticulated combinations of them are often formed. The scalariform septum is found, according to Sanio, not only in reticulately thickened vessels and those with bordered pits, as was previously supposed, but also in spiral vessels (*e.g.* in Casuarina, Olea, Vitis) where turns of the spiral band pass immediately into the scalariform markings. The loosening of the spiral band of the first-formed spiral vessel in stems and leaf-stalks of rapid growth, appears to depend solely on the loosening of the band from the thin quickly-growing wall which is common to the vessel and the adjoining cells. If the band could be unrolled owing to the absorption of this wall, the adjoining cells must necessarily be opened. If the septa of the separate vascular cells are placed very obliquely, the latter assume a prosenchymatous appearance (Fig. 85), and the more this is the case the more does the vessel appear discontinuous. In the xylem of Ferns this is often carried to so great an extent that, after isolation of the single cells by maceration, it would be easy to believe that it is not the remains of vessels, but fusiform prosenchyma that is left (Fig. 29); but here also all kinds of transitions occur to the typical scalariform septa[1]. Vessels with prosenchymatous constituents now form the immediate passage to the vascular wood-cells (Tracheïdes). If the form of the cells is such that there is no longer any difference between the longitudinal wall and septum, which is possible only in decidedly prosenchymatous forms, then the perforations of the cells which lie above and next one another are no longer different in form; rows of cells no longer arise in an especially marked manner resembling continuous tubes, but whole masses of cells (bundles, &c.) are connected with one another by means of open bordered pits. This occurs in an especially marked manner in the tracheïdes in the wood of Coniferæ (*vide* Figs. 25, 26, p. 25). There is no other difference between these and true vessels; for vessels when they have bordered pits behave in reference to the side-walls exactly like tracheïdes when they have open bordered pits (Fig. 27). The separate elements

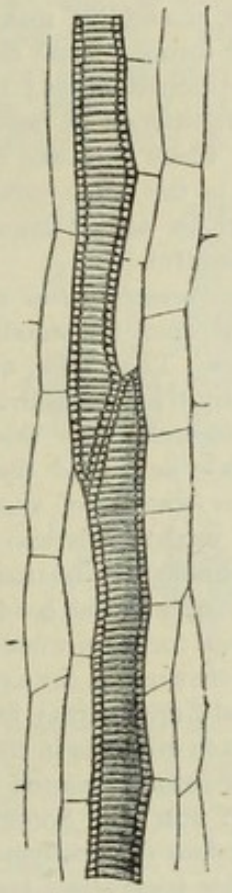

FIG. 85.—From the very young fibro-vascular bundle of a young leaf-stalk of *Scrophularia aquatica*; part of a spiral vessel surrounded by procambium; two spirally thickened cells are in prosenchymatous apposition; by the elongation of the leaf-stalk the turns of the spiral band now lying close to one another are drawn apart; the spiral band becomes detached from the thin wall which is common to the vessel and to the adjoining cells, and so a spiral band is formed capable of unrolling.

[1] Cf. Dippel in the Amtlichen Bericht der 39. Vers. der Naturforscher u. Aerzte. 1865 (Giessen), Feb. 3, Figs. 7–9. Dippel's observations on Cryptogams and the whole description of the formation of vessels here given, their passage into Tracheïdes, and especially the fact that the air-conducting tracheal forms have open bordered pits,—even when the parenchymatous constituents of a vessel are united not by large cavities, but by narrow fissures, &c. or are connected with one another (and are hence not closed cells, as Caspary thinks),—compel us to consider as erroneous Caspary's supposition of the absence of vessels in Cryptogams and many Phanerogams. (Cf. Caspary, Monatsberichte d. k. Akademie der Wissenschaften in Berlin, July 10, 1862.)

of the vessels of Ferns composed of prosenchymatous cells (Fig. 29) may be correctly designated tracheïdes.

The *Fibrous* cell-forms of the xylem are always prosenchymatous and fusiform, very thick in comparison with their diameter, with usually simple, but sometimes bordered pits, the pits small; always without a spiral band; and during the repose of vegetation containing starch. Next to the middle lamella of their partition-walls there more often lies an unlignified gelatinous thickening-mass which is coloured red-violet by Schultz's solution, resembling many bast-fibres; these cells are generally much longer than the vascular forms. Sanio distinguishes here also two forms;—the simple (Libriform), and the partitioned fibres; the latter are distinguished from the former by their cavity being partitioned by several thin septa, while the common wall of the whole fibre is thick. These fibre-like cell-forms are found in the wood of dicotyledonous trees and shrubs in the most various intermixture with the vascular elements and the other forms to be named immediately. Whether wood-fibres occur in Cryptogams is at least doubtful.

The *Parenchymatous* cell-forms of the xylem are widely distributed, and especially abundant when the woody substance of the fibro-vascular bundles attains a considerable thickness. They arise, according to Sanio, in the wood of Dicotyledons and Gymnosperms by transverse division of the cambium-cells before their thickening commences. The sister-cells show this origin chiefly by the mode in which they are arranged; when completely developed they are thin-walled, with simple closed pits. Their contents in winter consists of starch, often associated with chlorophyll, tannin, and crystals of calcium oxalate. It also happens sometimes that the cambium-cells on the xylem-side of the bundle become transformed without transverse division into parenchymatous, thin-walled, simply pitted, conducting, elongated cells, which must also be considered as parenchymatous forms of wood-cells[1]. To this last type are also to be referred the parenchymatous elements in the xylem portion of the closed fibro-vascular bundles of Monocotyledons and Cryptogams; but these thin-walled, mostly elongated, conducting cells do not in this case originate in the cambium (since this, according to the terms in customary use, is absent from the closed bundles), but immediately from the procambium of the bundle (Fig. 83, near *S*). Sometimes the wood-parenchyma resulting from the cambium of Dicotyledons (parenchyma of the xylem portion) attains a stronger development, while only a few vessels and tracheïdes are formed: this occurs in the thick napiform roots of the radish, carrot, beet, and dahlia, and in potato-tubers. The apparent pith of these organs corresponds, in its origin, to the woody substance of a dicotyledonous tree; but the elements of the xylem are not, or only slightly, lignified; the succulent contents and the thin soft cell-walls scarcely give this xylem the appearance of an analogue of the ordinary woody substance, although there can be no doubt about this analogy.

The Layers of Phloëm of the fibro-vascular bundle show, when fully developed, similar cell-forms to the xylem portion; the sieve-tubes correspond to the vessels, the bast-parenchyma to the wood-parenchyma, the true bast-cells to the woody fibres. In the phloëm as in the xylem, the different cell-forms may arise in the most various intermixture, sometimes in alternate layers, sometines irregularly. A very general cell-form in the phloëm is the *Cambiform*, consisting of narrow, usually elongated, thin-walled, succulent cells which sometimes appear, in very thin bundles, to form the only constituent of the phloëm. When this last is perfectly developed, regular latticed cells arise, which are not always to be easily distinguished from true sieve-tubes; the formation of the latter has been already explained in Figs. 23 and 24. The perforation of their older sieve-discs, especially on the septa, which may lie obliquely or transversely to the longitudinal rows of cells, can be easily proved by laying thin sections in concentrated sulphuric acid, especially if the preparation is saturated

[1] Sanio applies to these cells the term 'Ersatzzellen.'

with iodine-solution[1]. The cell-walls become dissolved, the protoplasmic mucilage remains behind coloured brown, and may be recognised in the form of fine strings of mucilage filling up the pores of the sieve-disc (Fig. 86, *p*). Those cells may provisionally (after Von Mohl) be called latticed-cells in which similar formations of wall are visible, even although the previous perforation of the narrow crowded pits (lattice) cannot be proved. To this category belong the so-called 'Vasa propria' in the fibro-vascular bundle of Monocotyledons (Fig. 81, *v*), and the form of cells discovered by Dippel in Cryptogams, and called by him bast-vessels. (Dippel, *l. c.*) The latticed cells or sieve-tubes frequently have sieve- or latticed discs in their longitudinal walls also, when two cells of this kind are placed in juxtaposition side by side; these discs are thinner portions of the cell-wall which show a fine puncturing or lattice-like thickening; whether in these cases actual perforations also occur is still undetermined. These cell-formations (cambiform, latticed cells, sieve-tubes) may, in combination with the phloëm-parenchyma in which they are imbedded, or which sometimes forms thicker layers, be included in the term *Soft-bast*, in opposition to the true bast which is sometimes entirely absent (as in Cucurbita), but in other cases is very abundantly developed (*e. g.* stem of *Helianthus tuberosus*, Tilia, &c.), and consists of elongated, prosenchymatous, fibre-like, flexible, tough, firm cells, usually greatly thickened. In Dicotyledons they are generally arranged in bundles, frequently forming layers alternating with soft-bast (as in the grape-vine); but sometimes, especially in the later portions of the phloëm, which are formed by the cambium, they occur also in separate fibres (as in the stem and tuber of the potato). The middle lamella of the partition-wall of two fibres is generally lignified or cuticularised (not dissolving and turning yellow with iodine) when they are closely crowded; but in other cases it forms a mucilaginous 'intercellular substance' in which the cells (in transverse section) appear imbedded (*e. g.* the laburnum according to Sanio, Coniferæ). The true bast-fibres of the phloëm, like the fibres of the wood, may become partitioned by subsequent septa (as in the vine, occidental plane, horse-chestnut, *Pelargonium roseum*, *Tamarix gallica*, according to Sanio, *l. c.* p. 111). As the wood-cells are often found branched after isolation by maceration, so also are the bast-fibres, which frequently attain greater freedom at the expense of the surrounding soft tissue (*Abies pectinata*, according to Schacht). Sometimes the bast-cells are short and lignified when more decidedly thickened, and very hard (tuberous roots of Dahlia). In Apocynaceæ (*e. g.* Vinca) the very long bast-cells are alternately wider and narrower, and also distinctly striated (on laticiferous bast-cells *vide infra*). The true bast-cells of the Equisetaceæ, Ferns, and Lycopodiaceæ (found by Dippel) are but little developed, the external thickening-layers of their walls being apparently generally mucilaginous[2] (or developed as intercellular-substance).

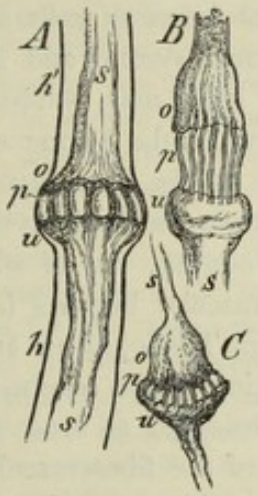

FIG. 86.—Combinations of sieve-tubes, showing the perforation of the septa after solution of the cell-wall by sulphuric acid. *A* and *B* from the leaf-stalk of Cucurbita; *C* from the stem of Dahlia. At *A* the cell-wall *h h'* is not yet completely absorbed; *s'* the protoplasmic mucilage, *o* and *n* accumulation of it on the upper and under side of the septum; *p* the strings of mucilage, which unite these accumulations and fill up the pores of the sieve-discs (cf. Figs. 23 and 24).

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[1] Cf. Sachs, in Flora, p. 68, 1863, and other proofs of the perforation in Hanstein, Die Milchgefässe, Berlin, pp. 13 et seq., 1864.

[2] There is no reason for describing, as is done by many writers, as bast the hypodermal fibres of Equisetum, the brown-walled prosenchyma in the fundamental-tissue of the stem of Tree-ferns and *Pteris aquilina*, and other cell-formations which do not at all belong to the fibro-vascular bundles.

All that has hitherto been said concerns only the elongated elements of the fibro-vascular bundle; the radially extended elements (xylem- and phloëm-rays) are a peculiarity of the open fibro-vascular bundles of Dicotyledons and Conifers.

Sect. 17. **The Fundamental Tissue** (Grundgewebe).—By this name I designate those masses of tissue of a plant or of an organ which still remain after the formation and development of the epidermal tissue and the fibro-vascular bundles. The fundamental tissue consists very commonly of thin-walled succulent parenchyma filled with assimilated food-materials; but not unfrequently it is thick-walled; sometimes separate portions assume the form of string-like tissues which consist of sclerenchymatous strongly lignified prosenchyma cells. The most various forms of cells and tissues may arise in the fundamental tissue as in the epidermal system and the fibro-vascular bundles; a portion of the fundamental tissue itself may persist from the commencement in a condition capable of division, while the surrounding portion passes over into permanent tissue; or special layers of the fundamental tissue, long after it has been transformed into permanent tissue, may again become subject to cell-division, and a generating tissue thus be produced, out of which originate, not only new fundamental tissue, but also fibro-vascular bundles (*e.g.* in Aloineæ).

In Thallophytes and many Muscineæ the whole mass of tissue, with the exception of the outermost layer, which is often developed as epidermal tissue, may be considered as fundamental tissue; but in these cases, in consequence of the absence of the fibro-vascular bundles, this distinction has but little practical value. In Mosses with string-like formations in the stem it may appear doubtful whether these are to be considered as peculiar forms of the fundamental tissue or as very rudimentary fibro-vascular bundles. In Vascular plants, on the other hand, the independence and peculiarity of the fundamental tissue, in contradistinction to the epidermal system and the fibro-vascular bundles, is at once apparent; it here fills up the interstices of the fibro-vascular bundles within the space enclosed by the epidermal tissues. Where the fibro-vascular bundles are closed and show no increase in thickness (as in many Ferns), the tissue is frequently the most largely developed; where, on the other hand, closely crowded fibro-vascular bundles, by the development of cambium, produce in succession large masses of layers of wood and phloëm (as in stems and roots of many Conifers and Dicotyledons), the fundamental tissue becomes a constantly less important portion of the whole organ. The disposition of the fibro-vascular bundles in stems is commonly of such a nature that the fundamental tissue is separated into an inner pith-portion, surrounded by the bundles, and an outer cortical layer enveloping the bundles. Since the bundles are not in contact laterally, or only partially so, there still remain between them portions of the fundamental tissue which connect the pith with the cortex, and are termed Medullary Rays. If the fibro-vascular masses of an organ form an axial solid cylinder, as occurs in some stems and in roots, the fundamental tissue is developed only as cortex.

(a) *Critical.* The whole course of my description of the tissue-system requires the introduction of the idea of a 'Fundamental Tissue.' It has, in fact, long been required, since it was often necessary, in anatomical descriptions of the collective masses of the tissue which are neither epidermal nor fibro-vascular bundles, to distinguish them by some common term. Many writers employ the term Parenchyma in this sense in opposition to the fibro-vascular bundles and the epidermis; but this usage is not scientific;

the fibro-vascular bundles often contain parenchyma also, and *vice versâ*, the fundamental tissue is not always parenchymatous but sometimes distinctly prosenchymatous. We have, moreover, to deal here not with forms of cells, but with the contrast of different systems of tissue, each of which may contain the most various cell-forms. I must compare somewhat more closely my description and use of terms with those of Nägeli. It might be supposed that Nägeli's Protenchyma is synonymous with my fundamental tissue; but this is not the case; the protenchyma of Nägeli is a much more comprehensive idea; everything which I call fundamental tissue is protenchyma; but all protenchyma is not fundamental tissue. Nägeli[1] says, for example, that he would call the primary meristem and all parts of the tissue which arise immediately from it (*i. e.* only through the medium of secondary meristem, but not of cambium) Protenchyma (or Proten); the cambium, on the other hand, and everything which directly or indirectly originates from it Epenchyma (or Epen). When Nägeli thus defined these terms, he was dealing with a description of fibro-vascular bundles, and it is intelligible that he on this occasion included everything which does not belong to the fibro-vascular bundles under one common name (Proten). But our business is to give a uniform description of the various differentiations of the tissues of plants; and there is no reason for bringing into prominence only the contrast between fibro-vascular and non-fibro-vascular masses (Epenchyma and Protenchyma), and for considering as less important the other differentiations; the protenchyma of Nägeli therefore splits up, according to me, into three kinds of equal value with his epenchyma. The primary meristem is as completely opposed to the fibro-vascular masses as to the epidermal and fundamental tissues, for the three systems of tissue arise by differentiation out of the still undifferentiated primary meristem. The conception of Proten, after the primary meristem has been eliminated from it, might be applied equally to the epidermal and the fundamental tissues; but I see no reason which compels us to bring into prominence this contrast alone; nature rather indicates that the differentiation between epidermal and fundamental tissues is as essential as that between fibro-vascular bundles and fundamental tissue. From all this it follows that primary meristem, epidermal tissue, fibro-vascular bundles, and fundamental tissue are conceptions of equal value; in each of the three differentiated tissues we find the most various forms of cells; and secondary meristem may also arise in each. In the fibro-vascular bundles the cambium is of this nature, the whole of the young epidermis is a generating tissue in as accurate a sense as the cambium; if this latter forms vessels, wood, bast, &c., the former produces hairs, stomata, prickles, &c. The phellogen, belonging to the epidermal system, arises still more decidedly as a generating tissue; finally even in the fundamental tissue a portion may persist for a considerable time as generating tissue, or may subsequently produce such a tissue (*e. g.* the meristem of the stems of Dracæna), which brings about its increase in thickness and thus forms new fibro-vascular bundles.

(b) *Examples.* The relationship of the three systems of tissue may be observed very simply and undisturbed by subsequent new formations in the foliage-leaves of Ferns and of most Phanerogams; in these the fundamental tissue is generally the prevailing system, and is developed into different cell-forms. Isolated fibro-vascular bundles separated by the fundamental tissue traverse the leaf-stalk, and are distributed through the blade; in the former they are generally surrounded by a broad-celled thin-walled parenchymatous fundamental tissue extended axially; this also forms sheath-like envelopes around the stronger bundles of the blade, which are conspicuous on the under-side of the leaf as the Veins; but the finer branches, and the finest of all, run through the so-called mesophyll, *i. e.* a peculiar form of the fundamental tissue distinguished by containing chlorophyll and by its thin cell-walls. Not unfrequently single cells of the fundamental tissue of the leaf-blade assume very peculiar forms (*e. g.* the larger stellate cells in the leaf of *Camellia*

[1] See his Beiträge zur wissenschaftlichen Botanik, Heft 1, p. 4.

japonica, the erect post-like cells upon which the stomata of the leaves of *Hakea* are, as it were, supported). All these tissue-formations are enveloped by the epidermis, and frequently also by hypodermal tissues. In the carpellary leaves of Phanerogams there occurs commonly a more manifold differentiation of the fundamental tissue; I will instance only the formation of the so-called stones of Drupaceæ. The stone is here the inner layer of tissue of the same foliar structure of which the outer layers form the succulent flesh of the fruit; both are the fundamental tissue of the carpel, the former sclerenchymatous, the latter parenchymatous and succulent, both being traversed by fibro-vascular bundles. Equally clear is the structure in the stems of Ferns, among which the Tree-ferns and *Pteris aquilina* are of special interest, because the fundamental tissue occurs in them in two quite different forms; its preponderating mass consists, *e. g.* in *Pteris aquilina* (Fig. 80) of a thin-walled colourless mucilaginously succulent parenchyma, in winter rich in starch, in which there also run, parallel with the fibro-vascular bundles, filiform or strap-shaped lines of thick-walled prosenchymatous dark brown bundles of sclerenchyma. They have nothing in common with the fibro-vascular bundles, but are only a peculiar form of the fundamental tissue which also often occurs elsewhere in Cryptogams in prosenchymatous forms. The tendency to prosenchymatous development of the cells of the fundamental tissue occurs also especially in the stems of Lycopodiaceæ. In *Selaginella denticulata* (Fig. 87, *A*) the axial fibro-vascular bundle is surrounded by a very loose parenchyma which forms large intercellular spaces; this innermost portion of the fundamental tissue is enveloped by a thin-walled tissue without interstices, which shows itself on longitudinal section to be developed prosenchymatously; the cells are pointed above and below, and penetrate to a considerable distance between one another; towards the circumference they become gradually narrower and more pointed; the outermost are dark-walled and form the epidermal system which gradually passes over into this fundamental tissue. In *Lycopodium*

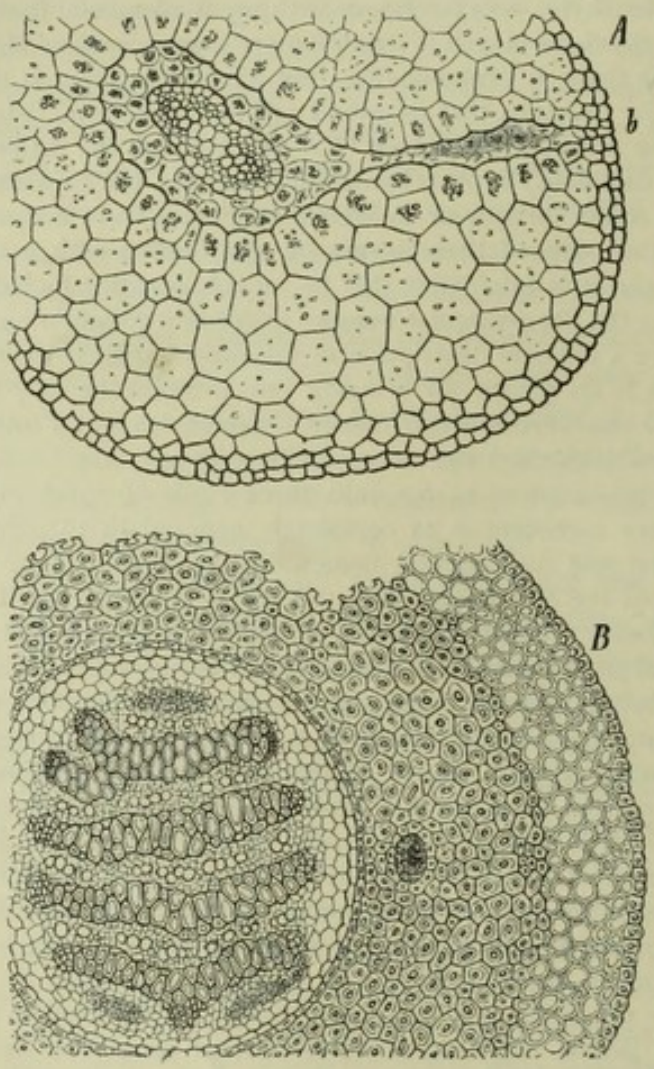

FIG. 87.—*A* transverse section of the stem of *Selaginella denticulata*; the fibro-vascular bundle is not yet fully developed; the vessels are already lignified on both sides, but not yet in the centre; *l* air-conducting intercellular spaces in the parenchyma enveloping the bundle; towards *b* the part of the tissue corresponding to the bundle which bends outwards to the leaf. *B* transverse section of the mature stem of *Lycopodium chamaecyparissus*, the axial tissue-cylinder consists of densely crowded and coalescent fibro-vascular bundles; the four parts of their xylem are quite separated, forming four bands on the transverse section, between and around which are found the narrower cells of the phloëm. The phloëm portions of the four bundles have coalesced; between each pair of xylem-bundles is seen a row of wider cells, the latticed cells or sieve-tubes; the narrow cells lying on the right and left edge of each xylem portion are spiral-vessel-cells (also in *A*). In the thick-walled prosenchymatous fundamental tissue which envelopes the axial cylinder, is seen the dark transverse section of a thin fibro-vascular bundle which bends outwards to a leaf; it consists almost exclusively of long spiral-vessel-cells (× about 90).

chamæcyparissus (*B*) the axial cylinder, which consists of several fibro-vascular bundles, is surrounded by a thick layer of greatly thickened prosenchyma; in the young stem the cells are similar to those of Selaginella; but here also an enormous thickening adds to the prosenchymatous form of the cells of the fundamental tissue; this is also enveloped by a layer of tissue, the cells of which are thin-walled and not prosenchymatous; this layer is a descending continuation of the fundamental tissue of the leaves, which envelopes the stem everywhere and is itself covered by an evidently developed epidermis.

(c) *The Cells and Tissues* of the system of the fundamental tissue have not yet undergone a comparative and comprehensive investigation, like those of the fibro-vascular bundles. Out of the very scattered material I select the following for the information of the beginner.

Irrespectively of many altogether special phenomena, it is chiefly in connexion with the true epidermal tissue on the one hand and the fibro-vascular bundles on the other hand that the differentiation of the fundamental tissue takes place; certain forms of this tissue occur as strengthenings, or at least as accompaniments of the epidermal tissue, and have already been described as *Hypoderma*; other masses of tissue accompany the separate fibro-vascular bundles as partially or entirely closed envelopes or sheaths, which I term generally *Bundle-sheaths*. In the same manner the whole remaining internal space of the organ concerned is commonly filled up by other forms of tissue, which do not, as for the most part the two former do, occur in the form of layers, but in masses; these I will designate simple *Intermediate Tissue* (Füllgewebe). Each of these combinations of tissue may be composed of very different forms.

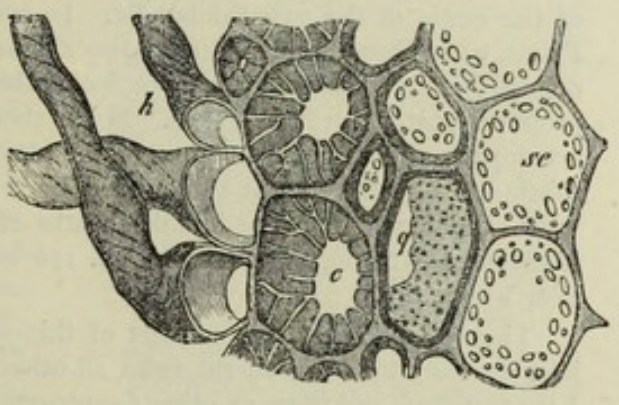

FIG. 88.—Transverse section through the underground stem of *Pteris aquilina*; *h* root-hairs; strongly thickened brown-walled cells beneath the epidermis; *q* one lying deeper and less strongly thickened; a part of the wall is seen in front; *se* cells of the deeper layers containing starch, forming the passage to the inner colourless parenchyma of the fundamental tissue.

The *Hypoderma* appears sometimes as thin-walled succulent watery tissue (as in leaves of Tradescantia and Bromeliaceæ). In Dicotyledons (stems and leaf-stalks) it commonly consists of collenchyma, the cells of which are

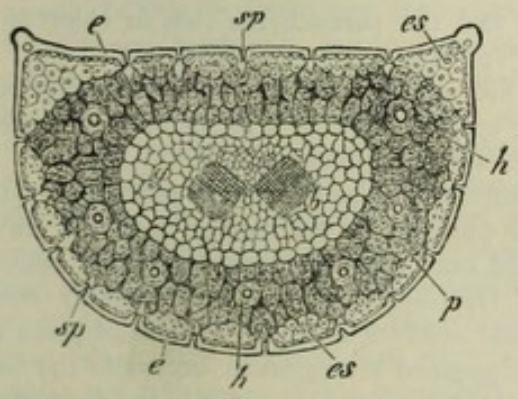

FIG. 89.—Transverse section of the acicular leaf of *Pinus Pinaster* (x about 50); *e* epidermis; *es* hypodermal fibrous bundles; *sp* stomata; *h* resin-passages; *g b* colourless inner tissue containing two fibro-vascular bundles.

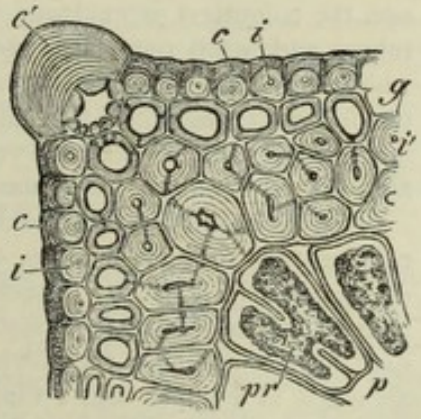

FIG. 90.—The left-hand corner of the previous figure magnified (800); *c* outer cuticularised layers of the epidermis-cells; *i* inner non-cuticularised layers; *c'* very strongly thickened outer wall of the epidermis-cells situated at the corner; *g i* the hypodermal cells; *g* the central lamella: *i'* the stratified thickening-mass; *p* parenchyma containing chlorophyll; *pr* its contents contracted.

longitudinally extended, narrow, and thickened in the angles by a mass capable of great swelling; or the hypodermal fundamental tissue is developed in a sclerenchymatous

manner, as in the stem of *Pteris aquilina*, or it occurs in the form of thick-walled but flexible fibres, and forming either layers and bundles (stem of Equisetum, leaf of Coniferæ, Fig. 89), or in long isolated fibres, similar to true bast-fibres (leaf of Cycadeæ). In all these cases the cells of the hypoderma are extended longitudinally; but when it is required in addition to produce very resisting layers, the cells often extend vertically to the surface of the organ, and, increasing greatly in thickness, form layers of closely arranged prisms, as in the pericarp of Marsilea and Pilularia and the testa of the seeds of Papilionaceæ. Isolated cells of the same kind are sometimes found in the hypoderma, as accompaniments of the stomata and air-cavities (*e. g.* in leaves of Hakea).

The *Bundle-sheaths* are commonly formed of a single layer of cells, which is in close contact with and envelopes each separate fibro-vascular bundle (Fig. 83); or, when these are arranged in a circle in the transverse section of the stem, forms an envelope common to the whole in contact only with the phloëm-layers (Fig. 82). The longitudinal walls of these simple bundle-sheaths placed radially always show in transverse section a black point, in consequence of a peculiar folding of the wall. The walls of these cells are mostly thin, but lignified or otherwise altered; in the thinner vascular bundles of Ferns on the side facing the bundle they are often much thicker and brown. In many Equiseta (*e. g. E. hyemale*) a continuous bundle-sheath runs along the inner side of the circle of the vascular bundle. In many Monocotyledons, especially Grasses and Palms, each fibro-vascular bundle, the xylem and phloëm of which are soft-walled and delicate, is surrounded by a layer, consisting of several strata of firm, long, lignified prosenchymatous cells (Fig. 81). Much stronger layers of brown-walled sclerenchyma accompany the vascular bundles in the stem of Tree-ferns. The axial fibro-vascular substance of all roots is surrounded by a simple bundle-sheath generally with thin walls (Fig. 117). (On the bundle-sheaths cf. Caspary, Jahrbuch für wissen. Botanik. I. Hydrilleen.—Sanio, Bot. Zeitung, pp. 176 et seq., 1865.—Pfitzer, Jahrbuch für wissen. Bot. VI. p. 297.)

The *Intermediate Tissue* consists of thin-walled succulent parenchyma with intercellular spaces which are absent from all other forms of tissue; in the stem, however, of Lycopodiaceæ and of many other Cryptogams the intermediate tissue consists of prosenchyma, and this is then either thin-walled as in Selaginella, or thick-walled as in Lycopodium. In so far as the intermediate tissue is parenchymatous, it may be termed simply parenchyma of the fundamental tissue or Fundamental Parenchyma. Two principal forms of this may be distinguished, which are nevertheless united by transitional forms, *viz.* the colourless parenchyma which occurs in the interior of large succulent stems and tubers and in all roots and succulent fruits, and the parenchyma rich in chlorophyll which forms the superficial layers beneath the epidermal tissues of stems and fruits. In the foliage-leaves, when thin and delicate, it fills up the space between the upper and lower epidermis; if they are very thick, as in species of Aloe, it forms only the superficial layers, while the inner mass of tissue is colourless parenchyma.

Not unfrequently there occur in the fundamental parenchyma very peculiar isolated cells, groups of cells, bundles, or bands. For example, in the mesophyll of the leaves of Camellia (Fig. 16, *P*) branched thick-walled cells appear; similarly formed spicular cells occur in the parenchymatous tissues of Gymnosperms, and are especially abundant in Welwitschia; the polyhedral stone-cells (sclerenchyma) in the flesh of pears are arranged in groups; and a similar isolated or grouped arrangement occurs in the bark of many trees; the brown-walled prosenchymatous sclerenchyma-cells in the fundamental parenchyma of the stem of Tree-ferns and of *Pteris aquilina* appear arranged in the form of bundles and bands. The sclerenchyma in the carpel of stone-fruits (the tissue of the stone in Prunus, Cocos, &c.) forms closed massive layers. To this description must also be referred many peculiarly thickened cells which occur here and there in the parenchyma, as well as the fibrous cells of the anther-walls, if these do not rather belong to the epidermal system. (Further material will be found in Schacht, Lehrbuch der Anatomie und Physiologie der Gewebe, 1856; Thomas, Jahrbuch für wissen-

schaftliche Botanik, IV. p. 23; Kraus, ditto, IV. p. 305, and V. p. 83; Borscow, ditto, VII. p. 344.)

(d) *New formations in the fundamental tissue.* The collective fundamental tissue in the stem of the higher Cryptogams, in the stem of most Monocotyledons and of many Dicotyledons, as well as in all leaves, and in all roots not yet changed by growth in thickness, originates immediately from the primary meristem of these organs by further development, simultaneously with the fibro-vascular bundles and the epidermal tissues. In the stems and roots of many Phanerogams endowed with growth in thickness, it occurs, however, that within the fundamental tissue, either originally or subsequently, meristem is formed, out of which secondary fundamental tissue, together with secondary fibro-vascular bundles, is then produced. This behaviour is seen very clearly in the stem of Dracæna, Aletris, Yucca, Aloe, Lomatophyllum, and Calodracon [1]. In Dracæna and Aletris isolated fibro-vascular bundles are formed in the primary meristem of the apex of the stem, while the whole fundamental tissue which surrounds them and separates them from the epidermis is transformed into parenchyma, and passes over into permanent tissue; but after considerable time (in *Aletris flagrans* about 4–5 cm. below the apex of the stem, in *Dracæna reflexa*, according to Millardet, as much as 17–18 cm. below the apex) a fresh formation of meristem begins in one of the cell-layers of the fundamental tissue which immediately surround the outermost fibro-vascular bundles; the permanent cells concerned in it divide repeatedly by tangential walls; and there arises (seen in transverse section) a girdle of meristem (Fig. 91, *x*), the cells of which are arranged in radial rows. In this meristem new fibro-vascular bundles are produced; one, two, or more adjoining cells of the transverse section dividing repeatedly by longitudinal walls in various positions. Out of the procambium-bundles which arise in this manner the cells of the fibro-vascular bundles proceed immediately; the intermediate meristem passes over likewise into permanent tissue, and indeed into strong-walled parenchyma, which now forms the secondary fundamental tissue between the secondary fibro-vascular bundles. Since the cells of the thickening-ring which face inwards pass over in centrifugal succession into permanent tissue, while the outermost divide repeatedly, the whole ring continually moves centrifugally, and leaves behind the new bundles and parenchyma-cells. In Yucca Millardet found the origin of the ring of meristem (thickening-ring) as little as 3mm. below the apex

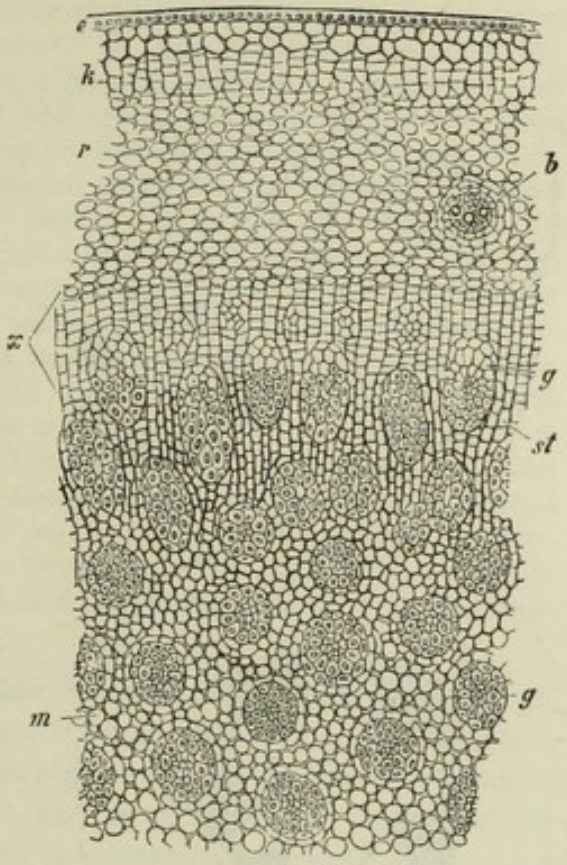

FIG. 91.—Part of the transverse section of a stem of Dracæna (probably *reflexa*) about 13 mm. thick and 1 metre high, about 20 cm. below the summit. *e* epidermis; *k* cork (periderm); *r* cortical portion of the fundamental tissue; *b* transverse section of a fibro-vascular bundle, bending out to a leaf; *m* the primary fundamental tissue (pith); *g* the primary bundles; *x* the girdle of meristem in which very young fibro-vascular bundles are to be seen, while the older ones *g* have already partially or entirely passed out of it, its lower part becoming transformed into radiately arranged fundamental tissue (*st*).

[1] Compare Millardet's description, Sur l'anatomie et le développement du corps ligneux dans les genres Yucca et Dracæna (Extrait des Mém. de la société impér. des sciences nat. de Cherbourg, F. XI, 1865; and Nägeli, Beiträge zur wissen. Botanik. Heft 1, p. 21).

of the stem; in Calodracon, according to Nägeli, while the bundles and the fundamental tissue become differentiated at the apex of the stem, a ring of meristem remains over, which subsequently produces new bundles and secondary fundamental tissue. In Dicotyledons and Conifers similar phenomena arise still more frequently and with many complications, the consideration of which I shall take up in Book II. Only one example may here be described, since it will serve to show the relationship of the fundamental tissue to the fibro-vascular bundles from a new point of view. In the hypocotyledonary segment of the stem of *Ricinus communis* there is found on transverse section, at the commencement of germination, a ring of generating tissue (Fig. 92, *A*, *x*), by which the fundamental tissue

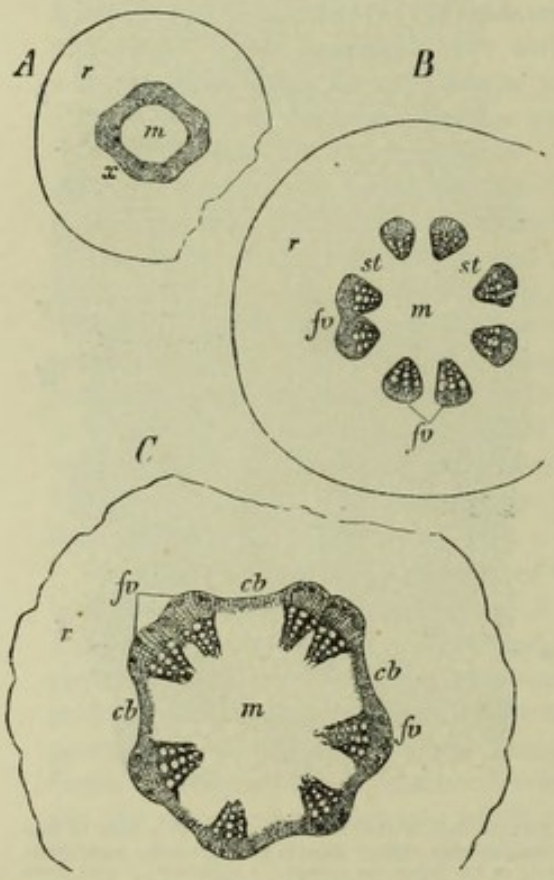

FIG. 92.—*Ricinus communis*; transverse section through the centre of the hypocotyledonary segment at various stages of germination; *A* after the appearance of the root beyond the testa of the seed; *B* after the hypocotyledonary segment has attained a length of about 2 cm.; *C* at the end of germination; *m* pith, *r* cortex, *x* generating ring of tissue (corresponding to Sanio's thickening ring); *st* medullary rays; *fv* fibro-vascular bundles; *cb* connecting bands of secondary meristem, producing xylem and phloëm later, and forming true cambium.

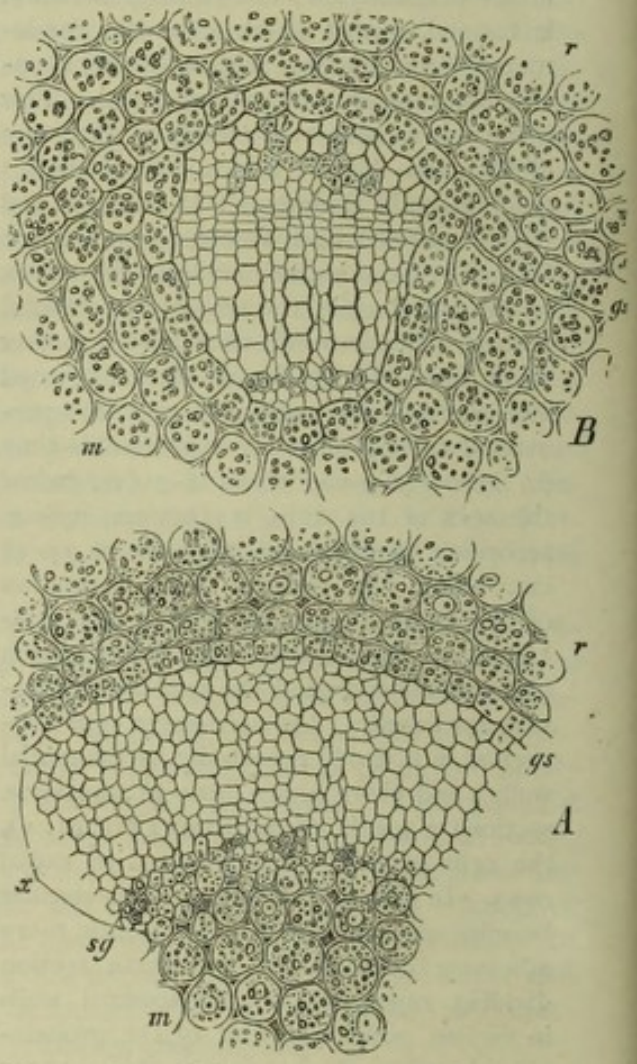

FIG. 93.—*A* a part of Fig. 92, more highly magnified; *sg* spiral vessels; *gs* bundle-sheath; *B* the same; true cambium is being formed by tangential divisions in the fibro-vascular bundle now isolated; the other letters as in Fig. 92. Compare Fig. 82 (p. 95), which represents a part of Fig. 92 *C*, magnified to the same degree as Fig. 93.

is divided into pith (*m*) and bark (*r*); at this time eight groups of narrow spiral vessels already indicate the differentiation of as many fibro-vascular bundles; subsequently the generating tissue (*B*) becomes differentiated into eight completely isolated fibro-vascular bundles (*fv*) and as many intermediate portions of parenchymatous fundamental tissue, which is in no way distinguished from that of the pith and the cortex (cf. Fig. 93, *B*); the fibro-vascular bundles are now also separated by medullary rays. This condition, however, does not last long, for as soon as the segment of the stem has become longer and thicker, and the granular materials of the fundamental tissue are mostly consumed, repeated divisions by tangential walls commence in those portions of the medullary

rays which lie between the cambium-layers of each pair of adjoining bundles (Fig. 92, *C*, *cb*). A bridge of secondary meristem is thus, as it were, established between the cambium layers of the bundles; and thus a closed ring of generating tissue is again formed, which also occasions the thickening of the portion of the stem, and may hence be termed a 'Thickening-ring'; but its origin is somewhat different to that in Dracæna and its allies. In them the thickening-ring has its origin entirely in the secondary meristem which was formed from the fundamental tissue, and the newly formed fibro-vascular bundles lie in the thickening-ring; here, on the other hand, the thickening-ring (*C*, *cb*) consists of cambium which lies in the vascular bundles, and of secondary meristem which proceeds from the fundamental tissue. Here, therefore, the thickening-ring passes through the fibro-vascular bundles; but the fundamental tissue which generating the parts required to complete the ring between the bundles has itself only shortly before been formed from a generating tissue. Subsequently the cambium of the bundles constantly produces new xylem, the meristem between them does the same, and thus is formed a closed ring of xylem (*i. e.* a hollow cylinder), which continually increases in thickness; simultaneously the same thickening-tissue forms constantly towards the outside new layers of phloëm. As soon as this takes place, all perceptible distinction ceases between the original cambium of the bundles and the intermediate secondary meristem; or a closed cambium-ring is formed. The fibro-vascular masses which are now constantly formed accumulate greatly, while the original fundamental tissue diminishes more and more in mass. By the increase in size of the fibro-vascular substance in the segment of the stem, the epidermis and the cortical parenchyma become passively extended; their cells grow rapidly in a tangential direction; but their original form is again restored as they become divided by radial walls; and thus also division is subsequently brought about in the whole portion of the original fundamental tissue and the epidermis, by the processes which take place in the fibro-vascular substance. Fig. 56 (p. 69) represents these phenomena in the thickened hypocotyledonary segment of the stem of the sunflower; the figure however is equally available for *Ricinus*.

Sect. 18. **Laticiferous and Vesicular Vessels, Sap-conducting Intercellular Spaces, Glands.**—Like other forms of cells and tissues, those of which we are speaking occur both in the fundamental tissue and in the fibro-vascular bundles, and even in the epidermal system; and by a strict carrying out of the morphology of tissues these forms would also be considered as constituents of the three systems. If we nevertheless treat them both separately and together, the object is to place more conspicuously in the foreground their prominent physiological peculiarities. They show manifold transitions both to the forms of tissue of the system within which they lie, and among one another. The more simple vesicular vessels which occur especially in the parenchyma of the fundamental tissue of many Monocotyledons differ only by the greater length of the cells and by their union in rows from the surrounding parenchyma-cells; when more mature the cells of these rows coalesce; the septa become absorbed; and thus longer tubes, mostly placed near the epidermis, are formed. From these to the true laticiferous vessels is only a step. They are also the result of the coalescence of rectilinear or branched anastomosing rows of cells. These canals, filled with milky sap, lie abundantly in the phloëm-portion of the bundles, and accompany them through all parts of the plant, forming in it a continuous system. They occur also in xylem (*e. g.* Carica), where, originating from the coalescence of parenchyma-cells, they form an envelope round the vessels, and even penetrate into the cortex by means of the medullary rays; in other cases again they form part of the fundamental tissue of the pith or cortex.

Their walls are generally very thin when they arise from the coalescence of parenchyma-cells which has already taken place in the primary meristem; they may, however, become thick, and it scarcely admits of a doubt that in many cases (as Apocynaceæ and Euphorbiaceæ) the bast-fibres themselves become transformed into laticiferous vessels; according to Hanstein it is even probable that in some Aroideæ vessels of the xylem assume the form and function of laticiferous vessels. The morphological signification of these organs may thus be very various; physiologically they have this in common, that they contain dissolved and finely divided substances (emulsions) which find in them open courses for rapid motion. The same object is, however, also obtained in the plant by the cells pouring out the substances they contain into specially formed intercellular spaces, which, like the laticiferous vessels, may form a connected system of channels in the plant. These also are produced sometimes in the parenchymatous fundamental tissue, sometimes in the xylem, sometimes in the phloëm of the bundles; but they are easily distinguished from the former by the peculiar arrangement of the surrounding cells. The latex contained in them may be limpid, mucilaginous, or gummy (*e.g.* Araliaceæ), or there is mixed with it an emulsion of resin-forming materials (as in Umbelliferæ); or the passage contains a resin-producing ethereal oil (as in Coniferæ), or other odoriferous and coloured fluids of oily nature (*e.g.* Compositæ, Umbelliferæ). Glands are distinguished from the latex-vessels hitherto mentioned by their not presenting channels or systems of channels, but being local formations. Separate cells or roundish groups, whose partition-walls frequently become absorbed, may take the form of glands, so that here again, by the process of coalescence of cells, arise receptacles for special substances (mostly strongly odoriferous, viscid, oily, or coloured). Glands may arise anywhere in the tissue; and if they belong to the epidermis may discharge their secretions outwardly.

(a) *Laticiferous and Vesicular Vessels*[1] show, as has already been mentioned, such numerous and various transitions, that it would be desirable to be able to include them under a common term, such as Latex-sacs.

The Cichoriaceæ, Campanulaceæ, and Lobeliaceæ possess very perfectly developed laticiferous vessels, belonging to the fibro-vascular bundles, which they accompany throughout the whole plant as reticulately anastomosing tubes, imbedded, in the case of the Cichoriaceæ in the outer, in that of the two other families in the inner phloëm-layer. Their form is best recognised by boiling sections of these plants for some minutes in dilute solution of potash; the reticulations are then clearly recognised in the transparent tissue (Fig. 94), and it is easy to separate them entirely in large pieces. In the Papayaceæ (Carica and Vasconcella), the laticiferous vessels, on the other hand, run through the system of the fibro-vascular bundles; they,—*i.e.* the cells by the coalescence of which they are formed—are repeatedly produced in layers from the cambium with the other elements of the xylem; the pitted and reticulately thickened wood-vessels alternate with them. The branches of the laticiferous vessels envelope these in all directions, and are sometimes firmly fixed to their surface; but in addition horizontal branches of these bundles also penetrate the medullary rays; and these terminate

[1] J. Hanstein, Monatsberichte der Berl. Akad. 1859.—Ditto, Die Milchsaftgefässe u. verwandten Organe der Rinde. Berlin 1864.—Dippel, Verhandlungen des naturwiss. Vereins für Rheinland u. Westphalen. 22. Jahrg. vols. 1–9.—Ditto, Entstehung der Milchsaftgefässe u. deren Stellung im Gefässbündelsystem. Rotterdam 1865.—Vogel, Jahrb. für wissen. Bot. vol. V. p. 31.

towards the primary cortex in scattered ramifications or recurrent knots, as also in the pith if the stem is hollow. As in the last-named families, there is developed in the horizontal partition-walls which the pith-tissue forms at the origin of each leaf-stalk in the hollow of the stem, a rich reticulation of laticiferous vessels which penetrates across the horizontal partition-wall in countless ramifications and in several layers one over another, and connects the sacs of the medullary rays and of the whole wood-cylinder. In the Papaveraceæ (Chelidonium, Papaver, Sanguinaria) the laticiferous vessels are also very perfectly developed; they are not here, however, as in the families just named, united in band-like groups, but they run mostly at a greater distance from one another, dispersed through the phloëm and the surrounding parenchyma; single ones appear also in the pith, but do not penetrate into the xylem; lateral outgrowths and cross-anastomoses are found seldom in the stem, but abundantly in the leaves, and especially in the carpels in which close-meshed reticulations are formed in the parenchymatous fundamental tissue (Unger); similarly also in the cortex of the root. In this family, especially in the root-parenchyma of *Sanguinaria canadensis*, the origin of the laticiferous vessels from the coalescence of cell-rows (absorption of the walls between adjoining cells), may, according to Hanstein, be proved; imperfect unions occur in this case, in consequence of which the sacs appear bead-shaped. The richly developed system of the laticiferous vessels of the Urticaceæ, especially of Ficus and Humulus, runs in the cortex in close proximity to the fibro-vascular bundles of the bast, in Ficus also in the pith, but not in the wood; but they are neither so abundant nor so evidently segmented as in the Papaveraceæ, nor so regularly combined into a close-meshed net-work as in the Cichoriaceæ; they rather run within each segment of stem almost singly and uninterruptedly as uniform tubes, only occasionally putting forth a branch or uniting with another tube. In the nodes and leaves, on the other hand, they form numerous ramifications, sometimes united into a network; or small, fine, obtuse prolongations, as in the Cichoriacæ. In the thicker leaves of many figs they are widely dispersed through the parenchyma, and extend to close beneath the epidermis. The laticiferous vessels of Euphorbiaceæ are so far similar to these that they also belong to the branched description, and are abundantly distributed through the parenchyma of the fundamental tissue; but they are distinguished by possessing thicker walls, and being similar, in transverse section, to the bast-fibres. Developed most abundantly in the neighbourhood of the bast-fibre-bundles, they sometimes entirely replace them (*Euphorbia splendens*); from

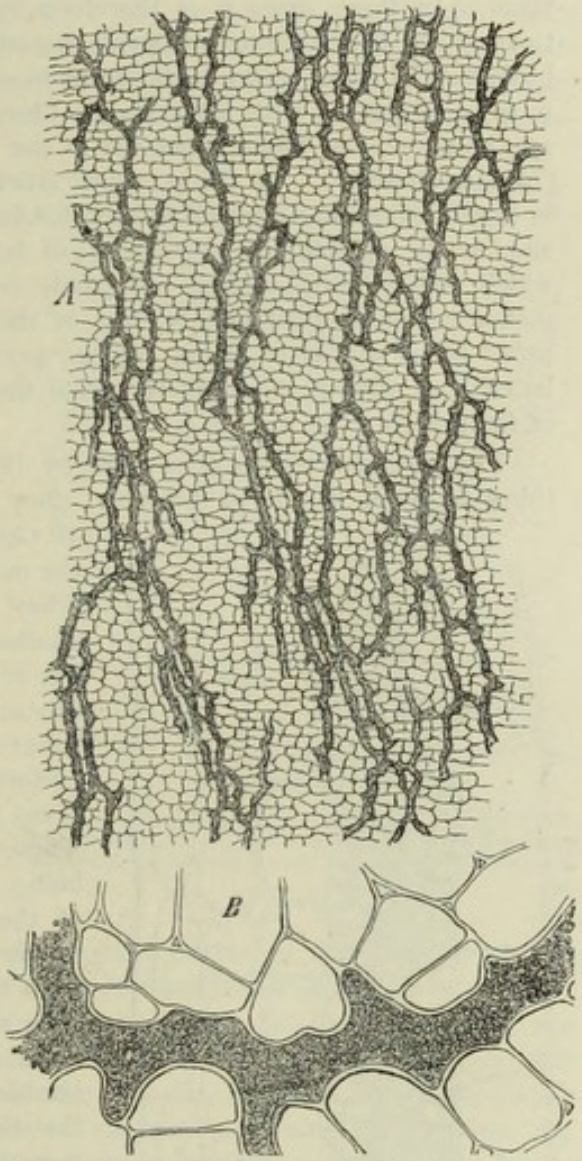

FIG. 94.—*A* tangential transverse section through the phloëm of the root of *Scorzonera hispanica*; a number of laticiferous vessels anastomosing laterally among one another run through the parenchymatous tissue; *B* a small piece of a laticiferous vessel with the adjoining parenchyma-cells, more strongly magnified.

them they run into the cortex and pith, forming, especially in the nodes of the stem and the cushions of the leaves, numerous ramifications. Still more similar to the bast-fibres are the laticiferous vessels of the Asclepiadæ and Apocynaceæ; some are pointed at both ends; sometimes also they have, like them, thickened and characteristically striated walls; they are found sometimes actually in the place of true bast-fibres, sometimes united with them into one bundle (of the phloëm), or surrounding them. In these cases it is therefore by the presence of the latex that the relationship of these metamorphosed bast-elements to true laticiferous vessels is established; the more milky their contents, the thinner becomes the wall (Hanstein, *l. c.* p. 21). Together with these simple fibre-like tubes, branched and anastomosing ones are, however, also found, especially in the nodes of the stem, the pith, and the cortex (*Nerium Oleander*). In the Aroideæ laticiferous vessels united into a network occur in the fibro-vascular bundles and the fundamental tissue; but some genera, as Caladium and Arum, exhibit the peculiarity of laticiferous tubes running within the xylem, which, from their position and partly from their structure, must be considered as metamorphosed spiral vessels; but in the fundamental tissue there also occur simple broad tubes similar to these. In the genus Acer the sieve-tubes are transformed into laticiferous vessels, as is inferred from their position in the phloëm and the structure of their walls.

The vesicular vessels discovered by Hanstein in species of Allium resemble sieve-tubes in form if not in position; they contain (evidently at least in the bulbs of *A. Cepa*) latex, and in some other respects resemble the more simple laticiferous vessels of Dicotyledons. They consist of long broad cells which touch one another at their broad ends and there have sieve-like or latticed septa; where two vessels are in lateral contact, the longitudinal walls have also a pitted structure similar to the sieve-tubes (Fig. 95); the perforation of the septa, *i. e.* the formation of open pores, is, however, doubtful in the species of Allium. These vesicular vessels permeate the scales of the bulb; at their base they anastomose, like those of the foliage-leaves and flower-stalks, into long nearly parallel rows, which are generally separated from the epidermis by 1–3 layers of cells. Similar rows are formed by the vesicular vessels of Amaryllideæ (Narcissus, Leucojum, Galanthus); they resemble, however, the laticiferous vessels in this, that the septa of the rows of cells become partially, sometimes entirely, absorbed; but their latex is not milky, and contains numerous needle-like crystals of calcium oxalate (raphides). To these must be added numerous other structures in Monocotyledons which bear scarcely any other resemblance to laticiferous vessels; in some genera of Liliaceæ (Scilla, Ornithogalum, Muscari) the vesicular vessels often form shorter interrupted rows of cells, and in the bulbs themselves larger isolated parenchyma-cells, similar to the former in containing raphides. That the cells containing raphides can, however, actually unite into tubes, which morphologically altogether resemble laticiferous vessels, is shown in the Commelynaceæ. Here rows of cells which are early distinguished from those which surround them by containing raphides arise in the young parenchyma of the fundamental tissue of the internodes and leaves; they no longer divide; while their neighbours continue to become shorter by septa, they remain

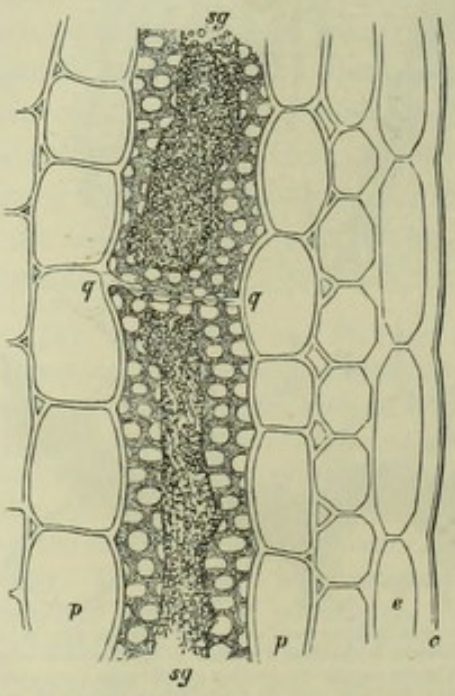

FIG. 95.—Longitudinal section through the bulb-scale of *Allium Cepa*; *e* the epidermis; *c* the cuticle; *p* parenchyma; *sg* the latex of the vesicular vessel coagulated by solution of potash; *q q* its septum; the longitudinal wall exhibits a pitted structure; it separates the vesicular vessel, in this case very visible, from one lying behind it.

longer, and their septa become absorbed, according to Hanstein, by the growth of the whole organ, by which the cells are extended. Thus long continuous tubes, filled with raphides of enormous length, arise out of the rows of cells of the fundamental tissue containing crystals.

(b) The term *Glands*[1] is applied to single cells or groups of cells which are strikingly distinguished by their contents from the surrounding tissue, especially when they contain odoriferous, strong tasting, coloured, oily, or resinous substances, which find no further use in changes connected with nutrition or growth. Usually the cell-walls also show certain differences from those of the adjoining cells, or they directly participate in the formation of the cavity and of the secretion which it contains, they themselves becoming absorbed. A sharp boundary-line can hardly be drawn, especially between unicellular glands and single cells with peculiar contents (*e.g.* tannin, crystals) dispersed through the tissue. It is more sharply marked in those that are compound; in them the mass of tissue which contains the products of secretion is usually surrounded by peculiarly developed layers, by which the whole is clearly marked off and individualised from the surrounding tissue; while generally the proper gland-tissue, surrounded by it, is at length absorbed, and forms a cavity filled by the products of absorption of the cell-walls, and by the coalescing cell-contents. The secretion may collect in the interior of the gland itself, as oil of camphor in single cells of the parenchyma of the leaf of *Camphora officinarum*, oil of citron in the cavities of the large compound glands in the rind of the fruit of species of Citrus; or it may be discharged externally, like the viscid excretion of the epidermis on the stem of *Lychnis viscaria*, the nectar of many nectaries, and the blastocolla of the viscid hairy covering of many leaf-buds (*vide infra*).

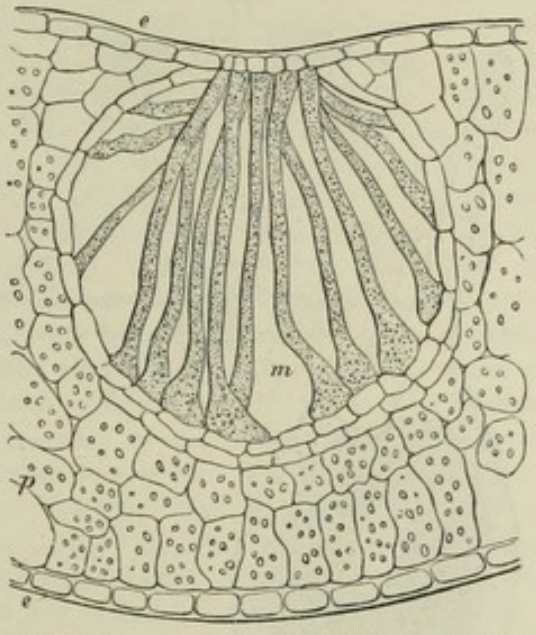

FIG. 96.—Transverse section of the leaf of *Psoralea hirta*; *e e* epidermis; *p* parenchyma containing chlorophyll; *m* receptacles of latex combining to form a gland. (After Hildebrand, *l. c.*)

Glands may be classified according to their position as internal (*i. e.* lying in the interior of the tissue), and superficial; but doubtful instances occur. In both cases the gland may consist of a single cell or a group of cells. Instances of internal simple glands are the camphor-cells just mentioned, those of rhubarb containing chrysophane, the gum-cells of Cactaceæ, orchis tubers (salep), and the crystalliferous cells whose cavity contains mucilaginous substances together with masses of crystals (sect. 11). Internal compound glands are, on the other hand, those that contain essential oils in the rind of the fruits of Citrus, as well as those covered only by the epidermis on the upper side of the leaves of *Dictamnus Fraxinella*. The former are to be recognised, even in the young ovary, as roundish groups of cells, the contents of which are distinguished by turbid protoplasm and small drops of oil; the walls of these cells soon swell, then become fluid, and thus form a spacious spherical space filled with mucilage and drops of essential oil suspended in it. The layers of cells that surround the cavity form an envelope, which marks it off sharply from the rest of the tissue. The formation of the internal glands of Dictamnus (Fig. 96 *c*) commences with only two cells, one of which belongs to the young epidermis, the other to the next layer of parenchyma; the former

[1] [See also J. B. Martinet, Organes de sécrétion des végétaux: Ann. des Sci. Nat. 5th ser. vol. XIV.—Ed.]

furnishes on its part two layers of cells, the outer of which (*d*) forms a continuation of the epidermis, while the inner (*c*) contributes to the formation of the tissue of the gland, which, in its principal mass, originates by divisions of the two mother-cells of the gland (*p p*); the enveloping layer of the gland is here scarcely developed, as is shown in Fig. 96 *c*, *C*. On the flower-stalks, bracts, and sepals of the same plant are formed large sessile or shortly stalked glands of somewhat ovoid form, bearing at their apex a single hair (Fig. 96 *b*). They always arise, as Rauter has shown, from a single cell of the young epidermis which divides first vertically then tangentially (Fig. 96, *A*); thus two layers are formed, the outer of which represents a continuation of the epidermis, while the inner produces, by further divisions, the tissue of the

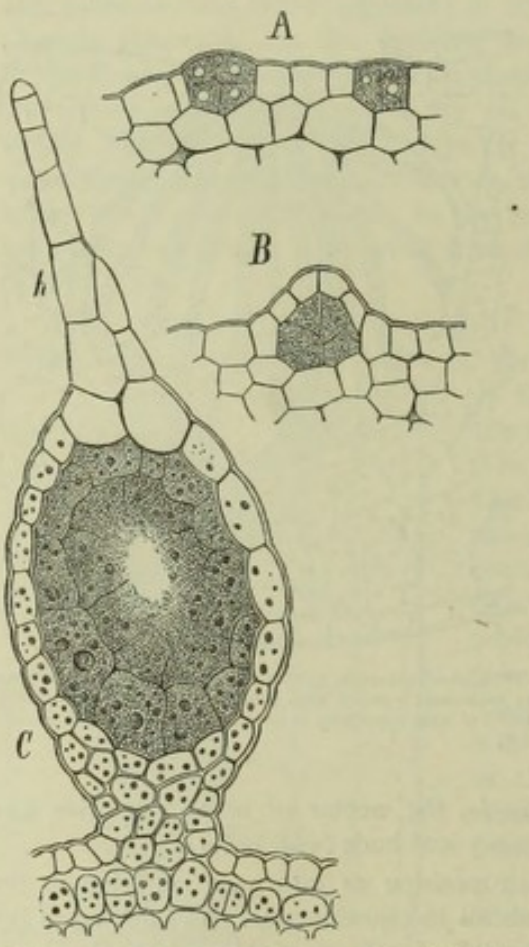

FIG. 96 *b*.—Glandular hair of *Dictamnus Fraxinella* (after Rauter). *A* and *B* earlier stages of development; *C* mature gland, with the hair at its apex.

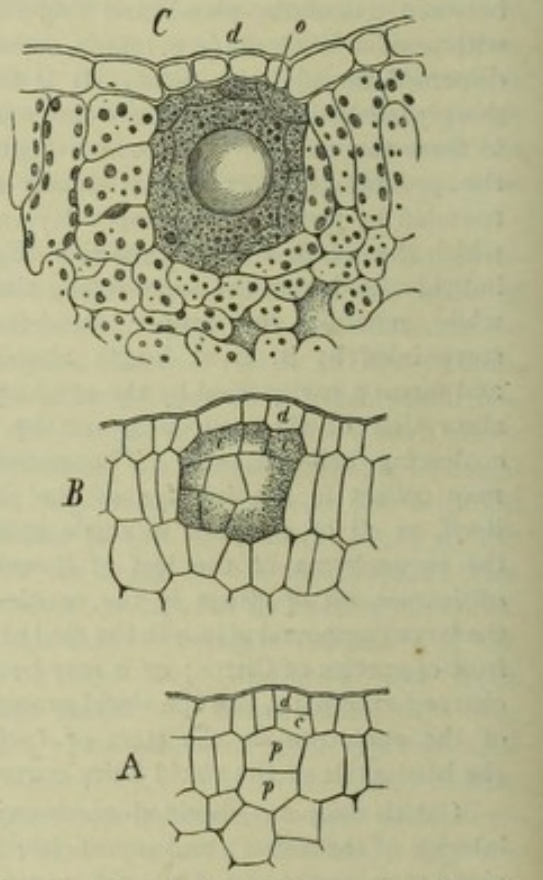

FIG. 96 *c*.—Internal gland of *Dictamnus Fraxinella* (after Rauter). *A* and *B* early stages of development, *C* mature gland; *d* the covering layer, developed as a continuation of the epidermis; *c* and *p* mother-cells of the gland-tissue; *e* a large drop of ethereal oil.

gland (*B*); in the further course of development, the whole substance of the gland now becomes, as it were, forced outwards above the surface of the organ (*C*); and when, finally, the secreting tissue is absorbed, a cavity is formed filled with mucilage and drops of essential oil, and now surrounded only by the continuation of the epidermis. Whether the substance of the gland is to be considered as a portion of the hair which it bears must remain undecided; it is also doubtful whether the gland should be termed an internal or an external one. Similar to glands in their origin are the gum-passages and gummy swellings of diseased stone-fruit. Grégorieff found the seat of the formation of the gum in them to be principally the soft bast of the fibro-vascular bundles which permeate the fruit-pulp; the cell-walls become absorbed after they have swelled up, indefinitely bounded cavities filled with gum are thus formed, which sometimes exude their contents externally through the flesh of the fruit when the production of gum is excessive.

Under the head of Superficial Glands should perhaps be included all those which

discharge their secretion immediately outwards, as the groups of cells which secrete the nectar of many nectaries, *e.g.* those at the base of the petals of *Fritillaria imperialis*, and at the base of the ovary of Nicotiana. The superficial glands are represented frequently and in many different forms by glandular hairs, to which a large number of leaves and stems owe their viscid character, and many leaf-buds their gummy or balsamic coatings. Not unfrequently odoriferous viscid substances collect in the globular terminal cells or knobs of simple glandular hairs; in other cases the odoriferous oily secretion penetrates through the cell-wall, and raises the cuticle in the form of bladders, collecting beneath it as a clear fluid, while the cells which produce it partially or entirely disappear, as in Salvia, Cannabis, and Humulus (the last on the perianth of the female flowers). We are indebted to a careful work of J. Hanstein's[1] for an accurate knowledge of the glandular hairs on the leaf-buds of many trees, shrubs, and herbs. The parts of the bud are coated by a gummy substance, or one composed of gum-mucilage and drops of balsam, which he calls Blastocolla, while the glandular hairs which produce them he terms Colleters. These multicellular shortly stalked hairs springing from an epidermal cell may expand upwards in a strap-shaped manner (Rumex), or may bear cells arranged in a fan on a kind of mid-rib (Cunonia, Coffea), or may form spherical or club-shaped knobs (*Ribes sanguineum*, *Syringa vulgaris*); in *Platanus acerifolia* branched rows of cells occur, the roundish terminal cells of which become glandular. The colleters attain their full development at a very early period in the bud, when the leaf-structures and portion of the stem out of which they spring are still very young, and consist of tissue which is yet scarcely differentiated. They are borne especially by the enveloping scales of the leaf-buds (Aesculus), by the stipules which precede the leaves in development (Cunonia, Viola, Prunus), the ochreæ (Polygonum), or the young leaves themselves (Ribes, Syringa). The secretion of the colleters is a watery mucilage in Polygonum, in the rest it is mixed with drops of balsam (resin). Gum-mucilage always arises from the conversion of a membranous layer lying beneath the cuticle of the colleter, the substance of which swells on addition of water, and raises the cuticle in places into small bladders (Rumex), or detaches it continuously from the hair as a large bladder; finally the cuticle bursts, and the mucilage escapes and envelopes the buds; the uninjured inner layer of cell-wall can, on its part, form a cuticle, beneath which a membranous layer again separates, and the process is repeated. Where balsam is also excreted, it may be recognised even in the cells of the hair; but it appears outside the cell-wall in drops as a deposit in the mucilage, or forms the principal mass of the secretion. Frequently also the young epidermis itself between the colleters participates in these processes (Polygonaceæ, Cunonia); or these latter are entirely absent, and the blastocolla is produced exclusively from the epidermis; thus arises, for instance, the greenish balsam on the bud-scales and foliage-leaves of poplars.

(c) *The Sap-conducting Intercellular Passages*[2]. It has already been explained in Fig. 66 (p. 76), that the 'resin passages' are intercellular spaces, arising usually from the separation of four cells; and they generally acquire a peculiar morphological character from the fact that the cells remain for a considerable time capable of division, and, obeying a common law of growth, form groups the arrangement of which may differ essentially from those by which they are surrounded. The development of the cell-walls is also different, as occurs especially in the resin-passages in the wood of Coniferæ. Here the cells which surround the passage are originally like pitted tracheïdes; but their walls remain thin and unlignified, their cavity enlarges, and their original position is obliterated by their growth. The contents of the cells which enclose the passage are more or less like those of the passage itself, since they escape from the one into the other. In Helianthus and other Compositæ it is a yellow or red intensely odoriferous oil; in Umbelliferæ a mixture of gum-mucilage and oily or resinous sub-

[1] Ueber die Organe der Harz- und Schleimabsonderung in den Laubknospen, Bot. Zeitg. 1868, no. 43 et seq. Compare the very instructive illustrations to this paper.

[2] Müller in Jahrb. für wissen. Bot. V. p. 387. 1867.—Thomas, ditto, IV. pp. 48–60.

stances (gum-resin); in Coniferæ and Terebinthaceæ a clear balsam, which hardens, on exposure to the air, into a firm resin.

The resin-passages run mostly in straight lines, or follow the course of the fibro-vascular bundles; apparently they only rarely anastomose. They so far resemble the simpler laticiferous vessels, that they may also form continuous systems running through the whole plant. When they occur in the parenchyma of the cortex and the pith which is formed from the primary meristem, they are mostly distributed at nearly equal distances through the transverse section of the stem, forming a circle; when produced in phloëm or xylem, they may recur periodically as elements of this system, and, so to speak, be formed in layers, *i.e.* in concentric circles, as, *e.g.* in the wood of Pinus, and in the phloëm of Coussonia.

The occurrence of these passages is limited to certain groups; they are found in a high state of development in Coniferæ and Cycadeæ, Terebinthaceæ, Umbelliferæ, Araliaceæ, and Compositæ.

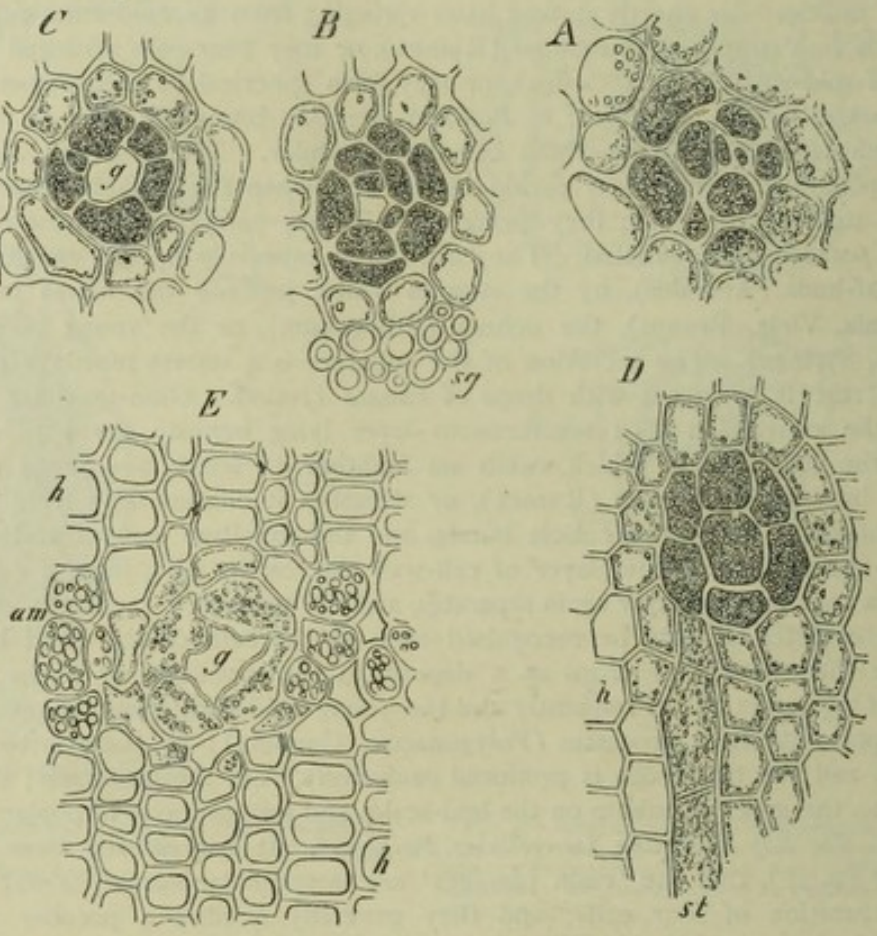

FIG. 97.—Transverse section of resin-passages (*g*) at the base of a first year's branch of *Pinus sylvestris* (×55⅓). *A*, *B*, *C* passages lying in the periphery of the pith (*sg* spiral-vessels of a fibro-vascular bundle); at *A* the formation of a passage has not taken place, but the cells destined for its formation are there, their walls having become weaker; *D* wood-cells (*h*) enclosing a group of resin-cells, not forming a passage (*st* a medullary ray); *E* part of the wood containing a resin-passage (*g*); next it wood-cells containing starch (*am*), forming in the wood a zone passing in a tangential direction from one passage to another.

When the passages lie in a tissue which undergoes rapid growth in diameter, they not unfrequently attain a considerable size in this same direction; as, *e.g.* in the primary cortex and leaf of Pinus (Fig. 60, *b*), Cycas, &c. When, on the other hand, the growth of the tissue in diameter is inconsiderable, as in the wood of Pinus, the intercellular space which has become enlarged into a passage remains also small (Fig. 97, *B*, *C*, *g*). In the pith of the first-year's twigs of Pinus groups of cells are also found which resemble, in contents and form, the environing cells of resin-passages, but do not separate from one another, and thus do not form a passage. In this case the wood which is already formed prevents a subsequent extension of the pith in diameter, and thus the space is wanting which would be necessary to the formation of the intercellular space (Fig. 97, *A*, *D*).

SECT. 19. **The Primary Meristem and the Apical Cell** [1].—At the growing ends of shoots, leaves, and roots, the forms of cell-tissue hitherto described do not yet exist; here is found a uniform tissue, the cells of which are all capable of division, rich in protoplasm, with thin and smooth walls, and containing no coarse granules. This tissue is termed Primary Meristem; it is a meristem because all the cells are capable of division, and must be considered primary (rather, perhaps, proto-meristem) because it presents the primary condition of the tissue, out of which the different forms of the permanent tissue are successively formed by differentiation. If the structure of the plant is in general simple, as in Algæ and Characeæ, the cell-forms arising from the primary meristem only differ slightly from one another. If the plant belongs to a higher type, as in Vascular Cryptogams and Phanerogams, from the uniform undifferentiated primary meristem proceeding from the growing apex layers of tissue of a different character first originate, within which, by further development of their cells (at a still greater distance from the primary meristem), the different cell-forms of the epidermal and fundamental tissue, as well as of the fibro-vascular bundles, finally arise. The differentiation takes place so gradually, and at such a different time in the various layers of the tissue, that no definite limitation of the primary meristem proceeding from the apex is possible. As growth proceeds at the end of shoots, leaves, and roots, portions of the primary meristem become gradually transformed further backwards into permanent tissue; but the primary meristem is always again renewed by the production of new cells close to the apex. Nevertheless whole organs, the apical growth of which soon ceases, may at first consist entirely of primary meristem, which finally passes over altogether into permanent tissue, so that no primary meristem is left. Examples of this are furnished by the development of the fruit of Mosses, of the sporangia of Ferns, and even of most leaves and fruits of Phanerogams.

The terminal portion of an organ with permanent apical growth, consisting entirely of primary meristem, is termed the *Punctum Vegetationis*; not unfrequently (but by no means always) it projects as a conical elongation, and is in this case distinguished as the Vegetative Cone.

The production and renewal of the primary meristem commence with the cells lying at the apex of the *punctum vegetationis*; and, by the manner in which this happens, two extreme cases may be distinguished, which are however united by transitional forms. In the one case, the usual one with Cryptogams though not without exception, *the whole of the cells* of the primary meristem trace their origin back to a single mother-cell, lying at the apex of the *punctum vegetationis* and

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[1] Nägeli, Die neueren Algensysteme. Neuenburg 1847.—Cramer in Pflanzenphysiol. Untersuchungen, Heft III. p. 21. Zürich.—Pringsheim, Jahrb. für wissen. Bot. III. p. 484.—Kny, ditto, IV. p. 64.—Hanstein, ditto, IV. p. 238.—Geyler, ditto, IV. p. 481.—Müller, ditto, V. p. 247.—Rees, ditto, VI. p. 209.—Nägeli und Leitgeb, in Beiträge zur wissen. Bot. Heft IV. München 1867.—J. Hanstein, Die Scheitelzellgruppe im Vegetationspunkt der Phanerogamen (in the Festschrift der niederrh. Ges. für Natur- und Heilkunde. Bonn, und Monatsübersicht of the same Society, July 5, 1869).—Hofmeister, Bot. Zeitg. p. 441, 1870.—Leitgeb, Sitzungsb. der Wiener Akad. 1868 and 1869, and Bot. Zeitg. nos. 3 and 34, 1871.—Reinke in Hanstein's Botan. Untersuchungen, Heft III. Bonn 1871.

called the *Apical Cell.* In some Cryptogams, on the other hand, and in Phanerogams, there is no single apical cell of this character. Even when a cell lies at the apex, it is not, as in the former case, distinguished by its greater size; and, what is of greater importance, it cannot be recognised as the single original mother-cell of all the cells of the primary meristem, nor even of a definite layer. We may distinguish, therefore, between the *Punctum Vegetationis* with and without an Apical Cell.

(a) *Punctum Vegetationis with an Apical Cell.* The formation of the primary meristem out of the apical cell may be brought about, as will be shown hereafter, in different ways, but it generally results from the repeated rhythmical division of each apical cell into two *unequal* daughter-cells. One of the two daughter-cells remains from the first similar to the mother-cell (the apical cell), and includes the apex; it is immediately enlarged by growth till it equals the previous apical cell in size, and then again divides, and so on. This process produces the appearance as if the apical cell always remained intact; and this has been assumed in ordinary language, although the apical cell existing at any time is only a daughter-cell of the preceding one. The other daughter-cell on the other hand appears from the first like a piece cut off from the back or side of the apical cell, generally in the form of a disc or angular plate, and is hence called the *Segment*[1]. In the simplest case the segment may, on its part, remain undivided; and then the whole tissue which is produced from the apical cell appears in the form of a simple thread or row of cells, as in some Algæ, Fungus-hyphæ, and hairs. But generally the segment is also again divided into two cells, each of which again breaks up into two, and this process is mostly repeated many times in the daughter-cells, until a more or less extensive mass of tissue is produced from the segment. The primary meristem now consists of such portions of tissue. A very simple case of this kind is shown in Fig. 98, where the

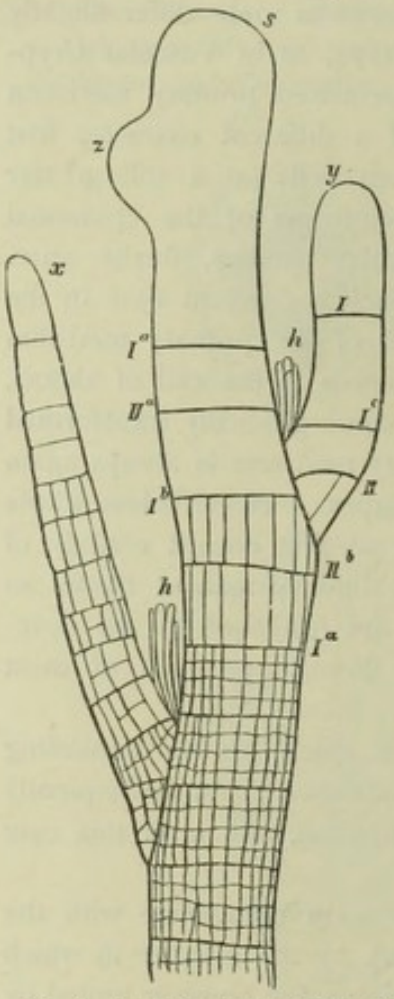

FIG. 98.—A branch of the thallome of *Stypocaulon scoparium* with two branchlets *x* and *y*, and the rudiment of a third branchlet *z* (after Geyler); all the lines indicate cell-walls.

[1] The portions of wall which enclose a segment-cell are different in their nature and origin, and behave differently in their subsequent growth. Each segment possesses two walls which were originally division-walls of the apical cell; they are generally parallel to one another, and are called the *Principal walls* of the segment; the older faces the base, the younger the apex of the organ. Another portion of the wall of the segment is a part of the outer wall of the apical cell; it may be termed the *Outer wall* of the segment. Where the segments arise as transverse discs of an apical cell, the process is very complicated, from the segmentation taking place on two or three sides; the segments have in this case also side-walls as well as the two principal walls and the outer wall, which intersect at oblique angles within and below. The side-walls are portions of the principal walls of older adjoining segments, which are always bounded by the youngest partition-wall of the apical cell, and this is at the same time the youngest principal wall.

apical cell, here very large (*s*), growing straight out from its base, is divided by septa (I^a, I^b), and thus forms the segments which lie in a row one over another; but each of these last is again immediately broken up by a septum (II^a, II^b) into two disc-shaped cells, and in each of these there arise numerous small cells by the formation of vertical and afterwards horizontal walls (as may be seen in the figure), further back from the apex; and it is easily seen how the whole branch is built up of portions of tissue, each of which is composed of a single segment. The same takes place on the lateral branchlets (*x*, *y*), which in this case arise originally from lateral protuberances from the apical cell. These processes are remarkably clearly seen in Stypocaulon, in the first place because only one row of segments is formed lying one over another, and in the second place because the segments themselves are transformed into portions of tissue without at the same time growing, as is usually the case; distortions often occur from the growth of the segments, which render difficult an investigation of the processes of division.

Figs. 99 and 100 show us a case in which the apical cell is divided alternately right and left by oblique walls so as to produce two rows of segments attached to one another in a zigzag manner by their inner and lower sides, but separated to some distance in front; in the angle which the two youngest segments enclose lies the apical cell (*s*). Fig. 99 shows the end of a shoot of *Metzgeria furcata* in the act of bifurcation; each fork ends in an apical cell (*s*); the segments and the masses of tissue which are formed from them are drawn just as they appear to the eye under the microscope in the superficial view of the flat strap-shaped shoot. But from the course of the cell-walls and the resulting grouping of cells around the apical cell the diagram represented in Fig. 100, *A*, is deduced, in which the distortions of the cell-walls occasioned by growth are omitted, and hence genetic relationships are represented more clearly. For further information Fig. 100, *B*, is added, which also represents diagrammatically the longitudinal section of the apical region, at right angles to the broad surface of the strap-shaped shoot. This longitudinal section bisects, behind the apical cell, the central nerve (Fig. 99, *n*, *n'*), which consists of several layers of cells, while the lateral expansions of the shoot are only one layer in thickness. The origin of the tissue is now clear from the diagrammatic Fig. 100, *A* and *B*, if it is observed in the first place that the portions of the surface indicated by *m*, *n*, *o*, *p*, and *q* are the segments of the apical cell (*s*) which were formed successively in the same order, so that *m* represents the oldest, *q* the youngest segment. From each segment a small piece is at first cut off behind by a wall oblique to the axis of the shoot; from the zigzag row of these inner divisions arises the mid-rib of the shoot, which attains a thickness of several layers of cells, each division first of all splitting up by a wall parallel to the surface of the shoot into two cells lying one over another; each of these cells on its side again divides in the same manner. Divisions at right angles to the surface of the shoot (Fig. 100, *B*) are then also formed in the uppermost and undermost of the cells produced in this way; an outer small-celled layer (covering the upper and under side) becomes formed on the mid-rib, surrounding an inner bundle which consists of longer cells. While the posterior sections of the segment produce the tissue of the nerve, the tissue

of the flat lateral portion (Fig. 99, *f*, *f'*) proceeds from the sections in front which face the margin of the shoot; and this tissue is only one cell-layer in thickness, no division taking place in it parallel to the surface of the shoot. All the divisions in these marginal sections of the segment are, on the contrary, at right angles to the surface of the shoot, and are produced by the marginal section first of all breaking up into two cells lying close to one another (cf. Fig. 100, *A*, *o*), each

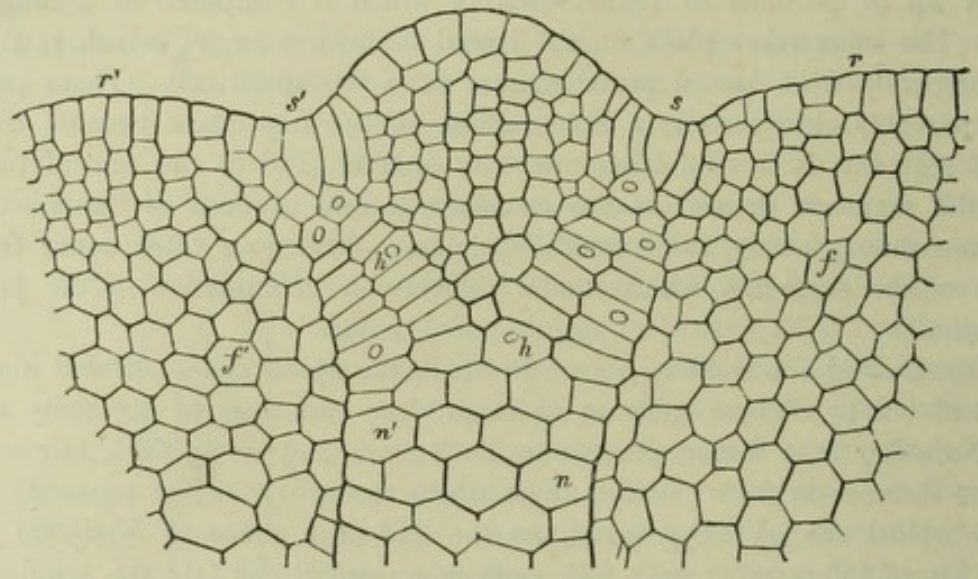

FIG. 99.—Apical region of a shoot of *Metzgeria furcata* in the act of dichotomous branching, looked at from the surface (after Kny). The shoots consist of a single layer of cells (*f f*), which is however penetrated by a mid-rib *n n'*, three to six layers in thickness.

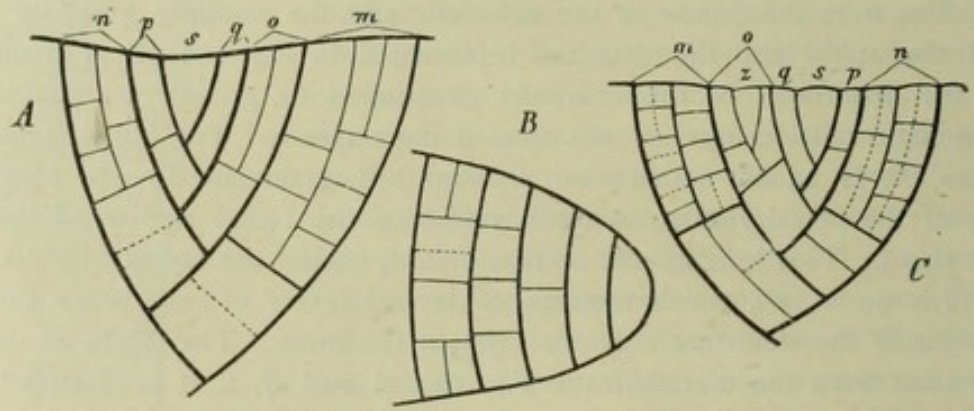

FIG. 100.—Diagrammatic representation of the segmentation of the apical cell, and of the first divisions in the segment of *Metzgeria furcata* (after Kny). *A* apex seen from the surface; *B* the same in vertical longitudinal section; *C* an apex in the act of dichotomous branching; a new apical cell is formed in the third-youngest segment.

of which then forms several shorter cells by repeated bipartition, and these may again undergo further division according to the activity of the growth. In general the first divisions only of the segment are constant; the further course of cell-multiplication is, according to the minute investigations of Kny, subject to many deviations. Since the tissue which is produced from the marginal sections assumes a prominent position during growth, it results that the apical cell lies, with the youngest segments, in a depression of the outline of the shoot; and thus we have here a simple example of the depression of the *punctum vegetationis* in the tissue which grows more luxuriantly around it, such as often occurs to a much greater extent in Fucaceæ, Ferns, and Phanerogams. The differentiation of the tissue out

of which the shoot of *Metzgeria furcata* is built up does not attain a high degree; the perfectly developed cells of the margin and of the mid-rib are only slightly different from one another; but it should be mentioned that this differentiation is brought about very early, even in the first division of the segment, so that the marginal tissue and the latest continuation of the mid-rib can be followed close up to the apical cell. Fig. 100, *C*, finally, affords an opportunity of learning the mode of formation of a new apical cell out of a cell of the meristem, a case which occurs often enough in Mosses and higher Cryptogams; while the thallome of Stypocaulon (Fig. 98) shows how the apical cell of the lateral shoot grows immediately from the apical cell of the principal process as a lateral protuberance, which is then cut off by a wall. In *Metzgeria furcata*, as is shown by the statements of Hofmeister, Kny, and Müller, it appears that the origin of a new apical cell may be brought about in a different manner; Fig. 100, *C*, shows the case described by Kny. In the third-youngest segment (*o*), which is formed from the apical cell (*s*), the customary separation into a nerve-mother-cell and a division belonging to the margin of the tissue has first taken place; the latter then breaks up, as is usually the case, into two cells lying close to one another; but the new apical cell is constituted by the appearance of a curved wall in one of these marginal cells of the second rank; and this wall comes into contact behind with the previous one, thus cutting out a wedge-shaped piece (*z*), which assumes at once the function of the apical cell of a new shoot. (We shall recur, in Chap. III, to this case of spurious dichotomy.)

In the Equisetaceæ and many Ferns, the axis of the shoot terminates in a comparatively very large apical cell, which is bounded by four walls—an outer one overarching the apex, spherically triangular, and free, and three converging obliquely below and within, which form at the same time the upper principal walls of the youngest segment (Fig. 101, *A*, *D*); the apical cell has hence the form of a segment of a sphere, or of a three-sided pyramid with spherical base turned upwards. The three plane principal walls of the apical cell are of different age; one is always the oldest, one younger, and the third the youngest. The next division-wall arises in the apical cell, and is parallel to the oldest wall; a segment is formed bounded by two triangular principal walls, an arched outer wall, and two nearly oblong side-walls[1]; after the apical cell has again grown to its original size a second division follows parallel to the next-younger principal wall, which is followed again, after fresh renewal of the apical cell, by a division parallel to the youngest principal wall. Three segments are now formed, placed somewhat like the steps of a winding staircase; each is in contact with a principal wall of the apical cell; and in this manner the divisions are repeated; and since each segment takes in a third of a circuit of the winding staircase, the segments out of which the stem is built up all lie in three straight rows parallel to the axis, each embracing a third of the diameter of the stem. In Fig. 101, *B* and *C*, the segments are numbered *I*, *II*, *III*, &c., according to the order of their formation, and are represented as they appear when the apex of the stem is seen from above and

[1] These side-walls are pieces of the principal walls of the previously existing adjoining segments, as is seen in *B* and *C*.

without (not in transverse section), or as if the arched surface of the apex were removed and spread out flat. If the segments are followed according to the order of their numbering, and the path thus described is indicated by a continuous line, a spiral is obtained, which is in reality an ascending spiral line, because each segment lies higher than the older ones, as is shown in Fig. 101, *D*, where, however, only two rows of segments are to be seen from without. The formation of tissue begins by each segment breaking up, soon after its production, into two

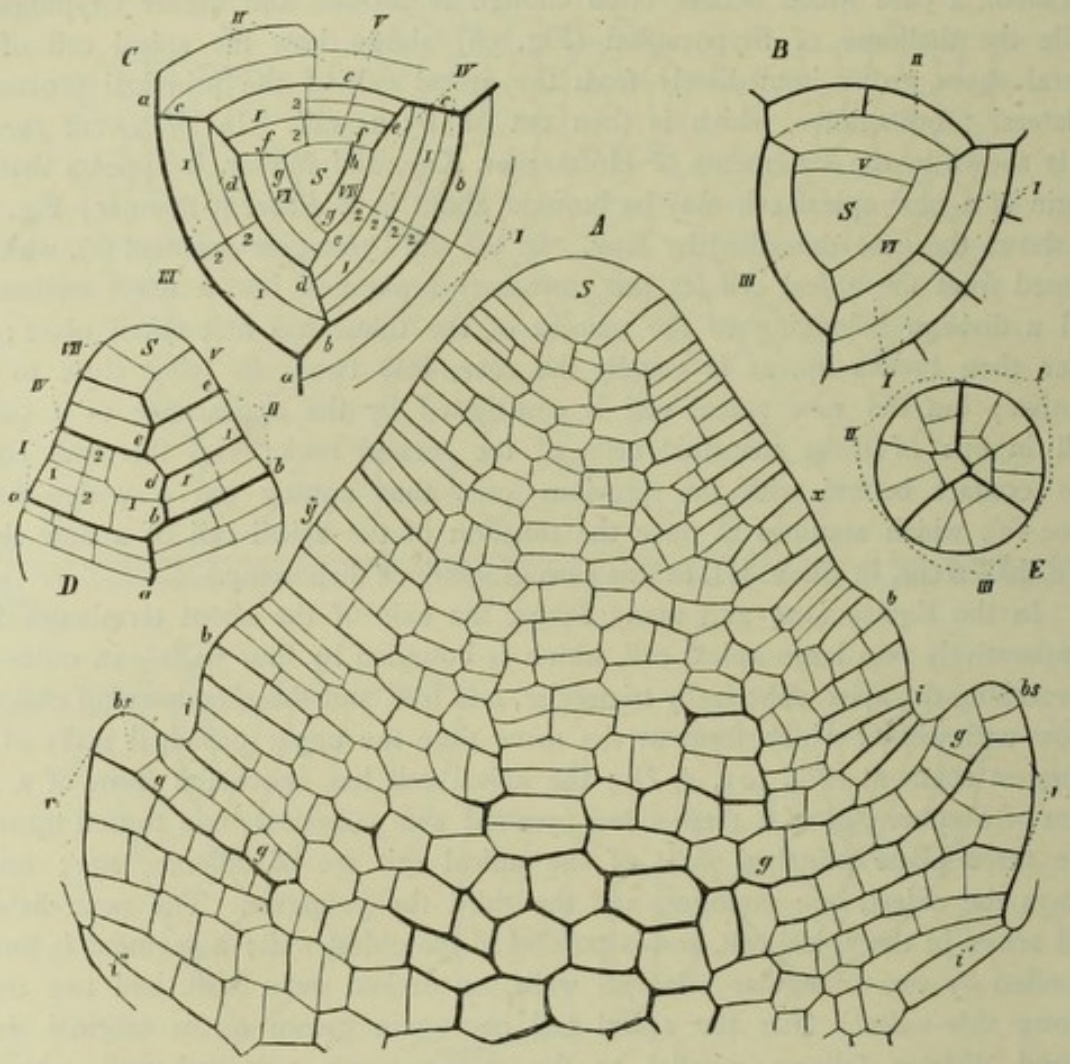

FIG. 101.—Apical regions of the stem of an Equisetum; *A* longitudinal section of an underground very strong bud of *E. Telmateia*, in September (×550); *B* view of the apex from above (both from nature); *C*, *D*, *E* the same of *E. arvense* (after Cramer). *C* diagrammatic ground-plan of the apical cell and of the youngest segment; *D* external view of a slender stem-apex; *E* transverse section through this from *I* to *D*; *S* is in all cases the apical cell, *I*, *II*, *III*, &c. the segments; 1, 2, 3, &c. the division-walls in the segments in the order of their formation; *x*, *y*, *b*, *bs* in *A* the first rudiments of leaves.

equal plates, a division-wall springing up parallel to the principal walls, indicated in *B*, *C*, and *D* by 1, 1. Since in each of these two half-segments which lie one on another the further processes are almost exactly the same, it is necessary to keep in view only one half. Each half of the segment becomes divided first of all by a vertical curved wall, which meets internally a side-wall, externally the centre of the outer wall of the segment. Since three segments compose one section of the stem, and each half-segment breaks up in this manner into two cells, the section of the stem now appears as if composed of six cells or sextants, whose walls are placed nearly radially, forming a six-rayed star, as is shown in the transverse section

Fig. 101, *E*. Hence the walls by which this division is brought about are called sextant-walls; in *C* and *D* they are indicated by the figure 2. The sextant-cells are still further broken up by vertical walls into an outer larger and an inner smaller cell (Fig. 101, *E*); and thus the foundation is laid of the two layers of tissue into which the primary meristem separates, *viz.* into an outer and an inner layer, as is clearly shown in Fig. 101, *A*. In the outer layer the divisions parallel to the principal walls and in vertical radial direction at first preponderate; in the inner layer the divisions are less numerous, so that the cells become more uniform in diameter. This inner mass of tissue, arising from the inner sections of the sextants, is the pith which splits as the stem developes, dries up, and thus causes its hollowness; from the outer layer of tissue of the primary meristem are also formed downwards the cortex, the system of the fibro-vascular bundles, and later the epidermis[1]. The external conformation also of Equisetum is brought about by the outermost layer of the primary meristem, as has already been shown in Fig. 101, *A*, where the protuberances *x*, *y*, *b*, *bs* represent the rudiments of the leaves; processes to which I shall recur at length hereafter. Here it need only be mentioned that each three consecutive segments undergo at an early period a small vertical displacement, of such a nature that they form, at least with their outer surfaces, a diagonal belt, which becomes arched and is the origin of a leaf-sheath.

As a final example of the formation of the primary meristem from an apical cell, we may now consider the processes that take place at the growing end of a Fern-root, with which the greater number of roots of Cryptogams agree in the main.

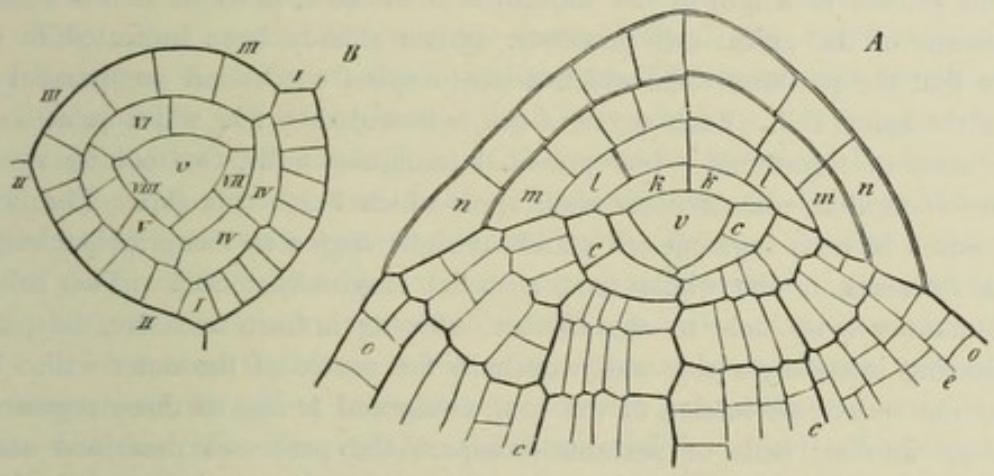

FIG. 102.—Apical region of a Fern-root; *A* longitudinal section through the end of the root of *Pteris hastata*; *B* transverse section through the apical cell and adjacent segments of the root of *Asplenium Filix-fœmina* (after Nägeli and Leitgeb).

Fig. 102, *A*, shows the axial longitudinal section through a Fern-root, with the point turned upwards. From the apical cell *v* arises not merely the tissue of the substance of the root (*o*, *c*), but also the root-cap *k*, *l*, *m*, *n*, a mass of tissue which covers like a helmet the *punctum vegetationis* of every root. The apical cell in this case resembles those of the stem of Equisetaceæ and of many other Cryptogams, in so far as it presents a three-sided pyramidal segment of a sphere; this form is sufficiently

[1] Compare Book II, Class of Equisetaceæ, and the formation of their tissue.

seen by comparing the longitudinal section *A* with the transverse section *B* (*o*). Here also three straight rows of segments are formed by successive divisions of the apical cell, which are numbered according to their order in age, *I*, *II*, *III*, &c., in Fig. *B*; and here also a spiral is described by the line connecting the centres of the consecutive segments. The great difference between the root and the apex of the growing stem of Cryptogams lies however especially in this, that in the former the apical cell not only produces these segments which build up the tissue of the root[1], but other segments also which build up the root-cap. These latter are cut off from the apical cell by septa in such a manner that they cover them like a cap; every such segment belonging to a root-cap is hence termed simply a Cap-cell. According to the investigations of Nägeli and Leitgeb, it appears to be the rule that whenever three segments have been formed (from the substance of the root), a new cap-cell arises; but this rule is not always strictly adhered to.

The cap-cell increases quickly in breadth, and its form, originally spherically-triangular in transverse section, passes over into a circle. It is simultaneously divided into two equal halves by a wall vertical to its original surface and hence parallel to the axis of the root; in each of these halves a longitudinal wall again springs up vertical to the former, by which four square cells are formed. Each quadrant again breaks up into two cells (octants), the further divisions varying in different species. In the layers of the cap which follow one another, the direction of the quadrants is not the same but alternate; *i. e.* the quadrant-walls of one layer deviate from those of the preceding and following ones by about 45°.

The growth in length of the substance of the root, in so far as it is occasioned by divisions of the apical cell, proceeds, as has already been indicated, in such a manner that the partition-walls which arise in spiral succession are parallel to the sides of the apical cell. Each segment-cell is bounded by five walls, as at the apex of the stem of Equisetum,—two principal triangular walls, two oblong side-walls, and one somewhat convex outer wall, upon which lies a root-cap. The first wall which arises in each segment-cell stands at right angles to the principal walls, and is, with reference to the whole root, a radial longitudinal wall. Two cells arise in this manner lying close to one another, differing in form and size, the partition-wall meeting internally a side-wall, externally the centre of the outer wall. In this manner the transverse section of the root, composed at first of three segment-cells, breaks up into six cells or sextants (compare the processes described above in the stem of Equisetum); three of these sextants reach to the centre of the section; but the three which alternate with them do not. The sextant-walls are seen in Fig. 102, *B*, in the segments *IV*, *V*, *VI*, *VII*, as dividing lines of the outer wall; in a transverse section made deeper they would form, together with the three side-walls of the three segments, a six-rayed star, similar to that in Fig. 101, *E* (compare Book II, Equisetaceæ, diagram of root). Each sextant-wall is next divided again by a wall parallel to the surface of the root into an inner and an outer cell; in the transverse section of the root at this stage (*i. e.* in the corresponding transverse section beneath the apex), twelve cells can therefore be recognised, of which the six

[1] They are bounded by thicker lines in the longitudinal section *A*.

outer ones form a peripheral layer, and the six inner ones a central body. The longitudinal section, Fig. 102, *A*, shows this wall at *c c*, and it may thus be seen how the mass of the substance of the root is broken up by it into an outer layer *o c* and an inner thick bundle *c c c c*. Out of the former arises by further division a tissue which becomes differentiated further backwards into epidermis *o* and cortex (between *o* and *c*); the axial bundle *c c c c*, on the other hand, which is the result of further longitudinal divisions of the inner sections of the sextants, forms the procambium-cylinder of the root, in which arise the vascular bundles. In this case also the first separation of the subsequent masses of tissue is occasioned by the first divisions of the youngest segments; but a comparison of the corresponding process in the stem of Equisetum shows that the mass of tissue which is formed from the central portions of the sextant, has quite a different signification; and the same is the case with the peripheral layer. A further insight into the origin of the forms of tissue of the root out of these portions of the primary meristem will be afforded in the consideration of Ferns and Equisetaceæ.

In conclusion, it may be remarked that the segments of the apical cell, where they arise in two or three rows, have at first a position oblique to the ideal axis of the organ, and enclose an angle open towards the apical cell; but, in consequence of growth, the position of the segments generally changes so that they come to lie gradually more transversely, and finally at a certain distance from the apical cell the principal walls lie at right angles to the axis of the organ. The process is not clearly shown in Figs. 101 and 102; but more evidently in examples to be brought forward later (*e.g.* Fig. 142).

(b) *Puncta Vegetationis without an Apical Cell* occur generally in Phanerogams. The apical region of growing shoots, leaves, and roots consists of a primary meristem, the cells of which are very small in proportion to the circumference of the whole *punctum vegetationis*, and very numerous. It has not yet been demonstrated whether only the cells next the apex can be traced back to a single primary mother-cell, although sometimes undoubtedly one cell lying at the apex is distinguished by somewhat greater size and by its figure. In many shoots the surface of the apex seen from above shows an arrangement of the superficial rows of cells which to a certain extent points to this one cell as their common primary mother-cell; but even if this were the case, which is by no means proved, it is, on the other hand, altogether impossible to connect genetically the inner layers of cells also with this cell. The peculiar significance of the apical cell of Cryptogams lies in the fact that all the cells of the primary meristem furnish evidence of different degrees of descent from it.

But as in Cryptogams certain layers of the primary meristem are prepared by the first divisions of the segment-cells to pass over into the differentiated tissue-systems further backwards from the apex, so also in Phanerogams a definite arrangement of the cells is brought about in the primary meristem of the *punctum vegetationis* of such a kind that the single layers of the primary meristem, when followed further backwards, have a genetic relation with the epidermal tissue, the cortex, and the fibro-vascular bundles, and may be recognised as the first rudiments of them. The outermost layers run uninterruptedly over the apex of the *punctum vegetationis*, overarching an inner mass of tissue of the primary meristem, which

latter, on its part, sometimes runs out beneath the apex into a single cell (in Hippuris and *Udora canadensis*, according to Sanio), but usually terminates in a somewhat subordinate group of cells.

While in Cryptogams with an apical cell, an evident cell of this kind is first of all formed where a lateral outgrowth (shoot, leaf, root) is about to be newly formed on the *punctum vegetationis*, in Phanerogams, on the other hand, a whole group of cells, including inner and outer layers, becomes developed at the spot in question, so that even at the first commencement of an organ, no one predominating apical cell can be recognised (Fig. 103, *k k*). After Sanio[1] had investigated these processes in Phanerogams, Hanstein[2] studied them in a more general and detailed manner, and has recently shown especially that even in the embryo of Phanerogams the first divisions take place in such a manner as to exclude from the first the existence of an apical cell; on the other hand, a differentiation into an outer layer and an inner nucleus of tissue soon manifests itself[3].

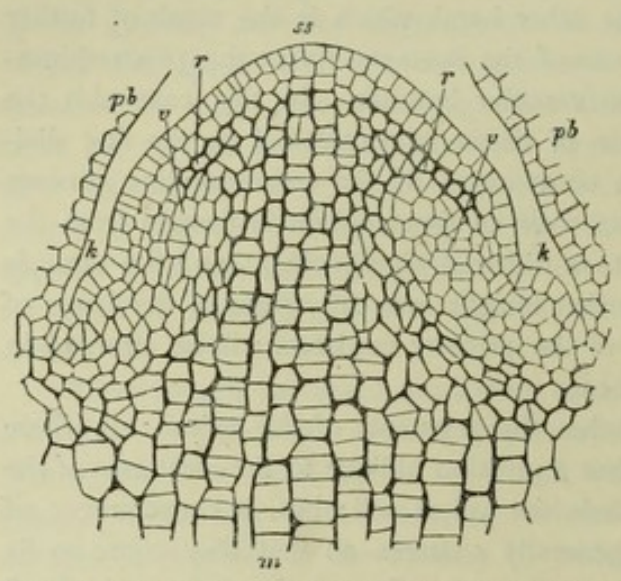

FIG. 103.—Longitudinal section through the apical region of the stem of an embryo of *Phaseolus multiflorus*; *ss* apex; *pb* part of the two first leaves; *k k* their axillary buds.

The outermost layer of the primary meristem which covers the *punctum vegetationis* together with its apex is the immediate continuation of the epidermis of the older part which lies further backwards; it may therefore be termed the Primordial Epidermis; Hanstein has however already applied to it the name Dermatogen. It is distinguished by the circumstance that divisions occur in it exclusively at right angles to the surface (it is only at a subsequent period that tangential divisions also sometimes occur when the epidermis consists of several layers).

Beneath the Primordial Epidermis are generally found one or more layers which also cover the apex continuously, and out of which the cortex originates further backwards from the apex (Fig. 112, *r r*, p. 141); they represent therefore the Primordial Cortex; Hanstein calls this layer of the primary meristem the Periblem. Enclosed and overarched by this is a nucleus of tissue, which may be followed out as an immediate continuation of the fibro-vascular bundles, and of the pith enclosed by them, as is shown in Fig. 112, where the later woody tissue (*f f*), together with its vessels (*g g*) and the pith (*m*), run out into a group of primary meristem, which, lying behind the apex (*s*), is covered by the primary epidermis and the primary cortex. The thickening-ring of Sanio mentioned in an earlier paragraph, in which the first fibro-

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[1] Sanio, in Bot. Zeitg. pp. 184 et seq. 1865.

[2] J. Hanstein, Die Scheitelzellgruppe im Vegetationspunkt der Phanerogamen. Bonn 1868.

[3] J. Hanstein, Monatsber. der niederrh. Gesell. July 5, 1869. For further details see the general characteristics of Phanerogams in Book II.

vascular bundles arise, thus corresponds to the outer layer of this inner tissue-nucleus (which Hanstein terms Plerome), when a pith is formed. If no pith is formed, as in many roots and some shoots (*e. g.* Hippuris, Udora, &c.), the whole of the plerome is developed into procambium, and this into an axial fibro-vascular cylinder, in which two or more vascular bundles and bast-bundles are then formed.

The origin of the root-cap in Phanerogams may be considered, according to the recent investigations of Hanstein and Reinke, simply as a luxuriant growth of the primordial epidermis (the dermatogen) localised at the apex, in such a manner that the part of the dermatogen which covers the apex of the root divides periodically by tangential walls. Thus the dermatogen splits at the apex into two layers of cells, the outermost of which developes into a (many-celled) cap the Root-cap,

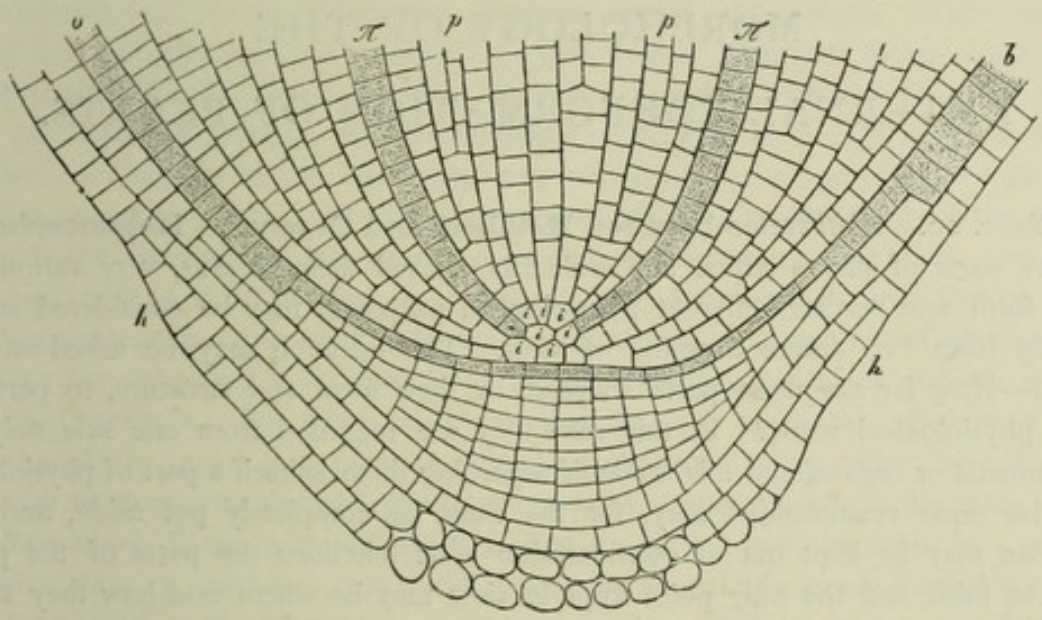

FIG. 104.—Longitudinal section of the apical region in the young root of the sunflower (after Reinke); *h h* the root-cap; *b b* (figured dark) the dermatogen; *p p* the plerome; its inner (dark) layer *π π* the pericambium; between *π* and *b* lies the periblem; *i i* the primary mother-cells, the origin of the periblem and plerome.

while the inner layer at first again performs the functions of the dermatogen, until a new splitting of the layer at the apex causes the formation of a new stratum, which again, on its part, as in Cryptogams, becomes separated by tangential divisions into several layers, as is exemplified in Fig. 104. (On the origin of secondary roots from the pericambium, Fig. 104, *π π*, cf. sect. 23.)

According to the description here given, which can only serve as a preparation to the beginner in a few examples for what follows, it might almost appear as if the processes in the *punctum vegetationis* of Phanerogams were essentially different from those in Cryptogams, a hypothesis which I however do not accept. On the one hand the careful investigations of Nägeli and Leitgeb in Lycopodiaceæ (*l. c.*) on this point prove that in this family the significance of the apical cell in the production of the primary meristem is different from that in other Cryptogams, and approximates to that which occurs in Phanerogams; and on the other hand the apical cell of Cryptogams may, equally with the apical cell-group of Phanerogams, be considered the starting-point of the first differentiation of the layers of tissue.

CHAPTER III.

MORPHOLOGY OF THE EXTERNAL CONFORMATION OF PLANTS.

Sect. 20. **Difference between Members and Organs**[1]. **Metamorphosis.** —The parts of plants which are ordinarily termed their Organs, very various in their form and serving different physiological purposes, may be considered scientifically from two different points of view. The question may be asked at the outset—How far are these parts adapted, by their form and structure, to perform their physiological work? In this case they are regarded from one side only as instruments or organs, and this mode of regarding them is itself a part of physiology. Or else these relationships may, for the time, be completely put aside, and the question may be kept out of consideration what functions the parts of the plant have to fulfil, and the only point kept in view may be where and how they arise, in what manner the origin and growth of one member are related in space and time to those of another. This mode of regarding them is the morphological one. It is obvious that this mode is as one-sided as the physiological; but investigation and description require, here as everywhere else in science, abstractions of this kind; and they are not only not hurtful, but even of the greatest assistance to investigation, if the investigator is only clearly conscious that they are abstractions.

In this chapter we shall concern ourselves exclusively with the morphological consideration of the parts of a plant.

But before we proceed to a more minute investigation, it will be useful to get a somewhat more exact comprehension of the relationship between the physiological and the morphological view.

Morphological investigation has led to the result that the infinite variety of the parts of plants, which in their mature state are adapted to altogether different functions, may nevertheless be referred to a few *Original forms*, if regard is paid to their development, their mutual positions, the relative time of their formation,

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[1] Nägeli und Schwendener, Das Mikroskop, p. 599. Leipzig 1867.—Hofmeister, Allgemeine Morphologie der Gewächse, sect. 1, 2. Leipzig 1868.—Hanstein, Botanische Abhandlungen aus dem Gebiete der Morphologie u. Physiologie, Heft I. p. 85. Bonn 1870.

and their earliest states; that, for instance, the thick scales of a bulb, the cuticular appendages of many tubers, the parts of the calyx and corolla, the stamens and carpels, many tendrils and prickles, &c., are, in these respects, altogether similar to the green organs which have been termed simply leaves (foliage-leaves). All these structures are therefore equally called leaves; and this designation is frequently justified by the fact that many of these organs, under peculiar conditions, actually become transformed into green leaves[1]. Since the green organs which are termed leaves in popular language (the foliage-leaves) may be considered as the primary form of leaves or as leaves *par excellence*, the remaining structures, which are also recognised as leaf-like, are termed changed, transformed, or *metamorphosed* leaves. The same is also the case with those parts to which the leaves are attached, and from which they grow as lateral appendages. They appear sometimes as cylindrical or prismatic slender greatly elongated stems, sometimes as thick roundish tubers, or are often hard and lignified (trunks). In other cases they are soft and flexible, either embracing other firm bodies (bines), or firmly attached to them (as in the ivy); they may also occur as sharp spines or as tendrils (as the grape-vine). All this is connected with the mode of life of the plant, and with the functions of the structures under consideration. But if the one characteristic only is kept in view that they all bear leaves which arise below their growing apices, an agreement is found as important as complete, which may for the time be altogether abstracted from the physiological functions and the corresponding structure. But when once this abstraction is made, the agreement may be denoted by applying a common name to all those parts which bear leaves; they may be termed Stem-structures (Caulomes) or simply Axes. In the same sense therefore in which, for example, the tendril of a pea is a leaf, the tuber of a potato is also a stem or axial structure; and just as the tendril of a pea is termed a metamorphosed leaf, so the tuber of a potato may also be called a metamorphosed stem.

The same is the case with the hairs as with the leaves and axes; the distinguishing characters of root-hairs, woolly hairs, prickles, glandular hairs, &c., is that they all originate as outgrowths of epidermis-cells. If we now go a step further, we may term all appendages of other parts which originate as outgrowths of epidermis-cells, whatever their form and function, Hairs (Trichomes). Thus the so-called paleæ and sporangia of Ferns are trichomes; or, if the ordinary filiform hairs are considered the original form, they are then metamorphosed hairs. It does not necessarily follow that the hairs grow from a true epidermis; it may be held sufficient that they arise from single superficial cells; and thus the number of the external appendages termed trichomes is still further increased.

As in the case of stems, leaves, and hairs, we may speak also of metamorphosed roots; they are usually filiform long and slender, but sometimes thick and tuberous; usually they grow beneath the ground, but also sometimes above ground, even in an upward direction. Nevertheless, under all circumstances roots maintain so striking a similarity to their typical forms that the term metamorphosed is but seldom applied to them.

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[1] It was these phenomena which first called Goethe's attention to the metamorphosis of leaves; at present the doctrine of metamorphosis rests on a better scientific foundation.

This mode of investigation, applied to Vascular Cryptogams and Phanerogams, has shown that all the organs of these plants may be referred to one of these morphological categories; every organ is either Stem (Axis), Root, Leaf, or Hair. Mosses have no root in a morphological sense, although they possess organs which completely fulfil the functions of roots; on the other hand most Mosses have leaves which grow on stems (axes). In Algæ, Fungi, and Lichens, the body of the plant has generally appendages which may be termed hairs; but roots in the morphological sense are always absent, and the idea of the leaf, as understood in higher plants, can no longer be rightly applied even in those cases where the external form of the mature parts is similar to the foliage-leaves of higher plants (*e. g. Laminaria digitata*, &c.). It is now agreed to apply to those vegetable structures in which the morphological distinction of stem and leaves cannot be carried out in the present state of our knowledge (and from which true roots are always absent), the morphological term Thallus or Thallome. In contradistinction to Thallus-plants (Thallophytes), all plants in which leaves can be morphologically distinguished might be termed Phyllophytes; the name Cormophytes has, however, been given in preference to them. From what has been said it will be seen that the thallophyte is only distinguished from a cormophyte by the lateral outgrowths which occur somewhere or other on it not presenting sufficient morphological distinctions from the part which bears them, to permit us to term them leaves in the same sense as in the more highly differentiated plants. But as the morphological distinctions of stem and leaf are not yet sufficiently established even in higher plants, it is impossible to draw a sharp boundary between Thallophytes and Cormophytes, and indeed it is certain that one does not exist.

If now we accept the ideas Thallome, Stem (Caulome), Leaf (Phyllome), and Hair (Trichome)[1], in the senses indicated, it can no longer be said that the leaf is the organ for this or that function; for leaves may undertake all possible functions; and the same remark applies also to the other parts. It is therefore on all accounts inexpedient simply to call the thallomes, stems, leaves, and hairs organs, for many of them have in fact no function at all. In order to avoid this mode of expression, which is confusing and foreign to morphology, it is obviously best to speak in this sense not of Organs, but of Members. The term Member is used when we speak of a part of a whole in reference to its form or position and not to any special purpose it may serve. In the same manner, from a morphological point of view, stems, leaves, hairs, roots, thallus-branches, are simply members of the plant-form; but a *particular* leaf, a *particular* portion of the stem, &c., may be an organ for this or that function, which it is the province of physiology to investigate.

The morphological nature of a member is best recognised in its earliest stages of development, and by its relative position in the series of processes of growth; the morphological definitions depend therefore essentially on the history of development.

The older a member becomes, the more obvious becomes its adaptation to a definite function, the more completely is its morphological character often lost. In

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[1] Cf. Nägeli und Schwendener, Das Mikroskop, II. p. 591.

their earliest states the members to which the same morphological names are applied (*e. g.* all the leaves of a plant) are extremely similar to one another; at a subsequent period all those distinctions arise which correspond to their different functions. With reference to these relationships we may now obtain a definition of Metamorphosis which can be used in a scientific manner: — *Metamorphosis is the varied development of members of the same morphological significance resulting from their adaptation to definite functions.*

(a) The conceptions of Stem, Leaf, Root, Trichome, as at present employed in botany, result from the consideration of highly developed plants the different members of which actually present considerable diversities, from a purely formal point of view; but if the attempt is made to apply these conceptions in the same manner to the less differentiated plants, Hepaticæ, Algæ, Lichens, and Fungi, many difficulties arise, depending principally on the fact that the members of the thallome sometimes display striking resemblances to leaves, hairs, stems, and even roots, while other characteristics of these parts are absent. In a word, transitions occur from the members of Thallophytes which are morphologically but slightly differentiated to the highly differentiated members of Cormophytes. In the members which we term stem, leaf, root, hair, it is clear that those differences are only augmented which also occur, though in a lesser degree, in the more homogeneous ramifications of the thallome especially of the higher Algæ; absolute distinctions between thallomes and leaf-bearing axes are not to be found. It is therefore a matter of convenience where the boundary-line is drawn.

(b) The expressions Thallome, Caulome, Phyllome, Trichome, Root, designate, as has been said, several ideas, from the definition of which are eliminated all those properties of the members which are calculated only for definite functions, while a few characteristics only, which concern their origin and mutual position, are kept in view. Parts which are physiologically entirely different may therefore be morphologically *equivalent*, and, *vice versâ*, physiologically equivalent organs may fall morphologically under quite different conceptions. The statement, *e. g.* that the sporangia of Ferns are trichomes, means only that their origin, like that of all hairs, is from the epidermis-cells; in this characteristic hairs and the sporangia of Ferns are morphologically equivalent. On the other hand the underground hairs of Mosses and true roots are physiologically equivalent; both serve for the absorption of nourishment and the fixing of the plant in the ground, although the former fall under the morphological conception of trichomes, the latter of roots.

(c) General ideas, like those considered here and in the sequel, depend always on abstractions, the practical clearness of the particular ideas from which they have been obtained by abstraction is therefore necessarily wanting in them. How far the abstraction may be carried is more or less arbitrary; and the only correction for this arbitrariness lies in a reference to the usefulness of the idea for scientific reasoning. Those ideas are the most useful which, from the greater precision of the definition, and from their greater clearness, include the greatest possible number of particular cases; for in this manner is that complete general comprehension of the phenomena most easily obtained which must precede a closer examination of them. The definitions in the following paragraphs are given from this point of view.

Sect. 21. **Leaves and Leaf-forming Axes**[1].—The members of the plant which are called Leaves (Phyllomes) in Characeæ, Mosses, Vascular Cryptogams, and

[1] Nägeli u. Schwendener, Das Mikroskop, pp. 599 et seq. Leipzig 1869.—Hofmeister, Allgemeine Morphologie der Gewebe, sect. 2. Leipzig 1868.—Pringsheim, Jahrb. für wissen. Bot. III. p. 484. Derselbe über Utricularia. Monatsber. der Berliner Akad. Feb. 1869.—Hanstein, Bot. Abhandlungen. Heft I. Bonn 1870.—Leitgeb, Botan. Zeitg. no. 3, 1871.

Phanerogams, are related to the axis or stem from which they are derived in the manner described in the following paragraphs.

(1) *The Leaves always originate below the growing apex of the stem as lateral outgrowths*, either singly or several at the same height, *i.e.* at an equal distance

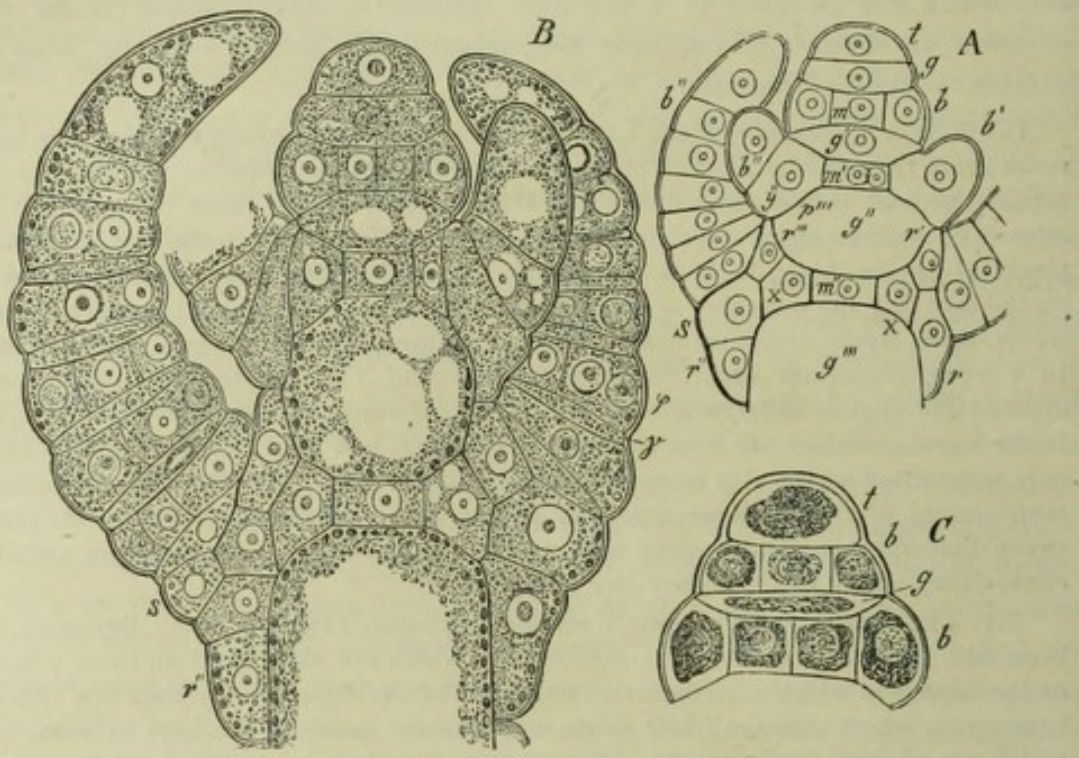

FIG. 105.—Longitudinal section through the apical region of three primary shoots of *Chara fragilis*; *t* the apical cell, in which segments are formed by septa; each segment being further divided by a curved septum into a lower cell no further divisible which developes into an internode *g' g'' g'''*, and an upper cell which produces a node *m m'* and the leaves. Each node-cell produces a whorl of leaves of different ages. (For a more exact description, see Book II. Characeæ.)

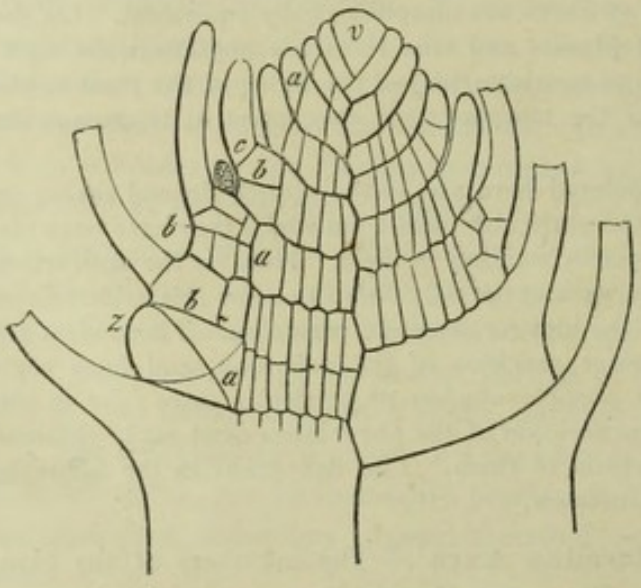

FIG. 106.—Longitudinal section through the apical region of a stem of *Fontinalis antipyretica*, a Moss growing in water (after Leitgeb); *v* the apical cell of the shoot, producing three rows of segments which are at first oblique and afterwards placed transversely (distinguished by a stronger outline). Each segment is first of all broken up by the division *a* into an inner and an outer cell; the former produces a part of the inner tissue of the stem, the latter the cortex of the stem and a leaf. Leaf-forming shoots arise beneath certain leaves, a triangular apical cell *z* being formed from an outer cell of the segment, which then, like *v*, produces three rows of segments; and each segment here also forms a leaf. (A more exact description in Book II, under Mosses.)

from the apex; in the latter case they form a whorl the single leaves of which may differ in age, as in Chara and Salvinia, and in the leaf-whorls of many flowers.

(2) *So long as the punctum vegetationis of the shoot grows in a straight line at the apex, the portion of the shoot which produces leaves lengthens, and the leaves arise in acropetal order; i.e.* the nearer the leaves are to the apex, the younger they are; in this case leaves are never produced at a greater distance from the apex than those already in existence. It is only when, as not unfrequently happens with the flowers of Phanerogams, the growth in length of the shoot

ceases or becomes weaker at the apex, and when, at the same time, an active growth continues in a transverse zone or at a place beneath the apex, that new leaves can become interpolated between those already in existence [1].

(3) *The Leaves always originate from the Primary Meristem of the Punctum*

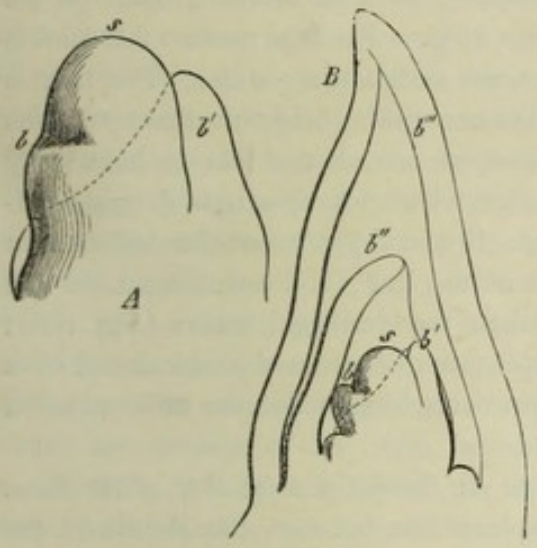

FIG. 107.—Apical region of two primary shoots of maize. Apex of the very small-celled vegetative cone, out of which the leaves b, b', b'', b''' arise as multicellular protuberances, which soon embrace the stem, and envelope it and the younger leaves like a sheath. In the axil of the third youngest leaf b'' the youngest rudiment of a branchlet is visible as a roundish protuberance.

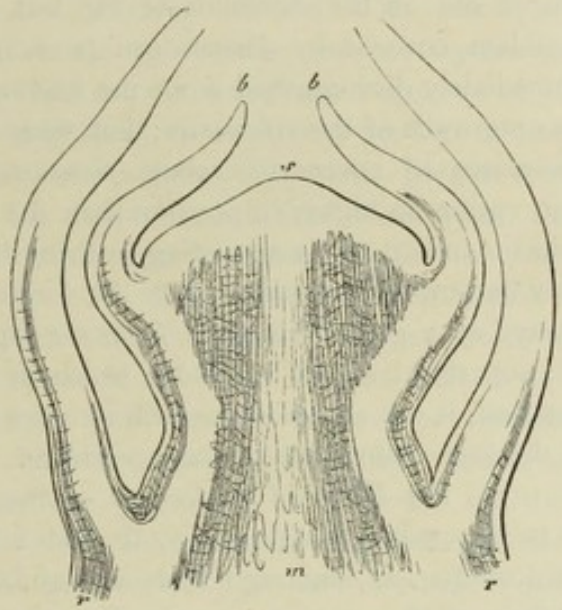

FIG. 108.—Longitudinal section of the apical region of the primary stem of the sunflower, immediately before the formation of the flowers; a the apex of the broad *punctum vegetationis*; b b the youngest leaves; r the cortex; m the pith.

Vegetationis, never from those parts of the stem which already consist of fully differentiated tissues. In Characeæ, Mosses, &c., before or during the first divisions of their segments the leaves become visible close beneath the apical cell, as protuberances, the outer portion constituting an apical cell, out of the segments of which are formed the leaves. In Vascular Cryptogams a many-celled vegetative cone often overtops the youngest rudiment of a leaf (*e.g.* strong Equisetum buds, Salvinia, many Ferns and Selaginellæ). In Phanerogams (Figs. 107, 108, 109) this is general; in them the rudiment of the leaf does not begin with an apical cell standing out beyond the vegetative cone, as in Cryptogams, but a roundish or broad cushion is formed, which from its very first origin consists of numerous small cells capable of division.

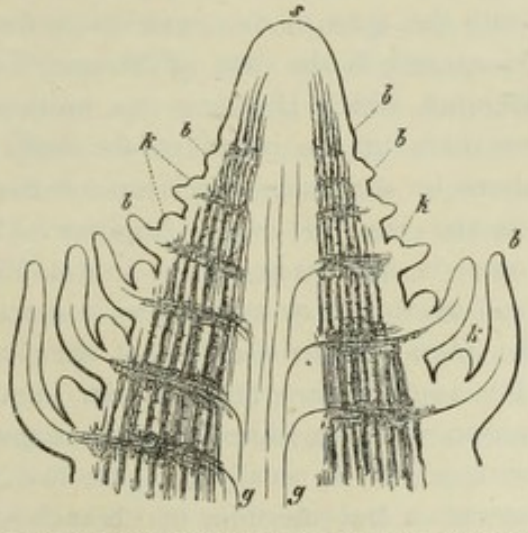

FIG. 109.—Longitudinal section through the apical region of an upright shoot of *Hippuris vulgaris*; s the apex of the stem; b, b, b the leaves (verticillate); k k the buds in their axils, which all develope into flowers; g g the first vessels (the dark parts of the tissue indicate the inner rind with its intercellular spaces).

(4) *The Leaves are always Exogenous Formations, i. e.* the rudiment of the

[1] Since phenomena of this kind are confined to the flowers and inflorescence of Phanerogams their consideration may for the time be postponed.

leaf never has its origin in the interior of the tissue of the stem, and is never covered by layers of tissue of the stem, like roots and many shoots. In Cryptogams it is usually one superficial cell (*i. e.* superficial before the differentiation of the epidermis) which forms the foliar protuberance. In Phanerogams a mass of tissue bulges out as the rudiment of the leaf, consisting of a luxuriant growth of the periblem covered by dermatogen (sect. 9, Fig. 103). By this means the leaf is immediately distinguished from the hair in its most rudimentary state. The hair is an outgrowth of the epidermis; but since in Phanerogams the primordial epidermis (dermatogen) covers the whole *punctum vegetationis* above the leaves, hairs may also spring up higher in position than the youngest leaves from single dermatogen-cells (as in Utricularia according to Pringsheim). But in Cryptogams the dermatogen only becomes differentiated after the formation of the leaf; and hence the hairs are always at a greater distance from the apex than the youngest leaves (Fig. 106); the superficial cell of the stem, which in Cryptogams becomes the apical cell of a new leaf, is not an epidermis-cell, since its origin dates long before the differentiation of the tissue into epidermis and periblem.

(5) *The Tissue of the Leaf is continuous in its formation with that of the Stem.* It is impossible, histologically, to find a boundary line between the stem and the base of the leaf, although such a boundary line must be assumed ideally. If the surface of the stem is imagined to be continued through the base of the leaf, the transverse section thus caused is called the *Insertion of the Leaf.* The continuity of the tissue of stem and leaf is an evident consequence of the early origin of the leaf below the apex of the *punctum vegetationis* before the differentiation of its tissue began. An inner mass of tissue is usually formed close beneath the apex of the stem before the formation of the leaf, and to this mass may be applied in the case of Mosses, Equisetaceæ, and other Cryptogams, the term Plerome, which Hanstein has proposed for Phanerogams (sect. 19). This takes no share in the origin of the leaf, and the continuity of its tissue is brought about by the outermost layers of the primary meristem, in which also the fibro-vascular bundles usually originate. When, however, the inner stem-tissue (plerome) is itself transformed into a fibro-vascular body, as in Hippuris (Fig. 109) (and notably in many Mosses), a continuity is subsequently brought about between the fibro-vascular bundles of the leaves and this innermost tissue of the stem (Fig. 109). When fibro-vascular bundles are formed in the stem having no connexion with the leaves, they are termed by Nägeli 'cauline bundles'; but in Phanerogams it is usually the case that each fibro-vascular bundle describes a curve beneath a leaf-insertion, one branch of which bends into the leaf, while the other branch runs downwards into the stem (Fig. 109, *g g*); the latter is called by Hanstein the inner leaf-trace, and the whole bundle is a 'common' one, *i. e.* common to both stem and leaves; both common and cauline bundles may run through the same shoot (as in Ferns, Cycadeæ, and Piperaceæ). In the fully developed shoot the cortical layers of the stem, at least the outer ones, bend outwards into the leaf without obvious interruption, and form its fundamental tissue; in the same manner the epidermis passes over continuously from the stem to the leaf. When the stem produces fibro-vascular bundles, the leaves are usually also provided with them; they remain without vascular bundles only when they are arrested early in their

growth, and persist as small scales, as in Psilotum and in many small leaf-scales of Phanerogams.

(6) *The Leaves usually grow more rapidly in length than the shoot which produces them does above their insertion* (Figs. 106, 107, 108). If the leaves are formed quickly one after another, they envelope and overarch the end of the shoot, and thus form a *Bud*, in the centre of which lies the leaf-forming *punctum vegetationis*. This bud-formation depends at the same time on the more rapid growth of the outer or under side of the leaves in their young state, by which they become concave on the inner (afterwards the upper) side, and adpressed upwards to the stem. It is only when perfectly developed, by the latest extension of their tissue, that the leaves turn outwards in the order of their age, and thus escape from their position in the bud. If the portions of the stem that lie between the insertions of the leaf undergo at the same time a considerable, and often very great extension, the leaves, when escaping from their position in the bud, become placed at a distance from one another, and a shoot results with extended internodes. In such cases the section of the stem in which the leaf-insertion lies usually undergoes a different development from the intermediate portions; these zones are then termed the Nodes, the intermediate portions the Internodes or interfoliar portions (*e. g.* Characeæ, Equisetaceæ, Grasses). If the stem remains entirely undeveloped between the leaf-insertions, it possesses no proper free upper surface, and is entirely enveloped by leaf-insertions (as in *Aspidium Filix-mas*); but more commonly this is only apparently so from the internodes being very short, as in many palm-stems. The internodes may be present immediately after the first formation of the leaves, when the consecutive leaves or leaf-whorls appear at considerable distances in height from one another, as in Chara[1] and Zea (Fig. 107); or they may originate only after further development of the stem-tissue, as in Mosses (Fig. 106) and Equisetaceæ, where each segment of the apical cell of the stem arches outwards and forms a rudiment of a leaf, so that the leaf-rudiments follow immediately one after another; and it is only by further differentiation that the lower portions of the segment become developed into the free portions of the surface of the stem, as is clearly shown in Fig. 106. The formation of a bud in the way described above is suspended when on the one hand the leaves are added very slowly one after another, and on the other hand the stem grows rapidly in length between the youngest leaf-rudiments or even before the appearance of the youngest; so that there is always only a slightly developed leaf near the apex, as in the underground creeping shoots of *Pteris aquilina* (*vide* Book II, Ferns).

(7) *Every leaf assumes a form different to that of the Stem which produces it, and to that of its lateral Shoots.* This is usually so conspicuous that no further description is needed. Nevertheless one point must be mentioned which often causes difficulty to the beginner. It not unfrequently occurs that lateral shoots of certain plants present a great similarity to the foliage-leaves of other plants in form and physiological properties, as the flat lateral shoots which bear the flowers in Ruscus, Xylophylla, *Mühlenbeckia platyclada*, &c.; but the course of development shows

[1] I consider in Chara, as in Mosses and universally, that the cortex belongs originally to the stem, and not to the leaf.

that these apparent leaves must, from their position, be lateral shoots, themselves producing leaves; and the leaves of these plants are usually of quite a different form from these leaf-like branches. The phrase 'leaf-like' has in these cases usually no distinct morphological, but only a popular meaning; and what will be said under paragraph (8) may be applied here. The branches or leaf-forming lateral shoots arise in a very different manner in different plants; but very commonly they have this in common with leaves, that their origin is equally in the primary meristem of the *punctum vegetationis* as lateral and exogenous outgrowths; that they are formed, like the leaves, in acropetal succession; and that the differentiation of their tissue proceeds continuously with that of the mother-shoot. They are distinguished, however, from the leaves of the same plant by the place of their origin, by their much slower growth,—at least at first (later they may overtake the leaves),—and by their relations in point of symmetry, of which we shall speak hereafter. The leading fact, however, is that the lateral shoot repeats in itself, by the formation of leaves, all the relations hitherto named between leaf and stem, and appears therefore as a repetition of the mother-shoot, although in other physiological relationships it is very different.

(8) *The morphological conceptions of Stem and Leaf are correlative;* one cannot be conceived without the other; Stem (Caulome) is merely that which bears Leaves; Leaf (Phyllome) is only that which is produced on an axial structure in the manner described in paragraphs 1–7 [1]. All the distinguishing characters which are applicable to the definition of Caulome and Phyllome express only mutual relationships of one to the other; nothing is implied as to the positive properties of either. If we compare with one another all the things which we call leaves, without reference to the stems to which they belong, we are unable to find a single characteristic which is common to them all and which is wanting in all stems. But that which is common to all leaves is their relation to the stem. Hence the ideas Phyllome and Caulome cannot be obtained by comparing with each other the positive properties of leaves and the positive properties of stems, or by laying stress on the points which they have in common and on those wherein they differ. But these ideas are obtained by observing exclusively leaves in their relation to the stem which produces them, and stems in relation to the leaves produced from them. In other words, the expressions Stem and Leaf denote only certain relationships of the parts of a whole—the Shoot; the greater the differentiation, the more clearly are Stem and Leaf distinguished. The measure of the difference is usually arbitrary; but if we confine ourselves to those plants to which the term leaf is applied in ordinary language, the distinction of leaves from stem depends on the relationships named in paragraphs 1–7; and in this sense certain lateral outgrowths in many Algæ may be termed Leaves, and the axial structures which produce them Stems (*e. g.* Sargassum). But when the difference between the outgrowths and the axial structures which produce them is less, one or several of the relationships mentioned in paragraphs 1–7 disappear; and it becomes doubtful

[1] There are, for instance, thallomes strikingly similar to certain leaf-forms, as those of Laminaria, Delesseria, &c.; they are, however, not leaves, since they are not formed on a stem as lateral structures.

whether the expressions Leaf and Stem ought still to be used; and when finally the similarity preponderates, the whole shoot is no longer called a Leafy Stem, but a Thallome. A branched thallome has the same relation to a leaf-bearing stem as a slightly differentiated to a highly differentiated whole.

The differentiation of the external forms of the members of the shoot into Stem and Leaf is to a certain extent independent of the internal differentiation which brings about the different forms of tissue and the cell-divisions, as is shown in the comparison of Mosses and Characeæ with Phanerogams. The internal segmentation may be reduced to a minimum of cell-divisions, or may altogether disappear; in the latter case the single cell presents itself as a shoot, the lateral outgrowths of which behave as leaves, and the axial part as stem, as, for example, in Caulerpa amongst Algæ. What has been already said as to the continuity of the tissue of the stem and leaf, and its origin from the primary meristem, must here be understood in an extended sense. In place of the primary meristem we have the *punctum vegetationis* of a single cell continuing its growth at the apex, and instead of the differentiation of tissue the development of the older cell-wall and of its contents. Caulerpa consists of a single cell-utricle, which grows as a creeping stem and puts out lateral leaf-like protuberances and tubular hairs which perform the function of roots, the whole enclosing a continuous cell-cavity without partition-walls[1].

(a) The leaves, like the shoots, grow at first at the apex, *i. e.* at the free end opposite the place of their origin. This apical growth continues indefinitely in many thallomes and leaf-forming axes until checked by some external cause; this is especially the case in the primary shoots of Fucaceæ, pleurocarpous Mosses, Characeæ, the rhizome of Equisetaceæ, Ferns, the main stems of Coniferæ and many Angiosperms. If the primary shoots themselves bear organs of reproduction, the apical growth generally ceases with their development, as in many acrocarpous Mosses, the fruit-stalks of Equisetaceæ, the haulms of grasses which bear the inflorescence, and in all cases in Angiosperms where a primary shoot ends in a flower. The lateral shoots are usually of limited growth; the growth frequently ceases without any external cause, and especially when they bear reproductive organs, become transformed into spines, or are very different in their shape from the primary shoot, as the horizontal lateral branchlets of many Coniferæ, the leaf-like shoots of Phyllocladus, Xylophylla, Ruscus, &c.

In by far the greater number of cases the apical growth of leaves ceases early, the apex itself becoming transformed into permanent tissue. In Ferns, however, the apical growth of the leaves usually continues, and in many genera is even unlimited, the apex of the leaf always remaining capable of development, and not becoming transformed into permanent tissue, as in Nephrolepis; in Gleichenia, Mertensia, Lygodium, and Guarea, the growth of the apex of the leaf is, as in many shoots, periodically interrupted, and again renewed in each period of vegetation.

(b) Besides the apical growth, there always exists however, both in stems and in leaves, an interstitial growth, the parts produced by the apical growth thus increasing in size and becoming further developed. The development of the internodes of the stem depends almost exclusively on this, as indeed is shown by the crowded position and the shortness of the internodes in the bud; the interstitial growth generally appears at first very rapid, and the increase in size occasioned by it is often very considerable; but it usually soon ceases, and the tissues become differentiated into unchanging permanent forms. Not unfrequently, however, a basal zone of internodes (as in Grasses, *Equisetum*

[1] Cf. Nägeli, Zeitschrift für wissenschaftliche Botanik und neuere Algensysteme.

hyemale, &c.), and in many cases the base of the leaf also, remains for a long time in the condition of primary meristem, while the parts nearer to the apex, long since transformed into permanent tissue, have attained their full growth. In this manner a subsequent basal increase in length, often continuing for a long time, is occasioned in parts which have long ceased to grow above; this occurs in a peculiarly marked manner in the long leaves of many Monocotyledons (Grasses, Liliaceæ, &c.) which are sheath-like in their lower part; and to a smaller degree in many Dicotyledons (*e. g.* Umbelliferæ). Where, as in Ferns, and in a lower degree in many pinnate leaves of Dicotyledons, the apical growth long remains active, the basal interstitial growth usually soon ceases, and, *vice versâ*, continues the longer the earlier the apical growth comes to an end. Two extreme cases may therefore be distinguished in leaves, although closely connected by intermediate forms; the predominantly basifugal or apical and the predominantly basal growth.

If the interstitial growth continues at one part of the surface of the leaf, and attains there a maximum which then decreases, a bag-like projection of the surface of the leaf is formed, which is termed a spur, such as occurs in many petals (as Aquilegia, Dicentra, &c.).

(c) Before the tissues which are differentiated from the condition of primary meristem assume their definite forms, a rapid growth usually takes place in their cells, which is no longer accompanied by cell-division; the size of the cells is not unfrequently increased by this means ten or even a hundred-fold and more. This process, which is mainly dependent on the rapid increase of the watery sap, may be termed *Extension*, in contradistinction to the growth of the younger cells which is contemporaneous with their divisions and which always precedes the extension. On this extension depends the rapid unfolding of the parts of the bud, which had long before been formed in their main outlines, but had remained small. The buds very often remain a long time in a condition of rest, until a rapid unfolding of the leaves and internodes already formed suddenly takes place; as, for instance, in the germination of many seeds, and in the persistent buds of many trees (Aesculus), bulbs (Tulip), and corms (Crocus, &c.), formed in the summer and germinating in the spring after long rest in winter.

(d) The axis of length or growth of a member (as will further be shown in a special paragraph), is an imaginary line passing from the centre of the base to its apex. The entire growth both of leaves and of stems is usually most rapid in the direction of this line; they are therefore for the most part longer than they are wide or thick. In stems the growth is most often nearly equal along all diameters; they assume therefore cylindrical, prismatic, or bulbous roundish forms. It is, however, sometimes the case that the growth in length advances much more slowly than that in diameter; and then the stem becomes tabular or flat, as in many bulbs, the corms of Crocus, and especially in Isoëtes. It is only in the lateral shoots of higher plants with very limited growth that the internodes grow mainly in the directions of a plane which includes the axis of length, and thus become leaf-like, as in Ruscus, Xylophylla, &c.

In leaves the growth usually preponderates in all the directions of a plane which cuts the stem transversely, and is mostly symmetrical right and left of a plane which includes the axes of length both of the leaf and the stem; the common form of leaves is therefore that of thin plates symmetrically divided into two longitudinal halves. There also occur, however, cylindrical and roundish tuber-like leaves, in which the growth has been nearly equally rapid in all diameters at right angles to the axis of the leaf (*e. g.* *Mesembryanthemum echinatum*).

Sect. 22. **Hairs (Trichomes)**[1] is the term given in the higher plants to those outgrowths which arise only from the epidermis, *i. e.* from the layer of cells

[1] Rauter, Zur Entwickelungsgeschichte einiger Trichomgebilde, p. 33. Vienna 1871.—Compare also sects. 15 and 19 (b).

which always remain the outermost in roots, stems, and leaves, whether these outgrowths occur as simple utricular protuberances, rows of cells, plates of cells, or masses of tissue, or have the physiological character of woolly envelopes of the young leaves, root-like absorbing organs (Mosses), glands, prickles, or spore-capsules (Ferns).

The hairs may originate from the primary meristem of the *punctum vegetationis*, or from young leaves and lateral shoots, if an external layer of cells has already been differentiated as dermatogen, as in Phanerogams. But they may originate also in much older parts the tissue-systems of which have already become further differentiated, and which exhibit intercalary growth, because in such cases the epidermis long remains generative; *e.g.* produces stomata and allows of cell-division.

When hairs spring from the *punctum vegetationis*, they are usually formed after the leaves, *i. e.* further from the apex than the youngest leaves; but it also happens in Phanerogams that they are developed above the youngest leaves and nearer to the apex, the outermost layer of cells of the *punctum vegetationis* having in this case already become differentiated as dermatogen (as in Utricularia according to Pringsheim). In Mosses and Vascular Cryptogams also, where the leaves become visible long before the differentiation of the external layers of tissue, the hairs do not show themselves on the surface of the stem till a later period and further from the apex.

If the hairs arise in the neighbourhood of the apex of a *punctum vegetationis* or on a zone of interstitial basal growth (as in the sporangia of Hymenophyllaceæ), they may be arranged according to a definite law, which is not the case with hairs that spring from older organs, or at least not evidently so.

Hairs are always strikingly different in their form from the leaves and lateral shoots of the same plant, although they sometimes bear a certain resemblance to these organs of other plants. The development in size of a single hair is usually extremely small compared to that of the member which produces it; even the mass of all the hairs of a leaf, a root, or a stem, is generally quite inconsiderable compared to its weight.

(a) The woolly and glandular hairs in buds are distinguished by a remarkably rapid growth; they are often perfectly formed long before the parts of the bud unfold, but then they generally die off; the persistent hairs which remain during the life of the leaves are formed much more slowly, and are marked by a great variety of form. The root-hairs are formed at a considerable distance from the *punctum vegetationis* of the root, often 1–2 cm. from the apex, and mostly die off after a few days or weeks, so that the older parts of the roots of even annual plants are destitute of living hairs. The existence of these hairs is connected with the activity of the roots in the ground.

The root-hairs which spring from the stems of Mosses are marked by a very long continued apical growth, and often by repeated branching. They consist of cells divided into rows by oblique septa, and, viewed physiologically, replace the root system of vascular plants. These root-hairs of Mosses are remarkably endowed with the generative principle, and behave in many respects like the Protonema, a means of propagation peculiar to Mosses; like it, they produce gemmæ, which, when exposed to light, grow into leafy stems. If the root-hairs themselves come to the surface (*e.g.* by turning up a sod) they put out rows of cells rich in chlorophyll, on which also gemmæ are produced.

(b) Thallophytes, when they consist of a mass of tissue, also form true hairs, like Cormophytes; but when the thallome consists only of one layer of cells, or, like Caulerpa

and others, is unicellular, one can no longer speak of an external layer corresponding to the epidermis; and its hair-like outgrowths cannot therefore be considered as trichomes in the same sense as those of the higher plants. Nevertheless it is customary to speak in such cases also of hairs, when the outgrowths are thin and long, destitute of chlorophyll, and otherwise dissimilar to the thallus which produces them. On the other hand structures occur in highly organised plants which are closely analogous to many forms of hairs in their physiological, and partly also in their morphological properties, but which differ from true hairs in not originating from single epidermis cells, but consist of massive outgrowths of the tissue which lies beneath the epidermis, remaining however covered by a continuation of it. Examples of such structures, which may perhaps be distinguished by the term *Emergences*, are afforded, according to Rauter, by the prickles and glandular hairs of roses, and perhaps also of the various species of Rubus. Closely related to these are probably the warts, tubercles, and knobs on the surface of many fruits (*e. g.* of Euphorbiaceæ, Ricinus). They resemble the leaves and branches of Phanerogams in their origin, but hairs in their later formation, and in their occurrence on stems as well as on leaves, and in their irregular disposition. For spines, which must not be confounded with prickles, cf. sect. 28.

Sect. 23. The term **Root**[1] is applied in botanical morphology, in contrast to its use in popular language, only to such outgrowths of the substance of the

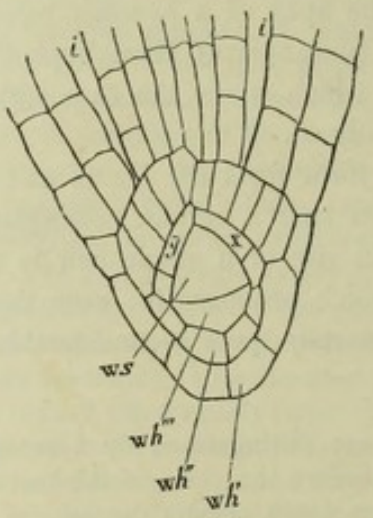

Fig. 110.—Longitudinal section of the young primary root of the embryo of *Marsilea salvatrix*; *ws* the apical cell, *wh'*, *wh''*, *wh'''* the still simple root-cap; *x*, *y* the last segments of the substance of the root; *i i* intercellular spaces.

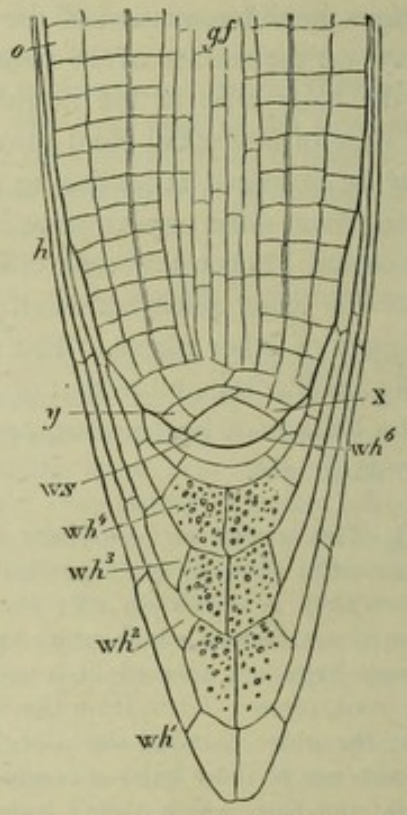

Fig. 111.—Longitudinal section of a somewhat older primary root of *Marsilea salvatrix*; *ws* apical cell; *wh*1 + *wh*2 the first, *wh*3 + *wh*4 the second, *wh*6 the third layer of the root-cap; each layer now consists of two divisions; *x y* the youngest segments of the substance of the root; *o* epidermis; *g f* fibro-vascular bundles; *h* the part of the root-cap which extends furthest back.

plant as are clothed at their growing apex with a layer of tissue, the *Root-cap* already described in sect. 19. Roots do not form leaves or other exogenous

[1] Nägeli und Leitgeb in Nägeli's Beiträgen zur wissen. Bot. Heft IV, 1867.—Hofmeister, Morphologie der Gewebe, sect. 5. Leipzig 1868.—Hanstein, Botan. Abhandlungen, Heft I. Bonn 1870.—Dödel, Jahrb. für wiss. Bot. VII, pp. 149 et seq.—Reinke, Wachsthumgeschichte der Phanerogamenwurzel in Hanstein's Botan. Untersuchungen, Heft III. Bonn 1871.—[La Racine: Ph. van Tieghem: Ann. des Sci. Nat., 5th series, XIII, 1871.]

leaf-like structures; their epidermis-cells, on the contrary, generally develope into long sacs, the root-hairs. The apex of each newly constituted root lies beneath the surface of the organ from which the root proceeds[1]; the root, when just formed, is usually covered with thick layers of tissue, which it breaks through in its further growth. Hence the roots are always endogenous formations, by which character they are distinguished from all trichomes and leaves, and from most lateral shoots.

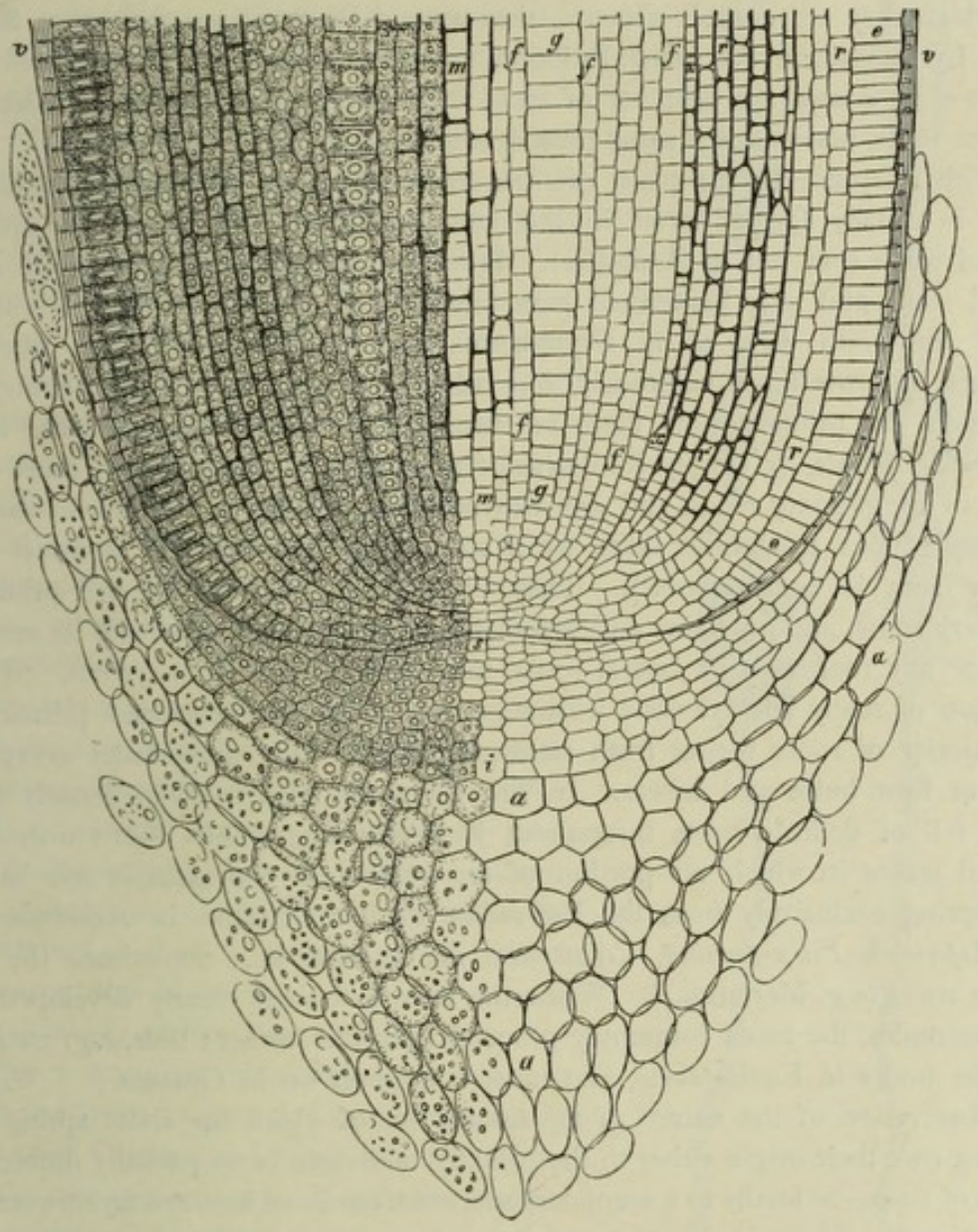

FIG. 112.—Longitudinal section through the apex of a root of maize; *a a* outer and older portion of the root cap; *i i* inner and younger portion; *s* apex; *m g f* the plerome; *m* becomes the pith, *g* a vessel, *f* wood; *x r* the cortex which is produced from the periblem at the apex; *e e* epidermis, continued into the dermatogen at the apex: *v v* thickened outer wall of the epidermis; (the origin of the root-cap from the dermatogen is not evident here; the figure was drawn long before this discovery).

Roots occur only in those plants the tissue of which is penetrated by fibro-vascular bundles; and they themselves therefore always contain fibro-vascular bundles; but these latter differ from those of the stem and leaves in the first

[1] I choose this expression because it appears to fit the primary root of the embryo of Vascular Cryptogams.

vessels being formed nearer to the circumference of the bundle, whereas the later bundles are always formed further inside, and hence centripetally in reference to the diameter of the root. Where bast-bundles occur, they arise in the cavities between the primary vascular bundles at the circumference of the fibro-vascular mass (Fig. 116, p. 146).

Although roots are generally distributed among vascular plants the higher Cryptogams and Phanerogams, there occur even in these groups single species from which they are entirely absent; thus among Rhizocarpeæ the genus Salvinia, among Lycopodiaceæ the genus Psilotum, among Orchideæ *Epipogium Gmelini* and *Corallorrhiza innata* are destitute of roots; the little *Lemna* (*Wolffia*) *arrhiza* does not form roots, and is at the same time destitute of vascular bundles.

With reference to the place of their formation roots are remarkably variable; a root is usually formed even in the young embryo which proceeds from the fertilised ovule (but not in Orchideæ). It appears at the posterior end of the embryonal stem, and may be termed generally the Primary Root, whether it remains weakly and soon dies, as in Cryptogams and Monocotyledons, or whether it continues to grow more vigorously, like all other roots, as in many Dicotyledons. But besides the primary roots, there are usually formed in addition a large number of *Secondary* Roots, or simply Roots (since they are a thousand times more numerous than the primary roots, and are also of much greater importance to the plant, it is superfluous to denote them by a special name, where the contrast to the primary root is not required). They arise in the interior of the primary or secondary roots, and on stems and leaf-stalks. The primary root with its secondary roots, or any root with its lateral roots, may be termed a Root-system. With the exception of many Dicotyledons with a persistent strongly developed primary root, the majority of roots spring from stems, especially when these latter creep, float, climb, or form bulbs and tubers. In Tree-ferns the stem is often densely covered with a felt of delicate roots throughout its whole length. In Ferns with densely crowded leaves in which no portion of the surface of the stem is left bare, the roots spring exclusively from the leaf-stalks, as, for example, in *Aspidium Filix-mas*, *Asplenium Filix-fœmina*, *Ceratopteris thalictroides*, &c.; sometimes the fronds put out roots (*e.g.* Mertensia)[1]. When the stem possesses clearly developed nodes and internodes, the roots commonly proceed from the former; thus, *e.g.* exclusively from the nodes in Equisetaceæ, and most commonly so in Grasses.

Observation of the nature of the tissues out of which the roots spring shows that they owe their origin either to the primary meristem, or to partially differentiated masses of tissue, or finally to a secondary meristem enclosed between layers completely differentiated. The primary roots of the embryos arise from quite undifferentiated primary meristem; the lateral roots of Cryptogams, as Nägeli and Leitgeb have shown, originate near the *punctum vegetationis* of growing roots, where the differentiation of their tissues first begins. With Phanerogams the same is the case, but stems may also produce roots near their *punctum vegetationis*, where the differentiation of their primary meristem first commences; this occurs in the case of the creeping

[1] A leaf of *Phaseolus multiflorus* cut off at the pulvinus and placed in water developed from the cortex of the intersected pulvinus an abundant root-system, and remained living for some months.

stems of Rhizocarps and of *Pteris aquilina*. Roots are formed much further backwards from the *punctum vegetationis*, where the tissue is already completely differentiated from a secondary meristem, in older portions of the stem, and especially when mutilated, or when the environment is dark and damp.

The order of development of the secondary roots is, according to Nägeli and Leitgeb, distinctly acropetal in the mother-roots of Cryptogams, where they arise near the apex; new roots are probably never formed in these plants between those already in existence in the mother-root. The same is, probably, always the case where roots are produced in the primary meristem or near the *punctum vegetationis* of the stem (as in Pilularia, Marsilea, Cereus, &c.). But even where their origin is further from the apex, as with the secondary roots in the primary root of Phanerogams and in many stems (*Zea Mais*, &c.), they generally appear in acropetal order; but by subsequent disturbance roots may arise adventitiously, *i. e.* in abnormal positions, as especially on older primary roots of Dicotyledons.

Secondary roots usually make their appearance on the exterior of the fibro-vascular bundles; the fibro-vascular bundle of the secondary root is then placed at right angles, or nearly so, to those of the mother-organ; the cortex is then only incompletely continuous with that of the latter, the epidermis not at all so. The case is different in the primary roots of embryos, which are formed early and mostly so near the surface of the embryo that a complete continuity is possible in all the tissue systems between stem and primary root; but in Grasses and some other Phanerogams, the first root arises so deep in the interior of the embryonal substance that it is enclosed in the fully developed embryo of the ripe seed by a thick sac-like layer of tissue (Fig. 114, *ws*), which is ruptured on germination (Fig. 113, *ws*), and is known by the name of Root-sheath (Coleorhiza). Similar formations occur also in the first secondary roots of the germinating plants of *Allium Cepa* and occasionally elsewhere. But the secondary roots which are formed deeper in the tissue in other cases

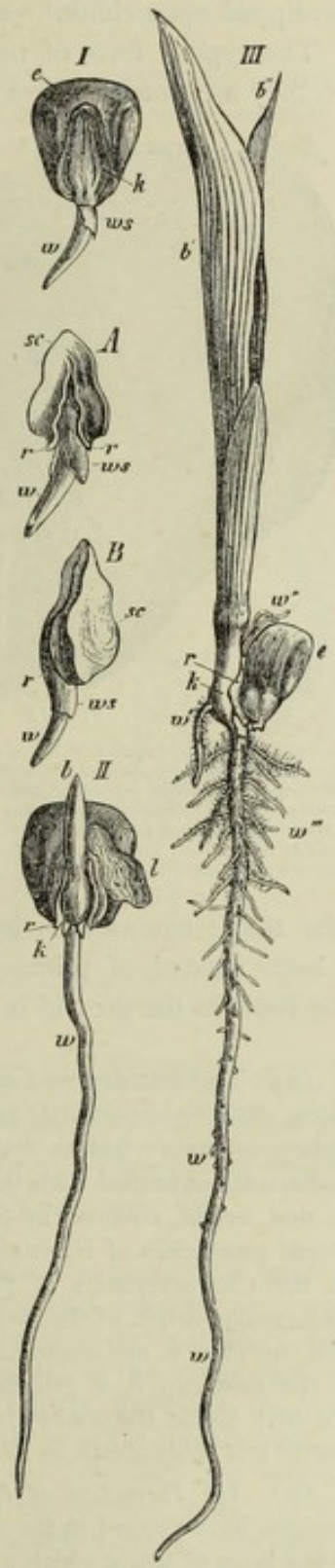

FIG. 113.—Germination of maize in the order *I*, *II*, *III*; *A* and *B* the embryo separated from *I*, in *A* seen in front, in *B* from the side; *w* the primary root; *ws* its root-sheath; *w'*, *w''*, *w'''* secondary roots; *e* the part of the seed filled with endosperm; *k* the plumule; *sc* scutellum of the embryo; *r r* its open margins; *b b' b''* the first leaves of the embryo-plant (natural size).

simply break through the layers of tissue which cover them, and then project from a two-lipped open chink.

The typical form of roots is filiform and cylindrical; their section is circular when they are not compressed from without. It is only when the roots undergo a subsequent increase in thickness, and serve as store-houses, as in many Dicotyledons and Monocotyledons, that the original filiform shape is changed into the fusiform or into tuberous swellings (as in turnips, tuberous roots of Dahlia, Bryonia, Asphodelus, &c.).

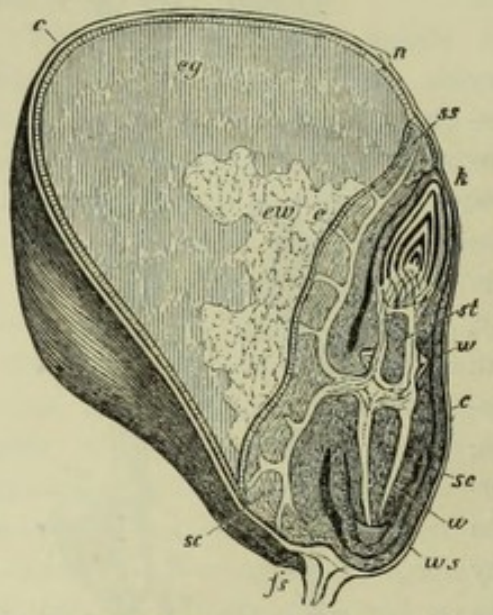

FIG. 114.—Longitudinal section of the grain of *Zea Mais* (× about 6); *c* pericarp; *n* remains of the stigma; *fs* base of the grain; *eg* hard yellowish part of the endosperm; *ew* whiter less dense part of the endosperm; *sc* scutellum of the embryo; *ss* its point; *e* its epidermis; *k* plumule; *w* (below) the primary root; *ws* its root-sheath; *w* (above) secondary roots springing from the first internode of the embryo-stem *st*.

Roots rarely form chlorophyll (*e. g.* in Menyanthes), and even then only in small quantities; usually they are quite colourless, not only when they grow in the ground, but also in water or air.

A subsequent basal growth appears never to occur in roots as it does in many leaves and internodes when once the regions near the apex have been transformed into permanent tissue. Interstitial growth behind the apex often continues, however, for a long time (in Lycopodiaceæ according to Nägeli and Leitgeb). The extension of the tissue commences immediately behind the terminal part of the root which has been formed of primary meristem—an arrangement by which the elongation of the roots in the ground is essentially assisted.

(a) The primary root of the embryo of most Phanerogams gives the impression of being entirely superficial, as if its apex were the actual posterior termination of the embryonal stem; but its first origin is endogenous; for the posterior termination of the embryo is connected with the 'pro-embryo' in Phanerogams, and the primary root is, at its first origin, covered by this. (A more exact account of this, according to the most recent researches of Hanstein on the formation of the embryo will be given in Book II, on the Characteristics of Phanerogams.) There was formerly some doubt as to the endogenous origin of the primary root of Ferns and Rhizocarps; but when it is observed that the root is not constituted as such until the apical cell has thrown off the first layer of the root-cap, it is evident that in this case also the apex of the new root lies from the first inside the embryonal tissue. (Compare the illustrations of the embryos of Ferns and Rhizocarps in Book II.)

(b) *The Formation of Lateral Roots* in a mother-root commences—as Nägeli and Leitgeb have proved in the case of Cryptogams, and Reinke in the case of Phanerogams,—in a layer of tissue which must be considered the outer layer of the plerome (or procambium), and is called Pericambium. In Cryptogams the secondary roots originate in acropetal succession from definite single cells of the pericambium, which lie before the vascular bundles, oblique divisions arising in them by which the three sides of the new apical cells that lie behind are marked off; a transverse division follows immediately, by which the first layer of the root-cap of the new lateral roots is separated. The apical cell of the secondary root formed in this manner and already provided with a root-cap, forms new

segments, from which the cap arises, as has already been shown in sect. 19, Fig. 102, p. 123. The roots of Lycopodiaceæ do not produce any lateral roots, they branch instead dichotomously at the apex (Fig. 130, p. 161).

In Phanerogams, the commencement of a lateral root is indicated by the splitting of several cells of the pericambium of the mother-root by tangential walls, so that the pericambium is divided there into two layers (Fig. 115, *A*). The outer layer is immediately formed into dermatogen (*d*), which afterwards forms the layers of the root-cap by tangential divisions; while the outer layer of cells which proceeds from the young dermatogen always constitutes a layer of the root-cap (*C b*). The inner layer of cells, resulting from the splitting of the pericambium (*A*, *n n*), which faces the vessels of the bundles of the mother-root, then also splits again into two layers (*B*); and further longitudinal and transverse divisions follow, by which the primary meristem of the young root is formed. This soon divides into three parts; a basal part by which the young root remains in connexion with the vascular bundle of the mother-root (*D*, *m m*), and an anterior mass of tissue which becomes differentiated into pericambium and plerome (*D*, *p p*). While the young root lengthens in a direction transverse to the axis of the mother-root, somewhat obliquely downwards, it compresses the cortical tissue (*D*); the innermost layer of cortex (*A–D*, *r*) resists disorganisation longest, and, at least at first, follows the growth of the young root, surrounding it in a sheath-like manner till it is destroyed. Finally, therefore, the young root lengthens and its apex protrudes through the cortical tissue of the mother-root.

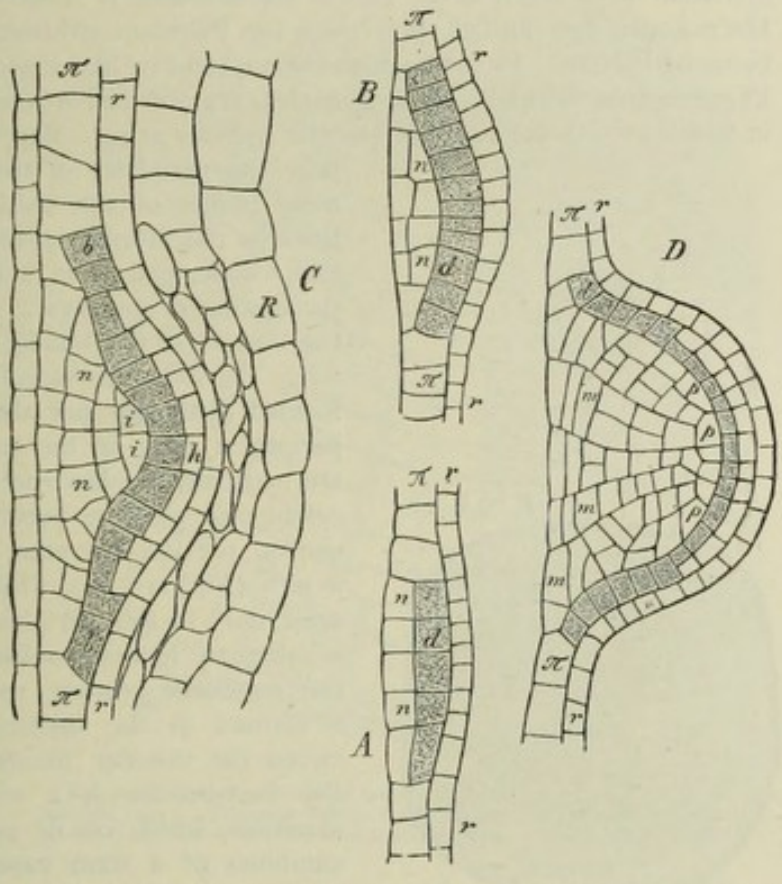

FIG. 115.—Mode of formation of the lateral roots in a mother-root of *Trapa natans* (after Reinke). *A* the pericambium (π) bounded by the innermost cortical layer splits into dermatogen (*d*) and an inner layer *n*, which in *B* is already again divided. *C* young root enclosed in the tissue of the mother-root; *R r* cortex of the latter; π the pericambium of the mother-root from which the secondary root has been formed; *h* the first layer of its root-cap, *d* its dermatogen. *D* secondary root in a further stage of development, surrounded only by the innermost cortical layer *r* of the mother-root; *p p* its periblem, in the middle of the plerome; *m m* the tissue that supplies the connexion with the mother-root.

In stem-formations lateral roots arise either from the interfascicular cambium (*e. g.* in *Impatiens parviflora* immediately above the soil in the primary stem), or from the outermost phloëm-layer of the fibro-vascular bundles, which is more commonly the case. These layers of tissue then behave like the pericambium of a mother-root (*e. g. Veronica Beccabunga*, *Lysimachia nummularia*, the ivy, according to Reinke).

(c) Whilst the formation of the root-cap, as has already been shown in sect. 19, continues from the apex of the root, its outermost layers of tissue pass over into permanent tissue; the cells retain simple forms, but their walls become thicker, and swell up in the outermost cell-layers of the cap, become gelatinous, and thus cause the apex of the root to appear viscid; finally they die and become detached.

In aërial and underground roots the root-cap is closely attached to the substance of the root by its oldest layers which generally extend backwards; in the roots of Lemnaceæ, Stratiotes, and some other plants which float on the water, it forms a loose sheath which envelopes the body of the root high up, and is only fixed below to the apex of the root.

(d) We have already, in sect. 19, touched on the manner in which the primary meristem of the apex of the root is differentiated in Angiosperms into three layers, the Dermatogen (primordial epidermis), the Periblem (primordial cortex), and the interior tissue or Plerome. In roots which remain slender, like those of Cryptogams and of many Phanerogams, the whole of the plerome is transformed into an axial fibro-vascular cylinder, in which two, three, or more vascular bundles arise. The vessels are formed first of all near the periphery of the bundle, at two, three, or more points of the section, and afterwards further towards the interior, until the rows of vessels meet in the middle, and form a diametral row, or a star of three, four, or six rays[1]. The lateral roots appear on the outside of the bundle in front of the primary vessels. Between the vascular bundles bast-bundles are formed (although not always) somewhat later in the peripheral gaps of the axial fibro-vascular cylinder. On originally thicker roots of Phanerogams the axial cylinder or plerome becomes again differentiated; its central portion becomes parenchymatous and forms a pith (Fig. 116, *m*), while vascular and bast-bundles arise only in the peripheral portion. When a root is able to increase subsequently in thickness, like the napiform primary roots of Dicotyledons, there is formed in the thickening-ring *x* (Fig. 116) between the vascular bundles *g* and on the inside of the bast-bundle *b*, a secondary meristem, a true cambium, which on its part behaves exactly like the cambium of a stem capable of subsequent increase of thickness; it produces inwardly in a centrifugal direction xylem, outwardly bast, especially phloëm. Fig. 116 shows at *A* the transverse section of the primary root of a bean before the increase in thickness has begun; and at *B* after the growth has continued for some weeks; between the thin pith *m* and the primary cortex *pr* a four-rayed woody substance has been formed; the four intermediate 'medullary rays' correspond to the original woody bundles *gg* which have not continued to develope centrifugally; the primary bast-bundles are still visible in *B*, *b*; but in addition, the cambium has produced a layer of phloëm with secondary bast-fibres *b'*. The strong primary root of the maize also produces, as has already been shown in Fig. 104, sect. 19, by the differentiation of the plerome, a pith-like substance *m*, surrounded by a fibro-vascular hollow cylinder *x*, in which are formed vessels and elongated wood-cells. Bast-cells are here not so clearly visible as in Phaseolus, or not at all. Fig. 117 shows the transverse section of the same root, somewhat higher than the longitudinal section in Fig. 112. No subsequent increase in thickness takes place in this case, nor is such active cambium formed in the fibro-vascular bundle as in Phaseolus. These are only some of the

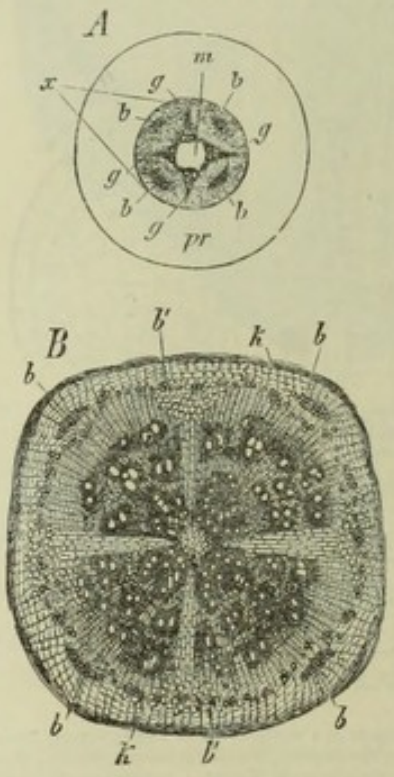

FIG. 116.—Transverse section of the primary root of *Phaseolus multiflorus* (slightly magnified). *A* a few centimeters above the apex of the root; *B* higher up on a much older root; *pr* primary cortex; *m* pith; *x* thickening ring; *g g g g* primary vascular bundles; *b b b b* primary bast bundles; *b'* secondary bast; *k* cork.

[1] In the thin embryo-roots of Triticum and other Grasses, an apparent central (axial) vessel is formed.

simpler cases of the differentiation of the tissue of the root, which it is desirable to mention here especially on account of the formation of pith which is usually entirely absent from slender roots. Generally also the pith disappears in thicker roots when they become more slender as they increase in length; the hollow cylinder of fibro-vascular tissue ends in a solid bundle.

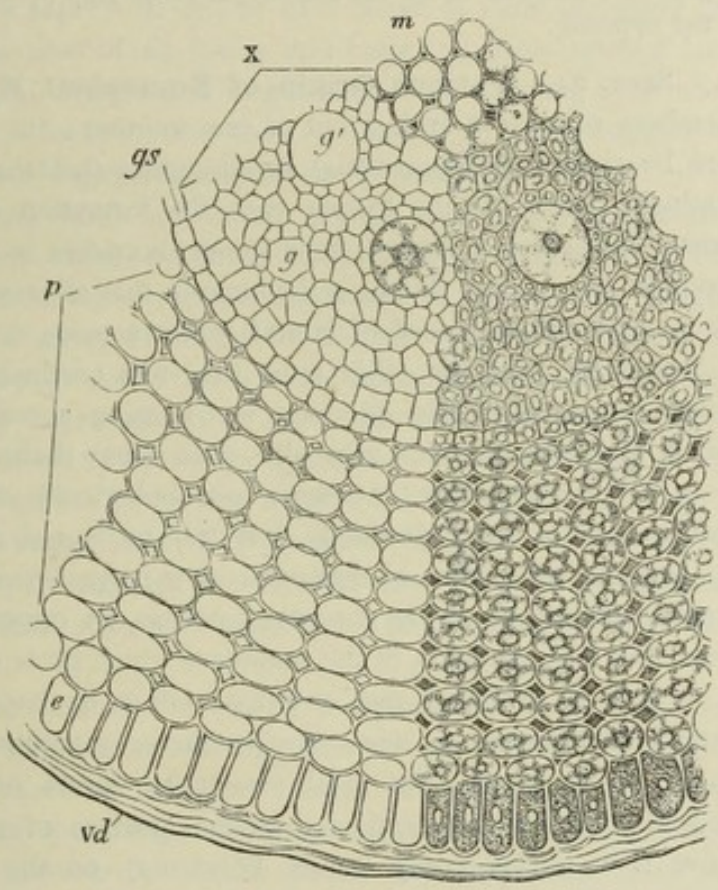

FIG. 117. — Part of a transverse section of the primary root of *Zea Mais* not far from the apex; *e* epidermis with its strongly swollen outer walls *vd*; *p* the cortex; *g s* bundle sheath; *m* the pith; *x* the thickening ring in which lie the vessels *g g'*.

(e) The roots are generally clearly distinguished from the leaf-forming shoots by the characteristics mentioned above; there occur, however, a few transitional forms which show that roots can become directly transformed into leaf-bearing shoots, as in *Neottia nidus-avis*, where older lateral roots of the stem throw off their root-caps and form leaves beneath the apex (Reichenbach, Irmisch, Prillieux, Hofmeister). On the other hand, leaf-forming shoots cease to produce leaves, as in many Hymenophyllaceæ (according to Mettenius); these leafless growing shoots form root-hairs, and assume the habit of true roots (whether they actually form a root-cap is doubtful); in these species true roots are wanting. In *Psilotum triquetrum* Nägeli and Leitgeb have shown that the apparent roots are only underground shoots, on which more or less evident traces of leaf-formation may be recognised; they are similar to true roots in function and in the formation of tissue, but have no root-cap, and, when they come to the light above ground, continue to grow in the manner of ordinary leaf-shoots. In the Selaginellæ also, the same investigators have shown the presence of leafless shoots (root-bearers) which grow downwards, and do not form root-caps until they touch the ground (cf. Book II. Lycopodiaceæ).

We thus see that transitional formations between roots and leaf-shoots are found even in highly differentiated plants. But even in Algæ the thallus is often fixed to its substratum by organs of attachment which may be compared with roots in their habit and in many functional properties, not only in the case of the large Fucaceæ and Laminariæ, but also in the unicellular Vaucheria and Caulerpa.

In reference to the confirmation of the Theory of Descent brought forward at the conclusion of this work, it is of great importance to know that members differing to the greatest extent morphologically and physiologically are connected by transitional forms, and that, especially in the branched thallomes of Algæ, starting points are to be found for all the differentiations of the higher plants. Distinctions which, in the ramifications of the Alga-thallus, are only of a weak, undefined, and rudimentary character, increase more and more in the higher plants; points which can be sharply defined in the latter become indistinguishable when we are considering the more simple Thallophytes. The more

the attempt is made to set up sharply defined ideas for single forms, the more does one become convinced that all definition, all limitation, is arbitrary, and that Nature presents gradual transitions from the indistinguishable step by step to the distinct, and finally to the opposite.

Sect. 24. **Various Origin of Equivalent Members**[1].—(1) The different members of a plant spring out of one another; the member produced may therefore be similar (homogeneous), or dissimilar (heterogeneous) to the member which produces them. In the former case the formation of new members is ordinarily termed Branching. A root, for instance, branches in the production of new roots, a shoot in that of new shoots, a thallome in that of new thallomes; in the same sense the production by a leaf of lateral leaf-structures must also be considered a case of branching. On the other hand the stem produces also leaves, roots, and hairs; leaves not unfrequently produce leaf-forming shoots, sometimes roots, generally hairs; leaf-forming buds may also arise from thallomes (as in Mosses), and from roots. Since, therefore, members morphologically dissimilar—stem, leaf, root, trichome—do not differ absolutely, but only in degree, the difference between Branching and the production of dissimilar new parts, between homogeneous and heterogeneous growth, must be conceived not as an opposition, but only as a gradually increasing differentiation of the members which grow out of one another.

(2) New members may originate either by lateral budding or by dichotomy. Lateral budding occurs when the producing member, after its previous increase in length at the apex (the axial structure), forms outgrowths *below* it, which, at their first origin, are weaker than the portion of the axial structure which lies above them. Dichotomy (rarely Polytomy), on the other hand, is caused by the cessation of the previous increase in length of a member at the apex, and by two (or more) new apices arising at the apical surface close to one another, which, at least at first, are equally strong, and develope in diverging directions. Lateral budding may form structures which are similar or dissimilar to the axial structure; and thus there arise, by lateral budding from the stem—leaves, roots, hairs, branches; from the leaf—leaflets, laciniæ, lobes, hairs, sometimes leaf-forming shoots, or even roots. Dichotomy, on the contrary, never produces structures which are dissimilar to the producing structure; the divisions of a root produced by dichotomy are both roots, those of a leaf-forming shoot both leaf-forming shoots, those of a leaf both leaf-structures; dichotomy hence always falls under the conception of Branching in the above narrower sense.

Dichotomous branching is very common among Thallophytes, especially Algæ and the lower Hepaticæ; among Phanerogams it occurs only exceptionally; among Vascular Cryptogams it appears to occur in Ferns (*e.g.* the leaves of *Platycerium alcicorne*); but it is the only mode of branching in all shoots and roots of Selaginellæ, Lycopodia, and in the roots of Isoëtes. (For further details of lateral branching and dichotomy see the conclusion of this section and sect. 25.)

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[1] Compare the literature mentioned in the previous sections, and in addition, H. von Mohl, Linnæa, p. 487, 1837.—Trécul in Ann. des Sci. Nat. vol. VIII. p. 268, 1847.—Peter-Petershausen, Beiträge zur Entwickelungsgeschichte der Brutknospen. Hameln 1869.—Braun and Magnus, Verhandlungen des Bot. Vereins der Provinz Brandenburg 1871 (on Oaniopsis). [Warming: Recherches sur la ramification des Phanérogames. Danish with French abstract. Copenhagen 1872.]

(3) The origin of lateral members, whether similar or dissimilar to the producing member, is either *exogenous* or *endogenous*. It is the former when they are formed by lateral outgrowth of a superficial cell or of a mass of cells including the outer layers of tissue, as in the case of all leaves and hairs and most normal leaf-forming shoots. A member is of endogenous origin when it is covered, even when in a rudimentary condition, by a layer of the tissue of the producing member, as in all roots, all lateral shoots of Equisetaceæ, and in adventitious buds.

(4) Lateral members of any kind are almost always formed in considerable numbers on the axial structure which produces them, and even repeatedly one after another, because the producing structure continues to increase in length, and the conditions are repeated along its length for similar equivalent outgrowths. Thus the stem, so long as it continues to grow at the apex, produces leaves, hairs, often even roots, and generally lateral shoots in great numbers, one after another; roots usually form in succession many lateral roots, branching leaves usually several laciniæ. If the apical growth ceases early, the number of the lateral members is also limited; thus the short primary stem of *Welwitschia mirabilis* produces only two leaves. When the increase in length of the stem is very slow, the formation of lateral shoots from it is sometimes altogether suppressed, as in Isoëtes, Botrychium, and Ophioglossum.

(5) An axial structure may produce the lateral members which are equivalent to one another in such a manner that either only one always arises at the same level or several; in the first case the members formed in succession are termed solitary, in the second case all the similar members arising at one level form a whorl or verticil. Leaves often occur in whorls, shoots less frequently, roots occasionally (in the primary roots of Phanerogams). Within the same whorl the members may arise either simultaneously, as the petals and stamens of many flowers, the whorl of foliage-leaves of many Phanerogams; or the members of a whorl may be successive, as those of Characeæ and Salvinia. A whorl is a true one when the level of the axial structure is originally such, as occurs in both the last-named plants and in many flowers; spurious whorls, on the other hand, are such as are formed by displacement and unequal growth of the axis, as in the Equisetaceæ, where leaves, roots, and shoots arise from transverse zones (nodes) which are themselves formed by displacement of three segments of the stem [1].

(6) Similar and equivalent lateral members usually arise on the common axial structure in *acropetal* or basifugal order, *i. e.* the younger a member is the nearer it is to the apex; counting from below upwards the members occur in the order of their age. The lateral members which are formed from the *punctum vegetationis* of an axial structure sufficiently near the growing apex are apparently always acropetal; but the order is disturbed when lengthening at the apex ceases and new formations occur at the primary meristem below, as in many flowers. The lateral members formed at a greater distance from the growing apex of the axial structure are sometimes, but not always, acropetal. Since branching and

[1] The three segments, which form the contour of the stem, stand at first at different heights, but arrange themselves, as Rees has shown, in a transverse zone (node), which forms outwardly a circular cushion, the rudiment of the leaves (cf. Book II. Equisetaceæ).

the formation of lateral members out of the *punctum vegetationis* occur in nearly all plants, and by their regular repetition at definite points of the growing axis determine the external form of the plant, they may be considered as normal, in opposition to the *adventitious* production of members which takes place at the older parts of the axial structure at a distance from the apex and without definite order. Such new formations are of equal importance in the external form of the plant, and though adventitious are often of great importance in a physiological point of view. Adventitious shoots are generally formed in the interior near the fibro-vascular bundles of the shoot, leaf, or root, and are therefore endogenous; but it does not follow from this that all endogenous shoots are adventitious. All the shoots of Equisetum are endogenous in their origin, but are not adventitious, since they are produced in the primary meristem below the apex of the mother-shoot, and in a perfectly definite order. It is equally incorrect to call all roots adventitious although they arise in the interior of the stem leaves or roots. They are adventitious only when they occur in older parts; when they arise close to the growing point of a mother-root or a stem, they are arranged in strictly acropetal order, and are for that reason not adventitious. When a member grows on a basal zone and produces lateral members from it, they may be arranged in basipetal order, *i. e.* the younger a lateral member is the nearer it will be to the base, as the sporangia on the columella of Hymenophyllaceæ (according to Mettenius), or the laciniæ of the leaves of Myriophyllum.

(7) When in the higher plants a new individual is formed which is destined for permanent and independent vegetation, a leaf-forming axis is first constituted, that is, a shoot on which roots, hairs, and lateral shoots then arise. In all vascular plants this first shoot (the primary stem) arises immediately out of the sexually produced embryo; it appears therefore as if the externally unsegmented embryo is to be considered as itself a primary shoot-axis[1]. In Mosses, on the other hand, the sexually produced embryo becomes transformed into the so-called Moss-fruit, a structure without leaves, roots, or branches, the sole function of which is the formation of spores. A new Moss-plant is, on the contrary, constituted by the formation of a leaf-bearing shoot out of a branch of the alga-like Protonema, which branches, strikes root (by root-hairs), and is independently nourished. The shoot first produced, which developes the rest of the shoots and roots, is termed the primary shoot, and its portion of the stem the primary stem, when it is more strongly developed than its lateral shoots, as in most Ferns, Cycadeæ, Coniferæ, Palms, and Amentaceæ. The primary shoot produces lateral shoots of the first order, these again lateral shoots of the second order, and so on. Nevertheless it often happens that lateral shoots of any order become independent, take root, and become detached from the primary shoot; they then assume all its peculiarities, and may equally be considered as primary shoots. But it also happens that the primary shoot itself is arrested at an early period, while new orders of shoots proceed from it which gradually become stronger, as in many bulbous and tuberous plants. Shoots which become detached from the mother-plant in a but slightly developed condition, and then continue to grow by independent nourish-

[1] Compare what will be found under Rhizocarpeæ and Angiosperms in Book II.

ment, while they repeat the peculiarities of the primary shoot, are called Gemmæ or Bulbils; they are often adventitious shoots; but bulbils may be shoots of normal origin, as those of many species of Allium.

Now that we have already spoken of the origin of leaves, hairs, and roots, and entered sufficiently into detail on the more important points (sects. 20, 21, 22), it only remains to go a little further into the various modes of origin of leaf-forming shoots.

(a) *The Formation of Leaf-forming Axes from Thallomes* (without the medium of a germ-cell) occurs only in the Muscineæ, especially in Mosses. From their spores, but

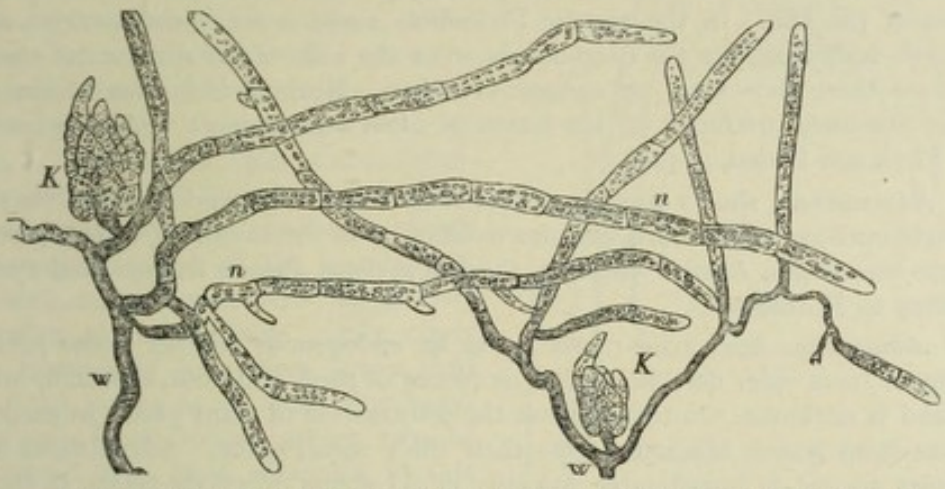

FIG. 118.—*Mnium hornum* (×50); *w w* parts of root-hairs of mature plants which have put out protonema-threads *n n* when the sod has been inverted in damp air; on these are formed the leaf-buds *K K*.

also from the root-hairs and other parts, are developed Conferva-like segmented filaments (Fig. 118, *nn*) growing at the apex, and branching. These often continue to grow for a long time, obtaining their nourishment independently, and sooner or later produce short lateral branches, generally at the base of longer branches. The apical cell, in which elsewhere segmentation of the filament is always produced by septa, is in them divided by oblique walls, and a usually triangular pyramidal apical cell of the stem is thus formed, the oblique segments of which at once develope into leaves; and thus shortly stalked leaf-buds arise (Fig. 118, *K K*), which at once take root by root-hairs, and become developed into independent Moss-stems.



FIG. 119.—*Asplenium decussatum*; middle part of a mature leaf; its mid-rib *st* bears the laciniæ *l l*; at the base of one the bud *K* is formed, which has also already put out a root (natural size).

(b) In many Ferns leaf-shoots arise *from Leaves*, and especially when branching of the stem seldom or never take place, as in *Aspidium Filix-mas*, *Asplenium Filix-fœmina*, *Pteris aquilina*, &c. In these species the buds spring singly out of the lower parts of the leaf-stalk at a greater or less height above its insertion. In other species it is the lamina which mostly produces numerous buds, generally in the axils of the laciniæ, as in *Asplenium decussatum* (Fig. 119), *A. Bellangeri*, *A. caudatum*, *Ceratopteris thalictroides*, or on the surface of the leaf itself, as in *Asplenium furcatum*, &c. In all these cases the buds produced on the leaves

are exogenous in their origin, and those on the leaf-stalks of the first-named species arise at an early period, while the leaves are still very young, out of single superficial cells[1]. These shoots take root while they still remain in connexion with the mother-leaf, but sooner or later become detached (in *Aspidium Filix-mas* and *Pteris aquilina* often only after some years, when they have already acquired considerable strength, and the base of the mother-leaf finally dies off and decays).

In Phanerogams buds generated on the leaves also occur, although much more rarely. The best known are those which are formed abundantly in the indentations of the leaves of *Bryophyllum calycinum*; according to Hofmeister[2] they arise before the complete unfolding of the leaf as small masses of primary parenchyma in the deepest parts of the incisions of the leaf. In the aquatic *Utricularia vulgaris* weak shoots arise, according to Pringsheim[3], mostly in the neighbourhood of the axils of the divisions of the leaf; in both cases these shoots are of exogenous origin. Nothing is known of the development of the buds produced on the leaves of *Atherurus ternatus* or *Hyacinthus Pouzolsii* (Döll, Flora von Baden, p. 348).

(c) Adventitious shoots springing *from Roots* are always endogenous; they arise in the neighbourhood of the fibro-vascular bundles or in the cambium, as in Ophioglossum, *Epipactis microphylla*, *Linaria vulgaris*, *Cirsium arvense*, *Populus tremula*, and *Pyrus Malus* (according to Hofmeister).

(d) *Adventitious Buds* arise moreover in an endogenous manner under peculiar circumstances from older detached leaves or pieces of stem and root, especially when kept damp and in darkness. On this depends the propagation of many plants in gardens, as of Begonias from leaves, Marattias from their thick stipules, &c. Adventitious buds also sometimes appear in considerable quantity in old stems of woody plants, in the cushion which projects between the bark and the wood, especially if the stem is cut off above the root. The branchlets which break out in old stems of Dicotyledons and Monocotyledons are, however, often not true adventitious shoots, but old dormant 'eyes' which have been left behind, having been formed at an earlier period as normal exogenous axillary buds, when the stem itself was still in the bud-condition; they had become enveloped by the bark as the stem increased in thickness, and carried on a feeble existence, until placed in a condition for active growth by a favourable accident, as the removal of the stem above them (Hartig).

(e) In the genus Isoëtes the leaf-forming shoot arises exclusively from the fertilised germ-cell or embryo, and forms neither normal lateral buds out of the stem nor any from the leaves or roots, nor any kind of adventitious buds.

(f) *The Normal Formation of Lateral Shoots* from the primary meristem of the *punctum vegetationis* of the mother-shoot is endogenous only in Equisetaceæ, elsewhere it is always exogenous. The Equisetaceæ stand in this respect quite alone in the vegetable kingdom; with the exception of the weak primary shoot which is developed out of the embryo, all their lateral shoots are of endogenous origin (Fig. 120, *KK'*); they are developed out of a cell in the interior of the tissue of the stem near to the *punctum vegetationis* somewhat later than the youngest leaf-cushions, and afterwards break through the base of the older leaf-sheaths.

With this exception all normal lateral shoots produced at the vegetative cone of the bud or in its neighbourhood (in the bud) are, like the leaves, exogenous[4].

(g) The lateral shoots which normally arise below the growing apex of a mother-shoot are always arranged acropetally, like the leaves, with which they exhibit various relationships as to position, age, and number.

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[1] Hofmeister, Beiträge zur Kenntniss der gef. Kryptogamen. II. Leipzig 1857.

[2] Hofmeister, Allgemeine Morphologie, p. 423.

[3] Pringsheim, Zur Morph. der Utricularien; in Monatsb. der k. Akad. der Wissen. Berlin 1869.

[4] [Leitgeb has recently described the endogenous formation of branches amongst the Hepaticæ: Ueber endogene Sprossbildung bei Lebermoosen. Bot. Zeitg. 1872.—Ed.]

(*a*) The numerical relationship of the lateral shoots to the leaves which are formed along with them on the same axis is so far variable that the number of the former may be either equal or unequal to that of the latter. If the number is unequal, a greater number of leaves than of branchlets usually arises on the same axis; in Mosses, Ferns, Rhizocarpeæ, Cycadeæ, and Coniferæ a much larger number. A branchlet may arise whenever a perfectly definite number of leaves has been formed, as in many Mosses and some Ferns, or the formation of a branchlet results when the increase in length of the primary shoot and the formation of its leaves ceases for a time, as in the genus Abies, and is subsequently renewed. When the leaves stand in whorls, the number of the lateral shoots may be equal to that of the members of the whorl, as in Equisetaceæ, or it may be smaller, as in Characeæ. Only rarely is the number of branchlets larger than that of the leaves, as in some Monocotyledons and Dicotyledons, where two or more lateral buds often arise side by side above a leaf (Fig. 122), or one above another (as in *Aristolochia Sipho*, Gleditschia, &c.). In most Monocotyledons and Dicotyledons the number of the lateral branchlets (with the exception of the flower-shoots) is, at first, equal to that of the leaves; but usually only a much smaller number attain a higher development.

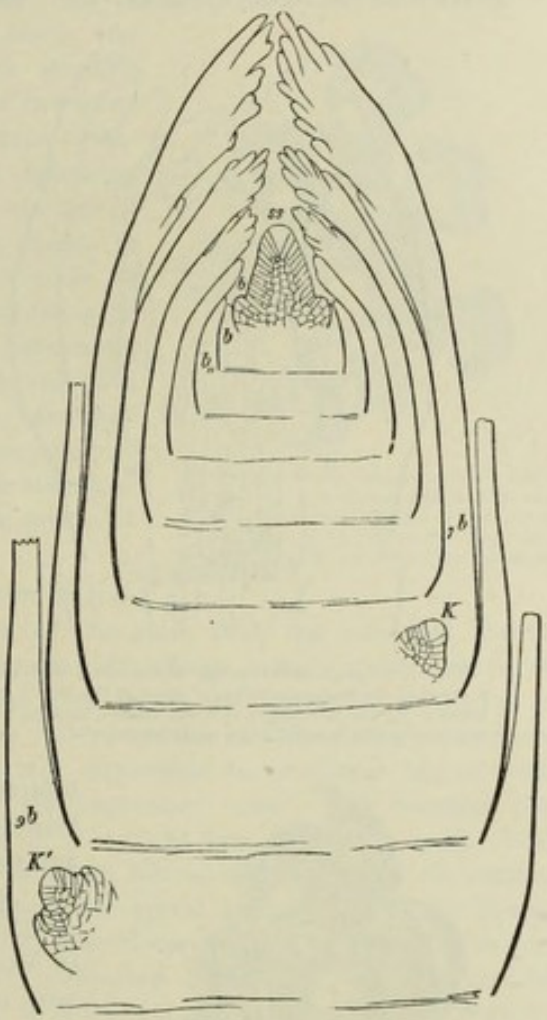

FIG. 120.—*Equisetum arvense;* longitudinal section of an underground bud in March; *ss* the apical cell of the stem; *b*—9*b* its leaves; *K K''* two endogenous lateral buds exposed by the cut. The youngest rudiments of buds are to be found, however, at *b''*, and they have probably begun to be formed even at a greater height (×50).

(*β*) A relationship in position exists between the origin of the leaves and the normal lateral shoots of a common mother-shoot, since a constant arrangement is found of leaves and shoots in each species and often in whole classes of plants, the shoots being always produced either below, beside, or above the leaves. The lateral shoots arise below the leaves (according to the acute investigations of Leitgeb[1]), probably in all Mosses, as well as in the Hepaticæ Radula and Lejeunia; the shoot springs (as shown in Fig. 106, *z*) out of the lower part of a segment of the stem the upper part of which has developed into a leaf. In Fontinalis this occurs below the median line (the symmetrically dividing plane) of the leaf, in Sphagnum laterally below one half of the leaf. According to the same observer, the lateral shoots arise in place of a half-leaf beside the remaining half, in many Hepaticæ of the section Jungermannieæ (Frullania, Madotheca, Mastigobryum, *Jungermannia trichophylla;* Leitgeb, Bot. Zeitg. p. 563, 1871). If each tooth in the leaf-sheaths of an Equisetum is considered to be a leaf, the buds originate at the side of the leaves and between them, for they break through the leaf-sheaths between the median lines of the teeth.

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[1] Leitgeb, Beiträge zur Entwickelungsgeschichte der Pflanzenorgane in Sitzungsber. der kais. Akad. der Wissen. zu Wien, Bd. 57, 1868, and Bd. 59, 1869; and Bot. Zeitg. no. 34, 1871. See also more in detail, Book II. Mosses.

In the Characeæ, Monocotyledons, and Dicotyledons, the normal lateral branchlets spring out of the axil of the leaf, *i. e.* above the leaves, in the acute angle which the leaf forms with the stem (Figs. 121, 123). Usually only one is formed above the middle of the

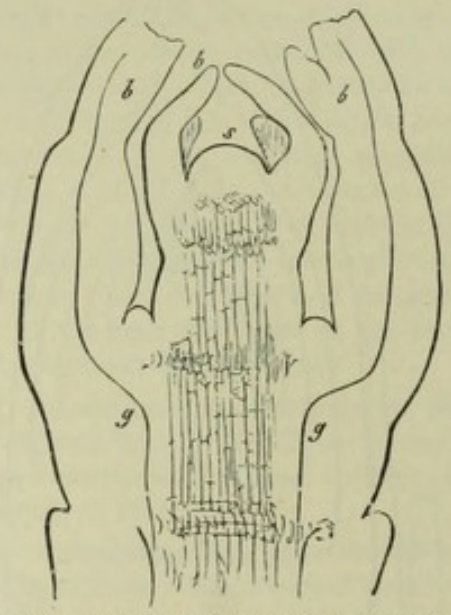

FIG. 121.—Longitudinal section of the apical region of a shoot of *Clematis apiifolia*; *s* apex of the stem; *b b* leaves; *g g* the first traces of spiral vessels, bending out uninterruptedly from the stem to the leaves.

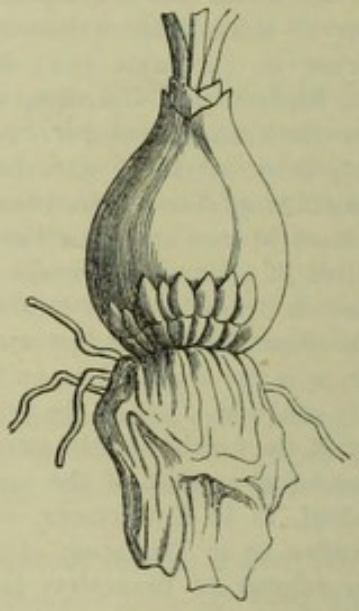

FIG. 122.—Bulb of *Muscari botrioides*; one of the lower bulb-scales is thrown back, in order to show the numerous buds standing side by side in its axil.

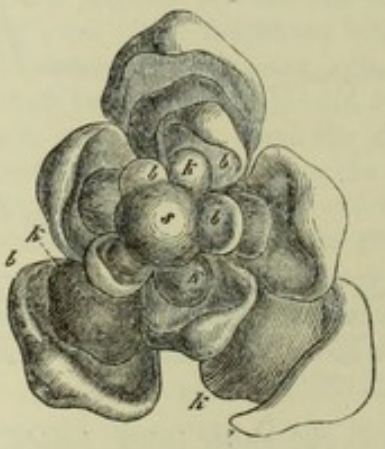

FIG. 123.—Apical region of a primary shoot of *Dictamnus Fraxinella*, seen from above; *s* apex of the primary shoot; *b b b* the young leaves; *k k* their axillary buds, the two youngest leaves have not yet axillary buds.

insertion of the leaf, or 2-3 one above another; sometimes several are formed side by side above the middle and right and left of it, as in the bulbs of Muscari (Fig. 122), and the flowers in the axils of the bracts of species of Musa. Such branchlets are called axillary shoots; in Monocotyledons and Dicotyledons the branching is, with few (and usually doubtful) exceptions, axillary.

(γ) If we except some inflorescences in Phanerogams, the general rule that *The normal Lateral Shoots appear later than the youngest Leaves* determines the relationship in age[1]. This is the case in Characeæ, Mosses (according to Leitgeb), Equisetaceæ, and the vegetative shoots and most inflorescences of Phanerogams, as is shown in Figs. 106, 107, 109, 120, 121, 123. In Mosses it is clear that the youngest branches stand at a greater distance from the apex of the stem than the youngest leaves. In the other groups named a different relationship would be possible; but in these cases it may also happen that the youngest lateral buds are almost always at a greater distance from the apex than the youngest leaves; or, in other words, the youngest leaves stand between the youngest lateral shoot and the apex. If the position of the branchlet is axillary, it would also be possible that when the formation of leaves ceases, the youngest axillary shoot would be observed to stand above the youngest leaf; but this would not prove that it was in this case formed earlier.

[1] Hofmeister indeed maintains the contrary (Allgem. Morphologie, p. 911, 1868). Since that, however, the Mosses have been shown by Leitgeb to be exceptions; and I constantly find in vegetative shoots and many inflorescences of Phanerogams young leaves above the youngest axillary buds.

If the formation of leaves is very feeble, as in the inflorescence of Grasses and some Papilionaceæ (*Amorpha fruticosa*), the lateral shoots may become visible earlier than the leaves in the axis of which they stand; the same is the case, according to Hofmeister, in Casuarina, Dianthus, *Orchis Morio*, and Salix (in the inflorescence or on vegetative shoots). In Cruciferæ, finally, the floral axes and the branches of the raceme spring from the primary shoot without any formation of bracts preceding or following (Fig. 124). But since in by far the greater number of Phanerogams the normal branching of the shoots is always axillary and subsequent to the formation of leaves, the above-named exceptions may, according to the principles of the theory of descent, be considered of little importance, since the leaves concerned (the bracts or leaves with buds in their axils) have lost their physiological signification, become useless, and at length entirely disappear. In such cases, the morphological character which is peculiar to a whole group of plants is usually altered in particular cases.



FIG. 124.—Young inflorescence of *Isatis tinctoria*, seen from above; *s* apex of the axis of the inflorescence; the flower buds shoot out beneath it (in whorls of four); the youngest are still simple leafless protuberances.

(δ) The fact that lateral shoots arise far most frequently at a greater distance from the apex of the stem than the youngest leaves, distinguishes them sufficiently from dichotomous branchings which must always of necessity arise above the youngest leaf. But even when the formation of leaves is observable later than the branching, as in the inflorescences of Gramineæ, or is even completely suppressed as in Cruciferæ, it is still impossible to confound lateral with dichotomous branching, if, as in these cases, the vegetative cone greatly overtops the youngest lateral apex, and continues to grow in a straight line (Figs. 107, 109). Still more distinctly conspicuous is the distinction between lateral branching and dichotomy when the generating stem-axis ends in a broad flat apical surface, as in the young capitula of Compositæ. Here the lateral shoots (the flowers) are so small relatively to the mother-shoot, and from the first at so great a distance from its apex (the centre of the apical surface), and placed so uniformly on all sides of it, that in this case the mother-shoot must be regarded as the independent centre of all new formations. The idea of dichotomy supposes that the mother-shoot ceases as such, and that two shoots, *at first at least equally strong*, continue growth in length in diverging directions in its place.

If it is desired to include lateral branching from the *punctum vegetationis* and dichotomy of the apex under one common term, in order to distinguish them from the lateral formation of branches from older portions of the stem, leaves, or roots, the expression *Terminal Branching* commends itself, which I have already employed in this sense in the first edition of this book.

SECT. 25. **Different capacity for Development of the members of one Branch-system**[1]. — Systems of members bearing the same name originate by branching; out of a root a root-system originates, out of a shoot a shoot-system; when a leaf branches, we get a pinnate, digitate, divided, lobed, or incised leaf, &c. It becomes therefore necessary to examine the more important relationships of form of such a system, if we for the time take into account only the relative size and capacity for development of the branches of the various orders. We may here leave adventitious branchings entirely out of consideration; for it appears clear from

[1] Nägeli und Schwendener, Das Mikroskop, p. 599. Leipzig 1867.—Hofmeister, Allgemeine Morphologie der Gewebe, § 7. Leipzig 1868.—Kaufmann, Bot. Zeitg. p. 886. 1869.—Kraus, Medic.-Phys. Soc. in Erlangen. Dec. 5, 1870.

these observations that they play no essential part in the whole external conformation; we have therefore only to do with the branchings which arise at the end of a growing shoot, leaf, or root, or with terminal branchings.

The terminal branches may be referred (as has already been shown in sect. 24, div. 2) to two principal forms, dependent on the origin of the branching by dichotomy or by lateral shoots; branch-systems of the first kind we will call simply *Dichotomies*, of the second kind *Monopodia*.

A Dichotomous Branch-system, according to the definition given in sect. 23, is the result of the cessation of the growth at the apex in the direction previously taken, and its continuation in two diverging directions at two newly constituted apical points, which arise close beside the previous one; as is very clearly shown in Fig. 125[1]. We will distinguish the two newly formed branches by the term Bifurcations, the member which produces them we will call the Base of the bifurcation. From the nature of the case every base can only bifurcate once; but every branch may again become the base of a new bifurcation[2].

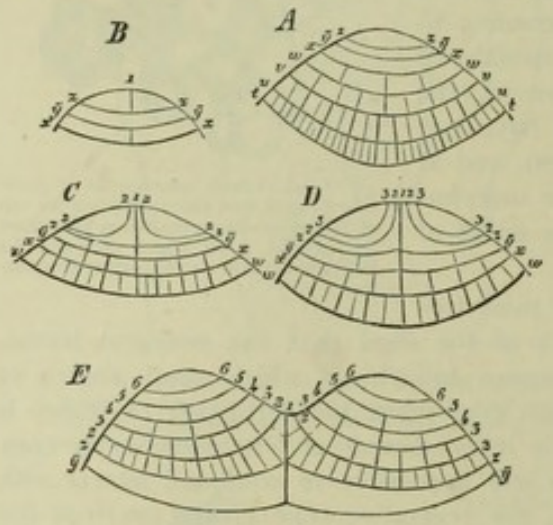

FIG. 125.—Dichotomy of the thallus of *Dictyota dichotoma* after Nägeli); the order of development is according to the letters *A—E*; the letters *t—x* indicate the segmentations of the apical cell before it dichotomises; 1 is the division-wall by which the dichotomy commences; 2—6 the segments of the new apical cells.

A *Monopodium* arises when the generating structure, following the direction of its previous axis of growth, continues to grow at its apex, while lateral structures of the same name grow beneath it in acropetal succession, the longitudinal axes of which are placed in an oblique or transverse direction to that of the generating member. The generating member, since it continues to grow during the branching, may form numerous lateral members; for all these it is the common base; hence the name Monopodium (Figs. 109, 113, 124). Every lateral branch may again branch in the same manner, and thus itself become a monopodium of the second order. Just as the dichotomy may consist of numerous bifurcations, so may a monopodium consist of several orders of monopodial branching.

These definitions refer only to the rudimentary condition of the branchings,

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[1] Since we have to give here a narrower application to the term Direction of Growth, it will be necessary to compare the following section on Direction of Growth and Symmetry.

[2] In Cryptogams with apical cells it may be thought that dichotomy must necessarily be brought about by longitudinal division of the apical cell. When the segments arise by transverse division this is actually the case, as is shown in Fig. 125; but when the segments are arranged in two or three rows, this would necessitate that the dichotomising wall proceeding from the apical surface of the apical cell should bisect its posterior angle, and thus have a position which is apparently universally avoided in cell-division. It is nevertheless possible that a true dichotomy may take place without this. Suppose the old apical cell, immediately after the formation of a new one near it, were to change the direction of its longitudinal growth, so that thus both apices diverge from the previous direction of growth; the old apical cell then represents the apex of a new direction of growth. From this it seems to me that we are peculiarly well able to arrive at the distinction between dichotomy and monopodium. *Mutatis mutandis* this is also true of Phanerogams which have no apical cell.

or the bud-condition of the branch-system. Not unfrequently the original character is maintained in their further growth, not only in dichotomous but also in monopodial systems. The two bifurcations develope, in the case of dichotomy, with equal strength and branch uniformly; in the case of a monopodium the primary axis continues to grow more strongly than all the secondary axes, and branches more luxuriantly. But it is very commonly the case that in a dichotomous system single bifurcations grow more weakly, or that in a system which starts on a monopodial plan some of the lateral axes, soon after their formation, grow more strongly and branch more luxuriantly than the primary axis. In such cases the original character of the branch-system becomes less and less evident as it developes; and it may happen that systems originally dichotomous have subsequently the appearance of monopodia, and *vice versâ*. It is therefore impossible to infer, without further evidence, the original form of a branch-system from its mature condition. It cannot be inferred from a maturely developed system whether it originated in dichotomy or in lateral branching. It will therefore be desirable to make here a simple classification of the most important changes which a branch-system undergoes during the development of its members.

(1) *The Development of Dichotomous Systems* may take place either in a forked or a sympodial manner; I call a system forked when at each bifurcation the two branches develope with equal strength, as in Fig. 126, *A*. The dichotomous system is developed sympodially when at each bifurcation one branch developes more strongly than the other; in this case the base of each successive bifurcation forms apparently a primary shoot, on which the weaker branches appear as lateral shoots (Fig. 126, *B*, *C*). The apparent primary shoot, which in fact consists of the bases of consecutive bifurcations, may on this account be termed a Pseud-axis or Sympodium[1]. Thus in *B* (Fig. 126) the sympodium is composed of the left-hand branches *lll*; in *C* of the alternate left and right-hand branches *lr*, *lr*. Whether the case represented in *B*, which, on account of its similarity to certain monopodial systems, may be termed a Helicoid (bostrychoid) Dichotomy, actually occurs is doubtful (probably however in the leaf of *Adiantum pedatum*). On the other hand the development represented in Fig. 126, *C*, is common in shoots of Selaginella, and, on account of its resemblance to some monopodial systems, may be termed a Scorpioid (cicinal) Dichotomy[2].

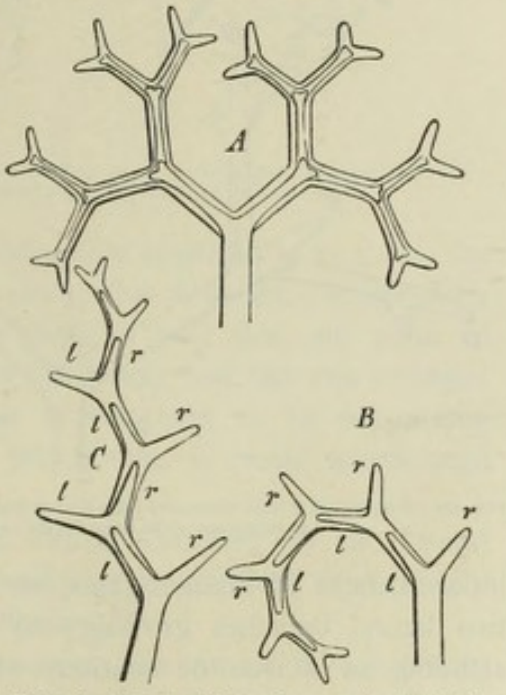

FIG. 126.—Diagram of the various modes of development of a dichotomy; *A* one developed by bifurcation; *B* a helicoid; *C* a scorpioid dichotomy.

[1] In opposition to the view expressed in my first edition, I now consider it more convenient to apply the term Sympodium only to the pseud-axis itself, and not to the whole branch-system; and the same in the originally monopodial systems.

[2] On Dichotomous Inflorescences cf. Book II. Phanerogams.

(2) *An originally monopodial branch-system* may develope in a racemose or cymose manner; and the cymose development may be either apparently dichotomous (or even apparently polytomous) or sympodial[1].

(a) A racemose system occurs when, with a monopodial origin, the mother-shoot, which is originally stronger, continues also to develope more strongly than all the lateral shoots, and when each lateral shoot of the first order behaves again in the same manner in respect to its lateral shoots of the second order, and so on. This occurs very clearly, for instance, in the stems of most Conifers (especially Pinus, Araucaria, &c.) and in the compound leaves of Umbellifers.

(b) The cymose development of a monopodial system, or a Cyme, depends on the fact that each lateral shoot, at first weaker, begins from an early period to grow more strongly than the mother-shoot above its point of origin; and, in consequence of this, also branches more vigorously than the mother-shoot, the growth of which then usually soon ceases. Two principal forms of Cyme may be distinguished, according as a Pseud-axis (Sympodium) is formed or not.

(*a*) When two, three, or more lateral shoots arise beneath the growing end of each shoot, which develope in different directions more strongly than their mother-shoot, the growth of which soon ceases, a false Dichotomy, or Trichotomy, or Polytomy arises. Fig. 127 represents the formation of a false dichotomy; the shoot *I* produces the shoots *II′*, *II″*, originally weaker, but soon growing more strongly, while the growth of *I* ceases; the same takes place with *III′* and *III″*. False dichotomies of this kind, which occur abundantly in the inflorescences of Phanerogams, are termed by Schimper Dichasia. But instead of two lateral branches growing out in opposite directions, three or more shoots standing in a true or spurious whorl may develope more strongly than their mother-shoot, and thus arises an umbrella-shaped or umbellate system, such as is developed in a typical manner in the inflorescences of our native Euphorbias; a system of this kind may be called a Cymose Umbel.

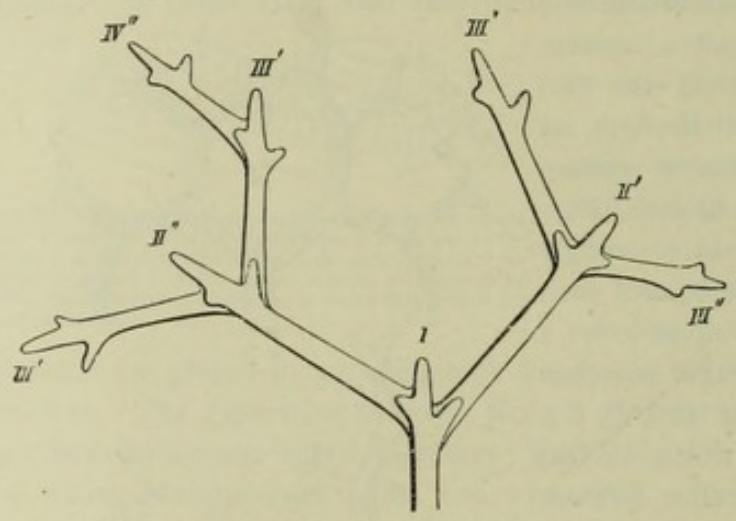

FIG. 127.—Diagram of a false dichotomy; the Roman numerals indicate the order of development of the shoots of the system.

(*β*) The sympodial development of an originally monopodial system occurs when *one* lateral shoot always developes with greater vigour than the portion of its mother-shoot which lies above its origin, as is shown, *e. g.*, in Fig. 128, *A*, where the lateral shoot 2–2 grows more strongly than the part 2–1 of its mother-shoot, and so on. Usually the portions of all the shoots which lie below their lateral branches develope more strongly than the terminal portions, as is shown in the

[1] Here also I deviate from the terminology of the first edition; not because that was incorrect, but because, by so doing, a greater facility is attained in the mode of expression.

figure by the thicker lines; the terminal portions (indicated by thin lines) often die off early; the thicker basal portions of the different ramifications which proceed from one another then commonly place themselves in a straight line, and have the appearance of a connected whole, like a primary shoot to which the terminal portions of each separate order of shoots are attached like lateral branches; the apparent primary shoot of the system is called the Sympodium or Pseud-axis. The latter consists, in Fig. 128, *B*, *e.g.*, of the pieces between 1–2, 2–3,

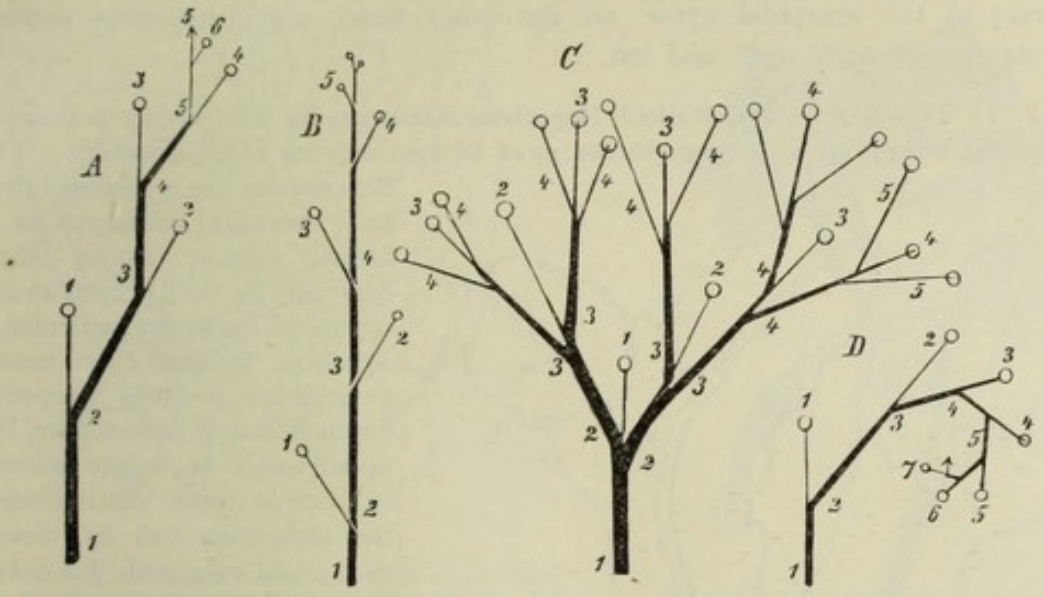

FIG. 128.—Cymose branchings represented diagrammatically; *A*, *B* scorpioid (cicinal) cyme; *C* dichasium; *D* helicoid (bostrychoid) cyme; the numerals indicate the order of succession of the lateral shoots which spring from one another [1].

3–4, 4–5; the weaker terminal portions of the respective branches 1, 2, 3, &c. are bent sideways. A comparison of Fig. *C* with *A* shows that between a sympodially developed and a spurious dichotomous system there is only this one point of difference, that in the latter each branch produces not only one but two stronger lateral branches. If in *C* one of the branches is imagined to be suppressed alternately left and right, the form *A* results, which then is easily transformed into *B*.

Sympodial systems appear in two different forms, according as the lateral shoots, the basal portions of which form the pseud-axis as they are continuously developed, arise always on the same side or on different sides.

If the sympodial ramification takes place always on the same side, *e.g.* always to the right, as in Fig. 128, *D*, or always to the left, the whole system is called a Helicoid Cyme (or bostryx); if, on the other hand, each branch which continues

[1] [Some difficulty will probably be felt with regard to Fig. D, which stands for a helicoid cyme in the text, but which is also identical with the scorpioid cyme of descriptive botany, and corresponds to the specific name 'scorpioides' given by Linnæus to several plants in which it occurs. The term scorpioid was introduced by A. P. De Candolle (Organographie, i. 415), to express a unilateral cyme the undeveloped portion of which is usually rolled up. This is the characteristic inflorescence of the Borraginaceæ, amongst which Myosotis has long been distinguished as 'scorpion grass' on this account. Bravais (Ann. de Sci. Nat. 2°. sér. vii. 197) distinguished the helicoid cyme, which he defined as having the successive flowers ranged in a spiral *round* the pseud-axis, while in the text above they are all placed in the same plane. Bravais amended De Candolle's definition of the scorpioid cyme by pointing out that the flowers are in two rows *parallel* to the pseud-axis.—ED.]

the system arises alternately right and left, as in Fig. 128, *A*, *B*, the system is a Scorpioid Cyme (or cicinus). If in these cases we have to do with leaf-forming shoots with a spiral arrangement of the leaves, a more exact definition of the terms right and left becomes needful. It is then necessary to imagine a median plane drawn through the longitudinal axis of each shoot and through that of its immediate mother-shoot; then in the helicoid cyme each following median plane always stands either right or left of the preceding one, following the course of the leaf-spiral; in the scorpioid cyme, on the other hand, the consecutive median planes stand alternately right and left.

(a) In Thallophytes and thalloid Hepaticæ, dichotomy is very widely prevalent; monopodial branchings also occur in the most various degrees of development. The dichotomies are unusually clear and generally developed in a forked manner among Algæ, especially in the Dictyoteæ, and species of Fucus (in particular *F. serratus*). In some there occurs a tendency towards sympodial development of dichotomies, but usually only at a late period; so that in those which branch the dichotomy can be clearly recognised even with the naked eye. The same is the case, among Hepaticæ, in the Anthoceroteæ, Riccia, Marchantia, and Metzgeria (Fig. 129), where the flat extension of the thallus or thallus-like stem arises between the young branches, first of all as a protuberance (f' f''), which however cannot be considered as a continuation of the shoot, since it has no apical cell or mid-rib; subsequently this protuberance disappears, as in f'' [1].

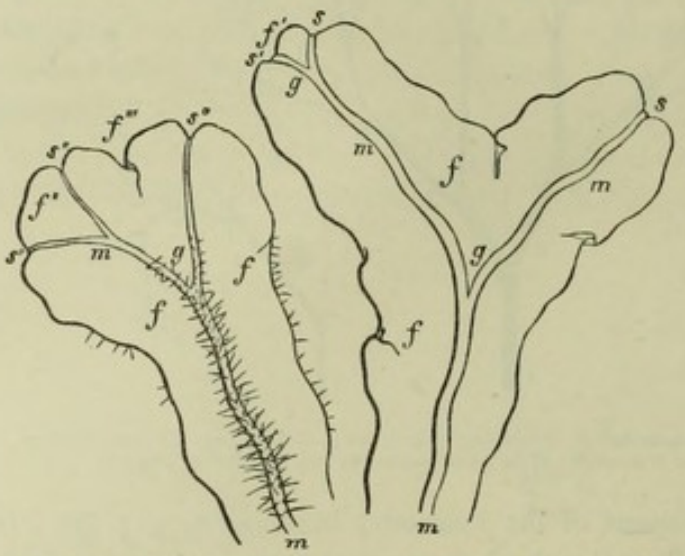

FIG. 129. — Flat dichotomously branched thallus of *Metzgeria furcata* (× about 13); *m m* mid-rib consisting of several layers, dichotomously branched at *g*; *s s* apical points of the branches; *f f* the wing-like expansions of the thallus, consisting of one layer of cells; *f' f''* the coherent wings between the mid-ribs of younger branches. (The left-hand figure is seen from below, the right-hand one from above.)

Decidedly monopodial (lateral) ramifications are particularly clear in filamentous Algæ, when the apical cell remains unbranched, and lateral branches grow only out of the individual cells (segments of the filament); as in Cladophora, Lejolisia, &c. It also however sometimes occurs that lateral branches proceed out of the apical cell itself, as is especially shown in Hypocaulon (Fig. 98, sect. 19). In other cases the branching of the apical cells is dichotomous, as in *Coleochæte soluta* (see Book II. Algæ).

(b) In the roots of Ferns, Equisetaceæ, and Rhizocarpeæ (according to Nägeli and Leitgeb), as well as in those of Conifers, Monocotyledons, and Dicotyledons, as far as is known, the branching is always at first monopodial, and even when further developed the mother-root generally remains stronger than its lateral roots; these root-systems are therefore developed in a racemose manner (Fig. 113, p. 143); this is seen very beautifully in the root-systems which proceed from the roots of Dicotyledons when they are allowed to germinate and to grow in water. Dichotomy of roots occurs only in Lycopodiaceæ, and probably in Cycadeæ, where they appear in their further development as systems of bifurcations. According to the most recent researches of Nägeli and Leitgeb,

[1] For the above-mentioned reasons I share Kny's view that the branching is in this case dichotomous. (Cf. Hofmeister, Allgemeine Morphologie, p. 433.)

it is still altogether doubtful whether the branching depends, even in Lycopodiaceæ, on true dichotomy[1]; but the root-branches of Lycopodiaceæ always arise so near to the apex, and they assume at so early a period the character of dichotomies developed in a forked manner that, until further investigation proves the contrary, they must be considered as such. It is scarcely necessary to mention in conclusion that when roots branch dichotomously the branches are at first covered by the original root-cap which fills up the bifurcation, as is shown in Fig. 130.

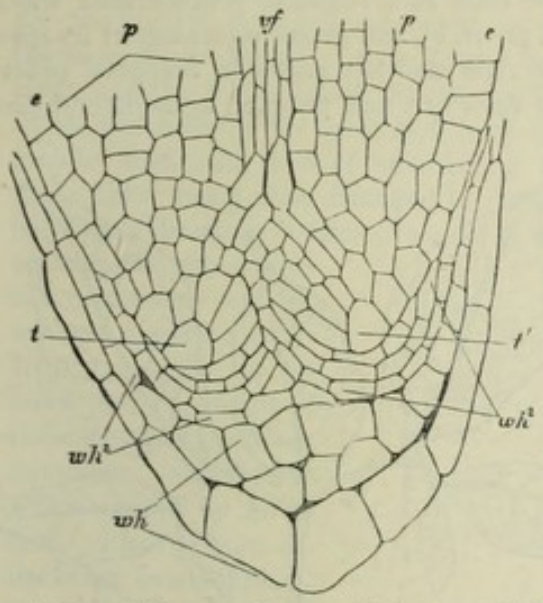

FIG. 130.—Dichotomy of the root of *Isoëtes lacustris* (after Hofmeister) (×400); *tt'* the apical cells of the branches; *wh* the old root-cap formed before the bifurcation; *wh2* the two root-caps of the branches, still covered by the former one; *e* epidermis; *p* parenchyma; *vf* fibro-vascular bundles of the root.



FIG. 131.—Part of a male flower of *Ricinus communis* cut through lengthways; *ff* the basal portions of the compoundly branched stamens; *a* their anthers.

(c) *Leaves.* Repeated bifurcations proceeding apparently from true dichotomy occur in the leaves of the Fern *Platycerium alcicorne*[2]; and, according to an older statement of Hofmeister, it appears that the branching of Fern-leaves generally commences dichotomously, although mature leaves mostly resemble a monopodium. On a mid-rib forming a continuation of the rachis are placed numerous alternating lobes, or secondary mid-ribs with secondary laciniæ. Since these branches are apparently always alternate and not opposite, and the terminal lobes of the leaves are frequently developed as equally strong bifurcations, leaves of this kind may be considered, according to Hofmeister's hypothesis, as dichotomies developed in a sympodial (and indeed a scorpioid) manner, the mid-rib representing the sympodium and the apparent lateral branchlets the weaker branches (as in Fig. 126, *C*); a process which is repeated in the laciniæ of the leaf itself when the leaf is doubly or many times pinnate. A similar interpretation may perhaps be permitted for the simply pinnate leaves of Cycadeæ. The repeated branching of the stamens in the male flowers of Ricinus appears, according to Payer[3], to proceed from dichotomy, and to a certain extent even polytomy, commencing at an early period.

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[1] Compare Nägeli's Beiträge zur wissen. Botanik, Heft IV. 1867. I would lay less stress on the relation of dichotomies to the apical cell, because the latter has scarcely the same decided signification in Lycopodiaceæ as in Ferns, Equisetaceæ, and other Cryptogams; and the apical growth apparently approaches nearer to that of Phanerogams.

[2] The leaf-stalk of *Adiantum pedatum* divides above into two equally strong branches, each of which forms a helicoid cyme of ramifications evidently arising by dichotomy; the weaker branches of the helicoid cyme stand upright and form each a mid-rib with numerous pinnate leaflets; and thus probably a scorpioid cyme produced by further dichotomy. This is one of the most beautiful forms of leaves, the history of the development of which would be of unusual interest.

[3] Payer, Organogénie de la fleur, pl. 108.

The separate stamens appear as roundish protuberances on the floral axis, and each of these immediately forms two or more roundish protuberances on its surface, after which the same process is again repeated. When fully developed, the stamens (Fig. 131) appear divided dichotomously or trichotomously upon long stalks, the branches being developed somewhat irregularly.

On an originally monopodial branching depends, on the other hand, the form of the pinnate, lobed, divided, cleft, and toothed foliage-leaves of Monocotyledons and Dicotyledons[1]. The leaf appears on the vegetative cone as a roundish protuberance which quickly broadens into a shell-like form (Fig. 132, *A*, *b*), and grows vigorously at its apex. Beneath the apex protuberances arise at the right and left angles in acropetal order; these also grow in the same manner at their apex (*f*), and produce again lateral pro-

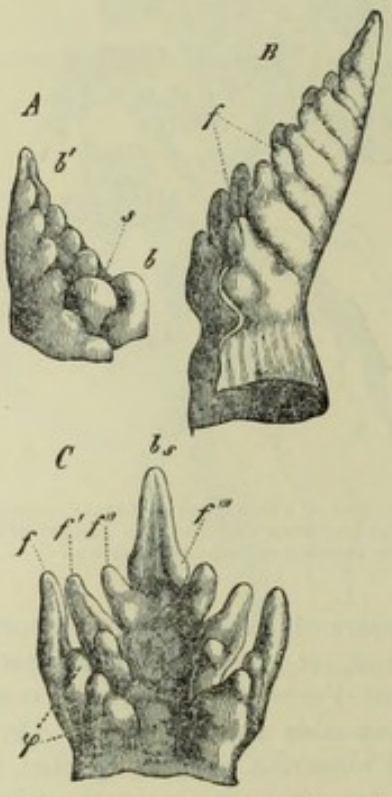

FIG. 132.—Development of the pinnate leaves of Umbelliferæ; *A*, *B* of *Pastinaca sativa*; *C* of *Levisticum officinale*; *A* the apical region of the primary stem; its vegetative cone is seen at *s*, its youngest leaf at *b*; *b'* youngest leaf but one with the pinnation commencing; *C*, *bs* the apex of the leaf; *f*, *f'*, *f''* the leaf-branches of the first order; φ of the second order.

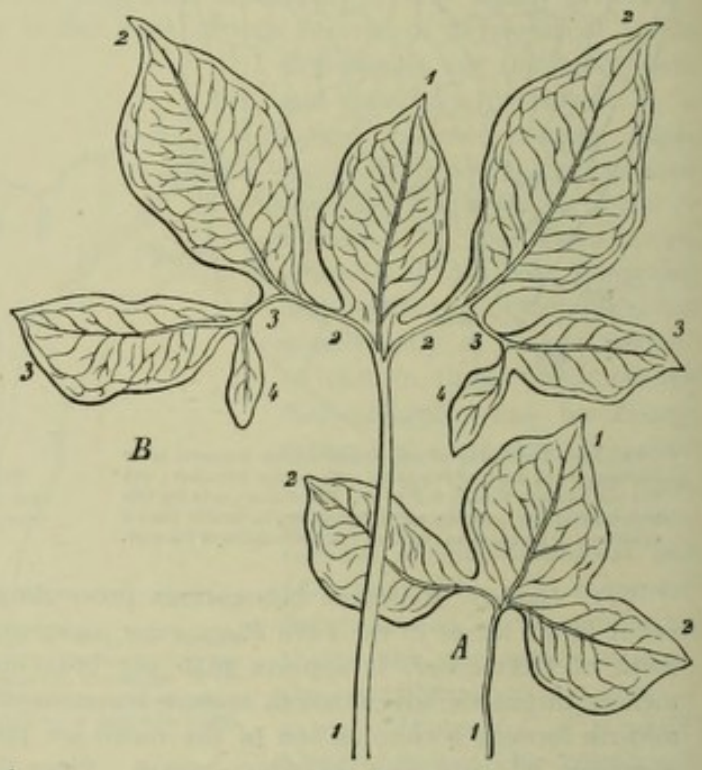

FIG. 133.—Leaves of *Amorphophallus bulbosus*; *A* with a simple, *B* with a threefold branching of the lamina.

tuberances of the second order (φ); and according to the extent to which the surface of the leaf is developed, these protuberances become lobes of a simple leaf or distinctly separated leaflets.

When two rows of lateral branches arise successively in the middle of the leaf, they generally remain weaker than it, and their lateral branches are also less numerous and weaker; the development of such an originally monopodial branching-system of leaves is therefore racemose. But the development may also be cymose, and may even lead to the formation of sympodia, especially when only one branch arises right and left on the leaf. This is the case, for instance, in the leaves of Helleborus, Rubus, and of several Aroideæ, as Sauromatum and Amorphophallus. Fig. 133 shows at *A* a weakly leaf of the last-named plant with only one branch on each side; but when the leaves attain a more vigorous development, as shown at *B*, each lateral lobe, 2 2, forms on its

[1] This was first shown in detail by Nägeli (Pflanzenphys Untersuch. von Nägeli und Cramer, Heft II.) in the leaves of *Aralia spinosa*.

outer side again a lobe of the third order, 3 3, which again produces a similar one of the fourth order, 4 4, and so on. According to the general definitions given above, the first branch of the leaf, 1, forms with 2 2 a dichasium; but each branch of the dichasium developes further only on one side, the new branches always arising either only on the left or only on the right side, 3 from 2 and 4 from 3; every lateral branch thus produces a sympodial system, and in fact a helicoid cyme.

If now the basal pieces 2, 3, 4, on both lateral shoots combined in a sympodial manner are imagined to be much shortened, so that the bases of the lobes 2, 3, 4 come close to the base of the lamina 1, then all the lobes of the leaf will appear to spring from one point, and the leaf is called digitate or fingered. It would appear, however, that such leaves also arise by the formation from the broad end of the young leaf itself first of a middle lobe, and then of new lateral lobes right and left from above downwards; these latter being thus arranged in the order of their origin, as in Lupinus, according to Payer's drawings (Organogénie de la fleur, pl. 104). If the lobes then remain united or have the appearance of a continuous lamella, we have a peltate leaf[1]. It is impossible to go more into the detail of these processes without numerous illustrations which cannot be given here. Fig. 134 may, on the other hand, explain, in conclusion, the origin of the quadripartite lamina of the leaf of *Marsilea Drummondi*, according to J. Hanstein's researches[2]. The leaf has its origin, in this case, in a cell of the vegetative cone of the stem, which, like the apical cell of the leaf, produces two rows of segments from which the right and left halves of the leaf are formed. Thus a broad cone first arises, growing at its apex, and bent towards the stem (*A*, *B*); when this which is the future leaf-stalk has attained a certain height, it increases in breadth right and left. Beneath the still growing apex, *D*, *bs*, a protuberance (*stb*) arises on both sides; and while the latter (destitute of an apical cell) becomes still more arched (*C*, *stb*) the apical growth of the leaf ceases (*C*, *bs*), its apical cell disappears, and soon two equally strong outgrowths arise near the apical point, which, like the earlier lateral ones, increase vigorously and grow out into broad lobes of the leaf. Thus arises a quadripartite lamina at the end of the leaf-stalk, the lateral lobes of which have resulted from lateral branching, but the middle ones by dichotomy. When more fully developed the four lobes remain small at their base, becoming much broader at the free margin; and, since the part of the leaf from which they originated remains short and narrow, they appear, in the mature leaf, to spring from a single point, the end of the leaf-stalk.

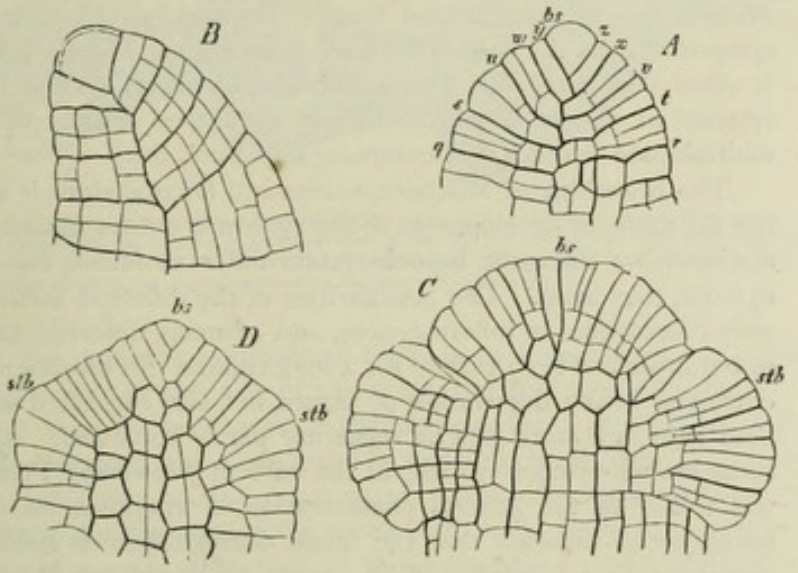

FIG. 134.—Development of the leaf of *Marsilea Drummondi* (after J. Hanstein). *A*, *C*, *D* seen from the inner surface; *B* longitudinal section vertical to *A*; *bs* apex of the leaf *q*—*z* the segments of the apical cell; *stb* lateral lobes of the lamina in their earliest state.

(d) *Branch-system of Leaf-forming Shoots.* The branching of the stem of Lyco-

[1] Compare further Trécul, Formation des feuilles, in Ann. des Sci. Nat. vol. xx. 1853; and Payer, *l. c.* p. 403; Entwickelung der Blattgestalten, Jena 1846.

[2] Jahrb. für wissen. Bot. vol. IV.

podiaceæ is dichotomous. In *Psilotum triquetrum* all the branches develope uniformly; it is the most regularly developed dichotomy found among vascular plants. In the Lycopodia the development is much more irregular, but always in such a manner that the bifurcation is conspicuous throughout; in the Selaginellæ, on the other hand, it is generally to be recognised only on the youngest branches, since the bifurcations are developed sympodially, and in fact as scorpioid cymes. This often happens (as in *Selaginella flabellata*) in such a manner that the entire outline of a branch consisting of numerous bifurcations assumes a form similar to that of a multipinnate Fern-leaf. The beginner who desires to obtain a clear idea of the different modes of development of a system produced from a dichotomous origin, especially the formation of sympodial forms out of dichotomies, could find no better object of study than the Selaginellæ which are cultivated in all hot-houses. On the branching of the stem of Ferns and Rhizocarps, reference should be made to the description of the respective classes in Book II.

The branching always originates monopodially in the stems of Characeæ, Equisetaceæ, and Coniferæ, and even with a racemose development. The branch-systems of Mosses also always proceed from a monopodial origin, but are sometimes developed sympodially (as the innovations of Acrocarpous Mosses beneath the floral organs). It is often very irregular, but sometimes occurs in such a manner that much-branched systems of shoots when racemosely developed assume defined outlines, like those of multipinnate leaves (Hylocomium, Thuidium, &c.).

The branching of Monocotyledons and Dicotyledons is always originally monopodial, but the mode of development of the system is extraordinarily variable; on the same plant and even on the same branch-system different forms, for example both racemose and cymose, may arise. The peculiarities of the different forms of development are usually very conspicuous in inflorescences, and of many different kinds; and since the attention of botanists has been turned for a long time in this direction, they are not only copiously employed in the description of plants, but also furnished with names, from which those used here in a more general sense are partly borrowed. A more special description of those branch-systems which, in the case of Flowering Plants are called Inflorescences, will follow in the general consideration of Angiosperms in Book II; here it is only necessary to mention that the forms distinguished as spikes, racemes, and panicles are especially clear examples of the racemose development, while those termed dichasia, cymose umbels (in Euphorbia), and scorpioid and helicoid cymes, and are examples of the sympodial development of monopodial branch-systems.

Every other form of (vegetative) branching of Flowering Plants may be regarded from the same point of view. The formation of sympodia is not unfrequently brought about by the arrest of the terminal portion or terminal bud of the shoot, while the nearest lateral bud developes all the more vigorously, and appears like a continuation of the mother-shoot, as in Robinia, Corylus, Cercis, and many other plants; in the lime the primary stem itself is a sympodium formed in this manner. If the flower-bearing shoots above ground die annually, while the underground portions remain in a living condition, underground sympodia sometimes arise composed of short thick basal portions of numerous larger shoots which have long since died off. This is the case, for instance, in *Polygonatum multiflorum*, the underground stem of which is known under the name of Solomon's Seal. In Fig. 135 is represented the front portion of one of these underground stems, those produced during eight previous years having disappeared. The stem denoted by the number 1866 is the lower portion of the upright aërial shoot bearing leaves and lateral flowers, which was in existence in that year; but this shoot is itself only the terminal part, its much thicker basal portion is denoted in the diagram *B* as seen from above by $n+2$; the thinner terminal part dies off in the autumn, and at *b*, *b*, beneath the numbers 1864 and 1865, are shown the scars which remain behind after the death of the similar earlier terminal parts. The portion here represented of the sympodium thus consists of the three basal portions n, $n+1$, $n+2$, of three shoots, each of which unfolded its aërial portion bearing leaves and flowers in the

year indicated. In the same manner will the bud $n + 3$ now become further developed; it springs from the axil of the leaf, the scar (insertion) of which is denoted by 9″. The basal portion of the shoot which proceeds from it will add a new piece to the sympodium, its terminal part will grow upwards and develope leaves and flowers, and will then die off. Just as $n + 3$ sprang from a leaf-axil as a lateral shoot from $n + 2$, so did this also spring from $n + 1$. Each of these shoots produced on its basal portion nine membranous colourless scale-like leaves[1] which are still partially retained in $n + 3$, while in n, $n + 1$, and $n + 2$, only their scars are to be seen; the numbers 1–9 indicate these in each year's growth. The new lateral shoot arises each year in the axil of the ninth and last scale-leaf, the succeeding leaves of which are then foliage-leaves on slender elongated internodes, while those of the basal portion between the membranous scale-leaves become thick and short. The leaves are in two rows on the basal parts, alternately right and left, as may be seen by their scars; if the position of the ninth leaf of the segment n is called left, then that of the segment $n + 1$ is right, that of the segment $n + 2$ left; the shoots which continue the sympodium are thus again alternately right and left; and hence the sympodium is in this case a scorpioid cyme.

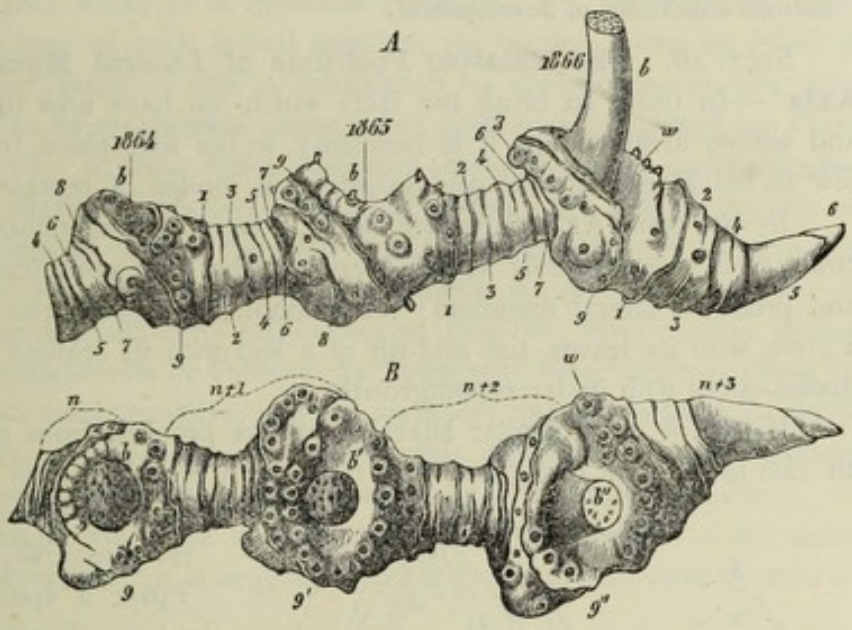

FIG. 135.—*Polygonatum multiflorum*; a front piece of a much longer rhizome consisting of four annual growths. *A* seen in profile, *B* from above; all the adventitious roots have been cut off, their position being indicated by the roundish warts. The numbers 1864, 1865, 1866 denote the years in which the respective pieces of the sympodium have grown.

It is evident that the processes of growth would remain precisely the same, if, at the close of each vegetative period, after the bud for the next year had attained sufficient vigour, the whole shoot, including its basal portion, had died off and decayed; then, of course, no sympodium would be formed, but the development of the underground buds would nevertheless be sympodial. This occurs, for instance, in our native tuber-forming species of Ophrys, but with the difference that if a sympodium were actually formed, it would be a helicoid cyme. The processes in Colchicum are similar but somewhat more complicated.

The explanation of processes of growth of this nature requires much space, as the above example shows; I must refer therefore to the labours of Irmisch mentioned below[2]. Where the leaves are clearly developed in Monocotyledons and Dicotyledons —and it is only in a few forms of inflorescence that this is not the case—it is almost always easy to understand the true nature of a branch-system even without microscopic examination; because, with but few exceptions, the branching is axillary; the position

[1] [Niederblätter or 'Cataphyllary leaves' of Henfrey; Braun's Rejuvenescence in Nature; in Ray Soc., Botanical and Physiological Memoirs, p. 4, 1853.]

[2] Irmisch, Knollen und Zwiebelgewächse. Berlin 1850.—Biologie und Morphologie der Orchideen. Leipzig 1853.—Beiträge zur Morphologie der Pflanzen. Halle 1854, 1856.—Papers in the Botanische Zeitung and the Regensburg 'Flora.' [Henfrey, Bot. Gaz. 1850, 1851.]

of the leaves then makes it sufficiently clear which is mother-shoot and which lateral-shoot in the sympodial pseud-axes. Sometimes, however, distortions occur (*e.g.* in Solanaceæ) which might lead to erroneous conclusions if reference was not made to the earliest conditions of development.

Sect. 26. **The Relative Positions of Lateral Members on a Common Axis**[1].—In order to bring the facts which we have now to consider into a clear and simple arrangement, it is necessary, in the first place, to explain the use of a few technical expressions and geometrical modes of representation.

By the term Axial Structure or Axis is to be understood, in future, when the contrary is not expressly stated, every member that continues to grow at its apex and produces lateral members; for example, a mother-root with its lateral roots, a stem with its leaves, the mid-rib of a leaf with its leaflets laciniæ or lobes, or a thallus-shoot with its lateral outgrowths.

If two or more similar lateral members proceed from one transverse zone of an axis in different directions, they compose a Whorl. A true whorl results when the zone of the axis which produces it is transverse from its origin (Fig. 136); a spurious or pseudo-whorl arises when the zone is the result of unequal development of the axis, or when lateral members which were formed side by side have become so far separated by subsequent unequal elongation of the axis, that they appear, in the mature state, distributed into different zones. Simultaneous Whorls are those whose members or rays are formed simultaneously (Fig. 136). Successive Whorls are formed when the members at a zone grow in succession either advancing right and left from one point of the periphery, as is shown in Fig. 137, and as occurs in the true leaf-whorls of Chara; or when the development takes place in a different order, as in the true leaf-whorls of Salvinia (*vide infra*), and in the three- or five-parted calyces of most Phanerogams.

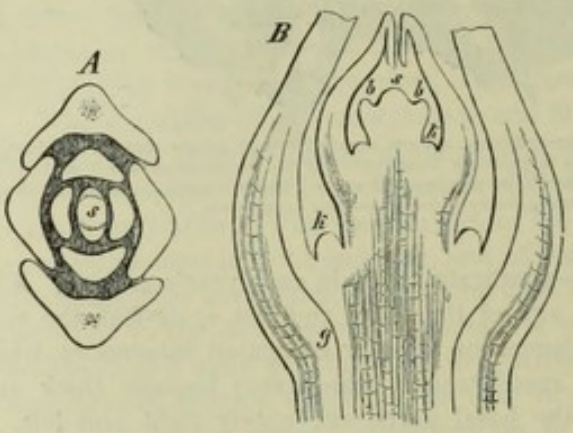

Fig. 136.—Apical region of a shoot of *Coriaria myrtifolia*; at *A* in transverse section, *B* in longitudinal section; *s* apex of the stem; *b b* leaves in pairs, *i.e.* in decussate whorls of twos; *k* axillary bud; *g* youngest vessel.

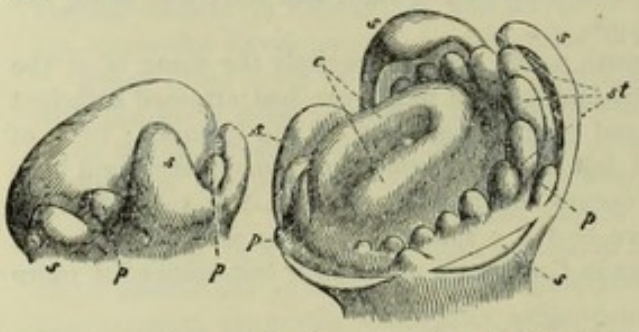

Fig. 137.—Development of the flower of the mignonette (after Payer); to the left a younger, to the right an older bud; from the latter the anterior sepals *s* have been removed, the posterior ones left; *p p* petals; *st* stamens, the posterior ones already large, the front ones not yet even in a rudimentary state; *c* the carpel or rudiment of the fruit.

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[1] Röper, Linnæa, p. 84. 1827.—Schimper-Braun, Flora, pp. 145, 737, 748. 1835.—Bravais, Ann. des Sci. Nat., vol. VII. pp. 42, 193. 1837.—Wichura, Flora, p. 161. 1844.—Sendtner, Flora, pp. 201, 217. 1847.—Brongniart, Flora, p. 25. 1849.—Braun, Jahrb. für wissen. Bot. I. p. 307. 1858.—Irmisch, Flora, pp. 81, 497. 1851.—Hanstein, Flora, p. 407. 1857.—Schimper, ditto, p. 680.—Buchenau, Flora, p. 448. 1860.—Stenzel, Flora, p. 45. 1865.—Numerous papers by Wydler, *e. g.* Linnæa, p. 153, 1843; Flora, 1844, 1850, 1851, 1857, 1859, 1860, 1863; and elsewhere.—Hofmeister, Allgemeine Morphologie der Gewebe, §§ 8, 9. Leipzig 1868. [Haughton, Manual of Geology.—

The lateral members are, on the other hand, isolated or scattered when each member stands on a different zone of the axis. If the surface of an axial structure (which sometimes is quite ideal, as in *Aspidium Filix-mas*, &c.) is imagined to be continued through the base of each lateral member, the section forms its *Plane of Insertion*. An imaginary point in this is considered its organic centre, but does not usually correspond to its geometrical centre; this point may be termed the *Point of Insertion* (cf. sect. 27). A plane which bisects a lateral member symmetrically, or divides it into two similar halves (sect. 28), and contains the axis of growth of the lateral member as well as that of the axial member, passes through the point of insertion, and is called the *Median Plane* of the lateral member in question. If members are so arranged at different heights on an axis that their median planes coincide, they form a straight row or Orthostichy; generally there are two, three, or more orthostichies on an axial structure, and the members are then said to be rectiserial. If there are no orthostichies, *i. e.* if the median planes of all the members intersect one another on an axis without coinciding, their arrangement is *solitary*.

The size of the angle which the median planes of two members of the same axis enclose is their *Divergence;* it is expressed either in degrees or as a fraction of

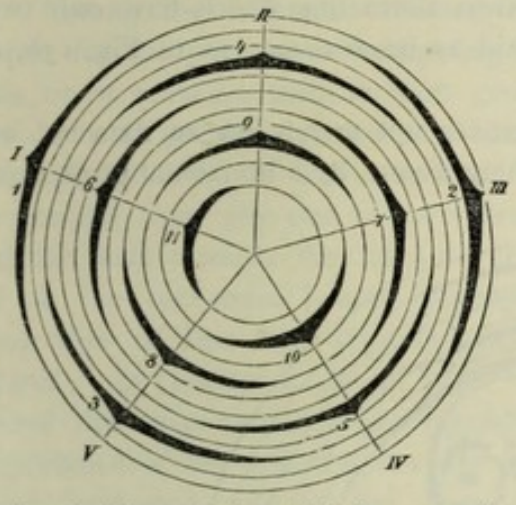

FIG. 138.—Diagrams of a shoot with the leaves arranged singly with a uniform divergence of $\frac{2}{5}$.

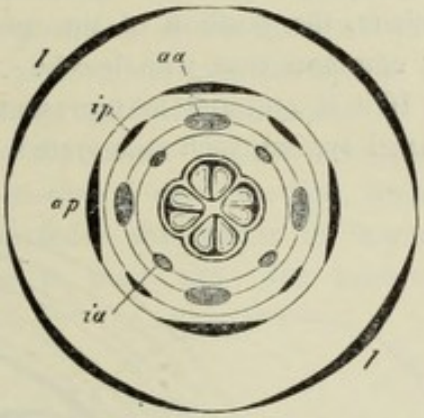

FIG. 139.—Diagram of the flower-stalk of *Paris quadrifolia*; *l l* whorl of the large foliage-leaves beneath the flower; *ap* outer, *ip* inner perianth-whorl; *aa* outer, *ia* inner stamens; in the centre is the rudiment of the fruit consisting of four carpellary leaves.

the circumference of the axis, which is then supposed to be a circle, although in fact this is not usually the case. In order to represent the divergences clearly, they may be drawn on the horizontal projection of the vertical axial structure, in the manner represented in Figs. 138 and 139. The transverse sections of the axial structure which bear the lateral members, in this case leaves, are denoted by concentric circles, and in such a manner that the outermost circle corresponds to the lowest, the innermost to the highest transverse section. On these circles, which thus represent the relative ages from without inwards according to their succession in the acropetal development of the axis, the places of the members are denoted by points, or the forms of the planes of insertion themselves may be approximately indicated, as in the figures. On such a projection or diagram the median planes

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Ellis, Mathematical Tracts.—A. Dickson, Trans. Royal Soc. Edinb. vol. XXVI. p. 505.—Chauncey Wright, Mem. Amer. Acad. vol. IX. p. 379.—H. Airy, Proceedings Royal Society, vol. XXI. p. 176. —Beal, American Naturalist, 1873, vol. VII. p. 449.]

of the members appear as radial lines, indicated in Fig. 138 by *I–V*. Since in this case several members stand upon each median plane, they are arranged in orthostichies; and these again are so placed that they divide the circumference into five equal parts. But if the members are considered in reference to their age, as indicated by the figures 1–11, it is seen that the divergence between 1 and 2 is $\frac{2}{5}$, as also is that between 2 and 3, between 3 and 4, and so on. The divergences are therefore all equal, or the members have in this case on the same axis the constant divergence $\frac{2}{5}$. In Fig. 139 the members are arranged in a quaternary whorl; on each circle or section there stand in this case four similar members with the divergence $\frac{1}{4}$; but the successive whorls are so placed that the median planes of one whorl exactly bisect the angle of divergence of the preceding and following whorls; the whorls here *alternate*, and all the members are arranged in eight orthostichies. If, on the other hand, two whorls stand one over the other in such a manner that their members fall into the same median planes, or cover one another, they are said to be *superposed*. Thus, for instance, the staminal whorl is superposed on that of the corolla in Primula; and in the primary roots of Phaseolus, Tropæolum, Cucurbita, and other Dicotyledons, there not unfrequently occur superposed whorls of lateral roots. When alternating whorls have only two members, the position of the members is said to be *decussate*, as in Fig. 136, a very common case with leaves.

If it is required to represent the divergences not merely on an axis but on an axial system, such as a system of leaf-forming shoots, by a horizontal projection,

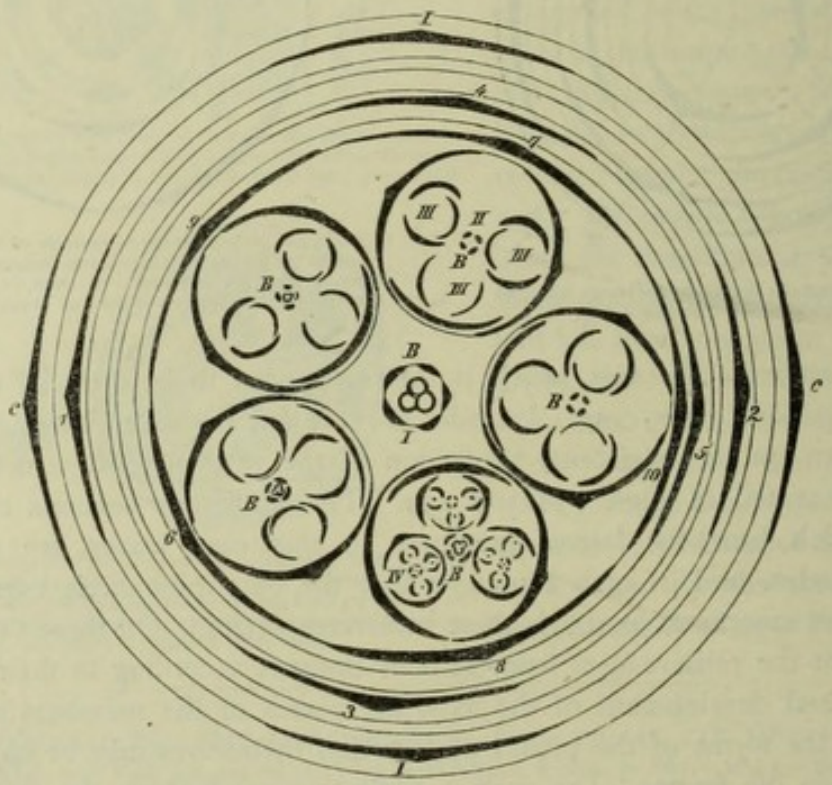

FIG. 140.—Diagram of a weakly plant of *Euphorbia helioscopia*; *c c* the cotyledons; *I, I* the first, 1—10 the later foliage-leaves; numbers 6—10 form one whorl; at *B I* in the centre is the terminal flower of the primary shoot; *B II* the terminal flower of one of the five axillary shoots; *III, III, III* the leaves of three axillary shoots of the second order.

it may be done on the same principle, as is shown in Fig. 140. Each system of concentric circles contains the members (in this case leaves) of an axis; the

lateral axes (here axial shoots) are interposed between the insertion of the respective leaves and their stem-axis.

If the axial members are greatly shortened, the view (from above) of an axis, with its lateral members, often itself supplies the diagram; as, for instance, in the leaf-rosettes of Crassulaceæ, and in most flowers. In other cases a transverse section through the bud enables the observer to examine the divergence of the leaves; but in many other cases the relative positions are more obscure, and can only be ascertained by careful examination. In addition to the study of the history of development, peculiar methods, depending on geometrical principles, are often necessary in order to represent the relative positions correctly and at the same time clearly.

There are also circumstances in which it is desirable, instead of representing the relative positions on a horizontal projection, to project them on the unwound surface of the axial structure, the latter being considered as a cylinder the surface of which is supposed to be flattened out. The transverse sections of the axis lying one over another are denoted on this surface by straight lines on which the positions of the members are drawn.

Among the different arbitrary constructions which may be attempted on paper, for the purpose of comparing the relative positions of the members of an axis, or of reducing them to short geometrical or arithmetical expressions, the following is of peculiar interest, and has been specially employed to denote the relative positions of the leaves and lateral shoots of the stem:—A line is imagined proceeding from any one of the older members in such a direction that, traversing the axis towards the right or the left, it includes the points of insertion of all the successive lateral members according to their age; the horizontal projection of this line is called the *Genetic Spiral;* in reality it is a helix [1] running round the stem more or less regularly. The importance of this construction has been very much overrated, and it has been employed where it is not only inapplicable to the elucidation of the history of development, but even where it has no longer even a geometrical meaning, and no longer assists a conception of the relative positions, but even makes it more difficult and complicated.

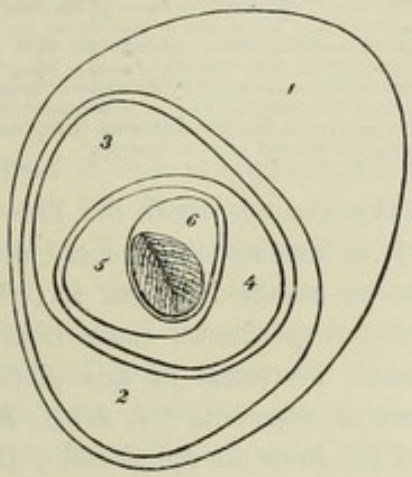

FIG. 141.—Transverse section through the convolution of the leaf-sheaths 1—6 of *Sabal ambraculifera*, in the centre of the section of a young leaf-blade. The arrangement of the leaves is a $\frac{2}{5}$ divergence. If the numbers 1—6 are united by a line, the genetic spiral is obtained.

When we are dealing with solitary leaves or shoots standing on the axis in three, four, five, eight, or more directions, and when the divergences are not too variable, the construction of the genetic spiral is of excellent service for a ready understanding of the position of the leaves (Fig. 141); and a more exact

[1] If the spiral winds from right to left, the right edge of the leaves is called the kathodic, the left (ascending) edge the anodic; the reverse in the spiral of an opposite direction seen from without.

knowledge of the peculiar properties of this ideal line may under these circumstances be of great use to morphology. In some cases it may be applied with advantage even to the relative position of whorls. But in a large number of cases other constructions appear much more natural, since they afford an easier explanation of the relative positions, and are more in accordance with the phenomena of growth. The construction of the desired genetic spiral is altogether impossible where the leaves are formed in simultaneous whorls[1], as the petals, stamens, and carpels of most flowers, or even in successive whorls where the members proceed from one point of the axis, and are formed in advancing order right and left, as in Characeæ and the flowers of Reseda (Fig. 137). In the successive whorls of *Salvinia natans* the construction of a genetic spiral would be equally impossible. Fig. 142, *B*, shows the diagram of the stem of this plant with three consecutive three-leaved whorls; in each of these the leaf w is formed first, then the leaf L_1, and finally the leaf L_2. If an attempt be made to construct the spiral, it must pass from w over L_2 across to L_1, then again in the same direction over w across to L_2; the figure thus formed is a circle, in which the divergences of successive leaves are very different. If we now pass to the next whorl, the line proceeds in a spiral direction to the next leaf w; but then, to retain the genetic succession in the second whorl, the line must be continued in an opposite direction; and this is repeated with every new whorl. It is evident that no clear conception can be obtained in this forced manner, and the whole construction appears altogether superfluous, since it is required by no feature in the history of development. The stem of this plant is constructed, as Pringsheim has shown, of two rows of segments (*G*, *H*, *J*, *K*, &c., in Fig. 142, *A*), which arise alternately right and left from the apical cell. Even before the formation of the leaves each segment undergoes various divisions, and in this manner sections of the stem are formed which alternately perform the functions of nodes and internodes of the stem. Each nodal section consists of the anterior half of an older segment and the posterior half of a segment next younger in age, as shown in the figure. An internode is formed of a whole segment of one row and of two half-segments of the other

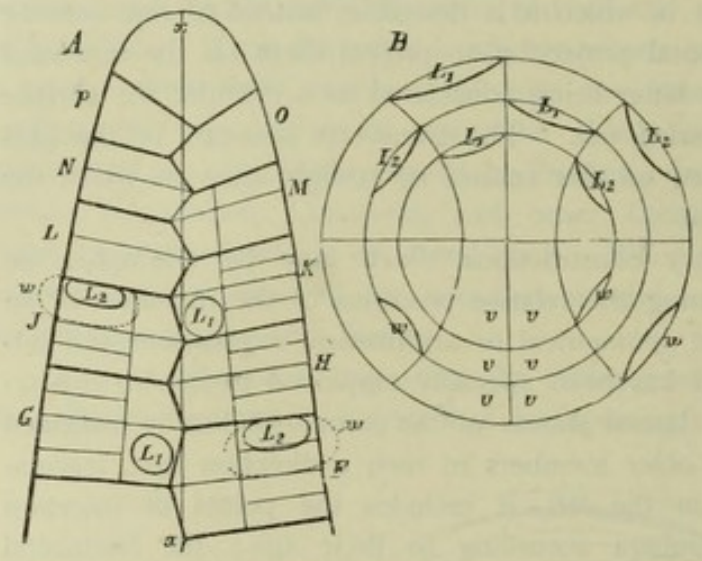

FIG. 142.—*A* the vegetative cone of the stem of *Salvinia natans*, regarded diagrammatically and looked at from above; *x x* projection of the plane which divides it vertically into a right and left half; the segments are indicated by stronger outlines, their divisions by weaker lines; the succession of the segments is denoted by the letters *F*—*P*; *B* diagram of the stem with three whorls of leaves, its ventral side indicated by *v v*; *w* the first-formed floating leaf; L_1 the aërial leaf formed next; L_2 the second aërial leaf of the same whorl formed last of all between the two first (after Pringsheim).

[1] Many writers employ even in such cases the conceptions borrowed from a spiral arrangement, considering arbitrarily as of successive origin the members of the whorl which arise simultaneously, by which means the path to more accurate knowledge is stopped.

row. Cells of the nodal sections occupying clearly-defined positions produce the leaves in the order stated. This development furnishes no evidence that the leaves are formed in spiral succession; the bilateral structure of the stem shows rather that a spiral construction is in this case altogether inadmissible. The same may be shown to be the case in Marsilea, where the creeping stem bears on its upper side two rows of leaves, while the under-side forms roots; the leaves borne on the upper side may in this case be united in the order of their age by a zigzag line broken right and left, which does not anywhere touch the leafless under-side of the stem, and corresponds also in its course to the bilateral structure of the stem. The spiral construction appears also to be meaningless in all those cases where it is indifferent whether the spiral be carried right or left. This is the case where the members are placed in two rows, with a constant divergence of $\frac{1}{2}$, and are thus arranged alternately in two orthostichies lying exactly opposite to one another, as is the case with the branchings of many thallomes (*e. g.* Stypocaulon, Fig. 98), the leaves of Grasses, the lateral shoots of Tilia, Ulmus, Corylus, &c. In all these cases of decidedly bilateral construction the genetic spiral may be imagined just as well and with the same divergence ascending right or left, by which of course it loses its importance for any morphological conclusion as much as if one supposed it to change its direction from leaf to leaf.

In upright free-growing axes with solitary leaves arranged in three, four, five, or more directions, the spiral construction appears especially natural; and this also agrees with the symmetrical relationships of plants, of which more will be said hereafter, as well as with the fact that the spiral construction proves to be opposed to nature in bilateral structures, especially in creeping or climbing stems, and in lateral branches.

In those cases in which the spiral construction may be employed naturally, *i. e.* in the least forced manner, to elucidate the relative positions of the members, two cases may be distinguished, according as the divergences are very unequal and change abruptly, or are nearly or quite equal to one another or only change gradually. In the first case the members appear to be arranged irregularly and without order, as the foliage-leaves on the stem of *Fritillaria imperialis* (Fig. 143), the flowers on the rachis of the raceme of *Triglochin palustre*, and in many Dicotyledons. When the change of divergence on the same axis is abrupt, it may also appear more natural to represent the position of the leaves by two homodromal spirals instead of one, as in many species of Aloe, where the shoots commence with leaves arranged in two rows and then pass over into complicated divergences, which lead finally to rosettes of leaves radiating on all sides. This occurs, *e. g.* in *Aloë ciliaris*, *latifolia*, *brachyphylla*, *lingua*, *nigricans*, and *Serra*. Fig. 144 shows the transverse section of a shoot of the last-named species; the first six leaves are arranged exactly alternately in two rows with a constant divergence $\frac{1}{2}$; at the 7th leaf this arrangement is suddenly changed; instead of being placed over 5, its position is between 5 and 6; but the 8th leaf exhibits the divergence $\frac{1}{2}$ from the 7th; the 9th again changes the divergence, instead of being placed over 7, it is between 7 and 6; the 10th leaf again diverges about $\frac{1}{2}$ from the 9th; and so it goes on. The leaves 7–15 are evidently arranged in pairs, the pairs being 7, 8; 9, 10; 11, 12; 13, 14; each pair

consists of two alternate (*i. e.* not opposite) leaves, the divergence of which is alike $\frac{1}{2}$; but the pairs themselves diverge from one another by smaller fractions.

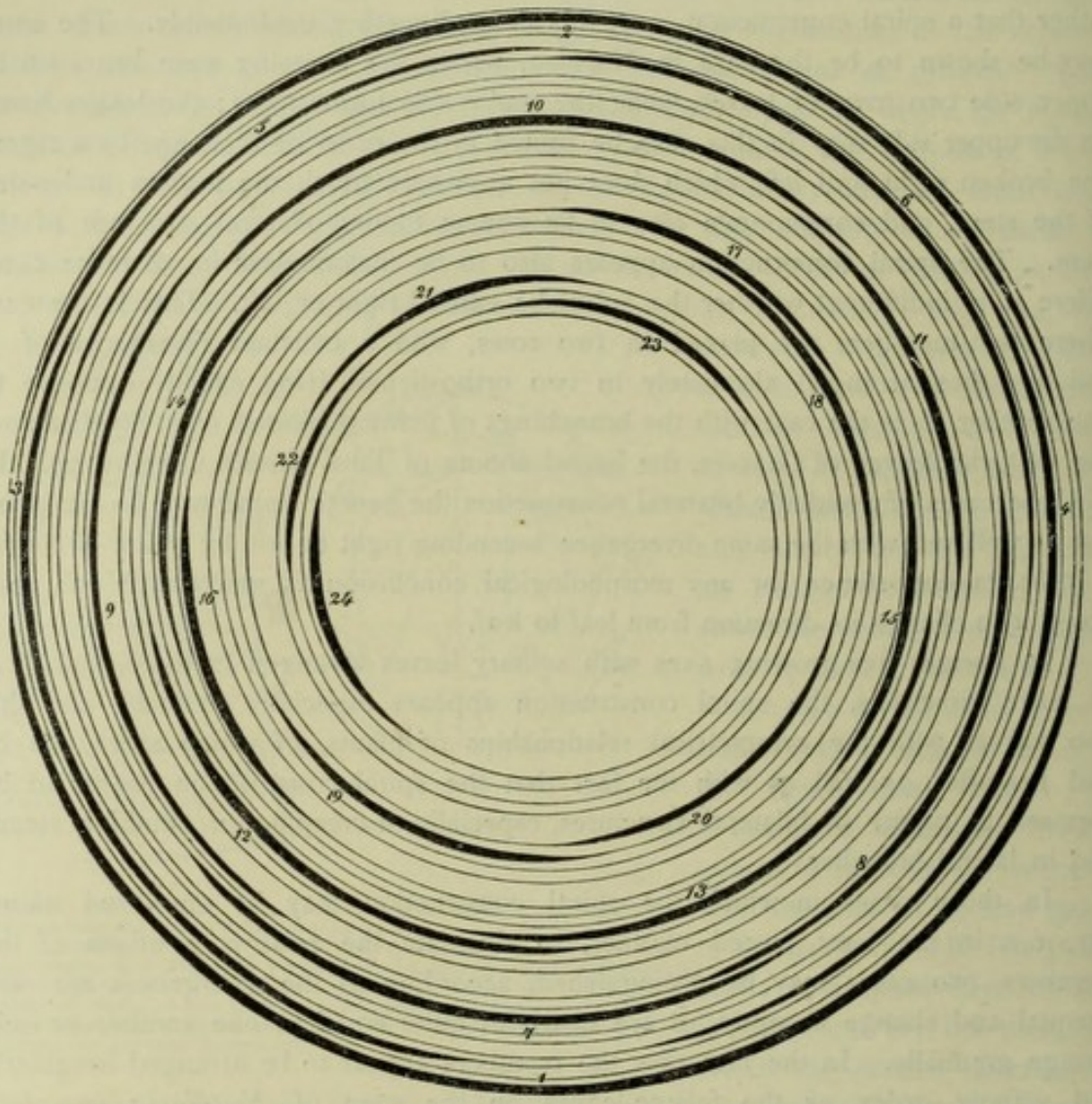

FIG. 143.—Diagram of a flower-stalk of *Fritillaria imperialis*, showing the divergences of the first twenty-four foliage-leaves; the relative lengths of the internodes are indicated by the larger or smaller distances between the circles.

If it is desired to unite all the leaves from 1–15 by a genetic spiral, an abrupt alteration of the divergence would be obtained within it. The relative positions are shown, however, more simply and clearly if, keeping in view the bilateral origin of the shoot, two spirals are constructed, each of which commences from one of the original orthostichies, and, so to speak, continues it in a spiral curve; the one contains all the leaves with an even number, the other those with an uneven number; the two are homodromal, running in the same direction round the stem. The bilateral origin of the shoot may be followed in this manner up to

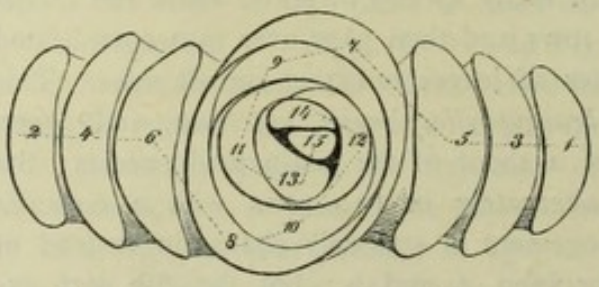

FIG. 144.—Transverse section of a shoot of *Aloë Serra*.

the rosette of leaves of the older shoot radiating on all sides. Similar relationships appear to exist in Dracæna and in some Aroideæ. At first sight such kinds of phyllotaxis appear as if the leaves were placed in two lines which have become changed by the torsion of the stem; but this hypothesis seems in this case scarcely admissible.

If we now turn, in conclusion, to those cases which clearly gave rise in times past to the erroneous hypothesis that the primary law of phyllotaxis is a universal spiral arrangement, we find the leaves placed singly, their divergences almost or quite equal or gradually passing over into some other value corresponding to the second case named above of spiral arrangement. In these cases the spiral construction affords a simple expression of the law of phyllotaxis; the only thing required is to name the constant angle of divergence; — according as this is $\frac{1}{3}$, $\frac{1}{4}$, $\frac{1}{5}$, $\frac{2}{5}$, $\frac{3}{8}$, &c., the phyllotaxis is termed simply one of $\frac{1}{3}$, $\frac{1}{4}$, $\frac{1}{5}$, and so on. It is usual in such cases for the divergence not to remain constant for all the members of an axis; shoots which form numerous leaves mostly begin with more simple arrangements, as $\frac{1}{2}$, and then pass over into more complicated ones, an arrangement being considered more complicated when the numerator and denominator of the fraction of divergence are larger. When the divergences between lateral members placed solitarily with spiral arrangement are equal, they must then also stand in straight rows, the number of which is expressed by the denominator of the angle of divergence. If, for instance, the divergence is a constant one of $\frac{3}{8}$, as in Fig. 145, there are eight orthostichies, the 9th member standing on the same median plane as the 1st, the 10th as the 2nd, the 11th as the 3rd, and so on. In a $\frac{2}{5}$ phyllotaxis, in the same manner, the 6th member stands over the 1st, the 7th over the 2nd, and so on. In some cases the orthostichies are very obvious, as, for instance, in Cacti with prominent angles, the angles corresponding to the orthostichies of the spirally arranged leaves, which, however, in this case mostly remain undeveloped. In verticillate leaves also the straight rows are mostly conspicuous if the shoot is looked at from above, as, for instance, in the decussate two-leaved whorls of *Euphorbia Lathyris*, and the cactus-like *E. canariensis*.

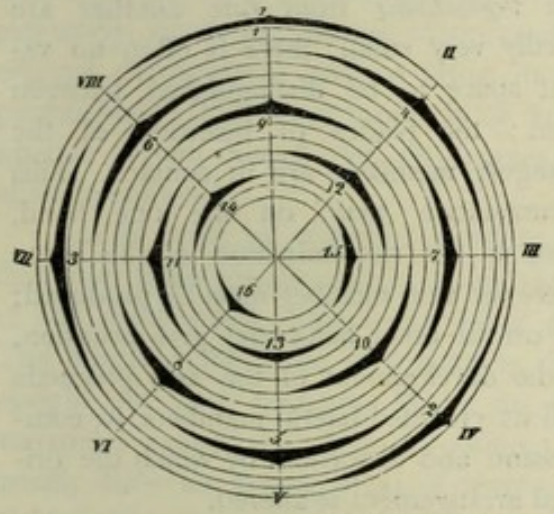

FIG. 145.—Diagram of a shoot in which the leaves have a constant phyllotaxis of $\frac{3}{8}$.

When the members of a spiral phyllotaxis with a constant angle of divergence stand sufficiently close to one another, spiral arrangements are easily seen and followed to the right and left which more or less conceal the genetic spiral. These rows are called Parastichies, and are particularly clear in the cones of species of Pinus, the leaf-rosettes of Crassulaceæ, the flowers of the sunflower and other Compositæ, and in the spadices of Aroideæ. They may be seen in every spiral phyllotaxis with a constant divergence, and can always be made clear in the diagram, or when the arrangement is represented on an unrolled cylindrical surface.

The considerations of these constructions leads to definite geometrical rules, by means of which the genetic spiral can be easily deduced from the parastichies[1].

It is evident that the constructions hitherto mentioned can only be more or less convenient aids to an understanding of the actual principles of the arrangement of leaves. But in order to obtain, with their assistance, a deeper insight into the processes of growth themselves of which these principles are the result, it is necessary to follow up the history of development, and in every single case to ask the question, what circumstances are the cause of a new member being formed just in this place and nowhere else. It may be well, therefore, to bring forward here some of the points which must be considered in reference to this view.

(1) The first question to consider is always the permanence of the order of succession which may occur at the time of the origin of the lateral members.

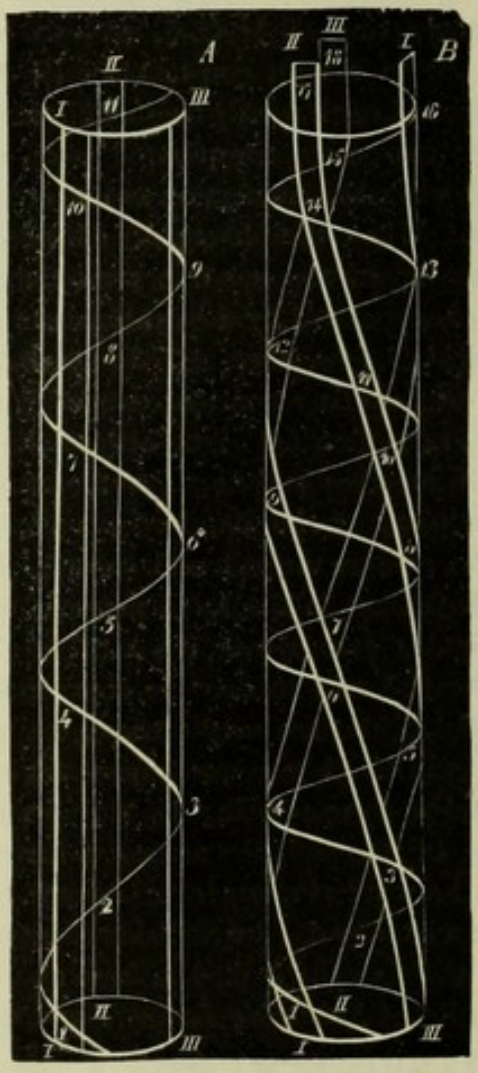

FIG. 146.—Diagrammatic representation of the orthostichies of a $\frac{1}{3}$ phyllotaxis; *A* before and *B* after the torsion of the stem. Each of the orthostichies *I*, *II*, *III* is indicated by a double line; the genetic spiral is single; where it crosses the orthostichy, the leaf-insertions are indicated by figures.

(2) Attention must be paid not only to the lateral deviation or divergence, but also to the longitudinal distance at which a new member is formed at the *punctum vegetationis* above the members next preceding it. The longitudinal distances of the youngest lateral structures of a *punctum vegetationis* from one another are usually very small; there is often no vacant space to be distinguished between them; the planes of insertion of the youngest members are in contact. This circumstance may, on the one hand, assist in the determination of the place where the next member must be produced; but on the other hand may give occasion, as the development of the axis proceeds with its crowded lateral members, to compression and distortion, by which the original arrangement is altered.

(3) By the increase in length of the common axis, members which were at first closely crowded become placed at a considerable distance from one another; others, in consequence of slower growth, remain closely packed, so that a different distribution occurs in different parts of the stem (as in the leaf-rosettes and flower-stalks of Crassulaceæ, Agave, Aloë, &c.). In the same manner the angle of divergence frequently becomes changed from the more rapid growth in thickness of the axial

[1] As the treatment of the subject is only of value to those who are practically concerned with phyllotaxis, I must refer to the detailed description in Hofmeister's Allgem. Morphologie, § 9.

structure on one side than on the other; and still more commonly by torsion around its own axis of growth. By such torsions lateral members, arranged at first exactly in straight rows, become displaced so that the orthostichies appear as if wound spirally round the axis. This occurs, for instance, according to Nägeli and Leitgeb, in the root-systems of Ferns, Equisetaceæ, and Rhizocarps, as well as in the three-rowed phyllotaxis of the Moss *Fontinalis antipyretica*, according to Leitgeb. But the most striking example is furnished by the stem of the screw-pine *Pandanus utilis;* in the bud, the numerous and already strongly developed leaves stand, as is shown by the transverse section, in three perfectly straight lines with the phyllotaxis $\frac{1}{3}$; but, as the development of the stem advances, it undergoes so severe a torsion that the three orthostichies are transformed into three strongly curved spiral lines running round the stem. In these and similar cases the change in the relative positions caused by the torsion of the axial structure is easily and certainly established. But when the positions are so related to the apex of the axial structure that the angle of divergence cannot be accurately estimated by an apical view from above, it must remain uncertain whether the position of the mature members is unchanged or has been altered by lateral displacement and torsion of the axis. A displacement, for instance, of about 9° of the circumference of the axis would be sufficient to alter the divergence from $\frac{2}{5}$ to $\frac{3}{8}$, a similar displacement of 1·3° would change the divergence from $\frac{5}{13}$ to $\frac{8}{21}$. When the phyllotaxis is very complicated and the number of the longitudinal rows very large, extremely small and almost inappreciable distortions are sufficient to destroy the original arrangement and to bring into existence altogether different systems of parastichies. This observation is of interest so far as it makes it seem doubtful whether certain complicated phyllotaxes are always due to the original arrangement of the members[1].

(4) It must be observed whether the position of newly-formed members or their later transformation shows any relation to the direction of the force of gravity, of the light which falls upon them, or of any pressure acting from without[2]. The effect of the force of gravity is that primary shoots which are in the main upright put forth radiating leaves on all sides; while such as have a decidedly horizontal growth, in which a rooting under-side is contrasted with an upper-side, usually show an arrangement of leaves on the latter in two rows, or one which is divided into two equal halves by a plane cutting the stem longitudinally (*e. g.* Salvinia, Marsilea, *Polypodium aureum*, *Pteris aquilina*, &c.). The horizontal lateral axes with leaves arranged in two rows on vertical primary shoots which have the leaves arranged in several rows (as in *Prunus Lauro-cerasus*, *Castanea vesca*, Corylus, &c.) show this kind of relationship less clearly, because an influence independent of gravity must in these cases be presumed of the primary upon the lateral axis, as is shown by the position of the leaves in the lateral buds before unfolding (see Fig. 147, p. 187).

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[1] [See Airy, Proc. Royal Soc. *l. c.*]

[2] Hofmeister (Allgemeine Morphologie, §§ 23, 24) has collected a series of facts which show relationships of this kind; but, both with reference to single facts and to the interpretation which he gives, I am decidedly of a different opinion, the reasons for which would carry me too far. (Cf. *infra*, sect. 27.)

(5) It must further be observed whether the first appearance of lateral members is preceded by phenomena connected with development which assist in the determination of the place of origin. Of this nature, for instance, is the connexion of the points of origin of the lateral roots on the outside of the fibro-vascular bundles by the course of which their succession is determined; and this again, in its turn, determines whether the lateral roots are arranged spirally or in whorls. Here the arrangement in longitudinal rows is clearly the general and primary one; the divergences and longitudinal distances are a secondary affair determined by special accessory circumstances. The point of origin of a lateral shoot is, on the other hand, in general primarily determined by its relation to the nearest leaf, in so far as it is formed beneath, beside, or above its median plane; forces of secondary importance determine whether lateral shoots are formed in connexion with each leaf or only with particular leaves of an axis, and so forth. The phyllotaxis of the lateral shoot may differ from that of its primary shoot, because the growth of the latter assists in influencing it; as, for instance, in the case of lateral shoots with phyllotaxis in two rows on primary shoots with an arrangement in several rows. Under this heading falls also the bilateral branching of leaves, whether those of the stem itself be bilateral or multilateral. The dimensions of the *punctum vegetationis* and the thickness of the axial structure derived from it may also be proportionate to the number of the rows of lateral structures; thus thicker mother-roots usually produce three or more rows of secondary roots, while thinner primary roots produce only two rows or even a smaller number. Thus, for instance, the roots of Cryptogams (according to Nägeli and Leitgeb), the thick primary roots of Zea, Phaseolus, Pisum, Quercus, &c., form three, four, five, six, or more orthostichies of lateral roots, which, on their part, are much thinner and produce fewer orthostichies. The same is not unfrequently the case with the phyllotaxis of stems. When the size of the *punctum vegetationis* increases, the leaves are arranged in a larger number of rows, as in the vigorous seedlings of many Dicotyledons, in Palms, *Aspidium Filix-mas*, &c. This is most strikingly exhibited in the many-rowed flower-heads of the sunflower on the four-rowed foliage-stem; the size of the *punctum vegetationis* undergoing a sudden and great increase at the period when the flower-head is being formed (Fig. 108, p. 133). But, *vice versâ*, the number of the rows of leaves decreases when the size of the growing end of the stem decreases in consequence of vigorous growth in length; this is shown, for instance, in the few-rowed long and slender flower-stalks which proceed from the many-rayed leaf-rosettes of species of Aloë, Echeveria, &c. If the insertion of the leaves or shoots embraces, at an early stage, a large part of the periphery at the *punctum vegetationis*, only a few rows of leaves are formed; if the insertion-planes are relatively small, the number of rows on the axis increases. This is illustrated by the many rows of small flowers on the spadix of Aroideæ or in the racemes of Trifolium, while the leaves of the same plants are in few rows, their insertions embracing the stem or being even broader. Hofmeister[1], to whom we owe the introduction of this point of view in the theory

[1] Allgemeine Morphologie, § 11, where particular cases are discussed in detail. This treatise is beyond question the most important that has hitherto been written on phyllotaxis; nevertheless, in my account, which necessary limits have confined almost to a mere sketch, I differ from Hofmeister's views even in some points of primary importance.

of phyllotaxis, states the general rule in the following words:—*New lateral members have their origin above the centre of the widest gaps which are left at the circumference of the punctum vegetationis between the insertions of the nearest older members of the same kind.* The rule is illustrated by the case of alternating whorls (especially of pairs crossing one another at right angles, or 'decussating'), or by that of alternating solitary leaves with a base which grows early in breadth, in Phanerogams, where the *punctum vegetationis* consists of small cells. Where, on the other hand, we have decidedly bilateral horizontal axes (as in *Pteris aquilina*, Salvinia, and Marsilea), or definite relations of the leaf-formation to the segmentation of an apical cell (as in Mosses), or distinctly successive formation of the members of a whorl (as in Chara, Salvinia, flowers of Reseda, &c.), the mechanical importance of the rule is, in my opinion, subordinate to the other causes which then have the greatest influence in determining the position of the new members. Independently of the points of view referred to in paragraphs 1–4, the genetic relationships indicated in this paragraph show that it is scarcely possible to find a single rule which will govern all cases of phyllotaxis. Causes which belong to altogether different categories must, according to circumstances, exercise the greatest influence in determining the point at which a new member is formed.

(6) I consider it a circumstance of primary importance that the same or very similar kinds of phyllotaxis may be brought into existence by very different combinations of causes, and positions apparently very different by very similar combinations of causes. Among the causes here referred to I understand the previous relative development of the axis and of its lateral members, the influence of the primary on the secondary axes, of pressure, gravitation, light, and similar conditions. The validity of this position becomes most evident when it is observed that the same or similar divergences of leaves or lateral shoots may occur universally in unicellular plants, in multicellular plants with a distinct apical cell, and in those in which the *punctum vegetationis* consists of a small-celled tissue without any definite relation to the segmentation of an apical cell, as in Phanerogams. The mechanics of the processes of growth must undoubtedly be different when the lateral branches of a Vaucheria are formed in two rows, and when the two rows of leaves of a Fissidens or of a Grass are produced in the same or a similar position, in which case the cell-walls in the primary meristem represent a multiplicity of causes of growth and of hindrances to it. The similar arrangement of the outgrowths under such different circumstances does not prove that the circumstances themselves are similar or of but little importance, but only that altogether different combinations of causes may lead to very similar relations of position. In Muscineæ and Vascular Cryptogams the relation of the formation of leaves to the segmentation of the apical cell is the more obvious the nearer to the apex the leaves originate. It is most obvious of all in Mosses, where each segment grows out into a leaf-forming protuberance immediately after its formation, and before further cell-division takes place. Here the immediate conditioning cause of the position of the leaves is the position of the leaf-forming 'segments' themselves; when these latter are formed in two alternating longitudinal rows, as in Fissidens[1], two rows or orthostichies of

[1] Lorentz, Moosstudien. Leipzig 1864.

alternating leaves arise with the divergence $\frac{1}{2}$. When the segmentation of the apical cell is into three rows, so that each new division-wall of the apical cell is parallel to the last division-wall but two, as in Fontinalis, two rows of leaves result, arranged spirally with the constant divergence $\frac{1}{3}$. When the apical cell is a three-sided pyramid, but the new walls which are formed in it are not parallel to those already in existence, but oblique, so that all the segments, *e. g.* on the anodic side are broader than those on the kathodic side, then the segments no longer lie in three straight rows, but either three spirals or one only can be recognised encircling the axis; and since each 'segment' in this case (*e. g.* in Polytrichum, Catharinea, and Sphagnum[1]), developes into a leaf, the leaves are formed in spiral arrangements, with divergences depending on the obliquity of the principal walls of the segments to one another[2]. These phenomena show clearly that when each segment produces a leaf, the phyllotaxis depends on the manner in which the new principal walls of the segments arise; and since the direction taken by the segmentation of the apical cell depends again on causes of which we are at present ignorant, the phyllotaxis must also finally be referred to these unknown causes. In certain cases a reason may be given why, when the segmentation of the apical cell is uniform, the positions at which the leaves are formed are nevertheless variable. The segments of the apical cell in Fontinalis lie, as in Equisetum, in three straight rows; but the solitary leaves stand in straight rows and spirally with the constant divergence $\frac{1}{3}$. In Equisetum, on the contrary, alternating whorls arise of leaves which have grown together in the form of a sheath, because here, as Rees has shown[3], the three segments of each cycle, arranged originally in a spiral manner from want of uniformity in growth, are finally placed on the same zone, from which a circular projection next grows out, on which the teeth of the sheath are formed. From the want of uniformity in the growth of the segments, the causes of which are at present unknown, still further differences, as compared with Fontinalis, are introduced, in consequence of which the development of the whorls themselves becomes alternate instead of superposed (as might be the case). If the processes which take place in Marsilea (as Hanstein has described them[4]) are compared with this, it is seen that the segmentation of the apical cell of the stem agrees in the main with that of Fontinalis and Equisetum; it is in three rows with a divergence $\frac{1}{3}$. As in Fontinalis, the leaves originate by a curving outwards of the segment-cells; but the leaves are in this case not arranged in three rows as in Fontinalis, nor in whorls as in Equisetum, but in two rows. The immediate cause of this must be sought in the fact that the stem, together with the *punctum vegetationis*, lies in a horizontal position; it has an upper and an under side The segments of the apical cell form two rows on the upper and one on the under side; but the former

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[1] Compare the admirable description by Leitgeb in the case of Sphagnum, in Sitzungsber. der kais. Akad. der Wissenschaften. Vienna, March 1869.

[2] Cf. Hofmeister, Allg. Morph. p. 494; and Müller, Bot. Zeitg. 1869, a general morphological study, t. IX. fig. 24. In such cases the behaviour of the apical cell can in fact be imagined as if it rotated on its axis, as I supposed in my first edition. The description there given does not however now appear to me suited to the beginner.

[3] Rees, Jahrb. für wissen. Bot. vol. VI. p. 216.

[4] J. Hanstein, in Jahrb. für wissen. Bot. vol. IV. p. 252.

produce leaves, the latter roots. The horizontal position of the stem and its bilateral development are here clearly the cause why the upper side only produces leaves; and since its segments lie in two rows, there are two rows of leaves, which we may imagine united by a zigzag line. But a further cause of the difference, as compared with Fontinalis and Equisetum, arises from the fact that in Marsilea it is not every segment of the two rows on the upper side that forms a leaf; but, according to Hanstein, certain segments remain sterile, and these form the internodes which are at first wanting in Fontinalis and Equisetum, and are only formed at a later period by further differentiation and intercalary growth. In *Pteris aquilina* and in Salvinia the segments of the apical cell of the stem are also formed, as in Fissidens, in two rows; but the phyllotaxis is in all cases very different. The effect of the difference of growth is first of all shown in the decidedly horizontal position of the stem of the last-named plants, and also in the circumstance that the segments themselves grow vigorously in thickness and length, and divide before the formation of the leaves commences; it is not from the segment-cells which are already in existence, but from certain products of their division at a great distance from the apex of the stem, that the leaves originate. This is common to Pteris and Salvinia; but in the divisions of the segments and in the total growth of the stem considerable differences between the two occur. *Pteris aquilina* forms on its thick underground horizontal shoots two alternating rows of leaves standing almost on the upper side, while Salvinia forms alternating whorls on its slender floating shoots, the members of the whorls showing a very peculiar order of succession corresponding to the bilateral arrangement and the horizontal growth of the axis.

The genetic forces which have an evident influence on the phyllotaxis of Cryptogams through the segmentation of the apical cell and the further behaviour of the segments, are wanting in Phanerogams, where the leaves spring from a small-celled *punctum vegetationis* the tissue of which behaves like an almost homogeneous plastic mass. The immediate causes which determine the spot where a leaf or shoot is to arise can no longer be referred in Phanerogams, step by step, to the behaviour of an apical cell. The most immediate visible causes lie rather in the position of leaves already in existence, in their increase in breadth, in the form and size of the vegetative cone, in its inclination to the vertical, and in its relation to the size of the mother-shoot, &c.—conditions which (as has already been mentioned under paragraph 5) have been treated in detail by Hofmeister. The rule enunciated by him, that lateral shoots arise above the middle points of the largest gaps left by the youngest contiguous shoots, gives an efficient cause for the determination of the place of origin of new members, and may be applied also to the first leaves of lateral shoots, which generally show a definite relationship to the mother-leaf, *i. e.* the leaf in the axil of which they are produced. In Monocotyledons, for instance, the first leaf of an axillary shoot usually stands on its posterior side, *i. e.* facing the mother-axis; in Dicotyledons, on the contrary, the axillary shoot generally begins with two leaves, which stand right and left of the median plane of the mother-leaf, and thus come in that free space between the mother-leaf and the primary axis which is least exposed to pressure.

As has now been shown by these brief indications, the investigations of

phyllotaxis have not at present got much further than to ascertain in each separate case the phenomena preceding and accompanying the origin of a member, as well as those forces which, from their direction, exercise an influence on the point of origin, and to lay down more general laws as the result of comparison in a sufficient number of cases. In these as in all other investigations into organisms, we are always however met at the very outset by a consideration of great importance which imposes itself upon us, I mean the *tout ensemble* of properties which define the character of the natural group, class, or order. By recognising a plant as a member of a particular class, *e. g.* Mosses, Ferns, Equisetaceæ, Rhizocarps, or Phanerogams, &c., an aggregate of properties is ascribed to it, which must be taken into account as such. If we pay special regard to the point of view opened out by the Theory of Descent, we must recognise the law of heredity and of the conformable endowment of the members with definite properties, the difficulty or even impossibility of demonstrating the causes of any morphological phenomenon in any other manner than historically. The organic forms are not the result of combinations of forces and materials given once for all, and always again presented in exactly the same manner, as in the case of a crystal which is first dissolved and then re-crystallised; but they are the result of combinations which repeat themselves hereditarily and which at the same time undergo change. To understand these it is necessary to refer to the past, and not only to the immediate present.

Abundant opportunity will be afforded in the description of the various classes in Book II for a more exact observation of particular relations of position; but what has now been said is sufficient as a preliminary. Some additional remarks on the Spiral Theory in the doctrine of phyllotaxis may however find a place here. It has already been shown that the construction required and employed in the spiral theory is not in all cases possible, being in some cases arbitrary and without relation to the history of development, and in others simply meaningless. Finally, only those cases admit of the application of the spiral theory without violence, in which the shoot forms three or more rows of leaves distributed singly and uniformly in all directions. The history of development often points to quite different constructions, even in those cases in which the spiral is still geometrically possible. But even in those cases in which the union of the leaves according to their order of succession in age by a spiral always running round the stem in the same direction is possible and even apparently useful, there is not in the relations of the history of development any sufficient reason for the hypothesis that the growth of the generating axis itself actually follows a spiral. This was for the first time refuted in detail by Hofmeister in the Bot. Zeitg. 1867, numbers 5, 6, 7, and the refutation is again repeated in his 'General Morphology,' p. 481. With reference to his descriptions it can only be stated that even a short abstract of them would occupy too much space for this text-book.

Closely connected with the spiral theory, which must be carefully distinguished from the doctrine of phyllotaxis, is another very peculiar mode of expressing the angle of divergence. It is thought, namely, that a natural law was found when it was remarked that some of the most commonly occurring constant divergences $\frac{1}{2}$, $\frac{1}{3}$, $\frac{2}{5}$, $\frac{3}{8}$, $\frac{5}{13}$, and some of the less common ones, as $\frac{8}{21}$, $\frac{13}{34}$, $\frac{21}{55}$, $\frac{55}{144}$ [1], &c. may be represented as

[1] It must be observed in reference to this that it remains uncertain whether such complicated divergences are ever so formed originally, or whether they are not always consequences of complicated displacements, in consequence of which the direct observation of the *punctum vegetationis* does not give in these cases a certain conclusion.

successive convergents of the continued fraction

$$\cfrac{1}{2+\cfrac{1}{1+\cfrac{1}{1+\ldots}}}$$

Were it possible to combine all kinds of phyllotaxis without exception in this manner into *one single* continued fraction, we should actually have a kind of natural law, in which there would be no relation of cause and effect, and which would hence stand out as an inexplicable curiosity. It is not however so bad. There are many such kinds which cannot be expressed by this continued fraction; and in order to carry out the method, new continued fractions have to be constructed, *e. g.*

$$\cfrac{1}{3+\cfrac{1}{1+\cfrac{1}{1+\ldots}}} \quad \text{or} \quad \cfrac{1}{4+\cfrac{1}{1+\cfrac{1}{1+\ldots}}} \quad \&c.;$$

of which indeed only one or two convergents are for the most part met with as actual angles of divergence. And since it is possible immediately to construct a new continued fraction for every phyllotaxis which cannot be arranged under those already in existence, it is of course possible to represent by this method all varieties of phyllotaxis; but it follows at the same time that the method itself thus loses all deeper significance. If only those divergences occurred on one and the same axis or on one system of axes which can be represented by convergents of one and the same continued fraction, or if the different values of one and the same continued fraction occurred exclusively in a genus, family, or order, the method would even in that case be of some value. But this is not the case. Since moreover no actual relationship of the method to the history of development, to the classification of plants, or to the mechanics of growth, has been established, in spite of numberless observations, it seems to me absolutely impossible to imagine what value the method can have for a deeper insight into the laws of phyllotaxis. But even as a mnemonic assistance it appears to me not only superfluous, but even disadvantageous, since the use of it diverts the attention from relationships which are of real importance[1].

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[1] [Chauncey Wright (Memoirs of Amer. Acad. ix. p. 389) has pointed out an interesting property of the series $\frac{1}{2}, \frac{1}{3}, \frac{2}{5}, \frac{3}{8} \ldots\ldots$ which includes all the more common arrangements of phyllotaxis. If the spiral line passing through successive leaves be traced the long way round, we obtain the complementary series $\frac{1}{2}, \frac{2}{3}, \frac{3}{5}, \frac{5}{8} \ldots\ldots$ the terms of which are successive convergents of the continued fraction

$$\cfrac{1+1}{1+\cfrac{1}{1+\cfrac{1}{1+}}} \quad \&c.$$

If we put this $= K$ then $K = \dfrac{1}{1+K}$

or $K^2 = 1 - K$

$\therefore 1 : K = K : 1 - K$

or K is the ratio of the extreme and mean proportion; and generally

$$K^n = K^{n-2} - K^{n-1}.$$

K is therefore the angular divergence which would effect 'the most thorough and rapid distribution of the leaves round the stem, each new or higher leaf falling over the angular space between the two older ones which are nearest in direction, so as to divide it in the same ratio, K, in which the first two or any two successive ones divide the circumference. Now $\frac{5}{8}$ and all successive fractions differ inappreciably from K.' Practically, therefore, all terms of the series above the third fulfil the condition of that leaf-distribution which is theoretically the most efficient.—Ed.]

Sect. 27. **Directions of Growth**[1].—(1) In every thallus, branch, stem, leaf, hair, and root, it is easy to distinguish between two opposite ends, the Base and the Apex. The base is the place where the member was first formed and began to grow; the apex lies in the direction which the growth follows. The direction from the base to the apex is the longitudinal direction of the member under consideration; a section made in this direction is called a longitudinal section. The transverse direction and section of the member are at right angles to the longitudinal ones.

(2) In every transverse section of a member there is a point about which the internal structure and external contour are so arranged that it must be considered as the *Organic Centre* of the transverse section. Every line drawn from this point towards any point of the circumference is a radius; every definite portion of the transverse section has one side facing the circumference and one facing the centre; these being usually developed in a different manner from the sides that face the radii, and hence easily distinguished from them. These relationships are recognised with ease in the transverse section of woody stems and roots, but can be easily made out in other cases also, even in unicellular plants and hairs. The organic centre of the transverse section does not usually coincide with the geometrical centre, as is easily seen in the transverse sections of most leaf-stalks and horizontal branches with an 'eccentric' pith.

(3) If a line be imagined uniting the organic centres of all the transverse sections of a member, this is the *Longitudinal Axis* or *Axis of Growth* of the member. The axis of growth may be a straight or a crooked line; in the younger parts (nearer the apex) it may be crooked, and again straight when further developed (further from the apex), (as in Salvinia and Utricularia) or the reverse. A plane which passes through the member in such a manner as to contain the axis is called an *Axial Longitudinal Section*. If the axis be curved in a plane, the latter coincides with the axial longitudinal section; if the axis is straight, the number of possible axial longitudinal sections is very large or even infinite.

Growth in the direction of the longitudinal axis is generally quicker and also generally lasts longer than in the transverse directions, as is clearly shown in most stems (haulms, flower-stalks, scapes, palm-stems), in long leaves, in all roots, and in most hairs and thallomes. This characteristic cannot however be used in the general definition; for there are cases in which it appears questionable whether the growth in the direction of the longitudinal axis is more intense or more prolonged than in the radial directions; as, *e.g.* in the stem of Isoëtes, and the prothallium of some Polypodiaceæ. But the characteristic is superfluous for the determination of the longitudinal axis; its direction can always be recognised by the position of the base and apex of a member; and its position on the transverse section (the organic centre) can be found without anything else being known about the relationships of growth. It is always possible, without even knowing the duration or intensity of the growth, to decide which is the longitudinal and which the transverse section of a

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[1] H. von Mohl, Ueber die Symmétrie der Pflanzen, in his Vermischte Schriften. 1846.—Wichura, Flora, pp. 161 et seq. 1844.—Hofmeister, Allgemeine Morphologie, §§ 1, 23, 24. Leipzig 1868.—Pfeffer, Arbeiten des botan. Instituts in Würzburg, p. 77. 1871.

member; this can indeed be determined from a very small fraction of it; in a Mammillaria, a Melocactus, or a Cereus, it is just as easy to determine the longitudinal axis of growth in early youth, when these Cacti are often as thick as they are long, as it is later when they are much longer than thick. This is also the case in the abbreviated axis of bulbs, in many tubers and corms (as Crocus), and in fruits, like those of many gourds, whose diameter is much greater than their length.

The growth of roots and stems in the direction of their longitudinal axis is generally unlimited, that of leaves and hairs mostly limited, although these relationships are sometimes reversed. When the growth is unlimited, the formations along the axis are usually constantly repeated, the segments formed one after another are similar, the lateral members that spring from them (branches, leaves, lateral roots, &c.) are uniform, or they exhibit in their development a repeated alternation, as, *e.g.* in Moss-stems, rhizomes of Equisetum, primary stems of Conifers, &c. When, on the contrary, the growth along the axis is limited and definite, the resulting segments are dissimilar, and their outgrowths exhibit progressive changes (metamorphosis). This occurs in most leaves, the basal portions of which are usually strikingly different in form from the parts nearer the apex; it occurs also in the stems of Angiosperms with terminal flowers, commencing, for instance, with the formation of radical leaves, proceeding to that of foliage-leaves, and then, through the bracts passing over into the production of floral leaves, closing with that of the carpellary leaves.

Axial growth is always limited when true dichotomy occurs at the apex; on the other hand the bifurcations repeat and continue the mode of development of their common basal portion (as in Fucus or Selaginella), although individual branches may terminate their growth without dichotomy by producing fruit.

(4) If an axial longitudinal section is imagined to pass through a member, the conformation right and left may be similar, like the right and left halves of the human body. If the two halves are so similar that the one is a reflected image of the other, they are *symmetrical*, and the dividing plane between them is called a plane of symmetry. In this strictest sense symmetry is very rarely found in plants (most nearly in many flowers and stems with decussating whorls); and accordingly the term is constantly employed in a laxer sense. Two, three, four, or a larger number of symmetrically dividing planes often pass through one member (a shoot or root), all of which intersect in the axis of growth. Such members are called polysymmetrical; so-called 'regular' flowers, stems with alternating whorls, and most roots, are polysymmetrical. If, on the contrary, it is possible to imagine only one symmetrically dividing plane, as in the flowers of Labiatæ and Papilionaceæ[1], in stems with leaves arranged in two rows, where the median plane of the two rows of leaves is at the same time the plane of symmetry, in the thalloid shoots of Marchantia, and in most leaves, the object is monosymmetrical, or simply symmetrical. Monosymmetry is however only a particular case of the ordinary bilateral structure; it consists in the processes of growth being perfectly similar to the right and left of an axial longitudinal section,

[1] A. Braun calls monosymmetrical flowers zygomorphic, an expression which is also elsewhere interchangeable with monosymmetrical.

but in such a manner that the two halves of the member do not lie exactly opposite to one another like reflected images. Thus, for example, the oblique leaves of Begonia are not symmetrical, although bilateral; the one half to the right of the mid-rib of the lamina is larger and of somewhat different shape to the other half to the left of the mid-rib; and the same is the case with the elm. A shoot with alternating leaves in two rows is also simply bilateral without being monosymmetrical; if it is divided at right angles to the common median plane of all the leaves, the two halves bear each one row of leaves; but the one is not the reflected image of the other, since the leaves of the two rows spring from different heights. Where a true monosymmetrical structure occurs, it may be considered a particular case of the bilateral; the latter, therefore, being the more common, is the more important phenomenon.

The same relationship occurs between polysymmetry and multilateral arrangement as between monosymmetry and bilateral arrangement; polysymmetry must also be considered only as a particular case of the multilateral structure. This latter is always present when several pairs of halves can be produced by axial longitudinal sections, so that the two halves of each pair are very similar to one another, but not exactly alike, like an object and its reflected image. Thus the short stems of Sempervivum, the leaf-rosettes of Æonium, the cones of species of Pinus with their scales, can be easily halved by numerous longitudinal sections, but the halves thus formed are never symmetrical, because the leaves and scales are arranged in a spiral manner, and a spiral can never be divided symmetrically; but in so far as the spirally arranged leaves stand in three, four, five, eight, thirteen, &c. orthostichies, the shoot itself may be said to be three-, four-, five-, eight-, thirteen-sided, &c.

The most common distinction is between bilateral and multilateral structures; in both cases the lateral arrangement may rise into symmetry, the former into monosymmetry, the latter into polysymmetry. The extremes are seen on the one side in roots with circular transverse sections, on the other side in most leaves and leaf-like shoots with only two symmetrical halves. If, however, in the case of roots regard is paid to the number of their fibro-vascular bundles, the apparently infinite number of their planes of symmetry may be usually reduced to two, three, four, or five.

To obtain a convenient mode of expression for relationships of this kind, each longitudinal section which produces two similar halves may be termed a principal section or principal plane; and if the two halves are symmetrical it is a symmetrical section or plane. Thus bilateral structures have one principal section, multilateral two or more principal sections.

(5) Lateral arrangement and relationships of symmetry may be looked at from two important points of view, according as the members of a plant are compared with one another, or are considered in reference to their relation with the external world, with gravity, light, pressure, and external circumstances.

If the members of a plant are compared with one another, it is seen, for example, that the principal sections of all the leaves may lie in one plane on opposite sides of the stem, in which case the shoot itself is bilateral; or they may lie in two planes, crossing one another at right angles, when the shoot is quadrilateral, as, for instance, when it bears decussate whorls of two members, a case which, in reference

to other relationships, is very near to that of bilateral arrangements, and may be termed a Double Bilateral arrangement. In these cases the principal sections of the leaves are also at the same time principal sections of the stem. In Salvinia, Marsilea, *Polypodium aureum*, and *Pteris aquilina*, on the contrary, the principal sections of the leaves, arranged in straight rows, lie right and left of the single principal section of the bilateral stem, which is in these cases closely connected with the horizontal growth.

The relationship of lateral arrangement and symmetry to the external environment of the plant is shown, for example, in the fact that multilateral shoots usually grow upright, while bilateral shoots generally lie horizontally, and in such a manner that the principal section is vertical. Many bilateral shoots cling on one side to a horizontal, oblique, or vertical support, as the Marchantiæ, Jungermanniæ, the ivy, &c.; and in that case the principal section is at right angles to the support. Bilateral structures, leaves or whole shoots and systems of shoots, generally form their two sides to which the principal section stands at right angles very differently in respect to the external world; so that, in addition to a right and left half (right and left of the principal section), there is also a clear distinction between an upper and under side, an attached and free side, a dark and light side; and it is in this respect that the dependence of lateral arrangement on external conditions is most clearly evident.

In each special case it must, however, be left for more exact enquiry to settle how far the position of the principal sections of the members of a plant are determined by internal relationships of growth, or by external influences[1], a question which can seldom be satisfactorily answered when not decided by experiment. To this end the researches on *Marchantia polymorpha*, begun by Mirbel in 1835, and carried on with great success by Dr. Pfeffer in 1870 (*l. c.*), are of peculiar interest. Dr. Pfeffer shows that the two flat sides of the gemmæ of this liverwort are identical; *i. e.* each of the two sides has the power of forming root-hairs when turned downwards or attached to a firm substance. Bilateral arrangement and differentiation of the upper and under sides are first developed in the flat shoot which springs from the gemma. The side of the shoot exposed to light, whatever its position, is under all circumstances the upper side which forms stomata, the dark side becomes the under side which produces root-hairs and leafy processes. Even after the lateral shoots have been formed, the two sides of the gemma itself are still of equal value. Similar relationships may also prevail in the germinating spores of creeping Jungermanniæ and in the formation of the prothallium of Ferns; but on this point more exact researches are still wanting. In Ferns only thus much is known that (according to Wigand) when the light is stronger from one side, the plane of the principal section falls in the direction of the strongest ray of light, and the axis of growth, with its apex, is turned towards the shade.

What has now been said will only serve as a definition of the most important ideas, and in illustration of the points of view from which observations must be made. The results obtained by them cannot be given in detail; and since a definite theory has not yet been elaborated by science, a more detailed description must deal with numerous

[1] Compare Hofmeister, Allgemeine Morphologie, §§ 23, 24. 1868.

peculiarities and critical explanations, for which we have here no space. A few important facts may, nevertheless, be briefly mentioned in addition.

(1) *In reference to the Direction of the Axis of Growth*, it appears to be the general rule that the origin of a new individual coincides with the beginning of a new direction of growth. This is very strikingly the case in the swarm-spores of Oedogonium (Fig. 4, p. 9), the longitudinal axis of which is transverse to that of the filament which produces it, and becomes the longitudinal axis of the new plant; and the same is the case with the origin of new filaments of Nostoc and Rivularia (cf. Book II. Algæ). In many Cryptogams, researches have not yet been made on this point, or it would carry us too far to mention them. It may be mentioned, merely by way of example, that the axis of growth of the embryo of Ferns and Rhizocarps is distinctly transverse to the axis of the archegonium. In Phanerogams the direction of growth of the embryonal stem is opposed to that of the ovule; the apex of the young stem is formed in a direction opposite to that of the ovule, and continues its growth in this direction. The formation of the fruit of Mosses forms an exception to this manner of growth, if it is considered as a new individual; but this appears very questionable; it grows in the same direction as the archegonium, and even in the direction of the axis of the stem when the archegonium is apical (*i.e.* in Acrocarpous Mosses).

A second remark relates to the fixation of the base of the axis of growth. In all lateral members and bifurcations the base is the fixed point at which the branching or new formation began; but even in the new formation of an axis of growth from swarm-spores and fertilised ovum-cells, the growth in a definite direction does not begin until a cell has become fixed. This occurs in all swarm-spores, which do not begin to grow up into sacs and filaments until their hyaline end, the anterior one in the swarming, has become fixed somewhere or other, even if only on the bounding surface of the water. The germinating spore also of Ferns and Equisetaceæ puts out at an early stage a root-hair which fixes it to the support (the macrospore of Rhizocarps and Selaginellæ does not require this in consequence of its weight). In a similar manner also the longitudinal growth of the embryo of Phanerogams does not begin until it has become attached at its posterior end to the apex of the embryo-sac. The embryo of Vascular Cryptogams produced by a sexual process fixes itself laterally by the portion called the foot into the tissue of the prothallium.

It is only in some Algæ of the simplest structure that there is no attachment of a point of the newly constituted plant to an external substance (for which purpose any portion of the generating body may serve). In this case the opposition of base and apex disappears; the growth may then produce a uniform arrangement in different and even opposite directions; simple threads result in which an anterior and posterior end can no longer be distinguished, as in some Desmidieæ and Diatoms, or in round families of cells, like Glœocapsa.

But when once a fixed point is established as a base, the increase of length takes place *uniformly* in one direction only from it; *i. e.* whatever grows in this direction is a member of a morphologically definite character. This does not however prevent the setting up of a new growth in the opposite direction; but the member which is formed in this direction is of a different nature morphologically; as occurs *e. g.* in the embryos of Phanerogams, in which, according to J. Hanstein's recent researches, the primary root in fact originates in such a manner that its longitudinal axis must be considered as the prolongation of that of the stem in a posterior direction[1].

(2) *In reference to the Relations of Symmetry*, the fact must be mentioned that dichotomous branching is frequently repeated in one and the same plane in thallomes (as in Fucaceæ and Metzgeria), stems (Marchantia, Selaginella), and leaves (in some Ferns). A different development then generally takes place on the two sides of the plane of

[1] By these observations the doubt expressed by me in the first edition as to the position of the primary root in the embryo is solved. (For further details see Book II, Phanerogams.)

dichotomy, one side of the shoot clinging closely to the ground or to upright bodies (as in Hepaticæ), or one side turns to the light, the other side to the shade (*e. g.* Selaginella); in such cases the shoots are also broader in the direction of the plane of dichotomy. Where no such different development of the two sides occurs, as in Lycopodium (especially *L. Selago* according to Cramer), the dichotomy of consecutive bifurcations may take place in different planes; and this is also the case with the roots of Lycopodiaceæ (cf. Nägeli and Leitgeb, and Pfeffer, *l. c.* p. 97).

As has already been mentioned, it is usually impossible, without experimental research, to determine whether the position of the principal section of bilateral shoots and leaves depends immediately on their relation to the mother-shoot, or is directly brought about by external conditions, such as pressure, gravity, and light[1]. The position of the principal section usually shows simultaneously definite relations to the mother-shoot, and to the direction of gravity, light, and pressure (the latter in clinging or climbing plants, as ivy, Jungermanniæ, &c.). It is therefore probable that internal and external causes generally cooperate to give a definite direction to the longitudinal axis of a member when first formed, as well as definite positions to its lateral shoots. As development advances, the relative positions may change, and may show new relations to the original axis and to external influences. On this point reference may be made to the horizontal lateral shoots of numerous woody plants among Dicotyledons with alternate leaves in two rows. Their principal section is vertical, their rows of leaves right and left. The axillary buds of these leaves which remain dormant through the winter show an altogether different disposition of their parts; the axis of the bud is parallel to that of the mother-shoot; it bears its leaves in two rows, one facing the sky and the other the earth (Fig. 147); the mid-ribs of the folded leaves are always turned outwards, away from the mother-axis; the principal axis of the whole bilateral shoot (the bud) is horizontal. But when the bud unfolds in the spring, a torsion of its axial structure takes place of such a nature that the principal section assumes a vertical position, the projecting mid-ribs of the leaves turn downwards, while the lobes of the lamina turn their sides, which were previously inclined towards one another, upwards; and thus the lateral shoot of a horizontal mother-shoot acquires the same position as this latter. The fact that the two rows of leaves within the lateral bud arise on the upper and under side, and consequently both in the vertical plane, may be referred to the immediate influence of gravity; but to this is opposed, among others, the fact that the position of the terminal bud[2] of the horizontal mother-shoot is usually from the first different. In Cercis and Corylus, for example, the terminal bud stands on the under side

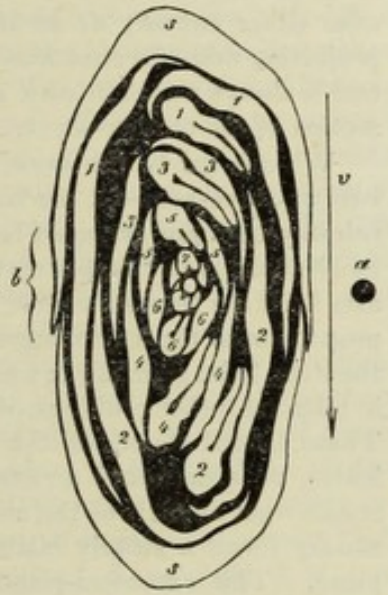

FIG. 147.—Lateral bud of a horizontal branch of *Cercis canadensis* (in December), in vertical transverse section; 1-7 the consecutive leaves with their pairs of stipules indicated in the same manner. The outer bud-scales have been removed, the two inner ones indicated by 3, 3. In the centre is the *punctum vegetationis* of the bud. *b* the position of the leaf in whose axil the bud grows; *a* axis of the mother-shoot; *v* direction of gravitation.

[1] This subject has been treated by Hofmeister (Allgemeine Morph. §§ 23, 24) from another point of view; but on consulting the facts themselves I find much that is not in agreement with his statements, and in their interpretation I arrive at essentially different conclusions which cannot be explained here in detail.

[2] It is for our present purpose the same whether the bud at the end of the horizontal shoot be its true terminal bud, or a lateral bud the development of which is induced by the withering of a terminal bud, as in Cercis and Corylus. In reference to the position of the terminal bud it is also indifferent that the lateral buds sometimes place their principal section not quite horizontally, but a little obliquely upwards and outwards, as in Corylus, Celtis, &c.

of the horizontal end of the branch, and its leaves lie right and left of the vertical principal section of the bud. The position of a terminal bud may be easily represented by turning Fig. 147 so that the mother-axis *a* lies above, the mother-leaf *b* beneath the bud (thus the apparently terminal bud becomes an axillary bud), and the direction of the vertical line *v* becomes horizontal. By this difference which exists from the very first in the position of the bud in horizontal bilateral mother-shoots, the *immediate* influence of gravity, as conjectured above, is excluded; but a useful arrangement is indicated by the fact that even in the bud all the parts are so arranged that by a single twisting of the axis during unfolding, they assume those positions which are most favourable for the functions of the leaves, and by which their inner surfaces are turned towards the light. In the terminal buds of such shoots this twisting is no longer necessary. Whether it is gravity or the influence of light on the growth which occasions during unfolding this torsion of the axis of the bud through 90° may for the time be left in doubt. But the most important result in reference to the starting-point of this observation is that the principal sections of the axillary buds of a bilateral mother-shoot may have positions greatly varying from the horizontal, and that, in consequence, the arrangement of the parts of the bud is originally independent of the direction of gravity; while, on the other hand, there results a perfectly definite relationship in the arrangement of the parts of the bud to the mother-axis. The axillary bud of such a shoot may arise either laterally or on the under or upper side[1]; all the leaves always turn their projecting mid-ribs outwards, away from the mother-shoot; the principal section of the bud is always placed in such a position that it is at the same time an axial longitudinal section of the mother-shoot.

We are led to the same conclusion by the study, among numerous other cases, of two or three-year-old seedlings of Thuja and other Cupressineæ. The leaves of the primary stem are arranged below in alternate whorls of fours, and consequently in eight longitudinal rows; higher up the whorls are alternate and of three leaves, and the primary axis itself has thus six rows. The axillary shoots, the number of which is very small in proportion to the leaves, appear, both in the eight-rowed and in the six-rowed region of the stem, to be generally in two rows, so that in reference to its branching the primary stem is bilateral (other positions of the branches occur, however, higher up, especially later). These lateral shoots of the first order begin at once with alternate whorls of two leaves, or a decussate arrangement, and always in such a manner that the first pair stands right and left of the mother-leaf. Every such lateral shoot of the first order now usually forms a strictly bilateral system of branching, which becomes extended into a plane. This extension-plane of the lateral system of shoots is usually horizontal in seedlings of *Thuja gigantea*, *T. Lobbii*, &c., and the principal section therefore vertical. But this is not without exception; lateral systems of shoots are formed here and there and extend in a vertical plane, the principal section of which is therefore horizontal; and this is sometimes repeated in single lateral shoots of the second order. Conversely I find on a strong seedling of *Cupressus Lawsoniana* seventeen lateral systems of shoots (standing in two opposite straight rows on the primary stem) which all extend in a vertical plane, while only one lower system of shoots is extended horizontally. These differences in the position of the principal section of lateral systems of shoots are not however brought about by torsions, which would easily be recognised from the phyllotaxis; they are original, and become permanent. Where a lateral shoot of the first order branches horizontally, the lateral shoots are produced only from the axils of the leaves that stand right and left; where it branches vertically, only from the axils of the leaves that stand above and below. Now since the principal sections of these lateral systems of branches have positions altogether different from the horizontal, it is scarcely possible to suppose

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[1] Axillary shoots are formed on the upper side of the mother-shoot near its base in Cercis, and bear inflorescences.

that gravity (or in this case light) has any immediate influence on the origin of the lateral branches of the second order. The vertical position of the principal section of the horizontal branching of the lateral shoots of the first order is much more constant in *Araucaria excelsa*; and here, as horticultural experience shows, we have a remarkably clear example of a phenomenon which may be considered as inherent to lateral arrangement;—lateral shoots of this kind, planted vertically as cuttings, take root and continue to grow vertically; but always produce, notwithstanding, only two-rowed lateral shoots; the branch which has once been produced as a lateral shoot does not become changed, when placed vertically, into a many-sided primary stem[1].

In conclusion I may add a few remarks on the different species of the genus Begonia, which show that in very closely allied forms the relationships of lateral arrangement of parts to external influences may be entirely different, while they remain unchanged when the members of the same plant are compared with one another. The leaves of Begonia are placed alternately in two rows; on thicker stems the two rows of leaves are nearer to one another on one side of the stem, and hence the other side of the stem appears naked; the shoot is thus not only bilateral, but it has a leaf-bearing anterior and a naked posterior side which are very unlike one another. The blade of the leaves is very unsymmetrical; one half is much larger than the other. The larger halves of all the leaves face the posterior side of the stem; and this can be used to distinguish the posterior and anterior sides even in slender-stemmed species, as *B. undulata* and *incarnata*, although in these cases the leaves are not nearer to one another on the anterior side, but follow exactly the divergence $\frac{1}{2}$. It is well to remark in the outset that the leaf-stalks of Begoniæ are moderately heliotropic, while on the contrary the axes of the shoot are scarcely curved by light. In thick axes heliotropism appears to be entirely wanting; in slender axes (*B. undulata* and *incarnata*) it is always very slight; some species with moderately thick stems, as *B. Verschaffeltii* and *B. manicata*, grow straight upright when the light comes from one side; very thick-stemmed species bend in different directions without reference to the direction of the light; slender-stemmed species allow their weak branches to hang down without always pointing in one definite direction.

If attention be now paid to the tendency of stems to bend in some one direction, the plane of curvature is found always to coincide with the principal section of the shoot which divides it into two similar halves, so that each half possesses one row of leaves. A definite relationship is also manifested between the tendency to bend and the relative thickness and length of the internodes. If the thickness of the internodes is always represented by 1, then, in the *upright* stems of *Begonia nitens*, *Möhringi*, and *sinuata*, their respective lengths are 9, 3·2, and 2; in the slightly curved *B. manicata* it is 1 or less; but in procumbent and strongly-curved stems as low as 0·7 (*B. hydrocotylifolia*), 0·4 (*B. pruinata*), and 0·2 (*B. ricinifolia*). In the slender-stemmed upright species the rows of leaves stand diametrically opposite to one another; in the slightly-curved thicker species they approach one another on the anterior side; in the very thick-stemmed species which are bent downwards the insertions of the leaves are placed entirely on the anterior side[2].

In the thick-stemmed species the stem curves downwards concavely, or lies horizontally upon the earth; but in this case it is always the leafless or posterior side which lies below and puts out adventitious roots (*e.g. B. ricinifolia* and *macrophylla*). In species on the other hand which have tall stems and slender internodes, the branches hang down, and in this case it is the posterior side which becomes convex and lies above (*B. undulata* and *incarnata*); or, in other words, if we regard the origin of the buds, *in the slender-*

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[1] [This is not without exception; see Gœppert, Acta Acad. Nat. Cur. 1868, p. 34, t. 1.—Ed.]

[2] The absolute measures of thickness run almost parallel to the above-named relative ones; the relatively thickest internodes are also usually absolutely the thickest, and these stems show the most decided tendency to a horizontal growth.

stemmed forms all the larger halves of the leaves when first formed turn upwards, while in the thick-stemmed forms they turn downwards. The want of symmetry of the leaves thus indicates, when the position of the bud is inclined, relationships opposed to the direction of gravity, and when the stem is upright no such relationship. In species with short internodes and thick stems only a few lateral shoots become developed, in those with slender stems a great many, as indeed constantly occurs in other cases (Cactaceæ, Palms, Ferns, and to an excessive extent in Isoëtes). The lateral arrangement of the lateral shoots exhibits the following relationships to that of the mother-shoot:—in all species the posterior side of the lateral shoot, and hence the larger half of the leaves, faces the mother-shoot; the principal section of a lateral shoot of slender-stemmed species is therefore at right angles to that of the mother-shoot. In thick-stemmed species, where the axillary shoots are nearer one another in front, the principal section of the lateral shoot makes an acute angle with the mother-shoot in front (and thus in procumbent forms, above). As the development progresses, the branches of slender-stemmed species retain nearly their original position; in thick-stemmed species where the anterior and posterior sides differ greatly, the lateral shoot twists in such a manner that its posterior side faces in the same direction as that of the mother-shoot.

I have no more precise information as to the mode of life of different species of Begonia, but suppose that those species in which the anterior and posterior sides are distinctly developed, and which do not cling to the ground, may have the power of climbing, like the ivy, although observations which I have had made for this purpose in the botanical garden at Würzburg have not yet led to any satisfactory result; partly because the plants were already too old, partly because the access of light was possibly too small on the anterior side. The researches detailed above on heliotropism do not negative the hypothesis that with *stronger* access of light from one side the stems of Begoniæ may possibly be negatively heliotropic. It appears moreover from the researches of Martius ('Flora brasiliensis,' fasc. XXVII, p. 394) that at least some Begoniæ cling to rocks and the stems of trees. (On positive and negative heliotropism see Book III, chap. 3, sect. 8.)

Sect. 28. **Characteristic Forms of Leaves and Shoots.** — The peculiarities of thallomes, leaves, axes, and roots which are common to whole classes, orders, or families (the so-called typical properties), are the subject of special morphology and systematic botany; on the other hand it is the province of physiology to study those relationships of organisation by which the members of the plant become adapted to perform definite functions. There are, however, some peculiarities of growth which recur in different divisions of the vegetable kingdom, or which present themselves in striking contrast to the ordinary phenomena, and are for this reason well adapted to bring into prominence the value of general morphological ideas. Peculiarities of this kind are termed *characteristic*, and they must be briefly mentioned here, chiefly in order to explain some scientific terms which will be used in Book II. We may limit our remarks to leaves and leaf-forming shoots, since the forms of the thallus will be treated in sufficient detail in the chapter on Thallophytes, and those of roots present only slight characteristic differences, to which reference has already been made; the characteristic form of hairs has already been alluded to in various ways.

(1) *Forms of Leaves.* When fully developed, leaves are usually flatly extended plates of tissue, the extension being generally in directions right and left vertically to the median plane or principal section, so that the surface of the leaf lies transversely (at right angles or obliquely) to the longitudinal axis of the stem. This is generally quite true for the base of flat leaves; but the upper part of the surface

of the leaf is sometimes itself extended in the directions of the median plane, so that the plane of extension coincides with an axial longitudinal section of the stem, as in the genera Ixia, Iris, &c. But sometimes the leaves are not flat, but conical or polyhedral; conical with almost circular transverse section in Characeæ, Pilularia, &c., polyhedral in some species of Mesembryanthemum and Aloë.

The outline of leaves is either simple or segmented; the former is the case when no definitely separated parts can be distinguished in the leaf; a leaf is 'segmented' when it consists of pieces of various shapes, which are more or less separated from one another. Leaves which are not flat are usually simple, as are also those which are flat but small, their length and breadth being inconsiderable relatively to the stem, and not exceeding a few millimetres or centimetres in absolute measurement. Larger leaves are usually distinctly segmented, and in general the degree of segmentation increases with the increase of size; the small simple leaves of Mosses, for instance, may be contrasted with the large segmented leaves of Ferns, the small simple leaves of Lycopodiaceæ and Coniferæ with the large compound leaves of Cycads, the small simple leaves of Linaceæ with the large much-divided leaves of the nearly-allied Geraniaceæ, &c. The segmentation of leaves usually consists in the separation of a basal portion which generally remains narrow, cylindrical, or prismatic, while an upper portion is flatly extended; the former being called the leaf-stalk or petiole, the latter the blade or lamina. Or the lower portion of the leaf has the form of a sheath, and forms a lamella enclosing the stem and younger leaves like a hollow cylinder. If the upper part is flatly expanded the leaf then consists of a sheath or vagina and a blade; it sometimes also happens that a stalk intervenes between the sheath-like basal portion and the lamina, as in Palms and some Aroideæ and Umbelliferæ. Segmentation into sheath, petiole, and blade may be distinguished as longitudinal from *lateral* segmentation, which consists of actual branching, as in pinnate, deeply lobed, or compound leaves, or of a rudimentary branching, as in indented, toothed, and sinuate leaves. Leaves are termed divided or compound in which the individual lateral pieces of the lamina are completely separated at their base; while those forms are termed lobed in which the lateral branches are only more or less projecting portions which unite at their base. If the individual branches of a branched leaf are sharply separated, each branch forms independently, so to speak, a leaf, and is hence distinguished as a *Leaflet*. The division, like the formation of lobes, may be repeated. If the branches are obviously arranged in two rows the leaf is said to be pinnate; pinnately-divided if it is a compound leaf; pinnately-lobed, pinnatisect, or pinnatifid if the divisions are incomplete; dentate, serrate, or crenate if the lateral projections are very small relatively to the lamina. If, on the contrary, the branches or lobes of the lamina are densely crowded at the end of the petiole, and radiate from it on all sides, the leaf is said to be digitate, palmately-lobed, &c. It is termed peltate when the lamina is fixed not by a portion of its margin, but by a point lying on its under surface (as in Tropæolum, Nelumbium, &c.). These are only a few of the more important forms; the beginner will find in every text-book a number of other distinctions and terms employed which are of importance in the special description of plants.

As occasional appendages, which indicate a still further segmentation of

leaves, must be mentioned Stipules, Ligular structures, and hood-like outgrowths.

Stipules may be considered as lateral branches of the leaves which arise at their very point of insertion; they stand in pairs right and left of the base of the principal leaf, either entirely isolated from it or united to it in growth; each single stipule is usually bilaterally unsymmetrical, and its shape is therefore such that it appears as the reflected image of the stipule belonging to the other side of the leaf. Stipules are not formed until after the origin of the principal leaf, but then grow much more rapidly, and attain their final development at an earlier period; hence they play an important part in the position of the parts in the bud. In vernation they either extend by their inner margins (those facing the median plane of the leaf) over the back of the principal leaf and cover it outside either partially or entirely, or they extend in front of and over the principal leaf (on the side facing the stem) right and left, and thus cover the parts of the bud next youngest in age. In one or the other of these modes chambers are not unfrequently formed by the stipules, in which the formation of the leaves is completed, and which they leave as they expand and unfold; and the stipules then either also unfold and remain or die and drop off.

The term *Ligule* is applied to a membranous outgrowth on the inner side of the leaf of Grasses at the point where the flat lamina bends out at an angle from the sheath; it stands transversely to the median plane of the leaf. Similar outgrowths are also found elsewhere, as on the petals of Lychnis and Narcissus (where they form the so-called corona), on the leaves of Allium, &c., and may be included in the general term of Ligular structures. In contrast to this outgrowths sometimes occur from the posterior (outer) side of leaves, as, for instance, the large hood-like appendages of the stamens in Asclepiadeæ.

It is only in some Mosses that the tissue of the leaf consists throughout of one layer of cells. Usually, especially in all large leaves, the tissue is formed of several layers, and then, in vascular plants, is distinguished into epidermis, parenchymatous fundamental tissue, and fibro-vascular bundles. The fundamental tissue is termed *Mesophyll;* the system of the fibro-vascular bundles running into the leaf forms the so-called *Venation.* In the leaves of many Mosses which otherwise consist of only one layer, there runs in the middle from the base towards the apex a bundle of several layers, also called the median vein; and in leaves of more complicated structure there is also usually a mid-rib which runs from the base to the apex of the lamina, and divides it more or less symmetrically into two similar halves. The same occurs in every lateral leaflet or in every branch or lobe of the lamina; from the mid-rib spring the lateral veins which run to the margin of the leaf. In larger leaves, especially those of Dicotyledons, the fibro-vascular bundles which traverse the mid-rib and its stronger branches are enclosed in a thick parenchymatous layer of tissue, the cells of which differ from those of the mesophyll. Usually these veins project on the under side of the leaf in the form of cushions, and the larger the whole lamina the more strongly are they constructed (especially the mid-rib). The finer veins, on the contrary, consist of single fibro-vascular bundles, often branching extensively, running through the mesophyll of the lamina itself. The kind of venation varies in different classes

of vascular plants, and is often very characteristic of large groups. This will be explained more in detail in the proper place.

In Characeæ, Muscineæ, and Vascular Cryptogams, all the leaves of a plant are usually similar, being either simple or segmented in the same manner, although the segmentation, especially in Ferns and Rhizocarps, is simpler in young plants and in those that are still weak than in the large leaves of mature plants. But it also happens, even in Cryptogams, that leaves of very different forms are found on the same plant. Thus some Mosses form colourless minute leaves on the underground creeping shoots, while in the neighbourhood of the organs of reproduction they often produce leaves of a different shape from those on the rest of the upright parts of the shoot. In the same manner the leaves on the underground shoots (stolons) of *Struthiopteris germanica* remain as thin membranous scales, which are replaced on the upright end of the stolon by large green pinnate leaves. In Salvinia each whorl forms two simple roundish leaves which rise into the air, and one that hangs down into the water and consists of filiform branches. Even in Coniferæ and Cycadeæ the variation in the leaves of one plant is much more common; while in Monocotyledons and Dicotyledons the shapes of leaves become extraordinarily variable, not only on the same plant but often on the same shoot.

The two most common forms of leaves are the Scales or 'Cataphyllary leaves'[1] and the Foliage-leaves.

The *Foliage-leaves*[2] are always distinguished by their green colour, owing to their containing abundance of chlorophyll (which however is sometimes concealed by red sap). It is these which, in popular language, are exclusively called leaves, and in descriptive botany are designated by the term 'folium.' Usually they are the largest foliar organs of the plant, lasting the longest, and distinguished by the greater degree of segmentation of the outline, as well as by more perfect formation of their tissue. As the chief vehicles of chlorophyll they are the most important organs of assimilation, and are always destined to be expanded to the light even when they are formed on underground *puncta vegetationis* (as in Sabal, *Pteris aquilina*, &c.). When small they are usually produced in great numbers on a shoot; as they increase in size their number and the rapidity of their growth diminishes in proportion. In this respect the numerous small leaves of Mosses may be compared with the few large leaves of Ferns, the numerous small leaves of Conifers with the few large ones of Cycads, &c.

Scale- or *'Cataphyllary-Leaves'* are usually produced on underground shoots and remain buried in the earth, although they also frequently occur above ground, especially as an envelope to the winter-buds of woody plants (as the horse-chestnut, oak, &c.). In the genus Pinus the primary stem and the strong lateral shoots form leaves of this kind only; the foliage-leaves appear on small axillary shoots (as tufts

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[1] [Henfrey, in his translation of Braun's 'Rejuvenescence in Nature' (Ray Soc., Botanical and Physiological Memoirs, 1853), first proposed to render the terms Hochblatt, Niederblatt, and Laubblatt by 'Hypsophyll,' 'Cataphyll,' and 'Euphyll.' The two first of these are useful additions to botanical terminology; the last, however, does not seem to the present translator to be required, being precisely equivalent to the term Foliage-leaf, which is already in general use.]

[2] Compare the characteristics of the formations of leaves in A. Braun, Verjüngung in der Natur, p. 66. Freiburg 1849-50. [Ray Soc., Bot. and Phys. Mem. 1853, p. 62.]

of acicular leaves); in Cycas scale-leaves alternate regularly on the stem with large foliage-leaves. Seedlings (as in the oak) and the lateral shoots of underground axes often begin with scales and only advance at a later period to the production of foliage-leaves (*e. g.* Struthiopteris, Ægopodium, Orchis, Polygonatum, &c.). In parasites and plants growing on decaying vegetable matter (Saprophytes) which are destitute of chlorophyll, the scales are the only foliar structures of the vegetative parts, the foliage-leaves being absent (*e. g.* Monotropa, Neottia, Corallorrhiza, Orobanche, &c.). Even in those plants whose foliage-leaves are much segmented the scales remain simple; they are distinguished by a broad base, usually diminutive length, the absence of prominent veins, and by forming no chlorophyll or only very little. They are colourless or yellowish, reddish, often brown; their texture is, according to circumstances, fleshy, succulent (as in some bulbs), membranous, or tough like leather.

In Phanerogams, especially in Monocotyledons and Dicotyledons, several other forms of leaves make their appearance as a preliminary to fertilisation—Bracts, Sepals, Petals, Stamens, and Carpels. The thick seed-leaves or Cotyledons will be spoken of in detail as a peculiarity of these classes.

From the point of view of the Theory of Descent we are justified in considering all other forms of leaves as subsequent metamorphoses of foliage-leaves. These latter are therefore regarded as the original typical leaves. When they lost their original function—the assimilation of food-materials—and served other purposes, they assumed at the same time other forms and other relationships of structure. The same is meant when certain tendrils and thorns are termed metamorphosed leaves:—*Leaf-tendrils* are leaves or parts of leaves which have become filiform, and possess the power of winding round slender bodies and thus of serving as climbing organs (as in Vicia, Gloriosa, *Smilax aspera*, &c.). *Leaf-thorns* are leaves which have developed into long, conical, pointed, hard, woody bodies; they take the place of foliage-leaves (Berberis) or represent metamorphosed stipules (*Xanthium spinosum*, some Acacias). These two kinds of metamorphosis occur almost exclusively in Flowering Plants (Angiosperms), the morphological and physiological perfection of which, in comparison to Cryptogams and Gymnosperms, is especially caused by the capability of their leaves to assume the most various forms.

(2) *Forms of Shoots.* The axis of leaf-bearing shoots is, when sufficiently developed, usually columnar with a cylindrical or prismatic surface. If the growth in length is very small in proportion to that in thickness, the short column forms a plate, the depth of which is shorter than its diameter, as in the bulbs of *Allium Cepa* and Isoëtes; if the growth in length is somewhat greater, with at the same time considerable increase of thickness, rounded or elongated masses are produced (as in the tuber of the potato and artichoke, the aërial stems of Mammillaria and *Euphorbia meloformis*); when the growth in length greatly preponderates we have stems, scapes, and filiform structures of various kinds. Very commonly the same shoot shows differences of this kind in the successive segments of its longitudinal growth; thus the stem of the onion, which is at first broad and tabular, afterwards rises as a high naked scape, the end of which in its turn remains short, and thus produces the capitular inflorescence; and in the same manner the thick tuber of the potato is only the swollen end of a slender filiform shoot. Among the

numerous deviations from the columnar form of the axis the conical is of peculiar interest. The conical stem is of two kinds; it may be slender at the base, increasing in thickness with further growth in length, so that each portion of the axis is thick in proportion to its youth; and the upright stem resembles a cone placed upon its point. The growing apex lies on the surface which is turned upwards, or rises above it as an upright cone. This form occurs in the stems of Tree-ferns, Palms, and very clearly in the maize and in many Aroideæ; it depends on the absence of a subsequent growth in thickness, while, as its age increases, the young tissue of the stem becomes constantly larger in circumference immediately beneath its apex; when this increase of strength at last ceases the circumference of the later increment of length remains the same, and the inverted conical stem continues to grow above in the form of a cylinder. The second form of conical stem is caused by a long-continuing subsequent growth in thickness together with the small circumference of the shoot at the *punctum vegetationis;* this occurs in Conifers and many dicotyledonous trees, the older stems of which are thick below but slender above, and thus resemble a slender cone placed on its base.

The habit of a shoot or of a segment of a shoot is usually in close relation to the number, size, and formation of its leaves. If the internodes are very short, but the leaves small and numerous, the surface of that portion of the axis is nowhere exposed, and the leaves only are seen, as in species of Thuja and Cupressus, and some Mosses (Thuidium); in such cases whole systems of shoots frequently have the appearance of multipinnate leaves. If the closely packed leaves are large, they form a rosette enveloping the end of the stem, while the older parts of the stem are clothed with the remains of the leaves, or are naked, as in Tree-ferns, many procumbent stems of species of Aspidium, many Palms, species of Aloë, &c.

If a comparison is made between the amount of development in bulk which takes place in the leaves and in the axis of a shoot, we find as extremes on one side, for example, the Cacti (Cereus, Mammillaria, Echinocactus, &c.) with gigantic axes and entirely abortive leaves, on the other side the Crassulaceæ with fleshy crowded leaves and comparatively weak stems; or on one side the underground tubers of the potato with scarcely visible scales, and on the other side the bulbs of Liliaceæ with fleshy scales which entirely envelope the short stem.

In reference to the formation of leaves which appear on the shoots, it must first be noted whether the same axis always produces only similar leaves or such as gradually vary in form. The first is the case, for example, in most Mosses, Ferns, Lycopodiaceæ, Rhizocarps, all Equisetaceæ, and most Conifers; the latter, on the other hand, occurs commonly in shrubby Dicotyledons. In Monocotyledons and Dicotyledons (to a certain extent even in Conifers) it not unfrequently happens that the different forms of leaves are distributed over different generations of shoots; certain shoots produce, for example, little or nothing but foliage-leaves, others produce only bracts with or without flowers (*e. g.* Begonia). In such cases the shoots may be designated, according to their leaves, scaly shoots, leafy shoots, bract-axes, flowers, peduncles, &c. On this point further details will be given in Book II.

It is of very common occurrence with Cryptogams and Angiosperms (not with Gymnosperms) for a persistent primary axis or system of shoots to continue

to grow underground, and to send up only at intervals long foliage-leaves or shoots, which subsequently disappear in their turn and are replaced by others. When such shoots or systems of shoots lie horizontally or obliquely on the ground, and produce lateral roots, they are called *Rhizomes* (Fig. 148) (as in Iris, Polygonatum,

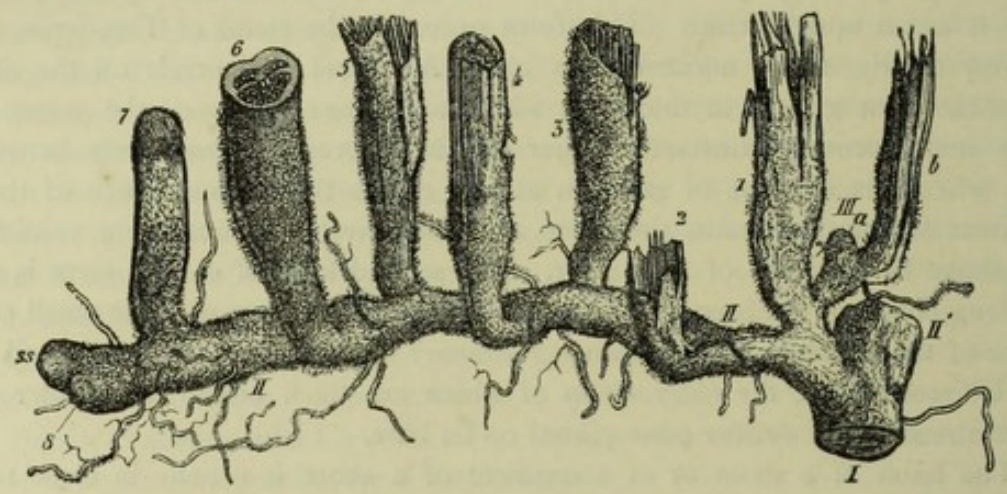

FIG. 148.—Rhizome of *Pteris aquilina*; *I, II, III* the underground creeping axes; *ss* the apex of one of them; 1-6 the basal parts of the leaf-stalks; *7* a young leaf; *δ* a decayed leaf-stalk, the basal portion of which is still living and bears a bud *III a*; the hairy threads are roots which arise behind the growing apex of the stem.

Pteris aquilina, and many other Ferns). Frequently they die at the posterior and continue to grow at the anterior end. Underground tubers and bulbs are more transitory structures, usually lasting only for one period of vegetation; the former are characterised by the preponderance of the axial mass with a very small amount of leaves, the latter, on the contrary, by the preponderance of leaves closely united round a short stem. If the lower parts of a plant produce slender lateral shoots with small scales growing upon or beneath the earth, and after rooting at a considerable distance from the mother-stock produce foliage-shoots or shoots stronger than themselves, they are called *Stolons*, as, for instance, in *Ægopodium Podagraria*, Fragaria, *Struthiopteris germanica*, and in Mnium and Catharinea among Mosses.

The greatest degree of variation from the ordinary forms of shoots is displayed by the leaf-like flat shoots and systems of shoots, and by the stem-tendrils and thorn-like shoots which occur frequently in Angiosperms. Leaf-like shoots are found in those Phanerogams in which large green foliage-leaves are wanting, and replace them physiologically; their axial structure is of considerable superficial extent, and they produce and expose to the light large quantities of chlorophyll; they generally bear only very small membranous scale-leaves. Examples may be found in Phyllocladus among Conifers, Ruscus among Monocotyledons, and among Dicotyledons in *Mühlenbeckia platyclada* (Polygonaceæ), Xylophylla (Euphorbiaceæ), Carmichaelia (Papilionaceæ), *Opuntia brasiliensis*, and *Rhipsalis crispata* (Cactaceæ), &c.

The *Stem-tendrils*, like the leaf-tendrils, are long, slender, filiform structures, which have the power of winding spirally round slender bodies in a horizontal or oblique position with which they come laterally into contact, and thus serve as climbing organs; they spring laterally from shoots which have not the form of tendrils, and are distinguished by the absence of foliage-leaves, their power of forming leaves

being mostly limited to very minute membranous scales. They are usually easily distinguished by their origin, position, and by the production of leaves, from the leaf-tendrils; cases, however, occur where the morphological nature of a tendril is doubtful, as, for instance, in Cucurbitaceæ. Peculiarly clear examples of stem-tendrils are to be met with in Vitis, Ampelopsis, and Passiflora. Shoots which bear strongly developed foliage-leaves on long slender internodes, and which have the power of winding in an ascending manner round upright supports, are not considered tendrils, but are called *Twining or Climbing Stems*[1]; and thus a distinction is drawn between Tendril-climbers (as Vitis) and Stem-climbers (as Phaseolus, Humulus, Convolvulus, &c.). In Cuscuta, where the primary shoot and all the lateral shoots except the inflorescences twine in the manner of tendrils and of climbing stems, and where foliage-leaves are also entirely suppressed, the peculiarities of tendrils and of climbing stems are to a certain extent united. A distinction similar to that between stem-tendrils and climbing stems is also possible in leaves; the foliage-leaves of the Fern-genus Lygodium, endowed with a continuous power of growth in length, behave completely like climbing stems, the climbing rachis of the leaf corresponding to a climbing axis, and the leaflets to its foliage-leaves[2].

The axial shoots of many Angiosperms have, like the leaves, the power of forming *Spines*, becoming transformed into conical, pointed, hardened bodies. This may take place either by the whole shoot or even a whole system of shoots becoming spiny, with suppression of the foliage-leaves, as in the branched spines of *Gleditschia ferox*, or by the shoot first producing foliage-leaves, growing in the ordinary manner, and finally finishing its growth in length by a spiny point, as in the lower axillary shoots of *Gleditschia triacanthos*, *Prunus spinosa*, and many others.

Among Phanerogams, especially among Monocotyledons and Dicotyledons, relative positions of the leaves and lateral shoots (as well as of roots), and mutual adhesions of members, constantly occur, which, as development advances or becomes mature, are in apparent contradiction to the typical laws of growth and position, *i.e.* to those which are the ordinary ones in these classes. It would be difficult even for a thoughtful and clever beginner to explain by the principles which have been regarded in this chapter as most universal, the structure, for instance, of an expanded flower of an Orchis, rose, Lamium, Salvia, and of many other plants, the structure of a partially or wholly ripe fig, or the phyllotaxis in the inflorescences of Asperifolieæ and Solanaceæ, and many others. But the history of development shows that even such cases may be ranged under these laws; and that the peculiarities of structures of this kind only arise during a later period of development, or in such a manner that they confirm general rules. The deviations from these rules are caused by the cessation of the growth of particular parts at an early period in their development, while others undergo a great advance; or they are caused by the adhesion of parts originally distinct. Although it is quite impossible to give general rules for the explanation of irregular formations, yet

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[1] Compare H. von Mohl, Ueber den Bau und das Winden der Ranken und Schlingpflanzen. Tübingen 1827. [See also Darwin, On the Movements and Habits of Climbing Plants, Journ. Linn. Soc. vol. IX.]

[2] Compare Book II, Ferns, and Book III, on the Physiological Signification of Tendrils and climbing Stems.

the causes which most commonly co-operate to produce these results may be mentioned; they may be termed *Displacement*, *Adhesion*, and *Abortion*. Very commonly the two first act simultaneously, and in many flowers combine with abortion to produce complex organs difficult to explain. It belongs to the most beautiful problems of morphology to refer such apparent exceptions to more general laws of development; and the determination of natural affinity, the fixing of the typical properties of whole classes, orders, and families, depends upon it. Since, however, these complicated phenomena belong almost exclusively to Angiosperms, and in them occur to much the largest extent in the flowers and inflorescences, the best place for a more detailed description will be when the characteristics of this class are under consideration. Some explanation may, however, be given here, by means of a few examples, of the use of the terms Displacement, Adhesion, and Abortion.

The diagrammatic Fig. 149 shows a branch-system developed sympodially and proceeding from an axillary shoot; 1, 1 being the first shoot with its two leaves 1^a and 1^b; in the axil of the leaf 1^b is developed the shoot 2, 2, with its two leaves 2^a, 2^b; in the axil of its leaf (2^b) again arises the lateral shoot 3, 3, with its leaves 3^a, 3^b, and so on. The parts of the stem of the shoots 1, 2, 3, 4, which proceed from one another, form a straight pseud-axis (sympodium) with the peculiarity that the mother-leaf in whose axis the lateral shoot

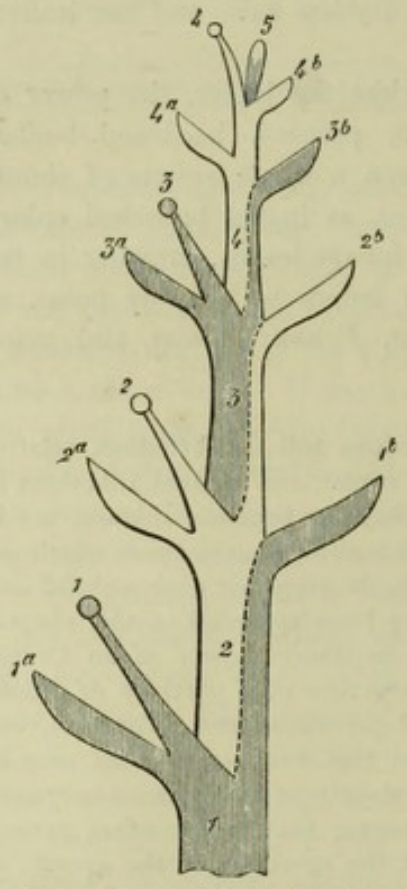

FIG. 149.—Diagram of the adhesion of leaves with the axial parts of their axillary shoots (after Nägeli and Schwendener; Das Mikroskop).

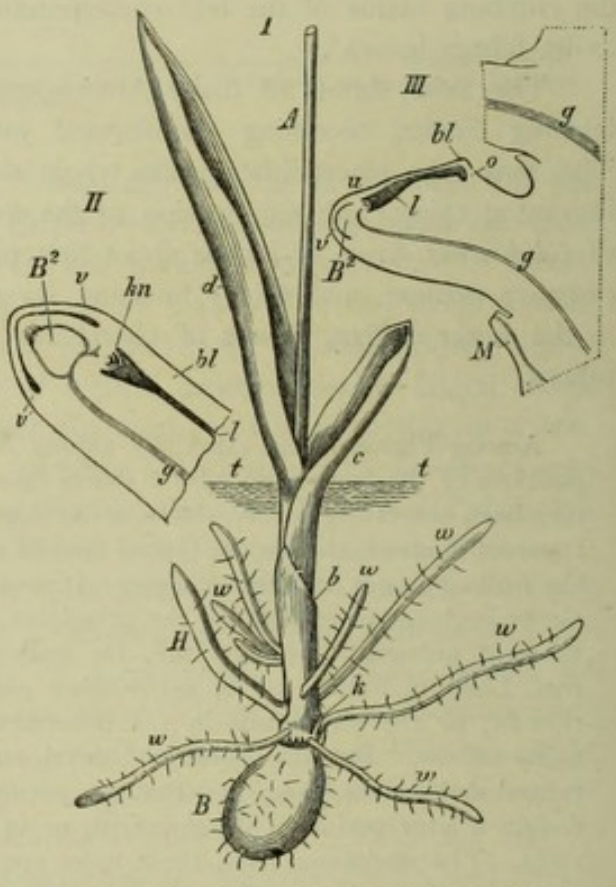

FIG. 150.—*Herminium Monorchis* (after T. Irmisch: Biologie und Morphologie der Orchideen. Leipzig 1853).

developes adheres to it, and is carried up by it for some distance. If we call the globular ends 1, 2, 3, 4 of the figure flowers, the whole is well adapted to represent diagrammatically the inflorescence of some Solanaceæ. If the leaves 1^a, 2^a, 3^a, 4^a are supposed to be removed, the diagram might stand for the primary branch of the inflorescence of Sedum. If, on the other hand, a lateral shoot is supposed to be formed in each case in the axil of the leaves 1^a, 2^a, 3^a, 4^a in the same manner as on the other

side with displacement of the mother-leaf, this would repeat diagrammatically in a simple manner the branching and phyllotaxis of Datura[1].

Still more complicated are the relationships in Fig. 150, where *I* represents the lower part of a flowering plant of *Herminium Monorchis*; *t t* is the surface of the ground, and what lies below this is therefore underground. *B* is a swollen spherical root, above which the leaf-forming shoot rises, which produces in its lower part slender lateral roots, *w*, *w*, *w*, as well as a sheath-like scale[2] *b*, and two foliage-leaves *c*, *d*, and continues higher as a slender scape *A*, bearing a raceme of flowers at its summit. Turning our attention exclusively to the structure *H*; we find it to be a shoot which contains the bud for the next year; for the whole plant *A*, *B*, in *I* dies off after flowering, a similar plant being produced the next year from the bud contained in *H*. *H* is therefore an axillary shoot of the scale *b*, an earlier condition being represented in Fig. *III*, where *M* represents the base of the leaf *b* cut through its median plane; *g* is a fibro-vascular bundle running from the primary axis to the bud *u*; *bl* is the first leaf of this bud *u* which is placed with its back to the mother-axis and forms a diminutive sheath enclosing the succeeding leaves of the bud *u*; B^2 is the young tuberous root with its root-sheath *v*. In order to understand the displacement which has already taken place, the whole lower part between *M* and *v* must be imagined shortened to such an extent that B^2 would be somewhere near the letter *g*; and the bud *u* must be supposed at the same time moved backwards towards *o*. By this means the normal position of the parts of *H* under consideration is restored, and it is intelligible that the channel *l*, which the base of the leaf *bl* encloses, is a consequence of the oblique direction outwards of the growth of the tissue lying between *o* and *u*, that the root-sheath *v* must be regarded as a part of the surface of the primary axis above *M*, and that in consequence B^2 has been formed in the tissue of the mother-axis beneath the bud *u*, and laterally on the fibro-vascular bundle *g*. In the normal position of the bud and root, the axis of growth of the latter would form almost a right angle with that of the bud, whereas by the displacement one forms a prolongation of the other. The growth of the mass of tissue lying between *g* and *u* now advances in the direction named, and the whole lateral shoot assumes the form represented in *H* (Fig. *I*); the still further change of position of the parts which takes place in consequence is explained by Fig. *II*, where *kn* represents the bud designated in *III* by *u*, *bl* the still more elongated sheath of the leaf *bl* in *III*; the channel *l* is the cavity of the leaf *bl* increased in breadth, and which, were there no displacement, would be entirely filled up by the bud *u* (or *kn*).

In order to make the following displacement which occurs very commonly more intelligible, reference should be first made to Fig. 108 (p. 133). This shows how the tissue beneath the apex extends to such a degree by a very considerable early growth in thickness, progressing equally in all directions, that the surface of the *punctum vegetationis*, which would otherwise be conically elevated, becomes almost level. The apical point thus comes to lie in the middle of a plane instead of at the point of a cone. In Helianthus this state of things remains nearly unchanged as the capitulum developes; but the abnormal growth increases in many cases to such an extent that the apical point eventually lies at the base of a deep hollow, the walls of which result from older masses of tissue which properly lie beneath the apex, growing upwards, and overarching the apex itself. This occurs, for instance, in the formation of the fig, which, as shown in Fig. 151, is a metamorphosed branch, the apex of which is at I^a still nearly level, at *II* has already been outstripped by a circular leaf-bearing cushion, and at III^a is depressed in the form of an urn. The apical point of this shoot lies in this case in the deepest part of the hollow, the inner side of which is properly only the prolongation of the outside of the fig, and bears in

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[1] [See Payer, Éléments de Botanique, p. 117.]

[2] A first scale in the axil of which the bud *k* stands is no longer to be seen.

consequence a large number of flowers (exogenous lateral shoots). In the nearly related genus Dorstenia the fig remains open; the margins of the tabular part of the axis which bears the small flowers do not arch over and unite.

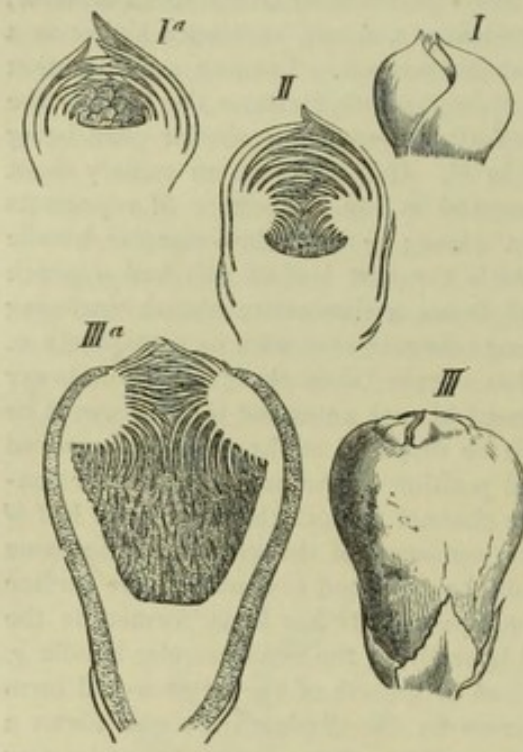

FIG. 151.—Development of the fig of *Ficus carica* (after Payer: Organogénie de la fleur).

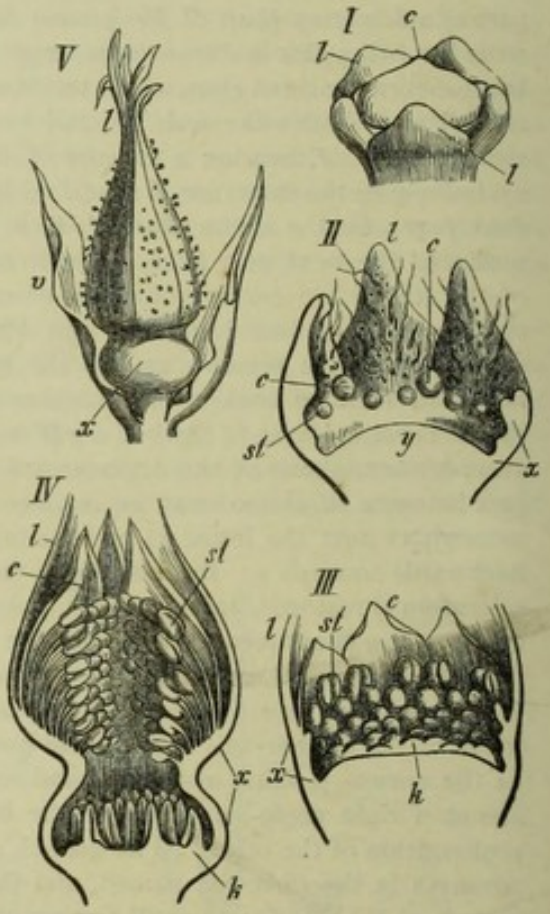

FIG. 152.—Development of the flower of *Rosa alpina* (after Payer: Organogénie de la fleur).

On a process very similar to the formation of the common fig depends the origin of perigynous flowers and of inferior ovaries. Fig. 152 represents this in the perigynous flower of a rose. *I* shows the very young shoot which is to develope into a flower, seen half from above and from the outside; the end of the shoot is thickly swollen; it has already produced the five sepals *l l*, and the five petals alternating with them are visible as little knobs, *c*, between which the apical region of the floral axis appears broad and flat. While the sepals grow quickly, the zone of the tissue of the axis out of which they spring becomes elevated in the form of a circular wall *x* in *II*, which afterwards contracts the opening above as seen in *IV*; an urn-shaped structure is thus formed which is known under the name of a hip, and is distinguished when ripe by its red or yellow colour and its sweet pulpy tissue. Here also the apical point lies in the middle of the bottom of the hollow, and the inner surface of the wall of the urn is a portion of the outer side of the floral axis which has been turned in. To this corresponds the acropetal succession of the leaves (which, however, is only adhered to in a general way). It is clear that if the apical point lies at *y* (in *II*), the succession of leaves (in this case stamens *st* and carpels *k*) from above downwards must be termed acropetal.

If an additional proof of what has just been said were wanted, it would be furnished by the history of development of the flowers of Geum, a genus very nearly related to the rose (Fig. 153). That part of the floral axis which bears the sepals *l*, the corolla *c*, and the stamens *a a*, is elevated in the form of a circular wall *y y*; but the apical region which in Rosa entirely ceases to elongate, becomes again elevated

as a conical body *x*, bearing at its summit the apical point of the floral axis. The order of succession of the leaf-structures is again acropetal, and in consequence the stamens *a* are formed on the inner side of the axis *y y* from above downwards, the carpels which succeed them on *x* from below upwards. In Geum and other Dryadeæ the urn *y y* spreads out at the time of fertilisation, its margin grows so vigorously in size that it expands in the form of a flat plate, and after the expansion its inner surface becomes the outer surface, in the middle of which the gynophore *x* rises like a cone, and in Fragaria afterwards swells out greatly, becomes fleshy, and forms the strawberry (a pseudocarp like the hip).

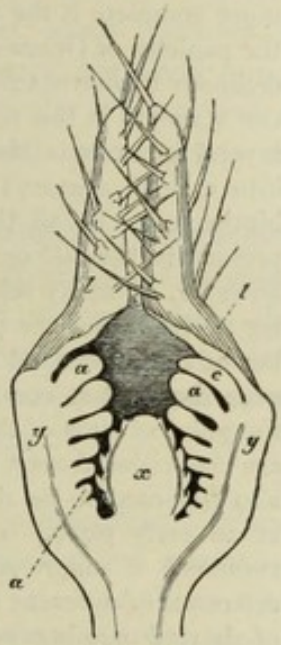

FIG. 153.—Longitudinal section of a young flower of *Geum rivale*.

It will be seen that the formation of the fig, the hip, and the subsequently flat receptacle of Geum depends on a displacement which is caused by vigorous growth of masses of tissue that arise in the form of zones beneath the *punctum vegetationis*. There is in these cases no such thing as adhesion of foliar structures (as is usually stated in works on descriptive botany). The so-called coherent corolla and calyx of gamopetalous or sympetalous (as well as gamosepalous or symsepalous) flowers, are not the result of cohesion; the petals (or sepals) are on the contrary formed in a whorl on the broad end of the young flower-stalk as isolated protuberances. That a gamopetalous corolla or gamosepalous calyx subsequently has the appearance of a bell having at its margin only as many teeth as there should be leaves, does not depend on lateral cohesion of the margins of the leaves, but on the fact that the whole annular zone of the young receptacle which bears the corolla (or calyx) grows up; the bell-shaped part therefore never consisted of isolated leaves, but is the common basal piece which is formed out of the floral axis as a whole, and shows at its margin the original still isolated leaves as teeth of the bell. The reverse is the case in the leaf-sheaths of Equisetum, where an annular wall originally projects round the axis, from which the separate leaf-teeth afterwards shoot out. In this case also the sheath cannot be considered as formed by the cohesion of previously isolated pieces, but the separate teeth of the sheath must rather be considered as branches of a single annular rudimentary leaf. A similar explanation applies to the bundles of stamens which are generally termed coherent stamens; there are, in fact, as many protuberances formed originally as there are bundles of filaments to be produced. These protuberances must be considered as the original staminal leaves which subsequently produce by branching a larger or smaller number of stalked anthers (as *e. g.* in Hypericum, Callithamnus, and many others). Cohesions of parts originally isolated are, as a rule, rare; examples are furnished by the coherent inferior ovaries of two opposite flowers of an inflorescence in *Lonicera alpigena*, the coherent fruits of *Benthamia fragifera* which grow to a large pseudo-berry, and the cohesion of the two stigmata in the flower of Asclepias to each other and to the anthers. The anthers of Compositæ are not truly coherent, but only glued together by their sides.

Much more common than actual cohesion is the abortion of members already formed. Thus, for instance, the paripinnate leaves of Leguminosæ[1] originate as imparipinnate leaves; the terminal leaflet which is finally aborted is at first in the bud even larger than the lateral leaflets; but, as development progresses, it is so retarded that in the mature leaf it overtops the origin of the highest lateral leaflets only as a minute point. In the

[1] Hofmeister, Allgemeine Morphologie, p. 546.

same manner the whole (branched) leaf-blades of many Acacias are also arrested, and are replaced by the petiole (phyllode), which is then expanded in its median plane. Still more complete is the arrest of the leaves from the axils of which spring the branches of the panicles of Grasses; and in this class whole flowers are often frequently aborted. In diclinous Phanerogams the unisexuality of the flowers usually depends on the abortion of the stamens in the female, of the carpels in the male flowers. Sometimes only one of several stamens is aborted, as in Gesneraceæ (*e. g.* Columnea, where it is transformed into a small nectary); and the same occurs with the carpellary leaves (*e. g.* in Terebinthaceæ). In all these cases the structure which is afterwards arrested is actually present in the bud or even later, but its further growth then ceases. The comparison, however, of nearly related plants shows that very commonly certain members are wanting in the flower the presence of which might be expected from the position and number of the others and from their presence in nearly related forms, although in such cases even the earliest condition of the bud does not show the absent member. Since from the point of view of the Theory of Descent it must be assumed that nearly related plants are descended from a common ancestral form, the absent member may in such cases be also supposed to be aborted, only the arrest of development which has once taken place at an early period is so complete and has become so hereditary, that even its first rudiment is suppressed. The true theory of the structure of many flowers, and the reference of different forms of flowers to common types, often depends on the restoration of aborted members of this kind; but to this we shall recur in detail in the Second Book, when treating of Phanerogams.

Sect. 29. **Alternation of Generations.**—When the growth of a plant has continued for some time, so that it has assumed a certain definite internal and external differentiation and conformation, a period at length arrives at which *single* cells become detached from the organic connexion, and cease to participate in the growth which they have hitherto shared as integral parts of the plant which has produced them. These cells begin, either immediately or after further preparation, an independent course of development. A structure thus arises which can no longer be considered a part of the connected conformation of the mother-plant, but a new plant which may be like or unlike the one which produced it.

Cells of this character which are separated from the organic structure of a plant, even if they do not always abandon the place where they were formed, are *Reproductive Cells;* and those plant-structures which result from similar reproductive cells, and are also like one another, form a *Generation.*

But it is only in some Algæ and Fungi that (according to the present state of our knowledge) all successive generations are similar and produce similar reproductive cells (*e. g.* in Nostocaceæ, Spirogyra, &c.). Even in most Thallophytes and in all Muscineæ and Vascular plants *the generations which proceed from one another are dissimilar*, or produce dissimilar kinds of reproductive cells, from which plant-structures of dissimilar habits of life and dissimilar conformation arise. In such cases several similar generations (A, A, A, &c.) may first of all appear in succession, the last of which brings forth a dissimilar generation (B), which, on its part, again produces a generation of the first kind (A), as, for instance, occurs in Vaucheria and Saprolegnia; or three or even four dissimilar forms of generation (A, B, C) succeed one another, until at last the first form (A) again appears. One form may repeat itself again several times (A, B, B, B, &c., C, A) before the production of a new one. This is the case in the Hypodermiæ among Fungi,

where the Uredo-form is produced from the Æcidium-form, and reproduces itself through several generations, till at length from the last Uredo a Puccinia springs as the third form of generation, and this, on its part, again produces an Æcidium. (Cf. Book II. Fungi.) The more common case among Algæ and Fungi, and the one exclusively met with among Muscineæ and Vascular Cryptogams is, however, for only two kinds of generations to alternate with one another, the form A producing B, B again producing A, and so on.

The whole process of development which passes through the successive dissimilar generations, and finally returns again to the first form, is called *Alternation of Generations;* each form of generation which follows and precedes a dissimilar one may be termed an *Alternate Generation.* The alternation of generations A B, A B, A B, &c., for example, consists thus of the two alternate generations A and B, and in like manner the alternation of generations A B B B &c. C, A B B B &c. C of the three alternate generations A, B, and C.

The reproductive cells either continue their development independently without foreign aid, and are then termed *Asexual Reproductive Cells,* and the generation from which they are directly and solely derived is called an *Asexual Generation;* or they are so constituted that they do not attain a condition in which they can develope without further union with another reproductive cell; in this case the reproductive cells are termed *Sexual,* and the form of generation to which they owe their origin a *Sexual Generation.* If the two sexual cells which unite to produce one capable of development are externally similar in form and size, the union is termed *Conjugation;* if, on the other hand, they are conspicuously dissimilar in form, size, and other respects, the union is termed *Fertilisation.* That one of the two sexual cells which performs active work and itself disappears after fertilisation is the *Male* or *Sperm-cell* (spermatozoid, antherozoid, pollen-grain); the one which is acted on by the former and becomes transformed into an Embryo which begins the new generation is the *Female* or *Germ-cell* (ovum, oosphere, germinal-vesicle)[1]. While the asexual reproductive cells usually become detached from the mother-plant and dispersed (hence called spores), in order to produce the new generation at a distance from it, the germ-cell, on the contrary, generally continues to lie in a special organ of the mother-plant (the oogonium, archegonium, ovule), there awaits fertilisation, and, afterwards still nourished by the mother-plant, commences the new process of vegetation (formation of embryo). It does, however, occur also in Algæ (*e. g.* in Fucaceæ) that the germ-cells escape before fertilisation, and produce the new generation without the help of the mother-plant.

If the relationship of asexual and sexual reproduction to the succession of generations is observed, it is seen that in the most simple plants asexual generations sometimes follow one another without intermission, as, *e. g.* in Nostocaceæ; while in other cases an uninterrupted series of sexual generations may succeed one another, as in Spirogyra. When alternation of generations occurs, in certain cases all the alternate generations may be asexual, as in Hydrodictyon (according

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[1] Compare Book III, on Sexuality.

to Pringsheim)[1], or several asexual generations may succeed one another, until finally a sexual generation is produced, as in Vaucheria, Mucorini, and Cystopus. The usual case, and the universal one among Muscineæ and Vascular Cryptogams is, however, for sexual and asexual generations to alternate regularly.

If the morphological conformation of alternate generations is more closely observed, it is seen that in the most simple plants the difference sometimes consists merely in the circumstance that one generation produces asexual spores while the other produces sexual organs, as in Vaucheria and Saprolegnia, where the morphological distinctions of the alternate generations are only observable in the preparation for reproduction. But even in the more highly organised Algæ and Fungi the alternate generations are mostly very dissimilar in their growth, and the difference is generally especially striking when one generation forms merely spores, the other sexual organs. Thus, for example, the sexual generation in Peziza (where the sexuality has been observed by De Bary, Woronin, and Tulasne) is a thread-like mycelium creeping upon the nourishing substratum, the second asexual generation being developed after fertilisation upon the mycelium in the form of a massive tissue, the receptacle with its numerous spore-sacs. In Muscineæ and Vascular Cryptogams, where the alternation of generations is more conspicuous than elsewhere, the sexual generation is always essentially dissimilar from the asexual generation of spores; and each of the two alternate generations follows an altogether different law of growth. In Mosses, for example, the sexual generation is a self-sustaining Cormophyte, usually lasting for years, and forming on its usually much-branched axis a number of sharply differentiated leaves, root-hairs, and finally the archegonia and antheridia; while the second generation, resulting from the fertilised ovum in the archegonium, presents itself in the form of a stalked capsule, in which the asexual spores are formed. This so-called Moss-fruit, although it exhibits a marked differentiation of tissue, is a thallus-structure, in which the segmentation into axis and leaf is entirely wanting. In Vascular Cryptogams, on the other hand, the sexual generation which proceeds from the spores is a small body of the simplest kind, without any considerable differentiation of tissue,—a thallus which usually never betrays a disposition to any external segmentation or branching. In Ferns, Equisetaceæ, and Ophioglossiaceæ, this organ, called the Prothallium, carries on an independent existence beneath or on the surface of the earth; in Rhizocarps and the Selaginellæ, on the contrary, it remains within the spore. In the female sexual organ (archegonium) of this first generation the second generation arises after fertilisation. In these cases it is always formed into a highly developed Cormophyte, usually possessing unlimited duration of life, and in Ferns often attaining large dimensions, and always forming a stem which produces highly organised foliage-leaves, roots, and hairs, and finally the spores in special receptacles.

It is one of the most important problems of morphology and systematic botany, not only to demonstrate the alternation of generations in different classes

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[1] From the general occurrence of sexuality, and from the circumstance that fertilisation has often been discovered where it was least expected, it must always be doubtful whether even those lowly organised Algæ and Fungi which we consider at present as altogether asexual do not under certain conditions develope sexual cells.

of plants, but also to compare the process according to definite principles, as will be done in detail in the Second Book. Here it is necessary only to remark that alternation of generations occurs even in Phanerogams; the Cycadeæ and Coniferæ are in this respect nearly related to Lycopodiaceæ, and through them we are also able to trace a repetition of the most important features of the alternation of generation of the highest Cryptogams in the formation of the seeds of Monocotyledons and Dicotyledons. It is sufficient only to remark that the Endosperm of Phanerogams corresponds to the Prothallium of Vascular Cryptogams (and thus to the sexual generation), while the Embryo which lies by the side of or enclosed in the endosperm may be compared to the asexual spore-forming generation of Ferns, Equisetaceæ, &c. In Phanerogams, as in Vascular Cryptogams, one generation (the endosperm or prothallium) is morphologically a thallus, the other a cormophyte, the rooting stem with its leaves and flowers.

Since the principal divisions of the life-history of each plant, and the decisive turning-points of the different formative processes, are given in the alternation of generations, a systematic representation of the natural relationship of plants—in other words the natural system—should primarily demonstrate and compare the homologies in the alternation of generations in different classes. This at the present time is attended with great difficulties in Thallophytes and Characeæ, and indeed is to a certain extent still impossible; but in Muscineæ, Vascular Cryptogams, and Phanerogams, it is practicable, and leads to the most unexpected and interesting results.

In the corresponding paragraph in the first edition I placed at the foundation of the definition of alternation of generations the phenomena which occur in Muscineæ and Vascular Cryptogams, and, to correspond with this, brought into prominence as the essential condition the change of the law of growth in the passage from one alternate generation to the other; this is true for many Thallophytes on the one hand, and for Phanerogams on the other. In this view, however, the intimate relation of the production of sexual and asexual reproductive cells to the alternation of generations was kept too much in the background, since alternation of generations in its simplest forms, as in Vaucheria, Saprolegnia, and the Mucorini, is simply almost invariably an alternation of sexual and asexual generations otherwise scarcely differing in their mode of growth. Although the earlier definition might, in its strict sense, be applied to these cases also, the representation attempted here appears to me clearer and more easily intelligible to beginners. The earlier definition permitted also the production of the Moss-buds on branches of the protonema to be comprised under the head of alternation of generations,—a case which, on the other hand, cannot be included under the definition here given, since the apical cell of a lateral branch of the protonema, which becomes transformed into the apical cell of the leaf-shoot, cannot be considered, without further explanation, as a reproductive cell in the above sense. But if the definition of alternation of generations should seem to be injured by the exclusion from it of this remarkable phenomenon, it must be specially noted, on the other hand, that the sharp differentiation of the Moss-buds from the protonema which produces them, and the passage to an entirely different law of growth, does not occur in the Hepaticæ. The structures in them homologous to the protonema frequently appear only as a preparatory and transitory germ-condition, just as germinating Fern-spores, especially those of Hymenophyllaceæ, first produce a filiform structure, at the apex of which is formed the flat prothallium. The protonema may therefore be considered, with the so-called *Pro-embryo*, as a peculiar process of growth interpolated in the alter-

nation of generations, and finding its analogue in the strongly developed pro-embryo of Gymnosperms and many Angiosperms. However important it may be from a scientific point of view to include the different phenomena under as few general terms as possible, this is only useful in actual investigation when the general terms are capable of a clear definition, and when they only include those things which agree with one another in such definite properties as distinguish them at the same time from other phenomena. I consider it, therefore, inconvenient to distinguish the differences between the shoots of a plant, such as scale-shoots, foliage-shoots, and flower-shoots, simply as alternations of generations. It would certainly be desirable to denote the fact that shoots of a definite kind regularly produce shoots of another definite kind by a scientific term. And were the term Alternation of Generations not already appropriated to the phenomena we have described, it might well be applied to this purpose; but it is not applicable to both, since it would then be equivocal and therefore scientifically valueless. The term Alternation of Shoots might, for instance, be applied, by analogy to this particular case of metamorphosis which is of such common occurrence among Phanerogams.

BOOK II.

SPECIAL MORPHOLOGY

AND

OUTLINES OF CLASSIFICATION.

GROUP I.

THALLOPHYTES.

Under this term are comprised Algæ and Fungi (Lichens being also included in the latter section); but the extraordinary variety of their forms and mode of life render it impracticable to characterise Thallophytes collectively by giving prominence to any special features of their growth or reproduction especially alternation of generations, as may be done in the succeeding groups. The most diverse forms of Thallophytes are nevertheless united by a strong and easily recognised bond of natural relationship;—transitional forms lead, through numberless gradations, from the simplest Algæ consisting of round isolated cells, not only to the highly differentiated members of the same class, but also, through the aquatic Fungi and Moulds, to the wonderful forms of the large Hymenomycetes, Gasteromycetes, and Ascomycetes, the external and internal structure of which deviates greatly from that of all other plants. A detailed account of these relationships would, however, be almost entirely unintelligible to the beginner, since it would presuppose not only a knowledge of the facts now to be explained, but also a more special acquaintance with numerous other forms which cannot be described here. A repeated study of the description of Thallophytes, Characeæ, Muscineæ, and Vascular plants, will exhibit clearly to the beginner the most prominent features of their affinities. One thing only must be mentioned at the outset,—that the term Thallophytes is an adequate one in so far as it points out one

prominent property of the external conformation of most Algæ and of all Fungi; but a sharp boundary line cannot be drawn in this respect between the Algæ and the group of Muscineæ. On the one side some Algæ show a clear differentiation of stem and leaf, while on the other side the vegetative part of many Hepaticæ is a very simple thallus. As little can a boundary line based on the structure of their tissues be drawn between Algæ on the one hand and Characeæ and Muscineæ on the other hand. It would be very easy to adduce a series of negative characteristics of Thallophytes; *i. e.* to show that certain properties are wanting in them which are found in all other plants or single groups; but this would only prove that Algæ and Fungi are neither Characeæ, Muscineæ, nor Vascular plants, but would tell us nothing respecting their affinity.

CLASS I.

ALGÆ[1].

The Algæ begin with the smallest and simplest forms of the Vegetable Kingdom; but they approach in different ways a more perfect development, and attain higher degrees of organisation, with frequently dimensions as considerable as are again found only in much more highly organised classes. This gradual approach towards a more perfect development takes very different courses; in some cases it is the differentiation of the individual cell, in others the mode of combination of the cells, in others again the external conformation, the variation of growth in different directions, but usually it is a combination of these conditions, by which more perfect structures proceed from simpler ones. The development of the mass of Algæ is also attained in different ways; sometimes the single individuals increase, at other times numerous individuals are united into a genetic and organic whole, which behaves as an individual. The former occurs especially in the forms which are morphologically and histologically more perfect (Fucaceæ), the latter in the simpler structures (Gelatinous Algæ, Nostocaceæ).

If we consider, first of all, the *Differentiation of the Individual Cell*, we find in the lowest grades of this class forms in which scarcely more can be recognised than a cell-wall containing a coloured protoplasmic substance, the latter always possessing a vacuole. Higher forms show the protoplasmic substance differentiated into colourless and coloured portions which contain granular substances, chiefly starch. A nucleus, absent from the lowest forms, is clearly present in the higher; the green protoplasmic substance assumes the most diverse forms, such as rings, bands, or stars; but generally, and even in the simpler forms, it breaks up into

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[1] For more comprehensive works on Algæ see Kützing. Phycologia generalis, Leipzig 1843.—Nägeli, Die neueren Algensysteme, Neuenburg 1847.—De Bary, Bericht über die Fortschritte der Algenkunde in den Jahren 1855, 56, 57, in Bot. Zeitg. 1858, Supplement, p. 55.—[Hassall, Hist. Brit. Freshwater Algæ, 1845.—Pritchard, Infusoria.—Rabenhorst, Flora Europæa, Algarum aquæ dulcis et submarinæ, 1864–68.]

grains (grains of chlorophyll), which are always present when cells are combined into tissues. The configuration of the cell-wall is much less varied than in other classes of plants, at least in so far as it depends on increase of thickness, stratification, and chemico-physical differentiation. In general a tendency prevails towards the transformation of the cell-wall into mucilage; and this process not unfrequently plays a most important part in the setting free of the reproductive cells. Lignification, on the other hand, occurs very rarely, perhaps never; greater firmness is attained only by deposition of silica (in the Diatoms), or of calcium carbonate (Acetabularia, Melobesiaceæ). Most of the Algæ of which the cells are united into tissues are ductile, flexible, and slimy. Sometimes the cell-wall (or single layers of it) is brightly coloured; its increase in thickness is generally almost uniform over the outside of the cell, but strong projections are often directed outwards. A localised increase in thickness on the inner side of the cell-wall is observable only in cells combined into tissues (*e. g.* Fucaceæ, Florideæ) in the formation of simple dots. A decided differentiation of the cell-wall into layers differing from one another in chemico-physical properties often occurs in the resting-spores (*e. g.* Vaucheria, Œdogonium, Spirogyra). The cuticularisation of the outer layers never advances far inwards, the cuticle generally remaining thin.

The Mode of Combination of the Cells with one another is more various among Algæ than in any other class of plants. In the most simply organised forms, where the vegetative cells which belong to one cycle of development are nearly alike, their combination into a tissue appears useless; they therefore not unfrequently separate from one another by division when first formed, and live isolated (so-called Unicellular Algæ). But in other cases, where the cells also show no perceptible diversity, they remain combined into tissues, either as rows (filaments) or plates, or masses of cells, according to the direction of growth and of the divisions perpendicular to this direction. Two modes of tissue-formation occur among the more lowly organised Algæ;—the enclosure of one cell within another, and the subsequent union of cells previously free. In both cases the cells form one family; in the former case, such as we find in Glœocapsa and Glœocystis, each cell, before it divides, forms a thick watery cell-wall, so that the second generation of cells appears as if enclosed in the cell-wall of the first generation, the third in that of the second generation, and so on. Sometimes the thick mucilaginous cell-walls run into one another in such a manner that their boundaries can no longer be distinguished (Volvocineæ); in other cases a row of cells in genetic connexion (a linear cell-family) forms in this manner an envelope of jelly around itself, or several coalesce into a larger lump of jelly, in which the strings of cells are imbedded (Nostoc). Less frequent is the union and subsequent common growth of cells previously isolated which have been formed by the division of one mother-cell; such a union forms a plate, as in Pediastrum, or a hollow net, as in Hydrodictyon. Larger masses of tissue not unfrequently arise in Algæ by the common growth of numerous rows or filaments of cells lying close to one another, and by their division in a corresponding manner; single filaments may in this manner become intimately combined (*Coleochæte scutata*), or may lie in loose juxtaposition (*Coleochæte soluta*). A tissue-like structure may even result from one and the same cell becoming variously branched, and its ramifications

becoming attached to one another in such a manner (as in Acetabularia or Udotea) that a section of the whole shows a number of cell-cavities, which however are all merely bulgings of a single cell. But none of these structures, which either actually constitute or only imitate a cellular tissue, have any great importance in the vegetable kingdom, being limited to single groups of Algæ; while aggregations of cell-filaments will be met with more completely developed among Fungi and Lichens. The more highly developed forms of Algæ, which at the same time have the power of forming large individuals,—as the various species of Fucus, Laminaria, Sargassum, and some Florideæ,—exhibit the usual mode of the formation of tissue which here makes its appearance for the first time in the vegetable kingdom, and is met with in a continuously increasing grade of development in Muscineæ and Vascular plants. The successive segments of the apical cell lying at the end of each branch of the thallus first form a primary meristem which then passes over into more or less diverse forms of permanent tissue, although these different forms show only slight indications of that specialized internal structure which we find partially even among the Muscineæ, and universally among Vascular plants. The whole tissue forms a kind of parenchyma, the cells of which, however, are everywhere densely compact, except where single large air-cavities are to be formed. A differentiation of this tissue into different systems is usually only so far indicated that the outermost layers consist of smaller and firmer cells, while the inner cells are often very large, and sometimes extremely long (as in some Florideæ).

The External Differentiation into Organs is only feebly indicated in the lowest Algæ; but, if we go through the different series of forms in the class, it passes through the most varied gradations. It is first manifested by the growth following the direction of one axis only, by which an elongated sac (Vaucheria) or, with the intervention of cell-division, a row of cells is formed. In this case the growth may either take place at all points (intercalary as in Spirogyra), or may be limited to a terminal cell, or may gradually cease at a greater distance from it. The external differentiation attains a higher grade when branching takes place; at first this is uniform, the branches resembling the axis in their mode of growth; in more highly differentiated forms it loses its uniformity, the lateral shoots developing in a manner different to the axis which produces them. Both may occur in a single cell, a row of cells, or a solid tissue. The external differentiation of the Algæ, as far as it is manifested in the formation of an axis with lateral outgrowths arranged according to certain laws, shows in its higher stages a differentiation which distinctly calls to mind the difference between stem and leaf, and to a certain extent even the formation of roots. In the genus Caulerpa these relationships are strikingly evident, although the whole thallome consists only of a single cell; it becomes differentiated into a creeping stem with leaf-like lateral branches arising in acropetal order, and root-like filaments growing downwards; and a similar differentiation occurs to a smaller extent even in Vaucheria. Much more varied is the differentiation of the lateral branches in those thallomes which consist of numerous cells (solid tissues), since they produce in definite order below their growing apex leaf-like appendages, or at places root-like shoots (Fucaceæ, the larger Florideæ, &c.). While the leaf-like members of the thallome may not be clearly distinguishable morphologically from actual leaves, the root-like members are at the same time always distinguishable from true roots as

long as the term root is arbitrarily applied only to the endogenous leafless shoots of Vascular plants provided with a root-cap; but without this arbitrary limitation it would be difficult to find a natural boundary-line between the root-like outgrowths of many Algæ and the roots of Cormophytes. For the sake of finding an expression for these relationships in Algæ, and partly also in Characeæ and Muscineæ, the leaf-like appendages might be termed Phylloids, the root-like appendages Rhizoids.

The Branching at the growing end of the thallus of Algæ may be lateral (monopodial) or dichotomous; very clear examples of both kinds of systems of branching occur among Algæ. In both cases the original character may be retained as the growth advances, so that the mature thallome is either monopodial or bifurcate; or in both cases the further development may be sympodial. The whole of the ramifications (uniform or not) lie more often in Algæ than in other classes of plants in one plane which bears a definite relation to the horizon, and is hence probably determined by gravity; this occurs, apparently, especially in dichotomies. Those cases are of special morphological interest where the branches of a true or spurious dichotomy are closely packed laterally, so that they form roundish discs lying upon the substratum, which continue to grow centrifugally at the margin (as in Coleochæte and Melobesiaceæ).

The Mode of Reproduction is not yet accurately understood in all families of Algæ, but in many it has been carefully investigated by distinguished observers and is even better known than anywhere else in the vegetable kingdom. As in the vegetative organs of the plant, so also in the reproductive, an enormous diversity is exhibited. Asexual reproduction is known in all the sections of Algæ, sexual reproduction in many, some of which belong to the simplest but most to the more highly developed groups; in numerous cases we find an alternation between asexual and sexual generations.

Asexual Reproduction is brought about either by motionless or motile spores. Motionless asexual reproductive cells are found not only in the very simply constructed Rivularieæ, but also in the most highly developed Florideæ (in this case generally as so-called Tetraspores). Motile reproductive cells (Swarm-spores or Zoospores), are especially common in those sections where the chlorophyll is not concealed by other colouring materials (Chlorosporeæ, Confervæ). They result from the contraction of the protoplasmic substance of certain cells (not unfrequently accompanied by division), which is then reconstructed as a primordial cell, and escapes through an opening in the wall of the mother-cell or, after its dissolution, into the surrounding water, where the naked swarm-spore now moves with a rotatory and at the same time progressive motion for some minutes, hours, or even days, until it finally comes to rest, becomes fixed to one spot, and germinates. In every swarm-spore there may be distinguished an anterior hyaline end, usually pointed, which is turned foremost during movement, and a posterior thicker rounded end provided with chlorophyll. The line which unites the two ends is the axis of growth of the swarm-spore, and of the embryo-plant which grows from it. When the swarm-spore comes to rest, it fixes itself by its anterior hyaline end, and forms there a hyaline organ of attachment (rhizoid), which is often branched, while the coloured posterior end becomes the free apex of the young plant. The rotating advancing movement is occasioned by Cilia, fine vibratile threads which are sometimes

very numerous but short, and cover the whole surface of the swarm-spore (Vaucheria), while sometimes they form a crest round the hyaline part (Œdogonium), but are most often fixed in pairs to the anterior margin and are then very long. Sometimes swarm-spores are of two sizes (Macro- and Micro-gonidia), indicating perhaps a sexual relationship as yet undemonstrated.

Sexual Reproduction is brought about in very different ways, the most important distinction being that the sexual cells may be either similar or dissimilar. In the first case the sexual reproduction is called Conjugation, in the second case Fertilisation or Impregnation. Conjugation occurs in Ulothrix[1], Chlamydococcus, Pandorina, and probably also in other Volvocineæ, by the coalescence of two free-swimming cells which perfectly resemble ordinary swarm-spores. In the conjugation of the Conjugatæ and Diatomaceæ, on the contrary, the conjugating cells are stationary; they are sometimes expelled in the form of primordial cells, and subsequently unite. But usually the walls of the cells concerned grow together, and their contents are reconstructed as primordial cells, one then passing over into the other and uniting with it. The product of this coalescence surrounds itself with a firm cell-wall, and is called a *Zygospore;* it generally germinates only after a long period of rest. Fertilisation, in the narrower sense of the term, is, except in the Florideæ, brought about by Oogonia and Antheridia. Oogonia are cells in which the female reproductive bodies or Oospheres are formed; the Antheridia are cells or masses of cells which produce the male reproductive bodies or Spermatozoids. The oospheres are formed, in Fucaceæ, several in one oogonium, out of which they are expelled before fertilisation; but in the other groups the whole contents of the oogonium are transformed into one oosphere, which contracts, becomes loosened from the cell-wall, and constitutes a primordial cell. This remains motionless within the wall of the oogonium, and there awaits the arrival of the spermatozoids, which enter by an opening previously formed in the wall of the oogonium, and unite with the oosphere. The part of the oosphere which faces the opening is hyaline, and takes up the spermatozoids; sometimes a hyaline mass of mucilage is expelled by the anterior end of the oosphere from the oogonium before fertilisation. The spermatozoids of Algæ which do not belong to the class Florideæ resemble swarm-spores, but are usually much smaller and provided with a red corpuscle; they swarm out of the antheridia, and some of them finally reach the oospheres, with which they coalesce. The oospheres are usually many hundred or even some thousand times larger than the spermatozoids. Algæ are distinguished from the rest of Cryptogams by their spermatozoids never being in the form of slender spiral filaments, but short, and rounded at least at their posterior end.

The sexual reproduction of the Florideæ differs greatly from that of most other Algæ, but the section of Nemalieæ forms the transition to Coleochæte. The antheridia of the Florideæ produce an immense number of small spermatozoids, which have no active motion, but are washed about by the water until at length some of them become attached to a Trichogyne, and empty their contents into it. The term Trichogyne is given to a long thin hair-like hyaline sac, which serves as a receptive organ, and springs from a structure which is called the

[1] Cramer, Bot. Zeitg. 1871, p. 76. (See under Volvocineæ.)

Trichophore. This latter is a body usually consisting of several cells, in or near which the results of the fertilisation become apparent, cell-filaments or masses of tissue shooting out near or beneath it, forming the receptacle, here termed the Cystocarp, in which the spores are subsequently formed. In one genus (Dudresnaya) the process is still more complicated, inasmuch as tubes first spring from the trichophore, which occasion the formation of the cystocarps only after conjugation with the terminal cells of other branches.

In other Algæ the result of the fertilisation is first of all the formation of a cell-wall round the oosphere, which thus becomes an oospore. In the Fucaceæ this is at once capable of germination; but in other cases it does not germinate until after a long period of rest, like most zygospores. The product of the oospore is, in the Fucaceæ, a new plant of apparently similar description to the mother-plant; in Œdogonium, on the contrary, it produces several swarm-spores, each of which forms a new cellular filament, of which in this case the plant consists. In Coleochæte the oospore after the resting period developes a mass of tissue from the cells of which the contents also escape as zoospores.

The Mode of Life of Algæ is determined and limited by the concurrence of two conditions, besides the specific requirements of temperature, *viz.* water and light. The greater number of Algæ are submerged aquatic plants, or, when otherwise, they still require water for certain processes of development, especially for their reproduction; sometimes certain vital phenomena are caused by moistening with water after the drying up of the cells. Light is a universal condition of the life of Algæ, inasmuch as they are all dependent on individual assimilation; in them, as elsewhere in the vegetable kingdom, this is brought about by chlorophyll, which, with the help of light, decomposes carbonic acid and evolves oxygen. Algæ are, therefore, never true parasites[1], although they very commonly live on the surfaces of other plants. This at the same time affords the only means for a sharp but artificial separation between Algæ and Fungi. From the section of Siphoneæ among the Algæ containing chlorophyll to the parasitic Phycomycetes among the Fungi destitute of chlorophyll there occurs so gradual a transition in their morphological characters that, without the characteristic colouring, the Siphoneæ and Phycomycetes would have to be included in one group; but the distinction between Algæ and Fungi would then be at once overthrown. There exists in fact, as may be concluded from what we have said, no definite boundary-line; but for the sake of clearness it is desirable to establish a conventional or artificial one; and this is best afforded by the presence or absence of chlorophyll. All Algæ contain chlorophyll, and have therefore the power of independent assimilation; all Fungi are destitute of chlorophyll, and are therefore parasites, or live on organised products of decomposition, and are in general independent of light in obtaining their nourishment. The chlorophyll is generally concealed from the sight in Algæ by the presence of substances of a different colour. The Nostocaceæ appear, in spite of their chlorophyll, bluish- or light-green, because they contain in addition a colouring material soluble in water, which by transmitted light appears

[1] [This proves however not to be absolutely true. Cohn has discovered a chlorophyllaceous Alga, *Chlorochytrium Lemnæ*, which is parasitic on Lemna. Archer has collected the literature of the subject in the Quart. Journ. Micr. Sc. 1873, p. 366 et seq.—Ed.]

of a beautiful blue, in reflected light (by fluorescence) of a blood-red colour. In addition to these two is found also a third yellow colouring material in small quantity, which also, in addition to chlorophyll, causes the colour of Diatoms. In Fucaceæ, according to Millardet, the chlorophyll, which is undoubtedly present, is concealed by this yellow and by a reddish-brown substance; the Florideæ appear of a beautiful rose-red, violet, or similar colour, because a red colouring material soluble in cold water is mixed with their chlorophyll in such quantities that the green colour of the chlorophyll is apparent only after this has been extracted. These coloured compounds are strikingly constant in large groups of distinct morphological character.

The *Classification* of Algæ[1] is at present in the utmost confusion; the older divisions of the class into the larger groups and families have, for the most part, been shown, by the recent researches of Thuret, Pringsheim, De Bary, Nägeli, and others, to be unsatisfactory; but these researches have not yet been carried sufficiently far to construct a new and complete classification of Algæ corresponding to the present requirements of science. The discovery of alternation of generations and polymorphism in some sections justifies the supposition that certain forms not as yet accurately known may be merely conditions of development of unknown cycles of forms, although hitherto considered distinct species and genera. For these reasons I do not, in the following pages, make a systematic review so much as a selection of typical forms round which the remainder group themselves.

The NOSTOCHINEÆ[2], in the broadest sense of the word, form thread-shaped or moniliform rows of cells, usually simple, rarely branched; the threads are free (in Oscillatoria), or enclosed in gelatinous sheaths, by the deliquescence of which they are often united into large colonies, which form either roundish or membranous wrinkled masses (*e.g.* Nostoc). The threads elongate by the longitudinal growth and transverse division of their cells; only in Seirosiphon and a few allies does any longitudinal division take

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[1] [The most recent general classification of Cryptogams is that of Cohn (see Hedwigia, Feb. 1872, Journal of Botany, 1872, p. 114). The Algæ allied to Nostocaceæ form the order Schizosporeæ. In this the family of the **Schizomycetes** finds a place, including the minute organisms known in a wide sense as Bacteria. For a detailed account of these organisms see Cohn, Beiträge zur Biologie der Pflanzen, Heft 2, 1872 (Quart. Journ. Micr. Sc. 1873, p. 156). Cohn defines Bacteria as chlorophyll-free cells of spherical, oblong, or cylindrical form, sometimes twisted or bent, which multiply themselves exclusively by transverse division, and occur either isolated or in cell-families. Bacteria make fluids milky unless they have nearly the same refractive index. Their diameter is not more than $\frac{1}{20000}$ in., and their length varies from twice to 100 times as much. They divide only longitudinally by elongating to double their normal length and subsequently pinching in; they never branch. The cells resulting from the division either separate or remain attached in chains. By the swelling up of their cell-membranes they may form a jelly-like mass or colony (Zooglæa). Most Bacteria present a motile and a motionless condition; their movements in the former are extremely various. The systematic place of these organisms is at present purely provisional. E. R. Lankester has shown (Quart. Journ. Micr. Sc. 1873, p. 408), from the investigation of a peach-coloured species which made its appearance in water containing decomposing animal remains, that the series of forms distinguished by Cohn cannot be maintained as distinct, and that they must either be regarded as 'a series of steps in the ontogenesis of a specific form, or they are a number of phases or "form-species" of a Protean organism.' Lister (Quart. Journ. Micr. Sc. 1873, pp. 393–4) believes that he has demonstrated the origin of Bacteria from a Fungus, a species of *Dematium*. On the other hand, Cohn has remarked the surprising resemblance of the microspores of an interesting Oscillarian Alga Crenothrix to Bacteria, although he is disposed to think that there is no genetic connexion between the two. (See Quart. Journ. Micr. Sc. 1873, p. 163.)—ED.]

[2] De Bary, Flora, 1863, pp. 553 et seq.—Thuret, Observations sur la reproduction de quelques Nostochines: Mém. de la Soc. Imp. des Sci. Nat. de Cherbourg, vol. V. Aug. 1857.

place, by which the threads come to consist of several rows of cells. The cells capable of division contain a homogeneous or granular protoplasm of a bluish-green or greenish-brown colour, consisting of a mixture of chlorophyll with the blue colouring substance already mentioned or with a yellow one. In Oscillatoria and its allies all the cells of a thread are alike; the thread itself is cylindrical, and the cells have the appearance of short transverse discs. In the other genera the threads are mostly moniliform, the cells spherical or ellipsoidal and of two different forms; the greater number are green and capable of division; between them occur, at greater distances, or at the end of the thread, colourless cells of considerable size and incapable of division, the Heterocysts. The Nostochineæ live in water, or more commonly on damp earth, bark, rocks, and walls, where they form gelatinous incrustations or masses. The mode of reproduction is known only in a few genera of this division.

Nostoc, which may be considered the type of **Nostocaceæ**, consists, when mature, of a large number of moniliform threads interwoven among one another and imbedded in a glutinous jelly, and thus united into colonies of a specifically defined form. New colonies are, according to Thuret, formed in the following manner:—The jelly of the old colony becomes softened by water, the portions of the threads lying between the heterocysts become detached, separate from the jelly, and straighten themselves, while the heterocysts themselves remain in the jelly. After they have entered the water, the old portions of the threads become endowed with motion like the Oscillatorieæ, and their exit is apparently caused by this movement[1]. The roundish cells of the filaments now grow transversely, *i. e.* vertically to the axis of the filament, become disc-like, and then divide, the division-planes being parallel to the axis of the old filament, which now consists of a series of short threads, the axis of whose growth is vertical to its own. The numerous threads which are thus formed continue to elongate and to increase the number of their cells; they then curve, place their two terminal cells in contact with those of the next row, and thus the whole unite into a single curved Nostoc-filament. Individual cells, apparently without any definite law, become heterocysts. In the meantime the gelatinous envelope of the new filament is developed, and the originally microscopic substance attains or even exceeds the size of a walnut by continuous increase of the jelly and divisions of the cells[2].

The history of the development of **Rivularieæ** has been observed by De Bary. *Rivularia angulosa* forms soft greenish-brown gelatinous masses, some of which swim freely in stagnant water, while others are attached; the former are about ½ mm., and spherical, the latter about the size of a nut and hemispherical. In the interior are found numerous threads arranged radially; they are moniliform, and are composed of roundish cells which, however, taper into an articulated hyaline hair at the peripheral end of each thread, while at the central end of the thread is a heterocyst or basal cell, so that each thread may be compared somewhat to a riding-whip. The pointed end of the thread does not grow, but the longitudinal growth and the increase in number of the transverse divisions continue further downwards as far as the basal cell. Fructification takes place nearly simultaneously in most of the filaments of a colony.

[1] These motile threads of Nostoc were seen by Janczewski to enter the young stomata on the lower side of the thallus of *Anthoceros lævis*, where they further developed into roundish coils. Such colonies of Nostoc have been known for a long time in cavities and in the tissues of different Hepaticæ (in Blasia, Pellia, Diplolæna, Aneura, Riccia), but have generally been considered endogenous gemmæ of these species, until Janczewski proved their true nature. Nostoc also establishes itself in the large porous cells of the leaves of Sphagnum. The entrance of Scytonemeæ into the parenchyma of the stem of a dicotyledonous plant, Gunnera, is brought about, according to Reinke, in a different manner; the deeper-lying parenchyma-cells of the circumference of the stem, themselves covered by layers of parenchyma, are densely filled with colonies of the Alga. (Bot. Zeitg. 1872, pp. 59 and 74.) [See also Ann. des Sci. Nat. 1872, p. 306, and Quart. Journ. Micr. Sc. 1873, p. 369.]

[2] [Archer has described the occurrence of 'spores' in *Nostoc paludosum* which were always placed singly between the heterocysts. Quart. Journ. Micr. Sc. 1872, p. 367.—Ed.]

The cells which lie immediately above the basal cell form a resting spore; it becomes thicker, and at the same time 10 to 14 times as long as thick, of cylindrical form and with rounded ends, and now forms, so to speak, the handle of the whip-shaped filament; its contents become denser, and darker from numerous granules, without, however, losing the bluish-green colour, and it surrounds itself with a compact firm membrane or sheath. At the commencement of the winter the cultivated plants disappear, only the *Spores* together with their sheaths remain behind, and commence germinating in January. The cylindrical cell divides first of all into 4, 6, 8, or 12 shorter cylindrical cells; the bipartition is then repeated in all the cells through several generations, until the filament which arises in this manner from the spore numbers from 120 to 150 cells. The cells have already begun to be rounded off, and the filament has become moniliform; as it lengthens it splits the envelope of the spore, or raises up its upper part like a cap, while the lower end of the filament remains in the sheath. With its increase in length the filament decreases in breadth. When it has attained double the length of the sheath, it escapes completely from it, and the terminal cells become pointed. The filament then splits up into from 5 to 7 pieces about equal in length and in the number of their cells; the pieces place themselves close to one another, until they form a bundle or tuft; then each piece begins to transform itself into a whip-shaped Rivularia-filament; one terminal cell becomes the basal cell; at the other end of the filament the cells elongate into an articulated hair. Various deviations from these normal processes occur however not unfrequently. The tuft of threads proceeding from a spore now forms a young mass of Rivularia, the threads of which are already imbedded in jelly. The multiplication of the filaments of a young growing mass takes place by apparent branching; *i. e.* one of the lower cells becomes a new basal cell; the piece of filament lying between it and the old basal cell developes into an independent filament, which places itself beside the mother-filament.

With respect to colour, habitat, and mode of life, as well as the tendency to form gelatinous envelopes, the **Chroococcaceæ** agree with the Nostocaceæ; the difference lies in their cells not being united into filaments. In Synechococcus, Glœothece, and Aphanothece, the cells of all the generations elongate and divide in the same direction, and would form filaments if they did not separate from one another. In Merismopœdia the generations of cells divide alternately in two directions, flat plates consisting of one layer being thus formed. In Chroococcus, Glœocapsa, and Aphanocapsa, the division takes place alternately in three directions, roundish families arising which are finally amorphous[1] (Fig. 154). The mass of layers of the softened gelatinous walls of the mother-cell surround the daughter-cells which proceed from it with their gelatinous envelopes which are also stratified, and thus form systems of layers enclosed in one another. The relations of growth now pointed out in the case of Nostocaceæ and Chroococcaceæ are repeated, in all essential particulars, in some other groups of very simple Algæ, the cells of which contain pure chlorophyll. The peculiar bluish- or brownish-green colour which the Nostocaceæ share with the Chroococcaceæ, is caused by a mixture of true chlorophyll with phycoxanthine and phycocyanine; the phycocyanine is diffused from dead or ruptured cells, and thus produces, for example, the blue stains on the paper round herbarium specimens of Oscillatorieæ. If the plants are crushed and an extract made with cold water, a solution[2] is obtained of a beautiful colour which is blue in transmitted and blood-red in reflected light. If the crushed plants, after extraction of the

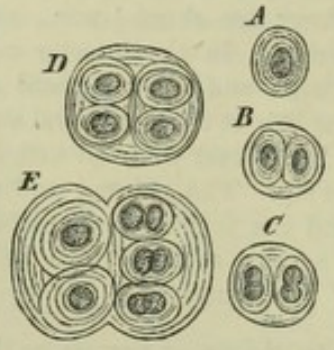

FIG. 154.—Mode of cell-division in Chroococcaceæ.

[1] Nägeli, Gattungen einzelliger Algen.—Braun, Verjüngung, p. 139.—Ray Soc. Bot. and Phys. Mem. 1853, p. 131.

[2] Cohn, Archiv für mikr. Anat. von Schultze, III, p. 12.—Askenasy, Bot. Zeitg. 1867, no. 29.

blue colouring-matter, are again extracted with strong alcohol, a green solution is obtained, which may be split up, as Millardet and Kraus have shown, into chlorophyll and phycoxanthine, if a large quantity of benzine is shaken up with it; this takes up the green chlorophyll and forms when again at rest an upper layer, while the lower alcoholic layer retains the yellow phycoxanthine[1].

The Hydrodictyeæ are a small group of Algæ to which belong without doubt the genera Hydrodictyon and Pediastrum, and, probably also according to Pringsheim some others whose cycle of development is not yet known. Their cells contain pure chlorophyll, and are distinguished by forming a large number of swarm-spores, which, when they come to rest, unite into a single family; this is tabular in Pediastrum; in Hydrodictyon it forms a wide-meshed sac-like net. They also produce in addition smaller swarm-spores which go through a long period of rest, and, in their further development, give rise to an alternation of generations. From the researches of A. Braun[2] and Pringsheim[3], the following process of development occurs in the case of *Hydrodictyon utriculatum*, which lives in stagnant or slowly flowing fresh water. In the mature state the thallome of this plant is a sac-like net several inches long; the individual cells, united only at their ends and forming four- or six-cornered meshes, are cylindrical and some lines long; all the cells of a net are sister-cells, formed simultaneously from one mother-cell. The mature cells have a firm compact wall, clothed with a thick layer of chlorophyll-green protoplasm, and enclosing cell-sap. In reproduction, the green protoplasmic sac in some cells of the net splits up into large naked daughter-cells, whose number reaches from 7000 to 20,000; but in other cells into smaller ones numbering from 30,000 to 100,000. Only the first or larger ones form new nets at once; they move first of all with a trembling motion within the mother-cell for about half an hour, and then form a daughter-net, which becomes free by absorption of the mother-cell-wall, and, under favourable conditions, attains its full size in three or four weeks, the separate cells elongating 400 or 500 fold. The smaller swarm-spores, on the contrary, leave the mother-cell and disperse, remaining in motion often for three hours. They are oval, and are furnished at the hyaline end with two long cilia; when finally at rest, they are spherical, and surround themselves with a firm cell-wall. In this state they may remain dried up for months, if protected from light. After remaining several months at rest, these spores begin slowly to grow, and a vacuole is formed in the green protoplasm. At first from $\frac{1}{120}$ to $\frac{1}{100}$ mm. in size, they attain a diameter of $\frac{1}{40}$ mm. Their contents split up by successive divisions into two or four portions, each of which forms a large swarm-spore. After a few minutes they come to rest, each large swarm-spore constituting a peculiar polyhedral cell, the angles of which grow out into long horn-like prolongations. These polyhedra make a considerable growth; their protoplasm becomes parietal and encloses a large sap-cavity; it finally splits up again into swarm-spores which move about with a creeping motion for 20 or 40 minutes within the inner layer of the wall of the polyhedron which protrudes from it as a hernioid sac; they then come to rest, and form a hollow net. These nets formed from the polyhedra consist of only from 200 to 300 cells, but otherwise behave in the manner described above. In some polyhedra smaller and more numerous swarm-spores are formed, but these also unite into a net.

The Volvocineæ[4] are, during the whole of their vegetative period, continually in

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[1] Millardet and Kraus, Comptes Rendus, LXVI, p. 505. [See also Sorby, Proc. Roy. Soc. XXI, p. 457.]

[2] A. Braun, Verjüngung, p. 146.—Ray Soc., Bot. and Phys. Mem. 1853, pp. 137, 190.

[3] Pringsheim, Mon. der königl. Akad. der Wiss. zu Berlin. Dec. 13, 1860. [Quart. Journ. Micr. Sc. 1862, pp. 54, 104.]

[4] Cohn, Ueber Bau und Fortpflanzung von *Volvox globator* in Berichte über die Verhand. der schlesischen Ges. für väterland. Cultur, 1856 (also in the Comptes Rendus, vol. XLIII, Dec. 1, 1856, and Ann. des Sci. Nat. 1857, p. 323).—Cohn, Ueber Chlamydococcus und Chlamydomonas (Protococcus),

motion, interrupted only by certain periods of repose; the motion, as is usually the case with swarm-spores, being caused by two cilia. They are, however, distinguished from swarm-spores by the cells—which either live isolated (Chlamydomonas, Chlamydococcus), or are united into angular and tabular (Gonium) or spherical families (Volvox, Stephanosphæra, Pandorina)—being surrounded, while in motion, by a membrane of cellulose, through which the cilia project free into the water, and produce by their vibrations the rotating and progressive movement of the single cells or of the whole family. This hyaline envelope of cellulose lies either in close contact with the green primordial cell (Chlamydomonas), or is separated from it by a colourless space (water?), from which fine threads of protoplasm run from one to the other, as in Stephanosphæra (Fig. 155, *VII*). As an example of the history of development, we may choose *Stephanosphæra pluvialis* (after Cohn and Wichura in Leopold. Akad. vol. XXVI, p. 1). This Alga occurs occasionally in rain-water in the hollows of large stones. When fully mature, Stephanosphæra (Fig. 155, *X*, *XI*) is a hyaline ball ('envelope-cell') in which,

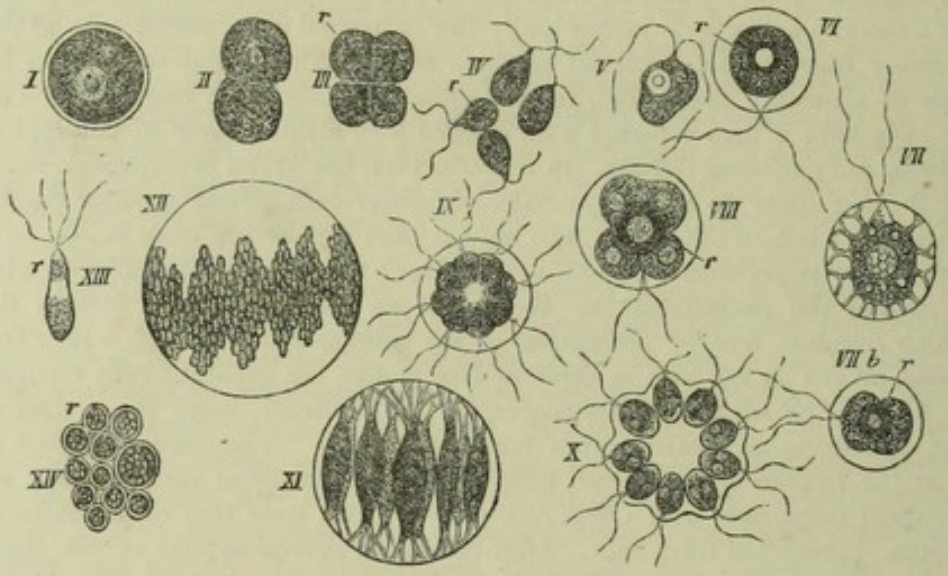

FIG. 155.—*Stephanosphæra pluvialis* (after Cohn and Wichura).

standing vertically to its horizontal diameter, lie eight (or more) chlorophyll-green primordial cells; these are fusiform (Fig. 155, *XI*), and attached to an equator of the envelope-cell at both their ends by branched threads of protoplasm. These primordial cells, derived from one mother-cell, form a family which rotates on the axis at right angles to the plane passing through them all. Out of each cell of a family of this kind is produced, so long as the conditions of vegetation (light, warmth, and water) are favourable, a new family which begins to be formed in the evening and is matured during the night. Each cell divides in succession into two, four, or eight cells, lying in the same plane and forming a disc divided into eight parts; they secrete a common envelope and develope their cilia. The cells separate from one another and their common envelope detaching itself become spherical; and thus eventually eight young families are found moving in circles within their mother-cell, until they are freed

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Berichte der schles. Ges. 1856.—Cohn und Wichura, Ueber *Stephanosphæra pluvialis:* Nova Acta Acad. nat. curios. vol. XXVI. p. 1. [Quart. Journ. Micr. Sc. 1858, p. 131.]—Pringsheim, Ueber Paarung der Schwärmsporen in Monatsber. der Berliner Akad. Oct. 1869.—De Bary, Bot. Zeitg. 1858, Supplement, p. 73. [See also on Volvox, Carter, Ann. Nat. Hist. 1839, vol. III. pp. 1–20.—Williamson in Phil. Soc. Manch. IX. p. 321; Trans. Micr. Soc. 1853, p. 45; Busk, Trans. Micr. Soc. 1853, p. 31. —On Stephanosphæra: Cohn, Ann. Nat. Hist. 2nd ser. X. pp. 321, 401; Archer, Quart. Journ. Micr. Sc. 1865, pp. 116, 185.—On Protococcus: Cohn, Ray Soc., Bot. and Phys. Mem. 1852.—On Pandorina, Henfrey, Trans. Micr. Soc. 1856, p. 49.]

by its rupture. Several generations of families endowed with motion are formed in this manner one after another. The succession of these generations is sometimes interrupted by the formation of Micro-gonidia; *i. e.* of small swarm-spores, which, resulting from repeated division of the primordial cells of a family, become completely isolated and dispersed. They are furnished with four vibratile cilia and each, secreting a cell-wall, finally passes into a roundish resting-cell, the fate of which is still unknown (Fig. 155, *XII*, *XIII*, *XIV*). The succession of generations of motile families is brought to an end by the formation of resting-cells. The separate primordial cells of the last motile family lose their cilia, and surround themselves with a firm closely-adherent cell-wall; they then resemble the cells of Protococcus, and are like the resting-cells which proceed from the small swarm-spores of Hydrodictyon. They accumulate at the bottom of the water, and there grow into larger green balls (Fig. 155, *I*), the colour of which passes over, when mature, into red. Only when these resting-cells have remained dry for a long time are they in a condition, when again moistened, to develope gradually generations endowed with motion; their contents divide into two, four, or sometimes eight parts, which, after absorption of the cell-wall, set up a motion as swarm-spores with two cilia (Fig. 155, *II*, *III*, *IV*). In the course of the day they surround themselves with a separable cell-wall, and in this condition the unicellular swarm-spores (Fig. 155, *V*, *VI*, *VII*) resemble those of the genus Chlamydococcus. After some hours each of these swarm-spores divides into two, four, or eight daughter-cells, which, lying in one plane, secrete a common cell-wall, and each developes two cilia; they then separate from one another, but remain enclosed in the common spherical cell-wall which has now separated itself from them[1]. After absorption of the mother-cell-wall the new family endowed with motion thus becomes free (Fig. 155, *VII b*, *VIII*, *IX*, *X*), grows in the course of the day, and forms in the night eight new similar families.

After Cohn and Carter had already detected phenomena in certain Volvocineæ (Volvox and Eudorina), which pointed to sexual union, Pringsheim has recently proved this to be the case with certainty in *Pandorina morum*, one of the commonest species. The sixteen cells of a family of Pandorina are closely crowded together, and surrounded by a thin gelatinous envelope out of which the long cilia project. The asexual multiplication results from the formation of a new sixteen-celled family in each cell of the mother-family; and the sixteen daughter-families become free by the absorption of the gelatinous envelope of the mother-family. The sexual reproduction is brought about in the same kind of way though with some points of difference; the gelatinous envelopes of the young families become softened, and the separate cells are thus freed and move each with its two cilia; these free swarm-spores are of very variable size, rounded and green at the posterior end, pointed hyaline and furnished with a red corpuscle in front, where they bear the two cilia. Among the crowd of these swarm-spores may be seen some which approach in pairs as if they were seeking one another. When they meet, their points come in contact, and they coalesce into a body at first biscuit-shaped, but gradually contracting into a ball; in this ball the two corpuscles are still to be seen, the hyaline part is relatively large, and both pairs of cilia are still present; but these all soon disappear. These processes last for some minutes. The green ball which results from the conjugation is an Oospore, and germinates only after a long period of rest. If the oospores, when dried up and of a red colour, are placed in water, the development begins after twenty-four hours; the exospore breaks up, as in Hydrodictyon; an inner membrane swells up like a bag, and allows the protoplasmic contents to escape in the form of a swarm-spore (more rarely after division into two or three). These swarm-spores which proceed from the oospore surround themselves with a gelatinous envelope, split up by successive divisions into sixteen primordial cells, and thus form new Pandorina-families.

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[1] [Archer has described, *l. c.*, pp. 7, 8, a remarkable amœboid phase which the primordial cells of Stephanosphæra undergo.—Ed.]

The CONJUGATÆ[1], a family of Algæ rich in genera and species, are distinguished by the occurrence of reproduction by *Zygospores*, in addition to the simple multiplication of cells by division; swarm-spores are not formed. In one section, comprising the Mesocarpeæ and the Zygnemeæ, the cells remain united, and form long unbranched threads, the cells of which are cylindrical, and only occasionally, where they are in contact with a firm surface, produce lateral root-like ramifications, as organs of attachment. In the Desmidieæ the mature cells consist usually of two symmetrical halves often separated by a constriction; the division takes place in this constriction or, at all events, symmetrically, each half becoming completely developed into a perfect cell. The external contour of these cells is very various; and since their divisions always take place parallel and in the same plane, as in the previous group, they form, when the cells are attached to one another, filiform rows; but very commonly they split up and live singly. A comparison of the unicellular Desmidieæ with those which possess a filiform arrangement and with the Zygnemeæ, shows clearly that it is a matter of subordinate importance whether cells live singly or united, *so long as they are similar to one another*. Each single cell of Spirogyra, like an isolated cell of Closterium, &c., constitutes an individual.

The cells of the Conjugatæ are distinguished by the most various configuration and the most beautiful arrangement of their masses of chlorophyll; it occurs in parietal spiral bands (Spirogyra), axile plates (Mesocarpus), a pair of radiate bodies (Zygnema), or plates arranged into stars (Closterium), &c. The zygospores are always resting-cells, germinating only after a long period of rest, even not till the next year. The formation of the zygospores results, in the Zygnemeæ, from a strong contraction of the protoplasmic substance in the manner shown in Fig. 6 (p. 10), although with some modifications in the different genera. In the Mesocarpeæ the conjugating protuberances unite in a similar manner, but the zygospore is formed by the accumulated contents of the canal becoming separated on both sides from the mother-cells by division-walls; and the central piece of the conjugating apparatus thus individualised is the zygospore[2]. In the Desmidieæ the zygospore is produced in the same manner as in the Zygnemeæ; it developes either one, two, or four new cells, each of which splits up into two equal daughter-cells capable of division.

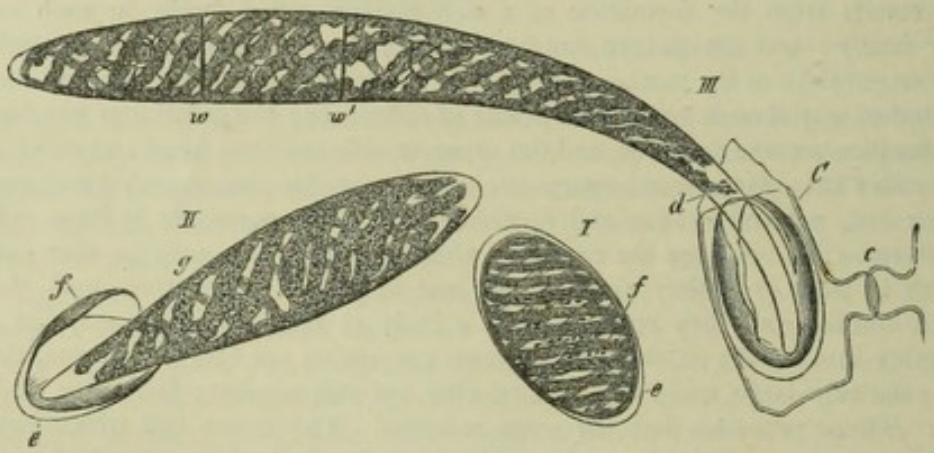

FIG. 156.—Germination of *Spirogyra jugalis* (after Pringsheim, Flora, 1852, no. 30); *I* a resting zygospore; *II* commencement of its germination; *III* the young plant further developed from a zygospore, which had been enclosed in the cell *C*, the conjugating apparatus being still visible; *e* outer cell-wall of the spore; *f* yellowish brown layer of the cell-wall; *g* the third and innermost layer of the cell-wall of the spore, which forms the germinating filament; *w w'* the first septa of the germinating filament, the posterior end *d* growing into a narrow appendage.

The genus Spirogyra (as an example of the *Zygnemeæ*) has already been described and figured several times in sect. 3 of Book I; the additional Fig. 156 will suffice,

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[1] A. de Bary, Untersuchungen über die Familie der Conjugaten. Leipzig 1858.

[2] [Two kinds of conjugation are distinguished; transverse, in which the cells belong to different filaments; longitudinal, in which they are parts of the same filament. See also Hassall, *l. c.*; Wittrock on Mesocarpeæ; Quart. Journ. Micr. Sc. 1873, p. 123.—ED.]

together with Figs. 5, 6, and 15 (pp. 10 and 17), to give an idea of the process of development of these plants.

Among the **Desmidieæ**[1] we may choose as an example for closer observation *Cosmarium Botrytis* (after De Bary, *l. c.*). The cells live isolated, and are symmetrically bisected by a deep constriction (Fig. 157, *X*), and are also compressed at right angles to the plane of constriction (*I*, *a*); in each half-cell are two grains of starch and eight discs of chlorophyll, which curve and converge in pairs running from two centres to the wall. The multiplication of the cells by division is brought about by the narrowest part of the constriction elongating a little, when the thicker outer layer of the cell-wall opens by a circular fissure; the two halves of the cell hence appear separated from one another and united by a short canal, the wall of which is a continuation of the inner layer of the walls of the half-cells. A septum soon appears in the piece which unites them, by which the cell is divided into two daughter-cells, each

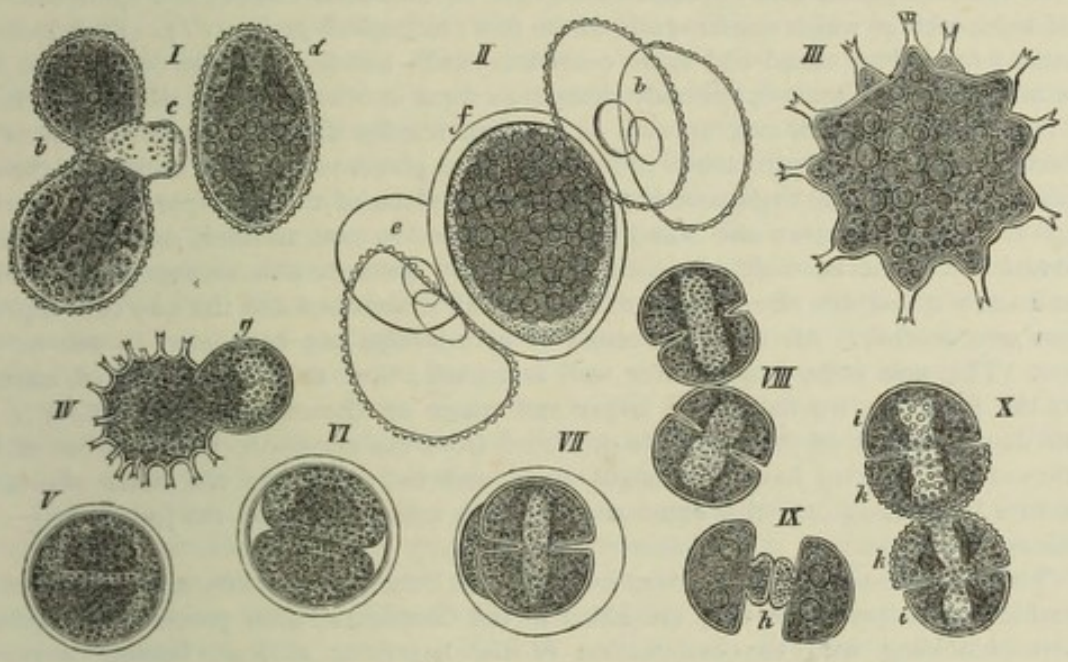

FIG. 157.—*Cosmarium Botrytis* (after De Bary, *l. c.*). (*I-III* ×390, *IV-X* ×190).

of which is a half of the mother-cell. The septum, at first simple, splits into two lamellæ, which immediately become convex towards one another (*IX*, *b*); each daughter-cell now possesses a small rounded outgrowth which grows gradually and assumes the form of a half-cell, so that each daughter-cell now again consists of two symmetrical pieces (*X*). While the wall is undergoing this growth, the discs of chlorophyll of the old halves grow into the newly-formed halves of the cell. The two grains of starch of the old half-cells elongate, become constricted, and each divides into two grains; of these four grains two pass over into the new half-cell, and all four again arrange themselves in the original symmetrical manner. *Conjugation* takes place between cells lying in pairs in a crossed position enclosed in thin jelly (Fig. 157, *I*). Each of the two cells emits from its centre a conjugating protuberance (*I*, *c*) which meets the other; these protuberances are formed by a delicate membrane which is a continuation of the inner layer of the cell, the firm outer layer of which is split (*I*, *c*). Both protuberances swell up into a hemispherical bladder while in contact with one another until the separating wall disappears, and the contents unite in the broad canal thus formed; the protoplasm becomes everywhere loosened from the cell-wall, and contracts into a spherical form. The united protoplasm appears as if

[1] [See also Ralfs, British Desmidieæ, 1848.—Archer in Pritchard's Infusoria.]

surrounded by a delicate gelatinous wall (*II, f*) by the side of which lie the empty cell-walls (*II, e, b*). The zygospore now becomes rounded into a ball; its wall forms, as it matures, three layers, an outer and an inner colourless layer of cellulose, and a middle firmer brown layer. This stratified cell-wall grows out at several points into spiny protuberances which are at first hollow and afterwards solid, each of them producing at the end a few small teeth (*III*). The starch-grains of the conjugating cells become transformed into fat in the zygospores. Germination commences by the protrusion of the colourless inner layer through a wide split in the outer layer (*IV*); the thin-walled sphere thus set free considerably exceeds the zygospore itself in size. In the contents of this sphere (*V*) may be recognised two masses of chlorophyll surrounded by fatty protoplasm which might have been distinguished even before their escape from the external layer of the zygospore. The contents now contract and become surrounded by a new wall (*V*) from which the older wall detaches itself as a thin vesicle. After some time the protoplasm becomes constricted by a circular furrow, and splits into two half-balls, each of which contains one of the two chlorophyll-grains (*VI*). Each half-ball remains for a time naked and again constricts itself; but this time the constriction does not advance to the centre; the body changes its form in other respects also, and each half of the germinating cell now appears as a symmetrically divided Cosmarium-cell (*VII*), which surrounds itself with a wall of its own. The planes of the constrictions of the two cells derived from the zygospore cut the dividing plane of the zygospore itself at right angles; they themselves also stand at right angles to one another, and therefore lie crossed in the mother-cell. In each of these the contents now arrange themselves in the manner above described; the mother-cell-wall is absorbed and the new cells separate from one another. All these processes of germination are completed in one or two days. The new cells, whose outer wall is smooth, now divide in the usual manner, but the newly grown halves are larger and rough on the outside (*VIII, IX, X*); the four daughter-cells of the two cells produced from the zygospore are therefore of two different forms; two have the halves equal and two unequal; the latter constantly produce by division one with equal and one with unequal halves; the former only cells with equal halves.

The **Diatomaceæ**[1] (Bacillarieæ) extremely rich in species follow naturally after the Desmidieæ; in particular they are allied to the Conjugatæ, their processes of development coinciding with the conjugation of the latter, or at least bearing a certain resemblance to it[2]. They also resemble the Desmidieæ in the configuration of their cells, in the manner of division, and in the mode of completion of the daughter-cells. Like the Desmidieæ, the similar cells of the Diatoms may be united into threads, or may live entirely isolated. The tendency of the Diatoms to secrete a thin jelly in which they live socially is found also in the Desmidieæ, although less strongly displayed. In the same manner the movements of Diatoms are not altogether dissimilar to those of the Desmidieæ, and even the silicification of the cell-wall, which is very strong in the former, is found, though to a smaller extent, in Closterium and other Desmidieæ; and the fine sculpturing of the silicious shell also finds an analogue, although in a coarser form, in the cell-wall of some Desmidieæ. The Diatoms are the only Algæ, except the Conjugatæ, in which the chlorophyll occurs in the form of discs and bands, but in some forms it is also found in grains, and the green colouring matter is concealed, like the chlorophyll-grains in Fucaceæ, by a buff-

[1] Lüders, Ueber Organisation, Theilung und Copulation der Diatomeen, Bot. Zeitg. 1862, no. 7 et seq.—Millardet and Kraus discuss their colouring-matter in Compt. Rend. vol. LXVI. p. 505; and Askenasy in Bot. Zeitg. 1869, p. 799.—Pfitzer in Heft II, of the Botanische Abhandlungen edited by Hanstein. Bonn 1871. [Quart. Journ. Micr. Sc., 1872, 1873.]

[2] [Thwaites first discovered the conjugation of the Diatomaceæ, Ann. Nat. Hist. 1847, vol. XX; see also Carter: Ann. and Mag. Nat. Hist. 1856. — Schmitz, Quart. Journ. Micr. Sc., 1873, p. 145.—Smith, Synopsis of British Diatomaceæ.—Ed.]

coloured substance, Diatomine or Phycoxanthine. One of the most prominent peculiarities of the Diatoms consists in their silicified cell-wall being composed of two separated halves or valves of unequal age, of which the older one is pushed on to the younger like the lid of a box. When the cell begins to divide, the valves separate from one another, and after the division of the contents into two daughter-cells, each of them forms a new layer on their plane of division which is adjusted by its turned-in margin (the girdle) to the girdle of the old valve of the mother-cell; this latter extends, like the lid of a box, over the newly formed valve; and the two valves of the two daughter-cells lie next one another. Since, according to Pfitzer, the silicious valves, which also contain some organic matter, do not grow, it is clear that the new cells must always become smaller from generation to generation. When they have thus attained a certain minimum size, large cells, the *Auxospores*, are suddenly formed; the contents of the small cells, leaving the silicious valves which fall away from one another, increase either simply by growth or by both conjugation and growth. After this the auxospores surround themselves with new valves. Since the large auxospores are of somewhat different shape to their smaller mother-cells and primary mother-cells, the first result of their division must necessarily be cells of a different form and with unequal halves, as in the Desmidieæ (Fig. 157). The origin of the auxospores has been more exactly followed out only in a few cases. It would appear that they are formed in very different ways, from two or from one mother-cell, simply or in pairs, with or without conjugation; they are alike only in so far that their size greatly exceeds that of the mother-cell. Diatoms are found in enormous numbers at the bottom both of the sea and of fresh water, and attached to the submerged parts of other plants. Besides the ordinary rotation of protoplasm in their interior, they also exhibit a creeping motion by means of which they crawl over hard bodies or push small granules along their surface. This occurs only in a line drawn along the length of the cell-wall, in which Schultze[1] supposes crevices or holes through which the protoplasm protrudes; and this, although not yet actually seen, probably occasions the creeping motion.

The genus Vaucheria[2] must be considered somewhat more in detail, as the best-known representative of a larger group, the **Siphoneæ**, which, in the mode of growth of their thallus, are nearly related to the Conjugatæ, but whose mode of reproduction is not yet sufficiently known. The thallus of Vaucheria consists of a single sac-like cell, variously branched, often several inches or a foot long, containing no nucleus, and developing on damp shady earth or in water. The fixed end is hyaline and branched in a wavy manner; the free part contains within the thin cell-wall a layer of protoplasm rich in chlorophyll-grains and drops of oil, and enclosing the large sap-cavity. This part of the thallus forms one or more main branches or stems which again branch beneath their growing point (*s*); only in *V. tuberosa* the branching is also dichotomous; though commencing monopodially the lateral branches often develope sympodially. Besides the occasional multiplication by the separation of branches or the regeneration of separated pieces of the thallus, reproduction is also brought about by asexual spores and by sexually produced oospores, and in such a manner that a long series of asexual generation usually proceeds from the latter, until at last sexual plants arise from asexual spores; but the sexual generation can also produce spores as well as oospores. The spores may be produced in very different ways, from the simple detaching of the end of a branch to the formation of zoospores. In *V. tuberosa* lateral branches (sometimes also forked branches) swell up to a considerable size through becoming filled with cell-contents, separate at the base, and put out one or more germinating tubes. In *V. geminata* the end of a branch swells up to an oval shape; its accumulated contents become separated by a septum; it contracts, and

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[1] [See Pop. Sci. Rev. 1866, p. 395.]

[2] Pringsheim, Ueber Befruchtung und Keimung der Algen. Berlin 1855, and Jahrbuch für wissen. Bot. II. p. 470.—Schenk, Würzburger Verhandl. vol. VIII. p. 235.—Walz, Jahrbuch für wissen. Bot. V. p. 127.—Woronin, Bot. Zeitg. 1869, nos. 9, 10.

forms a cell-wall of its own. These spores do not fall out; they either become freed by the decomposition of the sporangium-wall, or they fall off together with the sporangium; some days after their formation they put out one or two germinating-tubes. The spores of *V. hamata* are formed in the same manner, but after their formation the sporangium splits at its apex, the spore slips out with a jerk and remains at rest, to germinate the next night. In several other species (as *V. sessilis*, *sericea*, and *piloboloides*) true zoospores are formed. The preparations for them are similar to those in the last case; but the contents of the branch which has swollen into a zoosporangium do not become surrounded by a cell-wall, but contract, showing in the interior one or more vacuoli, and then escape as a naked cell from a fissure at the apex of the branch (Fig. 158, *A*, *sp*). The escaped primordial cell contains numerous grains of chlorophyll surrounded by a layer of colourless protoplasm, and is everywhere covered by delicate densely crowded short cilia. Their vibratile motion causes a movement of the large ellipsoidal zoospore (as much as $\frac{1}{2}$mm. long) about its longer axis, which sometimes, however, (as in *V. sericea*,) lasts only for $\frac{1}{2}$ to $1\frac{1}{2}$ minute. In *V. sessilis* the rotation begins, as I have

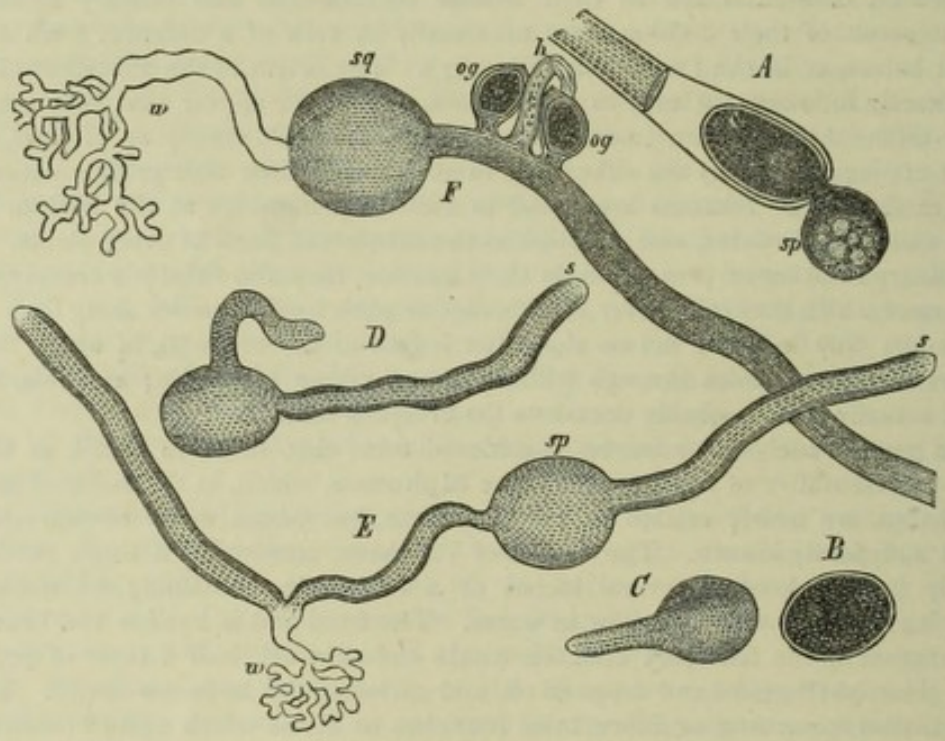

FIG. 158.—*Vaucheria sessilis* (× about 30).

distinctly seen, during the escape from the sporangium; and if the opening is too small, the zoospore splits into two pieces; both become rounded off; the outer piece rotates and swims out, while the inner piece rotates within the sporangium. As soon as the zoospores come to rest, the cilia disappear, and a cellulose-wall is produced (Fig. 158, *B*). The formation of the zoosporangia generally begins in the night; the spores escape in the morning, and their germination commences the next night. The spore puts out either only one or two tubes (*C*, *D*), or it forms on the other side at the same time a root-like organ of attachment (*E*, *F*, *w*). The *Sexual Reproduction* is brought about by oogonia (female cells) and antheridia (male cells). Both originate as twig-like protuberances from a branch or stem (Fig. 159, *A*, *B*), sometimes even on the germinating tube of the zoospore (Fig. 158, *F*, *og*, *h*). All the species of Vaucheria are monœcious, and the two kinds of sexual organs are mostly found very near together. The *Antheridia* usually arise[1] as the terminal cell of a branch by its transverse division, and contain very little

[1] In the *Vaucheria synandra* discovered by Woronin living in brackish water 2–7 small horns (antheridia) arise on the large ovoid terminal cell of a two-celled branch (Bot. Zeitg. 1869, nos. 9, 10).

or no chlorophyll (Fig. 159, *B*, *a*). From one part of the protoplasm of this antheridium-cell are formed the numerous spermatozoids, very small long bodies with two cilia (*D*). In several species the antheridia are curved like horns (*V. sessilis*, *geminata*, and *terrestris*); in others they are straight (*V. sericea*) or curved sacs (*V. pachyderma*). The *Oogonia* arise near the antheridia as thick protuberances (Fig. 159, *A*, *B*, *og*) filled with oil and chlorophyll. They swell up into an ovoid form (usually oblique), and finally the dense contents are separated by a septum from the base of the branch (*F*, *osp*). The green and granular mass collects in the centre of the oogonium; colourless protoplasm accumulates at its mouth, and withdraws from the cell-wall; the cell-wall

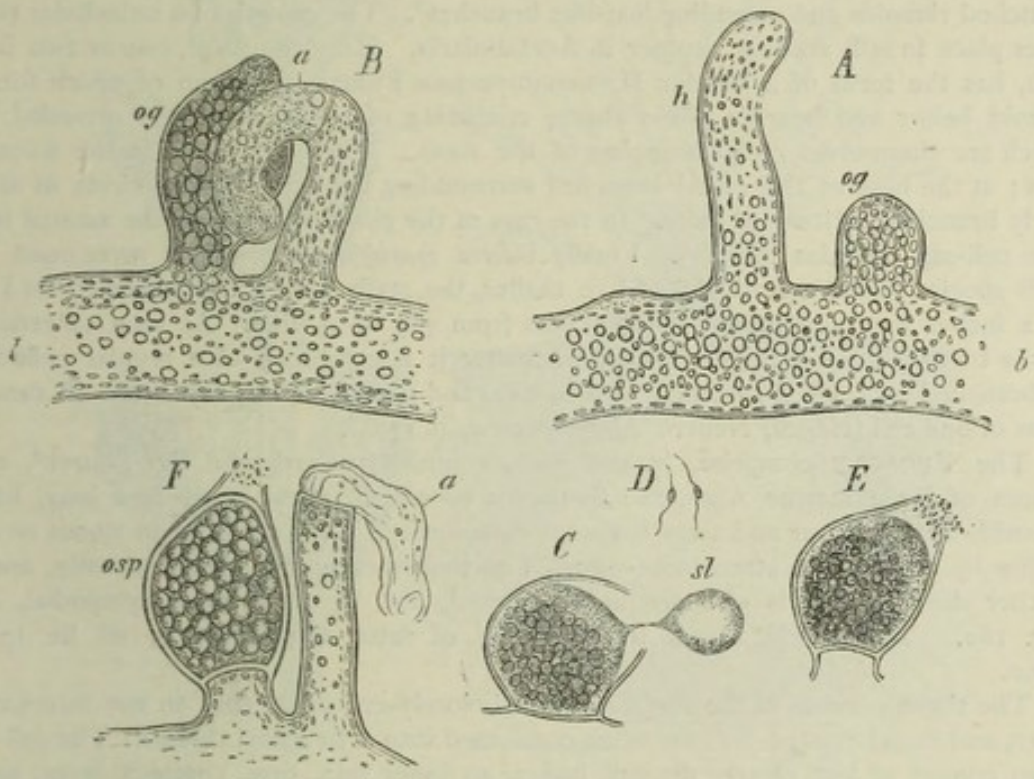

FIG. 159.—*Vaucheria sessilis*: *A*, *B* origin of the antheridium *a* on the branch *b*, and of the oogonium *og*; *C* an open oogonium expelling a drop of mucilage *sl*; *D* spermatozoids; *E* the spermatozoids collected at the mouth of the oogonium; *F*, *a* an empty antheridium; *osp* the oospores in the oogonium (*A*, *B*, *E*, *F* from nature, *C*, *D* after Pringsheim).

suddenly opens and swells up into a jelly, and at this moment the contents are transformed into an oosphere, contracting at the same time. In some species (as *V. sessilis*) a colourless drop of mucilage is expelled from the mouth (*C*, *sl*). At the same time that the oogonium opens, the antheridium also bursts and allows the spermatozoids to escape; these press through the thin mucilage, on which they collect (*E*), reach the oosphere, mingle with it, and disappear. The oosphere appears then to assume at once a sharp outline, and a double cell-wall may soon also be detected. The oosphere has transformed itself into an oospore; its chlorophyll assumes a red or brown-red colour, and the cell-wall thickens, so that three layers may generally be distinguished in it (Fig. 159, *F*, *osp*, the oospore in the oogonium). The formation of the oogonia and antheridia begins in the evening, and is completed the next morning; fertilisation is accomplished between 10 and 4 in the day.

In their processes of vegetation several other genera approach very near to Vaucheria, especially Botrydium. The young plant is (according to A. Braun: Rejuvenescence, p. 128) a spherical Protococcus-like cell; subsequently a hyaline prolongation is formed below which branches like a root and penetrates the earth, while the upper part swells up into an ovoid vesicle, in which the protoplasm forms, with the chlorophyll-grains, a parietal layer. From this arise, after the growth is matured, a number of zoospores

which are set free by the wall of the mother-cell becoming gelatinous and finally deliquescing. This is evidently a more simple mode of growth than that of Vaucheria. A higher degree of branching than in this latter is found in Bryopsis, which is also unicellular. This genus also forms on one side root-like organs of attachment, on the other upright much-branched stems (several inches in height) with unlimited apical growth; small branches with limited apical growth are formed on them in two rows or spirally, which clothe the stem like leaves, and after they have detached themselves from it, fall off; while in them are formed the numerous motile zoospores[1]. (A. Braun, *l. c.*) The branching of a single large cell is carried still further in the genus Caulerpa, which forms creeping stems growing at the apex with descending branched rhizoids and ascending leaf-like branches[2]. The growth of a unicellular thallus takes place in still another manner in Acetabularia. Here the plant, one or two inches high, has the form of a slender Hymenomycetous Fungus, the stem of which forms a rhizoid below and bears a pileus above, consisting of a disc of closely crowded rays, which are themselves radial branches of the stem. This ends above in the form of a boss; at the base of the radial branches surrounding the boss stands a circle of umbellately branched articulated hairs. In the rays of the pileus are formed the asexual spores (the cell-sap contains inuline). Finally *Udotea cyathiformis* must be mentioned here. This species forms a stalked leaf-like thallus, the stalk $\frac{1}{2}$ inch, the thallus from $\frac{1}{2}$ inch to 2 inches long and broad, its thickness from $\frac{1}{100}$ to $\frac{1}{20}$ line. As seen externally it seems to consist of a cellular tissue, in reality it is composed of a regular collocation of branched sacs, which, forming two cortical and one medullary layer, are all ramifications of one cell (Nägeli, Neuere Algensysteme, p. 177)[3].

The FUCACEÆ comprise, in the narrow limitation proposed by Thuret[4], a few genera of large marine Algæ, the thallomes of which, often many feet long, have a greenish-brown colour and a cartilaginous consistency. They are fixed to stones or other bodies by a branched attachment-disc. The thallomes branch dichotomously, and the further development is also frequently forked, but in other cases sympodial, as in Fig. 160. The ramifications, irrespectively of later displacements, all lie in one plane.

The tissue consists at the surface of small closely-crowded cells; in the interior it is laxer, and the elongated cells are often connected into articulated threads. The cell-walls often consist of two clearly distinct layers, an inner thin, firm, compact layer, and an outer gelatinous one, capable of swelling greatly in water, which fills up the interstices of the cells, and has the appearance of a more or less structureless 'intercellular substance'; it is clearly the cause of the slimy character which the Fucaceæ assume after lying for some time in fresh water. The granular cell-contents have been but little investigated; they appear to be mostly brown, but contain chlorophyll which is concealed by other colouring materials; from dead plants cold fresh water extracts a buff-coloured substance[5]. The tissue often becomes hollowed out internally into large cavities containing

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[1] Nägeli, Neuere Algensysteme. Neuenburg, 1867.

[2] Zeitschrift für wissensch. Bot. von Nägeli u. Schleiden, 1844, I. p. 134 et seq.

[3] [The remarkable fossil plant from Canada of Devonian age, *Prototaxites Logani*, was probably an enormous Siphonaceous Alga; see W. T. Thiselton-Dyer, Journ. of Bot. 1871, p. 252, and Carruthers, Monthly Micros. Journ. 1872, p. 160.—ED.]

[4] G. Thuret, Ann. des Sci. Nat. II. 1854, p. 197.

[5] In a recent paper (Comptes Rendus de l'Acad. des Sci. Feb. 22, 1869) Millardet showed that from quickly-dried and pulverized Fucaceæ an olive-green extract is obtained by alcohol, which, shaken up with double its volume of benzine and then allowed to settle, produces an upper green layer of benzine containing the chlorophyll, while the lower alcoholic layer is yellow and contains phycoxanthine. Thin sections of the thallus, completely extracted with alcohol, contain also a reddish-brown substance which in fresh cells adheres to the chlorophyll-grains, and can be extracted by cold water, more easily when the dried Fucus has been previously pulverized. Millardet calls

air which are forced outwards and serve as swimming bladders. The thallus has not, as far as I know, been further minutely examined; the outer conformation especially has been but little investigated from a morphological point of view. (Cf. Nägeli, Neuere Algensysteme.)

The mode of sexual reproduction is far better known through the labours of Thuret and Pringsheim. The antheridia and oogonia are formed in spherical hollows (Con-

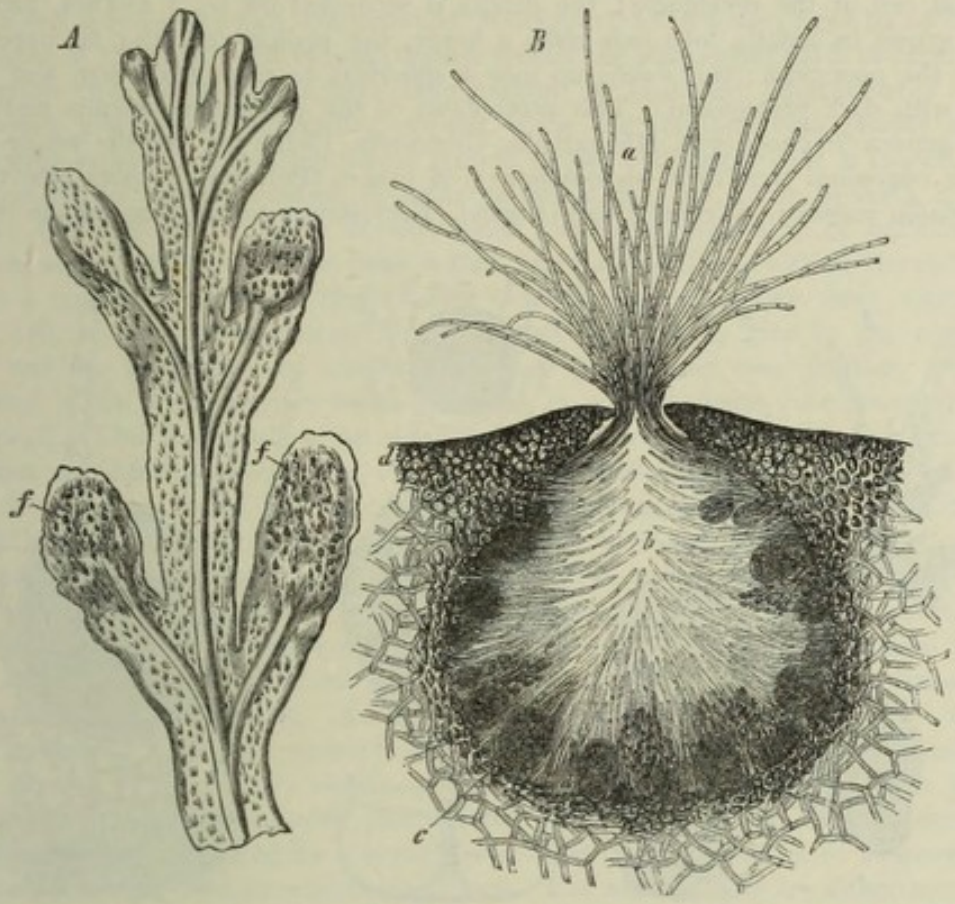

FIG. 160.—*Fucus platycarpus* (after Thuret); *A* end of one of the larger branches (natural size); *ff* fertile branchlets; *B* transverse section of a receptacle; *d* the surrounding epidermal tissue; *a* the hairs projecting from the mouth; *b* hairs in the interior; *c* oogonia, *e* antheridia (cf. Fig. 2, p. 3).

ceptacles) which make their appearance in large numbers and densely crowded at the ends of the longer forked branches or of lateral shoots of peculiar form. These receptacles are not formed in the interior of the tissue, but as depressions of the surface which become walled in by the surrounding tissue, and so overgrown that at length only a narrow channel remains, opening outwards. The layer of cells which clothes the hollow is thus a continuation of the external epidermal layer of the thallus; and since the filaments which produce the antheridia and oogonia sprout from it, these latter are, morphologically, trichomes. Some species are monœcious, *i. e.* both kinds of sexual organs are developed in the same receptacle, as in *Fucus platycarpus* (Fig. 160); others are diœcious, the receptacles of one plant containing only oogonia, those of another plant only antheridia (*e. g. Fucus vesiculosus*, *serratus*, and *nodosus*, *Himanthalia*

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this reddish-brown substance phycophæine. (Compare further the interesting treatise of Rosanoff, Observations sur les fonctions et les propriétés des pigments de diverses Algues, in Mémoires de la Société des Sci. Nat. de Cherbourg, vol. XIII. 1867; and Askenasy, Bot. Zeitg. no. 47, 1869.) [See also Sorby, Proc. Roy. Soc. 1873, vol. XXI. pp. 445, 454, 461.]

lorea). A number of hairs which grow in the receptacles among the sexual organs are long, slender, articulated, but unbranched, and project in *F. platycarpus* out of the mouth of the receptacle in the form of tufts (Fig. 160, *B*). The *Antheridia* are produced as lateral ramifications of branched hairs. Each antheridium consists of a thin-walled oval cell, the protoplasm of which splits up into numerous small spermatozoids; these are pointed at one end, each furnished with two motile cilia; in the interior they contain a red point. The formation of the *Oogonium* begins with the papillose swelling of a parietal cell of the receptacle; the papilla is separated off by a septum, and divides, as it grows in length, into two cells, a lower, the pedicel-cell, and an upper, which forms the oogonium; this swells up into a spherical or ellipsoidal form and becomes filled with dark protoplasm. This protoplasm of the oogonium remains undivided in some genera (Pycnophycus, Himanthalia, Cystoseira, Halidrys), and the whole contents of the oogonium thus form an oosphere; in others (Pelvetia) it splits into two, four (*Ozothallia vulgaris*), or eight pieces (Fucus). Fertilisation takes place outside the recep-

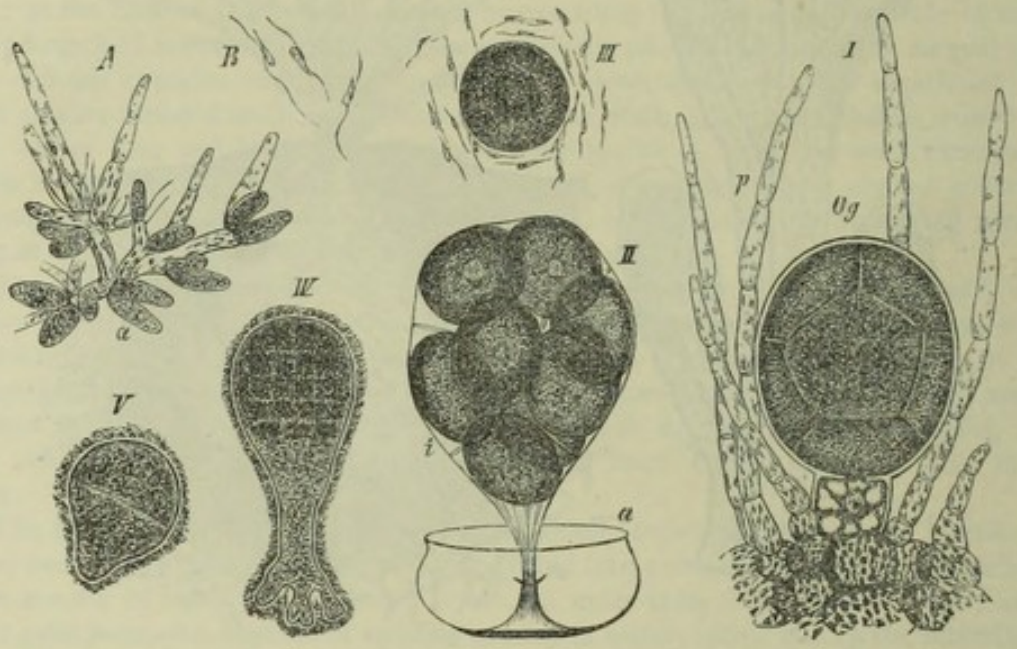

FIG. 161.—*Fucus vesiculosus* (after Thuret); *A* a branched hair bearing antheridia; *B* spermatozoids; *I* an oogonium, *Og* after the contents have divided into eight portions (oospheres), surrounded by simple hairs (*p*); *II* commencement of the escape of the oosphere; the membrane (*a*) has burst; the inner membrane *i* is ready to open (the two together constitute an inner layer of the cell-wall of the oogonium; *III* oosphere surrounded by spermatozoids; *IV*, *V*, germination of the oospore (*B* × 330, all the rest × 160).

tacles. The oospheres are expelled, surrounded by an inner membrane of the oogonium, and escape through the opening of the receptacle; the antheridia at the same time become detached, and collect in numbers before the mouth of the receptacle when the fertile branches are lying outside the water in moist air. When they again come into contact with the sea-water, the antheridia open and allow the spermatozoids to escape, the oospheres at the same time escaping from the envelope which still surrounds them, and which is then seen to consist of two separated layers (Fig. 161, *II*). The spermatozoids collect in numbers around the oospheres, become firmly attached to them, and when their number is sufficiently great, their movement becomes so energetic that they impart to the very large oosphere to which they are attached a rotatory motion which lasts for about half an hour. Whether the spermatozoids force themselves into the oosphere Thuret leaves undecided; but analogy with the processes observed by Pringsheim in Vaucheria and Œdogonium scarcely admits of a doubt that one or several of them mingle their substance with that of the naked ball of protoplasm. A short time after these processes are completed, the fertilised oosphere or oospore surrounds itself with a cell-wall, fixes itself to some body or other, and begins, without any period of rest, to germinate, and,

lengthening at the same time, undergoes first of all a transverse division followed by numerous other divisions. The mass of tissue thus formed puts out from the part on which it rests a root-like hyaline organ of attachment, while the thick free end forms the growing apex (Fig. 161, *IV*). The development of a fertile thallus from the oospore has not yet been observed; and the whole cycle of forms of the Fucaceæ has therefore not yet been certainly determined[1].

The Œdogonieæ[2] include at present only the two genera Œdogonium and Bulbochæte, a few species of which are common in stagnant fresh water, fixed by an organ of attachment at the lower end to solid bodies, mostly the submerged parts of other plants. The thallus consists of unbranched (Œdogonium) or branched (Bulbochæte) rows of cells, which multiply by intercalary growth, while the terminal cells readily elongate into hyaline bristles. The longitudinal growth of the cylindrical cells is caused by the formation of an annular cushion of cellulose inside the cell, close beneath its upper septum; the cell-wall ruptures at this place circularly; the ring of cellulose then stretches, and a broad transverse zone is thus intercalated in the wall of the cell. The process is constantly repeated immediately beneath the older very short upper piece of the cell, so that these pieces, forming small projections, give to the upper end of the cell the appearance of consisting of caps placed one over another, while the lower end of the cells appears to be enclosed in a long sheath (the lower old piece of cell-wall). This lower part of an elongated cell is always separated by a septum from the upper cap-bearing piece (Fig. 17, p. 22). In Bulbochæte the growth of all the shoots, even of the first which proceed from the spores, as far as it is connected with cell-multiplication, is limited to the division of their basal cell; so that the cells of each shoot must be considered at the same time as basal cells of the lateral shoot which stands upon them. The cells contain chlorophyll-grains and nuclei in a parietal layer of protoplasm. The *Reproduction* of the Œdogonieæ takes place by asexual swarm-spores and by oospores produced sexually. Both are formed, like the spermatozoids, in the cells of the filaments. An alternation of generations takes place in the following manner. From the oospores which have remained at rest for a considerable period several (usually four) swarm-spores are immediately formed, which produce asexual, *i. e.* swarm-spore-forming plants, from which again similar ones proceed, until the series of them is closed by a sexual generation (with formation of oospores); but the sexual plants produce swarm-spores as well. The sexual plants are either monœcious or diœcious; in many species the female plant produces peculiar swarm-spores (Androspores), out of which proceed very small male plants (dwarf males). Several generative cycles or only one may be completed in a vegetative period. The *Swarm-spore* is formed in an ordinary cell of the filament (sometimes even in the first cell, Fig. 162, *E*) by the contraction of its whole protoplasmic substance; it becomes free from the mother-cell, the cell-wall splitting by a transverse slit into two very unequal halves (as in the division of the cells) (Fig. 162, *A*, *B*, *E*). It is at first still surrounded by a hyaline membrane, which however it also breaks through. The swarm-spore is encircled at its hyaline end—the anterior end during the swarming—by a crest of numerous cilia. This end lies laterally in the mother-cell, and, after the movement ends, becomes the lower attached end which grows out into a rhizoid. The direction of growth of the new plant is thus at right angles to that of the mother-cell. The *Spermatozoids* are very similar in form to the swarm-spores, but much smaller (Fig. 163, *D*, z); their motion, due to a crest of cilia, is also similar. The mother-cells of the spermatozoids are cells of the filament, but shorter and not so rich in chlorophyll as the vegetative

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[1] [Thuret divided the olive-coloured sea-weeds (Melanosporeæ) into two groups, of which the Phæosporeæ (Laminaria, &c.) are distinguished by possessing zoospores, the Fucaceæ being destitute of them.—Ed.]

[2] Pringsheim, Morphologie der Œdogonieen in Jahrb. für wissen. Bot. vol. I. [Ann. des Sci. Nat. 1856, vol. V. p. 251.—Carter, Ann. and Mag. Nat. Hist. 1858, vol. I. pp. 29–39.]

cells; they lie either singly or in groups (sometimes as many as twelve) above one another in the filament. In most species each mother-cell of this description (antheridium-cell) divides into two equal special mother-cells, each of which produces a spermatozoid; they escape by the splitting of the mother-cell (as in the case of the zoospores) (Fig. 163, *D*). The androspores from which the dwarf male plants arise are produced from mother-cells similar to those which give birth to the spermatozoids (without formation of special mother-cells). After swarming they fix themselves to a definite part of the female plant, on or near the oogonium, and after germination produce at once the antheridium-cells, and in them the spermatozoids (Fig. 163, *A*, *B*, *m*, *m*). The

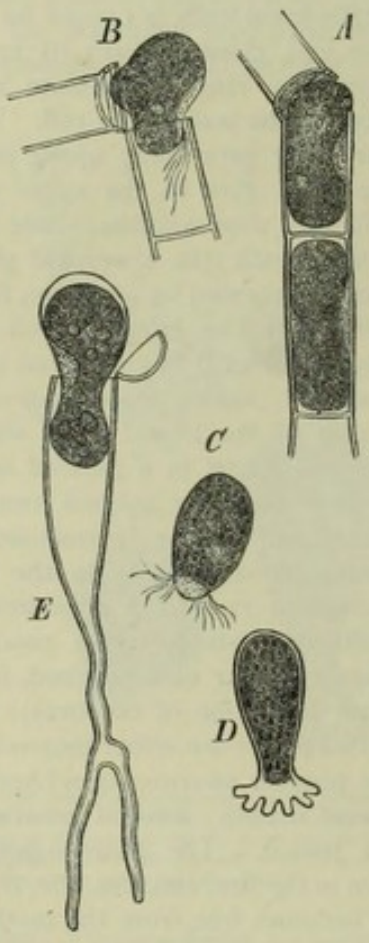

FIG. 162.—Development of the swarm-spores of Œdogonium (after Pringsheim). *A*, *B* their origin from an older filament; *C* free swarm-spore in motion; *D* commencement of its germination; *E* a swarm-spore formed out of the entire contents of a germinating plant (×350).

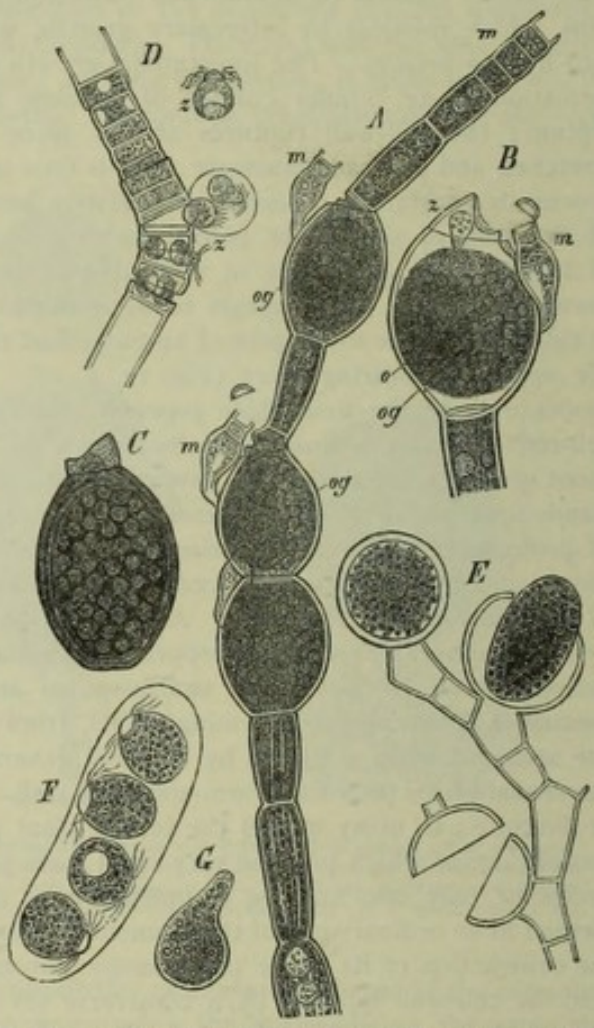

FIG. 163.—*A Œdogonium ciliatum* (×250) middle part of a sexual filament with an antheridium (*m*) at the upper end, and two fertilised oogonia (*og*) by the dwarf male plant *m*; *B* oogonium at the moment of fertilisation; *o* the oosphere, *z* the spermatozoid in the act of forcing its way in, *m* dwarf male plant; *C* ripe oospore; *D* piece of the male filament of *O. gemelliparum*, *z* spermatozoids. *E* branch of a hybernated plant of *Bulbochæte intermedia*, with one oogonium still containing a spore, another in the act of allowing it to escape; in the lower part an empty oogonium. *F* the four swarm-spores resulting from an oospore; *G* swarm-spores from an oospore come to rest (after Pringsheim).

Oogonium is always developed from the upper daughter-cell of a vegetative cell of the filament which has just divided, and immediately after the division swells up into a spherical or ovoid form. In Bulbochæte the oogonium is always the lowest cell of a fertile branch. This is not opposed to the law of growth above-mentioned, inasmuch as the mother-cell of a branch fulfils at the same time the function of its basal cell; the oogonium of Bulbochæte is never the first cell of a branch, since this is always developed as a bristle. The oogonium becomes at first more completely filled with contents than the remaining cells; immediately before fertilisation the protoplasm contracts and

forms, as in Vaucheria, the oosphere, in the interior of which the grains of chlorophyll are densely crowded. The part of the oosphere which faces the opening of the oogonium consists simply of hyaline protoplasm. The opening of the oogonium is produced in a variety of ways. In some species of Œdogonium and all of Bulbochæte its wall has an oval hole in its side, out of which the colourless part of the oosphere protrudes in the form of papillæ, and takes up the spermatozoids. In some species of Œdogonium (Fig. 163, *A*, *B*), on the other hand, the oogonium-cell splits, as when the swarm-spores are escaping; and the otherwise straight row of cells of the filament thus appears as if broken at this spot. In the lateral crevice appears some colourless mucilage, which the observer can actually see take the form of an open beak-like canal (Fig. 163, *B*, *z*), through which the spermatozoid enters. It mixes with the hyaline part of the protoplasm of the oosphere while it melts away. Immediately after fertilisation the oosphere surrounds itself with a membrane, which afterwards, like its contents, assumes a brown colour; but in Bulbochæte the contents of the oospore thus formed is of a beautiful red colour. The oospore remains enclosed in the membrane of the oogonium, which separates from the neighbouring cells of the filament and falls to the ground, where the oospore passes its period of rest. When it awakes to new activity, the oospore does not itself grow into a new plant; but in Bulbochæte, where this process has been observed, its contents divide into four swarm-spores, which escape together with the inner skin of the oospore, and after this latter is dissolved, swim about. After becoming stationary each grows into a new plant[1].

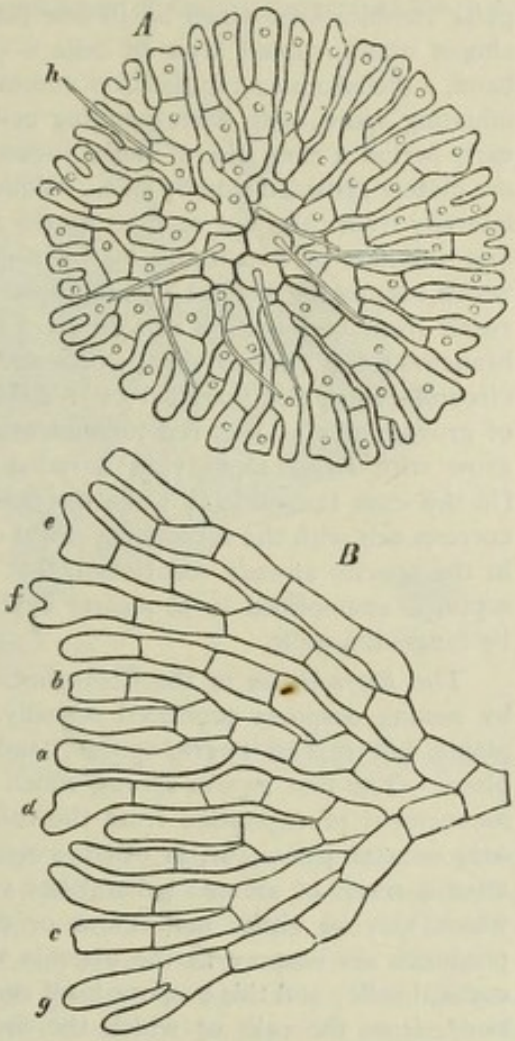

FIG. 164.—*A* an asexual plant of *Coleochæte soluta* (×250); *B* a piece of a similar disc; the letters *a-g* indicate the successive dichotomous branchings of the terminal cells (after Pringsheim).

The Coleochætæ[2] are small (about 1–2 mm.) fresh-water Algæ, chlorophyll-green and constructed of branched rows of cells, attached in standing or slowly running water to the submerged parts of other plants (*e.g.* Equisetum), and forming circular closely-attached or cushion-like discs Their chlorophyll assumes the form of parietal plates or of larger lumps; and the name of the genus Coleochæte (sheath-hair) is due to the circumstance that certain cells of the thallus form lateral colourless bristles fixed in narrow sheaths (Fig. 164, *A*, *h*). If the phenomena of growth of the different species are compared, two extreme cases are seen, united by

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[1] [**Confervaceæ** are a group of green filamentous Algæ. They are reproduced by zoospores (Cladophora, Chroolepus). Cohn has described the sexual reproduction of *Sphæroplea annulina* in Ann. des Sci. Nat. 4th ser. vol. V. 1856.—**Ulvaceæ** agree with Confervaceæ, but are expanded into a membrane (forming a tube in Enteromorpha) and are not filamentous. They are only known to be propagated by zoospores.—Ed.]

[2] Pringsheim in Jahrbuch für wissenschaftliche Botanik, vol. II. p. 1.

transitional forms. The one extreme is formed by *C. divergens*, which, as it developes from the spore, produces first of all creeping irregularly branched articulated threads, from which spring ascending articulated branches which are also irregularly branched; the whole thallus not assuming any definite form. In *C. pulvinata*, on the contrary, the thallus forms a hemispherical cushion; the cellular filaments which are the result of germination branch somewhat irregularly in one plane, but form something of a disc; from them rise up ascending articulated branches, which again branch and form the cushion. In the following species no ascending branches are formed, but those which cling to their support form a more or less regular disc. In *C. irregularis* this takes place by irregular ramifications which lie in one plane gradually filling up all the interstices, till an almost uninterrupted layer of cells is obtained. In *C. soluta* (Fig. 164), on the other hand, a dichotomous ramification commences in the two first daughter-cells of the germinating spore, with corresponding cell-division of such a nature that even at a very early period a close disc of radial forked branches is formed, which either lie loosely or are closely crowded side by side. While in the species already named the branches arise laterally from cells, but never from the terminal cell of a branch, in *C. soluta* we have the first instance of dichotomy in the regular disc-shaped centrifugal growth; a process which attains the highest development in *C. scutata*. In this species the first cells which result from germination remain from the first united laterally and do not form isolated branches; the circular disc, when once formed, continues to grow by increase of its circumference, the marginal cells dividing by radial and tangential walls. This mode of growth may be referred fundamentally to the law that the first twigs united laterally grow with equal rapidity in a radial direction, and then become divided by septa (in this case tangential); while the broadening of the terminal cell of each radial row corresponds with the succeeding radial division of a dichotomy. The law which prevails in the species already mentioned, that only the terminal cell of a branch is divided by septa, is exemplified in *C. scutata* by the marginal cells only of the disc being divided by tangential walls.

The *Reproduction* of the Coleochætæ is brought about by asexual swarm-spores and by resting oospores produced sexually. The oospores do not at once produce new plants, but several swarm-spores; and the following alternation of generations takes place:—The first swarm-spores, which arise in the early part of the year at the commencement of vegetation from the cells of the oogonia of the previous year, produce only asexual plants, or, in other words, only such as can form swarm-spores. Only after a series of asexual generations varying in length does a sexual generation arise, which may be either monœcious or diœcious according to the species. Fertilisation produces *one* oospore in the oogonia which clothe themselves with a peculiar layer of cortical cells; and this oospore itself again developes into a parenchymatous reproductive body, from the cells of which the first swarm-spores proceed in the next period of vegetation (Pringsheim). The swarm-spores (Fig. 165, *D*) may arise in all the vegetative cells of the Coleochætæ; in *C. pulvinata* especially from the terminal cells of the branches; they are always formed from the entire contents of the mother-cell, and escape through a round hole in its cell-wall.

The oogonium is always the terminal cell of a branch, and hence in *C. scutata* the terminal-cell of a radial row (Nägeli). The peculiar mode of its development is subject, according to the growth of the plant, to some, though subordinate, modifications. One species, *C. pulvinata* (Fig. 165), may first of all be examined somewhat more closely. The terminal cell of a branch swells up and at the same time elongates into a narrow bag (Fig. 165, *A*, *og*, to the left), which then opens (*og''*, to the right) and exudes a colourless mucilage. The protoplasm of the swollen part which contains chlorophyll forms the oosphere in which a nucleus is visible. The antheridia are formed at the same time in adjoining cells, two or three protuberances (*A*, *an*) growing out, which become separated by septa; each of the cells thus formed, which have somewhat the shape of a flask, is an antheridium; its entire contents form a spermatozoid (*z*) of oval

shape with two cilia; it is endowed with motion like a swarm-spore, but its entrance into the oogonium has not yet been observed. The effect of fertilisation is seen in the oogonium by its contents becoming surrounded with a membrane of its own, forming the oospore. This now grows considerably, and at the same time the formation of the cortical layer (*r*) of the oogonium commences, while out of the cells that support it proceed branches (*A*, *og''*) which cling closely to it. These again form branches which also cling closely and divide transversely; the branchlets of other branches also ramify (*B*); and only the neck of the oogonium does not become covered with the cortical layer. All this happens between May and July; later, the contents of the remaining cells of the plant disappear, and the walls of the cortical layer of the oogonium assume a deep

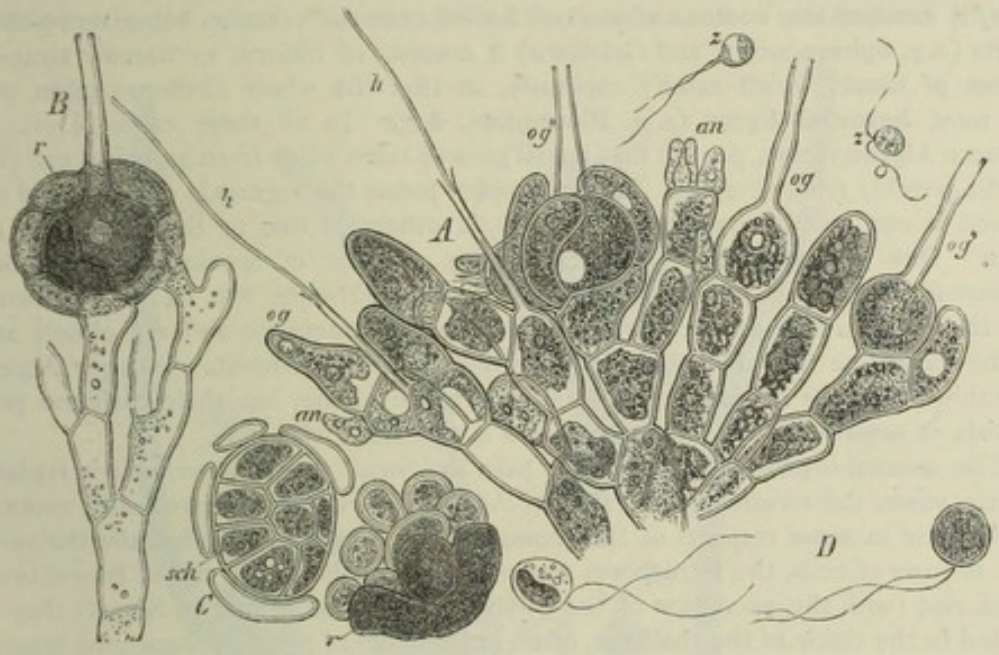

FIG. 165.—*A* part of a fertile thallus of *Coleochate pulvinata* (×350); *B* ripe oogonium enclosed in its cortical layer; *C* germinating oogonium, in the cells of which the swarm-spores are formed; *D* swarm-spores (*B-D* × 280) (after Pringsheim).

dark-brown colour. The further development of the oospore within the oogonium now covered with its cortical layer begins only in the next spring; a parenchymatous tissue is formed by successive bipartitions; the cortical layer splits and is thrown off (Fig. 165, *C*); and from each cell arises an ordinary swarm-spore, and from this again an asexual plant. *C. scutata* (the most abnormal species) deviates from these processes only so far that in it the oogonia provided with their cortical layer lie on the surface of the disc, and the antheridia are the result of divisions of disc-cells into fours.

The FLORIDEÆ[1] are a group of Algæ of extraordinarily variable form, belonging, with few exceptions (Batrachospermum, Hildenbrandtia[2]), to the sea. In the normal condition they are of a red or violet colour; the green colour of their chlorophyll is concealed by a red pigment[3], soluble in cold water. They are further distinguished from

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[1] Nägeli und Cramer, Pflanzenphys. Unters. Zürich, Heft I. 1855; Heft IV. 1857.—Thuret, Ann. des Sci. Nat. 1855, Recherches sur la fécondation, &c.—Pringsheim, Ueber die Befruchtg. u. Keimung der Algen, Berlin 1855.—[Quart. Journ. Micr. Sc. 1856, vol. IV. pp. 63, 124.]—Nägeli, Sitzungsb. der k. bayer. Akad. der Wissen.—Bornet and Thuret, Ann. des Sci. Nat. 5th series, vol. VII. 1867.—Solms-Laubach, Bot. Zeitg. nos. 21, 22, 1867.

[2] [Also Lemaneaceæ, Sirodot, Ann. des Sci. Nat. 5th ser. 1872, vol. XVI.—ED.]

[3] Rosanoff extracted the red colouring matter by cold water, and examined it accurately. In transmitted light it is carmine-red, in reflected reddish-yellow; the grains of chlorophyll also show

other Algæ by the absence of spermatozoids endowed with independent motion, and by the very remarkable female apparatus for fertilisation, which, however, in its simpler forms, shows considerable resemblance to that of the Coleochætæ.

The *Thallus* of the Florideæ consists, in the simplest forms, of branched rows of cells, which elongate by apical growth and transverse division of their apical cell, while the branching of the other cells not unfrequently developes sympodially. An apparent formation of tissue occurs in many Ceramiaceæ (C. Cramer, Physiolog. u. system. Untersuch. über die Ceramiaceen, Zürich 1863) from the branches growing closely adpressed to their mother-axes, and thus surrounding them with a cortex, reminding one of the formation of the cortex in Chara. In other Florideæ the thallome is a flat expansion of cells, but often consisting of several layers; in some (as Hypoglossum and Delesseria) it assumes the contour of stalked leaves, even the venation being represented; in others (*e. g.* Sphærococcus and Gelidium) it consists of filiform or narrow strap-shaped masses of tissue, which ramify copiously, so that the whole thallome often presents the most beautiful forms (*e. g.* Plocamium, &c.). In all these cases Nägeli asserts (Neuere Algensysteme, p. 248) that apical growth takes place from an apical cell (in Peissonelia possibly from several). In the simpler forms the segments of the apical cell are formed in one row by transverse divisions, in others in two or three rows by oblique walls. One group which comprises a large number of species, the Melobesiaceæ (Rosanoff, Mém. de la Soc. Imp. des Sci. Nat. de Cherbourg, vol. XII. 1856) forms disc-like thallomes, which grow centrifugally at the circumference and are closely attached to the substance on which they grow, which generally consists of larger Algæ; they resemble *Coleochæte scutata* in their size and mode of life, but their thallome generally consists of several layers, and the cell-wall is encrusted with lime.

The asexual organs of reproduction take the form of *Tetraspores*, which replace, in a certain sense, the swarm-spores of other Algæ, but are not endowed with motion, and remind one in some respects of the gemmæ of the Hepaticæ. When the thallome consists of rows of cells, the tetraspores are produced in the apical cell of lateral branches; in the rest (with the exception of the Phyllophoraceæ, according to Nägeli) they lie imbedded in the tissue of the thallome, often in branches of peculiar shape and densely congregated in great numbers. The tetraspores result from the division of a mother-cell, and are often arranged in it in the corners of a tetrahedron, but also frequently in a row, or like the quadrants of a sphere. Sometimes the four spores are replaced by only one or two, rarely by more than four (Nägeli); in the Nemalieæ they are altogether wanting.

The sexual organs, Antheridia and Trichogynes, are produced on other plants of the same species, thus pointing to an alternation of generations, and the sexual plants are frequently diœcious.

The *Antheridia* are either single cells at the end of the branches which consist of the

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fluorescence if left behind when the red colouring matter (the phycoërythrine) has escaped from them from injury to the cells; the whole plant also remains green when the red colouring matter has been extracted by water or destroyed by heat. (Rosanoff in Compt. Rend. April 9, 1866). Besides the chlorophyll-grains coloured red by phycoërythrine, Cohn found in Bornetia colourless crystalloids of an albuminous substance which are coloured a beautiful red by the colouring matter that escapes from the chlorophyll-grains when the cells are injured or killed. (Schultze's Arch. für mikr. Anat. III. p. 24.) Cramer had previously observed crystalloids of this kind in Bornetia which had been preserved in a solution of sodium chloride, and had accurately described them; according to him they are partly hexagonal, partly octahedral. (Vierteljahrschr. der naturf. Ges. in Zürich, VII.) Julius Klein (Flora, no. 11, 1871) found colourless crystalloids in *Griffithsia barbata* and *neapolitana*, *Gongoceras pellucidum*, and *Callithamnion seminudum*; and states that the red crystalloids which are also found outside the cell-cavity only appear after treatment with sodium chloride, alcohol, or glycerine, since their colourless matrix takes up the diffusible red colouring matter of the Florideæ. On Phycoërythrine see Askenasy, Bot. Zeitg. no. 30, 1867. [Sorby, Monthly Mic. Journ. vol. VI. 1871, p. 124. Van Tieghem has detected starch in the Florideæ, Compt. Rend. 1865.—Ed.]

longer rows of cells (as in Batrachospermum), each producing only one spermatozoid, or these mother-cells of the spermatozoids are congregated together in large numbers on a common axis as the terminal member of a very short branching-system (as in Ceramiaceæ according to Nägeli). In Nitophyllum Nägeli finds that they densely cover certain portions of the surface of the thallus consisting of a single layer of cells; in the Melobesiaceæ they are, like the tetraspores, produced in cavities which are formed by the overarching of the surrounding tissue. The roundish spermatozoids have no cilia and do not swarm, but are moved along passively by the water.

The development of the *Trichogyne* and of the capsule (Cystocarp) resulting from its fertilisation, may, first of all, be illustrated by an example, *Lejolisia mediterranea*, according to Bornet and Thuret[1]. The cystocarps consist of branches formed of only one or two cells, the apical cell being divided by a septum into a terminal cell (Fig. 166,

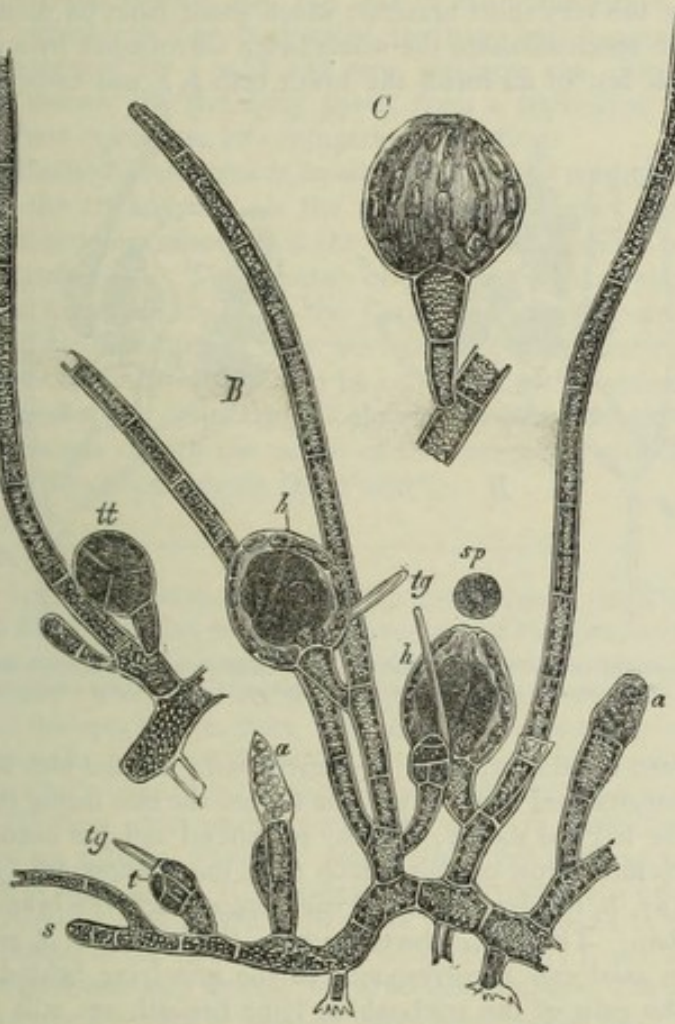

FIG. 166.—*Lejolisia mediterranea* (after Bornet, × about 150). *A* a small piece of a creeping filament with a root-hair and an upright branch; its lowest cell bearing a branchlet with tetraspores (*tt*). *B* a sexual (monœcious) plant; *w* a root-hair of the creeping stem, its apical cell situated at *s*, and its upright branches bearing the sexual organs; *a a* antheridia, the axial row of cells being however not indicated; *tg* trichogyne by the side of the apex *t* of the fertile branch; *h* the envelope of the cystocarp; *sp* a spore escaped from the cystocarp; *C* an empty cystocarp, its envelope consisting of rows of cells.

B, *t*) which no longer grows, and a broader cell which splits up by longitudinal walls into five cells, one central (axial) and four peripheral. One of the latter, the one turned away from the mother-filament, becomes coloured and filled with strongly refractive protoplasm, and then divides by septa into three cells lying one over another, and composing

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[1] Bornet and Thuret (*l. c.*) discovered these remarkable processes. The structure of the trichophore had long before been accurately described by Nägeli.

the Trichophore. The uppermost of these cells elongates into a hair-like continuation, the Trichogyne (*B*, *tg*, where the septa are not shown), which grows up beside the apical cell (*t*) of the fertile branch. The three other peripheral cells divide, after the fertilisation of the trichogyne, and develope into articulated branches, which grow upwards close to one another and form the peculiar 'Pericarp' (*C*) of Lejolisia. The spores arise in the centre of this pericarp as outgrowths of the central cell, the cells of the trichophore not participating in their formation. The trichophore is pressed aside by the cystocarp (*B*, *h*, *tg*), and hence at a later period the trichogyne occupies a lateral position.

The relative positions of the parts of the cystocarp are more clearly shown in the representation of *Herpothamnion hermaphroditum* copied from Nägeli (Fig. 167). On a primary branch *st* (in *A*) arises a branch *a*, bearing an antheridium (*an*) and a young cystocarp. The antheridium consists of an axial row of cells which is a prolongation of the branch, and of the very short branches which shoot from its members and bear the mother-cells of the spermatozoids, the whole being surrounded by a mucilaginous mass. The female branch first of all forms the lower cells *b*, *c*, and ends in the apical cell *i*;

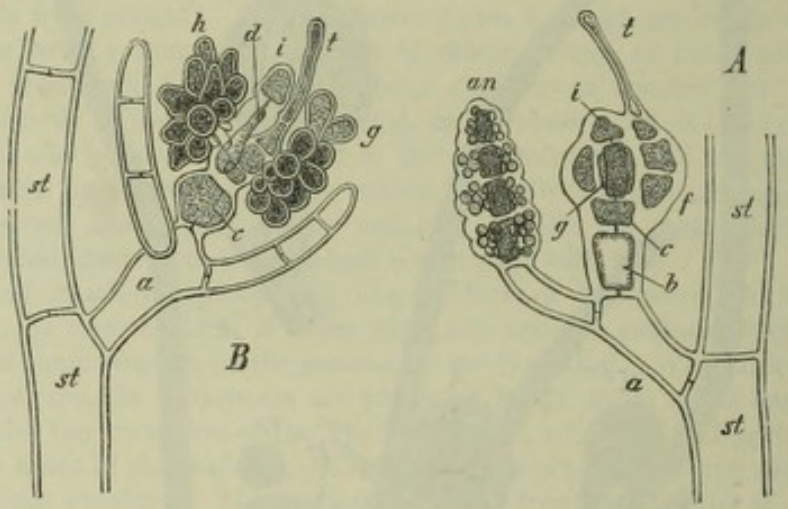

FIG. 167.—*Herpothamnion hermaphroditum*. *A* a branch with the rudiment of the cystocarp *f* and an antheridium *an*. *B* the mature cystocarp after fertilisation (after Nägeli in the Sitzungsberichte der k. bayer. Akad. 1861).

the last cell between *c* and *i* forms the cystocarp, being divided into four peripheral and one axial cell by longitudinal divisions; of the former the one facing the observer (*g*) and a lateral one on the left are shown; another peripheral cell has become transformed by transverse divisions into a row of cells, which form the trichophore (*f*), and the trichogyne *t*. In Fig. 167, *B*, fertilisation has already taken place, the branch *a* does not here bear an antheridium. The cell *c* corresponds to the cell *c* in *A*, and the apical cell *i* with *i* in *A*; the axial cell *d* corresponds to the one lying behind *g* in *A*; the trichogyne, *t*, and the cells of the trichophore lying beneath are still visible. From the two lateral cells which in *A* lie next the trichophore, the masses of spores, *g*, *h*, have arisen by the formation of very short branch-systems; beneath the cell *c* filaments shoot from the pedicel-cell *a*, and form the envelope of the cystocarp. It is clearly seen in both examples that, as the result of the fertilisation of the trichogyne, the masses of spores are produced not by this organ, but by neighbouring cells which lie deeper and do not in any way belong to the trichophore, but which originate in the same way, and that the formation of the envelope of the cystocarp is also a consequence of fertilisation. The fertilisation of the trichogyne takes place more immediately in the Nemalieæ to which Batrachospermum belongs[1]. In them there is no trichophore, but

[1] [Sirodot (Compt. Rend. May and June 1873) has found that the spores of Batrachospermum produce a Chantransia from which again the Batrachospermum is developed.—ED.]

the trichogyne replaces it. The lower swelling itself produces after fertilisation (according to Bornet and Thuret) the cystocarp, numerous articulated branches sprouting from it and forming a spherical ball (the Glomerulus), and the terminal members of this produce the spores; while beneath the trichogyne enveloping branches also arise (for further details on Batrachospermum see Solms-Laubach in Bot. Zeitg. nos. 21, 22, 1867). Thuret and Bornet found the most complicated and remarkable process of fertilisation in Dudresnaya. Here the cystocarps arise on altogether different branches from the trichophore; after the long spiral trichogyne at their base has been fertilised, branches shoot out from beneath it, which grow across to the fertile branches; each fertile branch has a spherical apical cell, and the 'tube connecteur' applies itself closely to this cell and afterwards continuing its growth becomes successively united with several other fertile branches. At the points of union the articulated 'tube connecteur' coalesces with the apical cell of the fertile branch, and the wall of both disappears. The part of the 'tube connecteur' which has thus conjugated swells up and becomes filled with protoplasm, which is separated by a wall and now produces the cystocarp. The 'tubes connecteurs' thus convey the fertilising power from a trichogyne to the other fertile branches, and produce cystocarps by conjugation with them.

The act of fertilisation itself consists, in all Florideæ, of a conjugation of the roundish spermatozoid with the trichogyne; *i. e.* the spermatozoid comes into contact with the trichogyne, the wall becomes absorbed at the spot, and the contents of the spermatozoid pass over into the trichogyne. This process of fertilisation takes place in the Nemalieæ at the base of the trichogyne itself; in the Ceramiaceæ and others in adjoining cells; in Dudresnaya in altogether different branches by means of the 'tube connecteur.' While the simpler processes in the Nemalieæ may be compared with corresponding processes in Coleochæte, the origin of the cystocarp of Lejolisia and Herpothamnion and of the more robust Florideæ reminds one of the origin of the receptacle produced by fertilisation in the Pezizæ and Erysipheæ among the Fungi[1].

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[1] [**Porphyreæ**. Janczewski (Mém. de la Soc. Nat. de Cherbourg, vol. XXI. p. 345, 1872, Ann. des Sci. Nat. 1873, vol. XXII) describes the reproductive organs of *Porphyra leucosticta* and *P. laciniata*. In the former the frond, consisting of a single layer of cells, produces octospores by the division of the contents of marginal cells. The octospores are set free by the softening and deliquescence of the mother-cell-walls and of the septa between them. When free they are destitute of a cellulose investment, and move by slow contractile changes of shape, only, however, very rarely putting out short pseudopodia. The octospores finally come to rest, develope a cell-wall, and germinate. The spermatozoids are developed in cells like those which produce octospores; there are usually however sixty-four from each mother-cell; they are spherical when free, destitute of a cell-wall, and without any mobility. Occasionally a portion of the contents of a mother-cell is converted into octospores, and the rest into spermatozoids. *Porphyra laciniata* differs from the preceding species in being diœcious. The segmentation of the contents of the mother-cells producing octospores is not, however, fully carried out. The antheridial mother-cells only produce thirty-two spermatozoids. The protoplasmic contents of the cells in the Porphyreæ are coloured violet by iodine solution (with KI). The endochrome is a mixture of chlorophyll and phycoërythrine. Porphyreæ appear to be connected with the Florideæ through the Dictyoteæ, all three agreeing in the immobility of their spermatozoids and spores (disregarding the amœboid movements of the latter), but distinguished by their female organs, which are quite distinct in the Dictyoteæ from those of the Florideæ, and perhaps do not require fertilisation; while they are absolutely wanting in the Porphyreæ, as far as our present knowledge extends.—Ed.]

CLASS II.

FUNGI[1].

The structural element from which the thallome of Fungi is built up consists of cellular filaments destitute of chlorophyll, endowed with apical growth, only rarely branching dichotomously, more usually abundantly by lateral shoots. These elementary constituents of Fungi are called *Hyphæ*. It is only in a single group of Fungi—forming the transition from the Siphoneæ among the Algæ to the typical Fungi—the Phycomycetes, that the hypha consists of a single undivided cell; in all other cases it is divided by transverse septa. The Hypha is thus usually a branched row of cells destitute of chlorophyll with a growing apical cell which divides transversely; intercalary transverse divisions, however, also occur in the cells. In the simplest forms, which have been termed Haplomycetes, including however mere conditions of development of higher forms, the whole thallome consists of a single hypha usually very much branched. The massive compact substance of many Fungi is formed by the aggregation of numerous hyphæ having a common growth; the larger Fungi are, without exception, examples of this. The hyphæ either run parallel to one another, or their numerous ramifications are interwoven in the most various modes. If these textures are very dense and the joints of the hyphæ therefore short and thick, and of a polyhedral form from pressure on opposite sides, the mass assumes the form of a parenchymatous tissue, the origin of which from hyphæ justifies its appellation of Pseudo-parenchyma. It is especially developed on the surface of larger Fungi as an epidermal system.

When the substance of a Fungus consisting of a number of hyphæ grows in length forming an apex at one point, this—as follows from what has been said—can never take place by means of *one* apical cell, but a certain number of hyphæ reach to the apex, where each lengthens by apical growth but in unison with its neighbours. If the substance of such a Fungus spreads out in the form of a disc growing at the margin, this is occasioned by the hyphæ proceeding from a centre lengthening radially and ramifying laterally in proportion to the growth of the circumference. Ramification rarely occurs in Fungi of this kind (*e. g.* in Clavaria and Xylaria); and in this case the individual branches are always similar to one

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[1] The most important works which include the whole class are Corda, Icones Fungorum, 6 vols. Prag 1837–1854.—Tulasne, Selecta Fungorum Carpologia, 3 vols. Paris 1861–1865.—De Bary, Morphologie u. Physiologie der Pilze, Flechten u. Myxomyceten, Leipzig 1866.—The most important papers on single sections are cited below.—De Bary's Ueber Schimmel u. Hefe, Berlin 1869, is also of general interest. [Berkeley, Outlines of British Fungology. London 1860.—Cooke, Handbook of British Fungi. London 1871.]

another; it never attains that differentiation into axes and dissimilar lateral leaf-like appendages which occurs in many Algæ. Much more common than ramification is, moreover, the tendency of the larger Fungi to the formation of compact roundish masses of tissue, in the interior of which a differentiation takes place into different layers and masses of tissue for the purpose of reproduction. Among the Gastero-mycetes structures unknown elsewhere in the vegetable kingdom and often highly curious are produced at the time of the ripening of the spores and for the purpose of their dissemination (*e. g.* Clathrus, Phallus, Geaster, Crucibulum) by the extension of inner masses of tissue, and by the deliquescence of certain portions of them and the rupture of outer layers (Peridia).

The whole process of development of a Fungus, whether it consists of a single branched hypha or of an aggregation of hyphæ, may be divided into two periods;—from the spore a Mycelium is first of all produced directly, or through the intervention of a Pro-mycelium; from this the reproductive receptacles afterwards grow.

The *Mycelium*, developed from the germinating filaments, and becoming very much branched, creeps in or upon the substratum which nourishes it, out of which it assimilates the useful materials. It usually consists of filaments simple or associated into the form of a pellicle (as Penicillium on fluids). In the Fungi with large compact receptacles, the mycelium often consists of thicker bundles each of which is composed of a number of parallel hyphæ (as in Phallus, Sphærobolus, Agaricus, &c.). The branches of the mycelium not unfrequently anastomose among one another; if simple by a kind of conjugation of one hypha with another. These mycelia can live for a shorter or longer time (often for years); they may produce reproductive receptacles only once or repeatedly (*i. e.* may be monocarpous or polycarpous). In the Haplomycetous forms the receptacles are simple branches of the hyphæ, which often arise from the substratum; in the rest of the class they appear as spherical aggregations of the branches of the mycelium at definite points, which then develope further independently in the most various ways, either remaining in the substratum (as in the truffle), or growing up above it. In some cases the young receptacle again puts out hyphæ, which, penetrating the substratum, form a secondary mycelium.

A peculiar form of the mycelium occurs in the Sclerotia, which were at one time considered as a special section of independent forms of Fungi. They form tuberous substances, and are not peculiar to any particular group of Fungi, but occur, in accordance with specific modes of life, in species of the most different groups, like bulbs and tubers among Phanerogams. The sclerotia arise out of ordinary mycelia by a dense interweaving of the hyphæ; they are hard bodies of definite form, the outer layer of which, mostly developed as pseudo-parenchyma, forms a kind of shell or skin. They are found, according to the habitat of the Fungus, on the surface or in the interior parts of other plants, as fallen leaves, or in the ground, and go through a period of rest, after which they produce receptacles and disappear, these latter being nourished from their substance.

If the *Receptacle* which proceeds from the mycelium consists of a simple or branched hypha, this latter bears, at the end of its ramifications, the spores, or, according to circumstances, the sexual organs. If the receptacle is composed of a

number of hyphæ, their spore-bearing branches grow close to one another and form level expansions called *Hymenia;* the separate fertile branches standing vertically upon the hymenial surface. According as the hymenium is formed upon the surface or in the interior of the receptacle, this latter is termed gymnocarpous or angiocarpous. The hymenial surfaces are generally greatly extended, and their form is highly characteristic of distinct groups of Fungi (*vide infra* under Gastromycetes, Hymenomycetes, Discomycetes). The hymenia never produce anything but asexual reproductive cells, the Spores; but the hymenium-bearing body itself may be the product of a sexual process (as in Peziza).

The mode of *Reproduction* of Fungi is even more various than that of Algæ. In those species the cycle of whose development is fully known, sexual and asexual reproduction occurs, or the latter is replaced by conjugation. In those cases where neither sexual reproduction nor conjugation has hitherto been observed, it may be assumed that our knowledge of the series of development is still incomplete, and that forms which are at present considered independent are really only members of an alternation of generations. The influence of the different modes of reproduction on the whole course of development and on the whole manner of life of the particular species is however so various that it does not permit a comprehensive description (as may be seen by comparing the examples below). It is important to note that it has been already ascertained that in many Ascomycetes the receptacles which bear the Ascospores are the result of a sexual process which takes place in connexion with the mycelium, so that the mycelium forms the first sexual, the receptacle the second asexual generation. In the Phycomycetes, on the other hand, the product of the sexual process is a resting cell (oospore or zygospore) similar to what is found in many Algæ; while the origin of the receptacle of the Ascomycetes corresponds essentially with that of the Florideæ. The spores produced asexually are very different in their origin and form; and in many Fungi two, three, or even four different forms of spores have been observed within one cycle of development. But since these relationships can only be made clear by examples, those facts only which are most important for nomenclature will be here mentioned. In several Phycomycetes swarm-spores are formed which, however, are wanting in all other Fungi. The motionless spores are either simply detached from the end of a branch of the hyphæ which is termed the Basidium,—and this detachment may be often repeated so that a basidium produces a chain of spores,—or the spores sprout from the basidium as short swollen separable branchlets, either successively or simultaneously (in this case in twos, fours, or larger numbers). This formation of spores depends finally on bipartition of the basidium. Essentially different from these Basidiospores [1] are the Ascospores, which arise by free cell-formation in the protoplasm of the sac-like swollen terminal cell (Ascus) of a branch of a hypha. With the development and escape of the spores the ascus disappears. Both the basidiospores and the ascospores, which often arise in the cycle of development of one species, may break up by subsequent

[1] To this category belong also the *Spermatia*, very small spore-like structures, which are mostly produced in large numbers by the Uredineæ and Ascomycetes; their function is, however, unknown.

(often early) division into several compartments, and thus become multicellular. Such spores, arising from rows or masses of cells, are termed Compound or Septate Spores. Each separate secondary cell of a spore of this description is usually capable of germination, and may be termed a Merispore. The formation of gemmæ also occurs not unfrequently, individual branches of a hypha breaking up by repeated transverse division into a row of cells which are capable of germinating.

The *Mode of Life* of Fungi is in all important features determined by the fact that they are destitute of chlorophyll, and therefore do not assimilate, but are adapted to take up the assimilated carbon-compounds of other organisms. This they effect either by their mycelia absorbing from the ground the partially decomposed exuviæ of animals and plants, or they grow upon or in excrementa, or are parasites; in the latter case they may attach themselves to living plants and animals, penetrate their tissues, and thus kill them or contribute to their further decomposition. In other cases their influence on their host is less injurious; they then cause peculiar degenerations in the plants whose tissues they inhabit (*Æcidium Elatinæ* causes, for example, the so-called 'witch-broom' of the silver fir, De Bary in Bot. Zeitg. 1867). The parasitism of Fungi runs through all degrees to the greatest extremes[1]; some of them live entirely within the tissues of plants and animals, and some are parasitic on other Fungi[2]. Since, in consequence of their want of chlorophyll, they do not require light for their nourishment, they may pass through all stages of development in complete darkness, if the escape of the spores or particular processes of growth do not require light, as is the case with truffles and numerous other underground Fungi. Some, however, need it for their morphological development, and do not fructify without its influence, while their mycelium on the other hand vegetates vigorously in the dark (as Rhizomorpha and many others).

With regard to the *Proximate Principles* for the construction of tissues, Fungi present, without exception, the peculiarity of never forming starch; but this is not immediately connected with their want of chlorophyll, since phanerogamic parasites like Cuscuta and Orobanche, although they form no chlorophyll[3], yet produce abundance of starch. Other substances usually occurring in large granules are also rare in their cells. The lime very commonly taken up by Fungi is almost always deposited on the surface of the hyphæ in the form of small crystalline granules of calcium oxalate.

The walls of the hyphæ are not generally turned blue by iodine or by iodine and sulphuric acid, or Schultz's solution; yet the cases where this occurs are not rare (De Bary, *l. c.* p. 7). The walls are usually thin, smooth, and without any perceptible differentiation into layers, although this latter occurs in the spores, especially the resting-spores, inasmuch as they form an exospore which is penetrated by the endospore when they germinate. The asci of the Pyrenomycetes are often

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[1] Compare what is said below on Lichens.

[2] On heteroecism, a peculiar form of parasitism, see below under Book II. On insect-destroying Fungi, *cf.* Tulasne, *l. c.*; De Bary, Bot. Zeitg. 1867; Oscar Brefeld, Untersuchungen über die Entwickelung der *Empusa Muscæ* and *E. radicans*, und die durch sie verursachten Epidemieen der Stubenfliegen u. Raupen. Halle 1871.

[3] [This statement requires modification; *vide infra*.—Ed.]

differentiated into an outer firm layer and an inner one capable of swelling in water. The wall is generally of a dark colour, but seldom or perhaps never actually lignified; it is usually tough, rarely hard and brittle. An important part is also played in Fungi by the formation of mucilage through the softening and swelling of the outer layers of the walls of the hyphæ. This occurs either in all the hyphæ of a Fungus, by which it acquires a gelatinous appearance, as among the Tremellini, or separate portions or layers of a larger mass of hyphæ are subsequently converted into mucilage, the inner structure of many Gasteromycetes, as has already been mentioned, depending on this change. This formation of mucilage takes place even on the spores, so that their mode of dissemination takes the form of a trickling mucilage in which they are enveloped (as in Sphacelia and Phallus). But most commonly the spores fall off dry, or are expelled singly or in masses, or are thrown out with violence (*e. g.* Pilobolus, Ascobolus, Sphærobolus).

Since the labours of Tulasne, De Bary, Woronin, and others, the *Systematic Grouping* of Fungi, as that of Algæ, has been completely remodelled. Whole sections of genera of the earlier systems are now recognised as simple forms of development in the alternation of generations of other forms, and the same fate is still threatened to many apparent species and genera. At present the classification proposed by De Bary, which corresponds to the present state of science, must be retained. The class of Fungi is thus divided into the following groups:—

I. Phycomycetes.
- Saprolegnieæ.
- Peronosporeæ.
- Mucorini.

II. Hypodermiæ.
- Uredineæ.
- Ustilagineæ.

III. Basidiomycetes.
- Tremellini.
- Hymenomycetes.
- Gasteromycetes.

IV. Ascomycetes.
- Protomyces. (?)
- Tuberaceæ.
- Onygeneæ.
- Pyrenomycetes.
- Discomycetes.

The characters of each more important division will be lllustrated in the following pages by one or two examples.

I. PHYCOMYCETES. In its morphological phenomena this order resembles Vaucheria. The Saprolegnieæ and Peronosporeæ form spherical oogonia at the ends of the mycelial branches, in each of which one or more oospores result from fertilisation. In (1) the **Saprolegnieæ**[1], which mostly grow on the bodies of insects putrefying in water, an alternation of generations takes place between the asexual individuals—which are the first formed and recur many times forming swarm-spores — and the sexual

[1] Pringsheim in Jahrb. für wissen. Bot. vol. I. p. 289, and vol. II. p. 205.—Hildebrand, ditto, vol. VI. p. 249.—Walz, Bot. Zeitg. p. 537, 1870.—Leitgeb, Jahrb. für wissen. Bot. vol. VII. p. 357.—Reinke in Schultze's Archiv für mikrosk. Anat. vol. V. p. 183.

individuals. These latter are in some instances monœcious, and the fertilisation is then brought about by antheridial branches, which perforate the oogonium, and allow the escape of the spermatozoids within it, or penetrate through holes already formed for this purpose in the wall of the oogonium. In other species the sexual generation is

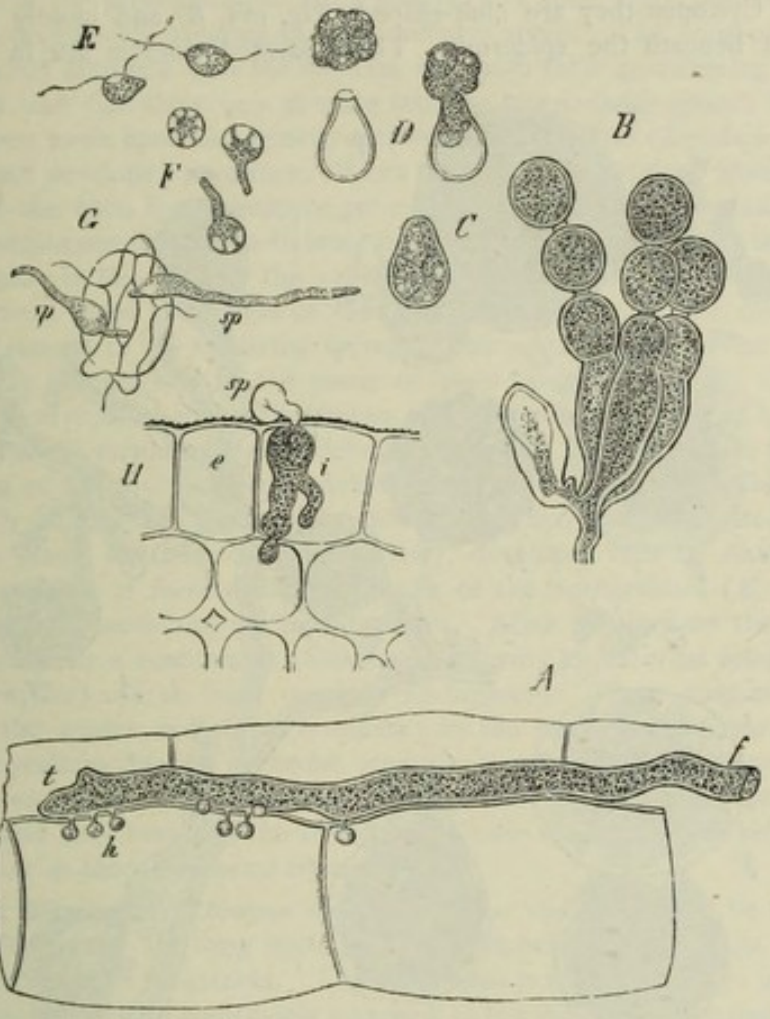

FIG. 168.—*Cystopus candidus*. *A* branch of the mycelium growing at the apex *t* with haustoria *h* between the cells of the pith of *Lepidium sativum*; *B* conidia-bearing branch of the mycelium; *C*, *D*, *E* formation of swarm-spores from the conidia; *F* swarm-spores germinating; *G* a swarm-spore germinating on a stoma; *H* swarm-spore of *Peronospora infestans* penetrating through the epidermis of a potato-stem (after De Bary, × 400).

diœcious, and in this case the male plant forms motile spermatozoids. Figs. 8 and 9 (pp. 12, 13) will sufficiently illustrate the essential points in the formation of zoospores and oospores. The oospores germinate directly after a period of rest[1].

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[1] [For the most recent study of the *Saprolegnieæ* the monograph of Max Cornu (Ann. des Sci. Nat. 1872, vol. XV) should be consulted. He divides them into groups: (i) *Saprolegnieæ* proper, having reniform zoospores with two unequal cilia attached, one before, the other behind, or oval zoospores with two equal cilia attached in front. The genera fall into two series according as their filaments are cylindrical or interrupted by constrictions (*e. g.* Rhipidium); in every case the wall of the filaments consists of cellulose, and is coloured blue by Schultz's solution. (ii) *Monoblepharidæ*, consisting of three species of the genus *Monoblepharis*, and having ovate zoospores furnished with a single posterior cilium; the wall of the filaments is not coloured blue by Schultz's solution. The sexual reproduction of the *Saprolegnieæ* proper presents two cases, according as the species is or is not provided with lateral branches. In the first case prolongations of the antheridia traverse the wall of the oogonium, which may or may not have been previously perforated. Max Cornu has never seen spermatozoids produced by the antheridium, which empties itself by an influx of its protoplasmic contents; the process

(2) The **Peronosporeæ**[1] live in the interior of Phanerogams, the branches of their unicellular mycelium growing between the cells of the tissue from which they draw their nourishment by peculiar organs of suction (Haustoria) (Fig. 168, *A*, *b*). The mycelium produces first of all asexual fertile branches which project above the surface; in Peronospora they protrude through the stomata and branch in an arborescent manner; in Cystopus they are club-shaped (Fig. 168, *B*) and closely packed, forming a hymenium beneath the epidermis. The separated Conidia are in some species of

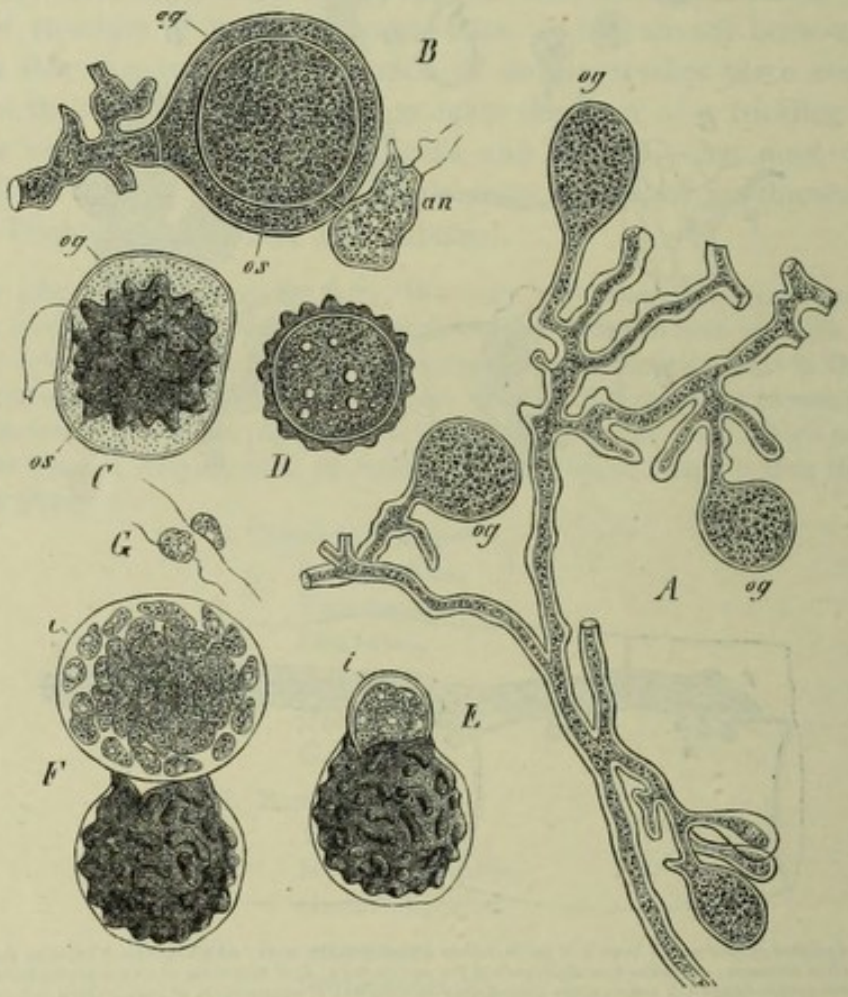

FIG. 169.—*Cystopus candidus*. *A* mycelium with young oogonia; *B* oogonium *og* with oosphere *os* and antheridium *an*; *C* ripe oogonium; *D* ripe oospore; *E*, *F*, *G* formation of swarm-spores from oospores; *i* endospore (after De Bary) (×400).

Peronospora simple spores, in others (as *P. infestans*), and in all species of Cystopus, they are not immediately capable of germination, but when in contact with water, as for instance drops of dew or rain, develope several zoospores (Fig. 168, *C*, *D*, *E*, *F*). In some species of Cystopus the terminal member of each row of conidia is capable of

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is in fact one of true *conjugation*. Where there are no lateral branches fertilisation would seem to be required by means of antherozoids. Max Cornu believes that the supposed spermatozoids discovered by Pringsheim really belong to an endophyte of the group *Chytridineæ*, which have often been identified with organs of the plants they infest. He thinks it probable that the spermatozoids closely resemble the zoospores in appearance, and have been overlooked in consequence. This is confirmed by the process of fertilisation in Monoblepharis, the spermatozoids are half the size of the zoospores, but of the same form. They creep with amœboid movements over the wall of the oogonium and fertilise the oosphere by blending with it. (See also Archer, Quart. Journ. Mic. Sc. 1867, p. 121. —Ed.]

[1] De Bary, *l. c.* p. 176, and Ann. des Sci. Nat. 4th series, vol. XX.

at once forming a filament in germination. The zoospores of *Peronospora infestans* are firmly attached, after swarming, to the cuticle of its host, surround themselves with a thin membrane, and penetrate by a small hole the outer wall of the epidermis (Fig. 168, *H*, *sp*), through which the germinating filament penetrates into the epidermis-cell with the whole of the protoplasm of the zoospore, and then, again piercing through the wall of the epidermis-cell, reaches the intercellular space. The zoospores of *Cystopus candidus* are firmly attached near the stomata and push their germinating filaments into its orifice, and thus find their way at once into the intercellular space; but unless the spores have been sown upon the (green) cotyledons of the host (*Lepidium sativum*, Capsella) they do not develope a mycelium. When the mycelium has once been formed in the parenchyma of the host, it continues to grow in it, and finally often spreads through the whole plant, putting out its conidia-bearing branches at various places in the stem, leaves, or inflorescence. In this manner the (unicellular) mycelium of *P. infestans*, for instance, can even hibernate inside the tubers of the potato, to undergo further development into germinating filaments in the following spring. The sexual organs of the Peronosporeæ are developed in the interior of the tissue of their host. Spherically dilated ends of branches of the mycelium shape themselves into oogonia (Fig. 169, *A*, *og*), in each of which an oosphere is formed out of a definite portion of the protoplasm (*B*, *os*). From another branch of the mycelium a branchlet grows towards the oogonium, swells, and becomes closely attached to it; and the thicker part becoming separated by a septum (just as takes place with the oogonium itself), developes into an Antheridium. As soon as the oosphere is formed, a fine branch of the antheridium (*B*, *an*) reaches it by penetrating the membrane of the oogonium. After fertilisation the oosphere becomes surrounded by a coat which thickens and forms an external rough dark-brown layer (the Exospore) and an inner one (the Endospore). These oospores remain dormant through the winter and then germinate; in the case of *Peronospora Valerianellæ*, they form a mycelium directly on moist ground; those of Cystopus, however, produce zoospores, the endospore (*i*) forces itself like a bladder out of the ruptured exospore (Fig. 169, *F*), and then bursting, the zoospores (*G*) are set free, which behave in exactly the same manner as those produced from conidia.

(3) Among **Mucorini**[1], *Rhizopus nigricans* (*Mucor stolonifer*) may be specially mentioned. It infests dead or dying parts of plants, especially fleshy fruits, which quickly decay in consequence of its attacks. The mycelium is from 1 to 3 cm. long, and forms stolon-like filaments, which are closely attached to the substratum by root-like branches that afterwards become septate, while each of the ascending branches 2 to 3 mm. in height bears a sporangium. The ends of these branches swell up into a sphere and become filled with protoplasm; the septum which separates this swelling from the branch becomes arched convexly into the cavity of the sporangium, in which numerous small spores now arise. These are set free by the giving way of the wall, and germinate only upon a substratum capable of nourishing them (not in pure water); putting out at once a germinating filament. They can, however, preserve their germinating power for months, if kept dry. When the mycelium has produced a number of sporangium-bearing filaments, the formation of the *Zygospores* begins beneath the white felt-like texture formed by it; where two of the firm mycelium-filaments touch, each puts out a swelling which is in close contact with that of the other. Both grow in this manner to a considerable size, and assume the form of a club; a septum then forms in each, by which the thick end is cut off as a conjugating cell. One of the two conjugating cells, which are in contact for some distance, is smaller than the other; the wall which separates them is then absorbed; and the two cells coalesce into a single cell (the

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[1] De Bary und Woronin, Beiträge zur Morph. u. Phys. der Pilze, p. 25. Frankfort 1866.—On *Pilobolus crystallinus*, cf. Cohn, Nova Acta Acad. Nat. Curios. vol. XV, pt. 1. p. 510. [Klein in Pringsheim's Jahrb. vol. VIII.—Van Tieghem and Le Monnier, Ann. des Sci. Nat. 1873, vol. XVII.]

Zygospore), which then increases (to $\frac{1}{3}$ mm.) and takes the form of a sphere flattened by the two supporting-cells. The exospore is thick and of a blue-black colour. The formation of zygospores takes place in May, June, and July, on stone-fruit and berries, and takes twenty-four hours for its completion. The germination of the zygospores has been observed in another genus, *Sporidinia grandis* (*Mucor Syzygites*), which infests fleshy Fungi. In this case they form a filament, on which is developed a system of sporangia with asexual spores; these then produce a mycelium which forms first zygospores and then again asexual spores. An alternation of generations thus takes place[1].

II. The HYPODERMIÆ[2]. The best known species of this order, *Puccinia graminis*, belonging to the family Uredineæ, may be taken as its type. Its development not only shows a distinct alternation of generations (although no sexual organs are as yet known), but also in combination with it, the heterœcism which occurs also in some other Fungi, but is not elsewhere so clearly defined. De Bary has given the term *Heterœcism* to that peculiarity by which one generation of a parasitic Fungus is developed exclusively on one host, or only on those which belong to a particular group, while another stage of development of the same species occurs only upon a different host.

On the leaves of *Berberis vulgaris* are found in the spring yellowish swollen spots, where dense masses of mycelial filaments are interposed between the parenchyma-cells (Fig. 170, *A* and *I*, the felted mycelium, lying between the cells, being indicated by dots). In these swollen spots are found two kinds of fructification, the *Spermogonia*, which are produced somewhat earlier, and the *Æcidia*. The spermogonia (Fig. 170, *I*, *sp*) are urn-shaped receptacles surrounded by a layer of mycelium as by an envelope; hair-like threads which clothe the cavity protrude in the form of a brush from the opening of the spermogonium, penetrating the epidermis of the leaf; the bottom of the spermogonium is covered with short mycelial branches, from the ends of which are detached numerous very small spore-like bodies, the *Spermatia*. The second form of

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[1] [On the Mucorini, the Memoirs of Brefeld (Botanische Untersuchungen über Schimmelpilze, Leipzig 1872), and Van Tieghem and Le Monnier (Ann. des Sci. Nat. 1873, vol. XVII, and Quart. Journ. Micr. Sc. 1871, pp. 49-76), should be consulted. The following particulars are extracted from the last cited memoir. The mycelium of the Mucorini always originates from an asexual spore. The zygospores never give rise in germinating to a mycelium, but always produce, as in other Fungi, and as also in Muscineæ, an asexual reproductive apparatus. The mycelium is at first always destitute of partitions; later, as the protoplasm disappears, septa make their appearance irregularly. The filaments occasionally anastomose; they may be wholly immersed in the nutrient medium or partly aërial. The mycelium of some species (*e.g.* Chætocladium), which are normally non-parasitic, have also the capacity of fixing themselves on the mycelium of other species and living parasitically. All the Mucorini develope sporangia upon aërial extensions of their mycelium, in which asexual spores originate by division of the protoplasm. In some genera (*e.g.* Thamnidium) these sporangia are of two kinds, but the spores they contain are similar. Peculiar asexual spores (Chlamydospores) also arise by local condensation of the protoplasm within the mycelium and in different positions. A single large echinulate or tuberculate chlamydospore may be formed within the extremities of all the branches of the aërial hyphæ; and this may for a long time be the only mode of reproduction exhibited (Mortierella). Zygospores arise from a true conjugation. They have been observed in six genera: Sporodinia (Ehrenberg, 1829), Rhizopus (De Bary, 1866), Mucor (*M. fusiger*, Tulasne, 1866, *M. Mucedo*, Van Tieghem and Le Monnier, Comptes Rendus, Apr. 8, 1872), Phycomyces (Van Tieghem and Le Monnier, 1872), Chætocladium and Piptocephalis (Brefeld, 1872). Before germination the zygospore requires a certain period of dryness and rest. After again becoming moist it produces without mycelium a system of sporangia having all the characters of those which the mycelium produces.—ED.]

[2] De Bary, in Monatsber. der königl. Akad. der Wissen. in Berlin, Jan. 12, 1865.—Ditto, Recherches sur le Développement de quelques Champignons parasites: Annales des Sci. Nat. 4th series, vol. XX, Div. 1.—Rees, Die Rostpilze der deutschen Coniferen. Halle 1809.

fruit is much larger, and was at one time considered a distinct genus of Fungi, and described under the name of Æcidium; but this term is now only used to designate a particular form of fruit in the cycle of development of Puccinia. These æcidium-fruits, which arise from the same mycelium as the spermogonia, lie at first beneath the epidermis of the leaf, where they form a tuberous parenchymatous body (*A*), also surrounded by an envelope of fine mycelial filaments. When mature the æcidium breaks through the epidermis of the leaf and forms an open cup, the wall of which (the Peridium, *p*) consists of a layer of hexagonal cells arranged in rows, and which are pro-

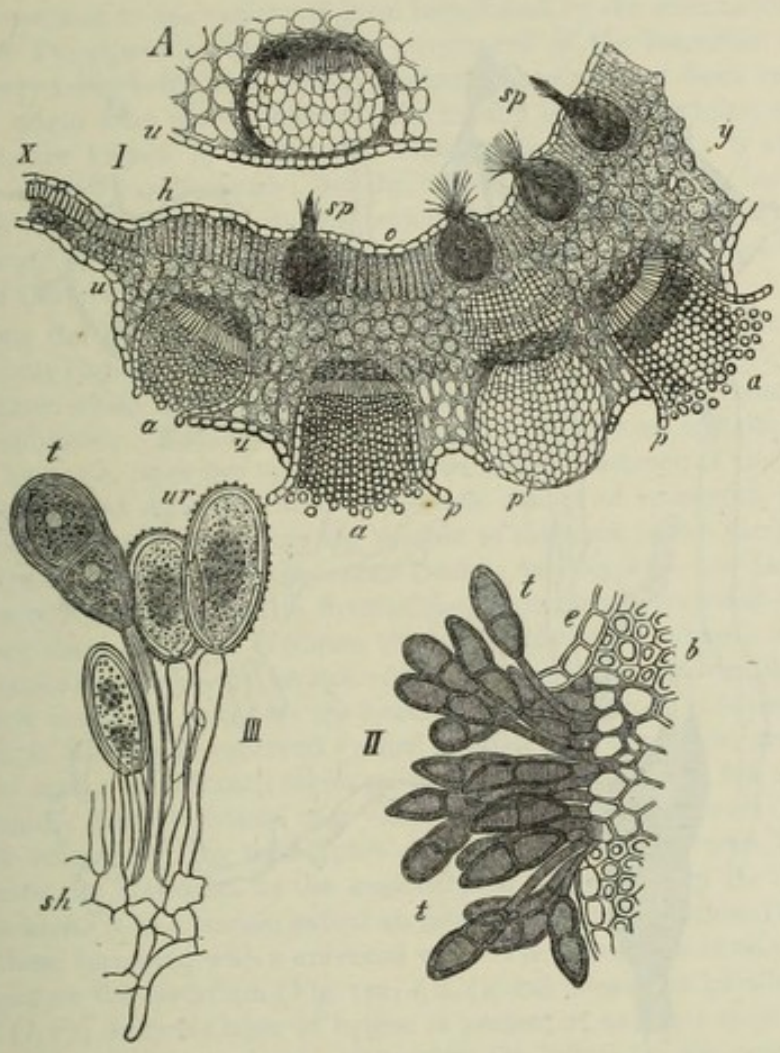

FIG. 170.—*Puccinia graminis*. *A* part of a vertical section of a leaf of *Berberis vulgaris* with a young æcidium-fruit; *I* section of leaf of Berberis with spermogonia *sp* and æcidium-fruits *a*; *p* their peridium; at *x* is the natural thickness of the leaf which is enormously thickened between *x* and *y*; *II* a mass of teleutospores on a leaf of couch-grass; *e* the ruptured epidermis; *b* the sub-epidermal fibres; *t* teleutospores; *III* part of a mass of uredospores *ur* with one teleutospore *t*; *sh* sub-hymenial hyphæ (*A* and *I* from nature; *II* and *III* after De Bary).

duced at the bottom of the cup from basidium-like mycelial ramifications. The bottom of the cup is occupied by a hymenium, the hyphæ of which have their apices exserted, and are continually detaching new conidia-like spores, which, originally of a polyhedral form in consequence of pressure from opposite sides, afterwards become rounded, and separate from one another at the opening of the cup (*I*, *a*). The peridium itself has the appearance of a peripheral layer of similar spores; its cells however remain united, and, like the spores, contain red granules. The æcidium-spores produced upon the leaves of Berberis do not develope a mycelium unless their germination takes place upon the surface of a leaf or stem of grass (as wheat or rye). The germinating filaments then penetrate through the pores of the stomata, and the mycelium produced in the paren-

chyma of the grass generates within 6 or 10 days a form of fruit which was also at one time considered a peculiar genus of Fungi, and called Uredo. These *Uredo-fruits* of *Puccinia graminis* form narrow long red cushions beneath the epidermis of the leaves and stems of Grasses; densely crowded hymenial branches rise upon the mycelium at right angles to the epidermis, and detach large ellipsoidal spores (the uredo-spores), the protoplasm of which contains red granules (Fig. 170, *III*, *ur*). These uredo-spores are dispersed after the rupture of the epidermis, and germinate after some hours upon the surface of the Grasses (Fig. 171, *D*); but in these they form new mycelia from which, in 6 or 10 days, new uredo-fruits again arise, while the germinating filaments of the spores

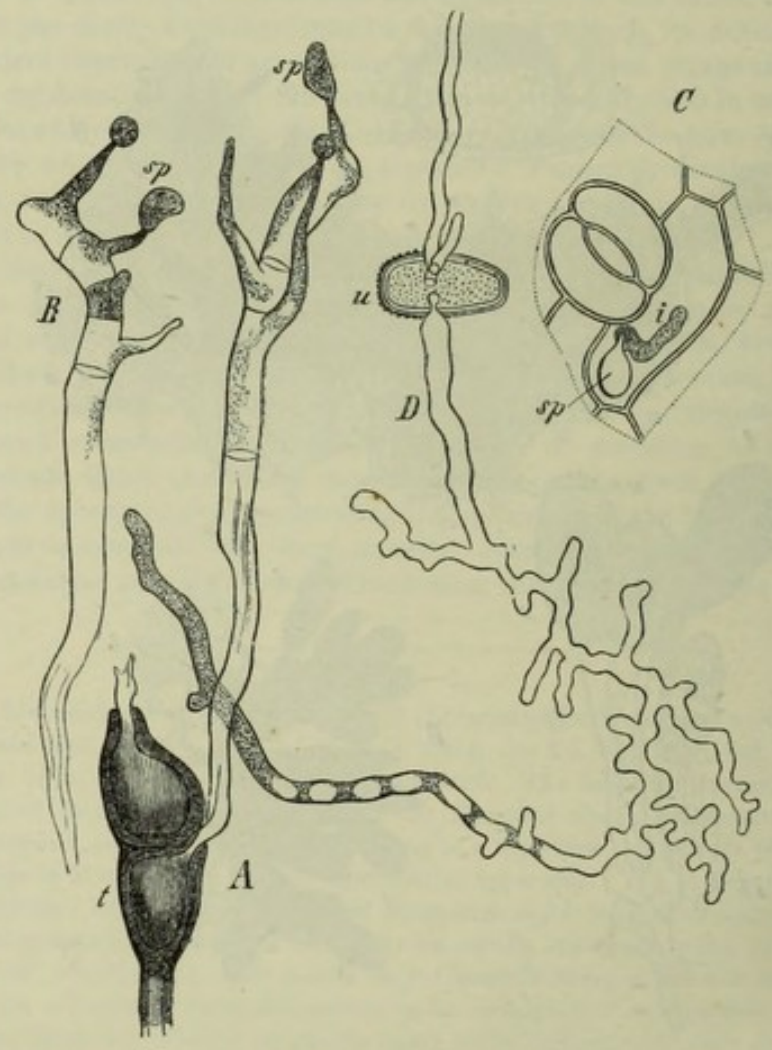

FIG. 171.—*Puccinia graminis*; *A* germinating teleutospore *t*, the pro-mycelium of which forms the sporidia *sp*; *B* a pro-mycelium (after Tulasne); *C* a piece of the epidermis of the lower surface of the leaf of *Berberis vulgaris* with a germinating sporidium *sp*; *i* its germinating filament penetrating the epidermis; *D* a germinating uredospore 14 hours after dissemination (after De Bary, *l. c.*).

penetrate into the interior through the stomata. While the Fungus is multiplying in this manner for several generations on Grasses during the summer in its uredo-form, the production of a new form of spores begins in the older uredo-fruits; long two-celled spores, the *Teleutospores*, being also formed near the roundish uredo-spores (Fig. 170, *III*, *t*). The formation of uredo-spores in the uredo-fruits then entirely ceases, and teleutospores only are produced (Fig. 170, *II*), and with them the period of vegetation closes. The teleutospores persist on the grass-haulms through the winter, and do not germinate till the spring; they emit from their two cells short septate germinating filaments (Fig. 171, *A*, *B*), at the ends of which, on slender branches, the *Sporidia* are produced. These sporidia develope a new mycelium only when they germinate on the surface of the leaves of the barberry; but their mode of germination differs from that of

the other forms of spores, their germinating filaments penetrating, as in the Peronosporeæ, into and through the epidermis-cells (Fig. 171, *C*, *sp* and *i*), and thus reaching the parenchyma. They there form a mycelium which produces the swelling of the leaf constituting the first stage which we considered; this mycelium again generating spermogonia and æcidium-fruits. (If within the cycle of this alternation of generations a fertilisation or conjugation occurs, it must probably be looked for on the mycelium in the barberry leaf, so that the æcidium-fruit would be the result of it.)

III. The Basidiomycetes. Although the largest and most beautiful Fungi belong to this order, yet their course of development is at present only very imperfectly known. In contrast to the variety of form occasioned by the alternation of generations in most other Fungi, and to the singular phenomena of the mycelium of the Ascomycetes, it is very remarkable that similar processes have not yet been established in this class. The origin from the mycelium of the usually large receptacles, and their further development, are known in their more conspicuous features, as is also the mode of germination of their basidiospores; but the history of the mycelium before it forms the receptacle is still unknown[1]. I must therefore content myself with a few morphological explanations of the development of the latter in the most striking forms of the Hymenomycetes and Gasteromycetes[2].

(1) Among the **Hymenomycetes**[3] the best known and most abundant species are those commonly known as Mushrooms. The structure which is usually called the Fungus is the receptacle which sprouts from a mycelium vegetating in the ground, or on wood or some other substance. Usually, but not always, the cap (pileus) is stalked; on its under-surface the hymenial layer lies upon projections of the substance of the pileus of various forms. In the genus Agaricus these projections consist of numerous lamellæ attached vertically and running radially from the summit of the stalk to the margin of the pileus; in Cyclomyces the lamellæ form concentric circles; in Polyporus and Dædalea they anastomose in a reticulate manner; in Boletus they form closely crowded vertical tubes; in Fistulina they stand alone; in Hydnum the lower side of the pileus is covered with soft dependent spines like icicles, the surface of which bears the hymenium, &c. In many cases the receptacle is naked; in others the lower side of the pileus is covered with a membrane which is afterwards ruptured (velum partiale), or the pileus and stalk are both enveloped in such a membrane (velum universale); or finally, in a few species (Amanita) both are found. This formation of a volva or veil is connected with the entire growth of the whole receptacle; the naked pilei are originally gymnocarpous, those covered by a veil indicate the transition to the angiocarpous receptacles of the Gasteromycetes[4]. *Agaricus variecolor* is to a certain extent an intermediate form between those with naked pileus and those furnished with a universal veil. The receptacle in this species arises as a slender cone on the mycelium (Fig. 172, *I*, *a*, *b*), and consists of parallel hyphæ growing at the apex (*I*, *c*); an outer layer of hyphæ is present at an early stage surrounding the whole body like a loose envelope; afterwards the apical growth ceases, the branches of the hyphæ turn outwards beneath the apex (*II*, *III*) and thus form the pileus (*IV*), the margin of which continues to grow centrifugally; the lamellæ are formed on its under-surface, the distance of the margin of the pileus from the stalk increasing, and the loose peripheral layer of hyphæ becomes stretched (*IV*, *v*), and forming a rudimentary universal veil. An example of the formation of a stalked pileus with a partial veil is afforded by the common mushroom (*Agaricus campestris*). Fig. 173 shows at *A* a small

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[1] [See however Oersted, Quart. Journ. Micr. Sc. 1868, p. 18.—Ed.]

[2] [On the **Tremellini**, see Tulasne, Ann. des Sci. Nat. 1872, vol. XV, p. 215; Journ. Linn. Soc. vol. XIII, p. 31.—Ed.]

[3] On the doubtful forms of spores of some Hymenomycetes not produced on basidia, see De Bary, Morph. u. Physiol. der Pilze, p. 190. On *Exobasidium Vaccinii*, a very simple Hymenomycete, parasitic on Vaccinium, see Woronin, Berichte der naturf. Gesells. Freiburg, 1867, vol. IV, p. 397.

[4] For further details on these processes see De Bary, Morph. u. Physiol. der Pilze, p. 16.

piece of the greatly extended reticulately anastomosing mycelium (*m*), from which sprout a number of receptacles; these are at first solid pear-shaped bodies (*a*) composed of young hyphæ all similar to one another. At an early stage the tissue of hyphæ gives way beneath the apex, leaving an annular air-cavity (*II, l*), the upper wall of which forms the under-side of the pileus; and from this the radial hymenial lamellæ grow downwards (*III, l*), filling up the air-cavity. The hyphæ run from the base of the whole receptacle to the margin of the pileus, forming the outer wall of the air-cavity; the tissue lying in the centre elongates into the stalk (*IV, st*), while the distance from it of the margin of the pileus constantly increases; the hyphæ which lie beneath the air-cavity that contains the lamellæ become stretched in consequence, and separate from the stem from below upwards, forming a membrane (*V, v*), running from the upper part of the stem

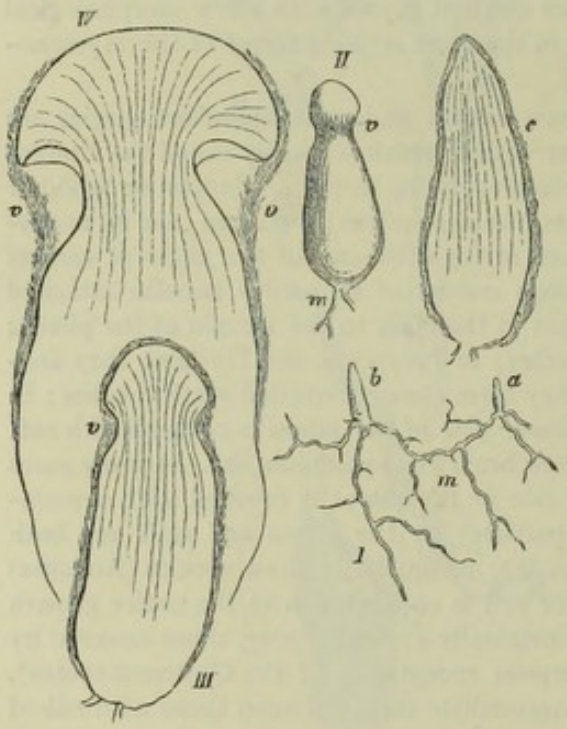

FIG. 172.—*Agaricus variecolor*. *I* mycelium *m*, with young receptacles *a b* (natural size); *c* longitudinal section of one of the latter (magnified); *II* an older receptacle, with commencement of the formation of the pileus; *III* the same in longitudinal section; *IV* a more mature pileus, *v* the veil. The lines in the sections indicate the course of the hyphæ.

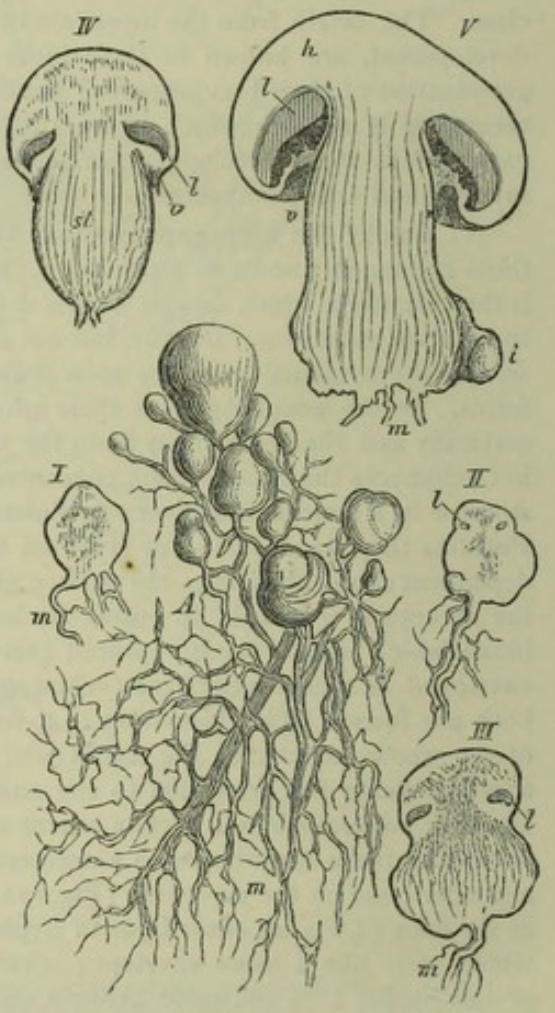

FIG. 173.—*Agaricus campestris* (natural size).

beneath the lamellæ to the margin of the pileus, into which their hyphæ are continued. When at length the pileus extends horizontally from the elongation of the tissues, the membrane (volva) becomes detached from its margin, and hangs from the stem like a ruffle. (Compare also Fig. 68, p. 81, *Boletus flavidus*.)

The hymenium, as has already been mentioned, covers the surface of the lamellæform peg-shaped or tubular projections of the under-side of the pileus. A transverse section of the latter across the hymenium gives, in all three cases, nearly the same figure, as is seen in Fig. 174, drawn from *Agaricus campestris*. *A* shows a piece of the disc of the pileus cut transversely, *b* the substance of the pileus, *l* the lamellæ; in *B* a piece of a lamella is more strongly magnified to show the course of the hyphæ. The substance of the lamella, called the *Trama* (*t*), consists of rows of long cells, which

diverge from the centre right and left to the outside, where the cells of the hyphæ are short and round, and form the sub-hymenial layer (*sh* in *B* and *C*). From these short cells spring the club-shaped cells (*q*), densely crowded and at right angles to the surface of the lamella, forming together the hymenial layer (*B*, *hy*). Many of these remain sterile, and are called *Paraphyses*, others produce the Spores and are the *Basidia*. Each basidium produces in this species only two, in other Hymenomycetes usually four spores. The basidium first of all puts out as many slender branches (*s'*) as there are spores to be formed; each of these branches swells at the end, the swelling increases and becomes a spore (*s''*, *s'''*), which falls from the stalk on which it was placed, leaving it behind (*s''''*).

On the formation of the tissue of this group only one further remark need be made; that in the receptacle of some Agaricineæ (*e.g.* Lactarius) some of the much-branched hyphæ are transformed into laticiferous vessels, from which large quantities of latex flow out when injured.

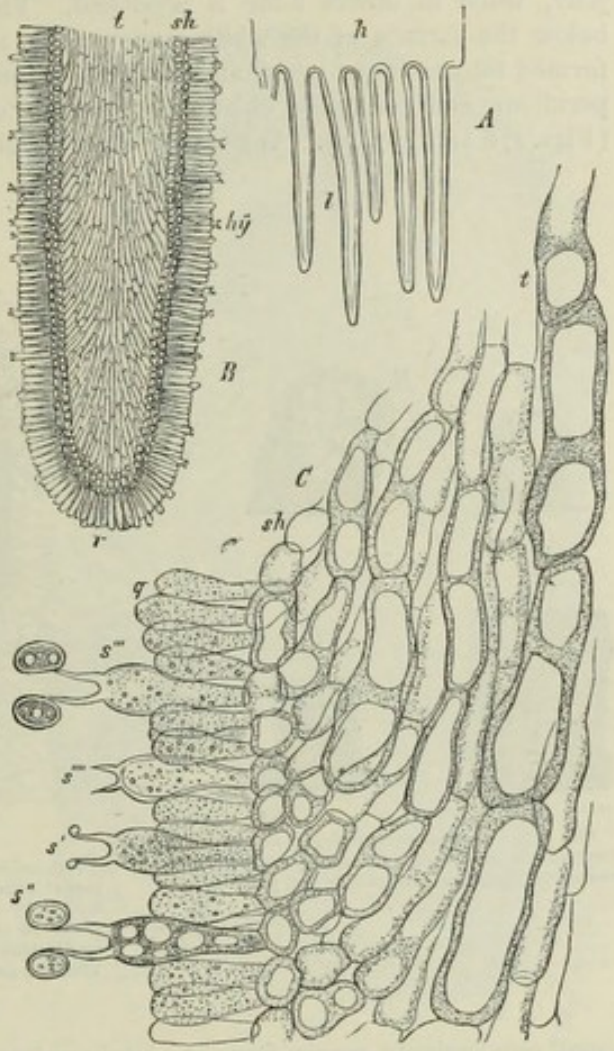

FIG. 174.—*Agaricus campestris*; structure of the hymenium; *A*, *B* slightly magnified; *C* a part of *B* (×350). The protoplasm is indicated by fine dots.

(2) The **Gasteromycetes** agree with the previous group in the mode of formation of their spores (eight spores are often produced on a basidium); but their receptacles are always angiocarpous. The hymenia are formed in the interior of the receptacle, which is at first usually spherical, or at any rate is not divided externally into distinct parts. The spores are disseminated by means of remarkable differentiations of the different layers, the growth of particular masses of tissue, or the simple bursting of the outer layer (the Peridium). The nature of these processes, which are extremely various in their external appearance, may be understood from two examples. The first example, *Cruci-bulum vulgare*[1], is selected from the beautiful **Nidularieæ**[2]. The mycelium forms a small white crust of branched hyphæ, which creep over the surface of wood. In the middle of the crust the filaments are interwoven into a roundish body, the rudiment of the receptacle; this grows by the intercalation of new branches of the hyphæ, and gradually assumes a cylindrical form. The outer threads form at an early stage yellowish-brown branches, which are again branched and directed outwards, forming a dense covering of hair. While the receptacle is becoming changed into a cylinder, a large number of brown threads shoot out from it externally to this (Fig. 175, *C*, *rf*), which form a firmly-woven layer, the outer peridium, and on the outside a dense mass of

[1] Compare Sachs in Bot. Zeitg. 1855.

[2] [See also Tulasne, Annales des Sci. Nat. 1844, vol. I, p. 1.]

erect hairs. The walls of the hyphæ of this part assume a dark colour, but the inner tissue remains colourless (Fig. 175, *A*); its apex increases in breadth, the hairs separate from one another, and the outer peridium ceases to exist at the apex (Fig. 176, *ap*). In the meantime the differentiation of the tissue commences in the interior of the Fungus, which is at first formed of densely-woven much-branched hyphæ, enclosing amongst them a considerable quantity of air which gives the whole a white appearance. Certain portions of the air-containing tissue become mucilaginous and freed from air; between the threads is formed in some places a hygroscopic transparent jelly, while in others none is produced. The conversion into mucilage begins first below the surface of the white nucleus (Fig. 175, *A*), and its outer layer is thus transformed into an inner peridium which is a colourless sac protruding from the dark outer peridium, and composed chiefly of branches of hyphæ running longitudinally upwards (Figs. 176 and 177, *ip*). While this differentiation is proceeding from below upwards,

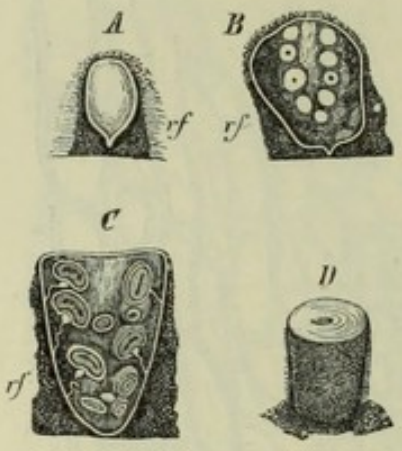

FIG. 175.—*Crucibulum vulgare*: *A*, *B*, *C* in longitudinal section (slightly magnified); *D* the entire plant nearly mature (natural size).

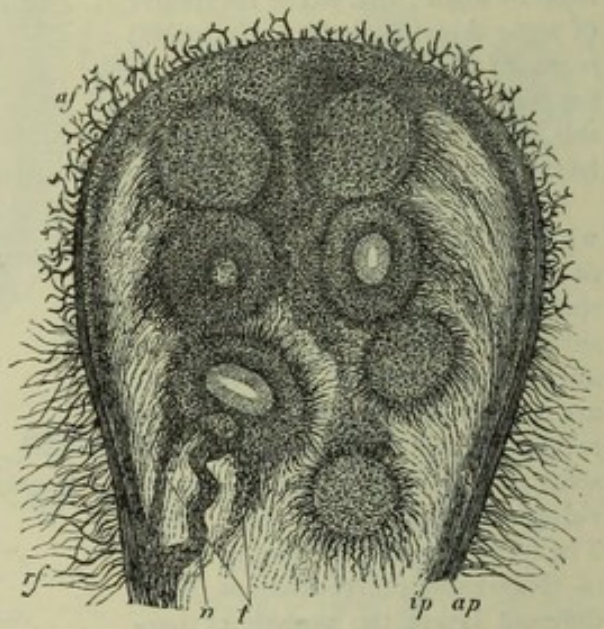

FIG. 176.—*Crucibulum vulgare*; longitudinal section through the upper part of a young receptacle (× about the same as Fig. 175, *B*). The section is seen by transmitted light; the dark parts in the interior are those where air occurs between the hyphæ; at the light parts a transparent mucilaginous substance free from air has formed between the hyphæ. The light parts of this figure are dark in the previous one.

small mucilaginous areolæ form at certain points in a deep layer of the white air-containing nucleus, also proceeding from below upwards, like all the succeeding differentiations (Fig. 175, *B*, and Fig. 176). The formation of mucilage advances at the same time from the inner peridium inwards, and leaves round each of the mucilaginous areolæ a border of air-containing tissue (Fig. 176), which afterwards developes, by the dense interweaving of its branched hyphæ, into a firm envelope consisting of two layers, in which the mucilaginous areola lies. For want of a better term, it may be called the Sporangium. While the centre of the Fungus is becoming changed into mucilage, the sporangia grow into lenticular bodies; a mucilaginous point has appeared at an early stage on the lower and outer part of each sporangium, and forms its umbilicus. From it a denser bundle of threads runs downwards to the peridium, the umbilical bundle (Fig. 176, *n*, and Fig. 177, *ns*); this is itself surrounded by a conical bag (*t*) which surrounds the bundle like a loose sheath. This sheath eventually becomes mucilaginous; the bundle runs upwards into the mucilaginous depression of the umbilicus, where it is resolved into its threads which are now more loosely connected. The mucilaginous tissue in the interior of each sporangium disappears, leaving a lenticular space similar in form to the sporangium itself;

and from the inner layers of the hyphæ of the sporangium branches now arise which are directed inwards and form the hymenium. Each sporangium is therefore clothed on its inner surface by a hymenial layer formed of paraphyses and basidia; each of the basidia produces four spores on short stalks. As the Fungus matures, the upper part of the peridium becomes stretched and flat, forming the Epiphragm, it afterwards ruptures and disappears, and the Fungus thus opens into a cup. The mucilage which surrounds the sporangia dries up, and the sporangia now lie free in the cup formed by the peridium, held by their umbilical bundles, which, when moistened, may be drawn out into long threads. If we imagine the sporangia more numerous and more closely packed and with less dense walls, we obtain an explanation of the roundish cell-like loculi which occur in the receptacles of other Gasteromycetes (as Octaviania, Scleroderma, &c.).

Still more remarkable are the changes produced in the **Phalloideæ** by internal differentiation of the tissues; but of these only the most important points can be illustrated in the case of *Phallus impudicus*. Here also the young receptacle, formed on the underground perennial mycelium which consists of thick threads, is at first a homogeneous convolution of threads, in which the differentiation begins and advances during growth. When the body has attained the size and form of a hen's or even a goose's egg, a longitudinal section gives the appearance represented in Fig. 178. The tissue consists at this time of different portions which may be classified into four groups — (1) The Peridium, composed of an outer firm, thick, white membrane (*a*), of an inner white, firm, but thin membrane (*i*), and of an intermediate thick layer of mucilaginous hyphæ (*g*) (the gelatinous layer). (2) The Spore-forming apparatus or Gleba (*sp*), bounded on the outside by the inner peridium (*i*), on the inside by a firm thick layer (*t*) from which walls project outwards united in a honeycomb manner dividing the gleba into a number of chambers. In these chambers the fertile branches of the hyphæ are found in great numbers, and on their basidia are formed four or more spores; so that, when ripe, the dark-green gleba appears to consist almost entirely of spores. (3) The Stem (*st*), formed of air-containing tissue hollowed into a large number of very narrow chambers; it is hollow, that is, its axial portion is transformed into a deliquescent jelly; the canal thus formed is open above in some individuals, in others it is closed by the inner peridium. (4) The Cup (*n*) forms a low broad column of firmer tissue, the outer part running upwards into the inner peridium, and sending up at the same time a layer which becomes softer between the stem and the inner membrane of



FIG. 177.—*Crucibulum vulgare;* longitudinal section through the upper part of the right side of the mature receptacle, showing the course of the filaments; for the sake of clearness the number of filaments has been reduced and their thickness increased.

the gleba (*t*); the base of the cup is continuous with the outer firm peridium. In this state the spores ripen; but for the purpose of their dissemination a great elongation of the stem (*st*) takes place; the peridium is ruptured at the apex, the gleba becomes detached from the inner peridium, this latter splitting at *x*, and the membrane *t* becoming detached below. The gleba is by this means raised up high above the peridium on the apex of the stem, while the stem attains the height of from 6 to 12 inches. This elongation is brought about by the widening of its chambers, which give the mature stem the appearance of a coarsely porous sponge; it increases in thickness in proportion to its increase in length. The spores now drop off the gleba in masses, the sporiferous hyphæ deliquescing into thick tenacious mucilage; till at last nothing remains of the gleba but the membrane (*t*) with its honeycombed walls, which depends like a frill from the apex of the stem, and is called the Pileus. The peculiarities in the detail of these processes exhibit the greatest variety in different species of the Phalloideæ, which may be investigated in Corda, *l. c.*, and De Bary, *l. c.* p. 84.

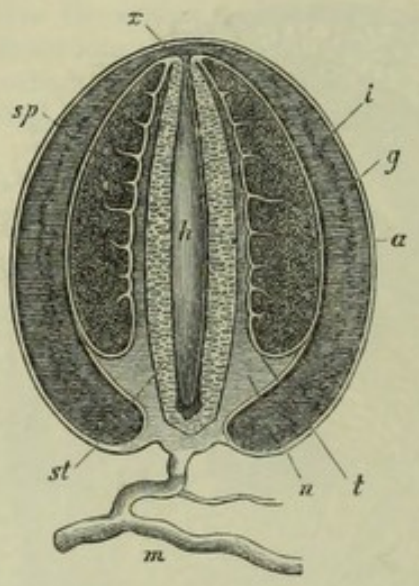

FIG. 178.—Longitudinal section of a nearly ripe plant of *Phallus impudicus* immediately before the elongation of the stem (⅔ the natural size); *a* outer layer of the peridium; *g* its gelatinous layer; *i* inner peridium; *st* the stem of the pileus *t* not yet elongated, covered by the white honeycomb-like ridges; *sp* the dark-green mass of spores (gleba); *h* hollow cavity of the stem, filled with watery jelly; *n* the cup in which the base of the stem remains after its elongation; *x* the place where the inner peridium becomes detached by the elongation of the stem; *m* mycelial thread.

IV. The ASCOMYCETES comprise a greater variety of forms than any other order of Fungi. Commencing with very simple forms comparable to some unicellular Algæ, as Endomyces, Saccharomyces, and Exoascus, they ascend to the truffles, morells, and Sphæriaceæ with receptacles formed of great masses of hyphæ, the internal and external structure of which is so various that a comprehensive description of them is impossible. The common characteristic by which all these different forms are connected is the asexual formation of spores in the interior of sacs by free-cell-formation. The Ascospores, however, belong only to one generation in the cycle of development of a species; for in large sections of the Ascomycetes there occur in addition Stylospores of a very different nature. The course of development generally shows in these cases a greater variation within a single species than occurs among the Hymenomycetes; and in many cases an alternation of generations has already been recognised, in so far as the receptacles in which the ascospores are produced owe their origin to a conjugation or sexual union which takes place on the mycelium (as in Erysiphe, Peziza, Ascobolus, Eurotium, &c.). Want of space compels me to limit my special descriptions to examples of only a few families of the order.

(1) The simplest forms of the Ascomycetes are the *Yeast-fungi* or Ferments of the genus **Saccharomyces**[1], which cause the alcoholic fermentation of the saccharine juices of plants (must, cider, &c.), of beer or of artificial solutions which contain sugar in addition to nitrogenous substances (albuminoids or ammonia-compounds) and mineral substances which form the food of plants. These Fungi consist of small roundish or ellipsoidal cells, which grow in fluids, and, in nourishing themselves, cause their decomposition, with formation of alcohol, carbonic acid, and other substances. Each

[1] Max Rees, Botan. Unters. über die Alkoholgährungspilze. Leipzig 1870. [Compare also Huxley on Yeast, Contemp. Rev. Dec. 1871; Pasteur, New Contributions to the Theory of Fermentation, Comptes Rendus, 1872, pp. 784–790, and Quart. Journ. Micr. Sc. 1873, p. 351.]

yeast-cell produces similar new cells by the protrusion of small projections at first resembling warts, which soon attain the form and size of their mother-cell, and sooner or later become detached from the narrow points of union. Usually they remain for a time united, and thus form combinations of shoots which may perhaps be considered as branched hyphæ with short, roundish, easily detached segments. When the supply of nourishment is less abundant,—for instance, when the yeast is grown on cut slices of potato, turnip, Jerusalem artichoke, or carrot, the yeast-cells grow to a more considerable size, their protoplasmic contents produce, by free-cell-formation, from 1 to 4 roundish spores, which, when placed in a fermentable fluid, immediately form new yeast-cells by branching and the detachment of the terminal cells. The fermentation of beer is produced by *Saccharomyces Cerevisiæ*, which occurs in two (cultivated) varieties, as yeast of the lower fermentation, which take place between 4° and 10° C., and as the yeast of the higher fermentation, which takes place at higher temperatures. The fermentation of wine and cider is caused by *S. ellipsoideus*, *conglomeratus*, *exiguus*, *Pastorianus*, and *apiculatus*, which are formed, together with other Fungi, on the surface of fruits, and thus find their way into the expressed juice[1].

(2) The **Tuberaceæ** form, like most Gasteromycetes (with which they may easily be confounded by the beginner), roundish, tuberous, bodies usually underground and often surrounded by the copiously branched mycelium. Nothing is known of the first appearance of the receptacle from the mycelium, and the development of the mycelium from the spore has also not been followed; no other kinds of spores than the ascospores have been met with. The receptacle is always angiocarpous. It consists, when mature, of an outer more or less thick peridium, in which an inner and an outer layer are usually distinguishable, the latter often provided with beautiful protuberances, and of a tissue of hyphæ enclosed within it, on branches of which the asci are formed. A very simple structure is shown in Hydnobolites. The receptacle here consists of a tissue formed of densely woven hyphæ, in which are everywhere imbedded numerous spore-mother-cells placed upon the branches of the hyphæ. Only the superficial layer of tissue, consisting of a fine down of sterile hyphæ[2], forms a kind of peridium. In Elaphomyces, where the peridium is firm and more highly developed, a mass of slender hyphæ with long cells springs from its inner side in every direction; here and there these are united more densely into larger discs and bundles projecting inwards; but there is no gleba divided into closed chambers. The cavities left in the tissue formed of slender filaments are everywhere loosely filled by the hymenial tissue, which consists of hyphæ 2 or 3 times thicker, formed of shorter cells, much bent and woven into balls, and bearing the asci on the ends of their branches. When ripe the whole hymenial tissue dissolves into jelly and disappears, while the mass of slender filaments remains as a delicate Capillitium between the loose dust consisting of spores. In another group a sterile matrix may be distinguished in the interior with a number of groups or nuclei of hymenial tissue imbedded in it, in which are again imbedded a number of asci springing irregularly from the ends of the branches. In Balsamia there is a thick peridium, and the interior is divided into many narrow curved air-containing chambers by means of thick plates of tissue which spring from the peridium, like the partition-walls of the Hymenogastreæ among the Gasteromycetes. To this is also related the genus Tuber; but the chambers clothed with the thick hymenium are very narrow, and much curved

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[1] [**Protomyces**, *P. macrosporus*, infests the foliage of some species of Umbelliferæ. Its mycelium is coloured blue by Schultz's solution and produces spherical asci, which enclose great numbers of minute spores. These spores conjugate in pairs, and the zygospore emits a germinating filament, which penetrates the epidermis of the host, and developes a new mycelium producing a new series of asci. See De Bary, Beiträge zur Morph. der Pilze, 1 Heft.—Ed.]

[2] This and what follows is after De Bary, Morph. u. Physiologie der Pilze, p. 91.—Compare also Tulasne, Fungi Hypogæi. Paris 1857.

and branched. The section of a truffle shows a dark matrix (the fertile tissue), in which run two kinds of branching veins;—the one opaque and destitute of air, composed of the main branches of the fertile hyphæ, spring from the inner surface of the peridium; the other white and air-conducting are prolonged to its outer surface. Hyphæ of the adjacent tissue begin to grow into these last-mentioned cavities from an early period, and have a white appearance in consequence of the presence of air filling up the spaces between them. The peridium of truffles is a strong shell consisting of pseudo-parenchyma, the outermost cell-walls of which are usually of a brown or black colour. The Asci of the Tuberaceæ are globular; and the spores, furnished with spines or honeycomb-like projections of the exospore, arise in indefinite numbers during a considerable period, and are without nuclei. The formation of spores shows some peculiarities, which are described by De Bary (*l. c.* p. 106; *cf.* also Tulasne, Fungi Hypogæi)[1].

(3) The **Pyrenomycetes**[2] usually produce in their asci, which are mostly long and club-shaped, eight spores formed simultaneously; they are not unfrequently septate. The asci are formed in the interior of small flask-shaped or roundish receptacles, which are here termed *Perithecia*. The contents of the perithecium are at first a delicate transparent tissue containing no air, which afterwards becomes compressed by the asci and paraphyses. These spring from a hymenium which clothes the wall of the perithecium or includes only its basal portion. The perithecia are either open from the first (in *Sphæria typhina*), or they are at first closed and afterwards form an orifice clothed with hairs, through which the spores escape (as in Xylaria); or finally the perithecium is ruptured to admit of their dissemination (*e. g.* Erysiphe). In one series of forms (Sphæriæ simplices, Pleospora, Sordaria, &c.) the perithecia originate singly or in groups from the filamentous inconspicuous mycelium; in others (as Claviceps), a so-called *Stroma* is first formed, *i. e.* a pillow-shaped, cap-shaped, arborescent, or cup-shaped receptacle, in which the perithecia usually arise in large numbers (Fig. 811). Besides the ascospores in the perithecia, other forms of spores are also produced by separation from the ends of filaments; *viz.* (1) *Conidia* (also septate) on filiform receptacles which spring from the mycelium or the stroma (Fig. 180, *c*); (2) *Stylospores*, essentially like the conidia (simple or septate), formed in the interior of conceptacles which are termed *Pycnidia*; and (3) *Spermatia*, formed in masses in depressed receptacles (Spermogonia), usually very small, often bacilliform or bent, apparently not capable of germination, and similar in their origin to the conidia and stylospores. The different forms of spores do not usually appear at the same time either on the same mycelium or the same receptacle; generally first conidia, then spermogonia, then pycnidia, finally perithecia, although each member of the series (except the perithecia) may be absent.

According to the most recent investigations of De Bary, Woronin, and Fuisting, it is probable that the perithecia of the Pyrenomycetes are always the result of a development caused by a peculiar sexual union not unlike that of the Florideæ. At present this has only been observed with certainty by De Bary in the genera Eurotium and Erysiphe; but in other genera very dissimilar in other respects to these, *viz.* in Sordaria and in *Sphæria Lemannea*, Woronin found similar processes of development on the

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[1] [**Onygenaceæ** are developed on animal substances, as feathers, horns, hoofs, hair, &c. The form of the general receptacle is that of a small round-headed nail. Externally it is smooth and the peridium is brittle, filled with branched threads producing asci at different points, which are soon absorbed, setting free the sporidia. See Berkeley, Outlines of Cryptogamic Bot. p. 272; Tulasne, Ann. des Sci. Nat. 1844, vol. I.—Ed.]

[2] Tulasne, Selecta Fungorum Carpologia. Paris 1860–65.—Woronin and De Bary, Beiträge zur Morph. u. Phys. der Pilze, 3rd series (on Sordaria, Eurotium, Erysiphe, &c.). Frankfort 1870. —Fuisting, Bot. Zeitg. 1868, p. 179.

mycelium, although the conjugation itself was not observed and the mode of origin of the asci remained doubtful. It is nevertheless certain that the receptacles of the last-named Pyrenomycetes are developed from an apparatus similar to the sexual organ of Eurotium and Erysiphe; and earlier statements of Fuisting contain at least indications that in other Pyrenomycetes also the perithecia may be the result of a sexual process.

Since the development of the Fungi belonging to this section undergo important modifications in the different genera, a comprehensive description would be altogether wanting in lucidity. I prefer therefore to explain the most important points in two very different examples.

One of the simplest of the Pyrenomycetes is *Eurotium repens* (Fig. 179); and but very slightly differing from Eurotium is *Aspergillus glaucus*, the history of whose de-

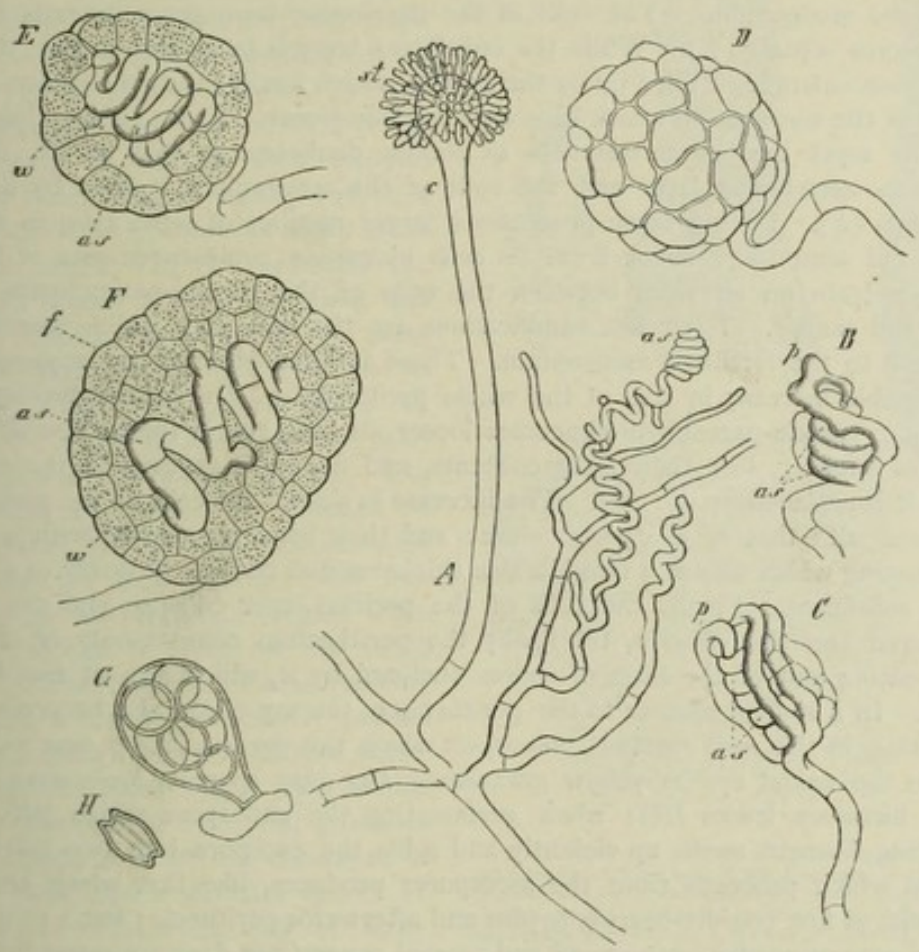

FIG. 179.—Development of *Eurotium repens* (after De Bary). *A* small portion of a mycelium, with the conidia-bearing hyphæ *c* and young ascogonium *as*; *B* the spiral ascogonium *as* with the antheridium *p*; *C* the same, beginning to be surrounded by the threads out of which the wall of the perithecium is formed; *D* a perithecium; *E*, *F* section of young perithecia, *w* parietal cells, *f* pseudo-parenchyma, *as* ascogonium; *G* an ascus; *H* an ascospore.

velopment has been described in detail by De Bary. Both species are found on the most various decaying or dead organic bodies, and are especially abundant on preserved fruit. The Fungus makes its appearance as a fine flocculent white mycelium overspreading the surface, from which the upright conidia-bearing hyphæ soon rise in large numbers. These swell in the upper part into a globular form, and on the upper half of the globe give rise to a number of peg-shaped projections, densely crowded and arranged radially, the *Sterigmata*, each of which produces gradually a long chain of greenish spores; so that finally the head of the receptacle is covered by a thick layer of them. During this formation of conidia, the sexual organs appear on the same mycelium. The female organ, called by De Bary the *Ascogonium* or Carpogonium, is the corkscrew-like end of a branch of the mycelium (Fig. 179, *A*, *as*), the coils of which become gradually

closer, until, when actually in contact, they form a hollow spiral (*B*, *C*). During this process about as many thin septa are formed as there are turns of the helix (*i. e.* 5 or 6). From the lowest coil of the ascogonium two slender branches now shoot out at opposite places, which grow upwards on the outside of the helix; one of these developes more quickly, reaches the uppermost coil, and becomes closely attached to it by its apex (*B*, *p*). This branch is the *Antheridium* (Pollinodium of De Bary). Conjugation takes place between its apex and the ascogonium, the cell-wall being absorbed at the point of contact, and the protoplasmic contents of the ascogonium and of the antheridium commingling. Soon afterwards new filaments sprout out from the lower part of the antheridium, as well as from the other branch, which increase in number, cling closely to the spiral (*C*), and finally entirely envelope it. From these filaments a layer of polygonal cells, the *Perithecium* (*D*), is formed by numerous transverse divisions, enveloping the ascogonium. The cells of the enveloping layer grow inwards as papillæ which become septate (*E*). While the enveloping layer is increasing in size, the cavity, which is thus enlarged, is filled up by the papillæ, which finally insert themselves between the coils of the ascogonium which have now become looser. These papillæ thus become divided by septa into numerous cells of similar diameter, so that at last the space between the enveloping layer and the coils of the ascogonium is filled by a pseudo-parenchyma (*F*). During these processes a larger number of septa arise in the ascogonium, and soon there shoot from its cells numerous commencements of branches, which penetrate on all sides between the cells of the pseudo-parenchyma, become septate, and ramify. Their last ramifications are the *Asci* (*G*), which therefore owe their origin to the fertilised ascogonium. These internal changes are accompanied by a considerable increase in size of the whole perithecium. During the development of the asci, the pseudo-parenchyma becomes looser, its cells round themselves off, become capable of swelling, lose their fatty contents, and finally disappear; in the ripe perithecium it is replaced by the asci. The increase in size of the cells of the parietal layer keeps pace with that of the perithecium; and they become covered with a sulphur-yellow coating which attains a considerable thickness and consists probably of a resinous or fatty substance. Finally the cells of the parietal layer collapse and dry up; the eight-spored asci also dissolve, till finally the perithecium consists only of the brittle yellow coating and of the mass of spores enclosed by it, which are set free by gentle pressure. In a similar manner to the perithecium, the mycelium also becomes covered by a coating, in this case chestnut colour, on which the perithecia are now individually visible to the naked eye as yellow granules. The ripe spores (*Ascospores*) have the form of biconvex lenses (*H*); when germinating the endospore which puts out the germinating filament swells up violently and splits the exospore into two halves. The mycelium which proceeds from the ascospores produces, like that which arises from the conidia, at first conidia-bearing hyphæ and afterwards perithecia; but a proper alternation of generations between sexual and asexual generations does not occur here[1].

For the different modes of origin of the perithecium in the Erysiphæ, Sphæriæ, and Sordariæ, I must refer to the treatises of Woronin and De Bary already mentioned, and now turn to the description of another pyrenomycetous Fungus the development and structure of which is much more complicated, *viz. Claviceps purpurea*[2], the Fungus which produces Ergot. Its development begins with the formation of a filamentous mycelium, which attaches itself to the surface of the ovary of Grasses, especially of rye, while still enclosed between the pales, covers it with a thick weft, and partially penetrates into its tissue, while the apex and often other parts of the ovary remain exempt

[1] [Brefeld appears to have obtained the perithecia of Penicillium. Bot. Zeitg. Apr. 5, 1872. —Ed.]

[2] Tulasne, Annales des Sci. Nat. vol. XX. p. 5.—Kühn's Mittheilungen des landw. Inst. in Halle, vol I. 1863.

from its attacks. The ovary thus becomes replaced by a soft white mycelial tissue which retains nearly its original form; the style being not unfrequently still borne on its summit. The surface of the tissue of the Fungus is marked by a number of deep furrows (Fig. 180, *A*, and *B*, *s*) and forms a large number of conidia on basidia arranged radially (*C*, *p*), imbedded in a mucilaginous substance which exudes between the pales. In this condition the Fungus had been at one time considered a distinct genus, and described under the name of Sphacelia. The conidia can germinate at once and immediately again detach conidia (*D*, *x*), which, according to Kühn, again produce a sphacelia in other Grasses. The mycelium of the sphacelia forms, when the production of conidia has reached its height, a thick felt of firmer hyphæ at the base of the ovary of the grass, which is at first still surrounded by the looser tissue of the sphacelia. This is the commencement of the Sclerotium or Ergot; its surface soon assumes a dark-violet colour, and grows to a horn-shaped body, often as much as an inch in length. In the meantime the sphacelia ceases to grow, its tissue dies and is ruptured beneath by the Sclerotium, and carried upwards on its summit, where it is placed like a cap (Fig. 180, *A* and *B*, *s*, sphacelia, *c*, sclerotium), and afterwards falls off. The hard ripe sclerotium now remains till the autumn, but is usually in a dormant state till the next spring; the formation of the receptacle begins when the sclerotium is lying on the damp ground. The receptacles arise beneath the skin, a number of closely packed branches being formed at definite points from the medullary hyphæ; the bundle breaks through the skin, and grows up to a receptacle or stroma consisting of a long stalk and a globular head. In the latter a large number of flask-shaped perithecia (Fig. 181, *B* and *C*, *cp*) appear, which do not possess a clearly-defined wall. Each perithecium is filled from the bottom by a number of asci, in each of which several slender thread-shaped spores are produced. These spores swell up in damp situations, and put out germinating filaments at several points. When they reach the young flowers of rye, or of other nearly allied grasses, Kühn states that the sphacelia arises from them, and the cycle of development is thus closed.

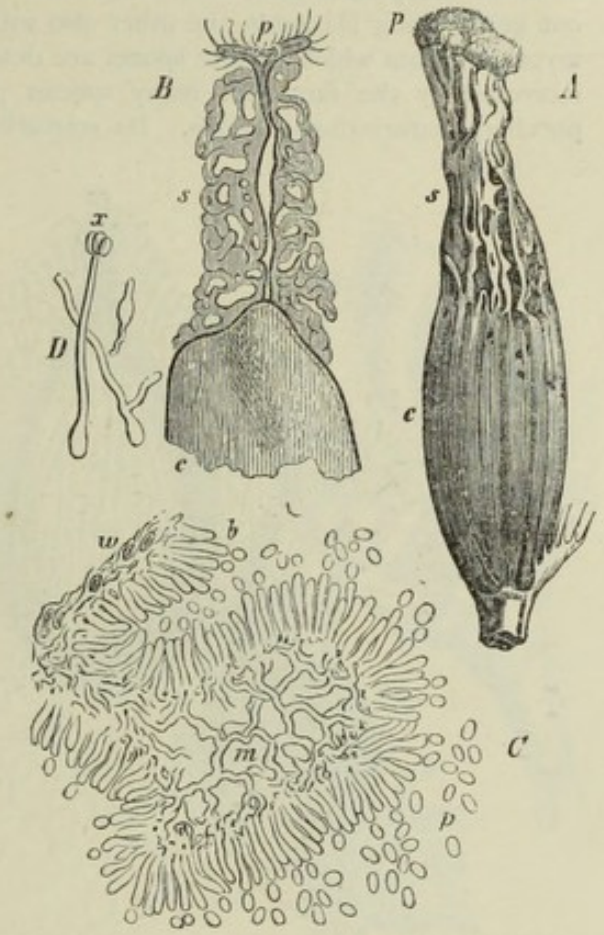

FIG 180.—*Claviceps purpurea*; *A* a young sclerotium *c* with the old sphacelia *s*; *p* the apex of the dead ovary of the grass; *B* longitudinal section of the upper part of *A*; *C* transverse section through the sphacelia, *m* its mycelium, *b* the branches from which the conidia are detached, *w* the wall of the ovary; *D* germinating conidia, forming secondary conidia *x*. (*A*, *B*, *C* after Tulasne; *D* after Kühn).

(4) The **Discomycetes**[1]. This section includes, together with a number of inconspicuous Fungi, the striking forms of the Helvelleæ and Morells, and the genus Peziza, enormously rich in species. In the two first-named genera the hymenial layer over-

[1] De Bary, Ueber die Fruchtentwickelung der Ascomyceten, Leipzig 1863, p. 11.—De Bary und Woronin, Beiträge zur Morphologie u. Physiologie der Pilze, 2nd series, pp. 1 and 82, Frankfort 1866.—Tulasne, Annales des Sci. Nat. 5th series, vol. VI. p. 247. 1866.—Janczewski, Bot. Zeitg. 1871, no. 18.

lays the surface of the folded pileus; in Peziza it clothes the concavity of the cup, which is either flat and sessile (Fig. 182) or stalked. The hymenium consists of paraphyses and asci, in which eight spores are usually formed simultaneously; the paraphyses generally appear earlier, but are finally crowded out by the asci. The spores sometimes possess nuclei, but are sometimes destitute of them (Fig. 182). The Discomycetes agree, however, with the Pyrenomycetes—from which they are principally distinguished by their gymnocarpous receptacles—in the occurrence of spermogonia, pycnidia, and conidia, as forerunners of the ascospores. In *Peziza Duriæana* two kinds of receptacles have even been observed, one with larger ascospores, which put out germinating filaments, the other also with ascospores, which, however, form a promycelium from which minute spores are detached. The variety of structure is further increased by the fact that many species produce sclerotia. *Peziza Fuckeliana* is a peculiarly interesting example. Its sclerotium is developed, according to De Bary, in

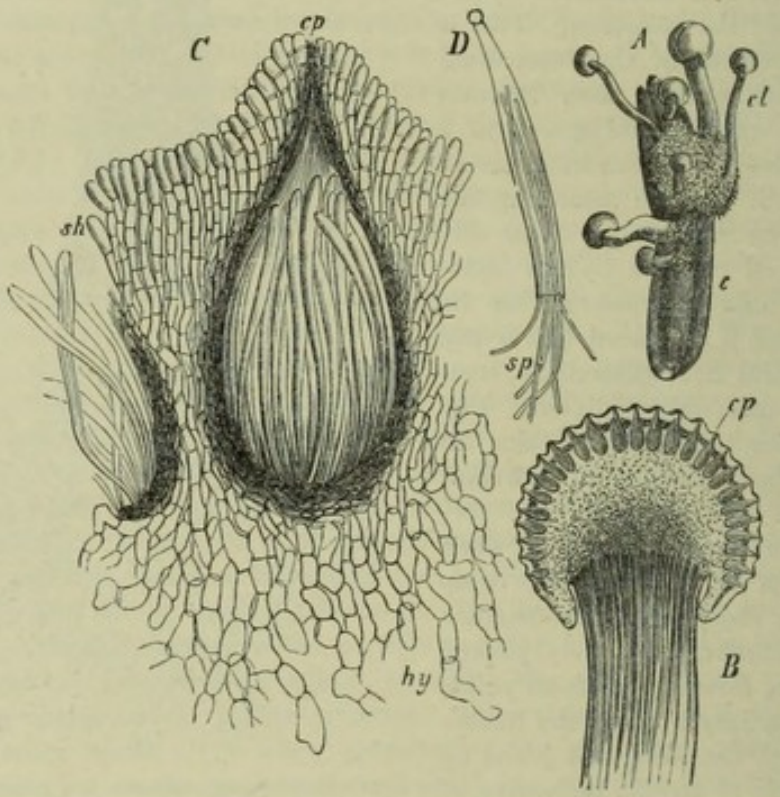

FIG. 181.—*Claviceps purpurea*: *A* a sclerotium forming a receptacle *cl* (ergot); *B* longitudinal section of upper part of a receptacle, *cp* the perithecia; *C* a perithecium with the surrounding tissue (greatly magnified); *cp* its orifice, *hy* hyphæ of the pileus, *sh* epidermal layer of the pileus; *D* an ascus ruptured and allowing the spores to escape (after Tulasne).

the tissue of decaying vine-leaves in autumn and winter; if it is placed when fresh, or after having been for some time at rest in the dry, upon the surface of damp ground, it begins after about twenty-four hours to put forth conidia-bearing hyphæ, and these prove to be identical with *Botrytis cinerea*. If, on the other hand, the sclerotium is buried beneath the surface of the soil to the depth of 1 cm., it does not put out conidia-bearing hyphæ of this kind, but produces, on the contrary, in the summer following its production, stalked trencher-shaped little cups, the ascus-bearing receptacles. Sclerotia sometimes again arise from the germinating filaments of the ascospores without any production of conidia. In other cases the mycelium which grows luxuriantly in the vine-leaves puts out Botrytis-threads at the same time that the formation of sclerotia takes place; from the germinating filaments of the conidia (of the Botrytis) De Bary always saw Botrytis again produced first of all, and its mycelium probably also forms sclerotia.

Like the perithecia of the Pyrenomycetes, the receptacles of the Discomycetes arise from a peculiar act of sexual union which takes place on the mycelium, so that the

mycelium is the sexual, the receptacle the asexual generation. This has indeed up to the present time been directly observed only in a series of the smaller species of Peziza and Ascobolus, but may well be assumed to exist also in the rest of the Discomycetes. In *Peziza confluens*, the species in which the sexual reproduction of the Ascomycetes was first discovered by De Bary in 1863, the process is as follows, according to De Bary's and Tulasne's exhaustive researches:—The mycelium of *P. confluens* grows on the ground; branches arise at particular points of its hyphæ which are directed

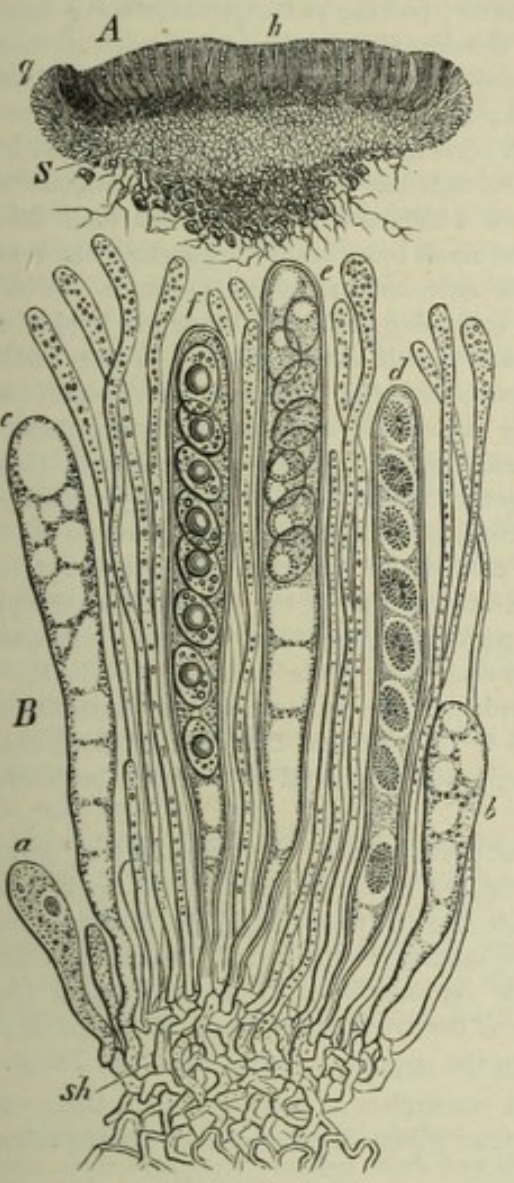

FIG. 182.—*Peziza convexula*; *A* vertical section of the whole plant (× about 20); *h* hymenium or layer in which lie the asci; *S* the tissue of the Fungus, surrounding the hymenium like a cup at its margin *q*; at its base fine filaments proceed from the tissue, which penetrate into the soil; *B* a small part of the hymenium (× about 500); *sh* sub-hymenial layer of densely interwoven hyphæ; *a*–*f* asci, with intermediate slender paraphyses, in which are red granules.

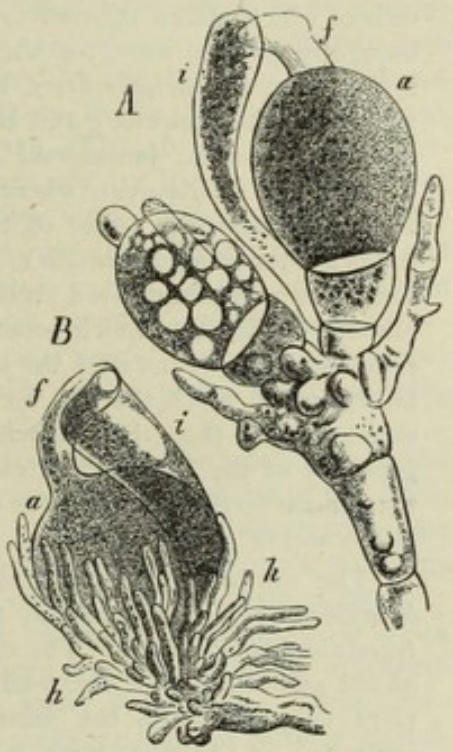

FIG. 183.—Conjugating apparatus of *Peziza confluens* (after Tulasne, very strongly magnified); in *B* is shown the commencement of the formation of hyphæ *h*, the result of fertilisation, from which the receptacle is developed.

upwards and again branch abundantly; at the end of the branchlets the organs of conjugation or fertilisation are produced in large numbers close together, forming rosettes. The terminal cells of the stronger branchlets swell up into ovoid vesicles (Fig. 183, *a*), which put out a usually crooked prolongation (*f*). From another cell of the same branch lying beneath this vesicle grows a club-shaped branchlet, the Antheridium, the apex of which (*i*) unites with the prolongation just mentioned. After this has taken place, a number of fine hyphæ (*b*) shoot out of the filament which

bears these organs, and these surround the rosette of the organ of conjugation, enclosing it in a dense felt. This felt forms the substance of the receptacle; upon its upper side densely crowded hyphæ immediately rise up to form the hymenial layer; finally the receptacle forms a Peziza-cup, which possesses somewhat the form represented in Fig. 183, and produces the ascospores in its hymenium. Woronin observed similar phenomena in *P. granulosa* and *scutellata*. In these species branches consisting of three or more cells arise from the mycelium; the terminal cell swells out into a globular or ovoid form, without, however, putting out a prolongation; from the cell lying beneath it arise two or more slender filaments which attach themselves closely to the former. By this means the conjugating apparatus is densely enveloped in numerous hyphæ which originate beneath it; and from them is developed the fruit-cup. In *Ascobolus pulcherrimus* the structure which corresponds to the structure *a f* in Fig. 183 consists of a vermiform body, which Tulasne calls the *Scolecite*. It is a branch of the mycelium, consisting of a row of short cells which are much broader than those of the mycelium. The adjacent threads put out small branches or Antheridia, the terminal cells of which attach themselves firmly to the anterior part of the scolecite. It is subsequently covered over, together with this fertilising organ, by branched hyphæ which spring from the neighbouring mycelium; and a ball is thus formed in the middle of which lies the scolecite; and this finally grows into the fruit-cup. To these observations of Woronin, Janczewski[1] has recently added the additional important fact that in *Ascobolus furfuraceus*, where the processes agree in other respects with those of *A. pulcherrimus*, the tissue of the cup, together with the paraphyses, proceeds from the branches of hyphæ which envelope the conjugating apparatus, and that, on the other hand, the asci are derived from a central cell of the scolecite. This cell puts out a number of filaments which penetrate between the meshes of the tissue of the receptacle, ramify extensively between the bases of the paraphyses, and there form the sub-hymenial layer, out of which the asci spring and grow up among the paraphyses. By this it is demonstrated that the scolecite corresponds to the ascogonium of Eurotium (and generally of the Pyrenomycetes); and it is to be expected that a structure similar to the female fertilising apparatus (Fig. 183, *a f*) will be proved to precede the formation of the asci of *Peziza confluens*.

The similarity of these processes to the formation of the reproductive organs of Florideæ, which I have already pointed out in the earlier editions of this book, was also recognised by De Bary. The chief difference lies in this—that in the Florideæ, instead of the antheridia, cells endowed with passive motion which detach themselves from the plant conjugate with the female organs of reproduction. The ascogonium (or the scolecite), on the other hand, is comparable to the trichophore in all the essential points by which both are at once distinguished from the oogonia of other Algæ and Fungi.

(5) LICHENS[2]. From the most recent researches of Schwendener[3], there can no longer be any doubt that the Lichens are true Fungi of the section Ascomycetes, but

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[1] [Annales des Sci. Nat. 1872, vol. XV, p. 198.]

[2] Tulasne, Mémoire pour servir à l'histoire organographique et physiologique des Lichens (Annales des Sci. Nat. 3rd series, vol. XVII).—Schwendener, Untersuchungen über den Flechtenthallus (in Nägeli's Beiträge zur wissensch. Botanik. 1860 and 1862.—Schwendener, Laub- u. Gallertflechten (Nägeli's Beiträge zur wissensch. Botanik. 1868).—Ditto, Flora 1872, nos. 11-15. [Quart. Journ. Micr. Sc. 1873, p. 235.]

[3] [The views of Schwendener have been corroborated by Bornet in an elaborate memoir published in the Ann. des Sci. Nat. 1873, vol. XVII. He also put them to a synthetical test by sowing the spores of *Parmelia parietina* upon Protococcus. About the fifteenth day the hyphæ were well developed and ramified. Wherever they met isolated cells of Protococcus or groups of them, they attached themselves either directly or by means of a lateral branch. They did this to the Protococcus only, neglecting altogether the other bodies which were mixed with it. Similar results

distinguished by a singular parasitism. Their hosts are Algæ, which grow normally in damp places but not actually in water, and belong, moreover, to very various groups (rarely Confervaceæ, frequently Chroococcaceæ and Nostocaceæ, more often Palmellaceæ, sometimes Chroolepus). The Fungi themselves (Lichen-forming Fungi) are not found in any other form than as parasites on Algæ; while the Algæ which are attacked by them, and which, when combined with the Fungus, are called *Gonidia*, are known in the free condition without the Fungus. When the species attacked by the Lichen-fungus is a filamentous Alga, and the development of the hyphal tissue is only moderate (as in Ephebe and Cœnogonium), the true state of the case is at once clear; and as Lichens of this kind have become better known, the suspicion has frequently arisen that they are in fact only Algæ infested by Fungi. In the Collemaceæ also attention has frequently been drawn to the identity of the gonidia with the moniliform filaments of Nostocaceæ; but in this case the nourishing Alga usually undergoes considerable changes of habit, at least in its external contour, from the influence of the parasitic Fungus, like *Euphorbia Cyparissias* from its parasitic Æcidium. But the greater number of Lichen-fungi prefer as hosts the Chroococcaceæ and Palmellaceæ which grow as stains and incrustations on damp ground, the bark of trees, and stones. The separate cells and groups of cells of these Algæ become so involved by the tissue of the Fungus, that they are at last only interspersed here and there in the dense hyphal tissue, or appear in it as a peculiar layer (the gonidial layer). The growth and multiplication of these Algæ, which thus become entirely enclosed by their parasites, is not hindered, but their development is disturbed in other ways. When, however, they are freed from their enclosing Fungus-tissue, their normal development proceeds, and in a few cases even the formation of zoospores takes place in them, a fact first observed by Famintzin and Baranetzky, but incorrectly explained. It is to Schwendener's knowledge of the facts, the result of researches extending over many years, that the correct interpretation is due in these cases of the relationship borne by the Lichen-forming Fungus to the gonidia, *i. e.* to the Alga which it attacks[1].

After these preliminary remarks the following description will be intelligible to the beginner. It is transferred, with but slight alterations, from the first edition of this book. We will consider first the Lichen as a whole, as it comes under observation, the nourishing Alga being distinguished as an elemental form of the thallus under the name Gonidia; and will afterwards discuss the nature of the nourishing Algæ more in detail.

The *Thallus* of Lichens is commonly developed in the form of incrustations which cover stones and the bark of trees, or penetrate between the lamellæ of the epidermis of woody plants, and then expose only the receptacles above the surface. These Crustaceous Lichens, as they are termed, have become so completely united in their growth

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were obtained when the spores of *Biatora muscorum* were sown upon Protococcus. Spores of Parmelia sown separately ramified much less and developed no chlorophyll; Protococcus, on the other hand, during the same period remained unchanged and put out no hyphæ. Tulasne, however, sowed the spores of Lichens and believed that he twice detected the formation of gonidia upon the hyphæ (Ann. des Sci Nat. 1852, XVII, pp. 96-98). De Bary indeed described the green gonidium as originating by the expansion of a short lateral branch of the hypha into a globular cell, which is shut off by a septum and assumes a green colour; once formed, it increases independently by division, and a number of the gonidia eventually lie without stipites in the interstices of the Lichen-tissue (Morph. u. Phys. der Pilze, pp. 258, 263-265). Berkeley also believes that the gonidia originate from the hyphæ, having had 'a good opportunity of ascertaining their development from the threads of the mycelium in specimens developed within the vessels of pine wood' (Introd. to Crypt. Bot. p. 373). For a careful *resumé* of all the recent literature of the subject by Archer, see Quart. Journ. Micr. Sc. 1873, p. 217. In this country Bentham has criticised Schwendener's view (Address to Linn. Soc. May 23, 1873), and Thwaites and Berkeley have also expressed their dissent (Gard. Chron. 1873, p. 1341).—Ed.]

[1] A few additional historical notes will be found at the end of this section.

to their substratum, at least on the under side, that they cannot be detached completely from it without injury to the thallus (Fig. 184, *A*, *B*, *C*). The crustaceous Lichen-thallus passes over, through various gradations, into that of the Foliaceous Lichens; the latter

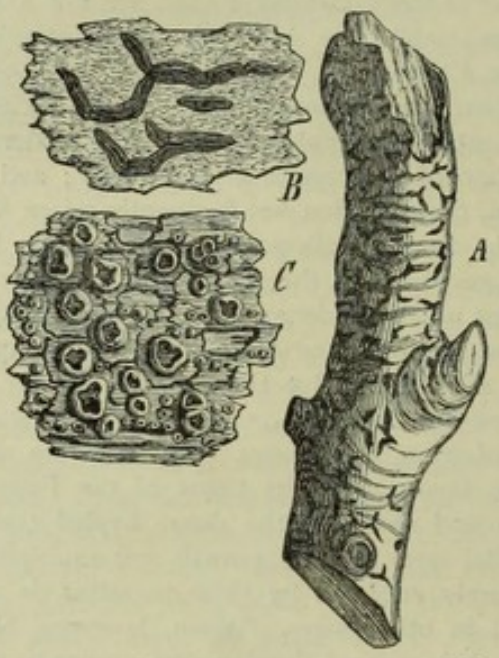

FIG. 184.—*A*, *B Graphis elegans*, a crustaceous Lichen growing on the bark of the holly; *A* natural size, *B* slightly magnified; *C Pertusaria Wulfeni*, another crustaceous Lichen (slightly magnified).

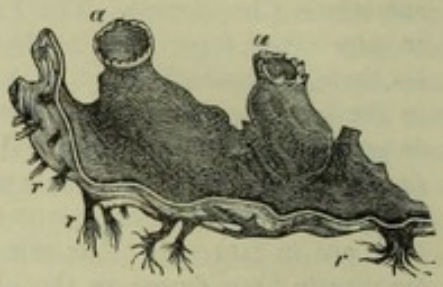

FIG. 185.—A piece of the foliaceous thallus of *Peltigera horizontalis*; *a* the apothecia; *r* the rhizines (natural size).

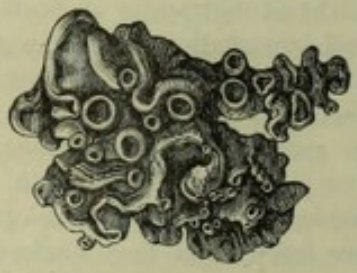

FIG. 186.—*Collema pulposum*, a gelatinous Lichen (slightly magnified).

forms flake-like expansions often curled, which can be completely detached from the ground, stones, moss, bark, &c., which support them, since they are attached to it only in places by a few organs of attachment, the *Rhizines*. The foliaceous thallus often

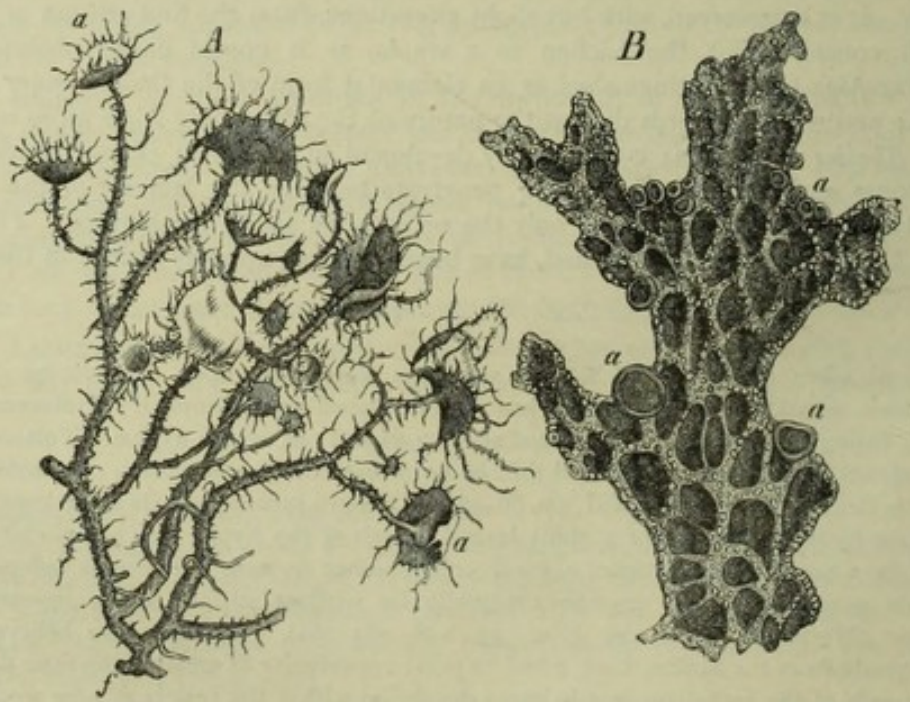

FIG. 187.—*A Usnea barbata*, a fruticose Lichen (natural size); *B Sticta pulmonacea*, a foliaceous Lichen (natural size) seen from beneath; *a* apothecia, *f* the attaching disc of *A*, by which the Lichen becomes attached to the bark of a tree.

attains considerable dimensions, in the large species of Peltigera and Sticta as much as a foot in diameter, and from $\frac{1}{2}$ to 1 mm. in thickness, and then generally assumes a circular form; at the growing margin it forms rounded indented lobes (Fig. 185 and Fig. 187, *B*).

A third form of the Lichen-thallus, also united with the previous one by transitional forms, is shown in the Fruticose Lichens, which are attached only at one spot and with a narrow base, and rise from it in the form of small much-branched shrubs. The branches of the thallus are either flat and ligulate, like the lobes of many foliaceous Lichens, or slender and cylindrical (Fig. 187). In Cladonia and Stereocaulon we have not so much a transition from the foliaceous to the fruticose thallus as a combination of the two, a foliaceous expansion of small size being first formed, the cup-shaped or fruticosely-branched thallus afterwards rising from this.

The thallus of Lichens can be dried so as to be pulverised without losing its vitality. When saturated with water it has generally a leathery consistence, is tough, elastic, and flexible; but a large number of genera, which are remarkable also in other ways, are slimy and gelatinous in this condition. These Gelatinous Lichens, as they are termed, form cushion-like masses with an undulated surface, and in their growth are sometimes more like the fruticose, sometimes more like the foliaceous Lichens. A typical form is shown in Collema, Fig. 186.

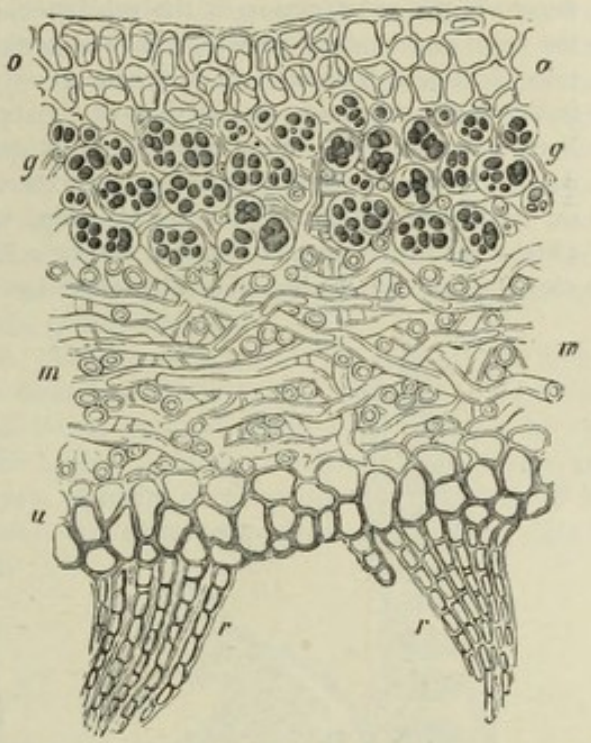

FIG. 188.—Transverse section through the foliaceous thallus of *Sticta fuliginosa* (×500); *o* cortical or epidermal layer of the upper side; *u* of the under side; *rr* rhizines or attaching fibres, springing from the epidermal layer and therefore trichomes; *m* the medullary layer, the hyphæ of which are seen cut, some transversely, some longitudinally. The upper and under cortical layers also consist of hyphæ, which however are much thicker, consist of shorter cells, and are united without interstices, forming a pseudo-parenchyma; *g* the gonidia (their light-green masses of protoplasm are coloured dark); each gelatinous envelope encloses several gonidia produced by division.

The disposition of the gonidia and hyphæ in a thallus may be such that these two structures appear about equally mingled (as in Fig. 189), and the thallus is in this case

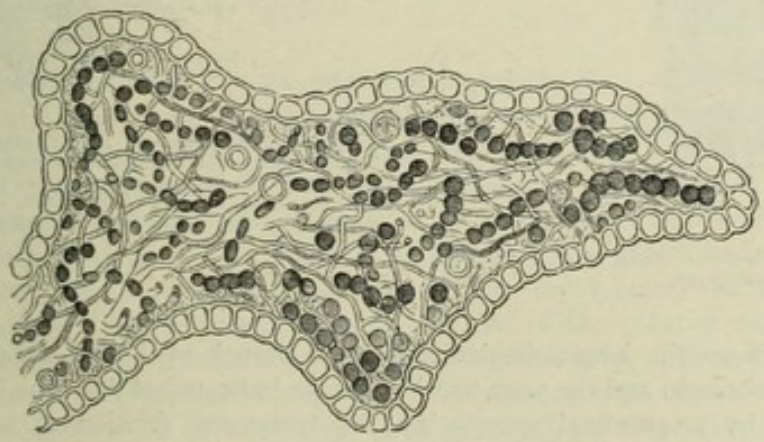

FIG. 189.—Vertical section of the gelatinous thallus of *Leptogium scotinum* (×500): an epidermal layer clothes the interior tissue, which consists mainly of shapeless and colourless jelly in which lie the coiled chains of gonidia; some of the larger cells of the chains are left white; between them run the fine hyphæ.

called Homöomerous; or the gonidia are crowded into one layer (as in Fig. 191), by which the hyphal tissue is at the same time separated according to circumstances into an outer and inner or an upper and under layer; the thallus-tissue is then stratified, and such Lichens are termed Heteromerous (Figs. 188 and 191).

The mode of growth, branching, and external structure of the Lichen-thallus may either be determined by the gonidia, the hyphæ being concerned only in a secondary degree in the construction of the substance, or it may happen that the hyphæ determine the form and mode of growth, while the gonidia have only a secondary share in the formation of tissue. The first mode occurs in only a few Lichens; the other mode of growth is the more common, and is that of the typical Lichens, especially of those that are heteromerous. In some homöomerous gelatinous Lichens (as Fig. 189) it appears doubtful whether the change in the external form proceeds more from the gonidia or from the hyphæ. This relationship, which, although both morphologically and physiologically important, has not hitherto had sufficient attention paid to it by lichenologists, will be made sufficiently clear by an examination of Figs. 190 and 192. In

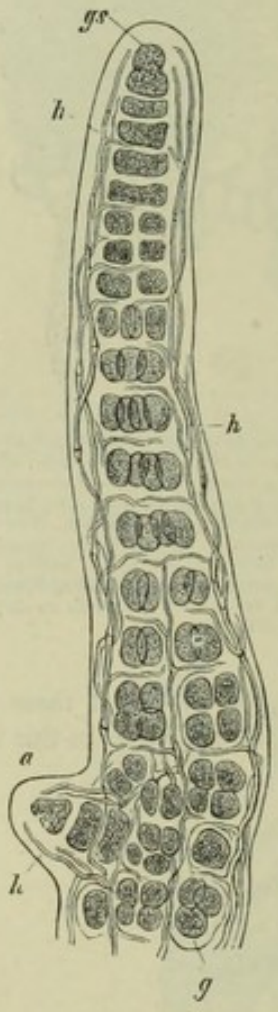

FIG. 190.—A branch of the thallus of *Ephebe pubescens* (×550).

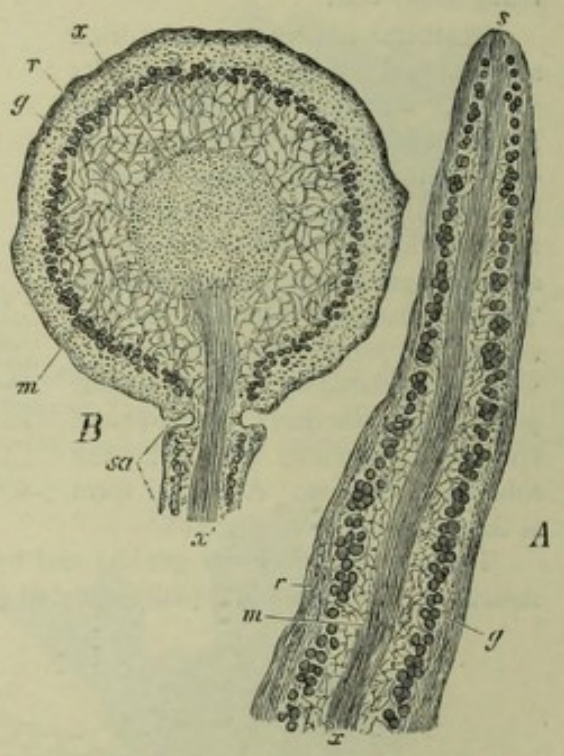

FIG. 191.—*Usnea barbata*; *A* longitudinal section of a slender branch, soaked in potash-solution; *B* transverse section of an older thallus-stem with the basal portion of an adventitious (or soredial) branch *sa* (×300); *s* apex of the branch, *r* the cortex, *x* the axial medullary bundle, *m* the loose medullary tissue, *g* the gonidial layer.

Fig. 190 is shown the longitudinal section of a branch of *Ephebe pubescens*; the large gonidia are left dark, and the very fine hyphæ are indicated at *h*. The branch increases at the apex by longitudinal growth and by transverse division of a gonidium (*gs*), which is here the apical cell of the branch. The cells produced from the apical gonidium afterwards divide parallel to the longer axis of the branch; still later divisions are formed in different directions, and thus groups of gonidia arise at some considerable distance from the apex of the branch. The fine hyphæ are represented in our figure as reaching to the apical cell; in other cases they come to a termination at a considerable distance beneath the apical gonidium. There are also only a few single hyphæ which follow the longitudinal growth of the branch; these grow within the gelatinous envelope which is evidently derived from the gonidia. At a considerable distance from the

apex of the branch the hyphæ first put forth lateral branches which penetrate between the single or grouped gonidia, forcing their way through the deliquescent mass of their gelatinous cell-walls. In this manner the whole form of the branch, its growth both in length and thickness, is determined by the gonidia; the hyphæ, from their small number and their fineness, produce scarcely any essential alteration either in the external form or the internal structure of the branch. This is clearly shown also in the origin of the lateral branches of the thallus of *Ephebe pubescens*. One of the exterior gonidia lengthens in a direction vertical to the axis of the parent-branch, and becomes the apical cell of the lateral branch, producing at the same time new cells by transverse divisions, as is shown in Fig. 190, *a*. Branches of the hyphæ which run into this cell turn in the same direction, and behave, in relation to the new apical cell, in the manner described above with respect to those of the primary branch.

In a manner similar to *Ephebe pubescens*, *Usnea barbata*, a fruticose Lichen, also forms a much-branched fruticose thallus. The branches of the thallus here also elongate by apical growth (cf. Fig. 191, *A*); but this is not brought about, as in Ephebe, by the gonidia, nor by a single apical cell. The hyphæ at the end of the branch which are nearly parallel and approximate at the apex, elongate each by the apical growth of its terminal cell, and thus produce in common the apical growth of the branch; this is

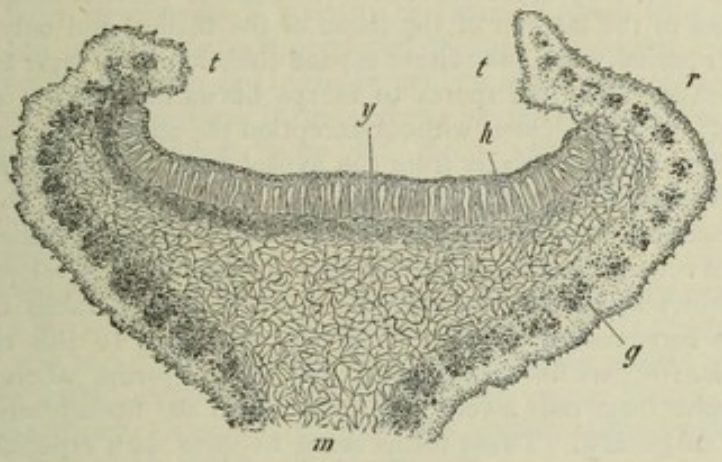

FIG. 192.—Vertical section of the gymnocarpous apothecium of *Anaptychia ciliaris* (× about 50); *h* the hymenium, *y* subhymenial layer and excipulum; all the rest belongs to the thallus; *m* its medullary layer, *r* its cortex, *g* its gonidia; at *tt* the thallus forms a cup-shaped rim round the apothecium.

followed further backwards by an intercalary growth, the result of the intercalary elongation of the hyphæ and of the formation of new branches in different directions. The hyphæ lie so close together near the apex that they form a compact mass without interstices; it is only at some distance from it that the hyphal tissue is differentiated into a very dense cortex of fibres interwoven on all sides, an axial bundle of densely-crowded threads running in the direction of length, and a looser layer (the medullary layer) furnished with air-containing interstices. The point below the apex where this differentiation of the hyphal tissue begins is also that of the point of commencement of the gonidial layer, which consists of small roundish green cells, collected in small groups in consequence of their increase by division. But these groups themselves lie in a layer between the medullary and cortical layers (*cf.* Fig. 191, *B*, the transverse section). Below the growing apex of the branch of the thallus there are only single gonidia, by the division of which the cells in the gonidial layer subsequently increase. It is evident therefore that in *Usnea barbata* the growth in length and thickness and the internal differentiation of the tissue depend entirely on the hyphæ, and that the gonidia behave like foreign bodies in the hyphal tissue; the formation of new branches proceeds also from the hyphæ and not from the gonidia. The branching may be dichotomous; and in this case the apical cells of the hyphæ converge towards two nearly adjacent points, and then continue to grow in corresponding directions, so that the two equal branches

form an acute angle. Adventitious branches arise laterally below the apex of the thallus, the cortical fibres forming at a particular point a new apex and subsequently growing outwards. Gonidia are also to be found below the new apex, while the base of the branch sends out medullary fibres and an axial bundle into the primary branch, so that the homologous forms of tissue of the two are continuous. The growth of Usnea may be compared, irrespectively of subordinate points, to that of the so-called stroma of the Xylariæ; the formation of the gonidia is a subordinate element in the structure of the whole.

In some crustaceous Lichens the thallus possesses in general no defined contour, and no external differentiation takes place; the thallus appears as a somewhat irregular aggregation of masses of gonidia traversed by hyphæ. In other crustaceous Lichens (as *Sporastatia Morio*, *Rhizocarpon subconcentricum*, *Aspicilia calcarea*, &c.), the thallus forms lobed discs which increase by centrifugal growth at the margin; the growing margin consists altogether of hyphal tissue, in which, further inwards masses of gonidia appear at a few isolated spots and gradually spread; the cortical tissue is indented at the circumference of the spots where the gonidia are formed. Isolated scaly pieces of a true Lichen-thallus then arise on a fibrous substratum called the Hypothallus[1].

The Formation of the Spores of Lichens takes place in receptacles termed *Apothecia*, similar to those of the Discomycetes, or in other cases to those of some Pyrenomycetes. They are formed in the interior of the tissue of the thallus, and only appear above its surface at a later period, when they either expand their hymenial layer to the air (Gymnocarpous Lichens), or allow the spores to escape outwards through an orifice (Angiocarpous Lichens). In all Lichens without exception the apothecium and all its essential parts derive their origin exclusively from the hyphal tissue; it is the Fungus alone that produces the receptacles; the nourishing Algæ, *i.e.* the gonidia, take no part whatever in it, or only in a secondary manner in so far as the thallus-tissue together with its gonidia grows like a wall round the apothecium and to a certain extent envelopes it (as shown in Fig. 192), or grows luxuriantly beneath the apothecium and raises it upon a kind of stalk above the surrounding thallus. The only exception to this endogenous origin of the apothecium occurs in Cœnogonium and similar forms, where it is impossible, because the hyphæ form only a very thin layer round the filamentous Alga which performs the part of gonidia. These forms serve to show with especial clearness, as we know from Schwendener's researches, that the receptacle of Lichens belongs exclusively to the hyphal tissue.

The history of the development of the apothecium is a branch of the inquiry attended with great difficulty, and in more than one point is still obscure[2]. It originates, in heteromerous Lichens, beneath the cortical layer, in the lower part of the gonidial zone, or, in some crustaceous Lichens, in the deepest part of the thallus in immediate contact with the substratum; in homöomerous gelatinous Lichens and in Ephebe it arises beneath the surface of the thallus. The commencement of the gymnocarpous apothecium is, in heteromerous Lichens, a very small roundish ball of confused interwoven hyphæ, on the outer side of which a tuft of very delicate hyphæ—the first paraphyses—rises at a very early period. The most external hyphal investment of this ball, and therefore surrounding the tuft of paraphyses and opening above (outwards), is termed by lichenologists the *Excipulum*. The further growth of the rudiment of the apothecium is now occasioned by the increase in size of the excipulum by the formation of new fibres, while new paraphyses are intercalated among those already formed and outside the tuft, the extension of the apothecium being the immediate result of the fresh formation of these bodies. The growth is first completed in the centre of the apothecium; at the outside it continues longer, often even after the appearance of the apothecium

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[1] See Schwendener, Flora, 1865, no. 26.

[2] What follows is taken from De Bary's account of his own researches, and from those of Schwendener and Fuisting.

above the surface of the thallus. The mother-cells of the spores, the asci, are formed, according to Schwendener and Fuisting, in a peculiar manner. 'Even in the young ball, and among the first rudiments of the paraphyses, thicker hyphæ are to be seen interwoven among the rest, rich in protoplasm, undivided by septa, and with numerous ramifications; the upright ends of the branches of these hyphæ which penetrate between the ends of the paraphyses, develope into club-shaped asci; they may hence be termed *Ascophorous hyphæ*. They are very readily distinguished from the paraphyses by their membrane being coloured blue by iodine after treatment with potash-solution, while that of the paraphyses remains colourless. They disappear at a very early period from the lower part of the rudiment of the apothecium, and remain only in one narrow layer which runs parallel to the upper surface of the apothecium, and extends below the lower ends of the ripe asci. In this layer they ramify in a centrifugal direction in proportion as the margin of the excipulum grows, and send out new asci among the new paraphyses. The first asci appear in the centre of the apothecium; and Schwendener states that no genetic connexion exists between the ascophorous hyphæ and those from which the paraphyses are derived; the two form separate systems but interwoven into one another[1].' The layer in which the ascophorous hyphæ run is called the *Sub-hymenial Layer;* the hymenium itself consists of the paraphyses and the asci taken together. The term *Hypothecium* is given to the mass of fibres lying beneath the sub-hymenial layer, and is often strongly developed through subsequent growth; it consists of hyphæ the branches of which end in the hymenium as paraphyses, and of the remains of the primary ball; when mature, it can scarcely be distinguished from the excipulum. The growing apothecium bulges more and more, and finally breaks through the layer of thallus which covers it; the hymenium and the margin of the excipulum appear above the surface of the thallus, or the part of the thallus which surrounds the excipulum rises and grows with it forming a bowl-like rim. Among the medullary hyphæ which surround the apothecium a number of gonidia subsequently appear in many Lichens, so that a gonidial zone runs beneath the apothecium. In Peltigera and Solorina even the young apothecium is expanded flat, its paraphyses project vertically towards the surface of the thallus, and the layer of thallus which covers them is finally lifted like a thin veil. In Bæomyces, Calycium, &c., the basal portion of the hypothecium is developed into a long stalk which elevates the apothecium.

The apothecium of Angiocarpous Lichens is so similar in its mode of development and in its mature state to the perithecium of the Xylariæ, that there is no need to give an exact description of it.

The club-shaped asci of Lichens are similar in every essential point to those of the Pyrenomycetes and Discomycetes; their wall is often very thick and capable of swelling; the spores (Fig. 193) arise simultaneously, as in those Fungi, by free-cell-formation, while a considerable portion of the protoplasm often remains unused in their production. The normal number of spores is eight, although sometimes only 1–2 (in Umbilicaria and Megalospora), 2 or 3 or from 4 to 6 (in several Pertusariæ); in Bactrospora, Acarospora, and Sarcogyne on the other hand their number amounts to some hundreds in one ascus. The structure of the spores is very various, but in general similar to that of the Ascomycetes; very commonly they are septate and multicellular; the exospore is usually smooth and often of various colours.

The spores are set at liberty by moisture penetrating the hymenium; they are suspended in the fluid which fills the ascus, and are expelled together with the fluid by

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[1] From the newly discovered processes in the formation of the reproductive organs of the Pyrenomycetes and Discomycetes, especially from the most recent statements of Janczewski on *Ascobolus furfuraceus* (*cf.* pp. 256 and 261), it may be assumed that the tubular hyphæ of the sub-hymenial layer arise from a yet undiscovered ascogonium or scolecite; and that thus the apothecium of Lichens is the result of a sexual process in a similar manner to the perithecia of the Pyrenomycetes and the fruit-cups of Peziza and Ascobolus.

the rupture of its apex. This expulsion is probably caused by the lateral pressure of the swollen paraphyses and the property of swelling possessed by the membrane of the ascus itself.

The germination of the spores of Lichens takes place by the endospore of each spore-cell putting out a filament which ramifies and creeps upon the damp substratum on which the spore is placed. The origin of the first gonidia has never been observed after the dissemination of the spores; but Tulasne sometimes found groups of gonidia at

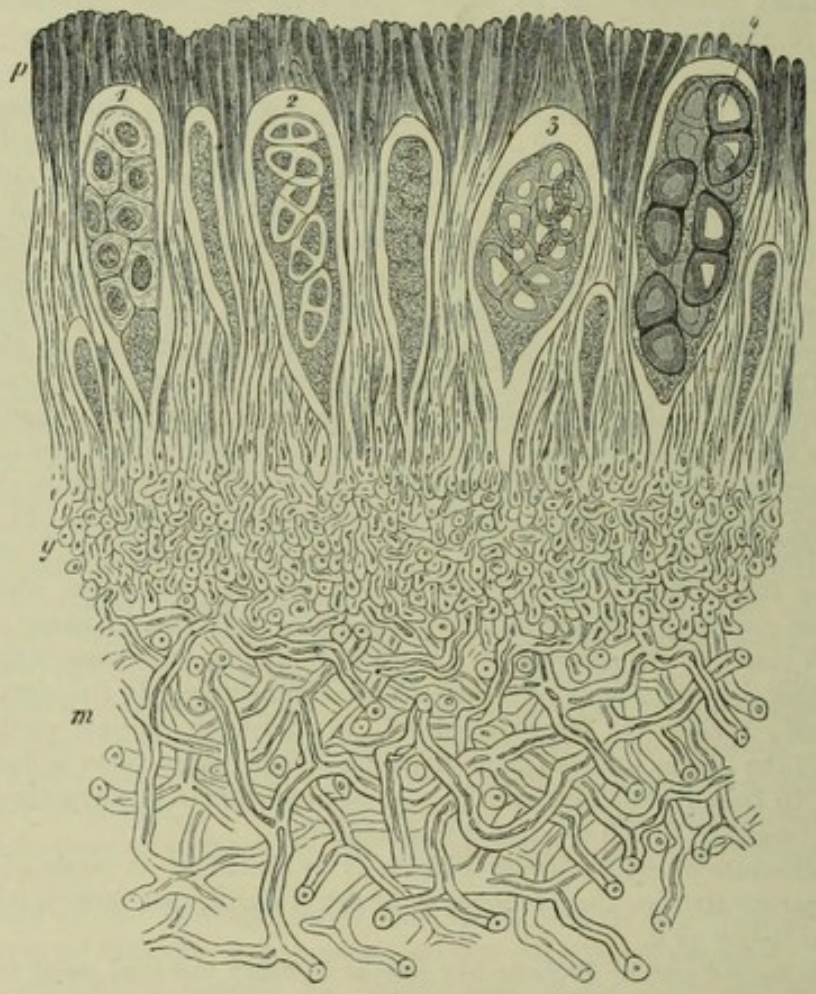

FIG. 193.—Vertical section of a small portion of the apothecium of *Anaptychia ciliaris* (× 550); *m* the medullary layer of the thallus; *y* the hypothecium, together with the sub-hymenial layer; *p* the paraphyses of the hymenium, their upper ends of a brown colour; among them are the asci in various stages of development; in 1 are the young spores not yet septate, in 2-4 the spores more fully developed; the protoplasm in which the spores are imbedded is contracted by the drying up of the Lichen before the preparation was made.

a later period upon the web of hyphæ derived from the spores; and even small rudiments of a thallus were observed; but the genetic connexion of the gonidia with the germinating filaments has not been made clear[1]. The mode of germination of the very large spores of some genera, Megalospora, Ochrolechia, and Pertusaria, differs from that of all the rest. They are simple, not septate, and densely filled with drops of oil (Fig. 194, *A*, *B*). Each spore puts out from different parts of its circumference in germination a great number, even as many as a hundred, germinating filaments. The formation of each begins with the appearance in the endospore of a cavity widening from within outwards,

[1] [Tulasne believed that he twice detected the formation of gonidia upon the hyphæ: Ann. des Sci. Nat. 1852, vol. XVII. p. 96.—ED.]

which becomes surrounded by a very delicate membrane and grows outwards in the form of a filament (Fig. 194, *A*, *B*).

Besides the apothecia with ascospores capable of germination, *Spermogonia* are also generally present in Lichens, as in Ascomycetes; they generally occur on the same thallus as the apothecia. There are cavities in the thallus (Conceptacles), globular, flask-shaped, or sinuous, and densely clothed and almost filled with sterigmata; from these sterigmata the spermatia are detached in very large numbers, and escape through

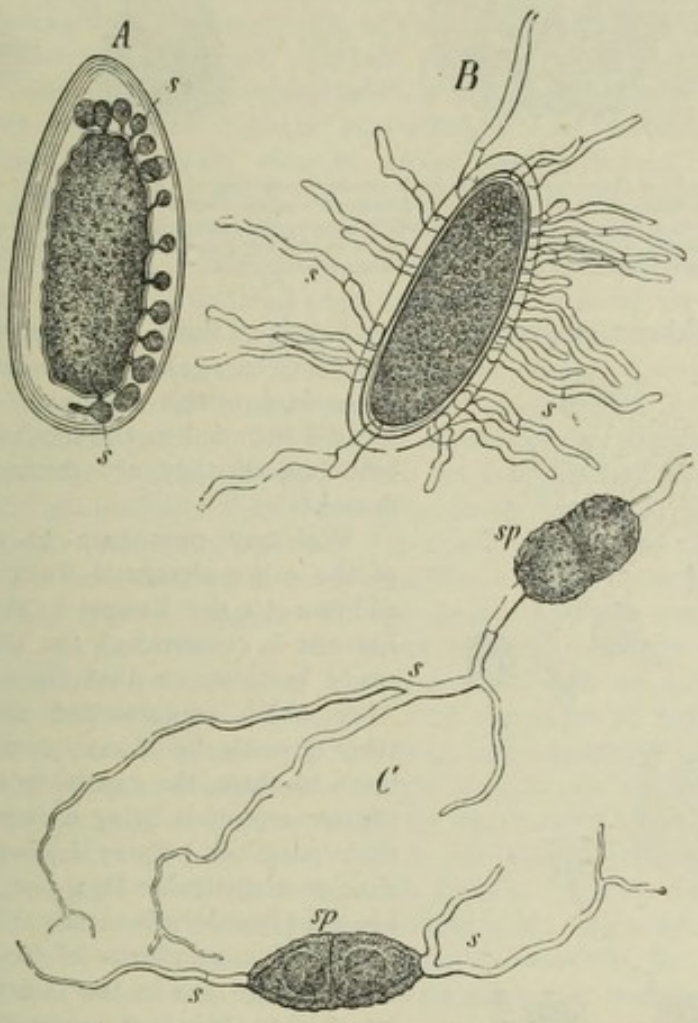

FIG. 194.—Lichen-spores germinating; *A* longitudinal section of a spore of *Pertusaria communis* after lying 34 hours in glycerine, *s* the first start of the germinating filaments; *B* spore of *Pertusaria leioplaca* with a number of germinating filaments (after De Bary, ×390); *C* germinating septate spores of *Solorina saccata* (after Tulasne).

a fine orifice in the spermogonium. Sometimes also conceptacles are found in which larger structures, more like spores, are detached from the sterigmata; receptacles of this kind are called *Pycnidia*. The signification of both is at present unknown.

Besides the spores, most Lichens also possess organs of a very great reproductive power, the *Soredia*. This term is applied to single gonidial cells or groups of gonidia which, surrounded by a weft of hyphæ, are pushed out of the thallus, and are able, without any further process, to grow into a new Lichen-thallus. The soredia are produced from the thallus in the non-gelatinous Lichens as a fine powder, forming sometimes dense pulvinate masses (as in Usnea, Ramalina, Evernia, Physcia, Parmelia, Pertusaria, &c.). In the heteromerous thallus the soredia appear in the gonidial layer; single gonidia, or sometimes several together becoming woven over by branches of hyphæ which cling closely to them and form an envelope of fibres. The gonidia divide repeatedly, and each daughter-cell is again woven over. This process is often repeated, the soredia accumulate in great numbers in the gonidial zone, and finally rupture the cortex. After escaping in

this manner, the soredia can still further multiply outside the thallus; but under favour-

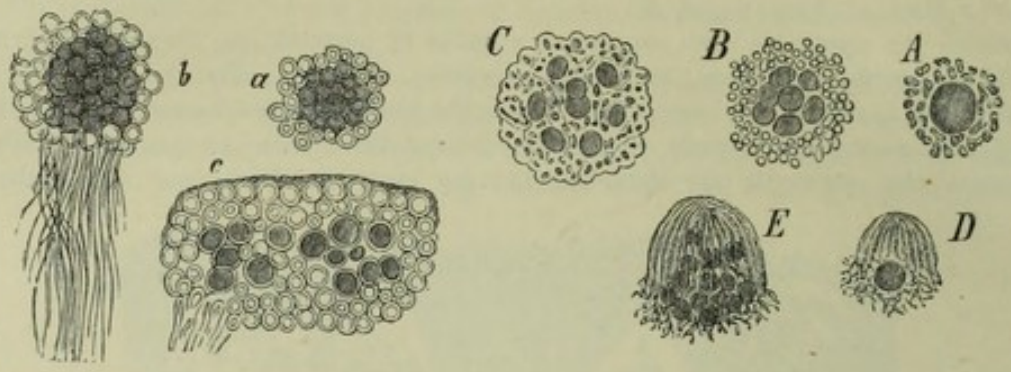

FIG. 195.—*A*—*D* soredia of *Usnea barbata*; *A* a simple soredium, consisting of a gonidium covered with a web of hyphæ; *B* a soredium, in which the gonidium has multiplied by division; *C* a group of simple soredia, resulting from the penetration of the hyphæ between the gonidia; *D*, *E* germinating soredia; the hyphæ are forming an apex of growth and the gonidia are multiplying; *a*-*c* soredia of *Physcia parietina*; *a* with an envelope of pseudo-parenchyma; *b* the envelope producing rhizines; *c* a young thallus formed from a soredium (after Schwendener, ×500).

able conditions either a single soredium or a mass of them grows out at once into a new thallus (Fig. 195). Schwendener states that in *Usnea barbata* this may occur while the soredia are still included in the mother-thallus; soredial branches, as they are termed, are thus produced.

We may now turn to the consideration of the other elemental form out of which, in addition to the Fungus-hyphæ, the thallus of Lichens is constructed, the *Gonidia*. It has already been shown that these are nothing but Algæ which are attacked and surrounded in their growth by Ascomycetes, and serve as hosts to them, the capability of assimilating inorganic materials being wanting on the part of their parasites. Every Lichen-forming Fungus chooses a particular Alga, just as other parasites like the Hypodermiæ mostly infest only particular hosts. The peculiarity of the parasitism of the Lichen-fungi lies in the fact that they are not attached to their host externally at any one particular spot, and do not penetrate into the cells themselves, but become woven round them, and thus enclose them in their hyphal tissue. Complete unions of growth however sometimes take place, single hyphæ becoming closely attached to the cell-walls of particular Algæ (or gonidia) (Fig. 196, *A g*, *B g*, *C g*), a phenomenon which led at one time to the assumption that the gonidia are themselves products of the hyphæ, the branches of which swell up in places to a globular shape, and form chlorophyll. The opposite view was also at one time held, that the hyphæ grow out of the gonidia (as, for instance, by me in Bot. Zeitg. 1855, on Collema). But these very rare phenomena may now be more easily explained as simple unions of growth of hyphæ and gonidia, and by no means stand in the way of the

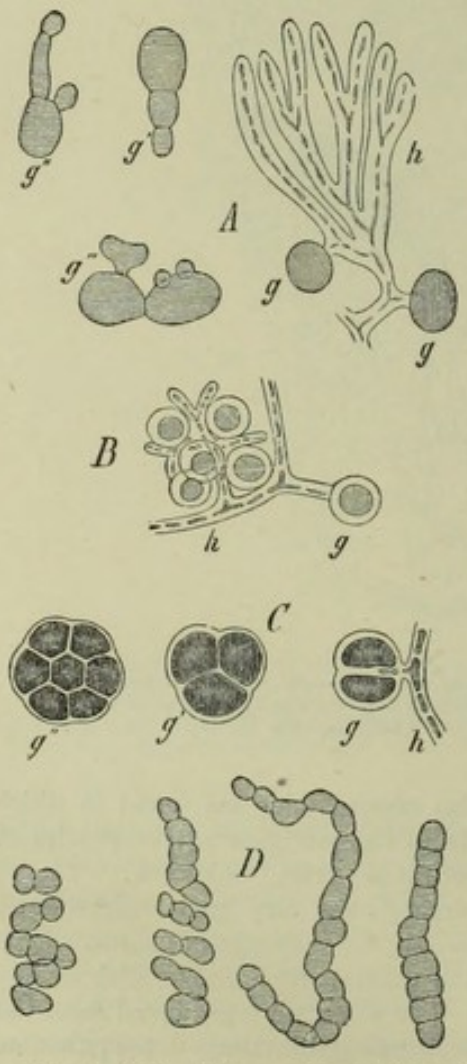

FIG. 196.—Various Lichen-gonidia; *A* of *Roccella tinctoria*, *g*-*g*^{III} in the act of multiplication, *g g* united with branches of hyphæ *h*; *B* of *Evernia divaricata* united with a branched hypha; *C* of *Usnea barbata* in the act of division, at *h* united with a hypha; *D* chain of gonidia of *Lichina pygmæa* (after Schwendener).

view that the gonidia are true Algæ, since the proofs of this are overwhelming.

Reviewing the views of older lichenologists, which may be found represented in detail in the writings cited below of Baranetzky and Schwendener; it may be mentioned, first of all, that De Bary (Handbuch der phys. Bot. vol. II. p. 291) had already arrived at the following alternative with respect to gelatinous Lichens, as Ephebe and similar forms:—'Either these Lichens are the perfectly developed fructifying states of plants the incompletely developed forms of which have hitherto been placed among Algæ under the names Nostocaceæ and Chroococcaceæ, or these last are typical Algæ which assume the forms of Collema, Ephebe, &c. Certain parasitic Ascomycetes penetrate them, extend their mycelium into the growing thallus, and often form an intimate attachment with those of its cells which contain phycochrome (as Plectospora, Omphalaria). In the latter case these plants may be called Pseudo-lichens.' From the last sentence of this quotation it follows that De Bary would not apply the latter alternative at all events to the heteromerous Lichens. Soon afterwards Famintzin and Baranetzky, and then the latter alone, published researches on the further changes which the gonidia of Lichens undergo when they are set free by the decomposition of the hyphal tissue in water[1]. Baranetzky comes to the conclusion that:—'The gonidia of the heteromerous chlorophyll-containing Lichens (as Physcia, Evernia, Cladonia, &c.), as well as of the heteromerous forms which contain phycochrome (*e.g.* Peltigera), and of the gelatinous Lichens (such as Collema), are capable of carrying on an entirely independent life outside the Lichen-thallus. When set free the Lichen-gonidia appear to expand their cycle of life; and thus the independently vegetating gonidia of Physcia, Evernia, and Cladonia produce zoospores.' He also found that all the ball-like masses of Peltigera-gonidia were afterwards transformed so as to become extremely like the interstitial cells of a Nostoc; and he did not doubt that this was their permanent condition. 'Some, perhaps many, of the forms hitherto described as Algæ must be considered as independently vegetating Lichen-gonidia, such as, for the present, the forms Cystococcus, Polycoccus, and Nostoc.' The researches of Schwendener, carried on in part earlier in part simultaneously and later, and conducted in the most careful manner, led to the opposite conclusion, that the gonidia are in fact Algæ which are more or less disturbed in their manner of life by the Fungus which becomes parasitic upon them. He first stated in the frankest and clearest manner that this was his opinion with respect to all Lichens in his treatise 'Ueber die Algentypen der Flechtengonidien' (Basel 1869). In this memorable work, which settled for the future the systematic position of the Lichens among the Ascomycetes, he gives a review of those genera of Algæ which were up to that time known as hosts of Lichen-fungi, in other words, as playing the part of gonidia:—

I. *Algæ with Blue-green Contents* (*Nostochineæ*).

Name of Group of Algæ.	Lichen on which they occur as Gonidia.
(1) Sirosiphoneæ . .	Ephebe, Spilonema, Polychidium.
(2) Rivularieæ . .	Thamnidium, Lichina, Racoblenna.
(3) Scytonemeæ . .	Heppia, Porocyphus.
(4) Nostocaceæ . .	Collema, Lempholemma, Leptogium, Pannaria, Peltigera.
(5) Chroococcaceæ .	Omphalaria, Euchylium, Phylliscum.

[1] Mémoires de l'Acad. Imp. des Sci. de St. Pétersbourg, 7th series, vol. XI. no. 9, and Mélanges biologiques tirés du Bulletin de l'Acad. Imp. de St. Pétersbourg, vol. VI. 1867.—[Ann. des Sci. Nat. 5th series, 1867, vol. VIII. pp. 137–144.]—Also Itzigsohn, Bot. Zeitg. 1868, p. 185.

II. *Algæ with Chlorophyll-green Contents.*

Name of Group of Algæ.	Lichen on which they occur as Gonidia.
(6) Confervaceæ . .	Cœnogonium, Cystocoleus.
(7) Chroolepideæ. .	Graphideæ, Verrucarieæ, Roccella.
(8) Palmellaceæ . .	Many fruticose and foliaceous Lichens: *e. g. Cystococcus humicola* on Physcia, Cladonia, Evernia, Usnea, Bryopogon, and Anaptychia[1]. Pleurococcus, on Endocarpon and various crustaceous Lichens.

Since anatomical and analytical research has led to this view of the nature of Lichens, the next step must be to complete synthetically the proof of its correctness by sowing the spores of the Lichen-fungi on or near those Algæ which serve as their gonidia, and to induce their germinating filaments and the hyphæ which proceed from them to invest the Algæ[2]. If in this manner a true Lichen-thallus is obtained, each fresh case in which this is successful would furnish a new proof of the correctness of Schwendener's theory. This synthetical method has already been adopted by Reess with the greatest success; for he has succeeded in growing in this manner the Lichen-thallus of *Collema glaucescens* both from germinating spores of the same species and from *Nostoc lichenoides*[3].

SUPPLEMENT.

MYXOMYCETES[4].

Under this head is included a numerous group of organisms which in many respects differ widely from all other vegetable structures, but, in the mode of formation of their spores, stand nearest to Fungi, on which account we may treat them as a supplement to that class. The Myxomycetes are remarkable in no ordinary degree from the fact that during the period of their vegetation and assimilation of food they do not form cells or tissues. The protoplasm, which in all other plants is also the general motive power of the phenomena of life, remains in them during the whole of this period perfectly free, collects into considerable masses, and assumes various shapes from the internal force residing in it, without becoming divided into small portions which surround themselves with cell-walls (or become cells). It is only when the protoplasm passes into a condition of rest in consequence of being surrounded by unfavourable conditions, or when it concludes its period of vegetation by the formation of the reproductive organs—its internal and external movements ceasing at the same time—that it breaks up into small portions which surround themselves with cell-walls, and which even then never form a tissue in the proper sense of the term.

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[1] See Schwendener in Nägeli's Beiträge, &c. 1868. Heft VI. pp. 110, 111.

[2] [See Bornet, Annales des Sci. Nat. 5th series, 1873, vol. XVII.—Treub, Bot. Zeitg. 1873, pp. 721–727.]

[3] Monatsberichte der königl. Akad. der Wiss. zu Berlin. Oct. 1871. Compare further, Schwendener, Flora, 1872, nos. 11 and 12. [Quart. Journ. Micr. Sc. 1873, p. 235; compare Archer, Quart. Journ. Micr. Sc. 1872, p. 367.]

[4] De Bary, Die Mycetozoen, in the Zeitschrift für wiss. Zool. vol. X. 1859; separate 2nd edition, Leipzig, 1863; (this work is the leading authority for the whole group). [Ann. Nat. Hist. 1860, vol. V. p. 233.]—Cienkowski in Jahrb. für wiss. Bot. vol. III. pp. 325, 400.—Oscar Brefeld, Ueber *Dictyostelion mucoroides*, Abhandlungen der Senkenbergischen Gesellschaft, vol. VII. Frankfort 1869.

The Myxomycetes live upon decaying and rotting vegetable substances, such as tan, rotten stems, and the like. While endowed with motion they either creep over the surface of the substratum, or live in hollows and pores in its interior; but for the purpose of reproduction they always come to the surface. When a Myxomycete is entering the reproductive condition, the whole of its protoplasm (the *Plasmodium*) becomes transformed into sporangia or large receptacles. In most Myxomycetes the sporangia have the form of round, longish vesicles, sessile or stalked, one or more millimetres in length; less commonly they form horizontal tubes either cylindrical or flattened. The structure of the walls of these sporangia is similar to that of ordinary cell-walls; they sometimes exhibit similar thickenings and stratification; they are colourless, or violet, brown, red, or yellow, according to

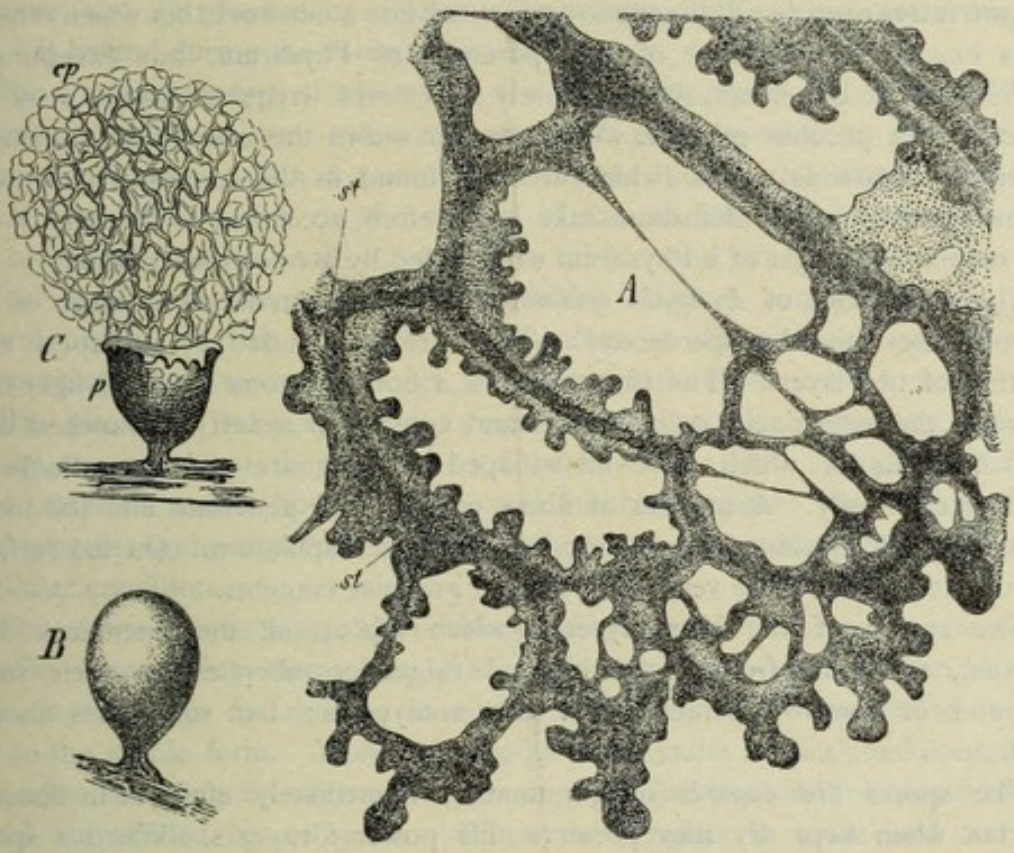

FIG. 197.—A plasmodium of *Didymium leucopus* (after Cienkowski, ×350); *B* a closed sporangium of *Arcyria incarnata*; *C* after rupture of the wall *p* and extrusion of the capillitium *cp* (after De Bary, ×20).

the species. In some, as Licea and Cribraria, the cavity of the sporangium is entirely filled with small spores; but generally the sporangium contains, besides the spores, a structure called the *Capillitium*, consisting sometimes of small thin-walled tubes anastomosing reticulately which are attached to the wall of the sporangium (*e.g.* Physarum); while in Arcyria (Fig. 197, *C*) the wall of these tubes is furnished with thickenings of an annular or wartlike or varying shape, projecting on the outside. The capillitium of the genus Trichia consists of separate long fusiform tubes not united to one another; their wall is thickened spirally like the spiral cells of higher plants. In the Stemoniteæ the pedicel which bears the sporangium is continued into it and forms the so-called *Columella*, from which the branches of the capillitium spring and anastomose reticulately. When the spores are being disseminated, the rupture of the wall of the sporangium and the expulsion of the

spores are assisted by the capillitium; its fibres, which in the unripe condition are irregularly folded, becoming straight and tense as they dry. After the rupture of the sporangium-wall, the capillitium becomes exposed in many cases as an extremely beautiful net-work (Fig. 197, *C*). The structure of the receptacles of Æthalium, Spumaria, and Didymium is different. Those of Æthalium (the so-called 'flowers of tan') are cake-shaped, not unfrequently a foot in length and breadth, and over an inch thick, but more often smaller and closely adherent to the substratum (generally tan). The cake is surrounded by a brittle skin several millimetres in thickness, which is at first bright yellow, afterwards brownish, and spreads itself over the substratum. The inside of this cake is composed of a dark-grey easily-pulverised mass (the spores) penetrated by yellow veins, and consists of tubes which are interwoven in all directions and united into a net-work, but which otherwise possess exactly the structure of the sporangia of Physarum, not excepting the capillitium. The cortex consists of densely interwoven irregular bundles or of tubes connected in a peculiar manner, which contain within the membrane an immense number of calcareous grains (which are also found in the sporangia), as well as a yellow pigment. The Æthalium-cake is therefore, according to De Bary, a tissue of the tubular sporangia of a Physarum surrounded by a calcareous cortex.

The receptacles of *Lycogala epidendron* bear a resemblance to those of some Gasteromycetes (the Lycoperdaceæ). They are surrounded by a papery cortex consisting of two layers. The inner layer is a homogeneous stratified light-brown membrane, the outer one is much thicker and consists of a weft of branched hollow fibres, the walls of which have cleft-shaped dots or are reticulate thickenings projecting externally. A number of fibres of this kind penetrate into the interior, piercing through the inner membrane, and form the capillitium. On the surface of the structure are firm large vesicles filled with granular contents.

The spores of the Myxomycetes, which fill up all the interstices of the capillitium, resemble, from the reticulated ridges or tubercles on their surface, the spores of some Tuberaceæ and Gasteromycetes; but sometimes they are smooth.

The spores are capable of germinating immediately after their dissemination; but when kept dry they preserve this power for years. When a spore is saturated with water it opens, and the whole of its protoplasmic contents escape as a roundish naked mass; but after some minutes it assumes another form, becomes long and pointed at one end, where it is provided with long cilia; it has, in fact, developed into a swarm-spore, which is either endowed with rotatory motion or creeps along changing its form like an Amœba. These swarm-spores multiply by division. But on the second or third day a new process begins; the swarm-spores cease dividing and unite, two or more of them coalescing—after they have gone over into the Amœba-form—into a homogeneous protoplasmic substance, also endowed with an Amœba-like motion, the Plasmodium. This increases, constantly absorbing into itself more swarm-spores and coalescing with other plasmodia. These plasmodia now creep along the surface of the nourishing substratum (Fig. 197, *A*), and the movements are essentially similar to those of the protoplasm which circulates in the large cells of plants, but are freer and more varied. This movement in position or 'creeping' is caused by arm-like protuberances

from the margin of the plasmodium, which increase by the protoplasm flowing into them from behind. These arms or branches coalesce laterally, anastomose, and form new projecting arms. When this has proceeded for a considerable time in the same direction, the whole plasmodium is found to have changed its position. In addition smaller tentacle-like arms, into which the inner granular protoplasmic substance does not penetrate, are also put out and again drawn in from the outside. Finally a streaming motion takes place in the interior of the larger arms or of the plate-like expansions of the plasmodium, the direction of which is constantly changing. The motile substance in the interior is granular and more watery; but the circumference of the plasmodium is formed of a hyaline layer (the marginal layer) destitute of granules and apparently denser, which is sometimes also surrounded by a layer of mucilage; this latter is not protoplasm, and is left behind during the creeping like the slime of a snail.

The greater number of plasmodia are colourless, many yellow (as *Æthalium septicum*) or reddish yellow; some are very small, scarcely visible to the naked eye, others, when mature, attain a size of some square inches, and those of *Æthalium septicum* sometimes collect on the surface of the tan into masses the size of the hand or larger, and one-half to one inch thick; and, in this state, may form spherical or Clavaria-like upright bodies, which however consist of soft cream-like protoplasm. In this condition the Æthalium is able to creep away from the tan upon plants even several feet high, and accumulate above on the leaves.

The plasmodia take up hard foreign substances which they enclose; and De Bary supposes that they obtain food in this way. The quantity of the absorbed materials seems, however, too small for this purpose; the residue of them are afterwards again expelled, especially when the plasmodium passes over into the cellular condition.

The swarm-spores may, under unfavourable conditions, be again transformed into cells, surrounding themselves with a cell-wall (*Microcysts*). When dry they remain in this state for months in a vital condition, and when placed in water revert to the motile form. Young plasmodia form, under similar conditions, 'solid-walled cysts,' dividing themselves into pieces of unequal size which become rounded off and surrounded by cell-walls. When the weather is moist and warm the plasmodium again creeps out of these cysts. The mature plasmodia finally arrive at a state of rest, forming bodies which De Bary calls *Sclerotia*, when the temperature and amount of moisture decrease. The plasmodium first of all draws in its arms and forms a sieve-like plate or mass of small irregular nodules, and the whole substance breaks up into a large number of roundish or polyhedral cells $\frac{1}{40}$ to $\frac{1}{30}$ mm. in diameter. The body thus formed is wax-like, gritty and dry. When placed in water the cell-walls again become absorbed, and the sclerotium reverts to the condition of a motile plasmodium.

When the mature plasmodia have lived for some time and been in motion on the surface of the substratum, they assume a firmer consistency, and after the net-like mass has collected, it either forms a cake, as in Æthalium, or puts forth outgrowths directed upwards, but always soft, of the form of the future sporangia. A firm membrane is formed on the outside, the capillitium and the spores in the inside. If the plasmodium contains lime, it is deposited in the form of granules

in the capillitium or in the wall of the sporangium. These processes are mostly completed in some hours; in Æthalium one or two hours is generally sufficient to transform the still motile plasmodium into the organs of reproduction; the water contained in the plasmodium is partially expelled in the fluid state, the remainder subsequently evaporates.

GROUP II.

CHARACEÆ[1].

CLASS III.

CHARACEÆ.

The Characeæ are submerged aquatic plants, rooting in the ground and growing erect, attaining a height of from $\frac{1}{10}$ metre to a metre, and containing abundance of chlorophyll. They are very slender, forming stems and leaves only $\frac{1}{2}$ to 2 mm. in thickness. With an alga-like habit, they possess a delicate structure, though sometimes attaining greater firmness from the deposition of lime on their surface. They live gregariously, mostly in crowded tufts at the bottom of fresh-water ponds, ditches, and streams; they may grow in deep or in shallow, in stagnant or in quickly flowing water; and are either annual or perennial.

In the greater number of species, which are distributed over all quarters of the globe, there prevails nevertheless so great a uniformity that they may all be arranged into two genera with some transitional forms; while, on the other hand, they are so different from all other classes of plants that they must be erected into a special group by the side of the Thallophytes and Muscineæ. Among the Thallophytes they would approach most nearly to certain groups of Algæ, but differ from all the members of that group in the form of their antherozoids; and in this respect resemble the Muscineæ, from which again they differ entirely in the structure of the antheridia and of the female organs of reproduction, as well as in that of their organs of vegetation.

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[1] A. Braun, Ueber die Richtungsverhältnisse der Saftströme in den Zellen der Charen in Monatsberichte der Berliner Akad. der Wiss. 1852 u. 1853.—Pringsheim, Ueber die nacktfüssigen Vorkeime der Charen, in Jahrb. f. wissen. Bot. 1864, vol. III.—Nägeli, Die Rotationsströmung der Charen, in dessen Beiträgen zur wissen. Bot. 1860, vol. II. p 61.—Thuret, Sur les anthéridies des cryptogames, Ann. des Sci. Nat. 1851, vol. XVI. p. 19.—Montagne, Multiplication des charagnes par division, ditto, 1852, vol. XVIII. p. 65.—Göppert u. Cohn, Ueber die Rotation in *Nitella flexilis*, Bot. Zeitg. 1849.—De Bary, Ueber die Befruchtung der Charen, Monatsber. der Berliner Akad. May 1871. [For additional Bibliography, see Lindley, Vegetable Kingdom, 3rd edit. p. 28.]

From the central cell of the fruit of Chara[1] the sexual leaf-forming plant is not immediately developed, but a *Pro-embryo* precedes it, which attains only small dimensions and consists of a single row of cells with limited apical growth. The stem of the *Leaf-bearing Sexual plant* springs from a cell which lies at some distance from the apex of the pro-embryo and grows in a direction nearly at right angles to that of its axis. The unlimited apical growth of the plant depends on an apical cell (Fig. 199, *C*, *t*) from which segments are cut off by septa. Each segment immediately divides again by a septum into two superposed cells, the lower one of which (*g*) always grows without further division into a long internode (frequently 5 to 6 cm. in length); the upper one scarcely lengthens, but is first divided in half by a vertical wall, and each half then divides by further successive septa so as to form a whorl of peripheral cells. From the node thus constituted the leaves are developed, each from a peripheral cell, and the normal lateral branches, which always originate from the axil of the first or of the two first leaves of the whorl. The leaves of such a whorl, from 4 to 10 in number, repeat in a modified manner the development of the stem, but their apical growth is limited. After the formation of a definite number of segments, the apical cell ceases to divide and grows into the terminal cell of the leaf which is usually pointed (Fig. 199, *A*, *b″*). From these leaves lateral leaflets may arise in a similar manner to that in which the leaves themselves have been formed from the stem; and the leaflets may again in turn produce others of a higher order. The successive whorls of a stem alternate, and in such a manner that the oldest leaves of the whorl, in the axils of which the branches stand, are arranged on a spiral line winding round the stem. Each internode also usually undergoes a subsequent torsion in the same direction. The lateral shoots, of which in Chara one is always developed in the axil of the oldest, in Nitella one in the axil of each of the two oldest leaves of the whorl, repeat the primary stem in all respects (Fig. 210, p. 287). It has already been mentioned that the leaves undergo a segmentation similar to that of the stem; they also consist at first of very short internodes which are afterwards greatly elongated (Fig. 199, *B*, *γ*), and are separated by inconspicuous transverse plates or nodes. From these the leaflets arise in whorls the members of which are formed in succession, but they are directly superposed one above another, and do

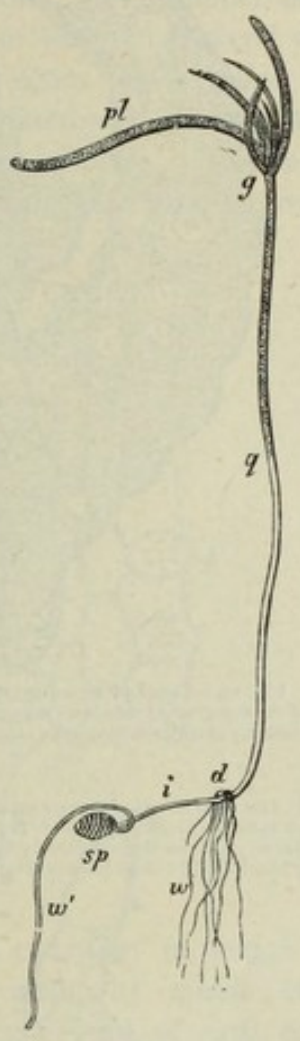

FIG. 198.—*Chara fragilis*; *sp* germinating spore; *i d q pl* together form the pro-embryo (*pl* is segmented, which is not clearly indicated in the drawing); at *d* are the rhizoids *w*; *w'* the so-called primary root; *g* the first leaves (not a whorl) of the second generation or leaf-bearing plant (after Pringsheim, × about 4).

[1] This has not yet been observed in Nitella.

not alternate like the whorls of primary leaves (Fig. 200, *C–E*, β). Each leaf begins with a node (the basal node[1]), by which it is united with the stem-node, just

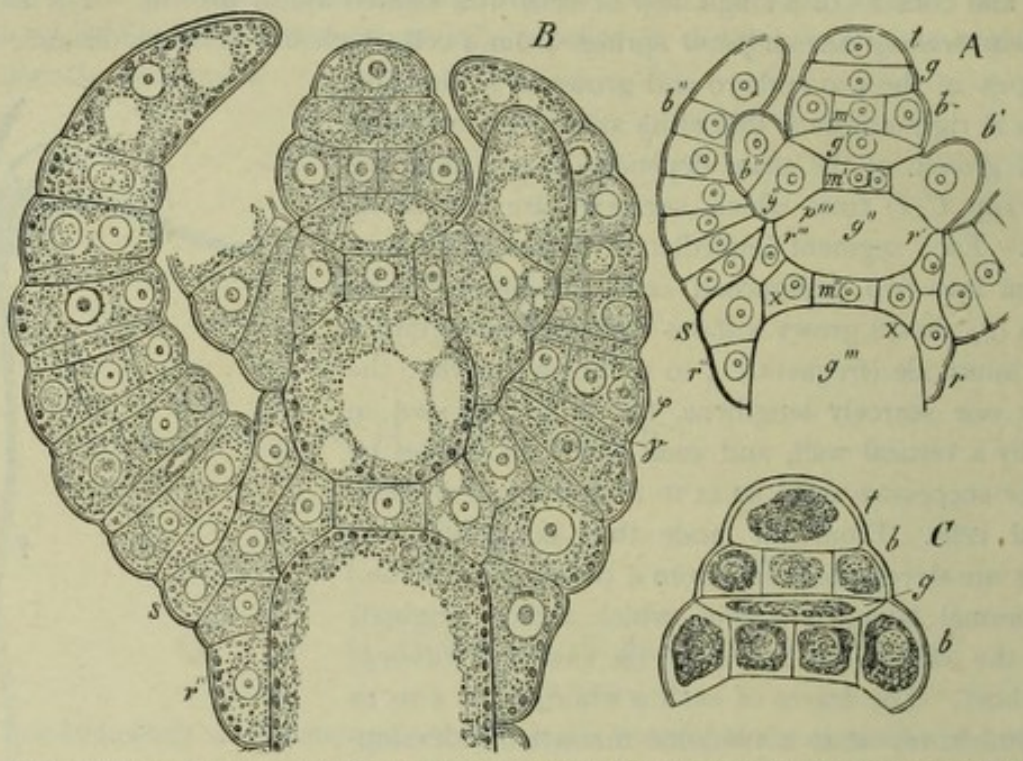

FIG. 199.—Longitudinal section through the bud of *Chara fragilis*; in *A* the contents of the cells have been removed; in *B* the fine-grained substance is protoplasm, the larger granules are chlorophyll; the formation of vacuoles is shown; in *C* the contents of the cells have been contracted by iodine solution (×500).

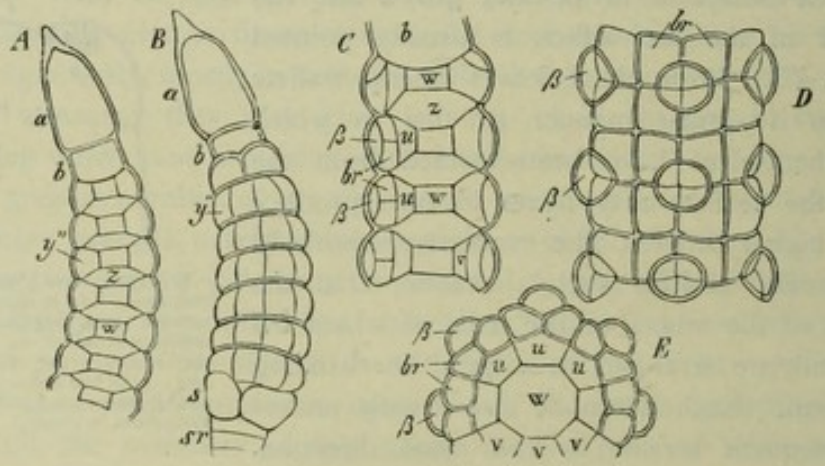

FIG. 200.—Leaves of *Chara fragilis*; *a* terminal cell, *b* penultimate cell of a leaf; *z* internodal cell; *w* cells of the leaf-node; *y''* mother-cell of a leaflet and of its basal node; from it arise *v* and *u* (the uniting cell), *br* the basal node which produces four simple cortical lobes and β the leaflet. *A* and *C* in longitudinal section, *B* an entire young leaf, external view, with the 'stipule' *s* and its descending cortical lobe of the stem *sr*; *D* external view of the middle part of an older leaf, though still young; *E* transverse section of a leaf-node, of the same age as *D*.

like each leaflet with its primary leaf. These basal nodes are the points of origin of the formation of the cortex which, in the genus Chara, covers the internodes

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[1] The cell *x* in Fig. 199, *A*, may however be considered also as the first internode of the leaf; then the nodes of the stem would consist only of the middle plate *m*, which is bisected by a longitudinal wall. A comparison with Muscineæ and Vascular Cryptogams leads however also to the supposition that the whole group of cells *x S r'' r'''* which proceeds from *y* belongs in common to the stem and leaf.

of the stem, but is wanting in Nitella. From the basal nodes of each leaf one cortical lobe which is morphologically individualised runs downwards, and one upwards[1] (Fig. 199, *B*, *r*, *r'*, *r''* and Fig. 201). In the middle of each internode therefore as many ascending cortical lobes as there are leaves in the whorl meet with the cortical lobes that ascend from the next whorl below. The number of the latter is, however, smaller, because the leaf in the axil of which the lateral shoot arises does not form an ascending lobe. The cortical lobes are in close contact laterally, and form a closed envelope round the internode, the ascending and descending lobes dove-tailing in a prosenchymatous manner. The formation of the cortex takes place so early that the elongating internode is covered

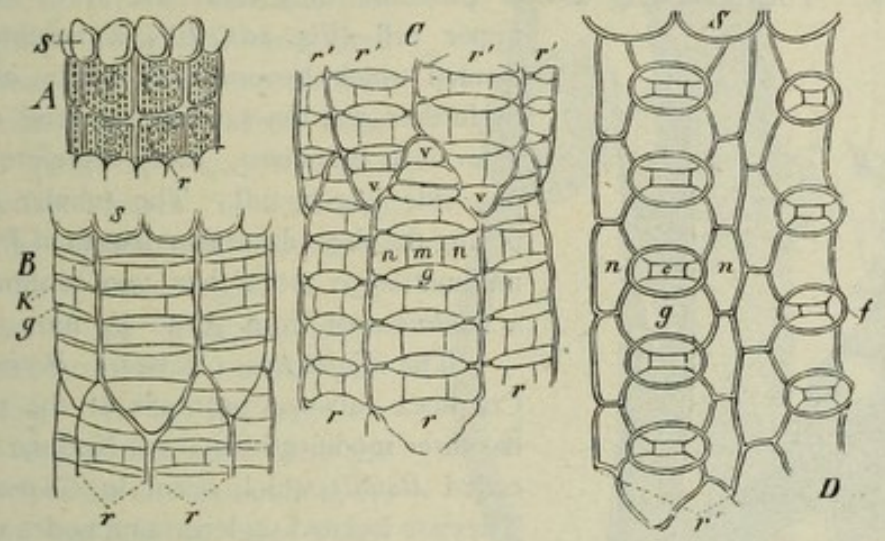

FIG. 201.—Development of the cortex of the stem of *Chara fragilis*; *A* a very young internode of the stem with the cortical lobe *r* still consisting of one cell; *B*—*D* its further development; *r r* signifies in all the figures the cortical lobes that ascend from the lower, *r' r'* those that descend from the upper leaves; *v v* the apical cell of each cortical lobe; *g g* its internodal cells, *n m n* the commencement of the formation of the node; *D c* the central cell of a cortical node; *S* signifies in all the figures the unicellular 'stipules' which spring in pairs from the base of the leaves.

by it from the first, the lobes keeping pace with its extension in length and thickness. Each lobe continues to grow, like the stem, by means of an apical cell, which becomes segmented by horizontal septa; out of each of the segments cortical internodal and nodal cells are formed by repeated divisions. The latter divide, by successive septa, into an inner cell, in contact with the internode of the stem, and three outer cells, the middle one of which commonly grows into the form of a spine or knob, resembling a leaf. The outer lateral cells of the cortical node, on the other hand, following the elongation of the internode itself, grow into longer tubes, so that each cortical lobe consists of three parallel rows of cells, the middle row however containing alternately short and long (internodal and nodal) cells. The cortex of the leaves is derived from the leaflets, and its formation is much simpler (Fig. 200, *C*–*E*, *br*). From the basal nodes of Chara other foliar structures also arise, both on the inner and outer side of the base of the leaf (Fig. 199, *S*), which Braun calls *Stipules;* they are always unicellular, and are sometimes very short, sometimes elongated.

[1] The first internode of every branch and leaf becomes covered with a cortex derived only from the descending cortical lobes of the next node above.

The nodes are the part from which all the lateral members of the Characeæ originate. The root-like structures or *Rhizoids* spring from the outer cells of the lower nodes of the primary shoot, and consist of long hyaline sacs growing obliquely downwards, and elongating only at their apex. They are formed by the outgrowth of flat cells at the circumference of the node, and are therefore attached to it by a broad base; but these bases of the stouter rhizoids themselves divide still further, giving rise, especially at the upper margin, to small flat cells from which slender rhizoids are developed. The rhizoidal tubes are segmented by only a few septa which lie far below the growing apex, and have at first an oblique position. The two adjoining cells abut one another like two human feet placed sole to sole. The branching always proceeds only from the lower end of the upper cell (Fig. 202, *B*); a swelling is here formed which becomes cut off by a wall, and by further division produces several cells which grow into branches; these therefore stand on one side like a tuft. The tubular cells composing the rhizoids attain a length of from several millimetres to more than two centimetres, with a thickness of from $\frac{1}{40}$ to $\frac{1}{10}$ mm.

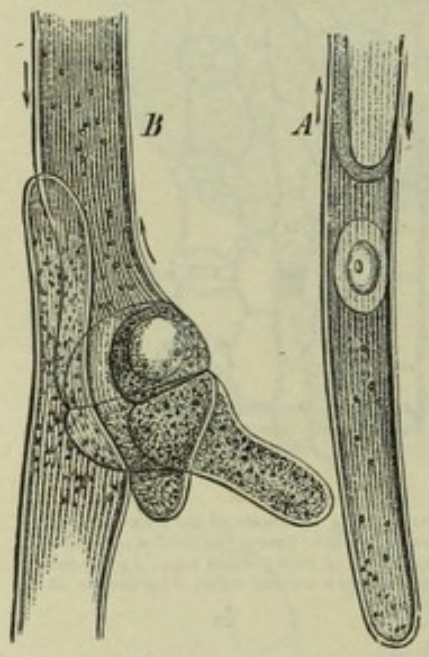

FIG. 202.—Rhizoids of *Chara fragilis*: *A* end in process of development: *B* a 'joint,' the lower part of the upper cell is branching (after Pringsheim, × 240). The arrows indicate the direction of the currents of protoplasm.

The *Vegetative* (*asexual*) *Reproduction* of Characeæ always proceeds at the nodes, and has three modifications:—(1) Nodular formations called *Bulbils* which occur in *Chara stelligera*. They are isolated underground nodes with greatly abbreviated whorls of leaves of beautiful regularity; their cells are densely filled with starch and other formative materials; new plants are produced from shoots laterally developed. (2) The *Branches with naked base* of Pringsheim. These are formed on old hibernating or on cut nodes of Chara in the axils not only of the oldest but also of the younger leaves of a whorl, and are in fact only slightly different from the normal branches, the greatest difference being in the partial or entire absence of the cortex of the lower internode and of the first whorl of leaves. The cortical lobes which descend from the first node of the branch often become detached from the internode and grow free, curling upwards, while the leaves of the lowermost whorl often do not form nodes. (3) The *Pro-embryonic Branches*. These spring, together with the last, from the nodes of the stem, but are essentially different from the branches, and have a similar structure to the pro-embryos which proceed from the spores. Like the last, they have only been observed in *Chara fragilis* (by Pringsheim). A cell of the node becomes elevated, and grows into a tube, and its apex becomes separated by a septum. In this growing terminal cell further divisions take place, till the 'apex of the pro-embryo' which proceeds from it consists of a row of from three to six cells. Beneath the apex of the pro-embryo (Fig. 203, *C*, *a*, *b*) the tube swells, and the distended part becomes separated by a septum as a cell, which Pringsheim calls the 'bud-rudiment,' (Fig. 203, *C*,

including the parts from *v* to *d*). This cell is now divided by two oblique walls into three cells, the middle one of which (*q*) lengthens into a tube (like an internode), while the upper and lower ones remain short. Out of the lower cell is afterwards formed a root-producing leafless node (Fig. 203, *d*, and Fig. 198, *d*), while the upper one, which lies between the apex of the pro-embryo *a b* and the elongated cell *q* becomes the axis of the new generation. It becomes arched on one side outwards, and divides in succession into the cells *I*, *II*, *III*, and *v*. Each of the cells *I*, *II*, and *III* becomes transformed by divisions into a disc of cells or transitional node, three of which thus stand over one another without intermediate internodes. Their lateral cells grow right and left, and form imperfect leaves of different lengths. The cell which lies outermost (Fig. 203, *C*, *v*) now begins to undergo a series of divisions, corresponding to those of a normal leaf-bearing shoot. It is, in fact, the mother-cell and at the same time the first apical cell of the new generation, *i.e.* of the sexual leaf-bearing plant which arises from the pro-embryo. The displacement indicated in Fig. 203, *C*, subsequently causes the apex of the pro-embryo to be pushed to one side; and since this apex has the appearance of a simple leaf uncovered by cortex, the further development of the lateral leaves which spring from the cells *I*, *II*, and *III*, brings about an appearance as if these different leaves together formed a whorl; and the bud of the lateral shoot thus comes to stand *apparently* in the centre of this pseudo-whorl (Fig. 203, *A*). If the structure which springs from the germinating spore is now compared with the pro-embryonic branch, the perfect homology cannot fail to be observed which Pringsheim pointed out in the parts that will be found indicated by the same letters in Figs. 198 and 203; but the pro-embryo of the spore has in addition a small node at the opening of the spore from which a rhizoid, sometimes called the primary root of Chara, springs (Fig. 198, *w'*).

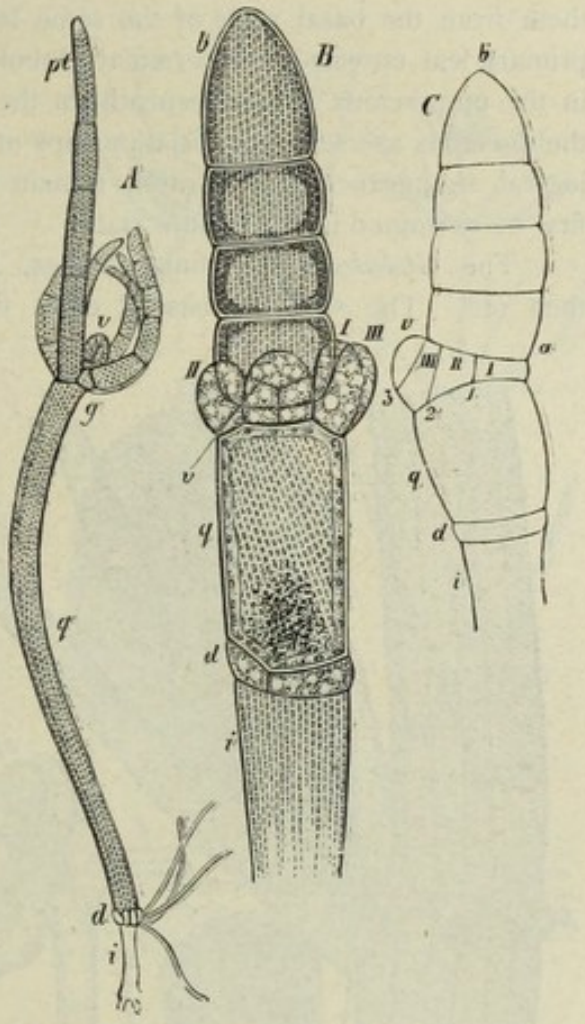

FIG. 203.—*Chara fragilis*; *A* an entire pro-embryonic branch; *i* the lowermost colourless cell below the root-node; *d* root-producing leafless node; *q* the long cell proceeding from the middle cell of the bud-rudiment; *pt* apex of the pro-embryo; *g* the pseudo-whorl of leaves, *v* the bud of the second generation of the leaf-bearing plant; *B* upper part of a young pro-embryonic branch; *i*, *d*, *q* as before, *b* apex of the pro-embryo; *I*, *II*, *III* the young leaflets of the transitional node, *v* the bud of the leafy stem; *C* still younger pro-embryonic branch; *i*, *d*, *q*, *b* as before; *I*, *II*, *III* the cells out of which the transitional nodes arise, *v* apical cell of the stem-bud (after Pringsheim, *B* × 170).

The *Sexual Reproduction* of the Characeæ results from organs which, in their development and definite form do not, in the present state of our knowledge,

correspond to those of Thallophytes, nor to those of Muscineæ or Vascular Cryptogams. To the male organs or Antheridia of Characeæ the term *Globules* is generally given; while the female organs, which are neither oogonia nor trichogynes nor archegonia, are usually called *Nucules*[1]. Globules and nucules stand on each side of the leaves; the globules are always the metamorphosed terminal cell of a leaf or lateral leaflet; the nucules spring, in the monœcious species, close beside them from the basal node of the same leaflet (Chara), or from the last node of a primary leaf crowned by a terminal globule (Nitella). The nucule therefore stands, in the monœcious Nitellæ beneath, in the Charæ above or beside the globule. In the diœcious species, these relationships of position of course fail; but the morphological significance and position remain unchanged. Both kinds of organs may first be examined in the mature state.

The *Globules* are globular bodies, ½ to 1 mm. in diameter, at first green, then red. The wall consists of eight flat cells, four of which, situated around the distal pole of the ball, are triangular, while the four situated around the base are quadrangular and become narrower below; each of these cells forms a segment of the shell of the ball, and they are hence called *Shields*. When unripe their inner face is covered with green grains of chlorophyll, which, in the ripe state, are of a red colour. Since the outer face is destitute of these grains, the outside of the ball appears clear and transparent (Fig. 204, *A*). From the lateral edges several folds of the cell-wall penetrate towards the middle of each shield, which gives them the appearance of being lobed in a radiate manner. From the middle of the inner face of each shield a cylindrical cell projects inwards, nearly to the centre of the hollow globule; these cells are called the *Manubria*. The flask-shaped cell which supports the globule also penetrates into the interior between the four lower shields; at the central end of each of the eight manubria is a roundish hyaline cell, the *Head;* and these twenty-

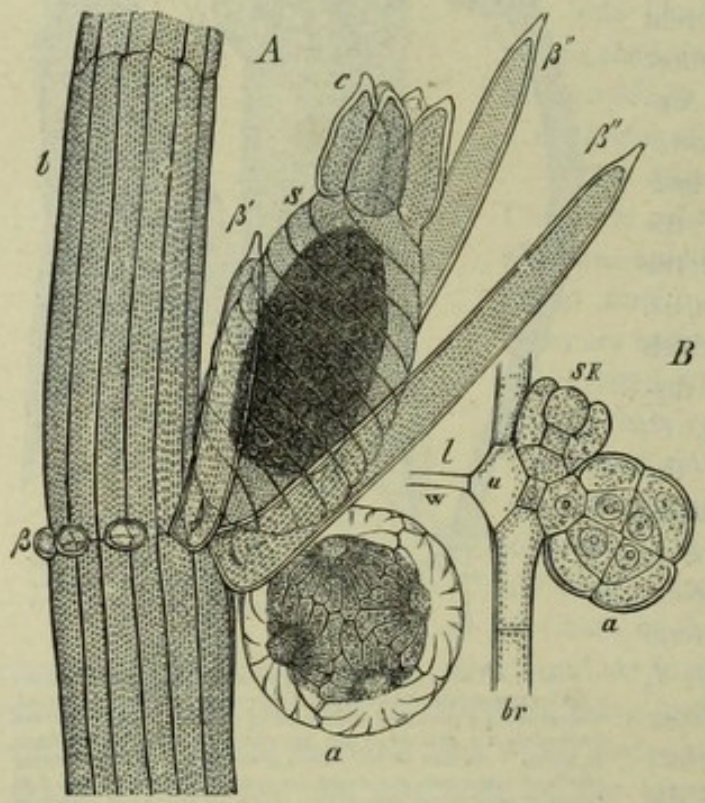

FIG. 204.—*Chara fragilis*; *A* middle part of a leaf *b* with a globule *a* and a nucule *S*, *c* its crown; *β* sterile lateral leaflet; *β′* large leaflets by the side of the nucule; *β″* the bracteoles, springing from the basal node of the nucule (× about 50). *B* a young globule *a* with a still younger nucule *SK*; *w* the nodal cell of the leaf, *u* the union-cell between it and the basal node of the globule; *l* cavity of the internode of the leaf; *br* cells of the leaf covered with cortex (× 350) (*cf.* Fig. 201).

[1] ['Spore-buds' of Sachs, 'ovum-buds' of De Bary.]

five cells form the framework of the globule. Each head bears in the centre six smaller cells (secondary heads), and from these grow four long slender whip-shaped filaments, which, being coiled round and round, fill up the interior of the globule (Fig. 205, *B*). Each of these filaments (the number of which amounts to about 200) again consists of a row of small disc-shaped cells (Fig. 205, *D*, *E*, *F*), numbering from 100 to 200. In each of these 20,000 to 40,000

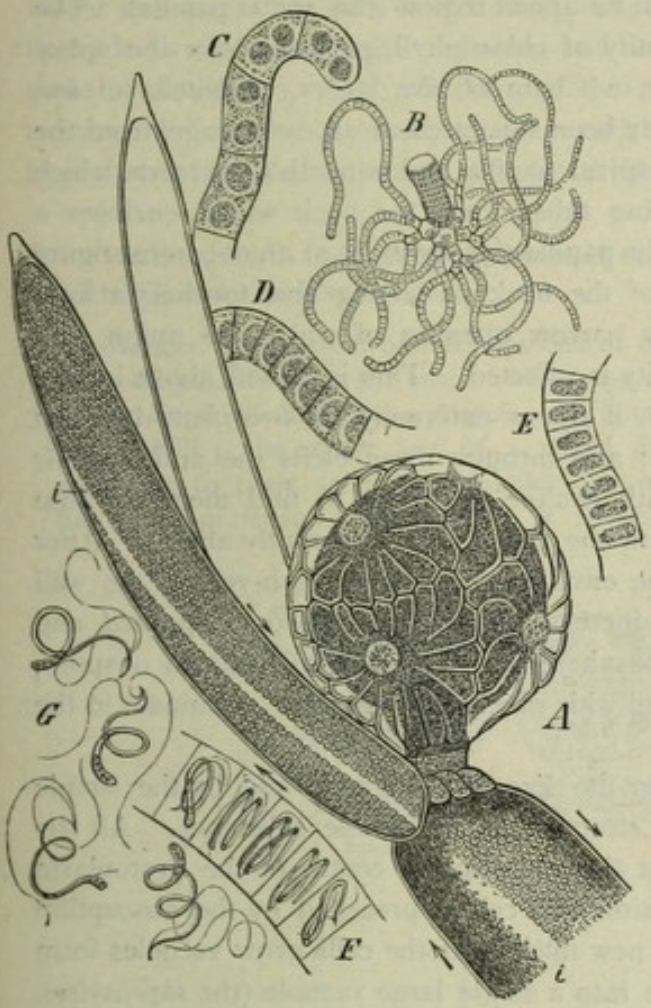

FIG. 205.—*Nitella flexilis*; *A* an almost ripe globule at the end of the primary leaf, by its side two lateral leaflets, *i* neutral lines; the arrows indicate the direction of the currents of protoplasm; *B* a manubrium with its head and the whip-shaped filaments, in which the antherozoids arise; *C* end of one of the young filaments; *D* middle part of an older one; *E* of one still older; *F* ripe antheridial filament with antherozoids *G* (*C*—*G* × 550).

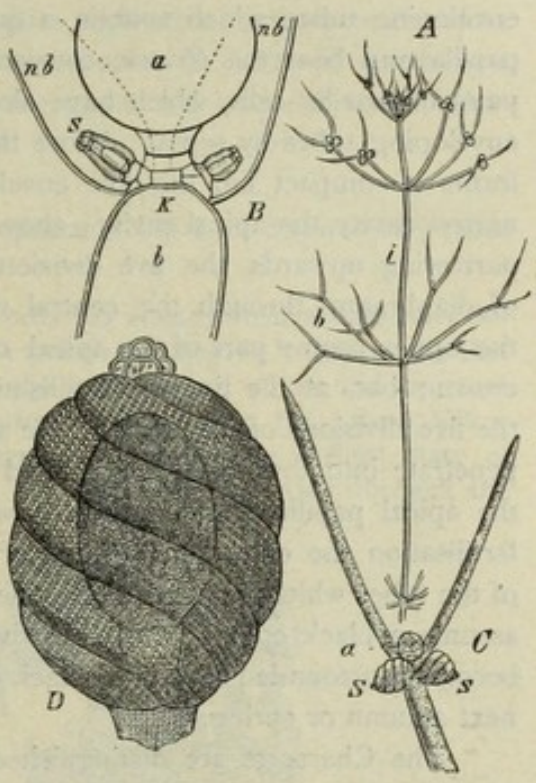

FIG. 206.—*Nitella flexilis*; *A* fertile branch (natural size); *i* internode, *b* leaves; *B* upper part of a fertile leaf *b* with the node *K*; on the node are two lateral leaves *n b*, and two very young nucules *S*; *a* a globule; *C* older leaf with two leaflets, a ripe globule *a*, and two unripe nucules *S*; *D* a half-ripe nucule more strongly magnified.

cells is formed an antherozoid, a slender spiral thread, thickened behind, and bearing at its pointed end two long fine cilia (Fig. 205, *G*). When perfectly ripe, the eight shields fall apart, their spherical curvature becoming diminished; the antherozoids leave their mother-cells and move about in the water. This breaking up appears generally to happen in the morning, and the antherozoids are in motion for some hours, till evening.

The mature *Nucule*, when ready for fertilisation, is a longer or shorter prolate spheroid; it is placed upon a short pedicel, visible externally only in Nitella, and consists of an axial row of cells, closely surrounded by five tubes which are coiled round it spirally. The whole must be considered as a metamorphosed shoot. The pedicel corresponds to the lower internode of a shoot; it bears a short nodal cell, from which the five enveloping tubes spring as like a whorl of leaves. Above the

nodal cell rises the peculiarly developed apical cell of the shoot, very large as compared to the other parts, and ovoid. At its base, immediately above the nodal cell, an inconspicuous hyaline cell is separated at an early stage in Chara; in Nitella a somewhat disc-shaped group of similar cells takes its place, which have been termed by Braun 'Wendungszellen.' The large apical cell of the nucule is filled with a number of drops of oil and grains of starch as well as with protoplasm; it contains pure hyaline protoplasm only in its apical region (the apical papilla). The enveloping tubes, which contain a quantity of chlorophyll, project above the apical papilla and bear the *Crown*, consisting in Chara of five larger, in Nitella of five pairs of smaller cells, which have already been separated at an early stage from the enveloping tubes by septa. Above the apical papilla and beneath the crown, which forms a compact lid, the five enveloping tubes form the neck which encloses a narrow cavity, the apical cavity; above the papilla this cavity is of an obconical figure narrowing upwards, the five divisions of the neck projecting and forming a kind of diaphragm, through the central very narrow opening of which the union with the upper roomy part of the apical cavity is effected. This is closed above by the crown; but, at the time of fertilisation, it opens externally by five clefts between the five divisions of the neck of the sac; and through these clefts the antherozoids penetrate into the apical space filled with hyaline mucilage, to find their way into the apical papilla of the oosphere, where the cell-wall is apparently absent. After fertilisation the chlorophyll-grains of the envelope become reddish-yellow, the wall of the tubes which lie next the oosphere increase in thickness, become lignified, and assume a black colour; and thus the oosphere, now transformed into an oospore, becomes surrounded by a hard black shell with which it falls off, to germinate in the next autumn or spring.

The Characeæ are distinguished by the size of their cells, and by the simple relations of the individual cells to the structure of the whole substance. All the young cells contain nuclei, which at first always lie in the centre of the protoplasm that fills up the whole cell; each bipartition of a cell is preceded by the absorption of the nucleus and the formation of two new nuclei. As the cells grow vacuoles form in the protoplasm which finally coalesce into a single large vacuole (the sap-cavity). The protoplasm, now clothing the wall as a thick layer, commences its rotatory motion which always follows the longest direction of the cell; the nucleus about this time becoming absorbed, while grains of chlorophyll are formed. With the growth of the whole cell these grains also grow and multiply by repeated bipartition; they adhere to the inner side of the outermost thin stationary layer of protoplasm, and take no part in the rotation of the layers which lie further inwards. The rotating protoplasm becomes differentiated, as the cell grows, into portions some very watery and others less watery and denser, the former appearing as hyaline cell-sap in which the latter float in the form of roundish larger or smaller lumps. Since these denser bodies are passively swept along by the rotating clear protoplasm, as may be seen from their tumbling over one another, the appearance is presented as if the cell-sap caused the rotating motion. Together with the denser lumps of protoplasm of less regular form, there are also a number of bodies of globular shape covered with delicate spines, consisting also of protoplasm. The current, as Nägeli has shown, is most rapid next the stationary parietal layer, and becomes

gradually slower towards the interior; hence the spheres and globules which swim in the thin rotating protoplasm tumble over one another, because they become immersed at different spots in layers of different rapidity. Dependent on the direction of the current, the grains of chlorophyll are arranged in longitudinal rows on the stationary layer, and are deposited so thickly that they form a stratum; they are absent only at the neutral lines (Fig. 205, *A*, *i*). These neutral lines mark the position where the ascending and descending portions of the rotating protoplasm of a cell run side by side in opposite directions and neutralise each other, and where therefore there is no motion. The direction of the rotatory motion in each cell stands in a regular relation to that of all the other cells of the plant, and hence to its morphological structure, as has been shown by A. Braun.

With regard to the various processes of development, I will here describe only those of the Globules and Nucules.

Globules. The order of development of the cells has already been exhaustively described by A. Braun in the case of *Nitella syncarpa* and *Chara Baueri;* it agrees with that of *Nitella flexilis* and *Chara fragilis.* In Nitella the terminal cell of the leaf becomes the globule; the oldest leaf of a whorl first forms its globule, the others follow according to their age; the globules are recognisable even in the earliest state of the whorl of leaves. In Fig. 207, *A*, is shown the longitudinal section through the

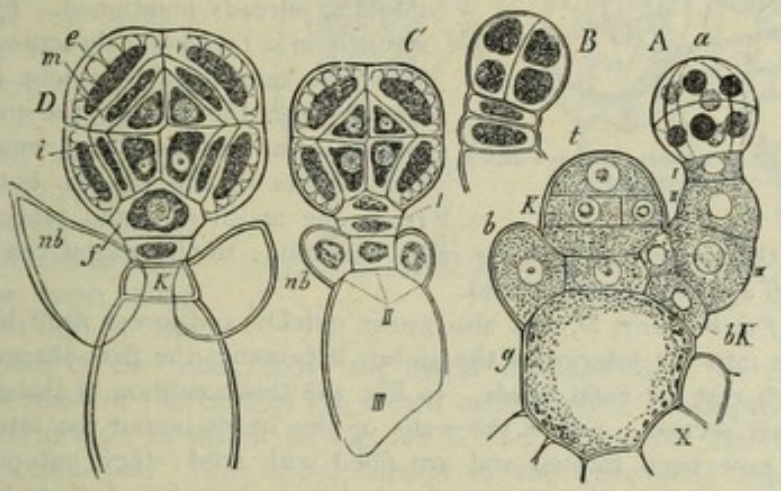

FIG. 207.—Development of the antheridia of *Nitella flexilis.* In *B*, *C*, and *D* the protoplasm has been contracted by glycerine.

apex of a branch, *t* being its apical cell; its last-formed segment has already been divided by a septum into a nodal mother-cell *K* and an internodal cell lying beneath it; beneath this lies the node with the last whorl of leaves; *b* is its youngest leaf, *bK* the basal node of the oldest leaf which already consists of the segments *I, II, III*; *a* is the terminal cell of this leaf which becomes transformed into the globule. While the globule is becoming developed, the leaf also undergoes still further changes which must be first considered. The segment *III* becomes the first internode of the leaf, *II* becomes a node from which are developed the lateral leaflets *n b* in *C* and *D*. The cell *I* divides into two (*C*, *I*), the lower of which remains short, while the upper grows into a flask-shaped cell (Fig. 207, *D*, *f*, and Fig. 208).

The globular mother-cell of the globule (Fig. 207, *A*, *a*) first of all divides into two hemispheres by a vertical wall passing through the axis of the leaf; these are divided into four segments by a vertical wall at right angles to the first; in each of the four quadrants a third division takes place horizontally and at right angles to the two last

walls; and the globule now consists of four lower and four upper octants of a sphere. Contraction by glycerine clearly shows that each of these divisions of the protoplasmic body is completely effected before the appearance of the cellulose-wall (Fig. 207, *B*); the second division even takes place before the wall has arisen between the two first-formed halves; and the four quadrants may be made to contract without any wall being visible between them. In Fig. 207, *B*, the third division has also taken place, the second vertical wall is already formed, and the two quadrants there visible are already divided; but no horizontal wall has yet appeared. In Fig. 207, *A*, *a*, are shown the eight octants in perspective together with their nuclei. Each octant now breaks up first of all into an outer and an inner cell (Fig. 207, *C*); the latter is again divided in all the eight octants (*D*), so that each octant now consists of an inner, a middle, and an outer cell (*D*, *i*, *m*, *e*). Up to this time the globe remains solid, and all the cells lie close to one another; but now commences an unequal growth, and with this the formation of intercellular spaces (Fig. 208). The eight outer cells (*e*) are the young shields, the side-walls of which show even at an earlier period the radial infolding already mentioned. They grow more strongly in a tangential direction than the inner cells, the outside of the globe increasing more rapidly than the inside; the middle cells (*m*), which form the manubria, remain attached to the centres of the shields, but are separated from one another by the tangential growth of the shields; they grow slowly in the radial direction; the innermost cell *i* of each octant is rounded off and becomes the head.

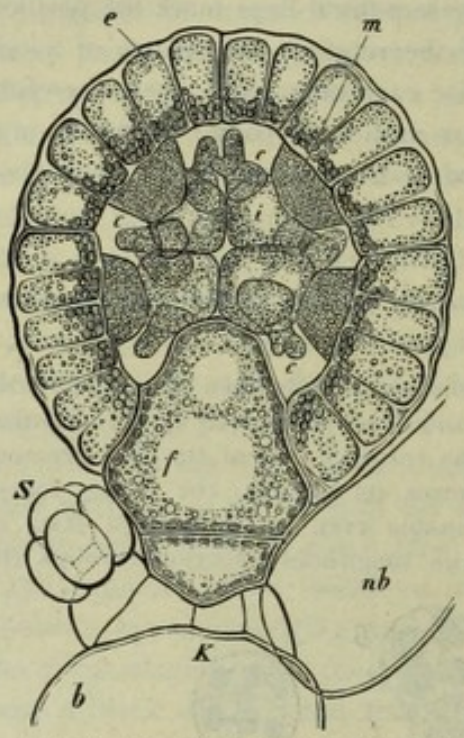

FIG. 208.—Antheridium of *Nitella flexilis* in a further stage of development (× about 500).

The cell *f* in Fig. 207, *D*, now also grows quickly, and forces itself between the four lower shields into the interior of the globe; it becomes the flask-shaped cell, upon the apex of which rest the eight heads. In Fig. 208 this condition of the globule is shown in longitudinal section; where the walls of the heads bound the intercellular spaces which have now been formed and are filled with fluid; they put out branches (*c*) which become septate, and again ramify; and these branches elongate by apical growth and also become septate. The lowermost cells swell up into a roundish shape, and form the secondary heads, upon which stand the whip-shaped filaments, consisting of the discoid cells which are the mother-cells of the antherozoids. (Compare Fig. 208 with Fig. 205, *B*.)

The globules of *Chara fragilis* are produced by metamorphosis of those leaflets which form the innermost row on a leaf, and in fact, as is shown in Fig. 210, the development advances downwards to the primary leaf. The succession of cells and the mode of growth show no noteworthy differences from those of Nitella; the flask-shaped pedicel is here placed on a small cell wedged in between the cortical cells, the central cell of the basal node of the leaflet, which Braun asserts to be present also in sterile leaves, where however I have not succeeded in finding it.

Antherozoids. The whip-shaped filaments in which the antherozoids arise, do not grow merely at their apex, but have also an intercalary growth. This is shown by the elongated cells in the middle of young filaments, each with two nuclei, between which no division-wall has yet been formed (Fig. 205, *C*). The longer the filaments become, the more numerous are their divisions, until at length the individual cells have the appearance

of rather narrow transverse discs. The further development of the contents of these mother-cells of the antherozoids progresses backwards from the end of the filament; the antherozoids are formed in basipetal order in each filament. At first the nucleus of each mother-cell lies in its centre, later it places itself in contact with the septa; the nuclei then disappear, and their substance becomes mixed with that of the protoplasm, which now forms a central discoid mass in the mother-cell, surrounded by a hyaline fluid (Fig. 205, *E*). From this is formed the antherozoid, in addition to which, when it is mature, there is no granular protoplasm[1]. The antherozoids begin to rotate even while within their cell, and escape out of it after the rupture of the antheridium; the filiform antherozoid has in Nitella 2 or 3, in Chara 3 or 4 coils; the posterior thicker end contains a few glistening granules.

The Development of the Nucules has already been described in detail by A. Braun; I have also studied it in *Nitella flexilis* and *Chara fragilis*. In *Nitella flexilis* it springs from the node of the leaf beneath the globule (Fig. 206, *B* and *C*); its origin is much later than that of the latter. Fig. 209, *A*, represents a very young nucule, the pedicel of which (*b*) bears the smaller nodal cell with the five rudiments of the enveloping tubes (*b*) (two only are shown here in longitudinal section). Above the nodal cell lies the apical cell (*s*) of the shoot, which represents the nucule. *B* represents a further stage of development, in which the first of the cells, designated by A. Braun the 'Wendungszelle,' has already made its appearance, and two septa have also appeared on the upper part of each enveloping tube; these upper short cells are raised up by the intercalary growth of the tubes, above the apical cell, and form the crown *K* in *C* and *D*. The lowest of the cells of the crown each forms a prolongation projecting inwards and downwards, as shown in Fig. 209 *C* and *D*, so that the whole nucule resembles a 'lobster-pot.' The spiral torsion of the enveloping tubes does not begin till a later period; the coils become gradually flatter while the apical cell of the nucule increases considerably in size and developes into the oosphere (Fig. 206). The development and fertilisation of the nucule of Chara has recently been described in detail by De Bary in the case of *C. fœtida*. Here also it consists, from an early stage of its development, of an axial row of three cells, and five others consisting each of two cells which form an envelope round it. The lowermost cell of the axial row is the nodal cell, the second remains small and colourless, and corresponds to the first 'Wendungszelle' in Nitella. It becomes in this case also, as De Bary's drawings show, separated by a somewhat oblique septum at the base of the apical cell (now the third of the axial row). Originally almost hemispherical, the apical cell grows first of all into the form of a narrow cylinder, and then becomes ovoid; it is provided, until it attains its full size, with a thin very delicate cell-wall; drops of fat and starch grains accumulate in its protoplasm. Its apex however remains free, and forms a

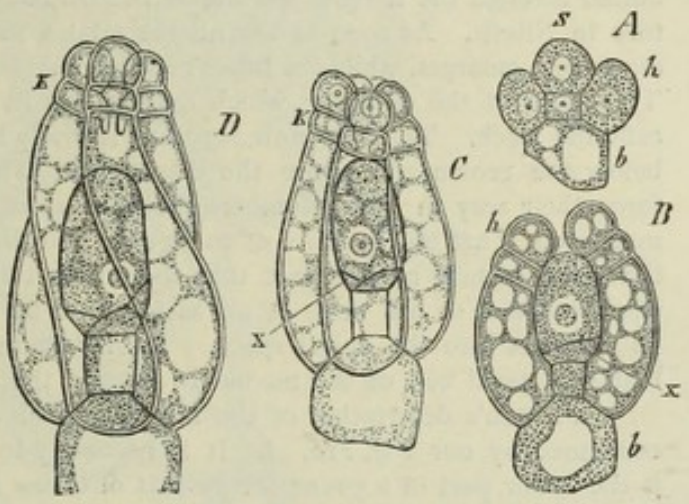

FIG. 209.—Development of the nucule of *Nitella flexilis* (× about 300); *x* 'Wendungszellen.'

[1] Compare the opposite view of Schacht, Die Spermatozoiden im Pflanzenreich, 1864, p. 30.

transparent finely granular terminal papilla, the receptive portion ; the apical cell of the nucule has therefore become transformed into an oosphere. The five enveloping tubes are from the first in close contact with the apical cell or oosphere; after each has become divided by a septum about half way up, the uppermost of the cells thus separated also become closely united with one another above the oosphere. This closing of the envelope takes place at least in *Chara fœtida*, before the 'Wendungszelle' has separated from the oosphere. The five upper cells of the envelope are at first as long as the five lower ones, and the septa which separate them lie about half way up the oosphere. As it now increases in size, the five lower ones become elongated into long tubes, which are at first straight but afterwards wind spirally round the oosphere. The five upper cells form the crown, which is elevated some distance above the apex of the oosphere. Between the crown and the apex of the oosphere the enveloping tubes grow inwards and increase in breadth, so that together they form, above the apical papilla of the oosphere, a thick diaphragm open only in the middle, by which a narrow space lying below the crown is separated from a still narrower one above the oosphere. The cells of the crown form a closed cover above the upper space; the upper and under space are united through the narrow opening in the diaphragm. De Bary found a similar structure in Nitella. As soon as the nucule attains its full size, the small space above the diaphragm enlarges, while the tubes between the diaphragm and the crown grow longer. This piece of the envelope, which only attains its full size at a later period, De Bary calls the Neck. The sacs now separate laterally from one another, forming five clefts below the crown and above the diaphragm. Through these clefts the antherozoids force their way in great numbers into the apical space, which is filled by a hyaline mucilage. That one or more of them even find their way into the oosphere is rendered the more certain by the fact that about this time its papilla is protected by a very weak cell-wall or has none at all, as is shown by the small pressure required to expel its contents into the apical space. It may therefore be considered as demonstrated that the apical cell of the nucule is actually the oosphere of Characeæ.

A. Braun's description of the morphological value of the nucule of Chara is fully confirmed by our Fig. 210, *A*. It is necessary to explain, in the first place, that this is the lower part of a young fertile leaf of *Chara fragilis*, together with the contiguous piece of the stem, and an axillary bud represented in longitudinal section; *m* is half of the nodal cell of the stem, *i* its upper, *i'* its lower internode, *sr* a descending, *y* an ascending cortical lobe; *sr'* the cortical lobe of the lower internode which descends from the leaf, *rK* a node of it; *i''* the first internode of the axillary bud which rests upon the cell *n* that unites the nodal cell *m* with the basal node of the leaf. The leaf shows its three lower internodes, *z*, *z*, *z*, still rather short; they eventually attain from 6 to 8 times this length. Between them are the nodal cells *w*, *w*; *v*, *v* are the cells which unite the leaf-node with the basal node of the leaflet β on the outer side of the leaf; *a* the corresponding cells on the inner side of the leaf; *br* the cortical lobes of the leaf, two of which go upwards and two downwards from each leaflet β; the lowermost internode of the leaf is however covered only by descending lobes; by the side of one of them stands the stipule *s*. *x*, *x* are the cortical lobes which descend on the inside of the internodes of the leaf, where the leaflets are transformed into globules, *a*, *a*; the ascending cortical lobes of the leaf are here absent, because one nucule always springs from the basal node of each leaflet. (Compare with this Fig. 204, *A* and *B*.) In reference to the origin of the nucule, A. Braun says (*l. c.* p. 69) that it springs from the basal node of a leaflet just as the branch does (in *Chara fragilis* from the basal node of a globule which stands in the place of a leaflet). As in the leaf which subtends a branch the ascending cortical lobes are wanting, so also in the leaflet which bears the nucule the cells forming the ascending portion of the cortex are also wanting. As it is the first leaf of the whorl on the stem that produces a branch in its axis, so it is also from the first (inner) leaflet of the whorl on the leaf that the nucule originates. The basal node of the globule in *C. fragilis* has, according to A. Braun, not four

peripheral cells, as in sterile leaflets, but five; an upper odd one which is first formed, two lateral ones which follow, and two lower ones which are formed last of all. Of these five cells only the two lower ones are developed into cells which form the cortex (of the leaves), the upper one, wanting in the sterile basal nodes, is the mother-cell of the nucule; but the two lateral ones are developed into leaflets which stand laterally between the globule and nucule (*cf.* Fig. 204, β''); these latter Braun calls Bracteoles. The mother-cell of the nucule now grows out of the axil of the globule, and divides

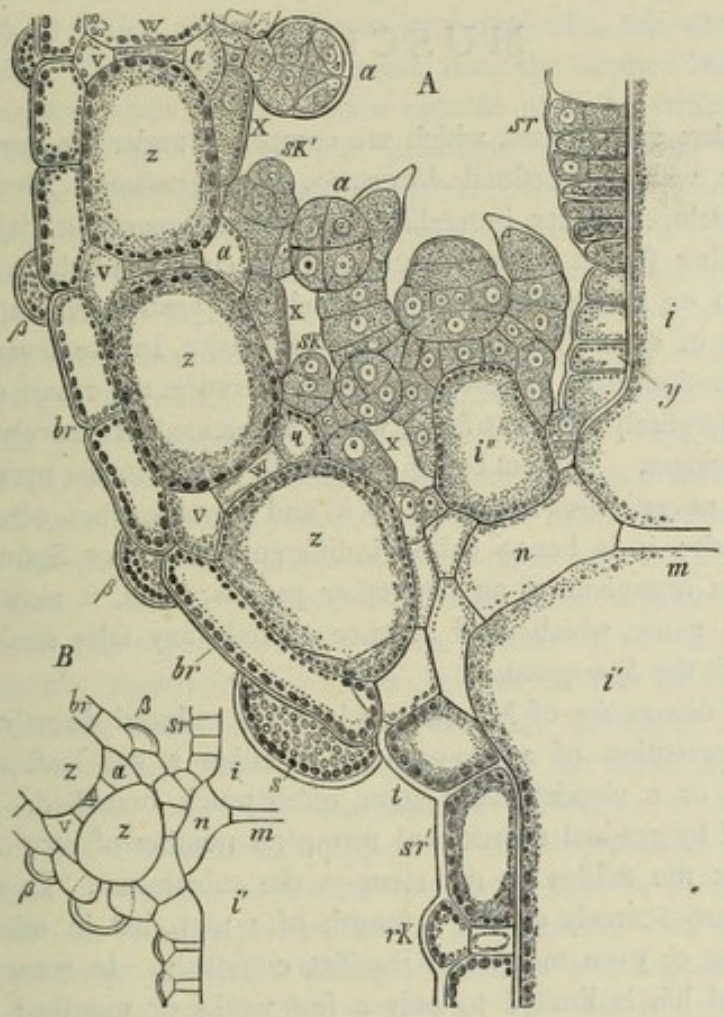

FIG. 210.—*Chara fragilis*: *A* lower part of a fertile leaf, a lateral bud springing from its axil; *B* lower part of a sterile leaf without an axillary shoot (in longitudinal section).

itself by a septum into an upper outer terminal cell and a segment which in its turn is broken up into two discs by a wall parallel to the previous one (Fig. 210, *A*, *SK*). The lower cell does not divide any further, it forms the concealed pedicel of the nucule, and corresponds to the first internode of a branch; but the upper one has the character of a nodal cell; it is divided by tangential walls into a zone of five outer and one inner cell (*SK'*); the former are the rudiments of the enveloping tubes, which are therefore morphologically leaves.

GROUP III.

MUSCINEÆ.

The Hepaticæ and Mosses, which are comprised under the term Muscineæ, are distinguished by a sharply defined *Alternation of Generations*. From the germinating spore is developed either immediately a sexual generation rich in chlorophyll and self-supporting (as in most Hepaticæ), or a confervoid thallus is first formed (the Pro-embryo or Protonema), out of which the sexual generation grows as a lateral shoot (as in some Hepaticæ and all Mosses). In the female sexual organ of this first generation there arises—as a new generation the result of fertilisation—a structure of an entirely different form, which is destined exclusively for the production of asexual spores. Without being organically united to the previous generation, this structure is nevertheless nourished by it, and appears, when observed externally, simply as its fruit; it is hence called indifferently Fruit or Sporangium. Since however it is an organism of an altogether peculiar kind, it may be desirable to give it a special name, which shall at once exclude any false analogy; I propose therefore to call it the *Sporogonium*.

The Sexual Generation of Muscineæ which is produced directly from the spore or with the intervention of a pro-embryo, is either a flat leafless thallus, as in many Hepaticæ, or a slender leafy stem, often much branched. In both cases, which are united by gradual transitional forms[1], a number of root-hairs are usually formed, which fix the thallus or the stem to the substratum. In some cases this vegetative structure scarcely attains a length of 1 mm., but in others as much as from 10 to 30 cm. or even more, and ramifies copiously. In some of the smallest forms its term of life is limited to only a few weeks or months; in most it may be termed unlimited, since the thallus or the leaf-bearing stem continually grows at its apex or by a process of renewal (Innovation), while the oldest parts die off behind. In this manner the branches become finally independent plants; and this, as well as the multiplication by gemmæ, stolons, detached buds, the transformation of hairs into pro-embryos (in Mosses), &c., serves not only to increase enormously the number of individuals formed by the asexual method, but is also the immediate cause of the social or cespitose mode of growth of these plants. Many Mosses in particular, even those which only rarely fructify, may in this manner form dense masses extending over considerable areas (as Sphagnum, Hypnum, Mnium, &c.).

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[1] From the great similarity of the true leafless thallus of some Hepaticæ to the thalloid stems of others furnished with leaves on the under side, it will be convenient to use the term 'thalloid forms' for both; the term including both a true thallus (*e.g.* Anthoceros) and also a thalloid stem (as in Marchantia).

The sexual organs are Antheridia and Archegonia. The mature *Antheridium* is a body with a longer or shorter stalk, of a spherical, ellipsoidal, or club-shaped form, the outer layer of its cells forming a sac-like wall, while each of the small and very numerous crowded cells enclosed within it developes an antherozoid. The antherozoids are freed by the rupture of the wall of the antheridium at the apex; they are spirally coiled threads thicker at the posterior and tapering to a fine point at the anterior end, at which are placed two long fine cilia, the vibrations of which cause their motion. The female organs, which since the time of Bischoff have been called *Archegonia*, are, when in a condition capable of being fertilised, flask-shaped bodies bulging from a narrow base and prolonged into a long neck. The wall of the ventral portion encloses the central cell, the protoplasm of which, contracting and rounding off, forms the oosphere. Above this begins a row of cells which passes through the neck in an axial direction, and is continued as far as the cells which form the so-called 'Stigma.' The cells of this axial row become broken up before fertilisation, and transformed into mucilage which finally swells up and forces apart the four stigmatic cells. In this manner an open canal is formed, which leads down as far as the oosphere, and enables the antherozoids to enter it. This mucilaginous axial row of cells occurs also in the archegonium of Ferns, but in Rhizocarpeæ and Lycopodiaceæ is reduced to a single rudimentary cell.

The great diversity in the origin of the sexual organs of Muscineæ is of extreme importance. In the thalloid Hepaticæ these organs arise below the growing apex from the superficial cells of the thallus or of the prostrate thalloid stem, or on specially metamorphosed branches (as in the Marchantieæ); in the foliose Jungermannieæ and in the Mosses not only the antheridia but also the archegonia may be formed from the apical cell of the shoot or from segments of it; in this case they may take the place of leaves, or of lateral shoots, or even of hairs. Thus the antheridia appear as metamorphosed trichomes in the axils of the leaves of Radula, as metamorphosed shoots in Sphagnum, as apical structures and also as metamorphosed leaves in Fontinalis. In the same manner the first archegonium of the fertile shoots of Andræa and Radula arises from the apical cell, the later ones from its last segments; and this is probably the case in Sphagnum.

Antheridia and archegonia are usually produced in great numbers in close proximity; in the thalloid forms of the Hepaticæ they are generally enveloped by later outgrowths of the thallus; in the foliose Jungermannieæ and in Mosses several archegonia are commonly surrounded by one envelope formed of leaves which is termed the *Perichætium*; in Mosses a male flower (sometimes a hermaphrodite one) is usually formed in this manner, while the antheridia of the Jungermannieæ and of Sphagnum stand alone. Very commonly, especially in the foliose kinds, *Paraphyses*, *i. e.* articulated threads or narrow leaf-like plates of cells, are formed in the male and female flowers by the side of the sexual organs. Besides the envelopes just named, there is also often in Hepaticæ (but not in Mosses) a so-called *Perianth*, which grows as an annular wall at the base of the archegonium, and finally surrounds it as an open sac.

The *Asexual Generation* or *Sporogonium*, arises in the archegonium from the fertilised oosphere or oospore. It first developes by repeated cell-divisions into an

ovoid embryo, growing at the end turned towards the neck of the archegonium, *viz.* the apex. Its final form is very different in different sections. In its lowest type (in Riccia) it is a globe, the outer cell-layer forming the wall, while all the inner cells become spores. In all other cases the sporogonium becomes differentiated externally into a slender stalk or *Seta* which penetrates into the bottom of the archegonium and even into the underlying tissue, and a Capsule (Urn or *Theca*) turned towards the neck of the archegonium, in which the spores arise. Together with the spores, long cells thickened by spiral bands, the *Elaters*, are also produced in most Hepaticæ. The internal differentiation of the spore-capsule is, in addition to this, very varied, and attains a very high degree of complexity, especially in the Hepaticæ.

While the sporogonium is developing, the ventral portion of the archegonium also continues to grow; its cells increase rapidly in number, and it thus becomes broader, enclosing the young sporogonium, and, in this condition, is termed the *Calyptra*. Its behaviour supplies distinctive characters for the larger groups. In the lowest Hepaticæ (Riccia) the sporogonium remains always enclosed in the calyptra; in the higher Hepaticæ it protrudes only after the ripening of the spores, its stalk elongating suddenly, and the capsule protruding from the ruptured calyptra for the purpose of disseminating the spores, the calyptra surrounding the base of the seta as a cup-like membranous structure. In the typical Mosses, on the other hand, the young sporogonium first assumes the form of a greatly elongated fusiform body, which, even before the development of the capsule, exerts a strong upward pressure upon the calyptra, which becomes detached at its base, and is raised up by the young sporogonium in various forms; the seta penetrates deep down into the tissue of the stem, by which it is surrounded as a sheath (*Vaginula*).

The spores of the Muscineæ arise *in fours;* the mother-cells—which had previously been united into a tissue with the surrounding cell-layers, but had become isolated even before the formation of the spores—show a rudimentary division into two previous to complete division into four. The number of the mother-cells and the place where they are produced in the sporogonium depends essentially on the internal differentiation of the latter. The ripe spores show a thin cuticle (the Exospore) provided with small excrescences, which is ruptured on germination by the inner layer of the cell-wall (the Endospore). Its contents consist, in addition to colourless protoplasm, of grains of chlorophyll, starch, and oil.

The *Differentiation of the Tissues* of Muscineæ is very various, and more considerable than in Algæ, but less so than in Vascular Cryptogams. Fibro-vascular bundles are not found; only in the stem and leaf-veins of the more perfect Mosses is an axial bundle of elongated cells differentiated, which may be considered as a slight indication of the fibro-vascular system. The Marchantieæ, on the other hand, show on the upper side of their thalloid stems, and the Mosses on their thecæ, a distinctly differentiated epidermis, which usually also forms stomata. The cell-walls of the Muscineæ are generally firm, often thick, tough, and elastic, and in this case frequently of a brown, bright red, or violet colour. The tendency towards the formation of jelly and mucilage, so general in the Thallophytes, is not found in the Muscineæ, with the exception of certain processes in the mother-cells

of the spores. Various forms of thickening are not uncommon, especially in the spore-capsule, as in the spiral bands of the elaters of Hepaticæ, and the formation of the epidermis and peristome of the thecæ of Mosses.

Classification of Muscineæ. The sexual generation is developed from the spore, generally after the previous formation of a pro-embryo. It is the longest-lived of the two generations, and constitutes the self-supporting vegetative structure of these plants, presenting either a flat dichotomously branched thallus, or a thalloid stem, or a filiform stalk furnished with two or four rows of leaves. True fibro-vascular bundles are not produced. The archegonia and antheridia are, except in the simplest thalloid forms, stalked multicellular bodies usually free, but sometimes buried in neighbouring masses of tissue from the subsequent growth of these latter. The central cell of the ventral part of the archegonium produces the oosphere by rejuvenescence of its protoplasmic body into a primordial cell. The antherozoids are spirally coiled threads with two cilia on the anterior pointed end.

The asexual generation or sporogonium arises from the oosphere within the actively growing ventral part of the archegonium, which becomes developed into the calyptra. The sporogonium is nourished by the sexual plant; it has therefore no independent existence, and appears externally as an appendage to it. It is usually a stalked capsule, in which (with the exception of Archidium) a number of cells are always developed into the mother-cells of the spores; and from these the spores are formed by division into four after bipartition has commenced but has not been completed.

(1) *Hepaticæ.* The sexual generation arises either directly from the spore or with the intervention of a small inconsiderable pro-embryo. It is developed as a flat dichotomously branched thallus or a thalloid stem, or finally as a filiform stalk furnished with two or four rows of leaves. This vegetative structure is usually broadly expanded and clings closely to the ground or to some other substratum; even when the stems grow erect there is still an evident tendency towards the formation of an upper (dorsal) and an under (ventral) surface. The mode of growth is hence always distinctly bilateral. The asexual generation or sporogonium remains surrounded by the calyptra until the spores are ripe; the calyptra is usually at length ruptured at the apex, and remains at the base of the sporogonium as an open sheath, while the free spore-capsule projects above its apex, to allow the escape of the spores. The mother-cells of the spores arise either from the whole of the cells except those of the single layer which forms the wall of the capsule, or the intermediate cells commonly become developed into elaters.

(2) *Mosses.* The sexual generation is developed from the spore with the intervention of a pro-embryo consisting of branched rows of cells and often vegetating for a considerable time independently, even when it has already produced leafy stems by lateral budding. The vegetative body is here always a cormophyte, a filiform stem furnished with leaves in two three or four rows, usually without any definitely indicated bilateral structure, and generally branched in a monopodial, never in a dichotomous manner. The asexual generation or sporogonium is only at first formed in the calyptra, afterwards this is usually ruptured below (at the vaginula), and raised up by the apex of the sporogonium, which covers it like a cap. The capsule, which is now first developed, produces the spores from an inner layer of tissue, while a large inner mass of tissue remains sterile, and forms the Columella. The wall of the capsule is covered by a distinctly differentiated epidermis, the upper part of which usually becomes detached from the lower part (the Urn) in the form of a cover, in order to allow the escape of the spores.

CLASS IV.

HEPATICÆ[1].

(1) The *Sexual Generation* is developed, in some genera, directly from the germinating spore, its first divisions resulting in the formation of a cellular lamina or a mass of tissue which fixes itself by root-hairs and produces the thallus by growth at its apex, as in Anthoceros and Pellia. In other cases the embryo which results from the divisions of the spore first forms a narrow ribbon-like lamina of cells, the apical cell of which becomes subsequently the apical cell of a stem, and the segments form leaves, as in *Jungermannia bicuspidata* (according to Hofmeister). Or again, the bud of a leafy stem springs immediately from the spore (*Frullania dilatata*). In other cases, on the other hand, a pro-embryo is formed; the endospore which grows out into the form of a tube produces a short articulated filament, on which the rudiments of the thallus are formed as lateral shoots, in a manner similar to the leaf-buds of Mosses on the protonema (*e. g. Aneura palmata*, Marchantia). In Radula the spore produces first of all a cake-shaped plate of cells, from which the first bud of the leafy stem shoots laterally (Hofmeister).

The vegetative structure of Hepaticæ is always formed in a distinctly bilateral manner; its free side, turned towards the light, is differently organised from that which faces and often clings closely to the substratum and is not exposed to light.

In the greater number of families and genera the vegetative structure is a broad, flat, or curled plate of tissue, varying in length from a few millimetres to several centimetres; and is either a true thallus without any formation of leaves, as in Anthoceros, Metzgeria, and Aneura, or lamellæform outgrowths arise on the under or shady side, which at the same time produces root-hairs; and these outgrowths may be looked on as leaves. For the sake of having a common expression for these forms extremely similar in habit, they may be comprised in the term *Thalloid*[2],

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[1] Mirbel, Ueber Marchantia, in the Mém. de l'Acad. des Sci. de l'Inst. de France, vol. XIII, 1835.—G. W. Bischoff, in Nova Acta Acad. Leopold. Carol. 1835, vol. XVII. pt. 2.—C. M. Gottsche, ditto, vol. XX, pt. 1.—Gottsche, Lindenberg u. Esenbeck, Synopsia Hepaticarum, Nürnberg, 1844. Hofmeister, Vergleich. Untersuchungen, 1851.—[On the Germination, Development, and Fructification of the Higher Cryptogamia: Ray Society, 1862.]—Kny, Entwickelung der laubigen Lebermoose; Jahrb. für wiss. Bot. vol. IV, p. 66, and Entwickelung der Riccien, ditto, vol. V, p. 359.—Thuret, in Annal. des Sci. Nat. 1851, vol. XVI (Antheridia).—Strasburger, Geschlechtsorgane u. Befruchtung bei Marchantia; Jahrb. für wiss. Bot. vol. VII, p. 409.—Leitgeb, Wachsthumsgeschichte der *Radula complicata;* Sitzungsber. der Wiener Acad. 1871, vol. LXIII.—Ditto, Bot. Zeitg. 1871, no. 34, and 1872, no. 3.—A portion of what is said about the apical growth of Jungermannieæ is derived from communications by letter from Leitgeb.

[2] [The term 'thalloid' is here, as on p. 292, preferred to the one in more general use 'frondose.'—Ed.]

in contrast to the *Foliose* Hepaticæ belonging to the family of Jungermannieæ, the vegetative structure of which consists of a small slender filiform stem, bearing distinctly differentiated leaves (Jungermannia, Radula, Mastigobryum, Frullania, Lophocolea, &c.). Between the thalloid and foliose forms of this family are some which present various stages of transition (as Fossombronia and Blasia).

The Leaves of all Hepaticæ are simple plates of cells, in which even the mid-rib usual in the leaves of Mosses is always wanting.

In most of the thalloid forms the growing apical region of each shoot (Fig. 211, *s*) lies in an anterior depression, produced by the more rapid growth in length and breadth of the cells which are derived right and left from the segments of the apical cell, while the masses of tissue which lie behind the apical cell in the central line of the shoot grow more slowly in length. Within this depression the terminal branching of the shoot also takes place; the branches originate from the youngest segments of the apical cell, which, from their position in the

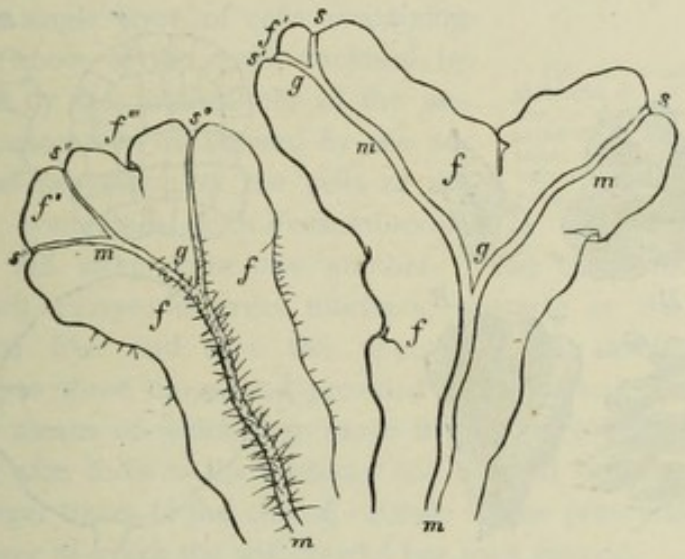

FIG. 211.—*Metzgeria furcata*; the right-hand figure seen from the upper, the left-hand figure from the under side; *m* the mid-rib; *s*, *s'*, *s''* the apical region; *f*, *f* wing-like expansion formed of a single layer of cells; *f' f'' f''' f'''* its development by branching (× about 10).

depression and their powerful growth, push aside the apex of the primary shoot, and form with it a fork (dichotomy). In the angle between the two bifurcations the permanent tissue increases more rapidly, and forms, so long as the two forks are still very short, a projection (Fig. 211, *f'*, *f''*) which overtops and separates its apical regions, but which, when the forks are longer, is in turn overtaken by them, and now appears as an indented angle of the older fork (*f*). The filiform stem of the foliose Jungermannieæ, on the other hand, ends in a bud as a more or less prominent vegetative cone, with a strongly arched apical cell. In this case also the lateral branches spring from individual mother-cells, which, however, do not originate from the youngest segments of the apical cell, but lie even at an early period below the apex; the branching is therefore, from its commencement, distinctly monopodial.

We shall speak, under the separate sections, of the form of the apical cell, which forms two, three, or four rows of segments; as well as of the origin of the

leaves and lateral shoots, since Leitgeb's researches show that great morphological differences occur in the different genera. For the same reason very little of a general character can be said, in addition to what has been mentioned above, on the habit and anatomical nature of the vegetative structure, which must therefore be considered under the separate families.

The *Asexual Propagation* of Hepaticæ is often brought about by the dying off of the thallus or stem from behind, the shoots thus losing their connexion and becoming independent. Adventitious shoots, arising in the thalloid forms from cells of the older marginal parts, become detached in a similar manner. The propagation by Gemmæ is very common and characteristic; not unfrequently a number of cells of the margin of the leaf of foliose Jungermannieæ (*e. g.* in Madotheca) simply detach themselves as gemmæ; in Blasia, on the other hand, as well as in Marchantia and Lunularia, peculiar cupules are formed on the upper side of the flat shoots exposed to the light, which are flask-shaped in Blasia, broadly cup-shaped in

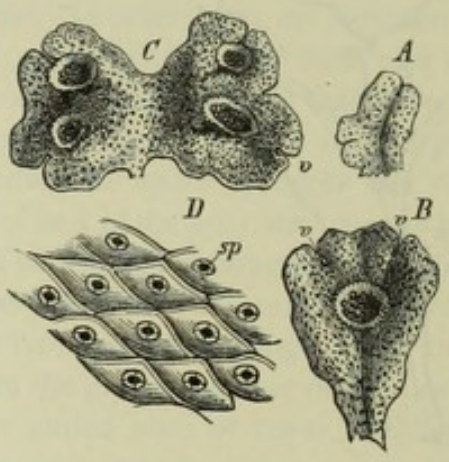

FIG. 212.—*Marchantia polymorpha*; *A*, *B* young shoots; *C* the two shoots which result from a gemma, with cupules; *v v* the depressed apical region; *D* a piece of the epidermis seen from above; *sp* stomata on the rhomboid plates (*A*-*C* x slightly; *D* more strongly).

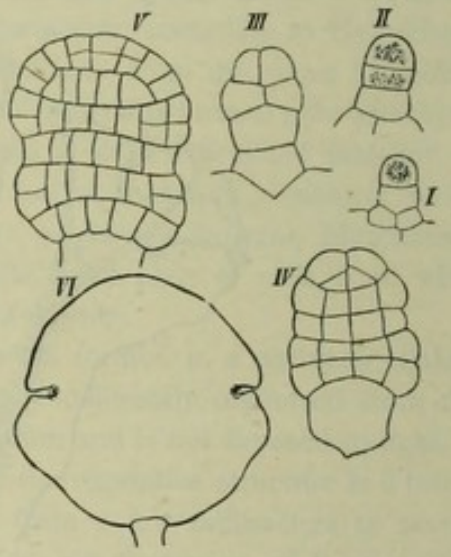

FIG. 213.—Development of the gemmæ of Marchantia.

Marchantia, crescent-shaped and deficient on one side in Lunularia. From the bottom of these cupules shoot out hair-like papillæ, the apical cells of which become transformed into a mass of considerable size constituting the gemma. (See Figs. 212, 213.) From the two depressions which lie right and left on the margin of the lenticular gemma (Fig. 213, *VI*) spring the first flat shoots (Fig. 212, *B*, *C*), when the gemmæ have fallen out of the cupule and lie exposed to light on damp ground.

The *Sexual Organs* are formed, in the thalloid forms, on the upper side exposed to light; in Anthoceros in the tissue of the thallus itself (endogenous); in the other thalloid forms from cells which project like papillæ and are of definite origin in reference to the segments of the apical cell. In the Marchantieæ branches of a very peculiar shape, which have a tendency to shoot upright from the flat stem, are formed, producing the antheridia on the upper, the archegonia on the

under side, and thus forming inflorescences distributed monœciously or diœciously. There is a general tendency in the thalloid Hepaticæ for the sexual organs to be depressed into hollows by overarchings of the surrounding tissue, and often opening externally only by a narrow mouth. An example of this is given in Fig. 214.

In the foliose Jungermannieæ the origin of the antheridia and archegonia is very various, and they are also enveloped in different ways. Further reference will be made to this in describing the different families.

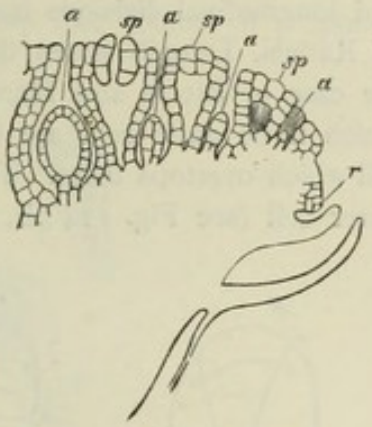

FIG. 214.—Anterior margin of the young antheridial disc of *Marchantia polymorpha*; *r* the growing margin; *a*, *a*, *a* the antheridia in different stages of development; *sp* the stomata above the air-cavities between the antheridia (after Hofmeister, ×300).

The *Antheridium* consists, in the mature state, of a pedicel surmounted by a globular or ellipsoid body; in those which are imbedded in the tissue the former is usually short, in the free forms it is long, and composed of from one to four rows of cells. The body of the antheridium consists of a wall formed of a single layer of cells containing chlorophyll; the whole of the space enclosed by it is densely filled by the mother-cells of the antherozoids; their escape is occasioned by the access of water and separation of the cells of the wall at the apex; sometimes, as in Fossombronia, these cells even fall away from one another. The small mother-cells of the antherozoids which escape in great numbers, separate in the water; the antherozoids become free, and have the appearance of slender threads curved spirally from one to three times, and provided at the anterior end with two long very fine cilia, by means of which they move in the water with a rotating motion. Usually they drag after them at the posterior end a small delicate vesicle, the origin of which Strasburger traces to the central vacuole in the protoplasm of the mother-cell, in the periphery of which the antherozoid has been formed.

The succession of cell-divisions in the formation of the antheridia has been shown by the researches of recent observers to present great diversities in the different genera; they agree, however, in the antheridium always making its first appearance as a papillæform swelling of a cell from which it is separated by a septum. This papilla thus detached again divides into a lower and an upper cell, the former of which produces the pedicel, the latter the body of the antheridium (parietal layer and mother-cells of the antherozoids).

There is also some doubt as to the succession of cell-divisions in the formation of the archegonia, since the observations of Leitgeb on Radula and those of Kny and Strasburger on Riccia and Marchantia do not entirely agree. An ultimate agreement may however be expected, since, on the other hand, Leitgeb's history of the development of the archegonia of Radula coincides with that studied by Kühn and Schuch in the Mosses[1]. It is certain that the archegonium, like the

[1] [Janczewski has made a series of comparative researches into the development of the archegonium of Muscineæ, Bot. Zeitg. 1872, p. 869 et seq.—ED.]

antheridium, makes its first appearance as a simple papilla, which, in the case of the first archegonium of an inflorescence of Radula, is itself the apical cell of the shoot. This papilla is detached by a septum, and is divided by a second septum into two cells, the lower one of which produces the pedicel, the upper one the ventral portion and neck of the archegonium. The lower cell undergoes numerous transverse and longitudinal divisions into several rows of cells. In the upper cell, in the case of Radula, Leitgeb states that there arise three (Kny and Strasburger assert in the case of Riccia and Marchantia four) somewhat oblique longitudinal walls, by which three outer cells are formed; these, on their part, enclosing an inner axial cell which overtops them. This latter is divided by a septum into an upper and a lower cell (see Fig. 214 bis, *B*). The lower cell is the central cell of the archegonium; the upper one subsequently divides cross-wise, and forms the apical stigmatic cells of the neck. While the three (or four) outer cells produce the wall of the ventral portion and neck of the archegonium by transverse and subsequently by longitudinal divisions—the whole thus increasing in height and diameter—the central cell divides into a lower and an upper cell; the former produces the oosphere by contraction and rounding off of its protoplasm; the upper one lengthens within the growing neck, and forms the axial row of cells, the conversion of which into mucilage forms at length the canal of the neck.

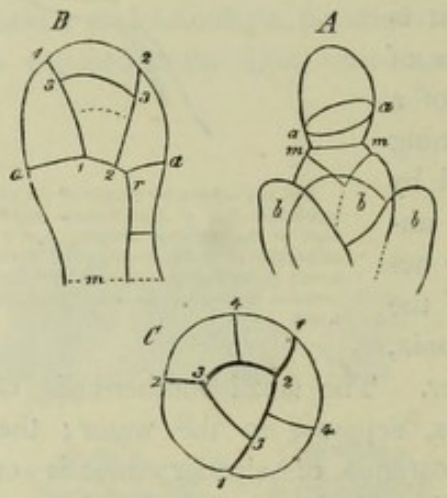

FIG. 214 bis.—First stage of development of the archegonium of Andreæa (after Kühn); *A* terminal archegonium arising from the apical cell of the shoot; *b b* the youngest leaves; *B* after the formation of the central cell and stigmatic cell; *C* transverse section of the young ventral portion.

(2) *The Asexual Generation* or *Sporogonium* arises and is entirely formed within the growing ventral portion of the archegonium, which from this time is termed the *Calyptra*. The sporogonium does not anywhere unite in its growth with the surrounding tissue of the vegetative structure of the sexual generation, even when its pedicel penetrates into its tissue.

The external form and internal structure of the sporogonium are very different in the different groups. In the Anthoceroteæ it is when mature an elongated two-valved pod projecting from the thallus. In the Ricciеæ it is a thin-walled ball entirely filled with spores, and, together with the calyptra, depressed in the thallus. In the Marchantieæ it is a shortly-stalked ball enclosing elaters as well as spores, and, after it has broken through the calyptra, bursting irregularly or opening by a circular fissure and detaching an operculum. In the Jungermannieæ it ripens even within the calyptra, but breaks through it and appears as a ball borne upon a long slender stalk; the receptacle consists, as in the Marchantieæ and Ricciеæ, when ripe, of a single layer of cells, but separates cross-wise into four lobes, to which the elaters remain attached. The elaters are, as in the Marchantieæ, long fusiform cells, the delicate colourless outer layer of which is thickened within by from one to three brown spiral bands.

The sporogonium also originates in different ways. The fertilised oosphere is always first divided in the archegonium into two cells, the upper of which, facing the neck, forms the growing apical cell; but this divides in very different ways in the different groups:—in Anthoceros by oblique walls inclined in four directions; in the Marchantieæ and Ricciеæ by walls inclined alternately in two directions; while the sporogonium of the Jungermannieæ contains, even in its very earliest stage, four apical cells lying beside one another like octants of a sphere,

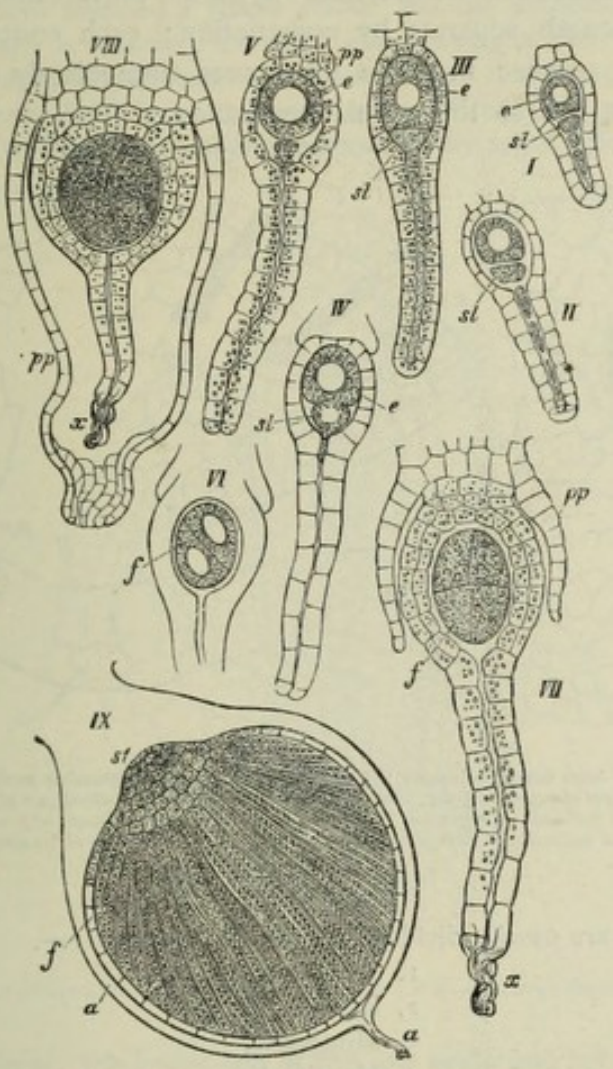

FIG. 215.—Later stage in the development of the archegonia and origin of the sporogonium of *Marchantia polymorpha*; *I, II*, young archegonia; *III, IV*, after absorption of the axial row of cells of the neck; *V* when ready for fertilisation; *VI-VIII* the cells of the mouth of the neck *x* relaxed after fertilisation; the fertilised oosphere *f* shows its first divisions. In these figures *st* is the lowest cell of the axial row in the neck which is last converted into mucilage; *e* in *I-IV* the central cell, in *V* the unfertilised oosphere; *pp* in *V-VII* the perianth in process of development; *IX* the unripe sporogonium in the ventral portion of the archegonium which has developed into the calyptra; *a* neck of the archegonium; *f* wall of the sporogonium; *st* its stalk; inside the sporogonium are the young elaters arranged in rays, among them the spores. (*I-VIII* × 300, *IX* about 30.)

which divide simultaneously by horizontal septa. When the young sporogonium has in this manner attained its destined height, and partially even at an earlier period, a number of divisions of different kinds take place in the segments of the apical cell, by which the structure is completed. The wall of the sporogonium also becomes differentiated from the tissue from which the mother-cells of the spores are to arise; if elaters are formed they originate from the same tissue, the cells ceasing to divide transversely at an earlier period and remaining long, while

the intermediate cells become rounded off and give rise to the mother-cells of the spores (Hofmeister).

The mode of division into four of the mother-cells of the spores also varies. Those of Anthoceros form at first two, and afterwards four, new nuclei (in addition to the primary nucleus), which are arranged tetrahedrally; the division-walls advance from without inwards, by which means the spherical mother-cell breaks up into four spores. In Pellia and Frullania, on the other hand, the division of the mother-cells commences by four protuberances arranged tetrahedrally, which at length separate by constriction; each contains a nucleus, and they form as many spores; in Pellia the spores immediately again divide several times, and thus give rise to the sexual generation.

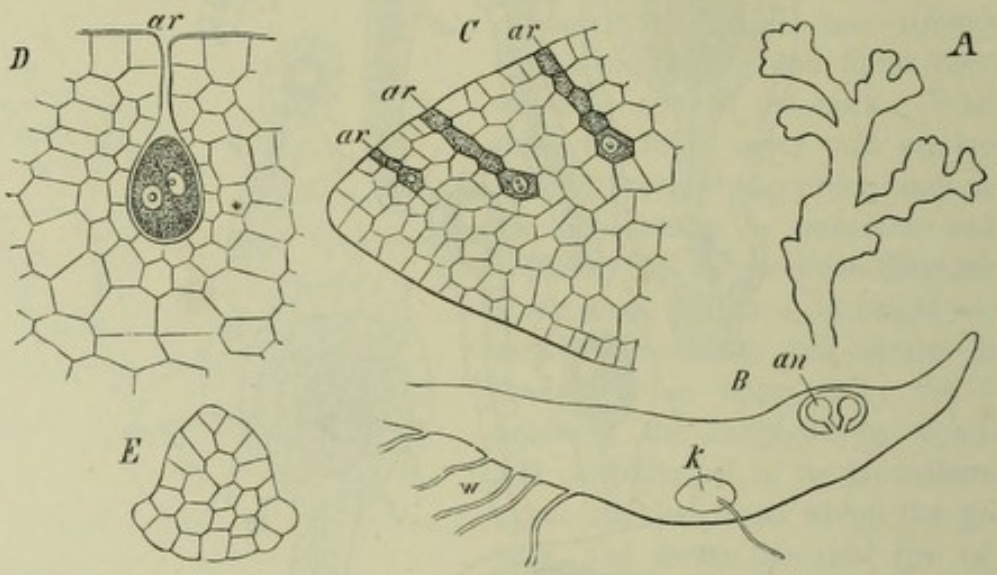

FIG. 216.—*Anthoceros lævis* (after Hofmeister); *A* a branched thallus; *B* longitudinal section of a shoot (×40); *an* antheridia beneath the layer of superficial cells; *C* longitudinal section through the apical part of a shoot; *ar* rudiments of archegonia (×500); *D ar* fertilised archegonium in the longitudinal section of a shoot, with rudimentary sporogonium consisting of two cells; *E* multicellular rudimentary sporogonium; *K* in *B* a colony of Nostoc settled in the tissue of the thallus.

The Hepaticæ are usually divided into five families, viz.:—

1. Anthoceroteæ,
2. Ricciеæ,
3. Monocleæ,
4. Marchantieæ,
5. Jungermannieæ,

of which the first four include only thalloid forms, the fifth both thalloid and foliose genera.

1. **Anthoceroteæ.** *Anthoceros lævis* and *punctatus*, which grow in summer on loamy ground, develope a perfectly leafless flat ribbon-like thallus, its irregularly developed ramifications forming a circular disc; the regularity of the (dichotomous) branching is disturbed by the adventitious shoots, which proceed from the margin of the thallus, and, in *A. punctatus*, also from the upper surface. The thallus consists of several layers, and the apical cells of the branches which lie in the anterior depressions are divided by walls inclined alternately upwards and downwards (Fig. 216, *C*). In each of the cells of the thallus, the upper layer of which does not become differentiated into an epidermis, only one mass of chlorophyll is formed, surrounding the nucleus. On the under side of the thallus, Janczewski states that stomata are formed close behind the

growing margin, through which filaments of Nostoc frequently penetrate, forming roundish balls in the tissue of the thallus (Fig. 216 *B*), which were at one time considered to be endogenous gemmæ. The antheridia and archegonia arise apparently without any definite arrangement in the interior of the upper side of the thallus. The formation of the antheridia commences by a circular group of cells of the outer layer separating from the subjacent tissue and thus producing a broad intercellular space, several of the lower bounding cells of which, after some vertical divisions, rise up in the form of papillæ, and form the antheridia, the position of which is represented in Fig. 216, *B*, *an*, their mode of formation in Fig. 214. It is only when the grains of chlorophyll in the walls of the antheridia have assumed a yellow colour and the antherozoids are mature, that the roof of the cavity is ruptured, the antheridia opening at their apex and allowing the antherozoids to escape. The archegonia are formed in a manner still more different from that of all other Hepaticæ (Fig. 218, *C*, *ar*). A row of cells perpendicular to the surface, resulting from the divisions of an upper segment of the apical cell of the shoot, becomes

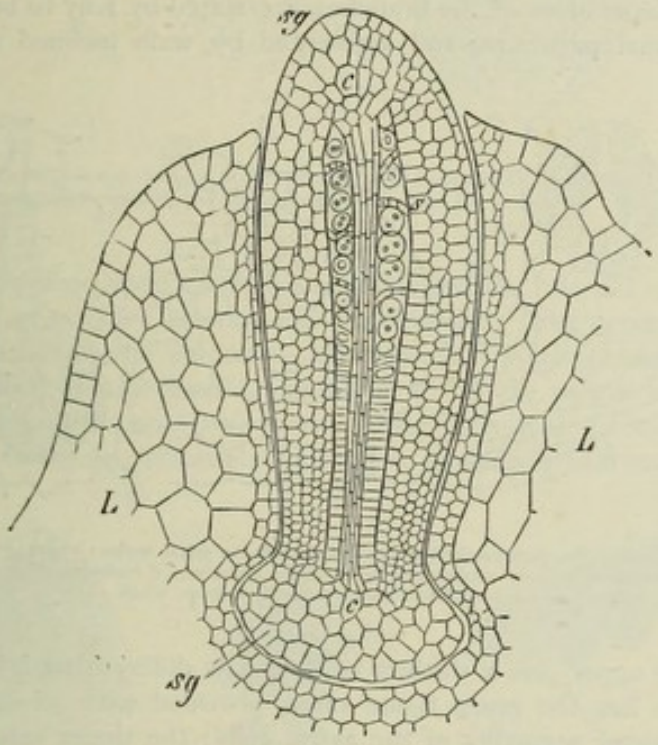

FIG. 217.—*Anthoceros lævis*; *sg* the young sporogonium; *L* the involucre (after Hofmeister, ×150).

filled with protoplasm; the lowest cell of this row swells and becomes the central cell of the archegonium. While this cell is growing and rounding off, the other cells of the row become absorbed; the canal of the neck (Fig. 216, *D*, *ar*) which conducts to the interior is thus formed, surrounded by six rows of cells. After fertilisation, the oosphere is first divided by an oblique wall; in the upper cell, which becomes the apical cell, other walls are formed inclining alternately right and left; but the walls afterwards arise in four alternating directions. While the immature sporogonium is thus becoming transformed into a multicellular body enlarged below (Fig. 216, *E*), the surrounding tissue of the thallus divides repeatedly and grows into an involucre which is arched upwards and through which the elongating sporogonium afterwards pushes its way. The sporogonium, which had hitherto consisted of homogeneous tissue, now becomes differentiated; the cylindrical *Columella*, consisting of from 12 to 16 rows of cells, is formed, its cells being elongated in an axial direction, while those of the surrounding layer become divided by horizontal walls, and form the mother-cells of the spores and elaters. The outer four or five layers of cells form the wall of the sporo-

gonium. Those cells of the layer surrounding the columella which are to become elaters undergo either one or several additional vertical divisions; the elaters are in this case transverse rows of cells in which *no* spiral bands are formed. The intermediate cells become rounded off and isolated progressively from the apex to the base of the sporogonium; and after they have still further increased in size, the division commences into four spores arranged tetrahedrally. The sporogonium extends and forms a pod some 15 or 20 mm. in height, the brown wall of which splits into two valves from above downwards.

2. The family **Monocleæ** appears, according to the 'Synopsis Hepaticarum,' to contain transitional forms between the Anthoceroteæ and the Jungermannieæ. The long sporogonium has a longitudinal dehiscence and no columella; and the sexual generation is either thalloid or foliose.

3. The **Ricciеæ** form a flat dichotomously branched but thalloid stem, floating in water or rooting in the ground, the apical cells of which, lying close to one another in the anterior depressions of the branches, are stated by Kny to become multiplied by vertical longitudinal partitions, and segmented by walls inclined upwards and down-

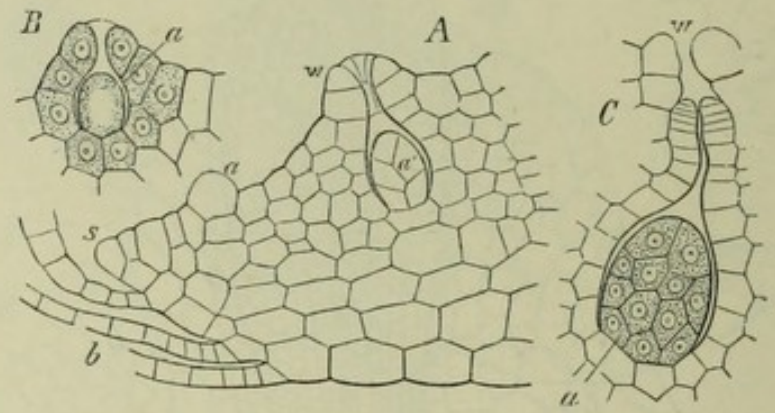

FIG. 218.—*Riccia glauca*; *A* vertical longitudinal section through the apical region; *s* apex, *b* leaves, *a* young antheridium, *a'* older antheridium already surrounded by involucral tissue *w*; *B* rudiment of an antheridium *a* already overarched; *C* young antheridium *a* in longitudinal section (after Hofmeister, ×500).

wards[1]. On the upper side a distinct epidermis is differentiated, but without stomata, and beneath this lies the green tissue often provided with air-cavities, which is derived from the upper segments of the apical cells; the under side is provided with a single longitudinal row of transverse lamellæ, which, resulting immediately from the lower segments of the apical cell, must be considered as leaves. Afterwards they split lengthwise and form two rows; between them arise a number of root-hairs with conical thickenings projecting inwards.

The archegonia and antheridia are formed on the upper side from young epidermal cells which grow into papillæ, and are overarched, in consequence of their mode of development, by the surrounding tissue (Fig. 218). This involucre sometimes forms an elevated neck above the sessile antheridia. The archegonia project, at the time of fertilisation, above the epidermis; subsequently they are arched over, and develope from

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[1] In a letter on the apical growth of Blasia, Leitgeb shows that this Liverwort possesses only one four-sided apical cell. He remarks:—'I entertain no doubt that in Hepaticæ also, which, according to Kny, have a row of apical cells (Pellia, Riccia), only *one* apical cell is really present, which divides as in Blasia. The deception may result from the lateral segments forming their first divisions in the same manner as the apical cell, by the formation of segments standing fore and aft. This led to the conclusion that the observer had before him in fact a row of apical cells.'

their fertilised oosphere the globular sporogonium with a wall consisting of a single layer of cells, and entirely filled with spores, without elaters. The spores are set free by the decay of the surrounding tissue.

4. The **Marchantieæ** have all a thalloid stem extended flat upon the ground; it is ribbon-like, dichotomously branched, possesses a mid-rib, and is always composed of several layers; the under side produces a number of hairs with conical thickenings

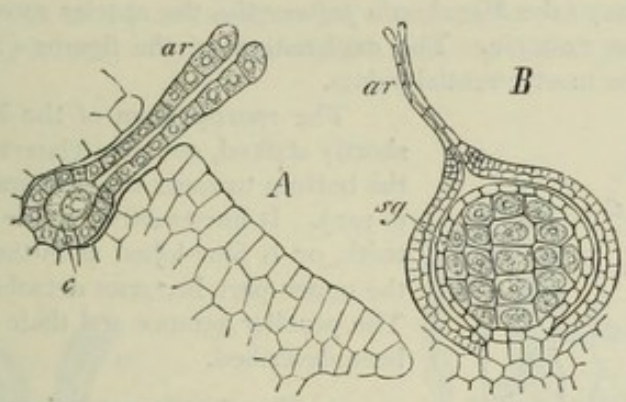

FIG. 219.—*Riccia glauca*; *A* apical region in vertical longitudinal section; *ar* archegonium; *c* oosphere (×360); *B* the unripe sporogonium *sg* surrounded by the calyptra, which still bears the neck of the archegonium *ar* (×300, after Hofmeister).

projecting inwards placed upon a spiral constriction of the internal cavity (Fig. 220 bis), and also two rows of leaf-like lamellæ, like the Ricciæ. The upper side is covered by a very distinctly differentiated epidermis, penetrated by large stomata of peculiar form. Each of these stands, in Marchantia, Lunularia, &c. in the centre of a rhombic plate; these plates are parts of the epidermis which overarch large air-cavities, from the bottom of which the cells containing chlorophyll spring in a conferva-like manner, while the rest

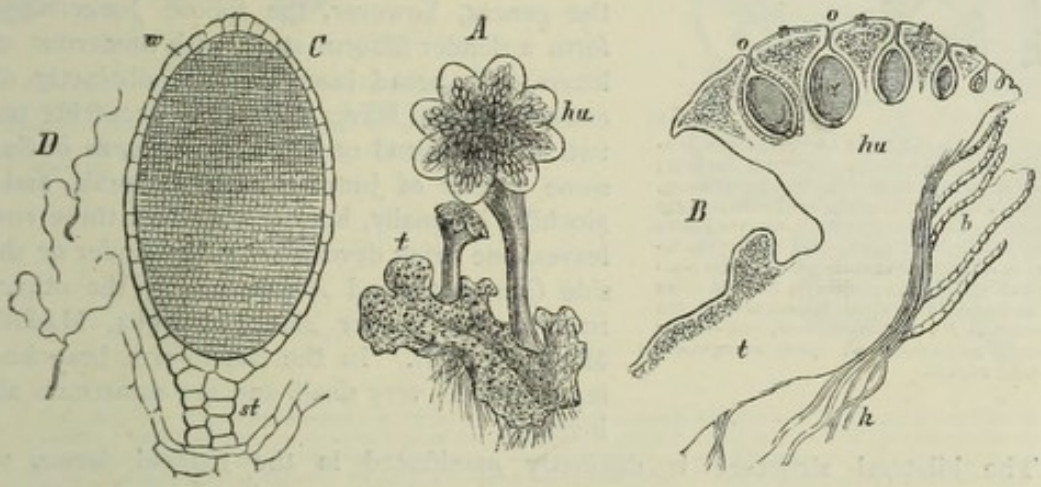

FIG. 220.—*Marchantia polymorpha*; *A* a horizontal branch *t* with two ascending branches which bear antheridial receptacles *hu*; *B* vertical section through an incompletely developed antheridial receptacle *hu* and the part of the thalloid stem *a* from which it springs; *b b* leaves; *h* root-hairs in a channel of the antheridial receptacle; *o o* openings of the hollows in which the antheridia *a* are placed; *C* a nearly ripe antheridium; *st* its pedicel; *w* the wall; *D* two antherozoids (these last, ×800).

of the tissue is destitute of chlorophyll and consists of long horizontal cells without interstices (*cf.* Fig. 65, p. 76).

The sexual organs of the Marchantieæ are borne on monœcious or diœcious receptacles. The antheridia, although springing from cells of the epidermis as in Riccia, are depressed in the upper side of the thalloid stem, and overarched by the surrounding tissue; they occur in larger or smaller numbers close together upon receptacles, which

are discoid or shield-shaped sessile or stalked branches that have undergone a peculiar transformation. The archegonia are only in the Targionieæ inserted at the apex of an ordinary shoot; in the other families they are produced on a metamorphosed branch, which rises like a stalk and developes in different ways at its summit. The summit bears the archegonia on its outer or lower side. With the variation in the form of the part which bears the archegonia is connected an equally varied mode of envelopment of the archegonia by involucres. Since it is impossible to describe these structures in a short space, we may take *Marchantia polymorpha*, the species most perfectly endowed in this respect, as an example. The explanation of the figures (220–222) will suffice to explain at least the most essential points.

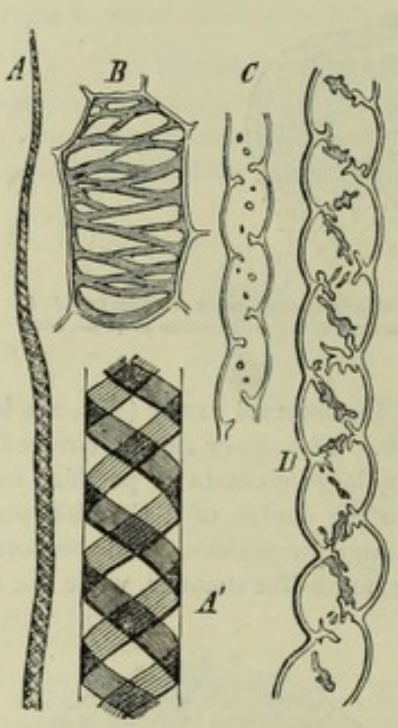

FIG. 220 bis.—Cell-forms of *Marchantia polymorpha* with thickenings projecting inwards; *A* an elater (one-half) from the sporogonium, with two spiral bands; *A'* a portion more strongly magnified; *B* a parenchyma-cell from the centre of the thallus, with thickenings projecting inwards in a reticulate manner; *C* a slender root-hair with thickenings projecting inwards, these are arranged on a spiral constriction of the cell-wall; at *D* a thicker root-hair, with thicker branched projections, and spiral arrangement still more evident.

The sporogonium of the Marchantieæ, usually shortly stalked, contains elaters which radiate from the bottom towards the circumference (*cf.* Fig. 215, p. 301). It bursts either at the apex with numerous teeth, or is four-lobed as in the Jungermannieæ, or the upper part becomes detached as an operculum. The peculiar gemmæ and their cupules have already been described.

5. The **Jungermannieæ**. In this family occur forms of which the vegetative structure is a true flat leafless thallus, as Metzgeria and Aneura, as well as transitional forms whose flat thalloid stem forms leaves on the under surface (Diplolæna), or whose stem, as in Blasia, elliptical in section in its early stage, becomes broad and leaf-like when older, and produces leaves on both surfaces. Closely allied to Blasia is a genus 'with a less dilated stem, though still always greatly flattened on the upper side, and bearing leaves only above.' The greater number of the genera, however, the foliose Jungermannieæ, form a slender filiform stem, with numerous sessile leaves with broad insertions but distinctly differentiated; these leaves commonly occurring only in two rows situated on the upper side, as in Radula, some species of Jungermannia, Lejeunia, and Plagiochila. Normally, however, we find three rows of leaves, one being developed on the under or shaded side (hence termed *Amphigastria*), the other two rows on the upper side (Frullania, Madotheca, Mastigobryum). In the flagelliform branches the leaves remain very small, and are sometimes almost invisible.

The bilateral structure is distinctly manifested in the thalloid forms, which mostly cling closely to the substratum, the sexual organs being formed only on the upper side or the one exposed to the light, rhizoids and leaves on the under or shaded side. In the foliose forms this tendency is also clearly shown, whether they cling closely to the substratum or rise from it obliquely. This bilateral structure is manifested not only in the different mode of the formation of the leaves on the two sides, and in the expansion of the ramifications in a single plane; but is also determined, both in the foliose and in the thalloid forms, by the growth of the apical region of the shoot. Even the youngest segments of the apical cell exhibit it, as is shown in the different organisation of the upper and under sides, and in the similarity (though not symmetrical) of the right and left sides of the shoot.

Enough has already been said on the position of the apical region in an anterior

depression in the thalloid forms, as well as on the termination of the filiform stem in the leaf-bud of the foliose genera. The form of the apical cell, and its segmentation in the thallus of Metzgeria, have been represented in detail in Figs. 99 and 100 (p. 120); in Aneura and Fossombronia it is also wedge-shaped. In Blasia, on the other hand, Leitgeb states that it is four-sided, and forms four rows of segments, a dorsal, a ventral, a right, and a left row. 'This may be most easily represented by supposing a wedge-shaped apical cell forming segments by walls inclined alternately upwards and downwards (towards the dorsal and ventral surfaces), as well as lateral segments from which the leaves proceed; a leaf is produced from the dorsal part of a lateral segment,

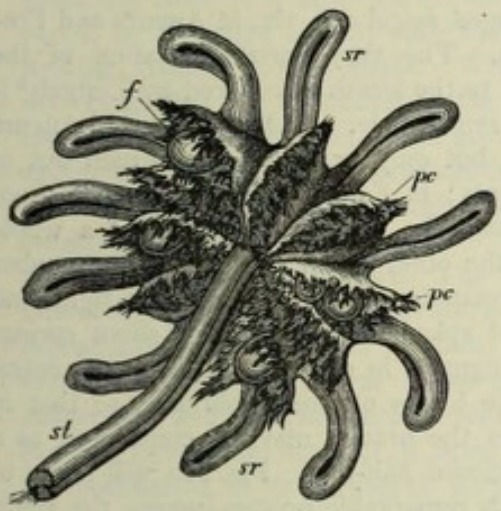

FIG. 221. — Female receptacle of *Marchantia polymorpha* seen laterally from below; *st* stalk with two channels; *sr* the radiate outgrowths of the disc; *pc* the intermediate perichætium; *f* sporogonia (× about 6).

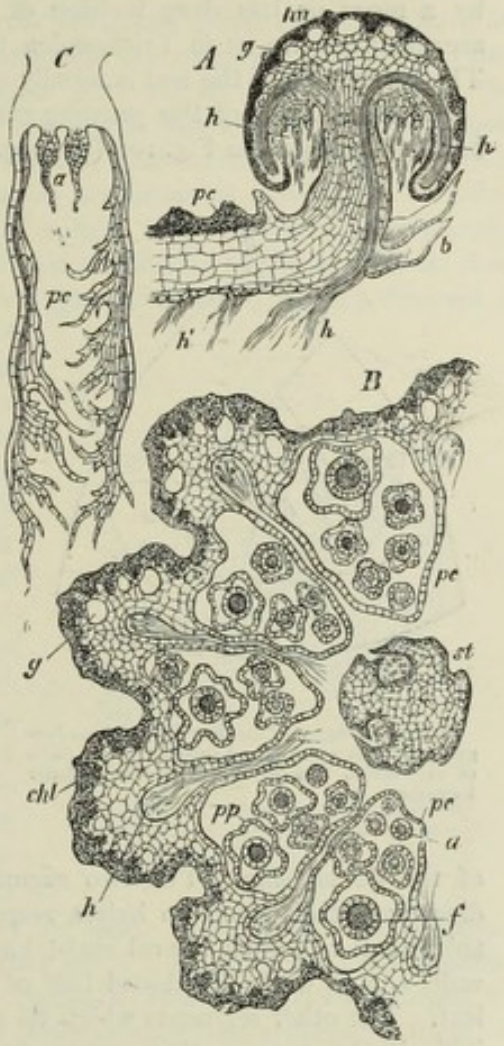

FIG. 222.—*Marchantia polymorpha*; *A* vertical section through a female receptacle *hh*, *bb* leaves; *h* root-hairs in its channel; *g* large cells between the air-cavities of the upper side; *B* horizontal section of half an older receptacle and of its stalk *st*; *chl* the chlorophyll-bearing tissue of the disc, large hyaline cells; *pc* the common perianth-leaves (*pc* in Fig. 221); *a* unfertilised archegonia; *pp* involucres of fertilised archegonia; *C* vertical longitudinal section through the receptacle; *a* two archegonia; *pc* general involucre of the archegonia, or perichætium.

a kind of leaf-tube from its central part, and a second leaf from its ventral part, though this last is more often absent' (Leitgeb, *in lit.*). It has already been mentioned that Leitgeb supposes this to be the mode of apical growth in those cases, like Pellia, where Kny thought he saw a *row* of apical cells.

In the Jungermannieæ with filiform stem and leaves arranged in two or three rows, the stem ends in a three-sided apical cell which forms three rows of segments in spiral succession; two rows being dorsal and lateral, while the third row forms the under or ventral side of the stem. The successive septa of each row of segments are parallel to one another, but the segments themselves are in straight rows, the rows being

parallel to one another and to the axis of growth of the stem[1]. In the species with leaves arranged in two rows a leaf springs from each of the lateral and dorsal segments; when the leaves are arranged in three rows each segment of the ventral side also produces a leaf, which is however smaller and of simpler structure and is also inserted transversely, while the insertion of the dorsal row of leaves is oblique to the axis of the stem, so that the lines of insertion of each pair form an acute angle. Before a lateral segment has developed a papilla from which the leaf is formed, it divides by a longitudinal wall into an upper and a lower half facing dorsally and ventrally, each of which now forms a leaf-papilla. Hence it arises that the leaves of Jungermannieæ are to a certain extent bisected or two-lobed; in the simpler leaves this is usually shown by a more or less deep incision of the anterior margin; but even when the leaves are quadripartite, as in Trichocolea, the primitive double origin can still be recognised. The lower lobe of the leaf is usually smaller, of peculiar form, and hollowed out.

The branching of the growing end of the shoot in the case of Metzgeria has already been represented in Fig. 100 (p. 120). According to Leitgeb it takes place in a similar manner also in the other thalloid forms with a wedge-shaped apical cell, viz. in Aneura and Fossombronia. The very variable relation of the branching to the leaves discovered by Leitgeb[2] is especially remarkable. In Metzgeria and Aneura no leaves, but only branches, are formed out of the segments; in Fossombronia the lateral shoot springs from the segment in place of a whole leaf; on the other hand, in the greater number of Jungermannieæ with filiform leafy stem and three-sided apical cell, the lateral shoot springs from the segment in place of the lower or ventral lobe of the leaves of the dorsal side, so that in these cases the branch may be considered as a metamorphosed half-leaf. Fig. 223 will serve to explain this remarkable process, where the apical view of a branching shoot is represented diagrammatically: *I, II . . . VI* are the segments of the apical cell *S* of the primary shoot; *II, V* being segments of the ventral, *I, III, IV, VI,* of the dorsal side. The two segments *I* and *III* are already divided by a longitudinal wall each into two halves respectively dorsal and ventral; and in the latter the apical cell *s* of each lateral shoot has already been constituted by the formation of the walls 1, 2, 3, while the dorsal half of each of these segments has developed into half a leaf. The other segments which do not form shoots develope normal two-lobed leaves. This is the process that occurs in Frullania, Madotheca, Mastigobryum, Lepidozia, Trichocolea, and *Jungermannia trichophylla*. A third type of branching occurs finally in Radula and Lejeunia, where the formation of leaves is not disturbed by the branching, the branches springing from *behind* the leaves at their base, and from the same segments.

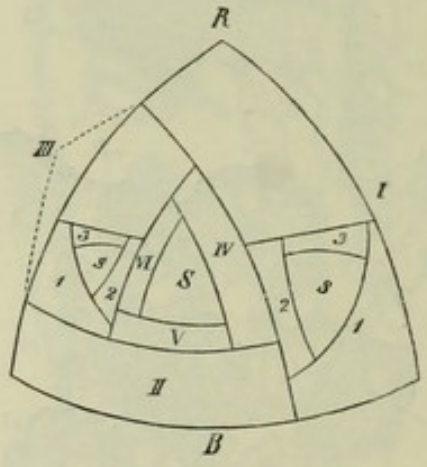

FIG. 223.—Diagram of the branching of those Jungermannieæ in which lateral shoots take the place of the ventral lobe of the dorsal leaves (after Leitgeb).

Besides these modes of ramification, which originate from particular outer cells of the segments of definite position, Leitgeb has recently discovered also an *endogenous* formation of shoots, springing sometimes as fertile branches from the ventral segments provided with amphigastria, while the exogenous shoots arise in the manner represented in Fig. 223, as, *e. g.* in Mastigobryum, Lepidozia, and Calypogeia; or they are formed

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[1] Compare in reference to this what follows with respect to Mosses.

[2] What follows is partially derived from Leitgeb's letters.

without the production of a ventral row of leaves, as in *Jungermannia bicuspidata* and other Jungermannieæ with leaves in two rows. In those especially belonging to the section Trichomanoideæ the fertile branches have an endogenous origin, and break out from the older parts of the stem as adventitious shoots; probably, however, their mother-cells always originate regularly in acropetal succession in the primary meristem of the vegetative cone, as in Mastigobryum and Lepidozia (like they do in Equisetaceæ). Finally, according to Leitgeb, the whole branching of many Jungermannieæ appears to depend exclusively on the endogenous production of branches.

The reproductive organs are distributed monœciously or diœciously, and are formed, in the thalloid genera, on the dorsal side of the shoot; in the foliose Jungermannieæ at the end of primary shoots or of special small fertile branches, which commonly have an endogenous origin on the ventral side. The antheridia are usually in the axils of the leaves, singly or in groups. The archegonia appear generally in large numbers at the summit of the shoot, either on those which bear antheridia below, or on special female branches, which in the Geocalyceæ are hollowed out in such a manner that the archegonia are sunk in a deep pitcher-shaped hollow, an arrangement which may be compared, to a certain extent, with the structure of a fig. This occurs in an especially striking manner in Calypogeia. Where this peculiar enveloping of the archegonia does not occur, they are concealed by the nearest leaves (the *Perichætium*); and a *Perianth* is usually formed in addition, which grows round the archegonia as a special membranous envelope. The development of these organs has been accurately described by Leitgeb in the case of *Radula complanata* (Fig. 224). The primary and lateral shoots both bear, as a rule, both kinds of reproductive organs; such a shoot is always at first purely vegetative, but forms after a time antheridia, and finishes with a female inflorescence. Less often, however, it again recurs, after the production of antheridia, to a vegetative development. The antheridia of Radula are metamorphosed trichomes; they stand singly in the axils of the leaves, and are completely enclosed in the hollow formed by the very concave lower lobe of the leaf. They arise from the club-shaped protuberance of a cell belonging to the cortex of the stem and lying before the leaf at its base. The female inflorescence of Radula always stands at the end of the primary or of a lateral shoot, and contains from three to ten archegonia, surrounded by a perianth, which is again enveloped by a perichætium of two leaves. The whole female inflorescence (the archegonia together with the perianth) is developed from the apical cell of the shoot and from its three youngest segments. The archegonia arise from the apical cell itself, and from the upper parts of its lateral segments; the lower parts, together with the ventral segment, are employed in the formation of the perianth. The further development of the archegonia and antheridia has already been described.

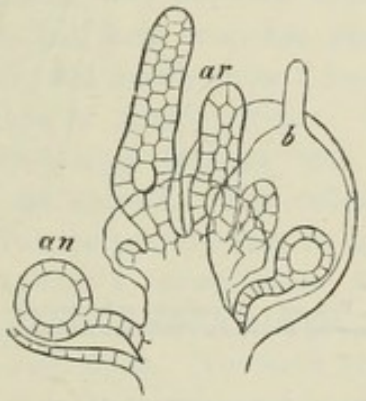

FIG. 224.—Inflorescence of *Radula complanata*; *ar* archegonium; *an* antheridium; *b* leaf (after Hofmeister).

In the species examined by Hofmeister the fertilised oosphere is first divided by a septum, *i. e.* at right angles to the axis of the archegonium. Only the upper of the two cells, the one towards the neck of the archegonium, becomes further divided; it becomes the apical cell of the sporogonium, and is sometimes again divided transversely once or twice before a longitudinal wall makes its appearance in it; the two cells thus formed are finally divided into four apical cells arranged as octants of a hemisphere.

The basal portion of the growing archegonium becomes swollen out and penetrates down into the tissue of the stem, being nourished and firmly enclosed by it (the Vaginula). As soon as the young sporogonium consists of a number of cells, its wall

becomes differentiated from the inner tissue which is to form the spores and elaters. In Frullania it is a single circular disc of cells lying transversely beneath the dome of the young sporogonium from which the vertical elaters, and by further divisions, the mother-cells of the spores arise, a process which reminds one of what occurs in Sphagnum. In most true Jungermannieæ there is, on the other hand, a column of tissue consisting of vertical rows of cells (surrounded by the wall of the sporogonium consisting of two layers), out of which the elaters and spores are formed. The elaters lie, in this case, horizontally, and radiate from the ideal longitudinal axis to the wall of the sporogonium (Fig. 225). In Pellia the inner fertile tissue forms, after the differen-

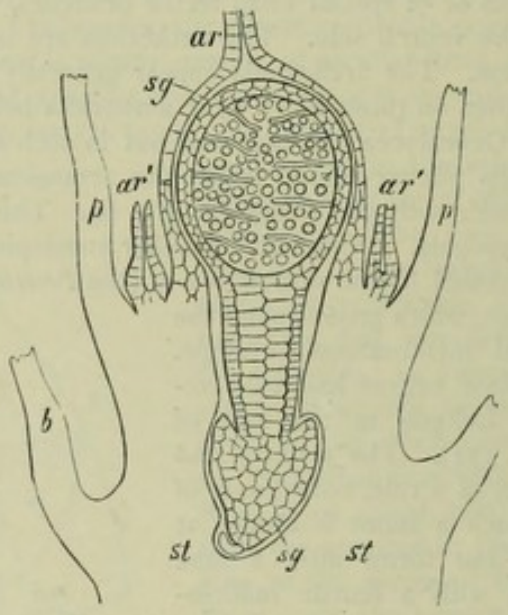

FIG. 225.—*Jungermannia bicuspidata*; longitudinal section of the unripe sporogonium *sg*, surrounded by the calyptra *ar*; *ar'* archegonia which have remained unfertilised; *p* base of the perianth; *st* stem; *b* leaf (after Hofmeister).

tiation of the wall of the sporogonium, a hemisphere, from the cells of which arise the spores and the elaters radiating from below upwards, in a similar manner to what occurs in the Marchantieæ.

By a rapid extension of the hitherto short pedicel, the calyptra is ruptured at the apex, and the globular sporogonium with the already ripe spores is raised up on it. Even while the spores are ripening, the inner layer of the wall of the sporogonium is absorbed; the single layer which still remains is ruptured at the apex, and splits into four (rarely more) longitudinal valves, which, flying asunder in the form of a star, carry with them at the same time the elaters, by which the spores are dispersed. The elaters, when mature, are long fusiform thin-walled cells, round the interior of which run from one to three brown spiral bands.

CLASS V.

MOSSES[1].

The spore produces a conferva-like thallus, the Pro-embryo or Protonema, from which the leaf-bearing Moss arises by lateral branching and differentiation into stem and leaf. On this plant the sexual organs are formed; from the fertilised oosphere proceeds the sporogonium, in which the spores are formed from a small portion of the inner tissue.

(1) *The Protonema* arises, in the typical Mosses, as a tubular bulging of the endospore, which elongates indefinitely by apical growth and becomes septate. The cells do not undergo any intercalary divisions, but form branches immediately behind the septa; and these also become septate, and usually show a limited apical growth; they may, in turn, produce ramifications of a higher order. The part of the endospore which lies opposite the germinating filament may develope into a hyaline rhizoid, which penetrates into the ground. The cell-walls of the protonema-filaments are at first colourless, but as the primary axes lie upon the ground or even penetrate into it, their cell-walls assume a brown colour, while the septa, previously at right angles to the axis of growth, become oblique, and assume positions inclined in different directions (Fig. 226, *B*, *h*). The cells above ground develope abundance of chlorophyll-grains; and the protonema is hence nourished independently by assimilation, and not only attains a considerable size in some genera, covering a surface of from one to several square inches like turf with its densely matted filaments, but its term of life is sometimes, as it were, unlimited. In most Mosses it altogether disappears after it has produced the leafy stems as lateral buds; but where these latter remain very small and have only a

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[1] W. P. Schimper, Recherches anat. et physiol. sur les Mousses (Strasburg 1848).—Lantzius-Beninga, Beiträge zur Kentniss des Baues der ausgewachsenen Mooskapsel, insbesondere des Peristoms (with beautiful illustrations) in Nova Acta Acad. Leopold. 1847.—Hofmeister, Vergleich. Untersuch. 1851. [On the Germination, Development, and Fructification of the Higher Cryptogamia, Ray Soc. 1862.]—Hofmeister, in Berichte der Kön. Sächs. Gesellsch. der Wissens. 1854.—Ditto, Entwickelung des Stengels der beblätterten Muscineen (Jahrb. für wissens. Bot. vol. III).—Unger, Ueber den anat. Bau des Moosstammes (Sitzungsber. der Kais. Akad. der Wissens. Vienna, vol. XLIII. p. 497).—Karl Müller, Deutschlands Moose (Halle 1853).—Lorentz, Moosstudien (Leipzig 1864).—Ditto, Grundlinien zu einer Vergleich. Anat. der Laubmoose (Jahrb. für wissen. Bot. vol. VI, and Flora 1867).—Leitgeb, Wachsthum des Stämmchens von *Fontinalis antipyretica* u. von Sphagnum; sowie Entwickelung der Antheridien derselben (in Sitzungsber. der Kais. Akad. der Wissens. Vienna 1868 and 1869).—Nägeli, Pflanzenphysiol. Untersuchungen, Heft I, p. 15.—Julius Kühn, Entwickelungsgeschichte der Andreæaceen (Leipzig 1870), (Mittheilungen aus dem Gesammtgebiet der Botanik von Schenk u. Luerssen, vol. I).

short term of life, as in the Phascaceæ, Pottia, Physcomitrium, &c., the protonema still remains vigorous after it has produced the leafy plants, and when the sporogonium has already been developed upon them. In such cases all three stages of the cycle of development are present simultaneously in genetic connexion. The Sphagnaceæ, Andreæaceæ, and Tetraphidei differ from the typical Mosses both in the structure of the sporogonia, and in the mode of formation of the pro-embryo. The spores of the Sphagnaceæ produce, at least when they grow upon a firm substratum, a flatly expanded plate of tissue, which branches in a crinkled manner at the margin, and produces from its surface the leafy stems. In Andreæa, according to the most recent investigations of Kühn, the contents of the spore divide, while still within the closed exospore, into four or more cells, and a tissue is thus formed similar to that produced from the spores of some Hepaticæ (as Radula and Frullania)[1]. Finally from one to three peripheral cells grow into filaments which

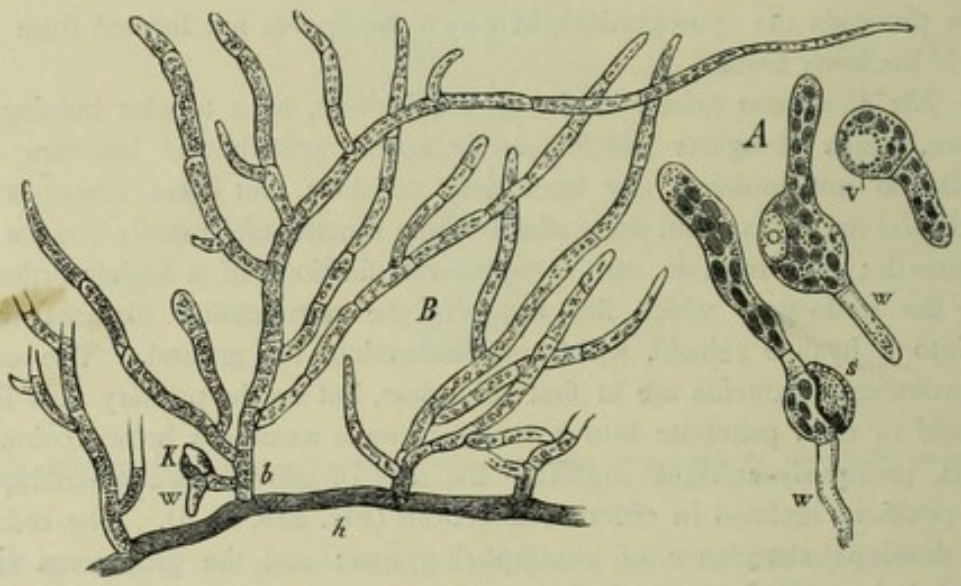

FIG. 226.—*Funaria hygrometrica*; *A* germinating spores; *v* vacuole; *w* root-hair; *s* exospore; *B* part of a developed protonema, about three weeks after germination; *h* a procumbent primary shoot with brown wall and oblique septa, out of which arise the ascending branches with limited growth; *K* rudiment of a leaf-bearing axis with root-hair *w* (*A* ×550; *B* about 90).

expand over the hard stony substratum. The branches of this protonema may now develope further in three different ways; longitudinal as well as transverse divisions arise, and irregularly branched cellular ribbons are formed; or, divisions also taking place in addition parallel to the surface of these ribbons, the pro-embryos developed in this manner as masses of tissue become erect and branch in an arborescent manner; finally, in a third form the leaf-like branches of the pro-embryo are plates of tissue of simple definite outline. Closely allied to this last form are the flat pro-embryos of Tetraphis and Tetradontium, which, as will be further shown in a following illustration, arise at the end of longer and slenderer filaments of a protonema[2].

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[1] In true Mosses also (as Bartramia, Leucobryum, Mnium, and Hypnum), the first septum of the protonema is formed, according to Kühn, even within the spore.

[2] Compare Berggren, Bot. Zeitg. 1872, nos. 23, 24.

(2) *The Sexual Generation, i. e.* the leaf-bearing plant which afterwards produces the sexual organs, originates from the lower cells of the lateral branches of the protonema; the apical cell of an elongated protonema-filament does not appear ever to become transformed so as to give rise to the leafy plant. Where a leafy plant is about to be produced, a short tube is formed from one of the lower cells, which, after being partitioned off, is divided by one or two more transverse septa; its apical cell thus becomes the apical cell of a bud, becoming divided by rapidly succeeding walls which intersect in opposite directions. In the Sphagnaceæ the bud arises in a similar manner from a marginal cell of the flat pro-embryo; in Tetraphis from the narrow base of a marginal cell; in Andreæa from lateral cells of the various kinds of pro-embryo except the leaf-like form. The cells cut off by the first oblique divisions are the first segments of the young stem, which either develope at once into leaves, or undergo only the first divisions into leaf-forming segments. Articulated rhizoids, which grow at once downwards, usually arise from these first segments after they have previously divided, and enable the young plant to take root.

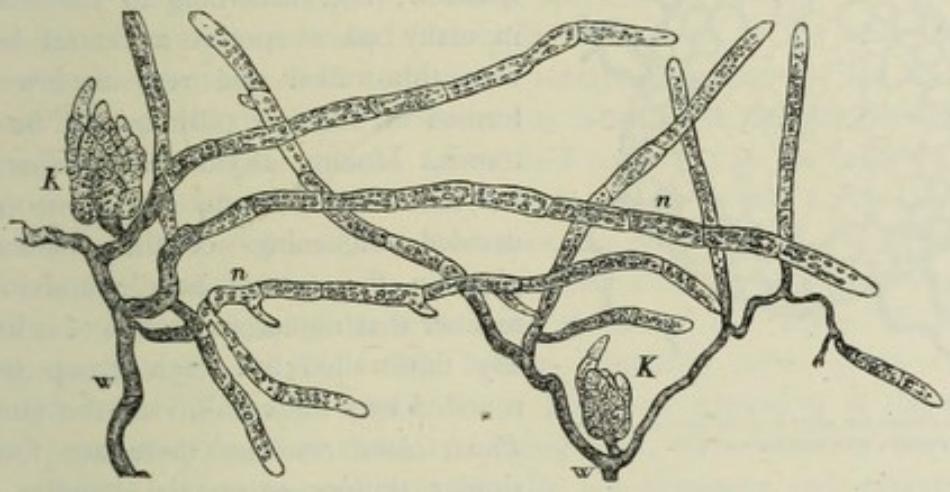

FIG. 227.—Production of rhizoids from the protonema of *Mnium hornum*, with leaf-forming buds *K*; *w w* the root-hairs of an inverted sod, from which shoot protonema-filaments *n n* (×90).

The apical cell of the stem is wedge-shaped in Schistostega and Fissidens, and produces two straight rows of alternating segments; in the rest of the Mosses it is a three-sided pyramid, with the bottom surface turned upwards (Fig. 106, p. 132). Each segment of the apical cell arches outwards and upwards as a broad papilla; this is cut off by a longitudinal wall (which Leitgeb calls a foliar wall), and developes, by further divisions, into a leaf, while the lower inner part of the segment produces, by further divisions, part of the inner tissue of the stem. Since each segment now forms a leaf, the phyllotaxis is determined by the position of the consecutive segments. In Fissidens two straight rows of alternate leaves are thus formed; in Fontinalis three straight rows with the divergence $\frac{1}{3}$, the segments themselves lying here in three straight rows with the $\frac{1}{3}$ arrangement, because each newly formed transverse wall is parallel to the last but three (both belonging to one segment). In Polytrichum, Sphagnum, Andreæa, &c., on the other hand, each new primary wall encroaches on the ascending side with regard to the leaf-spiral; the transverse walls of each segment are not parallel; the segments themselves do not lie, even

when first formed (without the assistance of any torsion of the stem), in three straight rows, but in three parallel spiral lines winding round the axis of the stem one above another; and the consecutive segments and their leaves diverge at an angle which, from what has been said, must be greater than $\frac{1}{3}$; the phyllotaxis is $\frac{2}{5}$, $\frac{3}{8}$, and so on [1].

The primary meristem of the stem situated beneath the *punctum vegetationis* which passes over into permanent tissue usually becomes differentiated into an inner and a peripheral mass of tissue, which are not generally sharply defined; the cell-walls of the peripheral and especially of the outermost layers are usually strongly thickened and of a bright red or yellowish red colour; the cells of the inner fundamental tissue have broader cavities and thinner walls more slightly or not at all coloured. In some Moss-stems this differentiation goes no further than into an outer skin consisting of several layers and a thin-walled fundamental tissue (*e. g. Gymnostomum rupestre*, *Leucobryum glaucum*, *Hedwigia ciliata*, *Barbula aloides*, *Hylocomium splendens*, &c., according to Lorentz); while in many other species a central bundle of very thin-walled and very narrow cells is formed in addition (Grimmia, Funaria, Bartramia, Mnium, Bryum, and others)[2]. In Polytrichum, Atrichum, and Dawsonia alone decided thickenings of the cell-walls take place in the central bundle and in such a manner that numerous groups of cells, originally thin-walled but each group itself surrounded by a thick wall, form the bundle. In *Polytrichum commune* there are found also similar thinner extra-axial bundles. Sometimes bundles of thin-walled cells run from the base of the leaf-veins obliquely downwards through the tissue of the stem as far as the central bundle, which Lorentz regards as foliar bundles (*e. g.* in *Splachnum luteum*, *Voitia nivalis*, &c.). If it is borne in mind that in some vascular plants fibro-vascular bundles of the most simple structure occur, and the similarity of the cambiform cells of true fibro-vascular bundles to the tissue of the central and foliar bundles in Mosses is considered, these latter may without doubt be held to be fibro-vascular bundles of the simplest kind.

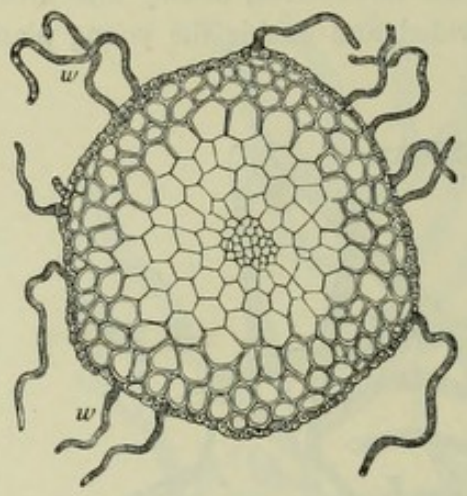

FIG. 228.—Transverse section of the stem of *Bryum roseum*, with root-hairs *w* (×90).

As has already been mentioned, the leaf originates from the broad papillose bulging of a cell of the stem which is separated by a longitudinal partition; a lower

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[1] If the position of each fourth division of the apical cell is kept in view, it gives the impression as if the apical cell rotated slowly on its axis, producing, at the same time, leaf-forming segments. (Compare on this subject the work of Leitgeb mentioned above, Lorentz's work, Hofmeister's Morphologie, p. 194, and Müller, Bot. Zeitg. 1869, pl. VIII.)

[2] It is stated by Lorentz that the pedicel of the sporogonium is always provided with a central bundle of this kind.

(basal) part of this cell is however concerned in the formation of the outer layers of tissue of the stem. The apical part of the papilla constitutes the apical cell of the leaf; it forms two rows of segments by partitions perpendicular to the surface of the leaf. The number of the segments thus formed, in other words, the terminal growth of the leaf, is limited, and the formation of tissue from the cells thus formed advances downwards, ceasing finally at the base. The whole of the tissue of the leaf is sometimes (as in Fontinalis) a simple layer of cells; but very commonly a vein, *i. e.* a more or less broad bundle, is formed from the base towards the apex, dividing the unilamellar lamina into right and left halves, and consisting itself of several layers of cells. The vein is sometimes composed of uniform elongated cells, but more often different forms of tissue become differentiated in it, among which are often formed bundles of narrow thin-walled cells similar to the central bundle of the stem, and these are sometimes continued to it through the external tissue of the stem as foliar bundles (*cf.* Lorentz, *l. c.*). The shape of the leaves of Mosses varies from almost circular through broadly lanceolate forms to the acicular; they are always sessile and broad at their insertion; usually densely crowded; only on the stolons of some species, the pedicels of the cupules of the gemmæ of Aulacomnion and Tetraphis, as well as at the base of some leafy shoots, do they remain small and remote (cataphyllary leaves). In the neighbourhood of the reproductive organs they usually form dense rosettes or buds, and then not unfrequently assume special forms and colours. In Racopilum, Hypopterygium, and Cyathophorum, there are two kinds of leaves, a row of larger upon one side, and a row of smaller leaves upon the other side of the stem. The leaves are not branched, but entire or toothed, rarely slit. In some kinds peculiar outgrowths are formed upon the inner or upper surface of the leaves; in *Barbula aloides* articulated capitate hairs. The lamina, which in other cases expands right and left from the median plane, is, in Fissidens, expanded in the median plane itself, proceeding from an almost sheathing base. The tissue of the leaf is, with the exception of the central vein, usually homogeneous and composed of cells containing chlorophyll, which sometimes project above the surface as mamillæ; in the Sphagnaceæ and Leucobryum the tissue is differentiated into cells of definite position, some containing air, others sap.

The mode of branching of the stem of Mosses is apparently never dichotomous, but also probably never axillary, although connected with the leaves. Even when the branching is copious the number of lateral shoots is nevertheless usually much smaller than that of the leaves; in many cases the lateral branches are definitely limited in their growth, leading sometimes to the formation of definite ramified systems similar to pinnate leaves (Thuidium, Hylocomium). When the primary shoot produces reproductive organs at the summit, a lateral shoot situated beneath it not unfrequently displays a more vigorous growth, continuing the vegetative system; and by such innovations sympodia are formed. It sometimes happens that stolons, that is shoots either destitute of or furnished with very small leaves, creep on or beneath the surface of the ground, elevating themselves at a later period as erect leafy shoots. The mode of branching is very various, and is closely connected with the mode of life. The morphological origin of the lateral shoots has been carefully investigated by Leitgeb in the case of Fontinalis and Sphagnum, and

admirably described. Since these two genera belong to very different sections, the results obtained in this case may be considered as of general application to the whole class. They agree in the fact that the mother-cell (which is at the same time the apical cell) of a branch originates beneath a leaf from the same segment as the leaf (Fig. 106, p. 132). In Fontinalis the branch arises beneath the median line of the leaf; but in Sphagnum beneath its cathodal half. In consequence of the further development of the mother-shoot, the lateral shoot in Sphagnum appears at a later period to stand by the side of the margin of an older leaf; and this is probably the explanation of the earlier statement of Mettenius that in *Neckera*

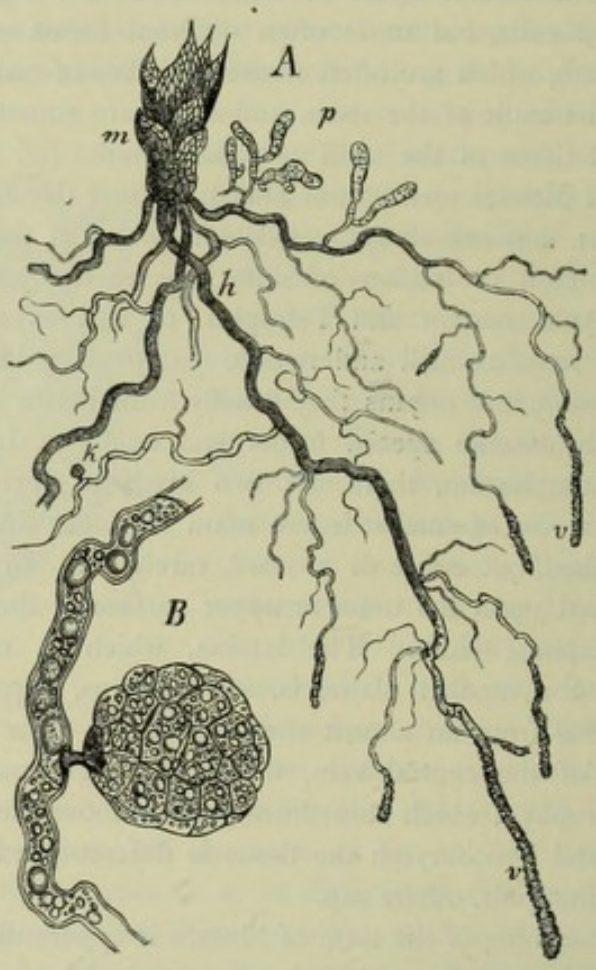

FIG. 229.—*A* young plant of a Barbula *m* with the root-hairs *h*, to the growing ends of which particles of earth have become attached; at *p* a superficial root-hair is putting out branches containing chlorophyll, in other words a protonema; at *k* a tuberous bud is growing from an underground branch of the root-hairs; *B* this bud more strongly magnified (*A* × 20; *B* × 300).

complanata, *Hypnum triquetrum*, *Racomitrium canescens*, and others, the lateral shoots stand by the side of the margins of the leaves. When the shoot arises beneath the median line of a leaf, and the leaves are arranged in straight rows, the further growth of the stem may cause it to seem as if the shoot originated above the median line of an older leaf, in other words as if it were axillary. Leitgeb states that articulated hairs arise in the genera named in the axils of the leaves, or perhaps more correctly at the base of the upper surface of the leaves.

The dimensions attained by the leaf-bearing axes and axial systems of Mosses show a wide range. In the Phascaceæ, Buxbaumia, and others, the simple stem

is scarcely 1 mm. in height; in the largest species of Hypnum and Polytrichum it is not unfrequently 2, 3, or more decimetres in length, and, if belonging to more than one axis, even longer owing to the formation of innovations and sympodia (Sphagnum). The thickness of the stem is less variable; $\frac{1}{10}$ mm. in the smallest, it scarcely exceeds 1 mm. in the thickest forms. For this reason, however, its dense tissue, coloured externally, is very firm, often stiff, always very elastic, and capable of offering long resistance to decay.

The Root-hairs (Rhizoids) play an extremely important part in the economy of Mosses. It is only in the otherwise very abnormal section of the Sphagnaceæ that they are very sparsely and poorly developed; in most other forms they occur in large numbers at least at the base of the stem, often clothing it completely with a dense reddish-brown felt. Morphologically the rhizoids are not sharply distinguished from the protonema[1]; and it will be seen further on that they, like it, are capable of forming new leafy stems. They arise as tubular protuberances from the superficial cells of the stem, elongate by apical growth, and are segmented by oblique septa; at the growing end the wall is hyaline, and particles of earth become attached to it in the ground; subsequently these fall off; the wall becomes thicker and brown; the latter being the case also with the aërial root-hairs. The cells contain a considerable quantity of protoplasm and drops of oil (Fig. 229, *B*); behind the septa branches proceed from the cells, often disposed in tufts, and in this case the individual threads are very slender. In many Mosses the root-hairs branch very copiously in the ground; they often form a dense inextricable felt; a felt of this kind may even arise above ground as a dense turf, and may serve as a soil for future generations. In Atrichum and other Polytrichaceæ, the stouter rhizoids coil round one another like the threads of a rope, the branches which proceed from them doing the same, and only the last and finest ramifications remain free.

The Vegetative Reproduction of Mosses is more copious and varied than is the case in any other section of the vegetable kingdom. It presents the peculiarity that the production of a new leaf-bearing stem is always preceded by the formation of a protonema, even when the propagation takes place by gemmæ. Exceptions are afforded only by the few cases in which leaf-buds become detached and commence immediately to grow.

In describing the different cases in detail, the first point that must be brought prominently forward is that both the protonema which proceeds from the spore itself and the leafy stems which spring from it are capable of reproduction of different kinds. The original protonema is so far an organ of reproduction that it may produce upon its branches a smaller or larger number of leafy stems in succession or simultaneously; sometimes the individual cells of the protonema-branch separate from one another after they have become rounded off into a spherical form, acquire thicker walls, and become for a time inactive (as in *Funaria hygrometrica*), forming, probably, at a later period again protonema-filaments. A

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[1] The rhizoids appear to be distinguished from the protonema only by the absence of chlorophyll and by their tendency to grow downwards; the protonema developes certain branches as rhizoids; and the rhizoids may, on their part, develope single branches as a protonema growing upwards and containing chlorophyll.

secondary protonema may, however, be formed from any root-hair when exposed to light in a moist atmosphere. It is not known whether, under such circumstances, the apical cell of the stouter rhizoids can itself undergo the change; but it is certain that the separate cells of the root-hairs form branches which behave in exactly the same manner as the protonema which proceeds from the spore form chlorophyll, and produce new leafy plants (*cf.* Fig. 226 and Fig. 229, *A*, *p*). In some species (Mnium, Bryum, Barbula, &c.) it is sufficient to keep a turf of moss damp for some days and turned downwards, in order to produce hundreds of new plants in this manner. Some apparently annual species, *e.g.* of Phascum, Funaria, and Pottia, persist perennially by means of their root-hairs; the plants disappear completely from the surface of the ground from the time that the spores become ripe till the next autumn, when the root-hairs again produce a new protonema, and upon this new stems arise.

A similar production of gemmæ from the roots occurs also, according to Schimper, in the felted protonema of some species of Polytrichum (*P. nanum* and *aloides*) on the slopes of hollow roads, and on that of *Schistostega osmundacea* in dark hollows. The root-hairs may also immediately produce leaf-buds, and behave, in this respect, exactly like the protonema. When the buds arise on underground ramifications of the root-hairs (Fig. 229, *B*) they remain in a dormant state, as small microscopic tuberous bodies filled with reserve food-material, until they chance to reach the surface of the ground, when they undergo further development (*e. g. Barbula muralis*, *Grimmia pulvinata*, *Funaria hygrometrica*, *Trichostomum rigidum*, Atrichum). The aërial root-hairs may, however, not only produce a protonema containing chlorophyll, but also leaf-buds without its intervention; and Schimper cites the remarkable fact that in *Dicranum undulatum* annual male plants are formed in this manner on the perennial clods of the female plants, and fertilise the latter.

Even the leaves of many Mosses produce a protonema, their cells simply growing, and the tubes thus formed becoming segmented. This occurs in *Orthotrichum Lyelli* and *obtusifolium;* in *O. phyllanthum* club-shaped tufts of protonema with short cells arise at the apex of the leaves; and the same phenomenon occurs in *Grimmia trichophylla*, Syrrhopodon, and Calymperes. In *Oncophorus glaucus* a dense felt of interlacing protonema-filaments is formed at the summit of the plant where the reproductive organs are produced, which arrests its further growth, and hence produces at a later period new clumps of young plants. In Buxbaumia, especially *B. aphylla*, the marginal cells of the leaves form a protonema enveloping them as well as the stem with its filaments. Lastly, even detached leaves, if kept moist, may emit a protonema, as for instance those of *Funaria hygrometrica*.

Gemmæ, which, like those of the Marchantieæ, are stalked fusiform or lenticular cellular bodies, occur in *Aulacomnion androgynum* at the summit of a leafless elongation of the leafy stem (*Pseudopodia*); in *Tetraphis pellucida* enveloped by an elegant cup composed of several leaves, out of which they subsequently fall. These latter then put forth protonemal filaments, which produce first of all a *flat proembryo;* and upon this finally new leaf-buds arise (Figs. 230, 231).

Finally the deciduous branch-buds of *Bryum annotinum* may also be considered as organs of reproduction; as also, according to Schimper, may the branches of

Conomitrium julianum and *Cinclidotus aquaticus*, which likewise have the power of detaching themselves.

The Sexual Organs of Mosses usually occur in considerable numbers at the end of a leafy axis[1], surrounded by enveloping leaves often of peculiar shape, and mixed with paraphyses. A compound structure of this kind may, for the sake of brevity, be called a 'Flower.' The flower of Mosses either terminates the growth of a primary axis (Acrocarpous Mosses), or the axis is indeterminate, and the flower is placed at the end of an axis of the second or third order (Pleurocarpous

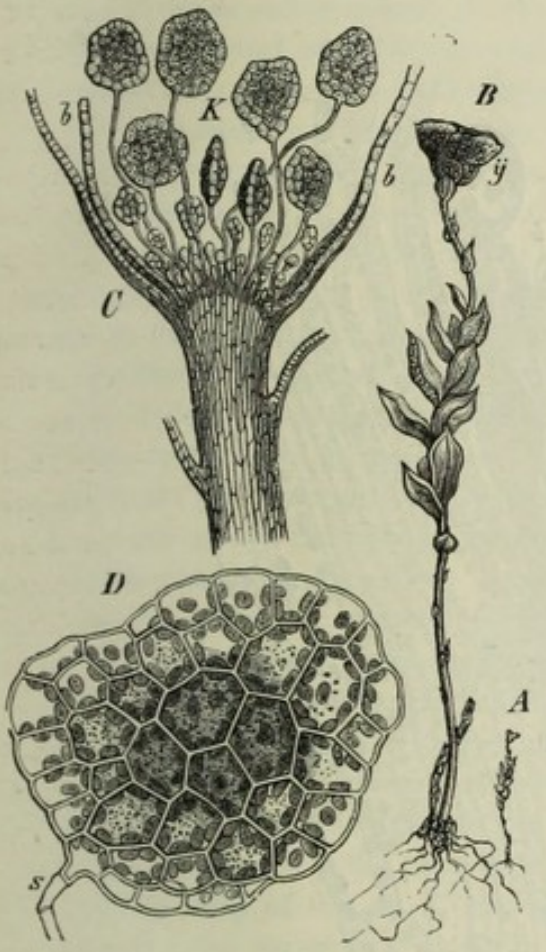

FIG. 230.—*Tetraphis pellucida*; *A* a plant producing gemmæ (natural size); *B* the same, magnified; *y* the cup in which the gemmæ are collected; *C* longitudinal section through the summit of the plant, *b* the leaves of the cup, *K* the gemmæ in various stages of development; the older ones are forced off their stalks by the later growth of the younger ones, and forced over the side of the cup; *D* a mature gemma (×500), consisting at the margin of one, in the centre of several layers of cells.

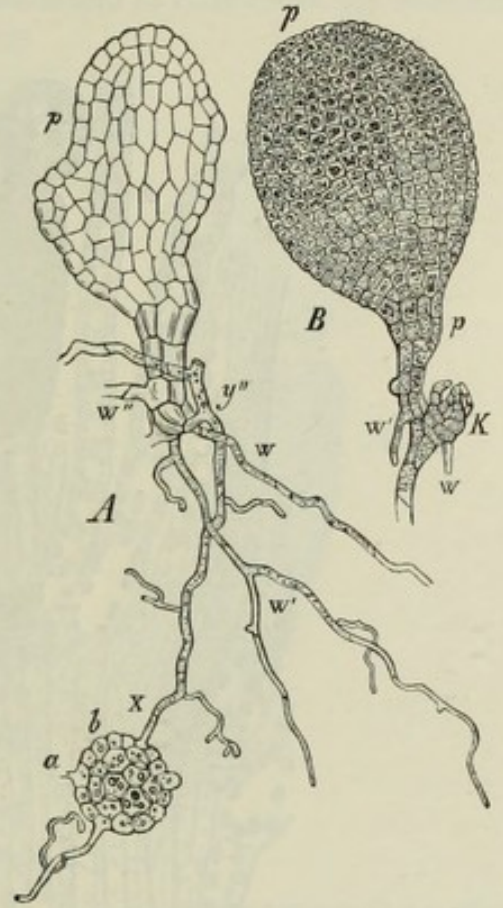

FIG. 231.—*Tetraphis pellucida*; *A*, *b* a gemma, detached from its stalk at *a*, the protonema-filament *x y* has been formed by the growth of a marginal cell of the gemma, and the flat structure *p* as a lateral outgrowth from the protonema; this has also put out root-hairs *w*, *w'*, *w''* (×100); *B*, *p* a flat pro-embryo from the base of which a leaf-bud *K* and root-hairs *w*, *w'* have sprung; the base of the pro-embryo often puts out a number of new flat pro-embryos before a leaf-bud is formed.

Mosses). Within a flower either both antheridia and archegonia are produced (bisexual flowers), or it contains only one kind of sexual organ, and the flowers may then be either monœcious or dicœcious. Sometimes the male flowers appear on smaller plants with a shorter duration of life (as *Funaria hygrometrica*, *Dicranum undulatum*, &c.). In external appearance the bisexual are similar to the female

[1] The male branches of Sphagnum form an exception (*vide infra*).

flowers, while the habit of the male flowers is altogether different. In the former the archegonia and antheridia occur either close to one another at the summit of the stem in the centre of the envelope (*Perichætium*), either in two groups, or separated by peculiar enveloping leaves, and the antheridia stand in the axils of these arranged in a spiral, surrounding the central group of archegonia. The form of the perianth is, in the female and bisexual flowers, that of an elongated almost closed bud, formed by several turns of the leaf-spiral. Its leaves are similar to the foliage-leaves, and become smaller towards the interior, but grow all the more vigorously after fertilisation. The male perianth (*Perigonium*) consists of

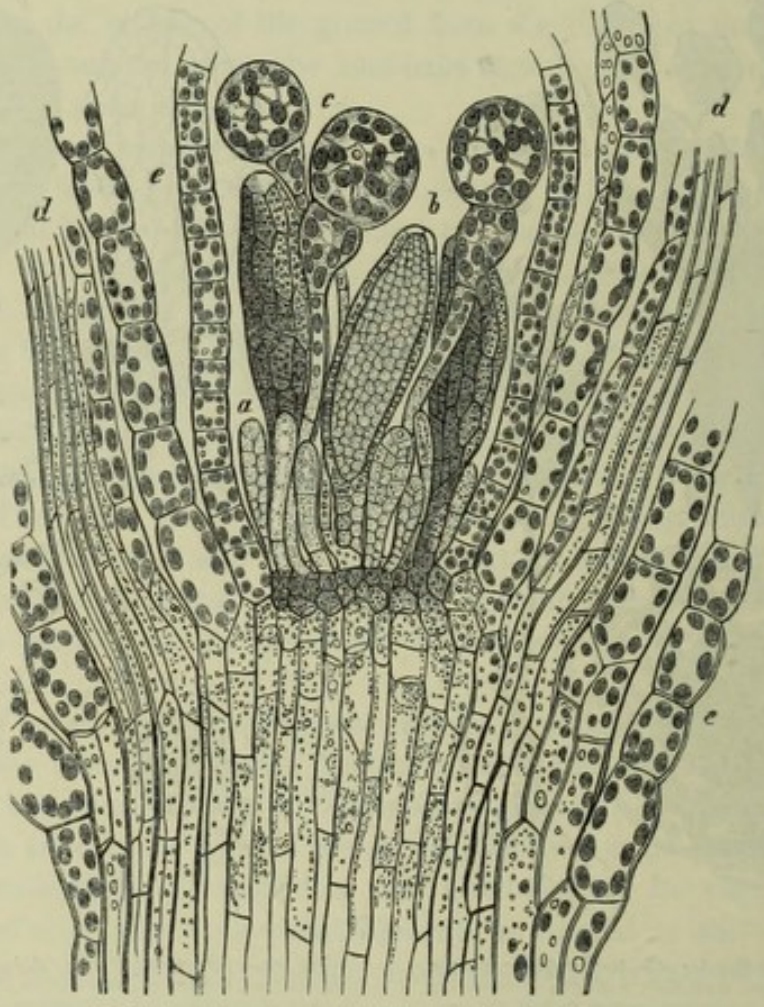

FIG. 232.—Longitudinal section of the summit of a very small male plant of *Funaria hygrometrica*; *a* a young, *b* a nearly ripe antheridium; *c* paraphyses; *d* leaves cut through the mid-rib; *e* leaves cut through the lamina (×300).

broader firmer leaves, and is of three different forms; usually it is bud-shaped, and resembles that of the female flower, but is shorter and thicker, its leaves often coloured red, and decreasing in size towards the outside; flowers of this type are always lateral. Those shaped like capitula are, on the contrary, always terminal on a stouter shoot and globular, their leaves are broad, sheathing at the base, thinner and recurved at the upper part; they become smaller towards the interior, and leave the centre of the flower, with the antheridia, free; these flowers are sometimes borne on a naked pedicel, a prolongation of the stem (Splachnum, Tayloria). Finally, the discoid male perigonia consist of perianth-leaves which are very different

from the foliage-leaves; they are broader and shorter, expanded horizontally at the upper part, delicate and of a pale green, orange, or purple colour; they are always smaller the nearer the leaf-spiral approaches the centre; the antheridia stand in their axils (Mnium, Polytrichum, Pogonatum, Dawsonia). The paraphyses stand between or by the side of the sexual organs; in the female flowers they are always articulated filaments; in the male flowers filiform or spathulate, and consisting, in the upper part, of several rows of cells.

The Antheridia are, when mature, stalked sacs with a wall consisting of a single layer of cells containing grains of chlorophyll, which however, in the ripe state, assume a red or yellow colour. In the Sphagnaceæ and in Buxbaumia the antheridia are nearly spherical, but in all other Mosses of an elongated club shape. In the Sphagnaceæ they open in the same manner as in the Hepaticæ; in the other orders by a slit across the apex, through which the antherozoids still enclosed in their mother-cells are discharged as a thick mucilaginous jelly. The interstitial mucilage dissolves in water, and the antherozoids escape from their mother-cells and swim about free.



FIG. 233.—*Funaria hygrometrica*; *A* an antheridium bursting, *a* the antherozoids (×350); *B* the antherozoids more strongly magnified, *b* in the mother-cell; *c* free antherozoid of Polytrichum (×800).

The careful investigations of Leitgeb show that the morphological significance of the antheridia is very various. In Sphagnum the mother-cell of the antheridium arises in exactly the same place in which a shoot would otherwise be formed, *i.e.* from the segment of the axis of the antheridial shoot which lies beneath the cathodal half of the leaf; the antheridia may in this case be considered as metamorphosed shoots. In Fontinalis, on the other hand, their morphological significance varies within the same flower; the one first formed is the immediate prolongation of the axis of the shoot, arising from its apical cell; the succeeding ones are developed from its last normal segments, and therefore resemble leaves in their origin and position; the last antheridia, finally, exhibit the morphological characters of trichomes, both in their variable number, their development as cells of the epidermis, and the want of definiteness in their place of origin. According to Kühn, Andreæa behaves in precisely the same way as Fontinalis. The mother-cell of the antheridium of Fontinalis is constituted as an apical cell forming two alternating rows of segments; in forming the oldest and terminal antheridium the apical cell changes from a triseriate to a biseriate segmentation. These segments are next divided by tangential walls in such a manner that the transverse section (which meets two segments) of the young organ shows four outer and two inner cells; the wall of the antheridium, one cell in thickness, arises from the former by further division; the small-celled tissue which produces the antherozoids from the latter.

Andreæa behaves also very similarly in these respects; the primary mother-cell of the antheridium appears as a papilla and is cut off by a septum; the lower cell produces a cushion-like support; the upper cell is again divided by a septum into a lower cell from the divisions of which the tissue of the stalk is formed, and an upper cell out of which the body of the antheridium arises; the formation of the latter takes place in the same manner as in Fontinalis. In Sphagnum the long stalk originates by transverse divisions of the growing papilla which produces the antheridium, the transverse divisions then dividing again in a cruciform manner.

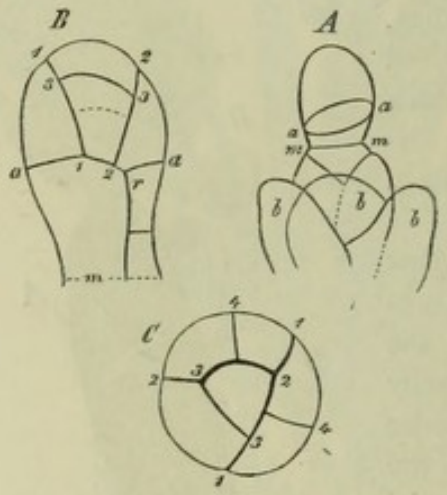

FIG. 234.—First stage of development of the archegonium of Andreæa (after Kühn); *A* terminal archegonium arising from the apical cell of the shoot; *b b* the youngest leaves; *B* after the formation of the central cell and stigmatic cell; *C* transverse section of the young ventral portion.

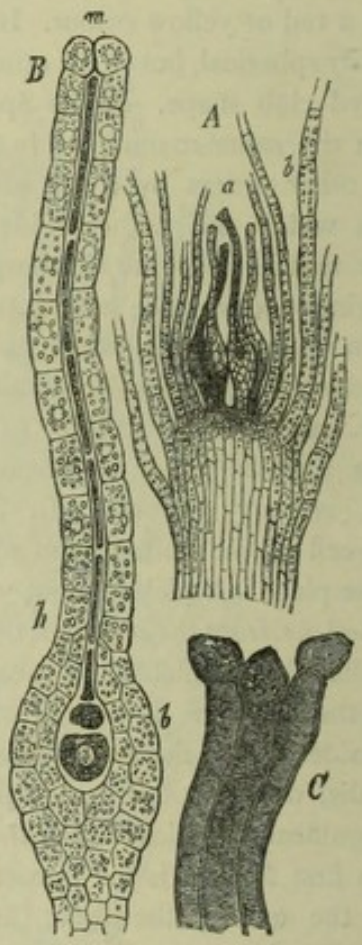

FIG. 235.—*Funaria hygrometrica*; *A* longitudinal section of the summit of a weak female plant (×100), *a* archegonia, *b* leaves; *B* an archegonium (×550), *b* ventral portion with the central cell, *h* neck, *m* mouth still closed; the cells of the axial row are beginning to be converted into mucilage (the preparation was made after lying three days in glycerine); *C* the part near the mouth of the neck of a fertilised archegonium, with dark red cell-walls.

The terminal cell then swells, and becomes divided by oblique walls of somewhat irregular position; a tissue is thus formed, which, at a subsequent period, consists also of a wall formed of a single layer of cells and an inner very small-celled tissue which produces the antherozoids.

The Archegonium consists when mature of a massive, moderately long base, which supports a roundish ovoid ventral portion; above this rises a long thin neck, generally twisted on its axis. The wall of the ventral portion, which consists, even before fertilisation, of a double layer of cells, passes up continuously into the wall of the neck consisting of a single layer of cells formed of from 4 to 6 rows (Fig. 235). Together they enclose an axial row of cells, the lowest of which, ovoid and lying

in the ventral portion, produces the oosphere from its protoplasmic substance by rejuvenescence, while the axial cells which lie above it become mucilaginous before fertilisation. This mucilage forces the four apical cells (stigmatic cells) of the neck apart, and thus opens the canal of the neck, allowing the antherozoids to penetrate to the oosphere. Fig. 235, *B*, shows the row of cells of the canal at the period when disorganisation is beginning, and when the stigmatic cells of the neck are still closed. In reference to the morphological significance of the archegonia, Leitgeb has already shown that at least the first archegonium of Sphagnum arises immediately from the apical cell of the female shoot; more recently Kühn found that in Andreæa the first is formed from the apical cell, the succeeding ones from its last segments, in the same manner as the antheridia of the same genus, and those of Radula and Fontinalis. According to preparations which Schuch obtained in the laboratory at Würzburg, the first archegonium arises also in typical Mosses from the apical cell of the shoot.

The order of succession of the cells in the construction of the archegonium has been studied in detail by Kühn in the case of Andreæa. According to his observations it is in the main similar to that stated by Leitgeb in the case of Radula, although there is a striking discordance in the statements in reference to the formation of the neck and of the row of canal-cells. In Fig. 234 is shown at *A* the origin of the first archegonium of Andreæa from the apical cell of the shoot; a septum (*m m*) has already separated the ovoid mother-cell, and a second oblique wall (*a a*) has divided this into a lower and an upper part; the former produces, by further divisions, the stalk or base of the archegonium; from the upper part proceed its neck and ventral portion. While this apical cell is increasing considerably in size, and especially in height, three oblique longitudinal walls (Fig. 234, *B*, 1, 1...2, 2...3, 3) next arise successively, by which a central cell is formed, arched and broader above, and surrounded by a three-celled wall (*cf.* Fig. 234, *C*, in transverse section). A septum now separates the upper part of the central cell like a lid, while the lower part is completely enclosed by this and the lateral ones. So far the statements of Kühn agree with those of Leitgeb in the case of the archegonium of Radula; but while, according to the latter, the central cell produces both the oosphere and the axial row of canal-cells, the upper ones forming only the stigmatic cells of the neck, and the three lateral ones the wall of the ventral portion and of the neck, Kühn states, on the contrary, that the upper cell continues to grow as the apical cell, developing successively new stages consisting each of three lateral cells surrounding a central canal-cell. Since, however, Kühn's drawings may be reconciled with the statements of Leitgeb in the case of Radula, it may, perhaps, be assumed that a fresh series of observations would show that after the separation of the first stigmatic cell the axial row is formed entirely from the central cell, the wall of the ventral portion and of the neck entirely from the three first lateral cells. A nearer agreement would thus be indicated not only with the Hepaticæ, but also with the higher Cryptogams[1].

[1] [According to Janczewski (Bot. Zeitg. 1872, p. 869) the archegonia of Mosses possess an apical growth which is wanting elsewhere in Cryptogams.—Ed.]

(3) *The Sporogonium*, which results from the fertilised oosphere, attains, in Sphagnum, almost perfect development within the actively growing ventral portion of the archegonium, which becomes transformed into the calyptra; but in all other Mosses the calyptra is torn away from the vaginula at its base, by the elongation of the sporogonium, usually long before the development of the spore-capsule, and (except in Archidium and its allies) is raised up as a cap. The neck of the archegonium, the walls of which assume a deep red-brown colour, still for some time crowns the apex of the calyptra. The sporogonium of all Mosses consists of a stalk (the *Seta*), and the spore-capsule (*Theca* or Urn); but the former is very short in Sphagnum, Andreæa, and Archidium, longer in most other genera, and with its base planted in the tissue of the stem, which, after fertilisation, grows luxuriantly beneath and beside the archegonium, forming a sheath-like protection, the *Vaginula*. The unfertilised archegonia may frequently be seen on the exterior slope of the vaginula, since only one archegonium is usually fertilised in the same flower, or it is only the one first fertilised that perfects its oospore. The capsule has in all Mosses a wall consisting of several layers of cells with a distinct epidermis which sometimes possesses stomata; the whole of the inner tissue is never used up in the formation of spores, even when, as in Archidium, it is subsequently supplanted by them; a large part of the central tissue remains as the so-called *Columella*, and it is at the circumference of this that the mother-cells of the spores are formed. The structure of the mature capsule, and especially the contrivances for dispersing the spores, are, however, so different in the various principal sections of Mosses that it will be better to consider them more closely separately, and the more so because by this means we shall at the same time arrive at the distinctive characters of the larger natural systematic groups.

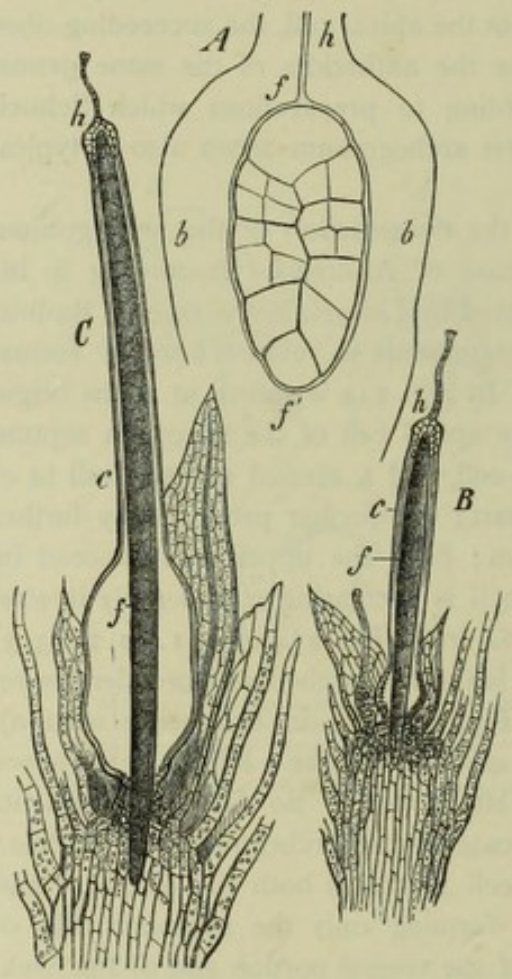

FIG. 236.—*Funaria hygrometrica*; *A* origin of the sporogonium *ff'* in the ventral portion *b b* of the archegonium; (longitudinal section ×500); *B*, *C* different further stages of development of the sporogonium *f* and of the calyptra *c*; *h* neck of the archegonium (× about 40).

In the mode of origin of the sporogonium there is, as might be expected, less variety. The oospore is first of all clothed with a cell-wall, continues to grow considerably, and is then divided by a (horizontal ? or) slightly inclined wall. Hofmeister asserts that in *Bryum argenteum* the upper cell (that facing the neck of the archegonium) is again divided once or twice by horizontal septa before the first oblique division, while in Phascum, Funaria, Andreæa, and Fissidens, this oblique septum is formed immediately after the first horizontal one. The apical

cell now forms two rows of segments by partition-walls inclined alternately, and these segments are next divided by radial vertical walls, followed by further numerous transverse divisions. By this process the young sporogonium growing at its apex is transformed into a multicellular body which is usually fusiform, the lower end not participating in the growth in length. A swelling of this lower end, such as usually occurs in Hepaticæ, takes place also in Sphagnum and Archidium. The apex of the sporogonium now becomes inactive, and beneath it the capsule is formed from a spherical, ovoid, cylindrical, or frequently unsymmetrical swelling which originates, in the typical Mosses, only after the elongation of the fusiform or cylindrical sporogonium, and after the raising up of the calyptra. The internal differentiation of this mass of tissue, at first homogeneous, forms the various tissues which compose the capsule of Mosses, and especially the mother-cells of the spores which first of all become isolated and then divide each into four spores. The contents of the mother-cell begin to divide into two, but this bipartition is usually not completed, the division into four taking place at once. The preparation for the formation of spores takes place simultaneously everywhere within the same capsule. The ripe spores are roundish or cubical, surrounded by a thin finely granulated exospore, which is of a yellowish, brownish, or purple colour. Besides protoplasm, they contain chlorophyll and oil. In Archidium, where only sixteen are formed in each capsule, they are about $\frac{1}{5}$ mm. in size, in the highly developed Dawsonia scarcely $\frac{1}{200}$ mm. (Schimper). When kept dry the spores often retain their power of germination for a long time, but when moist they frequently germinate after a few days, those of Sphagnum after two or three months.

The time necessary for the formation of the sporogonium varies greatly in the different species, but is usually very long in comparison with the small size of the body concerned. The Pottieæ blossom in summer, and ripen their spores in the winter; the Funariæ are perennially in blossom, and have constantly sporogonia in all stages of development, occupying for its completion probably 2 to 3 months; *Phascum cuspidatum* developes in the autumn from its perennial underground protonema, and ripens its spores in a few weeks before the winter. The bog Hypna, on the other hand (*H. giganteum*, *cordifolium*, *cuspidatum*, *nitens*, &c.), blossom in August and September, and ripen their spores in June of the next year; they often require ten months for the development of their sporogonia. *H. cupressiforme* bears in autumn at the same time flowers and ripe spores, and hence requires one year. The same length of time is required by Philonotis, and by some species of Bryum and some of Polytrichum which blossom in May and June[1].

Mosses may be distributed naturally into four parallel orders:—

1. Sphagnaceæ,
2. Andreæaceæ,
3. Phascaceæ,
4. Bryaceæ (True Mosses).

Of these the first includes a single genus, the second and third only a few; the fourth all the remaining extremely numerous genera. The first three groups recall, in many respects, the Hepaticæ; even the series of true Mosses commences with some genera

[1] Klinggräff, Bot. Zeitg. 1860, p. 344.

which still resembles that class; the lowest forms of all the groups exhibit many resemblances which are wanting in the most highly developed. We have therefore four diverging series.

1. The **Sphagnaceæ**[1] include only the single genus Sphagnum. When the spores germinate in water, a branched protonema is developed, on which the leaf-buds immediately appear laterally (Fig. 237, *C*). On a solid sub-stratum, on the other hand, the short protonema forms first of all a branching flat pro-embryo (Fig. 238), on which (as in Tetraphis) the leaf-buds appear. The leafy stems produce root-hairs only in the young state, the abundant protonema of true Mosses is entirely wanting. The stem, as it increases in strength, produces laterally, by the side of every fourth leaf, a branch, which, even at the very earliest period, is again much divided; tufts of branches arranged regularly thus arise which form a compact mass at the summit of the stem, but lower

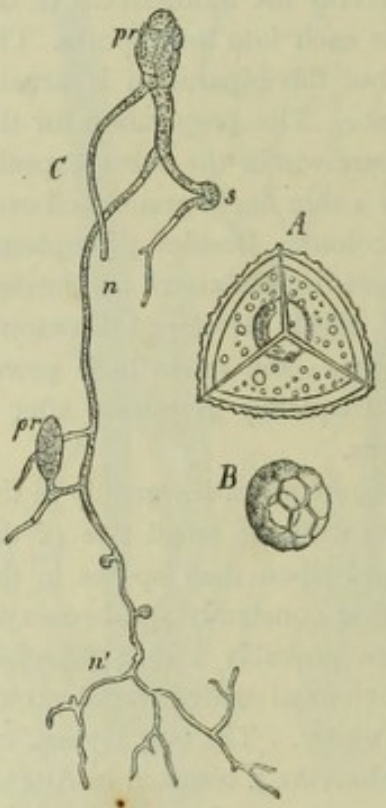

FIG. 237.—*Sphagnum acutifolium*; *A* a large spore, seen from the apex; *B* a small spore; *C* a protonema *n n'* resulting from the spore *s*; *pr* rudiments of young plants (after Schimper).

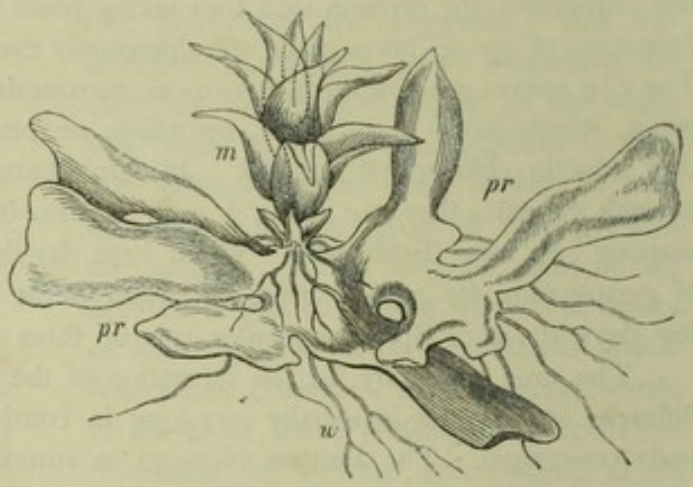

FIG. 238.—*Sphagnum acutifolium*; the flat pro-embryo *pr* with a young leafy stem *m* (after Schimper, × about 20).

down are more divergent. The separate branches develope in different ways; one is produced each year beneath the summit after the ripening of the fruit, and developes in a similar manner to the primary stem, growing up along with the prolongation of the latter, so that each year a false dichotomy takes place on the stem. These innovations afterwards become separated by the slow decay of the plant advancing from below, and constitute independent plants. Some of the branches of each tuft, however, turn downwards, become long, slender, and finely pointed, and are closely applied to the primary stem, forming a dense envelope around it; while other branches of each tuft turn outwards and upwards. The leaves spring from the stem and the branches from a broad base, and are usually arranged with a divergence of $\frac{2}{5}$; they are

[1] W. P. Schimper, Versuch einer Entwickelungsgeschichte der Torfmoose. Stuttgart 1858 (with many beautiful plates).

tongue-shaped or apiculate, and, with the exception of the first on the young stem, are composed of two kinds of cells arranged regularly. The young leaf necessarily consists of homogeneous tissue; but as the development progresses the cells of the veinless lamina become differentiated into large broad cells about the shape of a long lozenge, and into narrow tubular cells, running in the midst of the former, bounding them, and united with one another into a network; they are, as it were, squeezed in among the larger ones. The larger cells lose the whole of their contents, and hence appear colourless; their walls show irregular narrow spiral bands with the turns some distance apart, as well as large dots, each of which has a thickened edge, while the part of the cell-wall which closes the dot is absorbed. Large holes usually circular are thus formed in the cell-wall of the colourless cells. The intermediate tubular narrow cells retain their contents, form grains of chlorophyll, and thus constitute the tissue of the leaf,



FIG. 239.—*Sphagnum acutifolium*; part of the stem below the apex; *a*, *a* the male branches, *b* leaves of the primary stem; *ch* perichaetial branch with old still closed sporogonia (after Schimper ×5-6).

the entire area of which is, however, smaller than that of the colourless tissue (Fig. 240). The stems consist of three layers of tissue, the innermost of which is an axial cylinder of thin-walled colourless cells elongated in a parenchymatous manner; it is enveloped by a layer of thick-walled, dotted, firm (lignified?) prosenchymatous cells, with their walls coloured brown. The epidermal tissue of the stem, finally, consists of from 1 to 4 layers of very broad thin-walled empty cells, which, in *S. cymbifolium*, possess spiral threads and round holes similar to those of the leaves (*cf.* Fig. 70, p. 82). These colourless cells, both those of the leaves and of the epidermal layer of the stem and of the branches, serve as a capillary apparatus for the plant, through which the water of the bogs in which it grows is raised up and carried to the upper parts; hence it results that the Sphagna which always grow erect are

penetrated with water to their very summits like a sponge, even when their tufts stand high above the surface of the water.

The Archegonia and Antheridia of Sphagnum arise on the fascicled branches, as long as they are still near the summit of the primary stem and belong to the terminal tuft. The time of flowering is mostly in autumn and winter, but is not exclusively confined to these periods. The antheridia and archegonia are always distributed on different branches, sometimes even on different plants, and in this case the male and female plants form large distinct patches. When the primary stem does not continue to grow during the development of the sporogonia in dry weather, growth still takes place subsequently at the terminal tuft; but when the supply of water is great and vigorous increase of length takes place, the fertile branches diverge from one another, and are consequently found lower down on the stem; and the sporogonia and older male inflorescences are thus removed to a distance from the summit, although at the time of flowering they stand near it. The branches which bear the antheridia are generally

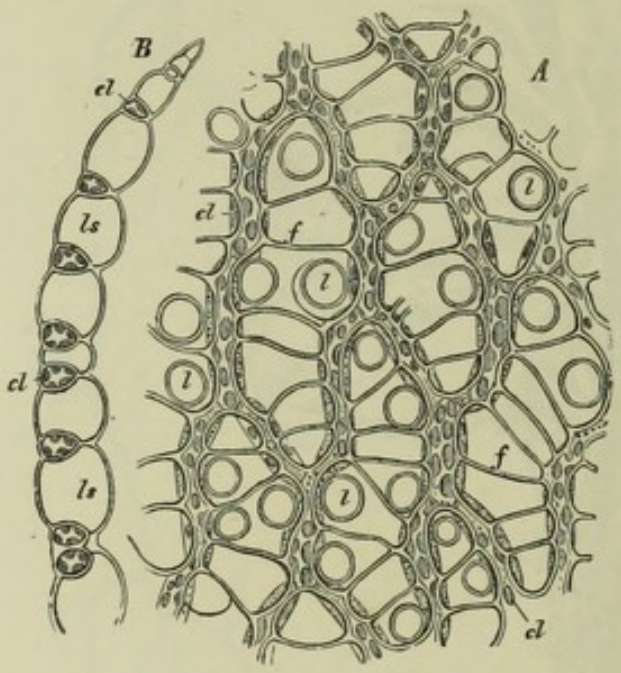

FIG. 240.—*Sphagnum acutifolium*; *A* a portion of the surface o the leaf seen from above, *cl* the tubular cells containing chlorophyll, *f* the spiral bands, *l* the holes in the large empty cells; *B* transverse section of a leaf, *cl* the cells that contain chlorophyll, *ls* the large empty cells.

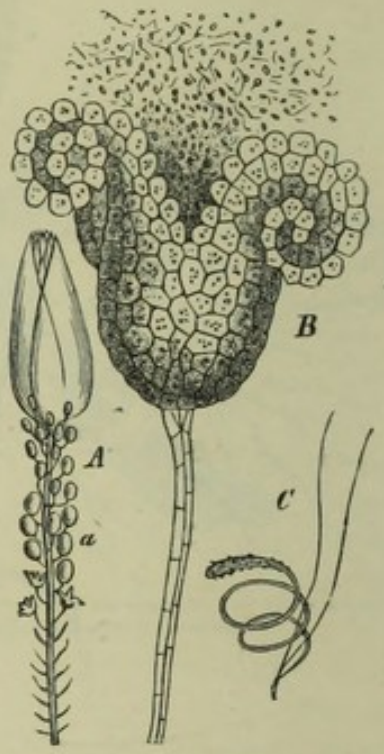

FIG. 241.—*Sphagnum acutifolium*; *A* a male branch, with the leaves partially removed in order to show the antheridia *a*; *B* an open antheridium (very strongly magnified); *C* a free motile antherozoid (after Schimper).

conspicuous externally by their imbricated leaves forming beautiful densely crowded orthostichies or spiral parastichies; the leaves are generally yellow, bright red, or especially dark green, and can hence be easily recognised (Fig. 239, *a a*). The antheridia stand, on the mature shoot, *by the side of* the leaves; they are never terminal, and are found only in the middle part of the male branch, one standing beside each leaf; the male branch may therefore continue to grow at the summit, and become an ordinary flagellate branch. This position of the antheridia, and still more their roundish form and long pedicel, causes the Sphagnaceæ to resemble some Jungermannieæ; the mode in which they open (Fig. 241) recalls the Hepaticæ even more than the true Mosses. The archegonia arise at the blunt end of the female branch, the upper leaves of which form a bud-like envelope; but the young perichætial leaves are still contained within this at the time of fertilisation, although they afterwards become further developed. The archegonia are exactly like those of the rest of the

Mosses; several of them are usually fertilised in one perichætium, but only one perfects its sporogonium. This development occurs within the perichætium; the summit of the branch then begins to rise, grows out into a long naked receptacle, and elevates the sporogonium contained in its calyptra high above the perichætium. This so-called *Pseudopodium* must not, however, be confounded with the seta of other Mosses. At Fig. 242, *B*, is shown in longitudinal section the nearly ripe sporogonium developed within the calyptra. Its lower part forms a thick base imbedded in the end of the pseudopodium which is transformed into the vaginula. The origin of the spore-mother-cells is a cap-shaped layer of spherical cells beneath the apex of the spherical theca; the part of the inner tissue which is found beneath it forms a low nearly hemispherical column, which is in this case also termed the Columella, although it is distinguished from the columella of true Mosses by not reaching to the apex of the theca. The mode of the formation of the spores from the mother-cells resembles that of true Mosses; but there occur, besides the ordinary (large) spores, also smaller spores in special smaller sporogonia, which owe their origin to a further division of the mother-cells (*cf.* Fig. 237, *B*). The theca opens by the detachment as a lid of the upper segment of the ball, which is sometimes more strongly convex. The calyptra, which closely surrounds the growing sporogonium as a fine envelope, is ruptured irregularly.

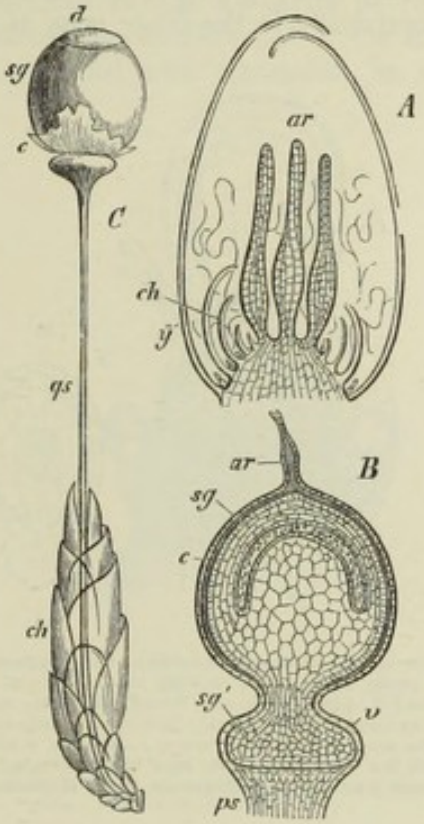

FIG. 242.—*A*, *B*, *Sphagnum acutifolium*; *A* longitudinal section of the female flower, *ar* archegonia, *ch* perichætial leaves still young, *y* the last perichætial leaves or perigynium; *B* longitudinal section of the sporogonium *sg*, the broad base of which *sg'* remains in the vaginula *v*, while the capsule is surrounded by the calyptra *c*, upon this is the neck of the archegonium *ar*, *ps* the pseudopodium; *C Sphagnum squarrosum*, ripe sporogonium *sg* with its lid *d* and ruptured calyptra *c*, *qs* the elongated pseudopodium growing from the perichætium *ch* (after Schimper).

2. The **Andreæaceæ**[1] are small cespitose Mosses which are very leafy and much branched; their very shortly stalked theca is elevated, as in Sphagnum, above the perichætium on a leafless pseudopodium. The long apiculate theca raises up the calyptra in the form of a pointed cap, as in the true Mosses, while the short seta remains buried in the vaginula. The body of the young sporogonium becomes differentiated into a parietal tissue consisting of several layers which surrounds the simple layer of the spore-mother-cells without any intermediate cavity, and a central mass of tissue, the columella; in the same manner as in the Sphagnaceæ the layer of cells which produces the spores is bell-shaped and closed above, the columella terminating beneath it. The ripe theca does not open by an operculum, but by four longitudinal slits at the sides; four valves are thus formed united at the apex and at the base, which are closed in damp, but open in dry weather.

3. The **Phascaceæ** are small Mosses, the short stems remaining attached to the protonema until the spores are ripe; they may be considered as the lowest form of the following group, to which the genus Phascum forms the transition. They are, however,

[1] J. Kühn, Zur Entwickelungsgeschichte der Andreæceen. Leipzig 1870.

all distinguished by their theca not opening by an operculum, but allowing the escape of the spores only by its decay. While in the genera Phascum and Ephemerum[1] the internal differentiation of the theca corresponds essentially to that of true Mosses, although more simple, the genus Archidium displays a more considerable deviation, and as an interesting transitional form may be examined a little more closely[2]. The very short pedicel of the sporogonium swells, as in Sphagnum and Hepaticæ; the roundish theca ruptures the calyptra laterally, without raising it up as a cap. Archidium agrees with the true Mosses in the formation in the theca of an intercellular space running parallel to its lateral surface, which separates the wall from the inner mass of tissue. The latter appears as a column continuous at the foot and apex with the wall of the theca. But while in the true Mosses a layer of cells parallel to this intercellular space produces the spore-mother-cells, it is here only a single cell lying eccentrically in the inner mass of tissue that becomes the primary mother-cell of all

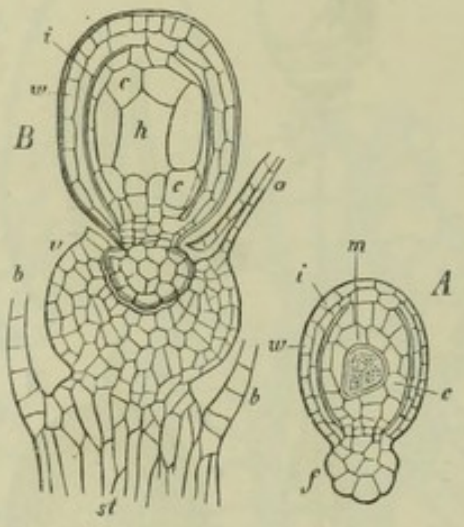

FIG. 243.—*Archidium phascoides*; *A* longitudinal section of the young sporogonium, showing the mother-cell *m* of the spores; *B* longitudinal section through the young sporogonium withits calyptra and vaginula, *f* base of the sporogonium, *w* wall of the theca, *i* intercellular space, *c* columella, *h* hollow out of which the spore-mother-cells have fallen, *v* vaginula, *st* stem, *b* leaves, *a* neck of the archegonium. After Hofmeister (×200).

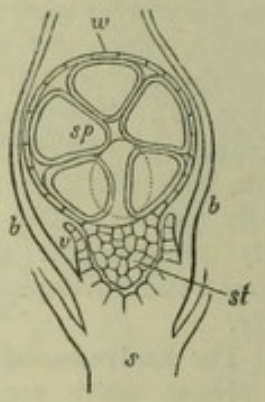

FIG. 244.—*Archidium phascoides*; longitudinal section through a nearly ripe sporogonium, *w* its wall, *sp* its spores, *v* the vaginula, *b* leaves of the stem. After Hofmeister (×100).

the spores (Fig. 243, *A*). It swells considerably, and supplants the other cells, until it lies free in the hollow of the theca; it then divides into four cells, each of which produces four spores. The wall of the primary mother-cell remains entire, while the sixteen spores grow, and fill up the whole of the theca, the inner cell-layer of which is also absorbed (Fig. 244).

4. In the **Bryaceæ** or True Mosses the sporogonium is always stalked, and the pedicel is usually of considerable length. The pedicel (*Seta*) is cylindrical, obtusely pointed below, and firmly implanted in the vaginula; the theca always opens by the detachment of its upper part as a lid (*Operculum*); the operculum is either simply and smoothly detached from the lower part of the theca, or a layer of epidermal cells termed the *Annulus* is thrown off in consequence of the swelling of their inner walls, and the operculum in this way separated from the theca. Most commonly, after the operculum has fallen off, the margin of the theca appears furnished with appendages of very regular and elegant form arranged in one or two rows; the separate append-

[1] J. Müller, in Jahrbuch für wiss. Bot. 1867, vol. VI. p. 237.
[2] Hofmeister, in Bericht der königl. Sächsisch. Gesellsch. der Wiss. 1854, April 22.

ages are termed *Teeth* or *Cilia*, the whole together the *Peristome*; if the peristome is wanting, the theca is said to be gymnostomous. The theca is at first a solid homogeneous mass of tissue; the differentiation of its interior begins with the formation of an annular intercellular space which separates off the wall of the theca consisting of several layers of cells; but the wall remains attached above and below to the columella. The intercellular space is traversed by rows of cells which stretch across from the wall of the theca to the inner mass of tissue; they resemble most nearly protonemal filaments, or those of Algæ, but have been formed by simple differentiation of the tissue of the theca. They contain grains of chlorophyll like the inner cell-layers of the wall. The outer layer of the wall of the theca is developed into a very characteristic epidermis strongly cuticularised externally. The third or fourth layer of cells of the inner mass of tissue, which is thus separated from the annular air-cavity by two or three layers of cells (forming the spore-sac), produces the mother-cells of the spores. They are first of all distinguished by being densely filled with protoplasm, in which

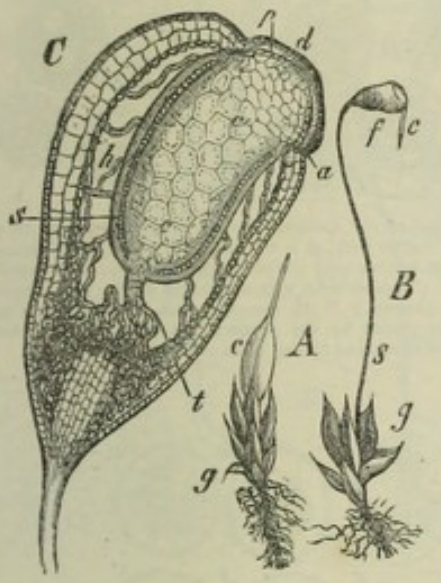

FIG. 245.—*Funaria hygrometrica*; *A* a young leafy plant *g* with the calyptra *c*; *B* a plant *g* with the nearly ripe sporogonium, *s* its seta, *f* the theca, *c* the calyptra; *C* longitudinal section of the theca bisecting it symmetrically; *d* operculum, *a* annulus, *p* peristome, *c c'* columella, *h* air-cavity, *s* the primary mother-cells of the spores.

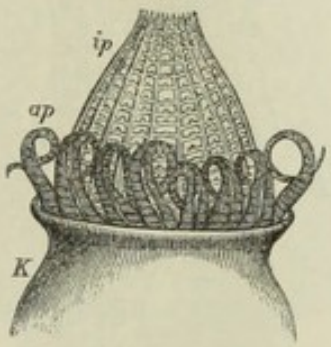

FIG. 246.—Mouth of the theca of *Fontinalis antipyretica*; *ap* outer peristome, *i* inner peristome. After Schimper (×50).

lies a large central nucleus, and are attached without interstices to the surrounding tissue in a parenchymatous manner. From their division proceed the spore-mother-cells, which are isolated by the deliquescence of the cell-walls, and then swim in the fluid contained in the spore-sac, till they form the spores by repeated division. The *Spore-sac* is the term given to those layers of cells by which the large air-cavity is separated from the spore-mother-cells. It seems convenient to consider the layers which bound the spore-cavity on the axial side (Fig. 247, *i*) also as a part of the spore-sac; its cells contain on both sides starch-forming grains of chlorophyll. The inner large-celled tissue, which contains but little chlorophyll, and is thus surrounded on all sides by the spore-sac, is distinguished as the *Columella*. The spore-sac is ruptured by the casting off of the operculum, but the columella remains dried up, and in Polytrichum there remains also a layer of cells, the *Epiphragm*, attached to the points of the teeth of the peristome, and covering the opening of the theca.

We must now examine somewhat more closely the origin of the Peristome. In those genera which, like Gymnostomum, do not form a peristome, the parenchyma which fills up the inner space of the operculum is homogeneous and thin-walled; when

the theca is ripe, it contracts and dries up at the bottom of the operculum, which is formed essentially only of the epidermis; or it remains attached to the columella and forms a thickening at its summit, which projects over the opening of the theca; or again it forms a kind of diaphragm, which closes the mouth of the theca after the casting off of the operculum (Hymenostomum). The transition to the genera provided with a true peristome is furnished by Tetraphis. In this genus the firm epidermis of the upper conical part of the theca falls off as the operculum, while the whole of the internal tissue of the operculum, the two outer layers of which are thick-walled, splits across into

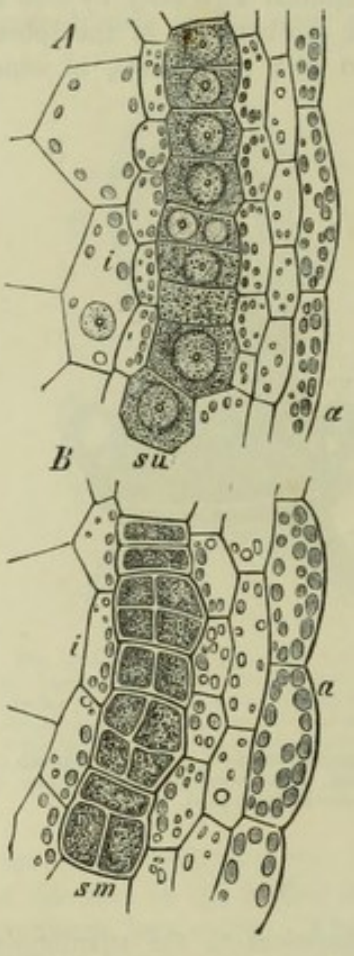

FIG. 247.—*Funaria hygrometrica* transverse section through the spore-sac; *A*, *su* the primary mother-cells; *B*, *sm* the spore-mother-cells not yet isolated; *a* outer side, *i* inner side of the spore-sac (×550).

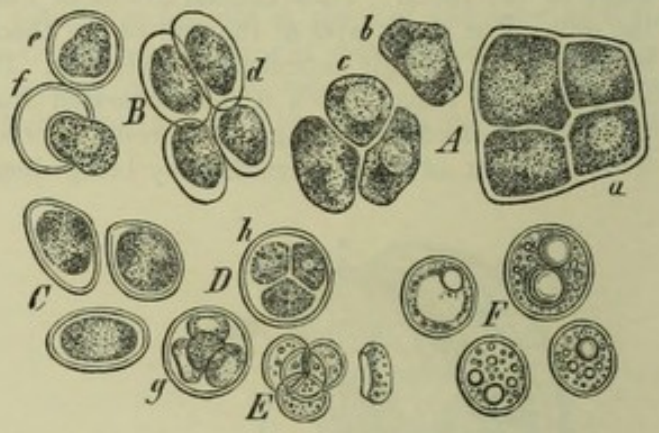

FIG. 248.—Development of the spores of *Funaria hygrometrica* observed in very thin glycerine; *A* mother-cells, at *a* still united, at *b* and *c* the separation has commenced; *B* isolated mother-cells clothed with cell-walls; at *f* expelling the protoplasmic contents; *C* mother-cells with indication of the commencement of the bipartition of the contents; *D* the contents have divided into four lumps of protoplasm, still surrounded by the primary cell-wall, but they themselves are naked; *E* the spores enveloped by cell-walls; *F* ripe spores (×550).

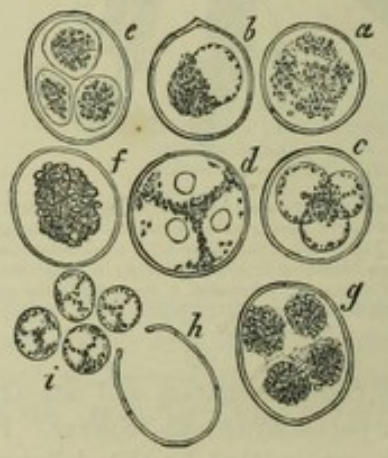

FIG. 249.—Various states of division of the mother-cells of the spores of *Funaria hygrometrica*, observed in water, the progress of development indicated by the letters *a*—*i*.

four valves. These are also termed by systematists a peristome, although their origin and structure are widely different from that of the true peristome in other genera. For, except in the Polytrichaceæ, neither the teeth nor the cilia consist of cellular tissue, but only of thickened and hardened parts of the walls of a layer of cells, which is separated by some layers of thin-walled cells from the epidermis which forms the operculum; the latter layers, as well as the delicate parts of the former, becoming ruptured and disappearing, while the thickened parts of the wall remain after the casting off of the operculum. This will be rendered clear by an example. Fig. 250 represents a part of the longitudinal section which bisects the theca of *Funaria*

hygrometrica symmetrically, corresponding to the part in Fig. 245, *C*, designated *a*; *e e* is the reddish-brown epidermis strongly thickened on the outside; at the part where it bulges its cells are of a peculiar shape, forming the ring or annulus; *se* is the tissue

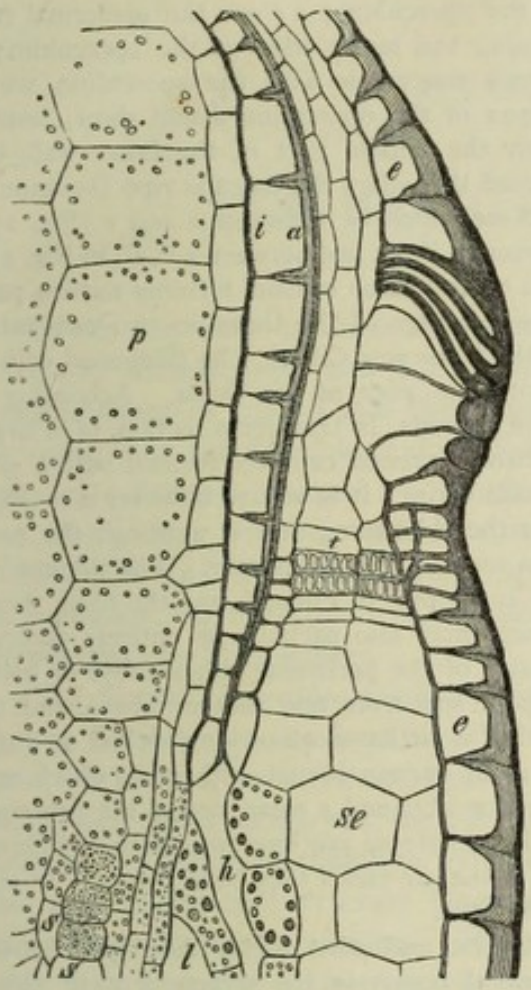

FIG 250.—*Funaria hygrometrica*; part of a longitudinal section of an unripe theca.

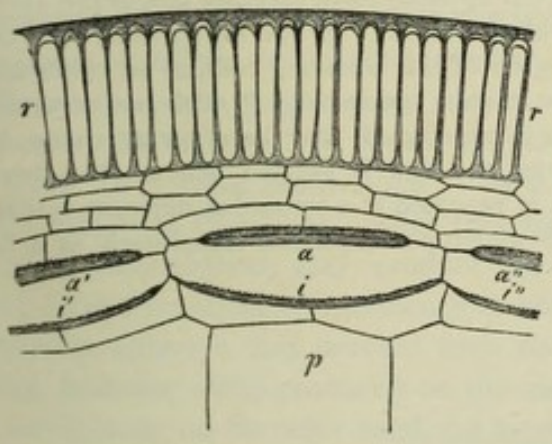

FIG. 251.—*Funaria hygrometrica*; part of a transverse section through the operculum.

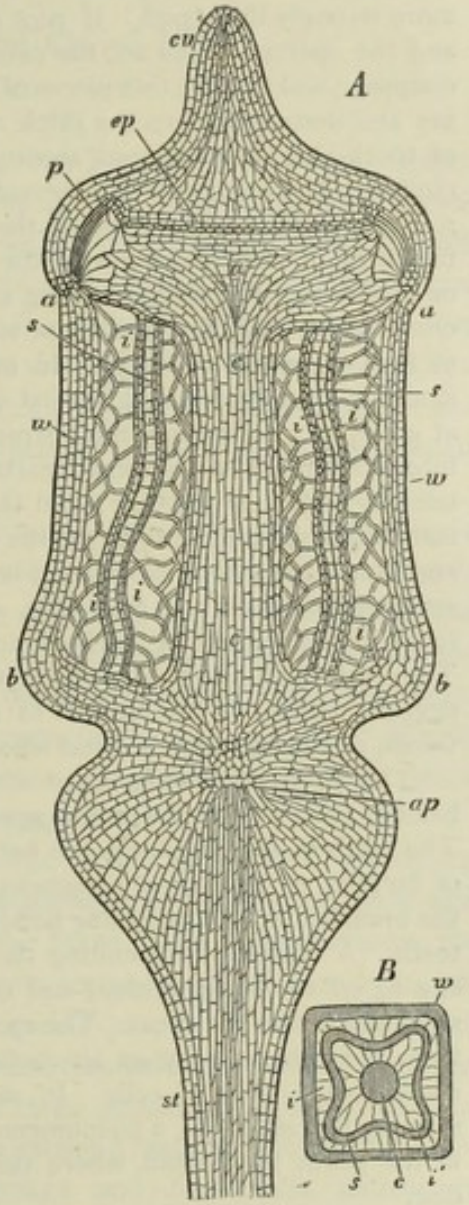

FIG. 252.—*A* longitudinal section of the theca of *Polytrichum piliferum* (after Lantzius-Beninga, ×15); *B* the transverse section (× about 5); *w* wall of the theca, *cu* operculum, *c c* columella, *p* peristome, *ep* epiphragm, *a a* annulus, *i i* the air-cavities penetrated by alga-like cellular filaments, *s* spore-sac, containing the primary mother-cells of the spores, *st* the seta, the upper part of which forms the apophysis *ap*.

lying between the epidermis of the theca and the air-cavity *h*; the large-celled tissue *p* is the prolongation of the columella within the cavity of the operculum; at *S* are seen the uppermost spore-mother-cells; directly above the air-cavity *h* rises the layer of cells

which forms the peristome; its walls (*a*), which face outwards, are strongly thickened, and of a bright red colour; the thickening is continued also partially along the septa; the longitudinal walls which lie on the axial side of the same layer of cells (*i*) are also coloured, but less strongly thickened. In Fig. 251 is shown further a part of the transverse section through the basal part of the operculum; *r r* are the epidermal cells placed immediately above the annulus, forming the lower edge of the operculum; *a* and *i* the thickened parts of the layer of cells concentric with the operculum, which form the peristome. A section near the apex of the operculum would show, instead of the broad thickening-masses *i*, *i'*, *i''*, only the middle part of the inner wall, but more strongly thickened. If now it is supposed that when the theca is ripe the annulus and the operculum fall off, the cells *p* and those which lie between *a* and *e* (Fig. 250) disappear, and that the thin pieces of wall between *a*, *a'*, *a''*, and between *i*, *i'*, *i''*, in Fig. 251, are also destroyed, then the thick red pieces of wall alone remain, forming sixteen pairs of tooth-like lobes pointed above, crowning the edge of the theca in two concentric circles. The outer row are termed Teeth, the inner row Cilia. The thickened cells at *t*, Fig. 250, unite the base of the teeth with the edge of the theca. According as the layer of cells which forms the peristome consists, in transverse section, of a larger or smaller number, and according as one or two thickened cells are formed within each one of these cells, the number of teeth and cilia varies; it is always however a multiple of four, generally 16 or 32. In many cases the thickening at *i* is wanting; the peristome is then simple, and formed only of the teeth of the outer row. The thickenings at *a* are very commonly much stronger than is the case in Funaria, and the teeth therefore stouter. The thickened parts of the wall may also partially or entirely coalesce laterally with one another; and then the parts of the peristome either above or below form a membrane; in this case the teeth appear split from one another above, and the endostome (the inner peristome) is composed of a lattice-work of longitudinal or transverse ridges instead of cilia (Fig. 246). A great variety is met with here, which may easily be understood by the beginner when he has obtained a clear idea of the principle. The inner and outer sides of the teeth of the peristome are hygroscopic to a different degree; hence, as the amount of moisture in the air varies they bend inwards or outwards, or sometimes in a spiral whorl, as in Barbula.

The genus Polytrichum, to which the largest and most highly developed Mosses belong, differs from the other genera in several points in the structure of its theca. The teeth of the peristome are composed not simply of single pieces of membrane, but of bundles of thickened prosenchymatous cells; these bundles are horseshoe-shaped; the branches of two adjoining bundles directed upwards form together one of the 32–64 teeth. A layer of cells uniting the points of the teeth (Fig. 252, *ep*) remains, after the casting off of the operculum and the drying up of the adjoining cells, as an epiphragm stretched across the theca. The spore-sac is, in some species (*e.g. P. piliferum*), separated from the columella by an air-cavity, which is penetrated, like the outer air-cavity, by conferva-like rows of cells. In most species the seta is swollen beneath the theca, forming the *Apophysis*, a phenomenon which is repeated in a somewhat different manner in the genus Splachnum, where this part is sometimes expanded transversely as a flat disc.

GROUP IV.

VASCULAR CRYPTOGAMS.

Under this term are included in one group the Ferns, Equisetaceæ, Ophioglossaceæ, Rhizocarpeæ, and Lycopodiaceæ. As in the Muscineæ, the process of development is divided into two generations which are extremely different both morphologically and physiologically. From the spore proceeds first of all a sexual generation; from its fertilised archegonium is produced in the second place a new plant, which does not form sexual organs, but in their place a number of spores. In the Ferns and Equisetaceæ these spores are all alike; the Rhizocarpeæ and Lycopodiaceæ, on the contrary, produce two kinds of spores, large and small, Macrospores and Microspores.

The *Sexual Generation* which is developed from the spore always preserves, in Vascular Cryptogams, the form of a thallus; it never attains, as in the more highly developed Mosses, to a differentiation into stem and leaf, but remains small and delicate, and closes its life with the commencement of the development of the second generation. It appears, therefore, externally as a mere precursor of further development, as a transitional structure between the germinating spore and the variously differentiated second generation. Hence the name *Prothallium* has been given to this first or sexual generation of Vascular Cryptogams.

If now the five classes are considered in the order mentioned above, the remarkable fact appears—and it is one of great importance in comparing them with the group that follows—that, in proceeding from the Ferns to the Lycopodiaceæ, the development of the prothallium becomes continually simpler and its morphological differentiation less pronounced. In the Ferns and Equisetaceæ the prothallium resembles the thallus of the lowest Hepaticæ. These prothallia sometimes continue to grow for a considerable time; they contain a large amount of chlorophyll, and form numerous root-hairs. After they have thus attained sufficient vigour by independent nourishment, they produce the Archegonia and Antheridia, usually in considerable numbers. A tendency to become diœcious is then manifested in these prothallia, although they proceed from similar spores; both kinds of sexual organs being, however, often produced on the same prothallium. In the Rhizocarpeæ and Lycopodiaceæ, on the other hand, the separation of the sexes is already prefigured by the two kinds of spores, the Macrospores being female, in so far as they develope a very small prothallium, which produces exclusively archegonia, or sometimes only a single one. The female prothallium of the Rhizocarpeæ is a small appendage of the macrospore, formed in its interior but afterwards developed externally although nourished by it; in Selaginella and Isoëtes, which belong to the

Lycopodiaceæ, the prothallium is developed in the spore itself, filling it up with a mass of tissue, the archegonia becoming exposed only by the splitting of the cell-wall of the spore. The microspores of this section produce the antherozoids after a previous endogenous formation of cells, which must be regarded as a rudimentary prothallium.

The *Archegonia* of Vascular Cryptogams are, like those of the Muscineæ, masses of tissue, consisting of a ventral part which encloses the oosphere, and of a neck, usually short and composed of four longitudinal rows. The two groups differ in the fact that in Vascular Cryptogams the tissue of the wall of the ventral part is formed from the prothallium itself; and the ventral part of the archegonium is therefore enclosed in the tissue of the sexual generation, the neck only projecting beyond it. The neck and central cell arise from an epidermal cell of the prothallum; the protoplasm of the central cell divides in this case also into two unequal portions; the lower larger one becomes by rejuvenescence the oosphere, while the upper small portion, the canal-cell, penetrates between the rows of cells of the neck and becomes converted into mucilage (after having, in the case of Ferns, produced, according to Strasburger, at least an indication of an axial row of cells). The mucilage thus produced in the neck finally swells up considerably, drives apart the four apical cells of the neck, and is expelled; an open canal is thus formed, leading from without to the oosphere; the expelled mucilage appears to play an important part in the conduction of the 'swarming' antherozoids to the opening of the neck. Fertilisation is always effected by means of water, which determines the opening of the antheridia and archegonia, and serves as a vehicle for the antherozoids. The advance of these latter as far as the oosphere, and even their entrance into and coalescence with its protoplasm, has been directly observed in the different groups.

The *Antherozoids* are, like those of the Muscineæ, spirally coiled threads usually with a number of fine cilia on the anterior coils. In the cases hitherto observed they arise from the peripheral part of the protoplasm of their small mother-cells, a central vesicle of protoplasm, containing starch-grains, remaining behind, which, adhering to a posterior coil of the antherozoid, is often dragged along by it, but is detached before its entry into the archegonium. The mother-cells of the antherozoids arise, in Ferns and Equisetaceæ, in the antheridia, which project free from the prothallium as roundish masses of tissue; but in the Ophioglossaceæ are imbedded in the prothallium. Among Rhizocarpeæ, Salvinia forms a very simple antheridium proceeding from the microspore, while the Marsileaceæ and Selaginelleæ produce their antherozoids within the microspore itself; but in the latter only after a few-celled mass of tissue has been formed in it which must be considered as a rudimentary prothallium (Millardet).

The Asexual Generation which produces Spores arises from the oospore or fertilised oosphere in the archegonium. In Ferns, Equisetaceæ, and Rhizocarpeæ, its earliest divisions, the rudiments of the first root, the first leaf, and the apex of the stem, can be recognised, while at the same time a lateral outgrowth of its tissue, called the Foot, commences at the bottom of the ventral part of the archegonium, and draws from the prothallium the first nourishment for the young plant. The ventral part of the archegonium at first grows vigorously (except apparently

in the Selaginelleæ), enveloping the embryo, until this latter finally protrudes free, leaving, however, for some time, the foot still attached to it as a nutritive organ. This process offers an unquestionable analogy to the formation of the calyptra of the Muscineæ. While, however, the spore-producing generation of the Muscineæ remains a mere appendage of the sexual plant, appearing, in a certain sense, as its fruit, the corresponding generation of Vascular Cryptogams developes, on the contrary, into a conspicuous, highly organised, independent plant, which frees itself at a very early period from the prothallium, and obtains its own nourishment. It is this asexual generation which is called, in ordinary language, simply the Fern, Equisetum, &c.; it always consists of a leafy stem, usually producing a number of true roots; roots may, however, occasionally be entirely absent, as in some species of Hymenophyllum, and in Psilotum and Salvinia. In many cases, especially in Ferns, Equisetaceæ, and (especially the extinct) Lycopodiaceæ, the spore-producing generation attains great dimensions with an unlimited term of life; only a few species are (like Salvinia) annual.

The *Leaves* are either simple, unsegmented, or variously branched (Ferns, Ophioglossaceæ). There does not, however, occur so great a variety in the forms assumed by the leaves in the same plant due to metamorphosis as in Phanerogams.

The *Roots* usually arise in acropetal succession on the stem (or on the leaf-stalk in some Ferns), and branch monopodially or dichotomously; they always remain nearly uniform in size, the first root never attaining the dimensions of a tap-root, as in many Phanerogams.

The *Differentiation of the Systems of Tissue* attains a high degree of perfection for the first time in this group of plants. The epidermis, fundamental tissue, and fibro-vascular bundles are always clearly distinct, and are composed of cells of various forms. The fibro-vascular bundles are closed; their phloëm usually surrounds the xylem of each separate bundle like a sheath.

The *Branching of the Stem* is very different in the different classes of Vascular Cryptogams, and will be considered hereafter; it may be remarked here that axillary branching probably does not occur in the same sense in which the term is applied to Phanerogams.

The *Production of the Sporangia* is, in most cases, evidently a function of the leaves; in a few cases (as Pilularia) this mode of origin is, however, still doubtful. In their form and mode of envelopment by neighbouring organs the sporangia show considerable differences; but within each class their characters are very constant.

It is clear from what has now been said that the sporangium of Vascular Cryptogams is equivalent, from a physiological but not from a morphological point of view, to the sporogonium of Mosses. This latter forms by itself the whole of the asexual generation of Mosses; while the sporangium of Vascular Cryptogams is a relatively small outgrowth of a foliar structure of the asexual generation which consists of stem, leaf, and root. The mode of origin of the mother-cells of the spores is also different from that in the Muscineæ, though the spores themselves are produced in the mother-cells in a manner more like that which occurs in Muscineæ. The spore-mother-cells of Vascular Cryptogams also become isolated from their combination into a tissue, and divide into four spores, an indication of a division into two generally preceding that into four. The distinction between

macrospores and microspores in the Lycopodiaceæ and Rhizocarpeæ is manifested only after the division into four of the mother-cells, which were previously alike in the case of both kinds of spores.

Vascular Cryptogams form a group connected with one another by very obvious bonds of relationship, but may be divided into five parallel and diverging series or classes. In the formation of a prothallium the Ferns and Equisetaceæ show a marked affinity with the lowest stages of development of the Muscineæ. The Rhizocarpeæ and Lycopodiaceæ diverge in this respect greatly from these classes, and in their mode of sexual reproduction form a transition to Phanerogams,—from Spore-plants to Seed-plants, as will be shown when treating of the general characteristics of the latter.

The proof that what is termed the Moss-fruit, *i. e.* the sporogonium, is, from its position in the alternation of generations, the equivalent of the entire leafy and rooting spore-producing plant of Vascular Cryptogams, was brought forward by Hofmeister as long ago as 1851 (Vergleichende Untersuchungen, p. 139[1]). In connexion with the relationships pointed out by him between the Lycopodiaceæ and Coniferæ, this discovery is one of the most fertile in results that has ever been made in the domain of morphology and classification. The researches of Pringsheim and Hanstein on the development of Rhizocarps, carried out with great acuteness and deep penetration, those of Nägeli and Leitgeb on the roots of Vascular Cryptogams, and of Cramer on the apical growth of the stem of Equisetaceæ and Lycopodiaceæ (with which the more recent labours of Rees made under Nägeli's superintendence agree), have not only contributed to a more accurate knowledge of this group of plants, but have especially cleared up the fundamental morphological facts. Since the appearance of the first edition of this book, our knowledge of the alternation of generations has been enriched by Millardet's discovery of the male prothallium in Selaginella; and the labours of Millardet, Strasburger, and Kny have resulted in a more complete acquaintance with the development of the sexual organs and of the process of fertilisation itself in its details.

The following systematic review will serve as a preliminary introduction to the group of Vascular Cryptogams:—

The sexual generation is developed from the spore, and is a thalloid structure of small size; the archegonia have their ventral part imbedded in this prothallium; the antherozoids are spirally-coiled threads, generally furnished with a number of cilia at their anterior pointed end. The asexual generation, resulting from the fertilisation of the oosphere in the archegonium, produces the spores, and is differentiated into stem, leaves, and roots. The branching of the stem is not axillary; its tissue is differentiated into epidermis, fundamental tissue, and closed fibro-vascular bundles; the sporangia are products of the leaves; the mother-cells of the spores arise from a central cell or from a mass of sporangial tissue, and form the spores by division into fours after previously showing a tendency towards bipartition.

I. Isosporous Vascular Cryptogams.

Only one kind of spore is produced; the prothallium vegetates for a considerable time independently of the spore, and produces antheridia and archegonia.

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[1] [On the Germination, Development, and Fructification of the Higher Cryptogamia, and on the Fructification of the Coniferæ, by W. Hofmeister; translated by F. Currey; Ray Soc. 1862, p. 434.]

(1) *Filices* or *Ferns*. Prothallium above-ground, green, monœcious; branching of the stem probably at first dichotomous; exogenous adventitious buds formed on the leaves; the sporangia are trichomes of the leaves, which are stalked, usually large and branched, and are characterised by the long continuance of their apical growth.

(2) *Equisetaceæ*. Prothallium above-ground, green, monœcious or diœcious; branching of the stem exclusively by endogenous verticillate lateral buds; leaves very simple, verticillate, forming sheaths; the sporangia are produced in groups on the margin of metamorphosed leaves, and constitute a terminal fructification.

(3) *Ophioglossaceæ*. Prothallium underground in the two known cases, not green, monœcious; the stem has apparently no provision for branching; the leaves have a stalked lamina and a sheathing base; the sporangia are produced on a branch of the leaf, and constitute a spike or panicle.

II. Heterosporous Vascular Cryptogams.

Macrospores and microspores are produced; the macrospore produces the female prothallium and nourishes it, the prothallium never becoming independent; the microspores produce a rudimentary prothallium which does not become free, and in which the antherozoids are formed.

(4) *Rhizocarpeæ*. The female prothallium protrudes from the cavity of the spore, and remains attached by its lower side to the macrospore; its size is less than that of the spore; the sporangia are produced in numbers in the interior of hollow receptacles (sporocarps), and produce either a single macrospore or a number of microspores; the sporocarps are appendages of the leaves.

(5) *Lycopodiaceæ*. Macrospores are known to occur only in two sections, the Selaginelleæ and Isoëteæ; the prothallium in these cases fills the cavity of the macrospore, and only the part which bears the archegonia protrudes; the terminal branching of the stem is dichotomous, or there is no provision for branching (Isoëtes); the sporangia are produced singly on the upper side of the leaves near their base; the macrosporangia produce a few macrospores, the microsporangia a large number of microspores.

CLASS VI.

FERNS[1].

The Sexual Generation or Prothallium is a thalloid structure containing chlorophyll and obtaining its nourishment independently; its development presents striking resemblances to that of the simpler Hepaticæ, and to a certain extent even to the formation of the pro-embryo of some Mosses. It produces simple tubular unarticulated root-hairs, and finally antheridia and archegonia. Its development and the duration of its life may embrace a considerable space of time, especially when the archegonia are not fertilised.

When the spores germinate, which usually does not take place till a considerable time after dissemination (but in Osmunda after only a few days) the cuticularised exospore, generally provided with ridges, bosses, spines, or granulations, splits along its edges; the endospore, which now protrudes and is not unfrequently already divided by septa, produces the prothallium, either immediately, as in Osmunda, or after the preliminary formation of a filamentous pro-embryo, which presents in Hymenophyllaceæ certain resemblances to that of the Andreæaceæ and of Tetraphis among Mosses. The development of the prothallium has been more exactly investigated only in the Hymenophyllaceæ, the Polypodiaceæ, and also in Osmunda and Aneimia; and the considerable differences which have thus been established necessitate separate descriptions.

In the Hymenophyllaceæ the contents of the spore are divided, even before germination, into three cells meeting in the centre; in some species of Trichomanes small cells are cut off at three points of the circumference, while a large central

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[1] H. von Mohl, Ueber den Bau des Stammes der Baumfarne (Verm. Schriften, p. 108).—Hofmeister, Ueber Entwickelung und Bau der Vegetationsorgane der Farne (Abhandlungen der königl. Sächs. Gesells. der Wissen. 1857, vol. V).—Ditto, Ueber die Verzweigung der Farne (Jahrb. für wissen. Bot. vol. III. p. 278).—Mettenius, Filices Hort. Bot. Lipsiensis (Leipzig 1856).—Ditto, Ueber die Hymenophyllaceen (Abhandlungen der königl. Sächs. Ges. der Wissen. 1864, vol. VII).—Wigand, Botanische Untersuchungen (Braunschweig 1854).—[On the Germination, Development, and Fructification of the Higher Cryptogamia, &c. Ray Society, 1862, pp. 128-266.]—Dippel, Ueber den Bau der Fibrovasalstränge in the Berichte deutscher Naturforscher u. Aerzte in Giessen, 1865, p. 142.—Rees, Entwickelung des Polypodiaceensporangiums (Jahrb. für wissen. Bot. 1866, vol. V. p. 5).—Strasburger, Befruchtung der Farnkräuter (Jahrb. für wissen. Bot. 1869, vol. VII, p. 390).—Kny, Ueber Entwickelung des Prothalliums und der Geschlechtsorgane, in the Sitzungsberichte der Gesellschaft naturforschender Freunde in Berlin, Jan. 21 and Nov. 17, 1868.—Kny, Ueber Bau und Entwickelung des Farnantheridiums (Monatsberichte der kais. Akad. der Wissen. Berlin, May 1869).—Kny, Beiträge zur Entwickelungsgeschichte der Farnkräuter (Jahrb. für wissen. Bot. vol. VII. p. 1).

cell remains undivided. The cells develope into germinating filaments, bursting the exospore in three directions; these filaments then grow at their apex, and become segmented by septa; only one of them however generally attains a more decided development, the others soon assuming the form of hairs. In *Hymenophyllum tunbridgense* the former frequently developes finally into a cellular plate; but in other species it forms a much-branched conferva-like protonema, on which flat prothallia 2 to 6 lines in length and $\frac{1}{2}$ to $1\frac{1}{2}$ in breadth are formed as lateral shoots. Each cell of the filament may give rise to a branch which is given off behind the anterior septum, and is at once separated by another septum. Some of these branches continue to grow like the mother-shoot indefinitely, others end in becoming hairs; a larger number are transformed into flat prothallia, but most develope into root-hairs. Here and there the rudiment of a filamentous branch becomes converted into an antheridium, or even into an archegonium. At the apex of the flat prothallia spherical cells arise in *Trichomanes incisum* on marginal flask-shaped cells: these must probably be considered as organs of propagation; but the marginal cells of the flat prothallia may develope into root-hairs and new protonemal filaments, and also into new flat shoots. The root-hairs are mostly short, with brown walls, and produce at their end lobed attaching-discs or branching tubes.

In the Polypodiaceæ and Schizæaceæ the endospore developes into a short articulated filamentous pro-embryo, at the end of which, even at an early stage, a more or less considerable increase in breadth takes place; a plate of tissue is thus formed consisting at first of only one layer, which soon assumes a broadly cordate or even reniform shape, and has its growing apex situated in an anterior depression. Its apical cell forms two rows of segments right and left, by walls which are perpendicular to the surface, and from their further divisions the flat tissue is produced. The power of rejuvenescence of the apical cell is, however, limited; it ends in the formation of a septum by which a new apical cell is formed, which then divides by longitudinal walls, and thus forms a row of apical cells lying side by side which occupies the bottom of the depression of the prothallium-disc, in the same manner as in the thallus of Pellia. The root-hairs are all lateral structures, springing in large numbers from the under-side of the posterior part of the prothallium; among them are the antheridia, which in this case are only rarely marginal. The archegonia are also produced on the under-side, but on a cushion behind the anterior depression formed of several layers; in Ceratopteris several cushions are formed bearing archegonia.

Osmunda (examined minutely by Kny, and compared with the preceding, *l. c.*) is distinguished in the first place from the Polypodiaceæ and Schizæaceæ by the absence of the pro-embryo. The endospore undergoes divisions at the very commencement of germination, which form a plate of tissue of which a posterior cell is converted, as in Equisetaceæ, into the first root-hair. The succeeding root-hairs arise from marginal cells and on the under-side of superficial cells of the prothallium, the apical growth of which follows a similar course to that of Polypodiaceæ. The mid-rib consisting of several layers is characteristic of Osmunda, penetrating the ribbon-like prothallium from the posterior end to the apex, and producing a large number of archegonia on both sides. The antheridia spring partly from the margin, partly from the lower surface with the exception of the mid-rib.

Like many thalloid Hepaticæ, the prothallia of Ferns also produce adventitious shoots from single marginal cells; this happens with especial profusion in Osmunda, where the adventitious shoots become detached, and play the part of vegetative organs of reproduction.

The prothallia show a tendency to be diœcious, which is manifested in the fact that all the spores from a sporangium sometimes produce prothallia bearing antheridia only (as in *Osmunda regalis*); while in other cases the archegonia appear later and in smaller numbers, and are fertilised by the antheridia of younger prothallia.

The *Antheridia* are, speaking morphologically, trichomes; they are produced in the same manner as the root-hairs, as outgrowths of the marginal or superficial cells of the prothallia; in the Hymenophyllaceæ they are also produced on the protonemal filaments. The projection is usually separated from the mother-cell by a septum, and swells up spherically at once or after the formation of a pedicel. In some cases the mother-cells of the antherozoids are formed at once in this globular cell; but it usually undergoes still further divisions[1], in consequence of which the wall of the antheridium consists of a single layer of cells surrounding the central cell. The cells of this wall form grains of chlorophyll on their inner face, while the central cell of the antheridium divides further into the mother-cells of the antherozoids, which, however, are not numerous. The dehiscence of the ripe antheridium is the consequence of a rapid absorption of water in the parietal cells, which swell up violently and compress the contents of the central cell till the antheridium is ruptured at the apex. The antherozoid-cells thus escape, and out of each of them is set free an antherozoid coiled spirally three or four times. The finer anterior end of each antherozoid is provided with a number of cilia; the thicker posterior end often drags with it a vesicle furnished with colourless granules, which subsequently falls off and remains at rest, while the filament alone continues in motion. Strasburger states that this vesicle is formed from a central part of the contents of the mother-cell, the parietal protoplasm of which forms the filament and its cilia. The vesicle is hence properly not a part of the antherozoid; it is only attached to it, and swells up strongly in water by endosmose, as is shown in Fig. 253.

The *Archegonium* arises from a single superficial cell of the prothallium, which is at first only slightly arched and is divided by a wall parallel to the upper surface. The lower of the cells thus formed is the central cell of the archegonium; the upper

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[1] These divisions take place in a very remarkable manner. In the hemispherical mother-cell of the antheridium of *Aneimia hirta*, an arched wall arises, by which it is divided into an inner hemispherical cell, and an outer one which covers the former like a bell; the latter is then split up by a transverse annular wall into an upper lid-like and a lower hollow cylindrical cell. The same thing occurs in Ceratopteris; in other cases, as in *Asplenium alatum*, a funnel-shaped wall is formed in the hemispherical mother-cell of the antheridium, and with the end of the funnel above the wall of the mother-cell; the upper part of this is cut off by a level septum as a covering cell; two, or even three, funnel-shaped walls may be formed in succession, so that the parietal layer of the antheridium consists of two or three superposed funnel-shaped cells and a covering cell (as in Fig. 253). The mode of formation of the antheridium-wall is quite different in Osmunda, where it consists below of two or three cells, upon which rest several of the upper cells which result from the division of the stigmatic cell (Kny, *l. c.*).

and outer one produces by further divisions the neck, which, when mature, consists of four rows of cells meeting in its axis. A layer of cells is formed by division of the cells surrounding the central cell, corresponding to that of the wall of the ventral part of the archegonium of Muscineæ. The further changes which take place within the central cell, and the formation of the canal of the neck, are described by

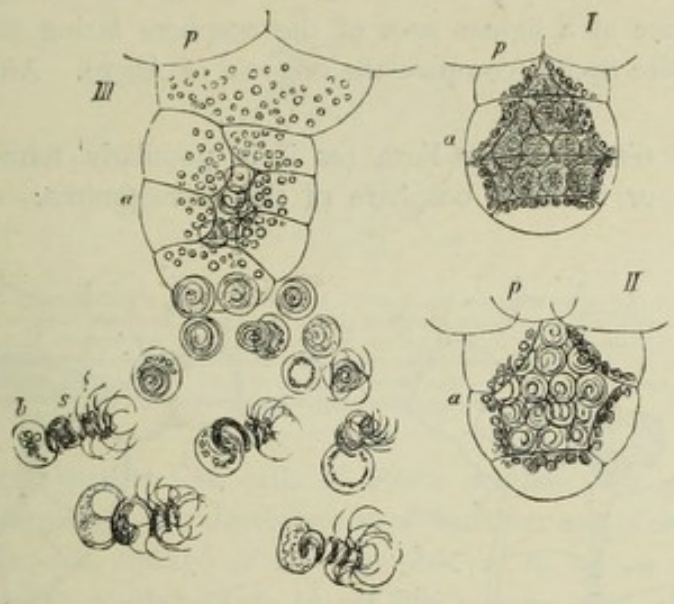

FIG. 253.—Antheridia of *Adiantum Capillus-Veneris* (× 550), in longitudinal optical section; *I* not yet ripe; *II* the antherozoids already mature; *III* the antheridium burst, the parietal cells greatly swollen radially, the antherozoids mostly escaped; *p* prothallium, *a* antheridium, *s* antherozoid, *b* the vesicle containing starch-grains.

Strasburger and Kny in the works already mentioned, in accordance with my earlier observations; so that the drawing, Fig. 255, given in my first edition, can be retained; it is completed by Fig. 254, borrowed from Strasburger, which represents a younger condition of development. The contents of the central cell are divided

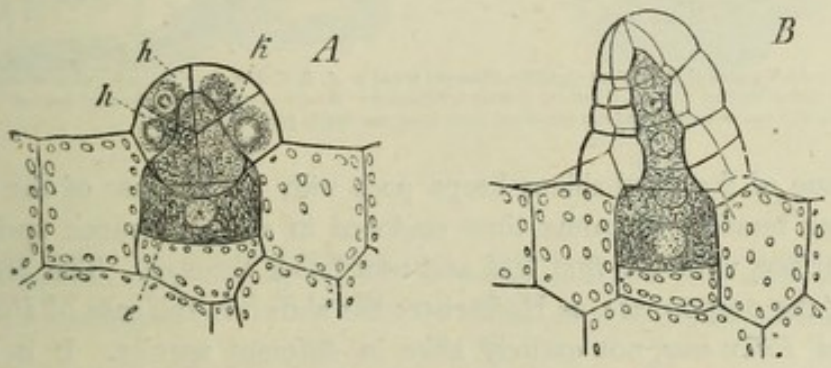

FIG. 254.—Young archegonia of *Pteris serrulata* (after Strasburger); *e* the oosphere, *h h* the neck, *k* the canal-cell.

into two unequal portions; the larger and lower one (Fig. 254, *A*, *e*) is at first broad, almost discoid, and afterwards becomes round; it is the oosphere. The other portion (*k*), which is at first smaller, grows in between the four rows of cells of the neck, forcing them apart; it thus forms a canal filled with mucilaginous protoplasm, in which a row of nuclei arises, but without the corresponding cell-

divisions taking place. The substance of this *Canal-cell*, as it is termed, is finally completely converted into mucilage, swells and forces the apical cells of the neck apart, escapes, and remains collected before the opening of the neck. The antherozoids are retained by this mucilage and collect in large numbers before the archegonium; a number force themselves into the canal of the neck, often finally stopping it up; a few reach the oosphere, force themselves into and disappear in it. The entrance takes place at a lighter spot of the oosphere facing the neck, which is termed the Receptive Spot[1] (compare the oogonia of Algæ). After fertilisation the neck closes.

The Asexual Generation or Fern (as it is popularly termed) is developed from the oospore or fertilised oosphere of the archegonium. At first the sur-

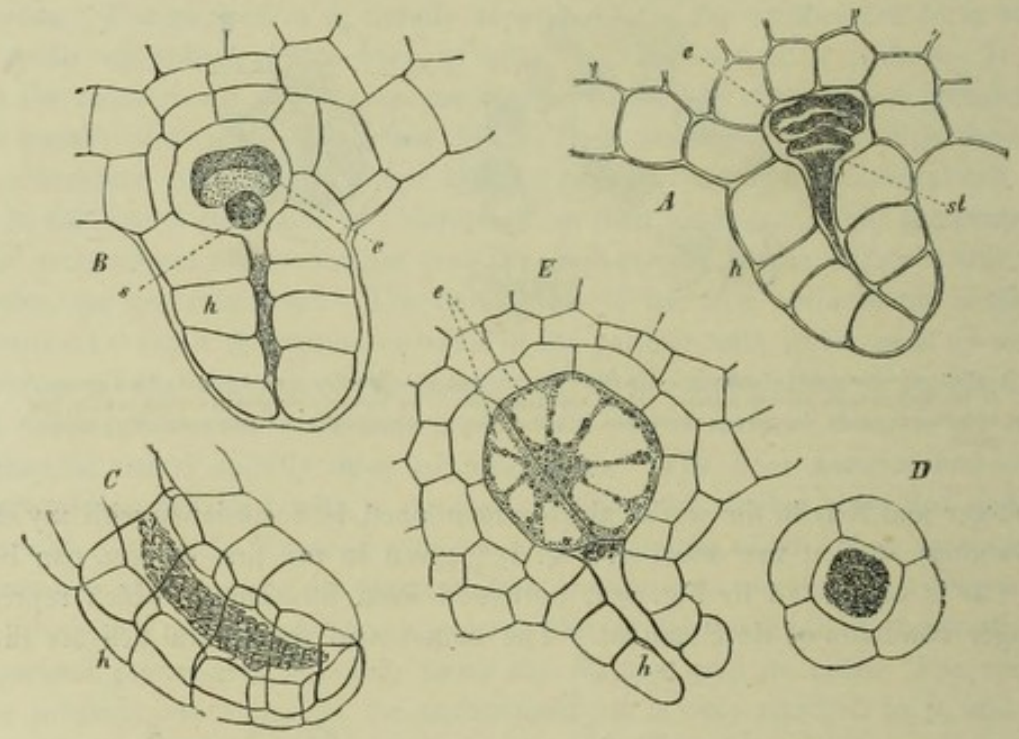

FIG. 255.—Archegonia of *Adiantum Capillus-Veneris* (×800); *A*, *B*, *C*, *E* in longitudinal optical section; *D* in transverse optical section; *A*, *B*, *C* before, *E* after fertilisation; *h* neck of the archegonium, *st* mass of mucilage, *e* oosphere; *E*, *e* the two-celled embryo (observed after lying one day in glycerine).

rounding tissue of the prothallium keeps pace with the increase of the oospore, so that this latter remains for some time enclosed in a protuberance springing from the under surface, until the first leaf and root break through. The first processes of division of the oospore are, as Hofmeister has shown in the case of *Pteris aquilina* and *Aspidium Filix-mas*, not entirely alike in different species. It is certain that the first division-wall of the oospore is transverse to the longitudinal axis of the prothallium, and inclined to it obliquely; as shown in Fig. 255, *E*, its inclination is the same as that of the neck of the archegonium. It is also certain that each

[1] Strasburger states that the act of fertilisation may be observed especially clearly in Ceratopteris; the forcible entrance of the antherozoids as far as the oosphere had previously been seen by Hofmeister.

of the two daughter-cells is at once divided again by transverse septa, so that the segmented oospore or embryo now consists of four cells placed as quadrants of a sphere, and which are bisected by a longitudinal section. In Fig. 256 these first transverse divisions are indicated by thicker lines, the embryo being seen in longitudinal section. The explanation of the figure points out the interpretation which

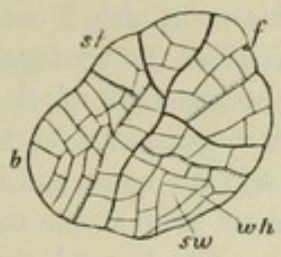

FIG. 256.—Vertical longitudinal section of the embryo of *Pteris aquilina* (after Hofmeister, Entwickelung und Bau der Vegetationsorgane der Farne, p. 607): the thicker lines are sections of the first three division-walls by which the embryo is divided into four cells. The lower anterior cell forms, according to Hofmeister, the leaf *b* at the apex of the stem *st*; from the lower posterior cell is produced the root, *sw* being its apical cell and *wh* its root-cap. In Pteris, the foot *f* is formed from the two upper of the first four cells. In *Aspidium Filix-mas*, the same author states that these processes diverge still further from those in the Rhizocarps.

Hofmeister gives to the first four cells of *Pteris aquilina*, which the reader may compare with the corresponding development of Salvinia and Marsilea; but it must not be forgotten that the embryo of the Fern lies, so to speak, on its back. Although it is impossible in this place to go into a more minute description, it is still necessary at least to point out the resemblance between the embryo of Ferns and that of Rhizocarps.

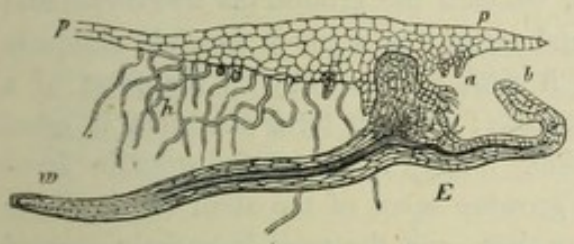

FIG. 257.—*Adiantum Capillus-Veneris*; vertical longitudinal section through the prothallium *pp* and the young Fern *E*; *h* root-hairs, *a* archegonia of the prothallium, *b* the first leaf, *w* the first root of the young plant (×about 10).

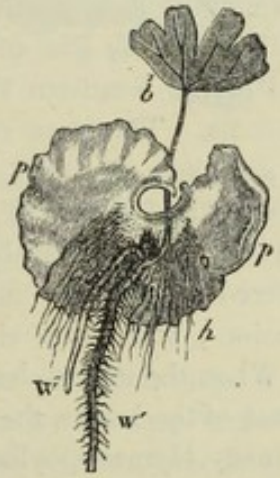

FIG. 258.—*Adiantum Capillus-Veneris*; the prothallium *pp* seen from below with the young Fern attached to it; *b* its first leaf; *w' w''* its first and second roots; *h* root-hairs of the prothallium (×about 30).

If we neglect for the moment the points which are still doubtful in the significance of each of the first four cells of the embryo, it is certain that one of them which is inferior[1] and posterior becomes the mother-cell of the first root, and that the apical cell of the stem lies immediately in front of and above the base of the leaf,

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[1] The terms posterior, anterior, superior, inferior, refer also to the prothallium, the apex of which is turned in front, and its archegonia-bearing surface downwards.

and that the upper part of the embryo between the apex of the stem and the base of the root becomes transformed into a special organ, the Foot, by which the young plant attaches itself to the tissue of the prothallium, in order to draw nourishment from it, while the first roots and leaves are being put out. This foot or apparatus for obtaining nourishment, which I consider a lateral structure, is called by Hofmeister the first axis of growth, or primary axis of the Fern; the leaf-bearing axis arises upon it as a lateral shoot. But on this point also I consider, in opposition to the views of this distinguished morphologist, that the analogy with the processes described by Pringsheim in Salvinia must not be lost sight of; I must refer to the description of the origin of the embryo in the archegonium given under the Rhizocarpeæ.

The first parts of the stem and the roots and leaves, which are now developed in succession from the embryo, are very small, and remain so; those which are formed later are gradually larger. The leaves become constantly more complex in form, and the structure of the stem more intricate as the new additions to it increase in diameter. The first parts of the stem, like the first leaf-stalks, contain each only one axial fibro-vascular bundle; the later ones a larger number. In this manner the Fern continues to gain strength, not by subsequent increase of size of the embryonic structures, but by each successive part attaining a more considerable size and development than the preceding ones; until at length a kind of stationary condition is arrived at in which the newly-formed organs are nearly similar to the preceding ones. The following observations refer especially to this mature condition of Ferns.

The mature Fern is, in some Hymenophyllaceæ, a small delicate plant, not much exceeding in dimensions the larger Muscineæ; in other sections the fully grown plants attain the size of considerable shrubs; some species, natives of the Tropics and of the Southern Hemisphere, assume even a palm-like habit, and are called Tree-ferns. The stem creeps on or beneath the ground (as in Polypodium and *Pteris aquilina*), or climbs up rocks and stems; in some it ascends obliquely (*e.g. Aspidium Filix-mas*); in Tree-ferns it rises up vertically in the form of a column. The roots are usually very numerous; in Tree-ferns the stem is often entirely covered by a dense mantle of them. They arise on the stem in acropetal succession; sometimes close to the growing apex of the stem (as in *Pteris aquilina*). When the internodes remain very short, and the stem is entirely covered with the bases of the leaves, the roots arise, as in *Aspidium Filix-mas*, from the leaf-stalks. In many Hymenophyllaceæ which have no true roots, branches of the stem assume a root-like structure. In creeping and climbing species the leaves are separated by distinct internodes which are sometimes very long; in thick, ascending, and vertical stems, the internodes are usually undeveloped, and the leaves so crowded that no free portion of the stem remains uncovered, or only a very inconsiderable one. The leaves of Ferns are usually characterised by a circinate vernation, and they only unrol in the last stage of their growth; the mid-rib and the lateral veins are curved from behind forwards. The forms of the leaves are among the most perfect in the whole vegetable kingdom; they manifest an enormous variety in their size, the lamina being usually deeply lobed, branched, or pinnate. In comparison with the stem and the slender roots they are mostly very large, and sometimes attain extraordinary dimensions, even a length of from 10 to 20 feet (as in

Pteris aquilina, Cibotium, and Angiopteris). They are always stalked, and continue their growth at the apex for a long time; the leaf-stalks and the lower parts of the lamina are often completely unfolded while the apex is still growing (as in Nephrolepis). This apical growth is not unfrequently interrupted periodically (*vide infra*); in Lygodium the leaf-stalk or the rachis even resembles a twining stem growing for a long period, the pinnæ presenting the appearance of leaves. The amount of metamorphosis of the leaves is, notwithstanding, very inconsiderable; on the same plant the same forms of leaves, mostly foliage-leaves, are constantly repeated; scale-like leaves occur on underground stolons (*e. g.* in *Struthiopteris germanica*), and in many cases the fertile leaves (those which bear sporangia) assume special forms. Such differences as occur in most Phanerogams are not found in the development of the leaves of one plant; *Platycerium alcicorne* must, however, be mentioned, as having the foliage-leaves alternately developed as broad plates closely applied to the supporting surface and as long dichotomously branched ribbon-shaped

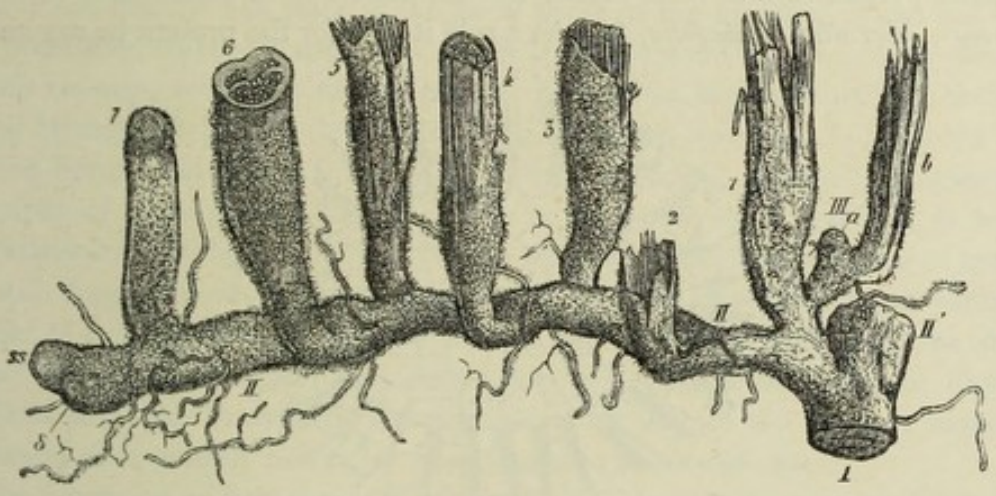

FIG. 259.—*Pteris aquilina*, a part of the underground stem with leaves and bases of the leaf-stalks (reduced about one-half); *I* older portion of the stem bearing the two bifurcations *II* and *II'*, *ss* the apex of the weaker branch *II*; beside it the youngest leaf-rudiment 8; 1-7 the leaves of this branch, one being developed in each year; 1-5 the leaves of earlier years, which have already died off at some distance from the stem; 6 the leaf of the present year with unfolded lamina, the stalk having been cut off; 7 the young leaf for next year; at the apex of the stalk is the lamina still very small and entirely clothed with hairs. The leaf-stalk *I* bears a bud *IIIa*, which has developed a leaf *b* that has already died off. The more slender filaments are roots. All the parts shown in the figure are underground.

erect leaves. Among the various forms of trichomes of Ferns those termed *Paleæ* are especially striking, from their great numbers and from being frequently flat and leaf-like; the younger leaves are generally entirely covered and concealed by them.

After these preliminary particulars, we may now turn to a consideration of the mode of growth of the separate organs.

The growing end of the stem sometimes far outruns the point of attachment of the youngest leaves, and then appears naked, as in *Polypodium vulgare*, *P. sporodocarpum*, and other creeping Ferns, as well as in *Pteris aquilina*, where, according to Hofmeister, it frequently attains in old plants a length of several inches without bearing leaves. Mettenius states that in many Hymenophyllaceæ leafless prolongations of the axis of this kind have been taken for roots. In other cases, on the contrary, especially in Ferns with an erect growth, the increase in length of the stem is much slower, its apex remaining enclosed in a leaf-bud. The stem generally ends in a flat apex; sometimes, as in Pteris, it is even imbedded in a funnel-shaped

elevation of the older tissues (Fig. 261, *E*). The apex of the stem is always occupied by a clearly distinguishable *Apical Cell*, which is either divided by walls alternately inclined, and then resembles, when viewed from above, the transverse section of a biconvex lens; or it is a three-sided pyramid, with a convex anterior surface and three oblique lateral surfaces, which intersect behind. The outlines of the segments, which are in the first case in two, in the second case in three rows, or arranged with more complicated divergences, soon disappear in consequence of numerous cell-divisions and of the displacement caused by the growth of the masses of tissue and leaf-stalks surrounding the apex. The apical cell, for instance, of *Pteris aquilina*, is wedge-shaped, the segments on the horizontal stem forming a right and a left row; the edges of the apical cell face upwards and downwards (Fig. 260). The same is also the case, according to Hofmeister, in *Niphobolus chinensis* and *rupestris*, *Polypodium aureum* and *punctulatum*, and *Platycerium alcicorne*. In *Polypodium vulgare* he states that it is sometimes wedge-shaped, sometimes pyramidal with three faces; the last-named form occurs also in *Aspidium Filix-mas*, *Marattia cicutæfolia*, &c. As a rule it may for the present be assumed that

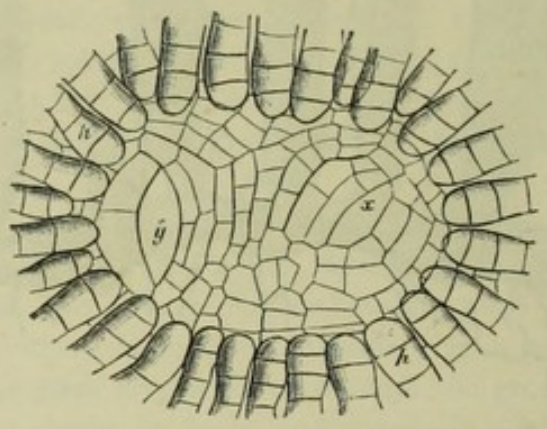

FIG. 260.—Apical view of the end of the stem of *Pteris aquilina*; *y* the apical cell of the stem; *x* the apical cell of the youngest leaf; *h h* hairs which cover the apical region surrounded by a cushion of tissue.

creeping stems with a bilateral development have a wedge-shaped apical cell, upright or ascending stems with radiating rosettes of leaves one that is a three-sided pyramid.

The further relationships of the segments of the apical cell of the stem to the origin of the leaves and to the building up of the tissue of the stem itself, are still but little known in detail. It cannot be doubted that each leaf results from a single segment only, and that this segment-cell is devoted from an early period to the formation of the leaf, but it appears doubtful whether the segments always form leaves, and if not what proportion of sterile segments precedes one from which a leaf is developed.

The phyllotaxis of Ferns sometimes corresponds to the rectilinear arrangement of the segments of the apical cell. Thus the distichous arrangement of the leaves of *Pteris aquilina*, *Niphobolus rupestris*, and of some species of Polypodium, corresponds to the biseriate segmentation of the apical cell of the stem. But where the phyllotaxis is complicated and spiral and the apical cell a three-sided pyramid, as occurs in *Aspidium Filix-mas*, the same processes may take place as in those Mosses

which have their leaves arranged in many rows with a triangular apical cell, such as Polytrichum[1].

The *Terminal Branching* of the stem which occurs in all Ferns Hofmeister considers to be dichotomous. The branches arise very near the end of the stem, and are, at least at first, like the primary stem, so that the branching is a bifurcation. That the branches are independent of the leaves is inferred by this writer from the fact that the ends of the stem of *Pteris aquilina*, which are leafless and often several inches long, regularly fork. These forks are, in this and in many other cases, not axillary; and where, in other Ferns, they appear axillary, we must assume, with Hofmeister, that the forking has taken place immediately in front of a youngest leaf, and that the fork which stands before the leaf developes to a smaller, while the other (a prolongation of the primary stem) does so to a greater extent. Thus, in other words, the apparent axillary branching of some Ferns must be considered as a consequence of the sympodial development of dichotomous ramifications which take place in the plane of insertion of the leaves. The branching at the end of the stem does not usually take place in the same plane as the insertion of the leaf immediately preceding, and the branch then stands laterally on the stem beside the leaf. To this class belongs, according to Mettenius's description, the extra-axillary branching of those Hymenophyllaceæ which have their leaves in two rows. That which distinguishes Ferns from Phanerogams with axillary branching, especially Angiosperms, is the rarity of terminal branching. While in the latter every leaf-axil, at least in the vegetative region, bears a bud, even the apparently axillary branches of creeping Ferns with long internodes occur mostly only at great distances, being wanting in a number of intermediate leaves. In those Ferns where the growth of the stem is slow and the apical region of considerable size, especially in erect species like *Aspidium Filix-mas* and Tree-ferns, the terminal branching of the stem is reduced to a minimum, or is entirely absent, or occurs only in abnormal cases.

The formation of new shoots from the bases of leaf-stalks must be distinguished from the normal terminal branching of the stem. These have nothing to do genetically with the stem, any more than the formation of adventitious shoots from the lamina of the leaves (*vide infra*).

The *Development of the Leaf* is decidedly basifugal and apical, the further growth being also basifugal. The leaf-stalk is first formed; at its apex the lamina begins subsequently to show itself; its lowest parts are formed first, its higher parts in basifugal succession. The extraordinary slowness of this growth is very remarkable, finding its parallel only among the Ophioglossaceæ. In old plants of *Pteris aquilina* the formation of the leaf commences fully two years before its unfolding; at the commencement of the second year only the leaf-stalk is as yet in existence, about one inch high, its growth having taken place up to this period from an apical cell which is divided by oblique walls in alternating directions; in the summer of the second year the lamina arises for the first time at the apex of this rod-like body, and may be found hidden in the form of a minute disc beneath the long hairs. It immediately bends downwards at its apex, and hangs

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[1] See Hofmeister, Allgemeine Morphologie, p. 509; and Bot. Zeitg. 1870, p. 441.

down like an apron from the apex of the stalk (Fig. 261, *B*, *C*, *D*). Its growth now proceeds underground, so that it does not begin to unfold till the third spring, when it is raised above ground by the elongation of the leaf-stalk. The whole of the leaves of a rosette of *Aspidium Filix-mas* have been in course of formation two years before their unfolding; the leaf-stalk is in this case also formed in the first year, and the first formation of the lamina takes place on the oldest leaves of the young rosette.

The basifugal apical growth of the lamina of Fern-leaves is however most conspicuous when it continually advances for a considerable time without attaining a definite conclusion while the lower parts of the lamina have long been fully developed, as in Nephrolepis. The periodical interruption of the apical growth of the lamina already mentioned occurs in many species of Gleichenia and Mertensia, where the development of the leaves remains stationary above the first pair of

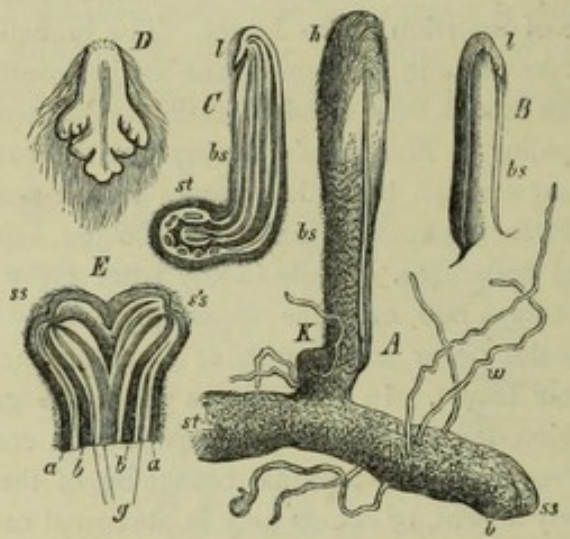

FIG. 261.—*Pteris aquilina*; *A* the end of a stem *st*, the apex lying at *ss*; by its side at *b* is the rudiment of a leaf, *bs* the stalk of a leaf in the second year, at *h* its lamina enveloped by hairs, *K* a bud at the back of the leaf-stalk, *w* roots; *B* a young leaf in the second year, *bs* its stalk, *l* its small lamina with the hairs removed; *C* longitudinal section of a similar leaf, connected with the transverse section of the stem *st*, *bs* and *l* as in *B*; *D* the lamina of a leaf in the second year seen in front, *i. e.* on the upper side (× about 5); the first divisions have begun to be formed; *E* horizontal longitudinal section of a fork of the stem, *ss s's* the two apices, *a a* brown epidermal tissue, *b b* brown sclerenchyma, *g* fibro-vascular bundles. (*A*, *B*, *C* natural size.)

pinnæ (and when the pinnation is compound is often repeated in the several orders of branching); so that the apex, forming apparently a bud in the fork, either remains altogether undeveloped, or is only incompletely developed in a succeeding period of vegetation, and then again in the same manner. This intermittent development of the leaves may apparently extend over many years (see Braun, 'Rejuvenescence,' p. 114). According to Mettenius, the lamina of some Hymenophyllaceæ is capable of unlimited development, and is annually renewed. In Lygodium the primary branches of the lamina remain also in a bud-like condition at the end after the formation of each pair of pinnæ of the second order, while the rachis of the leaf grows without limit and resembles a twining stem.

The branching of the lamina of Fern-leaves is not unfrequently forked in the mature state, as in Platycerium, Schizæa, &c.; but Hofmeister refers also the pinnate forms to dichotomous branching at the commencement, which becomes sympodial with further development, a right and left fork being alternately weaker in its growth.

and forming the lateral pinnæ; while the branches, the growth of which is favoured, form the rachis of the leaf or of the branch of a leaf[1].

The *Formation of Adventitious Buds*, which do not result from the terminal branching of the stem, is, in Ferns, connected with the leaves. These buds make their appearance on the leaf-stalk or on the lamina itself. The shoots of *Pteris aquilina* which spring from the leaf-stalk (Fig. 261) stand at the back of the

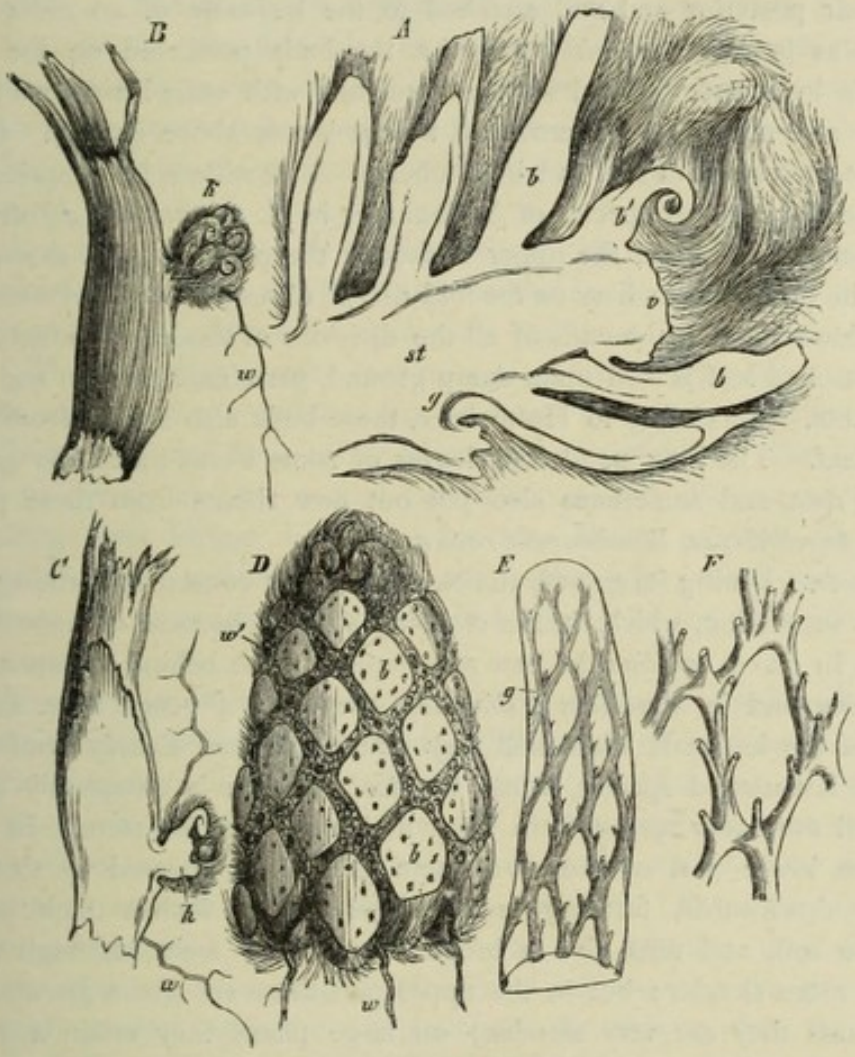

FIG. 262.—*Aspidium Filix-mas*; *A* longitudinal section through the end of a stem, *v* the apical part of the stem *st*, *b b* leaf-stalks, *b'* a young leaf still rolled up, the rest enveloped in long paleæ, *g* fibro-vascular bundles; *B* a leaf-stalk of the same plant broken off, bearing at *h* a bud with several leaves, *w* a root of this bud; *C* a similar leaf-stalk cut through lengthways, bearing a root at *w* and a bud at *h*; *D* end of a stem with the leaf-stalks cut off with the exception of the youngest leaves of the terminal bud in order to show the arrangement of the leaves, the spaces between the stalks *b b* are filled with numerous roots which themselves all spring out of the stalks; *E* end of a stem the cortex of which has been peeled off in order to show the net-work of fibro-vascular bundles *g*; *F* a mesh of this net-work slightly magnified, showing the basal portions of the bundles which pass into the leaves.

individual leaf-stalks near the base; in *Aspidium Filix-mas* (Fig. 262) they arise at a moderate height above the insertion, usually on one of the lateral edges of the leaf-stalk. In both cases Hofmeister states that they are formed on the young

[1] It must be observed here also that Hofmeister applies the term 'dichotomy' in a much wider sense than is usually done. New examinations of a large number of species are greatly to be desired, both in reference to the formation of leaves and to the terminal branching of the stem.

leaf-stalk even before the first appearance of its lamina, and before the differentiation of its tissue. A single superficial cell of the leaf-stalk is the mother-cell of the new shoot; and as the surrounding tissue of the leaf-stalk grows like a wall around them, they may, as in Pteris, be placed in a deep depression, where they sometimes remain dormant for a long period. Even when the leaf has long died away, the leaf-stalk still remains succulent above the bud, and filled with food-materials; and in *Aspidium Filix-mas* vigorous stems are not unfrequently found with a number of leaves at their posterior end still attached to the leaf-stalk of an older stem. In some cases, as in *Struthiopteris germanica*, the buds produced on the leaf-stalks develope into long underground stolons furnished with scale-leaves, which become erect at the end and unfold a crown of foliage-leaves above ground. In *Nephrolepis undulata* they swell at the end into tubers. Adventitious buds spring from the lamina, especially in many species of Asplenium; in *A. furcatum*, *e.g.*, often in large numbers from the middle of the upper surface of the pinnæ; in *A. decussatum* from the base of the pinnæ (or axillary on the mid-rib?). *Ceratopteris thalictroides* not unfrequently produces buds in the axils of all the divisions of the leaves, which, especially when the detached leaf is laid upon damp ground, germinate rapidly, and grow into vigorous plants. According to Hofmeister, these buds also spring from superficial cells of the leaf. The long pendulous leaves of some Ferns touch the ground with their apices, root, and sometimes also put out new shoots from these points (*e.g.* *Chrysodium flagelliferum*, *Woodwardia radicans*, &c.).

The *Roots*. During its growth the stem is usually constantly forming new roots in acropetal succession, which, in the creeping species, become at once fixed to the substratum. In *Pteris aquilina* the new roots appear close behind the apex, and, both in this species and in *Aspidium Filix-mas*, they also proceed from the adventitious buds of the leaf-stalk while still very young. It has already been mentioned that, in the last-named species, when the mature stem is completely covered by leaf-stalks, all the roots spring from them and not from the stem. In Tree-ferns especially the lower part of the erect stem is entirely covered by slender roots, which grow downwards, forming an envelope several inches thick before they penetrate the soil, and thus give a broad base to the stem although it is there really much more slender; but in the upper part there are also a great many roots. In small plants they are very slender; on large plants they attain a diameter of from 1 to 3 mm.; they are cylindrical, generally covered with a number of root-hairs which form a kind of felt, and are of a brown or black colour. The history of the growth of Fern-roots has been studied by Nägeli and Leitgeb[1]. The apical cell is a three-sided pyramid, with a convex equilateral base. The segments or layers of the root-cap detached by convex septa parallel to the base first separate into four cells placed crosswise, so that those of successive layers alternate by about 45°; each of the four cells of a layer then splits up into two external and one internal (central one), so that the layer is now formed of four internal cells arranged in a cross, and of eight external cells. Further divisions may then follow;

[1] Sitzungsber. der bayr. Akad. der Wiss. Dec. 15, 1865. Compare with what follows the diagram of a root given under the Equisetaceæ, which serves in the main also for Ferns and Rhizocarps; also in addition p. 123.

the central cells of the layer grow more quickly in an axial direction, and may become divided by transverse septa, by which the layer is made to consist of two or more strata in the middle. The formation of a layer is generally followed by that of three root-segments before a further new layer is formed; these segments, corresponding to the faces of the three-sided apical cell, lie in three straight longitudinal rows. Each of these triangular tabular segments includes a third of the circumference of the root, and is first divided by a radial longitudinal wall into two unequal portions. The transverse section of the root now shows six cells, three of which meet in the centre, while the other three do not reach quite so far. Each of these six cells is then divided by a tangential wall (parallel to the surface) into an inner and an outer cell; the inner ones form the fibro-vascular bundle, while the six outer cells form the rudiment of the cortex. If the root becomes thick, the six cortical cells divide by radial walls; if it remains slender, this division does not take place. The six or twelve cortical cells are now divided by a tangential longitudinal wall, and the fibro-vascular bundle is enclosed by two layers of cells, the outer of which forms the epidermis, the inner the fundamental tissue of the cortex. The epidermis usually continues to consist of one layer only, dividing only by walls vertical to the surface; but in some Ferns (*e. g.* Polypodium, Blechnum, and Cystopteris) the layer of epidermal cells is doubled. The layer of cells between the epidermis and the central bundle becomes double, an outer and inner cortex resulting from further divisions. In most Ferns, however, the distinction between the two layers cannot be made out in the fully grown root; though in some the inner cortex consists of thick-walled long cells, the outer cortex of thin-walled short ones.

The *Fibro-vascular Bundles* consist at first, as has been mentioned, of six cells in transverse section; these are each divided simultaneously by a tangential wall into an outer tabular and an inner cell. From the further divisions of the outer cell proceeds a tissue which Nägeli and Leitgeb call Pericambium, and the cells of which are characterised in the fully developed root by their thin walls and by their granular and mucilaginous contents. They are broad, but short. From the six inner cells proceeds the prolongation of the true fibro-vascular bundle; they divide in all directions, the divisions advancing in centrifugal succession; the peripheral cells are considerably smaller, after the completion of the division, than the inner ones. The formation of vessels begins with their production at two or three points of the circumference lying diametrically opposite one another on the inner side of the pericambium; it proceeds either at first right and left (tangentially), or centripetally, a diametral row of vessels being thus formed. In slender roots this may proceed no further than the production of the first vessel; in thicker roots one or more broad vessels lie in the centre, which only become woody at a later period. The peripheral cells and the narrow ones that lie between the vascular bundles form the phloëm-layer of the bundle by the thickening of their walls. The roots of Ferns branch in a monopodial manner only; the lateral rootlets arise in acropetal succession on the outside of the primary vascular bundle, and are therefore usually arranged in two rows, rarely in three or four. The mother-cells of the lateral rootlets belong to the innermost layer of the cortex, and are separated from the vascular bundle of the primary root by the pericambium; the rootlets originate very near

the apex, when the vessels are not yet in existence. Adventitious lateral rootlets (arising behind those already formed) do not occur. The mother-cell of a lateral rootlet first of all forms its three-sided pyramidal apical cell by three oblique divisions; the first layer of the cap being then formed from it. When two primary vascular bundles arise in a lateral rootlet, they lie right and left in reference to the primary root. The cortex of the primary root is simply penetrated, no root-sheath being formed.

The fibro-vascular bundles are always formed singly and in the axis of the root, even in very slender filiform stems, as in those of Hymenophyllaceæ, and in the young plants of larger species. When the stems of the latter and their leaf-stalks

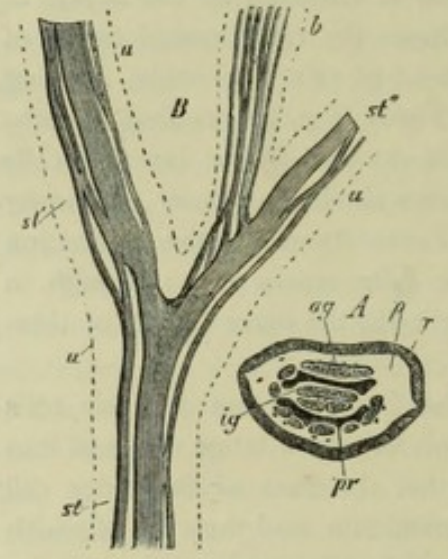

FIG. 263.—*Pteris aquilina*; *A* transverse section of the stem, *r* its brown sheath (the layer of sclerenchyma beneath the epidermis), *p* the soft colourless parenchyma of the fundamental tissue; *ig* inner fibro-vascular bundles; *ag* upper broad primary string of the outer bundle; *B* the separated upper fibro-vascular bundle of the stem *st* and of its branches *st'* and *st''*, *b* bundles of the leaf-stalk, *u u* outline of the stem (natural size).

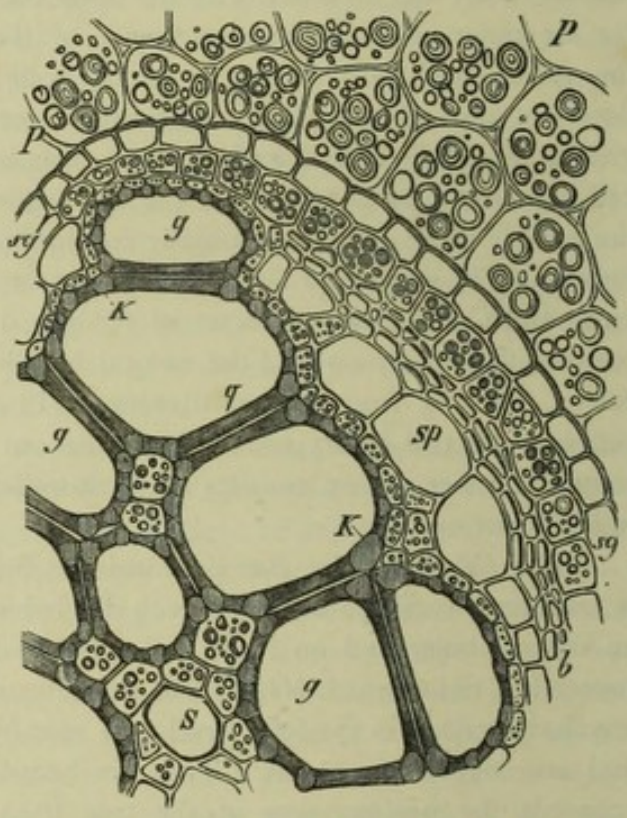

FIG. 264.—A quarter of the transverse section of a fibro-vascular bundle from the stem of *Pteris aquilina*, with the adjacent parenchyma *P* containing starch, *sg* the bundle-sheath, *b* the layer of bast, *sp* the large sieve-tubes, *g g* the large vessels thickened in a scalariform manner, *S* a spiral vessel surrounded by cells containing starch (×300).

become thicker with increase of growth, a network of anastomosing bundles is formed in place of the central bundle, presenting, in typical cases, a wide-meshed hollow cylinder, by which the fundamental tissue of the stem is separated into an outer cortical layer and an inner medullary portion (Fig. 262, *A* and *E*). Not unfrequently, however, isolated scattered bundles also arise in addition; thus in *Pteris aquilina* two strong broad cauline bundles are formed within the medullary portion (Fig. 263, *A*, *ig*), and in Tree-ferns a number of filiform bundles are scattered through it which enter into the leaf-stalk through the meshes of the primary bundle[1].

[1] For a more special description see Mettenius on Angiopteris, in Abhandlungen der königl. Sächs. Gesellsch. der Wiss. 1864, vol. VI.

The primary bundles which form the cylindrical network already mentioned are mostly ribbon-shaped, broad, and, in the case of Tree-ferns, commonly have their margins curved outwards. From these margins spring the more slender filiform bundles which enter the leaf-stalk, and are more numerous in proportion to its thickness. These may also coalesce laterally into plates of different forms (as in *Pteris aquilina*), or may run separately side by side. The leaf-stalk always corresponds to an opening of the meshes of the cylinder of the primary bundle. The thick bundles which run through the stem appear to be all cauline. Hofmeister found in *Pteris aquilina* that they exhibit the same distribution on the leafless elongated ends of the stem as on its leafy parts, a proof that the distribution does not depend on the leaves, as in Phanerogams. The end of the bundle may even be followed up to near the apical cell of the stem, in places where the nearest leaf-stalks have not yet begun to form bundles.

The fibro-vascular bundles of Ferns are, like those of all Vascular Cryptogams, closed; they consist of a mass of xylem, completely enveloped by a layer of phloëm. Besides a few narrow spiral vessels, lying in the foci of the elliptical transverse section, the xylem consists of vessels with bordered pits which usually resemble transverse clefts (scalariform vessels), their ends being mostly obliquely truncated, or fusiform and pointed. Between the vessels lie narrow thin-walled cells, which contain starch in winter. The phloëm, in addition to cells similar to those last named, contains wide sieve-tubes or latticed cells, and at the circumference narrow, bast-like, thick-walled fibres. The whole bundle is usually enclosed by a distinct sheath of narrower cells (vascular bundle-sheath); the latter often, but not always, have the walls which face the bundle strongly thickened and of a dark reddish-brown colour.

The *Fundamental Tissue* of the stem and of the leaf-stalks consists, in some species (as *Polypodium aureum* and *vulgare*, and *Aspidium Filix-mas*), entirely of thin-walled parenchyma; in others (as Gleichenia, species of Pteris, and Tree-ferns), string-like, ribbon-shaped, or filiform portions of the fundamental tissue become differentiated, the cells of which undergo great thickening, and become brown-walled, hard, and prosenchymatous. Mettenius aptly terms them sclerenchyma. In the stem of *Pteris aquilina* (Fig. 263, *A*) two thick bands of sclerenchyma of this description (*pr*) lie between the inner and outer fibro-vascular bundles, and fine threads of sclerenchyma appear on the transverse section of the colourless parenchyma as dark points. In other cases (as in *Polypodium vacciniifolium* and in Tree-ferns), dark layers of sclerenchyma, the nature of which was in these cases first correctly recognised by H. von Mohl, form sheaths round the fibro-vascular bundles. The outer layer of the fundamental tissue of thicker stems and leaf-stalks lying beneath the epidermis, is often dark brown and sclerenchymatous, forming a hard firm sheath, as again, for instance, in *Pteris aquilina* (Fig. 263, *A*, *r*) and Tree-ferns. In order to facilitate, in spite of this firm coat, the communication of the outer air with the inner parenchyma which is rich in assimilated food-materials, it is, in *Pteris aquilina*, interrupted along two lateral lines, where the colourless parenchyma rises to the surface. In Tree-ferns, on the other hand, according to H. von Mohl, depressed cavities appear on the enlarged base of the rachis of the leaf, where the sclerenchyma is replaced by a loose and pulverulent tissue.

It may be mentioned here in addition, as an isolated histological peculiarity, that in *Aspidium Filix-mas*, according to Schacht, roundish stalked glands occur in the fundamental tissue of the stem, which I have also noticed in the green parenchyma of the leaves, and on the pedicels of the sporangia of the same Fern (Fig. 266, *C*, *d*).

The lamina of the leaf consists in Hymenophyllaceæ only of a single layer of cells, as in Mosses; in all other Ferns it is formed of several layers. Between the upper and under epidermis lies a spongy parenchyma containing chlorophyll, the *Mesophyll*, penetrated by the fibro-vascular bundles which form the venation of the leaf. The epidermis of Fern-leaves is distinguished by containing chlorophyll, and by the peculiarities of the stomata already spoken of in the part of this work relating to tissue (Fig. 76, p. 89). The course of the veins is very various; sometimes they run branching dichotomously at acute angles, or spreading like a fan upwards and sideways, without anastomosing and without forming a mid-rib; more often the undivided lamina, or a division of the lobed, incised, or pinnate leaf, is penetrated by a distinct median vein though but slightly projecting, from which spring more slender branches, which themselves again ramify monopodially or in a forked manner, and run to the margins. The finer veins frequently anastomose like those of the leaves of most Dicotyledons, and divide the surface into areolæ of characteristic appearance.

The *Trichomes* of Ferns are produced in a great variety of positions. True root-hairs, simple unarticulated tubes, arise, not only on the roots themselves, but also on underground stems and on the bases of leaf-stalks (as in *Pteris aquilina* and Hymenophyllaceæ). On aërial creeping stems and on the leaf-stalks the numerous usually brownish or dark-brown flat multicellular hairs, the *Paleæ*, occur, soon becoming dry, often entirely enclosing the buds, and attaining a length of from 1 to 6 cm. (as in Polypodium, Cibotium, &c.). Long strong bristles are sometimes found on the lamina (in *Acrostichum crinitum*), and very often fine, delicate, articulated hairs. Finally, the sporangia themselves are trichomes.

The *Sporangia* of Ferns are, from a morphological point of view, trichomes of the leaves. They arise from epidermal cells, and are usually stalked capsules, the wall of which, when mature, consists of but a single layer of cells. A ring of cells belonging to the wall of the capsule and running across or obliquely or lengthwise is generally developed in a peculiar manner, and is then termed the *Annulus*. By its contraction when dried up the capsule bursts (at right angles to the plane of the annulus). Sometimes, instead of the annulus, a terminal or lateral group of the cells of the wall of the capsule is developed in a similar manner.

The sporangia are generally combined into groups, each group being termed a *Sorus;* the sorus contains either a small definite number or a large indefinite number of sporangia, and among them also very commonly some slender articulated hairs, the *Paraphyses*. The whole sorus is very generally covered by an excrescence of the epidermis, the true *Indusium;* in other cases the false indusium consists of an outgrowth of the tissue of the leaf itself, and is then composed of several layers, and even has stomata; or the covering of the sorus is simply the result of the margin of the leaf being recurved or rolled over it. In Lygodium each separate sporangium is covered by a pocket-shaped growth of the tissue of the leaf

like a bract[1]. Sori are not usually formed upon all the leaves of the mature plant; sometimes groups of fertile and sterile leaves alternate in regular succession, as in *Struthiopteris germanica*. In some cases the sori are uniformly distributed over the whole of the lamina, in others they are connected with definite portions of it. The fertile leaves may be in other respects like the sterile ones, or they may be strikingly different from them; and this difference is not unfrequently occasioned by the partial or entire failure of development of the mesophyll between and near the fertile veins; the fertile leaf, or the fertile part of the leaf, then appears like a spike or panicle furnished with sporangia (*e. g.* Osmunda, Aneimia). The sporangia generally arise from the epidermis of the veins of the leaf, and especially on the under side of the lamina; but in the Acrostichaceæ they spring both from the veins and from the mesophyll; in Olfersia they cover both surfaces of the leaf at the sides of the mid-rib, or in Acrostichum only the under side. When, as is usually the case, the veins are the only parts that bear the sporangia, the fertile veins may be like the sterile ones, or may undergo a variety of changes at the spots where they bear the sori; they may be swollen into a cushion (forming a receptacle), or they may project beyond the margin of the leaf, as in the Hymenophyllaceæ. The sorus may be



FIG. 265.—Under side of a lacinia of a leaf of *Aspidium Filix-mas*, with eight indusia *i* (×2).

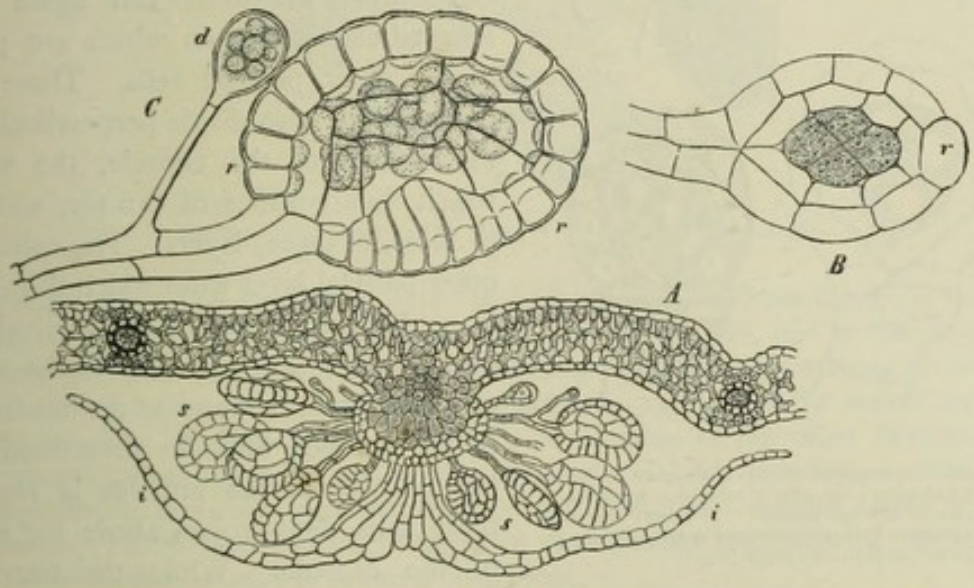

FIG. 266.—*Aspidium Filix-mas*. *A* transverse section of a leaf with a sorus consisting of the sporangia *s* and the indusium *i i*; right and left in the mesophyll of the leaf are two small fibro-vascular bundles, the sheath of which shows the dark brown thickenings on the walls that face inwards. *B* a young sporangium, its annulus standing vertically to the plane of the paper, *r* its apical cell; in the interior four cells are seen resulting from the division of the central cell; *C* lateral view of a nearly ripe sporangium, *r r* its annulus, *d* the stalked gland peculiar to this species; within the sporangium are seen the young spores already formed.

seated on the end of a vein, which then frequently puts out two branches in the angle of which is placed the sorus, or it may be formed on the back and below the ends

[1] Athough these points of structure are employed in systematic botany as characters of families, their morphology is at present but little known. A history of the development of the sori of Marattia, Kaulfussia, and Danæa, consisting of so-called united sporangia, is an especial desideratum.

of the veins; or the sorus may run for a considerable distance by the side of the veins. Sometimes the fertile veins run close to the margin of the leaf, in other cases close to the mid-rib of the lamina.

The *Development* of the sporangium[1] is accurately known only in the Polypodiaceæ; it arises there from a papillose outgrowth of one of the epidermal cells from which the sorus originates. Rees has shown that before the formation of the sporangium the epidermal cell concerned has been already divided cross-wise; the papilla is cut off by a septum, another septum arising, after further elongation, in the mother-cell of the sporangium thus formed; the lower cell forms the pedicel, the upper cell the capsule of the sporangium. The pedicel is usually transformed, by intercalary transverse divisions and longitudinal walls, into three rows of cells; the nearly hemispherical mother-cell of the capsule is next transformed, by four successive oblique divisions, into four plano-convex parietal cells and a tetrahedral inner cell; in the former further divisions follow perpendicular to the surface, while the inner cell again forms four tabular segments which are parallel to the outer parietal cells. These inner parietal cells also divide perpendicularly to the surface of the capsule, the wall of which thus consists of two (or, according to Rees, of three) layers. The cells of the outer parietal layer from which the annulus is to be formed are further divided by parallel walls perpendicular to the surface of the sporangium and to the median line of the annulus, until the prescribed number of cells of the annulus is reached; these cells then project above the surface of the capsule. While the tetrahedral central cell is now producing by successive bipartitions the mother-cells of the spores, the cells of the inner parietal layers are absorbed, and the cavity of the sporangium is considerably enlarged by this means and by the superficial growth of the outer parietal layer; so that the mass of mother-cells (according to Rees there are always twelve), floats entirely free in the fluid that fills the sporangium (Fig. 266). For the further peculiarities ex-

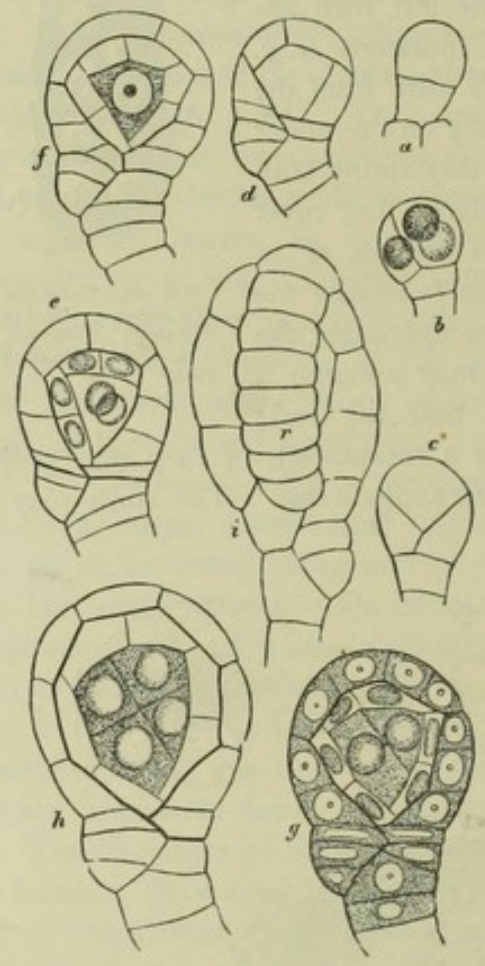

FIG. 267.—Development of the sporangium of *Asplenium Trichomanes*; the order of succession according to the letters *a-i*; in *i* the annulus *r* is shown; the other figures are seen in optical longitudinal section, and the annulus is perpendicular to the paper (×550).

[1] When the first sporangia are ripening, all stages of development of the younger ones may be found in the same sorus side by side.

hibited, reference must be made to the work of Rees already quoted; the illustrations, Figs. 266 and 267, had already been drawn on the wood when his more detailed investigations were published, and confirm his statements on all essential points. It is impossible, as has already been maintained, that the mother-cells of the spores can arise by free cell-formation. Each mother-cell is, in *Aspidium Filix-mas* (Fig. 268, *I*), provided with an evident nucleus; after its absorption (*II*), two new large clear nuclei arise (*III*), between which an evident line of separation is sometimes to be seen. After the absorption of these nuclei which show the commencement of a bipartition, four new smaller nuclei appear (*IV*), the mother-cell splitting up into four spore-cells (*V*), the relative position of which varies (as is shown in Figs. *VI*, *VII*, and *VIII*). The spore now becomes clothed with its cell-wall, which is differentiated into an endospore consisting of cellulose and a cuticularised brown exospore furnished with ridges (*IX*), and chlorophyll is formed within the spore. The spores of many Polypodiaceæ are distinguished by the long period during which they retain their power of germination, and by the slowness of this process; those of Hymenophyllaceæ often begin to germinate while still in the sporangium.

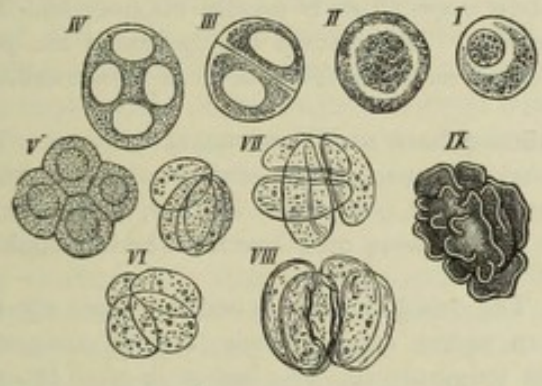

FIG. 268.—Development of the spores of *Aspidium Filix-mas* (× 550).

The Systematic Classification of Ferns, as generally given in handbooks, is based artificially on the form of the mature sporangium for the families, and of the sorus for the genera; only those groups which have already been repeatedly mentioned are accurately known. It appears certain that the Hymenophyllaceæ contain the lowest forms most nearly allied to the Muscineæ; the genetic relationship of the other families with the Hymenophyllaceæ and with one another has not yet been ascertained; but the Hymenophyllaceæ probably form the starting point for two or more series of families. Mettenius (Filices Horti Botanici Lipsiensis) distinguishes the following families, which I adopt with some alteration in the arrangement:—

1. Hymenophyllaceæ.
2. Gleicheniaceæ.
3. Schizæaceæ.
4. Osmundaceæ.
5. Marattiaceæ (*vide infra*).
6. Cyatheaceæ.
7. Polypodiaceæ.

In the characters of the families which follow, I have adopted the diagnoses of Mettenius, but at the same time give prominence to a few facts which may serve to complete the morphological statements already made.

1. **Hymenophyllaceæ.** The sporangia have an oblique or transverse complete annulus; and therefore burst with a longitudinal slit; they are formed on a prolongation of the fertile vein (the *Columella*), projecting beyond the margin of the leaf,

which is surrounded by a cup-shaped indusium. The antheridia and archegonia are formed for the most part on the surface of the prothallium, and chiefly from its marginal cells. The archegonia are borne on a cushion formed of several layers of cells. The mesophyll of the leaves usually consists of a single layer of cells, and is then necessarily destitute of stomata, which do however occur in Loxsoma on the leaf, which then consists of several layers. The stem is generally creeping and mostly very slender, and furnished with an axial fibro-vascular bundle. True roots are not present in all the species where they are absent, the stem itself is clothed with root-hairs: a large number of species of Trichomanes are described by Mettenius as rootless, and in these cases the ramifications of the stem assume a deceptive root-like appearance. The development of the axes precedes by a long space that of the leaves; several internodes have usually completely ended their growth while the leaves belonging to them are still very small; and these apparently (or actually?) leafless shoots often branch further to a great extent. The formation of the tissue of these families shows also many peculiarities, concerning which reference must be made to Mettenius (Hymenophyllaceæ, *l. c.*). The fertile end of the veins of the leaf projecting beyond its margin, or the columella, elongates by intercalary growth, and the newly formed sporangia are, in a corresponding manner, produced in basipetal succession. They are arranged in a spiral line on the columella. The sessile sporangia are biconvex, and are attached to the columella by one of their convex surfaces. The annulus projecting in the form of a cushion which separates the two convexities is usually oblique, and divides the circumference into two unequal portions. In Loxsoma the sporangia are pear-shaped and distinctly stalked. Paraphyses occur only in a few species of Hymenophyllum.

2. The **Gleicheniaceæ** have sessile sporangia with a complete transverse annulus, and hence a longitudinal dehiscence. The sori are dorsal, without indusium, and mostly formed of a few, sometimes of only three or four, sporangia. The innovation of the lamina of the leaf has already been mentioned. The leaf-stalk is not articulated.

3. **Schizæaceæ.** The ovoid or pear-shaped sporangia are sessile or shortly stalked; the annulus forms an apical cap-like zone, and is complete and circular, and the dehiscence is therefore longitudinal. The leaf-stalk of all the species contains only one fibro-vascular bundle. In Lygodium the climbing leaf-stalk is indefinite in its growth; its primary branches end in a lamina which is not circinate, and in *L. tenue* is transformed into a leaf-stalk with indefinite growth. The two pinnæ at the base of each primary branch of the leaf have a flatly expanded lamina definite in its growth. The fertile segments are spicate, and each bears on its under side two rows of sporangia, each of which is placed in a pocket-shaped outgrowth of the tissue of the leaf. To this order belong also Schizæa and Aneimia.

4. **Osmundaceæ.** The sporangia are shortly stalked, unsymmetrically rounded, and furnished on one side, instead of the annulus, with a peculiarly developed group of cells beneath the apex; on the other side they split longitudinally. In Osmunda the fertile leaves or leaf-stalks are contracted, that is, their mesophyll is not developed; in Todea they resemble the sterile ones.

5. **Cyatheaceæ.** The sporangia have a complete, oblique, eccentric annulus, and transverse dehiscence; the indusia are variable or absent; the sorus generally on a strongly developed receptacle. The leaf-stalk is usually not articulated, passing gradually into the stem. The genera Alsophila, Hemitelia, and Cyathea, include species with columnar stem (Tree-ferns), and large, often compoundly pinnate, leaves.

6. **Polypodiaceæ.** The sporangia have a vertical (*i. e.* longitudinal) incomplete annulus, and therefore split transversely. Mettenius distinguishes five sub-divisions of this family, which contains the largest number of species of any:—

(a) *Acrostichеæ*. The sori cover the surface and veins of the under side or of both sides, or are placed upon a thickened receptacle which stands on the vein. There is no indusium. (Acrostichum, Polybotrya.)

(b) *Polypodieæ*. The sori occupy either the whole length of the veins, or special anastomosing branches of it, or the back or thickened end of a vein. They are naked, or with a lateral indusium. (Polypodium, Adiantum, Pteris.)

(c) *Asplenieæ*. The sori are unilateral on the course of the veins, and are covered by a lateral indusium, or rarely without any; or they extend at their apex over the back of the veins, and are covered by an indusium springing from it; or they occupy special anastomosing branches of the veins, and are unilateral and covered by an indusium free on the side of the vein. The leaf-stalk is not articulated. (Blechnum, Asplenium, Scolopendrium.)

(d) *Aspidieæ*. The sori are dorsal on the veins, covered with an indusium, or terminal and without indusium. (Aspidium, Phegopteris.)

(e) *Davallieæ*. The sori are terminal on a vein or at a fork, and are furnished with an indusium; or are placed on an intramarginal anastomosing bend of the veins, and covered with a cup-shaped indusium, free at the outer margin. (Davallia, Nephrolepis.)

The **Marattiaceæ**, hitherto included among Ferns, must, from the earlier statements of Russow and the more recent investigations of Luerssen (Habilitationsschrift, Leipzig 1872), be separated from them, and classed with the Ophioglossaceæ (and Equisetaceæ), in consequence of the entirely different mode in which their sporangia are formed. The large sporangia of Marattia are placed singly on lateral veins of the pinnæ, to which they are attached by a narrow ridge-shaped base (pedicel). Two longitudinal rows of loculi contain the spores, which are not formed, as in the true Ferns, from a single primary mother-cell (central cell), but from a mass of tissue composed of primary mother-cells, filling up the loculus. The single loculus of the sporangium of Marattia corresponds so far to the single sporangium of Ophioglossum. A nearer affinity to the Ophioglossaceæ may be indicated by the stipular structures of the Marattiaceæ, which, while entirely foreign to Ferns, exhibit a certain resemblance to those of the Ophioglossaceæ.

[The classification of Mettenius given above will serve as a guide to the principal morphological differences between the various types of Fern structure. The student may however consult Hooker and Baker's Synopsis Filicum (London, 1868) for a systematic arrangement more in accordance with our present extended knowledge of species, though still, no doubt, artificial.—Ed.]

CLASS VII.

EQUISETACEÆ[1].

The *Sexual Generation* or Prothallium. The spores of the Equisetaceæ which have just attained the ripe condition (they retain their power of germination only for a few days), show, when sown in water or on damp soil, the preparatory phases of germination after only a few hours. In the course of some days the prothallium becomes developed into a multicellular plate, the further growth of which then proceeds very slowly. The spore, which contains a nucleus and grains of chlorophyll, increases in size as soon as germination commences, becomes pear-shaped, and divides into two cells, one of which is smaller with scarcely any except colourless contents, and soon developes into a long hyaline root-hair (Fig. 269, *I*, *II*, *III*, *w*), while the anterior and larger cell includes all the chlorophyll-grains of the spore which multiply by division. This cell produces by further divisions the primary plate of the prothallium, which increases by apical growth and soon branches (*III–VI*). The process of multiplication of the cells is therefore apparently extremely irregular; even the very first divisions vary; sometimes the first wall in the primary apical cell which contains chlorophyll is but little inclined with respect to the longitudinal axis of the young plant (in *E. Telmateia* the axis sometimes dichotomises); in other cases, on the contrary, this cell developes into a longish tube, the apical part of which is cut off by a septum (occasionally in *E. arvense*). The further growth is brought about by one or more apical cells dividing by septa, and longitudinal walls are subsequently formed in the segments in an order very difficult to determine. Ramification takes place by the bulging out of lateral cells, which then continue their growth in a similar manner. The chlorophyll-grains increase simultaneously by division in the cells. The young

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[1] G. W. Bischoff, Die kryptogamischen Gewächse (Nürnberg 1828).—W. Hofmeister, Vergl. Unters. (1851).—Ditto, Ueber die Keimung der Equiseten (Abh. der königl. Sächs. Gesell. d. Wiss. 1855, vol. IV. p. 168).—Ditto, Ueber Sporenentwickelung der Equiseten (Jahrb. für wiss. Bot. vol. III. p. 283).—[Germination, Development, and Fructification of the Higher Cryptogamia (Ray Society), pp. 267–306]. — Thuret (in Ann. des Sci. Nat. 1851, vol. XVI. p. 31).—Sanio, Ueber Epidermis und Spaltöffnungen des Equis. (Linnæa, vol. XXIX. Heft 4).—C. Cramer, Längenwachsthum und Gewebebildung bei *E. arvense* und *sylvaticum* (Pflanzenphys. Unters. von Nägeli und Cramer, 1855, vol. III.).—Duval-Jouve, Hist. Nat. des Equisetum (Paris 1864).—H. Schacht, Die Spermatozoiden im Pflanzenreich (Braunschweig 1864).—Max Rees, Entwickelungsgeschichte der Stammspitze von Equisetum (Jahrb. für wiss. Bot. 1867, vol. VI. p. 209).—Milde, Monographia Equisetorum, in Nova Acta Acad. Leop. Carolinæ, 1867, vol. XXXV.—Nägeli und Leitgeb, Entstehung und Wachsthum der Wurzeln (Beitr. zur. wissen. Bot. von Nägeli, Heft IV. München 1867).—Pfitzer, Ueber die Schutzscheide (Jahrb. für wissen. Bot. vol. VI. p. 297).

prothallia are, in *E. Telmateia*, usually narrow and ligulate, and consist of but a single layer of cells. The older prothallia are, both in this and in other species, branched in an irregularly lobed manner; one of the lobes takes, sooner or later, the lead in growth, becomes thicker and fleshy, consisting of several layers of cells, and puts forth root-hairs from its under side.

The prothallia of the Equisetaceæ are, in general, diœcious. The male prothallia remain smaller, attaining a length of a few millimetres, and produce archegonia only in exceptional cases on shoots of later origin (Hofmeister). The female prothallia are larger (as much as $\frac{1}{2}$ inch); Hofmeister compares them to the thallus of *Anthoceros punctatus*, Duval-Jouve to a curled endive-leaf. Duval-Jouve states that the antheridia appear about five weeks after germination, the archegonia much later. These statements refer especially to *E. arvense*, *limosum*, and *palustre*; according to the same writer, the prothallia of *E. Telmateia* and *sylvaticum* are broader and less branched; those of *E. ramosissimum* and *variegatum* slenderer and more elongated.

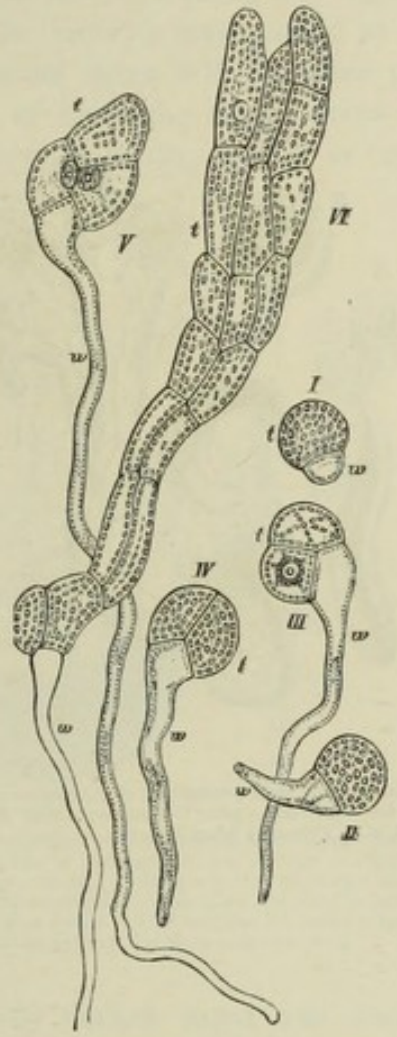

FIG. 269.—First stage of development of the prothallium of *Equisetum Telmateia*; *w* the first root-hair; *t* rudiment of the prothallium. The order of development follows the numbers *I*—*VI* (× about 200).

The *Antheridia* arise at the end or margin of the larger lobes of the male prothallium. The apical cells of the enveloping layer of the antheridium contain but little or no chlorophyll; they separate from one another on the addition of water (like those of Hepaticæ), to allow the escape of the antherozoids, which are still enclosed in vesicles and number from 100 to 150. The hindermost and thickest of the two or three coils of the antherozoid, which is larger in this class than in all other Cryptogams, bears an appendage on the inner side which Hofmeister terms an undulating Float, Schacht a thin-walled vesicle of protoplasm, and which contain granules of starch and sap (compare with Ferns and Lycopodiaceæ).

The *Archegonia* are developed from single cells of the anterior margin of the thick and fleshy lobes of the female prothallium. As the tissue of the prothallium beneath them continues its growth, the archegonia come, as in Pellia, to stand on its upper surface. The mother-cell of the archegonia, after it has become much curved, divides by a wall parallel to the surface of the prothallium; the lower of the two daughter-cells, which is entirely sunk in the tissue of the prothallium, becomes the central cell; from the outer one is formed the neck, consisting, at a subsequent period, of four parallel rows of cells. The four upper cells become very long; the four middle ones remain shorter; the four lower

ones scarcely elongate at all, and contribute, by their multiplication, like the cells of the prothallium which surround the central cell, to the formation of the wall of the ventral part of the archegonium, which consists of one or two layers. The oosphere is produced in the central cell, the contents of which it gradually displaces. The four upper long cells of the neck curve radially outwards, when the canal of the neck is being formed, like a four-armed anchor[1]. Immediately after fertilisation the canal of the neck closes, the oosphere, the nucleus of which disappears (and

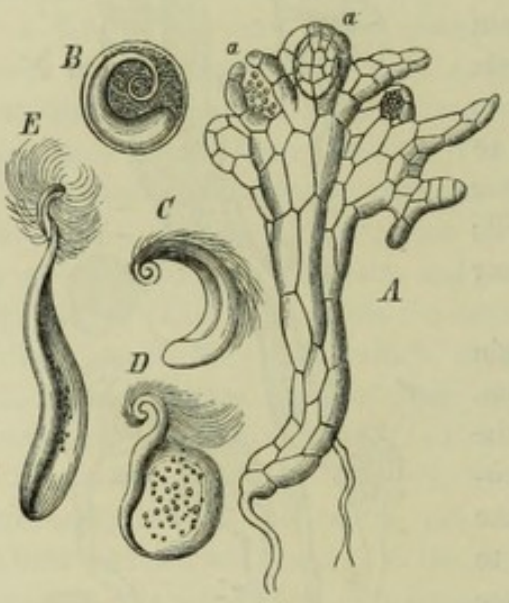

FIG. 270.—A male prothallium of *Equisetum arvense* with the first antheridia *a* (after Hofmeister, × 200); *B—E* antherozoids of *E. Telmateia* (after Schacht).

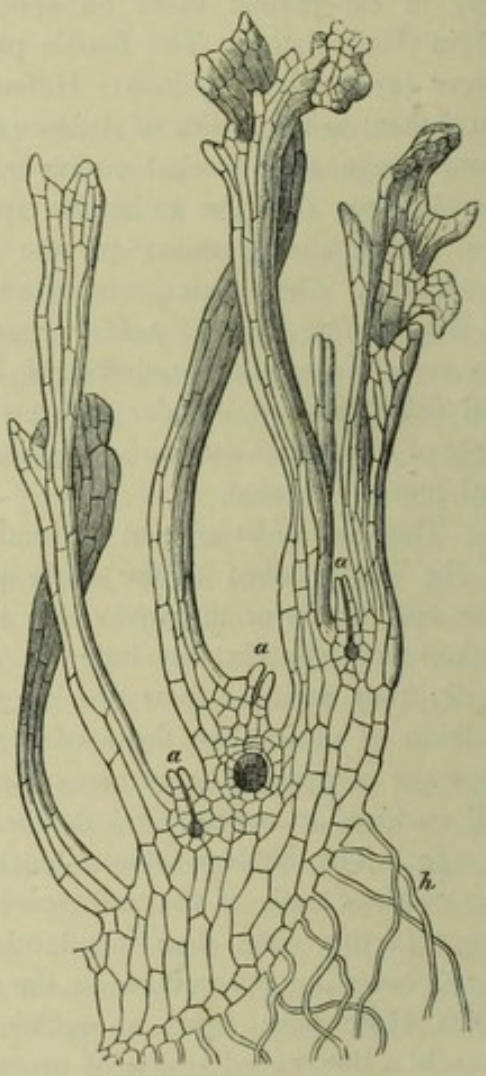

FIG. 271.—Lobe of a highly developed female prothallium of *Equisetum arvense* cut through vertically (after Hofmeister, (× about 60); *a a a* two abortive and one fertilised archegonium, *h* root-hairs.

which has now become the oospore), enlarges, and the cells of the wall of the ventral part of the archegonium which surrounds them begin rapidly to multiply.

Development of the *Asexual Generation* of Equisetum The formation of the embryo from the oospore is the result of divisions, the first of which is inclined to the axis of the archegonium, and is followed, according to Hofmeister, in each of the two cells by a division-wall placed perpendicularly to the first. The embryo appears

[1] Recent investigations are wanting from the point of view taken in Ferns and Rhizocarps. From analogy, however, the existence of a 'canal-cell' may be inferred here also.

to be composed of four cells arranged like the quarters of a sphere. The same author states that the foot, which he terms in this case also the primary axis, arises from the lower quarter, the rudiment of the first shoot from one of the lateral ones, turning upwards immediately afterwards and producing as the rudiment of the first leaf a projecting girdle, which then grows out into three teeth (Fig. 272 *B*). The first root now (?) arises from an *inner* cell of the tissue. It may here be remarked that this observation of Hofmeister's would establish, on the one hand, an essential difference between the mode of formation of the first root in Equisetaceæ and in other Vascular Cryptogams; while, on the other hand, the origin of the first leafy axis from one of the quarters of the embryo corresponds to the behaviour of Ferns and Rhizocarps, and hence does not agree with the other processes of growth of the Equisetaceæ, since in all of them the other shoots are developed from inner cells of the tissue. Duval-Jouve maintains, in fact, in opposition to this view, that the first leaf-bearing axis has a lateral origin in the interior of the already multicellular embryo, so that even the first shoot of Equisetum would be of endogenous origin. The unaccountable errors of this writer on the subject of apical growth render his statements of but little value in contrast to those of Hofmeister; the question is however, in any case, deserving of further inquiry.

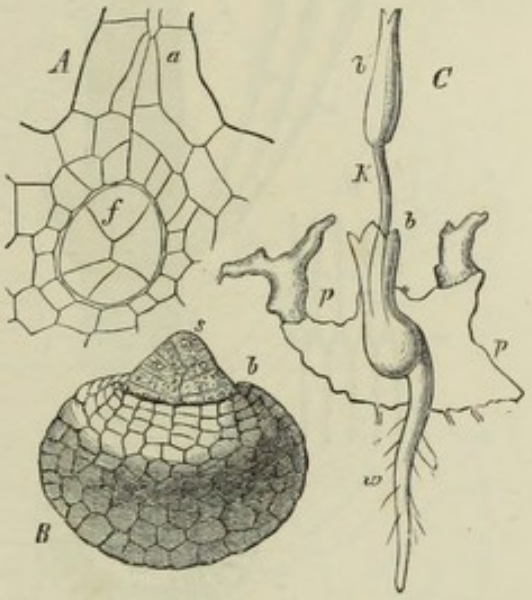

FIG. 272.—Development of the embryo of *Equisetum arvense* (after Hofmeister); *A* archegonium cut through vertically with the embryo *f* (× 200); *B* embryo further developed and separated, *b* rudiment of a leaf, *s* apex of the first shoot (× 200); *C* vertical section of a plate of a prothallium *p p*, with a young (asexual) plant, *w* its first root, *b b'* its leaf-sheaths (× 10).

The first leaf-bearing shoot grows upwards, and forms from ten to fifteen internodes with sheathing leaves ending in three teeth. It soon produces at its base a new stronger shoot with four-toothed sheaths (as in *E. arvense*, *pratense*, and *variegatum*, according to Hofmeister), which in turn gives origin to new generations of shoots, developing constantly thicker stems and sheaths with a larger number of teeth. Sometimes the third or one of the succeeding shoots penetrates downwards into the ground, forming the first perennial rhizome, which again produces from year to year new underground rhizomes and ascending leafy shoots.

In order to facilitate the understanding of the *Mode of Growth of the Stem and Leaves*, it is necessary to glance in the first place at their structure in the mature state. Every axis of an Equisetum consists of a series of joints (internodes) usually hollow and closed at their base by a thin septum. Each internode passes upwards into a leaf-sheath embracing the next internode, the sheath being split at its upper margin into three, four, or usually a larger number of teeth. From each tooth of the sheath a fibro-vascular bundle runs vertically downwards into the internode as far as the next node, parallel with the other bundles of the same internode; at the lower

end each bundle splits into two short diverging arms, by which it unites with the two neighbouring bundles of the next lower internode, where they descend into it from their sheath-teeth. The joints of the stem and their leaf-sheaths therefore alternate; and since in each joint the arrangement of bundles, leaf-teeth, projecting longitudinal ridges, and depressions or furrows, is exactly repeated in the transverse section, the different parts of a joint always correspond to the intervals between the homologous parts of the next upper and next lower joint. If the internode has projecting longitudinal ridges on its surface, one of these always runs downwards from the apex of each leaf-tooth parallel with the others as far as the base of the internode; between each pair of leaf-teeth commences a furrow or channel, which also continues as far as the base of the internode. The projecting

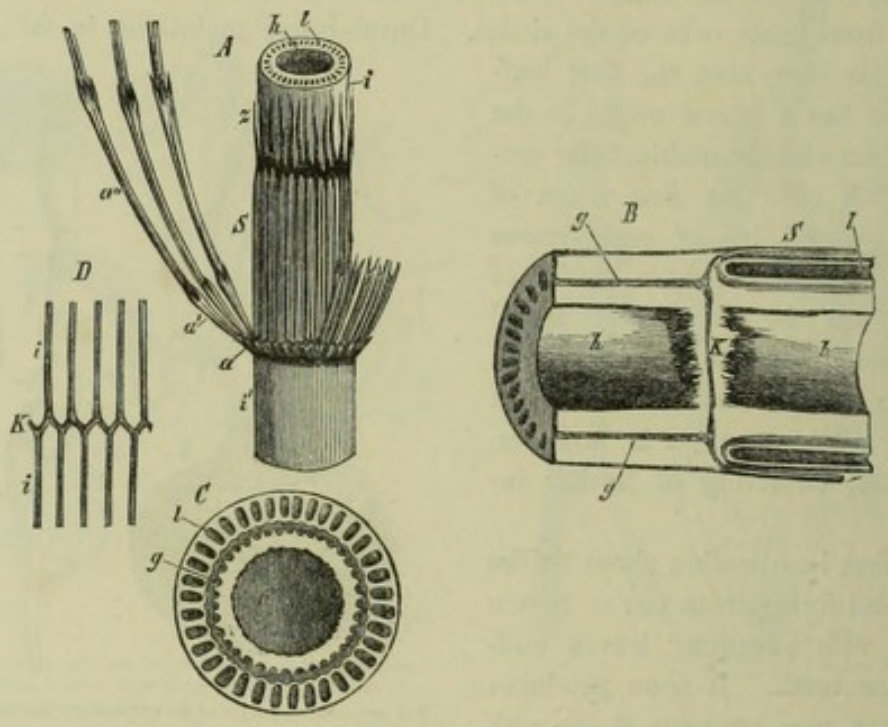

FIG. 272 a.—*Equisetum Telmateia*; *A* piece of an upright stem (natural size), *i i'* internodes, *h* its central cavity, *l* lacunæ of the cortex, *S* leaf-sheath, *z* its apex, *a a' a''* the lower internodes of young leaves; *B* longitudinal section of a rhizome (× about 2), *h* septum between the cavities *h h*, *g* fibro-vascular bundle, *l* lacunæ of the cortex, *S* leaf-sheath; *C* transverse section of a rhizome (× about 2), *g* and *l* as before; *D* union of the fibro-vascular bundle of an upper and lower internode *i i'*, *K* the node.

ridges lie on the same radii as the fibro-vascular bundles, each of which contains an air-canal; the depressions or furrows lie on the same radii as the lacunæ of the cortical tissue (which are sometimes wanting), and alternate with the fibro-vascular bundles. The branches and roots spring exclusively from within the base of the leaf-sheath; and as this forms a whorl, the branches and roots are also verticillate. The branches are all of endogenous origin; they arise in the interior of the basal tissue of the leaf-sheath, upon radii of the stem which alternate with the fibro-vascular bundles, and thus also with the teeth of the sheath. A root may arise beneath the bud of each branch; both break through the leaf-sheath at its base. All the joints of the axis agree in these respects, however they may be modified as underground rhizomes, tubers, ascending stems, leafy branches, or sporangiferous axes.

The end of the stem enveloped by a large number of younger leaf-sheaths terminates in a large apical cell, the upper wall of which is arched in a spherical manner, while below and at the side it is bounded by three almost plane walls. The apical cell has therefore the form of an inverted triangular pyramid, the upturned basal surface of which is a nearly equilateral spherical triangle. The segments are cut off by walls which are parallel to the oblique sides of the apical cell, that is, to the youngest primary walls of the segment; the segments, disposed

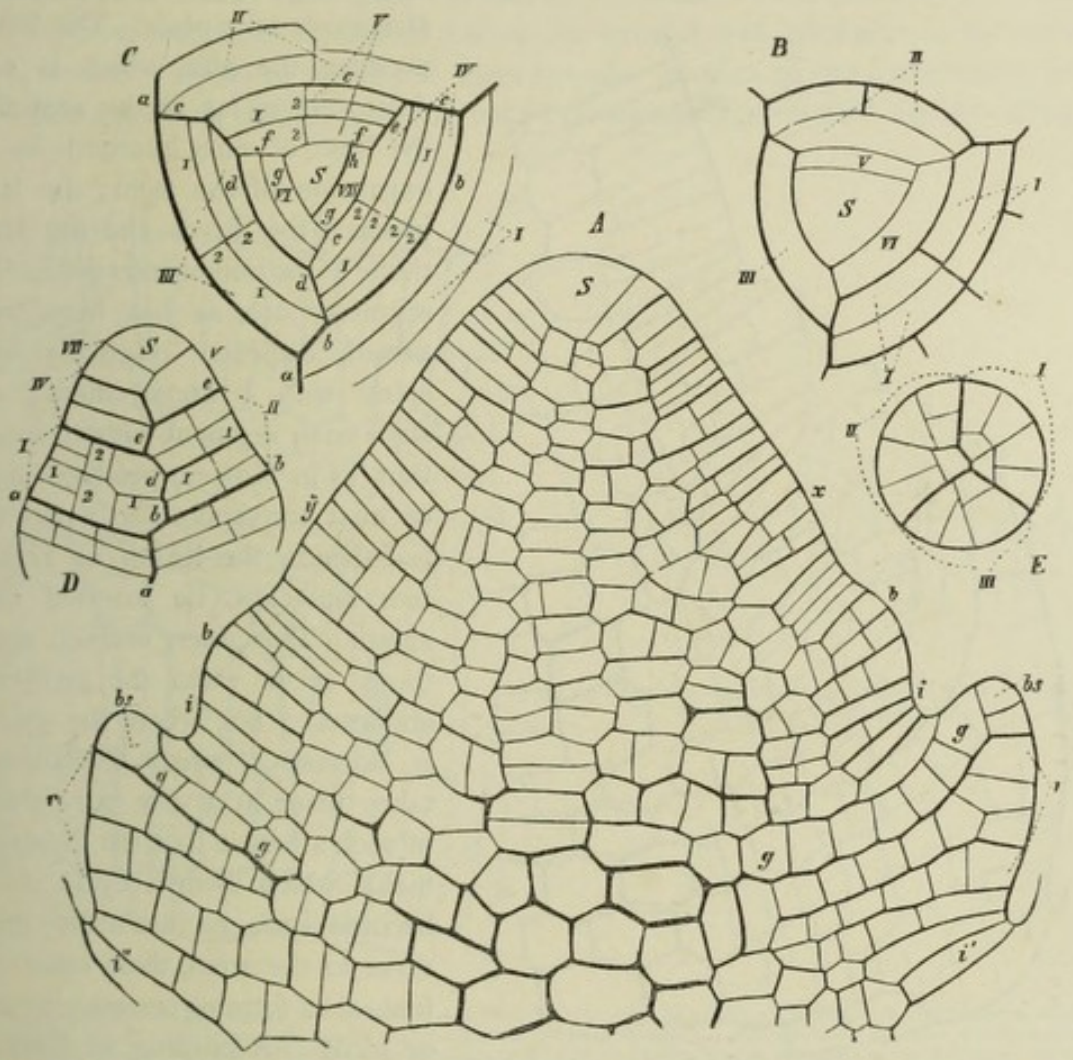

FIG. 273.—*A* ongitudinal section of the end of a stem in an underground bud of *Equisetum Telmateia*; *S* apical cell, *xy* first indication of the girdle from which the leaves are subsequently formed, *b b* a more advanced and distinctly marked foliar girdle, *bs* the apical cells of a strongly projecting foliar girdle, *r r* rudiment of the cortical tissue of the internodes, *g g* rows of cells from which the leaf-tissue and its fibro-vascular bundle proceed, *i i* the lower layers of cells of the segment which take no part in the formation of leaves (from nature); *B* horizontal projection of the apical view of the end of a stem of *E. Telmateia*; *s* apical cell, *I—V* the successive segments, the older ones still further divided; *C* horizontal projection of the apical view of *E. arvense*; *D* optical longitudinal section of the end of a very slender stem; *E* transverse section of the end of a stem after the formation of the vertical and first tangential walls. (*C, D, E*, after Cramer; the Roman numerals indicate the segments, the Arabic numerals the walls formed in them in the order of their succession; the letters the primary walls of the segments.)

in a spiral $\frac{1}{3}$ arrangement, lie in three vertical rows. Each segment has the form of a triangular plate with triangular upper and under walls, rectangular lateral walls lying right and left, and an outer rectangular wall which is curved. Each segment is first divided—as was shown by Cramer and Rees and confirmed by myself—by a wall parallel to the upper and under surfaces into two equal plates lying one above another, and consequently each half the height of the undivided segment. Each

half-segment is then again halved, in the most usual case, by a vertical nearly radial wall. The segment now consists of four cells, two of which lie one above the other and reach as far as the centre, but the other two do not because the vertical wall is not radial but intersects one of the lateral walls of the segment (the anodal wall) (Fig. 273, *E*). Divisions now take place without any strict rule in the four cells of each segment parallel to the primary and the lateral walls; and tangential divisions also soon make their appearance, by which the segment is split up into inner and outer cells, in which further divisions afterwards take place. The former produce the pith, which is soon destroyed as far as the septum at the base of each internode by the expansion of the stem; the latter produce the leaves and the entire tissue of the hollow internodes. The segments are, as has been mentioned, disposed originally in a spiral with $\frac{1}{3}$ arrangement; and since each segment without exception (as in Mosses) produces a leaf or what corresponds to a part of a leaf-sheath, the leaves of Equisetum must also be inserted on a spiral. This does, in fact, sometimes occur when the growth is abnormal; but when the growth is normal, a small displacement takes place at a very early period, of such a nature that the three segments which form a cycle always become arranged into a disc transverse to the stem, their outer surfaces thus forming an annular zone or girdle. According to Rees, to whom this observation is due, the three segments of each cycle are formed in rapid succession, while a longer time elapses between the formation of the last segment of the preceding and that of the first of the succeeding cycle. Thus by the unequal growth of the segments in longitudinal direction each cycle of segments or turn of the spiral produces a whorl, which therefore, strictly speaking, is a pseudo-whorl, because resulting from subsequent displacement. Each whorl of segments now forms a leaf-sheath, and the corresponding internode or joint of the stem. The above-mentioned divisions take place in the three segments during their arrangement into a transverse disc, each segment becoming converted into a mass of cells

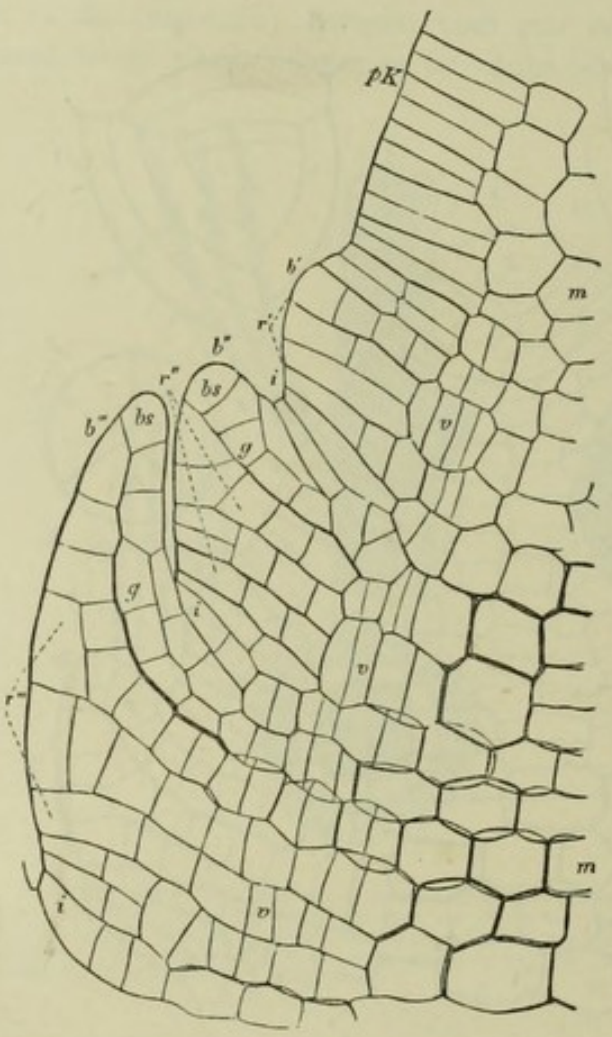

FIG. 274.—Left half of a radial longitudinal section beneath the apex of an underground bud of *Equisetum Telmateia* in September; *pK* lower part of the vegetative cone, *b' b'' b'''* leaves, *bs* their apical cells, *r' r'' r'''* the cortical tissue of the corresponding internodes; *m m* pith, *v v v* thickening ring, *g g* layer of cells from which the fibro-vascular bundles of the leaf-tooth arises.

consisting of from four to six layers. As soon as the transverse zone is formed, the formation of the leaves commences by the growth of the outer cells of the segments. They form an annular wall; one of the upper transverse cell-layers of the whorl of segments projects outwardly, forms the apex (the circular apical line) of the wall (Figs. 273, 274, *bs*), and those of its cells which lie most on the outside (the apical cells) divide by walls inclined alternately towards and from the axis. The circular apical line becomes more and more elevated, and thus the annular wall becomes a sheath enveloping the end of the stem. This same layer, of which the outermost cells form the apical line of the annular wall, produces in the interior of the sheath a tissue in which the fibro-vascular bundles of the leaf-sheaths arise. The lower transverse cell-layers of the whorl of segments grow only slightly outwards

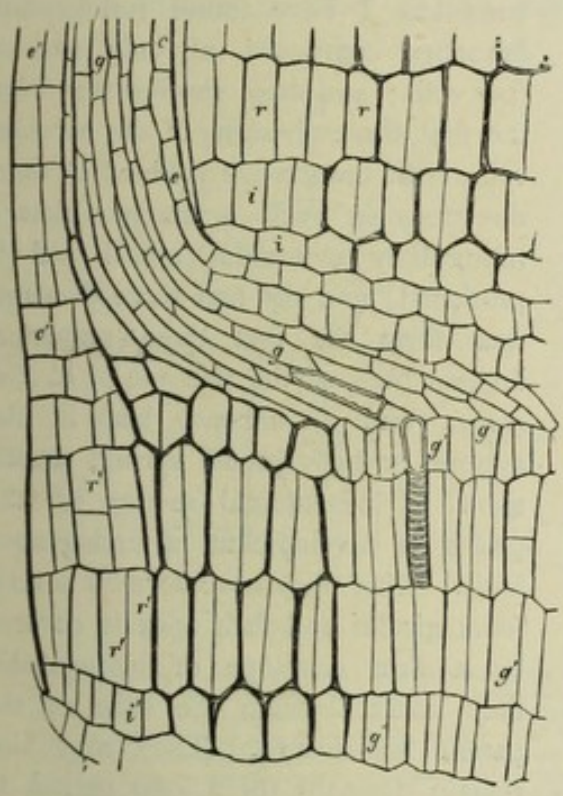

FIG. 275.—The same as Fig. 274. but at a greater distance from the apex, showing a further advance of the differentiation of leaf-sheath and internode; *r r* cortex of the upper, *r' r' r'* cortex of the lower internode, *e e* the inner, *e' e'* the outer epidermis of the leaf-sheath, *g g* the foliar portion of the fibro-vascular bundle, *g' g' g'* its descending portion belonging to the internode; the first annular vessel is formed at their point of meeting.

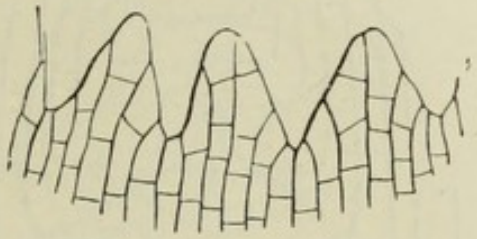

FIG. 276.—External view of three teeth of a young leaf-sheath of *Equisetum Telmateia*.

and upwards, become divided by vertical and afterwards rapidly by transverse walls, to produce the tissue of the internode, which passes gradually into that of the leaf. A vertical layer of this tissue forming a hollow cylinder (Fig. 274, *v v*) is distinguished by numerous vertical divisions; it forms a ring of meristem (or thickening-ring in Sanio's sense), in which the vertically descending fibro-vascular bundles of the internode are formed. These bundles form the prolongations of those of the leaf-teeth, which they meet, as shown in Fig. 275, *g g'*, at an obtuse angle, and coalesce to form curved 'common' bundles. The layers of cells which lie outside this ring of meristem that gives rise to the bundles produce the cortex of the internode, in which air-conducting canals soon arise. Even at an early period

the first rudiments of the sheath-teeth appear as protuberances at regularly distributed points, each of them ending in one or two apical cells (Fig. 276)[1].

The Equisetaceæ are the only class of plants the *Branching* of which depends exclusively on the formation of *endogenous* lateral buds. These are formed in the tissue of the youngest foliar girdle at points alternating with the sheath-teeth long before the differentiation of the fibro-vascular bundles. The position of the spot where they originate has not yet been precisely determined; it is probably a cell of that layer from which the fibro-vascular bundles originate. Hofmeister was the first to show that each bud proceeds from a single cell of the inner tissue; and although I have myself never seen it in a unicellular condition, I have found rudimentary branches composed of only two or four cells; and these showed that even the first three divisions of the mother-cell of the branch are inclined in three directions in such a manner that a triangularly pyramidal apical cell is produced; and the first three divisions thus form the first three segments. Lateral buds of the rhizome of *E. Telmateia* and *E. arvense*, late in the autumn or early in the spring, usually show in longitudinal section all the stages of development of endogenous buds. After they have formed several foliar girdles and their apex is covered by a firm envelope of leaf-sheaths, they break through the base of the parent leaf-sheaths. They may also remain dormant for a long period, as is shown by the circumstance that buds break out when the underground nodes of ascending stems are exposed to the light. It may be assumed that there is always as large a number of buds in a rudimentary condition as there are sheath-teeth. On the erect leafy stems of *E. Telmateia*, *E. arvense*, and other species, they all attain complete development, and produce the numerous slender green leafy shoots of these species; in other species the development of the branches is more sparing; some, as *E. hyemale*, usually form no aërial lateral shoots at all except when the terminal bud of the stem is injured, and then the

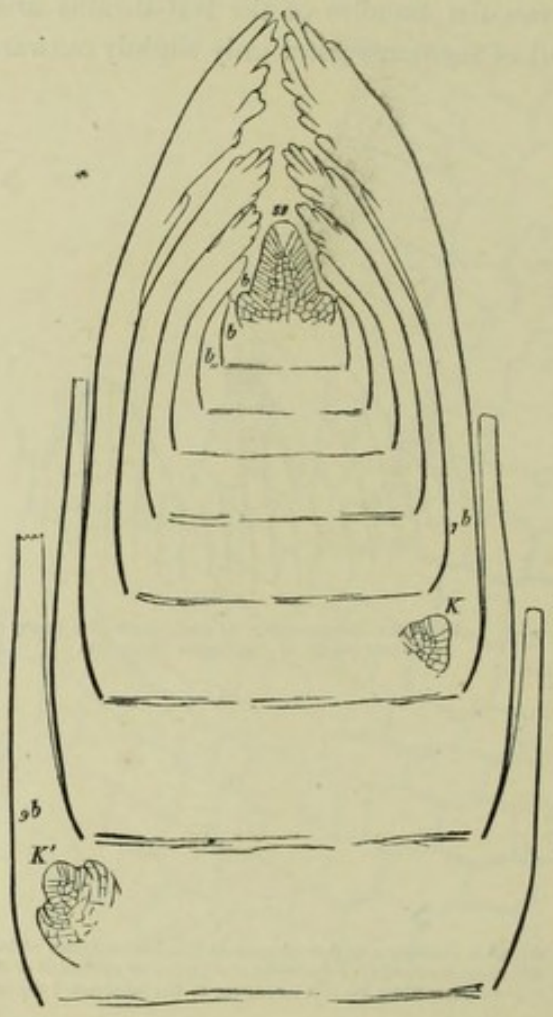

FIG. 277.—Longitudinal section through an underground bud of *Equisetum arvense*; *ss* apical cell of the stem, *b*–*9b* the leaves; *K K'* two buds; the horizontal lines across the stem indicate the position of the septa (diaphragms).

[1] On the original number and subsequent increase of the sheath-teeth, &c., compare Hofmeister and Rees, *l. c.*

node next below produces a shoot. Branches do not usually make their appearance on rhizomes in the form of complete whorls, but in twos or threes; but on the other hand they are more vigorous and become either new rhizomes or ascending stems. Since in the cases first mentioned the buds arise like the leaves in strict acropetal succession, it may be assumed that where the production of shoots is only induced at a later period by accidental circumstances, the buds have up to that time remained dormant in the interior.

The *Roots* arise in whorls, each immediately below a bud; but they may also often be suppressed, and may be developed, according to Duval-Jouve, even on aërial nodes, by humidity and darkness. Their development has been studied by Nägeli and Leitgeb (*l. c.*); in its earliest stages, which are represented diagrammatically in Fig. 278, it resembles essentially that of Ferns. The cortex is differentiated into an inner and an outer layer; the former forms air-conducting

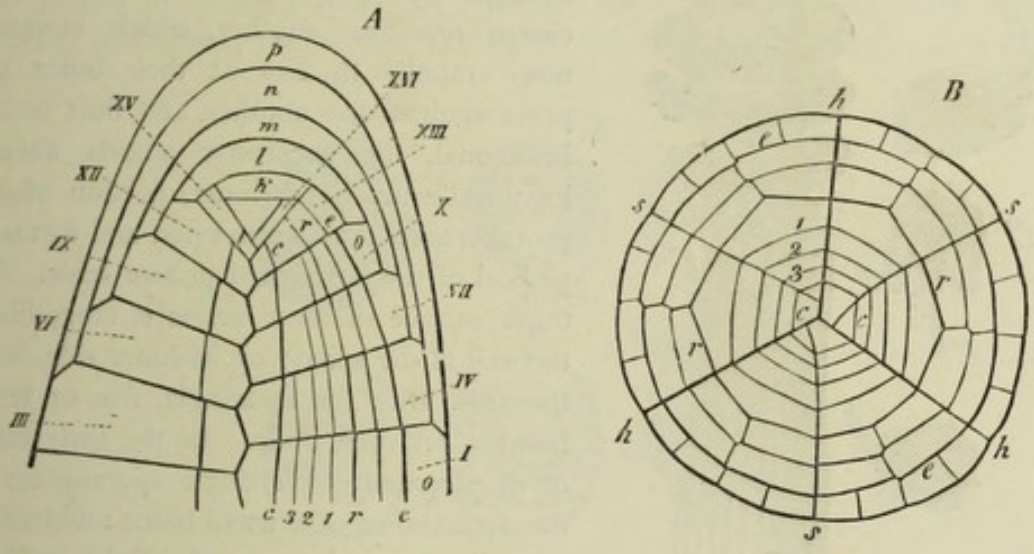

FIG. 278.—Diagram of the succession of cell-divisions in the apex of the root of *Equisetum hyemale* (after Nägeli and Leitgeb) (this diagram will serve also in the main for Ferns and for Marsilea). *A* longitudinal section; *B* transverse section at the lower end of *A*; *h h h* the primary walls, *s s s* the walls of the sextant-segments, indicated in *A* by the figs. *I*—*XVI*, *k l m n p* the layers of the root-cap, all the further divisions being omitted; *c c* in the interior of the root indicates the cambium-walls by which the primary fibro-vascular bundle is divided from the cortex of the root, *e* the boundary-wall between the epidermis *o* and the cortex (epidermal wall), *r r* boundary-wall between the outer and inner cortex (cortical wall), 1, 2, 3, the successive tangential walls by which the inner cortex is divided into several layers, the radial divisions being omitted.

intercellular spaces, at first arranged, like the cells themselves, in radial and concentric rows, and afterwards combining by the rupture of the cells into a large air-cavity surrounding the central fibro-vascular bundle. As the fibro-vascular bundle of the root developes, (seen in transverse section,) each of the three primary cells which alone of the six reach the centre is first of all divided by a tangential wall, so that the rudiment of the vascular bundle now consists of three inner and six outer cells. The six outer cells produce a cambial tissue in which the formation of vessels begins, commencing from two or three points of the circumference and advancing towards the interior. Last of all one of the three inner cells forms a broad central vessel; and phloëm is produced in the circumference of the vascular bundle. The branching of the root is, as in Ferns, strictly monopodial or acropetal; but since there is here no 'pericambium,' the lateral roots arise in contact with the outer vessels.

The *Sporangia* of Equisetaceæ are outgrowths of peculiarly metamorphosed leaves, and are generally formed in numerous whorls at the summit of ordinary shoots or of those specially destined for this purpose. Above the last sterile leaf-sheath of the fertile axis an imperfectly developed leaf-sheath is first of all produced (Fig. 279, *a*), a structure corresponding in some degree to the bracts of Phanerogams. The development of this structure is sometimes more sometimes less leaf-like; foliar girdles are formed above it in acropetal succession beneath the growing end of the shoot, projecting however but slightly, as in the ordinary formation of leaves of Equisetum. A larger number of protuberances project from each of these girdles, corresponding to the teeth of the ordinary leaf-sheaths; and thus several whorls of hemispherical projections are formed lying closely one over another, which, increasing more rapidly in size at their outer part, press against one another, and thus become hexagonal, the successive whorls alternating; while the basal (inner) portion of each protuberance remains slender, and forms the pedicel of the hexagonal peltate scale. The outer surface of these scales is tangential to the axis of the spike; on its inner side, facing the axis, arise the sporangia, five or ten in number on each scale. In the early stages of development each single sporangium has the appearance of a small blunt multicellular wart, the internal tissue of which[1] produces the spore-mother-cells which become isolated, while of the three exterior cell-layers which at first envelope it only the outermost finally remains as the wall of the sporangium or spore-sac. The mother-cells of the spores, connected together in groups of fours or eights, float freely in a fluid which fills the sporangium and is interspersed with granules. The processes that take place in the mother-cells up to the time of the formation of the spores have already been described in detail in Chap. I (see Fig. 10, p. 14). It was there shown how the division into four of the mother-cells is preceded by a bipartition which is at least indicated in Equisetum, in a manner analogous to the corresponding process in Ferns. The ripe sporangium opens by a longitudinal slit on the side which faces the pedicel of the

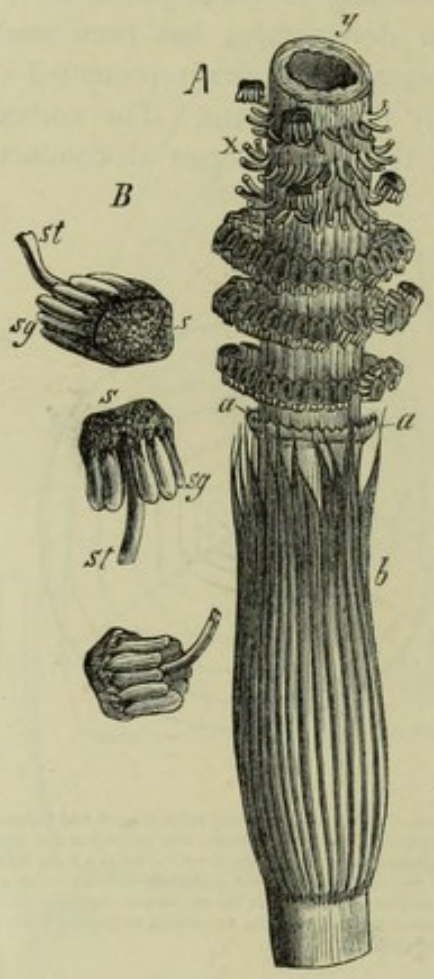

FIG. 279.—*Equisetum Telmateia*; *A* upper part of a fertile stem with the lower half of the spike (natural size), *b* leaf-sheath, *a* the annular 'bract,' *x* the pedicels of peltate scales which have been cut off, *y* transverse section of the rachis of the spike; *B* peltate scales in various positions (slightly magnified); *st* the pedicel, *s* the peltate scale, *sg* the sporangia.

[1] The formation of the spore-mother-cells from a single original central cell which occurs in Ferns and Rhizocarps, has been contrasted by Russow with that of Equisetum (compare p. 358).

peltate scale. The very thin-walled cells of the wall have previously formed spiral thickening-ridges on the dorsal, annular ones on the ventral side of the sporangium, arising, according to Duval-Jouve, in the case of *E. limosum*, with extraordinary rapidity immediately before the dehiscence. The development of the spores of Equisetum, after they have made their appearance as naked primordial cells by the division into four of their mother-cells, shows the peculiarity of a successive formation of distinct coats. Each spore forms first of all an outer non-cuticularised coat capable of swelling, which, splitting subsequently into two spiral bands, forms the so-called *Elaters*, a second and third coat soon afterwards making their appearance within it. All three lie at first closely one upon another like successive layers of a single coat; but when the spore is placed in water, the outer one, even at this period, swells up strongly and becomes detached from the others (Fig. 280, *B*). The three coats may be easily distinguished even in the quite fresh spore when placed in distilled water (*A*), (in the case of *E. limosum*), the outer one (1) being colourless, the second (2) light blue, and the third (3) yellowish. As

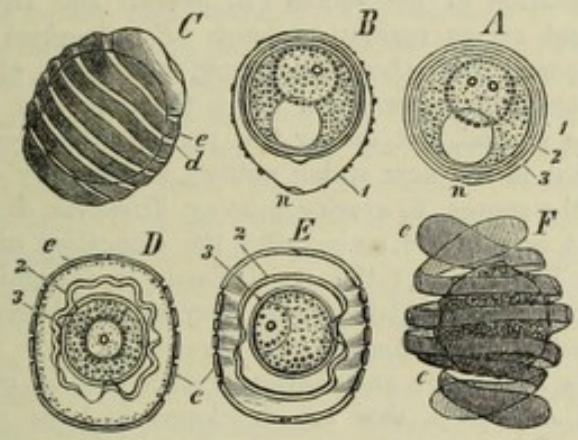

FIG. 280.—Development of the spores of *Equisetum limosum* (×800); *A* unripe spore with three coats just placed in water; *B* the same after two or three minutes in water, the outer coat having become separated, a large vacuole is seen by the side of the nucleus; *C* commencement of the formation of the elaters on the outer coat *c* (=1 in Figs. *A* and *B*); *D*, *E* the same stage of development in optical section after lying twelve hours in glycerine, *c* the outer coat; 2, 3, the inner coats separated from one another; *F* the outer coat split into spiral elaters, coloured a beautiful blue by Schultz's solution.

the development advances, the outer coat is separated like a loose investment from the body of the spore (*C*, *d*, *e*), and at the same time its division into elaters is first indicated. The optical longitudinal section shows that the spiral thickening-bands of this coat are separated only by very narrow spaces of thin membrane (*D*, *E*); these at length entirely disappear, and, when the surrounding air is dry, the thicker parts separate from one another as spiral bands, forming when unrolled a four-armed cross; they are united by their centre, and attached there to the second coat. It is probably this spot which may be recognized even in the unripe spore in the form of an umbilical thickening (*n* in *A* and *B*). In the fully developed elaters an external very thin cuticularised layer may be distinguished. They are extremely hygroscopic; when the air is damp they are rolled round the spore, but when dry are again unrolled. When this alternation takes place rapidly (as when lightly breathed on under the microscope), the spores are set in active motion by the bendings of the elaters. If spores, the outer coat of which

has not yet become split up into elaters, but which already show the corresponding differentiations (*D*, *E*), are allowed to lie for some time in glycerine, the spore contracts considerably, surrounded by its inner coat, while the second cuticularised coat raises itself from the former in folds. The inner coat is differentiated into an outer granular cuticularised exospore, and an inner endospore of cellulose.

Very little need be said about the *Classification* of Equisetaceæ, as all existing forms are so nearly related to one another that they may be included in a single genus, Equisetum. Even the Equisetaceæ of earlier geological periods, the Calamites, show, in the little that is still discernible of their organisation, the closest agreement with existing forms.

The *Habit* of the Equisetaceæ is, like their morphological structure, of a very characteristic kind. In all the plant is perennial by means of creeping underground rhizomes, from which ascending aërial shoots rise annually, mostly lasting only for one period of vegetation, less often for several years. The sporangiferous spikes appear either at the summit of these axes, which are at the same time the organs of assimilation, or on special fertile shoots which, when destitute of chlorophyll and unbranched, die after the dissemination of the spores (*E. arvense* and *Telmateia*), or throw off the terminal spike and act as vegetative shoots (*E. sylvaticum* and *pratense*). The fertile axes are developed from the underground internodes of the erect vegetative axes; they remain during the summer, in which the latter are unfolded, in the bud-condition beneath the ground, but during this period either develope their sporangiferous spikes so far that in the next spring nothing is necessary except elongation and the dissemination of the spores (*E. arvense*, *pratense*, *Telmateia*, &c.), or the spikes attain their full development only in the spring after the elongation of the axes which bear them (*E. limosum*). The habit of the aërial shoots is determined especially by the number and length of the verticillate usually very slender lateral branches; in some, as *E. hyemale*, *trachyodon*, *ramosissimum*, and *variegatum*, they are generally entirely wanting; in others, as *E. palustre* and *limosum*, rather few, in others again, as *E. arvense*, *Telmateia*, and *sylvaticum*, they are developed in large numbers. The height of this leafy stem is in our native species mostly from 1 to 3 feet; in *E. Telmateia*, where the ascending axis of the sterile shoots is colourless and destitute of chlorophyll, it attains a height of 4 or 5 feet and a thickness of about ½ inch; while the green slender leafy branches are even in this case scarcely ½ line thick. The tallest stems are produced by *E. giganteum* in South America, as much as 26 feet high, but only about the thickness of the thumb, and are kept in an upright position by neighbouring plants. The Calamites were as lofty, and as much as 1 foot thick. The rhizomes mostly creep at a depth of from 2 to 4 feet beneath the ground, and extend over areas 10 to 50 feet in diameter; but are also found at a much greater depth. They prefer damp, gravelly, or loamy soil, their thickness varying from 1 to 2 lines to as much as ½ inch or more. The surface of the internodes of the rhizome is, in some species, as *E. Telmateia* and *sylvaticum*, covered with a felt of brown root-hairs, which also clothe the leaf-sheaths of the underground part of ascending stems, a peculiarity which reminds one of Ferns. In some species, as *E. limosum* and *palustre*, the surface is smooth and shining, while in others it is dull. The ridges and furrows of the aërial stems are usually but little developed on the underground stems; sometimes the rhizomes are twisted. The central canal of the internodes is sometimes wanting in the rhizomes; but the lacunæ of the fibro-vascular bundles (carinal canals) and those of the cortical parenchyma (vallecular canals) are always present; the air which the tissues require and which is not found in the usually very compact soil is carried by these canals from the surface to the underground organs. As in the case of the spikes, the formation of the branches of the leafy stems has already commenced entirely or at least for the greater part in the preceding year in the underground bud, so that in the spring the internodes of the

ascending axis have only to extend and the slender lateral branches to unfold, as may be seen with especial ease in *E. Telmateia*. All the more important cell-formations and the processes of morphological differentiation thus take place underground; the aërial unfolding has for its main purpose only the dispersion of the spores and assimilation in the leafy shoots, by the exposure of the cortex, which contains chlorophyll, to light. The rapid growth of the upright stems in the spring is brought about especially by the simple elongation of the internodal cells already formed, although permanent intercalary growth of the internodes sometimes also takes place, and especially at their base within the sheaths. The tissues often remain there for a long time in the young state, and in *E. hyemale* the internodes, still short and lighter in colour after passing through the winter, push themselves out of their leaf-sheaths; the shorter they were before the winter, the more they elongate afterwards.

Special Organs for Vegetative Propagation, like those of Mosses, are not found in the Equisetaceæ any more than in Ferns; but every part of the rhizome, and the underground nodes of ascending stems, are adapted for the production of new stems. In some species some of the underground shoots swell up into ovoid (*E. arvense*) or pear-shaped (*E. Telmateia*) tubers about the size of a hazel-nut; Duval-Jouve states that these occur also in *E. palustre*, *sylvaticum*, and *littorale*, but in other species (*E. pratense*, *limosum*, *ramosissimum*, *variegatum*, and *hyemale*) they have not yet been observed. The tubers are produced by the rapid increase in thickness of an internode at the end of which is situated the terminal bud; this may repeatedly form tuberous internodes so that the tubers become moniliform, or they may develope simply as a rhizome, or sometimes a central internode of a rhizome is developed in a tuberous manner. The parenchyma of these tubers is filled with starch and other food-materials; they may apparently long remain dormant and form new stems under favourable circumstances.

Among the *Forms of Tissue* of the Equisetaceæ the epidermal system and the fundamental tissue are in particular developed in a great variety of ways. The fibro-vascular bundles, which in Ferns are so thick and so highly organised, especially in their xylem-portion, appear to be less developed in the Equisetaceæ; they are slender, the lignification of the xylem-portion very slight (as in many water and marsh plants); the firmness of their structure is chiefly due to the epidermal system with its highly developed epidermis, and to the hypodermal fibro-vascular bundles. What follows has special reference to the internodes; the leaf-sheaths are usually similarly constituted in their lower and central parts; at the teeth the tissue is simpler and more uniform.

The *Epidermal Cells* are mostly elongated in the direction of the axis, and are arranged in longitudinal rows separated by transverse or slightly oblique walls; the boundary-walls of the adjoining cells are often undulating. The epidermis of the underground internodes is almost always destitute of stomata, and consists of cells with either thick or thin walls, usually brown, which, in some species, as *E. Telmateia* and *arvense*, develope into delicate root-hairs. The epidermis of the deciduous sporangiferous stems of the species just named is similar to that of the rhizome and without stomata; and the same is the case with the upright colourless sterile stem of *E. Telmateia*. In all the aërial internodes which contain chlorophyll, the leaf-sheaths, and the outer surface of the peltate scales, the epidermis possesses numerous stomata which always lie in the channels, never on the ridges, and are arranged in longitudinal rows either single or lying close to one another. On the ridges the epidermal cells are long, in the channels between the stomata shorter. All the cells, even those of the stomata, have their outer walls strongly silicified, and exhibit very often on their outer surface protuberances of various forms, which are also and indeed peculiarly strongly silicified. These protuberances resemble fine granules, bosses, rosettes, rings, transverse bands, teeth, and spines; on the guard-cells they usually occur in the form of ridges, running at right angles to the orifice. The guard-cells are generally partially overreached by the neighbouring epidermal cells. The mature stoma appears to be formed of two pairs of guard-cells lying one over another; Strasburger asserts that these four cells

arise from one epidermal cell, and lie at first side by side at the same level. Only at a later period the two inner ones (the true guard-cells), become pressed inwards and overreached by the two outer ones which grow more rapidly. Bundles or layers of firm thick-walled cells (Hypodermal Tissue) are of common occurrence beneath the epidermis of rhizomes, of upright stems, and of their leafy shoots (with the exception of the deciduous sporangiferous stems). In the rhizomes they form a continuous stratum of brown-walled sclerenchyma consisting of several layers; in the aërial internodes they are colourless and are developed with especial prominence in the projecting ridges.

The *Fundamental Tissue* of the internodes consists in the main of a colourless thin-walled parenchyma occurring only in the rhizomes, the deciduous sporangiferous stems, and the colourless sterile axes of *E. Telmateia*. The green colouring of the other shoots is caused by layers consisting of from 1 to 3 strata of parenchyma containing chlorophyll (the cells lying transversely). This green tissue lies especially beneath the furrows, corresponding to the stomata, and forms on a transverse section ribbon-shaped masses concave outwardly; in the slender leafy branches, where the ridges sometimes cause the transverse section to have a stellate outline (*e.g. E. arvense*) the tissue containing chlorophyll is in excess. The vallecular canals, which correspond to the furrows, arise in the fundamental tissue by separation and partially by rupture of the cells; they may be absent from the slender leafy branches.

The *Fibro-vascular Bundles* are arranged, in a transverse section of the internodes, as in Dicotyledons, in a circle, each corresponding to a ridge of the surface, between the cortical canals but somewhat nearer the centre. In the axis of the sporangiferous stems, where the diaphragms are wanting, they run in the same manner, and bend out singly into the pedicels of the peltate scales (as in the sheath-teeth). The bundles of a shoot are all parallel to one another; each bundle is the result of the coalescence of two portions; one of these belongs to the leaf-sheath and developes in the median line of one of its teeth from below upwards; the other portion developes in the internode itself from above downwards. At the angle where the two portions meet, the formation of tissue begins in both, and thence advances in opposite directions; the lower end of each bundle unites by two lateral commissures with the two next alternate bundles of the next lower internode; and the Equisetaceæ have therefore only 'common' bundles. In transverse sections these bundles resemble the fibro-vascular ones of Monocotyledons, especially of Grasses; the first-formed annular, spiral, or reticulated vessels belonging to the inner side, together with the thin-walled cells which separate them, are subsequently destroyed, and a canal (carinal) remains in their place traversing the whole length of the fibro-vascular bundle on its inner side. Right and left of this lie on the outside a few not very broad vessels thickened reticulately; external to the canal lies the phloëm-part of the bundle, formed of a few wide sieve-tubes and narrow cambiform cells, and at the circumference of a few thick-walled narrow bast-like cells. These are all enveloped by a prosenchymatous tissue. A vascular-bundle-sheath, as it is termed, either surrounds each bundle or (varying with the species) runs continuously outside the circle of all the bundles; sometimes (as in *E. hyemale*, &c.), a similar layer of tissue is found on the inner side of the circle of bundles as well.

[Professor W. C. Williamson is led by a study of the internal organisation of Calamites and Calamodendra[1] to the conclusion that in England at least we have but one group of these fossil plants. When young their vascular zone, separating a medullary from a cortical parenchyma,

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[1] [On **Fossil Equisetaceæ**, see Williamson, Mem. Lit. Phil. Soc. Manch. 3rd ser. vol. IV, pp. 155–183; Ditto, Trans. Roy. Soc. vol. CLXI, pp. 477–510.—Coemans, Journ. Bot. 1869, pp. 337–340.—Dawson, Ann. Nat. Hist. 4th ser. vol. IV, pp. 272–273.—Grand'Eury, Ann. Nat. Hist. 4th ser. vol. IV, pp. 124–128; Compt. Rend. vol. LXVIII.—M°Nab, Journ. of Bot. 1873, pp. 72–80.—Ed.]

was scarcely more than a thin ring of longitudinal canals, each of which had a few vessels at its outer border In this state the structure of the plant presented a close resemblance to that of a recent Equisetum. But as the plant grew in size, new vessels were added to the exterior of the pre-existing bundles, so that each of the latter became the starting-point of a woody wedge which continued to grow peripherally until it assumed large dimensions. In some specimens these wedges measure fully two inches between the canal marking their medullary angle and their peripheral or cortical base. Each wedge is composed of vertical radiating laminæ of barred or reticulated vessels separated by cellular rays. The medullary portion became fistular, as in the recent Equisetaceæ at an early age, and the fistular cavities becoming filled with sand or mud, the very thin layer of medullary cells which remained did not prevent the sand from moulding itself against the inner angles of the vertical woody wedges, and thus produced the longitudinal grooves so characteristic of the casts commonly seen in collections. In such specimens most of the vegetable elements disappeared during fossilisation, and what remained in the shape of a thin film of coal moulded itself upon the medullary cast, and gave to the specimens the appearance of having had corresponding grooves upon their outer bark surfaces. No single example of a specimen of which the internal organisation is preserved—and we now possess these in great numbers—sustains this conclusion. Wherever the true bark is preserved it exhibits an outline indicating a smooth surface.

The longitudinal woody wedges of each internode alternated their arrangement at each node; the wedges of one internode becoming vertically superposed on the larger cellular masses separating the wedges in the nodes above and below. At each node an irregular verticil of vascular bundles left the vascular zone to supply some peripheral organs, probably branchlets; but besides these diverticula, in one large group an exceedingly regular verticil of canals, with circular or oblong sections, proceeded from the central fistular cavity through the woody zone to the bark. One of these canals occupied the uppermost end of each of the large cellular rays which separated the vascular wedges of each internode. In the common fossils these canals are indicated by a very regular verticil of small round or oblong impressions, which some writers have erroneously associated with roots, and others with vascular bundles going to leaves or branches. But they never contained any vascular tissues whatever. Of the leaves of Calamites we have no knowledge, although some have identified them with those of Asterophyllites and Sphenophyllum.

Professor Williamson has only obtained one example of a fruit which he can with confidence identify with Calamites (*Volkmannia Dawsoni*, Williamson, in Mem. Lit. Phil. Soc. Manch. 3rd ser. V. p. 28). It is a strobilus the structure of the axis of which corresponded most closely with that of a young Calamitean shoot. At each node it has a curiously perforated disk fringed with numerous peripheral bracts. From each disk there projects vertically upwards a ring of slender sporangiophores, around each of which were clustered three or four sporangia full of spores. These sporangia are so compactly compressed that a transverse section of this fruit presents the appearance of a compact mass of spores, amongst which the outlines of the sporangia are traceable with difficulty. Whilst he has failed to find any true stem in which the surface of the bark was fluted, that of the internodes of this fruit was undoubtedly so. He has not obtained more than half-a-dozen examples of Calamite-stems in which the outer bark is preserved. Nearly all the specimens are absolutely decorticated. Hence we cannot speak with certainty as to what may have been the condition of the surface of the bark in many of these plants. The flutings of the fruit-bark do not, like those seen in the carbonaceous film covering the common casts, correspond in number and position with those caused by the woody wedges, since two vascular bundles are located in each projecting ridge of the axis of the former structure, instead of one as in the latter.

Mr. Carruthers believes the fruits figured by Mr. Binney, Professor Schimper, and himself, under the several names of *Calamodendron commune*, *Calamostachys Binneyana*, and *Volkmannia Binneyi* (Journ. of Bot. 1867, pp. 349–356), to belong to Calamites; and he further regards the spores as having been furnished with elaters similar to those of Equisetum. Professor Williamson is unable to agree with either of these conclusions. He considers the supposed elaters to be merely fragments of the torn mother-cells of the spores, and that the affinities of these fruits are with the Lycopodiaceæ rather than with the Equisetaceæ.—Ed.]

CLASS VIII.

OPHIOGLOSSACEÆ[1].

The Sexual Generation. The prothallium is at present known only in *Ophioglossum pedunculosum* and *Botrychium Lunaria*. In both cases it is developed underground. It is destitute of chlorophyll, and forms a parenchymatous mass of tissue which, according to Mettenius, has at first, in the species first-named, the form of a small round tuber, out of which is subsequently developed a cylindrical vermiform shoot, which grows erect underground, is rarely and slightly branched, and elongates by means of a single apical cell. When the apex appears above

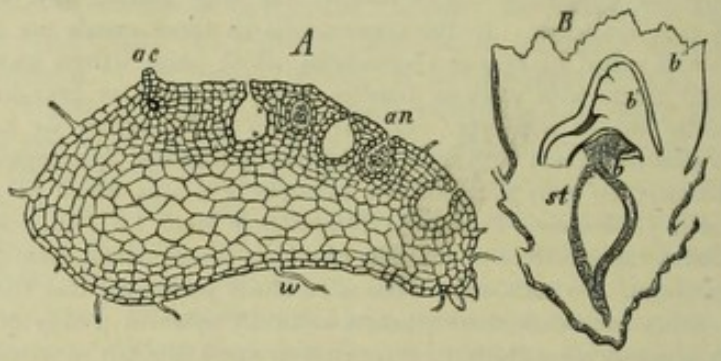

FIG. 281.—*Botrychium Lunaria*; *A* longitudinal section of prothallium (×50), *ac* an archegonium, *an* an antheridium, *w* root-hairs; *B* longitudinal section of the lower part of a young plant dug up in September (×20); *st* stem, *b b' b''* leaves (after Hofmeister).

ground and becomes green, it forms lobes and ceases to grow. The tissue of this prothallium is differentiated into an axial bundle of elongated, and a cortex of shorter parenchymatous cells, and the surface is clothed with root-hairs. With a transverse diameter of $\frac{1}{2}$ to $1\frac{1}{2}$ lines, it attains a length of from 2 lines to 2 inches. The prothallium of *Botrychium Lunaria* is, according to Hofmeister, an ovoid mass of firm cellular tissue, the greatest diameter of which does not exceed $\frac{1}{2}$ line, and is often much less (Fig. 281, *A*). It is light brown externally, yellowish white internally, and provided on all sides with sparse moderately long root-hairs. These prothallia are monœcious; each one produces a number of antheridia and archegonia, which are distributed with tolerable uniformity over the

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[1] Mettenius, Filices horti botanici Lipsiensis. Leipzig 1856, p. 119.—Hofmeister, Abhandlungen der königl. Sächs. Gesellsch. der Wissens. 1857, p. 657.—[On the Germination, Development and Fructification of the Higher Cryptogams, Ray Soc. 1862, pp. 307-317.]—On the probably near relationship between this class and Marattiaceæ, see p. 361.

whole of its upper surface, with the exception, in *O. pedunculosum*, of the small primary tuber; in Botrychium it is the lower side which chiefly bears antheridia. The *Antheridia* are cavities in the tissue of the prothallium covered externally by a few layers of cells, and in Ophioglossum only slightly projecting beyond the surface. In this genus the mother-cells of the antherozoids originate by repeated divisions from one or two cells of the inner tissue (covered externally by one or two layers of cells); they form a mass of tissue of roundish form. The antherozoids are similar in form to those of the Polypodiaceæ, but larger; they escape through a

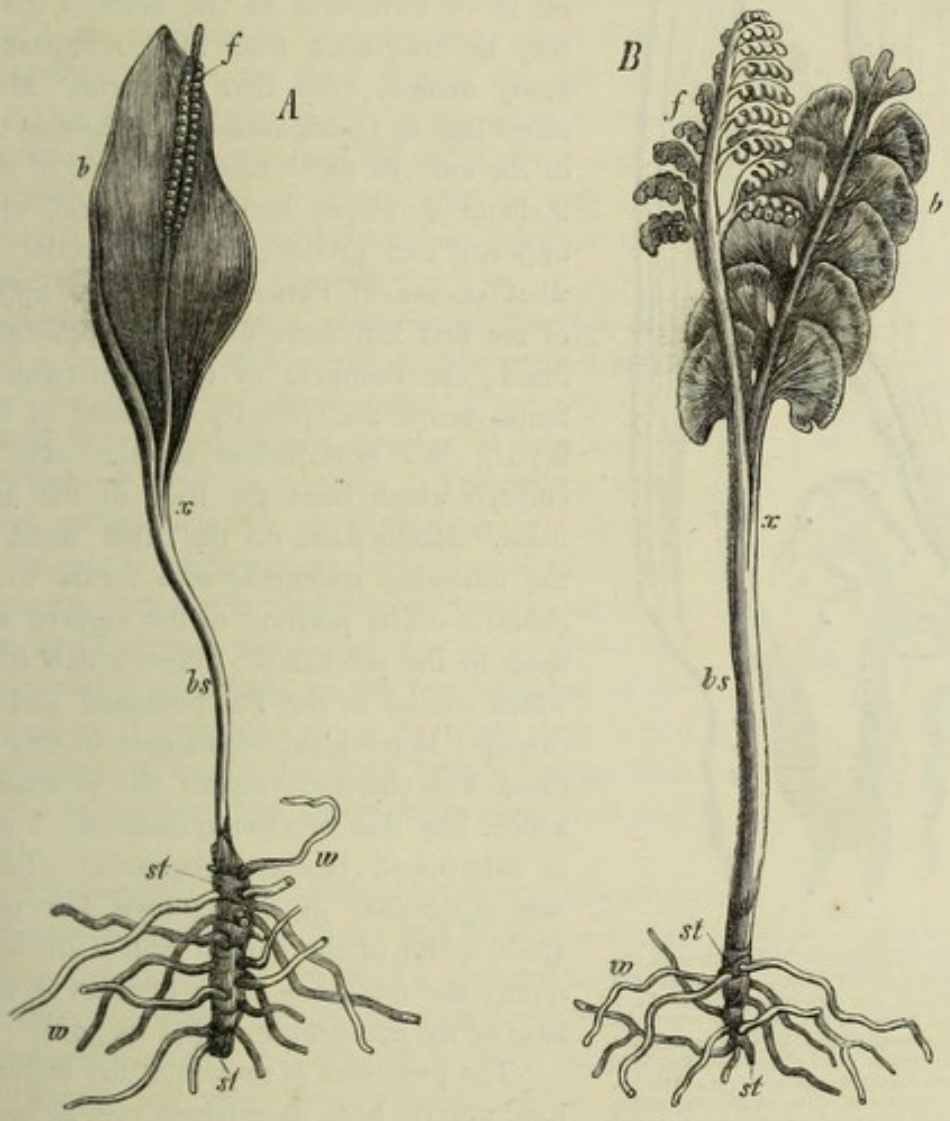

FIG. 282.—*A Ophioglossum vulgatum; B Botrychium Lunaria* (both natural size); *w* roots, *st* stem, *bs* leaf-stalk, *x* point where the leaf branches off, the sterile lamina *b* separating from the fertile branch or receptacle *f*.

narrow opening in the cover of the antheridium. The *Archegonia* are apparently developed in a similar manner to those of other Vascular Cryptogams. Mettenius saw in Ophioglossum instances in which they consisted of two cells, a superficial cell and one lying below it; this latter, he considered, became the central cell, the former producing the neck of the archegonium. Four covering cells of the central cell arranged in the form of a cross are first produced, which are then transformed, by further divisions, into four vertical rows each consisting of two or

more cells, and thus form the neck. The wall of the ventral part which surrounds the central cell is formed by divisions of the cells of the prothallium which surround it; the ventral part is therefore completely imbedded, and only the neck, which is usually very short, projects above the surface. Mettenius asserts that in Ophioglossum a prolongation of the oosphere (probably a canal-cell, as in Ferns and Rhizocarps), penetrates into the lower part of the neck.

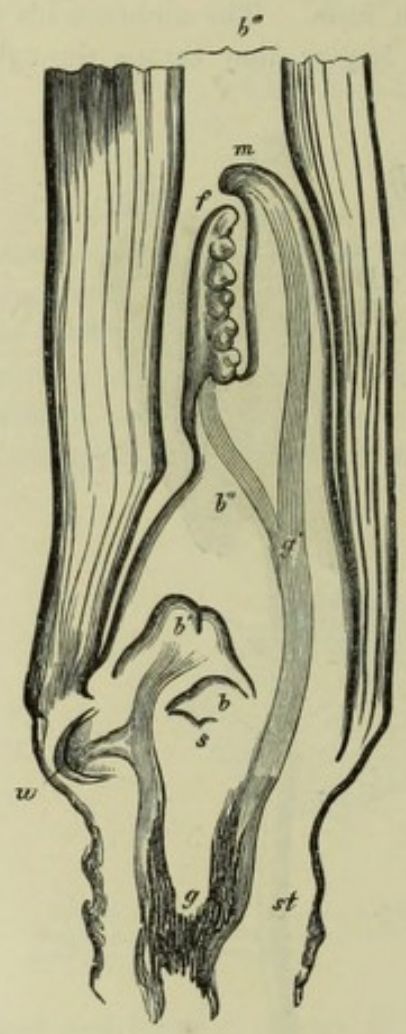

FIG. 283. — Longitudinal section through the lower part of a mature plant of *Botrychium Lunaria*. *st* stem, *g g'* fibro-vascular bundles, *w* a young root, *b* apex of the stem, *b b' b'' b'''* the four leaves already formed, *b'''* the one unfolded during the present year: *b'* shows the first indication of the branching of the leaf; in *b''* this has advanced further; *m* is the median line of the sterile lamina, having already its lobes right and left which are not shown; *f* the fertile lamina with the young ramifications, on which the sporangia will be produced (x about 10).

The Asexual Generation. The first divisions of the oospore are not known; but the mode of formation of the embryo differs, as may be concluded from the circumstances already named, from that of Ferns. Mettenius states that in *Ophioglossum pedunculosum* the end of the embryo which faces the apex of the prothallium developes into the first leaf, while the opposite end produces the first root. Unlike what occurs in Ferns, the concave upper side of the first leaf faces the neck of the archegonium; the rudiment of the stem (which Mettenius terms the 'primary rudiment of the embryo'), lies nevertheless on the side of the embryo which faces the base of the archegonium. Hofmeister, on the other hand, makes the following statement with regard to Botrychium:—'The position of the embryo with respect to the prothallium differs widely from that which occurs in the Polypodiaceæ and Rhizocarpeæ; Botrychium approaches in this respect those Vascular Cryptogams the prothallium of which, like that of Ophioglossaceæ, is destitute of chlorophyll (Isoëtes, Selaginella). The *punctum vegetationis* of the embryo lies near the apical point of the central cell of the archegonium; the first roots arise beneath it, near the base of the archegonium' (*l. c.* p. 308).

The processes of growth of the mature plant have not yet been ascertained with as much certainty as in other Vascular Cryptogams. In *Ophioglossum vulgatum* and *Botrychium Lunaria* the erect stem, buried deep in the earth and growing very slowly in length, appears never to branch. Even the comparatively thick roots rarely branch, and it is not known whether the branching is then monopodial or dichotomous. The flattened apex of the stem, surrounded by the insertions of the leaves, is buried deeply in the leaf-sheaths, and shows, in *Ophioglossum vulgatum*, according to Hofmeister, a three-sided pyramidal apical cell as seen from above. The leaves have a sheathing base, and each is completely enclosed in

the next older one, as shown in Fig. 283 in the case of *Botrychium Lunaria*. In Ophioglossum the relative positions of the parts at the end of the stem are still more complicated, from the fact that the rudimentary leaves, while completely enclosed one within another, produce ligular structures which grow together so completely that each leaf appears as if enclosed in a kind of chamber formed by the cohesion of the ligular parts of leaves of different ages, recalling a similar structure in Marattia. These cohesions however leave an opening at the apex of each chamber; the apex of the stem is therefore exposed to the air through a narrow canal (Hofmeister).

As soon as the leaves have attained a certain age, each leaf bears a collection of sporangia, which form a branch springing from the axial side of the leaf (in *O. palmatum* two or more such 'fertile segments' are formed). In the genus Ophioglossum both the outer sterile and the fertile branch of the leaf are unbranched or only lobed (*O. palmatum*); in the genus Botrychium both are again branched and in parallel planes (Fig. 282, *A* and *B*). The earlier hypothesis of a cohesion of the two leaf-stalks of a fertile and of a sterile leaf is at once negatived by the history of development (Fig. 283), and would lead to very complicated theories of stem-branching, of which we have no evidence. The history of development rather indicates, as Hofmeister first showed, that the receptacle originates on the inner side of the leaf. In the mature state the fertile leaf-branch either separates from the sterile (green) one at the base or at the middle of the lamina (*O. pendulum*), or the two branches of the leaf appear as if separated deep down to their origin (*O. bergianum*), or, finally, the fertile branch springs from the middle of the leaf-stalk (*Botrychium rutæfolium* and *dissectum*).

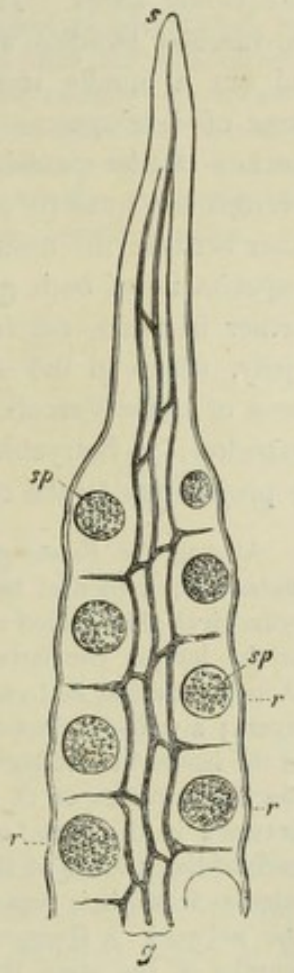

FIG. 284.—Longitudinal section through the upper part of a spike of *Ophioglossum vulgatum*: *s* its free apex, *sp* the sporangial cavities, *r* the part where they burst transversely; *g* the fibro-vascular bundles (× about 10).

The *Sporangia* of the Ophioglossaceæ are so essentially different from those of Ferns and Rhizocarps that these plants cannot, for this reason, be arranged in either of these classes; whether they differ as greatly from those of the Equisetaceæ and Lycopodiaceæ is yet to be proved by the history of their development. They agree with the sporangia of all Vascular Cryptogams in the one point of belonging to the leaves. The history of their development is not yet accurately known; but from the half-ripe states which I have been able to examine in *B. Lunaria* and *O. vulgatum*, it is evident that the sporangia cannot be products of single epidermal cells, as in Ferns and Rhizocarps, but that their origin more resembles that of the pollen-sac of the anthers of many Angiosperms. Each sporangium is, in Botrychium, an entire lobe of a leaf, the inner tissue of which produces the mother-cells of the spores. A longitudinal section through the unripe so-called spike of *O. vulgatum* (Fig. 284) shows that the outer layer of the wall of the sporangium is a continuous

prolongation of the epidermis provided with stomata and covering the whole of the fertile branch of the leaf. At the places where the lateral transverse line of dehiscence subsequently appears in each sporangium, these epidermal cells are elongated radially, and the whole layer exhibits an indentation at first scarcely perceptible. The spherical cavities which contain the masses of spores are imbedded in the tissue of the organ, and are therefore entirely surrounded by its parenchyma; this is found also in several layers on the outer side where the transverse fissure subsequently arises. The middle part of the parenchyma is penetrated by three fibro-vascular bundles which anastomose with one another into long meshes, and send out a bundle transversely between each pair of sporangial cavities. The course of development is the same in Botrychium, if the separate sporangiferous branches of the panicle are compared with the spike of Ophioglossum. The sporangia are similarly placed on them in two rows and alternate; only they project further because the tissue between each pair of sporangia is but slightly developed. In specimens of both genera preserved in spirits the young spores still connected together in fours, are found imbedded in a colourless, granular, coagulated mass of jelly, which in the living plant clearly corresponds to the fluid in which the spores of other Vascular Cryptogams float before they are ripe. The spores are tetrahedral; in Botrychium they are provided, even in a very early state, with knob-like projections on the cuticularised exospore.

Among the *Forms of Tissue* of the Ophioglossaceæ, the prevailing one is parenchymatous fundamental tissue. It consists, especially in the leaf-stalk, of long, almost cylindrical, thin-walled succulent cells with straight septa and large intercellular spaces; in the lamina the latter are, in *O. vulgatum*, very large, and the tissue spongy. In *O. vulgatum* and *B. Lunaria*, the epidermal tissue nowhere possesses special hypodermal layers; a well-developed epidermis with numerous stomata on the upper and under side of the leaves immediately covers the outer layers of the fundamental tissue. The fibro-vascular bundles of *O. vulgatum* form, according to Hofmeister, a hollow cylindrical network in the stem, on which the leaves are arranged spirally, with a $\frac{2}{5}$ phyllotaxis; each of the meshes of this network corresponds to a leaf, and gives off to it the foliar bundles from their superior angle. The whole of the tissue which fills up the meshes of the network is frequently transformed into scalariform vessels, so that considerable lengths of the stem then form a closed hollow cylinder; this sometimes occurs on one side only. The leaf-stalk is penetrated by from 5 to 8 slender fibro-vascular bundles, which, in transverse section, are arranged in a circle, and between which the fundamental tissue presents wide lacunæ. Each of these bundles has on its axial side a strong fascicle of narrow reticulately thickened vessels, a broad fascicle of soft bast (phloëm) lying on their peripheral side. In the sterile lamina the slender bundles branch copiously and anastomose into a network; they run into the mesophyll which contains chlorophyll, without forming projecting veins. The slender stem of *B. Lunaria* has the same structure as that of Ophioglossum; its vascular bundles appear to be only the lower ends of the foliar bundles (Fig. 283). In each leaf-stalk, which has a conical hollow below obliterated above, arise two broad ligulate bundles, which split above, below where the leaf divides into the fertile and sterile laminæ, into four narrower bundles. Each of these latter consists of a broad axial fascicle of tracheïdes thickened in a scalariform or reticulated manner, which is enveloped by a thick layer of phloëm. This layer shows an inner stratum of narrow cambiform cells, while the outside is formed of soft thick-walled bast-like prosenchyma (as in Pteris and other Ferns). In the lobes of the sterile lamina the bundles split repeatedly dichotomously, and run through the mesophyll without forming projecting veins.

Habit and Mode of Life. The number of leaves which appear each year is small, and constant in the species; thus *O. vulgatum* and *B. Lunaria* unfold only a single leaf annually, *B. rutæfolium* two, a sterile and a fertile one; *O. pedunculosum* from 2 to 4 (Mettenius). The extremely slow development of the leaves is remarkable; in *B. Lunaria* each leaf requires four years, of which the three first are passed underground; in the second the two branches (the sterile and fertile laminæ) are formed, and further developed in the third; in the fourth year they for the first time rise above ground (Fig. 283), the process reminding one of the slow formation of the leaves of *Pteris aquilina;* the same occurs in *O. vulgatum.*

Vegetative Reproduction takes place in Ophioglossum by means of adventitious buds from the roots. *O. pedunculosum* is so far monocarpous that, after the production of fertile leaves, it as a rule dies down, but maintains a perennial existence by means of the root-buds (Hofmeister). Most species are only, reckoning from the base of the stem to the apex of the leaf, 5 or 6 inches high; a few attain the height of a foot; *B. lanuginosum* of the East Indies is stated by Milde to be 3 feet high; the leaf is three or four times pinnate, and the stem contains from 10 to 17 fibro-vascular bundles.

CLASS IX.

RHIZOCARPEÆ[1].

1. *The Sexual Generation* of Rhizocarps is developed from spores of two different kinds; the smaller spores produce antherozoids, and are therefore male; the larger spores, which exceed the smaller kind several hundred times in size, produce a small prothallium, which never separates from them, and forms one or several archegonia; the macrospores may therefore be considered to be female.

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[1] G. W. Bischoff, Die Rhizocarpeen u. Lycopodiaceen (Nürnberg 1828).—Hofmeister, Vergleich. Untersuch. 1851, p. 103.—[On the Germination, Development, and Fructification of the Higher Cryptogams, Ray Soc. 1862, pp. 318–335.]—Ditto, Ueber die Keimung der *Salvinia natans* (Abhand. der königl. Sächs. Gesellsch. der Wissensch. 1857, p. 665).—Pringsheim, Zur Morphologie der *Salvinia natans* (Jahrb. für wissensch. Bot. vol. III. 1863).—J. Hanstein, Ueber eine neuholländische Marsilia (Monatsber. der Berliner Akad. 1862, Ann. des Sci. Nat. 4th series, vol. XX, 1863, pp. 149–166).—Ditto, Befruchtung u. Entwickelung der Gattung Marsilia (Jahrb. für wissensch. Bot. vol. IV, 1865).—Ditto, Pilulariæ globuliferæ generatio, cum Marsilia comparata (Bonn 1866).—Nägeli u. Leitgeb, Ueber Entstehung u. Wachsthum der Wurzeln bei den Gefässkryptogamen (Berichte der bayer. Akad. der Wissensch. 1866, Dec. 15, and Nägeli's Beiträge zur wissensch. Bot. vol. IV. 1867).—Millardet, Le Prothallium male des Cryptogames vasculaires (Strasbourg 1869).—A. Braun, Ueber Marsilia u. Pilularia (Monatsber. der königl. Akad. der Wissensch. Berlin, Aug. 1870).—E. Russow, Histologie u. Entwickelung der Sporenfrucht von Marsilia (Dorpat 1871). [Strasburger, Ueber Azolla, mit 7 Tafeln. Jena 1873.]

The development of the *Antherozoids* is preceded, in the genus Salvinia, by the formation of a very rudimentary male prothallium. The microspores lie imbedded in a mass of granular hardened mucilage, which fills up the whole of the microsporangium; they do not escape, but each of them emits from its endospore a tube which pierces the mucilage and the wall of the sporangium and forms a septum at its curved end (Fig. 285, *A* and *B*). The terminal cell of the tube thus produced is again divided by an oblique wall, after which the protoplasm contracts in the two cells (which Pringsheim together calls the antheridium), and splits up by repeated bipartition into four roundish primordial cells, each of which forms an antherozoid.

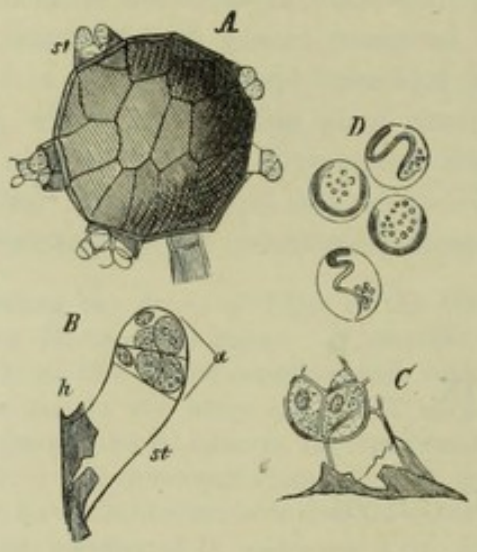

FIG. 285.—*Salvinia natans*; *A* an entire microsporangium, the tubes of the microspores *st* breaking through (× about 100); *B* one of these tubes *st* protruding from the envelope of the microsporangium *h* (× about 200), *a* the antheridium still closed; *C* tube with the empty antheridium; *D* antherozoids (× 500) (after Pringsheim).

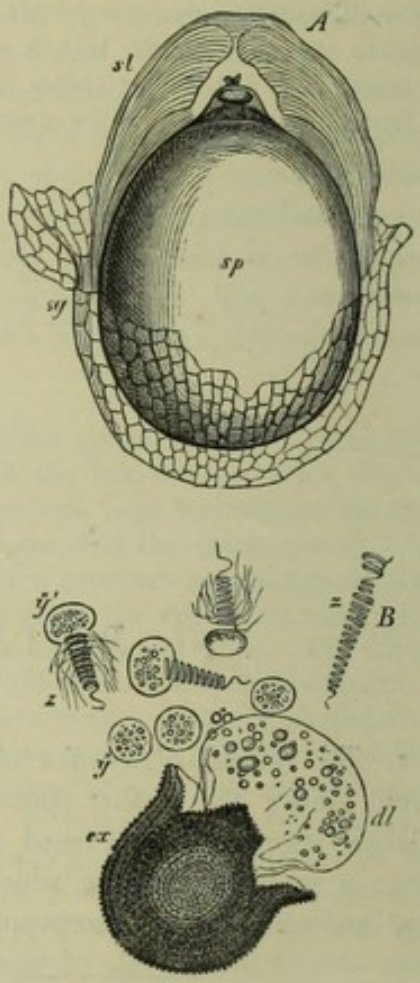

FIG. 286.—*Marsilea salvatrix*; *A* macrospore *sp* with its mucilaginous envelope *sl* and the apical papilla projecting into its funnel: in the papilla is a broad yellowish drop, *sg* the ruptured wall of the macrosporangium (× about 30). *B* a microspore burst after the escape of the antherozoids; *ex* the exospore, *dl* the protruding endospore containing granules, *z*, *z* the spiral antherozoids, *y*, *y* their vesicles containing starch-grains. The mucilaginous envelope of the microspore is no longer in existence (× 550). (The exospore does not show the regular arrangement of the protuberances, which is indicated erroneously in the figure.)

In addition a small portion of the contents remains inactive in each of the two cells. The antheridial cells burst by transverse slits to allow the escape of the antherozoids. The spirally curved body of the antherozoid lies in (?) a vesicle, which, according to Pringsheim, it does not leave even during the 'swarming.' In Marsilea and Pilularia the antherozoids are produced in the interior of the microspores themselves; their protoplasmic contents contract into a longish round lump placed eccentrically, which separates into eight primordial cells by three successive

divisions at right angles to one another; each of the latter is divided into four portions disposed tetrahedrally. The 32 smaller primordial cells which are formed in this manner became surrounded with thin cell-walls, and are the mother-cells of the antherozoids (Hanstein). This cellular body which produces the antherozoids is called by Millardet the Antheridium, since he considers the space between it and the endospore filled with sap (in which at first a number of starch-granules lie) as a rudimentary indication of a male prothallium, a view which, although it sounds singular, appears confirmed by the behaviour of the microspores of Isoëtes and Selaginella. As in Ferns, we find also in Rhizocarps only a portion of the contents of the mother-cell applied to the formation of the antherozoid. According to Millardet[1], this portion assumes the form of a roundish turbid lump consisting of protoplasm and starch-granules, which, during the formation of the antherozoids, becomes gradually clearer, and, when the latter escape from the mother-cell, forms a vesicle consisting of the unused protoplasm and the starch-granules lying in it. In Pilularia, where the antherozoid is a thread coiled four or five times, this vesicle remains attached to the mother-cell. In Marsilea, on the contrary, it adheres to the posterior coils of the corkscrew-like antherozoid, which is coiled 12 or 13 times; and is often carried about with it for a considerable time by its swarming motion, but finally becomes detached. When the antherozoids are formed in their mother-cells, the exospore bursts at the apex, the endospore swells up as a hyaline bladder, which finally bursts and allows the escape of the antherozoids (Fig. 286, *B*).

The *Female Prothallium* is formed within the apical papilla of the macrospore from a small part of its protoplasm, and only partially emerges at a later period from the spore-cavity, but remains united with the latter, closing it by its basal surface, for the purpose of using up the food-materials (starch-grains, fatty oil, and albuminous substances) which are stored up there. The separate stages in the first formation of the prothallium are still in many respects not clear; but it is certain that it arises from a collection of protoplasm in the cavity of the papilla; this protoplasm immediately breaks up into several cells, which, according to Hanstein (in Marsilea and Pilularia) become clothed only at a later period with cell-walls and thus form a tissue. The further processes seem to me, according to the statements of Pringsheim, Hanstein, and Hofmeister, compared with my own observations on *Marsilea salvatrix*, to be briefly:—the tissue of the prothallium is for a certain time completely enclosed in the apical papilla of the macrospore, covered above by the epidermal layers of the apex of the spore itself, and shut off from the spore-cavity below by a lamella of cellulose which is stretched across like a diaphragm and is attached at the circumference to the endospore. By the further growth of the prothallium the epidermal layers of the papilla are ruptured above, the dorsal part of the prothallium projects into the funnel-shaped cavity which is left by the absence of the thick epidermal layers of the macrospore; subsequently the diaphragm arches convexly, and the prothallium is thus pushed further outwards. This is the present state of our knowledge with respect to the position of the prothallium in the macrospore. (Compare the explanations of the figures further on).

[1] For the different view adopted by Hanstein, *vide l. c.*

The prothallium of *Salvinia natans*[1] attains a much more considerable size than that of the two other genera already mentioned; it is destitute of chlorophyll, and forms a number (which may even be large) of archegonia in definite positions. After it has broken through the membrane of the papilla, it appears seen from above, as three-sided between the three torn lobes of the exospore; one of these sides is anterior; the two posterior sides meet behind at an acute angle; a line from this angle to the centre of the anterior side runs above the elevated saddle-shaped back of the prothallium, and forms its median line. The anterior side projects above the back, and, where it meets the two posterior sides, the two angles grow subsequently into long wing-like prolongations hanging down by the sides of the macrospore. The first archegonium makes its appearance on the median line of the elevated back immediately behind the growing anterior side of the prothallium;

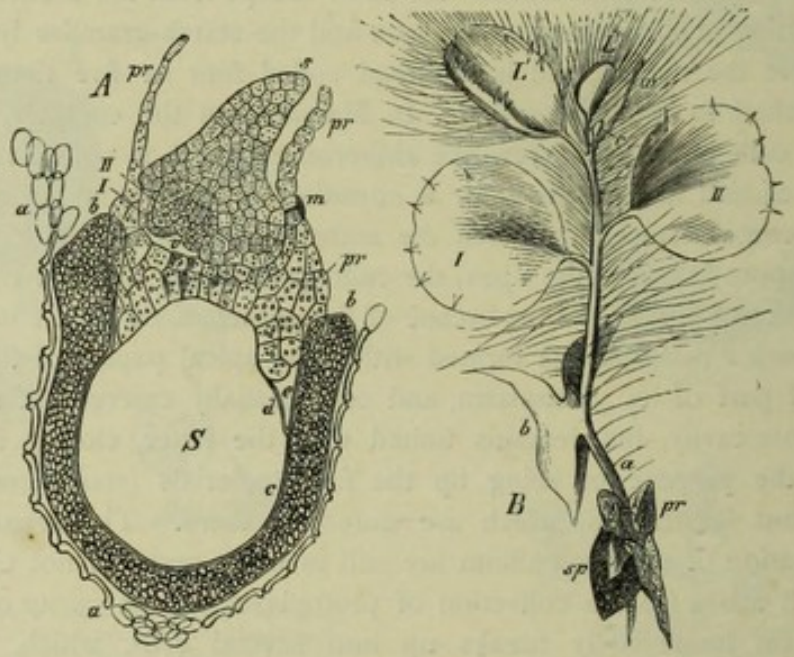

FIG 287.—*Salvinia natans* (after Pringsheim). *A* longitudinal section through the macrospore, prothallium, and embryo in the median line of the prothallium (× about 70), *a* layer of cells of the sporangium, *b* exospore, *c* endospore, *c* its prolongation, *d* the diaphragm mentioned above which separates the prothallium from the spore-cavity, *pr* the prothallium already broken through by the embryo, *I*, *II* its two first leaves, *s* the scutiform leaf; *B* an older seedling with the spore *sp* and prothallium *pr* (× 20), *a* the pedicel, *b* the scutiform leaf, *I*, *II* first and second single leaves, *L*, *L'* aërial leaves of the first whorl, *w* submerged leaf of the first whorl.

two other archegonia then invariably appear right and left of the first, so that they stand in a transverse row parallel to the anterior side. If one of these archegonia is fertilised there is an end of the growth of the prothallium; but if this does not happen, the prothallium continues to grow on its anterior side, and from 1 to 3 new transverse rows of archegonia are produced, each of which contains from 3 to 7. The long central cell of each archegonium lies obliquely in the tissue of the prothallium, so that the outer (neck) end faces backwards, its inner deeper end facing the anterior surface. At this latter point lies at a subsequent period the apical cell of the embryonal stem. Young archegonia have the apex of their central cell

[1] All that is said about Salvinia is from Pringsheim, *l. c.*

covered with four superficial cells arranged in the form of a cross; in each of these latter a wall arises inclined from without inwards, followed in each inner cell by another similar partition (Fig. 288 *I*, *a*, *b*, *c*). By the succeeding growth these cells are transformed into four rows each consisting of three segments lying one above another (*II*, *III*), the lower of which are termed 'closing cells,' the upper pair the neck (*III*, *h*). In the meantime a new cell arises at the apex of the central cell, which, with its conical point, forces itself between the closing cells (*I*, *d*, *III*, *d*), and forms the canal-cell, first discovered by Pringsheim. It becomes transformed into mucilage, which escapes from the canal laid open by the throwing off of the neck. The whole contents of the central cell (*I*, *II*, *III*, *e*) becomes the oosphere. After fertilisation has been accomplished, the canal again closes by the lateral approximation of the closing cells.

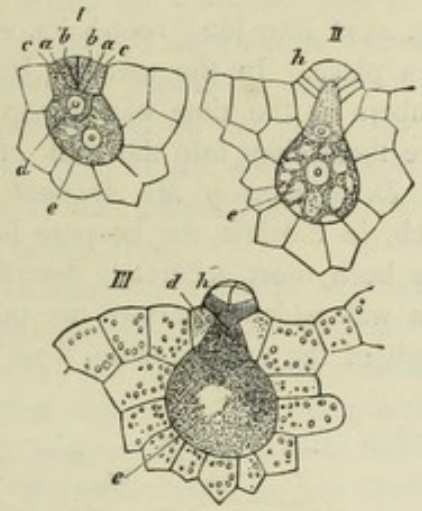

FIG. 288.—Development of the archegonia of *Salvinia natans* (after Pringsheim, ×150).

The prothallium of Marsilea and Pilularia is developed as a hemispherical mass of tissue from the apical papilla of the macrospore, after it has ruptured the cell-walls of the spore at that place (Fig. 290, *A*, *B*), and remains buried at the bottom of the funnel formed from the outer membranes of the macrospore. Even at an early period, before the rupture, Hanstein asserts that the large central cell may be recognized in it, surrounded, in its entire circumference, at least at first, by a single layer of cells, so that the prothallium bears originally in this case only a single archegonium. The central cell is here also covered by four cells arranged as a cross, which form at the same time the apex of the whole prothallium. By a similar process to that which occurs in Salvinia, they form the free neck-portion (which in Marsilea projects only slightly, in Pilularia very much) and the closing cells of the archegonium. Above the central cell, the protoplasm of which contracts, a small canal-cell is visible, according to Hanstein, penetrating between the closing cells, and behaving as in Salvinia. Even Hanstein was unable to recognize any further cell-formation within the central cell; the whole of

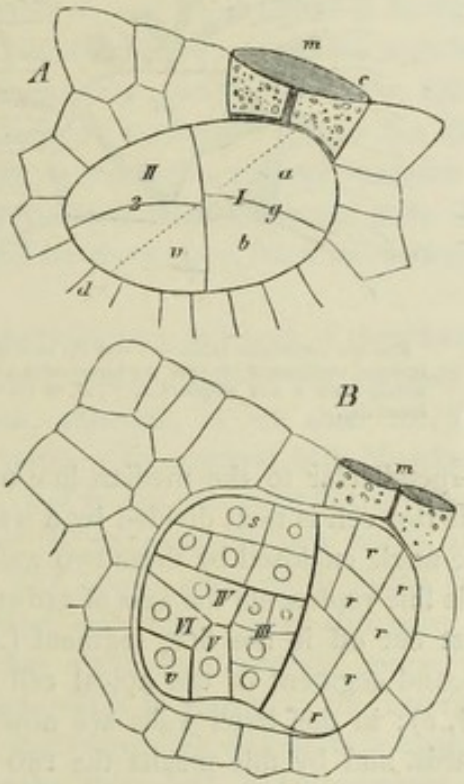

FIG. 289.—*Salvinia natans*; median longitudinal section through the prothallium and young embryo; *A* after the first three divisions of the oospore, *I* the first segment divided by the wall *y* into the cells *a* and *b*; *II* the second segment, cut off by the wall 2 from the apical cell *v*; *cd* axis of growth; *B* embryo in a further stage of development, *r r r* first stage of the foot, *s* apical cell of the scutiform leaf, *III*—*VI* the succeeding segments, *v* apical cell of the stem, *m* in *A* and *B* the closing cells of the archegonium (after Pringsheim).

its protoplasmic body is converted into the oosphere. After fertilisation the layer of tissue of the prothallium surrounding the central cell becomes double; a few granules of chlorophyll arise in it, and the outer cells grow in *Marsilea salvatrix* (Fig. 291) into long root-hairs, which are especially luxuriant when no fertilisation takes place. In the case of *Marsilea salvatrix* the antherozoids collect in large numbers at the time of impregnation in the funnel above the prothallium, and force themselves into the neck of the archegonium[1].

Development of the Asexual Generation. The first processes of division by which, in Salvinia, the oospore is transformed, after fertilisation, into the embryo, have been most accurately described by Pringsheim. The first division is effected by a wall which separates the posterior piece of the oospore, above which is the mouth of the archegonium, from the anterior piece, which is usually larger; it is

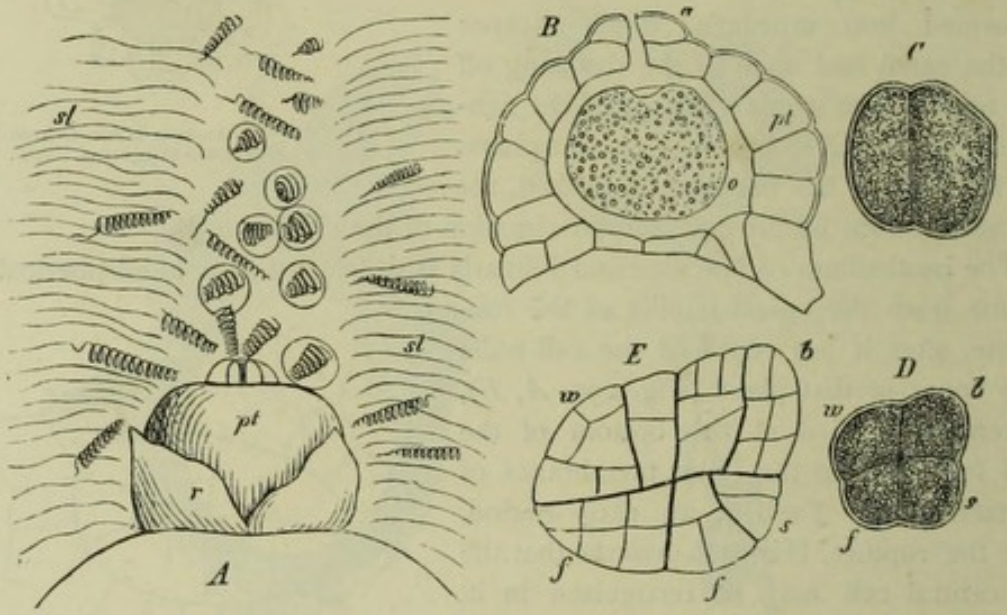

FIG. 290.—*Marsilea salvatrix*; *A* *pt* the prothallium projecting through the ruptured membrane *r* of the spore; *sl* the layers of mucilage which form the funnel, with a number of antherozoids; *B* vertical section of a prothallium *pt* with an archegonium *a* and oosphere *o*; *C*, *D*, *E* young embryos, *s* apex of the stem, *b* leaf, *w* root, *f* foot (*B*—*E* after Hanstein).

perpendicular to the median line of the prothallium and to its basal surface. The anterior cell is next divided by a wall nearly at right angles to the previous one. If the angle enclosed by these two walls is bisected by a straight line (Fig. 289, *A*, *c*, *d*), this line represents the axis of growth of the stem; the posterior piece of the oospore first cut off is the first segment (*A*, *I*), the cell cut off by the second wall is the second segment of the apical cell of the stem which now lies in front and below (*A*, *v*); in this latter walls are now formed inclined alternately upwards and downwards, and by this means the two rows of segments are formed out of which the structure of the stem of Salvinia is gradually developed. In Fig. 289 *B* are shown, at *III*, *IV*, *V*, and *VI*, these segment-cells undergoing still further division. No root is developed either at this period or subsequently; Salvinia is absolutely rootless.

[1] For further details see Hanstein, Jahrb. für wiss. Bot. vol. IV.

In order to understand the subsequent processes of growth, Fig. 287 must be compared with Fig. 289. The growing embryo bursts the prothallium; from the whole of the first segment (Fig. 289 *B*, *r*, *r*, *r*) arises the so-called *Foot* of the young plant (Fig. 287 *a*); from the whole of the second segment is formed a peculiar foliar structure, differing from all the subsequent leaves, the *Scutiform leaf* (Fig. 287 *B*, *b*), by the growth of which the terminal bud of the stem becomes directed downwards (Fig. 287 *A*, *v*). The anterior part of the embryo faces the anterior side, its posterior part the posterior side of the prothallium; its axis of growth lies in the same plane with the median line of the latter.

The first divisions of the embryo of *Marsilea salvatrix* agree in all essential points, according to Hanstein's observations and my own, with those of Salvinia; and Hanstein states that this is also the case with Pilularia; but in both these genera the rudiment of the first root is visible at once in the first segment. The stem in these genera also creeps or floats in a horizontal direction from the first, as in Salvinia, forming a number of roots in acropetal succession. Fig. 290 shows the first divisions of the embryo of *Marsilea salvatrix*. The oospore is divided by a nearly vertical wall into an anterior larger and a posterior smaller cell; the former splits up by an almost horizontal wall into an upper segment which forms the first leaf; the latter (*i. e.* according to the type of Salvinia the first segment of the apical cell of the stem) also splits up into two cells, lying one over the other, the upper of which produces the first root. The union between embryo and prothallium is brought about by the foot, which is formed out of the posterior inferior segment together with the posterior half of the anterior inferior segment (Fig. 290 *Eff*). The apical cell of the stem, the anterior half of the anterior inferior segment, Fig. 290 *Es*, thus lies, after the formation of the first three segments, between the anterior margins of the first leaf and of the foot. In the stage represented in Fig. 299 (p. 398) this origin of the first leaf, first root, and foot, may still be recognised from the arrangement of the cells.

The further growth of the three genera, otherwise very different in their habit, agrees in maintaining the bilateral structure already manifested in the embryo in connection with the decidedly horizontal growth, although, as we shall see, the position of the apical cell and of its segments varies. In contrast with Muscineæ and Equisetaceæ, but in accordance with Ferns, a leaf is not produced in the Rhizocarpeæ from every segment of the stem; some of the segments remain sterile, and these then go to the formation of internodes. The leaves grow, as in Ferns and Ophioglossaceæ, basifugally by means of an apical cell which forms two rows of alternating segments. Before the development has assumed a constant course, an increase of vigour of the young plant takes place, which is shown in the enlargement of the leaves and the greater perfection of their forms, as well as in a change of their relative positions. But in order to make this clear, it is necessary to observe separately Salvinia on the one hand, and the Marsileaceæ (Marsilea and Pilularia) on the other.

The embryo of Salvinia, as long as it is enclosed in the prothallium, forms, as we have seen, the segments of its apical cell alternately above and below; but when the apex of the stem is exposed in consequence of its elongation, a torsion takes place to the extent of about 90°, so that the two rows of alternate segments of the

apical cell lie right and left, a peculiarity which has also been observed by Hofmeister in *Pteris aquilina*. The first leaf is the scutiform leaf mentioned above, which is placed medio-dorsally; then follow a second and third aërial leaf standing singly, after which the definite verticillate arrangement of the leaves at length commences at the fourth node; each whorl thereafter consists of a submerged leaf springing on the ventral side (right or left), which at once branches, and forms a tuft of long filaments hanging down into the water; while two other leaves have quite flat laminæ and spring from the dorsal side, touching the water only with their under surface (Fig. 295). These three-leaved whorls alternate, and thus form two rows of ventral submerged, and four rows of dorsal aërial leaves. Their succession in age in the whorl, and the position of the whorls (antidromal among themselves) is indicated in Fig. 290 *a*. The node of the stem which produces a whorl of leaves, is, as was shown by Pringsheim, formed of a transverse disc of the long

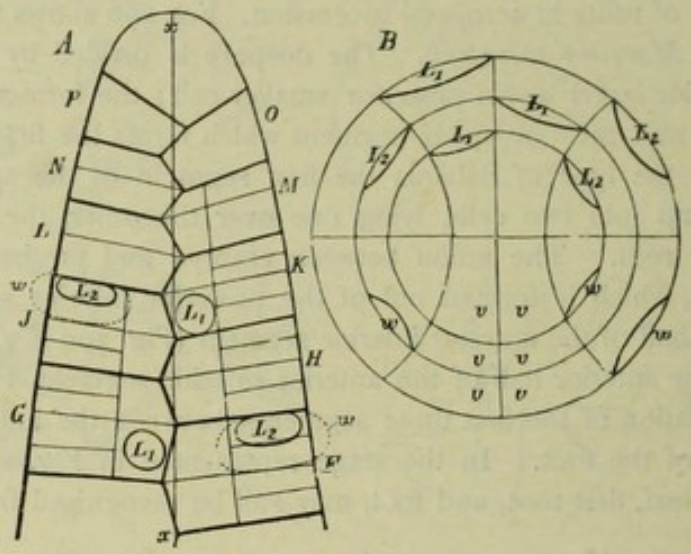

FIG. 290 *a*.—*A* the vegetative cone of the stem of *Salvinia natans*, regarded diagrammatically and looked at from above; *x x* projection of the plane which divides it vertically into a right and left half; the segments are indicated by stronger outlines, their divisions by weaker lines; the succession of the segments is denoted by the letters *F*—*P*; *B* diagram of the stem with three whorls of leaves, its ventral side indicated by *v v*; *w* the first-formed submerged leaf; L_1 the aërial leaf formed next; L_2 the second aërial leaf of the same whorl formed last of all between the two first (after Pringsheim).

vegetative cone, which, in its length (or height) corresponds to a half-segment, while each internode corresponds to the whole height of a segment. Each nodal disc, as well as each internode, consists of cells of the right and left row of segments of different ages; in Fig. 290 *a* an internode is formed of the segment *H* on the right side, of the anterior half of the older segment, *G*, and of the posterior half of the younger segment, *J*, on the left side; the next internode is the product of the whole of the left segment, *L* and of the two halves of *K* and *H* lying to the right; the intermediate nodal disc which forms the leaves *w*, L_1, L_2 consists, on the other hand, of the anterior half of the left older segment *J* and of the posterior half of the right younger segment *K*; in the preceding and succeeding node the relationships are the same, right and left being transposed. In each whorl the submerged leaf is the oldest, the one further from it of the two aërial leaves the second; the nearer aërial leaf is the last formed. Each leaf arises from a cell of definite position,

which becomes arched outwards (Fig. 291, B, L_1, L_2), and, becoming the apical cell of the leaf, forms a row of segments on each side.

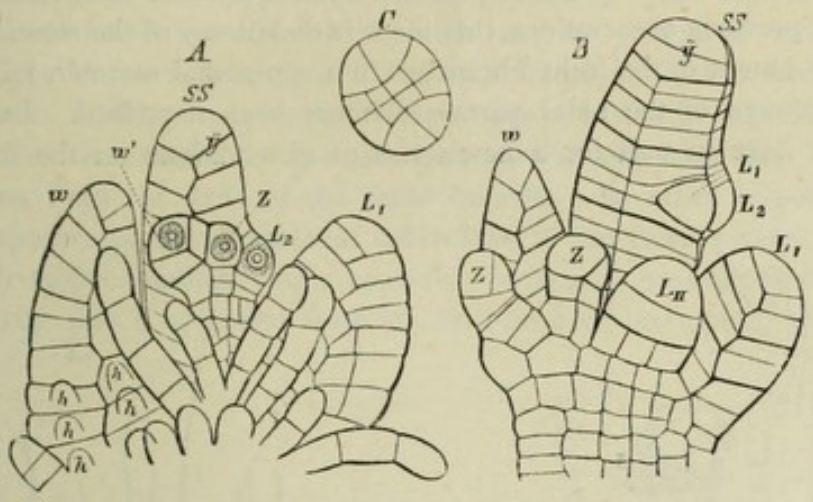

FIG. 291.—Apex of the horizontal floating stem of Salvinia (after Pringsheim); *A* ventral side, *B* dorsal side, *C* transverse section of the long vegetative cone, *SS* apical cell of the stem, *y* its last septum, *w* submerged leaf, *Z* its lateral teeth, *L L* aërial leaves, *h h* hairs.

In Marsilea the apical cell of the embryo is so placed that dorsal and ventral segments in two rows are at first formed from it by walls inclined upwards and downwards; the dorsal median leaf also proceeds from the first dorsal segment. But a different arrangement is soon produced as the plant increases in strength; the apical cell of the stem forms segments arranged in three rows with a $\frac{1}{3}$ divergence, and in such a manner that one row of segments comes to lie below (ventrally), while the two other rows form the dorsal side of the stem; the ventral side of the stem forms roots in strictly acropetal succession, the youngest being found near the apex of the stem. On the dorsal side of the stem the leaves arise in two alternating rows, some of the dorsal segments remaining at the same time sterile and serving for the formation of internodes[1]. The first leaf of the young plant, arranged on the median line and without a lamina, is followed, in the biseriate arrangement which now results, by a number of young leaves with a short stalk and a lamina at first entire but afterwards divided into two and four lobes; normal leaves circinate in their development are then for the first time formed with a long stalk and a quaternate lamina. In the processes which have now been described, Pilularia agrees, according to Hanstein's observations, with Marsilea, except that all the leaves remain destitute of a lamina (Fig. 293); they are long, conical, filiform, and at first rolled up spirally forwards.

The *Branching* of Rhizocarps is similar to that of Ferns. Pringsheim states that in Salvinia terminal branching never occurs; new shoots arise, on the contrary, exclusively from the basal part of the submerged leaves, each leaf of this description forming a shoot on the side which faces the nearer aërial leaf; every branch produces at once a trimerous whorl of leaves. The branching of the Marsileaceæ has been termed by Hanstein axillary, a designation with which, however, I am unable to agree. The lateral shoots have altogether the appearance of springing from the

[1] Compare the corresponding processes in Radula and other foliose Jungermannieæ, p. 309.

stem itself, and very near to the leaves; but at a later period they appear lateral near the leaves, not axillary; and, as regards their first origin, which has not yet been accurately ascertained, I am inclined to think, from some of Hanstein's figures and from my own previous observations, that there is dichotomy of the stem, which, with a cymose development of the forked branches in a sympodial manner, might well lead to the arrangement of the older parts which has been described. But here, as in the Ferns, we have to wait for a new series of observations on the first origin of the branches.



FIG. 292.—Anterior part of the stem of *Marsilea salvatrix* with leaves (reduced one-half); *K* terminal bud, *bb* leaves, *ff* sporocarps springing from the leaf-stalks at *x*.

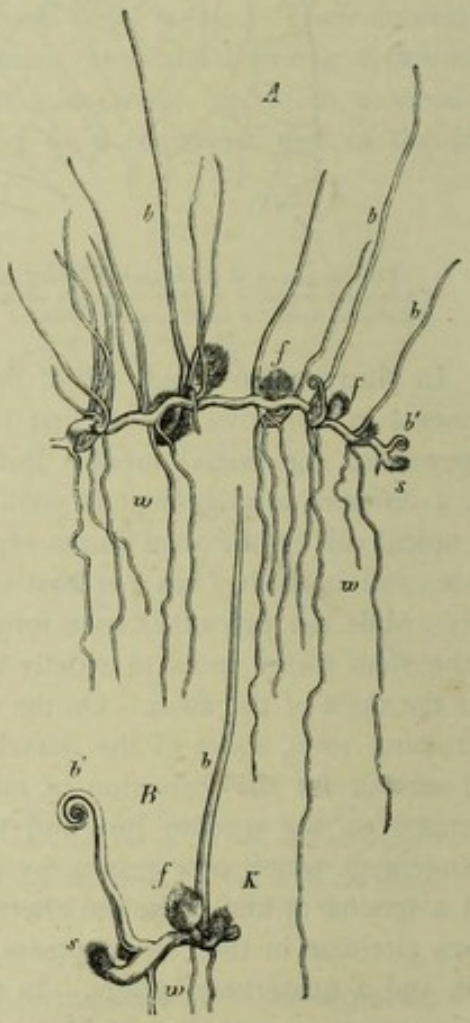

FIG. 293.—*Pilularia globulifera*; *A* natural size, *B* end of a shoot magnified, *s* terminal bud of the stem, *bb* leaves, *w* roots, *f* sporocarps, *K* lateral bud.

The *Growth of the Roots* of Marsileaceæ, and their monopodial branching, agrees with that of Ferns and Equisetaceæ in all important points (Figs. 293 *a*, 293 *b*).

The *Sporangia* of Rhizocarps are formed in hollow, capsular, stalked receptacles, closed on all sides, usually termed *Sporocarps*. In Salvinia they are metamorphosed teeth of the submerged leaves; in Marsilea their stalks (which in this genus are sometimes very short, but occasionally very long) spring from the outer or lower side of the leaf-stalk, or they appear quite at its base and by the side of the

leaf-stalk. These fruit-stalks may be simple, bearing only one sporocarp, or forked and bearing several; those situated on the leaf-stalks are mostly divided, while the basal ones bear only one sporocarp. This peculiarity finds its analogue in the Ophioglossaceæ; the fruit-stalks of Marsilea may be compared with the 'fertile segments' of the leaves in that class. The sporocarps of Salvinia and Marsilea are therefore always of foliar origin; in Pilularia they are shortly-stalked and axillary, or grow on the ventral side of the insertion of the leaf, and their fibro-vascular bundles spring from the axils of the foliar bundles. In other respects the structure of the sporocarps shows material differences in the three genera. In Salvinia (Fig. 294, *B*) they contain a single spacious cavity; at its bottom a stalk arises, which swells up into a spherical form in the centre of the cavity, and contains a

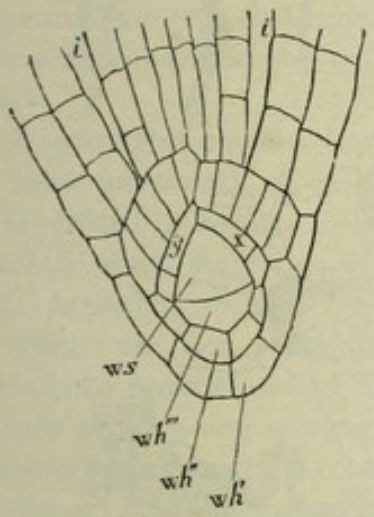

FIG. 293 *a*.—Longitudinal section of the young primary root of the embryo of *Marsilea salvatrix*; *ws* the apical cell, *wh'*, *wh''*, *wh'''* the still simple root-cap; *x*, *y* the last segments of the substance of the root; *i i* intercellular spaces.

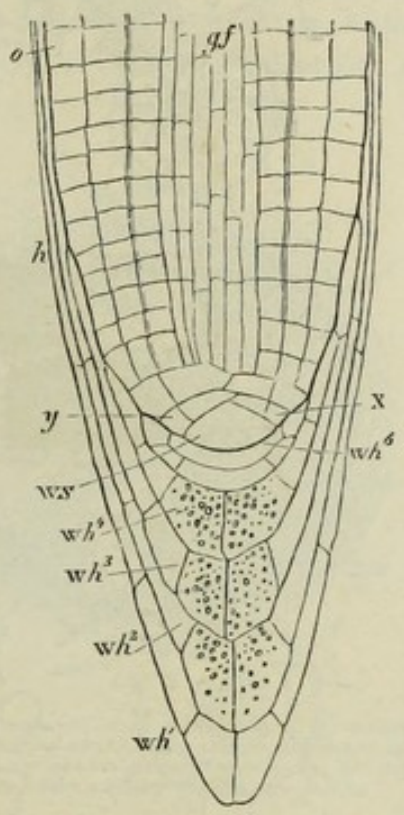

FIG. 293 *b*.—Longitudinal section of a somewhat older primary root of *Marsilea salvatrix*; *ws* apical cell; *wh*1 + *wh*2 the first, *wh*3 + *wh*4 the second, *wh*6 the third layer of the root-cap; each layer now consists of two divisions; *x y* the youngest segments of the substance of the root; *o* epidermis; *g f* fibro-vascular bundles; *h* the part of the root-cap which extends furthest back.

prolongation of the axial fibro-vascular bundle of the tooth of the leaf, the termination of which is the sporocarp; on this spherical swelling are formed a number of sporangia, which produce exclusively macrospores or microspores within the same sporocarp. In Salvinia therefore the difference of sexes of the spores reaches back to the sporocarps themselves. In Pilularia the cavity of the sporocarp is divided into vertical compartments (*i. e.* parallel to the axis); in *P. minuta* it is bilocular, in *P. americana* trilocular, in *P. globulifera* quadrilocular; each chamber bears on its peripheral side a cushion running from the base to the apex of the sporocarp and projecting inwards, behind which runs a fibro-vascular bundle. On this cushion a number of sporangia are formed, the lower of which produce macrospores, the upper microspores. A cushion of this kind bearing sporangia may be

compared to the sorus of a Fern. In Marsilea the processes are still more complicated. In this genus the sporocarp has somewhat the form of a bean, the stalk running up one of its edges (Fig. 292). The interior of the sporocarp may be compared somewhat to two book-cases placed parallel to one another, and separated by a wall, or to a chest in which bags are placed horizontally and side by side in two vertical rows: each of the smaller transverse compartments contains a sorus, the placenta of which extends on its external face from the dorsal to the ventral edge

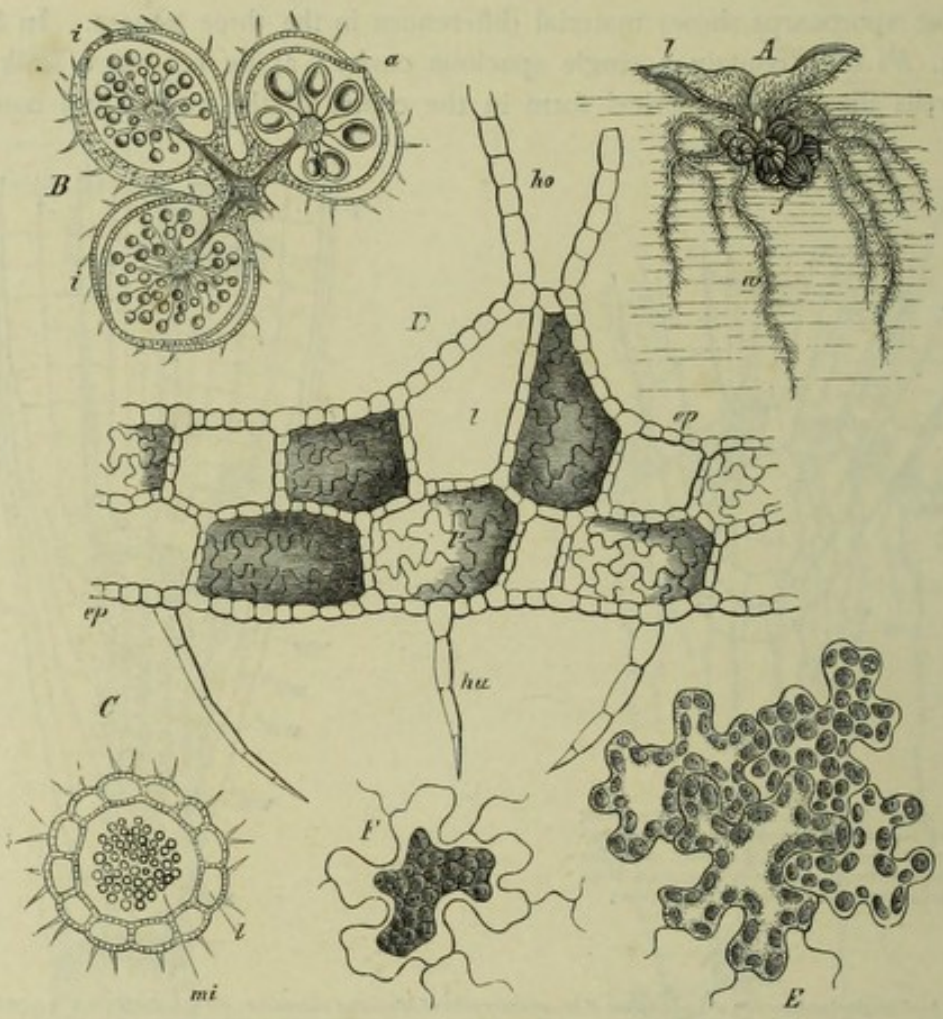

FIG. 294.—*Salvinia natans*; *A* transverse section of a stem bearing a whorl of leaves, *l* aërial leaves, *w* submerged leaf with several teeth, *f* sporocarps on it (natural size); *B* longitudinal section through three fertile teeth of a submerged leaf, *a* a sporocarp with macrosporangia, *i i* two sporocarps with microsporangia; *C* transverse section of a sporocarp with microsporangia *mi*; *D* transverse section of an aërial leaf, *hu* hairs of the under side, *ho* hairs of the upper side, *ep* epidermis, *l* air-cavities, the dark ones show the vertical walls of the tissue in the background (*B*—*D* ×10); *E* cells of a lamella of tissue in the leaf; *F* one of the cells after contraction of the contents in glycerine.

of the sporocarp, and projects inwards in the form of a ridge; along the centre the placenta bears a row of macrosporangia, and on either side of this rows of microsporangia. (On the part played by these compartments in germination, *vide infra* Fig. 300.) Corresponding to each placenta a fibro-vascular bundle runs on the inner side of the envelope of the sporocarp, springing from the primary bundle which runs along the dorsal edge and branches towards the ventral edge.

Our knowledge of the history of development of the sporocarps is still very imperfect. With respect to that of Salvinia it is known that an annular zone becomes

elevated on a tooth of the submerged leaf simultaneously all round, which grows up, envelopes the tooth, and closes it; the enclosed end of the tooth swells into a globular form, and the sporangia arise as trichomes from it. Dr. Pfeffer, who confirms in this respect the statements of Griffith and Mettenius (as stated in a letter received from him) compares, as A. Braun also did, the envelope of the sporocarp of Salvinia to the integument of an ovule. I consider, however, that a closer and better comparison may be drawn with the indusium of the Hymenophyllaceæ. If a resemblance can thus be traced between the sporocarp of Salvinia and the indusiate sorus of this family of Ferns, Braun shows, on the other hand, that the much more complicated sporocarps of Marsilea and Pilularia must be considered as metamorphosed leaves with united pinnæ and bearing the sporangia on their upper sides in a definite relation to the course of the veins or vascular bundles, in the same manner as among the Polypodiaceæ. It appears also from the history of development given by Russow (otherwise not very clear) that in Marsilea at an early period the compartments of the sorus open outwards by narrow apertures.

The sporangia arise, as has already been mentioned, from some of the superficial cells of the placenta or part to which the sorus is attached. According to my observations, which are not yet entirely completed, the order of development of the cells in the young sporangium of Pilularia is very similar to that in Polypodiaceæ. After the formation of the pedicel and mother-cell of the capsule, two circular series of oblique divisions arise in them, by which a double parietal layer of cells and a tetrahedral central cell are formed. While the former are broken up by radial walls into a number of cells, and the size of the capsule increases, the central cell first divides into two, and then, by successive bipartitions, into eight spore-mother-cells, which become isolated in the cavity of the sporangium which is filled with granular fluid, and assume a round form. The inner parietal layer remains in the condition of a delicate epithelium till the time of the formation of the spores, but disappears when they are ripe; so that here also the wall of the sporangium finally consists of only one layer. In Marsilea and Pilularia, where the envelope of the sporocarp is very hard, it remains thin and colourless, the sporangia forming small hyaline sacks; in Salvinia, where the wall of the sporocarp is thin and delicate, the cells of the wall of the sporangium assume, at the period of ripeness, greater consistency and a brown colour, as in Ferns. Until the commencement of the division of the spore-mother-cells into four, the development of all the sporangia proceeds similarly; the differentiation into macrosporangia and

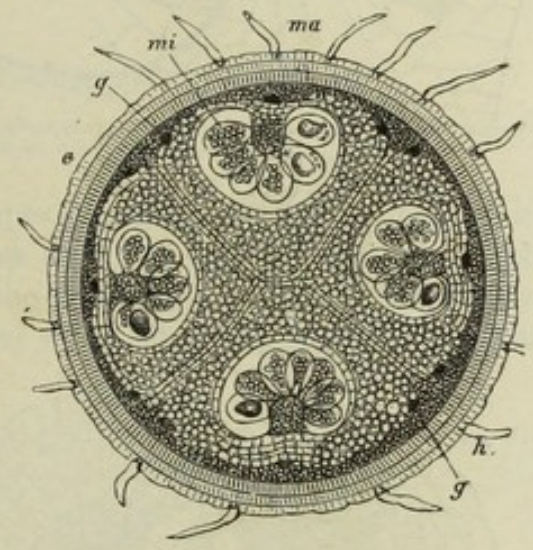

FIG. 295.—Transverse section of the sporocarp of *Pilularia globulifera* below the middle, where the macrosporangia and microsporangia *ma* and *mi* are intermingled; *g* the fibro-vascular bundles, *h* hairs, *e* epidermis of the outer surface.

microsporangia arises, at least according to observations made on Pilularia, in the following manner[1]: — If a microsporangium is about to be formed, each of the mother-cells is broken up into four tetrahedral spores, which all develope into microspores; in the macrosporangium, on the contrary, the mother-cells remain, with one exception, undivided; this one first of all divides in exactly the same manner as the mother-cells of the microspores (Fig. 297, *I*); but only one of the four daughter-cells developes any further; in the three others the formation of a rough exospore is commenced covered by an outer gelatinous layer; this latter soon becomes absorbed, the three abortive spores are arrested in their development (Fig. 297, *II*, *III*), while the fourth at once increases rapidly in size, and grows into an ovoid sac at first thin-walled, exceeding several hundredfold the size of the three sister-cells. The remainder of these abortive sister-cells usually remain for some considerable time shrivelled up and hanging to the apex of the macrospore, and may even sometimes be found on it when ripe. The macrospore of Pilularia is at first entirely clothed with one coat, but after it has attained about one-third of its ultimate length, it has two, an inner compact brown and an outer hyaline one. While the spore is growing, this hyaline coat forms a dome-shaped projection at the apex of the spore (Fig. 298 *b'*) and at the same time a third coat (*c*) is formed, which is very evidently composed of radiating prisms. These prisms are short at the lower part of the spore, but much longer below its apex, and there form a collar, surrounding the dome-shaped projection (*b'*) already mentioned. On the latter also appears a thin gelatinous layer with a prismatic structure, which however is not very clear. Finally, when the spore has attained almost its full development, it becomes surrounded with a fourth

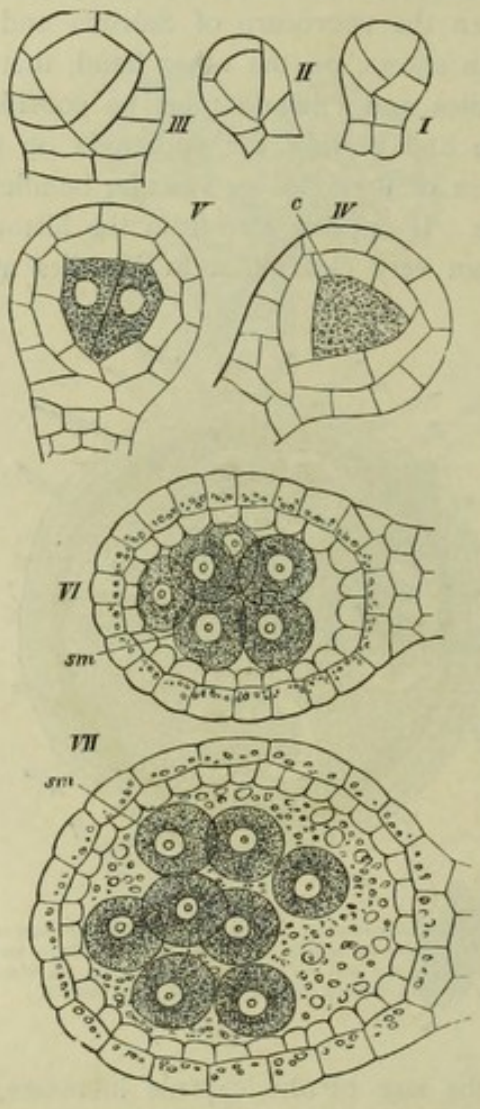

FIG. 296.—Development of the sporangium of *Pilularia globulifera*, all the figures in optical longitudinal section; *c* central cell or primary mother-cell of the spores, ; *sm* mother-cells of the spores (×550).

[1] On the corresponding processes in Marsilea, see Russow, *l. c.*—Russow takes the opportunity of objecting that in the formation of the spores of the higher Cryptogams I do not assume the existence of special mother-cells. I can only reply that I never anywhere assume their existence, principally because the idea of a special mother-cell is always superfluous, and is not in accordance with our present cell-theory.

thick hyaline gelatinous coat which also shows a prismatic structure (*d*), but at the same time a concentric stratification. This coat is also not continuous over the apex, but rises above it on all sides forming the outer part of the funnel-shaped entrance to the apex of the spore. About this time the dome-shaped bladder-like

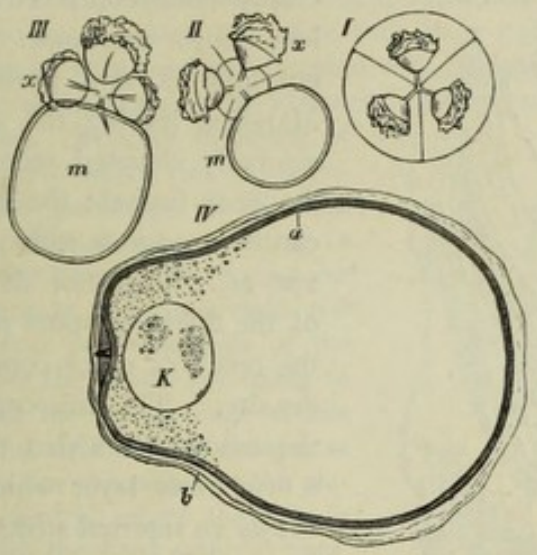

FIG. 297.—Development of the macrospore of *Pilularia globulifera*; *x* the abortive sister-cells, *m* the macrospore, *K* its nucleus, *a* the inner, *b* the outer coat.

widening of the second coat (*b'*) at the apex appears to burst and to empty itself; in its place is found on the ripe spore (as shown in Fig. 298 *b'*), a conical plicate wart; the true apical papilla, in which the prothallium is formed on germination, is formed by an arching of the inner coat which now takes place. The prismatic

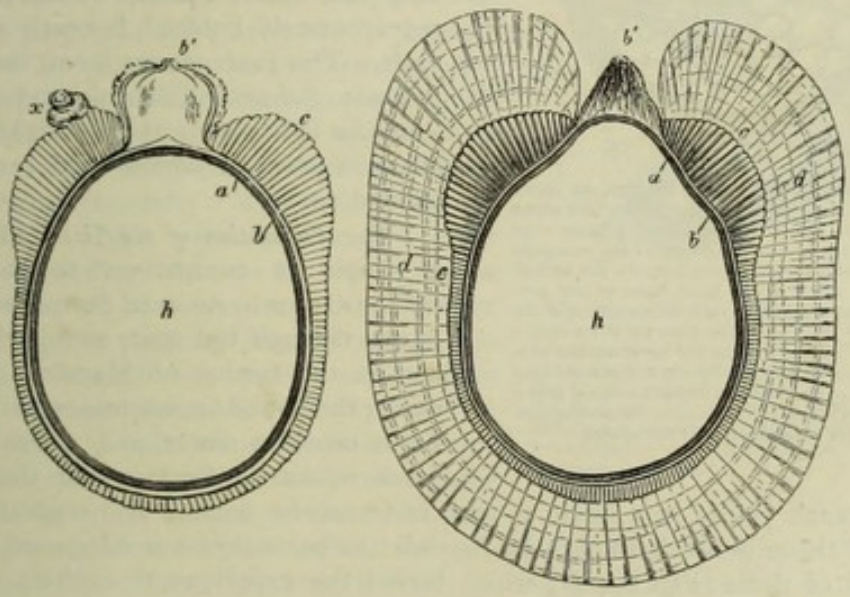

FIG. 298.—Further development of the macrospore of *Pilularia globulifera*; *h* cavity of the spore, *a* the first inner coat, *b* the second, *c* the third, *d* the fourth coat (×80).

structure of the two outer coats of the spore may be considered as an evidence of intersecting lamellar systems perpendicular to the surface of the spores of denser and softer substance; the third concentric lamellar system is here clearly visible only on the outer coat. The structure of the exospore of Marsilea may also

be understood in the same manner. A uniformly thick envelope is formed round the spore with the exception of the apex (Fig. 299 *ex*), consisting of distinct prisms arranged radially, the walls of which are, however, much denser, so that the whole layer gives the impression of a honeycomb; but the prisms are not hollow, like empty honeycomb-cells, but are filled with a less dense substance. A hyaline gelatinous envelope is also present in the spores of Marsilea, leaving the apex free, but is considerably elevated around it, and thus forms the deep funnel; the concentric stratification can be seen in it with peculiar clearness (Fig. 286 *sl*). I cannot doubt that the structure of the thick exospore of Salvinia is also only the result of more complicated differences in density. The microspores so far resemble the macrospores that their exospore has also a firm inner layer which is cuticularised and shows an internal structure depending on difference of density. This layer is surrounded in Marsilea by a thick, in Pilularia by a thin hyaline envelope capable of swelling in water.

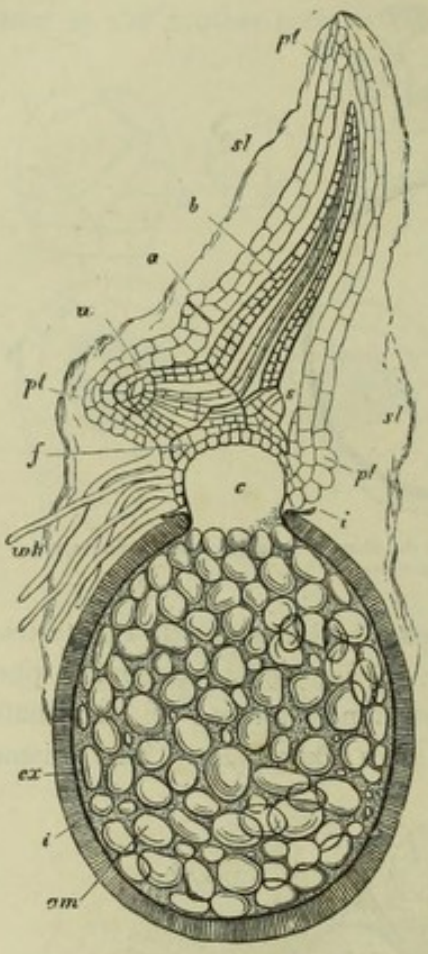

FIG. 299.—Longitudinal section through the spore prothallium and embryo of *Marsilea salvatrix* (×about 60); *am* starch-grains of the spore, *i* inner coat of the spore burst above into lobes, *ex* the exospore consisting of prisms, *c* the cavity beneath the arched diaphragm on which is the basal layer of the prothallium. *pl* the prothallium, *wh* its root-hairs, *a* the archegonium, *f* the foot of the embryo, *w* its root, *s* the apex of its stem, *b* its first leaf by which the prothallium becomes extended, *sl* the mucilaginous envelope of the spores which at first forms the funnel above the papilla, and which still envelopes the prothallium 50 hours after the dissemination of the spores.

The Class Rhizocarpeæ contains, besides the genera that have already been mentioned, only one other, Azolla, which, although not yet accurately known [1], is nearly allied to Salvinia. The four genera form, therefore, two groups; *Salvinieæ* (Salvinia and Azolla), and *Marsileæ* (Marsilea and Pilularia); the further characteristics of which need not be further alluded to.

The *Formation of the Tissue* of Rhizocarps is simple in comparison to their external differentiation. An axial fibro-vascular bundle passes through the root, stem, and leaf-stalk, and in the lamina of Marsilea dichotomises many times and anastomoses at the margin. As is usual in water and marsh plants, the parenchymatous fundamental tissue contains large air-canals placed in a circle as seen in transverse section and separated by radial lamellæ of tissue one cell thick. In Salvinia the parenchyma is composed everywhere of lamellæ of tissue (Fig. 294 *D*) which bound the capacious air-cavities that lie one over another in the aërial leaf like cells of a honeycomb. The outer layer of cells is differentiated into an epidermis with hairs and stomata on the leaves and walls of the sporocarps; the stomata are small and of very peculiar form [2].

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[1] [See Strasburger, Ueber Azolla: Jena 1873.—Ed.]

[2] On the peculiar interstitial striæ of the leaves of Marsilea see Braun (*l. c.*, p. 672); on the histology of the sporocarp see Russow, *l. c.*

The structure of the sporocarp of *Salvinia natans* was sufficiently explained by Fig. 294, *B*, *C*. The sporangia are set free by the decay of the whole plant during winter; the macrospores fill up the sporangium, and do not become detached from it even during germination. The structure of the sporocarp of the Marsileæ (the species mentioned are perennial) determines at the same time a remarkable mode of dehiscence and dispersion of the spores, which must be briefly explained. Beneath the epidermis of the wall of the sporocarp, which is at first very hairy and provided with stomata, lie two or three layers of thickened and lignified cells elongated radially, which form a very hard sporocarp-wall, in the case of Marsilea scarcely permeable by water (compare Figs. 295 and 300). Beneath lie layers of parenchymatous cells, into which run the fibro-vascular bundles of the sporocarp; in *Pilularia globulifera* there are twelve in all, ascending as meridian lines from the base to the apex, one lying beneath each placenta, and a pair right and left of each of the four partition-walls of the sporocarp. In Marsilea the bundle belonging to the pedicel runs along the dorsal edge of the sporocarp, and sends out right and left transverse anastomosing branches corresponding to the placentæ, as far as the ventral edge; they lie in the parenchyma beneath the hard external testa. The apparent median partition of the sporocarp of Marsilea is not an independent structure, but consists of the walls of the compartments of the sporocarp which meet on the median plane; these are themselves composed of large cells, the outer layer of whose cell-wall is thin and solid, while the inner become converted into mucilage and are capable of swelling. The compartments of the sporocarp are small longish sacs lying transversely in it in two rows one over another, and attached by their anterior and posterior ends to a cushion of tissue which fills up the angle at the dorsal and ventral edges of the sporocarp, and runs round its cavity. The inner layers of the cell-walls of this cushion have also great capacity for swelling. If now by any injury to the hard testa of the sporocarp, the entrance of water becomes possible, the cushion and the walls of the compartments begin in a short time (about 10 minutes) to swell so violently that first of all the testa is split along the ventral edge into two valves, the annular cushion detaching itself from the inner surface of the testa, enlarging in consequence of the swelling, and protruding from the slit in the form of a ring (Fig. 300 *B*). The compartments of the sporocarp are attached at both ends to the inner periphery of this ring; but they are all torn off on one side by its gradual expansion; it now stretches to a great size, increasing at the same time in thickness, and usually subsequently breaks, as shown in Fig. 300 *C*, unrolling into a straight or vermiform linear body, and bearing the alternating compartments of the sporocarp in contiguous pairs. Each of these compartments contains on its outer side the projecting ridge on which the sporangia grow (*D*, *E*); both the macrospores and microspores escape from the sporangia and from the sac of the sporocarp which envelopes them;

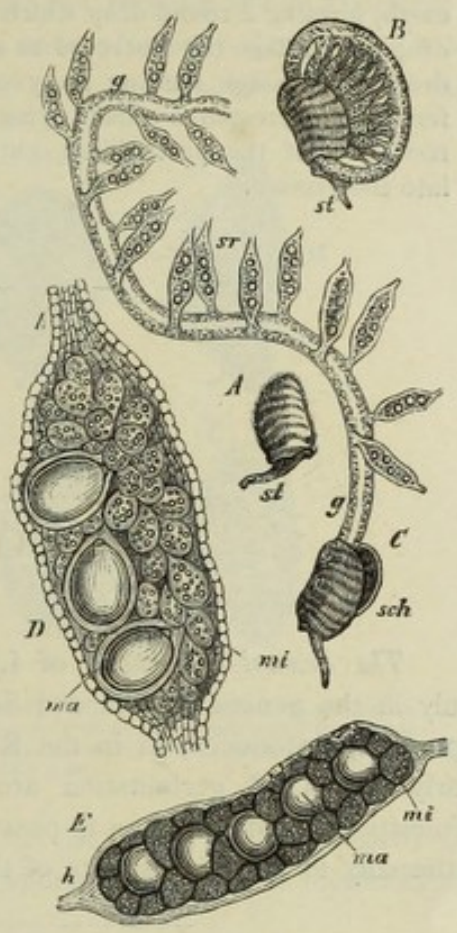

FIG. 300.—*Marsilea salvatrix*: *A* a sporocarp (natural size), *st* the upper part of its pedicel; *B* a sporocarp which has burst in water and is protruding its gelatinous ring (after Hanstein); *C* the gelatinous ring *g* ruptured and extended, *sr* compartments of the sporocarp; *sch* testa of the sporocarp; *D* a compartment of an unripe sporocarp with its sporangia; *E* one from a ripe sporocarp; *mi* microsporangia, *ma* macrosporangia.

their outer gelatinous envelope, which surrounds the exospore, swelling up. Their size being thus increased, they glide out, and escape into the surrounding water, where the germination of *Marsilea salvatrix* begins and completes its course with extraordinary rapidity. With a favourable summer temperature, antherozoids and archegonia ready for fertilisation are formed within 12 or 18 hours. Hanstein was the first to describe these processes accurately; I have myself repeatedly seen them in sporocarps, for which I am indebted to him[1]. To him also we owe the knowledge of a similar though in many respects different process in *Pilularia globulifera*. In this species the sporocarps lie on or beneath the ground; they burst at the apex into four lobes, and exude a tough hyaline mucilage which escapes only when the sporocarp is buried in the earth, forming a round drop which continues to increase in size for some days. In this drop of mucilage the macrospores and microspores rise to the surface and germinate, the drop of mucilage melting away only after fertilisation has been accomplished. The fertilised macrospores remain lying on the ground, and are temporarily fixed to it by the root-hairs of the prothallium, until the first true roots of the young plant penetrate into the ground.

CLASS X.

LYCOPODIACEÆ[2].

The Sexual Generation of Lycopodiaceæ is, up to the present time, known only in the genera Isoëtes and Selaginella; in these large female and small male spores are produced, as in the Rhizocarpeæ. In the genus Lycopodium only the early stages of germination are known, and that only in one species; like Tmesipteris and Psilotum, it possesses only one kind of spore, which corresponds externally to the microspores of the first-named genera[3]. These differences would

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[1] [See Hanstein in Ann. des Sci. Nat. 1863, vol. XX, pp. 149-166.—Ed.]

[2] Hofmeister, Vergleichende Untersuchungen, 1851.—[Germination, Development, and Fructification of the Higher Cryptogamia, Ray Soc. pp. 336-399.]—Mettenius, Filices horti bot., Lips. 1856.—Cramer, Ueber Lycopodium Selago in Nägeli and Cramer's Pflanzen-phys. Unters. Heft 3, 1855.—Hofmeister, Entwickelung der Isoëtes lacustris in Abhandl. der königl. Sächs Gesellsch. der Wissensch. vol. IV, 1855.—De Bary, Ueber die Keimung der Lycopodiaceen, in Berichte der naturf. Gesellsch. zu Freiburg-in-Br. 1858, Heft IV.—Nägeli u. Leitgeb, Ueber Entstehung u. Wachsthum der Wurzeln, in Nägeli's Beiträge zur wissensch. Bot. Heft IV, 1867.—A. Braun, Ueber Isoëtes in Monatsber. der Berl. Akad. 1863.—Milde, Filices Europæ et Atlantidis, Leipzig 1867.—Mettenius, Ueber Phylloglossum, Bot. Zeitg. 1867.—Millardet, Le prothallium male des cryptogames vasculaires, Strassburg 1869.—Juranyi, Ueber Psilotum, Bot. Zeitg. 1871, p. 180.—Pfeffer, Entwickelung des Keims der Gattung Selaginella in Hanstein's Botanische Abhandlungen, Heft IV, 1871.

[3] [J. Fankhauser (Bot. Zeitg. 1873. pp. 1-6) has described the hitherto unknown prothallium of Lycopodium, which is underground and destitute of chlorophyll. In September he found it more or less preserved and still attached to young plants less than three inches high, growing in moss in a damp wooded locality near Langenau in Emmenthal. He describes it as a yellowish white irregularly lobed structure, furnished sparingly with small root-hairs. The under side is comparatively

be sufficient to divide the Lycopodiaceæ into two classes, and to include the genera Lycopodium, Psilotum, Tmesipteris, and the less known Phylloglossum in the highest class of higher Cryptogams, if the difference were an actually existing one; but at present it rests only on an insufficient knowledge of these genera, which are otherwise closely allied to Selaginella in the mode of formation of their tissue, in the dichotomous branching of their stem and root, in the nature of their leaves, and in other characters. We must therefore, until our knowledge is more complete, consider all these genera as members of one class.

The *Microspores* of Isoëtes and Selaginella do not produce the mother-cells of the antherozoids immediately from their contents, as was formerly thought. To the treatise of Millardet mentioned in the foot-note we owe our knowledge of the fact,

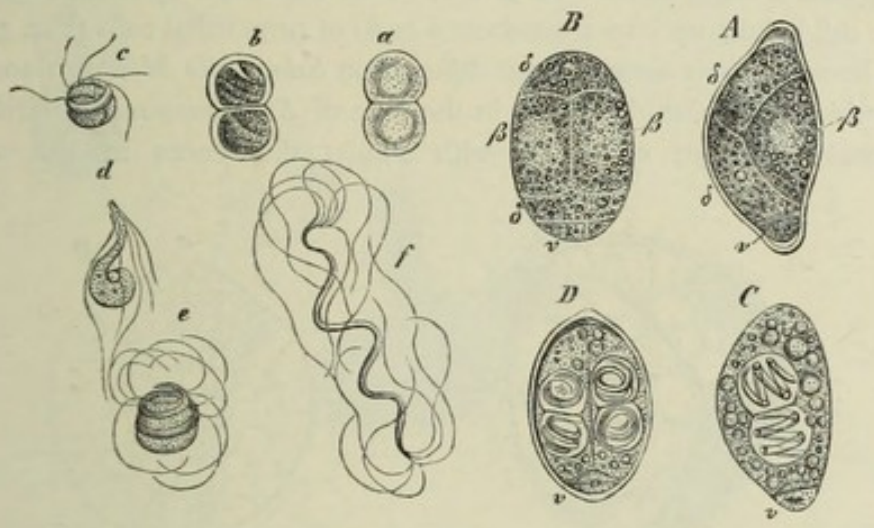

FIG. 301.—Germination of the microspores of *Isoëtes lacustris* (after Millardet). *A* and *C* microspores seen on the right side, *B* and *D* on the ventral face; *A* and *B* show the formation of the antheridium, δ δ its dorsal cells, β β its ventral cells, *C* and *D* the formation of the antherozoids, β and δ have disappeared; *v* is the vegetative cell (prothallium of Millardet); *a*—*f* development of the antherozoids (*A*—*D* and *a*—*d* × 580, *e* and *f* × 700).

so important in connection with the relationship of the higher Cryptogams to the Gymnosperms, that at the period when the microspores are ripe, their contents are

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smooth, while the upper has numerous grooves and protuberances. In these grooves the antheridia and archegonia are situated. A vertical section through the prothallium shows that the cellular structure is formed of three regions; the uppermost, in which the antheridia and archegonia are developed, consists of thin-walled cells poor in cell-contents; the cells of the middle layer are rather smaller, and filled with dark granular contents rich in fatty matter; those of the lowermost region are somewhat elongated parallel to the surface, and their contents are turbid and finely granular. Starch does not appear to be present in any part of the prothallium. The antheridia are filled with innumerable antherozoid-mother-cells; the antherozoids are only slightly twisted and are stout compared with those of Selaginella. The archegonia were not observed, but the position they would occupy was indicated by that of the germinating plants, and it seems probable that they are not sunk completely in the tissue of the prothallium. In general only one embryo is produced from each prothallium, but it appears that a second may be produced from a second prothallium when the first is abortive. The reproduction of Lycopodium appears, therefore, to bear the greatest resemblance to that of Ophioglossaceæ. Berkeley remarks (Introd. to Crypt. Bot. p. 549) that Ophioglosseæ 'are plainly connected with Clubmosses by Rhizoglossum, a Cape genus which has precisely the habit of Phylloglossum (Lycopodiaceæ), consisting of a few subulate leaves and a pedunculate spike of sporangia.'—ED.]

transformed into a mass of tissue consisting of but few cells. One of these cells remains sterile, and may be considered a rudimentary prothallium; while from the others originate the mother-cells of the antherozoids, and these may therefore be looked on as a rudimentary antheridium.

The microspore of *Isoëtes lacustris* breaks up, after hibernation, into a very small sterile cell and a large one comprising the whole of the rest of the contents (Fig. 301 *A—C*). The former (*v*), cut off by a firm wall of cellulose, does not undergo any further considerable changes; the latter, on the other hand, splits up into four primordial cells without cell-walls, of which the two ventral ones produce each two antherozoid-mother-cells, and therefore four in all. Pfeffer has confirmed the statements of Millardet that in Selaginella, long before the spores escape from the sporangium, a small sterile cell is first of all separated by a firm wall, while the other large cell breaks up into a number (6 to 8) of primordial cells (Fig. 303 *A—D*). He found, however, their arrangement different in *Selaginella Martensii* and *caulescens* from that which Millardet described in the case of *S. Kraussiana*, a variation which seems immaterial when compared with similar differences in the antheridium

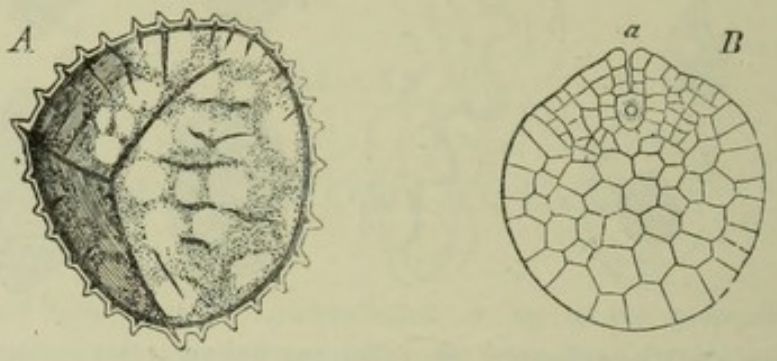

FIG. 302.—*Isoëtes lacustris* (after Hofmeister); *A* macrospore, two weeks after its escape from the sporangium, rendered transparent by glycerine (×60); *B* longitudinal section of the prothallium four weeks after the escape of the macrospore, *a* archegonium (×40).

of Ferns. The essential difference between the results of the two observers consists in this:—that, according to Millardet, only two of the primordial cells produce the mother-cells of the antherozoids, which then, increasing in number, cause the absorption of the rest of the primordial cells, and fill up the spore; while Pfeffer found, in his species, that all the primordial cells underwent further division, and contributed to the formation of the antherozoids. As to the latter they were both in accordance. In Isoëtes the antherozoids are long and slender, attenuated, and splitting up at both ends into a tuft of long slender cilia; in Selaginella they are shorter, thick behind, finely drawn out in front, and divided there into two long fine cilia. In the perfectly mature condition the antherozoids are rolled up into an elongated helix or into a short spiral. The mode of their formation in the mother-cells is the same in both genera, and agrees in essential points with that of Ferns. A cell-nucleus is not present at the time when the antherozoid is first formed; the contents of the cell are perfectly homogeneous; the antherozoid originates from a shining scarcely granular mass of protoplasm which encloses a vacuole, the cilia at one end being formed first, and the spiral body becoming differentiated from before backwards by a kind of splitting of the protoplasm. The antherozoid is

originally curved spirally round the central vacuole; this latter, surrounded by a fine membrane, not unfrequently remains attached to the posterior end of the antherozoid after it has escaped, and is carried along by it. The movement does not last longer than five minutes in the antherozoids of Isoëtes, in Selaginella from one-half to three-quarters of an hour. From the commencement of germination till the complete maturity of the antherozoids there is, in Isoëtes, an interval of about three weeks; the same period from the dissemination of the spores is necessary in Selaginella.

The *Macrospores* produce the female prothallium, which is an endogenous struc-

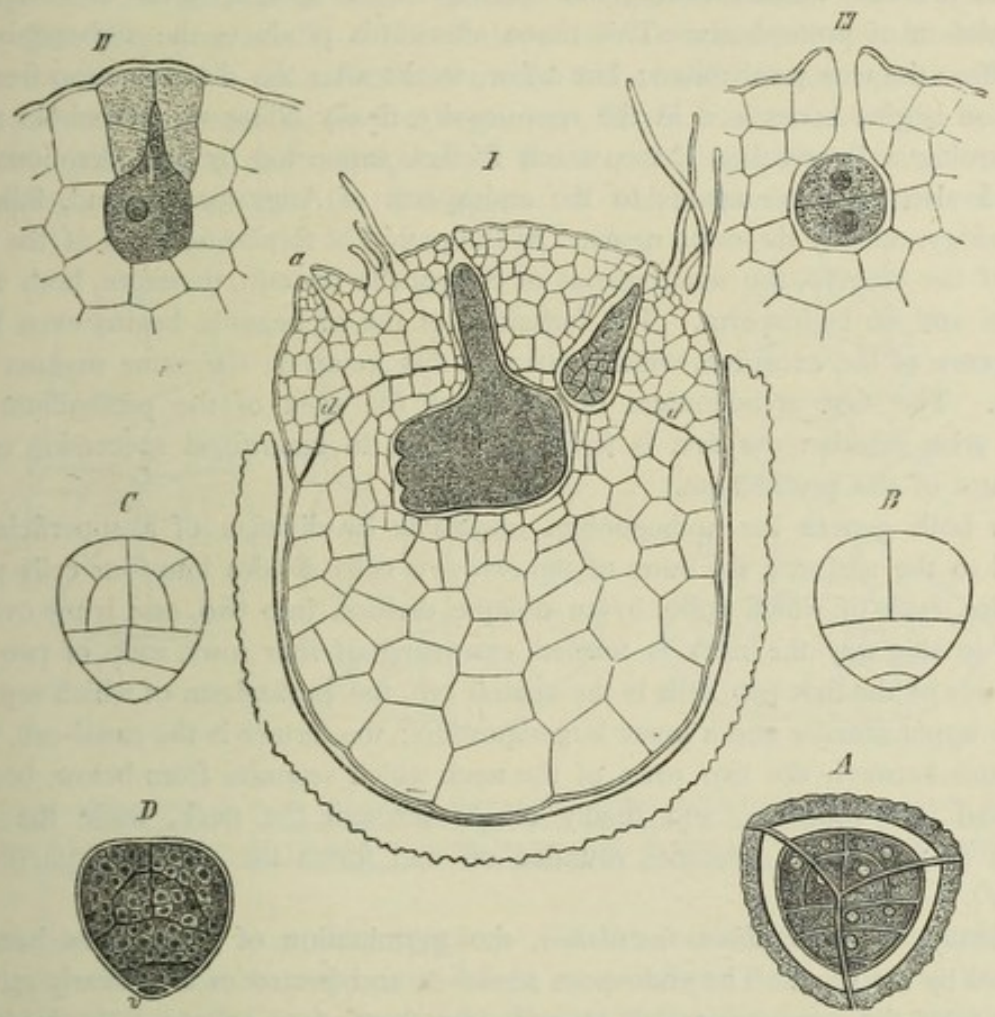

FIG. 303.—Germination of Selaginella (after Pfeffer); *I—III, S. Martensii, A—D, S. caulescens; I* longitudinal section of a macrospore filled with the prothallium and 'endosperm,' *d* the diaphragm, *e e'* two embryos in process of formation; *II* a young archegonium not yet open; *III* an archegonium with the oospore fertilised and divided once; *A* a microspore showing the primordial cells; *B C* different views of these divisions; *D* the mother-cells of the antherozoids in the perfect antheridium.

ture in a still higher degree even than is the case with Rhizocarps. In this respect and in the mode of its development, it shows a still greater resemblance to the tissue that fills up the embryo-sac of Gymnosperms, and even of Angiosperms. In Isoëtes the cavity begins to be filled with cellular tissue a few weeks after the escape of the macrospores from the decaying macrosporangium; the cells of this tissue are all at first still naked (without cell-wall); they appear to become enclosed in firm cell-walls only when the whole cavity of the endospore is filled with them (Fig. 302). In the meantime the endospore thickens, becomes differentiated into layers, and

assumes a finely granular appearance, phenomena which, as Hofmeister insists, are exhibited in like manner in the embryo-sacs of Coniferæ. The spherical prothallium now swells up, the three convergent edges of the exospore burst lengthwise and thus form a three-rayed fissure, where the prothallium is covered only by the membranous endospore; this also peels off, and softens, finally exposing the corresponding part of the prothallium. At its apex appears the first archegonium; if this is not fertilised, several others are subsequently formed at its side. In Selaginella, even when the macrospores are still lying in the sporangium, the apical region is found to be clothed with a small-celled meniscus-shaped tissue which is probably formed, during the ripening of the spores, by the division of an accumulation of protoplasm. This tissue afterwards produces the archegonia, and is therefore the true prothallium; but a few weeks after the dissemination free cell-formation begins beneath it in the spore-cavity, finally filling up the whole cavity, and forming a large-celled tissue, which Pfeffer, supported by considerations with which I also agree, compares to the endosperm of Angiosperms, and, following this analogy, calls by the same name. At the period of fertilisation and of the formation of the embryo, the macrospores of Selaginella contain, therefore, both a prothallium and an endosperm. The formation of the archegonia begins even before the rupture of the exospore, which occurs in this genus in the same manner as in Isoëtes. The first archegonium originates at the apex of the prothallium; the others arise, whether the first is fertilised or not, in centrifugal succession on the free parts of the prothallium.

In both genera the archegonium originates by division of a superficial cell parallel to the surface; the outer of the two new cells divides into four cells placed crosswise, each of which splits by an oblique division into two, one lying over the other; in this way the neck is formed, consisting of four rows, each of two cells. The lower of the first two cells is the central cell, the protoplasm of which separates into an upper smaller and a lower larger portion; the former is the canal-cell, which penetrates between the two rows of the neck which separate from below, becomes converted into mucilage, and finally breaks through the neck, while the lower portion of protoplasm becomes rounded off and forms the naked oosphere (Fig. 303, *II*).

Finally, in *Lycopodium inundatum*, the germination of the spores has been observed by De Bary. The endospore stretches, and protrudes as a nearly spherical vesicle from the exospore which is split into three deep lobes; it is divided by an upper partition-wall into a hemispherical basal cell which does not undergo any further changes, and an outer cell which continues to grow as the apical cell and forms two short rows of alternating segments by walls inclined alternately in two opposite directions. Each segment is broken up by a tangential wall into an inner and an outer cell, so that the prothallium consists finally of four short cells forming an axial row, surrounded by two rows of lateral cells, and by the basal and the apical cell. De Bary was unable to follow the further stages of development; and it is therefore still impossible to form a judgment on the true nature of this structure. [See, however, *supra*, p. 400.]

The Asexual Generation. The mode of formation of the embryo is, as has been said, known only in Isoëtes and Selaginella. The first division of the oospore

differs from that of Ferns and Rhizocarps, taking place perpendicularly to the axis of the archegonium. According to Hofmeister, each of the two cells first formed is divided in Isoëtes in a plane at right angles to that of the first division, the relation of which to the first root, the first leaf, the stem, and the foot of the embryo, requires yet further elucidation. The formation of the embryo of Selaginella has recently been investigated in detail by Pfeffer. From an elongation of the upper half of the oospore is formed the *Suspensor*, a body which is wanting in all other Cryptogams, but universally present in Phanerogams, and through which Selaginella consequently approaches flowering plants. The suspensor seldom remains a simple cell; a smaller or larger number of divisions usually takes place in its lower part (Fig. 304, *A–D*). The embryo itself originates from the lower half of the oospore, which must itself be considered as the primary apical cell of the stem, and the suspensor as its first segment. By the elongation of the suspensor and the compression and absorption of the surrounding cells, the mother-cell of the embryo is forced into the endosperm, in which the embryo now undergoes

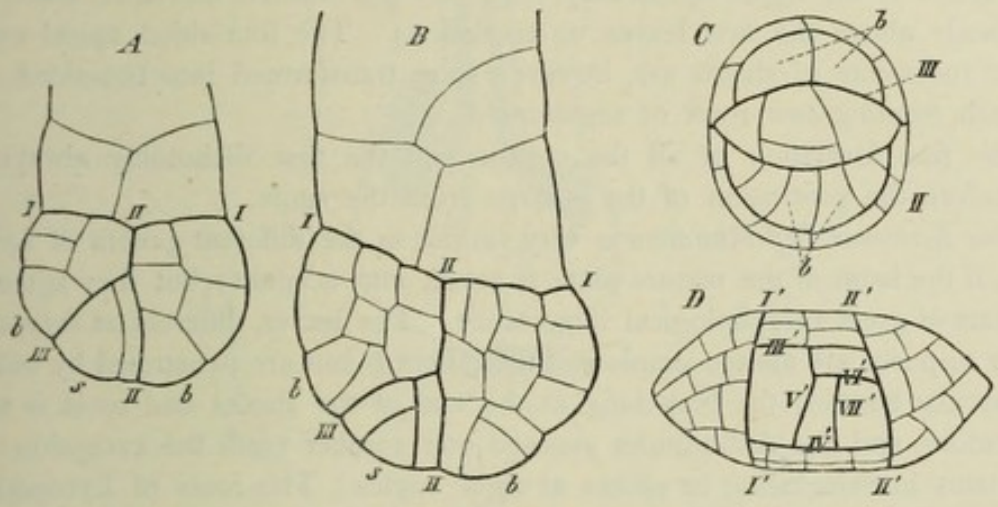

FIG. 304.—Formation of the embryo of *Selaginella Martensii* (after Pfeffer); *A*, *B* lower part of the suspensor with the first much-divided segments of the embryo and the apical cell *s* of the future stem; *bb* the first leaves; *C* apical view of the same; *D* the apex seen from above in the act of forming two new apical cells, right and left; *I*, *II*, *III* the primary walls of the primary apical cell; *I'—VII'* the longitudinal walls by which the two new apical cells are formed.

further development, as in Phanerogams. In the mother-cell of the embryo two segments are in the meantime cut off by two oblique walls; out of each proceeds an embryo-leaf (cotyledon), and a longitudinal half of the hypocotyledonary segment of the stem; the foot and root originating besides from the older segment. Between the two segments in front lies the two-edged apical cell of the stem (Fig. 304, *A*, *B*). While the two segments are becoming transformed by a number of cell-divisions into masses of cells, of which an inner mass very soon separates itself as the procambium of the axial bundle and a peripheral mass as dermatogen and periblem, a swelling is produced laterally beneath the first leaf, forming the foot; by its increase the stem is forced over to the other side (that of the younger segment); so that the apex comes to lie horizontally, and afterwards is even directed upwards (Fig. 303 *I*); and finally the bud, with its first leaves, the cotyledons, grows out upright from the apical part of the macrospore when the embryo begins to increase in length. The first root is formed a considerable time

afterwards between the foot and the suspensor. It is lateral, and its apical cell is formed from an inner cell of the older segment; but the first layer of its root-cap originates from the splitting into two layers of the overlying dermatogen; the later layers of the root-cap arise from the apical cell of the root itself.

It has already been mentioned that in Pteris and Salvinia the position of the apical cell of the growing stem is placed at an angle of about 90° with respect to that of the embryo. Something of the same kind occurs in Selaginella; the apical cell which lies between the rudiments of the first two leaves is divided by walls in such a manner that a four-sided apical cell is formed (Fig. 304 *C*, *D*), the segments of which arise in decussate pairs. In the fifth or sixth segment a second four-sided apical cell is now formed by a curved wall with the convexity turned towards the primary apical cell, so that a longitudinal section through the two apical cells cuts at right angles the common median line of the first leaves, and that of the original two-edged apical cell. Each of the two four-sided apical cells now developes into a branch of the first dichotomy; but neither of the segments continues to grow in the direction of the hypocotyledonary segment; the division, therefore, takes place immediately above the first leaves or cotyledons. The four-sided apical cells of the two rudiments of shoots are, however, soon transformed into two-sided apical cells each forming two rows of segments[1].

The first formation of all the organs and the first dichotomy always take place before the protrusion of the embryo from the spore.

The *External Differentiation* is very various in the different genera of Lycopodiaceæ, if the habit of the mature plant is taken into account; but they agree in a few points of great morphological importance. The leaves, different as they appear in other respects, are always simple and unbranched, and are penetrated by only one fibro-vascular bundle; the branching at the end of the shoots and roots is always dichotomous, and the dichotomies succeed one another (with the exception of the older states in Selaginella) in planes at right angles. The roots of Lycopodiaceæ are, at present, the only ones known to dichotomise in the whole vegetable kingdom[2]. The difference of habit depends especially on the relative size of the leaves and on the different rapidity of the growth of the stem in length. One extreme is afforded in this respect by the genus Isoëtes, with its extremely short unbranched stem, growing scarcely at all in length but much in breadth, its dense rosettes of leaves, which are of considerable and often of very great length and the number of which is often very large, and its numerous roots; the other extreme occurs in Psilotum, where the stem regularly dichotomises, remains slender, grows much in length, but forms only very small leaves and no true roots at all. In Selaginella and Lycopodium the leaves are not large but nevertheless strongly developed, and the repeatedly dichotomising branches are densely covered with leaves, and produce numerous roots in acropetal succession. Very different from

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[1] The new wedge-shaped apical cells of the two first branches lie parallel to the primary apical cell of the embryo, as also do the apical cells of the succeeding branch. The second and succeeding planes of dichotomy therefore cross the first at a right angle, but only at the outset; since, by a twisting of the first branches, their dichotomies come into the same plane as the first.

[2] According to Reinke, however, some adventitious roots of Cycadeæ do dichotomise.

these genera in appearance is Phylloglossum, a small Australian plant only a few centimetres in height, which puts out a stem from a small tuber, and produces a rosette of a few long leaves and one or more lateral roots, then lengthens into a slender scape, and bears above a small-leaved spike of sporangia. The plant is renewed by lateral adventitious shoots, consisting of a tuber and a leafless rudiment of a bud; and in this respect resembles our native Orchideæ.

The *Stem* is distinguished in Isoëtes, as has already been mentioned, by its extraordinarily small growth in length, with which is connected, in this as in other cases, an absence of branching; no internodes[1] are formed, the leaves with broad bases of insertion constituting a thick rosette, without leaving between them any surface of the stem bare. The upper region of the stem, which is furnished with leaves, has the form of a shallow funnel, depressed in the centre or apex (Fig. 305).

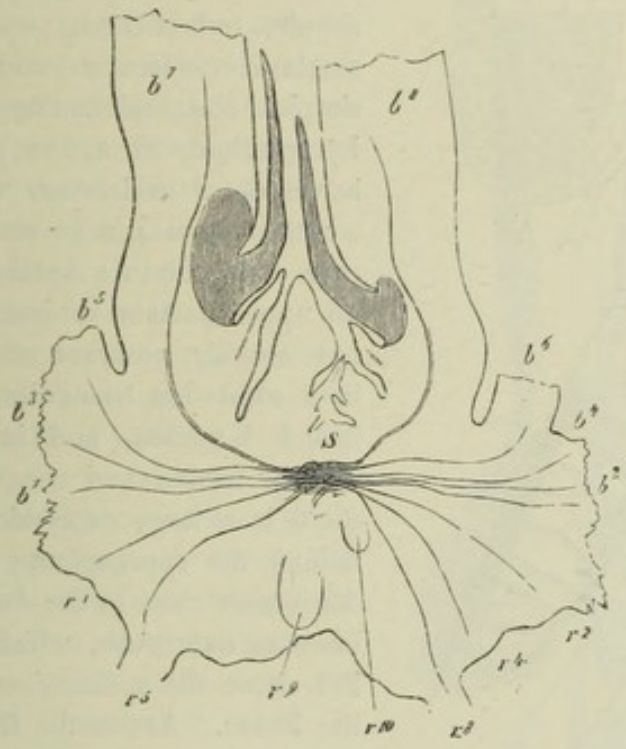

FIG. 305.—Longitudinal section of *Isoëtes lacustris* at right angles to the fork of the stem ten months old (after Hofmeister). *S* stem, *b*1—*b*8 leaves, *r*1—*r*10 roots (×30); the ligula of the two developed leaves is shaded.

The increase in thickness, the long continuance of which distinguishes the stem of Isoëtes from that of all other Cryptogams, is brought about by a layer of meristem lying inside, surrounding the central vascular body, and continually producing new layers of parenchyma on the outside. This takes place especially in two or three directions, so that two or three corresponding masses of tissue are formed, slowly dying off on the outside, between which lie as many deep furrows meeting on the ventral side of the stem. From these a large number of roots are produced in rows in acropetal succession.

In Selaginella, Lycopodium, Tmesipteris, and Psilotum, the stem remains slender, but lengthens rapidly by a great number of dichotomies, and forms distinct

[1] The same occurs in Ophioglossaceæ and the short tuberous Cactaceæ.

internodes. In Selaginella the end of the stem rises above the youngest leaves as a slender cone; in Lycopodium it is blunt and flat. The branches of the dichotomies grow with equal vigour in Psilotum, and often also in Lycopodium; but in the latter genus and in Selaginella some of the branches develope into primary stems or branches, which either assume a creeping position as rhizomes or an ascending one as aërial stems. In Selaginella a tendency prevails to sympodial scorpioid development of the dichotomous systems of branches (see p. 157) which not unfrequently leads to the system of abundantly branched shoots developed bilaterally in one plane attaining a definite outline, and a corresponding resemblance to a compoundly pinnate leaf. The small size of the leaves in these genera causes the general habit to be mainly dependent on the development of the systems of branches.

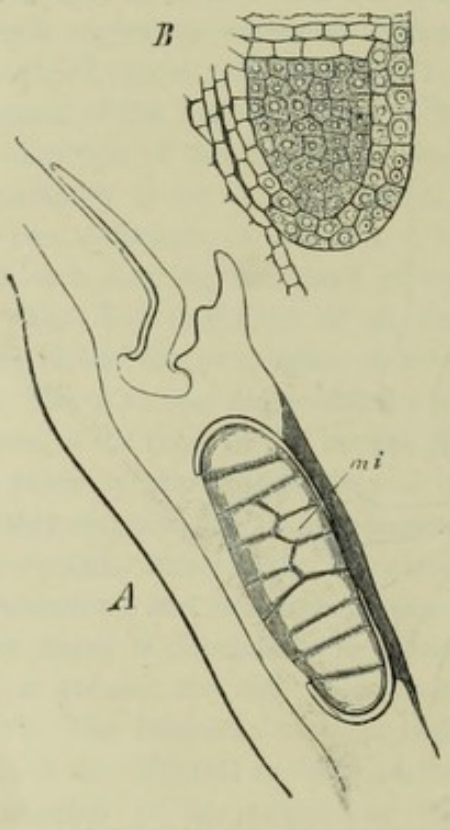

FIG. 306.—*A* longitudinal section through the base of a leaf of *Isoëtes lacustris* with its microsporangium *mi* still unripe; *B* longitudinal section of the lower part of a young sporangium (×300) (after Hofmeister).

The *Leaves* of Lycopodiaceæ are always simple, unbranched, penetrated by only a single fibro-vascular bundle, terminating in a simple point, and ending, in Selaginella and Lycopodium, in a fine awn. The largest leaves occur in Isoëtes, where they attain a length of from 4 to 60 cm. They are in this case divided into a basal part or sheath, and an upper part or lamina. The sheath does not entirely embrace the stem, but rises in a somewhat triangular form from a very broad insertion, and is acuminate; it is convex behind and concave in front, where there is a large depression, the *Fovea*, containing the sporangium; the margin of this depression rises in the form of a thin membranous outgrowth, which, in many species lies above the sporangium and envelopes it, the *Velum*. Above the fovea and separated from it by a 'saddle,' lies a smaller depression, the *Foveola*, the lower margin of which forms a lip, the *Labium*, while from its bottom an apiculate membranous structure, the *Ligule*, with a cordate base, is prolonged beyond the foveola (Fig. 306, *A*). The lamina of the leaf, containing chlorophyll, into which the sheath passes above, is narrow and thick, almost cylindrical, but flattened in front, and penetrated by four wide air-canals, which are divided by septa. This form is exhibited by the fertile leaves of all the species of Isoëtes; a rosette of such leaves is produced annually; but between each pair of annual whorls is formed a whorl of imperfect leaves, which consist, in *I. lacustris*, of only a small lamina, but in the terrestrial species are destitute even of this, and may therefore be considered as scale-like hypsophyllary leaves (phyllodes).

The leaves of Selaginella are never more than a few millimetres in length, and are usually cordate at the base with a narrow insertion, acuminate, and from lanceo-

late to ovate in form. In the greater number of species the sterile leaves are of two different sizes, the ventral leaves attached to the under or shaded side of the obliquely ascending stem are much larger than the dorsal leaves on the upper side exposed to the light (Fig. 307, *A*). Both kinds taken together form four longitudinal rows (*vide infra*). On its upper side and near the base each leaf bears a ligule; the point of attachment of the sporangium is below this on the fertile leaves. The fertile leaves form a quadrangular terminal spike, are uniform in size, and usually of somewhat different form from the sterile ones. This difference is more striking in those species of Lycopodium (*L. clavatum*, &c.) which form a terminal spike of sporangia, the leaves of which are usually yellow or at least not green, and broader and shorter than the sterile foliage-leaves. In other species however (*L. Selago*, &c.) the sporangia are seated in the axils of the ordinary foliage-leaves, without forming an externally distinguishable spike. The form of the leaves of Lycopodium, although always simple, is also very various in the different species, in some cases resembling the acicular leaves of Conifers, in others broad, and always spreading on all sides. In Psilotum all the leaves are rudimentary, very small, membranous, and scale-like, even the fibro-vascular bundle is wanting in them; on the underground shoots of these plants, which assume a root-like appearance (true roots are altogether wanting, *vide infra*), the formation of leaves is still more completely suppressed, and is often only recognizable by the arrangement of the cells near the *punctum vegetationis*. Tmesipteris, which is allied to Psilotum, possesses, on the other hand, large strong leaves.



FIG. 307. — *Selaginella inæqualifolia*; *A* fertile branch (one-half natural size); *B* apex in longitudinal section bearing microspores on the left, macrospores on the right (magnified).

The *Phyllotaxis* is either spiral or decussate. In Isoëtes the rosettes are arranged spirally, with the divergences $\frac{3}{8}$, $\frac{5}{13}$, $\frac{8}{21}$, $\frac{13}{34}$, the fractions becoming more complicated the larger the number of leaves that are annually formed. In Lycopodium the arrangement is also spiral; and the number of orthostichies is frequently considerable; but not unfrequently the leaves form in this genus pseudo-whorls in spiral succession, which appear as decussate pairs (*L. complanatum*) or as alternating whorls of numerous leaves, as in *L. Selago*, where the forked branches begin with pseudo-whorls of three leaves, but then produce others with four and finally five leaves. In the species of Selaginella which have their leaves arranged in four rows, each dorsal and ventral leaf form together a pair, whose median plane, however, does not intersect that of the next

pair at right angles but obliquely, an arrangement which is often clearly seen on old shoots of *S. Kraussiana*.

The *Apical Growth* of the stem takes place, in Isoëtes, Selaginella, and Psilotum, by means of an apical cell. That of *Isoëtes lacustris* is, according to Hofmeister, two-edged when the stem has two furrows; in the species with three furrows it is a three-sided pyramid. In young plants the leaves stand accordingly in the first case in two, in the second case in three rows; but later the phyllotaxis becomes more complicated and spiral, indicating perhaps that in the older stem the primary walls of the segments are arranged in regular succession, in the same manner as in those Hepaticæ which have a three-sided apical cell and a complicated phyllotaxis. In those species of Selaginella which have the leaves in four rows, the apical cell of the stem is, according to Pfeffer, two-edged (Fig. 308, *A*, *B*). The two rows of segments here form an elevated vegetative cone, at the base of which the rudiments of the leaves first appear at the height of the fourth or fifth

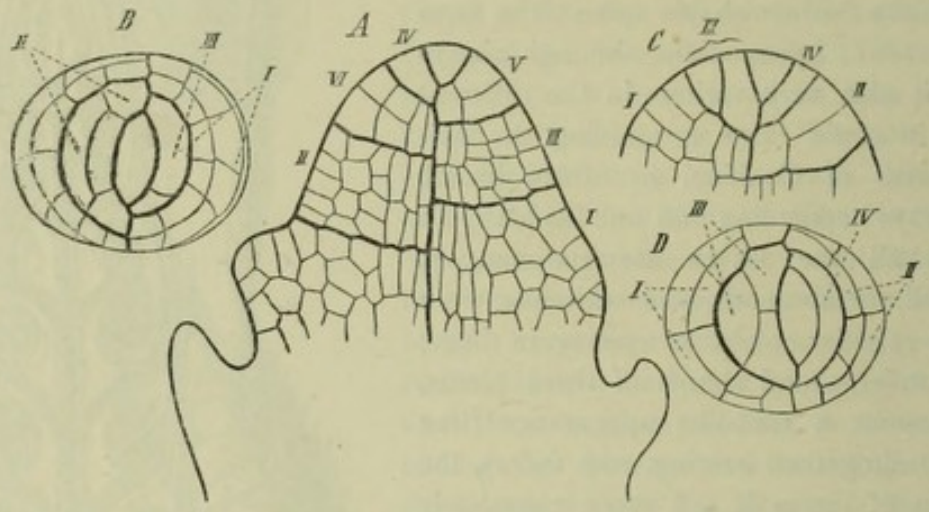

FIG. 308.—Apex of the stem of *Selaginella Martensii* (after Pfeffer); *A* longitudinal section of the end of the stem with the first rudiment of the leaves; *B* apex of the stem seen from above; *C* dichotomy of the apical cell seen from the side; *D* the same seen from below. The primary walls of the segments are denoted by darker lines; the segments themselves are numbered with Roman figures.

segment. The two edges of the apical cell are directed upwards and downwards (on the obliquely ascending shoot). The relationship of the leaves to the segments has not yet been entirely made out. The two leaves of each pair arise obliquely; one above, the other below, and alternately right and left; where the pairs cross obliquely, each embraces about a fourth of the circumference of the stem. Divisions then take place which are directed obliquely upwards and downwards, and a row of apical cells is thus formed, by means of which the growth of the leaf is continued (Fig. 308, *A*). The dichotomy of the shoot is caused by a second two-edged apical cell being formed from the youngest segment (Fig. 308, *C*, *D*). The two shoots which are thus formed grow right and left of the previous direction of growth, and all the successive dichotomies take place in one and the same plane.

In *Psilotum triquetrum* the root-like underground shoots have been investigated by Nägeli and Leitgeb in relation to their apical growth. They found a small three-sided apical cell, the divisions of which however advance (as in Polytrichum

and Sphagnum), in the anodal direction, and thus produce rows of segments arranged spirally.

In *Lycopodium clavatum*, finally, the same authorities thought they recognised a small apical cell, but were uncertain whether it was two- or four-faced. Pfeffer, on the other hand (as he informs me in a letter), did not find an apical cell in either *L. clavatum*, *annotinum*, or *Chamæcyparissus*; and Cramer's experience was the same with *L. Selago*. The dichotomy begins in this case by two small-celled papillæ rising on the flat apex of the shoot, and growing up into the two shoots of the dichotomy.

The gemmæ or bulbils of *L. Selago*, which subsequently fall off, are probably products of the leaves, not of the stem; they are apparently axillary. It appears however to result from Cramer's description and drawings that they spring from the basal part of the leaf itself—at least this is indicated by the circumstance that the vascular bundle does not spring from the cauline but from the foliar bundle. The additional circumstance that sporangia are developed on the earlier leaves of a year's growth, bulbils on the later ones (the branch continuing to grow for years without dichotomising), appears further to justify the supposition that the bulbils occupy morphologically the same position as the sporangia, which in Lycopodium unquestionably originate from the leaves, and are not axillary.

The *Roots* of Lycopodiaceæ show very remarkable morphological peculiarities; they are the only roots at present known the branching of which is (apparently or actually) dichotomous; the successive dichotomies lie in planes crossing at right angles. A second peculiarity are the *Rhizophores* of Selaginella and the root-like shoots of Psilotum. All these phenomena have been investigated by Nägeli and Leitgeb (*l. c.*).

Psilotum triquetrum is a plant perfectly destitute of roots, forming however a number of underground shoots which serve the purpose of roots and are extremely similar to them. On the shoots of the rhizome which approach the surface of the ground may be detected with a lens minute leaves of a whitish colour and acicular shape; the deeper root-like shoots have a blunter end, on which no trace of leaves can be detected, even with the lens. While the anatomical structure of the superficial shoots corresponds to that of the true stem of these plants, in these deeper shoots the vascular bundles are united into an axial group, as in true roots. The shoots which bear visible rudiments of leaves may turn upwards, become green and transformed into ordinary foliage-shoots, while the root-like shoots, which are more slender, may also turn upwards, become thicker, and assume the appearance of the ordinary superficial rhizome-shoots. In this point therefore they differ at once from true roots, but still more in the absence of a root-cap. They terminate in an apical cell, which forms oblique segments alternating in different directions. The most important point, however, is that these shoots really possess rudiments of leaves which consist of only a few cells and do not project above the surface, but remain concealed in the tissue. They are best recognised in longitudinal section, when they are seen to consist of an apical cell and from two to five cells with the characteristic arrangement of leaf-cells. Similar rudimentary leaves consisting of but few cells occur also on the ordinary rhizome-shoots, where, however, they do not undergo further development, especially when the end of the shoot appears

above ground. The root-like shoots branch like the ordinary ones; a cell is cut off by an oblique wall from one of the youngest segments, and forms the apical cell of the new shoot.

All the species of Selaginella possess true roots; but in some, as *S. Martensii* and *Kraussiana*, they arise on a structure which Nägeli calls the Rhizophore, and which has no root-cap. In *S. Kraussiana* the rhizophores spring from the dorsal side of the stem, nearly at the base of the weaker fork of each dichotomy, curl themselves round it, and then grow downwards; it is only rarely in this species that two of these organs arise near one another. *S. Martensii*, on the other hand, forms at each fork two rhizophores, one on the dorsal and one on the ventral side (the plane which passes through them is perpendicular to the plane of dichotomy), but usually only the ventral one undergoes further development, while the dorsal generally remains in the form of a small protuberance. The rhizophores arise very near the *punctum vegetationis*, probably at the same time as the branches of the dichotomy; unlike the roots, they are exogenous structures which, when young, possess a distinct apical cell. This is probably two-edged, but soon ceases to form new segments, the further growth being effected by intercalary divisions of the segments and elongations of the cells which proceed from them. After the cessation of the apical growth, the end of the still very short rhizophore swells up into a spherical form; its cell-walls become thicker, and in the interior of the swelling the first rudiments of the true roots originate, which however do not break through until the rhizophore has attained such a length by intercalary growth that its swollen end penetrates into the ground. The cells of this terminal part become disorganised and deliquesce into a homogeneous mucilage, through which the true roots penetrate into the ground. The rhizophores, as Pfeffer has shown (in *S. Martensii*, *inæqualifolia*, and *levigata*), are often transformed into true leafy shoots, which at first show some deviations from the normal structure in their first leaves, but afterwards continue to grow as normal shoots, and even produce sporangiferous spikes.

In *Selaginella Kraussiana*, *cuspidata*, and some other species, there are no rhizophores, but the roots spring immediately from the places nearest the ground where the stem forks and dichotomises, like the rhizophores of *S. Martensii*, even before they reach the ground. These roots are also formed very early, near the *punctum vegetationis*, probably at the same time as the branches of the stem. The roots which spring immediately from the stem, as well as those which proceed from the rhizophores, branch dichotomously, and in such a manner that the planes of the successive dichotomies cross one another at right angles. The branchings of the roots follow one another very quickly, and at the end of the mother-root are densely crowded; the apical cell is difficult to detect, but is probably, like those of the stem and of the rhizophore, two-edged. It soon ceases to form segments; the increase of length of each fork of the root takes place therefore almost exclusively by intercalary growth. Similar phenomena are observable in the roots which proceed from the furrows of the stem of Isoëtes, and which dichotomise three or four times in planes at right angles to one another. Nägeli and Leitgeb failed to find in them any apical cell distinguished by its form or size, although they considered the existence of a two-edged apical cell probable. In *Lycopodium clavatum* the roots spring

from the ventral side of the creeping stem without any fixed rule; they fork when they have attained a length of 3 or 4 centimetres, but probably not until they come in contact with the ground. Their plane of dichotomy stands (as in *Selaginella levigata* and *cuspidata*) at right angles to the longitudinal axis of the stem (in Isoëtes it is, on the contrary, parallel to it); the succeeding branches are either also dichotomous, or sympodial; in the latter case the real or apparent lateral branches appear distributed either in decussating pairs or singly with a divergence of $\frac{1}{2}$ or $\frac{1}{4}$. The position of these lateral roots has not been correlated with the arrangement of the fibro-vascular bundles of the mother-root. This, together with the circumstance that the young ramifications are densely crowded at the end of the mother-root, appears to exclude the supposition that the branching is monopodial; and in any case the process is more like that which occurs in Selaginella and Isoëtes. Above ground these roots are of a bright green colour. It is very difficult to prove the existence in them of an apical cell; yet Nägeli and Leitgeb conclude that one is present, having the form of a four-sided pyramid, the segmentation of which would influence the peculiar position of the root-branches.

The *Sporangia* exhibit considerable differences in the different genera of the class, both in their position on the fertile branch, and in their development and mature form. But they agree in a single sporangium being always formed in the axil of a leaf; and they are distinguished by their size from those of all other Cryptogams.

The sporangia of Isoëtes are sessile in the fovea of the leaf-sheath, to which they are attached by their dorsal line (Fig. 306 *A*). They are unquestionably products of the leaves; the outer leaves of the fertile rosettes produce only macrosporangia, the inner ones only microsporangia, the former containing a large number of macrospores. Both kinds of sporangia are imperfectly segmented by threads of tissue (*Trabeculæ*) which cross from the ventral to the dorsal side. The sporangia do not dehisce, but the spores escape by the decay of the wall.

In Selaginella the sporangia are shortly stalked roundish capsules, their origin being still doubtful, whether from the base of the leaf or from the stem itself, perhaps variable in the different species. The macrosporangia contain usually four, less often two or eight macrospores. In the division of Articulatæ the lowermost sporangium only of a spike produces macrospores; in the other divisions there are several macrosporangia.

The remaining genera have, as has been mentioned, only one kind of sporangium, the contents of which bear a greater resemblance, in Lycopodium to the microspores of Selaginella, in Psilotum to those of Isoëtes. The sporangia originate, in Lycopodium, from the leaf itself; they consist, as in Selaginella, of only one compartment, and split into two valves at the apex or on the anterior surface. In Psilotum the sporangia are described as trilocular, and as placed in the axil of a bipartite leaf; Juranyi's recent researches seem, however, to show that three sporangia are here seated round the end of a short branch, which at the same time forms below them two leaflets on the outer side. In Tmesipteris the elongated sporangium is seated on a stalk (shoot?) bearing two leaves right and left of it.

The history of development of the sporangia is still incomplete in many points. It is important to observe at the outset that Hofmeister considers that the sporangium of Lycopodiaceæ arises from a single cell of the leaf or stem, and that he

traces back also the origin of the spores in Selaginella to a single primary mother-cell, which is the central cell of the sporangium. All that is known in addition about Lycopodium and Psilotum is that the first point is at least not universal, while Russow, I think rightly, has doubts about the latter.

In Isoëtes the sporangia originate, according to Hofmeister, from the leaves in their very earliest stage. A single cell produces the mass of tissue, of which two outer layers of cells (Fig. 306 *B*) become the wall of the sporangium, while strings of cells running transversely form the trabeculæ. The numerous cells which lie between the latter still remain united into a tissue, increase in number, and form the

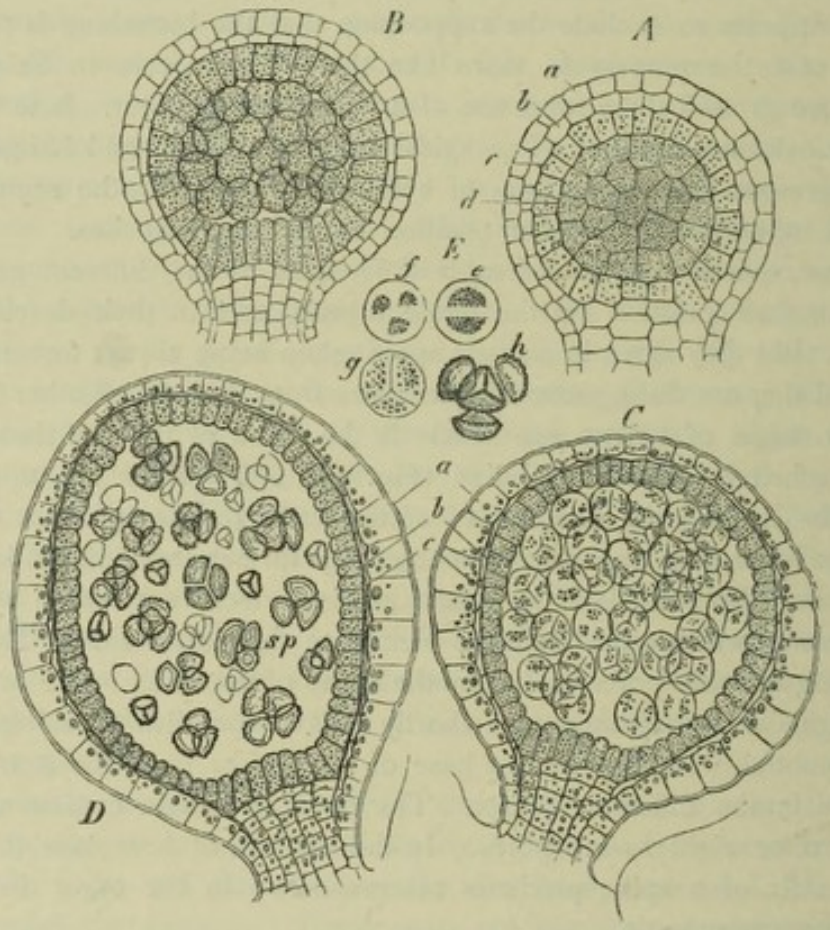

FIG. 309.—Development of the sporangia and spores of *Selaginella inæqualifolia*; the order of succession is indicated by the letters *A*—*D*; *A* and *B* serve for all the sporangia, *C* and *D* for the microsporangia only: *E* division of the mother-cells of the microspores, *h* four nearly ripe spores; in *A*, *C* and *D*, *a*, *b*, *c* are the three layers of the wall of the sporangium, *d* the primary mother-cells (*A*, *B* and *E* × 500; *C* and *D* × 200).

mother-cells of the spores; they finally become isolated and rounded off. The spores are formed by a repeated bipartition of these spore-mother-cells in planes at right angles to one another.

In Selaginella again, according to Hofmeister, the sporangium springs from a mother-cell which belongs to the periphery of the stem. In later states the sporangium is inserted in the axil or even in the base of the leaf. As in Isoëtes, the fibro-vascular bundle of the leaf runs beneath the sporangium, without sending a branch into it (*cf.* Psilotum, *infra*). I was unable, even in the youngest which came under my observation, to recognise a central cell which could be considered the mother-cell of the spores; on the contrary, even in very young sporangia a separation

of the tissue could be observed into a central mass and a wall consisting of three layers; the cells of the former soon become isolated and rounded off, and if a microsporangium is under observation, they all divide, after previous indication of a bipartition (Fig. 309 *E*, *e*, *f*) into four spores arranged in a tetrahedron, which retain this arrangement until they are ripe (*g*, *h*). In the macrosporangia, on the contrary, one of these mother-cells grows more vigorously, divides, and produces the four macrospores, while the rest of the mother-cells remain undivided; but, at least in *S. inæqualifolia*, continue to exist for a considerable period by the side of the much larger macrospores. These latter also retain until their dispersion their primitive position at the corners of a tetrahedron which they owe to the division of the mother-cell. Weakly macrospores are very commonly to be found in otherwise normal spikes of sporangia. The three cell-layers of the wall of the sporangium continue to exist until the spores are ripe, while in the case of Ferns the inner layers, as we know, are destroyed during the formation of the spores.

The youngest rudiments of sporangia which I could detect in *Lycopodium Chamæcyparissus*—but which I have frequently examined—have the appearance of broad protuberances of the upper side of the young leaf, at first very flat, and in this case it is quite clear that they do not belong to the axil of the leaf nor to the stem itself; the fibro-vascular bundle of the leaf passes beneath them, and it appears as if in this case the sporangium is not produced from a single superficial cell. In the youngest, and even in older states, where it already projects as a flat segment of a sphere, the epidermis of the leaf is continuous over the sporangium, constituting its parietal layer. While the sporangium becomes more and more protuberant, this layer undergoes numerous divisions at right angles to the surface. Even in the youngest stages there can be recognised, beneath the swelling of the epidermis, a layer of cells, out of which, as the growth of the protuberance advances, a spherical group of large cells is formed, which divides in all directions to form the mother-cells of the spores. The processes appear to be still the same when the sporangium has grown to a considerable size and is almost spherical in radial section; at that time a tangential division is seen here and there in the parietal layer, which, in the mature state, clearly consists of at least two layers. Older stages of development have not come under my notice; what I have here stated was deduced from the observation of some longitudinal sections of very young spikes preserved in glycerine.

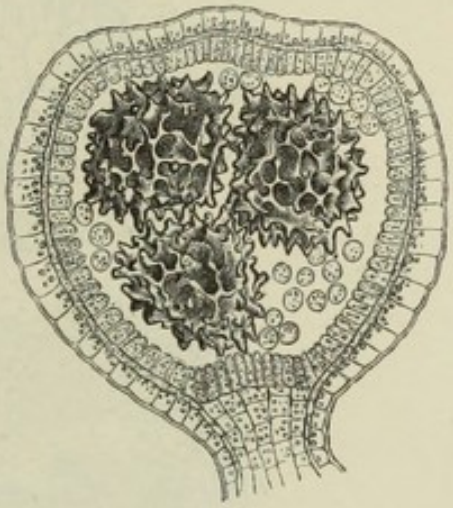

FIG. 309 *b*. — A nearly ripe macrosporangium of *Selaginella inæqualifolia*; the fourth spore which lies behind is not indicated (× 100).

In Psilotum the short branches on which the apparently trilocular sporangia arise appear as papillæ on the vegetative cone, which, according to Juranyi, possess, as well as the vegetative branches, a three-sided apical cell. A bundle from the

fibro-vascular bundle of the mother-shoot runs into these papillæ, without, however, reaching more than half their height. The two small leaves of this fertile shoot, which at one time were thought to be a bipartite leaf, originate separately on the papillæ, and unite only at a later period. The papilla itself consists, even at a rather late period, of a homogeneous tissue which becomes separated, in a similar manner to the anthers of Phanerogams, into parietal layers and three groups of spore-mother-cells. Three loculi are thus formed, protruding strongly outwards

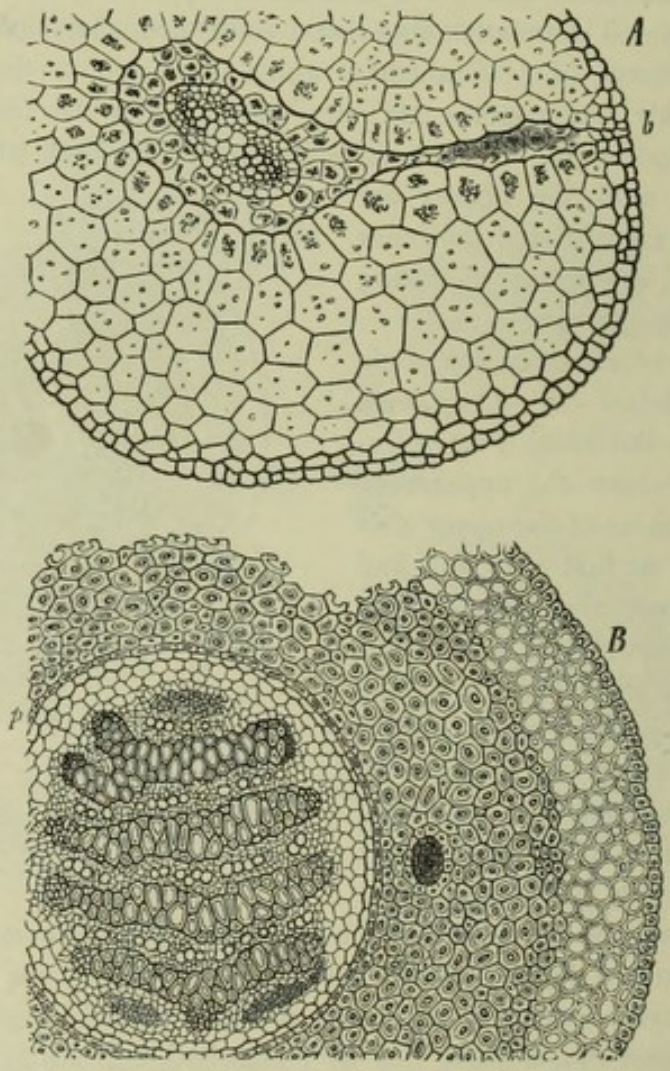

FIG. 310.—*A* transverse section of the stem of *Selaginella denticulata*, the central vessels of the bundle not yet lignified; *B* transverse section of the stem of *Lycopodium Chamæcyparissus* (×150).

and separated by longitudinal walls and by an axial mass of tissue. These three loculi I consider to be as many sporangia which are formed round the summit of the fertile shoot, through which the axial fibro-vascular bundle ascends.

The Systematic Classification of Lycopodiaceæ can only be regarded as provisional until the mode of germination of the remaining genera is accurately known. As we have seen, they may in the meantime be arranged into two groups:—

A. *Lycopodieæ*; with only one kind of spores.
Lycopodium, Tmesipteris, Phylloglossum, Psilotum.

B. *Selaginelleæ*, with two kinds of spores.
Selaginella, Isoëtes.

As to the *Forms of Tissue* in Lycopodiaceæ[1], it may be remarked that the fibro-vascular bundles which penetrate the stem belong exclusively to it or are 'cauline.' They may be followed in the procambial condition close beneath the apical cell to the apex of the stem and the youngest leaves. This I have found to be the case in *Selaginella inæqualifolia* and *Martensii* and in *Lycopodium Chamæcyparissus*; and, according to Nägeli, the fibro-vascular bundle of Psilotum is also cauline, since no branches pass from it into the leaves (Nägeli, Beitr. p. 52). Proceeding downwards from the apex of the stem, it is seen that the leaves which are already more developed each form a procambial bundle which applies itself to that of the stem. In the angle where they meet the formation of spiral vessels begins, and advances downwards into the stem, outwards

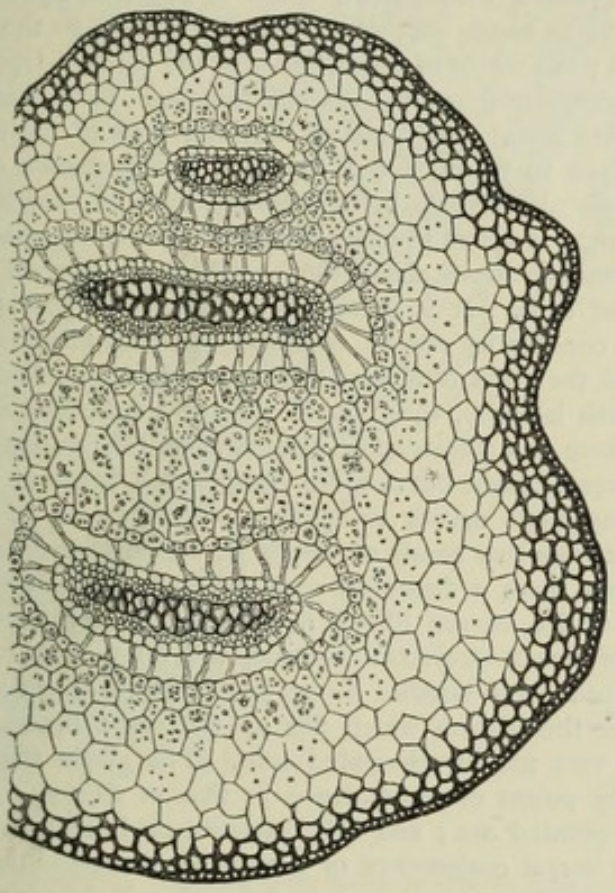

FIG. 311.—Transverse section of the stem of *Selaginella inæqualifolia* (×150).

into the leaf. In their procambial origin part of the fibro-vascular bundles of Lycopodium and Selaginella are therefore cauline, and part foliar; but the formation of the first spiral vessels takes place as if they were 'common' (*cf.* Equisetum). The first spiral vessels of the cauline bundle arise near its edges; the formation of the wider vessels, which are thickened in a scalariform manner, proceeds from them in a centripetal direction as seen in a transverse section. This occurs in different ways according to the nature of the cauline bundle, which is very simple in *Selaginella denticulata*

[1] On the development of the tissues in the roots, especially on the eccentric position of the fibro-vascular bundles in those of Isoëtes, compare Nägeli and Leitgeb, Beiträge zur wissensch. Bot. 1867, Heft IV.

(Fig. 310 *A*), *Kraussiana*, and *Martensii*; and in these cases it has, in transverse section, an elongated elliptical form. The first narrow spiral vessels arise nearly in the two foci of the ellipse; from these points two alternating rows of much wider scalariform vessels proceed inwards and become very slowly lignified, until a vascular band formed from a double row of woody vessels lies within the fibro-vascular bundle. The outer much narrower elongated cells of the bundle do not become woody; they form the phloëm, the outermost peripheral layer of which consists of much wider cells. In *Selaginella inæqualifolia* (Fig. 311), three fibro-vascular bundles lie parallel and side by side in the stem, each resembling the single bundles of the species mentioned before. In *Lycopodium Chamæcyparissus* (Fig. 310 *B*) a fibro-vascular cylinder occurs in the stem; four parallel transverse bands of xylem lie in it, each of which consists of a double row of wide scalariform vessels, with narrow spiral vessels also right and left at its ends. Each of these transverse bands corresponds in all respects to the single fibro-vascular bundle of Selaginella; the whole of the cylinder in the stem of Lycopodium is therefore made up by a coalescence of four fibro-vascular bundles. In the same manner the whole of the densely lignified tissue which fills up the interstices of the fibro-vascular bundles and forms an envelope to them, is the result of a coalescence of as many layers of phloëm, each fibro-vascular bundle being enveloped by its own layer. Between each pair of transverse bands of xylem lies also a row of wider cells, which may be recognised on longitudinal section as sieve-tubes; the periphery of the whole of the phloëm is also formed of wider cells. It is therefore beyond doubt that the axial cylinder of *L. Chamæcyparissus* consists of several coalescing parallel fibro-vascular bundles[1]. If the three bundles in the stem of *S. inæqualifolia* are imagined laid side by side and to have united in growth laterally, they would present a precisely similar structure. In *Lycopodium Selago* there is a similar axial cylinder, but the groups of vessels do not in this case form transverse bands, but a more complicated figure in a transverse section; otherwise the arrangement agrees completely with that of *L. Chamæcyparissus* (*cf.* Cramer). In *L. clavatum* two bands of vessels lie in the tranverse section of the axial cylinder, and between them a diametral row of wider cells (sieve-tubes). The outer fibro-vascular bundles are curved like a horseshoe: from the concavity which faces outwards a group of vessels projects: between the three arms so formed of each of these horseshoe-shaped outer bundles lie again two rows of wider cells (sieve-tubes), while all the rest of the phloëm which fills up the space between the fibro-vascular bundles consists of very narrow elongated cells. The single fibro-vascular bundle of Selaginella has many points of resemblance to that of Ferns (*e.g. Pteris aquilina*), as Dippel has already pointed out; and this resemblance is only partially obliterated in Lycopodium by the lateral coalescence of several fibro-vascular bundles[2].

Only one bundle bends out into each leaf, forming, in Selaginella and Lycopodium, an axial bundle through the mid-rib, and, as has been said, uniting with the outer edge of a cauline bundle.

In Selaginella the fibro-vascular bundles are surrounded by large spaces which contain air, into which transverse rows of cells pass out to the bundle like buttresses from the surrounding fundamental tissue. In Lycopodium these air-cavities are wanting. The fundamental tissue of both genera consists of elongated cells with oblique septa dove-tailed into one another in a prosenchymatous manner. In Selaginella the cell-walls are thin, the cavities wide, and there are no intercellular spaces; in Lycopodium the walls of the fundamental tissue are usually much thickened, especially in the part that

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[1] A similar explanation may also be given of the complicated fibro-vascular bundle of the thickish roots of *L. clavatum*, as described by Nägeli and Leitgeb.

[2] I found a stem of *Pteris aquilina* in which the two inner cauline bundles had coalesced laterally to such an extent as to form a hollow cylinder, enclosing a part of the parenchymatous fundamental tissue as medulla.

surrounds the axial cylinder; in *L. Chamæcyparissus* this thickening of the walls is remarkably great (Fig. 310 *B*)[1].

The epidermis of the stem consists, in Selaginella, of long prosenchymatous cells, and has no stomata; these occur only in a few rows on the under side of the leaves right and left of the mid-rib (Fig. 46, p. 47). The epidermis of the leaf consists of cells

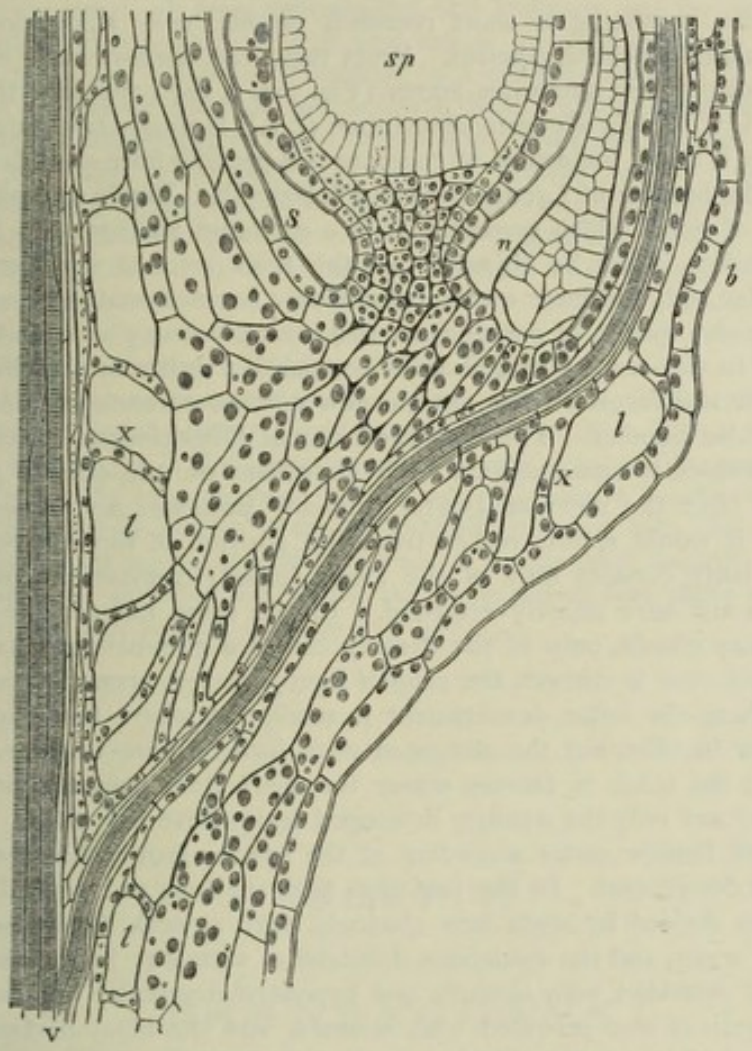

FIG. 312.—*Selaginella inæqualifolia*: longitudinal section through the right side of the axis of a spike *S*, the base of the leaf *b*, the ligule *n*, and the sporangium *sp*; *V* point where the cauline and foliar fibro-vascular bundles unite; *l* air-conducting intercellular spaces; *X* series of cells traversing the spaces.

containing chlorophyll, the lateral walls of which are beautifully serpentine. In *L. Selago*, on the other hand, the large and comparatively few stomata are distributed over the

[1] [Hegelmaier, in an exhaustive treatise on the morphology of the genus Lycopodium (Bot. Zeitg. 1872, p. 773 *et seq.*), describes the stem as consisting of a fibro-vascular cylinder surrounded by a thick cortex, the first being formed of a number of bundles penetrating a thin-walled and narrow-celled tissue. The central cylinder is composed of two parts, distinguishable from an early period and even when the tissue is mature, *viz.* a comparatively small external and a much more strongly developed axial portion, the latter consisting of the true fibro-vascular bundles with inter-fascicular tissue. The first of these two parts, which must not be confounded with the inner layers of the cortex, surrounds the central part of the cylinder as an enveloping sheath, and Hegelmaier proposes for it the term 'Phloëm-sheath,' retaining, with previous writers, that of 'phloëm' for the interfascicular tissue. This phloëm-sheath (Fig. 310 *B*, *p*) is separated from the phloëm by a cylindrical layer which unites together the outer convex surfaces of the fibro-vascular bundles, and is distinguished from it by its cells being shorter, with thinner walls and larger cell-cavities.—ED.]

whole of the under side of the leaf. The chlorophyll in the cells of the leaf of Selaginella often forms only a few—sometimes only one or two—masses variable in form; the margin of the leaf consists, in this genus, of only a single row of cells, which, as in Mosses, develope in the form of teeth or hairs.

To this brief description must be added a few further words with respect to Isoëtes. The short stem of the mature plant contains an axial woody body which can scarcely be termed a bundle, consisting of short roundish vascular cells united loosely, and with spiral or reticulated thickening-bands. From these the fibro-vascular bundles proceed, one into each of the very numerous leaves (Fig. 305, p. 407) and into the roots. Notwithstanding H. v. Mohl's accurate description (*l. c.*), Hofmeister's statements, and my own researches, it is still impossible to compare this peculiar fibro-vascular body morphologically with the bundles of Lycopodium and Selaginella. But in opposition to the view that the layer of tissue which surrounds it is a cambium analogous to that of Dicotyledons and Conifers, it may be objected that this thick layer of meristem which invests the fibro-vascular body produces on the outside only parenchymatous fundamental tissue, by which the outer masses of parenchyma that annually decay away and become brown are replaced. In this respect this tissue is comparable rather to the thickening-ring of Dracæna, which also forms on the outside new cortical parenchyma and on the inside new fibro-vascular bundles. The true cambium of Dicotyledons, on the other hand, produces fibro-vascular structures in both directions, on the outside phloëm, on the inside xylem. But the stem of Isoëtes probably possesses no proper fibro-vascular bundle at all; it would appear rather, from the position of the vessels, that the axial fibro-vascular body consists only of the lower (inner) commencements of the foliar bundles, which are here densely crowded. In the same manner the basal disc-like woody body may consist only of the densely crowded commencements of the radical bundles. If this view is correct, the class of Lycopodiaceæ presents two extremes, one in Psilotum, where the foliar development is small, and where there are, according to Nägeli, no foliar bundles, but the elongated stem forms a fibro-vascular bundle belonging to it only; the other in Isoëtes, where the short stem possesses no cauline fibro-vascular bundle, and only the strongly developed leaves have one each. The structure of the leaves of Isoëtes varies according as the species grow submerged in water, in marshes, or on dry ground. In the first case they are long and conical, penetrated by four air-cavities divided by septa into channels, with a weak fibro-vascular bundle in the axis of the organ, and the epidermis destitute of stomata: in the second case they are similar, but provided with stomata and hypodermal vascular bundles; in the third case the epidermis is also provided with stomata, and the basal portions of the dead leaves (phyllopodes) form a firm black coat of mail round the stem.

[Professor W. C. Williamson has contributed the following note on the **Carboniferous Lycopodiaceæ**:—'The large and varied group of the Lycopodiaceous plants of the Coal Measures exhibits so many modifications that it is difficult to give a brief statement of their characteristic features. But so far as the Lepidodendroid and Sigillarian forms are concerned, our British forms all exhibit one type of internal organisation. In the very young state each twig has a central bundle of scalariform vessels surrounded by a 'bark,' which usually exhibits an inner parenchymatous layer surrounded by a more prosenchymatous one, which is again invested by a second but more unequal parenchyma. Bundles of vessels given off by the central vascular axis proceed to each of the leaves. As the twig enlarges the central axis invariably expands into a vascular cylinder, its interior becoming occupied by a cellular parenchyma of large size, and which now occupies the position and exhibits the appearance of a true medulla. The parenchyma of the leaves appears to be an extension of the outermost parenchyma of the bark. The above remarks appear to represent the common history of all the Lepidodendroid plants up to a certain stage of their growth. Beyond this stage their histories vary somewhat in the different groups. In some forms, *e.g.* those to which the Haloniæ belong, the branches attain considerable dimensions without undergoing any great change in their internal organisation; but in others a new development of vascular tissue invests the central cylinder at a period which seems to have varied in different species. This new growth takes place in successive

layers, which are arranged in vertical laminæ disposed in radiating planes separated by tracts of muriform parenchyma; successive additions are made to the outer margins of the woody wedges previously formed through the agency of a pseudo-cambial layer of the innermost 'bark.' These exogenous growths continued until the woody zone attained to a great thickness in the larger trunks. These exogenous layers took no part in supplying the leaves with vessels. The foliar bundles invariably pass through them on their way from their source in the inner non-radiated vascular cylinder to the leaves. It being now admitted that Stigmaria was the general form of root of Lepidodendroid and Sigillarian types it is necessary to correlate its tissues with those of the aërial stem. It contains a 'medulla' surrounded by a cylinder composed of radiating vascular laminæ separated by cellular rays, and enclosed in a thick 'bark.' Large vascular bundles are given off from the vascular wedges to supply the rootlets. Thus the structure of the root differs from that of the aërial stem in two ways. (1) The inner vascular cylinder of the latter, characterised by the non-radiating arrangement of its vessels, by the absence of 'cellular rays,' and by the numerous foliar bundles which it gives off to the leaves, is altogether wanting in the former. On the other hand, the exogenous zone of the stem is prolonged into the roots, retaining all its more important features. These however are modified in two ways—1st, in the absence of small passages for the transmission of foliar bundles of vessels; and, 2nd, in their replacement by much larger spaces having a lenticular section, and through which large vascular bundles, directly derived by enlarging from the exogenous laminæ themselves, pass outwards to the succulent rootlets. That Lepidostrobi are the fruits of Lepidodendroid plants is certain. Equally so is it that many of the former produced microspores in the upper sporangia of each cone, and macrospores in those occupying its basal end. The incalculable myriads of these macrospores found in many coals renders it probable that a very large number of the Lepidostrobi possessed both kinds of spores; indeed it is far from certain that any of them did otherwise. In the great majority of cases the sporangia of these fruits are shrivelled and empty, the spores having been shed; and this renders it impossible to say what their original character was[1].'—Ed.]

GROUP V.

PHANEROGAMS.

The Alternation of Generations in Phanerogams is concealed in the formation of the Seed, which, at least in its earliest stage, consists of three parts:—(1) The *Testa*, which is a part of the mother-plant; (2) The *Endosperm*[2]; and (3) The *Embryo*, the result of the development of the oospore or fertilised embryonic vesicle (oosphere).

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[1] [For the literature of the Carboniferous Lycopodiaceæ see Brongniart, Archives du Mus. d'Hist. Nat. vol. I, and Journ. Bot. vol. VII, pp. 3–8.—King, Edin. New. Phil. Journ. vol. XXXVI. —Hooker, Mem. Geol. Surv. vol. II.—Carruthers, Monthly Mic. Journ. vol. I, pp. 177–181 and 225–227; Quart. Journ. Geol. Soc. vol. XXV, pp. 248–254.—Williamson, Phil. Trans. vol. CLXII, pp. 197–240.—Thiselton Dyer, Quart. Journ. Mic. Sc. 1873, pp. 152–156.—Ed.]

[2] The only reason why the ripe seeds of many Dicotyledons do not contain any endosperm is because it has already been absorbed and supplanted by the rapidly growing embryo before the seeds become ripe; while in others this absorption happens only on germination after the ripening of the seeds, *i. e.* on the unfolding of the embryo; more rarely the formation of endosperm is from the first rudimentary.

In Vascular Cryptogams we have already seen the sexual generation which results directly from the spore or prothallium losing more and more of its character of an independent plant. In the Ferns, Equisetaceæ, and Ophioglossaceæ it grows independently of the spore, often for a considerable period; in the Rhizocarpeæ and Lycopodiaceæ, where male and female spores are formed, it arises in the interior of the spore, the female prothallium still protruding in the former out of the cavity of the macrospore, but remaining united with it; while in Isoëtes it fills up the interior of the macrospore as a mass of tissue which only bursts the cell-wall of the spore in order to render the archegonia accessible to the antherozoids. In the Cycadeæ and Coniferæ this metamorphosis is carried one step further; the prothallium[1], which is now known as the Endosperm, remains during its whole existence enclosed in the macrospore or Embryo-sac; it produces before fertilisation archegonium-like structures, the 'Corpuscula,' in which the Germinal or Embryonic Vesicles arise. The processes which take place in the embryo-sac of Monocotyledons and Dicotyledons appear somewhat different, and bear a greater resemblance to what takes place in the macrospore of Selaginella. In this genus, besides the prothallium which produces the archegonia, there arises subsequently, by free cell-formation, another tissue which fills up the rest of the space of the macrospore; to this tissue the endosperm of Monocotyledons and Dicotyledons, which is formed by free cell-formation only after fertilisation, appears to correspond; the prothallium of Selaginella does not appear to have anything to correspond to it in Angiosperms, the embryonic cells or 'Germinal Vesicles' arising immediately from the protoplasm of the embryo-sac[2]. If, therefore, the embryo-sac is the representative of the macrospore, that part of the ovule in which the embryo-sac arises (the nucleus) must be considered the equivalent of the macrosporangium. But, as in the formation of the seeds of Monocotyledons and Dicotyledons, certain processes of development (the formation of the archegonia or 'corpuscula'), being no longer necessary, are suppressed, and the embryonic vesicle is produced immediately from the embryo-sac as the analogue of the macrospore, so also the production of the embryo-sac immediately from the tissue of the nucleus of the ovule is more direct. Its production is due to the simple increase in size of an inner cell of the nucleus which here replaces the sporangium. But while even in the most highly developed Cryptogams the macrospore still becomes detached from the tissue of the mother-plant, and the full development of the prothallium takes place only after the dissemination of the spores, so that the embryo always arises in structures distinct from those of the mother-plant, the embryo-sac (or macrospore) of all Phanerogams remains, on the contrary, enclosed in the ovule, the endosperm in the embryo-sac, and the embryo in the endosperm. In this manner arises that structure peculiar to Phane-

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[1] The analogy of the endosperm with the prothallium of the higher Cryptogams was first shown by Hofmeister (Vergleich. Untersuch. 1851), [Germination, Development, and Fructification of the Higher Cryptogamia, Ray Soc. 1862, p. 438.]

[2] Compare Pfeffer in Hanstein's Botanical Dissertations, Heft IV, p. 24. The 'Antipodal Cells' in the embryo-sac of Angiosperms may probably be considered as the last occasional occurrence of the rudiment of the true prothallium, and the occasional filamentary apparatus of the embryonic vesicles as the last rudiment of the canal cell.

rogams, the *Seed*, the testa of which, the product of the envelopes of the ovule, closely invests both endosperm and embryo. The whole becomes separated from the mother-plant after the embryo has attained a certain very variable degree of development. Germination consists in the further development of the embryo at the expense of the endosperm.

If, on the other hand, the microspores of Selaginella and Isoëtes are compared with the pollen-grains of Phanerogams, a series of analogies is again seen which becomes intelligible on comparing the intermediate phenomena presented by Gymnosperms. Indications of the male prothallium and antheridium are indicated, as Millardet and Pfeffer have shown, by certain cell-divisions which may also be recognised in a still simpler form in the pollen-grain of Gymnosperms, but which do not occur in Angiosperms. Like the microspores, the pollen-grains contain the male fertilising principle, which, passing into the oosphere or embryonic vesicle, causes it to develope the embryo; but a great difference is displayed in the mode in which the fertilising substance is conveyed. In Cryptogams the fertilising substance takes the form of spermatozoids or antherozoids endowed with motion and adapted to force themselves, with the assistance of water, into the oosphere through the open neck of the archegonium. In Phanerogams, where the embryonic vesicle is enclosed in the embryo-sac and ovule, and in Angiosperms is also surrounded by the wall of the ovary, such a conveyance of the fertilising element would not serve the purpose intended; the pollen-grains are therefore themselves conveyed to the female organ by foreign agencies, such as the wind, mechanical contrivances in the flowers, and especially insects; and then germinating like spores, they emit their pollen-tubes, which, penetrating through the masses of tissue of the female organ, finally reach the embryo-sac, and transmit by diffusion the amorphous soluble fertilising substance into the embryonic vesicle. The analogy of pollen-grains to spores becomes still more evident when we examine the mode of origin of both. The mass of tissue in which the pollen is formed, the pollen-sac, shows, not only in its morphological but also in its anatomical relationships, a striking resemblance to the sporangium of Vascular Cryptogams. As in the latter the spore-mother-cells are formed by the isolation of cells previously combined, so also are the mother-cells of the pollen; and as the former themselves produce the spores by division into four, usually after previous indication of a bipartition, the pollen-cells are produced from their mother-cells in a similar manner. Moreover, in the points here indicated Gymnosperms again appear as a connecting link between Cryptogams and Angiosperms; the pollen-sacs of Cycadeæ and of some Coniferæ resembling, in form and position, the sporangia of some Vascular Cryptogams.

The general result of these observations is that the Phanerogam, with its pollen-grains and its embryo-sac, is equivalent to the spore-producing (asexual) generation of the heterosporous Vascular Cryptogams. But as in Vascular Cryptogams the sexual differentiation first makes its appearance (in Ferns and Equisetaceæ) on the prothallium only, and next (in Rhizocarpeæ and Lycopodiaceæ) on the spores themselves, so, in Phanerogams, this process is carried back a step further, the sexual differentiation arises still earlier, being manifested not only in the formation of embryo-sac and pollen-grains, but also in the difference between ovule and pollen-sac, and even earlier in the distinction between male and

female flowers, and last of all in the diœcious condition of the plants themselves[1].

The fertilised embryonic vesicle of Phanerogams is not directly developed into the embryo; it first of all produces a pro-embryo, the *Suspensor*,—growing towards the base of the embryo-sac and dividing,—which we have already met with in Selaginella, and on the apex of which arises a mass of tissue at first almost globular, and from which the embryo is developed. The development of the embryo usually proceeds, even before the maturity of the seed, to such an extent that the first leaves, the primary axis, and the first root, can be clearly distinguished. It is only in parasites and saprophytes devoid of chlorophyll that the embryo usually remains rudimentary until the dissemination of the seeds without discernible external differentiation; while in those Phanerogams which contain chlorophyll the embryo not unfrequently attains a very considerable size and external differentiation (as in Pinus, Zea, Aesculus, Quercus, Fagus, Phaseolus, &c.) Independently of any curving of the embryo, the primary apex of its stem always lies originally pointing towards the bottom of the embryo-sac (the base of the ovule); the first root (primary root) coincides with a posterior prolongation of the primary stem; it faces the apex (micropylar end) of the embryo-sac, and is of distinctly endogenous origin, inasmuch as its first rudiment at the posterior end of the embryo is covered by the nearest cells of the pro-embryo.

The *Apical Cell* of the *punctum vegetationis*, which is easily recognized in many Algæ, in Characeæ, Muscineæ, Ferns, Equisetaceæ, and Rhizocarpeæ, as the primary mother-cell of the tissue, has already, as we have seen, lost its significance in the Lycopodiaceæ. The apical growth of the axes, leaves, and roots of Phanerogams can no longer be referred to the activity of a single apical cell from which the whole primary meristem has proceeded. Even in those cases where a single cell (not, however, of preponderating size) occupies the apex, and the arrangement of the superficial cells of the *punctum vegetationis* appears to point to it as the primary mother-cell, it is nevertheless by no means to be assumed that all the cells, and especially the internal mass of the primary meristem, has proceeded from it. The primary meristem of the *punctum vegetationis* consists of a large number of usually very small cells, more or less evidently disposed in concentric layers; an outer simple layer, the dermatogen, may be recognized in Angiosperms as the immediate continuation of the epidermis of the older parts, and is continuous even over the apex of the *punctum vegetationis*. Beneath it lies a second layer of tissue (the periblem), consisting usually of a few layers of cells, which covers the apex and passes lower down into the cortex; this envelopes a third inner mass of tissue (the plerome) terminating beneath the apex as a single cell[2] (Hippuris, &c.) or as a group of cells; and out of it proceeds either an axial fibro-vascular body (in the roots and stems of water-plants), or the descending arm of the fibro-vascular bundles. In harmony with this the root-cap does not proceed, as in Cryptogams, from transverse divisions

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[1] Compare what is said on Dichogamy in Book III.

[2] As in so many other respects, here also Isoëtes shows an affinity to Phanerogams, as is evident from Nägeli and Schwendener's researches on the apical growth of roots. (Compare Nägeli's Beiträgen, 1867, Heft IV, p. 136.)

of an apical cell, but arises, on the contrary, in Gymnosperms from a luxuriant growth of the layers of periblem of the root and from their splitting away towards the apex, and in Angiosperms from a similar process in the dermatogen[1]. Even the first rudiments of lateral structures, leaves, shoots, and roots, cannot be traced back in Phanerogams to a single cell in the same sense as in Cryptogams. They are first observable as protuberances consisting of a few or a larger number of small cells; the protuberance which is to form a shoot or a leaf shows, even when it first begins to swell, an inner mass of tissue which is connected with the periblem of the generating vegetative cone, and is covered over by a continuation of the dermatogen.

The normal *Mode of Branching* at the growing end of the shoot, leaves, and roots, is, with few exceptions, monopodial. The generating axis continues to grow as such, and produces lateral members (shoots, lateral leaf-branchings, lateral roots) beneath its apex; some cymose inflorescences appear however to be the result of dichotomous branching. It is possible also that in Cycadeæ the branching of the stem and leaves may be dichotomous. The monopodial branching of the axes is usually axillary; *i.e.* the new rudiments of shoots appear above the median plane of very young (but not necessarily the youngest) leaves, in the angle which they form with the shoot, or somewhat above it. In Gymnosperms every axil of a leaf does not usually produce a shoot; sometimes (in Cycadeæ), the branching of the stem is reduced to a minimum. In Angiosperms, on the contrary, it is the rule that every axil of a foliage-leaf (*i.e.* one not belonging to the flower) produces a lateral shoot (sometimes even several side by side or one above another); but commonly the axillary buds, once formed, are inactive, or develope only at later periods of vegetation. In addition to the above-mentioned cases of apparent dichotomy, there are in Angiosperms only a few cases of actual or apparent extra-axillary branching, which will be mentioned when discussing the characteristic features of this class.

Phanerogams are distinguished from Cryptogams by an extraordinarily varied and complete metamorphosis of members bearing the same name; and this is connected with the almost infinite variety in the mode of life, and the strict differentiation of the physiological functions of these plants; and the same is the case with the differentiation of tissues, which in Phanerogams greatly exceeds even that of Ferns. In these respects also Gymnosperms assume an intermediate position between Cryptogams and the rest of Phanerogams.

What has now been said will serve to explain on one hand the distinction between Vascular Cryptogams and Phanerogams, on the other hand the points in which they agree, and the affinity of the two groups in their main outlines. In order, however, to facilitate the comprehension by the student of the characteristics of the separate classes of Phanerogams which are now to be described, we must in the first place keep in view a few of their peculiarities, which have at present only been briefly touched upon, and attempt to settle the nomenclature, which has become to some extent obsolete and out of harmony with the most recent theories.

The *Flower*, in the broadest sense of the term, is composed of the sexual organs and the axial structure which bears them. When the leaves which stand immediately

[1] See Hanstein, Bot. Abhandl. Heft I, and Reinke, Göttinger Nachr. 1871, p. 533.

beneath the sexual organs on the same axis differ from the rest of the leaves of the plant in their arrangement, form, colour, or structure, and are physiologically connected with fertilisation and its results, they are considered as belonging to the flower, and are termed collectively the Floral Leaves or *Perianth*. The separate flowers are distinguished from the *Inflorescence* by including, together with their sexual organs and perianth, only one axis, while the inflorescence is an axial system with more than one flower[1]. Röper has termed the *tout ensemble* of the male sexual organs of a flower the *Andrœcium*, that of the female organs the *Gynœceum*. When a flower contains sexual organs of both kinds it is called *hermaphrodite* or *bisexual*; if it contains only male or only female sexual organs, and is therefore *unisexual*, it is termed *diclinous*; when flowers of both sexes occur on the same individual plant, the species is *monœcious*, when on different individuals it is *diœcious*. Usually the apical growth of the floral axis ceases as soon as the sexual organs make their appearance, and frequently even earlier; the apex of the floral axis is then concealed, and is often deeply depressed in the centre of the flower; but in abnormal cases (and normally in Cycas) the apical growth of the floral axis recommences, again produces leaves, and sometimes even a new flower; and a *Proliferous Flower* is thus produced. The sexual organs and perianth of a flower are usually crowded (arranged in rosettes either spirally or in whorls); the part of the floral axis which bears them remains very short, no internodes being in general distinguishable in it; and it not unfrequently expands into the form of a club or disc, or becomes hollow, and this part of the floral axis is called the *Torus* or *Receptacle*. In Coniferæ and Cycadeæ (occasionally also in Angiosperms), it is however sometimes elongated to such an extent that the sexual organs appear loosely arranged along an axis in the form of a spike. Beneath the receptacle the axis is mostly elongated and more slender, either entirely naked or bearing one or two small leaves or *Bracteoles*. This part of the axis is the *Peduncle*; if it is very short, the flower is said to be sessile. No shoots usually arise from the axils of the floral leaves, even when they are produced in all the other leaf-axils of the plant; there occur, however, abnormal cases (which are not very uncommon) of axillary branching or prolification even within the flower.

The *Male Sexual Cells* (*Pollen-grains*), which are equivalent to the microspores of the higher Cryptogams, arise in receptacles corresponding to the sporangia in those plants, and may be termed in general *Pollen-sacs*. These are at first solid masses of tissue in which, as in the sporangia, an inner mass of cells becomes differentiated into the mother-cells of the pollen-grains (at first by more vigorous growth of the single cells), while the surrounding layers of tissue become developed into the wall of the pollen-sac. It has already been mentioned that the mother-cells of the pollen become separated and detached from the tissue (though this rule is subject to exceptions), and then produce the pollen-cells by division into four after actual bipartition or at least an indication of it. A special description of these processes will be given under the heading of the separate classes; at present we must however premise a few facts relative to the morphological nature of the pollen-sac. Like the sporangia of most Vascular Cryptogams, the pollen-sacs of Phanerogams are usually products of the leaves, which however mostly undergo in this case a striking metamorphosis, remaining much smaller than all the other leaves. A leaf which bears pollen-sacs may be termed a Staminal Leaf or *Stamen*; the most recent researches have, however, shown cases in which the pollen-sacs arise on the elongated floral axis itself, as Magnus has illustrated in the case of Naias, Kaufmann in Casuarina, and Rohrbach in Typha; in these cases it is still doubtful whether the pollen-sacs may not be the only surviving portions of

[1] In some cases it is however difficult to distinguish between a flower and an inflorescence; as in some Coniferæ, and especially in Euphorbia. (On the latter, see Warming in Flora 1870, no. 25; Schmitz, ditto 1871, nos. 27, 28; and Hieronymus, Bot. Zeitg. 1872, no. 12.) [E. Warming, Er Koppen hos Vortemælken en Blomst eller en Blomsterstand, Köbenhavn 1871.]

otherwise completely abortive staminal leaves[1]. In the Cycadeæ the pollen-sacs grow singly or in groups on the under side of the relatively large stamens, often in large numbers, resembling in position the sporangia on Fern-leaves. In the Coniferæ the stamens have still more lost the appearance of ordinary leaves; they remain small, and form several or only two relatively large pollen-sacs on the under side of the lamina which is still distinctly developed. In Angiosperms the stamen is usually reduced to a slender weak and often very long stalk called the *Filament*, bearing two pairs of pollen-sacs at its upper end or on both sides beneath the apex, which are included as a whole under the term *Anther*; the anther therefore usually consists of two longitudinal halves, united and at the same time separated by a part of the filament termed the *Connective*. The two pollen-sacs of each half of the anther are contiguous throughout their length, and frequently both halves of the anther are in close apposition. The separate pollen-sacs then appear as compartments of the anther, which is in this case quadrilocular, in contrast to those anthers (of rare occurrence) in which each half contains only a single pollen-sac, and which are therefore bilocular.

The *Embryo-sac*, the analogue of the macrospore, is the result of a very considerable enlargement of an inner cell of the nucleus of the ovule, which itself corresponds to the macrosporangium of heterosporous Cryptogams. The nucleus is a small-celled mass of tissue of usually ovoid form, and enclosed, with a few exceptions, in one or two envelopes, each of which consists of several layers of tissue. These envelopes or *Integuments* grow round the young nucleus from its base, and form at its apex—where they approach and often greatly overtop it—a canal-like entrance, the *Micropyle* or *Foramen*, through which the pollen-tube forces its way, in order to reach the apex of the embryo-sac. Very commonly the nucleus, enclosed in its integuments, is seated on a stalk, the *Funiculus*; but this is sometimes wanting, and the ovule is then said to be sessile. The funiculus is, with a few exceptions (Orchideæ), penetrated by an axial fibro-vascular bundle which usually ceases at the base of the nucleus. The external form of the ovule when in a state for fertilisation is very various. Independently of outgrowths of various kinds at the funiculus and the integuments, the direction of the nucleus (together with its coatings), with respect to the funiculus, is of especial importance. The ovule is *orthotropous* when the nucleus is in a direct line with the funiculus, and the apex of the nucleus is the apex of the entire ovule. Much more frequently the ovule is *anatropous*; *i.e.* the apex of the nucleus, and therefore the micropyle which projects beyond it, faces the point of origin of the funiculus, which runs along the side of the nucleus, so that the ovule appears as if sharply curved at its base; and the integuments (or at least the outer one), have united in growth with the ascending funiculus, which, so far as this union is complete, is termed the *Raphe*; the nucleus itself being in this case straight. Much less common is the *campylotropous* ovule, where the nucleus itself (together with its coatings) is curved; its apical part, and therefore its micropyle, facing the base, but without any lateral cohesion with the funiculus. These are, however, only the most striking forms, which are united by transitional states. The place from which the ovules spring is called the *Placenta*, and belongs to the axis of the flower, or more commonly to the carpels themselves. The placentæ often do not show any peculiar phenomena of growth; but more commonly they project like cushions, and may thus assume the appearance of special organs, finally becoming detached from the surrounding tissue. While, after fertilisation, both the endosperm and the embryo are undergoing simultaneous development in the embryo-sac, the former most commonly increases considerably in size, and supplants the surrounding layers of tissue of the nucleus (sometimes even of the inner integument); and the tissue of the integument which is not displaced, or usually only certain definite layers of it, becomes then developed into the *Testa*. If a portion of

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[1] [For instances of the production of pollen-grains in abnormal positions, even in ovaries or in the ovules themselves, see Masters, Vegetable Teratology, Ray Soc. London 1869, pp. 182–188. —Ed.]

the tissue of the nucleus, filled with food-materials, remains unchanged until the seed is ripe, it is distinguished as the *Perisperm;* its food-materials, although lying outside the embryo-sac, are consumed by the embryo during germination; and the perisperm may then act physiologically as the representative of the endosperm[1]. The seeds, *e.g.*, of Cannaceæ and Piperaceæ, contain perisperm. Sometimes the ovule, during the period of its development into a seed, is enveloped from below by a new coating, which usually itself surrounds the tough testa as a soft mantle, and is termed the *Aril.* Of this nature is the red pulp which surrounds the hard-shelled seed of the yew; and the origin is the same of the so-called 'mace' of the nutmeg, the seed of *Myristica fragrans.*

If we now turn our attention to the morphological nature of those structures from which the ovule immediately springs, we find a considerable variety. Only rarely does the orthotropous ovule appear as the prolongation or terminal structure of the floral axis itself, so that the nucleus forms directly the vegetative cone of the latter, as in Taxus and Polygonaceæ. It is more usual for the ovule to grow laterally on the floral axis, thus corresponding in position to a leaf, as in Juniperus, Primulaceæ, and Compositæ. But the most common case is where the ovules spring from undoubted leaves—the carpels—and usually from their margin, like pinnæ from the leaf (this is very clear, *e.g.* in Cycas), more rarely from their upper (or inner) side (as in Butomus, Akebia, Nymphæa, &c.). If the ordinary morphological definitions are applied to these relationships, we should have in the first-named case ovules of an axial nature, or they would be metamorphosed caulomes[2]; where they spring laterally from the axis, they would have to be considered as metamorphosed entire leaves; and where they proceed laterally from the margins of carpellary leaves, as metamorphosed pinnæ. For those ovules which spring from the surface of carpels there is no clear analogy with any purely vegetative structures (*i. e.* with any that do not subserve the purpose of fertilisation); though in this case we may be reminded of the sporangia of Lycopodiaceæ. It appears, however, possible to regard some ovules, as, for instance, those of Orchideæ, as metamorphosed trichomes (like the sporangia of Ferns and Rhizocarps). The ovules, finally, of some Cupressineæ, which appear to have an axillary position on the carpels, have not yet been sufficiently investigated with respect to their true relationships. In some cases the morphological interpretation is supported by malformations which not unfrequently occur. Cramer, to whom we are indebted for an admirable investigation of this question, has shown that the ovules of Primulaceæ and Compositæ, which arise laterally beneath the apex of the axis of the flower, become gradually transformed into entire leaves of the ordinary form; and that in the same manner the ovules of Delphinium, Melilotus, and Daucus, which spring laterally from the margins of the carpellary leaves, may become developed into ordinary parts of the lamina, as laciniæ or leaflets. It appears on the other hand significant that nothing of the kind has yet been observed in those ovules which have been interpreted above as metamorphosed portions of the axis or as trichomes. The development not only of normal, but still more plainly that of abnormal ovules, shows further that a morphological distinction exists between the nucleus on the one hand and the funiculus together with the integuments on the other hand. In those anatropous ovules which may be regarded as metamorphosed leaves or parts of leaves, the nucleus makes its appearance of a new lateral structure inserted on the body

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[1] [The endosperm and perisperm are generally both included in English text-books under the term 'albumen,' a term which should by all means be avoided, as conveying the idea of a definite chemical composition, whereas that of the endosperm varies greatly.—Ed.]

[2] Cramer,—Bildungsabweichungen bei einigen wichtigeren Pflanzen-familien, u. die morphologische Bedeutung des Pflanzeneies (Zürich 1864),—is inclined to consider all ovules as metamorphosed leaves or parts of leaves. To this view I have already expressed some hesitation in the first edition of this book; the description here given, which differs from the earlier one, is derived as much as possible from direct observation.

of the ovule, and when this latter becomes developed in a leaf-like manner it appears as an outgrowth of the surface of the leaf. This fact, the morphological importance of which was first insisted on by Cramer, is however not universal, as is especially shown in the development of the ovules of Orchideæ, the nucleus of which unquestionably corresponds to the apex of the entire ovule, although it becomes anatropous by subsequent curvature; still less possible does it appear to consider the nucleus of the orthotropous ovule of Taxus and Polygonaceæ as a lateral formation, since it is obviously an elongation of the apex of the floral axis (see Angiosperms).

The *Carpellary Leaves* are the foliar structures of the flower which stand in the closest genetic and functional relationship to the ovules. They either produce and bear the ovules, or are constructed so as to enclose them in a chamber, the *Ovary*, and to form the apparatus for the reception of the pollen, or *Stigma*. The distinct morphological significance of the carpellary leaves is clearly seen by a comparison of the genera Cycas and Juniperus. In Cycas the carpels resemble the ordinary leaves of the plant, and the ovules are produced on their margins and remain entirely exposed; in Juniperus the ovules spring from the floral axis itself, corresponding, even in their position, to a whorl of leaves, but the preceding whorl of carpellary leaves swell up after fertilisation, and envelope the seeds in a pulpy mass, the berry-like 'fruit' of these plants. In Primulaceæ the ovules spring from the elongated floral axis itself, and thus correspond in their position to entire leaves; they are however enclosed, even at the period of their formation, by an ovary, consisting of the carpels and an elongated style bearing the stigma. In most other Dicotyledons and Monocotyledons the ovules are seated on the revolute margins of the carpels which have grown together into an ovary, and which therefore in these cases both produce and enclose the ovules. But notwithstanding these very considerable morphological differences, the carpellary leaves are always alike physiologically in being excited by fertilisation to further development during the maturing of the seeds, and in taking a certain share in their future history.

Pollination and Fertilisation. The mutual action on one another of the pollen and the embryonic vesicle of Phanerogams, the latter already formed in the embryo-sac, results in two phenomena of extreme importance, to be carefully distinguished from one another: Pollination and Fertilisation. By *Pollination* is meant the conveyance of the pollen from the anthers to the stigma of Angiosperms or to the nucleus of Gymnosperms. The pollen is detained there by a viscid substance, or often by hairs, and the emission is thus brought about of the pollen-tube which in Gymnosperms penetrates at once the tissue of the nucleus, but in Angiosperms grows downwards through the tissue of the stigma and the frequently very long style in order to reach the ovules; it then forces itself into the micropyle and advances as far as the embryo-sac. It is only when it reaches the embryo-sac (in Gymnosperms however it penetrates still more deeply) that fertilisation of the embryonic vesicle results. A considerable time, occasionally even months, often elapses between pollination and fertilisation; but commonly only a few days or hours.

Pollination is rarely effected by the wind alone; in this case large quantities of pollen are produced in order to secure the result, as in many Coniferæ; in a few cases the pollen is thrown on to the stigma by the bursting of the anthers (*e.g.* in some Urticaceæ); but the means usually employed is that of insects. For this purpose special and often very complicated contrivances are met with to allure insects and attract them to visit the flowers; and at the same time the object is accomplished of always conveying, where possible, the pollen to the stigma of a different flower to that which produced it (even when they are hermaphrodite). In reference to this object the parts of the flower also assume definite forms and positions, which will be followed out further in Book III. Here it need only be mentioned that insects are especially attracted to visit flowers by the nectar secreted in them; this usually sweet juice is generally produced deep down among the foliar structures of the flower, and the form of the parts is generally so contrived that the insect, while it is obtaining the nectar, must

place its body in certain definite positions by which it at one time brushes the pollen out of the anthers, at another time attaches it to the stigma of another flower. The diversity in the forms of flowers depends especially on these relationships, a comparatively simple plan of structure lying at the base of them all. The organs which secrete the nectar, the *Nectaries*, are therefore of extreme importance in the life-history of most Phanerogams; they are, nevertheless, usually very inconspicuous, and,—which is very significant with respect to the relationship of morphology with physiology,—notwithstanding their enormous physiological importance, they are attached to no definite part of the flower in a morphological sense; almost every part is able to perform the function of a nectary. This term therefore does not denote a morphological but a purely physiological idea. The nectary is usually only a small spot at the base of the carpels (as in Nicotiana), or of the stamens (as in Rheum), or of the petals (*e.g.* Fritillaria) which, without becoming more prominent, produces the nectar; but frequently it is in the form of glandular protuberances of the floral axis between the insertion of the stamens and petals (as in Cruciferæ and Fumariaceæ). A particular organ, *e.g.* a petal, is often transformed, for the purpose of secreting and storing up the nectar, into a hollow receptacle, forming a spur-like protuberance (*e.g.* Viola); or all the perianth-leaves become developed into hollow or pitcher-like nectaries (as in Helleborus), or they assume the most wonderful forms, like the petals of Aconitum.

Even before fertilisation, pollination is usually followed by striking changes in the parts of the flower, particularly in the gynæceum, and especially when the parts concerned are delicate; thus the stigmas, style, and corolla wither, the ovary swells up (as in Gagea and Puschkinia), and the like. The most striking result of pollination is shown in many Orchideæ, where the ovules are only formed as a consequence of this process.

Those changes however which are excited by the entrance of the pollen-tube into the embryo-sac, in other words by *Fertilisation*, are still more energetic and varied; the embryonic vesicle developes into the embryo; the endosperm—formed previously in Gymnosperms—originates in Angiosperms only subsequently to fertilisation; the ovules grow along with the ovary, their layers of tissue are differentiated, become lignified, pulpy, dry, &c. The increase in size of the ovary, which is frequently enormous (in Cucurbita, Cocos, &c., several thousand times in volume), shows in a striking manner that the results of fertilisation extend to the rest of the plant, in so far as it affords the materials of nourishment. Striking changes in form, structure, and size take place after fertilisation, especially in the carpels, placentæ, and seeds; but very frequently similar changes result also in other parts. Thus, *e.g.*, it is the receptacle that constitutes the fleshy swelling which is called the strawberry, on the surface of which are seated the small true fruits; in the mulberry it is the perianth of the flowers that swells up to form the succulent coating of the fruit; in Taxus it is a cup-shaped outgrowth of the axis beneath the ovule (the aril) that surrounds the naked seed with a red fleshy coating, &c. Popular usage includes under the term *Fruit* all those parts which exhibit a striking change as the result of fertilisation, especially when they separate as a whole from the rest of the plant; in ordinary language the strawberry, as well as the seed of the yew surrounded by its aril, the fig, and the mulberry, are all fruits. Botanical terminology limits the idea of Fruit within narrower boundaries, which, however, are not yet sharply defined. In the most exact use of botanical terms, the whole of the gynæceum which ripens in consequence of fertilisation may be termed the Fruit. When the gynæceum consists of coherent carpels or of an inferior ovary, the flower produces a single entire fruit; if the carpels do not cohere, each forms a part of the fruit, or a fruitlet. This limitation of the term is often, however, inconvenient; and it would seem preferable to give it a definition which will vary in the different sections.

The point to be most clearly borne in mind by the student is that the fruit is not a new plant-structure. All the parts of the fruit which are morphologically determinable originate and assume their morphological character before fertilisation; the result of fertilisation is merely a physiological change in the parts. The only new

parts in a morphological sense are the embryo and the endosperm, which are produced in the ovule.

The *Inflorescence*. When a shoot which has previously formed a large number of foliage-leaves terminates in a flower, the flower is said to be *terminal;* if, on the other hand, a lateral shoot developes at once into a flower, with one or at most a few bracteoles beneath it, the flower is termed *lateral*. Sometimes the first primary axis which proceeds from the embryo terminates in a flower; but more often the axis continues to grow, or its growth comes to an end, without forming a flower; it is only lateral shoots of the first, second, or a higher order that terminate in flowers. In the first case the plant may be termed, in reference to the formation of its flowers, uniaxial, in the other cases bi-, tri-axial, &c. When a plant produces only terminal flowers, or when the lateral flowers spring from the axils of single large foliage-leaves, they are said to be solitary. When, on the other hand, the flowering branchlets are densely crowded, and the leaves within this region of ramification are smaller and of a different form and colour from the others, or are entirely absent, an *Inflorescence* arises in the narrower sense of the term, usually sharply differentiated from the vegetative region of the plant, and not unfrequently assuming very peculiar forms which require a special terminology. This occurs however only rarely among Gymnosperms, the formation of multifloral inflorescences of peculiar form being characteristic of the more highly developed structure of Angiosperms; and it will therefore be convenient to defer a more detailed classification and definition of inflorescences until we are treating of that class.

With reference also to the *Forms of Tissue*, one point only need be mentioned here, in which Gymnosperms and Angiosperms agree. The *Fibro-vascular Bundles* of Phanerogams exhibit the characteristic peculiarity that every bundle which bends outwards to a leaf is only the upper arm of a bundle which runs downwards into the stem; in other words, we have here 'common' bundles, each of which has one arm that ascends and bends out into the leaf, and another which descends and runs down into the stem; the latter is called by Hanstein the 'inner leaf-trace' [see p. 134]. In the most simple cases (*e. g.* in most Coniferæ) only one bundle bends out into each leaf; but when the insertion of the leaf is broad, or the leaf is large and strongly developed, a larger number of bundles pass from the stem into the leaf, in which they ramify when the lamina is broad. The bundles are usually thicker at the spot where they pass from the stem into the leaf than lower down in their course. Each bundle of this kind may pass downwards through only one internode or through several; in the latter case an internode with several leaves standing above it contains the lower parts of bundles which bend outwards above into leaves of different height and different age. The descending foliar bundle seldom has its lower extremity free; it is usually attached laterally to the middle or upper part of a lower (or older) bundle. This may take place by the bundle splitting below into two arms which anastomose with the lower bundles; or the thin ends of the descending bundles may intercalate themselves between the upper parts of older foliar bundles; or each bundle may bend right or left and become finally joined laterally to a lower bundle. In this manner the foliar bundles, originally isolated, are united laterally in the stem into a connected system; and this, when copiously developed, gives the impression of having arisen by branching, whereas it arises in fact from the coalescence of separate portions originally distinct.

Besides the descending arms of the common bundles, others may however occur in the stem of Phanerogams; first of all net-works (as in Grasses) or girdle-like reticulations (as in Rubiaceæ or Sambucus) are frequently formed in the nodes of the stem by horizontal bundles. Furthermore, longitudinal bundles may become differentiated in the stem, which have nothing to do with the leaves; and the mode of formation of these 'cauline bundles' may vary greatly. They originate either at an early period in the primary meristem of the stem, immediately after the foliar bundles and in the pith (as in Begoniaceæ, Piperaceæ, and Cycadeæ), or only at a much later period in the

outer layers of the stem when this has continued to increase in thickness, outside the foliar bundles (as in Menispermaceæ, Aloineæ, and Dracæna).

The further development of the foliar bundles varies in Monocotyledons on the one hand and in Gymnosperms and Dicotyledons on the other hand. In the former they are closed; in the latter a layer of formative cambium remains, which, in stems that increase rapidly in thickness and become woody, usually prolongs itself across the medullary rays so as to form a perfect ring (the cambium-ring), and then produces regularly new layers of phloëm on the outside and of xylem on the inside. In the primary roots and the stouter lateral roots of Gymnosperms and Dicotyledons, an increase of thickness also takes place by the subsequent formation of a closed cambium-ring, which, like that of the stem, is not found in Cryptogams, and commonly leads to the formation of strong persistent root-systems, which are more often replaced physiologically in Monocotyledons by rhizomes, tubers, and bulbs. With the persistent increase in thickness is connected, finally, the active and extensive production of cork, a process foreign both to Cryptogams and to Monocotyledons. It will be more convenient, however, to defer the special discussion of these points also until we are treating of the characteristics of the separate classes.

The distinguishing characteristic of Phanerogams, as contrasted with Cryptogams, lies in the formation of the Seed. This organ is developed from the ovule, which, in its essential part the nucleus, produces the Embryo-sac, and in this the Endosperm and the Embryonic Vesicle. The latter is fertilised by the Pollen-tube, an outgrowth of the Pollen-grain, and, after first growing into a Pro-embryo, produces the Embryo. The phanerogamic plant which is differentiated into Stem, Leaves, Roots, and Hairs, corresponds to the spore-forming (asexual) generation of Vascular Cryptogams; the Embryo-sac to the Macrospore; the Pollen-grain to the Microspore; the Endosperm is equivalent to the female Prothallium; and the Seed unites in itself, at least for a time, the two generations, the Prothallium (Endosperm), together with the young plant of the second (sexual) generation (the Embryo).

Flowering Plants may be first of all classified as follows:—

I. Phanerogams without an Ovary.

The ovules are not enclosed before fertilisation in a structure (the Ovary) resulting from a cohesion of carpellary leaves. The endosperm arises before fertilisation, and forms archegonia (*i. e.* 'corpuscula'), in which the embryonic vesicles originate. The contents of the pollen-grains are divided before the formation of the pollen-tube, corresponding to the formation of the microspores of Selaginella.

Class XI. **Gymnosperms.** The first leaves produced from the embryo are arranged in whorls of two or more.

A. *Cycadeæ.* Branching of the stem very rare, or entirely suppressed; leaves large, branched.

B. *Coniferæ.* Axillary branching copious, but not from all the leaf-axils; leaves small, not branched.

C. *Gnetaceæ.* Mode of growth very various; flowers similar in many respects to those of Angiosperms.

II. Phanerogams with an Ovary.

The ovules are produced in the interior of a structure (the Ovary) formed by the cohesion of carpellary leaves (often only of one carpel, the margins of which have become coherent), bearing at its summit the stigma upon which the pollen-grains germinate. The endosperm is formed after fertilisation at the same time as the

embryo, both remaining for a time rudimentary. The contents of the pollen-grain do not divide. The branching is almost always axillary and from the axils of all the foliage-leaves; it is rarely extra-axillary.

Class XII. **Monocotyledons.** The first leaves produced from the embryo are alternate; endosperm usually large; embryo small.

Class XIII. **Dicotyledons.** The first leaves of the embryo form a whorl of two (or are opposite); endosperm very often rudimentary, often entirely absorbed by the embryo before the ripening of the seeds.

CLASS XI.

GYMNOSPERMS.

This class embraces, in the orders Cycadeæ, Coniferæ, and Gnetaceæ, plants of strikingly different habit, but evidently closely allied in their morphological structure. In the peculiarities of the mode of formation of their tissue, and especially of their sexual reproduction, they occupy an intermediate position between Vascular Cryptogams and Angiosperms, while they approach Dicotyledons among the latter especially in their anatomical structure.

The *Pollen-grains* suggest a homology with the microspores of Selaginella, their contents undergoing before pollination one or more divisions into cells which resemble a very rudimentary male prothallium. One of these cells grows into the pollen-tube when the pollen-grain has reached the nucleus of the ovule. The pollen-sacs are always outgrowths from the under side of structures unquestionably foliar (staminal leaves), and bear a striking resemblance in many cases to the sporangia of some Vascular Cryptogams. They are produced either in larger or smaller numbers or in pairs on a staminal leaf, without cohering in their growth.

The *Ovule*, which is almost always orthotropous, and usually provided with only one integument, appears to be either the metamorphosed end of the floral axis itself, or originates laterally beneath its apex (or is apparently axillary), or it grows from the upper surface or margins of the carpels. These never cohere so as to form a true ovary before fertilisation, although during the ripening of the seeds they often increase considerably in size, close together, and conceal the seeds, usually separating again when they are mature in order to allow them to fall out; the cases are, however, not rare in which the seeds remain quite naked from first to last. The embryo-sac is formed beneath the apex of the ovule which consists of small-celled tissue and remains enclosed until fertilisation by a thick layer of the tissue of the nucleus. Sometimes the formation of several embryo-sacs commences in one nucleus, but

only one of them attains its full development. The Endosperm arises by free cell-formation long before fertilisation in the embryo-sac which is distinguished by its firm wall; but the cells soon become combined into a tissue and increase by division. Within this mass of tissue, corresponding to the endogenous prothallium of Selaginella, arise the *Archegonia* (or Corpuscula[1]) in larger or smaller numbers. Strasburger states that each of these bodies is formed from an endosperm-cell lying at the apex of the embryo-sac, which increases considerably in size and produces the neck and central cell of the archegonium by division. According to the same authority a small upper portion of the central cell beneath the neck is even separated as the canal-cell. Whether, as Strasburger asserts, the whole contents of the central cell are to be considered as the oosphere, or whether, as Hofmeister thinks, the embryonic vesicles arise in it by free cell-formation, must for the present remain unsettled; although the first-named opinion would correspond more closely with the analogy in other respects so remarkable with the heterosporous Vascular Cryptogams[2]. After the pollen-tube has penetrated the tissue of the nucleus and forced itself as far as the archegonium (corpusculum), where its fertilising material is conveyed to the central cell by diffusion, the *Pro-embryo* is formed by division of a cell that lies in the lower part of the central cell. The pro-embryonic cells are at first small, but the middle or upper ones develope into long *Suspensors*, which, pushing the lower ones before them, break through the central cell below, and penetrate into a softened part of the endosperm. Sometimes the suspensors which are produced side by side separate, and each produces at its apex a small-celled rudiment of an embryo. On this account, and also because several archegonia are often fertilised in one endosperm, the unripe seed contains several rudimentary embryos of which, however, only one usually increases greatly in size, the others withering away.

During the development of the embryo, the endosperm becomes filled with nutrient materials and increases greatly in size; the embryo-sac which encloses it grows at the same time, and finally entirely absorbs the surrounding tissue of the nucleus; the integument, or an inner layer of it, becomes developed into a hard shell, while frequently (in naked seeds) its outer mass of tissue becomes fleshy and pulpy and gives the seed the appearance of a drupaceous fruit (*e.g.* Cycas, Salisburia). The effect of fertilisation not unfrequently extends also to the carpels or other parts of the flower, which grow considerably, forming fleshy or woody coatings to the seeds, or cushions beneath them.

The ripe *Seed* is always filled with the endosperm, in which the embryo lies and is distinctly differentiated into stem, leaves, and root. It fills up an axial cavity of the endosperm, is always straight, its radicle being turned towards

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[1] [The central cells of the archegonia of Gymnosperms were discovered by Robert Brown in 1834. He called them corpuscula or embryoniferous areolæ (Miscellaneous Botanical Works, vol. I. pp. 567 and 570). The structure of the neck of the archegonium was made out by Hofmeister, who applied to it the term rosette (On the Higher Cryptogamia, p. 411). Archegonium and corpusculum do not seem exactly synonymous, since the latter, properly speaking, is only equivalent to the central cell of the former. Henfrey termed the central cells 'secondary embryo-sacs' (Elementary Course, 2nd edition, p. 608).—Ed.]

[2] More will be said on this subject under Coniferæ.

the micropyle, its plumule towards the base of the seed. The first leaves which the embryonal stem produces stand in a whorl, consisting generally of two opposite, but not unfrequently of three, four, six, nine, or more members. The radicle does not project through the split testa of the seed until the period of germination; the bud which is formed between the *Cotyledons* or first leaves at the apex of the stem is forced out by their elongation, the cotyledons still remaining concealed in the embryo, and remaining in it until its food-materials have been completely consumed by the embryo. Sometimes they remain concealed there as organs which have become useless; but in Coniferæ they are drawn out by the elongation of the embryonal stem and brought above the surface of the ground, where they unfold as the first foliage-leaves. The cotyledons of Coniferæ become green even within the seed in complete darkness, the formation of chlorophyll taking place, as in Ferns, without the assistance of light. It is not known whether the same thing occurs also in Cycadeæ and Gnetaceæ. The young plant, freed from the seed, consists of an erect stem, passing below insensibly into the vertically descending tap-root, from which numerous secondary roots soon proceed in acropetal order, usually forming finally a powerful root-system. The embryonal stem grows vertically upwards, and is usually not only unlimited in its growth, but is much stouter than all the lateral shoots, even when these are formed in abundance, as is the case with Coniferæ. In the remarkable Gnetaceous Welwitschia the apical growth however altogether ceases at a very early period, and even the production of new leafy shoots is suppressed, as is usually the case also in Cycadeæ.

The *Flowers* are usually developed on small lateral shoots, often of a high order of ramification; terminal flowers occur on the primary stem only in the Cycadeæ (and in them not exclusively). They are always diclinous; the plants themselves monœcious or diœcious. The male flower consists of a slender axis usually greatly elongated, on which the staminal leaves are arranged in large numbers usually spirally or in whorls. The female flowers are remarkably different in their external appearance, and usually very unlike those of Angiosperms. A kind of perianth of rather delicate leaves occurs only in Gnetaceæ; in Coniferæ and Cycadeæ it is wanting or is replaced by scales. But what makes the female flowers peculiarly strange, independently of the absence of an ovary, is the elongation of the floral axis, on which the foliar structures are placed not in concentric circles as in Angiosperms, but in a distinctly ascending spiral arrangement, or in alternating whorls when they are numerous. When only a few ovules are produced on a naked or small-leaved inflorescence, as in Podocarpus and Salisburia, the last trace of resemblance in habit to the flowers of Angiosperms ceases. But to clearly understand the matter it is only necessary to retain distinctly in mind the definition of a flower, viz. an axis furnished with sexual organs.

On the formation of tissue in Gymnosperms see the remarks at the conclusion of the description of the whole class.

A. CYCADEÆ[1].

The *Embryo*, enclosed in the large endosperm, possesses two opposite unequal cotyledonary leaves, which lie with their inner surfaces face to face, cohering towards their apices. The tendency of the subsequent foliage-leaves to branch is sometimes displayed even in these cotyledons, a rudimentary lamina being formed on the larger one, with an indication of pinnæ (as in Zamia, Fig. 313 *B'*). The seed germinates when laid in moist earth, but only after a considerable interval; the testa splits at the posterior end and allows the emission of the primary root, which at first grows vigorously downwards, but sometimes assumes afterwards a tuberous form or produces a system of thicker fibrous roots. According to Fig. 313 *C* borrowed from Schacht, and a more recent statement by Reinke, the branching of the primary root is laterally monopodial; Miquel, however, asserts the existence of bifurcations of the more slender roots in older plants of *Cycas glauca* and Encephalartos, which is also confirmed by Reinke's investigations into the history of their development. By the elongation of the cotyledons which remain in the endosperm and absorb their nourishment from it, their basal parts and the intermediate plumule are pushed out of the seed. The portion of the axis which bears the cotyledons, as well as that which developes above them, remains very short, but a considerable lateral increase of size takes place beneath the apex due to a large development of parenchymatous tissue. The stem thus acquires the form of a roundish tuber which it retains even at a later period in some species; but in most it lengthens in the course of years into an erect tolerably stout column which sometimes attains a height of some metres. This slow increase in height, together with the considerable increase in thickness of the growing end, is correlated with the absence of a tendency to branch as in other similar cases (Isoëtes, Ophioglossum, *Aspidium Filix-mas*, &c.). The stem of Cycadeæ usually remains perfectly simple, although old stems sometimes divide into branches of equal stoutness. But when several flowers are formed at the summit, this evidently depends on branching; and, as far as one is able to judge from drawings, it is probable that this branching is dichotomous. In old or sickly plants small bulbous or tuberous gemmæ are not

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[1] Miquel, Monographia Cycadearum, 1842. [Ditto, On the Sexual Organs of the Cycadaceæ; Journ. of Bot. March and April 1869.]—Karsten, Organogr. Betracht. über *Zamia muricata*, Berlin 1857.—Mohl, Bau des Cycadeen-stammes (Vermischt. Schrift. p. 195).—Mettenius, Beiträge zur Anatomie der Cycadeen (Abhandl. der königl. Sächs. Gesellsch. der Wissensch. vol. VII, 1861).—[W. C. Williamson, Contributions towards the history of *Zamia gigas*, Trans. Linn. Soc. vol. XXVI, 1870.—Carruthers on Fossil Cycadean Stems from the Secondary Rocks of Britain, *ibid.*]—On the structure of the pollen see Schacht, Jahrb. für wissensch. Bot. vol. II, p. 142 et seq.—Kraus, Ueber den Bau der Cycadeenfiedern (Jahrb. für wissensch. Bot. vol. IV).—Reinke in Nachrichten der königl. Gesellsch. der Wissensch. in Göttingen, 1871, p. 532.—De Bary, Bot. Zeitg. 1870, p. 574.—Juranyi, Bau u. Entwickelung des Pollens bei Ceratozamia (Jahrb. für wissensch. Bot. vol. VIII, p. 1382).

unfrequently found at the base of the stem under or above ground, the morphological nature of which is still doubtful; in Miquel's opinion it is not impossible that they spring from old leaf-scales, and have therefore nothing to do with the branching of the stem.

The whole of the surface of the stem is furnished with leaves arranged spirally; no internodes can be distinguished. The leaves are of two kinds; dry, brown, hairy, sessile, leathery scales of comparatively small size, and large, stalked, pinnate or pinnatifid foliage-leaves. The scales and the foliage-leaves alternate periodically; a rosette of large foliage-leaves is produced annually or biennially, and among these the terminal bud of the stem is enveloped with scales, under protection of which the new whorl of foliage-leaves is slowly formed. This alternation begins at once on germination in Cycas and other genera, a number of scale-leaves following the leaf-like cotyledons, and enveloping the bud of the seedling; after these a pinnate though small foliage-leaf is then usually developed, which is again followed by scales. It is only as the strength of the plant increases after several years' growth that the foliage-leaves are produced in whorls constantly increasing in size, and forming, after the older ones have died off, the palm-like crown of leaves, the scales which stand above them enclosing at the same time the apical bud of the stem. In this bud the foliage-leaves are so far formed beforehand, that when they at length burst the bud they only have to unfold, this process then occupying only a very short time, while one or two years elapse before the unfolding of the next rosette of leaves. The leaves which proceed from the bud are in Cycas and other genera circinate like those of Ferns; in others the rachis of the leaf only is rolled up; in others, finally, as Dion, the growth of the leaf is straight, its lateral leaflets being also straight before expansion[1]. The unfolding is, as in Ferns, basifugal, and, probably in consequence of this, there is also a permanent apical growth and a basifugal development of leaflets. The leaflets are usually simple, and generally stand alternately on the rachis, which is often 1 to 2 metres long. The mode in which the lamina terminates above points

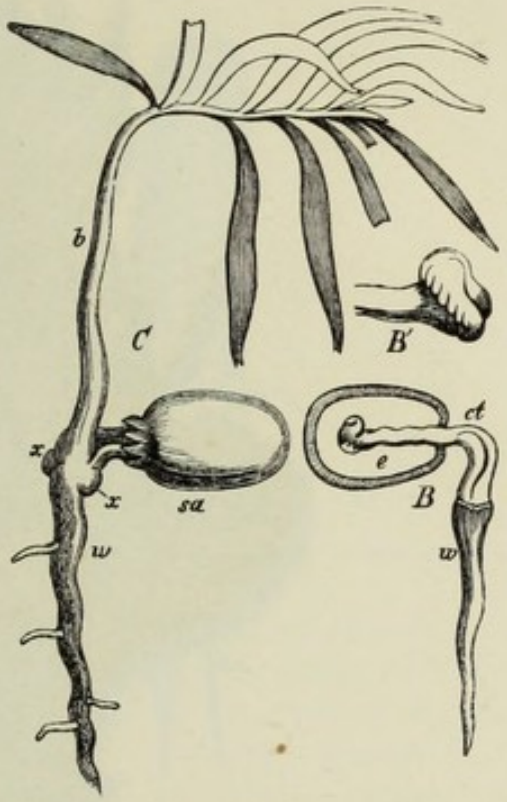

FIG. 313.—Germination of *Zamia spiralis* (after Schacht, reduced). *B* commencement of germination, *ct* the cotyledons coherent above their elongated base, one of them having at its apex (magnified at *B'*) an indication of a pinnate lamina; *C* seedling six months old; *sa* seed, *w* the primary root, *b* the first pinnate leaf, *x x* rudiments of the adventitious roots which afterwards grow upwards.

[1] [This statement is not quite exact. In Zamia and Encephalartos the leaves are not circinate in vernation; and even in Cycas it is only the leaflets and not the rachis that is so.—ED.]

to a dichotomous branching of the leaf, the rachis of which may therefore be considered as a sympodium composed of the basal portions of the successive bifurcations, while the lateral leaflets represent the bifurcations of the lamina of the leaf, the growth of which is arrested and flattened. The whole leaf would therefore be a dichotomous cymose branch-system. Researches into the history of its development are however wanting, as in the case of the branching of the stem and root.



FIG. 314.—A carpel of *Cycas revoluta* (reduced about ½); *f* pinnæ of the leaf-like carpel; *sk* ovules replacing the lower pinnæ; *sk'* an ovule further developed.

The *Flowers* of the Cycadeæ are always diclinous and diœcious; both kinds of flowers appear at the summit of the stem, either singly as in Cycas as terminal flowers of the primary stem, or in pairs or larger numbers as in *Zamia muricata* and *Macrozamia spiralis*, where they may perhaps be regarded as metamorphosed bifurcations of the stem[1]. The flower consists of a strong conical elongated axis,

[1] The hypothesis that the male flower of *Cycas Rumphii* is one, the leaf-bud by which the stem is prolonged the other bifurcation of the dichotomising apex of the stem, is not supported by De Bary's recent researches.

sometimes supported on a naked peduncle, but densely covered in other parts by a large number of staminal and carpellary leaves arranged spirally.

In Cycas the female flower is a rosette of foliage-leaves which have undergone but slight metamorphosis (Fig. 314), the apex of the stem developing again first of all scale-leaves, and then new whorls of foliage-leaves; the stem, therefore, grows through the female flower, or furnishes an instance of prolification. The separate carpels are, indeed, much smaller than the ordinary foliage-leaves, but are essentially of the same structure; the lower pinnæ are replaced by ovules, which attain, even before fertilisation, the magnitude of a moderate-sized ripe plum, the

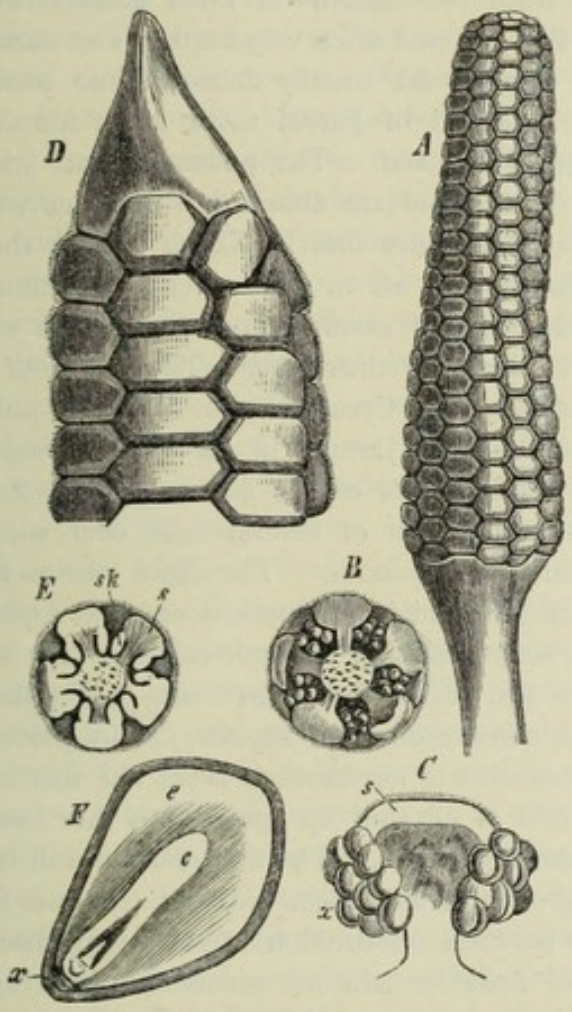

FIG. 315.—*Zamia muricata* (after Karsten). *A* a male flower (natural size); *B* transverse section of one; *C* one of its stamens with the pollen-sacs *x* and the peltate expansion *s* (seen from below); *D* the upper part of a female flower (natural size); *E* transverse section of one, *s* the peltate placenta of the ovules *s k*; *F* longitudinal section of a ripe seed; *e* endosperm, *c* cotyledons, *x* the folded suspensor.

fertilised seed acquiring the dimensions and the appearance of a moderate-sized ripe apple, and hanging quite naked on the carpel. Whether the male flower of Cycas also exhibits prolification I do not know, and it seems improbable; the very numerous staminal leaves are much smaller, 7 to 8 cm. long, and undivided; they expand considerably from a narrow base and terminate in an apiculus. They are furnished on the under side with a number of densely-crowded pollen-sacs; the whole flower is from 30 to 40 cm. long.

The male and female flowers of the remaining genera of Cycadeæ resemble fir-cones externally. The comparatively slender floral axis rises as a rachis on a

short naked peduncle, and on this are seated the numerous staminal or carpellary leaves (Fig. 315). The axis terminates with a naked apex which undergoes no further development (Fig. 315 *D*). The stamens are, indeed, but small in comparison to the foliage-leaves of the same plant, but are, nevertheless, the largest which occur anywhere among Phanerogams. In Macrozamia, as in Cycas, they are from 6 to 8 cm. long, and as much as 3 cm. broad; they spring, with rather a narrow base, from the floral axis, and expand into a kind of lamina, terminating in an apiculus (Macrozamia) or in two curved points (Ceratozamia), or the lower part of the stamen is thinner and stalk-like and bears a peltate expansion (Zamia). They are also distinguished from the stamens of most other flowering plants by their persistence, becoming lignified and often very hard. The numerous pollen-sacs on the under side of the stamens are usually collected into small groups numbering from two to five, like the sori of Ferns, these again forming larger groups on the right and left side of the leaf. The pollen-sacs are globular or ellipsoidal, usually about 1 mm. in size, and are attached with a narrow base to the under side of the stamen; Karsten states that in *Zamia spiralis* they are even stalked. They dehisce longitudinally, and are in all respects much more like the sporangia of Ferns than the pollen-sacs of other Phanerogams, from which they also differ in the firmness and hardness of their wall. The mode of development of the pollen-sacs and pollen-grains of Cycadeæ was till lately unknown; it has only quite recently been observed by Juranyi in *Ceratozamia longifolia*. The pollen-sacs are formed on the under side of the stamens in the form of small papillæ, probably consisting from the first of several cells over which the epidermis of the surface of the leaf is continuous. The inner tissue is next differentiated (as in the sporangia of Lycopodiaceæ, Equisetaceæ, and Ophioglossaceæ) into an outer layer of smaller cells enclosing a larger-celled tissue; since the cells of the latter continue to grow and divide in all directions, the mother-cells of the pollen are finally isolated, but densely crowded together, as in Dicotyledons. The mode of division of the mother-cells is nevertheless more like that of Monocotyledons in this respect, that they first of all split up successively into two daughter-cells, each of which again undergoes bipartition. The first division-wall is formed, as in Dicotyledons, by the slow growth of an annular ridge of cellulose, formed in the depression produced by the previous constriction of the protoplasm of the mother-cell; but in each of the two daughter-cells the second partition appears to be formed simultaneously, as in Monocotyledons. The four young pollen-cells are now freed by the rapid absorption of the cell-wall which surrounds and separates them. The pollen-grains, when free from their mother-cells, are unicellular and spherical; but, during their further growth, the contents, enclosed by an extine and intine, divide into two cells, a smaller and a larger one, each possessing a nucleus. The smaller of these two cells, lying on one side against the intine of the pollen-grain, becomes arched on the opposite side, and projects in the form of a papilla into the larger one. This smaller cell now again undergoes a transverse division parallel to the first, and this is sometimes followed by a second; a two- or three-celled body is thus formed, attached on one side to the intine, and projecting into the cavity of the larger cell, as in Abietineæ, from which, however, Ceratozamia differs in the fact that, as in Cupressineæ, the large cell, formed by the first division of the

pollen-grain, developes into the pollen-tube, the mass of small cells remaining inactive in the pollen-grain. In *Cycas Rumphii*, Encephalartos, and Zamia, the pollen-grain also splits up, according to De Bary, into a larger and a smaller cell, the latter also in this case again dividing once, and the larger cell developing into the pollen-tube. The spot where the intine which developes into the pollen-tube breaks through the extine, lies exactly opposite the mass of small cells (the secondary cells of the pollen-grain); the extine is in this place thinner, and in the dry pollen-grain deeply folded in, so that the transverse section of the dry pollen-grain is kidney-shaped. During the absorption of water however which precedes the formation of the pollen-tube, the pollen-grain again assumes a spherical form.

The carpellary leaves are arranged spirally or in apparent verticils, closely crowded on the axis of the female flower. Those of Cycas have already been described; in Zamia, Encephalartos, Macrozamia, and Ceratozamia, the carpels are much smaller, and each bears only two ovules, attached right and left to a peltate expansion which terminates a slender pedicel (Fig. 315). The ovule is always orthotropous, and consists of a large nucleus and a thick integument the inner layer of which (in contrast to that of other Phanerogams) is penetrated by a number of fibro-vascular bundles. The micropyle is a slender tube, formed by the prolongation of the contracted margin of the integument beyond the summit of the nucleus. According to De Bary's recent researches a second inner integument appears to exist in the case of *Cycas revoluta*. But little is known about the formation of the embryo-sac, or of the endosperm, which is strongly developed long before fertilisation, or of the large central cells, easily visible to the naked eye (in Cycas from 3 to 4 mm. long), or finally of the long suspensors. The main point is that in all these respects Cycadeæ agree essentially with Coniferæ. The central cells are formed in large numbers in the same endosperm, but not until the ovule has already attained a considerable size. The suspensors, each of which gives rise to several rudimentary embryos, but only one of which developes into a perfect embryo, may still be detected in the ripe seed as a ball of long threads, the central cells themselves being also discernible even in the ripe seed.

In consequence of the form and position of the carpels, the ovules are covered and concealed before and after fertilisation, except in Cycas; at the period of pollination, which is apparently brought about by insects, the carpels separate from one another, and the micropyle excretes a fluid to which the pollen-grains adhere. The outer layer of the testa is usually fleshy, the inner one hard, and the seed therefore resembles a plum, with its surface often brightly coloured.

B. CONIFERÆ[1].

Germination. The endosperm surrounds the embryo in the form of a thick-walled sac open at the radicular end; the embryo lies straight in the central cavity of

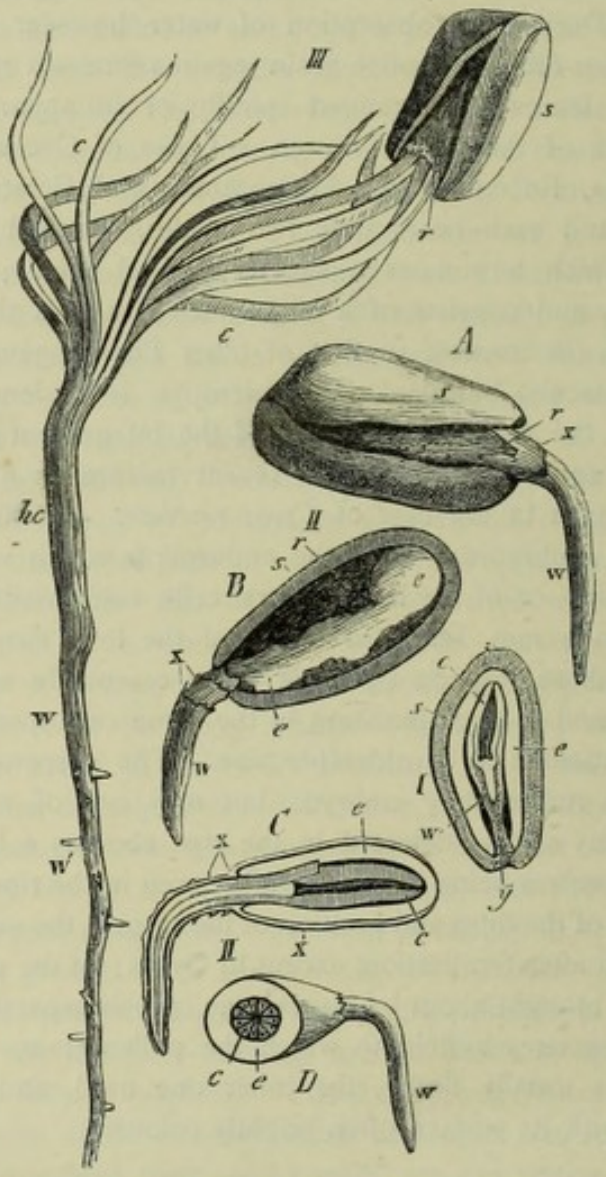

FIG. 316.—*Pinus Pinea*; *I* longitudinal section through the middle of the seed, *y* the micropylar end; *II* commencement of germination, emergence of the root; *III* completion of germination, after the endosperm has been absorbed (the seed lay at too small a distance below the surface, and was therefore raised up by the cotyledons when the stem began to grow); *A* shows the ruptured testa *s*, *B* the endosperm *e*, one half of the testa having been removed, *C* longitudinal section of the endosperm and embryo, *D* transverse section at the commencement of germination; *c* the cotyledons, *w* the primary root, *x* the embryo-sac pushed out by it (ruptured in *B*), *hc* hypocotyledonary portion of the axis, *w'* secondary roots, *r* red membrane within the hard testa.

the endosperm; its axis is continuous behind with the rudiment of the primary root, and bears at its anterior end a whorl of two or more cotyledonary leaves, between

[1] For the structure of the flowers, see R. Brown, On the Plurality and Development of the Embryos in the Seeds of Coniferæ: Misc. Bot. Works, London, 1866, vol. I, pp. 567-576.—H. von

which it terminates in a roundish apex (Fig. 316 *I*). The Taxineæ and most Cupressineæ and Araucarieæ have two opposite cotyledons, although in some Cupressineæ there are from three to nine, and in some Araucarieæ whorls of four cotyledons; while among the Abietineæ there are rarely so few as two, more often four or even as many as fifteen. To refer this larger number of cotyledons to the division of two opposite ones, as Duchartre proposes, is entirely opposed to the other processes of leaf-formation in these plants, especially to the common occurrence of whorls consisting of several leaves on the growing axis of seedlings.

When placed in damp soil the endosperm swells up, bursts the testa at the radicular end of the embryo, which is then pushed out by the elongation of the axis, and grows into a strong descending tap-root, from which lateral roots proceed, succeeding one another rapidly in acropetal succession, and subsequently branching. This is the commencement of the root-system of Conifers, which is frequently strongly developed and persistent. After the emergence of the root, the cotyledons elongate in their turn, push out their bases from the seed and the end of the axis that lies between them; but they themselves remain in the endosperm until it has been absorbed. In *Araucaria brasiliensis* the hypocotyledonary portion of the axis remains short, and the cotyledons remain contained in the seed; in most Conifers, on the contrary, this portion becomes greatly elongated, making a sharp bend in an upward direction, pierces the soil, and draws the cotyledons with it. As soon as these are exposed to light, the hypocotyledonary portion straightens itself, the whorl of cotyledons expand, and, having become green while still underground, act as the first foliage-leaves of the seedling, the apex of its axis having in the meantime formed a bud with new leaves (Fig. 316).

Mode of Growth and External Differentiation. The terminal bud of the stem of the seedling grows more rapidly, though frequently interrupted, than the lateral shoots which arise subsequently. The primary stem is thus a direct prolongation of the axis of the embryo; it never ends in a flower, but grows indefinitely at the summit, becoming thickened to a corresponding extent by the activity of a cambium-ring, and thus becomes a slender cone attaining a height of 100, 200, or even more feet[1], and a diameter at the base of 2 or 3 or as much as 20 feet. On this highly-developed primary axis, the lateral axes of the first order are produced;

Mohl, Vermischt. Schrift. pp. 25 and 49.—Schacht. Lehrb. der Anat. u. Phys. vol. II. p. 433.—Eichler in Flora 1863, p. 530 [and Nat. Hist. Rev. 1864, pp. 270-290; Flora 1873, and Trans. Bot. Soc. Edin. 1873, pp. 535-541.—Dickson, Trans. Bot. Soc. Edin. VI, p. 420; New Phil. Journ. 1861, pp. 198, 199.—J. D. Hooker, On the Ovary of Siphonodon in Trans. Linn. Soc. XXII, pp. 137, 138.—Caspary in Ann. des Sci. Nat. 4th series, vol. XIV, p. 200, and Flora 1862, p. 377.—Brongniart, Bull. Bot. Soc. France XVIII, p. 141.—Van Tieghem, Ann. des Sci. Nat. 5th series, vol. X.] For the fertilisation, Hofmeister in Vergl. Unters. 1851 [On the Germination, Development, and Fructification of the Higher Cryptogams, Ray Soc., pp. 400–433].—Strasburger, Die Befruchtung der Coniferen, Jena 1869. For the pollen, Schacht in Jahr. f. wiss. Bot. vol. II, p. 142.—Strasburger, Ueber die Bestäubung der Gymnospermen, Jenaische Zeitschr. vol. VI. Also in addition: [Zuccarini, Morphology of the Coniferæ, Ray Soc. Rep. and Pap. on Bot. 1845.]—Pfitzer, Ueber den Embryo der Coniferen, Neiderrhein. Ges. für Natur. u. Heilk. Aug. 7, 1871.—Reinke, Ueber das Spitzenwachsthum der Gymnosperm-Wurzeln, Göttinger Nachr. 1871, p. 530.—[Strasburger, Die Coniferen u. die Gnetaceen; eine morphologische Studie, Jena 1872.—Eichler, Sind die Coniferen gymnosperm oder nicht? Flora 1873.]

[1] [The trunk of *Sequoia* (*Wellingtonia*) *gigantea* of California attains the height of 400 feet.—Ed.]

often periodically in terminal rosettes (pseudo-whorls) or distributed irregularly and branching again in the same manner. Each primary axis usually grows more vigorously than its secondary axes; and hence the collective form of the system of branching, as long as the primary axis continues to grow vigorously, is that of a panicle of conical or pyramidal form. While in Cycadeæ the branching is almost entirely suppressed, the peculiar form and beauty of Conifers depends chiefly on the branching, the more so as the leaves are almost always small and inconspicuous, serving only, as far as the outward appearance of the plant is concerned, as a clothing to the system of branching. The branching is always axillary; but Conifers differ from Angiosperms in not producing buds in nearly all the leaf-axils; in Araucaria and some species of Taxus, Abies, and other genera, it is chiefly or exclusively the youngest leaf-axils of a year's growth which produce branches, and these grow vigorously. In *Juniperus communis*, indeed, buds occur in most of the leaf-axils, but only a few develope. In *Pinus sylvestris* and its allies shoots are formed only in the axils of the scale-like lower leaves which are borne exclusively by the primary stem and the permanent woody branches, remaining however very short, and producing two, three, or more acicular foliage-leaves, from the axils of which no lateral shoots are produced. In Larix, Cedrus, and Salisburia, buds are formed in the axils of a considerable number—but not nearly all—of the foliage-leaves, a few growing rapidly, and serving for the development of the primary branch, while others remain very short, and form annually a new rosette of leaves without lateral buds. In Thuja and Cupressus also, which are distinguished by their copious branching, the number of small leaves is still very much larger than that of the axillary shoots. Many Conifers exhibit a very regular arrangement of those branches of different orders which arrive at their full development, the symmetry of the whole tree being at the same time increased by their difference in size. The branches of the first order on the upright primary stem are frequently formed in pseudo-whorls of several members at the conclusion of each period of vegetation, the same process being frequently repeated on the branches themselves (*e.g. Pinus sylvestris*, *Araucaria brasiliensis*, and especially *Phyllocladus trichomanoides*, and many others); more commonly a tendency to bilateral ramification appears on the horizontal branches of the first order (as in *Abies pectinata*); and not unfrequently besides these strong branches from which the framework of the tree is constructed, smaller ones are also formed between them (*e. g.* in *Abies excelsa*). In many cases the arrangement and growth of the branches are more irregular; the greatest deviation from this type being shown in the Cupressineæ, especially Cupressus, Thuja, and Libocedrus, in which the tendency to bilateral ramification[1] is seen even on the primary stem, which is more perfectly developed on the lateral shoots. Branch-systems of three or four orders of shoots are developed in one plane in such a manner that a system of this kind assumes a definite contour and somewhat the appearance of a pinnate leaf. In Taxodium the foliage-leaves are formed in two rows on slender branches a few inches in length; in *T. distichum* these fall off in the autumn together with

[1] In many species also of Abies and Pinus there is an evident tendency to bilateral development in the horizontal lateral shoots, the spirally arranged leaves inclining over to the right and left, and thus forming two comb-like rows.

their leaves, thus presenting a still greater resemblance to pinnate leaves. Finally Phyllocladus produces on all its verticillate shoots only small colourless scale-like leaves, from the axils of which, but beneath the terminal bud, whorls of shoots spring with limited power of growth, developing their bilateral side-shoots in the form of flat lobed foliage-leaves. These remarks, incomplete as they are, may suffice to turn the attention of the student to the phenomena of the branching, which are moreover easily observed.

The *Leaves* (with the exception of the floral leaves) are either all foliage-leaves containing chlorophyll, as in Araucaria, Juniperus, Thuja, &c.; or all colourless or brownish scales, as in Phyllocladus, where the foliage-leaves are replaced by leaflike shoots; or, finally, scales and foliage-leaves are very frequently formed at the same time, and even on the same shoots (as in Abies), where the scales only serve the purpose of protecting the buds; or the two forms are distributed on different axes, as in the true pines (Pinus) the permanent woody shoots of which produce only membranous scales, the axils of which develope sterile foliage-shoots which afterwards die off. The foliage-leaves of Conifers are mostly small, of simple structure, and scarcely ever compound; they are smallest and at the same time most numerous in the Cupressineæ, where they form a dense covering to the axes of the branchlets (as Thuja, Cupressus, &c.); in most of the Abietineæ (as Taxus and Juniperus) they are larger, more sharply separated from the axis, narrow and comparatively thick, usually angular and prismatic (acicular); intermediate forms between these acicular leaves and the broad expanded leaves of Thuja occur in *Araucaria excelsa*, &c. In Podocarpus and Dammara the leaves are flat and broader, and in Salisburia they are stalked and even two-lobed, with a deeply emarginate apex as if from dichotomous division. Not unfrequently, especially in the Cupressineæ, the foliage-leaves of the elongated primary axis are different in form from those higher up the same axis and from those on the lateral shoots; in Thuja, *Juniperus virginiana*, Cupressus, &c., the former are acicular, patent, and of considerable size, the latter very small and closely adpressed to the axis; the youthful foliage sometimes recurs on isolated branches of adult plants. The axis of the shoot within the bud is so densely covered with the bases of leaves that no free portion of the surface of the axis is visible between them. When the axis has attained a considerable length on the unfolding of the bud, the bases of the leaves generally grow at the same time in length and breadth, so that they entirely cover the surface of the enlarged shoot also, clothing it with a green cortex, in which the parts belonging to the separate leaves can be distinctly recognised. This is especially clear in Araucaria and many species of Pinus, but is very common also in other genera; in Thuja, Cupressus, Libocedrus, &c., the axis of the shoot is also completely covered with these leaf-cushions; but the free parts of the leaves are very small and often project only as short points or projections. The phyllotaxis is spiral in the Abietineæ, Taxineæ, Araucarieæ, Podocarpus, &c.; the Cupressineæ bear whorls which, above the cotyledons, contain generally from three to five leaves, but usually fewer at a greater height on the primary axis. The secondary axes usually begin at once with decussate pairs, which, in bilateral shoots, are alternately larger and smaller (as in Callitris and Libocedrus); in Juniperus and Frenela the whorls on the secondary axes also consist of from three to five leaves, and are alternate; the

pairs of leaves of Dammara stand at an acute angle to one another. The foliage-leaves of most Conifers are very persistent, and may live for several years, their leaf-cushions keeping pace in growth for a long time with the increase in size of the axis; in Larix and Salisburia the leaves alone are deciduous in autumn, in *Taxodium distichum* the axes that bear them are also deciduous.

The *Flowers* of Coniferæ are always diclinous; either monœcious, as in the Abietineæ and Thuja, or diœcious, as in Taxus, Salisburia, and *Juniperus communis;* the male are usually much more numerous than the female flowers. They are never terminal on the primary stem, differing in this respect from those of Cycadeæ; even the larger woody branches bear only rarely, as in *Abies excelsa*, terminal (in this case only female) flowers. Usually the flowers are produced at the apex of small foliage-shoots of the last order, or in the leaf-axils of the stronger foliage-shoots. In Thuja, for instance, male and female flowers appear at the end of small short

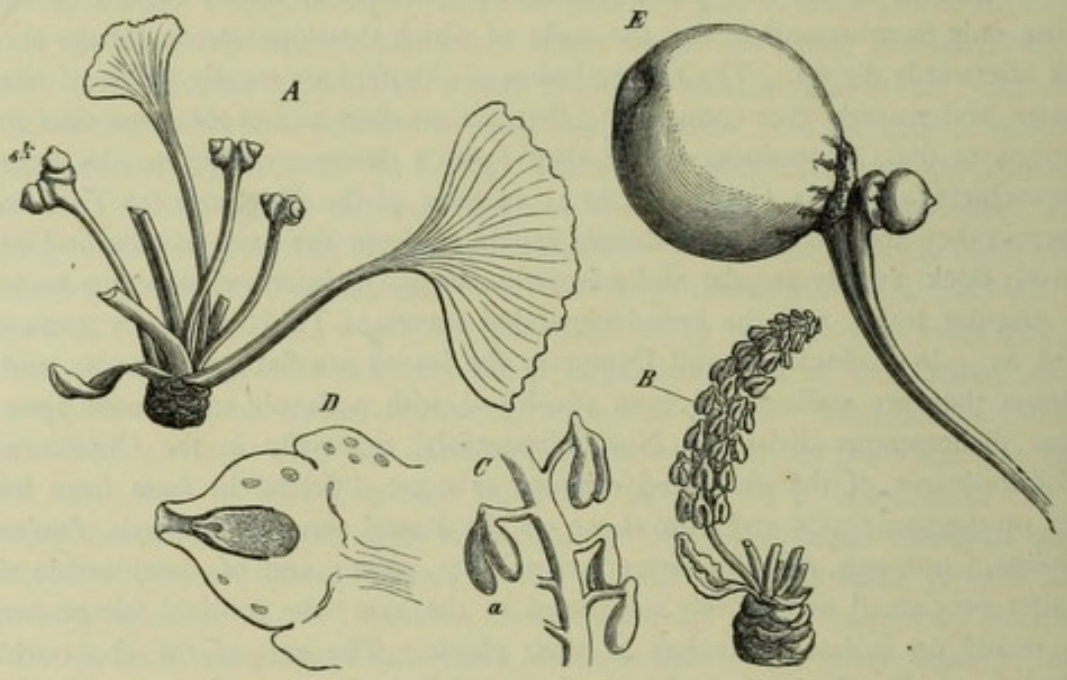

FIG. 317.—*Salisburia adiantifolia* (natural size). *A* a short secondary foliage-shoot with female flowers, on the naked axes of which are placed the ovules *ik*; *B* a male flower; *C* part of one magnified, *a* the pollen-sacs; *D* longitudinal section of an ovule magnified; *E* a ripe seed with an abortive one by its side on the floral axis.

green shoots of the bilateral system of branches; in Taxus and Juniperus, on the other hand, in the axils of foliage-leaves of larger shoots; in *Abies pectinata* they are found on the under side of shoots of a higher order at the summit of older trees, both kinds in the axils of foliage-leaves, the female flowers singly, the male in larger numbers. The flowers of *Pinus sylvestris* and allied species appear in the place of the undeveloped branches (tufts of leaves) which stand in the axils of the scales of growing woody shoots, the males usually in groups forming an inflorescence the primary axis of which is the mother-shoot, the female flowers generally more scattered. In Salisburia the flowers appear exclusively on the short lateral branches which annually form new rosettes of leaves, and they are situated in the axils of the foliage-leaves or of the inner bud-scales (Fig. 317, *A* and *B*).

The part of the floral axis immediately beneath the organs of reproduction is densely covered with scales or foliage-leaves in the female plant of Taxus, Juniperus,

&c. (Figs. 318, 319); but is developed as a naked stalk in the Abietineæ, Salisburia, the male plant of Taxus, Podocarpus, &c. (Fig. 317 *A*, *B*). The flowers of Coniferæ resemble those of Cycadeæ in the peculiarity that the axis elongates even at the part that produces the organs of reproduction; if these are numerous, the whole flower presents the appearance of a long cone, resembling externally a catkin; and this term is indeed given to it in the superficial language of many systematists, although the catkin of Dicotyledons is an inflorescence, the pseudo-catkin of Conifers



FIG. 318.—*Taxus baccata*; *A* male flower (magnified), *a* the pollen-sacs; *B* a stamen seen from below with open pollen-sacs; *C* piece of a foliage-shoot with leaf *b*, from the axil of which springs the female flower, *s* its envelope of scales, *sk* the terminal ovule; *D* longitudinal section of the same (magnified), *i* integument, *kk* nucleus of the ovule, *x* a rudimentary axillary ovule; *E* longitudinal section through a more mature ovule before fertilisation, *i* integument, *kk* nucleus, *e* endosperm, *m* aril, *s* upper scales of the envelope.

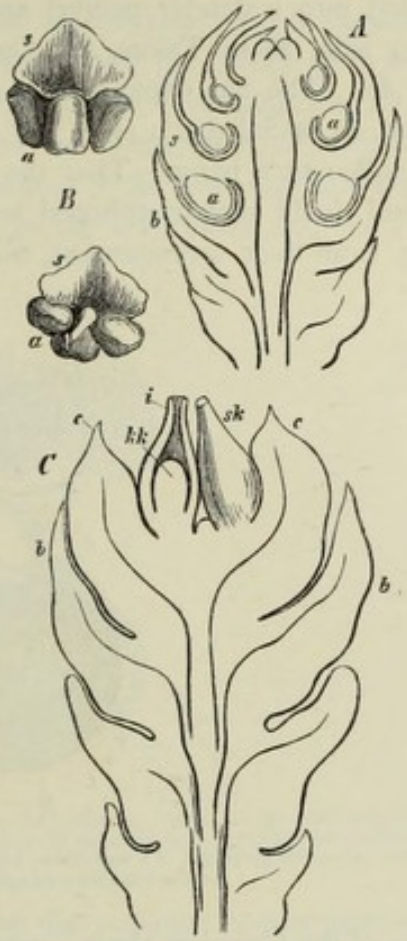

FIG. 319.—*Juniperus communis*; *A* longitudinal section of a male flower, *B* (upper figure) a stamen seen from the front and the outside, (lower figure) seen from the back of the axis; *C* longitudinal section of a female flower; *a* the pollen-sacs, *s* the peltate lamina of the stamen, *b* lower leaves of the floral axis, *c* carpels, *sk* ovules, *kk* nucleus, *i* the integument (*A* and *C* × about 12).

a single flower. In Angiosperms the flowering shoot usually undergoes a very peculiar development at its summit, the portion of the axis which bears the flower (the receptacle) remaining very short and broad, and the floral leaves and organs of reproduction being formed in positions which differ greatly from those of the foliage-leaves; in Coniferæ the distinction between a floral and a foliage-shoot is much less, and this is especially conspicuous in the arrangement of the leaves; if those of the foliage-branches are arranged spirally, so also are usually those of the flowers, as, *e.g.*, in the Abietineæ; if, on the contrary, as in the Cupressineæ,

they occur in alternating whorls, the staminal and carpellary leaves are arranged in the same way. In *Juniperus communis* even the ovules, here the representatives of whole leaves, are arranged in alternating whorls. But, occasionally, as in Taxus, greater differences are to be observed in the phyllotaxis of the flowering shoot as compared with that of the foliage-shoots.

The *Male Flowers* always consist of a distinctly elongated axis provided with staminal leaves, and ending above in a naked apex (Fig. 319 *A*). The stamens are mostly more delicate and of a different colour from the foliage-leaves, and are usually divided into a slender pedicel and a peltate lamina bearing the pollen-sacs on its under side, as in Taxus, the Cupressineæ, and Abietineæ (Fig. 318 *B*, 319 *A*, *B*, 320 *A*). The flat expansion at the end of the pedicel may, however, be entirely absent, as in Salisburia (Fig. 317 *C*), where it is reduced to a small knob on which the pollen-sacs hang. That the parts which bear the pollen-sacs in Coniferæ are beyond doubt metamorphosed leaves, is evident not only from their form, but still more from their arrangement, which has already been spoken of. If the staminal

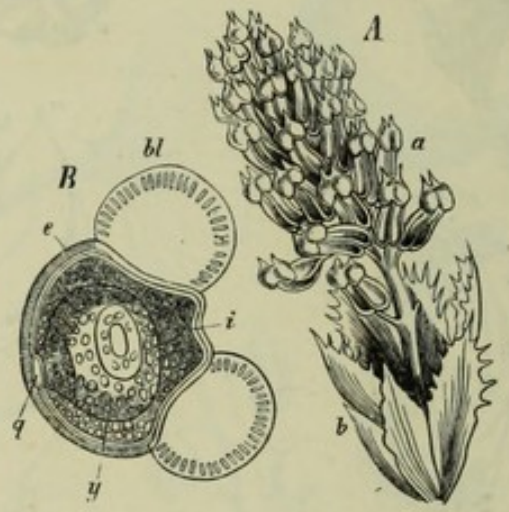

FIG. 320.—*Abies pectinata*; *A* a male flower, *b* the delicate bud-scales forming a perianth, *a* the stamens; *B* a pollen-grain (after Schacht), *e* its extine, forming the two large vesicular protrusions *bl*.

leaves of the Cycadeæ show a resemblance in more than habit to the sporangiferous leaves of Ferns, those of Coniferæ may perhaps be compared to the parts that bear the sporangia of Equisetaceæ; and not unfrequently, as in Taxus, Juniperus, &c., the resemblance of the male flowers to the inflorescence of Equisetum is as striking in external appearance as in the actual agreement between them from a morphological point of view. The pollen-sacs, of the structure and development of which but little is at present known, usually hang, with a narrow base, on the under side of their support, and do not cohere in their growth; their number is usually much smaller than in Cycadeæ, but much more variable than in Angiosperms; in the yew the peltate part of the staminal leaf bears from three to eight, in the juniper and most Cupressineæ three roundish pollen-sacs (Figs. 318, 319). Those of Pinus, Abies, and their allies lie in pairs parallel or placed obliquely to one another, right and left of the pedicel, which here resembles the connective of Angiosperms; in Araucaria and Dammara, on the other hand, the long sausage-shaped pollen-sacs hang in larger numbers free beneath the peltate limb. The

wall of the pollen-sacs is usually delicate, and finally dehisces longitudinally to allow the escape of the pollen-grains, which are produced in extraordinarily large numbers, since they have usually to be carried by the wind to the female organs of the same or of another tree. The pollen-grains which happen to fall on the opening of the micropyle of the ovules are retained by an exuding drop of fluid, which about this time fills the canal of the mycropyle, but afterwards dries up, and thus draws the captured pollen-grains to the nucleus, where they immediately emit their pollen-tubes into its spongy tissue. In the Cupressineæ, Taxineæ, and Podocarpeæ this contrivance is sufficient, since the mycropyles project outwardly; in the Abietineæ, where they are more concealed among the scales and bracts, these themselves form, at the time of pollination, canals and channels for this purpose, through which the pollen-grains arrive at the micropyles filled with fluid (*cf.* Strasburger, *l. c.*). The large number and lightness of the pollen-grains enables them to be carried great distances by the wind; in the true pines and the Podo-

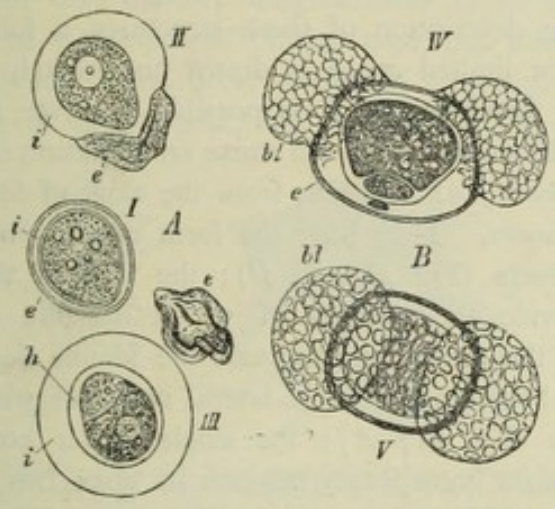

FIG. 321.—*A* pollen-grain of *Thuja orientalis* before its escape from the pollen-sac, *I* fresh, *II*, *III* after lying in water, the extine *e* having been stripped off by the swelling of the intine *i*; *B* pollen-grain of *Pinus Pinaster* before its escape, *e* the extine with its vesicular protrusions *bl*.

carpeæ their capacity for transport is increased by the vesicular hollow protrusions of the extine, as represented in Fig. 321, *IV*, *V*, *bl*.

The *Mode of cell-division in the interior of the pollen-grain* of Coniferæ, to which allusion has already been made, is still but imperfectly known; especially now that we know more, through Millardet's researches, of the male prothallium of Selaginella and Isoëtes, it is greatly to be desired that fresh observations should enable us to compare with them the corresponding structures in Coniferæ. Schacht asserts that in Taxus, Thuja, and Cupressus, only one division-wall (Fig. 321 *A*) arises at right angles to the longest diameter of the pollen-grain; one of the daughter-cells is much smaller than the other, and the larger of the two developes into the pollen-tube. In Larix, Pinus, Abies, and Podocarpus, two daughter-cells of very different size are also first of all formed. But the septum between them arches into the cavity of the larger one, and the protuberance (the papilla of the smaller cell) is cut off by a partition; a third cell is thus formed lying in the cavity of the larger of the two primary cells, grows at its apex, and again divides. A three- or four-celled body (or row of cells) is thus formed in the cavity of the pollen-grain,

and is attached to the wall of the grain by a very small basal cell; the apical cell (Fig. 320 *B*, *y*) finally enlarges and developes into the pollen-tube. The basal cells of this row appear, after they have lost their contents (in Pinus and Abies), like narrow slits in the thick wall of the pollen-grain, a phenomenon which requires further explanation (see Fig. 320, *B*, *q*, and 321 *IV*, *e*). A peculiarity which distinguishes the pollen-grain of Conifers from that of Angiosperms lies in the rupture and final stripping off of the cuticularised extine by the swelling of its intine (Fig. 321, *I*, *II*, *III*). Even in this apparently insignificant fact a resemblance is again seen to the microspores of Cryptogams, and especially to those of Marsileaceæ, in which the swelling endospore protrudes from the exospore.

The structure of the *Female Flowers* is very different in the different sections of Coniferæ, and in some cases the homology of the separate parts is still doubtful. The position of the ovules, as far as can be judged from advanced stages of development, is, in particular, very variable, and with this is again connected the fact that different opinions may be entertained as to the part which should be called the carpel. The following description of these structures, a full discussion of which is not permitted by our limited space, is drawn immediately from the observation of advanced stages of development; it is possible, however, that the direct observations of the most rudimentary stage will cause an alteration in some points.

The female flowers of Taxus spring from the axils of foliage-leaves belonging to elongated woody shoots. They have the form of short branches covered with decussate scale-like bracts (Fig. 318, *C*, *D*); the axis of the shoot ends in an apparently terminal ovule, the nucleus of which has the appearance of being the vegetative cone of the axis. In Salisburia the female flowers spring from the axils of foliage-leaves belonging to short lateral branches which annually produce new rosettes of leaves (Fig. 317 *A*); the single flower consists of a stalk-like elongated axis which bears immediately beneath its apex two or more rarely three lateral ovules. Neither in this genus nor in Taxus are there any foliar structures close to the ovules which either from their position or from any other circumstance can be regarded as carpels. In the genus Podocarpus small flowering shoots are developed, springing in *P. chinensis* (according to Braun) from the axils of foliage-leaves, in *P. chilina* from the axils of very small scale-leaves at the end of elongated leafy shoots; they consist of an axial structure slender and stalk-like below, club-shaped above, and bearing three pairs of very small decussate scales. The floral axis terminates between the upper pair; the ovules, in this case anatropous, with their micropyle turned downwards and towards the floral axis, spring from the axils of this pair; one ovule however is usually abortive, and the flower becomes one-seeded. In Phyllocladus the lower lateral branchlets of the leaf-like flattened shoots are transformed into female flowers which are raised upon a pedicel and are swollen above into the form of a club, the large ovules standing (according to a drawing of Decaisne's[1]), in the axils of small leaves. In these two genera the small scales from the axils of which the ovules spring may be regarded as carpels, if it is thought necessary to assume the existence of these organs.

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[1] [See Le Maout and Decaisne's Descriptive and Analytical Botany, edited by Dr. Hooker, London 1873, p. 747.]

The ovules of *Juniperus communis* (Fig. 319, *C*) stand in whorls of threes beneath the naked extremity of the floral axis, the flower springing as a little shoot from the axil of a foliage-leaf, and its axis bearing whorls of three leaves. The ovules apparently alternate with the three leaves of the upper whorl, and hence must, from their position, be themselves considered as metamorphosed leaves; these leaves of the upper whorl swell after fertilisation, grow together and become fleshy, forming the pulp of the juniper-berry in which the ripe seeds are entirely enclosed; they may therefore be termed carpels. In the other Cupressineæ the flower consists of decussate whorls of two or three leaves, which grow considerably after fertilisation and attain a considerable size, enveloping the seed and forming a pericarp which may therefore correctly be said to be formed of carpels. In Sabina the pericarp is fleshy and berry-like, as in Juniperus; in the other genera, on the other hand (Thuja, Cupressus, Callitris and Taxodium), the carpels become woody and assume the form of stalked peltate scales, or of valves separating from one another longitudinally (Frenela); these are closely approximate during the development of the seed, but afterwards open to allow the ripe seeds to fall out. The erect ovules of Cupressineæ sometimes appear to stand in the axils of the carpels; but it is clear in other cases that they

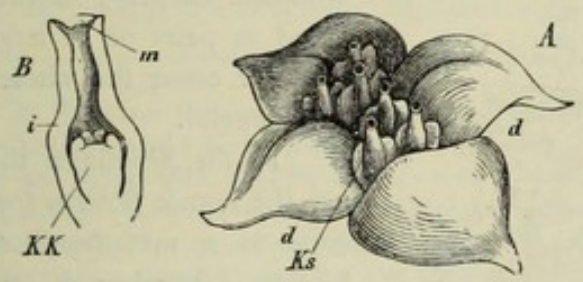

FIG. 322.—*Callitris quadrivalvis*; *A* female flower (magnified); *d d* two pairs of decussate leaves (carpels) in the axils of which are six ovules (*Ks*); *B* vertical longitudinal section of an ovule through its broader diameter; *KK* the nucleus still without an embryo-sac; *i* the tubular elongated integument with the micropyle *m*.

spring from the carpels themselves, either low down near their point of insertion or at a greater height. In Sabina and *Callitris quadrivalvis* (Fig. 322) only two decussate pairs of carpels separate like a star at the time of flowering; in Sabina the ovules stand in pairs in the axils of the two lower carpels, right and left of their median line, some of them being frequently abortive. In *Callitris quadrivalvis* a pair occurs on each of the lower carpels and a pair higher up; but this position can only be explained by further investigation of the history of their development. In Thuja and Cupressus there are three or four decussate pairs of carpels, in Taxodium a still larger number; in Thuja and Taxodium two erect ovules are situated at the base of each of the central pairs of carpels, springing from the right and left of their median line; in Cupressus there are a considerable number at the base of each carpel. In *Juniperus drupacea* and *Frenela verrucosa* the fruits (in the collection at Würzburg) consist of alternating whorls of three carpels, opening, in the last species, after the seeds become ripe, like a six-lobed capsule. Each carpel is swollen on its inner side into a thick placenta ascending from the base to the apex, and bearing numerous winged seeds which stand in transverse rows of threes; there are from four to six of these rows on each carpel, the whole inner side therefore bearing seeds nearly up to the apex.

So far as the relative positions of the parts of the flower can be explained without going back to their earliest stage, a great diversity is thus shown in the two families of Taxineæ and Cupressineæ; the ovule is terminal in Taxus, lateral beneath the summit of the axis in Salisburia, carpellary leaves appearing to be entirely absent. In Podocarpus and Phyllocladus they are indicated indeed, as small scales, the ovules springing from their axils; but they are small and do not at any time constitute a pericarp. A structure of this kind, in the form of a berry or of a chambered woody fruit, is indeed formed after fertilisation in the Cupressineæ, the carpels either becoming fleshy and growing together (as in Juniperus and Sabina), or becoming woody and closing in laterally by their peltate expansions (as in Cupressus, Thuja, and Callitris), or presenting the appearance of the lobes of a unilocular capsule (*e.g.* Frenela); but the carpels are in these cases at first entirely open. In *Juniperus communis* the ovules form a whorl alternating with the carpels; in the other genera they stand in pairs or in larger numbers at their base, or cover the whole of their inner side (as Frenela).

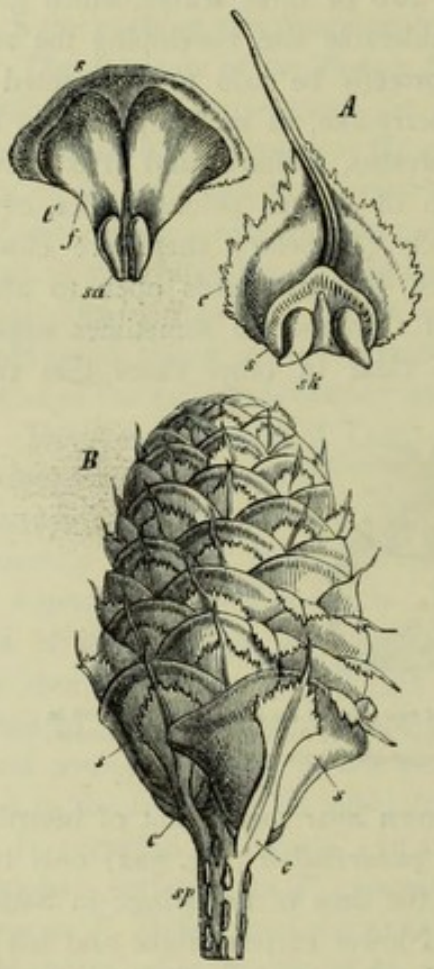

FIG. 323.—*Abies pectinata* (after Schacht). *A* a leaf detached from the female floral axis seen from above, with the seminiferous scale *s* bearing the ovules *sk* (magnified); *B* upper part of the female flower (or cone) in the mature state; *sp* floral axis or axis of the cone, *c* its leaves, *s* the largely developed seminiferous scales; *C* a ripe seminiferous scale with the two seeds *sa*, *f* the wing of the seed (reduced).

In the Abietineæ the well-known cones are the female flowers (or rather fruits). The cone is a metamorphosed shoot, its axis bearing a number of crowded woody scales arranged spirally, the ovules arising on them rarely singly, usually in pairs, occasionally in larger numbers. In the Pineæ (Abies, Picea, Larix, Cedrus, and Pinus) the seminiferous scales (Fig. 323, *A*, *B*, *s*) appear as axial structures in the axils of bracts (*c*) which spring from the axis of the cone; but the examination of very young cones of *Abies pectinata* shows that the seminiferous scale itself arises as a protuberance at the base of the bract (*c*), and is therefore not axillary. While the bract afterwards grows very little or not at all, this protuberance increases greatly, and produces on its upper surface two ovules which are attached to it by one side with the micropyle towards the axis of the cone. The seminiferous scale of these genera must therefore be considered as a greatly developed placenta growing out of a carpel (Fig. 323 *A*, *B c*) which is very small or even abortive[1]. According to

[1] Braun, Caspary, and Eichler consider the seminiferous scale in Pinus and Larix as itself a flower; *i.e.* as a short axis which has coalesced with its two carpels, and stands in the axil of the

this view the whole cone is a single flower with a number of small open carpels (hitherto considered as bracts), which are far outstripped in their growth by their seminiferous placentæ (the scales). In the other Abietineæ also, the female flowers of which I have had no opportunity of examining, it may be concluded from the descriptions that the cone is a single flower with numerous seminiferous scales arranged spirally, not springing from the axils of leaves, but growing immediately out of the axis of the cone, and therefore themselves leaves and of a carpellary nature. Eichler (*l. c.*) says, in reference to Dammara, Cunninghamia, Athrotaxis, and Sequoia:—'The scales of a cone are in these genera all of one kind; they consist simply of open carpels; and, in order not to introduce confusion into the definition of a flower, the whole of what is found on the axis, in other words the whole cone, must be considered a single flower; and this is also necessary in the case of the Araucarieæ, the Cupressineæ, and the male "catkins" of all Coniferæ[1].' In Araucaria each scale (or carpel) bears only a single ovule, which, according to Eichler, is so enveloped by it that the only opening left is that of the micropyle which faces the axis of the cone; in Cunninghamia there are three ovules, in Athrotaxis from three to five, in Sequoia from five to seven, in Sciadopitys as many as seven or eight on one scale, and their micropyle here also faces the axis of the cone. In Dammara the scale bears, according to Endlicher[2], only one ovule which,

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bract (*c* in our figure). In that case the cone of these genera, in contradistinction to that of the other Coniferæ and of Cycadeæ, would be an inflorescence (*cf.* Caspary in Ann. des Sci. Nat. 4th series, vol. XIV, p. 200, and Flora, 1862, p. 377); but this view I have already contested more in detail in my first edition, p. 427. It is impossible to consider the seminiferous scale of Pinus and Abies itself as a single carpel. In opposition also to the most recent views of Mohl (Bot. Zeitg. 1871, p. 22), I cannot bring myself to consider the seminiferous scale of the true Abietineæ as a coherent structure formed of two leaves of an undeveloped branch.

[1] Eichler thinks that an exception must be made in favour of Podocarpus and Cephalotaxus.

[2] [Van Tieghem has been led by studying the distribution of the bundles in the different parts of the female bud of Coniferæ to the opinion—different from that expressed by Sachs—that the female flower throughout this group of plants is in every case constructed after a single fundamental type which has undergone various secondary modifications. He has given in a note to his French translation of the present work the following abstract of the conclusions which are worked out in greater detail in his paper already cited in the Annales des Sciences Naturelles.

Neither the axis of the female bud nor its leaves or bracts of the first order ever bear ovules. It is always upon structures arising from the axils of these bracts that the ovules make their appearance. This establishes a fundamental distinction between Cycadeæ and Coniferæ. In the former group it is always the leaves of the female bud of the first order that produce the ovules directly. While therefore we may regard the female bud in Cycadeæ as well as the male as contributing a single flower, this does not hold good in the case of Coniferæ. We may if we please regard the male bud of Coniferæ as a single flower, but the female bud is an inflorescence. The structure which bears the ovule in Coniferæ is always a foliar organ—the first and only leaf of an axis which undergoes no further development. This leaf, which is more or less largely developed beyond the circumscription of the ovule or ovules which it bears, is an open carpel and in itself constitutes the whole female flower. It is always inverted, that is to say, it arises upon the suppressed axis which bears it with its ventral face opposite to and united with the ventral face of the primary bract. When the ovules do not terminate the carpel, it is upon its structurally dorsal—but in respect of position upper—face that they arise, just as it is upon its structurally dorsal—but in respect of position lower—face that the pollen-sacs arise upon the stamen.

This is the general type. It remains to consider the principal secondary modifications which are superinduced upon it in the different genera.

The axillary branch, which is reduced to its first leaf, is most frequently of the first generation

like those of Sequoia and Sciadopitys, are inserted near the apex and hangs down free[1].

The *Ovules*, as we have already seen, are in the Podocarpeæ anatropous and furnished with two integuments; in the rest of Coniferæ they are orthotropous and possess only one integument; in the Cupressineæ and Taxineæ they are erect, in the Abietineæ inverted, with the micropyle towards the base of the scale, to which the ovules are usually attached on one side. In these cases there is no funiculus, and the ovule consists only of the small-celled nucleus and one integument, which usually projects above it and forms a comparatively wide and long micropylar canal, through which the pollen-grains reach the apex of the nucleus, which is sometimes depressed (see Figs. 317, 318, 319, 322). Lateral outgrowths of the integument not unfrequently cause the ovule, and afterwards the seed, to appear winged on both sides, as in *Callitris quadrivalvis* (Fig. 322), Frenela, &c. The wing-like appendage of the seed of Pinus and Abies, on the other hand, is the result of the detaching of a plate of tissue from the seminiferous scale, which remains attached to the ripe seed.

The *Embryo-sac* is formed by the considerable enlargement of a cell of the nucleus lying nearly in its axis, and usually at some depth and at a considerable distance from its apex. In the Abietineæ and Juniperus it arises beneath the point at which the integument separates from the nucleus; the embryo-sac is in these genera usually the result of the transformation of one cell only; while in Taxus, according to Hofmeister, several sacs are always formed; several cells which lie one over another in a short axial row increase in size, and become isolated and filled with protoplasm; only one of these, however, usually continues to grow in

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in respect to the axis of the female bud; but it is also sometimes of the second (Taxus) and may even be of the third order (Torreya). The carpel itself is either entirely distinct from the parent bract (the *Pineæ*, *Taxineæ*) or the two leaves are united together by their ventral surfaces and are only separate towards their summit (*Cupressineæ*, *Sequoieæ*, *Araucarieæ*). This difference merely depends upon a different localisation of the intercalary growth of the two leaves; it is a difference the same in kind as that which separates a dialypetalous corolla from a gamopetalous one. Whether free or united with the bract, the carpellary leaf bears its ovules sometimes towards its base (*Cupressineæ*), sometimes towards its middle (*Pineæ*), sometimes towards its summit (*Araucarieæ*); each represents a lobe, more or less developed, of the dorsal face of the carpel.

In the *Taxineæ* the ovules terminate the carpellary leaf; they result in this case from the transformation of its whole entire limb, whether each half of the limb forms an ovule (Salisburia, Cephalotaxus), or whether the entire limb has only produced a single one (Podocarpus, Phyllocladus, Taxus, Torreya, &c.). In this case it is evidently only the petiole of the ovuliferous leaf which represents the carpel; if the petiole is long (Salisburia) the carpel is obviously developed; but if it remains very short (Cephalotaxus, Podocarpus, Phyllocladus, Taxus, Torreya, &c.) the carpel is almost absent—in other words, the carpellary leaf is reduced to a sessile limb completely converted into a single ovule (Podocarpus, Taxus, &c.) or into two ovules (Cephalotaxus). The number of the ovules which each carpellary leaf bears, as well as the number of carpellary leaves themselves, that is to say, of the female flowers which enter into the composition of the inflorescence, both vary, and may even be simultaneously reduced to unity, which is the ordinary case in Taxus.—Ed.]

[1] [For a review of the literature of the question whether the ovules of Coniferæ are really naked or whether there is a true ovary, see Eichler, 'Sind die Coniferen gymnosperm oder nicht, in 'Flora' for 1873, translated in Trans. Bot. Soc. Edin. 1873, pp. 535–541. Dr. Eichler here, in opposition to the contrary view of Strasburger, sums up the whole argument strongly in favour of the opinion that the Conifers are really gymnospermous.—Ed.]

order to form the permanent embryo-sac. The nucleus of the embryo-sac is soon absorbed, fresh nuclei being then formed in the parietal protoplasm, and free cell-formation takes place round them. These cells soon unite laterally, grow in the radial direction, and divide in such a manner that the embryo-sac is filled with parenchymatous tissue. In those Coniferæ in which the seeds take two years to ripen, as *Pinus sylvestris* and *Juniperus communis*, the endosperm formed in the first summer is again absorbed in the spring, the protoplasm of the primary endosperm-

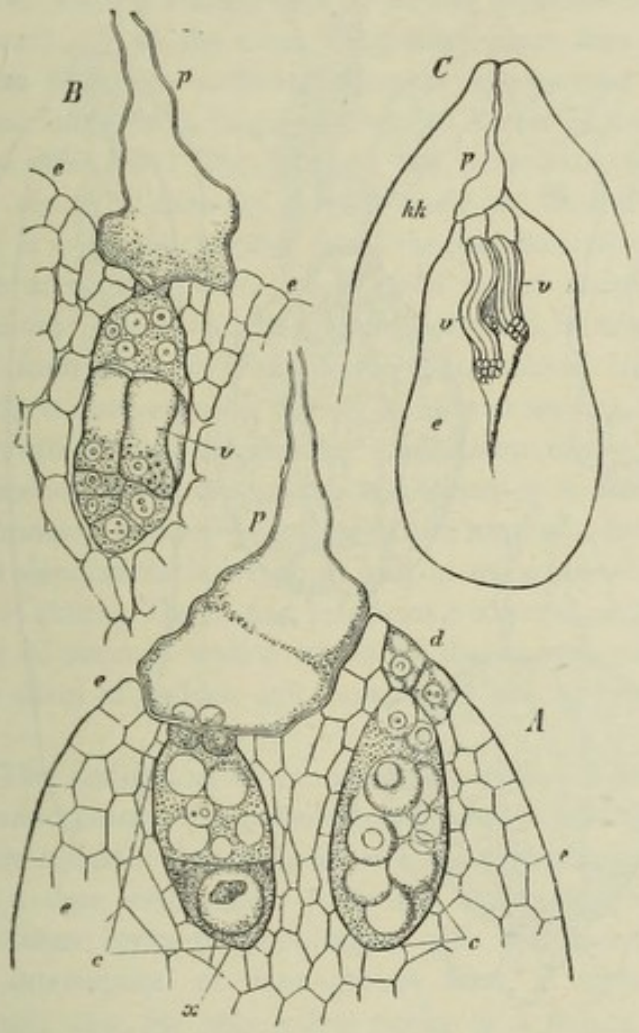

FIG 324.—*Taxus canadensis* (after Hofmeister). *A* longitudinal section through the upper end of the endosperm *e e* and the lower end of the pollen-tube *p*, *c c* the archegonia, *d* their stigmatic cells, the left archegonium is fertilised, *x* rudiment of the pro-embryo (June 5). (×300). *B* part of the endosperm with an archegonium, the pro-embryo of which *v* is already further developed, *p* the pollen-tube (June 10) (×200); *C* longitudinal section of a nucleus (June 15), *k k* nucleus, *e e* endosperm, *p* pollen-tube, *v v* two pro-embryos proceeding from two archegonia (×50).

cells is set free by the deliquescence of their cell-walls, and forms by division a number of new cells which, in May of the second year, again fill with parenchymatous tissue the embryo-sac now considerably increased in size.

According to Strasburger's recent researches, the mother-cells of the 'corpuscula' (archegonia[1]) arise in the embryo-sac by free cell-formation in the same manner as the first endosperm-cells; but the septa by which the latter are transformed into a multicellular tissue are not produced. The cells grow, on the other hand, more vigorously, and divide near their apex where they touch the embryo-sac; a large inner

[1] [See foot-note to p. 434.]

(lower) cell is thus formed, the central cell of the archegonium, and an upper small one, lying next the embryo-sac from which the neck of the archegonium is formed[1]. In *Abies canadensis* this neck remains simple and unicellular, and elongates considerably with the increase in size of the surrounding endosperm; but usually the original cell which constitutes the neck divides into several cells which either lie only in one plane (Figs. 324 *A*, *d*, 325 *I*, *d*), the 'stigmatic cells,' or form several layers lying one over another (as in *Abies excelsa* and *Pinus Pinaster*). Seen from

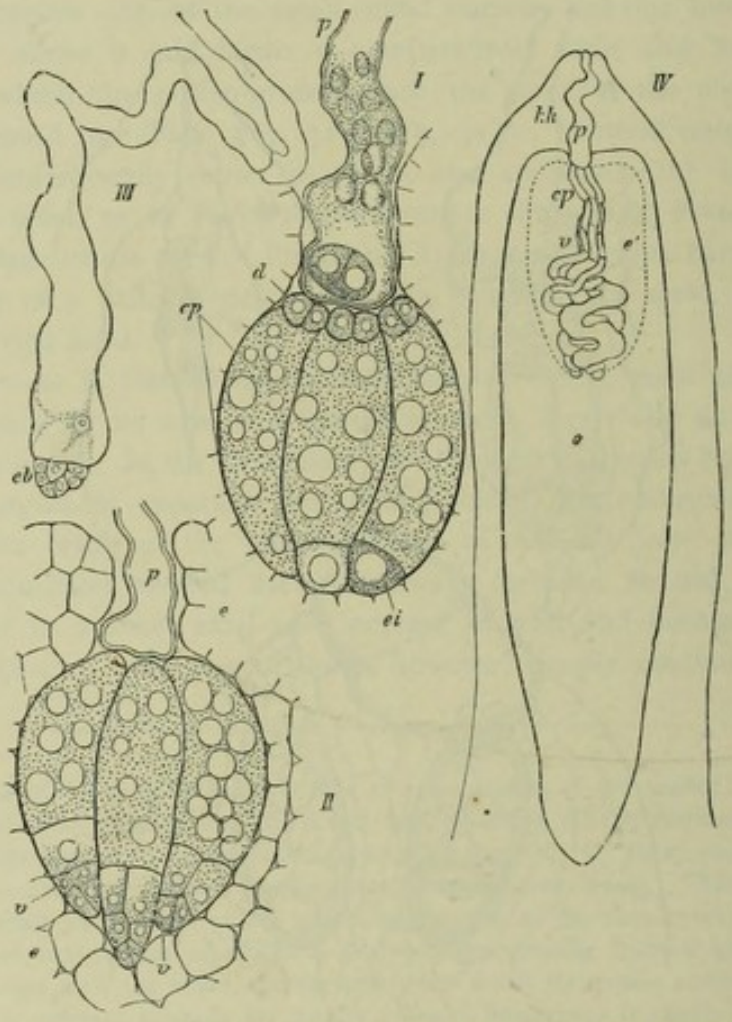

FIG. 325.—*Juniperus communis* (after Hofmeister). *I* three archegonia *cp* close beside one another, in two of them the fertilised embryonic vesicle *ei* is imbedded in the upper end, *d* stigmatic cells, *p* pollen-tube (July 28) (×300). *II* a similar section, *e e* the endosperm, *v v* the pro-embryos; *III* lower end of one of the longitudinal rows of cells of a pro-embryo with the rudiment of the embryo *eb*; *IV* longitudinal section of the nucleus *k.k*, *e* the endosperm, *e'* portion of the endosperm that is broken up, *p* pollen-tube, *cp* the archegonia, *v* the pro-embryos (beginning of August) (×80).

above the neck appears to form a four-celled, or, in *Abies excelsa*, even an eight-celled rosette. The homology of the archegonium 'corpuscula' with the archegonium of Vascular Cryptogams, already established by the earlier investigations of Hofmeister, is carried a step further by Strasburger, who discovered the formation also of a canal-cell. He considers that the part of the protoplasmic contents of the large central cell which lies immediately beneath the neck are separated from the rest by division, and a small cell is thus formed shortly before fertilisation (*i. e.*

[1] Hofmeister (Vergleichende Untersuchungen, p. 129) gives a somewhat different account of the origin of the archegonium [Germination, &c., p. 410].

before the access of the pollen-tube to the endosperm); this cell being clearly equivalent to the canal-cell so often mentioned in Vascular Cryptogams which is afterwards converted into mucilage[1]. In *Abies canadensis* and *excelsa* and *Pinus Larix* this canal-cell is, according to Strasburger, very evident; while in the Cupressineæ (Thuja, Juniperus, and Callitris), its demarcation from the rest of the contents of the central cell is only slight. As in those Vascular Cryptogams where the ventral part of the archegonium is plunged in the tissue of the prothallium, the neighbouring cells become transformed by further divisions into a parietal layer surrounding the central cell, so the same thing takes place also in the endosperm of Coniferæ. In the Abietineæ each archegonium is separated from an adjacent one by at least one, often by a large number of layers of cells: those of the Cupressineæ, on the other hand (Fig. 325, *cp*), are in lateral contact. The archegonia of Taxus are short; in those of the Abietineæ the central cell is elongated; in the Cupressineæ it becomes angular from the pressure of the adjacent cells. The number of the archegonia which are formed in the endosperm beneath the apex of the embryo-sac is very various; Hofmeister and Strasburger state that in the Abietineæ it is from three to five, in the Cupressineæ from five to fifteen (according to Schacht it may even be thirty); in *Taxus baccata* from five to eight. The continuous growth of the surrounding endosperm causes the formation of funnel-shaped depressions above the archegonia, which in some Abietineæ are but shallow, in *Pinus Pinaster*, *P. Strobus*, &c., deep and narrow. In these species each of the funnel-shaped depressions leads down only to the neck of one archegonium; in the Cupressineæ (Callitris, Thuja, and Juniperus), where they lie closely crowded together, the cluster of them is walled round by the endosperm, and a funnel is formed common to them all, which still remains closed by the cell-wall of the embryo-sac.

Fertilisation. The pollination of the ovules takes place before the archegonia are formed in the endosperm; the pollen-grains, having reached the apex of the nucleus, put out their tubes at first only for a short distance into its tissue; their growth is then for a time suspended. After the archegonia are completely developed, the pollen-tubes begin to grow again into the endosperm in order to reach them. This interruption of their growth lasts, in those Coniferæ whose seeds ripen in a single year, for only a few weeks or a month; when the seeds take two years to ripen, as in *Juniperus sibirica* and *communis*, and *Pinus sylvestris* and *P. Strobus*, until June of the next year. Whilst the pollen-tubes penetrate through a loose portion of the tissue of the nucleus, their width gradually increases at their lower end, their wall becoming at the same time thicker; until at length they meet the wall of the embryo-sac which has now become soft, break through it, penetrate into the funnel of the endosperm mentioned above, and attach themselves firmly to the cells of the neck of the archegonia. In the Abietineæ and Taxineæ each pollen-tube fertilises only one archegonium; and several tubes therefore penetrate into the funnel at the same time; in the Cupressineæ on the contrary one pollen-tube suffices for the fertilisation of the whole group of archegonia beneath the broad

[1] In Figs. 324 and 325, which are transferred from the first edition, the canal-cell is not indicated.

funnel of the endosperm. The tube entirely fills up the funnel and applies itself to the necks of the whole group of archegonia; short narrow protuberances from the wide pollen-tube now grow into the separate necks of the archegonia, forcing the stigmatic cells from one another and destroying them, and at length reaching the central cell. The same process takes place in the Abietineæ and Taxineæ; the pollen-tube, after widening again, becoming narrower and entering the neck of only one archegonium, whence it penetrates finally as far as the central cell. A thin spot may be observed at the extremity of this protuberance of the thick-walled pollen-tube, which obviously facilitates the escape of the fertilising substance by diffusion; and this is probably assisted by the pressure exerted by the tissue which lies above on the part of the pollen-tube outside the archegonium. Hofmeister states that a few free primordial cells (Fig. 325, *I*) are sometimes formed in the end of the pollen-tube, which he was inclined to consider as rudimentary indications of mother-cells of antherozoids (corresponding somewhat to those in Salvinia); but Strasburger denies the existence of bodies of this kind, and admits only the presence of a number of grains of starch in the protoplasm at the end of the pollen-tube. In reference also to the processes in the central cell of the archegonium, the statements of these two observers differ. According to Hofmeister a number of primordial cells arise in the protoplasm of the central cell, all of which he considers to be embryonic vesicles (oospheres); one of these, however, is distinguished from the rest even before fertilisation by its size and contents; it lies in the upper or middle part of the central cell, but after fertilisation sinks to its base and adheres closely to it, filling up the lower part of the central cell as the rudiment of the embryo, while the remaining embryonic vesicles perish. Strasburger, on the contrary, considers the whole protoplasmic contents of the central cell as the 'oosphere,' and regards Hofmeister's numerous embryonic vesicles only as vacuoli (vesicles of protoplasm). The effect of fertilisation is manifested first of all in the central cell by the turbidity of the protoplasm and by the formation of granular bodies in it; these collect in the lower part of the central cell, which then becomes separated by a septum from the larger remaining part, and forms the rudiment of the pro-embryo. Our figures, which are borrowed from Hofmeister (Fig. 324, *A*, *x*, and 325, *I*, *ei*, the rudiment of the pro-embryo mentioned above), may point to both explanations; that of Strasburger, however, is most in accordance with the processes that take place in the archegonium of the highest Cryptogams, as well as with those in the embryo-sac of Angiosperms, and connects the two. My own observations, however, are not sufficient to decide definitely in favour of one or the other view.

The further development of the rudiment of the pro-embryo (Fig. 324, *A*, *x*, and Fig. 325, *I*, *ei*), is brought about by longitudinal divisions at right angles to each other, which are soon followed by transverse divisions; a mass composed usually of three layers of cells is thus formed at the base of the central cell; the bottom of the cell is broken through by a considerable extension of the uppermost (in Taxus and Juniperus) or middle cells (Abietineæ) of the pro-embryo (Fig. 324, *B*, *v*); these cells elongate, continue to grow, and transverse divisions are formed in them (Fig. 325, *IV*, *v*), and penetrate into the softened part of the endosperm, bending in different directions. In Taxus the elongated cells of the pro-embryo

remain for a long time adjacent and united, the pro-embryo producing only a small-celled rudiment of an embryo at its apex (Fig. 324, *B*, *C*); while in the Abietineæ (Abies, Pinus) and Cupressineæ (Thuja, Juniperus) the elongated cells of the pro-embryo separate from one another, continue to grow in this condition, and each forms the rudiment of an embryo at its apex[1] (Fig. 325, *IV*, *v*, *III*). By this means several embryos can be produced from one embryonic vesicle; the number within a single endosperm being increased by the simultaneous fertilisation of several archegonia. Polyembryony, which is rare among Angiosperms, is thus the typical condition among Conifers and generally among Gymnosperms, but only in the very earliest stage; for usually only one of the rudiments developes into a vigorous embryo, such as has already been described. During its development the endosperm also continues to grow vigorously; its cells become filled with reserves of food-material (fat and albuminoids); the embryo-sac which surrounds it grows at the same time, and finally supplants the tissue of the nucleus, the tissue of the integument hardening at the same time into the testa. In Salisburia, however, an outer strong layer of tissue forms the pulpy envelope which causes the seed to resemble a drupe. The elongated cells of the pro-embryo usually disappear during these processes, but according to Schacht are permanent in Larix.

During the period that the seeds are ripening, the carpels and the placentæ also continue to grow and to undergo changes in texture. In Taxus a red aril which afterwards becomes pulpy grows round the ripening seed (Fig. 318 *m*); in Podocarpus the part of the floral axis that bears the scales and the seeds, and which was already considerably swollen, becomes fleshy; in Juniperus and Sabina the carpels themselves form the blue 'berry' which envelopes the seeds: in most other Cupressineæ the carpels grow, close up laterally and become woody; and the same occurs in those Abietineæ which are without bracts (in respect to Cunninghamia, *vide supra*); while in Pinus, Abies, Cedrus, and Larix, it is the placental scales which after fertilisation grow vigorously, outstripping in their growth the true carpels (bracts), become woody, and form the mature cone. In all these cases (except Podocarpus, Salisburia, and Taxus), the seed is closely and firmly enclosed during ripening by the carpels or placental scales; it ripens within the fruit, the parts of which do not again separate or become detached in order to allow of the escape of the seeds until they are completely ripe (as in *Abies pectinata*).

So long as we are still in doubt as to the nature of the female flowers of various genera, the systematic arrangement of the Coniferæ can only be considered as provisional; Endlicher (Synopsis Coniferarum, 1847) distinguishes the following families:—

First Family. **Cupressineæ.** Leaves, including those of the flowers, opposite or verticillate (in Division *e* single); flowers monœcious or diœcious; stamens terminating in a shield-like expansion bearing pollen-sacs in twos or threes or larger numbers; female flower consisting of alternate whorls of carpels, bearing at their base or on their inner surface two or a larger number of erect ovules (in *Juniperus communis* the ovules

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[1] See in addition Schacht, Lehrbuch der Anat. u. Phys. vol. II, p. 462. According to Pfitzer (*l. c.*) the young rudiment of the embryo has at first an apical cell, which however soon disappears; in the Abietineæ the mode of formation of the embryo is from the first like that in Angiosperms.

are alternate with the three carpels on the floral axis); embryo with two, rarely three or nine cotyledons.

(a) *Juniperineæ*. Fruit berry-like (Juniperus, Sabina).

(b) *Actinostrobeæ*. Carpels united into valves; afterwards separating as a four- or six-rayed star (Widdringtonia, Frenela, Actinostrobus, Callitris, Libocedrus).

(c) *Thujopsideæ*. Carpels partially overlapping one another (Biota, Thuja, Thujopsis).

(d) *Cupressineæ veræ*. Carpels peltate and polygonal in front (Cupressus, Chamæcyparis).

(e) *Taxodineæ*. Carpels peltate or overlapping; leaves alternate (Taxodium, Glyptostrobus, Cryptomeria).

Second Family. **Abietineæ**. Leaves usually acicular and arranged spirally, singly, or in twos, threes, or rosettes on special short shoots; flowers monœcious, rarely diœcious; stamens numerous, with two or more long pollen-sacs; female flower consisting of a number of scale-like placentæ arranged spirally, which are either themselves carpels or are the result of the coalescence and lignifying of small carpels; micropyle of the ovule turned towards the base of the placenta; embryo with from two to fifteen cotyledons.

(a) *Pineæ*. Seeds in pairs on a scale-like placenta which springs from a small open carpellary leaf (Pinus, Abies, Tsuga, Larix, Cedrus).

(b) *Araucarieæ*. Seed single on the carpel, and enveloped by it (Araucaria).

(c) *Cunninghamieæ*. Seeds single or numerous on a carpel (Dammara, Cunninghamia, Athrotaxis, Sequoia, Sciadopitys).

Third Family. **Podocarpeæ**. Leaves acicular or broader, and arranged spirally; flowers monœcious or diœcious; stamens short, with two roundish pollen-sacs; female flower consisting of an axis swollen above with small scale-leaves, from the axils of which (?) the ovules spring; embryo dicotyledonous.

Podocarpus (Dacrydium, Microcachrys).

Fourth Family. **Taxineæ**. Leaves arranged spirally, acicular or often of considerable breadth; in Phyllocladus there are no foliage-leaves, these being replaced by leaf-like branches; flowers always diœcious; stamens of various forms, bearing two, three, four, or eight pendent pollen-sacs; female flowers always consisting of a naked axis or of one furnished with small leaves, bearing the erect ovules terminally or laterally; ripe seed enclosed in a fleshy aril or with the outer layer of the testa fleshy; embryo dicotyledonous.

Phyllocladus, Salisburia, Cephalotaxus, Torreya, Taxus.

C. GNETACEÆ.

This order includes three genera which differ strikingly in habit. The Ephedræ are shrubs with no foliage-leaves and with long, slender, cylindrical green-barked branches; at the joints of the stem are two opposite minute leaves which grow together into a bidentate sheath, and from their axils the lateral branches spring. In Gnetum the leaves are also opposite on the jointed axes, but large and stalked, with a broad lanceolate lamina and feather-veined venation. Thirdly, *Welwitschia mirabilis*, so remarkable a plant in many other ways, possesses only two

foliage-leaves (probably the cotyledons) of immense size. They are extended on the ground and become divided into strips as they become old; the stem remains short, rising only slightly above the ground, and is broad above with a furrow across the top, while it is tuberous below, and passes into the tap-root[1].

The *Flowers* of Gnetaceæ are unisexual, and are arranged in dicœcious (Ephedra) or monœcious inflorescences; the inflorescence has a well-defined form, and in Ephedra and Gnetum springs from the axils of the opposite leaves. The male flower of these genera consists of a small bifid perianth, in the middle of which rises a staminal column, which in Gnetum is bifurcate above and bears two bilocular anthers, in Ephedra a larger number crowded into a head. The female flower of Gnetum (Eichler, in Flora 1863, p. 463), like that of Ephedra, also possesses a perianth, flask-shaped in the former, obscurely trigonous in the latter genus; it envelopes a central ovule possessing in the case of Ephedra one integument, in that of Gnetum two, the inner of which is elongated like a style. The more exact morphology of these flowers is still doubtful. The endosperm of Ephedra is said by Schacht to produce only one archegonium, and the contents of the longish pollen-grain to divide like those of the Abietineæ. In Gnetum the inflorescence, which springs from the axil of the foliage-leaves, consists of a jointed axis with verticillate leaves, in the axils of which the flowers, male and female, are agglomerated. The inflorescence of Welwitschia[2] is a dichotomously branched cyme

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[1] For a full description of this remarkable plant see J. D. Hooker in Trans. Linn. Soc. vol. XXIV.

[2] [According to Professor W. R. M'Nab, 'The cones of Welwitschia consist of numerous opposite and decussate bracts, with a sessile flower in the axil of each of the bracts. The perfect flowers in the male cone consist of two outer perianth leaves (calyx) placed right and left, two inner ones (corolla) placed anteriorly and posteriorly, six stamens united below, and two carpels anterior and posterior, the conical end of the axis projecting as a rudimentary axile ovule surrounded by the two carpels. The outer parts of the perianth are first developed, appearing as two shoulders at the very base of the young floral branch. The flower next in age has the floral axis more elongated, the outer parts of the perianth larger, and a distinct swelling is visible above the outer parts. These swellings are anterior and posterior, and much larger than the outer parts. Above the inner parts of the perianth the axis is expanded, and contracts near the rounded apex. The expanded portions are superposed on the outer lateral parts of the perianth, and are the two primordial staminal cushions. These cushions are semilunar, and in the earlier stages show no trace of division into three. At this stage the parts of the perianth rapidly enlarge and cover in the central parts of the flower. A projection now forms anteriorly and posteriorly, the first indication of the two carpels. The next stage shows the two staminal cushions each forming three elevations, the central one larger than the two lateral ones. The six stamens are thus produced by the branching of two primordial stamens. In the next stage the carpels elongate and cover in the *punctum vegetationis*, ultimately developing the peculiar style and stigma-like process. The axis elongates slowly and forms a conical projection which is undoubtedly a rudimentary axile ovule, but it never shows any appearance of an embryo-sac.'

In the female flowers, which are produced in different cones from the male flowers, the development is very different. A very short stalk is developed in the female, which is wanting in the male; then two shoulders are developed exactly like the two outer parts of the perianth in the male flower, to which Dr. Hooker considered them to be equivalent. Judging from the construction of the male flower, Professor M'Nab was disposed to accept this view; but with hesitation, as he could not account for the stalk-like process. Strasburger however concludes that they are carpels, and in that M'Nab quite concurs. Above the carpels the axis elongates slightly, and a ring is formed surrounding the *punctum vegetationis*. This ring is the ovular integument. Comparing the two flowers, it will be seen that in the male there are four series of parts, in the female the three outer

nearly a foot in height, rising above the insertion of the two enormous leaves on the periphery of the broad apex of the stem. The branches of the inflorescence are terete and jointed, spring from the axils of the bracts, and bear upright longish cylindrical cones; these are furnished with from seventy to ninety broadly ovate scale-leaves standing closely one above another in four rows, a single flower being seated in each axil, male and female in different cones. The male flowers are pseudo-hermaphrodite, and possess a perianth consisting of two pairs of decussate leaves; the lower ones are entirely free, sickle-shaped and pointed, the upper ones broadly spathulate and coherent at their base into a compressed tube. Within this tube are six stamens monadelphous at the base, with cylindrical filaments and terminal spherical bilocular anthers, which dehisce above the apex with a three-armed fissure; the pollen-grains are simple (?) and elliptic. The centre of the flower encloses a single erect orthotropous sessile ovule with broad base, and with no other investment than a simple integument, which is drawn out into a style-like tube with a margin expanded in a discoid manner; the nucleus however has no embryo-sac, or is sterile. In the female flowers the perianth is tubular, greatly compressed, somewhat winged, and altogether undivided; there is no indication of any male organ; the ovule (in this case of course possessing an embryo-sac) is entirely enclosed in the perianth, and is similar in its external form to that of the male flower, but with this difference, that the elongated point of the integument is only simply slit, not expanded into the form of a plate. When ripe the cone is about two inches long and of a scarlet colour; the scales are persistent; the perianth enlarges considerably and becomes broadly winged; its cavity is narrowed above into a narrow canal, through which the apex of the integument passes. The seed is of the same form as the unfertilised ovule, and contains abundant endosperm, in the axis of which lies the dicotyledonous embryo; the embryo is thick at the radicular end, and is there attached to the very long spirally coiled suspensor. The formation of endosperm commences in the embryo-sac even before fertilisation; archegonia are formed which grow out of the embryo-sac to the number of from twenty to sixty, and penetrate into the canal-like cavity of the nucleus; there they are fertilised by the pollen-tubes which have grown to meet them, the pro-embryos being then formed in the lower part of the central cells, the (coiled) suspensors attaining a length of three inches. Although from two to eight archegonia are fertilised, only one embryo is developed.

The Formation of Tissue in Gymnosperms. From the abundant though still unsifted material I will only adduce a few particulars as a contribution to the special characteristics of this section.

The *Fibro-vascular Bundles*[1] are similar in their structure to those of Dicotyledons.

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series are wanting and only the carpels remain. But in the male flower the carpels are anterior and posterior, while in the female they are lateral. This is to be explained by the fact that the carpels are here the first leaves of the branch, and that it is very rare (except in Grasses) that the first leaves of a shoot are anterior or posterior, and not lateral. The ovular integument of the female flower is wanting in the male. While therefore the male flower is complex, the female is remarkably simple.

For further details see Transactions of the Linnean Society 1873, vol. XXVIII, pp. 507-512. —Ed.]

[1] Mohl, Bau des Cycadeenstammes (Verm. Schr. p. 195).—Kraus, Bau der Cycadeen-Fiedern

There is a system of bundles common to the stem and leaves; the portions which descend into the stem forming a circle, where a closed cambium-ring is produced by the formation of interfascicular cambium. This ring causes the permanent growth in thickness of the stem. The ascending portion, which curves out into the leaf itself, assumes in Cycadeæ more or less the character of a closed bundle, while in the leaves of many Coniferæ it at least retains the appearance of an open bundle. No exclusively cauline bundles are produced in the stem of Coniferæ or of Ephedra; but in Cycadeæ and Welwitschia bundles arise in the older stem which are nothing but ramifications of the common bundles, although in their further development, to a great extent, independent of them. Thus in the tissue of the pith of some Cycadeæ slender isolated bundles occur; while in some a system of thicker branches of bundles is developed in the bark which may form there in old age one or more apparent rings of wood. As far as we can judge from Hooker's description, bundles occur in the bark of Welwitschia which owe their origin to a layer of meristem enveloping the whole stem. The Coniferæ, as has been mentioned, possess only common bundles, the descending portions passing through a number of internodes, and then joining others lower down either unilaterally or on both sides by splitting into two arms and turning to both sides. The leaves of Coniferæ, when narrow, contain only one fibro-vascular bundle from the stem, which then usually splits into two halves running parallel to one another; when the leaves are broader, two (Salisburia, Ephedra) or even three bundles occur; when the leaf forms a flat broad lamina, as in Salisburia and Dammara, the bundles ramify in it, but without forming a net-work; in Salisburia they repeatedly branch dichotomously. In Coniferæ these bundles seldom form prominent veins, but run through the middle of the tissues of the leaf. In the two gigantic leaves of Welwitschia there are a number of bundles, the parallel ramifications of which run into the middle layer of tissue. In the large pinnate leaves of Cycadeæ there are also several bundles which curve nearly horizontally within the cortical parenchyma, and split into a number of stout bundles in the leaf-stalk when it is thick; these bundles exhibit a beautiful arrangement when seen in transverse section (in *Cycas revoluta*, *e. g.* in the form of an inverted Ω). They run parallel in the rachis of the pinnate leaf, and give off branches into the pinnæ, where they either run parallel in the middle layer of tissue (as in Dion) or dichotomise (*e. g.* Encephalartos); while in Cycas they form a mid-rib projecting beneath. The course of the bundles in the leaf therefore shows a decided resemblance to that of many Ferns.

The substance of the wood of the stem is formed from the descending bundles, which are at first completely isolated, but soon coalesce into a closed ring by portions of cambium which cross the medullary rays. The primary wood or xylem, termed the Medullary Sheath, which consists of the xylem-portions of the descending arms of the common bundles, contains, in all Gymnosperms, as in Dicotyledons, long narrow vessels with annular or spiral thickening-bands, while further outwards occur scalariform or reticulately thickened vessels. The secondary wood produced from the cambium-ring after the cessation of growth in length consists, in Cycadeæ and Coniferæ, of long tracheïdes grown one into another in a prosenchymatous manner (*cf.* p. 25) with a few large bordered pits, which are usually circular, at least when the wood is mature. Every possible stage of transition occurs between these tracheïdes (p. 99) and the spiral vessels of the medullary sheath. The secondary wood of Cycadeæ and Coniferæ is distinguished from that of Dicotyledons by the striking peculiarity that it is composed only

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(Jahrb. f. wiss. Bot. vol. IV. p. 329).—Geyler, Ueber Gefässbundelverlauf bei Coniferen (ditto, vol. VI. p. 68).—Thomas, Vergl. Anat. des Conifer-Blattes (ditto, vol. IV. p. 43).—Mohl, Ueber die grossen getüpfelten Röhren von Ephedra (Verm. Schr. p. 269).—J. D. Hooker, On Welwitschia (Trans. Linn Soc. vol. XXIV.).—Dippel, Histologie der Coniferen (Bot. Zeit. 1862 and 1863).—Rossmann, Bau des Holzes (Frankfurt-a-M. 1863).—Mohl, Bot. Zeit. 1871.

of this a prosenchymatous form of cells[1]); and that the wide dotted vessels composed of short cells are wanting which penetrate the dense narrow-celled masses of the wood of Dicotyledons. In the younger stems of Cycadeæ the tracheïdes with broad bordered pits and hence with a more or less scalariform wall, are very much like the long prosenchymatous vessels of Vascular Cryptogams; and this resemblance extends even to the tracheïdes of Coniferæ, so far as they are distinctly prosenchymatous, although the smaller number and round form of the bordered pits shows a more marked difference (pp. 25–27). The bordered pits of Coniferæ are usually developed only on the wall which faces the medullary rays, in one or two rows, but in Araucaria in larger numbers and densely crowded. In the structure of the secondary wood, as in that of their flowers and in their habit, Gnetaceæ approach Dicotyledons; in Ephedra broad vessels occur in it together with the usual tracheïdes in the inner part of the ring of wood, but their component cells are separated by oblique septa, and are therefore still prosenchymatous, and are penetrated by several roundish holes; their lateral walls show bordered pits like the tracheïdes, and furnish a striking evidence that the true vessels in the secondary wood of Dicotyledons are connected by intermediate forms with the vessels of Vascular Cryptogams formed from prosenchymatous cells. It is stated that in the wood of Welwitschia tracheïdes with doubly bordered pits are entirely wanting, and that it contains in their place thick-walled 'porous vessels.'

The rays of the secondary wood of Coniferæ are very narrow, often only one cell in breadth; the cells are strongly lignified, and their lateral faces in contact with the adjoining tracheïdes are provided with closed dots. In Cycadeæ the rays are broader, and their tissue bears a closer resemblance to the parenchyma of the pith and cortex; their number and width cause the whole substance of the wood to appear spongy, and its parenchymatous cells to be strongly curved in different directions when cut across. The phloëm-portion of the fibro-vascular bundles of Gymnosperms resembles that of Dicotyledons; it is mostly composed of true strongly-thickened bast-fibres, cambiform cells, latticed-cells, and parenchymatous cells; while in Coniferæ they are formed in alternate layers. Usually the soft bast predominates.

The *Fundamental Tissue* of the stem of Gymnosperms is separated by the ring of wood into pith and primary cortex. Both are very strongly developed in Cycadeæ, especially the pith, and consist of true parenchyma, while the woody portion is considerably smaller. In Welwitschia the parenchymatous tissues appear also to prevail; but the greater part of their substance can only originate from the meristem-layer of the stem already mentioned. A large number of so-called spicular cells occur dispersed in all the organs of this remarkable plant, they are fusiform or branched and greatly thickened; and a number of beautifully developed crystals are found imbedded close to one another in their cell-wall. Similar structures also occur in Coniferæ (p. 66).

The parenchymatous fundamental tissue of Coniferæ decreases greatly with the increase in age of the stem (and of the root). With the exception of the pith, which is here small, the stem consists exclusively of the products of the cambium-ring, since the primary cortex, and afterwards also the outer layers of the secondary cortex which always have a subsequent growth, are used up in the formation of cork. In the stem of Cycadeæ, the increase of which in thickness is inconsiderable, the formation of cork is also very small; in Welwitschia it appears to be entirely wanting (?).

Sap-conducting Intercellular Passages are widely distributed in Gymnosperms; their structure is that which has been explained generally at pp. 73 and 115. In Cycadeæ they are found in all the organs in large numbers, and contain gum, which exudes from incisions in thick viscid drops; in Coniferæ they contain oil of turpentine and resin. In this latter order they occur in the pith of the stem, in the whole substance

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[1] Wood-parenchyma is not formed, or only in small quantity.

of the wood, and in the primary and secondary cortex, as well as distributed through the leaves (p. 105); always following the direction in length of the organs, like the gum-passages of Cycadeæ. In many Conifers with short leaves roundish resin-glands also occur in them (as in Callitris, Thuja, and Cupressus, according to Thomas); in Taxus the resin-canals are entirely wanting[1].

The *Leaves* of Cycadeæ and Coniferæ are covered by a firm epidermis, usually strongly cuticularised, and furnished with numerous stomata, each with two guard-cells. In the Cycadeæ the guard-cells are more or less deeply depressed, and the stomata occur only on the under side of the lamina, and are either irregularly scattered, or arranged in rows between the veins (Kraus). In the leaves of Conifers the guard-cells are also, according to Hildebrand (Bot. Zeit. 1869, p. 149), always depressed in the epidermis; and the stoma has hence always a border (*cf.* p. 86). In Coniferæ the stomata are developed either on both or only on one side of the leaf; when the leaf is broad, as in Dammara and Salisburia, they are irregularly scattered; when the leaves are acicular they mostly lie in longitudinal rows; and in the large leaves of Welwitschia they are also arranged in rows. The firm texture of the leaves of Cycadeæ and Coniferæ is due to a hypodermal layer (p. 105), often strongly developed, consisting of

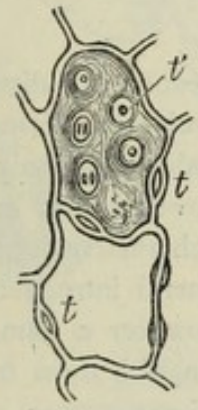

FIG. 326.—*Pinus Pinaster*; two cells of the colourless parenchyma surrounding the fibro-vascular bundle of the leaf; *t t* the dot-like structures cut across, *t'* the same seen from the surface.

strongly-thickened, generally long, fibre-like cells lying parallel to the surface; in the leaf of Welwitschia this hypoderma consists of spongy succulent tissue penetrated by bundles of fibres, which acquires its hardness from a mass of spicular cells. The chlorophyll-tissue of the leaves lies beneath this layer, and is developed on the upper side of the leaves of Cycadeæ and of the broader leaves of Coniferæ as the so-called Pallisade-tissue; *i. e.* its cells are elongated in a direction vertical to the surface of the leaf and are densely packed together. In Pinus, Larix, and Cedrus the cells which contain chlorophyll exhibit the infoldings of the cell-wall which have been already

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[1] [Van Tieghem (Ann. des Sci. Nat. 1872) distinguishes the six following modifications of the distribution of the secretory organs in Coniferæ:—1. No canals in the root nor stem: Taxus. 2. No canals in the root; canals in the cortical parenchyma of the stem: Cryptomeria, Taxodium, Podocarpus, Dacrydium, Torreya, Tsuga, Cunninghamia. 3. No canals in the root; canals in the cortical parenchyma and in the pith of the stem: Salisburia. 4. A secretory canal in the root; canals in the cortical parenchyma of the stem: Cedrus, Abies, Pseudolarix. 5. Canals in the wood of the fibro-vascular bundles of the root and stem; canals in the cortical parenchyma of the stem: Pinus, Larix, Picea, Pseudotsuga. 6. Canals in the liber of the fibro-vascular bundles of the root and of the stem; canals in the cortical parenchyma of the stem: Araucaria, Widdringtonia, Thuja, Cupressus, Biota. In Cycadeæ the canals are found disseminated through the cortical parenchyma of the stem; the pith of Cycas appears destitute of them. In their distribution they resemble therefore that which occurs in the second class of Coniferæ.—ED.]

mentioned at p. 72 (Fig. 60). The middle layer of the tissue of the leaf, in which also the fibro-vascular bundles run, has usually a peculiar development in Gymnosperms; in Cycadeæ and Podocarpeæ it consists of cells elongated in a direction transverse to the axis of the leaf and to the bundles, but parallel to the surface of the leaf, leaving large intercellular spaces (Transfusion-Tissue of Mohl). In the acicular leaves of the Abietineæ the fibro-vascular bundle, split into two, is enveloped by a colourless tissue, which is sharply differentiated from the surrounding chlorophyll-tissue (Fig. 89, *gb*, p. 105). It is parenchymatous, and is distinguished by the large number of peculiar pit-like markings (Fig. 326)[1].

ANGIOSPERMS[2].

Monocotyledons and Dicotyledons are distinguished from Gymnosperms by the following characters:—their ovules are formed within a receptacle, the *Ovary;* the endosperm originates in the embryo-sac only after fertilisation, the pollen-grain emits its pollen-tube as an outgrowth of its inner cell-wall (intine) without any previous internal cell-formation;—characteristics, the immense importance of which has already been shown in the general introduction to Phanerogams. Concurrent with these distinctions there are however a number of other peculiarities in these plants taken as a whole which distinguish them from all other vascular plants; and this is especially the case with the structure of the flowers and the fruit, the normal morphological characters undergoing such peculiar combinations and changes that a more detailed description of them must precede the special description of the two classes which they include.

The Flower as a whole[3]. The flower of Angiosperms is rarely terminal, *i. e.* the primary stem, which is a prolongation of the axis of the embryo, rarely terminates in a flower, making the plant uniaxial. When this is the case a sympodial or cymose inflorescence is usually developed, new axes with terminal flowers arising beneath the first flower; but it is more common for only axes of the second, third, or a higher order to terminate in a flower, so that the plant may in this respect be termed bi-, tri-, or multi-axial.

While in Gymnosperms the flowers are typically unisexual or diclinous, hermaphroditism largely prevails among Angiosperms, although monœcious and diœcious species, genera, and families are not uncommon. The male flowers are sometimes essentially different in structure from the female flowers (as in Cupuliferæ and Cannabineæ), but in most cases the unisexuality arises merely from the partial or

[1] For further details, see Mohl, Bot. Zeit. 1871, Nos. 1, 2.

[2] From ἀγγεῖον, a receptacle, capsule, ovary, and σπέρμα, seed.

[3] The most important and comprehensive work on the flowers of Angiosperms is Payer's Traité d'Organogénie de la Fleur (Paris 1857) with 154 plates.

entire abortion either of the androecium or the gynæceum, the flower being in other respects constructed on the same type (Fig. 327, *A*); and in such cases it also frequently happens that hermaphrodite flowers are developed in addition to the male and female (polygamous species, as the ash, Acer, *Saponaria ocymoides*, &c.). But even in the greater number of cases where the male and female organs are completely developed in hermaphrodite flowers and functionally perfect, fertilisation takes place by the conveyance of the pollen of one flower to the gynæceum of other flowers or even of other individuals of the same species, because either pollination within the same flower is impossible in consequence of special contrivances (such as dichogamy), or because the pollen is potent only in the fertilisation of

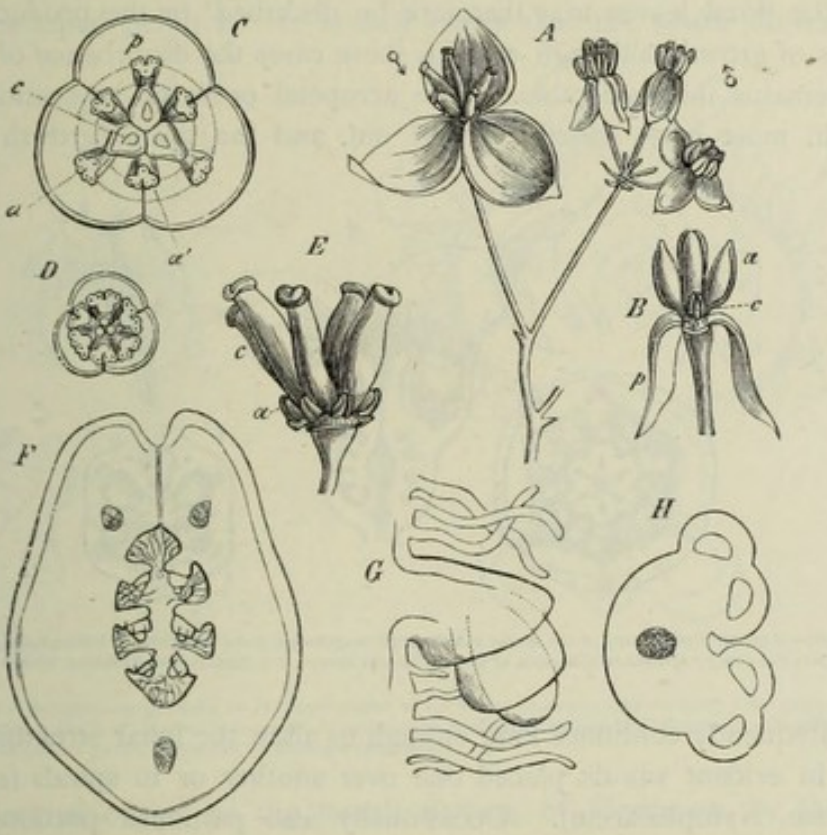

FIG. 327.—*Akebia quinata*; *A* part of an inflorescence, ♀ female, ♂ male flowers; *B* a male flower cut through lengthwise, *c* its sterile carpels; *C* horizontal section of a female flower (magnified); *D* horizontal section of a male flower; *E* gynæceum of the female flower with the sterile stamens *a*; *F* an ovary cut through horizontally; *G* an ovule; *H* horizontal section of an anther; *a* (in *B* and *C*) the outer, *a'* the inner stamens, *c* (in *E*) the carpels; *p* (in *B* and *C*) the perianth.

ovules of another flower (as in Orchideæ, Corydalis, &c.). To these phenomena we shall recur more in detail in the Third Book, when speaking of the physiology of sexual reproduction.

While in Gymnosperms the floral axis is usually elongated to such an extent that the sexual organs, especially if numerous, are evidently arranged one above another in alternate whorls or in spirals,—in Angiosperms, on the contrary, the floral axis which bears the floral envelopes and sexual organs is so abbreviated that space can only be found for the various foliar structures by a corresponding expansion or increase in size of the receptacle or torus; this receptacle swells even before and during the formation of the floral leaves in a club-shaped manner, and is not unfrequently expanded flat like a plate or even hollowed out like a cup in such a

manner that the apex of the axis is placed at the bottom of the hollow (*cf.* Fig. 152, p. 200), while the cup thus formed encloses the carpels (as in perigynous flowers), or even takes part in the formation of the ovary, which is then inferior (Fig. 328). But in every case, owing to the abbreviation of the axis, the separate parts do not usually stand one above another, but rather in concentric whorls, or in scarcely ascending spirals, for which reason the explanation of the relative positions expressed by a diagram in the sense explained on p. 167 appears the most obvious. This abbreviation of the axis is also obviously the immediate cause of the numerous cohesions and displacements which are nowhere met with so frequently as in the flowers of Angiosperms. The small development of the floral axis in length depends on the early cessation of its apical growth; the acropetal or centripetal order of succession of the floral leaves may therefore be disturbed[1] by the production of intercalary zones of growth, although even in these cases the disturbance of the ordinary regularity remains inconsiderable. The acropetal order of succession is however even here in most cases strictly carried out, and the apical growth of the floral

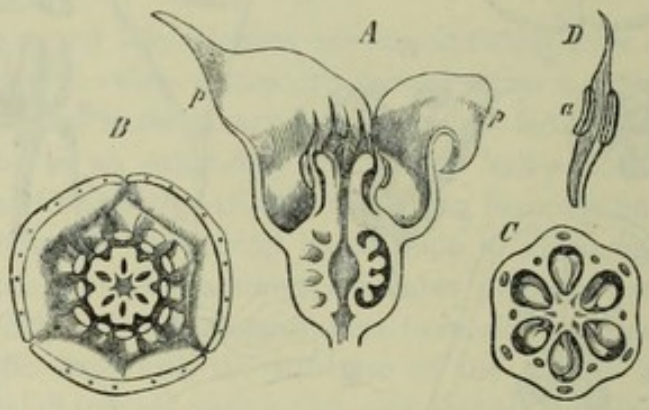

FIG. 328.—*Asarum canadense*; *A* the flower cut through lengthwise, *p* the perianth; *B* horizontal section of the flower above the ovary; *C* horizontal section of the sex-locular ovary; *D* a stamen with its lateral anther-lobes *a*.

axis not unfrequently continues long enough to allow the foliar structures to arrange themselves in evident whorls placed one over another or in spirals (*e.g.* Magnolia, Ranunculaceæ, Nymphæaceæ). Occasionally also particular portions of the axis are greatly elongated within the flower, as the portion between calyx and corolla in Lychnis (Fig. 330 *bis*, p. 472), in Passiflora that between corolla and stamens, in Labiatæ that between stamens and ovary.

The flower of Angiosperms, like that of Gymnosperms, is a metamorphosed shoot, a leaf-bearing axis; but this section of the vegetable kingdom is especially characterised by the high degree of metamorphosis which the floral shoot has undergone, and by the very peculiar characteristics and the different arrangement of the foliar structures as contrasted with those of the purely vegetative shoots. As far as external appearance goes, the flower of Angiosperms is an altogether peculiar structure, sharply differentiated as a whole from the rest of the organism. This peculiar appearance is due not only to the special properties of its axis,

[1] The cases adduced by Hofmeister (Allgemeine Morphologie, § 10) of the absence of strict acropetal succession in the foliar structures all belong to this category.

but especially to the presence of the floral envelopes, and most of all to the circumstance that the foliar structures of the flower are arranged, with rare exceptions, in the form of whorls, even when the leaves of the vegetative shoots are alternate or distichous, or disposed in other similar arrangements. Each of the distinct appendicular organs of the flower, viz. the perianth, andrœcium, and gynæceum, is usually represented by several members arranged in concentric circles or a spiral; so that one or more perianth-whorls are immediately succeeded within by one or more whorls of stamens, and these by the gynæceum in the centre of the flower. One or other of these whorls may however be absent, or each of the separate whorls may be represented by only a single member, as in Hippuris (Fig. 330), where only one stamen and one carpel are contained within a scantily developed perianth. It is only rarely that the whole flower is reduced

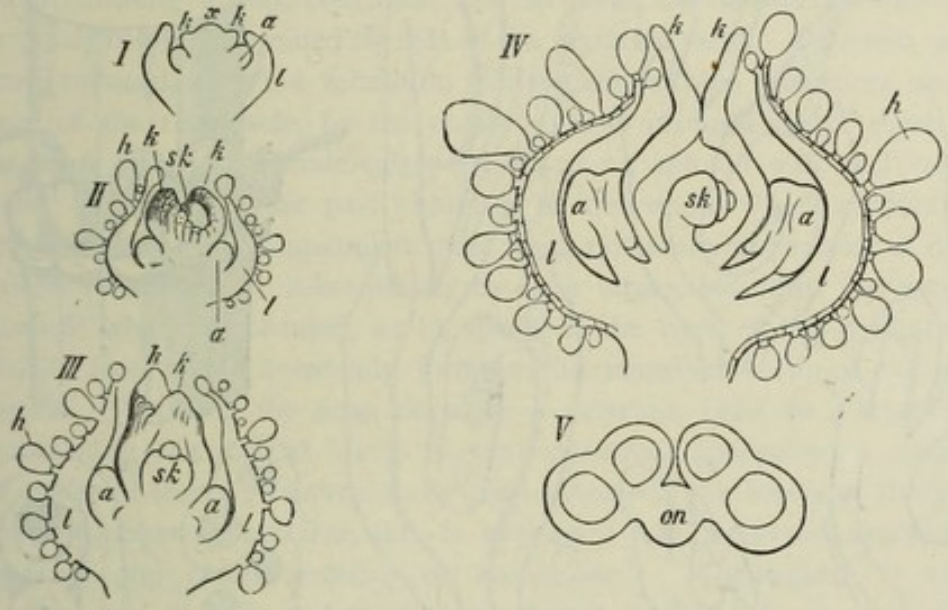

FIG. 329.—*Chenopodium Quinoa*; *I—IV* development of the flower (in longitudinal section), *l* the calyx furnished with glandular hairs *h*, *a* anthers, *k*, *k* carpels, *sk* ovule, *x* apex of the floral axis, *V* horizontal section of an anther with four pollen-sacs on the connective *on* (strongly magnified).

to a single sexual organ, as the female flowers of Piperaceæ, or the male and female flowers of some Aroideæ; it is much more commonly the case that the flower is composed of successive whorls of members disposed from without inwards (or from below upwards), consisting of the same or multiples of the same number[1], radiating from the centre on all sides like a rosette, a property which is frequently partially obscured at a subsequent period by bilateral development and abortion.

The Floral Envelope or *Perianth* is only rarely entirely wanting, as in the Piperaceæ and many Aroideæ; more often it is simple, *i. e.* it consists of only one whorl of two, three, four, five, or rarely a larger number of leaves (as in Figs. 327, 328); in this case the perianth is frequently inconspicuous and composed

[1] [To this peculiarity of structure the term 'symmetrical' is generally applied in English text-books; in the present work however this word is used in a very different sense, namely in reference to any structure (foliar or floral) which can be divided into two similar halves, or the parts of which are radially disposed around a central point; see p. 183.—ED.]

of small green leaves, as in the Chenopodiaceæ and Urticaceæ, but is sometimes large, of delicate structure and brightly coloured (petaloid), as in Aristolochia, Mirabilis, &c. But in both classes of Angiosperms (Monocotyledons and Dicotyledons) the perianth is usually composed of two alternating whorls consisting of the same number of leaves, two, three, four, five, or rarely more. In most Dicotyledons and many Monocotyledons the form and structure of these two whorls is very different; the outer whorl or *Calyx* consisting of stouter, green, usually smaller leaves (*Sepals*), while the inner whorl or *Corolla* is more delicate, and is formed of white or bright-coloured, usually larger leaves (*Petals*). It is however more convenient, for the sake of brevity, as Payer has already suggested, to designate the inner whorl as

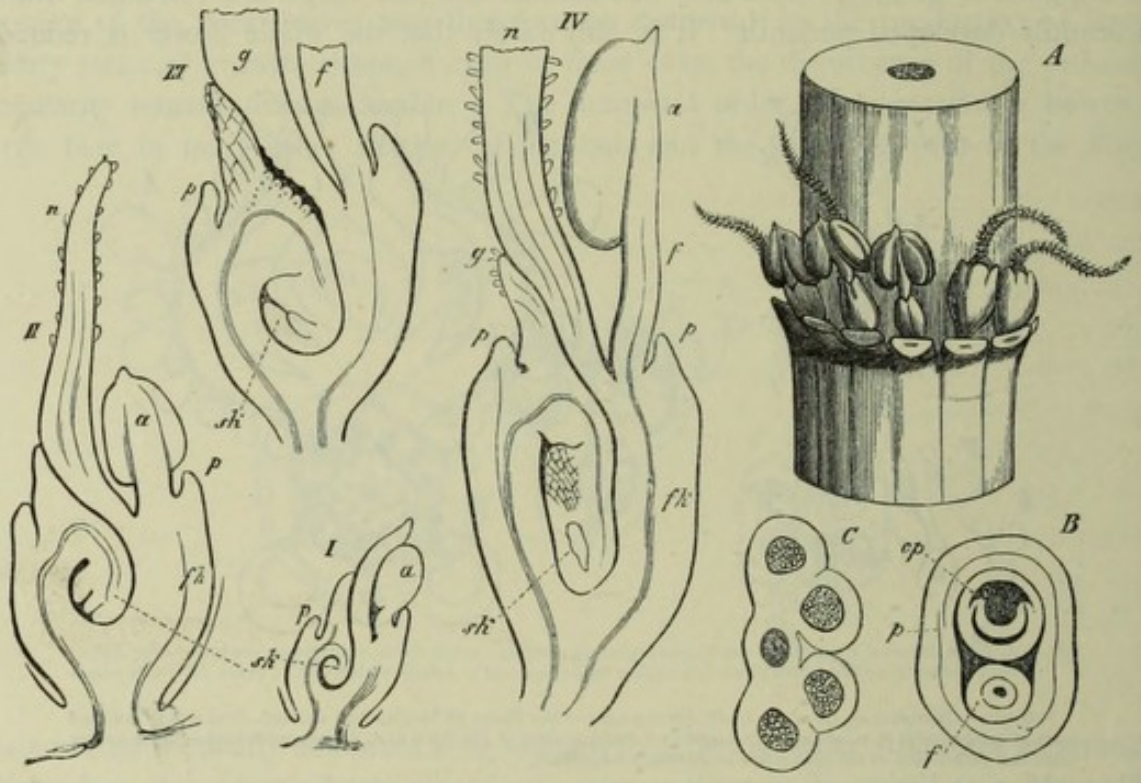

FIG. 330.—*Hippuris vulgaris*; *A* piece of an erect stem, the flowers standing in the axils of the whorl of leaves (which have been cut off); *B* horizontal section of a female flower above the ovary, *p* perianth, *cp* carpel; *C* horizontal section of the anther; *I—IV* longitudinal section of flowers in various stages of development, *a* anther, *f* filament, *g* style, *n* stigma, *p* perianth, *fk* the inferior ovary, *sk* the pendulous and anatropous ovule.

corolla, the outer whorl as calyx, even in those cases where the structure of the two is the same[1]; and this is the more necessary since the contrast of structure referred to is frequently wanting, both whorls being either sepaloid, as in Juncaceæ, or both petaloid, as in Lilium; in Helleborus, Aconitum, and some other species, the outer whorl or calyx alone is petaloid, the inner whorl or corolla being transformed into nectaries. In some Dicotyledons the perianth does not consist of alternating whorls, but of a smaller or larger number of turns of spirally arranged leaves, the number of which is then usually large or indefinite; the outer or lower leaves of this spiral arrangement may in this case also be sepaloid, the inner ones alone petaloid (*e.g.* Opuntia), or they may all be petaloid (as in Epiphyllum

[1] The substantives calyx and corolla then designate the position of the whorl, the adjectives sepaloid and petaloid the nature of the part.

and Trollius), or a gradual transition takes place from the sepaloid through the petaloid to the staminal structure (as in Nymphæa).

But besides the usual sepaloid and petaloid form and structure of the perianth-leaves, there occur other considerable deviations from the ordinary foliar structure. Thus, for example, the (imperfect) perianth of Grasses consists of very small delicate colourless membranous scales (the *Lodicules*), that of some Cyperaceæ is replaced by hair-like bristles, the *Setæ;* in the place of the calyx of Compositæ a crown of hairs, the *Pappus*, surrounds the corolla; and it has already been mentioned that the petals of Aconitum, Helleborus, &c., are transformed into nectaries of a peculiar form.

Whether the perianth consist of one or two whorls, the leaves of the same whorl have very commonly the appearance of being coherent or of coalescing with one another, forming a cup, bell, tube, and so forth, the number of the coherent sepals or petals being determined by that of the marginal teeth. Coherent perianth-whorls are produced, after the formation of the distinct foliar structures at the circumference of the receptacle, by the common zone of insertion of these distinct structures being raised up by intercalary growth as an annular wall, and forming, as it continues to develope, the part common to the whole whorl of floral leaves. The coherent tubular or campanulate part does not therefore consist of originally free portions which cohere subsequently by their edges, but from the very first it forms a whole which is intruded, so to speak, at the base of the perianth-leaves; the originally free leaves eventually forming the marginal teeth of the common basal portion. Applying the term Sepal to a calycine, Petal to a corolline leaf, a calyx consisting of coherent leaves is *gamosepalous* or *synsepalous*, a corolla consisting of coherent leaves *gamopetalous* or *sympetalous;* if the leaves of the perianth-whorl are not coherent, but free, this is expressed by the terms *eleutherosepalous* or *aposepalous*, and *eleutheropetalous* or *apopetalous*[1]. When there is only one perianth-whorl, and it is desired to state whether it consists of coherent or of free leaves, the terms *gamophyllous* or *symphyllous* and *eleutherophyllous* or *apophyllous* may be used. It sometimes happens moreover that two perianth-whorls coalesce into one, so that, for example, two alternating trimerous whorls have united into a six-toothed tube (as in Hyacinthus, Muscari, &c.).

If the leaves of the outer and inner whorls are free (not coherent), and if the distinction between calyx and corolla is clearly marked, then, in addition to the structural distinctions already named, other differences of form are also usually to be observed. The sepals have generally a broader base, are sessile, usually of very simple outline and pointed at the apex; the petals have mostly a narrower base, their upper portion is often very broad, and a distinction is not unfrequently apparent of claw (*unguis*) and blade (*lamina*), and the lamina is often divided or otherwise segmented. At the point where the lamina bends back from the unguis, ligular structures are often formed on the inner or upper side, which are then, when treating the flower as a whole, comprised under the term *Corona*, as in Lychnis

[1] The terms 'polysepalous' and 'polypetalous' are objectionable, since these terms do not express the contrast correctly; still more so are 'monosepalous' and 'monopetalous,' as applied to the coherent whorls, because they have no reference to the true nature of the phenomenon.

(Fig. 330 *bis*), Saponaria, Nerium, Hydrophylleæ, &c. When the corolla itself is gamopetalous, the parts of the corona also coalesce, as in Narcissus, where it is very large.

The complete form of the perianth, especially when its structure is decidedly petaloid and its dimensions considerable, always stands in a definite relation to pollination by the aid of insects [or birds]; and large, brilliantly coloured, odoriferous flowers only occur where the fertilisation is brought about by this means. The purpose of these properties is to attract insects to visit the flowers; and the infinitely varied and often wonderful form of the perianth is especially adapted to compel certain positions of the body and certain movements on the part of insects of a definite size and species when searching for the nectar, by which the conveyance of pollen from flower to flower is unintentionally accomplished by them. We shall recur in detail to these physiological questions in the Third Book.

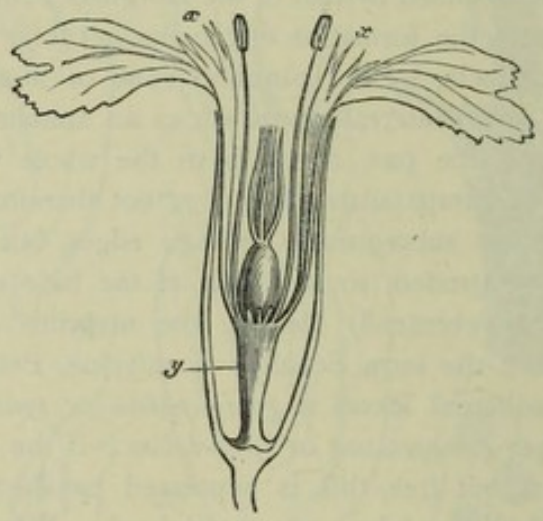

FIG. 330 *bis*.—Longitudinal section through the flower of *Lychnis flos-Jovis*; *y* the elongated portion of the axis between calyx and corolla; *x* ligule of the petals or corona.

The radial or bilateral symmetry of the perianth is usually associated with that of the other parts of the flower, and will therefore be discussed in connection with it.

Besides the perianth in the narrower sense which we have hitherto considered, there are often additional envelopes to the separate flowers. In the Malvaceæ and some other plants the true calyx appears to be surrounded by a second calyx (*Epicalyx* or Calyculus), the morphological homology of which, however, varies. In *Malope trifida*, for example, the three parts of the epicalyx represent a sub-floral bract with its two stipules; in *Kitaibelia vitifolia*, the six-parted epicalyx consists (according to Payer) of two such sub-floral leaves with their four stipules. But the epicalyx may be purely illusory from the production of stipular structures by the true sepals, as in Rosa and Potentilla. In *Dianthus Caryophyllus* and some other species a kind of epicalyx results from two decussate pairs of small bracts which are found immediately beneath the calyx; in the terminal flowers of Anemone a whorl of bracts stands at a short distance below the flower, which takes the form in the nearly allied *Eranthis hyemalis* of a kind of epicalyx[1]. The epicalyx of

[1] [The garden Clematis known as 'Lucie Lemoine' possesses a well-marked seven-leaved involucre which has evidently originated from the growth of the axis above the outermost whorl of the multiplied petaloid sepals.—ED.]

the small flowers of Dipsacaceæ is of special interest, each being surrounded, within the crowded inflorescence, by a membranous tube, which here forms the epicalyx. Sometimes, after the perianth and sexual organs have begun to be formed, an elevation of the flower-stalk, at first annular, is formed below the flower, growing up afterwards in the form of a cup or saucer, and bearing scaly or spiny protuberances. A structure of this kind is called a *Cupule;* and the cup in which the acorn of the various species of oak is seated is of this nature[1]. In this case the cupule surrounds only one flower, in the sweet-chestnut and beech on the other hand it encloses a small inflorescence. This spiny cupule afterwards splits from above, separating into lobes, to allow the escape of the fruit which has ripened within it. When an inflorescence is surrounded by a peculiarly developed whorl or rosette of leaves, as in Umbelliferæ and Compositæ, this is called an *Involucre;* when a single sheathing leaf envelopes an inflorescence springing from its axis, it is a *Spathe*. Both involucre and spathe may assume a petaloid structure, the former, for example, in *Cornus florida*, the latter in Aroideæ.

The *Andrœcium* is composed of the assemblage of the male sexual organs of a flower. Each separate organ is called a *Stamen*, and consists of the *Anther* and its stalk the *Filament*, which is usually filiform, but sometimes expanded like a leaf. The anther consists of two longitudinal halves (anther-lobes) placed on the upper part of the filament right and left of its median line; and the portion of the filament which bears the lobes of the anthers is distinguished as the *Connective*.

The lateral position of the stamens on the floral axis (the receptacle) is quite unmistakeable in all hermaphrodite and in most exclusively male flowers. Their lateral position, their exogenous origin from the primary meristem next the *punctum vegetationis* of the floral axis, their acropetal order of development, and the frequent monstrosities in which the stamens assume more or less the nature of petals, or even of foliage-leaves[2], place it beyond doubt that they must be considered morphologically as foliar structures, and make it convenient to term them Staminal Leaves; the filament, together with the connective, being considered as the leaf, of which the two anther-lobes are appendages. From a morphological point of view it is therefore indifferent whether the filament (or true leaf) greatly preponderates in size, or is inconsiderable as compared to that of the anther. Only very recently three cases have become known in which the anther appears itself to be a product of the floral axis, and the stalk which corresponds to the filament is the floral axis itself. According to Magnus[3], the vegetative cone of the male floral axis of Naias becomes transformed into quadrilocular anthers by the formation of pollen-mother-cells in four peripheral longitudinal strips of its tissue. Kaufmann had previously described a somewhat similar process in the case of the anther of Casuarina; and, according to Rohrbach[4], the apex of the floral axis of Typha either itself developes into the anther, or it first of all branches and then forms an anther on each branch. It would carry us too far to give reasons for the doubt already expressed (p. 426),

[1] On the development of the acorn-cup see Hofmeister, Allgemeine Morphologie, p. 465.

[2] [On 'phyllody' and 'petalody' of stamens see Masters, Vegetable Teratology, Ray Soc. 1869, pp. 253–256, and 285–296.—Ed.]

[3] Magnus, Bot. Zeitg. 1869, p. 771.

[4] Rohrbach, in Sitzungsber. der Gesellsch. naturf. Freunde in Berlin, Nov. 16, 1869.

whether these facts are sufficient to establish the axial character of these anthers; and these cases may, therefore, be considered for the present as exceptions to the foliar nature of stamens. But, besides, the morphological homology of the separate parts of the ordinary stamens is not yet altogether determined, more precise investigations into the history of development being still wanting in this direction. Cassini and Röper consider the two anther-lobes as the swollen lateral halves of the lamina of the stamen; their loculi would therefore in that case be mere excavations in the tissue of the leaf; the pollen-mother-cells become differentiated inside the young tissue of the leaf, like the spore-mother-cells in the fertile segment of the leaf of Ophioglossaceæ. According to this view the furrow between the two pollen-sacs of an anther-lobe (see Fig. 327, *H*) would correspond to the margin of the staminal leaf; but this cannot be the case[1], at least not always, according to Mohl's observations. When the stamens become transformed into petals (by the so-called 'doubling' of the flower) as in the rose, poppy, *Nigella damascena*, &c., it may be observed with certainty that the anterior and posterior loculi do not stand opposite one another, which would be the case if one belonged to the upper, the other to the under side of the staminal leaf; but that both are formed on the upper surface, the anterior loculus nearer the median line of the leaf, the posterior one nearer its margin. It is further observable that in such cases the two pollen-sacs of an anther-lobe do not always stand close to one another, but that they are frequently separated by a tolerably broad piece of the leaf, and that this intermediate piece contracts in the normal state into the partition-wall between the two pollen-sacs. The greater stress must be laid on these observations of Mohl, because in them the abnormal development only shows more plainly what can often enough be seen in a horizontal section of the anther and connective of normal stamens, *viz.* that the pollen-sacs of an anther-lobe evidently belong to *one* side of the stamen; it appears, however, that they must in some cases be referred to the under (Fig. 327, *C*, *H*), in others to the upper side (Fig. 330 *C*). The origin of the pollen-mother-cells and the development of the wall of the separate pollen-sacs calls to mind so vividly in all essential features the corresponding phenomena in the sporangium of Lycopodiaceæ and even of Equisetaceæ, that it may be assumed, until more exact observations bring something different to light, that each pollen-sac (*i. e.* each loculus with its wall) corresponds to a sporangium, and hence also to a single pollen-sac of Cycadeæ and Cupressineæ; and that therefore the anther usually consists of four pollen-sacs springing side by side from the anterior or posterior side of a staminal leaf, the sacs lying in pairs so close to one another right and left of the connective, that they coalesce more or less laterally to form one anther-lobe. But before we pass on to the consideration of the pollen-sacs and their contents, we must again recur to the discussion of the entire stamen and andrœcium.

The stalk of the anther (the filament with its connective) is either simple or segmented. The simple filament may be filiform (Fig. 329) or expanded into the form of a leaf (Fig. 328), sometimes even very broad, as in Asclepiadeæ and Apocynaceæ; or it may be broad below (Fig. 332 *f*) or above; it generally terminates between the two anther-lobes, but is not unfrequently prolonged above

[1] H. v. Mohl, Vermischte Schriften, p. 42.

them (Fig. 328 *D*) as a point, or in the form of a long appendage as in the oleander. If the upper part of the stalk, the connective, is broad, the two anther-lobes are distinctly separated (Figs. 328, 331); if it is narrow, they lie close to one another. The articulation of the stalk is very commonly the result of the connective being sharply separated from the filament by a deep constriction; the connection of the two is then maintained by so thin a piece that the anther, together with the connective which unites the anther-lobes, swings very lightly as a whole on the filament (versatile anther). The point of connection may be at the lower end, at the centre (Fig. 332), or at the upper part of the connective; sometimes the detached connective attains a considerable size, and forms appendages beyond the anther (Fig. 333, *A*, *x*), or it is developed between the two lobes like a cross-bar, so that the filament and connective form a T, as in the lime, and to a much greater extent in Salvia, where the transversely extended connective bears an anther-lobe on one arm only, while the other is sterile and is adapted for a different purpose. Whether the anther-lobes are parallel depends on the mode of their connection with the

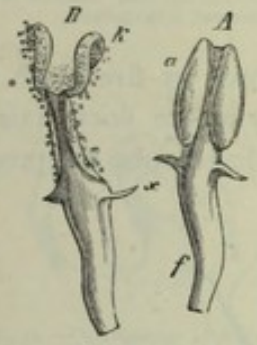

FIG. 331.—Stamen of *Mahonia Aquifolium*; *B* with the anther open (by recurved valves).

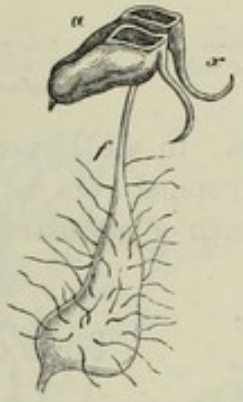

FIG. 332.—Stamen of *Arbutus hybrida*, anther open (by pores); *x* appendage.



FIG. 333.—Stamens of *Centradenia rosea*; *A* a larger fertile one, *B* a smaller sterile one of the same flower.

connective; if they are so, they are usually attached to the connective for their whole length; or in other cases they are separated above, or free below and coherent above, in which case they may become placed at such a distance from one another that the two lobes lie in one line above the apex of the filament, as in many Labiatæ. Not unfrequently the filament also has appendages; as, for example, the membranous expansions or appendages right and left below in Allium which resemble stipules, or a hood-shaped outgrowth behind as in Asclepiadeæ, or ligular structures in front as in *Alyssum montanum*, or conical prolongations beneath on one side as in Crambe, or on both as in Mahonia (Fig. 331 *x*).

A phenomenon of great importance from a morphological point of view is the branching of stamens which occurs in many Dicotyledons, a peculiarity of structure which was erroneously confounded by the older botanists with their cohesion, although the two are fundamentally distinct. Sometimes the branching of stamens takes place, like that of foliage-leaves, bilaterally in one plane, right and left of the median line, so that the branched stamen has a pinnate appearance, as in Calothamnus (Fig. 334 *st*), where each division bears an anther. In other cases the branching takes place in a kind of polytomy, as in Ricinus (Fig. 335), where the separate stamens arise in the form of simple protuberances from the receptacle, each

one repeatedly producing new protuberances, which at length develope by intercalary growth into a compoundly and repeatedly branched filament; the ends of



FIG. 334.—Longitudinal section of the flower of Calothamnus; *f* the ovary, *s* calyx, *p* petals, *g* style, *st* branched stamens.

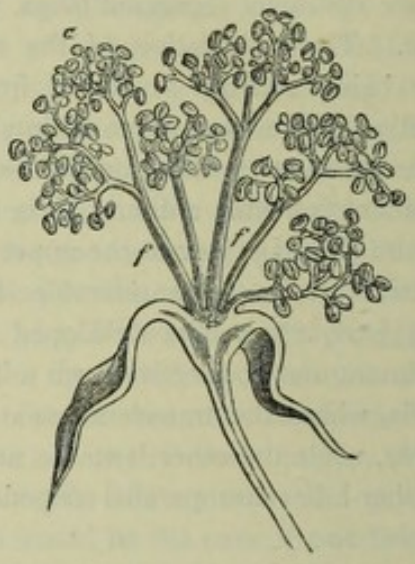

FIG. 335.—Part of a male flower of *Ricinus communis* cut through lengthways; *ff* the basal portions of the compoundly-branched stamens; *a* the anthers.

the branches all bearing anthers. In the Hypericineæ, three or five large broad protuberances (Fig. 336, *II–V*, *a*) spring from the periphery of the floral axis after the formation of the corolla, on each of which smaller roundish knobs are produced

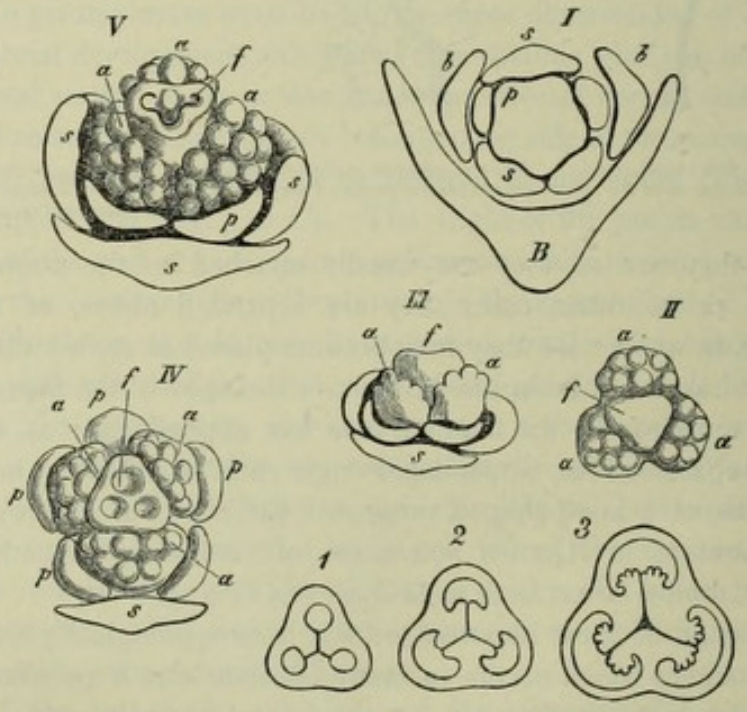

FIG. 336.—Development of the flower of *Hypericum perforatum*; *I* young flower-bud in the axil of the bract *B*, with its two bracteoles *b b*, *s* the sepals, *p* first indication of the petals; *II* middle part of a somewhat older bud, *f* rudiment of the ovary, *a*, *a*, *a* the three stamens with the rudiments of their branches arising as protuberances; *III* a flower-bud of nearly the same age as in *II*, but seen from the side, *s* a sepal, *a a* the stamens, *f* the ovary; *IV* and *V* flower-buds in further stages of development, the letters indicating the same as in *I*, *II*, and *III*; 1, 2, 3 ovary in various stages of development cut through horizontally.

in basipetal succession from its apex; these latter become the filaments, each of which eventually bears an anther, and are connected at their base with the primordial protuberance of which they are branches. A horizontal section through the flower-

bud before the opening of the flower shows, especially in *Hypericum calycinum*, the numerous filaments which spring from one original protuberance densely crowded into one bundle. In this and many similar cases the common primordial basal portion of the stamen remains very short, while the secondary filaments lengthen considerably and subsequently present the appearance of a tuft springing from the receptacle, the true nature of which can only be ascertained by the history of its development. If, on the contrary, the primordial basal portion lengthens, as in Calothamnus, the whole stamen is easily recognised as branched even in the mature condition.

Of no less importance for understanding the entire plan of structure of a flower, and especially the relations of number and position which actually occur, is the cohesion of stamens which grow side by side in a whorl. In Cucurbita, for example, there are, in the earliest stage, five stamens, but at a later period only three are found, two of which are, however, broader than the third; these are each the result of the lateral coalescence of two stamens. In this case the filaments

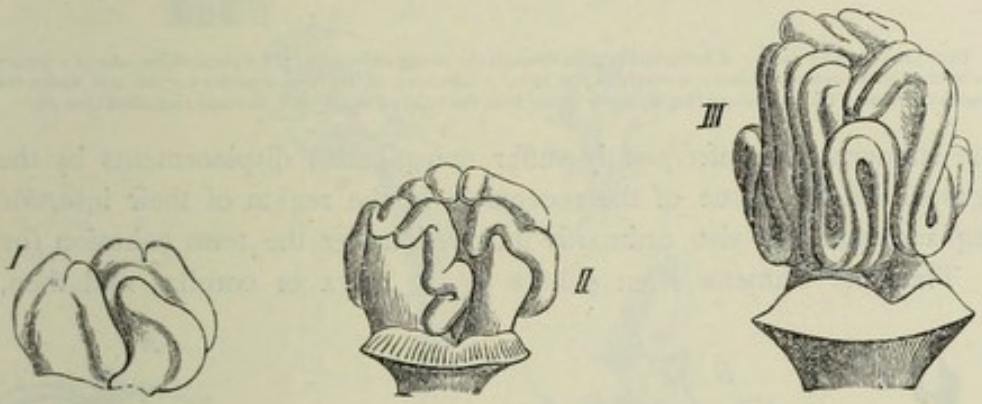

FIG. 337.—Development of the andrœcium of *Cucurbita Pepo* (after Payer); in all the figures the simple stamen is to the right, behind and to the left two double ones. The anthers grow vigorously in length and form vermiform coils.

become combined into a central column, on which (as is shown in Fig. 337, *III*) the pollen-sacs grow more rapidly in length than the filaments, forming vermiform coils.

The relationships are much more complicated and more difficult to understand when cohesion and branching of the stamens occur simultaneously, as in Malvaceæ. In *Althæa rosea*, for instance, the filaments form a membranous closed tube which completely envelopes the gynæceum; springing from this tube are five vertical and parallel double rows of long filaments, each of which (Fig. 338, *B*) again splits into two arms (*t*), and each of these arms bears a single anther-lobe. The history of development and a comparison with allied forms shows that the tube is formed by the lateral coalescence of five stamens; but the coherent margins produce double rows of lateral ramifications, in other words, of filaments, which then again split into two arms. A horizontal section of the young staminal tube (Fig. 338, *A*) shows plainly these double rows of split filaments; the part (*v*) which lies between two of these must be considered as the substance of a stamen, the margins of which each bear right and left a simple row of filaments as laciniæ or branches[1]. In

[1] The strangeness of this conception will disappear if the structure is recalled of a unilocular ovary with numerous carpels coherent at the margins, *e.g.* Viola, where the ovules arise in double rows on the lines of junction (the placentæ). What takes place in one case in the inside in reference to the ovules takes place in the other case on the outside in the formation of the filaments.

the lime, where the five primordial stamens also branch at the margins, and form anthers on their branches, the stamens remain free, but in other respects the phenomena are altogether similar (*cf.* Payer *l. c.*)

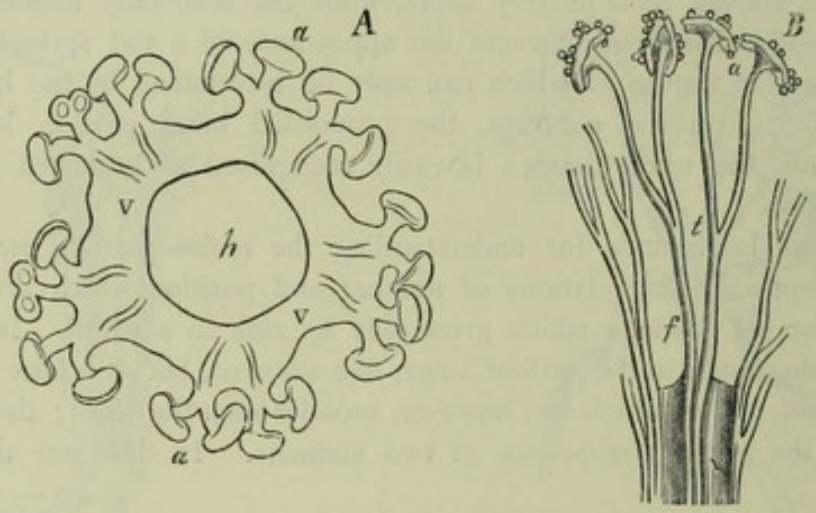

FIG. 338.—*Althæa rosea*; *A* horizontal section through the young androecium; *B* a piece of the tube of a mature androecium with several stamens; *h* cavity of the tube, *v* substance of the tube, *a* anthers, *t* the spot where the filament divides, *f* the spot where two filaments spring from the tube (*A* much more strongly magnified than *B*).

The stamens not unfrequently suffer conspicuous displacements by the intercalary growth of the tissue of the receptacle in the region of their insertion; and such displacements are also ordinarily included under the term cohesion (or adhesion)[1]. Thus the stamens often adhere to the calyx or corolla; and then, when

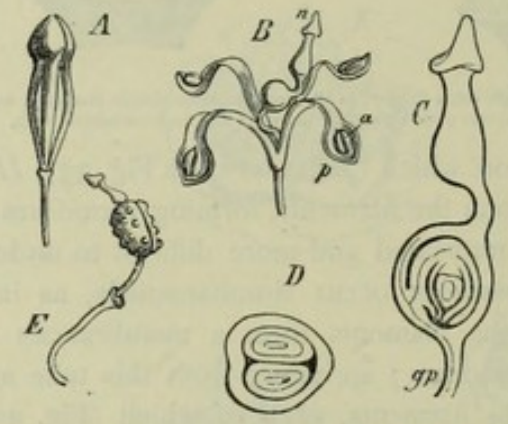

FIG. 339.—Flower of *Manglesia glabrata*; *A* before opening; *B* open; *C* the gynaeceum, *gp* the gynophore; *D* horizontal section of the ovary; *E* fruit ripening on its pedicel.

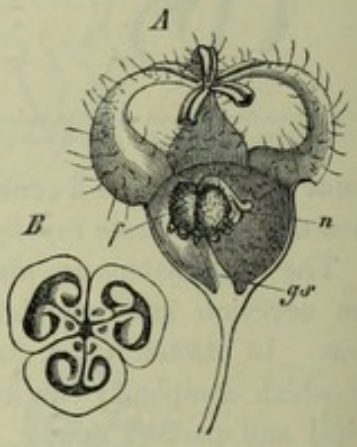

FIG. 340.—Flower of *Sterculia Balanghas*; *A*, *gs* the gynophore, *f* ovary, *n* stigma; *B* horizontal section of the ovary.

mature, the filaments appear as if they sprang from the inside of the perianth; the earliest stages of development show, however, that the perianth-leaves and the stamens spring in succession and separately from the receptacle; it is not till a later period that intercalary growth begins at the part of the receptacle from which both spring; in this manner a lamella grows up which structurally forms the basal portion of the perianth-leaf, and which at the same time bears the stamen, so that the

[1] [It has come to be the usage in English works on descriptive botany to apply the term 'cohesion' to the apparent union of organs of the same kind, 'adhesion' to the apparent union of organs of a different kind.—ED.]

appearance is presented as if the stamen sprang from the centre of its inner surface. This is shown in Fig. 339, *B*, where *p* is a perianth-leaf and *a* an anther sessile upon it; the two stand at first distinct on the young receptacle one over the other; the portion of leaf lying beneath *a* and *p* is not formed till a much later period by intercalary growth, and pushes up at the same time the true perianth-leaf *p*, and the stamen *a*. This kind of adhesion is especially frequent in those flowers whose petals have also become coherent laterally into a tube, such as Compositæ, Labiatæ, Valerianaceæ, &c. On the other hand, the stamen may also become 'adherent' in various ways to the gynæceum. In *Sterculia Balanghas* (Fig. 340) this structure is only apparent, depending simply on the small stamens, which are placed close beneath the ovary, becoming raised up together with it by the elongation of a part of the receptacle; from their small size they appear like a mere appendage of the large ovary; the part which bears both the organs, the *Gynophore*, is therefore in this case an internode of the floral axis. Much more complicated is the history

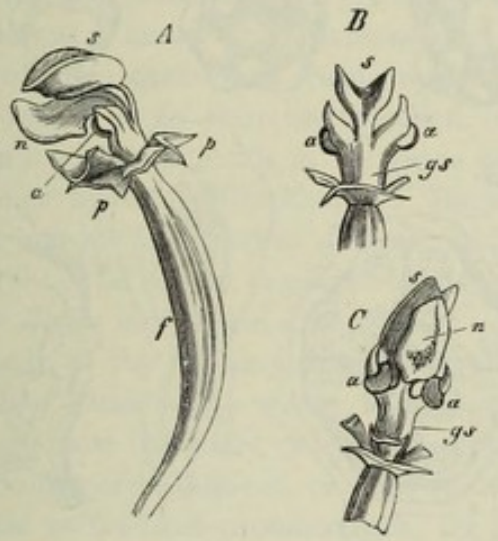

FIG. 341.—Flower of *Cypripedium Calceolus* after removal of the perianth.

of the formation of the true *Gynostemium* (column) which is formed above an inferior ovary, as in the Aristolochiaceæ, and especially in the Orchideæ, where these adhesions and displacements of the parts of the flower are also combined with abortion of certain members. Since these relationships will be explained in the sequel, the examination of Fig. 341 will suffice for the present, where the flower of Cypripedium is represented from the side (*A*), from behind (*B*), and from front (*C*), after removal of the perianth (*p p*). *f* is the inferior ovary, *gs* the gynostemium, resulting from the adhesion of three stamens—two of which (*a a*) are fertile, while the third (*s*) forms a sterile staminode—with the carpel, the anterior part of which bears the stigma (*n*). In this case the gynostemium consists entirely of coherent foliar structures, or of the basal portions of the staminal and carpellary leaves, both of which spring from the upper margin of the hollowed-out receptacle which constitutes the inferior ovary[1].

[1] Compare the account of the development and significance of the flowers of Orchideæ in the sequel.

The size and form of the stamens frequently varies within one and the same flower; thus, for instance, in the Cruciferæ there are two shorter and four longer (tetradynamous), in the Labiatæ two larger and two shorter (didynamous) stamens; in Centradenia, as was shown in Fig. 333, *A*, *B*, they are not only of different size, but are also differently segmented. A correct conception of the history of development and a comparison of the relationships of number and position in nearly allied plants enable one to apply the term stamen even to structures which have no anther and therefore want the ordinary physiological character of stamens. Thus, for example, in Geranium there are two whorls of fertile stamens, while in the nearly related genus Erodium those of one whorl are without anthers. Such sterile stamens or *Staminodes* generally undergo further metamorphosis, by which they become unlike the fertile ones and not unfrequently petaloid, as the innermost staminal leaves of

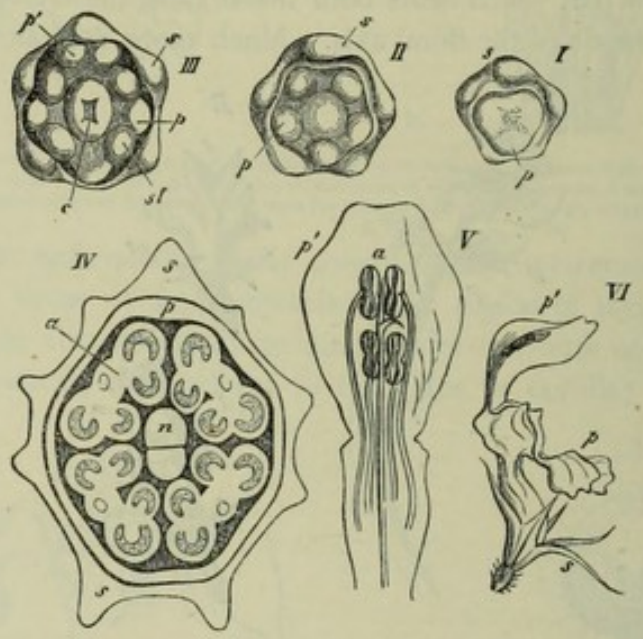

FIG. 342.—Various stages of development of the flower of *Lamium album*; *I*, *II*, *III* very young buds seen from above; in *I* the rudiments of the sepals *s* are formed, in *II* those of the petals *p*, in *III* those of the stamens *st* and of the carpels *c*; *IV* horizontal section of an older bud, *s* tube of the gamosepalous calyx, *p* that of the gamopetalous corolla; *a* anthers, *n* stigmas; *V* upper lip of the corolla with the epipetalous stamens; *VI* entire mature flower seen from the side.

Aquilegia; or assume very peculiar forms, as in Cypripedium (Fig. 341 *s*). In some Gesneraceæ a glandular structure or nectary is found in place of the posterior stamen (compare the drawing of Columnea, Fig. 385). Metamorphoses of this kind may be considered as the first steps to a condition of abortion, the final stage of which is the production of a vacancy at the spot where the stamen should be, as in the Labiatæ, an order closely allied to the Gesneraceæ, where, in the place of this staminode there is no structure whatever; instead of the five stamens to which the plan of construction of the flower points, there are only four, even the rudiment of the fifth, the posterior one, being suppressed, as is seen in Fig. 342[1]. Phenomena of this kind altogether justify the hypothesis of abortion in those cases also where

[1] [Peyritsch however (Sitzungsb. der k. Akad. der Wissen. zu Wien, 1872) infers, from the constant reversion to fours in the peloric flowers of Labiatæ, and from other considerations, that the original type of the flower is tetramerous.—ED.]

the absent organ does not disappear in the course of development, but never comes into existence at all, if the hypothesis of the suppression of the part is confirmed by a comparison of the relationships of number and position in nearly-allied plants. The hypothesis of an abortion of this kind was, however, for the first time placed on a firm basis by the theory of descent.

The number of stamens in a flower is only rarely so few as one or two; it is usually larger, and equal in number to that of the perianth-leaves, and they are then arranged in the form of rosettes, either spirally or in whorls. If the arrangement of the perianth-leaves is spiral, that of the stamens is usually the same, and the number of the latter is then very commonly large and indefinite, as in Nymphæa, Magnolia, Ranunculus, Helleborus, &c.; but in this case they are sometimes also few in number and definite.

Much more often, however, the stamens are arranged in one or more whorls, those in one whorl being then usually equal in number and alternate with those in the other whorls, and with the perianth-leaves [symmetrical flowers of English text-books]. There are, however, numerous deviations from this rule [unsymmetrical flowers of English text-books] occasioned frequently by the abortion of particular members or of whole whorls, or by their multiplcation, or by the superposition of consecutive whorls; and not unfrequently in the place of a single stamen two or even more will arise side by side (*dédoublement*). These phenomena, which are often difficult to make out, are nevertheless of great value in the determination of natural affinities, and will be still further examined in the sequel.

Development of the Pollen and of the Anther-wall[1]. The description given in this place will apply only to the ordinary cases in which the pollen is formed in separate grains in the four loculi of the anther, and falls out of the anther after it has opened; some of the more important exceptions will be mentioned hereafter.

Immediately after the perianth-leaves, or their innermost whorl, first become visible on the receptacle as roundish protuberances, the rudiments of the stamens make their appearance in a similar manner, but usually obtain a considerable start in growth of the corolla, which not unfrequently remains for a considerable time in a very rudimentary condition. The form of the stamen, which consists of homogeneous primary meristem, very soon shows the outlines of the two anther-lobes united by the connective; the filament is still very short, subsequently it also grows slowly, and it is only just before the expansion of the flower that it elongates very rapidly by vigorous intercalary growth. When the four pollen-sacs make their appearance externally on the young anthers as longitudinal protuberances, a layer of cells becomes differentiated in the direction of their length[2], through

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[1] Nägeli, Zur Entwickelungsgeschichte des Pollens; Zürich 1842.—Hofmeister, Neue Beiträge zur Kenntniss der Embryobildung der Phanerogamen, II. Monocotyledonen.

[2] I am indebted to a letter from Dr. Warming for the following account of the first origin of the mother-cells of the pollen:—'The mother-cells of the pollen originate by the division of the cells of the outermost or sub-epidermal layer of the periblem from one to three times by tangential walls, the outermost of the cells which are thus formed being also divided by radial walls. In those plants which have been more minutely examined (Hyoscyamus, Datura, Cyclanthera, Euphorbia) the innermost layer of these cells becomes immediately converted into the primary mother-cells of the pollen, the inner of the layers which lie between them and the epidermis becoming absorbed,

a stronger growth and slower production of divisions, which are formed more rapidly in the surrounding meristem. This layer consists of the primary mother-

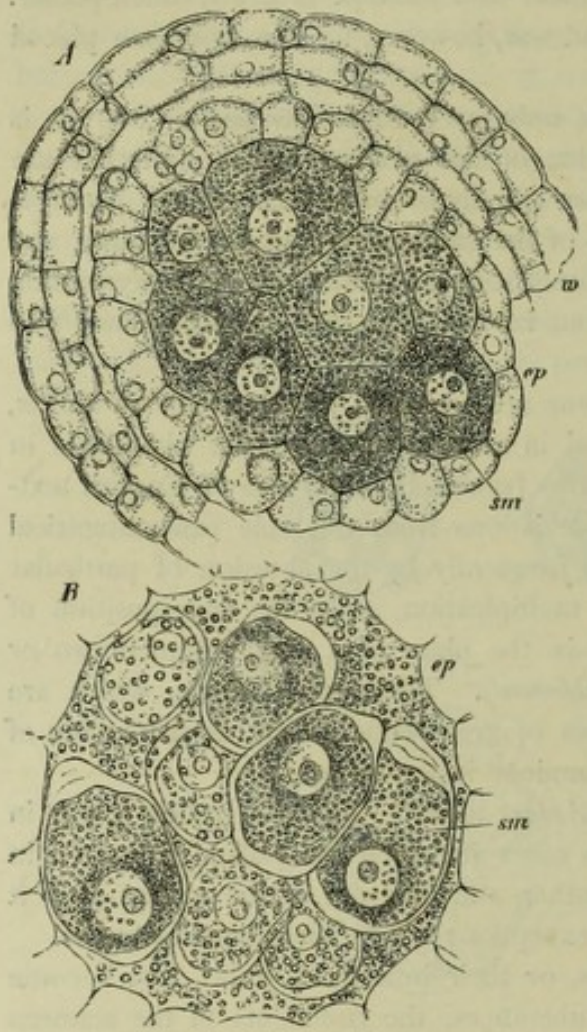

FIG. 343.—*Funkia cordata*; *A* transverse section through a young pollen-sac before the isolation of the mother-cells *sm*, *ep* the epithelium which clothes the anther-lobe, *w* wall of the pollen-sac; *B* the anther-lobe after isolation of the mother-cells *sm*; *ep* indication of the epithelium (× 500).

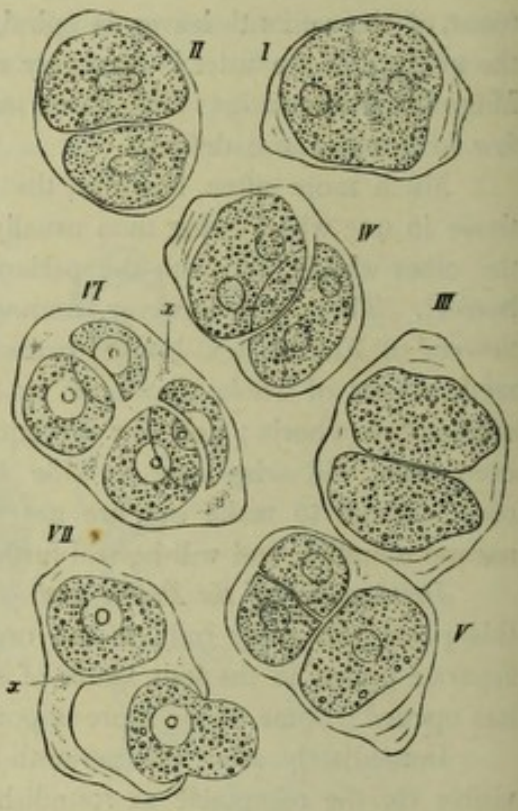

FIG. 344.—Mode of formation of the pollen of *Funkia ovata* (× 550). In *VII* the wall of the daughter-cell has absorbed water till it has burst; its protoplasm is forcing itself out through the fissure, and is lying before it rounded off into a spherical form.

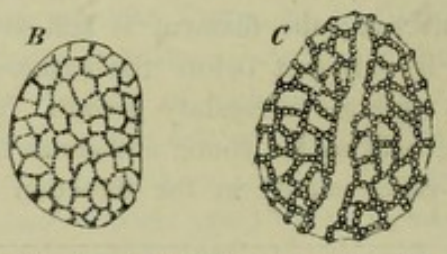

FIG. 345.—*B* a young pollen-cell of *Funkia ovata*; the thickenings which project outwardly are still small, in the older pollen-cell *C* they are larger; they are arranged in lines connected into a net-work.

cells of the pollen, which produce, by a few further divisions, a longish assemblage of mother-cells united into a tissue (Fig. 343, *A*, *sm*; Fig. 346, *m*); the whole large-celled mass being surrounded on the outside by a small-celled tissue consisting of

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so that usually only one layer remains; and this, together with the epidermis, forms the wall of the anther.'

several layers, the future wall of the pollen-sac (Fig. 343, *A*). The innermost layer, which is continued round the whole mass of mother-cells, is transformed at an early

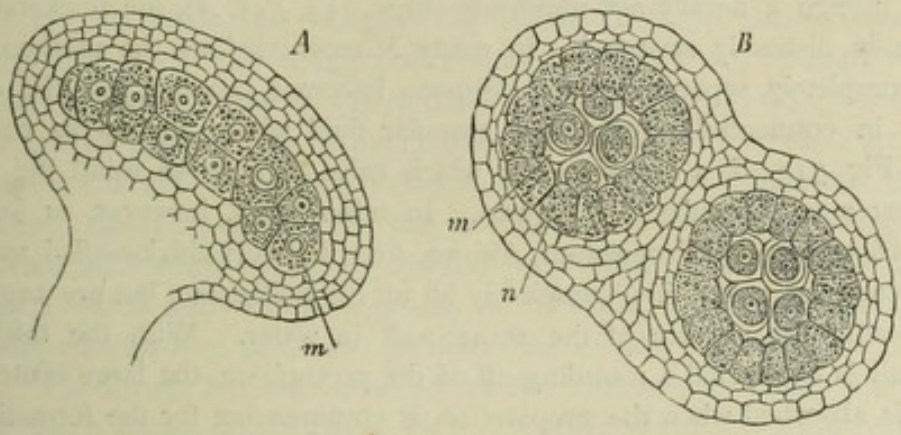

FIG 346.—*A* pollen-sac of *Althæa rosea* seen from the side; *B* transverse section of an anther-lobe showing the two pollen-sacs, *m* the mother-cells of the pollen, in *A* still united into a tissue, in *B* already divided each into four pollen-cells, *n* the epithelium of the pollen-sac. Each anther-lobe, consisting of two pollen-sacs, is here borne on a long branch of the filament.

period into a delicate thin-walled epithelium (*ep*) filled with coarse-grained protoplasm, the cells of which usually divide radially and elongate, but are afterwards destroyed

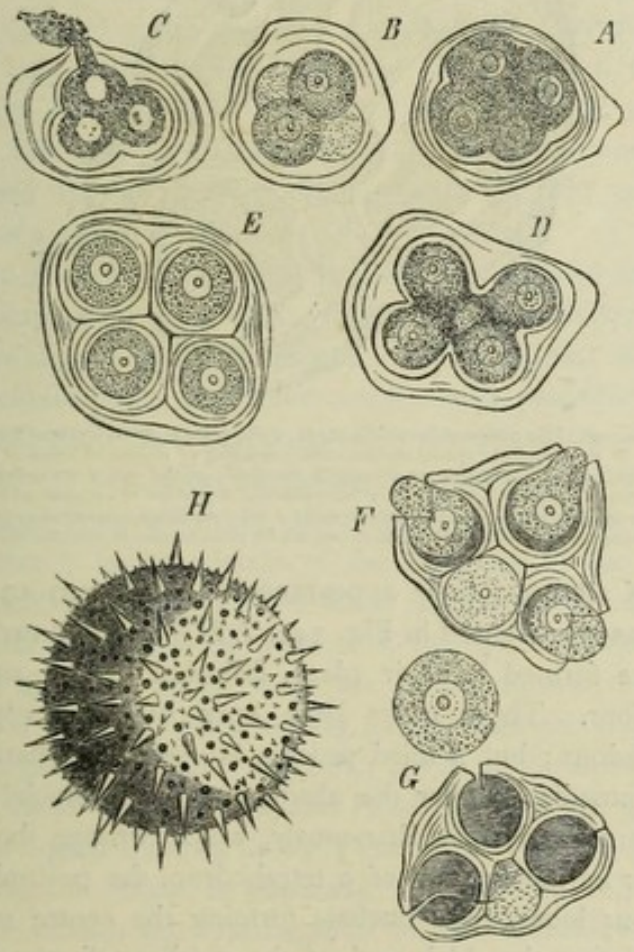

FIG. 347.—*Althæa rosea*; *A—E* division of the mother-cells of the pollen into four; *F* and *G* a tetrahedron, the walls of whose special mother-cells have burst under the influence of water, and have allowed the protoplasmic body of the young pollen-cells to escape; *H* a mature pollen-grain seen from without magnified to the same extent (*cf.* Fig. 11, p. 14).

like the inner layer of cells in the sporangium of Vascular Cryptogams. The development of the outer cell-layers which subsequently cause the rupture of the wall

does not take place till a much later period. The mother-cells of the pollen are at first large and their walls thin (Fig. 343, *A*, *sm*); but these increase considerably in thickness, though generally not uniformly (Figs. 344, 347, *A*), the thickening matter being usually distinctly stratified. In many Monocotyledons the mother-cells now become completely separated, the pollen-sac becomes broader, and the cells float singly or in connected groups in a granular fluid which fills up its cavity, as is shown in Fig. 343, *B*, a phenomenon which calls strongly to mind the formation of the spores of Vascular Cryptogams. In other cases, however, as for instance in many Dicotyledons (Tropæolum, Althæa, &c.), the very thick-walled mother-cells do not become isolated; they completely fill up the pollen-sac, but are usually found separated after the rupture of the anther-wall in water. With the thickening of the cell-wall is connected a rounding-off of the protoplasm, the large central nucleus of which is absorbed when the preparation is commencing for the formation of the pollen-cells. Instead of the nucleus which has disappeared by absorption, either two

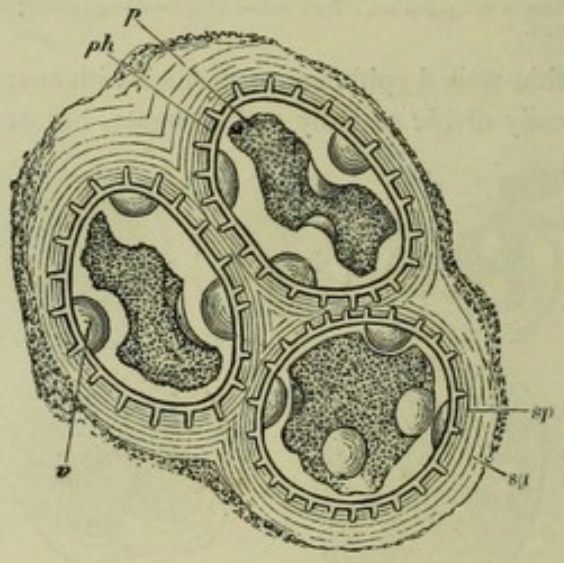

FIG. 348.—Mother-cell of the pollen of *Cucurbita Pepo*: *sg* the outer common layers of the mother-cell in the ac of being absorbed; *sp* the so-called 'special mother-cells,' consisting of masses of layers of the mother-cell which surround the young pollen-cells; they also are afterwards absorbed; *ph* the wall of the pollen-cell; its spines grow outwards and penetrate the special mother-cell; *v* hemispherical deposition of cellulose on the inside of the pollen cell-wall, from which the pollen-tube is afterwards formed; *p* the protoplasm contracted (×550). (The preparation was obtained by making a section of an anther which had lain for some months in absolute alcohol.)

fresh nuclei first of all make their appearance and undergo an immediate simultaneous bipartition (as represented in Fig. 344, *I*, *II*), or these two are again absorbed and four nuclei are formed in their place, followed by the simultaneous division of the cell into four. These cases have been observed especially in Liliaceæ among Monocotyledons; but a third process is especially characteristic of Dicotyledons, in which, immediately after the absorption of the nuclei of the mother-cell, four fresh nuclei are formed simultaneously, which arrange themselves at different points of a plane or in the corners of a tetrahedron, the protoplasm becoming then constricted into four lobes, each nucleus forming the centre of one of the lobes. During this constriction the thick wall of the mother-cell grows inwards, following the constriction of the protoplasm, until at length the four lumps of protoplasm which have become rounded off during the division lie quite distinct in four cavities of the mother-cell (Fig. 347, *A*–*E*). The mass of cellulose now becomes differentiated round each of the daughter-cells of the tetrahedron into concentric systems

of layers (the so-called 'special mother-cells'), and these are again enveloped by layers which are common to the whole tetrahedron (Figs. 347 *E*, 348). If the tetrahedra have lain for some time in water, the masses of layers usually burst, and the protoplasmic contents of the young pollen-cells are forced out through the fissure, and become rounded off into a sphere (Figs. 344 *VII*; 347 *F*, *G*). Soon after the conversion of the mother-cells of the pollen into a tetrahedron, each protoplasmic mass becomes clothed with a new cell-wall, at first very thin and not continuous with the inner layers of the wall of the mother-cell, as is shown by its becoming detached from them when caused to contract by alcohol. This is the true cell-wall of the pollen, which now increases greatly in thickness, and becomes differentiated into an outer cuticularised layer and an inner one of pure cellulose, the *Extine* and the *Intine*. The former becomes covered on the outside with spines (Fig. 348, *ph*), warts (Fig. 345), ridges, combs, &c.; while the latter frequently forms considerable thickenings which project inwards at particular spots (Fig. 348, *v*), and at a later period are employed to form the pollen-tube. During these processes the masses of layers forming the envelope of the tetrahedron become slowly absorbed, their substance is converted into mucilage, and they at length entirely lose their form; their disorganisation may commence either on the inner (as in Fig. 344, *VII*, *x*) or outer side (Fig. 348, *sg*) of the wall of the mother-cell. By the absorption of the chamber in which the young pollen-cells have hitherto been enclosed, they now become free, separate, and float in the granular fluid which fills up the cavity of the anther; and within this they now attain their definite development and size. The fluid being thus used up, the mature pollen-grains finally fill up the cavity of the anther in the form of a powdery mass.

The ripe pollen-grain of Angiosperms[1] does not undergo any further divisions, like that of Gymnosperms; it remains unicellular; the pollen-tube is developed immediately on the stigma as a protuberance of the intine, which perforates the extine at certain definite spots that have usually been prepared beforehand. The spots where this perforation takes place are often more than one, or even very numerous (Fig. 349 *a*, 350 *o*); yet, notwithstanding the possibility of the formation of this number of pollen-tubes from one grain, only one usually grows to an extent sufficient to effect impregnation. Independently of the sculpture of the extine itself which has already been mentioned, the external form and structure of the outer coat of pollen-grains depends chiefly on the number of the spots at which the perforation takes place, on the mode in which these are arranged, and on the circumstance whether the extine is at these spots merely thinner and the intine projects in the form of a wart (Fig. 349), or whether roundish pieces of the extine become detached in the form of a lid, as in Cucurbitaceæ and Passiflora (Fig. 37, p. 33), or whether it splits into bands by spiral fissures, as in Thunbergia (Fig. 38, p. 34), &c. At the points of perforation the intine is generally thicker, often forming hemispherical protuberances which furnish the first material for the formation of the pollen-tube (Fig. 350, *i*), or the extine only forms thinner longitudinal striæ which fold inwards

[1] For more minute details see Schacht, Jahrb. für wissensch. Bot. II, p. 109, and Luerssen, ibid. VII, p. 34.—[Fritzsche, Beiträge, zur Kenntniss des Pollen, Berlin, 1832.—Mohl, Beiträge zur Anatomie u. Physiologie der Gewächse, 1st Heft, Bern, 1834.]

when the pollen-grain becomes dry (as in Gladiolus, Yucca, Helleborus, &c.). Very commonly however the intine is uniformly and continuously thickened, as in Canna, Strelitzia, Musa, Persea, &c.; and in this case, according to Schacht, no definite spots are prepared beforehand where the perforation is to take place. The number of these peculiarly organised points of perforation is definite in each species, often in whole genera and families; there is only one in most Monocotyledons and a few Dicotyledons, two in Ficus, Justicia, &c., three in the Onagrarieæ, Proteaceæ, Cupuliferæ, Geraniaceæ, Compositæ, and Borragineæ; four to six in Impatiens, Astrapæa, Alnus, and Carpinus, while the number is large in Convolvulaceæ, Malvaceæ, Alsineæ, &c. (see Schacht, *l.c.*). The extine is rarely smooth, more often marked

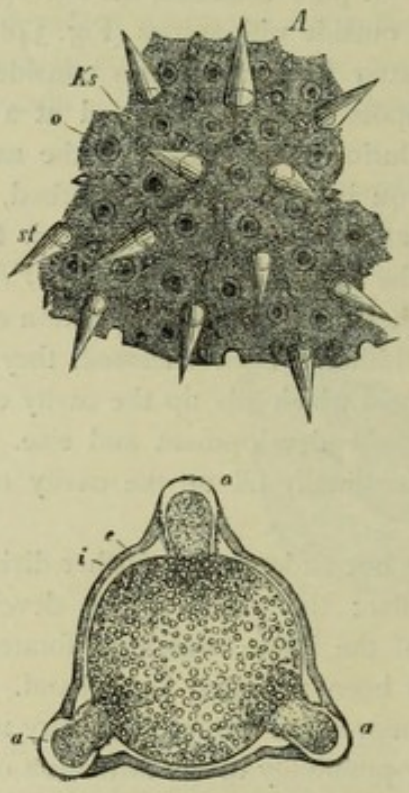

FIG. 349.—Transverse section of a pollen-grain of *Epilobium angustifolium*: *a* the points where the intine *i* protrudes, the intine being there thicker and the extine *e* thinner (× 500).

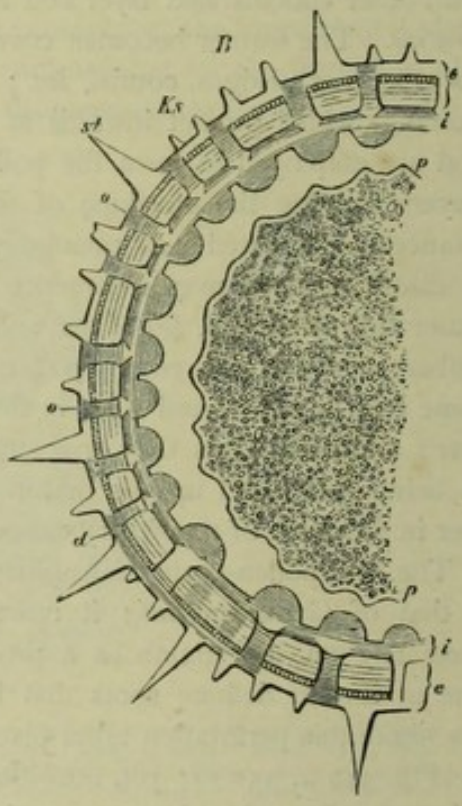

FIG. 350.—Pollen-grain of *Althæa rosea*: *A* a piece of the extine seen from without; *B* the half of a very thin section through the middle of the pollen-grain, *st* large spines, *Ks* small spine of the extine, *o* perforations through the extine *e*, *i* the intine, *p* the protoplasm of the pollen-grain contracted (× 800).

on the outside by the sculpture to which reference has already been made. When it is very thick, layers of different structure and texture may frequently be detected, and differentiations sometimes occur in a radial direction, penetrating the thickness of the extine (Fig. 350), and giving it in some cases the appearance of consisting of rod-shaped prismatic pieces or of honeycomb-like lamellæ, &c. These peculiarities of structure recall those of the exospore of Marsileaceæ, and probably only depend, as in that case, on a further development of the radial striation, accompanied possibly by subsequent absorption of the soft areolæ and hardening of the denser parts (see p. 30). The contents of the ripe pollen-grain, the *Fovilla*[1] of the older

[1] [On the constitution of the 'amyloid corpuscles' in the fovilla of pollen see Saccardo, Nuovo Giornale Botanico Italiano, 1872, p. 241.—ED.]

botanists, usually consists of a dense coarse-grained protoplasm in which grains of starch and drops of oil may be recognized. When the grain bursts in water, the fovilla escapes in masses connected by mucilage and often in long vermiform threads. The surface of the extine is commonly found coated with a yellow oil, or of some other colour, often in evident drops, which renders the pollen viscid and adapted to be carried by insects from flower to flower; in only a comparatively few cases is it quite dry and powdery, as in Urticaceæ and many Grasses, where it is projected with violence from the anthers or simply falls out.

At the time when the pollen-grains are nearly mature, and the flower-bud is preparing to open, the wall of the pollen-sacs undergoes a further development[1]. The outer layer of cells or epidermis always remains smooth-walled (see Fig. 351, p. 489); the inner layers or endothecium are also smooth if the anther does not dehisce. If on the other hand it opens by recurved valves (Fig. 331 *k*, p. 475), the cells of the innermost layers only of these valves are provided with thickening-bands (or are fibrous); while, when the pollen-sacs dehisce longitudinally, the whole of their endothecium contains fibrous cells. There is usually only one such layer, sometimes several; in *Agave americana* as many as from eight to twelve. The thickening-bands of the fibrous cells which project inwards are usually wanting on their outer wall; on the side-walls they are generally vertical to the surface of the pollen-sac; on the inner wall they run transversely and are united in a reticulate or stellate manner. Since the epidermal cells contract more strongly when the ripe anther-walls dry up than those of the endothecium which are provided with thickening-bands, they exert a force which has a tendency to make the anther-wall bulge outwards and give way at its weakest point. The modes in which the anthers open are very various, and are always intimately connected with the other contrivances which are met with in the flower for the purpose of pollination with or without the agency of insects. Sometimes only a short fissure (pore) is formed at the apex of each anther-lobe, as in Solanum, Ericaceæ (Fig. 332, p. 475), &c., through which the pollen of both the contiguous pollen-sacs escapes; but more commonly the wall gives way in the furrow between the two sacs (the suture) along its whole length, the tissue which separates them becoming at the same time more or less destroyed, and thus both pollen-sacs dehiscing at the same time by the longitudinal fissure (Fig. 351). It is this phenomenon that has given rise to the erroneous description of these anthers as being bilocular; but if nomenclature is to have a scientific basis, they must be termed quadrilocular, in contrast to the really bilocular anthers of Asclepiadeæ and the octilocular ones of many Mimoseæ. Sometimes again the anther-lobes open at the apex by a pore which results simply from the destruction of a small portion of tissue at this spot (Hofmeister). In other respects we still want a detailed and comparative investigation of these processes, which are very various and of great physiological importance; only the additional remark need be made here, that it is very important from a systematic point of view whether the anthers open inwards towards the gynæceum (introrse), or outwards (extrorse), the difference depending on the position of the suture and hence on that of the pollen-sacs on the inner or outer side of the filament.

[1] Compare H. v. Mohl, Vermischte Schriften, p. 62.

In several families of Monocotyledons and Dicotyledons more or less considerable deviations[1] occur from the course of development of the pollen and from its final structure which has been here described. Naias and Zostera deviate only to this extent, that no thickening of the wall of the mother-cells takes place, and that the pollen-cells themselves are very thin-walled, acquiring in Zostera a very strange appearance from assuming, instead of the ordinary rounded form, that of long thin tubes lying parallel to one another in the anther. The deviations are more considerable in the formation of compound pollen-grains. The origin of these is either that only the four daughter-cells (pollen-cells) of one mother-cell remain more or less closely united, like the pollen-tetrahedra (four-fold grains) of some Orchideæ, Fourcroya, Typha, Anona, Rhododendron, &c.; or the whole contents of one primary mother-cell remains unseparated and forms a mass of pollen consisting of eight, twelve, sixteen, thirty-two, or sixty-four connected pollen-cells, as in many Mimoseæ and Acacieæ[2]. In these cases the cuticle or extine is more strongly developed on the outer surface of the daughter-cells lying at the circumference of the mass, and covers the whole as a continuous skin; while only thin ridges of the cuticle project from this skin inwards between the separate cells. In the various sections of Orchideæ every gradation occurs from the ordinary separate pollen-grains of Cypripedium, through the four-fold grains of Neottia, to the Ophrydeæ, where all the pollen-grains which are formed from each primary mother-cell remain united, and thus a number of pollen-masses lie in one pollen-sac; and finally to the *Pollinia* of the Cerorchideæ, where all the pollen-grains of a pollen-sac remain united into a cellular mass. In this case, as in the Asclepiadeæ with only bilocular anthers, where the grains of each pollen-sac are firmly united by a waxy substance, it is obvious that the pollen cannot be dispersed, nor can the pollen-masses fall out spontaneously from the anthers; but the flower is provided with very peculiar contrivances by means of which insects in search of honey extract from the pollen-sac the pollinia or the masses of pollen which are glued together, and again get rid of them on to the stigmas of other flowers of the same species (see Book III on Sexual Reproduction).

The Female Sexual Apparatus or *Gynæceum*[3] of the flowers of Angiosperms consists of one or more closed chambers in which the ovules are formed; the lower, hollow, swollen part of each separate seed-chamber which encloses the ovules is called the *Ovary;* the place or the mass of tissue from which the ovules spring directly into the ovary is a *Placenta.* Above the ovary the seed-vessel narrows into one or more thin stalk-like structures or *Styles,* which bear the *Stigmas;* these are glandular swellings or expansions of various forms which retain the pollen that is carried to them, and by means of the moisture which is excreted from them induce the emission of the pollen-tubes.

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[1] In reference to what follows compare Hofmeister, Neue Beiträge, pt. II. (Abhand. der könig. Sächs. Gesellsch. VII); also Reichenbach, De pollinis orchidearum genesi, Leipzig 1852; and Rosanoff, Ueber den Pollen der Mimosen (Jahrb. für wissensch. Bot. VI, p. 441).

[2] In many Mimoseæ the anther is, according to Rosanoff, octilocular, two pairs of small loculi being formed in each anther-lobe; the pollen-cells of each pollen-sac remain united into a mass.

[3] Compare with this Payer's view (Organogénie de la fleur, p. 725), which differs in some essential points.

The Gynæceum is always the final structure of the flower. When the floral axis has attained a sufficient length, the gynæceum is formed at its apex; if the axis is flat, disc-like, or expanded, it stands in the centre of the flower; if it is hollowed out or cup-shaped, the gynæceum is placed at the bottom of the hollow, in the centre of which lies the apical point of the floral axis. In the diagram of the flower, Figs. 351 *I*, and 353 *B*, where each outer circle represents a lower transverse section, and each inner circle a higher one, the gynæceum necessarily appears always as the innermost central structure of the flower, the longitudinal displacements on the floral axis being neglected in the construction of the diagram.

When the axial part of the flower, the *Receptacle* or Torus, is so elevated in the

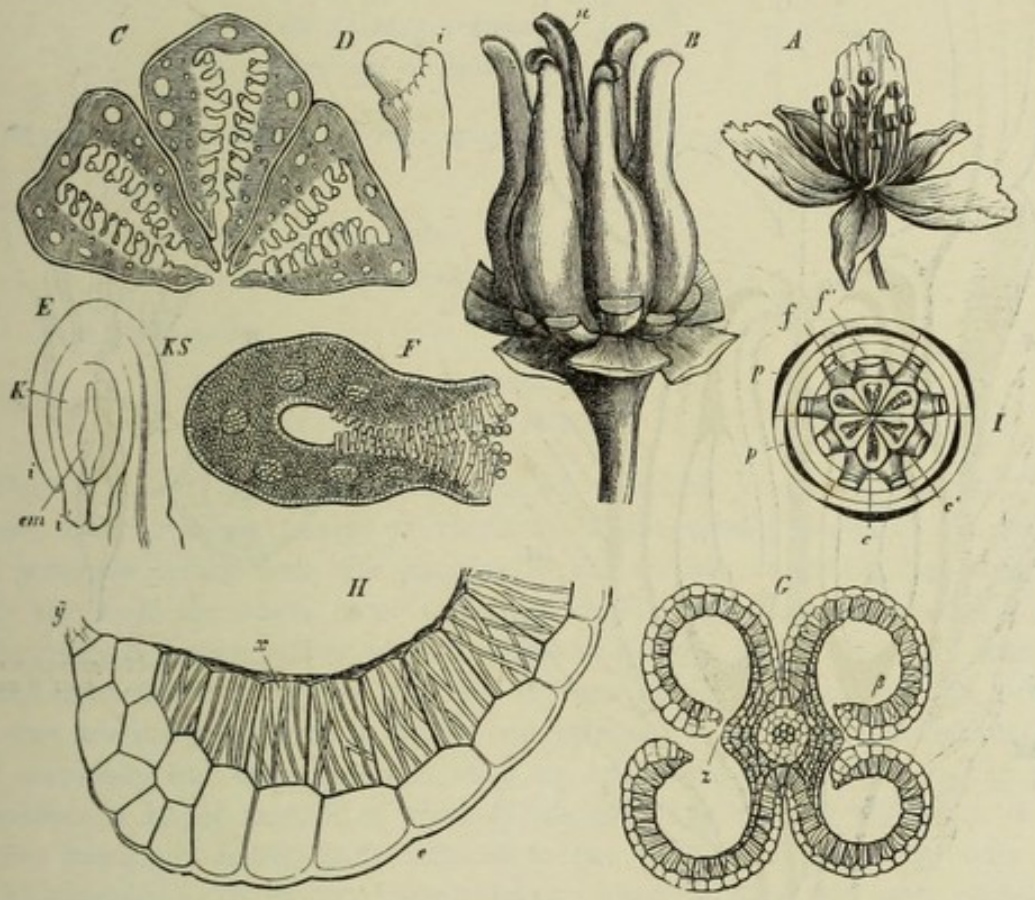

FIG. 351.—*Butomus umbellatus*: *A* flower (natural size); *B* the gynæceum (magnified), the perianth and stamens removed, *n* the stigmas; *C* horizontal section through three of the monocarpellary ovaries, each carpel bearing on its inside a number of ovules; *D* a young ovule; *E* an ovule immediately before fertilisation, *i i* the integuments, *K* the nucleus, *KS* the raphe, *em* the embryo-sac; *F* horizontal section through the stigmatic portion of a carpel (strongly magnified), pollen-grains attached to the stigmatic hairs; *G* horizontal section of a quadrilocular anther, but the valves *z* are so separated at β that it then appears bilocular; *H* part of an anther-lobe (corresponding to β in *G*), *y* the point where it has become detached from the connective, *e* the epidermis, *x* the fibrous layer of cells (endothecium); *I* diagram of the entire flower; the perianth *p p* consists of two alternate whorls of three leaves, as also does the androecium, but the stamens of the outer whorl *f* are double, those of the inner whorl *f'* simple and thicker; the gynæceum also consists of two whorls of three carpels, an outer *c* and an inner whorl *c'*; there are therefore six alternate whorls of three, the members of the first staminal whorl being doubled.

centre that the base of the gynæceum lies evidently above the stamens, or at least in the middle of the androecium, the perianth and the androecium, or even the whole flower, is said to be *hypogynous* (Fig. 351). When, on the contrary, the receptacle is hollowed out like a cup or saucer, bearing the perianth and stamens on its annular margin, while the gynæceum springs from the bottom (Fig. 353 *A*), the flower is said to be *perigynous*. It is obvious that intermediate forms are possible between extreme cases of hypogynous and perigynous flowers; and these are in fact

common, especially among Rosifloræ. In both these forms of flower the gynæceum is free, the receptacle taking no part in the formation of the wall of the ovary, although this appears to be the case externally in some perigynous flowers, as Pyrus and Rosa. The flower finally is *epigynous* when it possesses an actually inferior ovary. This latter is distinguished from the ovary which is buried in the receptacle of perigynous flowers by its wall being formed of the receptacle itself hollowed out into the form of a cup or even of a long tube. The carpels, which in the case of the free superior ovary form its whole wall, spring in the inferior ovary

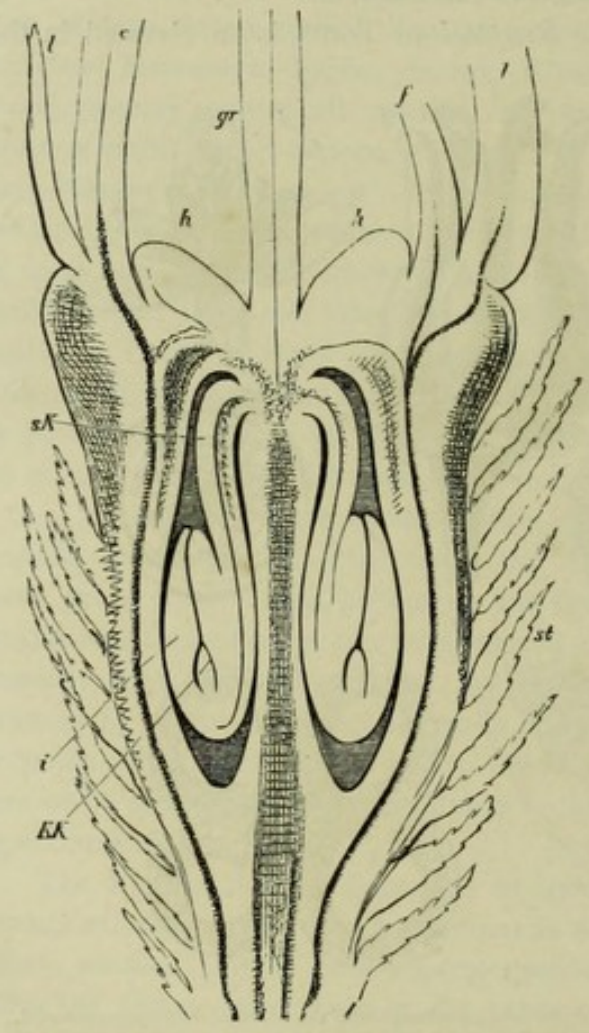

FIG. 352.—Longitudinal section through the inferior ovary of *Eryngium campestre*; *l* sepals, *c* petals, *f* filament, *gr* style, *h* disc, *K K'* nucleus of the ovule, *i* integument.

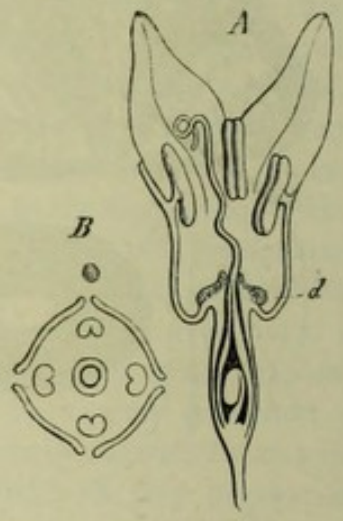

FIG. 353.—Flower of *Elæagnus fusca* *A* longitudinal section, *d* disc; *B* diagram.

(like the perianth and the andrœcium) from the margin of the hollow receptacle, and only close up the cavity above, where they are prolonged into the style and bear the stigmas (Fig. 352). Intermediate forms are also not uncommon between the superior ovary of hypogynous and the inferior ovary of epigynous flowers; the ovary may, for example, be composed in its lower half of the receptacle, in its upper part of the coherent carpels; transitional forms of this kind are found especially among Saxifragaceæ.

It will be easier to understand the different forms of the gynæceum if the more important ones are considered separately; and for this purpose the following classification may be made:—

I. **Gynæceum Superior;** flower hypogynous or perigynous.

A. Ovules attached to the carpels.

a. Ovary monocarpellary;

(α) flower with one ovary,
(β) flower with two or more ovaries.

b. Ovary polycarpellary;

(γ) ovary unilocular,
(δ) ovary multilocular.

B. Ovules attached to the floral axis;

(ϵ) ovule solitary, terminal,
(ζ) ovules one or more, lateral.

II. **Gynæceum Inferior;** flower epigynous.

C. Ovules parietal;

(η) ovary unilocular,
(θ) ovary multilocular.

D. Ovules axile;

(ι) ovule solitary, terminal,
(κ) ovules one or more, lateral.

The *Superior Gynæceum* is constructed essentially from a peculiar foliar structure, the carpellary leaves or carpels. These usually produce the ovules, which generally spring from the margins of the carpels, as in Fig. 354, but frequently also from the whole inner surface, as in Fig. 327 *F* (p. 467), and Fig. 351 *C*. The ovary is *monocarpellary* when it consists of only a single carpel, the margins of which are coherent, so that the mid-rib runs along its back, and the ovules, when they are marginal, form a double row opposite to it. The inflexed margins of the carpellary leaf may, however, swell up into thick placentæ (as in Fig. 355) and produce a larger number of rows of ovules. The number of ovules is, on the other hand, not unfrequently reduced to two (as in Amygdalus), or only one (*e.g.* Ranunculus). In monocarpellary flowers there is only one such carpellary leaf, as in Figs. 353, 354; in polycarpellary flowers there may be two, three, or more, or even a very large number: if the number is two, three, or five, they usually stand in a whorl; if four, six, or ten, they are generally arranged in two alternating whorls (see Fig. 351, *B*, *I*). When the number of monocarpellary ovaries in a flower is considerable, as in Ranunculaceæ, Magnolia, &c., the part of the axis which bears them is commonly elongated (to a very considerable extent for example in Myosurus), and their arrangement is then spiral. The monocarpellary ovary is originally always unilocular, though it may subsequently become multilocular from the production of ridges by the luxuriant growth of the inside of the carpel, which divide the cavity longitudinally into compartments, as in Astragalus, or transversely, as in *Cassia fistula*. Ovaries of this kind may be distinguished as monocarpellary with spurious loculi, but ought not to be called polycarpellary.

A *polycarpellary* ovary is always the result of the union of all the carpels of a flower, the number being usually two, three, four, or five, arranged in one whorl, and the floral axis terminating in the midst of them. If the separate carpels remain open, and cohere in such a manner that the right margin of one unites with the left margin of another, the result is a *unilocular* polycarpellary ovary. The placentation

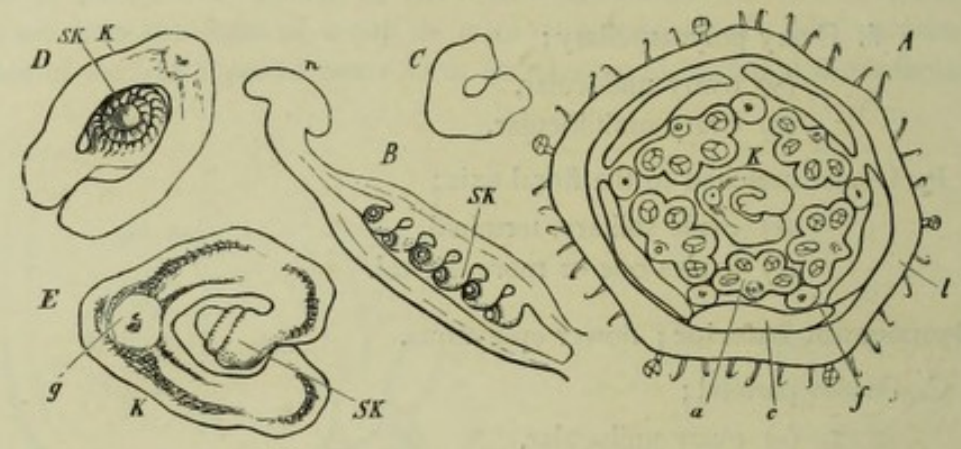

FIG. 354.—*Phaseolus vulgaris*; *A* horizontal section through the flower-bud, *l* calyx-tube, *c* corolla, *f* filaments of the outer, *a* anthers of the inner staminal whorl, *K* carpel; *B* longitudinal section of the carpel, with the ovules *SK* and stigma *n*; *C*, *D*, *E* horizontal sections of carpels of different ages, *SK* the parietal ovules, *g* mid-rib of the carpel.

is in this case parietal when the coherent margins project only slightly inwards, as in Reseda, Viola, &c. But if the coherent margins of the carpels project further inwards, the cavity of the ovary becomes imperfectly multilocular, the chambers being connected with one another in the centre, as in Papaver, where the imperfect dissepiments are covered on both sides by a number of ovules. A *bi-* or *multilocular*

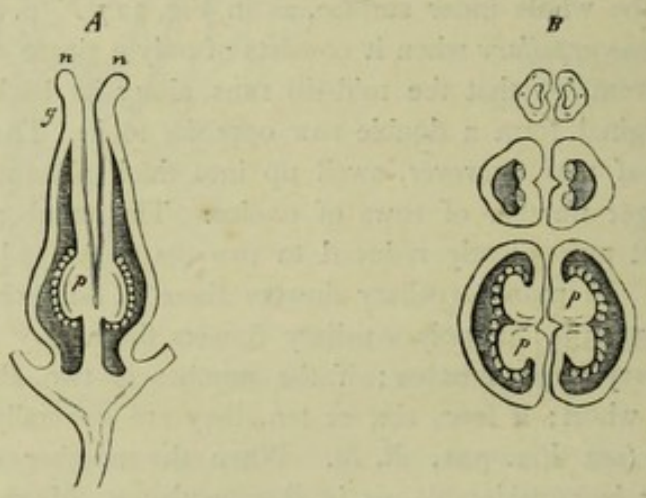

FIG. 355.—Gynæceum of *Saxifraga cordifolia*; *A* longitudinal section, *g* style, *n* stigma; *B* horizontal section at different heights, *p* placenta.

polycarpellary ovary results when the margins of the carpels project inwardly so far that they meet or cohere either in the axis or periphery of the ovary, the elongation of the floral axis in the centre frequently contributing to this result. The mode of cohesion of the carpels in multilocular ovaries may vary greatly in other respects, according as it takes place along the whole length of their inflexed margins, or only below, while the upper parts resemble a whorl of monocarpellary

ovaries (Figs. 355—358). Since the margins of the carpels which meet in the centre become developed into the placentæ, the ovules make their appearance in the central angles of the loculi, as is seen in Fig. 357; but very commonly the margins of the carpels which turn in as far as the centre then split into two

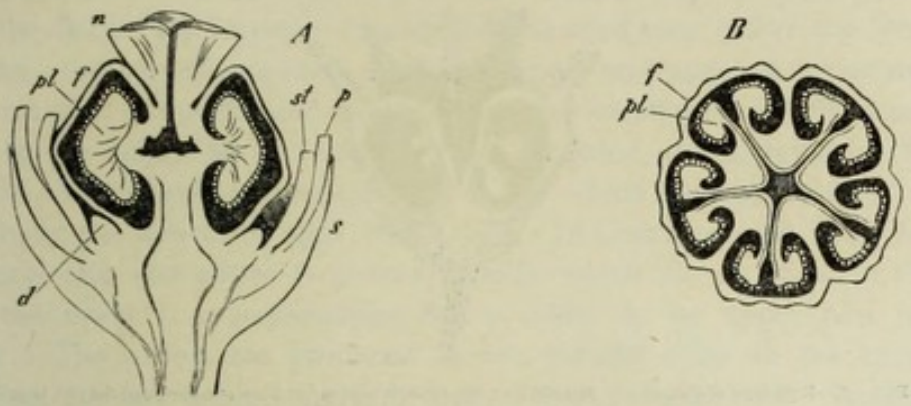

FIG. 356.—Gynæceum of *Pyrola umbellata*; *A* longitudinal section, *s* sepals, *p* petals, *st* filaments, *f* ovary, *n* stigma, *d* nectar-glands; *B* horizontal section through the ovary, *f* the wall, *pl* placentæ.

lamellæ which are bent back and swell out into placentæ in the middle of the loculi, as is shown in Fig. 356. It is clear that in this case the two placentæ within

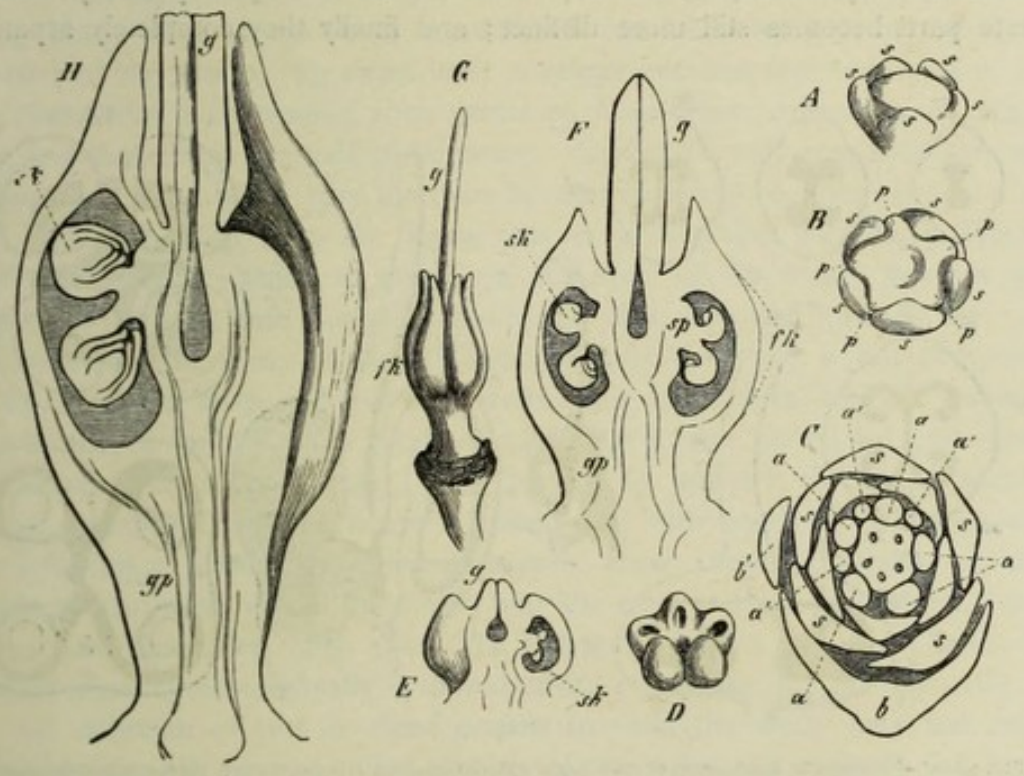

FIG. 357.—*Dictamnus Fraxinella*; *A* young flower-bud, with rudiments of sepals *s*; *B* older flower-bud, with rudiments of petals *p*; *C* still older state, with rudiments of the five stamens *a*, five more stamens *a'* arise between them, of which three are already visible; *b* the bract, *b'* a bracteole; *D—H* development of the ovary *fk*, *sk* ovules, *gp* gynophore, *g* style.

each loculus correspond to the margins of the same carpel which forms the outer wall of the loculus.

Spurious dissepiments may arise in polycarpellary as in monocarpellary ovaries; if the polycarpellary ovary consists of two loculi, it may thus become quadrilocular, or five original loculi may become divided into ten. The first case is universal in

Labiatæ and Borragineæ. Fig. 359 shows that the ovary is formed of two coherent carpels, the margins of which (*I–IV*) projecting inwards form a right and a left placenta (*pl*); on each of these placentæ which correspond to the margins of the carpels a posterior and an anterior ovule are produced, but an outgrowth from

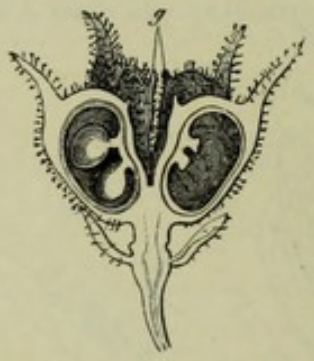

FIG. 358.—Ripe fruit of *Dictamnus Fraxinella*: the anterior carpel has been removed and the two lateral ones opened; *g* gynobasic style (natural size).

the mid-rib of the carpel (*IV, VI, x*) inserts itself between the two ovules belonging to each loculus, dividing it into two one-seeded lobes. Since at a subsequent period the outer part of the wall of each of the four lobes bulges strongly outwards and upwards (*B*), the separation of the bicarpellary ovary into four separate parts becomes still more distinct; and finally they completely separate as

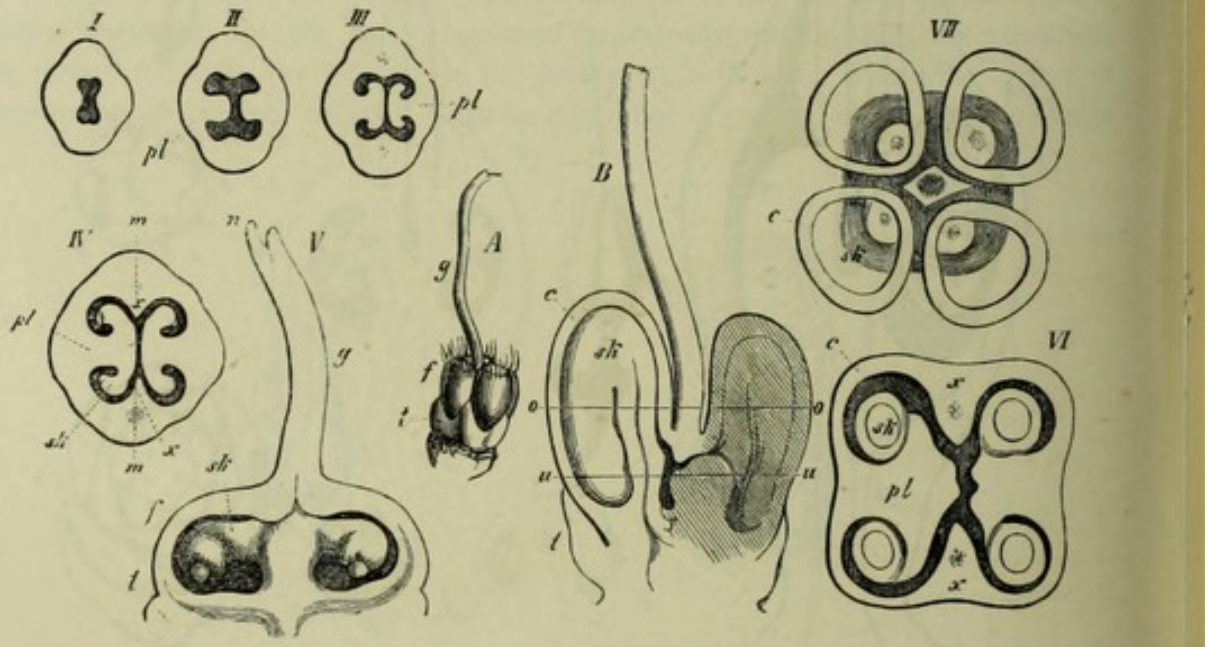

FIG. 359.—*I–VII* stages of development of the ovary of *Phlomis pungens*, *V* in longitudinal, the rest in horizontal section; *A* a gynæceum seen from without ready for fertilisation; *B* the same in longitudinal section, the lines *u u*, *o o* correspond to the horizontal sections *VI* and *VII*; *pl* the placenta, *x* the spurious dissepiment, *f* loculi, *sk* ovules, *c* wall of the carpel, *t* disc, *g* style, *n* stigma.

one-seeded lobes of the fruit; while in Borragineæ the separation is still more complete. The division of the five loculi of the ovary of Linum into ten by spurious dissepiments is not so perfect, the projections from the centres of the carpels not reaching the central axis of the ovary.

Before passing to the consideration of ovaries with axile placentation, it should

be mentioned that there are cases in which the present state of our knowledge does not enable us to decide with certainty whether the ovules arise from the axis or from the margins of the carpels which have become united to it; and these doubtful cases are possibly more numerous than is generally thought. Payer's observations on Cerastium and Malachium show that in Caryophylleæ the expanded apex of the floral axis becomes considerably elevated even before the formation of the carpels; the carpels are then seen in a whorl, and attached by means of their coherent margins to the elevated axis; each forms what may be described as a pocket attached to the axis. As the axis becomes elongated, the margins of the carpels form radial dissepiments separating the pockets, which widen into loculi; and the carpels finally rise above the apex of the axis. In Cerastium and other genera the dissepiments also rise above it as free lamellæ which do not meet in the centre, so that the ovary is quinquelocular below, while in the upper part it remains unilocular. The ovules are produced in two parallel rows on the axial face of each loculus, this face being apparently formed from the axis itself. In some genera of Caryophylleæ it seems probable that the placentæ are axile, while in others they would appear rather to be carpellary.

Among *Superior Ovaries with axile Placentation*, those of Typha, Naias, and Piperaceæ[1] require especial mention. In these cases the very simple female flower consists (with the exception of the perianth of Typha, which is replaced by hairs) of nothing but a small lateral shoot transformed into an ovary with a central ovule. The apex of the axis of this shoot itself develops into the terminal nucleus of the ovule, round which an annular zone grows up from below, overarches it, closes up above, and thus forms the wall of the ovary. In Typha only one style and stigma surmount the ovary, which may therefore be considered to be composed of a single carpel which rises up from the floral axis as an annular zone. In Piperaceæ however the stigma, which is sessile on the apex of the ovary, is often placed obliquely or divided into several lobes; and this, like the two or four styles which surmount the ovary of Naias[2], indicates that the ovary is not composed of one but of several carpels, which first make their appearance, like the leaf-sheaths of Equisetum, as an unbroken ring, which only at a later period becomes resolved at its upper margin into teeth. This hypothesis appears the more admissible since, in other Angiosperms where a comparison with nearly allied forms justifies us in inferring a number of coherent carpels, these carpels originate as an undivided annular zone which developes into the ovary, style, and stigma; as, for instance, in Primulaceæ (Fig. 360). In Polygonaceæ, on the other hand, where the ovary also forms eventually a closed cavity containing the central ovule (Fig. 361), the cohesion of two or three carpels to form the ovary may not only be recognised from the corresponding number of the styles and stigmas; but separate carpels appear at first distinct on the floral axis, and only amalgamate in the course

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[1] Magnus, Zur Morphologie der Gattung Naias (Bot. Zeit. 1869, p. 772).—Rohrbach, Ueber Typha (in Sitzungsber. des Gesells. naturf. Freunde Berlin Nov. 16, 1869).—Hanstein u. Schmitz, Ueber Entwickelung der Piperaceenblüthen (Bot. Zeit. 1870, p. 38).

[2] I am unable to understand why Magnus calls the coating of the ovary 'perianth.'

of their growth, their zone of insertion becoming elevated as a ring. Since the wall of the ovary does not in any of these cases forms placentæ from the number and position of which the number and position of the carpels might otherwise be more easily determined, we are thrown back on the direct observation of the first stages of development and on the numbers of the styles and stigmas. Failing this, the solution of the question depends on morphological relationships which are still by no means made out with sufficient certainty, notwithstanding the numerous researches which have been made on the development of the flower.

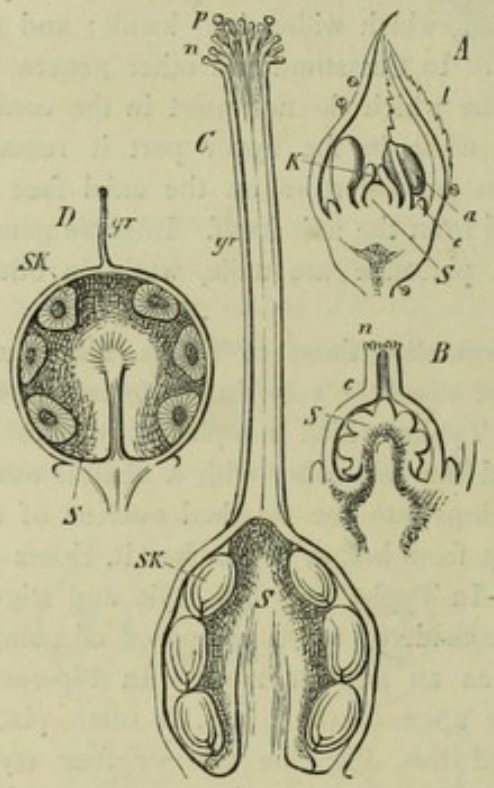

FIG. 360.—*Anagallis arvensis*: *A* longitudinal section of a young flower-bud, *l* sepals, *c* corolla, *a* anthers; *K* carpel; *S* apex of the floral axis; *B* the gynæceum further developed, the stigma *n* being now formed, and the ovules on the central placenta *S*; *C* the gynæceum ready for fertilisation, *p* pollen-grains on the stigma *n*, *gr* style, *S* central placenta, *SK* ovules; *D* unripe fruit, the placenta *S* has become fleshy and swollen so as to fill up the spaces between the ovules.

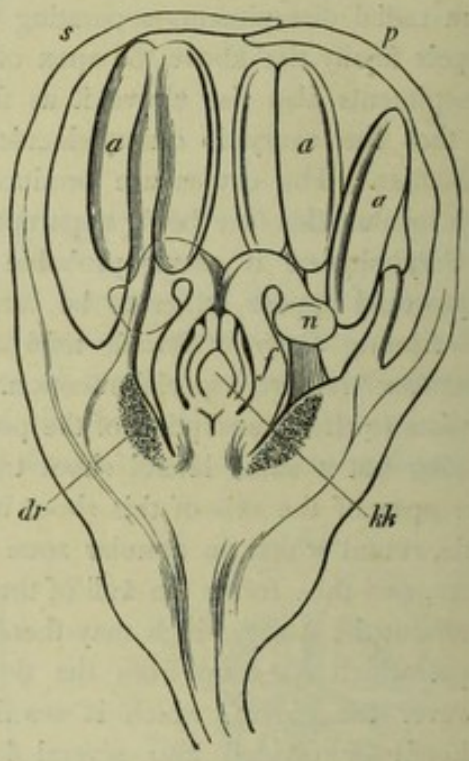

FIG. 361.—Longitudina section of the flower of *Rheum undulatum*: *s* leaf of the outer, *p* of the inner perianth-whorl; *a a a* three of the nine anthers, *f* ovary, *n* stigma, *k k* nucleus of the ovary, *dr* glandular tissue at the base of the filaments forming the nectaries.

Besides the number of the carpels which have coalesced to form the ovary, it is a question of interest whether in any particular case the ovules have been produced laterally on the floral axis or as its terminal structure. In the cases of Piperaceæ, Polygonaceæ, Naias, Typha, &c., where only a single ovule springs from the base of the ovary, it is evident that this must be the terminal structure of the floral axis; and the investigations of Hanstein and Schmitz, Magnus, Rohrbach, and Payer, have proved in addition that not only the ovule as a whole, but the nucleus itself, must be considered as a terminal structure. It must not, however, be inferred from this that every ovule which springs from the base of the cavity of the ovary necessarily forms the apex of the floral axis; for it is conceivable that the axis itself may have ceased to grow, but has produced an ovule at the side of its apex, a case which we shall meet with further on in the inferior ovary of Compositæ.

In a few cases the floral axis rises free within the spacious cavity of the ovary and produces ovules laterally, as occurs in Primulaceæ (Fig. 361) and Amaranthaceæ (in Celosia, according to Payer).

The *Inferior Ovary* of epigynous flowers results from the retardation or complete suppression of the apical growth of the young floral axis, its peripheral tissue rising as an annular zone, and producing on its free margin the perianth, stamens, and carpels (Figs. 362, 363). The hollow structure which is thus formed, and which is at first open above, is afterwards covered over by the carpellary walls which close in above it; the apex of the floral axis lies at the bottom of the elongated

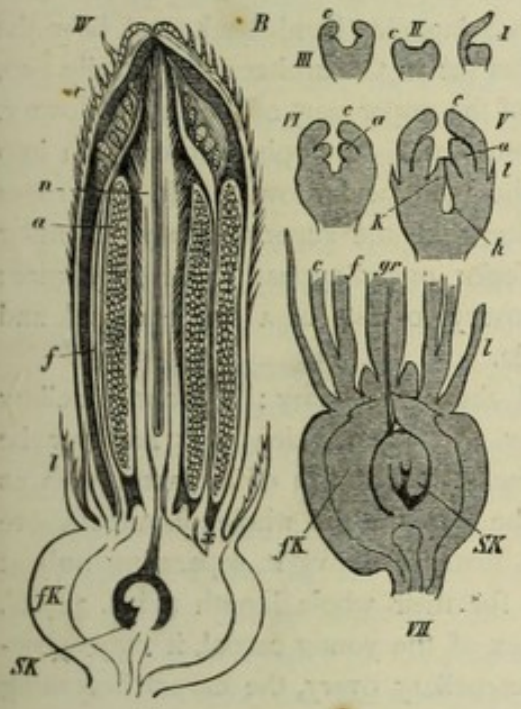

FIG. 362.—*I-VII* stages of development of the flower of *Helianthus annuus*: *l* calyx, *c* corolla, *f* filaments, *a* anthers, *x* basal portion which afterwards developes into the lower part of the tube of the corolla which bears the epipetalous stamens, *fK* the inferior ovary, *SK* the ovule, *h* carpel, *gr* style.

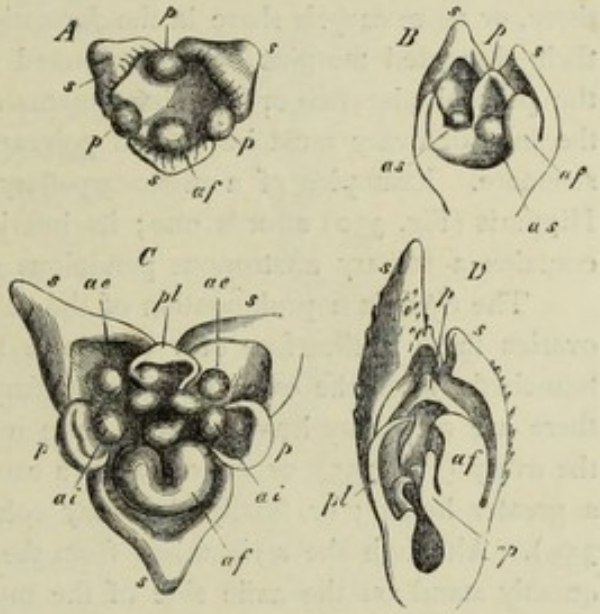

FIG. 363.—*A-D* stages of development of the flower of *Calanthe veratrifolia* (after Payer): *A* and *C* seen from above, *B* and *D* in longitudinal section, *s* sepals, *p* petals, *pl* the petal which developes into the labellum, *af* the single fertile anther, *ae* and *ai* abortive anthers of the outer and inner whorl; in *B as* are the sterile stamens, in *D cp* one of the three carpels.

cup-shaped or tubular cavity. Notwithstanding this striking displacement of the axial parts, the structure of the inferior ovary resembles that of the free polycarpellary ovary in almost all respects; it may also be either unilocular or multilocular—if unilocular, the placentation may be either basilar or lateral. When the placentation is basilar, the ovule sometimes appears as if it were the terminal structure of the apex of the axis; as for instance the erect ovule of Juglandeæ. In Compositæ, on the other hand, the position of the single anatropous ovule is not terminal but lateral; the apex of the floral axis may often be clearly made out as a small elevation beside the funiculus, and in abnormal cases it undergoes further development into a leaf-bearing shoot[1]. In Samolus the apex of the axis rises within the

[1] Cramer, Bildungsabweichungen und morphologische Bedeutung des Pflanzen-Eies (Zurich 1864). —Köhne, Die Blüthenentwickelung der Compositen, Berlin 1869. — Buchenau, Bot. Zeit. 1832, No. 18 *et seq.*

unilocular inferior ovary as in the superior ovary of other Primulaceæ (Fig. 360), and bears a number of lateral ovules. If the placentæ of the unilocular inferior ovary are parietal, they form on the wall two, three, four, five or more ridges from above downwards or from below upwards, and bear two or a larger number of rows of ovules (as in Opuntia or Orchideæ). These placentæ, which project more or less into the interior, may be regarded as the prolongations of the margins of the carpels on the inside of the ovary. A similar explanation may be given of the longitudinal dissepiments of the multilocular inferior ovary; the same differences occur in them as those which have already been described in the case of the superior ovary; for they may either meet in the middle and bear the ovules in the axile angles of the loculi, or they may split into two lamellæ, bend back, and bear the ovules in the middle of the cavity of the loculus (as in Cucurbitacæ). Usually two, three, or more carpels share in the formation of the upper part of the inferior ovary, their elongated margins being prolonged inwards and developing downwards into the parietal placentæ or the dissepiments of the multilocular ovary. In such cases the inferior ovary must be termed polycarpellary, like the superior ovary of similar structure. Examples of a monocarpellary inferior ovary appear to be very rare; Hippuris (Fig. 330) affords one; its inferior ovary consists of a single carpel, and contains a solitary anatropous pendulous ovule.

The *Style* is a prolongation of the carpel above the ovary; in monocarpellary ovaries there is therefore only one style (Figs. 351, 353), which may however be branched; when the ovary is polycarpellary, the style consists of as many parts as there are carpellary leaves; these parts may be free for the whole distance above the ovary (Fig. 355), or coherent for a certain distance above it, separating only at a greater height; or, finally, they may cohere for their whole length (Figs. 357 *G*, 359). Although the style arises from the apex of the young carpel, it may subsequently stand on the axile side of the monocarpellary ovary, the carpel becoming considerably bulged outwards by the more rapid growth of the dorsal side of the ovary (as in Fragaria and Alchemilla). If this occurs with the separate carpels of a polycarpellary ovary, the ovary itself appears to be depressed in the middle, and the style rises from the depression (Figs. 356, 357). In Labiatæ and Borragineæ this peculiarity is especially conspicuous, the four lobes of the bilocular ovary forming strong protuberances (Fig. 359, *A*, *B*), so that the style finally appears to spring from between four parts of the ovary which seem to have scarcely any connection with one another, and is hence termed a *gynobasic* style.

The style may be hollow, that is, it may be penetrated by a channel consisting of a narrow elongation of the cavity of the ovary, as in Butomus (Fig. 351, *B*, *E*), where it opens on the hairy surface of the stigma; or in Viola (Fig. 364), where the channel is broad, and opens above into the hemispherical cavity of the stigma; or in Agave and Fourcroya, where the style is hollow throughout its whole length, and open to the stigma, the simple channel dividing below into three tubes which run into the loculi of the ovary, a phenomenon which occurs also in other Liliaceæ[1]. In other cases it is at first hollow, as in Anagallis (Fig. 361, *B*), but becomes

[1] Zuccarini, Nova Acta Ac. Leopold, XVI, pt. II, p. 665.

afterwards filled up by the growth of the tissue. There is usually no channel to be detected in the style when the pistil is ready for fertilisation, or at least not in its upper part ; in the place of this its centre is occupied by a mass of loose tissue, the 'conducting tissue,' down which the pollen-tubes grow till they reach the cavity of the ovary. The external form of the style is usually cylindrical, filiform, or columnar, sometimes prismatic or ribbon-shaped; in the Irideæ it generally attains a considerable size; in Crocus it is very long, tripartite above, each division being deeply hollowed out like a cup; while the genus Iris is distinguished by its three free broad petaloid coloured styles. Sometimes the portion of the style which belongs to each carpel branches, as in Euphorbiaceæ, where a tripartite style, each arm of which bifurcates, corresponds to the three carpels. The style frequently remains very short, and then has the appearance of being a mere constriction between the ovary and stigma, as in Vitis.

The *Stigma*, in the narrower sense of the term, is the part of the style which is destined for the reception of the pollen. When pollination takes place it is covered with a viscid secretion, and usually with delicate hairs or short papillæ, constituting a glandular structure which is sometimes merely a peculiarly developed portion of the surface of the style, sometimes a special organ of very variable appearance attached to it. The form of the stigma always has an intimate connection with the mode of conveyance of the pollen by insects or otherwise, and can be understood and explained only when these facts are taken into consideration. A few specially interesting cases will be described in Book III; it is sufficient now to mention that the surface of the stigma forms the exit of the open channel of the style when there is one; if this channel is closed or entirely absent, the stigma has the appearance of a superficial glandular structure upon or beneath the apex of the style or of its arms. If these arms are long and slender, and covered with long hairs, the stigma has the form of a pencil or tuft of hairs or feathers, as in Grasses; in Solanaceæ and Cruciferæ the moist surface of the stigma covers a knob-like indented thickening at the end of the style; in Papaver it forms a many-rayed star on the lobed style. Sometimes the stigmatic portion of the style is greatly swollen, as in the Asclepiadeæ, where the two monocarpellary and distinct ovaries cohere by the stigmas; the true stigmatic surface into which the pollen-tubes penetrate lies in this case concealed on the under side of the stigma[1].

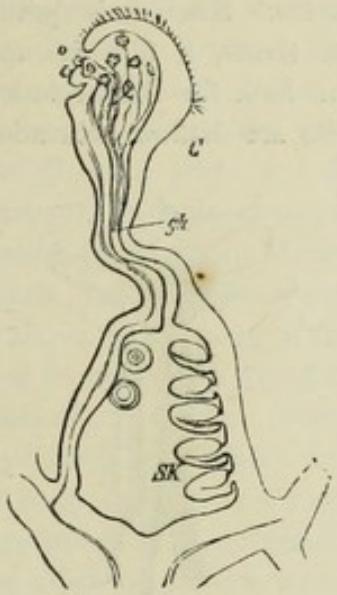

FIG. 364.—Longitudinal section through the gynæceum of *Viola tricolor*; *SK* the anatropous ovules, *gk* channel of the style, *o* its opening: in the hollow of the stigma which is filled with the stigmatic secretion are pollen-grains which are putting out their pollen-tubes.

[1] On the position of the lobes of the stigma in relation to the placentæ in different plants, see Robert Brown, Misc. Bot. Works, Ray Soc. 1867, vol. I, pp. 553-563.

The *Nectaries*. Wherever pollination is effected by insects, glandular organs are found in the flowers which secrete odoriferous and sapid (generally sweet) juices, or contain them within their delicate cellular tissue from which they are easily sucked out. These juices are included under the term *Nectar*, the organs which produce them being the Nectaries. The position, form, and morphological significance of the nectaries are very various, and always stand in immediate relation to the special contrivances for the pollination of the flower by means of insects. The nectaries are often nothing but glandular portions of tissue on the foliar or axial parts of the flower; very often they project in the form of cushions of more delicate tissue, or take the form of stalked or sessile protuberances; or whole foliar structures of the perianth, of the androecium, or even of the gynæceum, are transformed into peculiar structures for the secretion and accumulation of the nectar. Since it is quite impossible to treat these organs morphologically in general terms, a few examples may serve to show the student where he will have to look for the nectaries in different flowers. In *Fritillaria imperialis* the nectaries are shallow excavations on the inner side of the perianth-leaves near their

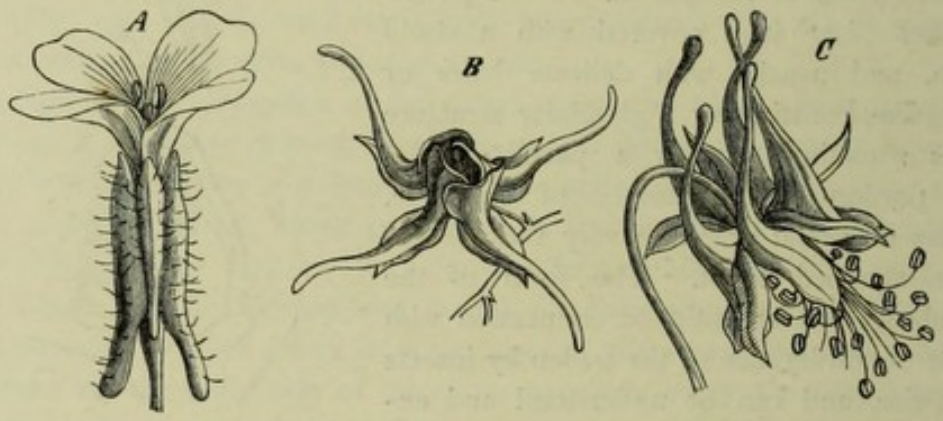

FIG. 365.—Flowers with spurred sepals (*A*) and petals (*B*, *C*); *A Biscutella hispida*, *B Epimedium grandiflorum*, *C Aquilegia canadensis*.

base, large clear drops of nectar exuding from them; in *Elæagnus fusca* a glandular annular cushion on the gamophyllous perianth (Fig. 353 *d*); in Rheum slight glandular protuberances at the base of the stamens (Fig. 360 *dr*); in Nicotiana an annular callosity at the base of the superior ovary; in the Umbelliferæ a fleshy cushion surrounding the bases of the styles united above the inferior ovary (Fig. 352 *h h*, p. 490); in Compositæ they are also at the base of the style (Fig. 362). In Citrus, *Cobæa scandens*, Labiatæ, and Ericaceæ, the nectary appears as a development of the floral axis or disc in the form of an annular zone beneath the ovary (Figs. 356 *d*, 359 *A*, *x*), &c.; in Cruciferæ and Fagopyrum in the form of four or six roundish or club-shaped outgrowths or warts between the filaments, &c. An abortive stamen is converted into a nectary in the Gesneraceæ; in *Cucumis Melo* (the melon) the whole androecium is replaced in the female and the gynæceum in the male flowers by a similar organ. As a rule the nectaries occur deep down among the other parts of the flower; and when they secrete nectar, it collects at the bottom of the flowers, as in Nicotiana and Labiatæ. Frequently, however, special hollow receptacles are constructed for this purpose, as is especially the case with the bag-like appendages of the perianth-leaves (Fig. 365), usually called Spurs. In

Viola only one of the perianth-leaves forms a hollow spur, into which the appendages of two stamens are prolonged and secrete the nectar. The cup-shaped stalked petals of Helleborus and the slipper-shaped petals of Nigella excrete at the bottom of their cavity the nectar which gathers there.

The *Ovule* of Angiosperms usually consists of a clearly developed, sometimes even very long stalk or *Funiculus* (as in Opuntia and Plumbagineæ)—which, however, is sometimes entirely wanting, as in Grasses—and one or two integuments which enclose the nucleus. The ovules of most gamopetalous Dicotyledons have one, those of almost all Monocotyledons two integuments; a third envelope, the *Aril*, is frequently formed subsequently (as in Myristica, Euonymus, *Asphodelus lutea*, *Aloë subtuberculata*, &c. When the ovule is the terminal structure of the floral axis, and has a short funiculus, it is orthotropous, as in Piperaceæ and Polygonaceæ; the campylotropous form, *i. e.* where the nucleus together with its integuments is itself curved, is comparatively rare, but occurs in Grasses, Fluviales, Caryophylleæ, &c. The usual form of the ovule of Angiosperms is the anatropous; the nucleus together with its integuments is inverted, so that the micropyle faces the point of origin of the funiculus from the placenta (Figs. 351 *E*, 352, pp. 489, 490); in this case the funiculus runs up the side of the ovule, coalesces with it, and is termed the *Raphe*. The micropyle is frequently, especially in Monocotyledons, formed by the inner integument only of the nucleus; but sometimes, especially among Dicotyledons, the outer integument grows also above the opening of the inner one, and the channel of the micropyle is then formed at its outer part (the *Exostome*) of the outer, at its inner part (the *Endostome*) of the inner integument. When there are two or three integuments, the innermost (the *Primine* of Mirbel) is always formed first, then the outer one (the *Secundine*), and finally, usually at a much later period, the Aril; the order of development is therefore basipetal in reference to the axis of the ovule. The transverse zone from which the single or the two true integuments spring, is termed the *Chalaza* (more correctly the base of the ovule).

The integuments are usually only a few layers of cells in thickness, and have the appearance, especially when they enclose a large nucleus, of thin membranes (Fig. 351, *E*). But when only one integument is developed, the nucleus usually remains very small, while the integument becomes thick and solid, extending far beyond the nucleus, and forming, before fertilisation, the principal mass of the ovule, as in Hippuris (Fig. 330, p. 470), Umbelliferæ (Fig. 352, p. 490), and Compositæ (Fig. 362, p. 497).

There is still much doubt about the history of development of the separate parts of the ovule; the following may be stated as certain or at least probable. In the formation of the erect orthotropous ovule the apex of the floral axis rises within the ovary as a roundish or conical ovoid protuberance which forms the nucleus; an annular wall grows up first, and finally envelopes the nucleus and extends beyond it as an integument. If a second outer integument is formed in addition, this arises in a similar manner, and grows up around the first (as in Piperaceæ, Polygonaceæ, &c.). The anatropous ovule may be at first a straight or slightly curved projection of tissue (as in Fig. 366, *I*), but immediately becomes evidently curved at the spot where the first or the single integument springs from it (Fig. 366, *II*, *III*, *IV*); the apical part enclosed by the integument then forms the

nucleus, while the subjacent basal part becomes the funiculus. As the integuments arise, the curvature becomes gradually stronger, and the nucleus becomes inverted even before the outer integument has entirely developed. This latter is therefore not formed on the side next to the raphe, but clothes all the free part of the ovule, right and left of the raphe (Fig. 366, *V, VI, VII*). Cramer was the first to point out that anatropous ovules may originate in another way (and this is probably the most common case), the ovule developing as a secondary lateral projection

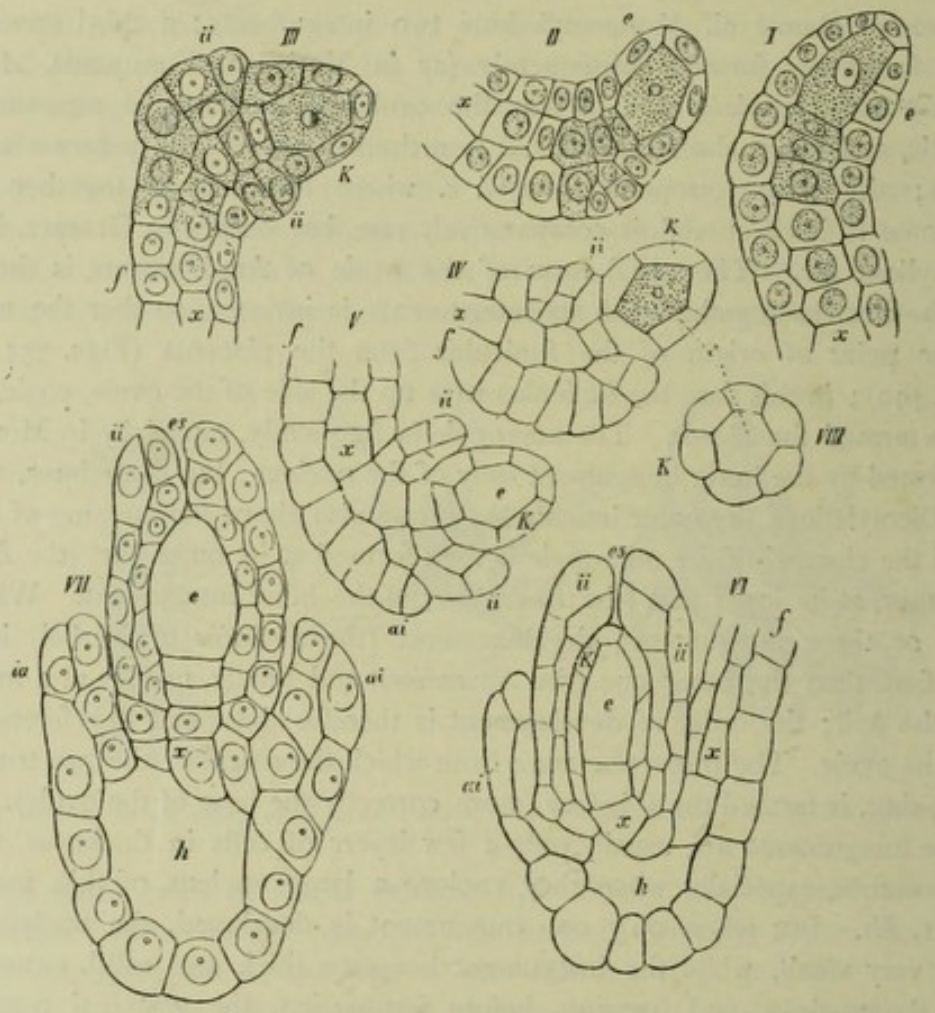

FIG. 366.—*I—VII* stages of development of the ovule of *Orchis militaris* (× 550); *I—VI* seen from the side in longitudinal section, *VII* from the front, the funiculus being behind, *VIII* a horizontal section of *I*; *x x* the axial row of cells, the upper one of which becomes the embryo-sac *e*, *f* the funiculus, *ii* the inner, *ai* the outer integument, *K* the nucleus, *es* the micropyle, *h* an intercellular space: in *VII* the embryo-sac *e* has completely replaced the tissue of the nucleus.

beneath the apex of the young conical funiculus, and curving backwards subsequently towards the base of the latter. This inversion takes place while the single or the inner integument is enveloping the nucleus from the summit of the funiculus; the second integument, if there be one, then similarly clothes the free part (see Fig. 367, *B, C*). Köhne[1] has indeed thrown some doubt on the actual lateral origin of the nucleus, not only in Compositæ, but also in Solanum, Hedera, Fuchsia, Begonia, &c. I have, however, had the opportunity, not only previously, but also more recently, in Grigorieff's researches on Compositæ, of observing a number of

[1] Köhne, Ueber die Blüthenentwickelung bei den Compositen. Berlin 1866.

different stages of development in this respect, and not only of convincing myself that the funiculus arises laterally with respect to the apex of the floral axis, but also that the nucleus, when first visible, stands laterally also below the apex of the funiculus. It is possible that the observation of peculiarly favourable cases will remove the last remaining doubt on this point. Cramer has shown in a number of other instances that all stages of the metamorphosis of ovules occur when the flower is developed in a monstrous condition, leading also to the conclusion that the nucleus is a lateral structure on the funiculus of the ovule. Malformations of *Delphinium elatum*, where the ovules spring from the margins of the carpels, show that the carpel is transformed into a flat open pinnate leaf, the lobes of which are the metamorphosed ovules. The nucleus here springs from the upper or inner side of the lobe of the leaf which represents the transformed funiculus together with the integument. In Melilotus, *Primula chinensis*, and Umbelliferæ, Cramer

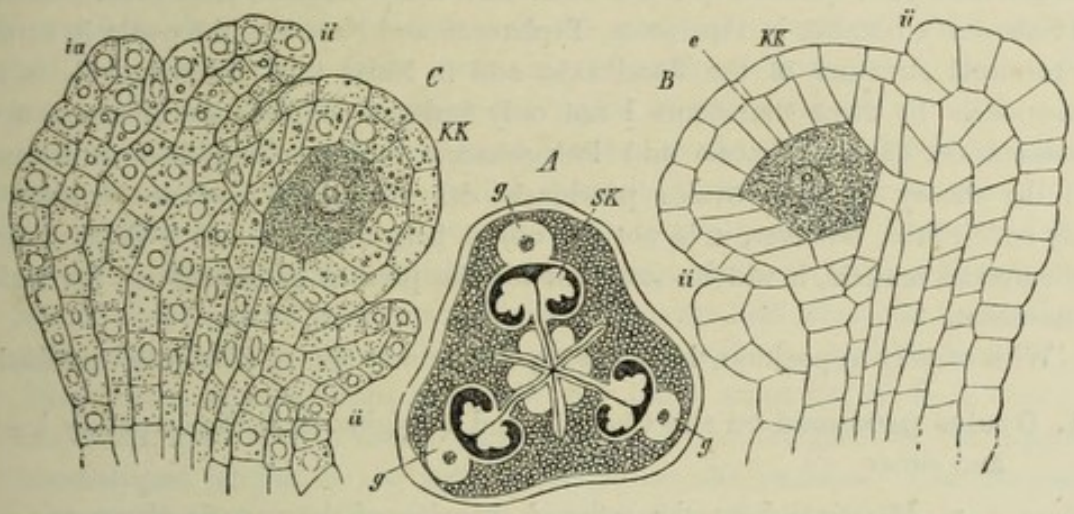

FIG. 367.—*Funkia cordata*; *A* horizontal section of the young superior trilocular ovary, two ovules *SK* are seen in each loculus, growing from the revolute margins of the carpels, *g* a fibro-vascular bundle surrounded by light-coloured parenchyma; *B* and *C* two successive states of the young ovule in longitudinal section, *KK* tissue of the nucleus, *ii* inner, *ia* outer integument, *e* embryo-sac (*A* slightly, *B*, *C* very highly magnified).

found the case to be the same[1]. Relying on this and other facts, and on the hypothesis that the ovule is never a terminal structure of the floral axis, Cramer[2] adopted the view that the ovule is either a metamorphosed leaf or part of a leaf (a tooth or outgrowth of the upper surface). The ovule of Primulaceæ and Compositæ he considered to be a whole leaf, and he supposed that closer observation would show the same to be the case in other flowers also, especially in those where the flower is said to possess a solitary 'reputed terminal ovule,' as Urtica (and Taxus), and perhaps also the Dipsacaceæ and others. The nucleus would in this case be a new formation on the surface of the ovular leaf, the funiculus would correspond to the base of this leaf, and the integuments to its upper part, which is folded once or twice in the form of a cup or hood round the nucleus. On the other hand he would consider as only portions of the leaf (teeth or outgrowths of

[1] Compare also H. von Mohl, Vermischte Schriften, pl. I, figs. 27–29.

[2] Cramer, Bildungsabweichungen bei einigen wichtigeren Pflanzenfamilien und die morphologische Bedeutung des Pflanzeneies (Zürich 1869, p. 120), where the literature of this subject has been carefully treated.

the upper surface) all those ovules which spring singly or in numbers from the margin or upper surface of carpellary leaves, as those of Cycadeæ, Abietineæ (?), Liliaceæ, Umbelliferæ, Ranunculaceæ, Resedaceæ, Cruciferæ, Leguminosæ, &c. In these cases the nucleus would be a new formation on the surface of the lobe, the funiculus would correspond to its base, and the integuments to its upper part folded once or twice round the nucleus in the form of a cup. Only in those few plants in which the ovule has no integument would the naked nucleus or entire ovule correspond to this lobe of the carpellary leaf. In the first edition of this book I expressed my agreement with Cramer's view, but with a reservation with respect to Orchideæ, being especially influenced by the importance which I then attached to the morphological equivalency of the nucleus in all Phanerogams. Further reflection has, however, deprived this reason of its importance; and I am the more induced to ascribe different morphological significations to the ovules, according to their mode of origin and their position (as has been shown by Magnus, Rohrbach, Hanstein, and Schmitz[1]), because in Piperaceæ, Typhaceæ, and Naiadeæ, the ovule is actually the terminal structure of the floral axis, and in Naias this terminal ovule is also anatropous. In these statements I not only find the confirmation of my own observations on Chenopodiaceæ and Polygonaceæ, but they are also in harmony with the theory that the ovules previously described by Payer as terminal are really so. Since, however, it is not my object here to enter into a detailed proof of theoretical matters, it will be sufficient for the present to summarise the various phenomena.

With respect to position, the following classes may first of all be distinguished:—

A. **Ovules produced on the Carpels** and springing from the carpellary leaves; and either

1. *Marginal*, from the reflexed margins of the carpels (Figs. 354, 355, 356, 359); or,
2. *Superficial*, from the whole of the inner surface of the reflexed halves of carpellary leaves, always apparently with the exception of the mid-rib of the carpellary leaf (Fig. 351).

B. **Ovules produced on the Axis** and springing from the prolongation of the floral axis within the ovary, the carpels themselves being sterile; these may be either—

3. *Lateral*, when they stand beside or below the apex of the floral axis, which either rises as a columella and bears a number of ovules (as in Fig. 360), or is arrested in its development, so that the single ovule appears terminal (as in Fig. 362); or,
4. *Terminal*, when the apex of the floral axis itself becomes the nucleus (as in Figs. 330, 361, and in Piperaceæ, Naias, Typha, &c.).

To which of these classes the ovules belong in any given plant must be decided in each separate case; the position on the margin of the carpels is by far the most common among Angiosperms, both the superficial and the axile position belonging

[1] These researches have been already quoted.

only to single families or genera. If these facts are compared with what occurs in Gymnosperms, the ovules of Cycadeæ must be classed with the marginal carpellary, those of many Cupressineæ with the superficial description; while those of Taxus are axile and terminal, and those of Salisburia lateral.

When the position of the ovules is given, so also is in general their morphological significance: the terminal ovules must be regarded as the terminal portion of the axis, the lateral as equivalents of whole leaves, the marginal as branches of leaves (laciniæ, pinnæ, or lobes); the superficial ovules may be included in the category of such foliar outgrowths as we have already found to occur in the form of sporangia among the Lycopodiaceæ[1]. The ovules of Orchideæ must however be included (like the sporangia of Ferns and Rhizocarps), under the category of trichomes, inasmuch as they owe their origin to single superficial cells of the parietal placentæ (according to Hofmeister) and have no fibro-vascular bundles in the funiculus. These explanations are so far confirmed by the occurrence of malformations, that the lateral axile and the marginal carpellary ovules are often enough transformed into foliar structures of ordinary form, while this appears never to occur with terminal or superficial ovules, or with those of Orchideæ.

These remarks have at present been confined to the ovule as a whole, although reference has already been made to the theory of Cramer on the various morphological relationships of the nucleus and of the other parts, the funiculus and the integuments. Malformations, which in this respect are even more instructive than the normal development, led Cramer to the conclusion that when the ovule appears to be the equivalent of a lateral branch or of the whole of a leaf, the funiculus and the integuments together correspond to the foliar structure in each case; the nucleus arises from it as a lateral outgrowth, while the integuments correspond to the hood-shaped lamina of the leaf, growing over the nucleus. The integument of a terminal ovule would therefore be equivalent to a leaf on the axial nucleus[2] (see also Hanstein and Schmitz, *l. c.*). But we cannot enter further here into these relationships.

The ovules are sometimes rudimentary; those of Balanophoreæ and Santalaceæ have no integument; the nucleus is naked, and in some species is itself composed of only a few cells. In Loranthaceæ the development does not even proceed so far as the formation of a distinctly differentiated ovule; the growth of the apex of the floral axis ceases so soon as the carpels begin to be formed; and the cohesion of these is such that it is scarcely possible to speak of a cavity of the ovary; the formation of the embryo-sac in the axial part of the tissue of the inferior ovary is the only indication that this spot corresponds to the ovule; and since more than one embryo-sac is formed, it still remains doubtful whether this mass of tissue must be regarded as the equivalent of one or of several ovules[3].

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[1] [The remarkable position of the ovule in *Hydnora* (*Prosopanche*) *americana*, immersed in the placental tissue, is comparable with the origin of the sporangium in Isoëtes (Fig. 306, p. 408). On Hydnora see De Bary, Abhandl. der naturf. Gesellsch. zu Halle, vol. X; Hooker, Journ. Linn. Soc. vol. XIV, p. 182.—Ed.]

[2] In this one case the ovule might be a bud in the ordinary sense of the word; *i. e.* the young state of a leaf-bearing axis.

[3] Hofmeister, Neue Beiträge I (Abhandl. der kön. sächs. Gesellsch. der Wissensch. VI).

The *Embryo-sac*[1] is formed by the early enlargement of a cell lying nearly in the centre of the young nucleus, the surrounding tissue remaining small-celled and for some time afterwards in the condition of primary meristem, the growth of the entire ovule being continued in this manner. In Orchideæ (Fig. 366, p. 502), where its structure is very simple, the young ovule consists of a single layer of cells surrounding an axial row; the uppermost of these latter cells becomes the embryo-sac, and begins to enlarge even before the integuments are developed from the peripheral layer. Hofmeister is inclined to apply this description to all ovules, and to consider the embryo-sac as being always developed from a cell belonging to an axial row which passes through the ovule. It is, however, very difficult to prove the existence of such an axial row of cells in very small-celled ovules, especially those of Dicotyledons; and even among Monocotyledons the description of the ovules of Orchideæ does not seem always to apply, as may be seen (Fig. 367, p. 503) in the case of Funkia. It also sometimes happens among Angiosperms—reminding one of the phenomena in Taxus among Gymnosperms—that several embryo-sacs are at first formed; this is the case, for instance, according to Tulasne, in Cruciferæ, where however only one attains full development. The multiplicity of embryo-sacs in the ovary of Viscum cannot at present be included under this head, since the absence of any differentiation of the ovule makes it uncertain whether the mass of tissue in the ovary to which we have already alluded must be regarded as the equivalent of one or of several ovules.

The further behaviour of the embryo-sac of Angiosperms differs in many ways from that of Gymnosperms. In Gymnosperms it remains surrounded by a thick layer of the tissue of the nucleus till after fertilisation has taken place; it is comparatively small, and is surmounted by a strongly developed nuclear protuberance. In Angiosperms, on the other hand, the embryo-sac has grown considerably even before fertilisation; it usually supplants the surrounding tissue of the nucleus so far that it remains enveloped by only a thin layer of it, or is even in actual contact with the inner surface of the inner integument, as in Orchideæ (Fig. 366, *VII*). In such cases the tissue of the apex of the ovule often still remains entire (as in Aroideæ), but frequently the apex of the embryo-sac bursts through it, and projects into the micropyle (as in Crocus and Labiatæ), or even grows out beyond it as a long tube (*e.g.* Santalum). The middle and lower part of the sac also frequently extends considerably; in many gamopetalous Dicotyledons it puts out vermiform appendages which penetrate into and destroy the tissue of the integument, as in Rhinanthus, Lathræa, and some Labiatæ. While this process of growth is proceeding, the protoplasm which at first fills up the whole sac becomes full of vacuoles; a large sap-cavity arises surrounded by a parietal mass of protoplasm, which accumulates especially in the apical prominence and at the bottom of the embryo-sac, while threads, in which currents are visible, radiate to the walls from the protoplasm which envelopes the nucleus.

After this state of things has arisen, but still long before fertilisation, and even before the development of the embryonic vesicles, one or more cells are formed in

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[1] The following is mostly founded on Hofmeister's Neue Beiträge (Abh. der kön. sächs. Ges. der Wiss. VI and VII).

many Angiosperms at the bottom of the sac by free cell-formation. These cells are called by Hofmeister the 'Antipodal Cells,' but their appearance is inconstant even within a very narrow circle of affinity. They do not participate in the subsequent formation of the permanent endosperm, but are either included in or excluded from it (as Mirabilis, Ranunculaceæ, &c.), or are absorbed (as in Crocus and Colchicum). In the first edition of this book I had already expressed the opinion that these cells may be considered as the true equivalent of the endosperm of Gymnosperms.

In the mass of protoplasm which fills up the apical prominence of the embryo-sac, the bodies are formed by free cell-formation whose impregnation gives rise to the production of the embryo, and which are usually termed the *Embryonic* or *Germinal Vesicles*. In a few cases, as in *Rheum undulatum*, only one of these bodies is produced, forming a round primordial cell with a large nucleus and concealed in the narrow apical prominence of the embryo-sac. Since after fertilisation the pro-embryo is at once formed from this cell, and from it the embryo, this primordial cell must at present be looked on as homologous with the oosphere among Cryptogams. But usually two embryonic vesicles are formed side by side in the embryo-sac, and in these cases they are generally not round, but longish, ovoid, or even greatly elongated, mostly with the narrower end closely attached to the cell-wall of the sac, while the other rounded end which contains the nucleus projects free into its cavity. In a few, but not many, genera the two embryonic vesicles are elongated to an unusual length and peculiarly organised, as in Watsonia, Santalum, Gladiolus, Crocus, Zea, Sorghum, &c.[1] While the lower free end which contains the nucleus becomes rounded off, and presents the ordinary appearance of a primordial cell, the other end (and this is especially striking in Watsonia and Santalum) projects as a slender tubular or caudate elongation into the micropyle or even beyond it. On this appendage may be observed a distinct longitudinal striation, consisting apparently of cellulose, about the nature of which there is still however some doubt. Schacht considers this striated appendage of the embryonic vesicles to be a special organ, which he calls the Filiform Apparatus, and ascribes to it an intermediate function in the process of impregnation. He states that the two filiform apparatuses project from the perforated apex of the embryo-sac; while Hofmeister asserts that they are still covered by a protuberance of the sac, and that the striation is a peculiar thickening of this part of the wall of the embryo-sac itself—a view which however appears hardly tenable, at least in the case of Watsonia and Santalum. Only the lower rounded part of each embryonic vesicle acts as an oosphere after the contact of the pollen-tube with the filiform apparatus; Schacht states that in Santalum both develope as often as only one, so far as to produce an embryo; usually however one is entirely abortive, and the filiform apparatus takes no part in the development which is brought about by impregnation; Schacht asserts that in *Santalum album* they are even separated by a septum which arises in the apex of the embryo-sac. Pringsheim and Strasburger have demonstrated that the filiform apparatus corresponds to the canal-cell in the archegonium of Cryptogams. According to this explanation—which seems to me probable—each of the two embryonic

[1] Schacht, Jahrb. für wiss. Bot. vols. I. and IV; Hofmeister *l. c.* vol. VII, p. 675.

vesicles would correspond to the essential contents of an archegonium such as that of Salvinia; the lower rounded part which subsequently developes would be the oosphere, and the upper appendage the canal-cell, which is in this case only separated from the former after impregnation. The very rare occurrence of the filiform apparatus in Angiosperms can scarcely be brought forward as an objection to the explanation; since in this case, as in the 'antipodal cells,' we have to do with an organ which has become rudimentary, and the occurrence of such organs is commonly observed to be very variable and inconstant. In the enormous majority of Monocotyledons and Dicotyledons the filiform apparatus of the embryonic vesicles is wanting, the number of these latter being almost invariably two, rarely three. They usually lie obliquely one over the other, one closely attached to the apical prominence of the embryo-sac, the other situated lower down and sideways, but adpressed to the former by its broad surface; both adhering by their peripheral end to the wall of the sac. The fertilising pollen-tube usually, as Hof-

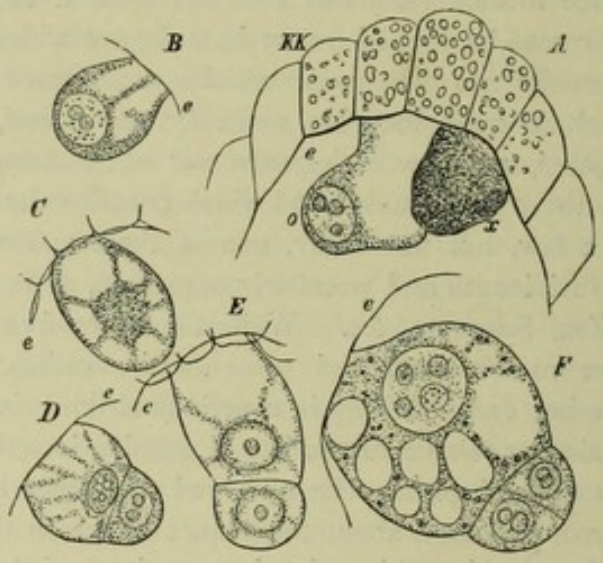

FIG. 368.—*Funkia cordata*; *A* apex of the embryo-sac *e*, covered with a layer of cells belonging to the nucleus *KK*, *x* the embryonic vesicle which is incapable of fertilisation, *o* the peculiarly shaped 'oosphere' with its nucleus; *B*, *C* 'oosphere' before, *D*, *E* after the first division; *F* the spherical pro-embryo with the two-celled rudimentary embryo (×500).

meister's and Schacht's drawings show, perhaps always, meets the apical embryonic vesicle (Fig. 368, *A*, *x*); but this does not then undergo further development, but disappears, while the one which lies lower down and at the side (*o*), and which is not touched at all by the pollen-tube, produces the pro-embryo, and subsequently the embryo. It appears therefore as if one of the two embryonic vesicles assume the function of the filiform apparatus or the canal-cell, while the other represents the oosphere. Sometimes even one embryonic vesicle is decomposed before impregnation takes place, as in *Funkia cordata* (Fig. 368); it resembles a lump of tough granular mucilage. Judging from Hofmeister's drawings, something of the same kind appears to occur also in other cases. In any case it is only one of the embryonic vesicles—that which produces the embryo—which can be looked on as the oosphere, since the other one, not merely occasionally but normally, has nothing to do with the formation of the embryo; its essential function appears to be merely to transmit the fertilising substance from the pollen-tube to the embryonic vesicle which is destined for further development. This remark refers however only to

function; the morphological significance of these parts is still undecided; and it remains at present doubtful whether the two embryonic vesicles correspond to those of Santalum and Watsonia; or whether the one which is destined to destruction must not rather be considered as the separated canal-cell, the other as the true oosphere.

In a few cases polyembryony occurs also among Angiosperms; but it is brought about in a way different from what occurs in Gymnosperms. A number of embryonic vesicles are formed in the parietal protoplasm of the embryo-sac before impregnation in *Funkia cærulea*, Scabiosa (according to Hofmeister) and Citrus; the formation of embryos is caused in them by the contact of the pollen-tube with the apex of the embryo-sac; but of the large number of rudimentary embryos, which is very considerable, especially in Citrus, only a few attain to a capacity for germination.

Fertilisation[1]. The pollen-grains which germinate on the stigma send out their tubes through the channel of the style where there is one, or more usually through the loose conducting tissue in its interior, down to the cavity of the ovary; frequently both in erect basilar (Fig. 361) and in pendulous anatropous ovules the micropyle lies so close to the base of the style that the descending pollen-tube can enter it at once. But more often the pollen-tubes have to undergo further growth after their entrance into the cavity of the ovary before they reach the micropyles of the ovules; and they are then guided in the right direction by various contrivances. We frequently find papillose projections of the placentæ or other parts of the wall of the ovary, to which the pollen-tubes attach themselves; in our species of Euphorbia a tuft of hairs conducts them from the base of the style to the neighbouring micropyle; in the Plumbagineæ, the conducting tissue of the style forms a conical descending outgrowth, which conducts the pollen-tube into the micropyle; and so forth.

Since every ovule requires one pollen-tube for its impregnation, the number of tubes which enter the ovary depends, speaking generally, on the number of the ovules contained in it; the number of pollen-tubes is however usually larger than that of the ovules; where these latter are very numerous, the number of pollen-tubes is therefore also very large, as in Orchideæ, where they may be detected in the ovary even by the naked eye as a shining white silky bundle.

The time that intervenes between pollination and the entrance of the pollen-tube into the micropyle depends not only on the length of the style, which is often very considerable (as in Zea and Crocus), but also on the specific characters of the plants. Thus, according to Hofmeister, while the pollen-tubes of *Crocus vernus* only require from twenty-four to seventy-two hours to penetrate the style which is from 5 to 10 cm. in length, those of *Arum maculatum* take at least five days, although the distance they have to go over is scarcely more than 2 or 3 mm., and those of Orchideæ require ten days or even several weeks or months, during which time the ovules first become developed in the ovary, or even are not formed till then.

The pollen-tube is usually very slender and thin-walled as long as it is increas-

[1] Besides the works of Hofmeister already quoted, see his historical account in Flora, 1857, p. 125, where the literature is collected.

ing quickly in length; after entering the micropyle its wall generally thickens rapidly and often considerably, chiefly, as would seem, by swelling, so that its cavity forms only a narrow channel. Hofmeister compares it, in this condition, to a thermometer-tube (as *e.g.* in Lilium, Cactus, and Malva); while sometimes the cavity of the tube becomes wider (as in Œnothera and Cucurbitaceæ). It consists of granular protoplasm, usually mixed with a number of starch-grains (the Fovilla).

Within the micropyle the pollen-tube either comes immediately into contact with the naked apex of the embryo-sac; or, as in Watsonia and Santalum, with the projecting filiform apparatus of the embryonic vesicles; but very commonly a portion of the tissue of the apex of the nucleus still remains through which it has to make its way to the embryo-sac. The wall is often weak at the apex of the embryo-sac, and is frequently inflexed by the advancing end of the pollen-tube, and in Canna is even perforated.

The contact of the pollen-tube with the apex of the embryo-sac or with the filiform apparatus of the embryonic vesicles is sufficient for the transmission of the fertilising substance; and the results of this process can usually be observed after a short time in the behaviour of the nucleus of the embryo-sac and of that of the embryonic vesicle. It frequently however occurs that a considerable time elapses after the entrance of the pollen-tube before the commencement of the development which is induced by it; several days or even weeks in many woody plants, as Ulmus, Quercus, Fagus, Juglans, Citrus, Æsculus, Acer, Cornus, Robinia, &c.; almost a year in the American oaks, the seeds of which take two years to ripen; in *Colchicum autumnale* the pollen-tube enters the embryo-sac at the latest at the beginning of November, but it is not till May in the next year that the formation of the embryo begins. (Hofmeister.)

Even the advance of the pollen-tube through the conducting tissue of the style and into the cavity of the ovary often causes extensive changes in the flower; if the perianth is delicate it usually loses at this time its freshness, fades, and afterwards entirely falls off; among Liliaceæ it is common for the ovary to commence growing actively even before the fertilisation of the ovules (Hofmeister); in Orchideæ not only is the active growth of the ovary, which often lasts for a considerable time, occasioned by pollination, but the ovules themselves are by it rendered capable of receiving impregnation; in some cases even their production is thus induced from the placenta which would otherwise remain sterile. (Hildebrand: see also Book III on the Sexual Process.)

Results of Fertilisation in the Embryo-sac; Formation of the Endosperm and Embryo. The first result of fertilisation seen in the embryo-sac is (as Hofmeister has shown) the disappearance of its nucleus; the action of the pollen-tube on the embryonic vesicle is only apparent later; the vesicle becomes enclosed in a cell-wall of cellulose if it did not possess one before fertilisation, as occurs sometimes, according to the same authority (*e.g.* in Nuphar, Tropæolum, Cheiranthus, Funkia, Crocus, &c.). The formation of the endosperm very commonly begins even before the division of the embryonic vesicle, at the latest during its transformation into the pro-embryo. In all Monocotyledons and most Dicotyledons the endosperm-cells are formed simultaneously in large numbers by free cell-formation within the parietal layer of protoplasm of the embryo-sac. They are at first globular and

unconnected with one another (Fig. 370); as they increase in size these primary endosperm-cells may at once fill up the sac, coming into contact with one another laterally and meeting in the middle (as in Asclepiadeæ and Solanaceæ); or new endosperm-cells may be again formed by free cell-formation within the parietal layer of cells first formed, which have already multiplied by division. They form an internal lining to the primary endosperm-cells until the whole space of the sac is filled up; if the sac increases greatly in size, as, for instance, in Ricinus and the large-seeded Papilionaceæ, the filling up with endosperm does not take place till

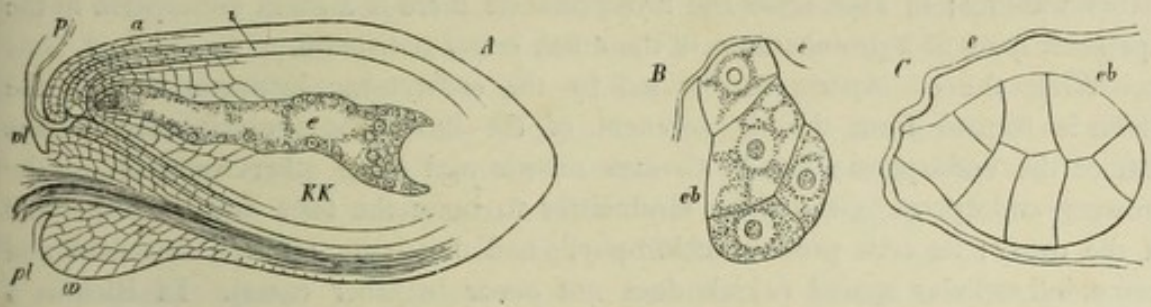

FIG. 369.—*Viola tricolor*: *A* longitudinal section through the anatropous ovule after fertilisation, *pl* the placenta, *w* cushion on the raphe, *a* outer, *b* inner integument, *p* the pollen-tube which has entered the micropyle, *e* the embryo-sac containing the embryo (to the left) and a number of young endosperm-cells; *B* and *C* the apical swelling of two embryo-sacs *e* with the embryo *eb* attached to it; the pro-embryo in *B* is two-celled.

later, and the centre of the sac is filled in the unripe seed with a clear vacuole-fluid. In the embryo-sac of the cocoa-nut, which grows to an enormous size, this fluid—the cocoa-nut-milk—remains until the seed is fully ripe, the tissue of the endosperm forming a layer only some millimetres in thickness, which lines the inside of the testa. The very narrow elongated embryo-sacs of plants with small seeds, as Pistia and Arum, are filled up by a single longitudinal row of cells formed by free cell-formation. In a large number of dicotyledonous plants (as Loranthaceæ, Oro-

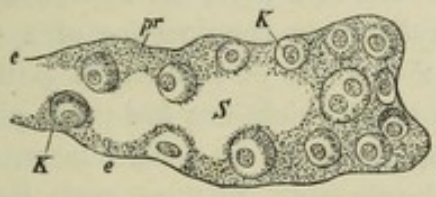

FIG. 370.—*Viola tricolor*, posterior part of the embryo-sac, *e* its cell-wall, *S* the cavity of the cell, *K*, *K* young endosperm-cells which have been produced in the protoplasm *pr*.

banchеæ, Labiatæ, Campanulaceæ, &c.), with long narrow tubular embryo-sacs, the space of the embryo-sac is first of all divided by two septa, further divisions succeeding in all or some of the cells thus formed; the tissue of the endosperm is produced from these last cells, and in this case often fills up only certain parts of the embryo-sac; or the sac is divided by a septum into two daughter-cells, the upper of which contains the rudimentary embryo, and produces endosperm in small quantities by free cell-formation (*e. g.* Nymphæa, Nuphar, Ceratophyllum, Anthurium[1]). In a few families only the formation of endosperm is rudimentary, and limited to the temporary appearance of a few free cells or nuclei, as in Tropæ-

[1] For further details of these processes described by Hofmeister, *vide infra*, under the characteristics of Dicotyledons.

olum, Trapa, Naïadeæ, Alismaceæ, Potamogetoneæ, Orchideæ; in Canna even this rudimentary production of endosperm appears to be suppressed.

During the formation of the endosperm, the embryo-sac usually increases in size, and thus displaces the tissue of the nucleus which still to a certain extent surrounds it; only in a few cases is the nucleus still partially or entirely preserved; it becomes filled with food-materials, like the endosperm, and replaces this latter as a reservoir of reserve-materials for the embryo. In Scitamineæ (*e. g.* Canna), this tissue, the *Perisperm*, is very strongly developed, while the endosperm is altogether wanting; in Piperaceæ and Nymphæaceæ there is a small endosperm in the ripe seed, lying in a protuberance of the much larger perisperm.

While the endosperm surrounded by the embryo-sac increases in size, the *Testa* is formed from the development of the integuments which accompanies that of the endosperm; but in *Crinum capense* and some other Amaryllideæ the growing endosperm is stated by Hofmeister to burst the testa and even the wall of the ovary; its cells produce chlorophyll, and the tissue remains succulent and forms intercellular spaces (which does not occur in other cases). In Ricinus a similar growth takes place when the ripe seed germinates in moist earth, bursting the testa (according to von Mohl); and the endosperm, previously ovoid and from 8 to 10 mm. long, is transformed into a flat broad sac 20 to 25 mm. in length, which surrounds the growing cotyledons until they have absorbed all the food-materials from it.

In Monocotyledons and many Dicotyledons the embryo remains small and either enveloped by the endosperm or lying by its side (as in Grasses); its cells, which are in close contact without intercellular spaces, become filled, until the seed is ripe, with a protoplasmic substance and fatty matter or starch or both, in which case they remain thin-walled; the endosperm then appears as the mealy (full of starch) or fatty nucleus of the ripe seed, the embryo being found by its side or within it; but it is often horny in consequence of a considerable thickening of its cell-walls which have the power of swelling (*e. g.* the date and other Palms, Umbelliferæ, Coffea, &c.) If this thickening has taken place to a very great extent, the endosperm may fill up the testa as a hard mass, forming, for instance, the 'vegetable ivory' in the Phytelephas. In these cases the thickening-masses of the endosperm-cells, which are absorbed during germination together with their protoplasmic and fatty contents, serve for the first nourishment of the embryo. The ripe endosperm, when copiously developed, has usually the form of the entire ripe seed, being uniformly covered by its testa; its external form is therefore generally simple, often round; although considerable deviations from this frequently occur, especially among Dicotyledons. Thus, for instance, the substance known as the 'coffee-berry' consists, with the exception of the minute embryo which is concealed in it, entirely of the horny endosperm; but this, as a transverse section shows, is a plate folded inwards at its margins. The marbled (ruminated) endosperm which forms the nucleus of the nutmeg (the seed of *Myristica fragrans*), and the areca-nut (the seed of the areca-palm), owes its appearance to the circumstance that an inner dark layer of the testa grows in the form of radiating lamellæ between narrow fold-like protuberances of the light-coloured endosperm. The ripe endosperm is either a perfectly solid mass of tissue, or it possesses an inner cavity, as in *Strychnos*

Nux-vomica, where, like the seed itself, it is broad and flat. This is clearly the result of the endosperm which grows inwards from the periphery of the embryo-sac leaving a free central space, which, as has already been mentioned, is very large and filled with fluid in the case of the cocoa-nut. In these cases the endosperm is therefore a hollow thick-walled sac, enclosing a roundish or flattened cavity.

In a large number of families of Dicotyledons, the first leaves of the embryo, the *Cotyledons*, grow, before the seeds are ripe, to so considerable a size that they displace the endosperm which was previously present, and finally fill up the whole space enclosed by the embryo-sac and the testa; while the axial part of the embryo, and the bud (plumule) that lies between the bases of the cotyledons, attain even in these cases only inconsiderable dimensions. In these thick fleshy or foliaceous cotyledons (which are then usually folded), the reserve of food-material accumulates, consisting of protoplasmic substance or starch and fatty matter, which is in other cases stored up in the endosperm, and is made use of during the development of the seedling. This storing of the cotyledons with so large a quantity of food-materials appears to take place by its transference from the endosperm; and hence the difference between those seeds which in the ripe condition contain no endosperm ['exalbuminous'], and those which do contain it ['albuminous'] consists essentially only in the fact that the food-material of the endosperm has passed over in the former case before germination into the embryo; while in the latter case this only takes place during the process of germination. The presence or absence of the endosperm in ripe seeds is more or less constant within large groups of forms, and is therefore of value in classification. Of the better-known families, for example, the Compositæ, Cucurbitaceæ, Papilionaceæ, Cupuliferæ (the oak and beech), &c., are destitute of endosperm. Sometimes also the embryo increases so greatly in size that the endosperm appears as a thin skin surrounding it.

We must now recur to the fertilised ovule in order to follow the formation of the *Embryo*. In Angiosperms, as in Gymnosperms, the embryonic vesicle is not immediately transformed into the embryo; the end which faces the micropyle coalesces in its growth with the wall of the embryo-sac at its apical swelling; its free end turned towards the base of the ovule then lengthens, and undergoes one or more transverse divisions. The *Pro-embryo*, or *Suspensor* as it is more frequently called, thus formed, usually remains short (Fig. 369, p. 511); sometimes, as in Funkia, its basal cell swells up into a globular form (Fig. 368, p. 508); in other cases (as, according to Hofmeister, in Loranthus) the embryonic vesicle lengthens, and penetrates to the considerably enlarged base of the long tubular embryo-sac, and there forms the embryonic vesicle within the endosperm. In those Dicotyledons where the endosperm is formed only at certain lower parts of the embryo-sac by division, a similar elongation of the embryonic vesicle is usual, although not to so great an extent (*e.g.* Pedicularis, Catalpa, Labiatæ). The apical cell of the two- or more-celled pro-embryo which is turned towards the base of the embryo-sac, and therefore also towards that of the ovule, is rounded off into a spherical form, a longitudinal or only slightly oblique division-wall first of all makes its appearance in it, indicating the commencement of the formation of the embryo (see also Fig. 14, p. 17). As this grows by rapidly repeated divisions, a spherical or ovoid mass of small-celled tissue is produced, on which the first foliar

structures, the cotyledons, subsequently arise, while the rudiment of the first root may be observed in the differentiation of the tissue at the boundary-line of the pro-embryo and embryo. The first cells of the embryo are not unfrequently disposed as if they had resulted from oblique divisions of an apical cell in two or three directions (Fig. 369 *C*), a supposition which is completely supported by the oblique position of the first septum of the apical cell in the pro-embryo; in Rheum I also found the apex of young embryos to present an appearance which suggested the existence of a three-faced apical cell. According to Hanstein's new and prolonged researches, the process is, nevertheless, different; he asserts that the first longitudinal wall, even

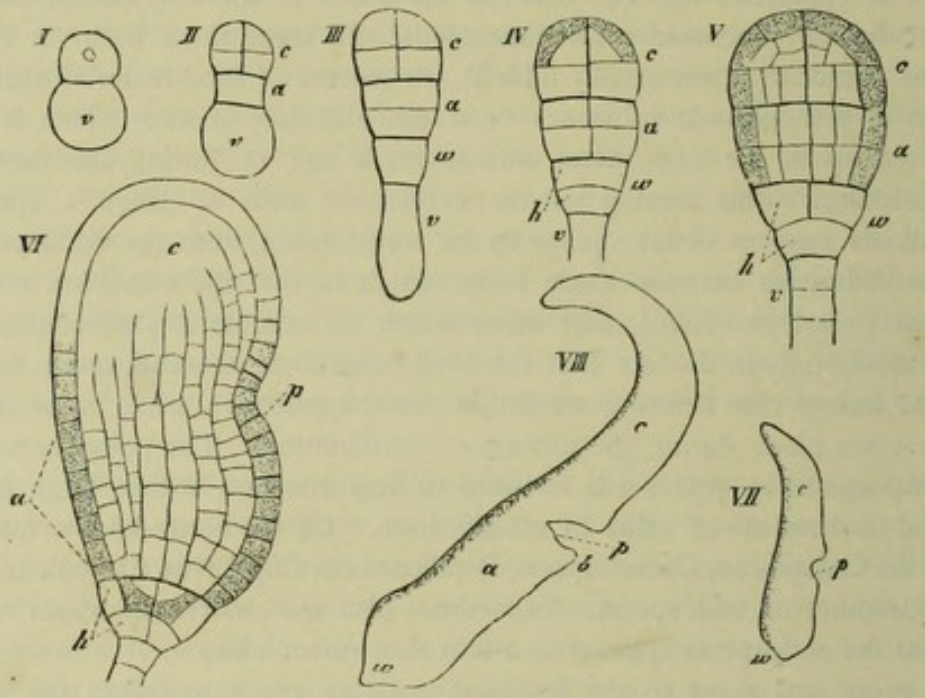

FIG. 371.—Formation of the embryo of Monocotyledons (Alisma) (after drawings by Hanstein); *I—VIII* various stages of development; *v* the pro-embryo, *h* the hypophysis, *w* the region in which the radicle is formed, *p* the region in which the plumule is formed, *c* cotyledon, *b* first leaf (*VII* and *VIII* much less magnified than the rest; the dermatogen is shaded).

when it stands obliquely to the last transverse wall, is still in the median plane of the body of the embryo which is being formed, and is frequently at right angles to the last transverse wall, and therefore in the axis of growth of the pro-embryo[1]. The formation of this median longitudinal wall in the primary embryonic vesicle completely excludes the possibility of a bi- or pluri-seriate segmentation of the apical cell. We learn from Hanstein that the mode of formation of the embryo of Monocotyledons may be seen remarkably clearly in Alisma. In Fig. 371, *II*, are shown, above the pro-embryonic cell *v*, two other cells *a* and *c* lying one over the other, the last of

[1] The description in the text is taken from Hanstein's preliminary publications (Monatsberichte der niederrhein. Gesellsch für Natur- und Heilkunde, July 15 and August 2, 1869), as well as from more detailed communications in letters. Professor Hanstein has also had the kindness to allow me the sight of a number of drawings; and, with his permission, the figs. 371–374 are copied from them. I have also had the opportunity, in the summer of 1869, of seeing preparations of Hanstein's similar to Fig. 372. Compare also Hanstein, Botanische Abhandlungen, Heft I, for a more detailed description of the development of the embryo in Monocotyledons and Dicotyledons. [See also Quart Journ. Micr. Soc. 1873, p. 51.]

which is already divided by a longitudinal and a transverse wall into four cells arranged like quarters of a sphere. A comparison of the states *II*—*V* shows that the further development advances first of all in a basipetal direction. A cell *w* or *h*, the result of intercalary division, which arises between the end of the pro-embryo and the body of the embryo *a c* already formed, is especially to be noted. It is from this that the root is subsequently developed. Hanstein calls it and the tissue which proceeds from it the *Hypophysis*. Before the body of the embryo undergoes any external differentiation, its primary meristem separates into a single peripheral layer (shaded in the drawing), and a tissue internal to this; the former is the primary epidermis or dermatogen, which continues to grow only at the surface and divides only in a radial direction; the figures *IV*—*VI* show that the dermatogen is marked off from the primary cells of the embryo by tangential divisions proceeding towards the base. The inner mass of tissue soon undergoes further differentiation; an axial string of tissue is produced by divisions, especially longitudinal, forming the plerome or tissue which subsequently produces the fibro-vascular bundles; the primary meristem lying between the plerome and the dermatogen, and which undergoes copious transverse divisions, is the periblem, *i. e.* the primary cortical tissue. At the same time that this differentiation of tissue is first indicated in the upper part *a c* of the embryo, it begins also in the hypophysis *h*. The lower layer of this hypophysis takes no part in the formation of the dermatogen, while from its upper layer (in *VI*) is formed a prolongation of the dermatogen and of the periblem of the body of the embryo, from which, as will be explained further on, the root is developed as a posterior appendage of the embryo. Hanstein designates the apical part *c* of the embryo the first cotyledon, at the base of which *b* the apex of the stem is afterwards formed laterally. But if the cotyledon is really the apical structure of the embryo, which seems to me to be not yet sufficiently established, it cannot possibly be a foliar structure, even if (as in Allium) it subsequently assumes altogether the appearance of a foliage-leaf.

The different stages in the development of the embryo from the embryonic vesicle are much more clearly seen in Dicotyledons than in Monocotyledons, the Grasses in particular among the latter presenting difficulties. Hanstein has singled out *Capsella Bursa-pastoris* for detailed description. Fig. 372 shows first of all that the mass of the embryo is developed from the spherical apical cell of the pro-embryo *v*, and in what manner this takes place; here also a basal cell *h* of the body of the embryo forms the hypophysis, from which the radicle is developed. The spherical primary cell of the embryo divides first by a longitudinal wall 1, 1 (in *I*—*IV*), followed in each of the two halves by a transverse division 2, 2, so that the body of the embryo consists at first of four quarters of a sphere, each of which next undergoes another tangential division, by which four outer cells are formed as the rudiment of the dermatogen, and four inner central cells (*II*). While the first only multiply by radial divisions, the inner mass of tissue grows in all directions, resulting at an early period in its differentiation into plerome (*III*, *IV*, *V*, shaded in the drawing), and periblem. The mass of tissue which is produced from the primary cell of the embryo thus increases rapidly by the multiplication of its cells, and two large protuberances (*V*, *c c*), the first leaves or cotyledons, soon make their appearance one on each side of the apex (*s*); the

apex of the stem exists for the present only as the end of the longitudinal axis of the embryo; an elevated piece of tissue, the vegetative cone of the stem, is not formed till later deeply enclosed between the cotyledons. The posterior or basal end of the axis of the embryo after the differentiation of its primary meristem into dermatogen, periblem, and plerome (*II*, *III*, *IV*), is, so to speak, open as long as this differentiation has not also taken place in the hypophysis (*h*); but finally it takes place in it also and in such a way (as is shown in Fig. 372, *V*), that

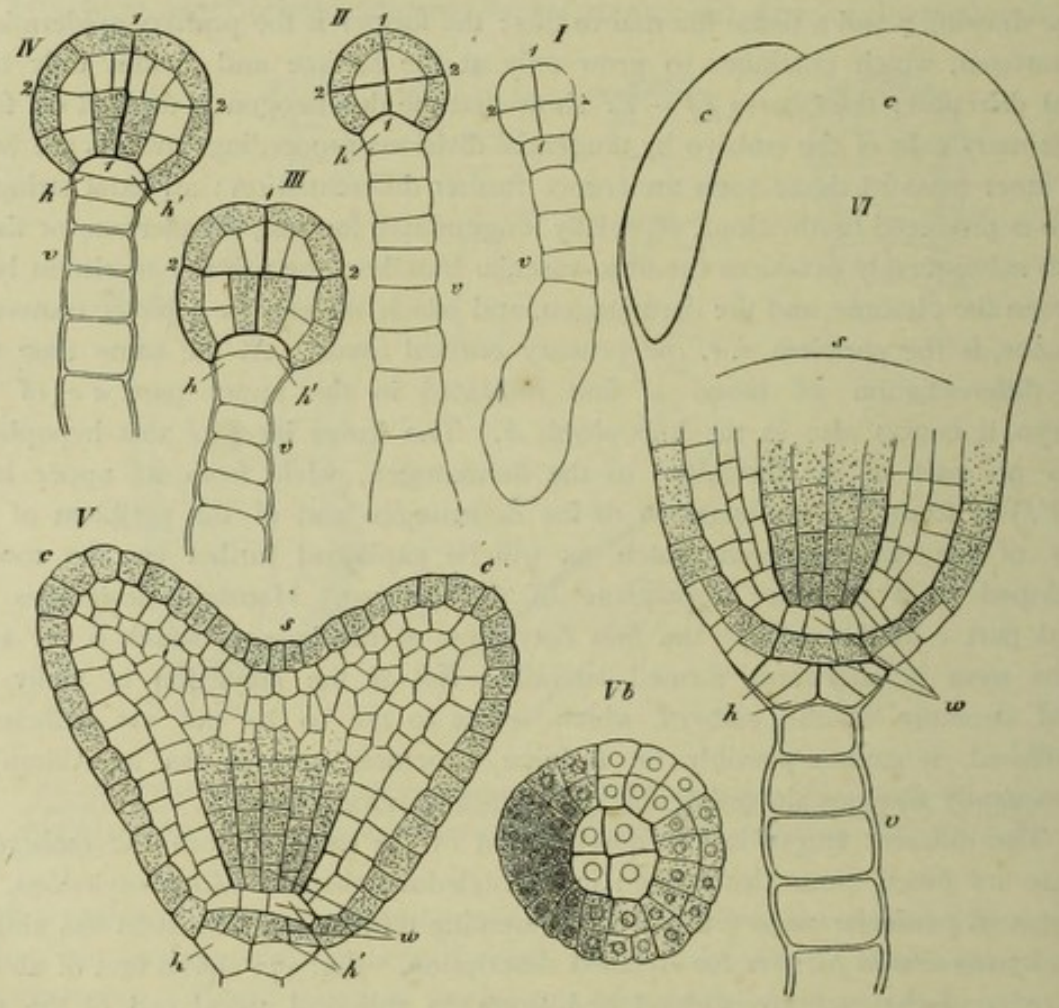

FIG 372.—Formation of the embryo of *Capsella Bursa-pastoris* (after Hanstein); *I*—*VI* various stages of development, *V b* apex of the root seen from below; 1, 1, 2, 2, the first divisions of the apical cell of the pro-embryo (suspensor), *h h* the hypophysis, *v* the pro-embryo, *c* the cotyledons, *s* apex of the axis, *w* root (the dermatogen and plerome are shaded dark).

the upper of its two cells breaks up into two layers (*h'*), the outer of which becomes continuous with the dermatogen of the axis, while the inner layer forms a prolongation of the internal axial tissue. The lower cell of the hypophysis (*h*) divides cross-wise (*V b*, seen from below) and may be regarded as a transitional structure between pro-embryo and root (appendage of the root) or as the first layer of the root-cap. Hanstein's description of the growth of the root-cap of Phanerogams, confirmed by Reinke[1], is of very great value, showing, as may be seen from

[1] Compare also Reinke, Wachsthumsgeschichte und Morphologie der Phanerogamenwurzel, in Hanstein's Botanische Abhandlungen, Bonn 1871, Heft III.

Figs. 373 and 374, that it is simply a luxuriant growth of the dermatogen. This peripheral layer of tissue, which elsewhere remains simple, and passes over into permanent tissue in forming the epidermis, increases in thickness, on the contrary, where it covers the *punctum vegetationis* of the root, and undergoes repeated tangential divisions (parallel to the surface). Of the two layers which are successively formed on each of these occasions, the outer becomes a layer of the root-cap (Fig. 373 *wh*, and Fig. 374, 2); the inner remains as dermatogen and again undergoes the same process. This dermatogen which covers the vegetative cone of the root behaves therefore like a layer of phellogen, with this difference, that the cells produced from cork-cambium become at once permanent cells, while those of the root-cap remain still capable of division; so that each layer split off as it were from the dermatogen forms a cap consisting of several layers of cells; its growth being most active in the centre, and diminishing towards the periphery. The splitting of the dermatogen into two lamellæ usually progresses from the

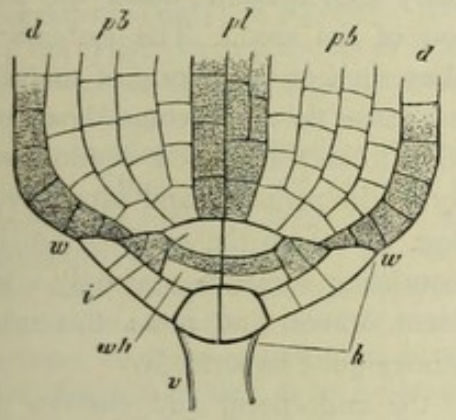

FIG. 373. — Diagrammatic representation of the formation of the primary root in Monocotyledons and its connection with the stem (after Hanstein); *v* pro-embryo, *h* hypophysis, *w w* line of separation of the root and stem, *wh* layer of the root-cap, *d* dermatogen, *p3* periblem, *pl* plerome.

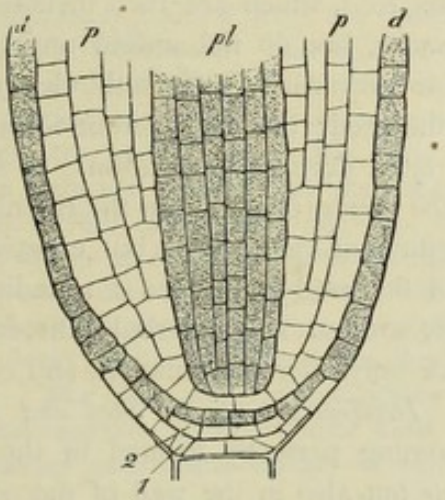

FIG. 374. — Diagrammatic representation of the formation of the embryo of Dicotyledons (after Hanstein); 1, 2, the first layer of the root-cap, *p* periblem, *d* dermatogen, *pl* plerome.

apex towards the periphery of the apex of the root; in the secondary roots of Trapa, Hanstein and Reinke state that the reverse is the case.

Lateral roots not unfrequently arise in the embryo even before the ripening of the seed, in addition to the primary root which we have hitherto alone considered; as, for instance, in many Grasses and some Dicotyledons (*e.g.* Impatiens, according to Hanstein and Reinke, Cucurbita from my own observations). In *Trapa natans* the primary root soon becomes abortive, lateral roots arising at an early period from the hypocotyledonary portion of the axis.

Hanstein and Reinke state that the lateral roots of Angiosperms have their origin in the pericambium, in Nägeli's sense of the term[1]. Their development was found in several plants to harmonise with this. In *Trapa natans*, for example, it is as follows:—A group of cells of the mantle of pericambium which consists of only one layer divides radially; the newly formed cells elongate in the same direction, and then divide tangentially; the outer of the two layers produces the dermatogen,

[1] Compare what was said on Fig. 115, p. 145.

the inner the body of the root. The dermatogen, pushed outwards by the development of the body of the root, produces the root-cap in the way already mentioned; the tissue of the body of the root itself which is covered by it becomes differentiated into plerome and periblem. The same process takes place in Pistia, and probably also in Grasses. Hanstein and Reinke do not find 'anywhere an apical cell which originates the growth, as in Cryptogams; a group of cells always obeys the common direction of growth.'

The variation in the size of the embryo in the ripe seed of Angiosperms has already been mentioned when speaking of the endosperm. The external differentiation sometimes goes no further than the rudiment of the root (radicle) at the posterior end of the stem of the embryo and the cotyledons (*e.g.* in Cucurbita, Helianthus, *Allium Cepa*, &c.), between which lies the naked *punctum vegetationis*. But frequently this latter undergoes further growth before the seed is ripe, and produces additional foliar structures (as in Grasses, Phaseolus, Faba, Quercus, Amygdalus, &c.), which are then included, in the ordinary nomenclature, under the term *Plumule*, but do not unfold until the germination of the seed. The systems of tissue are usually sufficiently clearly differentiated as such at the period of maturity of the seed; but the different forms of permanent tissue do not become developed till later, during germination. A striking exception to this advanced development of the young plant within the ripening seed is afforded by parasites and saprophytes destitute of chlorophyll, but especially by Orchideæ. In them the embryo remains until the seed is ripe as a roundish corpuscle consisting sometimes of only a few cells, without any external differentiation into stem, leaves, and root; this takes place only after germination, and even then sometimes quite imperfectly.

Development of the Seed and Fruit. While the endosperm and embryo are becoming perfectly formed in the embryo-sac, growth proceeds not only in the ovule but also in the wall of the ovary that encloses it. Since the testa is formed at the expense of the whole or part of the cellular layers of the ovular integuments, and presents extreme diversities in its structure, the ovule, together with its contents which have resulted from fertilisation, becomes the *Seed*. The wall of the ovary, the placentæ, and the dissepiments, not only increase in dimensions, but undergo the most various changes of external form and still more of internal structure. Together with the seeds they constitute the *Fruit*. The transformed wall of the ovary now takes the name of *Pericarp;* if an outer epidermal layer is specially differentiated it is called the *Epicarp*, and an inner one the *Endocarp;* while a third layer, the *Mesocarp*, frequently lies between these two. A number of typical kinds of fruit are distinguished according to the original form of the ovary and the structure of its tissue when ripe, the nomenclature of which will be given in the sequel. But sometimes the long series of deep-seated changes induced by fertilisation extends also to parts which do not belong to the ovary, and even to some which have never belonged to the flower. But as they are part of the fruit from a physiological point of view, and are usually associated with it as a whole, while sharply differentiated from the rest of the plant, a structure of this kind (such as the fig, strawberry, and mulberry) may be termed a *Pseudocarp*.

At a certain period either the fruit together with its seeds becomes detached from the rest of the plant, or the seeds alone separate from the dehiscent fruit; and

this is the period of maturity. In many species the whole plant dies down when the fruit is ripe, and a plant of this description is termed *monocarpic* (bearing fruit only once). Monocarpic plants may be distinguished into those which fructify in the first period of vegetation (*annual* plants), those which do not till the second year (*biennial* plants), and finally not till several or a large number of periods of vegetation (monocarpic *perennial* plants, as *Agave americana*). Most Angiosperms are however *polycarpic; i. e.* the vital power of the individual is not exhausted by the ripening of the fruit; the plant continues to grow and periodically fructifies afresh, or is polycarpic and perennial.

The Inflorescence. It is comparatively rare for the flowers of Angiosperms to arise singly at the summit of the primary shoot or in the axils of the leaves; peculiarly developed systems of branching are much more commonly produced at the end of the primary shoot or in the axils of its foliage-leaves, which usually bear a considerable number of flowers and are distinguished by their collective form from the rest of the vegetative system; in polycarpic plants these may even be thrown off after the ripening of the fruit. Such a system of branching is termed an *Inflorescence*. The habit of the inflorescence does not depend merely on the number, form, and size of the flowers which it bears, but also on the length and thickness of the branches of different orders, as well as on the degree of development of the leaves from the axils of which the branches spring. These leaves are generally much simpler in form and smaller than the foliage-leaves; frequently coloured (*i. e.* not green) or altogether colourless. They are distinguished as Hypsophyllary Leaves or *Bracts;* and in this term are frequently included the small leaves which spring from the pedicels and which often have no axillary shoots (*Bracteoles*). Leaves of this kind are sometimes entirely absent from the inflorescence or from certain parts of it; the ultimate floral axes or pedicels of the flowers are then not axillary, as in Aroideæ, Cruciferæ, &c. The most recent investigations by Kaufmann have shown that the very peculiar inflorescence of Borragineæ must be the result of dichotomous branching, although ordinary monopodial axillary branching occurs in their vegetative system.

A large number of different forms of inflorescence may arise by the combination in different ways of the determining characters already mentioned. Each form is constant in the same species, and is often characteristic of a whole genus or family; hence the form of the inflorescence often not only determines the habit of the plant, but is also of value in its systematic classification.

The most convenient basis for the classification of the forms of inflorescence is the mode of branching. This is less variable than the other features, and can be referred to a few types; it also affords distinctive characters for the principal groups, which might then be further sub-divided according to the length and thickness of the separate axes and other points.

With reference to the mode of branching, the first point to observe is that every inflorescence originates from the normal terminal branching of a growing axis; the mode of branching is always monopodial in Angiosperms with the exception of the cases mentioned under Division 14; *i. e.* the branches arise laterally beneath the apex of the growing mother-shoot. If the leaves on this shoot (the bracts) are conspicuously developed, the lateral axes arise in their axils; if they are inconspicuous or abortive, the lateral axes of the inflorescence are not axillary, but their mode of branching and growth remain the same as if the bracts were present; and it is usual, in framing the divisions, not to lay great stress on this circumstance. But the presence of bracts is of great practical value, since it assists in the recognition of the true mode of branching even in the mature inflorescence, inasmuch as the axillary shoot is always lateral. When the bracts are absent it is however often difficult to distinguish a lateral from a

primary axis, since the former often grows as vigorously as the latter, or even more so. In Section 24 of the chapter on General Morphology (p. 148 *et seq.*) the principles have been laid down according to which the various systems of branching may be generally classified; these will serve also in every respect for inflorescences, and form the basis of the characters of the larger groups in the following classification. Of the great number of separate forms of inflorescence only the more common ones, a nomenclature for which is already provided in systematic botany, will be enumerated[1].

A. **Racemose (monopodial), Centripetal, or Indefinite Inflorescences**, in the widest sense of the terms, result from the primary axis or rachis of the branching system producing a larger or smaller number of lateral shoots in acropetal succession; the capacity for development of each lateral shoot being smaller, or at least not greater, than that of the portion of the primary axis which lies above it.

a. *Spicate Inflorescences* arise when the lateral axes of the first order do not branch and are all floral axes; the rachis terminates with or without a flower.

(α) Spicate Inflorescences with elongated rachis:—

1. *The Spike:* Flowers sessile; rachis slender (as in some Grasses).
2. *The Spadix:* Flowers sessile; rachis thick and fleshy, usually enveloped in a large spathe; bracts generally undeveloped (Aroideæ).
3. *The Raceme:* Flowers distinctly stalked (*e.g.* Cruciferæ, without bracts; Berberis, Menyanthes, Campanula, rachis terminating in a flower).

(β) Spicate inflorescences with abbreviated rachis:—

4. *The Capitulum:* Rachis conical or tubular, or even hollowed out like a cup; flowers sessile; bracts frequently absent (Compositæ, Dipsacaceæ).
5. *The Simple Umbel:* Flowers stalked and springing from a very short rachis (*e.g.* the ivy).

b. *Panicled Inflorescences* arise when the lateral axes of the first order again branch and produce axes of the second and higher orders; every axis or only those of the last order may terminate in a flower; the capacity for development usually decreases from below upwards both on the lateral and on the primary axis.

(α) Panicled Inflorescences with elongated axes:—

6. *The true Panicle:* Axes and pedicels elongated (Crambe, grape-vine).
7. *The Compound Panicle made up of Spikes:* The elongated lateral axes bear sessile flowers (Veratrum, *Spiræa Aruncus*, the 'ears' of wheat, rye, &c.).

(β) Panicled Inflorescences with abbreviated axes:—

8. *Compact spike-like Panicle:* The very short lateral axes are arranged on an elongated primary rachis (the 'ears' of barley, Alopecurus, &c.).
9. *The Compound Umbel:* The very short rachis bears a densely compact umbel of secondary (partial) umbels usually with long stalks (*cf.* No. 5); if the compound umbel is surrounded by a whorl of leaves this is called the *Involucre;* a similar whorl surrounding the secondary umbel is an *Involucel* (secondary involucre); one or both may be absent; (most Umbelliferæ).

B. **Cymose, Centrifugal, or Definite Inflorescences** result from the primary axis branching beneath the first flower in such a manner that each lateral axis itself

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[1] Compare the dissimilar descriptions in Ascherson's Flora of the Province Brandenburg, Berlin 1864, and in Hofmeister's Allgemeine Morphologie, § 7.

terminates in a flower, after producing one or more lateral axes of a second order which in their turn terminate in flowers and continue the system in this manner; the development of each lateral shoot is stronger than that of the primary axis beyond the point of origin (see Figs. 127, 128, pp. 158, 159).

a. Cymose Inflorescences without a Pseud-axis: Two or more lateral axes are developed beneath each flower, terminating in flowers; lateral axes of a higher order continuing the system in the same manner.

10. *The Anthela:* An indefinite number of lateral axes are produced on each axis, and overtopping the primary axis develope in such a manner that the entire inflorescence does not acquire any definite shape (*e.g. Juncus lamprocarpus, tenuis, alpinus*, and *Gerardi, Luzula nemorosa*, &c.[1]). The anthela of these genera, as well as of Scirpus and Cyperus, exhibits a number of different transitional forms to the panicle and even to the spike, and on the other hand to the formation of cymose inflorescences with pseud-axes, *e.g.* in *Juncus bufonius*. The inflorescence of *Spiræa Ulmaria* is included in this form by myself and others.

11. *The Cymose Umbel:* A whorl of three or more equal axes springs from the primary one, secondary whorls of lateral axes being again produced from it, and the process being then again repeated (see Fig. 140, p. 168). The whole system resembles a true umbel in habit; very good examples are afforded by several species of Euphorbia, especially *E. Lathyris* and *helioscopia*. This form of cyme is not essentially distinct from the next, and in the highest orders of branching commonly passes into it; in *Periploca græca*, for example, even in the first ramification.

12. *The Dichasium:* Each primary axis produces a pair of opposite or nearly opposite lateral axes, which in their turn produce pairs of the second order, and so on. The whole system appears as if composed of bifurcations, especially after the older flowers have fallen off; as in Euphorbia, many Sileneæ, some Labiatæ, &c. The dichasium easily passes, in the first or a succeeding order of lateral axes, into a sympodial mode of development.

b. Cymose Inflorescences with a Pseud-axis (*Sympodial Inflorescences*). The axes of each successive order bear only one lateral axis of the next order. The basal portions of the consecutive orders of axes may lie more or less in a straight line, and may become thicker than the flower-stalk (above the branching). A pseud-axis or sympodium may thus become either straight or curved first in one direction and then in another, the flowers appearing to be produced on it as lateral shoots (see Fig. 128, *A, B, D*, p. 159). If the sympodium is clearly developed, it resembles a spike or raceme, from which however it is easily distinguished when bracts are present by their being apparently opposite to the flowers (as in Helianthemum); but displacement not unfrequently causes it to assume a different form (as in Sedum).

13. *The Unilateral Helicoid Cyme* is a sympodial cyme in which the median plane of each of the successive axes which constitute the system is always situated on the same side, whether right or left, with respect to the preceding one (see Fig. 128 *D*); as for instance, in the

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[1] Compare the careful description by Buchenau in Jahrb. für wissensch. Bot. p. 393 *et seq.* and Pl. 28–30.

primary branches of the inflorescence of *Hemerocallis fulva* and *flava*, and in the partial inflorescences of *Hypericum perforatum* which are themselves arranged in a panicle. (Hofmeister.)

14. *The Unilateral Cicinal* (*Scorpioid*) *Cyme* is one in which the successive axes arise alternately to the right and left of the preceding one (Fig. 128 *A*) as in Helianthemum, Drosera, Tradescantia, and *Scilla bifolia*. (Hofmeister.) The inflorescence of Echeveria belongs also to this kind of originally monopodial sympodium; the mature cyme has a pseud-axis on which the flowers are placed opposite the leaves. While the summit of each successive axis is converted into a flower, a lateral axis arises in the axil of the subtending leaf. This lateral axis developes further, forms a new leaf in a plane nearly at right angles to the last, and becomes transformed into a flower, while a lateral axis appears in the axil of its leaf which continues the development; the leaf which arises on this axis is in the same plane as the last but one. (Kraus.)

The inflorescences of Borragineæ and Solanaceæ differ both in their mode of development and in their external appearance from the plan described in *B b*. Kaufmann has already stated[1] that the inflorescence of some Borragineæ is the result of repeated dichotomy of the apex of an axillary bud; and Kraus has also shown[2] that the leafless inflorescence of Heliotropium and Myosotis is a monopodium, at all events when luxuriant. A thick and flattened vegetative cone developes two alternate rows of flowers *on its upper side;* on this side the longitudinal growth of the primary axis is at first stronger; and the younger part of the inflorescence is consequently rolled with its apex downwards in a circinate manner. An inflorescence which is formed in this manner, as will be seen from what has already been said, cannot properly be described as a scorpioid cyme, but corresponds rather to a raceme or spike which bears flowers only on one side of its rachis. The leafy scorpioid cymes of Anchusa, Cerinthe, Borrago, and Hyoscyamus are, on the contrary, the result of dichotomous branching; a leaf which stands on the primary axis ending in a flower bears in its axil a vegetative cone which is at first hemispherical; this becomes broader and dichotomises in a direction parallel to the surface of the leaf; one of the bifurcations becomes a flower, the other forms a new leaf at right angles to the last, and above it a dichotomy as before. The planes of dichotomy therefore cross one another at right angles; and this is the reason why the leaves always stand between the sympodial axis and the flower. Lateral displacements of the leaves begin at the second division and continue afterwards.

According to Kraus it is doubtful whether the sympodial inflorescences of Omphalodes and *Solanum nigrum* are the result of dichotomous or of lateral branching. On the side of the primary axis which becomes a flower a leafless lateral axis arises which continues to branch, and the right and left lateral axes of which are alternately transformed into flowers. Kraus entertains a similar doubt respecting weak inflorescences of Myosotis and Heliotropium (*vide supra*).

It will be seen from what has now been said, that within an inflorescence which consists of several orders of axes there may be produced not only different forms of one section, but forms belonging to both sections (*A* and *B*), mixed inflorescences being thus formed. Thus, for example, a panicle may form dichasia in its last ramifi-

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[1] Kaufmann, Bot. Zeitg. 1869, p. 886 [and Nouv. Mém. de la Soc. Imp. des Nat. de Moscow, XIII, p. 248. See also Warming, Recherches sur la ramification des Phanérogames, Vid. Selsk. Skr. 5 R. Afd. 10 (with French abstract). He confirms the view that the scorpioid cymes of Borragineæ and Hyoscyamus originate through dichotomy.—Ed.]

[2] Kraus, Sitzungsberichte der med.-phys. Soc. in Erlangen, Dec. 5, 1870. I have also derived a part of the above from correspondence with Kraus.

cations (as in some species of Silene); a dichasium may bear capitula (*e. g.* Silphium), or even in its first branches or in those of a higher order may pass into a helicoid or scorpioid cyme (as in Caryophylleæ, Malvaceæ, Solanaceæ, Linaceæ, Cynanchum, Gagea, Hemerocallis, &c.). The mode of branching of the inflorescence is in most cases different from that of the vegetative stem. Not unfrequently it passes abruptly from one to the other, but often through intermediate modes of branching.

In the older systems of nomenclature a number of other terms are given to various forms of inflorescence, such as glomerulus, corymb, &c.; but they all designate merely the habit or external form of the system, and must be referred, in a scientific description, to one or other of the above forms or to combinations of them.

Number and Relative Position of the Parts of the Flower. Just as the forms of branching of the inflorescence are usually different from those of the vegetative stem, the arrangement of the leaves of Angiosperms is also usually different on the shoot which constitutes the flower from that on other parts of the same plant. The cessation of the apical growth of the receptacle, its great increase in breadth, or even hollowing out, before and during the time when the perianth and the sexual organs are being formed, influences their order of succession and their divergence from one another. But since, notwithstanding the extraordinary variation of the other relations of form, the true position of the floral leaves varies but little—though it may often be difficult to determine—the knowledge of this position is often of great importance in the determination of the affinities of the species, and hence for purposes of classification. This is especially the case if we at the same time take into account the abortion of individual members which is here of so common occurrence, the multiplication of the parts which take place under certain circumstances, and their branching and cohesion.

In order to facilitate a description of these relationships, it is necessary to explain certain terms and methods of description.

In the first place it is important to denote the position of all the parts of a flower with respect to the mother-axis of the floral shoot. For this purpose the side of the flower which faces the mother-axis is termed the *posterior*, that which is most remote from it the *anterior* side. If a plane be imagined to divide the flower longitudinally from front to back, and to include the primary axis of the flower as well as that of the mother-shoot, this is the *median plane* of the flower, dividing it into a right and a left half. Floral leaves, as well as ovules and placentæ which are bisected longitudinally by the median plane are said to have a median position, either posterior or anterior. If another plane is now imagined at right angles to the first, and also including the axis of the flower, it may be termed the *lateral plane;* this plane divides the flower into a posterior and an anterior half, and parts which are longitudinally bisected by it are precisely lateral. The two planes which bisect the right angle between the median and the lateral planes may be called *diagonal planes*, and the parts which are bisected by them be said to have a diagonal position. Flowers usually have some of their floral organs placed exactly posteriorly or anteriorly, not so commonly exactly right and left or exactly diagonally; but usually other additional terms must be used, such as obliquely posterior or obliquely anterior.

If next the position of the parts of the flower with respect to one another be examined, their arrangement, as has already been mentioned, is either *spiral* or *verticillate*.

Flowers with a spiral arrangement of their parts are comparatively rare, and apparently occur only in certain orders of Dicotyledons (Ranunculaceæ, Nymphæaceæ, Magnoliaceæ, and Calycanthaceæ). Braun has termed such flowers *acyclic*, when the transition from one foliar structure to another, as from calyx to corolla or from corolla to stamens, does not coincide with a definite number of turns of the spiral (as Nymphæaceæ and *Helleborus odorus*); *hemicyclic* when it does so coincide. This latter term may also be employed when some of the foliar structures are actually cyclic (verticillate) others spiral, as in Ranunculus, where the calyx and corolla form two alternating whorls, followed by the stamens and carpels arranged spirally. Parts which have a spiral

arrangement sometimes occur in definite numbers, more often in larger indefinite numbers.

When on the other hand the parts of the flowers are arranged in whorls, the number of the whorls, as well as that of the members of each whorl, is constant in the same species, and within larger or smaller circles of affinity. When the number of members of each whorl is the same, and those belonging to the different whorls are placed one over another so as to form orthostichies, I adopt Payer's expression of *superposed* (instead of the ordinary one of 'opposite'). When the stamens are superposed on the calyx or corolla, they are termed respectively *episepalous* and *epipetalous;* if the members of a whorl fall between the median lines of those of the next whorl above or below, the whorls are *alternate;* and Braun calls those flowers *eucyclic* in which the members of all the whorls are equal in number and alternate. It also happens however that members of the same kind arise subsequently between those of a whorl already formed; as, for instance, five later stamens between the five earlier ones in *Dictamnus Fraxinella* (Fig. 357, p. 493), and probably in many eucyclic flowers with ten stamens. Members subsequently introduced in this manner into a whorl may be called *interposed.* (For further details, *vide infra.*)

The consideration of the number of the parts of the flower cannot be separated from that of their relative position. But before entering more minutely upon this subject, the construction of the Floral Diagram must be described.

The *Floral Diagram* is constructed differently according to the purpose it is intended to serve. Some treat it as a somewhat free drawing of an actual transverse section of



FIG. 375.—Diagram of the flower of Liliaceæ.



FIG. 376.—Diagram of the flower of Celastrus (after Payer).



FIG. 377.—Diagram of the flower of *Hypericum calycinum.*

the flower, and indicate on it not merely the number and position, but approximately the form, size, æstivation, cohesion, &c., of its parts. This purpose is however clearly best attained by preparing as accurate drawings as possible of actual transverse sections of the flower-bud, which will then also contain much that would be superfluous for observations of a certain kind. But if it is merely required to represent the number and position of the parts of the flower in such a manner as to render as easy as possible the comparison in this respect of a number of flowers, it is best to disregard all other properties, and to adopt one and the same plan for all diagrams, and that as simple as possible, so as to represent nothing but the variations in the relationships of number and position. This is the only purpose kept in view in the diagrams given in the remainder of this work, of which Figs. 375–377 may serve for the present as examples. They are constructed according to the rule already given on p. 167; the dot above the diagram always represents the position of the mother-axis of the flower; and the lower is therefore the anterior part. Although mere dots would be sufficient to indicate perfectly the number and position of the parts of the flower, different signs have nevertheless been chosen for the various separate organs, in order to render the explanation more readily visible to the eye. The leaves of the perianth are represented by arcs of a circle, a kind of midrib being indicated on each of the outer whorl of these, or calyx, merely in order to distinguish them at a glance from the inner whorl. The sign chosen for the stamens resembles a transverse section of an anther, but without reference to the position of the pollen-sacs or of their mode of dehiscence whether inwardly or outwardly. When the

stamens are branched, this is indicated by the signs being grouped, as in Fig. 377, where the five groups correspond to five branched staminal leaves. The gynæceum is treated as a simplified transverse section of the ovary, since it is thus most easily distinguished from the other parts; the marks within the loculi of the ovary indicate the ovules, which however are only represented in those cases where their actual position can be expressed by so simple a plan. The size, form, and cohesion of the separate parts are not taken into account at all. The construction of these diagrams is based partly on careful investigations of my own, but chiefly on the studies of Payer in the history of development (Organogénie de la fleur), as well as on the descriptions of other authors (Döll, Eichler, and Braun).

I draw a distinction between *empirical* and *theoretical* diagrams. The empirical diagram only represents the relative number and position of the parts, just as a careful observation shows them in the flower; but if the diagram also indicates the places where members are suppressed—which can only be determined by the history of development and by comparison with allied species, especially if it points out relationships which are entirely the result of theoretical considerations—I call it a theoretical diagram. If the comparison of a number of diagrams shows that, although empirically different, they nevertheless yield the same theoretical diagram, this common theoretical diagram may be termed the type or *typical* diagram according to which they are all constructed. I consider the careful determination of such types an important problem, the solution of which may be extremely useful in the classification of Angiosperms. When the type has once been ascertained, the theoretical diagrams which correspond to it may be treated

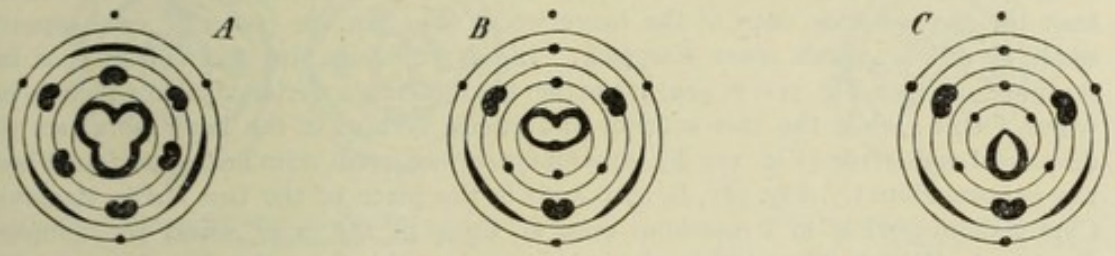

FIG. 378.—Diagram of the flower of a Grass; *A* Bambusa; *B* of most Grasses; *C* of Nardus (from Döll, Flora von Baden, vol. I, pp. 105, 133).

as derivative forms from which particular members have disappeared, or where they have been replaced by a number of members. From the stand-point of the theory of descent the type corresponds to a form still in existence or that has already disappeared, from which the species to which the derivative diagrams belong have arisen by degeneration (*i. e* by abortion[1]) or by multiplication of the parts.

A few examples will explain this. The flower of Grasses which is seated among the pales may be deduced, as is shown in Fig. 378, on the theory of the abortion of certain parts from the typical flower represented in Fig. 375, which is itself the typical diagram of Liliaceæ. *A* is the diagram of Bambusa, which only deviates from the type in the absence of the outer perianth-whorl which is indicated by dots. But in most other Grasses (*B*) the posterior leaf of the inner perianth-whorl (this whorl appearing generally only in the form of small colourless scales), the whole of the inner whorl of stamens, and the anterior carpel, are also wanting. In Nardus again (*C*), the anterior carpel only is present (as far as the pistil is concerned); all the absent parts are represented by dots,

[1] The construction of the diagram itself shows that the theory of abortion is justified even where the earliest state of the flower-bud gives no indication of the absent member, if the number and position of the parts present point distinctly to such a hypothesis. If the idea of abortion in this sense is not admitted, neither can the increase in number of individual parts, or their replacement by several, be allowed. It is only the theory of descent that gives a rational explanation of either fact, and that a very clear one.

and the diagram is therefore so far a theoretical one. If the dots are removed, we get the empirical diagram; the number and position of the carpels is here determined from those of the stigmas[1].

The flowers of Orchideæ can also be derived, like those of Gramineæ, from the type represented in Fig. 375, the empirical diagram of Liliaceæ, although their external form is so remarkably different. While in Grasses the perianth is especially degenerated or even partially abortive, in Orchids both whorls are developed in a petaloid, and like the whole flower in a zygomorphic or monosymmetrical manner. Of the androecium, which consists typically of two alternating whorls, each of three stamens, only a single stamen is completely developed in most Orchids (Fig. 379, *A*), viz. the anterior one of the outer

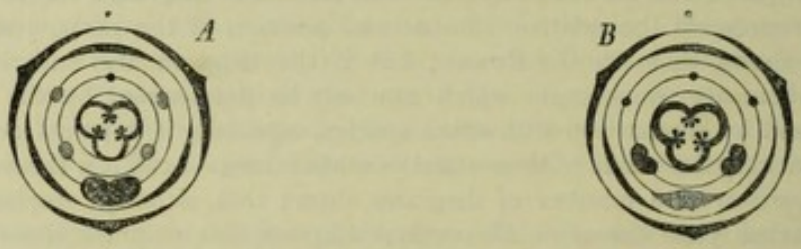

FIG. 379—Diagram of the flower of Orchideæ: *A* the ordinary structure; *B* that of Cypripedium (see Figs. 341 and 363): the dots indicate stamens which are altogether abortive, the shaded figures rudimentary stamens which become abortive or transformed into staminodes.

whorl, the others being abortive. Indications of these are however sometimes found in the young bud, as in *Calanthe veratrifolia* (according to Payer, *cf.* Fig. 363), where at least the two anterior ones of the inner whorl (but not the posterior one) appear as small elevations which soon disappear. In Cypripedium, on the contrary, a large staminodium (see Fig. 341, p. 479) takes the place of the anterior stamen which is elsewhere fertile; while the two anterior and lateral anthers of the inner whorl are fully developed and fertile (Fig. 379 *B*). In Ophrydeæ two small staminodes are found beside the gynostemium (*cf.* Fig. 387, *D*, *st*, p. 536) in the place of the two fertile stamens of Cypripedium; while in Uropedium even all three of the inner whorl are completely developed. (Döll.) The carpels which, by adhesion with the androecium form the gyno-



FIG. 380.—Diagram of the flower of Fumariaceæ (after Eichler).

stemium, are developed unequally, a difference which however is usually not discernible in inferior ovaries, and is therefore not indicated in the diagram. The student who desires to investigate these relationships for himself must observe that the long inferior ovary of most Orchids undergoes a torsion at the time of the opening of the flower, which causes the posterior side of the flower to assume an anterior position; but transverse sections even of advanced buds show clearly the true position of the parts of the flower in relation to their mother-axis.

The flowers of most Monocotyledons, like those of Orchids and Grasses, can be derived from a type which is actually seen in Liliaceæ, and which represents a flower

[1] Compare further, Döll, Beiträge, in the Jahresbericht des Mannheimer Vereins für Naturkunde, 1870, where an actual pentacyclic trimerous flower of Streptochæte is described.

consisting of five alternating whorls, each with three members, of which the two outer ones constitute the perianth, the two next the andrœcium, and the last the gynæceum; although the latter may sometimes be represented by two whorls. Occasionally instead of abortion an increase of number takes place in particular whorls, by the formation of one member instead of two (as in Butomus, Fig. 351, p. 489).

Increase in the typical number of the members of a whorl may arise in different ways, as the following examples will show. According to the detailed researches of Eichler[1], the flowers of Fumariaceæ may be referred to a type in which there are six decussate pairs of members (Fig. 380), viz.—

two median sepals,
two lower lateral (exterior) petals,
two upper median (interior) petals,
two lateral stamens,
two median (always abortive) stamens,
two lateral carpels.

The two lateral stamens are however represented in some genera (as Dicentra and Corydalis) by two groups, each consisting of three stamens, an inner one with an entire quadrilocular anther, and two lateral stamens each with a bilocular anther, a structure which Eichler explains on the hypothesis that the lateral stamens are only stipular structures, and therefore branches from the base of the middle one. In Hypecoum Eichler assumes a cohesion of each pair of opposite stipular stamens so as to form an apparent whorl of four stamens.

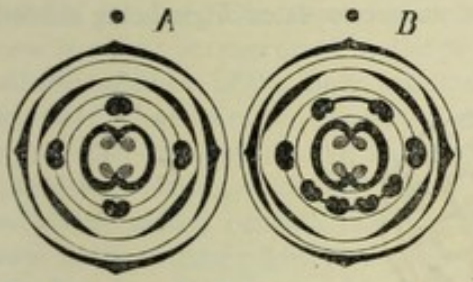

FIG. 381.—Diagram of the flower of Capparideæ; *A Cleome droseræfolia*, *B Polanisia graveolens* (after Eichler).



FIG. 382.—Diagram of the flower of Cruciferæ.

Eichler also deduces the flowers of Cruciferæ and Cleomeæ (a section of Capparideæ) from a type represented by Fig. 381 *A*, which is also the empirical diagram for *Cleome droseræfolia*, and for certain species of Lepidium, Senebiera, and Capsella. This typical flower consists of

two lower median sepals,
two upper lateral sepals,
four diagonal petals in one whorl,
two lower lateral stamens,
two upper median stamens,
two lateral carpels.

Deviations from this type are produced by the formation of two or more stamens in place of each of the upper (inner) ones; in the Cruciferæ usually two (Fig. 382), in the Cleomeæ sometimes two, sometimes more (Fig. 381 *B*). Such a replacement of one

[1] Eichler, Ueber den Blüthenbau der Fumariaceen, Cruciferen, und einiger Capparideen, in (Regensburg) Flora 1865, nos. 28–35, and 1869, p. 1.—Peyritsch, Ueber Bildungsabweichungen der Cruciferenblüthen, Jahrb. für wiss. Bot. vol. VIII, p. 117.

stamen by two or more is termed by Payer *Dédoublement*[1], by Eichler and others *Collateral Chorisis*, and must apparently be considered as a branching of very early origin. This view is confirmed in this case by the fact that in the Crucifer Atelanthera, the median stamens are only split and the two halves of each provided with half-anthers, while in Crambe each of the four inner stamens puts out a lateral sterile branch, which may be explained as the commencement of a further multiplication of the stamens such as actually occurs in the Crucifer Megacarpæa and in many Cleomeæ. Even if the way in which increase of the typical dimerous number of the inner whorl of stamens has been brought about be still obscure, it appears certain that the inconstancy of the number of the members of the staminal whorl proves that in Cruciferæ and Cleomeæ a deviation has arisen in this part of the flower from the typical dimerous number, while the other whorls have remained unchanged. The only deviation which occurs in the gynæceum of the Crucifers is in the genera Tetrapoma and Holargidium, where, besides the two lateral carpels, two median ones are also produced, thus forming a four-lobed ovary[2].

An essentially different kind of increase in the typical number of the members of a floral whorl may be caused by the formation in the still very young bud of new members of the same kind between those already in existence and on the same zone of the receptacle; *i.e.* by what we have already described as the *Interposition* of new members. This I found to occur, for example, in *Dictamnus Fraxinella* (Fig. 357), and is represented in the diagram, Fig. 383, by the stamens of later origin being shaded not so



FIG. 383.—Diagram of the flower of *Dictamnus Fraxinella* (*cf.* Fig. 357, p. 493).

dark as those of earlier origin. It may, I think, be inferred from Payer's descriptions and drawings that the same process occurs in the nearly related genus Ruta, and in the families Oxalideæ, Zygophyllaceæ, and Geraniaceæ included in the same circle of affinity; *viz.* that in these cases also five stamens are interposed between those already in existence. If the five interposed stamens are supposed to be removed, there remains in these families a regular pentamerous flower with four alternating whorls each consisting of five members, such as is found in the nearly related Linaceæ and Balsamineæ[3].

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[1] [The theory of an original dimerous symmetry in the flowers of Cruciferæ has been pushed still further by Meschaeff (Bull. Soc. Imp. Nat. Mosc.), who regards the four petals as also the result of a lateral dédoublement of a single pair (see Bentham, Ann. Address Linn. Soc. 1873).—ED.]

[2] [Holargidium is a section of Draba. According to Bentham and Hooker the four carpels of Tetrapoma are an abnormality not constant under cultivation. The same authors also mention the occasional occurrence of a similar abnormality in Brassica and Nasturtium.—ED.]

[3] Döll (Flora von Baden, vol. III. pp. 1175, 1177) and others suppose that a whorl has become abortive between the corolla and ovary in Rutaceæ and Oxalideæ, a hypothesis which is not supported by the history of development, and which is superfluous on our hypothesis. To assume abortion merely because certain whorls do not alternate seems to me to be going too far. Besides, the ten stamens of Epacrideæ and Rhodoraceæ cannot belong to two but only to one whorl in which five are of earlier origin, and five have been interposed. (Compare Payer, Organogénie de la fleur, pl. 118).

Floral Formulæ. The diagram may, under certain circumstances, be substituted, at least partially, by a formula composed of letters and numbers. In a floral formula of this kind the relative positions of the parts cannot indeed always be represented with accuracy; but it has the advantage that it can be expressed by ordinary printer's type, and, what is perhaps of greater importance, is capable of a wider generalisation, since the numerical coëfficients may be replaced by letters.

The construction and application of these formulæ will easily be made intelligible by a few examples[1].

The formula $S_3 P_3 St_{3+3} C_3$ corresponds to the diagram of the Liliaceæ, Fig. 375, and signifies that each of the two perianth-whorls—the outer whorl or sepals *S*, and the inner whorl or petals *P*—consists of three members, the andrœcium of two whorls each of three stamens *St*, and the gynæceum of three carpels *C*. The diagram shows in addition that these trimerous whorls alternate without interruption; but since this is the usual case with flowers, it need not be specially indicated. The formula $S_3 P_3 St_3^2{}_{+3} C_{3+3}$ gives the relative positions of the parts of the flower of *Butomus umbellatus* (Fig. 351, p. 489). It is distinguished from the previous one by the gynæceum consisting of two whorls of three carpels each, and the andrœcium having the typical three stamens of the outer whorl each replaced by two stamens, which is expressed by the symbol 3^2. The formula $S_0 P_3 St_{3+3} C_3$ corresponds to the diagram of the flower of Bambusa, Fig. 378 *A* (p. 525), and differs from that of Liliaceæ only in the suppression of the outer perianth-whorl, represented by S_0. The numerical relations of the parts of the flower of Orchideæ, Fig. 379 *A*, might be expressed by the formula $S_3 P_3 St_{\ddot{1}+0} C_3$, the symbol $St_{\ddot{1}+0}$ indicating that all the members of the inner staminal whorl are abortive, while on the other hand in the outer whorl the two posterior ones are suppressed, the anterior outer stamen being perfectly developed; the two dots over the number ï are meant to indicate that the absent members are the posterior ones; were the anterior ones deficient the dots would be placed beneath the number, as in the formula $S_0 P_{\dot{2}} St_{3+0} C_{\dot{2}}$ which corresponds to the ordinary flower of Grasses represented by the diagram Fig. 378 *B*. The formula $S_2 P_2 St_{2+2} C_2$ expresses the whorls consisting of decussate pairs which form the flower of *Maianthemum bifolium*; the formula $S_4 P_4 St_{4+4} C_4$ or $S_5 P_5 St_{5+5} C_5$ the flowers of *Paris quadrifolia*, in which all the whorls are either tetramerous or pentamerous. These and most other formulæ for the flowers of Monocotyledons may now be combined into a general expression $S_n P_n St_{n+n} C_{n\,(+n)}$, which signifies that the flowers belonging to this type are usually constructed of five alternating whorls each with the same number of members, two of which are developed in the form of perianth-whorls, two as staminal whorls, and generally only one as a carpellary whorl; the bracket $(+n)$ at the end of the formula indicating that a second carpellary whorl sometimes occurs in addition. The general number *n* may, as the examples which have been adduced show, have the value 2, 3, 4, or 5; 3 is the most common. If a considerable increase of the number of members takes place in a whorl, and if this number, as is then usually the case, is variable, this is expressed by the symbol ∞; thus the formula for *Alisma Plantago* is $S_3 P_3 St_{3+3} C_\infty$.

As has already been mentioned, no further indication is given of the position of the whorls when they alternate; when a departure from this rule occurs, this can be more or less accurately expressed by special symbols. Thus, for example, the formula for the flower of Cruciferæ, Fig. 382, might be represented by $S_{2+2} P_{\times 4} St_{2+2}{}^2 C_{2(+2)}$, the symbol $P_{\times 4}$ signifying that the decussate pairs of sepals are followed by a corolla consisting of one whorl of four petals, which are however arranged diagonally to the sepals. In order to express the superposition of two consecutive whorls, a vertical stroke might

[1] Grisebach (Grundriss der systematischen Botanik; Göttingen, 1854), has denoted the relative numbers of the parts of flowers in a different manner, placing the numbers of the members of a whorl simply one after another, and indicating cohesions by strokes.

be placed after the number of the first whorl; thus $S_5 P_5 \mid St_5^{v} C_5$ might represent the formula for *Hypericum calycinum* (Fig. 377, p. 524), St_5^{v} indicating that the andrœcium consists of five branched stamens which are superposed on the petals. If, finally, it is desired to signify that members of a second whorl are interposed at the same level between those of one already in existence, the number of the new members may be placed simply beside those of the original whorl; thus the formula $S_5 P_5 St_{5\cdot5} C_5$ would correspond to the diagram, Fig. 383, p. 528.

In the formulæ already given no cohesions of any kind have been indicated; they can however under certain circumstances easily be expressed by special symbols. Thus, in the formula for Convolvulus, $S_5 \widehat{P_5} St_5 \widehat{C_2}$, the sign $\widehat{P_5}$ indicates a gamopetalous corolla of five petals, $\widehat{C_2}$ a syncarpous ovary of two carpels. In the formula for the flowers of Papilionaceæ again $\widehat{S_5} P_5 St_{\widehat{5+4}+1} C_1$, the expression $St_{\widehat{5+4}+1}$ signifies that the five stamens of the outer and four of those of the inner whorl have united into a tube, while the posterior stamen of the inner whorl remains free[1].

The mode of writing the formulæ must vary according to the object which one has in view; the greater the number of relationships it is intended to express, the more complicated will they become; and care must be taken that they do not lose their clearness by being overladen by too many signs.

The examples of formulæ which have hitherto been adduced all illustrate cyclic flowers; those parts of flowers which are arranged spirally may be denoted by the symbol $\sim$ placed before them, and the angle of divergence may also be affixed to their number. Thus, for example, the relative numbers and positions of the parts of the flower of Aconitum, according to Braun's investigations, may be expressed by the formula $S_{\sim 2/5} P_{\sim 3/8} St_{\sim 8/21} \infty\ C_{\sim 3}$, which indicates that all the foliar structures of this flower are arranged spirally, and that the calyx consists of five sepals with the divergence $^2/_5$, the corolla of eight petals with the divergence $^3/_8$, and the andrœcium of an indefinite number of stamens with the divergence $^8/_{21}$. It would however be sufficient in this case, since the spiral arrangement runs through the whole flower, to place the symbol only once before the whole formula, thus $\sim S_{2/5} P_{3/8} St_{8/21} \infty\ C_3$.

In flowers with a cyclic arrangement of their parts a statement of the angle of divergence is generally unnecessary, since the members of each whorl usually arise simultaneously, and are arranged so as to divide the circle into equal parts. When they do not arise simultaneously but successively in the circle with a definite angle of divergence, as in most trimerous or pentamerous calyces, this can be indicated by placing the angle of divergence after the number of the members; thus the formula for Linaceæ would be $S_{5\,2/5} P_5 St_5 \underline{C_5}$. If, on the other hand, the members of a whorl are formed in succession from front to back, this may be shown by an arrow pointing upwards ↑, as in the formula for Papilionaceæ $S_5\uparrow P_5\uparrow St_5\uparrow_{+5}\uparrow C_1$. If they are formed in succession from back to front, the arrow may be made to point downwards ↓, as in the formula for Reseda $S_n\downarrow P_n\downarrow St_p\downarrow_{+q}\downarrow C_r$, where the number of the parts is expressed by letters instead of figures in consequence of its variability[2].

Order of Succession of the Parts of the Flower. The foliar structures arise on the axis of the floral shoot, as on other axes, in acropetal order below the growing apex. It is however not uncommon in the formation of flowers for the apical growth of the axis to cease altogether or to become extremely slow, while the receptacle continues to increase in breadth, and to develope transverse zones of intercalary growth. When this is the case the acropetal order of development is disturbed, and new whorls may become interposed between those already in existence. But even within the same floral whorl the individual members may be formed in a very different order of succession, according as the zone of the receptacle which bears the floral leaves is developed in a uniform

[1] See also Rohrbach, Bot. Zeitg. 1870. pp. 816 *et seq.*

[2] See Payer, Organogénie de la fleur; also our Fig. 137, p. 166.

manner all round (as in polysymmetrical flowers) or more rapidly on the anterior or the posterior side (which is especially the case in monosymmetrical or zygomorphic flowers).

In flowers with a spiral arrangement of their parts[1], disturbances of the acropetal order of development are of less importance the more numerous the parts with a spiral arrangement, and the longer the apical growth of the floral axis continues. Those members which have a spiral arrangement arise one after the other in ascending order; the angle of divergence may either be constant or may change. Thus, according to Payer, in Ranunculaceæ and Magnoliaceæ the perianth-leaves and stamens arise in a continuous spiral, but each whorl of stamens consists of a larger number of members than the whorls of perianth-leaves; thus, *e. g.*, in *Helleborus odorus*, where all the organs of the flower are arranged spirally, each whorl of the corolla consists of only thirteen petals, while each whorl of stamens numbers twenty-one. According to Braun the whorls of the calyx of *Delphinium Consolida* have a $^2/_5$ arrangement[2]; the divergence then undergoes a small change, but without materially deviating from $^2/_5$; the first whorl with this altered arrangement is the corolla; the three following ones are the stamens, and the spiral terminates with a single carpel. In the section Garidella of Nigella the first of the whorls with a $^2/_5$ angle of divergence is the calyx and the second the corolla; then follows a slight change in the angle to $^3/_8$, the stamens forming one or two whorls with this arrangement; and the spiral closes with three or four carpels. In the section Delphinellum of Delphinium the calyx constitutes a whorl with $^2/_5$, the corolla one with $^3/_8$ angle of divergence; then follow two or three whorls of stamens with the angle very near $^3/_8$, the spiral closing with three carpels. In the section Staphisagria of the same genus, and in Aconitum, the calyx forms a whorl with $^2/_5$, the corolla one with $^3/_8$ angle; the stamens stand in one or two whorls with the divergence $^8/_{21}$ or $^{13}/_{34}$; concluding with three, five, or rarely a larger number of carpels. It must be noted in reference to these arrangements that the members of successive whorls stand in orthostichies when the angle of divergence remains constant; but that the orthostichies pass into oblique rows when the divergence undergoes a small change.

The first thing to observe in cyclic flowers (*i. e.* those in which the parts are arranged in whorls) is the order of formation of the whorls with respect to one another, and then the order in which the members of each whorl are themselves formed; although the two are in fact closely connected. A disturbance of the acropetal order of succession in the formation of the whorls occurs when the carpels have begun to be formed before all the stamens which stand below them have been produced, as in Rubus, Potentilla, and Rosa[3], or when the calyx is not formed until after the andrœcium (as in *Hypericum calycinum* according to Hofmeister), or when the calyx is not observable until after the corolla has become considerably developed or even after the formation of the stamens and carpels, as in Compositæ, Dipsacaceæ, Valerianaceæ, and Rubiaceæ.

One of the most remarkable deviations from the general rule of the order of development of the floral whorls occurs in Primulaceæ, where five protuberances (primordia) appear on the receptacle above the calyx, each of which grows up into a stamen, while on the posterior or lower side of the base of each primordial stamen a lobe of the corolla subsequently appears. Pfeffer, who has observed this order of development (Jahrb. für wissensch. Bot. vol. VII, p. 194), considers that the same probably also happens in the pentandrous Hypericineæ and in Plumbagineæ; he therefore explains the corolla-lobes as posterior outgrowths of the stamens (a posterior ligular structure), such as, for

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[1] Compare Payer, Organogénie de la fleur, p. 70; *et seq.*; and Braun, Jahrb. für wissensch. Bot., Ueber den Blüthenbau der Gattung Delphinium.

[2] Compare with this what is said below respecting sepals and petals which are formed with the angle of divergence $^1/_3$ and $^1/_5$.

[3] Compare Hofmeister, Allgemeine Morphologie, pp. 436 *et seq.*, where Payer's observations on this point will also be found.

instance, occur on the stamens of Asclepiadeæ in the form of hood-shaped nectaries, where a true corolla is also present. The flowers of Primulaceæ would therefore be strictly apetalous in the morphological sense of the word, since their corolla is not a true floral whorl, but only an outgrowth of the staminal whorl. In other families of Dicotyledons, on the other hand, superposed corollas and andrœcia arise separately and in acropetal order; as, for instance, in Ampelideæ, probably also in Rhamnaceæ, Santalaceæ, and Chenopodiaceæ.

The individual members of a floral whorl may arise in succession from front to back or the reverse, especially when the flowers themselves are subsequently developed zygomorphically. Thus, for instance, in Papilionaceæ the anterior median sepal is formed first, then simultaneously one to the right and one to the left, and finally the two posterior ones; but before these last arise the two anterior petals appear, followed by the two lateral and finally the posterior one; and the andrœcium, consisting of two alternating whorls of five stamens each, is formed in the same manner from front to back[1]. In the Resedaceæ on the contrary (Reseda and Astrocarpus), Payer states that the petals, stamens, and carpels are developed from behind forwards on both sides (*cf.* Fig. 137, p. 166).

When the calyx consists of pairs of sepals, those of each pair are formed, as Payer has shown, simultaneously; but if the calyx consists of three or five sepals, they are usually formed one after another, and with the angle of divergence in one case $^1/_3$ in the other $^2/_5$; but the succeeding whorls, the petals stamens and carpels, usually arise as simultaneous whorls, with the exceptions already named and others still to be spoken of.

It is well to draw attention here to the circumstance that it does not follow from the order of succession advancing from one point, with a definite angle of divergence, say $^1/_3$ or $^2/_5$, that the arrangement is a spiral one[2]; it may just as well in such cases be a whorl. The nature of the arrangement depends on the circumstance whether the foliar structures in question are formed at the same height or not, *i. e.* at an equal distance from the centre of the flower; if this is the case, we have a whorl; but if the members arise in acropetal order at different heights, *i. e.* approaching the centre of the flower with each step in the divergence, the arrangement is a spiral one. The last appears to be actually the case in many calyces; but it is doubtful whether it ever occurs where the angle of divergence of the sepals is $^1/_3$ or $^2/_5$.

We must now refer again to the cases already mentioned, where new members of a whorl are formed between those already in existence and at the same height[3]. In the Oxalideæ, Geraniaceæ, Rutaceæ, and Zygophyllaceæ, an entire whorl of five stamens is thus interposed between those already present; according to Payer, in *Peganum Harmala*, a whorl of ten stamens is even formed in this manner, arising, not in pairs between the first five, but lower down at the bases of the petals; whether the later formed stamens arise on the same level with the first or lower down is obviously regulated according to the space afforded by the changes of form of the growing receptacle. A still further departure from the ordinary process occurs in the Acerineæ, Hippocastaneæ, and Sapindaceæ, where Payer asserts that a whorl of five stamens is first of all formed alternating with the corolla, in which an imperfect whorl of two or four stamens is subsequently interposed at the same height, as is shown by his illustrations. In Tropæolum, on the other hand, according to Payer and Rohrbach[4], three stamens first of all appear after

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[1] On the nearly related Cæsalpineæ see Rohrbach, Bot. Zeitg. 1870, p. 826.

[2] Compare the successive true whorls of Chara and Salvinia, pp. 279, 389.

[3] Compare also on this point Pfeffer, Jahrb. für wiss. Bot. vol. VIII, p. 205.

[4] Rohrbach (Bot. Zeit. 1869, Nos. 50, 51) however gives a different explanation to these observations from that mentioned here. The equal or greater distance at which the later stamens arise from the centre of the flower is a distinct proof that one cannot in this case suppose that the parts are produced in a spiral arrangement advancing from without inwards.

the formation of the petals, and then between them five others, the distance of which from the centre of the flower is however rather greater than that of the three earlier ones.

Symmetry of the Flower. If the observations which will be found on p. 166 *et seq.*, under the head of General Morphology are now applied to the floral shoot, it is seen that true symmetry and distinctly bilateral structure occur here far more commonly than on the vegetative shoots. In contrast to the lax mode of expression used by many botanists, I understand by Symmetrical Structures those which may be divided into two halves, each of which is an exact reflex image of the other. If a flower can be divided in this manner by only one plane, I call it simply symmetrical or *monosymmetrical;* if, on the contrary, it can be symmetrically divided by two or more planes, it is, as the case may be, doubly or *poly-symmetrical.* The happy expression *zygomorphic* already used by Braun may be applied equally to monosymmetrical flowers and to those polysymmetrical ones in which the median section produces halves of quite a different shape from those caused by lateral section (*e.g.* Dicentra). I apply the term *regular* to a poly-symmetrical flower only when the symmetrical halves produced by any one section are

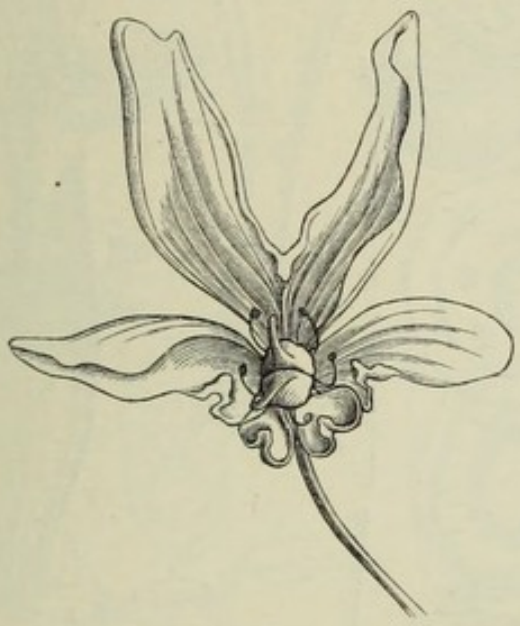

FIG. 384.—Flower of *Heracleum pubescens* with zygomorphic corolla.

exactly like or very similar to those produced by any other section; or—which comes to the same thing—when two, three, or more longitudinal sections divide a flower into four, six, or more equal or similar portions.

In exactly defining the symmetrical relations of a flower, the relative positions of the parts, as represented by the diagram, must first of all be distinguished from the entire form of the flower, such as is realised in the development of the organs.

If attention is paid first of all only to the relative positions of the parts, it is clear that they can never be distributed symmetrically in flowers with a truly spiral structure; while in hemicyclic flowers those members at least which are arranged in whorls may possibly be distributed symmetrically. If, on the contrary, the parts are all arranged in whorls, they are usually distributed monosymmetrically or polysymmetrically on the receptacle. Thus, for example, the diagram Fig. 375 (p. 524) can be divided symmetrically and irregularly by three planes, Fig. 376 by four, and Fig. 377 by five planes. The diagrams Fig. 378 *B* and *C*, as well as Fig. 379, can, on the contrary, be symmetrically halved by only one plane, which is at the same time the median plane. The diagram Fig. 380 can be divided by the median plane into two symmetrical halves which are

unlike those produced by the lateral section; this diagram is, like those in Figs. 378 *B, C* and 379, zygomorphic, but is doubly while these are only singly symmetrical.

The symmetry of mature unfolded flowers is indeed usually connected genetically with the relations of symmetry of the diagram (which represents only the position and number of the parts); as will be made clear by a comparison of Figs. 385 and 387 with Fig. 379 *A*. But inasmuch as the entire form of the mature flower is essentially determined by the shape, size, torsion, and curvature of the separate parts, these circumstances also exert a preponderating influence on the relations of symmetry of the open

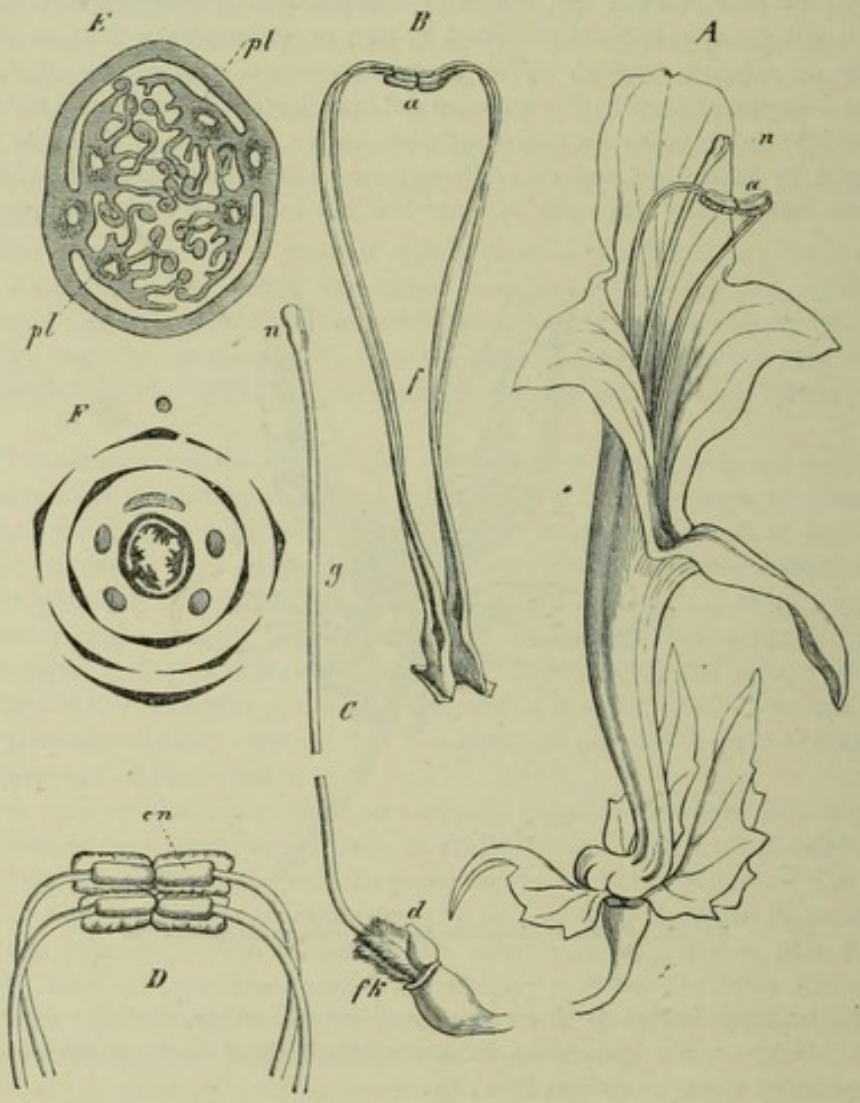

FIG. 385.—Zygomorphic flower of *Columnea Schiedeana*: *A* entire flower after removal of two sepals; *E* androecium; *C* gynæceum; *D* the coherent anthers magnified and seen from behind; *E* horizontal section of the ovary; *F* diagram; *a* anthers, *n* stigma, *g* style, *fk* ovary, *d* the staminode developed into a nectary, *pl* the lateral oblique placentæ.

flower, and to such a degree that even flowers that have their parts arranged spirally may become monosymmetrically zygomorphic in reference to their entire form, as is the case to a high degree, for example, in Aconitum and Delphinium. It must however be observed that the zygomorphism of the flower is here brought about principally or entirely by the calyx and corolla, the spiral arrangement of which may perhaps still be doubtful, but which always occupy so narrow a zone on the receptacle that their position may be considered practically to be verticillate. If, on the other hand, the floral axis is sufficiently elongated to show that the arrangement is a distinctly ascending spiral one, as in the perianth and androecium of Nymphæa and the androecium and gynæceum of

Magnolia, the subsequent development of the organs appears also not to show any zygomorphic nor indeed generally any kind of actually symmetrical arrangement.

The zygomorphic and monosymmetrical form occurs, on the contrary, very commonly in those flowers the parts of which are arranged in whorls. A very distinctly zygomorphic arrangement is not unfrequently united with a partial or entire abortion of particular members, as, *e. g.*, in Columnea, Fig. 385, and other genera of Gesneraceæ, where the posterior stamen is transformed into a small nectary; while in Labiatæ it is entirely wanting. This abortion is carried still further in Orchideæ, where, of the six typical stamens, only the median anterior one of the outer whorl or the two lateral anterior ones of the inner whorl are developed (see Fig. 379, p. 526). The final monosymmetrical arrangement is sometimes to a certain extent indicated by the order of their formation, even in the rudimentary condition of the parts of the flower, when their origin is not simultaneous in the whorl, and does not progress with a definite angle of divergence, but is so arranged that the development commences with one anterior or one posterior member, and then advances simultaneously right and left from

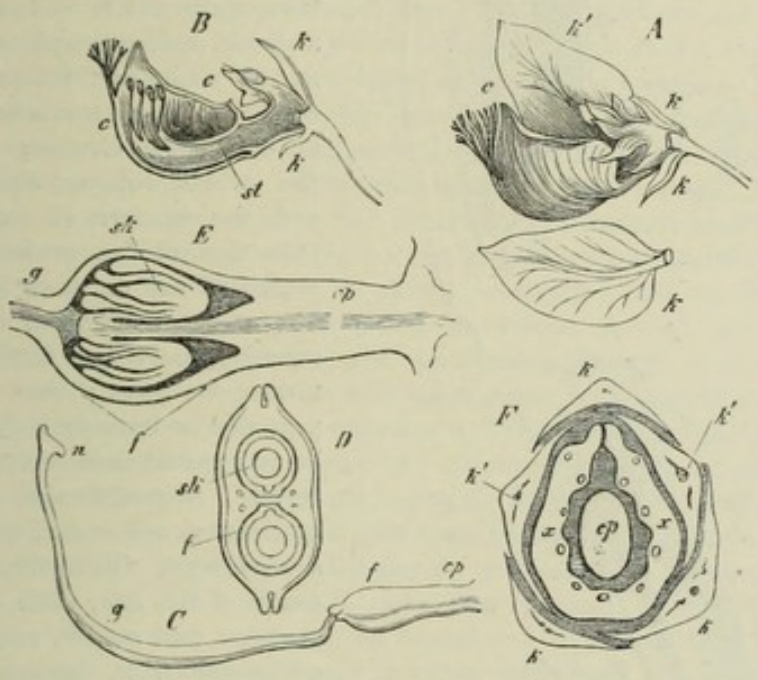

FIG. 386.—Zygomorphic flower of *Polygala grandiflora*: *A* entire flower seen from the side after removal of one sepal *k*; *B* flower divided symmetrically without the gynæceum; *C* the gynæceum magnified; *D* horizontal section of the ovary; *E* median longitudinal section of the ovary; *F* horizontal section of the flower; *k* calyx, *c* corolla, *st* staminal tube, *cp* gynophore, *f* ovary, *g* style, *n* stigma, *sk* ovules, *xx* the tube formed by the adhesion of the petals and stamens.

the median line towards the opposite side of the whorl. Examples have already been given of this arrangement in Papilionaceæ in the one case and Resedaceæ in the other.

In the zygomorphic flowers of Fumariaceæ, the diagram (Fig. 380, p. 526) is, as we have already pointed out, symmetrically divisible in different ways by two planes. The anterior and posterior halves, symmetrically similar to one another, are unlike the right and left halves, which again are symmetrically alike. This is the arrangement of the parts in the mature flower of Dicentra; in Fumaria and Corydalis the right side is developed differently from the left, one producing a spur, the other not; while the anterior and posterior sides remain symmetrical. In this case therefore the plane of symmetry coincides with a lateral section. In the zygomorphic flowers of some Solanaceæ the plane of symmetry and the median plane intersect at an acute angle. But by far the greater number of zygomorphic monosymmetrical flowers are so constructed that the median

plane coincides with a longitudinal section which divides the flower symmmetrically; as for instance in Labiatæ, Papilionaceæ, Orchideæ, Scitamineæ, Lobeliaceæ, Compositæ, Delphinium, and Aconitum[1]. The zygomorphic development is especially prevalent in the lateral flowers of spicate, racemose, or paniculate inflorescences; but is found also in those that are cymose and that have all the flowers terminal (Labiatæ and Echium). It seems as though the vigorous development of the principal rachis of the entire inflorescence — whether the final ramifications are cymose or not—often determines a zygomorphic development of flowers, as is shown in Labiatæ, Scitamineæ, and Aesculus. The formation of a vigorous pseud-axis appears to exercise a similar influence in the case of sympodial inflorescences (as in Echium).

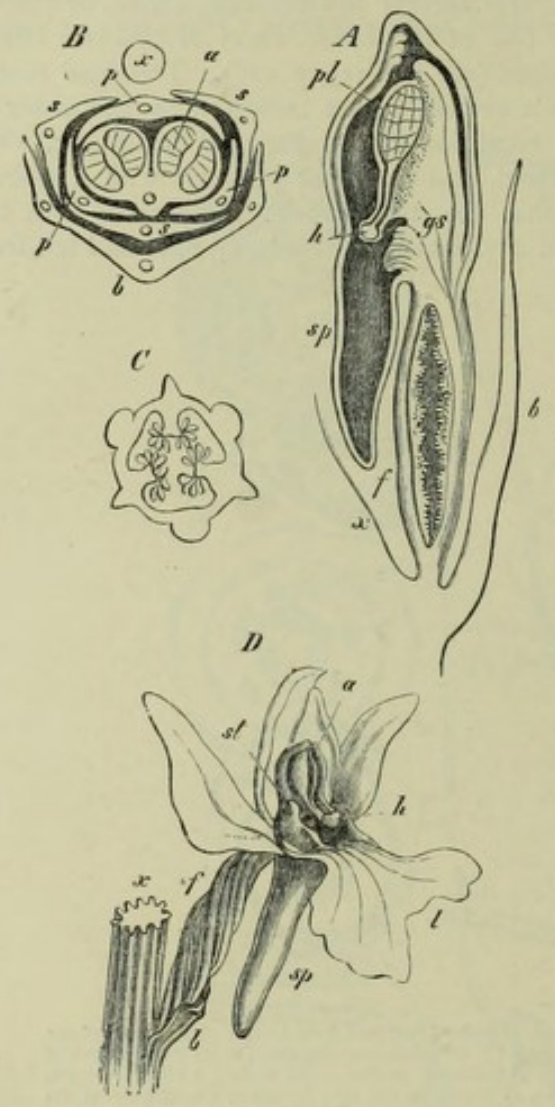

FIG. 387.—Zygomorphic flower of *Orchis maculata*: *A* bud divided symmetrically through the middle; *B* transverse section of the bud; *C* horizontal section of the ovary; *D* entire mature flower, one of the lateral perianth-leaves having been removed; *x* mother-axis of the flower; *b* bract, *s* outer, *p* inner perianth-leaves—the posterior one *l* becomes the labellum, *a* the single anther, *st* staminodes, *gs* gynostemium, *pl* pollinium, *h* its viscid disc, *sp* spur of the labellum, *f* the inferior ovary, twisted in *D* (compare the diagram Fig. 379, p. 526).

The *Fruit* of Angiosperms is the mature ovary which contains the ripe seeds and has undergone physiological changes as the result of fertilisation. The style and stigmas are frequently deciduous (as in Cucurbita, Grasses, &c.). Some of the ovules not unfrequently disappear, and the number of seeds is thus less than that of the ovules. When all the ovules of one or more loculi of a multilocular ovary disappear in the process of ripening, only the fertile loculus continues to grow; the others become partially or entirely suppressed, and can be recognised only with difficulty or not at all. A multilocular ovary may thus produce a unilocular, and often a one-seeded fruit. Thus from the trilocular ovary of the oak, each loculus of which contains two ovules, results a unilocular one-seeded fruit, the acorn. A less complete disappearance of two or four loculi together with their ovules occurs in the tri- or quinqui-locular ovary of the lime, the fruit usually containing only one seed.

Parts of the flower again which do not belong to the gynæceum, or even not to the flower, undergo changes resulting from fertilisation. The entire structure which is thus formed may be termed a *Pseudocarp*, and may be composed of a single fruit or of a number of true fruits together with the surrounding parts which have undergone peculiar development. Thus, for example, the strawberry is a pseudocarp, the axial part (or receptacle) of the flower

[1] In observations of this kind attention must be paid to torsions, such as occur in the ovary of Orchideæ, the flower-stalk of Fumariaceæ, the laburnum, &c.

swelling out and becoming fleshy, and bearing on its surface the true small fruits. In the 'hip' of the rose the hollow urn-shaped flower-stalk (again the receptacle) encloses the separate ripe fruits in the form of a red or yellow succulent envelope. The apple is also in the same sense a pseudocarp; and the mulberry results from a whole spike of flowers, the perianth-leaves of each separate flower swelling and becoming fleshy and enclosing the small dry fruit. In the fig the hollowed-out stalk of the whole inflorescence forms the pseudocarp, bearing the fruits inside.

Starting from the definition that a fruit is always the product of a single ripe ovary, it follows that several fruits may arise from one flower, whenever, namely, there is more than one monocarpellary ovary in the flower; in other words, when the flower is polycarpellary. The ripe gynæceum has in such cases been termed a multiple fruit, but it would be much better to apply to it the term *Syncarp*. Thus, for example, the small fruits resulting from the flower of Ranunculus or Clematis or the larger ones from the flower of Pæonia or Helleborus, form together a syncarp. Of a similar character is the blackberry, consisting of a number of drupe-like fruits, the product of a single flower. The fleshy receptacle of the rose-hip again encloses a syncarp, but the separate fruits constituting it are in this case dry and not fleshy. The syncarp must not be confounded with the pseudocarp resulting from an entire inflorescence, as in the cases of the mulberry and fig already named, or the pine-apple, or *Benthamia fragifera*.

The single multilocular ovary of a flower may undergo transformation so as to produce two or more parts, each containing seeds, and appearing like separate fruits, and hence termed *Mericarps*, while the whole fruit is called a *Schizocarp*. This separation may take place at a very early period in the process of the formation of the fruit; as in Tropæolum, where each loculus, enclosing a single seed, becomes rounded and at length entirely separated from the others as a closed mericarp; and in Borragineæ and Labiatæ, where each of the two carpels produces two one-seeded chambers, all four becoming at length completely separated, and surrounding the style as distinct mericarps (here called *Carceruli*); or the separation only takes place by the splitting and rupture of certain plates of tissue in the fully ripe fruit (as in Umbelliferæ and Acer), then termed a *Cremocarp*, where the fruit breaks up into two one-seeded halves or mericarps by the splitting of the dissepiment or 'carpophore' along its length. The quinquilocular fruit of Geranium splits up in the same manner into five one-seeded mericarps.

True single fruits are in general unilocular or multilocular, according as the ovary was divided or not. But the unilocular ovary may produce a multilocular fruit by spurious dissepiments, *i.e.* such as cannot be considered as the reflexed margins of the carpels; and the loculi of such a fruit may lie either one above another or side by side. The compartments, for example, of the legume (lomentum) of some Papilionaceæ and of *Cassia fistula* lie one over another, while the two spurious loculi of the legume of Astragalus lie side by side. A multilocular ovary may, *vice versâ*, produce a unilocular fruit by the suppression of one or more loculi, as in the oak and lime. A classification of fruits into monocarpellary and polycarpellary cannot therefore be carried out as it can be in ovaries; the terms having now a different application.

The wall of the ovary becomes the wall of the fruit or *Pericarp*. If sufficiently thick, it can generally be divided into two or three layers, the tissue of which is developed differently; the outer one, often nothing but the epidermis, is then called the *Epicarp*, and the inner one the *Endocarp*. If another one lies between these, it is called the *Mesocarp*, or when it possesses a fleshy character, the *Sarcocarp*.

Using the nomenclature which has now been described, we may classify all true fruits into two principal sections, and each of these again into subdivisions, according to whether the pericarp consists, when the fruit is ripe, of succulent fleshy layers or not, and whether the fruit dehisces in order to allow the escape of the seeds which become detached from the placentæ, or not; viz.—

A. Dry Fruits. Pericarp woody or tough and leathery, the cell-sap having disappeared from its cells.

a. **Dry Indehiscent Fruits.** The pericarp does not split open, but encloses the seed till germination; the testa is thin and membranous, and but little developed.

(α) One-seeded dry indehiscent fruits.

1. *The Nut* or *Glans:* the dry pericarp is thick and hard, and consists of lignified sclerenchymatous tissue; *e.g.* the hazel-nut.
2. The *Caryopsis* or *Achenium:* the dry pericarp is thin, tough, and leathery, in close contact with the seed, and separable or not from the testa; as the fruit of Compositæ, Grasses, the sweet-chestnut.

(β) Bi- or multilocular dry indehiscent fruits.

3. These are mostly *Schizocarps* splitting up into *Mericarps*, each of which resembles a nut or achenium; *e.g.* Umbelliferæ, Geraniaceæ. When the mericarp is winged, as in Acer, it is called a *Samara*.

b. **Dry Dehiscent Fruits** or **Capsules** in the more general sense. When the fruit is perfectly ripe, the pericarp bursts or splits to allow the escape of the seeds, which are themselves clothed with a strongly developed usually hard or tough testa. They generally contain more than one seed.

(α) Capsules with longitudinal dehiscence:—

4. The *Follicle* consists of a single carpel which splits along the ventral suture or coherent margins of the carpels which bear the seeds; as in Pæonia, Aquilegia, and *Illicium anisatum;* in Asclepias the thick placenta also becomes detached.
5. The *Legume* consists also of a single carpel, which however splits not only along the ventral but also along the dorsal suture, and thus separates into two halves; Leguminosæ.
6. The *Siliqua* consists of two carpels which form a bilocular fruit with a longitudinal dissepiment; the two halves of the pericarp separate from the dissepiment which remains behind; Cruciferæ.
7. The *Capsule* (in the narrower sense of the term) results from a unilocular polycarpellary or a multilocular ovary, and splits longitudinally into two or more lobes and valves, which separate from one another only partially from the apex downwards (as in Cerastium), or entirely to the base. If the fissures cause the dissepiment itself to split, the dehiscence is *septicidal* (as in Colchicum); if, on the contrary, the fissure is in the middle between each pair of dissepiments, the dehiscence is *loculicidal* (as in Tulipa and Hibiscus); if again a part or the whole of each dissepiment remains attached to a central column (which in the latter case is winged), from which the valves becomes detached, the dehiscence is *septifragal* (as in Rhododendron). If the capsule results from a unilocular polycarpellary ovary, the separation of the valves may take place either at the sutures corresponding to the septicidal dehiscence (as in Gentiana), or in the middle between them, corresponding to the loculicidal dehiscence (as in Viola).

(β) Capsules with transverse dehiscence:—

8. The *Pyxidium* opens by the separation of an upper part of the pericarp which falls off like a lid, while the lower part remains attached

to the flower-stalk in the form of an urn (*e.g.* Plantago, Hyoscyamus, Anagallis).

(γ) Capsules opening by pores:—

9. The term *Pore-capsule* might be given to those in which openings of small size result from small valves becoming detached at certain points of the pericarp; the small seeds being shaken out by the wind through these openings (*e.g.* Papaver, Antirrhinum).

B. Succulent Fruits. The tissue of the pericarp or certain layers of it remain succulent until the fruit is ripe, or assume a fleshy pulpy texture.

c. **Succulent Indehiscent Fruits.** The succulent pericarp does not burst, and the seeds therefore do not escape.

10. The *Drupe* or *Stone-fruit*. A mesocarp of fleshy texture and usually considerable thickness lies within a thin epicarp; the endocarp forms a thick hard layer (the stone, called also the *putamen*) which usually encloses only one seed with a membranous testa (the plum, cherry, peach, &c.).

11. The *Berry*. The rest of the tissue of the pericarp is developed in the form of a succulent pulp within a more or less tough or hard epicarp, the seeds being imbedded in the pulp and surrounded by a firm or even hard testa. The berry is distinguished in general from the drupe by the absence of a hard endocarp, and usually contains more than one seed (as the currant, gourd, pomegranate, potato-berry), but sometimes only one (as the date). Closely resembling the berry is the fruit of the various species of Citrus, sometimes called *Hesperidium*, the pericarp of which consists of a leathery outer layer and a pithy inner layer; at a very early period multicellular protuberances are developed from the innermost layer of tissue of the wall of the multilocular ovary, which gradually fill up the cavity of the loculi of the fruit with isolated but closely crowded succulent lobes of tissue, and form in this case the pulp.

d. **Succulent Dehiscent Fruits.** The succulent but not fleshy pericarp splits and allows the escape of the seeds which have usually a strongly developed testa.

12. The term *Succulent Capsule* might be given to those fruits the succulent pericarp of which opens by dividing into lobes, and allows the seeds to escape (as in the horse-chestnut and balsam).

13. The fruit of the walnut corresponds again to the drupe; the outer succulent layer bursts, a stony endocarp surrounding the thin-skinned seed. It might be called a *Dehiscent Drupe*.

14. The fruit of Nuphar bears more resemblance to a berry, but differs in the bursting of the outer firm layer of the pericarp; it may be termed a *Dehiscent Berry;* in *N. advena* this exposes an inner coating of each loculus of the fruit, which floats for some time on the water like a bag filled with seeds.

The enumeration here given includes only the more common forms of fruits; there are a number of others which cannot be placed exactly in any of the above categories, but to which no special name has been given[1].

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[1] [For other recent attempts to classify fruits, see Dickson, Brit. Assoc. Rep. 1871, also Nature, vol. IV. p. 347, and Journ. of Bot. 1871, p. 310; McNab, Nature, vol. IV, p. 475; and Masters, Nature, vol. V, p. 6.—Ed.]

The *Ripe Seed* depends, as respects its external nature, on the development of the pericarp. The testa is in general thicker, firmer, and harder in proportion to the softness of the pericarp, especially when this latter bursts to allow the dispersion of the seeds. When, on the contrary, the pericarp is tough or woody, and encloses the seeds until they germinate, as in the caryopsis, nut, drupe, and schizocarp, the testa remains thin and soft, as also when the endosperm is strongly developed and very hard and encloses a small embryo, as in the date and Phytelephas. The testa of the seeds of dehiscent fruits is usually covered by a distinctly differentiated epidermis; and it depends on the configuration of this epidermis whether the seed has a smooth appearance (as in the pea and bean), or displays a variety of sculpturing, such as pits, warts, bands, and so forth (as in Hyoscyamus, Datura, Papaver, Nigella, &c.). The epidermal cells of the seed not unfrequently grow into hairs; cotton consists, for example, of the long woolly hairs which clothe the seed of Gossypium; in some cases only a pencil-like tuft of long hairs is developed, as in *Asclepias syriaca*. The epidermal cells of some seeds, as the flax, quince, *Plantago Psyllium*, *arenaria*, and *Cynops*, contain layers of cellulose which have become converted into mucilage, swell up strongly with water, become separated, and envelope the seeds when moist in a layer of mucilage. Pericarps which are indehiscent and which contain small seeds not unfrequently assume a character closely resembling that of the testa of the seeds of dehiscent fruits; and this is especially the case with the achenium and caryopsis, which are hence popularly called seeds. The corona of hairs which serves as an apparatus for the dissemination of many seeds through the air is frequently developed in the caryopsis as an appendage of the pericarp (as the pappus of Compositæ, which properly replaces the superior calyx). The wings answering the same purpose which are formed during the development of the testa of some seeds in dehiscent fruits (seen in an especially beautiful manner in Bignonia) recur again on the pericarp of indehiscent fruits (as in Acer). The mucilaginous epidermis spoken of above of the seeds of dehiscent fruits recurs in the epidermis of the carcerulus of Salvia and other Labiatæ, &c. These and a number of other facts show that all that is essentially required in the development both of the pericarp and the testa is to furnish means for the dissemination of the seeds in various ways; structures which are morphologically very different thus attaining the same physiological development, while those which are morphologically similar attain the most various physiological development. A more detailed enumeration is therefore more in the province of physiology and biology than of morphology and classification.

To complete the subject of nomenclature, it only remains to remark that the part of the seed where it has become detached from the funiculus—usually easily distinguished after falling out—is termed the *Hilum* or umbilicus. The micropyle is often also to be recognized, lying, in anatropous and campylotropous seeds, close beside the hilum (as in Faba, Phaseolus, and Corydalis), generally as a wart pitted in the middle. When outgrowths occur on the seed, either along the raphe, as in *Chelidonium majus*, Asarum, Viola, &c., or as a cushion covering the micropyle as in Euphorbia, they are variously called *Crest*, *Strophiole*, or *Caruncle*. The *Aril* which envelopes the base of the ripe seed or the entire seed as a fleshy succulent mantle and is easily removed from the true firm testa, has already been described in detail.

CLASS XII.

MONOCOTYLEDONS.

The *Seed* of Monocotyledons usually contains a strongly developed endosperm and a comparatively small embryo; and this is exhibited in an especially striking manner in large seeds, such as those of Cocos, Phœnix, Phytelephas, Crinum, &c. In the Naiadeæ, Juncagineæ, Alismaceæ, and Orchideæ, the endosperm is wanting from the first; and in the Scitamineæ, where it is also wanting, it is replaced by a copious perisperm.

The *Embryo* is usually cylindrical, fusiform, and sometimes considerably elongated, and is then also curved spirally (*e.g.* in Potamogeton and Zanichellia); its form is not unfrequently that of an erect or inverted cone, in consequence of a considerable thickening of the upper end of the cotyledon. The axis of the embryo is generally very short and small in comparison to the cotyledon; in the Helobiæ on the contrary the axial portion of the embryo forms the greater part of it. At the posterior end of the axis is the rudiment of the primary root, in addition to which two or more lateral roots also originate in Grasses, which, like the primary one, are surrounded by a root-sheath (Fig. 114, p. 144). The embryo of Grasses is also distinguished by the presence of the *Scutellum*, an outgrowth of the axis beneath the cotyledon, which envelopes the whole of the embryo like a mantle, and forms a thick peltate plate on the posterior side where it is in contact with the endosperm[1]. In the Orchideæ, Apostasiaceæ, and Burmanniaceæ, the parts of the embryo of the ripe seed are not differentiated; it consists of a round mass of tissue on which the plumule is developed only during germination.

Germination[2] either begins at once with the lengthening of the roots—their protrusion causing in Grasses the rupture of the root-sheath which envelopes them, and which remains attached to the axis of the embryo as the *Coleorhiza* (Fig. 113, p. 143)—or, as is more commonly the case, the lower part of the cotyledon lengthens, and pushes the end of the root, together with the plumule which is enveloped by the sheath of the cotyledon, out of the seed (Fig. 388), while its upper part remains in the endosperm as an organ of absorption, until the endosperm is consumed. In Grasses, however, the whole of the plumule projects from the seed, the scutellum only remaining behind in it, in order to convey to the embryo the food-material contained in the endosperm.

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[1] [Van Tieghem (Ann. des Sci. Nat. 5th series, vol. XV, 1872) gives a useful summary of the various views which have been held with respect to the homology of the parts of the embryo of Grasses. He regards the scutellum as the cotyledon, and what Sachs considers the cotyledon as only its strongly developed ligule.—Ed.]

[2] See Sachs, Bot. Zeit. 1862 and 1863.

The growth of the primary root of Monocotyledons soon ceases even when it is very strongly developed during germination, as in Palms, Liliaceæ, Zea, &c.; lateral roots are produced in its place, springing from the axis, which are stronger the higher up they are produced on it. No such permanent root-system is

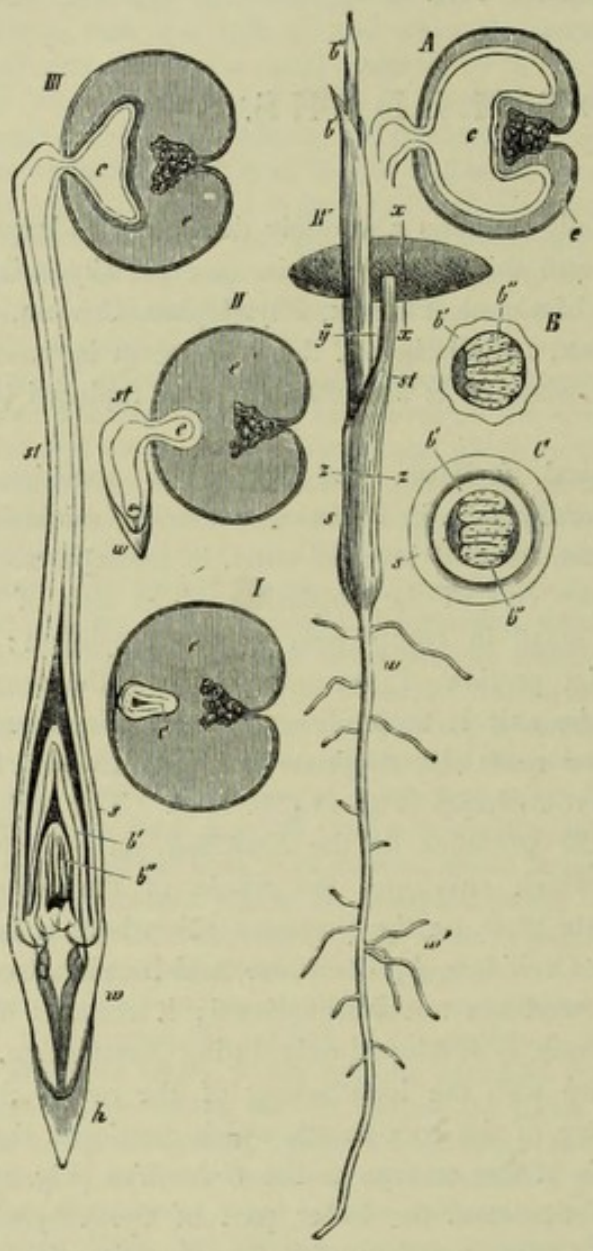

FIG. 388.—Germination of *Phœnix dactylifera*: *I* transverse section of the dormant seed; *III*—*IV*, different stages of germination (*IV* the natural size); *A* transverse section of the seed at *xx* in *IV*; *B* transverse section at *xy*, *C* at *zz*; *e* the horny endosperm, *s* the sheath of the cotyledon, *st* its stalk, *c* its apex developed into an organ of absorption which gradually consumes the endosperm and at length occupies its place, *w* the primary root, *w'* secondary roots, *b' b''* the leaves which succeed the cotyledon, *b''* becomes the first foliage-leaf: in *B* and *C* its folded lamina is seen cut across.

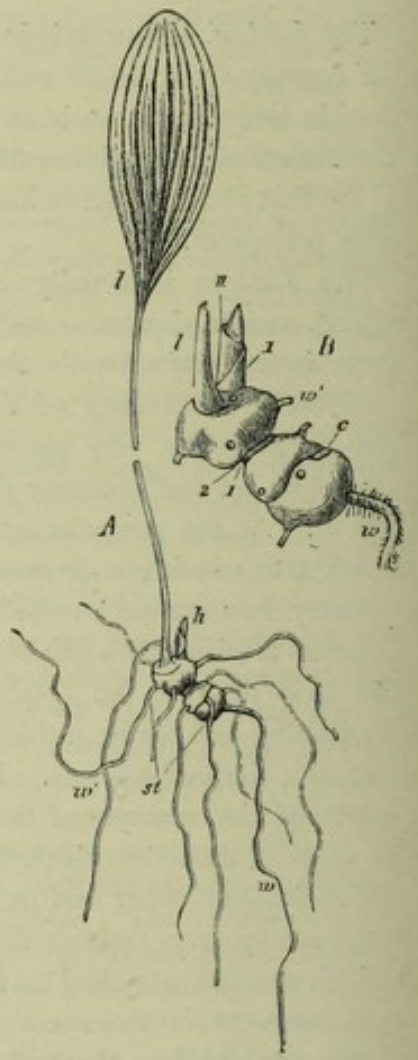

FIG 389.—Plant of *Polygonatum multiflorum* in its second year; *B* its stem magnified, *w* the unbranched primary root, *w'* lateral roots springing from the stem *st*, *l* foliage-leaf of the second year, *k* bud, *c* the scar where the cotyledon was attached, 1 and 2 scars of the first sheath-leaves which precede the foliage-leaf, *l*. *I*, *II* the succeeding sheath or cataphyllary leaves of the bud in *B*. (*Cf.* Fig. 135, p. 165.)

developed from the primary root of Monocotyledons as is found in Gymnosperms and in many Dicotyledons; sometimes no roots at all are produced, as in some Orchidaceous saprophytes destitute of chlorophyll (as Epipogium and Corallorhiza), which never possess any roots.

The plumule of the embryo is usually completely enclosed in a single

sheath-like structure, the first leaf or cotyledon, which developes either into a sheath-like cataphyllary leaf or at once into the first green foliage-leaf of the young plant (as in Allium). Within the cotyledon there is generally a second and sometimes (in Grasses) a third and fourth leaf, which protrude on germination out of the sheath of the cotyledon, increasing by intercalary growth at their base; these and the leaves which are formed subsequently are larger the later they are formed on the growing axis. The axis usually remains very short during germination without forming any distinct internodes (Allium, Palms, &c.), or it lengthens more rapidly and becomes segmented into evident internodes (Zea and other Grasses).

The increase in strength of the plant may take place by the powerful growth of the axis of the embryo itself, so that this at length forms the primary stem of the mature plant bearing the organs of reproduction, as for instance in most Palms, Aloes, Zea, &c. If the axis of the embryo remains short while it increases in strength, it may grow considerably in thickness and form a tuber (Fig. 389), or, if the bases of the leaves become thick (as in *Allium Cepa*), a bulb. If the axis of the embryo itself developes into the primary stem, whether into an upright one or a creeping rhizome, it first of all takes the form of an inverted cone, which is elongated or abbreviated according to the length of the internodes. This peculiarity, which belongs to Monocotyledons in common with Ferns, depends on the absence of any subsequent increase in thickness; the portions of the stem first formed retain their size, while each successive portion is larger; the diameter of the stem is therefore so much larger the nearer it is taken to the apex. As long as this growth proceeds, the stem continues to grow stronger; but sooner or later there comes a time when every portion of the stem acquires the same thickness as the previous one; the stem then becomes cylindrical, or, if it is compressed like some rhizomes, still with a uniform breadth. The lateral shoots exhibit the same peculiarity when they spring low down from the primary stem (as in Aloë, &c.). But the primary shoot which springs from the embryo not unfrequently disappears after producing lateral shoots which grow more vigorously than it and then again transfer the further growth to new shoots, which now produce from generation to generation thicker axes, larger leaves, and stouter roots, until at length a condition again results in which each successive generation of shoots produces others of equal strength. If the portions of the axes of the shoots beneath the points where the shoots of the next order arise are persistent, sympodia arise (as represented in Fig. 135, p. 165); but frequently each shoot entirely disappears after producing one of the next order, as for instance in our native tuberous Orchids (Fig. 150, p. 198), or in the crown-imperial (Fig. 390) or autumnal crocus (Fig. 391)[1].

The normal *Mode of Branching* of Monocotyledons is always monopodial and usually axillary[2]; a bud is generally formed in the axil of each leaf, but often

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[1] Further details of the great variety of modifications of these processes of growth will be found in Irmisch, Knollen und Zwiebelgewächse (Berlin 1850), and Biologie und Morphologie der Orchideen (Leipzig 1853).

[2] According to Magnus (Bot. Zeit. 1869, p. 770) the flower of Naias occupies exactly the place of

does not unfold, so that the number of branches visible is often less than that of the leaves (as in Agave, Aloë, Dracæna, Palms, many Grasses &c.). But sometimes several buds are formed in the axil of a leaf, and if the insertion of the leaf is broad these are placed side by side, as occurs in many bulbs (Fig. 122, p. 154). In Musa a number of flowers even stand side by side in the axil of a bract, and in *Musa Ensete* two rows one over the other. In the Spadicifloræ the bracts are often absent[1], and the ebracteate flowers stand on the rachis of the inflorescence, but are distinctly lateral in their origin. This is also the explanation of the branching of Lemna, which does not in general form any foliage-leaves, but the vegetative portion of the plant consists of disc-like or swollen portions of the axis containing chlorophyll which branch laterally out of one another, and are connected together only by slender stalks, or soon separate. The plane of

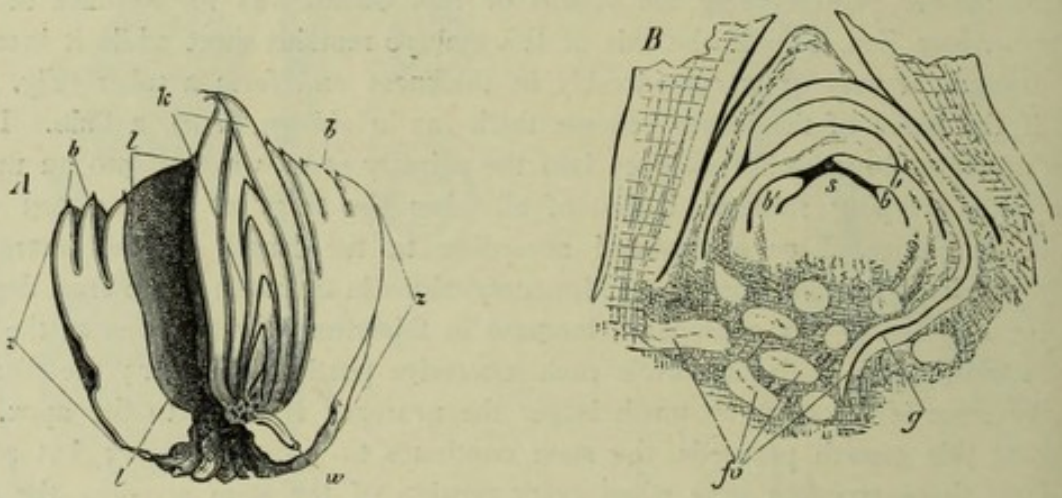

FIG. 330.—Bulb of *Fritillaria imperialis* in November: *A* longitudinal section of the whole bulb reduced, *z z* the coalescent lower portions of the bulb-scales, *b b* their free upper portions; the scales enclose a cavity *l* which contains the decayed flower-stem; next year's bud is formed in the axil of the innermost scale; its first leaves will form the new bulb, while its axis will develope into the flower-stem; the root *w* springs from the axis of this bud. *B* longitudinal section of the apical region of next year's bud, *s* apex of the stem, *b b' b''* youngest leaves.

ramification coincides with the surface of the water on which they float; each shoot produces only one or a pair of opposite lateral shoots, and the branching is therefore distinctly cymose, sympodial, or, as in *Lemna trisulca*, dichasial.

Besides the formation of shoots by the branching of the axis, adventitious shoots also sometimes occur on leaves which perform the function of gemmæ; as for instance on the margins of the leaves of *Hyacinthus Pouzolsii* and some Orchids (Döll, Flora p. 348)[2]. The large gemmæ which appear very regularly at the point of junction of the leaf-stalk and lamina, and at the base of the lamina of *Atherurus ternatus*, are especially striking. The small bulbs on the stem of

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the first leaf of a branch; but it appears from p. 771 as though the flower and the shoot that bears it were the bifurcations of a dichotomy.

[1] Compare under Dicotyledons p. 554

[2] [On the buds developed on the leaves of *Malaxis* which exhibit a striking resemblance to the ovules of Orchideæ, see Dickie, Journ. Linn. Soc. vol. xiv, pp. 1 and 180. Dr. Dickie considers the structure of these buds to favour the theory that the ovule is homologous to a bud, the nucleus-like body of the bud corresponding to an axis. See also Henslow on Malaxis, Mag. Nat. Hist. vol. I. 1829. pp. 441, 442.—Ed.]

Lilium bulbiferum are, on the other hand, normal axillary shoots, and probably the same is the case with those on the inflorescence of some species of Allium. Adventitious buds are stated by Hofmeister to occur on the roots of *Epipactis microphylla*.

The *Leaves* of Monocotyledons are seldom verticillate, though this occurs in the foliage-leaves of Elodea and the bracts of Alisma; they are very commonly arranged alternately in two rows, as in Gramineæ, Irideæ, Phormium, Clivia, Typha'

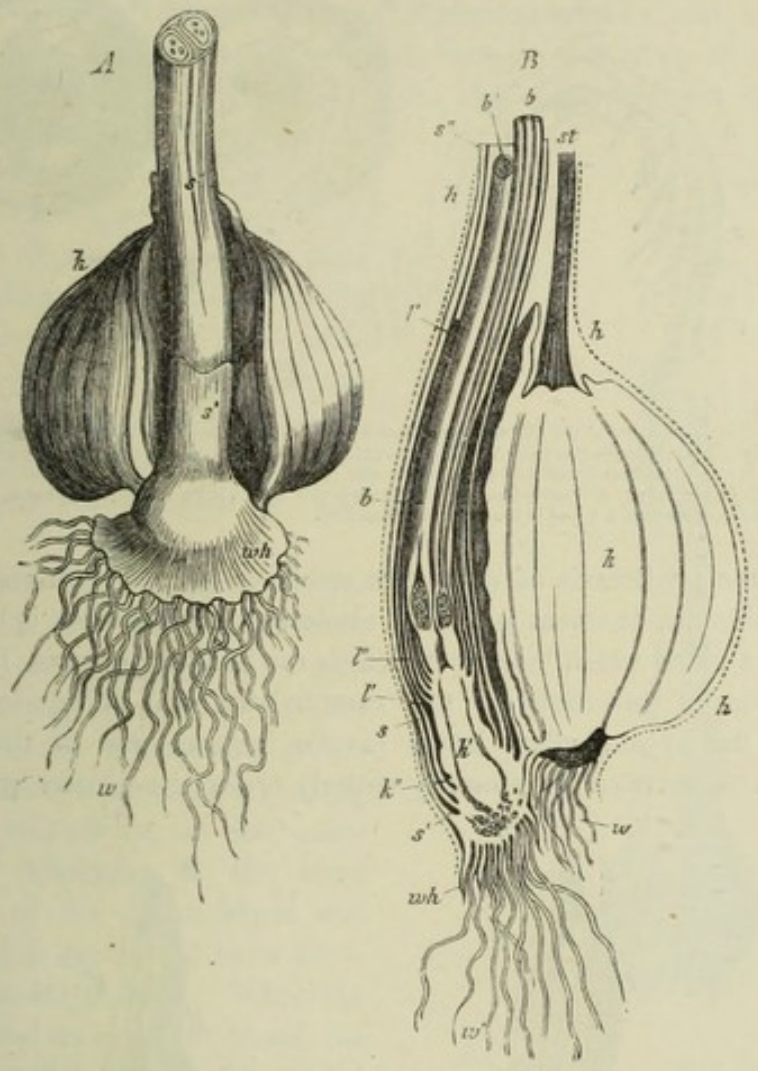

FIG. 391.—The underground part of a flowering plant of *Colchicum autumnale*: *A* seen in front and from without, *k* the corm, *s'*, *s''* cataphyllary leaves embracing the flower-stalk, *wh* its base from which proceed the roots *w*; *B* longitudinal section, *h h* a brown skin which envelopes all the underground parts of the plant, *st* the flower- and leaf-stalk of the previous year which has died down, its swollen basal portion *k* only remaining as a reservoir of food-materials for the new plant now in flower. The new plant is a lateral shoot from the base of the corm *k*, consisting of the axis from the base of which proceed the roots *w'*, and the middle part of which (*k'*) swells up in the next year into a corm, the old corm *k* disappearing; the axis bears the sheath-leaves *s*, *s'*, *s''* and the foliage-leaves *l'*, *l''*; the flowers *b*, *b'* are placed in the axils of the uppermost foliage-leaves, the axis itself terminating amongst the flowers. The foliage-leaves are still small at the time of flowering; in the next spring they emerge from the ground together with the fruits; the portion of the axis *k* then swells up into the new corm, on which the axillary bud *k''* developes into the new flowering plant, while the sheath of the lowermost foliage-leaf is changed into the brown enveloping skin.

&c. This arrangement either prevails over the whole shoot together with its secondary shoots, or occurs only at first, and then passes into spiral arrangements, which very commonly lead to the formation of rosettes radiating on all sides, as in Aloe (see Fig. 144, p. 172), Agave, Palms, &c. The arrangement with the angle of divergence $^1/_3$ is much rarer, but occurs in some species of Aloë, Carex, Pandanus, &c. Spiral arrangements with a smaller divergence than $^1/_3$ also occur

sometimes; as *e.g.* in Musa (in *M. rubra* the angle is, according to Braun, $^3/_7$ in the foliage-leaves, $^4/_{11}$ in the bracts), and Costus (where the angle of the foliage-leaves is from $^1/_4$ to $^1/_5$) &c. The axillary shoots of Monocotyledons mostly begin with a leaf in close contact with the primary axis and with its back turned towards it, and usually bicarinate. Of this character must be considered, for instance, the upper pale of the flower of Grasses, which is itself an axillary shoot of the lower

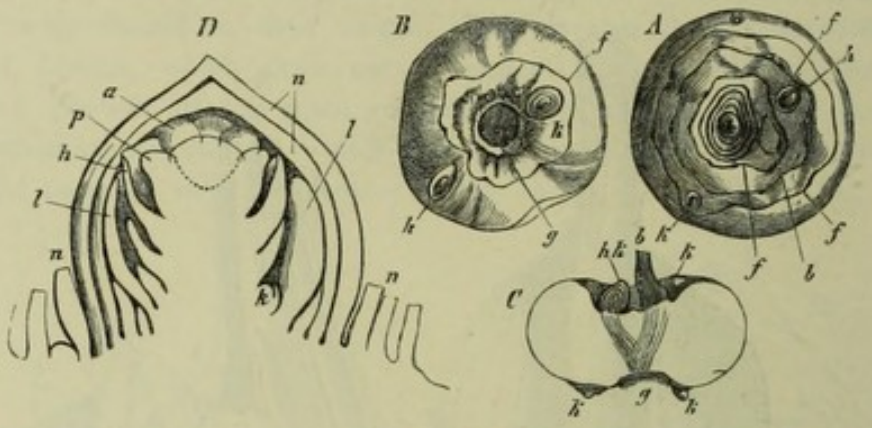

FIG. 392.—*Crocus vernus*: *A* the bulbous stem seen from above, *B* seen from below, *C* from the side and cut through lengthwise; *fff* the circular line of scars of the cataphyllary leaves, *k k* the corms which grow in their axils; *b* the base of the decayed flower- and leaf-stem, by its side (*kk* in *C*) next year's bud, from which a new corm and flower-stem will be produced; *D* longitudinal section through this bud, *n n* its cataphyllary leaves, *l l* foliage-leaves, *h* bract, *p* perianth, *a* anthers, *k* a bud in the axil of a foliage-leaf.

pale. When the phyllotaxis of successive orders of shoots is alternate in two rows, the result of this arrangement is that a whole system of shoots is bilateral, or may be divided by a plane which bisects the leaves (as in Potamogeton, Typha, &c.).

The mode of insertion of the cataphyllary and foliage-leaves, and very often that of the hypsophyllary leaves (as for instance that of the spathe which is of common occurrence) is generally entirely or for the greater part amplexicaul,

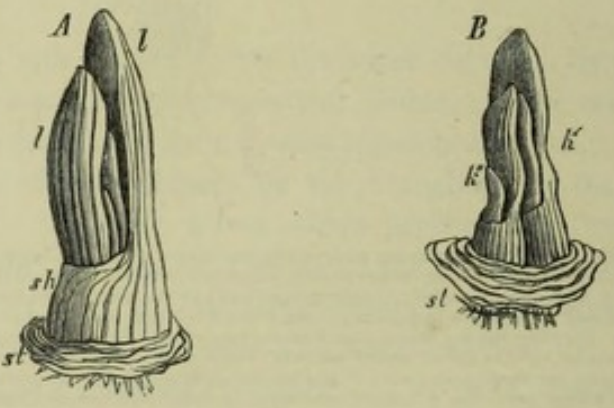

FIG. 393.—Bud in the inside of a bulb of *Allium Cepa*, the scales having been removed, *st* the short flat base of the stem on which the bulb-scales are inserted; *l* in *A B* lamina, *sh* the sheath of the foliage-leaves still short; in *B* the outer leaves have been removed, and an axillary bud *k''* has made its appearance in addition to the terminal bud *k'*.

and the lower part of the leaf is in consequence sheathing; and this is evidently connected with the want of stipules, which are so frequent among Dicotyledons. The cataphyllary and many of the hypsophyllary leaves are usually reduced to this sheathing part, which generally passes immediately into the green lamina in the case of the foliage-leaves; but in Scitamineæ, Palmaceæ, Aroideæ, and

some others, a long and comparatively slender stalk developes between the sheath and the lamina. When the leaf-stalk is absent, and the lamina sharply marked off from the sheath, a *Ligule* is not unfrequently present at the point where the two meet, as in Grasses and Allium (Fig. 394).

The lamina is generally entire and of a very simple form, commonly long and narrow (ligulate), rarely roundish and disc-shaped (*e. g.* Hydrocharis), or cordate or sagittate (as in Sagittaria and some Aroideæ). Branching of the lamina is a rather rare exception among Monocotyledons; and then takes the form either of lobes from a broad common base or less often of deep divisions, as in some Aroideæ (*e. g.* Amorphophallus, Fig. 133, p. 162, Atherurus, and Sauromatum). The division of the compound and pinnate leaves of Palms is not due to a branching occurring at an early stage, but to a splitting which takes place on unfolding, and is caused by the drying up of certain strips of tissue within the lamina, which is at first sharply folded up. The formation of the tendrils of Smilax appears, on the other hand, to depend on actual branching of the leaf-stalk.

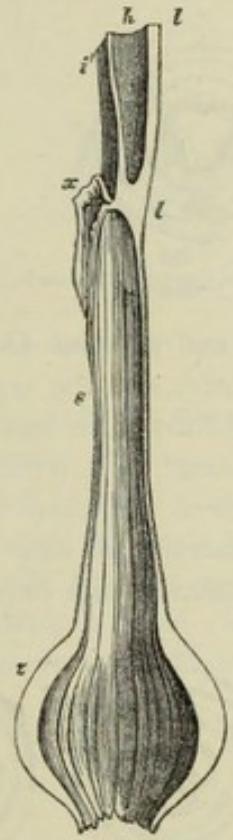

FIG. 394.—A leaf of *Allium Cepa* divided lengthwise; *z* the thickened base of the sheath, which persists as a bulb-scale after the upper part of the leaf has died down, *s* the membranous part of the sheath, *l* the hollow lamina, *h* hollow of the leaf, *i'* inner side of the lamina, *x* ligule.

The *Venation* of the foliage-leaves differs from that of most Dicotyledons, in the weaker veins not generally projecting on the under side of the leaf, but running through the mesophyll; in the smaller leaves there is even no projecting mid-rib. The mid-rib is, on the other hand, strongly developed in the large stalked leaves of the Spadicifloræ and Scitamineæ, and is permeated by a number of fibro-vascular bundles. When the leaf is ligulate and its insertion broad, the fibro-vascular bundles run nearly parallel to one another; in broader leaves without a conspicuous mid-rib they describe curves from the mid-rib to the margins (as in Convallaria). But when a strong mid-rib occurs in a broad lamina, as in Musa &c., the fibro-vascular bundles which run through it give off laterally smaller thin bundles, running parallel to one another in large numbers to the margin of the leaf. These parallel transverse nerves are sometimes united into a lattice-like network by short straight anastomosings (as in Alisma, Costus, and Ouvirandra, the mesophyll being absent within the meshes of the latter). It is only rarely (as in some Aroideæ), that projecting lateral veins are given off from the mid-rib, a finer reticulated venation springing from them.

The *Flower* of Monocotyledons usually consists of five alternating whorls each

with an equal number of members; viz. an outer and an inner perianth-whorl, an outer and an inner whorl of stamens, and a carpellary whorl, which is succeeded by a second carpellary whorl only in Alismaceæ and Juncagineæ. The most common typical flora formula is therefore $S_n P_n St_{n+n} C_{n\,(+n)}$. It is only in the Hydrocharideæ and a few other isolated cases that the number of whorls of stamens is larger. Where in other cases, as Butomus, an increase of the typical number of stamens occurs, this takes place by *dédoublement* without any increase of the number of whorls (Fig. 400 A).

The number of members in each whorl is two ($S_2 P_2 St_{2+2} C_2$), in only a very few cases scattered through the most different families (*e. g.* in Maianthemum and some Enantioblastæ; it is sometimes four or five (occasionally in *Paris*



FIG. 395.—Diagram of Scirpus (Cyperaceæ).



FIG. 396.—Diagram of Irideæ.



FIG. 397.—Diagram of Musaceæ.

quadrifolia and in some Orontiaceæ); but the usual number of members in each whorl is three, and the typical formula therefore $S_3 P_3 St_{3+3} C_{3(+3)}$. In the large section of Liliifloræ, in some Spadicifloræ, and in many Enantioblastæ, Juncagineæ, and Alismaceæ[1], this typical floral formula is at once obtained empirically; but in most others particular members or whorls are wanting; but the abortion of these is generally at once evident from the position of those that are present. In the Scitamineæ with only one or even with only half an anther (Fig. 398, 399)

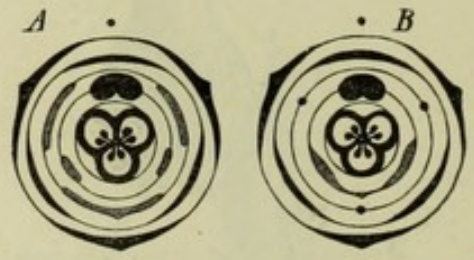

FIG. 398.—Diagram of Zingiberaceæ; *A* Hedychium (after Le Maout and Decaisne), *B* Alpinia (after Payer).



FIG. 399.—Diagram of Canna (Musaceæ), after Payer.

the rest of the members of the androecium are present or only partially deficient, but are transformed into petaloid staminodes. It has already been pointed out how the flowers of Gramineæ and Orchideæ can be traced back to the trimerous pentacyclic type; the theoretical diagrams here given (Figs. 395–402) will answer the same purpose for some of the other more important families.

If the pentacyclic flower with the formula $S_n P_n St_{n+n} C_{n(+n)}$ is considered as

[1] The dimerous flower of Potamogeton ($S_2 P_2 St_{2+2} C_4$) (see Hegelmaier, Bot. Zeit. 1870, p. 287) differs from the typical formula only to this extent, that the four carpels arise simultaneously, and are placed diagonally to the preceding pairs.

the typical one for Monocotyledons, it will be seen that the great majority of families the number of whose parts deviates from this type, do this only by the suppression of single members or of whole whorls, the typical position of those that still remain with respect to one another not being disturbed. The variety in the forms of flowers in this class is therefore brought about almost entirely by abortion[1]; and it is not uncommon for abortion to be carried to such an extent in Monocotyledons that nothing is left at last of the whole flower but a single naked ovary or a single stamen, as happens frequently in Aroideæ. In these cases a similar explanation of the relationships of the parts of the flower is approached and elucidated by the occurrence of flowers with the actual typical structure, and by a complete series of transitions caused by partial abortion. It is

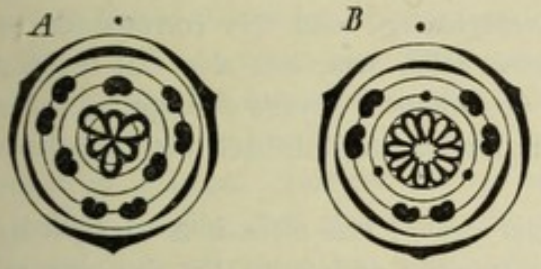

FIG. 400.—Diagram of Alismaceæ; *A* Butomus, *B* Alisma.



FIG. 401.—Diagram of Triglochin (Juncagineæ).

especially in small closely crowded flowers, as those of Spadicifloræ, Glumifloræ, &c., that so great a reduction of the typical number of members is observed; while in larger and more isolated flowers the number of members in each whorl is usually complete or even excessive (as Butomus and Hydrocharis), and deviations usually result from petals (or petaloid staminodes) being formed in the place of fertile stamens (*e. g.* Scitamineæ). With reference to the abortion which is often carried to so great an extent in small flowers, it may in certain cases even be doubtful whether



FIG. 402.—Diagram of Gymnostachys (Aroideæ), after Payer.

in an assemblage of stamens and carpels we have a single flower or an inflorescence consisting of several flowers reduced to a very simple state by abortion, as for example in Lemna.

When both the perianth-whorls are well developed, they are usually similar in structure; in large flowers they are generally delicate and petaloid and either brightly coloured or not (Liliaceæ, Orchideæ, &c.); in small flowers on the contrary they are firm, dry, and membranous, as in Juncaceæ, Eriocauloneæ, &c.

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[1] Compare what was said on Abortion at p. 201 and in the Introduction to Angiosperms.

Sometimes however the outer perianth-whorl is green and sepaloid, the inner whorl larger, delicate, and petaloid (Canna, Alisma, Tradescantia); in the very small and closely crowded flowers of the Glumifloræ, the perianth-leaves, when present, take the form of hairs (the setæ of Cyperaceæ) (Fig. 395), or of small membranous scales (the pales and lodicules of Grasses).

The *Stamens* generally consist of a filiform filament and a quadrilocular anther; though variations frequently occur, especially in the form of the filament and connective. Among the most striking deviations from the ordinary type are the petaloid staminodes of Cannaceæ and Zingiberaceæ. It has already been pointed out (pp. 426, 473), that the foliar nature of the stamens is subject to an exception in the Naiadeæ (at least in Naias) according to the researches of Magnus, and in Typha according to those of Rohrbach. The stamens of Monocotyledons scarcely ever branch, as is often the case in Dicotyledons; and this corresponds to the customary absence of branching in the other foliar structures also. If the diagram of the flower of Canna (Fig. 399), drawn according to Payer's description, is correct, the petaloid staminodes are branched; according to Rohrbach the (axial) stamen of Typha is also branched.

The *Gynæceum* has usually a trilocular ovary; less often it is tricarpellary but unilocular; in both cases it may be either superior or inferior, but the latter occurs only in plants with large flowers (Hydrocharis, Irideæ, Amaryllideæ, Scitamineæ, Orchideæ, &c.). The formation of three or more monocarpellary ovaries is limited to the alliance of the Juncagineæ and Alismaceæ, in which the ordinary number of members and of whorls of the gynæceum is also exceeded, reminding one of the Polycarpæ among Dicotyledons.

Adhesion and displacement are not so common in the flower of Monocotyledons, and usually not so complicated as among Dicotyledons; among the most striking phenomena of this nature are the formation of the gynostemium of Orchids; the cohesion of the six similar perianth-leaves into a tube in Hyacinthus, Convallaria, Colchicum, &c.; and the epipetalous and episepalous position of the stamens in the same plants and in some others. Adhesion of the stamens to the calyx or corolla occurs much less constantly in particular families among Monocotyledons than among Dicotyledons.

Terminal flowers to a leafy primary shoot occur very rarely among Monocotyledons (*e.g.* in Tulipa); terminal inflorescences are more common. The flower acquires a tendency to zygomorphism, especially as it increases in size; but this is often only feebly indicated, and attains its highest development in Scitamineæ and Orchideæ.

The *Ovules* of Monocotyledons usually spring from the margins of the carpels, rarely from their inner surface (as in Butomus); the single orthotropous ovules of Naias (according to Magnus) and Typha (Rohrbach) arise by the transformation of the end of the floral axis itself (see p. 496); in Lemna and in some Aroideæ one or more ovules stand at the bottom of the cavity of the unilocular ovary. The prevailing form of the ovule is anatropous; but in Scitamineæ, Gramineæ, and some other orders, campylotropous ovules occur; in the Enantioblastæ and a few Aroideæ they are orthotropous, either erect or pendulous. The nucleus is almost without exception enclosed in two envelopes (Crinum however forms an exception).

The *Embryo-Sac*[1] generally remains surrounded by one layer of the tissue of the nucleus till the time of impregnation; the apex is sometimes destroyed so that the embryo-sac projects (as in Hemerocallis, Crocus, Gladiolus, &c.); but, on the other hand, the apex not unfrequently remains as a cap of tissue covering the apex of the embryo-sac (as in some Aroideæ and Liliaceæ). In Orchideæ the growing embryo-sac completely destroys the layer of tissue that envelopes it together with the apex of the nucleus; and this happens after impregnation in all the other Monocotyledons that possess an endosperm, and in this case the embryo-sac sometimes advances even to the inner integument and destroys it (*Allium odorans*, Ophrydeæ).

In the greater number of Monocotyledons a copious development of endosperm-cells follows quickly after impregnation; these are all formed simultaneously, and remain free in the parietal protoplasm. When they lie near together they soon unite into a layer of tissue and divide tangentially, new cells being formed at the same time by free cell-formation on the inner side of the first layer which behave in the same manner, until at length the embryo-sac is filled with radial rows of cells the result of division. Narrow embryo-sacs are filled up by the growth of the first endosperm-cells; but sometimes the cells formed by free cell-formation in the parietal layer of protoplasm constitute at first a loose mass which fills up the embryo-sac and only closes up into a tissue at a later period (*e. g.* Leucojum, Gagea). The narrow embryo-sac of Pistia is filled up by a row of broad disc-shaped cells which lie in it like transverse compartments and are perhaps the result of division of the sac itself. In some Aroideæ only a part of the embryo-sac is filled with endosperm, the rest remaining empty.

The endosperm still continues to grow after it has filled up the embryo-sac, the seed which it fills increasing also in size. It has already been mentioned how considerable this growth is in Crinum (p. 512).

In all those Monocotyledons which form an endosperm (albuminous), it becomes closed up into a continuous tissue enveloping the embryo before this has completed its growth. By the growth of the embryo a part of the endosperm which surrounds it is again forced aside; and on this displacement depends the lateral position of the embryo in Grasses by the side of the endosperm, and the absence of this latter in some Aroideæ. But in all the other Monocotyledons which have no endosperm (exalbuminous), Naiadeæ, Potamogetoneæ, Juncagineæ, Alismaceæ, Cannaceæ, and Orchideæ, its formation is altogether suppressed, or transitory preparations for it only take place.

On the first origin of the embryo reference must be made to what was said in the Introduction to Angiosperms (p. 510); there are many points which are still doubtful in the formation of the plumule, scutellum (in Grasses), and root, from the original small-celled mass of tissue of the embryo.

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[1] See Hofmeister, Neue Beiträge (Abhandl. der königl. Sächs. Gesellsch. der Wissensch. vol. VII).

With respect to the *Formation of Tissue*[1], Monocotyledons differ from Dicotyledons and Gymnosperms chiefly in the course of the fibro-vascular bundles in the stem, and in the want of a true cambium-layer. A number of the common bundles (*i.e.* those common to the stem and leaves) enter the stem side by side from the broad insertions of the leaves, pass obliquely downwards into it, and then again bend outwards as they descend, approaching gradually the surface of the stem. The common bundle is usually thickest and most perfectly developed at the curved portion which lies deepest in the stem, while the arm which bends upwards into the leaf becomes thinner and simpler upwards, and the descending arm of the bundle behaves similarly downwards. Hence a transverse section of the stem which cuts through the different descending arms at different heights in their course, shows bundles of different structure and of various sizes. A radial longitudinal section through the bud or through mature stems with short internodes (as Palm-stems, thick rhizomes, bulbs, &c.), shows how the bundles which descend from different leaves, the curves of which lie at different heights, cross one another radially, some of them bending inwards where others are already turning outwards. In elongated internodes, as for instance those of the stalks of Grasses and of some Palm-stems (like Calamus), the long scapes of Allium, &c., the bundles run nearly parallel to one another and to the surface; the curves and intersections of the bundles may be easily distinguished at the apex of such stems, and localise themselves in the transverse plates or nodes which do not elongate between each pair of internodes. The nodes are not unfrequently traversed by a network of horizontal bundles; and this is very conspicuous in the maize.

The course of the fibro-vascular bundles which has now been described renders impossible the separation of the fundamental tissue of the stem into pith and cortex in the sense in which this occurs in Conifers and Dicotyledons. The parenchymatous fundamental tissue fills up homogeneously the spaces between the bundles which are generally numerous; but a separation takes place not unfrequently into an outer peripheral layer and an inner region, a layer of tissue being formed between the two the cells of which are thickened and lignified in a peculiar way (as for instance in most thickish rhizomes, in the hollow scape of Allium, &c.).

In consequence of their not being parallel, and of their scattered distribution in the transverse section of the stem, the descending bundles of Monocotyledons have not the power of coalescing into a closed sheath by connecting bands of cambium (interfascicular cambium), as is the case in other Phanerogams. In consequence of this the layer of cambium between the phloëm and xylem is also absent; the fibro-vascular bundles are closed. When a portion of the stem ceases to grow in length, the whole of the tissue of the bundles becomes transformed into permanent tissue (see *e.g.* Fig. 91, p. 107); and there is in consequence usually no subsequent increase in thickness; each portion of the stem, when once formed, maintains the thickness which it had already attained within the bud near the apex of the stem. But in Dracæna, Aloë, and Yucca, a renewed increase of thickness begins afterwards at a considerable distance from the apex of the stem, which may even continue for centuries and may cause a considerable though slow increase in its circumference. But this subsequent growth in thickness takes place in a way quite different from that which occurs in Gymnosperms and Dicotyledons;—a layer of the fundamental tissue parallel to the surface of the stem becomes transformed into meristem which continually produces new closed fibro-vascular bundles, and between them parenchymatous fundamental tissue (Fig. 91). A more or less evidently stratified network of slender anastomosing bundles is thus formed, the position and connection of which is easily recognised on stems which have been exposed

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[1] Von Mohl, Bau des Palmenstammes, in his Vermischte Schriften, p. 129.—Nägeli, Beiträge zur wissensch. Bot. Heft 1.—Millardet, Mémoires de la Soc. Imp. des Sci. Nat. de Cherbourg, vol. XI, 1865.

to the weather, and in which the parenchyma which fills up the interstices has decayed. This network of closely-placed closed fibro-vascular bundles now forms a kind of secondary wood which surrounds like a hollow cylinder the space in which the original fibro-vascular bundles of the stem run isolated and loose in the form of long threads. This thickening ring of the arborescent Monocotyledons resembles the secondary woody mass of Conifers and Dicotyledons in the fact that it belongs altogether to the stem and has no genetic connection with the leaves, differing in this from the original common bundles. An exception to the ordinary structure of Monocotyledons occurs in submerged water-plants (Hydrilla and Potamogeton), in which, according to Sanio (Bot. Zeitg. 1864, p. 223, and 1865, p. 184), an axial cauline bundle in the stem lengthens continuously, while the foliar bundles do not unite with it till a later period, a peculiarity which recurs in some dicotyledonous water-plants, and reminds one of the corresponding processes in Selaginella.

The *Systematic Classification*[1] of the sub-sections of Monocotyledons here adopted is that of A. Braun (in Ascherson's Flora of the province Brandenburg, Berlin 1864); but with the variation that the order Helobiæ there given is broken up into a series of orders. In short diagnoses of the orders only a few of the characters are specified which are most important from a systematic point of view; the figures placed within brackets refer to those attached to the families belonging to the order in which the characters named are present or absent. A complete account might have been given of the characters of the separate families of Monocotyledons; but since a similar treatment of the class of Dicotyledons would have far exceeded our limits, the mere enumeration of the families must, for the sake of uniformity, suffice.

SERIES I.—Helobiæ.

Water-plants; seed with little or no endosperm, but a strongly developed hypocotyledonary axis to the embryo. The number of parts of the flower usually vary from the ordinary type of Monocotyledons.

Order 1. **Centrospermæ** (so named from the central position of the seed in (1) and in Naias). Flowers imperfect, very simple, usually without a perianth; in (1) consisting of two stamens and a unilocular ovary (containing from 1 to 6 basilar ovules) surrounded by a sheath (perianth or spathe); ovary in (2) unilocular, usually one-seeded; seed with but little endosperm. The Lemnaceæ consist of small branched leafless floating vegetating bodies, generally with true pendent roots; the Naiadeæ are slender branched long-leaved submerged plants; this family is not definable systematically, and should be split up into several. (The Lemnaceæ should perhaps be united to the Aroideæ.)

Families: 1. Lemnaceæ.
2. Naiadeæ.

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[1] [The systematic classification adopted in this book is not one which the reader will find followed in any standard English work, either as respects Monocotyledons or Dicotyledons. The work now generally adopted as containing the most satisfactory system of distribution of the vegetable kingdom into classes, orders, and genera, is Bentham and Hooker's Genera Plantarum (London 1862-1873), which is however at present only completed so far as to include the Gamopetalæ with inferior ovary. In Dr. Hooker's edition of Le Maout and Decaisne's Traité Générale de Botanique (London 1873), will be found the outlines of this classification completed as far as relates to the classes and orders. De Candolle's Prodromus Systematis Naturalis Vegetabilium in 17 vols. (Paris 1818-1873), contains a description of every known species of Dicotyledons; Walpers' 'Repertorium' and 'Annales,' serving as supplements to the earlier volumes, which are far less complete than the later ones. For an admirable epitome and illustrations of the character of each of the natural orders see also Oliver, Illustrations of the Principal Natural Orders of the Vegetable Kingdom; London, 1874.—Ed.]

Order 2. **Polycarpæ.** Flowers pentacyclic or hexacyclic (2, 3); whorls in (1) dimerous and decussate, with four monocarpellary ovaries placed diagonally; in (2, 3) trimerous, or with a larger number of stamens and carpels (see p. 549); the gynæceum consists of three or more monocarpellary ovaries, which are one- or more-seeded; endosperm absent. Perennial floating water- or upright bog-plants, with large lattice-veined or long narrow (2) leaves.

Families: 1. Potamogetoneæ.
2. Juncagineæ.
3. Alismaceæ.

Order 3. **Hydrocharideæ.** Flowers diœcious or polygamous, with trimerous whorls, and perianth consisting of both calyx and corolla; male flowers of from one to four whorls of fertile stamens and within these several whorls of staminodes; female flowers with an inferior tripartite or six-chambered (3) many-seeded ovary; endosperm absent. Perennial submerged or floating water-plants with spiral or verticillate (1) leaves.

Family 1. Hydrocharideæ; with the subsections—
1. Hydrilleæ.
2. Vallisnerieæ.
3. Stratioteæ.

SERIES II.—Micranthæ.

Land- or bog-plants; the individual flowers usually very small and inconspicuous, but collected in large numbers in the inflorescence, and almost always referable to the dimerous or trimerous pentacyclic type.

Order 4. **Spadicifloræ.** Inflorescence a spadix or panicle with thick branches (4), generally enveloped in a large sometimes petaloid (1) spathe; bracts small or altogether absent; perianth never petaloid, usually inconspicuous or altogether abortive (1–3); sexual organs generally diclinous by abortion; fruit always superior and often very large (2, 4); the seed mostly large or of an immense size and with a very large endosperm; embryo small, straight. Mostly large strong plants with the stem strongly developed, chiefly above ground, and a great number of large foliage-leaves; in (1, 3, 4) they have a broad branched or apparently pinnate or compound lamina, a leaf-stalk and sheath, in (2) they are sessile, very long and narrow.

Families: 1. Aroideæ.
2. Pandanaceæ.
3. Cyclantheæ.
4. Palmaceæ.

Order 5. **Glumifloræ.** Inflorescence spicate or panicled, without a spathe; flowers very small and inconspicuous, usually concealed among thickly placed dry hypsophyllary leaves (glumes or pales) (2, 3); perianth absent, or replaced by hair-like structures or scales; fruit superior, small, one-seeded, dry and indehiscent (a caryopsis); embryo in (1) long and in the axis of the endosperm, in (2) by its side and very small, in (3) also by the side of the endosperm, but considerably developed and provided with a scutellum. Plants with persistent underground elongated rhizomes, and upright foliage-leaves in two or three (2) rows; (1) should perhaps rather be included in the fourth order.

Families: 1. Typhaceæ.
2. Cyperaceæ.
3. Gramineæ.

Order 6. **Enantioblastæ.** Flowers in crowded (4) cymose inflorescences, inconspicuous (1, 2), or conspicuous (3, 4), pentacyclic, and usually trimerous (in (1, 2) often dimerous); perianth-whorls glumaceous in (1, 2), developed into calyx and corolla in (3, 4); fruit a superior bi- or trilocular capsule with loculicidal dehiscence; ovule orthotropous, and the embryo (*βλάστη*) therefore opposite (*ἐναντίος*) the base of the seed. Plants with grass-like (1–3), or succulent habit (4).

Families: 1. Restiaceæ.
2. Eriocauloneæ.
3. Xylideæ.
4. Commelynaceæ.

SERIES III.—Corollifloræ.

Both the perianth-whorls conspicuous, usually large and petaloid; the two staminal whorls completely developed or partially wanting by abortion, and then replaced by staminodes; one carpellary whorl; the five whorls, with few exceptions, trimerous.

Order 7. **Liliifloræ.** Inflorescence very various, racemose or cymose; the large flowers sometimes single. Flowers pentacyclic and trimerous, except a few cases where they are dimerous, tetramerous, or even pentamerous; in (3) the inner staminal whorl is wanting; perianth-whorls similar, in (1) inconspicuous and membranous, but usually petaloid (2, 3, 5–8) and often large; sometimes all the six leaves are coherent into a tube (6 and elsewhere), often with epipetalous and episepalous stamens; ovary superior in (1, 2), inferior in the other families, usually forming a trilocular capsule or berry; embryo surrounded by endosperm. Plants of very various habit; with strong woody stems increasing in thickness in Aloë, Yucca, and Dracæna (2); more often with underground rhizomes, corms, or bulbs, from which spring leafy annual shoots; leaves mostly long and narrow, in (4) with a broad lamina and slender stalk.

Families: 1. Juncaceæ.
2. Liliaceæ.
3. Irideæ.
4. Dioscoreæ.
5. Taccaceæ.
6. Hæmodoraceæ.
7. Pontaderiaceæ.

Order 8. **Ananasineæ.** Flowers consisting of the typical five trimerous whorls; outer perianth-whorl developed into calyx, inner one into corolla; ovary trilocular and many-seeded, superior or inferior; embryo by the side of the endosperm; leaves long, often very narrow.

Family: 1. Bromeliaceæ.

Order 9. **Scitamineæ.** Floral whorls trimerous and zygomorphic; both perianth-whorls or only the inner one (2, 3) petaloid; of the stamens the posterior one of the inner whorl is abortive in (1), this alone being fertile in (2, 3) (in 3 with only half an anther), while the rest are changed into petaloid staminodes (see Figs. 397–399, p. 548); fruit inferior, trilocular, a berry or capsule; endosperm

absent, but replaced by a copious perisperm. Usually handsome, often very large (1) leafy shrubby plants springing from a persistent rhizome, with large leaves, generally divided into a broad lamina, leaf-stalk, and sheath.

Families: 1. Musaceæ.
2. Zingiberaceæ.
3. Cannaceæ.

Order 10. **Gynandræ.** The entire flower zygomorphic in origin and development; by the torsion of the long inferior ovary (1) the anterior side of the mature flower usually becomes posterior; both of the trimerous perianth-whorls petaloid, the posterior leaf of the inner one (the labellum) generally provided with a spur; of the six typical stamens of the two whorls only the anterior ones are eventually developed, and in (1) (with the exception of Cypripedium) the anterior one of the outer whorl is alone fertile and has large anthers, the two anterior ones of the inner whorl forming small staminodes; but in Cypripedium it is these latter that are fertile, the anterior one of the outer whorl forming a large staminode; in (2) the same occurs, or the three anterior ones are fertile; filaments of the fertile and sterile stamens coherent with the three styles into a gynostemium; pollen in single grains, tetrahedra, masses, or pollinia; ovary inferior and unilocular with parietal placentation (1) or trilocular with axile placentation (2); ovules anatropous; seeds very numerous, very small, without endosperm and with the embryo undifferentiated. Small herbs or larger shrubby plants; the tropical Orchideæ often epiphytal and furnished with peculiar aërial roots; our native species perennial with underground rhizomes or tubers; some Orchideæ are saprophytes destitute of chlorophyll, and a few have even no roots (Epipogium, Corallorhiza).

Families: 1. Orchideæ.
2. Apostasiaceæ.

The **Burmanniaceæ** with cymose inflorescence, three or six fertile epipetalous stamens, free tripartite style, and uni- or tri-locular inferior ovary, are allied to the Gynandræ by their small seeds without endosperm and their undifferentiated embryo; and in this order, which consists for the most part of small plants, there are some saprophytes destitute of chlorophyll.

CLASS XIII.

DICOTYLEDONS.

The ripe *Seed* of Dicotyledons contains either a large endosperm and a small embryo (as in Euphorbiaceæ, Coffea, Myristica, Umbelliferæ, Ampelideæ, Polygonaceæ, Cæsalpineæ, &c.); or the embryo is comparatively large, and the endosperm occupies but a small space (*e. g.* Plumbagineæ, Labiatæ, Asclepiadeæ, &c.); or, thirdly, the endosperm is entirely wanting, and the embryo fills up the whole of the

space enclosed by the testa, and thus, when ripe, often attains a very considerable size (*e.g.* Aesculus, Juglans, Cucurbita, Tropæolum, Cupuliferæ, Leguminosæ, &c.); though in small seeds it still remains of moderate dimensions (as in Cruciferæ, Compositæ, Rosifloræ, &c.). The absence of endosperm generally results from its absorption by the rapid growth of the embryo before the ripening of the seed; only in a very few cases is it rudimentary from the first (Tropæolum, Trapa). In Nymphæaceæ and Piperaceæ the embryo and the endosperm which surrounds it both remain small, the rest of the space within the testa being occupied by perisperm.

The *Embryo* generally attains but very small dimensions in the small-seeded parasites and saprophytes destitute of chlorophyll, and remains without differentiation until the time of ripening of the seed; in Monotropa it never consists of more than two cells, and even in *Pyrola secunda*, which possesses chlorophyll, only of from eight to sixteen (Hofmeister). The ripe seeds of Orobanche, Balanophora, Rafflesiaceæ, &c., contain a very small undifferentiated embryo in the form of a roundish mass of tissue; the embryo of Cuscuta is of moderate size and length, but the formation of leaves and roots on the filiform stem[1] is suppressed. The mistletoe (Loranthaceæ),

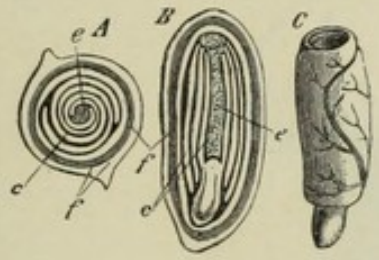

FIG. 403.—*Chimonanthus fragrans*: *A* horizontal section of the nearly ripe fruit; *B* longitudinal section of the same, *f* the thin pericarp, *e* remains of the endosperm, *c* cotyledons; *C* the embryo removed from the seed, showing the cotyledons rolled round one another, the radicular end below.

on the other hand, parasitic but containing chlorophyll, produces an embryo which is not only large but well-developed.

If the embryo of the ripe seed is differentiated, as is generally the case, it consists of an axis and two primary opposite leaves (cotyledons) between which the axis terminates as a naked vegetative cone (Cucurbita), or bears a bud which sometimes consists of several leaves (*Vicia Faba*, Fig. 405, Phaseolus, Quercus, &c.). Instead of the two opposite cotyledons, a whorl of three is not unfrequently formed in those plants which normally possess only two[2] (Phaseolus, Amygdalus, Quercus, &c.). The opposite cotyledons are usually alike in form and vigour; in Trapa however one remains much smaller than the other; and cases even occur in which only one has been formed, as in *Ranunculus Ficaria*[3], where it remains below in the form of a sheath, and in Bulbocapnos, a section of Corydalis. The two cotyledons generally form by far the larger part of the ripe embryo, so that the axis has the appearance

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[1] According to Uloth (Flora 1860, p. 265) the root-cap is also absent. On parasites see especially Solms-Laubach in Jahrb. für wissensch. Bot. vol. VI, p. 599 *et seq.*

[2] Numerous additional instances are given in the Bot. Zeitg. 1869, p. 875. [Masters, Vegetable Teratology, Ray Soc. 1869, p. 370.]

[3] Irmisch, Beitr"ge zur vergleichenden Morphologie der Pflanzen, Halle 1854, p. 12.

only of a small fusiform appendage between them; and this structure is especially striking when the embryo attains a very considerable absolute size in those seeds which possess no endosperm, and the cotyledons swell up into two thick fleshy bodies (as in Aesculus, Castanea, Quercus, Fig. 407, Amygdalus, *Vicia Faba*, Phaseolus, the Brazil-nut, &c.); but more often the cotyledons remain thin like shortly stalked foliage-leaves of simple form (as in Cruciferæ, Euphorbiaceæ, and Tilia, the last with a three- to five-lobed lamina). Most often they lie with their inner faces flat against one another (Figs. 404, 405); but are not unfrequently folded or wrinkled and curved backwards and forwards (as in Theobroma with thick, Acer and Convol-

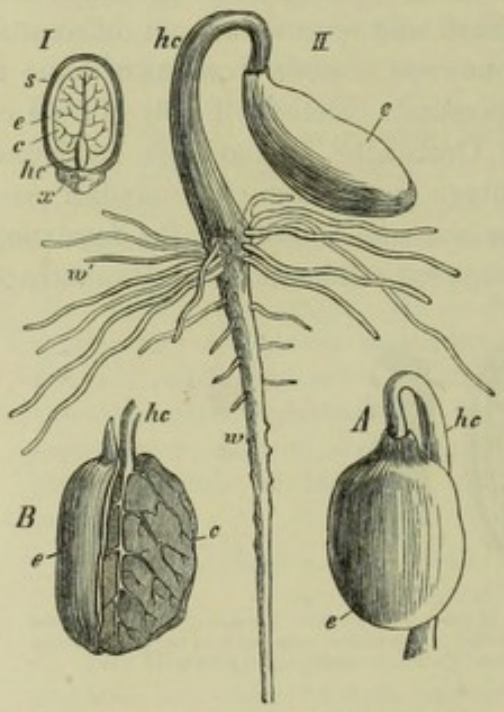

FIG. 442.—*Ricinus communis*: *I* longitudinal section of the ripe seed; *II* germinating seed with the cotyledons still in the endosperm (shown more distinctly in *A* and *B*), *s* testa, *e* endosperm, *c* cotyledon, *hc* hypocotyledonary portion of the stem, *w* primary root, *w'* secondary root, *x* the caruncle, an appendage of the seed characteristic of Euphorbiaceæ.

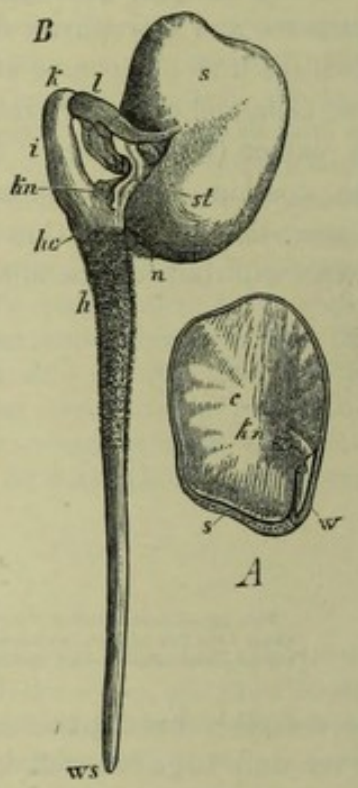

FIG. 405.—*Vicia Faba*: *A* seed with one of the cotyledons removed, *c* the remaining cotyledon, *w* radicle, *kn* plumule, *s* testa; *B* germinating seed, *s* testa, *l* a portion of the testa torn away, *n* hilum, *st* petiole of one of the cotyledons, *k* curved portion of the axis above the cotyledons, *hc* the very short hypocotyledonary portion of the axis, *h* the primary root, *ws* its apex, *kn* bud in the axil of one of the cotyledons.

vulaceæ, &c., with thin cotyledons); less often they are rolled spirally round one another.

The axis of the embryo beneath the cotyledons is generally elongated and fusiform, and when of this shape is described in works on descriptive botany as the *Radicle*. This fusiform body consists however in its upper and usually larger part of the hypocotyledonary portion of the stem, and only the lower posterior terminal piece, which is often very short, is the rudiment of the primary root (Fig. 406). The rudiments of the secondary roots can sometimes be distinguished in the tissue of the primary root (in Cucurbita, and according to Reinke in Impatiens).

Germination generally takes place—after the testa, or in dry indehiscent fruits the pericarp, has burst from the swelling of the endosperm or of the cotyledons them-

selves—by the elongation of the hypocotyledonary portion of the axis to such an extent as to push the radicle out of the seed, the root then beginning to grow rapidly and generally attaining a considerable length and forming secondary roots in acropetal succession, while the cotyledons and plumule still remain in the seed (Figs. 404, 405, 406). Thick fleshy cotyledons usually remain in the seed during germination, finally perishing after their food-material has been consumed (as in

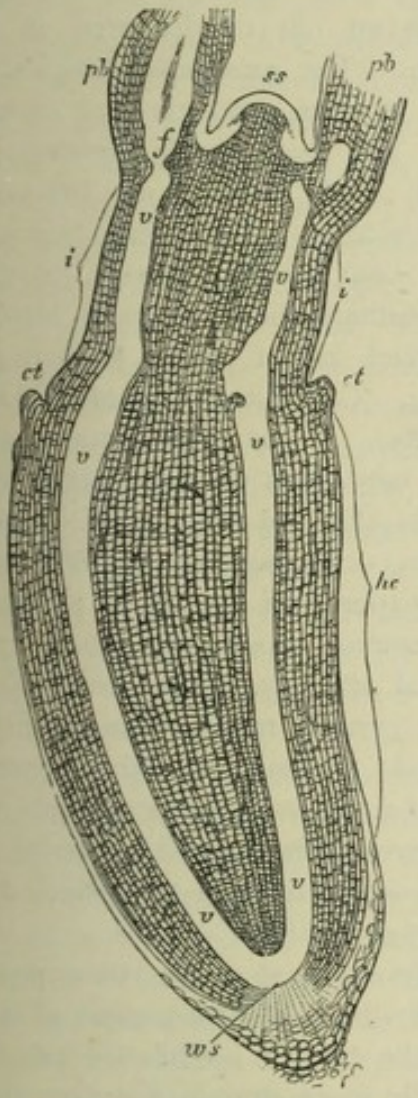

FIG. 406.—Longitudinal section of the axis of the embryo in the ripe seed of *Phaseolus multiflorus*, parallel to the cotyledons (× about 30). *ss* apex of the stem, *ws* of the root, *ct* cushion at the insertion of the cotyledons, *i* the first internode, *pb* the petioles of the first foliage-leaves, *v*, *v*, *f* the procambium of the fibro-vascular bundles.

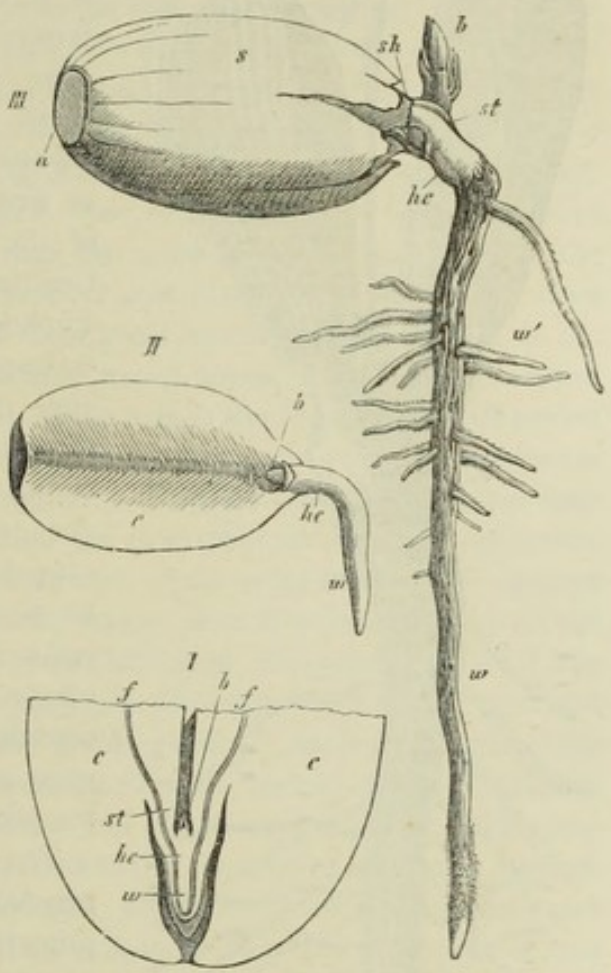

FIG. 407.—*Quercus Robur*: *I* longitudinal section of the embryo (magnified) after removal of the anterior half of both cotyledons *c*, *c*; the hypocotyledonary portion of the axis *hc* the primary root *w* and plumule *b* are concealed between the lower portion of the thick cotyledons; *st* petiole of the cotyledons; *II* seed at the time when germination is commencing (natural size), the pericarp and one cotyledon have been removed, the hypocotyledonary portion of the axis and the radicle have elongated; *III* further stage of germination, the plumule having emerged from the testa *sh* and pericarp *s* by the elongation of the petiole of the cotyledons *st*, *w* primary root, *w'* secondary roots.

Phaseolus multiflorus, *Vicia Faba*, Fig. 405, Quercus, Fig. 407). In this case the petioles of the cotyledons lengthen so much that the plumule which is concealed between them is pushed out (Fig. 407), and now grows upright so that the seed and cotyledons together have the appearance of being a lateral appendage of the axis of the embryo. But usually the cotyledons are destined for further development, especially when they are thin, and form the first foliage-leaves of the plant.

In order to liberate them and the plumule which lies between them from the seed, the hypocotyledonary portion of the axis increases considerably in length, making first of all a curve which is convex on the upper side (Fig. 404), because the cotyledons still remain in the seed while the lower end of the stem is attached by the root to the ground. Ultimately, by a final lengthening of the hypocotyledonary portion, the upper part of the axis together with the cotyledons is drawn out of the seed in a pendent position. The axis now straightens as it continues to grow, and the cotyledons expand in the air, the plumule developing more completely and pushing up between them. The cotyledons which thus become exposed to the light usually increase rapidly in size, and constitute the first green leaves of the plant, which are of simple form (*e. g.* Cruciferæ, Acer, Cucurbita, Convolvulaceæ, Euphorbiaceæ, &c). If the seed contains an endosperm, the cotyledons do not emerge till after it has been absorbed (Fig. 404). Many transitional forms occur between the different modes of germination now described; peculiar phenomena sometimes appearing which are caused by special vital conditions. In Trapa, for example, the primary root is from the first rudimentary, and remains altogether undeveloped; the hypocotyledonary portion lengthens considerably, curves upwards, and protrudes a great number of lateral roots in rows which fix the plant into the ground[1].

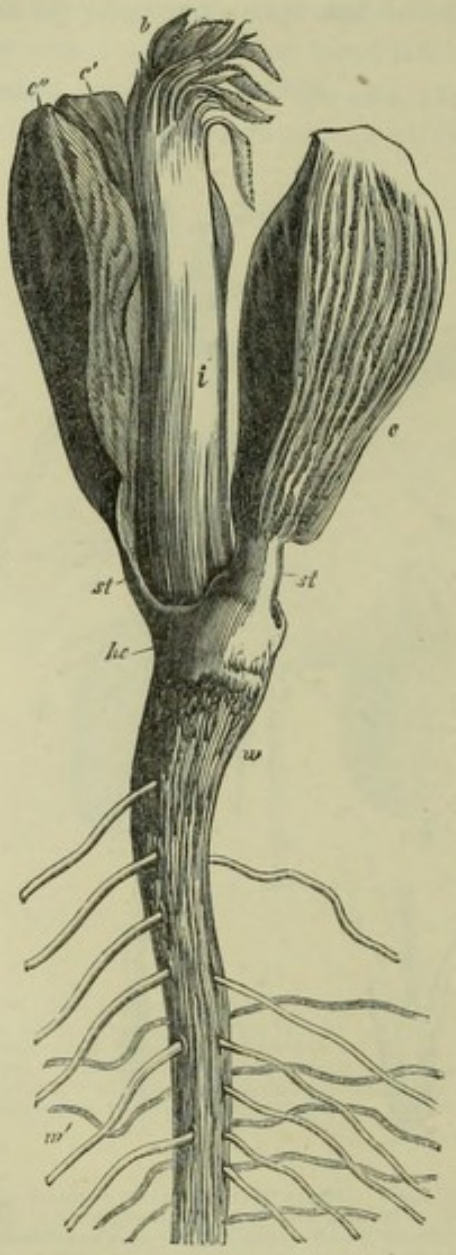

FIG. 408.—Almond-seed germinating, one of the cotyledons c' c'' being split; the letters as in Fig. 407, i the first internode strongly developed.

The further development of the young plant may take place by the rapid enlargement of the primary axis of the embryo. While the axis is growing, generally in an upright direction, the shoot which developes from the plumule becomes the primary stem of the plant, lengthening at the summit, and usually producing weaker lateral shoots (*e. g.* Helianthus, Vicia, Populus, Impatiens, &c.). When the main stem is perennial, it sooner or later ceases to develope further at the apex, or the lateral shoots nearest to the apex become equally strong. An arborescent head is thus formed, the main stem or trunk becoming denuded by the dying off of the lower branches, or the main stem continues to grow erect as a sympodium (as in Ricinus, the lime, &c.); or lateral shoots are formed at an early

[1] [See De Candolle, Organographie Végétale, Pl. 55.—Ed.]

period at the base of the primary stem which grow as strongly, and thus give rise to a shrubby plant. When the axis of the embryo grows vigorously, the primary root generally also grows vigorously in a downward direction[1]; and a *Tap-root* is thus formed, from which, as long as it increases in length, the lateral roots spring in great numbers in acropetal succession. When the growth in length of the tap-root ceases, adventitious roots become intercalated among the lateral roots already formed, and like them, grow vigorously, and may themselves produce lateral roots of higher orders. A strong root-system is thus produced with the primary root of the embryo for its centre, which endures as long as the stem itself. By the subsequent increase in thickness the primary stem (as well as its branches) assumes the form of a slender upright cone, the base of which rests on the base of the inverted cone formed by the primary root which has also increased in thickness. While these processes, which are here described in their main outlines, take place almost invariably among Conifers, a number of deviations occur, on the other hand, among Dicotyledons similar to those which have been spoken of under the head of Monocotyledons. The primary axis may die soon after germination or at the end of the first period of vegetation, the primary root often perishing as well, while the axillary shoots of the cotyledons or of subsequent leaves continue the life of the individual. Thus, for example, in the dahlia, a strong adventitious root is given out laterally from the hypocotyledonary portion of the axis at the close of the first period of vegetation of the young plant, and swells into a tuber; the primary root-system and the portion of the axis above the cotyledons disappear, and there remain only for the continuance of the life of the plant the new tuberous root, the hypocotyledonary portion of the axis, and the axillary buds of the cotyledons. The process is still more striking in *Ranunculus Ficaria*, where, after the development of the primary root, a tuberous lateral root is produced below the primary axis of the embryo, sheathed by a coleorhiza, and maintains its existence together with the axis, while the primary root and the first leaves perish. Among the numerous cases belonging to this category may be mentioned also *Physalis Alkekengi*, *Mentha arvensis*, *Bryonia alba*, *Polygonum amphibium*, and *Lysimachia vulgaris*[2]. The production of bulbs also occurs among Dicotyledons (as in species of Oxalis), though not so commonly as among Monocotyledons; of more common occurrence are tubers or swellings of underground branches, stolons, or rhizomes of greater or less thickness. The greater number of Dicotyledons have perennial underground roots or stems which send up periodically leafy and flowering shoots that die at the end of each period of vegetation. In all such cases, where the primary root-system of the seedling perishes, new roots are repeatedly developed from the stem; and the power possessed by most Dicotyledons of producing adventitious roots from the

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[1] One of the most remarkable exceptions is afforded by the genus Cuscuta, which has no primary root, the posterior end of the axis penetrating into the ground on germination, but soon dying off when the upper filiform portion of the stem has embraced the plant on which it becomes parasitic, and has fixed itself on to it by its short suckers; the plant afterwards grows vigorously and branches.

[2] The above is taken from Irmisch's detailed descriptions in his Beiträge zur vergleichenden Morphologie der Pflanzen, Halle, 1854, 1856; Bot. Zeitg. 1861; and elsewhere.

stem, especially when kept moist and dark, enables them to be reproduced to almost any extent from branches and portions of branches. Some species climb, like the ivy, by roots put out regularly from the weak stem which requires a support; others send out runners to a distance, on which the bud forms a new plant, as in the strawberry, the stem which is thus formed putting out roots. The order of succession of new roots from the stem is in general acropetal, but they do not usually make their appearance except at a considerable distance behind the growing bud; many Cactaceæ however not unfrequently produce them close below it.

The normal *Mode of Branching* at the end of growing shoots is monopodial; the branches are produced laterally beneath the apex of the *punctum vegetationis*. Up to the present time only one instance is known of dichotomous branching, and in that the bifurcations are developed sympodially; according to Kaufmann, the formation of the circinate inflorescence of Borragineæ depends, as has already been mentioned, on this mode of development. The normal monopodial branching is axillary; the lateral shoots are produced in the angle which the median line of the leaf forms with the internode. On a vegetative shoot at least one lateral shoot is produced in the axil of each leaf, although only a few of the axillary buds unfold. Sometimes other axillary buds are produced in rows above the original one; as, for instance, above the axils of the foliage-leaves in *Aristolochia Sipho*, Gleditschia, Lonicera, &c.[1], above the axils of the cotyledons in *Juglans regia*, and that of the larger cotyledon in Trapa. In woody plants the axillary buds destined to live through the winter are not unfrequently so completely surrounded by the base of the leaf-stalk that they are not visible until the leaf has fallen off, as in *Rhus typhinum*, *Virgilia lutea*, Platanus, &c., and are then called *Intrapetiolar Buds*. Besides the ordinary axillary branching, some cases are known among Dicotyledons of lateral and monopodial but *extra-axillary* branching. To this description belong the tendrils of Vitis and Ampelopsis which are produced (according to Nägeli and Schwendener) beneath the *punctum vegetationis* of the mother-shoot, opposite to the youngest leaf and somewhat later than it. In *Asclepias syriaca* and some other plants a lateral vegetative branch stands beneath the terminal inflorescence between the insertions of the foliage-leaves, which themselves also produce shoots in their axils. According to Pringsheim[2] lateral shoots arise on the concave side of the long spirally-curved vegetative cone of *Utricularia vulgaris* which he considers to be extra-axillary branches, while 'normal' shoots are formed in the axils of the leaves which stand in two rows on the convex side of the shoot or by their side. It appears to me however certain that these extra-axillary structures on the concave side of the mother-shoot are leaves of peculiar form[3], since inflorescences are produced in their axils.

The suppression of the bracts of the inflorescence, which is not uncommon,

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[1] See Guillard, Bull. Soc. Bot. de France, vol. IV, 1857, p. 239 (quoted by Duchartre, Eléments de Botanique, p. 408).

[2] Zur Morphologie der Utricularien. Monatsber. der königl. Akad. der Wissensch. Feb. 1869.

[3] This of course depends on what is considered leaf and what shoot; this is not however a matter of simple observation, but rather of conventional conceptions convenient for a special purpose.

cannot be placed in the same category as the cases just mentioned of extra-axillary branching, where large leaves in the axils of which buds are also formed exist near the extra-axillary lateral branches. Here, on the contrary, as for instance in Cruciferæ and the capitulum of many Compositæ, the formation of leaves on the axis of the inflorescence is itself entirely suppressed; there are no leaves in the axils of which the branches could stand. The branches are however produced as if the leaves were actually there; and there are reasons for supposing that we have here a case of abortion of the bracts in the same sense as the abortion of the posterior stamen of Labiatæ (p. 480), Musaceæ (Fig. 397, p. 548), &c. Since it is common for the hypsophyllary leaves on the inflorescence to remain very small and to disappear early, it would not be surprising, according to the theory of descent, that functionless organs of this kind should at length entirely disappear, their development being in such cases altogether suppressed, while the lateral branches which belong to them (according to the theory of descent typically axillary) should be strongly developed.

Adventitious buds are rare in Dicotyledons, as they are in Phanerogams generally. Those which are commonly formed with an exogenous origin in the indentations of the margins of the leaves of *Bryophyllum calycinum* are well known, and serve to propagate the plant. They sometimes occur (according to Peterhausen[1]) in *Begonia coriacea* in the form of small bulbs on the peltate surface of the leaf where the principal veins radiate[2]. On the adventitious buds on the leaves of Utricularia, Pringsheim's treatise already quoted may be consulted. Adventitious buds more often spring from roots, *e. g.* in *Anemone japonica*, *Linaria vulgaris*, *Cirsium arvense*, and *Populus tremula*, according to Irmisch[3]. The shoots which spring from the bark of the older stems of trees must not at once be set down as the development of adventitious buds; since the numerous dormant buds of woody plants may long remain buried and yet retain their vitality.

The *Leaves* of Dicotyledons exhibit a greater variety both in their position and their form than those of all other classes of plants put together. The ordinary phyllotaxis of seedlings begins with a whorl of two cotyledons, and continues either in decussate pairs or passes into a distichous arrangement or into whorls consisting of larger numbers or spiral arrangements with the most various angles of divergence. More simple arrangements, especially that of decussate pairs, are generally constant in whole families, the more complicated arrangements usually less constant. Axillary branches usually begin with a pair of leaves which are either opposite or alternate, and stand right and left of the median line of the mother-leaf.

It is quite impossible to give in a short space even a general account of the forms of leaves, even apart from cataphyllary leaves (scales on underground stems and those which envelope persistent buds), hypsophyllary leaves or bracts,

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[1] Beiträge zur Entwickelung der Brutknospen (Hameln 1869), where various examples are also given of axillary buds of Dicotyledons which form deciduous gemmæ; as in *Polygonum viviparum*, *Saxifraga granulata*, *Dentaria bulbifera*, *Ranunculus Ficaria*, &c.

[2] [The common method of propagating Begonias is by cutting or tearing the leaf, which, if then placed on moist soil, produces buds on the edges.—Ed.]

[3] [Irmisch, Bot. Gaz. III, pp. 146 and 160.]

and floral leaves; only a few of those forms of foliage-leaves can be mentioned here which are peculiar to or characteristic of Dicotyledons. The foliage-leaves are usually divided into a slender leaf-stalk (*petiole*) and a flat blade (*lamina*); the lamina is very commonly branched, *i. e.* lobed, pinnate, compound, or incised; and even where it forms a single plate (simple leaf) the tendency to branching is generally indicated by indentations, teeth, or incisions in the margin. The branching of the lamina has usually a distinctly monopodial origin, but its development may continue in a cymose manner, a helicoid succession of lateral lobes being formed on each side right and left of the centre of the leaf (as in Rubus, Helleborus, &c., see Fig. 133, p. 162). The sheathing amplexicaul base is not common in Dicotyledons (but occurs in Umbelliferæ); and the occurrence of *Stipules* in its place is more common. The cohesion of opposite leaves into a single plate pierced by the stem is not uncommon ('perfoliate' leaves, as in *Lamium amplexicaule*, *Dipsacus Fullonum*, *Lonicera Caprifolium*, species of Silphium, Eucalyptus, &c.); as well as the downward prolongation of the lamina of the leaves ('decurrent leaves'), which distinguishes the 'winged' stem of Verbascum, Onopordon, &c. The not uncommon 'peltate' leaf also scarcely occurs in so marked a manner in any other class (Tropæolum, *Victoria regia*, &c.). The power of Dicotyledons to develop from their foliage-leaves organs of the most diverse functions adapted to the most various conditions of life is seen in a very striking manner in the common occurrence of leaf-tendrils and leaf-thorns, and still more in the formation of the ascidia or 'pitchers' of Nepenthes, Cephalotus, Sarracenia, &c.

The *Venation* of the foliage-leaves (with the exception of the thick leaves of succulent plants) is distinguished by the numerous veins which project on the under side, and by their curvilinear anastomoses by means of fibro-vascular bundles running through the mesophyll itself. The mid-rib, which usually divides the leaf into two symmetrical but sometimes into very unsymmetrical halves, gives off lateral veins right and left; one, two, or three strong nerves, similar to the mid-rib, often springing in addition from the base of the lamina right and left of the median line. The whole system of the projecting veins of a foliage-leaf behaves like a monopodial branch-system developed in one plane, the interstices being filled up by the green mesophyll in which lie the anastomoses combined into a small-meshed network. Within the meshes still finer bundles are usually formed which disappear in the mesophyll. In membranous cataphyllary and hypsophyllary leaves and the perianth-leaves of the flowers the projecting veins do not usually occur; the venation is more simple and more like that of Monocotyledons[1].

The *Flower*[2]. In the great majority of Dicotyledons the parts of the flower are

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[1] [The structure of the leaf compared with that of the stem has been worked out by Casimir De Candolle, Archives des Sciences, 1868; the 'Student' for the same year contains an abridged translation of his paper.—Ed.]

[2] The floral diagrams given here are drawn partly from my own investigations, but chiefly from the researches of Payer into the history of development, assisted by Döll's Flora of Baden. The figures placed beneath the diagrams are intended to indicate the number and cohesion of the carpels as well as the placentation in those plants the diagram of which is otherwise the same.

arranged in whorls, or the flowers are *cyclic*; only in a comparatively small number of families (Ranunculaceæ, Magnoliaceæ, Calycanthaceæ, Nymphæaceæ, and Nelumbiaceæ) are all or some of them arranged spirally (*acyclic* or *hemicyclic*[1]).

In *Cyclic Flowers* the whorls are usually pentamerous, less often tetramerous, both numbers occurring in nearly-related plants. Dimerous or trimerous, or combinations of dimerous and tetramerous whorls are much less common than pentamerous, and are usually characteristic of smaller groups in the natural system.

When the floral whorls are tetramerous or pentamerous, they are generally four in number, and are developed as Calyx, Corolla, Andrœcium and Gynæceum. In dimerous or trimerous flowers the number of the whorls is much more variable, and then it is not uncommon for each organ to be made up of two or three whorls; while in the previous case the multiplication of the whorls is almost entirely confined to the andrœcium.

The corolla is frequently absent, and the flowers are then said to be *apetalous*. When the calyx and corolla are both present the number of their parts (sepals and petals) is almost always the same (Papaver is an exception); but this is not the case with the number of the whorls. In Cruciferæ, for example, the calyx consists of two decussate whorls of two sepals each, the corolla of one whorl of four petals. When the perianth and andrœcium are both present (whether the former consist of calyx only or of both calyx and corolla), the number of their parts is usually the same, or the flower is *isostemonous*, but the stamens are often more, rarely fewer in number than the parts of the perianth, and the flower is then *anisostemonous*. When the flower is tetramerous or pentamerous the number of carpels is usually less; when the flower is dimerous or trimerous, or when the parts are arranged spirally, the number of carpels is not unfrequently larger.

It will be seen from this brief outline that the relations of number and position in the parts of the flowers of Dicotyledons are very various, and cannot be referred, as is the case with Monocotyledons with but few exceptions, to a single type. Even the establishment of different types for the larger groups is attended with great uncertainty, since the knowledge of development necessary in order to refer particular forms of flowers to general formulæ is often wanting. The too universal application of the spiral theory to phyllotaxis even in the case of cyclic flowers has often increased the difficulty, and has even occasioned doubts which would not have arisen without the theory.

For the great majority of Dicotyledons the floral formula may be given $S_n P_n St_{n(+n+\ldots)} C_{n(-m)}$. This formula holds good for most pentamerous flowers and for those which are truly tetramerous (or octamerous as Michauxia); so that n is in these cases 5 or 4 (or 8 as the case may be). In the andrœcium an indefinite number of (alternating) whorls $St_{n(+n+\ldots)}$ must be assumed in order to include the large number of flowers in which the andrœcium consists of more than one whorl (as *e. g.* Fig. 420). The mode expressing the gynæceum $C_{n(-m)}$ is intended to show that very commonly the number of carpels is fewer than 5 or 4 (or 8 as the case may be); m may be of any value from 0 to n. In the majority of gamopetalous

[1] Compare pp. 523 and 531.

orders and elsewhere there are very commonly only two carpels; and in this case they stand in a median line posterior and anterior; but on the hypothesis that the typical gynæceum consists of five alternating carpels and has been reduced to two by abortion, one must stand in the median position in front, the other obliquely behind. A similar difficulty is also presented when the gynæceum consists of three or of only one carpel. It would carry us too far to detail the reasons which nevertheless determine me to retain the formula above given for the gynæceum of flowers of this description; it need only be mentioned that species or genera with the typical five carpels occur in the most diverse families and orders where a smaller number is the normal one.

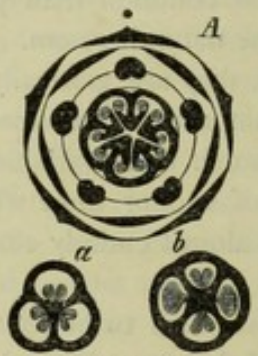

FIG. 409.—Diagram of Caprifoliaceæ; *A* Leycesteria, *a* Lonicera, *b* Symphoricarpus.



FIG. 410.—Diagram of Parnassia (Saxifragaceæ).

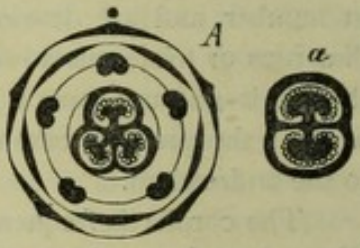

FIG. 411.—Diagram of Campanulaceæ; *A* Campanula, *a* Lobelia.

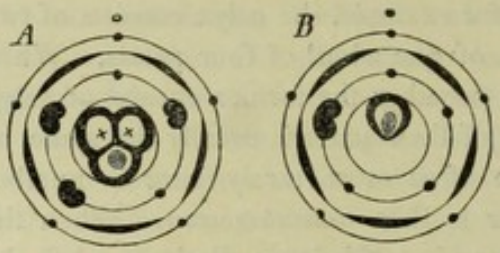

FIG. 412.—Diagram of Valerianaceæ; *A* Valeriana, *B* Centranthus.



FIG. 413.—Diagram of Cucurbitaceæ.



FIG. 414.—Diagram of Compositæ.



FIG. 415.—Diagram of some Rubiaceæ.



FIG. 416.—Diagram of Plantagineæ.

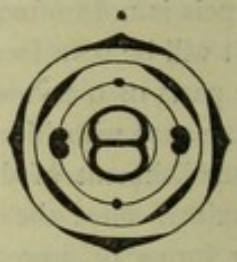

FIG. 417.—Diagram of Oleaceæ.



FIG. 418.—Diagram of Menispermaceæ.



FIG. 419.—Diagram of Cinnamomum (Lauraceæ).

The diagrams Figs. 409–419 represent a selection of cases which can be

reduced (if no further reference is made to the considerations mentioned above) to the general formula which here assumes the simpler expression $S_n P_n St_n C_{n(-m)}$. A comparison with nearly-allied forms leaves little room for doubt that the vacant spaces indicated by dots in the three outer whorls correspond to abortive members

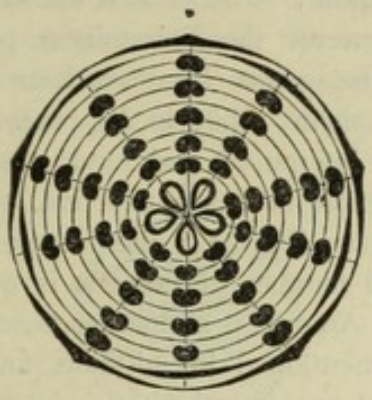

FIG. 420.—Diagram of Aquilegia (Ranunculaceæ).

in the sense already frequently indicated, even when the absence of these members is so complete that even the earliest stages of development of the flower give no indication of them. The same is the case also when the number of carpels is less than the typical one. Other cases however occur, as in the case of Rhus (Fig. 421),

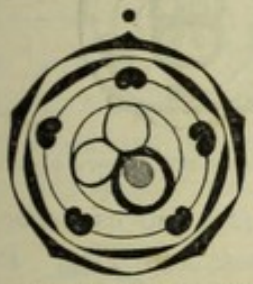

FIG. 421.—Diagram of Rhus (Anacardiaceæ).

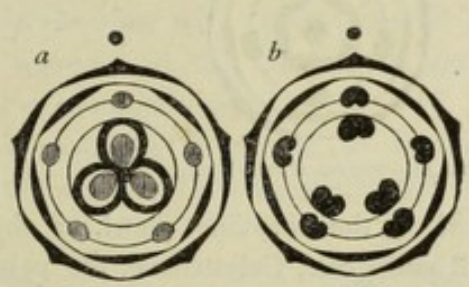

FIG. 422.—Diagram of Crozophora (Euphorbiaceæ), *a* female, *b* male flower.

where certain members, in this case two out of the three carpels, disappear in the course of development. *Crozophora tinctoria* (Fig. 422) is especially instructive in regard to the relationships here suggested, the flowers becoming diclinous from the stamens in the female flowers developing as sterile staminodes, which may be



FIG. 423.—Diagram of pentamerous Ericaceæ and Epacrideæ.



FIG. 424.—Diagram of Æsculus (Hippocastaneæ).

considered as the first step towards abortion, while in the male flowers the three carpels are replaced by as many fertile stamens (Payer).

Reference was made in the Introduction to Angiosperms (p. 481) to the interposition of a whorl of stamens between the members of a previously formed staminal

whorl; and it was mentioned that the interposed whorl has sometimes not the full number of members. These phenomena occur in various large groups of Dicotyledons[1]. In Fig. 423 the five stamens of the decandrous flower of the group of Bicornes which are interposed as a whorl of full number within the first whorl are indicated by the lighter colour. The same is the case with the larger number of Gruinales, among which however the Balsamineæ possess only the typical five stamens; the Lineæ and the genus Erodium have five additional rudimentary stamens interposed between them; while in *Peganum Harmala* and Monsonia the number of stamens in the interposed and outer whorl is doubled. The order Æsculineæ is of special interest in this connection, since in some of its families (Acerineæ and Hippocastaneæ, Fig. 424) the interposed staminal whorl remains incomplete, so that the total number of stamens is not a multiple of the typical fundamental number (five). Among pentamerous flowers Lythrarieæ, Crassulaceæ, and Papilionaceæ may be mentioned in addition, and among tetramerous ones Œnothereæ, in which a complete staminal whorl is interposed.

One of the most remarkable deviations from the ordinary structure takes the form in not a few families of Dicotyledons of the simple staminal whorl being



FIG. 425.—Diagram of Primulaceæ.



FIG. 426.—Diagram of Vitis (Ampelideæ).

superposed on the corolline whorl, as shown in Figs. 425, 426, and as occurs also in the Rhamnaceæ, Celastrineæ, the pentandrous Hypericineæ, and Tilia. Pfeffer[2] has shown that the two superposed whorls of Ampelideæ arise independently of one another and in acropetal order, while on the other hand in Primulaceæ they first appear in the form of five projections each of which forms a stamen, and from each of which a petal subsequently grows outwards[3]. In these cases we have no sufficient ground for the hypothesis that an alternating whorl has been suppressed between the two superposed ones; although in other cases this supposition is justified, or at least is very probable. Thus in the order Caryophyllineæ, families, genera and species occur in which the corolla is absent and the stamens are superposed on the sepals; and since in the same natural group species also occur with a corolla, it may be assumed that where the corolla is absent this is the result of abortion. The diagram of these plants (Figs. 427, 428) is complicated still further by the tendency which they exhibit to a *dédoublement* of the stamens and even of the carpels.

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[1] Payer's figures show that the interposed whorl, although of later origin, is sometimes exterior to the typical whorl. The main point is that the position and number of the other parts of the flower are exactly as if there were no interposed whorl.

[2] Pfeffer, Bot. Zeitg. 1870, p. 143; and Jahrb. für wissensch. Bot. vol. VIII, p. 194.

[3] Compare on this point what was said on p. 531. If the theory that is here objected to of the flowers of Primulaceæ is maintained, it is clear that the mode of expressing the floral formula must then be altered, and the diagram be somewhat differently drawn.

When a flower has more stamens than sepals or petals, this may be the result, as has already been mentioned, on the one hand of an increase in the number of staminal whorls (as in Fig. 420), or on the other hand, of the interposition of a perfect or imperfect whorl among the typical ones, or of *dédoublement* of the stamens (as in Fig. 427). These cases must be clearly distinguished from those in which a larger number of stamens results from the branching of the original ones, a phenomenon which is found in different sections of Dicotyledons, and is sometimes constant in whole families (see p. 475). Thus, for instance, in Dilleniaceæ



FIG. 427.—Diagram of Scleranthus (Paronychiaceæ).

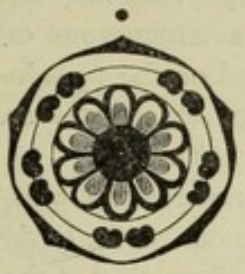

FIG. 428.—Diagram of Phytolacca (Phytolaccaceæ).



FIG. 429.—Diagram of Celosia (Amaranthaceæ).

(Fig. 430), Aurantiaceæ (Fig. 431), and Tiliaceæ (Fig. 432), each symbol which indicates a group of anthers corresponds to a single original stamen. In this case the number of original stamens is the same as that of the petals and sepals; but sometimes it is less (as in *Hypericum perforatum* with three staminal bundles in the pentamerous flower); so that an increase in the number of stamens is united with a decrease of the typical number of staminal leaves.

The branching of carpels is much less common than that of stamens. It occurs very clearly in Malvaceæ, where the typical number of carpels is five,



FIG. 430.—Diagram of Candollea (Dilleniaceæ).

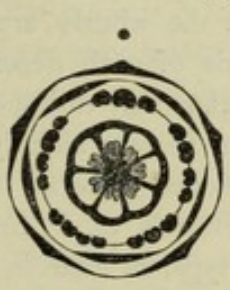

FIG. 431.—Diagram of Citrus (Aurantiaceæ).



FIG. 432.—Diagram of Tiliaceæ.

and they are often developed as such (as in Hibiscus). In some genera however (as Malva, Malope, and Althæa) five original rudiments of carpels first of all make their appearance in the form of a low cushion. Each of these forms very early a larger number of outgrowths lying side by side, and each of these produces a style and a one-seeded compartment of the peculiarly-shaped gynæceum[1].

This short sketch will be sufficient to show what variations are possible in the numbers and positions of the parts that may be included under the expression $S_n P_n St_{n\ (+n+\ldots)}\ C_{n\ (-m)}$, which, as has already been said, is especially characteristic of flowers with pentamerous or truly tetramerous whorls. True tetramerous flowers

[1] See Payer, Organogénie de la fleur, Pl. 6-8.

are allied not only to those that are octamerous (like Michauxia) but also to those with dimerous whorls, among which Œnothereæ may be especially mentioned. Of genera belonging to this family, Epilobium, for example, is constructed on the formula $S_{2+2}\ P_{\times 4}\ St_{4.4}\ C_4$, Circæa on that of $S_2\ P_2\ St_2\ C_2$; and Trapa, with the formula $S_{2+2}\ P_{\times 4}\ St_4\ C_2$, must also be included here. Although in Epilobium and Trapa the calyx really consists of two whorls, this pseudo-whorl formed of two decussate pairs is followed by the other whorls exactly as if it were a true tetramerous whorl. But other dimerous and tetramerous flowers exhibit a more considerable deviation from the type, inasmuch as the two dimerous perianth-whorls which develope as if they were a tetramerous calyx or corolla are followed by a staminal whorl which is superposed on the pseudo-whorl consisting of two decussate pairs, as in Urtica and other genera of the order, and in Proteaceæ with the formula $S_{2+2}\ St_4\ C_1$ (Fig. 339, p. 478).

Among the dimerous and trimerous flowers of the orders Polycarpæ and Cruciflorae, where they are the most perfectly developed, a tendency prevails for more than one whorl to go to the formation of the calyx, the corolla, the andrœcium, and even the gynæceum, a tendency which may be expressed by the formula $S_{p(+p+\ldots)}\ P_{p(+p+\ldots)}\ St_{p(+p+\ldots)}\ C_{p(+p+\ldots)}$; for example

Fumariaceæ, $S_2\ P_{2+2}\ St_{2+\ldots}\ C_2$.

Berberideæ,

Epimedium, $S_{2+2}\ P_{2+2}\ St_{2+2}\ C_1$

Berberis, $S_{3+3}\ P_{3+3}\ St_{3+3}\ C_1$

Podophyllum, $S_3\ P_{3+3}{}^2\ St_3{}^3{}_{+3}\ C_1$

Cruciferæ, $S_{2+2}\ P_{\times 4}\ St_{2+2}{}^2\ C_{2(+2)}$.

A large number of examples of this general formula are afforded by the family Menispermaceæ, in which the whorls are sometimes dimerous, sometimes trimerous, while sometimes whorls of each description occur in one flower; and where almost every one of the organs may disappear by abortion[1].

In addition to the trimerous flowers already mentioned, there are also some which come under the first-mentioned general formula $S_n\ P_n\ St_{n(+n)}\ C_{n\ (-m)}$; as, for example, Rheum with the formula $S_3\ P_3\ St_3{}^2{}_{+3}\ C_3$. Other trimerous flowers again appear to belong to a third type, as Asarum with the formula $S_3\ St_{3+6}\ C_6$.

When the number of staminal whorls is considerably increased, it not unfrequently happens that the number of stamens in each whorl also undergoes change, and complicated alternations arise. Flowers the structure of which is otherwise altogether different resemble one another in this respect, as is shown by the Papaveraceæ on the one hand (Fig. 433), and by Cistineæ and some Rosaceæ on the other hand.

The reduction of the flower to a simpler condition is often carried so far in many Dicotyledons (as in Monocotyledons) that each individual flower consists only either of an ovary with one or several stamens, or, when the arrangement

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[1] Eichler, Ueber die Menispermaceen, Denkschrift der k. bayer. Ges., Regensburg 1864.—Payer, Organogénie de la fleur, Pl. 45–49.—Eichler, Flora 1865, Nos. 2–8 *et seq.*

is diclinous, even only of a single ovary or of a single or several stamens; the perianth being either entirely absent (as in Salix and Piperaceæ) or reduced to a cup-like structure (Populus, the female flower of Cannabineæ &c.) or to hair-like

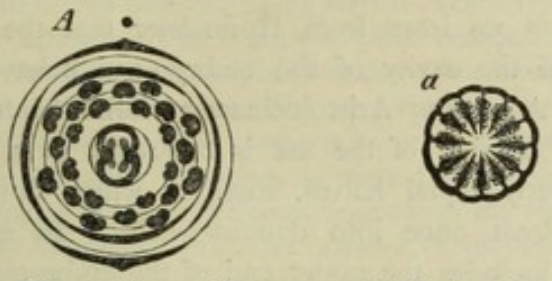

FIG. 433.—Diagram of Papaveraceæ; *A* Chelidonium, *a* Papaver.

scales among the sexual organs which represent the flower (*e. g.* Platanus). Flowers of this kind are generally very small and densely crowded in large numbers in the inflorescence (such as capitula, spikes, or catkins). In some cases it may even be doubtful whether we have an inflorescence or a single flower, as in the genus Euphorbia[1].

The development of the separate parts and the entire form of the flower in the mature state is so various that it is scarcely possible to state any general facts concerning them. The perigynous structure of the flower is peculiar to Dicotyledons, as is also the occurrence of hollowed axes of the inflorescence, like the fig and similar structures, and the cupule, which occur in some families, and are dependent on similar processes of growth.

The *Ovules* exhibit, in the different divisions of Dicotyledons, all those varieties of structure which have already been mentioned in the introduction. Very commonly, especially among the Gamopetalæ, the nucleus is covered by only one integument, which is then often very thick before impregnation. But on the other hand the third integument or aril is much more common than among Monocotyledons. When there are two integuments, the outer one,—differing again in this respect from most Monocotyledons—takes part in the formation of the micropyle, enveloping the exostome or entrance to it. In some parasites the ovules are rudimentary, and in many Balanophoraceæ are reduced to a naked few-celled nucleus; while in Loranthaceæ they are coherent with the tissue of the floral axis in the inferior ovary.

The behaviour of the *Embryo-sac*[2] before and after impregnation is similar in most Dicotyledons to that which occurs in Monocotyledons. The endosperm usually originates by free cell-formation, and is transformed by repeated divisions of the first cells which are formed in this manner into a more or less dense tissue, which fills up the embryo-sac either before or after the formation of the multicellular rudiment of the embryo. But in a very considerable number of families belonging to altogether different groups the embryo-sac exhibits on the one hand striking phenomena of growth, elongating considerably before impregnation into

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[1] See Payer, *l. c.* p. 529; [also foot-note to p. 426].

[2] Hofmeister, Jahrb. für wiss. Bot. vol. I, p. 185; and Abhandl. der kön. Sachs. Ges. der Wiss. vol. VI, p. 536.

a long tube, and emitting after impregnation one or more vermiform protrusions which penetrate into and destroy the tissue of the nucleus and of the integuments, or even protrude altogether out of the ovule (as in Pedicularis, Lathræa, and Thesium). On the other hand in those plants in which the endosperm originates by cell-division we learn from Hofmeister that the following variations occur:—'The whole of the cavity of the embryo-sac behaves like the first cell of the endosperm in Asarineæ, Aristolochiaceæ, Balanophoraceæ, Pyroleæ, and Monotropeæ; the first division of the sac is the result of a partition-wall which divides it into two nearly equal halves, each of which encloses a cell-nucleus and again divides at least once into daughter-cells. In other cases the first cell of the endosperm includes the upper end of the embryo-sac; the embryo-sac which has just been fertilised appears to be divided by a transverse septum into two halves, the upper one of which developes into the endosperm by a series of bipartitions; while no such bipartition of the lower one occurs in Viscum, Thesium, Lathræa, Rhinanthus, Mazus, Melampyrum, or Globularia. The first cell of the endosperm fills up the middle part of the embryo-sac in Veronica, Nemophila, Pedicularis, Plantago, Campanula, Loasa, and Labiatæ; its lower end in Loranthus, Acanthus, Catalpa, Hebenstreitia, Verbena, and Vaccinium.' In Nymphæa, Nuphar, and Ceratophyllum, the upper end of the embryo-sac is cut off from the rest of the space by a septum soon after impregnation, and the further development of the daughter-cells or endosperm takes place only in the upper part which also includes the 'embryonic vesicles.' This mode of formation of the endosperm differs however from that which occurs in the plants mentioned above, in taking place in the upper half of the embryo-sac by free cell-formation.

In the very large majority of true parasites (except Cuscuta) and saprophytes, the endosperm is formed by cell-division; in Cuscuta however by free cell-formation. Hofmeister states that only slight indications of the formation of endosperm are to be found in Tropæolum and Trapa.

The mode of formation of the *Embryo* of Dicotyledons, as it has now been elucidated by Hanstein's recent researches, has already been explained in the introduction to Angiosperms (see Fig. 372, p. 516). It need now only be stated in addition that in parasites destitute of chlorophyll and in some saprophytes the seeds become ripe before the embryo has emerged from the condition of a roundish mass of tissue still without external differentiation of parts (*e. g.* in Monotropa, Pyrola, Orobanche, Balanophoraceæ, and Rafflesiaceæ).

With reference to the *Formation of Tissue*[1], I will confine my remarks here to a description of the behaviour of the fibro-vascular bundles and of the mode in which the stem increases in thickness.

With the exception of a few water-plants of simple structure, in which a purely cauline fibro-vascular cylinder runs through the stem and increases in length at its

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[1] Hanstein, Jahrb. für wiss. Bot. vol. I, p 233 *et seq.*, and for the girdle-shaped combinations of vascular bundles Abh. der Berl. Akad. 1857, 8,—Nägeli, Beiträge zur wiss. Bot. Leipzig, Heft I, 1858; and Dickenwachsthum und Anordnung der Gefässstränge bei den Sapindaceen, München 1864.—Sanio, Bot., Zeit. 1864, p. 193 *et seq.* and 1865, p. 165 *et seq.*—Eichler, Denkschrift der kön. bayer. bot. Gesells. vol. V, Heft I, p. 20, Regensburg 1864.

summit, the foliar bundles originating from it later (in Hippuris, Aldrovanda, Ceratophyllum, and to a certain extent also Trapa, according to Sanio), it is the general rule that 'common' bundles are first formed, the ascending branches of which enter the stronger foliage-leaves generally in large numbers, and then pursue their course as isolated bundles in the leaf-stalk and mid-rib, giving off the secondary bundles which constitute the venation of the lamina[1]. The branches which descend into the stem mostly run downwards through several internodes, become first interposed between the upper parts of the older bundles, and sometimes (Fig. 434) first split and then coalesce laterally with the older bundles lower down. Sometimes (as in Iberis) every bundle is twisted in the stem and in the same direction, so that the bundles which have coalesced sympodially, belonging to leaves of different heights on the stem, ascend spirally within the bark. But most commonly they run parallel to the axis of the stem, until they anastomose with older bundles lower down. The bundles do not bend deeply into the inner tissue of the stem, but turn downwards and run parallel to one another at the same distance below the surface, so that they lie in one layer, which presents the appearance of a ring on transverse section separating the fundamental tissue into pith and primary cortex. The portions of the fundamental tissue which lie between the fibro-vascular bundles connect the pith with the primary cortex, and form the primary

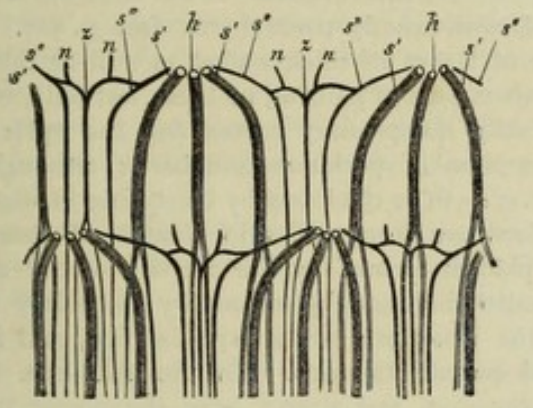

FIG. 434.—The course of the bundles in two internodes of *Sambucus Ebulus*: they lie in a cylinder which is here flattened out; each internode bears two opposite leaves, and each leaf receives from the stem a middle bundle *h h* and two strong lateral bundles *s' s'*; the descending arms of the bundles split and interpose between the lower bundles; there are in addition weaker bundles *s'' s''* united by horizontal branches, from which bundles *n n* ascend into the stipules. (After Hanstein.)

Medullary Rays. If there is no subsequent increase in thickness no further change takes place. But usually, even in annual stems (as Helianthus and Brassica) and invariably in woody stems and branches several years old, the subsequent increase in thickness begins after the elongation of the internodes. A layer of cambium is formed between the outer phloëm and the xylem which is turned towards the axis of each foliar bundle; the cambium layers of the bundles which are at first still separated by the medullary rays lying side by side in a ring, unite in a closed mantle of cambium; an interfascicular cambium is formed by divisions in the intermediate cells of the medullary rays, and bridges over the spaces between the separate layers of the cambium of the fibro-vascular bundles (see Fig. 82, p. 95). The *Cambium-ring* thus formed produces on the outside layers of phloëm, on the inside layers of xylem, while it is at the same time itself constantly increasing in diameter. All the tissue formed from the cambium-ring on the outside may be termed *Secondary Cortex*, all the xylem formed on the inside

[1] When several fibro-vascular bundles enter a leaf-stalk, they are generally widely separated by the fundamental tissue; but sometimes, as in the fig. the bundles are arranged in a circle on transverse section, and form a closed hollow cylinder which divides the fundamental tissue of the leaf-stalk into pith and cortex. Isolated fibro-vascular bundles also run into the pith of the leaf-stalk in the fig. as occurs also in some stems of Dicotyledons.

Secondary Wood; in opposition to the *Primary Cortex* which consists only of fundamental tissue, and the *Primary Wood* consisting of the isolated bundles of xylem of the foliar bundles which were already in existence before the formation of the cambium-ring. While the wood which is produced from this cambium-ring forms a hollow cylinder, the primary woody bundles project from the inside of the ring into the pith as ridges, and often cause it to present on transverse section the appearance of a star. The whole of these primary xylem-bundles are included in the term *Medullary Sheath;* and in the same sense one may adopt Nägeli's term of *Cortical Sheath* to express the whole of the primary bast-bundles at the point of junction of the primary and secondary cortex. The medullary and cortical sheaths increase in length with the internodes, and therefore generally consist of very long elementary structures;—the medullary sheath of very long annular, spiral, and reticulated vessels intermixed with long woody fibres; the cortical sheath containing bundles of long bast-fibres which become widely separated from one another by the increase in circumference of the stem, and which are often strongly thickened but long and flexible; in addition to these, long cambiform cells and elongated bast-vessels (latticed and sieve-tubes) occur in it. The structural elements of the secondary cortex are, like those of the secondary wood, shorter; in the secondary wood there are no annular or spiral vessels, these being altogether replaced by shorter and broader vessels with bordered pits, surrounded by wood-fibres intermixed with woody parenchyma (see p. 98). The secondary cortex forms either a number of layers of thick-walled as well as thin-walled bast-fibres, and partially parenchymatous masses of phloëm, or these last only, or the most various combinations of both. Finally the primary cortex and the epidermis are both generally supplanted by the formation of periderm and bark; although these may sometimes undergo a considerable growth in thickness by increasing in diameter at the same time that longitudinal divisions are formed (as in Viscum, *Helianthus annuus* &c.). The masses of xylem and phloëm formed by the activity of the cambium-ring are penetrated lengthwise in radial direction by secondary medullary rays consisting of horizontal cells which in the wood are not always lignified, and in the secondary cortex are generally soft and parenchymatous. In the one case they are called xylem-rays, in the other phloëm-rays, and always have the power of taking up assimilated food-materials. In proportion as the cambium-ring increases in size, the number of these rays increases; and the later layers of wood are always traversed by a larger number of rays. They are one or more layers of cells in thickness, and form thin vertical plates wedge-shaped at their upper and lower edges, which have the appearance in a longitudinal section of ribbon-like structures (the 'silver-grain'). In a tangential section the fibro-vascular bundles which run through the length of the stem are seen to form a network of elongated meshes, through which they pass (especially clearly seen in decaying cabbage-stumps). The medullary rays, like the fibro-vascular bundles, are added to by means of the cambium-ring outwards and inwards; and as the ring increases in thickness, it produces new rays between the old ones.

When the increase in thickness of a stem ceases periodically and is renewed with each new period of vegetation, as in our woody plants, a layer of wood is formed during each period of growth, (and usually also a secondary cortical layer) which is sharply marked off from those of the preceding and of the following year, and is called an *Annual Ring* of the wood. These annual rings are usually distinctly visible to the naked eye, because the mass of wood formed in the early part of each period of vegetation has usually a different appearance from that formed in the autumn, the latter being denser, the former less dense and generally with a greater number of vessels. The wood formed in the spring consists also of wider cells than that produced in the autumn, and the radial diameter of the cells is usually greater. The cells formed in the autumn appear compressed radially and broad in the tangential direction; their cavities are smaller, and hence, other things being equal, the thickness of their wall is greater. A given quantity of wood produced in the autumn is therefore denser than

a like volume formed in the spring[1]. While Dicotyledons differ so widely from Monocotyledons in the mode of increase of their stems in thickness, they agree almost entirely in this respect with Gymnosperms, except that in these latter there are no pitted vessels in the secondary wood. In this respect however, according to v. Mohl, Ephedra indicates a transition to Dicotyledons. The organisation of Dicotyledons shows also in some sense a higher stage of development in the greater varieties of the forms of cells of which the xylem and phloëm are composed.

A remarkable deviation from these normal processes is exhibited by the Sapindaceæ. In some plants of this order the stem has the ordinary structure; but in others a transverse section shows several smaller woody cylinders of various sizes outside the usual one and lying in the secondary cortex. Each of these increases in thickness, like the normal ones, by a cambium-layer which surrounds it. Nägeli supposes the cause of this structure to be that the primary fibro-vascular bundles of the stem do not lie in a circle on the transverse section, but in groups more towards the outside or inside. When the connecting bands of cambium are formed in the fundamental tissue, the isolated bundles become united on the transverse section, according to their grouping, into one (as in Paullinia) or several (*e.g.* Serjania) closed rings.

The cause of a large number of deviations of different kinds from the normal structure of the stem in Dicotyledons which occur in various families, is the formation of other cauline bundles of later origin in the stem besides the common bundles, either within the primary pith or outside the ring in which the common bundles lie. We owe to Nägeli a more exact knowledge of these cases, and more especially to the very exhaustive labours of Sanio, which form for the most part the basis, in addition to my own observations, of the following short sketch, without going in detail into special cases[2].

The phenomena may be classified into two groups, according as the secondary (cauline) bundles originate within or without the circle of the primary (common) bundles. Sanio calls the former the endogenous, the latter the exogenous mode of origin.

First Group. The secondary bundles are formed outside the primary bundles (exogenous).

a. The primary bundles lie near the axis of the stem, and remain more or less isolated, while the secondary bundles belong to a closed cambium-ring which continues to grow on the outside (originally a 'thickening-ring' in Sanio's sense). Examples are furnished by Mirabilis, Amaranthus, Phytolacca, and Atriplex.

b. The primary bundles lie in a ring on the transverse section and continue their growth by means of a closed cambium-ring, which however soon disappears. A new

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[1] The cause of this difference is not yet known; but I suppose that it depends simply on the difference in pressure to which the cambium and the wood are subjected from the surrounding cortex. This pressure is less in the spring, and constantly increases till the autumn. I have no direct measurements of this, but conclude it from the fact that the longitudinal fissures in the bark become wider in February and March, as may be clearly seen in the oak, maple, poplar, walnut, &c. I cannot here explain the cause of this; but in any case the bark, the longitudinal fissures of which have become wider in winter, must exert less pressure on the cambium in the spring, and the cells of the wood must therefore be able to extend more easily in a radial direction. The pressure which the bark exerts on the cambium must continually increase by the thickening of the ring of wood internally and the drying up of the bark in summer externally, and must affect the radial growth of the young cells of the autumnal wood. Further investigations which I am proposing to make will determine whether my theory is correct. This hypothesis, which I brought forward in the first edition, has recently been fully confirmed by the researches of H. de Vries. (See Flora 1872, no. 16, and sect. 15 of Book III of this work).

[2] [Oliver has collected the bibliography of the structure of the stem of Dicotyledons in the Nat. Hist. Rev. 1862, pp. 298–329, and 1863, pp. 251–258.—Ed.]

cambium-ring is then formed outside the one which has disappeared, and another one again outside this one when it has in turn disappeared. Several circles of fibro-vascular bundles are thus formed, continually increasing in number. In many Menispermaceæ (*e.g.* Cocculus), the new outer circle of vascular bundles together with its cambium-ring is developed from a ring of meristem which lies in the primary cortex and therefore outside the primary bast,—a phenomenon which is repeated in the primary cortex as its growth proceeds (Nägeli). In Phytolacca, on the other hand, and, according to Eichler, also in Dilleniaceæ, Bauhinia, Polygaleæ (Securidaca and Comesperma), Cissus, and Phytocrene, the successive circles of bundles originate in the secondary cortex. Phytolacca agrees moreover with the cases mentioned under *a* in the primary bundles lying also in the pith, and in the first closed ring which surrounds them being a secondary production due to increase in thickness.

Second Group. The secondary bundles arise early after the primary bundles further inwards or nearer the axis of the stem (endogenous).

a. Both the primary and the secondary endogenous bundles remain isolated; they are not united by a closed cambium-ring, but anastomose with one another, as in Cucurbita, Nymphæaceæ and Papaver (?). The transverse section of the stem bears a greater or less resemblance to that of a Monocotyledon, especially in Nymphæaceæ.

b. The primary bundles lie in a ring on the transverse section, and are united by a cambium-ring; the secondary bundles arise at an early period in the pith and remain isolated and scattered on the transverse section; they anastomose with one another and with the primary bundles in the nodes of the stem. Examples are furnished, according to Sanio, by Piperaceæ, Begoniaceæ, and Aralia.

The cell-forms of the phloëm and xylem of Dicotyledons have already been described in general terms (see p. 98 *et seq.*). Only two peculiar phenomena need be mentioned here. In Cucurbitaceæ, some Solanaceæ, and Nerium (and in a certain sense also in *Tecoma radicans*), a phloëm-tissue is found not only on the outside but also on the inside of the fibro-vascular bundles, which is developed with especial strength in Cucurbitaceæ. The isolated fibro-vascular bundles of the pith which are enclosed by the ring of wood sometimes show an abnormal arrangement of their phloëm and xylem. Thus, according to Sanio, *Aralia racemosa* has an endogenous circle of closed fibro-vascular bundles in which the xylem is outside and the phloëm inside. The isolated bundles in the pith of *Phytolacca dioica* on the other hand consist, according to Nägeli, on a transverse section, of a hollow woody cylinder which surrounds the phloëm on all sides and is itself penetrated by xylem-rays. The isolated fibro-vascular bundles of the pith in the rachis of the inflorescence of *Ricinus communis* also consist of a thin axial bundle of phloëm (?), surrounded by a sheath of cells (xylem ?) arranged in rays.

A layer of collenchyma is very common in Dicotyledons beneath the epidermis of the internodes and leaf-stalk.

The Classification of Dicotyledons[1] has now been carried out so completely that the smaller groups which are called Families[2], and which usually comprise genera very nearly related to one another, have been united into larger groups or orders; so that at present only a few families remain unplaced. The greater number of the orders can also be again arranged into larger groups which are clearly connected by actual relationship. Systematists have not however up to the present time agreed as to how many of these cycles of affinity should be established, so as to make the primary division of the whole class of Dicotyledons in accord with the requirements of scientific classification. The grouping of all Dicotyledons into three sections, Apetalæ, Gamopetalæ, and Eleu-

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[1] [See note to p. 553.]

[2] Le Maout and Decaisne's Traité général de Botanique, descriptive et analytique, is strongly to be recommended for a study of the diagnosis of the families [translated by Mrs. Hooker; London 1873].

theropetalæ, proposed by De Candolle and Endlicher[1], is now abandoned by most, although still much in use for practical purposes. A. Braun[2] placed among the Eleutheropetalæ the greater number of plants previously classed among Apetalæ; and Hanstein[3] has now distributed among them the remainder, so that the whole class consists of only two sub-classes, Gamopetalæ and Eleutheropetalæ. This classification however assigns far too great an importance to this particular point of structure, considering that on the one hand flowers occur among the Eleutheropetalæ which differ greatly from one another not only in this but also in every other respect; while on the other hand the most intimate relationship exists between particular sections of Eleutheropetalæ and of Gamopetalæ. I therefore think it convenient, while retaining the largest sub-divisions of the class, to employ also other characters in the classification; and to make use of the character drawn from the cohesion or non-cohesion of the petals in the subdivision of the largest group, that provided with two perianth-whorls. In the following classification Dicotyledons are split up into five divisions of equal systematic and morphological value, which should rather be arranged parallel to one another than in a single linear series. This classification has also, I think, a practical advantage; since the extraordinarily large number of families and orders can be more easily kept in the memory when they are at once arranged in several comprehensive groups of equal value.

DICOTYLEDONS.

I. **Julifloræ:**
- A. Piperineæ,
- B. Urticineæ,
- C. Amentiferæ.

II. **Monochlamydeæ:**
- A. Serpentarieæ,
- B. Rhizantheæ.

III. **Aphanocyclæ:**
- A. Hydropeltidineæ,
- B. Polycarpæ,
- C. Crucifloræ.

IV. **Tetracyclæ:**

(α) *Gamopetalæ:*
- A. Anisocarpæ,
- B. Isocarpæ.

(β) *Eleutheropetalæ;*
- C. Eucyclæ,
- D. Centrospermæ,
- E. Discophoræ.

V. **Perigynæ:**
- A. Calycifloræ,
- B. Corollifloræ.

The sections designated by capital letters correspond partly to single orders, partly to whole series of orders in the system referred to above.

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[1] Endlicher, Genera plantarum secundum ordines naturales disposita, Vindobonæ, 1836-1840; and Enchiridion botanicum, Lipsiæ—Viennæ, 1841.

[2] A. Braun, Uebersicht des natürlichen Systems, in Ascherson's Flora der Provinz Brandenburg, 1864.

[3] Hanstein, Uebersicht des natürlichen Pflanzensystems, Bonn 1867. In the first edition of this book I followed this work with but little deviation. Compare also Grisebach, Grundriss der systematischen Botanik.

I. Julifloræ.

Flowers very small or inconspicuous, crowded in dense inflorescences—spikes, capitula, or less often panicles—which are often of very peculiar form; naked or with a simple sepaloid perianth, and usually diclinous; the male and female flowers often different. Leaves simple.

A. *Piperineæ*. Flowers very small, in dense spikes subtended by bracts, without a perianth. The small embryo lies, surrounded by the endosperm, in a hollow of the copious perisperm. Herbs or shrubs, often with verticillate leaves.

Families: 1. Piperaceæ,
2. Saurureæ,
3. Chlorantheæ.

B. *Urticineæ*. Perianth simple, sepaloid, three- to five-partite, sometimes absent; stamens superposed on the segments of the perianth; flowers hermaphrodite or diclinous, and then the male and female flowers different (3), usually in densely crowded inflorescences, the female flowers in spikes, umbels, capitula (2) or sometimes panicles (3), not unfrequently developing into peculiar pseudocarps (as the mulberry, fig, bread-fruit, and Dorstenia). Fruit usually unilocular, rarely bilocular; ovules one or rarely two in each loculus; seed usually with endosperm. Large shrubs or trees[1]; leaves stalked, usually stipulate.

Families: 1. Urticaceæ,
Urticeæ,
Moreæ,
Artocarpeæ,
2. Platanaceæ,
3. Cannabineæ,
4. Ulmaceæ (including Celtideæ).

C. *Amentiferæ*. Flowers diclinous, epigynous, in compact panicles (false spikes); the female few-flowered inflorescence in (2) surrounded by a cupule. Fruit dry, indehiscent, one-seeded; seed without endosperm. Trees with deciduous stipules.

Families: 1. Betulaceæ,
2. Cupuliferæ.

II. Monochlamydeæ.

Flowers large and conspicuous and consisting of a simple more or less petaloid, usually gamophyllous perianth, one or more staminal whorls, and a polycarpellary ovary; carpels equal in number or double the segments of the perianth. The number of members of the whorls is derived from the typical numbers two, three, four, or five, and generally increases inwards. Ovary generally inferior and surmounted by a short thick columnar style, to which in the hermaphrodite flowers the stamens are usually partially or entirely adherent. Flowers often diclinous. Seeds numerous.

A. *Serpentarieæ*. Creeping or climbing plants with slender stems and large simple leaves; floral whorls dimerous and tetramerous (1) or trimerous and hexamerous; perianth-leaves free (1) or coherent into a tube; ovary of four or six loculi; embryo small but segmented.

Families: 1. Nepentheæ,
2. Aristolochiaceæ,
3. Asarineæ.

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[1] [The Urticeæ include a number of herbaceous genera.—Ed.]

B. *Rhizantheæ.* Root-parasites without chlorophyll or foliage-leaves, generally with stunted vegetative organs and very large solitary flowers or small flowers on a dense inflorescence (1); whorls dimerous to octamerous (1), trimerous (2), or pentamerous and decamerous (3); ovary with one or eight (1) loculi; the placentæ and anthers of very peculiar form; a very great number of small seeds with rudimentary embryo.

Families: 1. Cytineæ,
2. Hydnoreæ,
3. Rafflesiaceæ.

III. Aphanocyclæ.

Flowers hemicyclic or cyclic, or the parts arranged spirally; the members of each whorl usually free, not coherent with one another, or only in the gynæceum; perianth generally distinctly separated into calyx and corolla; the numbers of the parts in the four whorls very variable; stamens usually more in number than perianth-leaves; carpels forming generally one, several, or a large number of monocarpellary ovaries; in C the ovary is superior and bi- or quadri-locular. Ovules springing occasionally in all the sections from the inner surface of the carpels.

A. *Hydropeltidineæ.* Water-plants with solitary lateral and usually large flowers, the perianth-leaves and stamens variable in number and arranged spirally; ovaries several and monocarpellary (1, 2), or one only polycarpellary and multilocular; embryo small, surrounded by a small endosperm in a hollow of the perisperm.

Families: 1. Nelumbiaceæ,
2. Cabombeæ,
3. Nymphæaceæ.

B. *Polycarpæ.* Parts of the flowers arranged spirally or in whorls, when in whorls usually dimerous or trimerous, each organ generally consisting of more than one whorl, rarely in four pentamerous whorls (2); gynæceum consisting of one, several, or a larger number of monocarpellary ovaries, which are one- or many-seeded; embryo small; endosperm none (8), abundant, or very large (9).

Families: 1. Ranunculaceæ,
2. Dilleniaceæ,
3. Schizandreæ,
4. Annonaceæ,
5. Magnoliaceæ,
6. Berberideæ,
7. Menispermaceæ,
8. Laurineæ,
9. Myristicaceæ.

C. *Crucifloræ.* Perianth-whorls dimerous; in (3) and (4) corolla of four petals placed diagonally; staminal whorls two or more, each consisting of two stamens or divisible into two; ovary single, bi- quadri- or multi-locular; seed with (1, 2) or without endosperm.

Families: 1. Papaveraceæ,
2. Fumariaceæ,
3. Cruciferæ,
4. Capparideæ.

IV. Tetracyclæ.

Parts of the flower always arranged strictly in whorls; the typical number of whorls is four, the calyx, corolla, andrœcium, and gynæceum each consisting of a single whorl; whorls generally pentamerous, rarely tetramerous (very rarely dimerous or octamerous); any one of the whorls may be entirely wanting, or individual members may be abortive; this occurs most often with the stamens and carpels. Increase in number of the stamens usually takes place by the interposition of one perfect or imperfect whorl between the members of the typical whorl or a little outside it, or by doubling of the members, or by branching of the original staminal leaves; increase in number of the staminal whorls themselves is rare. All the whorls usually alternate, but the stamens are not unfrequently superposed on the petals. A tendency prevails in all the sections to a diminution of the number of carpels below that of the members of the perianth-whorls; very commonly there are only two, one anterior and one posterior. Ovary almost always single and polycarpellary, inferior or superior, unilocular or multilocular.

I. Gamopetalæ or Sympetalæ.

The petals united at the base into a tube or cup; corolla never wanting.

A. *Anisocarpæ*. The whorls or members of the whorls never larger than the typical number; calyx or some of the stamens sometimes abortive; carpels usually only two, one anterior and one posterior, or three and united into a single ovary[1].

a. Hypogynæ.

Order 1. Tubifloræ.

Families: 1. Convolvulaceæ (including Cuscuteæ),
2. Polemoniaceæ,
3. Hydrophyllaceæ,
4. Borragineæ,
5. Solanaceæ.

Order 2. Labiatifloræ.

Families: 1. Scrophulariaceæ,
2. Bignoniaceæ,
3. Acanthaceæ,
4. Gesneraceæ,
5. Orobancheæ,
6. Ramondieæ,
7. Selagineæ,
8. Globulariaceæ,
9. Plantagineæ,
10. Verbenaceæ,
11. Labiatæ.

Order 3. Diandræ.

Families: 1. Oleaceæ,
2. Jasminiaceæ.

Order 4. Contortæ.

Families: 1. Gentianaceæ,
2. Loganiaceæ,
3. Strychnaceæ,
4. Apocynaceæ,
5. Asclepiadeæ.

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[1] The orders are arranged mainly after Braun and Hanstein.

b. **Epigynæ.**

Order 5. Aggregatæ.

Families: 1. Rubiaceæ,
2. Caprifoliaceæ,
3. Valerianaceæ,
4. Dipsacaceæ.

Order 6. Synandræ.

Families: 1. Cucurbitaceæ,
2. Campanulaceæ,
3. Lobeliaceæ,
4. Goodeniaceæ,
5. Stylidieæ,
6. Calycereæ,
7. Compositæ.

B. *Isocarpæ.* Carpels equal in number to the sepals and petals, usually five, rarely four, and coherent into a generally superior ovary (except Order 1, Family 1, where there are only two median carpels); diminution of the number of stamens does not occur (except in Order 1, Family 1); in Orders 2 and 3, on the other hand, a perfect staminal whorl is usually interposed; in Order 1 the stamens are superposed on the petals, and a number of seeds spring from an elevated axial placenta in the unilocular ovary; in Orders 2 and 3 the ovary is multilocular and many-seeded.

Order 1. Primulineæ.

Families: 1. Lentibulariaceæ,
2. Plumbagineæ,
3. Primulaceæ,
4. Myrsinaceæ,

Order 2. Diosporineæ.

Families: 1. Sapotaceæ,
2. Ebenaceæ (including Styracaceæ).

Order 3. Bicornes.

Families: 1. Epacrideæ,
2. Pyrolaceæ,
3. Monotropeæ,
4. Rhodoraceæ,
5. Ericaceæ,
6. Vaccinieæ.

II. Eleutheropetalæ or **Dialypetalæ.**

Petals free, sometimes wanting.

C. *Eucyclæ.* Corolla very rarely wanting; stamens very commonly twice or three times as many as petals by the interposition of a perfect or even double (Orders 6, 7) whorl, or by the interposition of an imperfect whorl differing in number from the corolla (Order 5); the isostemonous stamens sometimes superposed on the petals (Order 4), or the original stamens branch (especially in Orders 2, 3, and 8); the number of carpels often the same as that of the sepals and petals (Orders 7, 8), but commonly less—two, three, or four; ovary unilocular with parietal placentæ in Order 1, in the others multilocular; seed generally without endosperm.

Order 1. Parietales.

Families: 1. Resedaceæ,
2. Violaceæ,
3. Frankeniaceæ,
4. Loasaceæ,
5. Turneraceæ,
6. Papayaceæ,
7. Passifloraceæ,
8. Bixaceæ,
9. Samydaceæ,
10. Cistineæ.

Order 2. Guttiferæ.

Families: 1. Salicineæ,
2. Tamariscineæ,
3. Reaumuriaceæ,
4. Hypericineæ,
5. Clusiaceæ,
6. Marcgraviaceæ,
7. Ternstrœmiaceæ,
8. Chlænaceæ,
9. Dipterocarpeæ.

Order 3. Hesperideæ.

Families: 1. Aurantiaceæ,
2. Meliaceæ (including Cedreleæ),
3. Humiriaceæ,
4. Erythroxylaceæ.

Order 4. Frangulineæ.

Families: 1. Ampelideæ,
2. Rhamnaceæ,
3. Celastrineæ,
4. Staphyleaceæ,
5. Aquifoliaceæ,
6. Hippocrateaceæ,
7. Pittosporeæ.

Order 5. Æsculineæ.

Families: 1. Malpighiaceæ,
2. Sapindaceæ,
   a. Acerineæ,
   b. Sapindaceæ,
   c. Hippocastaneæ,
3. Tropæolaceæ,
4. Polygalaceæ.

Order 6. Terebinthineæ.

Families: 1. Terebinthaceæ,
   a. Anacardiaceæ,
   b. Burseraceæ,
   c. Amyrideæ,

2. Rutaceæ,
    a. Ruteæ,
    b. Diosmeæ,
    c. Xanthoxylaceæ,
    d. Simarubeæ,
3. Ochnaceæ.

Order 7. Gruinales.

Families: 1. Balsamineæ,
2. Limnanthaceæ,
3. Linaceæ,
4. Oxalideæ,
5. Geraniaceæ,
6. Zygophyllaceæ.

Order 8. Columniferæ.

Families: 1. Sterculiaceæ,
2. Büttneriaceæ,
3. Tiliaceæ,
4. Malvaceæ.

Order 9. Tricoccæ[1].

Families: 1. Euphorbiaceæ,
    a. Euphorbieæ,
    b. Acalypheæ,
2. Phyllanthaceæ;
    a. Phyllantheæ,
    b. Buxineæ.

D. *Centrospermæ*. Corolla usually wanting [except in Fam. 6]; stamens fewer or more often more than the sepals, in the last case generally double as many (4 or 6); ovary usually superior and unilocular, with one or more basal often campylotropous ovules, less often multilocular with central placentation.

Order 1. Caryophyllineæ.

Families: 1. Nyctagineæ,
2. Chenopodiaceæ,
3. Amaranthaceæ,
4. Phytolaccaceæ,
5. Portulacaceæ,
6. Caryophylleæ:
    a. Paronychieæ,
    b. Scleranthеæ,
    c. Alsineæ,
    d. Sileneæ.

E. *Discophoræ*. Ovary inferior (Order 1) or half inferior or even superior, and then (Order 2, Family 5) carpels distinct; carpels as many as or fewer than sepals and petals (often two); when the ovary is inferior or half inferior a nectariferous disc usually occurs between the styles and the stamens; stamens equal in number to sepals and petals (Order 1) or twice as many, or even a still larger number; calyx-limb usually obsolete in Order 1; seed generally with copious endosperm.

[1] The position of this order is doubtful.

Order 1. Umbellifloræ.

Families: 1. Umbelliferæ,
2. Araliaceæ,
3. Cornaceæ.

Order 2. Saxifragineæ.

Families: 1. Saxifragaceæ (including Hydrangeæ, Escallonieæ, and Cunoniaceæ),
2. (?) Grossulariaceæ,
3. (?) Philadelpheæ,
4. (?) Francoaceæ,
5. (?) Crassulaceæ.

V. Perigynæ.

Flower displaying a tendency towards the perigynous structure. An annular body is elevated from the floral axis bearing the perianth and the stamens, and enveloping the gynæceum as a cup-, saucer-, or urn-like receptacle; or it becomes adherent in its growth to the carpels (B, Order 2, Family 2). In a few families which are placed here provisionally (B, Order 3, Families 4–6) the ovary is truly inferior.

A. *Calyciflorœ.* Perianth simple, either sepaloid or petaloid and usually tetramerous; the tubular receptacle is generally of the same nature, and in Family 3 is even quadripartite, corresponding to the four perianth-leaves and to the four stamens superposed on them (see Fig. 339, p. 478); stamens fewer than, as many as, or twice as many as the perianth-leaves; ovary monocarpellary, rarely bilocular, with one or a few seeds; seed with little or no endosperm.

Order 1. Thymelæineæ.

Families: 1. Thymelæaceæ,
2. Elæagnaceæ,
3. Proteaceæ.

B. *Corolliflorœ.* Calyx, corolla, and andrœcium placed on a flat (Order 1) or cup-shaped receptacle, or on one hollowed out into a deep urn-shape (Order 2 and in part 3), which is often (Order 2) thick and succulent (as in the apple, rose-hip, &c.); sepals distinct or coherent (Order 1); petals always distinct (corolla dialypetalous); the two perianth-whorls usually pentamerous, sometimes tetramerous; stamens as many as or twice as many as (Order 1) sepals and petals, or a much larger number (Order 2), in Order 3, Family 3, commonly branched; gynæceum composed of one (Order 1, and in part 3) or several or a large number of monocarpellary ovaries; or (in Order 3) ovary polycarpellary, and sometimes inferior (Families 4–6).

Order 1. Leguminosæ.

Families: 1. Mimoseæ,
2. Swartzieæ,
3. Cæsalpineæ,
4. Papilionaceæ.

Order 2. Rosifloræ.

Families: 1. Calycanthaceæ,
2. Pomeæ,
3. Rosaceæ,

4. Sanguisorbeæ,
5. Dryadeæ,
6. Spiræeæ,
7. Amygdaleæ,
8. Chrysobalaneæ.

Order 3. Myrtifloræ.

Families: 1. Lythrarieæ,
2. Melastomaceæ,
3. Myrtaceæ,
4. Combretaceæ,
5. Œnothereæ,
6. Haloragideæ.

} [1]

Families of unknown or very doubtful affinity.

Balanophoræ.	Hippurideæ.	Polygonaceæ.	Elatineæ.
Santalaceæ.	Callitrichaceæ.	Begoniaceæ.	Casuarineæ.
Loranthaceæ.	Ceratophyllaceæ.	Mesembryanthemeæ.	Myricaceæ.
		Tetragonieæ.	
Podostemoneæ.	Empetraceæ.	Cactaceæ.	Juglandeæ.

[1] The position of these families here is very doubtful.

BOOK III.

PHYSIOLOGY.

CHAPTER I.

MOLECULAR FORCES IN THE PLANT.

Sect. 1. — **The Condition of Aggregation of organised structures**[1]. Cell-walls, starch-grains, and protoplasmic structures consist, in their natural condition, at every point that can be seen even under the microscope, of a combination of solid material with water. If these organised structures are placed in a substance capable of removing water, a part of their aqueous contents is withdrawn; while, on the other hand, if they are in contact with aqueous solutions possessing certain chemical properties and of a proper temperature, they absorb more water. The volume alters with the change in the proportion of water; loss of water causes contraction, absorption of water a corresponding augmentation of volume. Since the absorption of water occasions a considerable elevation of temperature (air-dry starch rises 2° or 3° C. when mixed with water of the same temperature), it must be supposed that the water contracts as it is absorbed[2]. Within certain limits these variations in the proportion of water may occur without occasioning any permanent change in the molecular structure; but if, with a higher temperature and in the presence of chemical reagents, the proportion falls below a certain minimum or exceeds a certain maximum, permanent changes of the internal structure take place which can no longer be reversed; and the internal organisation of the body becomes partially or entirely destroyed.

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[1] See Sachs, Handbuch der Experimental-Physiologie, p. 398 *et seq.*—Nägeli u. Schwendener, Das Mikroscop, vol. II, p. 402 *et seq.*; compare also Book I of this work, p. 31 *et seq.*—Cramer, Naturforsch. Gesells. in Zürich. Nov. 8, 1869.

[2] Jungk, in Pogg. Ann. 1865. vol. 125, p. 292 *et seq.*

These facts, in connection with a number of other phenomena, first led Nägeli to the hypothesis that organised bodies consist of isolated particles or *Molecules* between which the water penetrates, and which are solid and relatively unchangeable, and invisible even with the most powerful microscopes. Every molecule of a saturated organised body is, on this hypothesis, surrounded by layers of water by which the adjacent molecules are completely separated from one another. These molecules may be supposed to be of various sizes, and it is evident *a priori* that, if the thickness of the aqueous envelope is the same, larger molecules will form a denser, smaller molecules a less dense substance; and it may therefore be concluded conversely that the layers and lamellæ of organised bodies of different thickness, especially those of the cell-wall and of starch-grains, are composed of molecules of different sizes; and the difference in the proportion of water in such cases leads to the hypothesis that the densest substance consists of molecules which are several thousand times larger than those of the more watery substance. As the molecules increase in size, the density of the whole substance is moreover increased by the smaller distance that intervenes between them, so that larger molecules are separated from one another by thinner layers of water. The changes in volume of organised bodies due to the removal of water or its absorption, depend, according to this view, on the fact that when swelling takes place the molecules are forced further apart by the water which penetrates between them; while, on the other hand, when water is removed they approach one another in proportion as the water is withdrawn from their interstices.

The forces which are concerned in these processes in the interior of an organised body may be divided into three kinds:—(1) the Cohesion within each separate molecule impermeable to water, which is itself an aggregate of smaller molecules and atoms; (2) the Attraction of the adjoining molecules for one another, in consequence of which they tend mutually to approach; and (3) the Attraction of the surfaces of the molecule for the absorbed water, which counteracts the mutual attraction of the neighbouring particles.

In starch-grains, cell-walls, and to a certain extent in crystalloids[1], the absorbed water is not deposited uniformly in all directions; the molecules are, on the contrary, forced further from one another in certain directions, as is clearly seen from the change of form of the whole, from the formation of fissures, &c. One of the most remarkable effects of the tensions thus caused in the interior of the body is the fact that when swelling takes place particular dimensions may even decrease; thus, for example, the layers of bast-fibres become very considerably shorter when they swell up under the influence of dilute sulphuric acid, the coils of the spiral striation becoming closer and larger in circumference. Crystalloids change their angles several degrees when they swell. These phenomena are explicable only on the supposition that the molecular forces in the interior of organised substances vary in intensity in different directions; and this again is conceivable only on the hypothesis that the form of the molecules is not spherical. Nägeli and Schwendener obtained a deeper insight into these laws by a very careful observation of the phenomena produced by

[1] [See Book I, pp. 49–57, on Crystalloids.]

polarised light in cell-walls, starch-grains, and crystalloids[1]. They inferred from these facts a crystalline structure of the individual molecules, and that the crystals are doubly refractive, and have two optic axes which are so arranged, at least in the greater number, that one axis of elasticity of the ether within each molecule of the starch-grains and cell-walls is placed radially, but the two other axes of elasticity tangentially. In crystalloids the molecules are probably arranged as in true crystals, but separated also by layers of water parallel to the faces or lines of cleavage.

The behaviour of grains of chlorophyll and of colourless protoplasm towards polarised light, as well as under the addition and removal of water, is at present but little known; and a more definite idea of the form of their molecules is therefore not yet possible.

The solid molecules of one and the same organised body which are separated by aqueous envelopes always vary in their chemical nature; so that at every visible point molecules which possess chemically different properties lie by the side of and among one another separated by layers of water. In starch-grains, cell-walls, and crystalloids this fact is inferred from the circumstance that certain substances are extracted by the application of certain solvents, while other substances remain behind, constituting what is called the skeleton. This skeleton is of course less dense than the original substance; and it is evident that the extraction has taken place at all visible points, without the external form or internal structure having undergone any essential change. Thus, for example, a skeleton of cellulose remains behind when the lignin has been extracted from wood-fibres by Schultz's maceration; and again, a skeleton of silica remains behind with all the optical properties of the cell-wall when the organic substance has been burnt away. In the same manner a grain of starch leaves behind a skeleton containing very little solid material when the granulose has been extracted by saliva or some other substance. From crystalloids also a skele in this sense of the term containing very little solid matter can be obtained by the solution of a part of their substance, especially of the colouring material contained in them. The properties of these skeletons show that the molecules which remain behind after solution of the rest still occupy essentially the same position and are endowed with the same forces as before; but it is probable that the extracted substance lay previously between these molecules without being contained in them. This view is also more or less probable in the case of chlorophyll-grains and protoplasm; in the former the fundamental protoplasmic substance remains behind as a very solid skeleton when the green colouring material is extracted by ether, alcohol, oil, &c. Very different substances are certainly combined in the protoplasm; and when a naked primordial cell secretes a cell-wall, it may be assumed that the molecules which form the cell-wall were previously distributed between those of the protoplasm, and only change their position and their chemical nature when they are secreted in the formation of the cell-wall; the protoplasm which remains behind retaining essentially its original properties. The same is the case when grains of starch or chlorophyll are formed in the protoplasm. A fundamental substance is clearly present in the protoplasm which always retains the

[1] Hofmeister (Handbuch der phys. Bot. vol. I, p. 348) has arrived at altogether different conclusions, with which I cannot agree.

essential properties of protoplasm; but various other substances penetrate between its molecules and are afterwards again separated. This is especially observable in the formation of zygospores and swarmspores.

The nutriment and growth of organised structures takes place, as has already been shown in Book I, by intussusception; the nutrient solution penetrates between the molecules already in existence, and either occasions by apposition an enlargement of the individual molecules; or new molecules of small size are produced in the spaces filled with water, which then increase by the apposition of new matter, or the increase takes place in both ways at different points. The increase in mass of the cell-wall, starch-grain, &c., is therefore brought about by the molecules being forced apart from within. Connected with the growth of the molecules already in existence and with the formation of new ones, is a continual disturbance of the osmotic equilibrium between the surrounding fluid (the cell-sap in the widest sense of the term, see p. 62), and that within the body, which has the effect of constantly drawing fresh particles from the surrounding fluid to the interior of the body which is undergoing augmentation.

Chemical processes in the interior of the growing body are also always connected with these processes of growth. The nutrient fluid which penetrates from without contains in fact the material for the formation of molecules of a definite chemical nature; but this material is chemically different from the molecules which it produces. Thus starch-grains are nourished by a fluid which clearly does not contain any starch in solution; and again the cell-wall grows by the absorption of substances out of the protoplasm which are not dissolved cellulose. The colouring matter of the chlorophyll arises in the interior of the chlorophyll-grain; and the substances by which the protoplasm is nourished by intussusception are clearly only produced in the interior of the protoplasm, as is shown in particular by naked plasmodia and by unicellular Algæ and Fungi. Growth by intussusception is therefore connected not only with a continual disturbance of the molecular equilibrium, but also with chemical processes in the interior of the growing structure. Chemical combinations of the most various kinds take place between the molecules of an organised body, so that they act upon and decompose one another. It is certain that all growth continues only so long as the growing parts of the cell are exposed to atmospheric air; the oxygen of the air has an oxidising effect on the chemical compounds contained in the organised structure; with every act of growth carbon dioxide is produced and evolved. The equilibrium of the chemical forces is also continually disturbed by the necessary production of heat; and this may also be accompanied by electrical actions. The movements of the atoms and molecules within a growing organised body represent a definite amount of work, and the equivalent forces are set free by chemical changes. The essence of organisation and of life lies in this:—that organised structures are capable of a constant internal change; and that, as long as they are in contact with water and with oxygenated air, only a portion of their forces remains in equilibrium even in their interior, and determines the form or framework of the whole; while new forces are constantly being set free by chemical changes between and in the molecules, which forces in their turn occasion further changes. This depends essentially on the peculiarity of molecular structure, which permits dissolved and gaseous (absorbed) substances to

penetrate from without into every point of the interior, and to be again conveyed outwards.

This internal instability attains its highest degree in chlorophyll-grains and protoplasm. In the former chemical processes take place with great energy and activity under the influence of light, such as the formation of the green colouring matter and of starch; and when deprived of light other chemical changes at once ensue, which terminate only with the complete destruction of the entire chlorophyll-grain. The remarkable properties of protoplasm, which we have already examined from different sides in discussing the structure of the cell, attain their climax in its spontaneous automatic power of motion, and in its capacity of assuming different forms and changing both its shape and its internal state, and therefore of bringing into action internal forces, even when corresponding impulses from without cannot be observed. It is impossible to enter here in detail into the explanation of these remarkable facts; but they will be understood, at least generally and to a certain extent, if it is borne in mind that neither the chemical nor the molecular forces are ever in equilibrium in the protoplasm; that the most various elementary substances are present in it in the most various combinations; that fresh impulses to the disturbance of the internal equilibrium are constantly given by the chemical action of the oxygen of the air; and that forces are continually being set free at the expense of the substance of the protoplasm itself, which must lead to the most complex actions in a substance of so complicated structure. Every impulse from without, even when imperceptible, must call forth a complicated play of internal movements, of which we are able to perceive only the ultimate effect in an external change of form.

The destruction of the molecular structure of organised bodies may take place in many different ways, and affords an insight into many physiological processes.

The most important forces by which the molecular condition of organic substances is permanently altered are changes in temperature, chemical reagents, and substances which have a powerful attraction for water. But these agencies do not in general cause destruction until they have exceeded a definite degree of intensity; while different changes of temperature and different states of concentration of the reagents not unfrequently give rise to phenomena differing not only in degree but even in kind. The effect of most external influences depends moreover to a great extent on the chemical nature of the substance which forms the material and molecular framework of an organised body. Cellulose[1] and starch may therefore be distinguished from crystalloids, chlorophyll-grains, and protoplasm, the former consisting mainly of carbo-hydrates insoluble in water, the latter chiefly of albuminoids.

(*a*) *Temperature* does not usually cause any striking or permanent change or destruction of organisation till it exceeds 50°, or sometimes even 60° C., and the substance affected is completely saturated with water. Air-dry organised bodies can generally bear much higher temperatures without injury. Thus, for example, dense starch-grains containing but little water are not converted into paste below 65° C., while the more watery grains undergo this change at 55° C. (Nägeli), the capacity for absorbing water and in consequence the volume then increasing enormously. Payen gives the increase in volume of starch in water of 60° C. as 142 p. c., at 70° to 72° C. as 1255 p. c., the starch originally containing, according to Nägeli, only from 40 to 70 p. c. water. Air-dry

[1] The cell-wall I suppose here and in the sequel to be neither cuticularised, lignified, nor converted into mucilage.

starch must be heated to nearly 200° C. before its power of absorbing water materially increases; but it is then changed chemically and converted into dextrine. The corresponding action of temperature on cellulose is not yet accurately known, but it is certainly different from that on starch. Like albuminoids, protoplasmic structures consisting for the most part of these substances are, when saturated, coagulated by a temperature of from 50° to 60° C., while when air-dry they can stand much higher temperatures without their molecular structure being destroyed[1]. The remarkable difference in the action of temperature on saturated starch on the one hand and on saturated protoplasm on the other hand must not be overlooked. In the former case the power of absorbing water is enormously increased; its structure becomes looser and more easily susceptible to chemical action; while the coagulation of protoplasm diminishes its power of absorbing water and the diffusibility of its molecules, and increases its power of resisting chemical action. This difference is also manifest when the change of molecular structure is caused by acids; and in this respect normal cellulose behaves in a similar manner to starch.

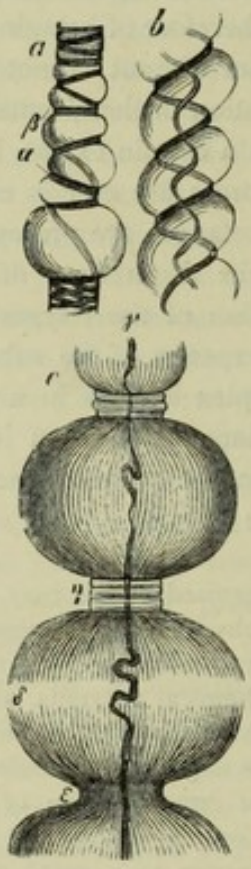

FIG. 435.—Bast-cells from a leaf of *Hoya carnosa* (see Fig. 32, p. 29); *a* and *b* after the commencement of the action of iodine and dilute sulphuric acid; *c*, when the swelling in dilute sulphuric acid has proceeded further. α and β in *a* are the outermost layer not capable of swelling, and coloured blue, which breaks up somewhat irregularly in these cases, but in *c* more regularly, into a spiral band, while the inner layers swell between them, and are coloured blue by iodine; γ in *c* is the cavity of the bast-fibre; ε and η are constrictions at points where the outer layer is especially firm; at δ the greatly swollen substance is beginning to become disorganised (×800).

(*b*) *Acids* (especially sulphuric acid) when greatly diluted cause starch-grains and cellulose at the ordinary temperature to swell up much more violently than pure water, without however destroying their organisation; and the previous condition returns when the acid is washed out. If, on the other hand, the acids are more highly concentrated, a violent absorption takes place in cellulose and starch-grains, and they pass into a pasty state. Protoplasmic substances, on the contrary, coagulate, as they do under the influence of higher temperatures. Concentrated sulphuric acid finally completely destroys the molecular structure of both with a smaller or larger amount of chemical change, and they deliquesce.

(*c*) *Solution of Potash* acts on starch-grains like sulphuric acid, especially in causing them to swell up. Its action on protoplasmic substances is on the other hand very different from that of acids; if the solution is dilute they swell up strongly or deliquesce, and this is especially the case with protoplasm and the nucleus of very young cells (the nuclei of older cells often resist the action strongly). But in a highly concentrated solution of potash protoplasmic structures often retain their form and apparently their structure; they neither coagulate nor deliquesce. The fundamental destruction of their molecular structure which has nevertheless taken place is evident from the fact that they immediately deliquesce if water is added copiously.

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[1] See Sachs, Handbuch der Experimental-Physiologie, p. 63 *et seq.*

(*d*) *Mechanical Influences.* Organised structures bear without injury small mechanical disturbances; they are either sufficiently elastic, like starch-grains and cell-walls, again to bring to equilibrium the changes which are thus caused in their internal tension and external form; or they are inelastic like protoplasm and chlorophyll-grains, and can then equalise small passive changes of form in another way. But stronger disturbances cause disruptions which cannot be again effaced. The molecular structure of the separated portions may however still be perfectly retained, as is shown by fragments of starch-grains and cell-walls. This is still more evident in motile protoplasm, where the separated portions of the previously continuous substance behave like so many individuals, and have the power of independent motion; as, for example, separated portions of plasmodia, the detached halves of the rotating protoplasm in the root-hairs of Hydrocharis when contracted by a solution of sugar, &c. In the same manner two or more separated portions of protoplasm may unite into a whole, as in the formation of large plasmodia and of zygospores, the impregnation of oogonia, &c. The only purely mechanical mode in which complete destruction of an organic structure can be accomplished is by crushing; *i.e.* by complete disseverance of its molecules and their subsequent promiscuous intermixture. In this case a chemical change usually directly follows the mechanical destruction of the molecular structure of the protoplasmic substance. In some cell-walls the mere interruption of continuity by a cut causes striking changes in the adjoining and the more distant parts; thus, according to Nägeli, cell-walls of Schizomeris that have been cut through become shorter and thicker to a remarkable extent.

(*e*) Changes in the molecular arrangement of organised structures caused by injurious influences determining their death are often accompanied by striking changes in their power of diffusion. With respect to starch and cellulose but little is known in this respect; but the phenomena connected with protoplasm, including the nucleus, are very remarkable[1]. Normal living protoplasm does not, for example, absorb any colouring material from the surrounding solution; but as soon as it has been killed by heat or by a chemical re-agent, the dissolved colouring material not merely penetrates into it, but accumulates in it to such an extent that the dead protoplasm appears of a much deeper colour than the surrounding solution of the colouring substance. Starch and cellulose, on the contrary, even in a fresh unchanged condition, absorb from a solution of iodine a comparatively much larger quantity of iodine than of the solvent, and become of a much deeper colour than the surrounding solution; the colour is also different, usually blue, while the surrounding solution is yellowish brown. The protoplasm which fills the cells and has been killed in any manner, by frost, heat, or chemical agents, is more permeable (whether cellulose is so also is not known); it allows the cell-sap, which in living and growing cells is always subject to high pressure, to filter out as if it had become porous. This is well seen when coloured cells or tissue are frozen or heated above 50° C.; they then allow their coloured contents to diffuse out, which they do not do when living.

(*f*) The true nature of the change which the molecular structure of moist organised bodies undergoes by heating above 50° or 60° C., or when they are made to swell up strongly by treatment with acids or alkalies, is considered by Nägeli to lie in the destruction of the crystalline molecules. In the case of starch-grains and cell-walls this view is supported by a few facts which have hitherto not been explained in any other manner. The increase of the power of absorbing water under such conditions is then explained on the hypothesis that the number of particles which attract water is increased and their size diminished by the destruction of the molecules; and this must necessarily be connected with an increase in the proportion of water and a corresponding increase

[1] Nägeli, Pflanzenphysiologische Untersuchungen, vol. I, p. 3 *et seq.*—Hugo de Vries, Sur la perméabilité du protoplasm des betteraves, Arch. Neérland vol. VI, 1871.

in volume. It is especially noteworthy that the denser layers of starch-grains and cell-walls become under these circumstances homogeneous with the least dense and most watery layers. But since the denser layers probably consist of large, the less dense layers of small molecules, the explanation may lie in the fact that the large molecules of the dense substance are broken up into a number of small molecules, and thus become similar to those of the less dense substance. The same explanation may be given of the fact that when the organised structure is changed by undergoing strong swelling, the optical properties of starch and cellulose also undergo change; their previous action on polarised light disappearing altogether. This is also explained if we suppose that under the action of these agents the molecules which produce the optical effect lose their form, and that their fragments are irregularly intermixed.

How far these views can be applied also to protoplasmic structures and their coagulation remains at present uncertain.

(*g*) The disorganisation of the molecular structure of organised bodies may take place gradually; and when it has exceeded a certain limit, a new substance is produced from the originally organised material, the molecular condition of which has, since the time of Graham, been termed *colloidal*. From the similarity which, according to Nägeli and Schwendener, exists between organised and crystalline bodies, it is not surprising that there are also mineral substances, which, like silica, are usually crystalline, but become under certain circumstances colloidal[1]. Organised bodies absorb water and other fluids, increasing at the same time in volume up to a certain maximum at which they are saturated; crystalline bodies dissolve in a definite minimum of water and produce a saturated solution which can be diluted *ad libitum*. Colloidal bodies show in this respect intermediate properties; they can be mixed with water in all proportions without any minimum or maximum. Solvents cause in organised and crystalline bodies a sudden passage from the solid to the fluid condition. Colloidal bodies pass from the solid to the fluid condition, when they are soluble, through all stages of softening; in a certain state when they contain but little water they are hard, then tenacious, then tough and scarcely fluid, finally when mixed with abundance of water perfectly fluid. Even in the fluid state they may be mucilaginous, cohering strongly to organic, less strongly to crystalline substances; and even when greatly diluted they diffuse very slowly, and some of them appear unable to penetrate organic membranes such as cell-walls. On drying they afford a homogeneous substance which differs greatly in its capacity for swelling and in its optical properties from the molecular structure of crystals and of organised bodies. In contradistinction to these latter, colloidal bodies may be considered amorphous internally as well as externally. Colloidal bodies occur abundantly in plants as products of the decomposition of organised bodies, and under certain circumstances they supply material for the production of new organised bodies. Thus gum-bassorin and perhaps also gum-arabic, as well as the mucilage of quince and linseed, result from the decomposition of cell-walls; perhaps also the formation of the substance of the cuticle must be included in this category. Viscin is the product of decomposed cellulose; the origin of colloidal pectin and caoutchouc is still unknown; but none of these substances are of any further use to the plant.

(*h*) *Traube's Artificial Cells*[2]. Among the most important of the phenomena belonging to the growth of the plant are those connected with the cell-wall; and everything which contributes to a more exact knowledge of its development must always be welcome. The researches of Traube, of which an abstract is here given, are of great interest from this point of view; even though it may not always be possible to transfer all the properties of his artificial cells to the real plant.

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[1] See, among other authorities, Graham, Phil. Trans. 1862; Journ. Chem. Soc. 1862.

[2] Traube, Experimente zur Theorie der Zellbildung u. Endosmose, in Arch. für Anat., Phys., u. wissensch. Medecin, von Reichert u. Du Bois 1867, p. 87 *et seq.*

Starting from Graham's observation that dissolved colloids cannot diffuse through colloidal membranes, and from the empirical fact that precipitates of colloidal substances are usually themselves colloidal, Traube found that a drop of a colloid *A* placed in a solution of a colloid *B* must become surrounded by a pellicle. If *A* is also more concentrated (or rather if its attraction for water is greater) the cell must become turgid, *i. e.* the precipitated pellicle must become stretched by the additional water that is absorbed; and the molecules of the pellicle thus become separated to such an extent that a fresh precipitate takes place between them which occasions increase in the superficies of the pellicle. For a more exact study Traube chiefly employed cells the pellicle of which consisted of a precipitate of gelatine tannate. For this purpose the tendency of the gelatine to coagulate was destroyed by boiling for thirty-six hours. A thick drop of this gelatine (called β) of the consistency of syrup was taken up by a glass rod, allowed to dry for some hours in the air, and then plunged into a flask half filled with a solution of tannic acid, into the cork of which the rod was fixed. The portion of gelatine which undergoes solution on the outside of the drop immediately forms a completely closed pellicle with the surrounding solution of tannin; and the water which penetrates through it constantly dissolves the gelatine within. In a dilute solution of tannin of 0·8 to 1·8 p.c. a tense pellicle which is not iridescent and is therefore thick is formed; in a concentrated solution of from 3·5 to 6 p.c. (in which therefore there is a smaller difference between the concentration of the two fluids) a thin flaccid iridescent pellicle is formed[1]. Traube found that the cells which are at first thick-walled go through various stages of development; they remain spherical so long as the nucleus of gelatine is not completely dissolved; a turbidity then sets in from above downwards owing to the solution of a part of the pellicle in the solution of gelatine which is more dilute in its upper part; the pellicle at the same time begins to collapse and to become iridescent; and finally the contents become clear and tension again takes place. After the lapse of some weeks the cell still allows gelatine to escape when torn. The greater the difference in the concentration of the two fluids, the firmer and more tense is the pellicle; *i.e.* the greater the intensity of the endosmotic attraction the greater is the number of layers of atoms which coagulate so as to produce the pellicle, and therefore the thicker it is.

With reference to the properties of the pellicle, Traube shows that all pellicles hitherto employed in experiments on diffusion have perforations[2], while the precipitated pellicles have only molecular interstices; and indeed these latter are, according to him, smaller than the molecules of the precipitate of which the pellicle is composed. But in spite of the greater density, the endosmose is quicker than with all other membranes, because they are thinner. The pellicle becomes firmer (stiffer?) when lead acetate or copper sulphate is added to the β gelatine. As soon as the molecules of the stretched pellicle have become so far separated by the pressure of the cell-contents which have increased in quantity by the action of endosmose that their interstices allow the passage of the two substances from which the pellicle is formed, these substances must obviously again at once mutually react upon one another at those points, and must

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[1] Only pellicles of gelatine behave in this way; all others are iridescent when tense.

[2] It is easy to convince oneself of the presence of actual perforations in pig-bladder, ox-bladder, the pericardium, amnios, collodion-membrane, or parchment, with which experiments on diffusion have hitherto usually been made, by stretching them over a wide glass tube, pouring in a column of water from 20 to 40 cm. high, and repeatedly drying the free surface of the membrane with filtering paper. Water is then almost always seen to ooze out at particular spots; a piece of membrane 2 or 3 cm. square is seldom water-tight. The perforations are still more evident if the tube is filled with a concentrated solution of common salt and the membrane dipped in water. Instead of a diffusion-current equal over the whole surface of the membrane, separate threads of the solution of salt are seen to sink down into the water. These experiments show how little dependence is to be placed on the researches hitherto made on membranes.

cause the production of new molecules of pellicle, which are deposited between those already in existence. Growth therefore takes place by intussusception, and is caused by the stretching of the pellicle, which stretching is on its part occasioned by endosmose. That the growth takes place not only by stretching but also by deposition Traube proved by replacing the tannic acid by water. As soon as this was done (*i. e.* as soon as the formation of new molecules of the precipitate in the pellicle was prevented, the endosmose still continuing) the growth ceased.

As long as the concentration of the contents of the artificial cell is everywhere the same, the pellicle remains everywhere equally thick, and the cell retains its spherical form. But when the contents are diluted, a denser solution is formed in the lower part of the cell, a more watery solution in the upper part. The pellicle becomes in consequence thinner above and therefore more extensible, because the difference of concentration is smaller there; hence the pellicle becomes more strongly stretched above and increases more rapidly in superficies, and protuberances directed outwards are not unfrequently formed. This may be expressed shortly by saying that endosmose takes place principally in the lower part of the cell, growth in the upper part. The difference however in the concentration in the interior of the cell which causes this is the consequence of the water which penetrates by endosmose not mixing at once uniformly with all parts of the interior solution, so that layers of different specific gravity lie one over another.

Further experiments showed that growing pellicle-precipitates having the form of cell-walls are produced also by mixing colloids with crystalloids[1]; *e.g.* tannic acid with copper and lead acetates, soluble glass with the same substances or with copper chloride, or finally crystalloids with one another, as potassium ferro-cyanide with copper acetate or chloride. Traube came to the conclusion that every precipitate the interstices of which are smaller than the molecules of its components must assume the form of a pellicle when the solutions of its components come into contact with one another. Since the pellicle-precipitates, as has already been mentioned, contain molecular interstices but no perforations, they are peculiarly well adapted for the study of endosmotic processes. They behave in this respect very differently from other membranes, being themselves often perfectly impermeable to the most diffusible substances, but allowing other chemical compounds to pass through them; and every kind of pellicle has in this respect its own peculiarities. Independently of the fact that every pellicle-precipitate is impermeable to the fluids from which it is itself produced, the β gelatine tannate is, moreover, impermeable for example also to potassium ferro-cyanide, but permeable to ammonium chloride, barium nitrate, or water. The pellicle of copper ferro-cyanide which is formed round a drop of copper chloride in potassium ferro-cyanide is impermeable to barium chloride, calcium chloride, potassium sulphate, ammonium sulphate, or barium nitrate, but permeable to potassium chloride or water. Traube considers that in the permeability of the pellicle-precipitates we have a means of determining the relative size of the molecules of different solutions, since only those molecules can pass through the pellicle which are smaller than its molecular interstices and therefore smaller than the molecules of the solutions which produce it.

If a small quantity of ammonium sulphate is added to a solution of β gelatine, and a small quantity of barium chloride to one of tannic acid, and the two mixtures thus obtained are themselves mixed, a pellicle is formed of calcium tannate, and on it a precipitate of barium sulphate which diminishes the size of the interstices; the two solutions which cause the deposit can no longer diffuse; but the incrusted pellicle is still permeable to the smaller molecules of ammonium chloride and water.

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[1] [The term 'crystalloid' is here used in the sense in which it was first employed by Graham, to indicate those substances—as opposed to 'colloids'—which may be susceptible of crystallisation, and which are endowed with the power of diffusion through a porous septum.—Ed.]

Traube maintains that there is no such thing as an endosmotic equivalent in the sense of the older theory. Endosmose is independent of any interchange, since it results entirely from the attraction of the dissolving substance for the solvent; and this attraction is invariable at the same temperature and may be termed *Endosmotic Force*. The endosmotic force of grape-sugar, for instance, is very great, that of gelatinous substances very small.

To these researches, which are of extreme importance in reference to vegetable physiology, and of which we shall make much use in the sequel, though with a cautious selection, Traube has added observations on the growth of the pellicle-precipitates of copper ferro-cyanide, the main results of which however I have been unable to confirm after a number of experiments.

If a drop of a very concentrated solution of copper chloride is dropped into a dilute solution of potassium ferro-cyanide, it immediately becomes coated with a thin brownish pellicle of copper ferro-cyanide which exhibits peculiar phenomena. It is more convenient to place small pieces of copper chloride in the ferro-cyanide solution, where a green drop is immediately formed at the expense of the water of the solution, producing the pellicle on its surface, and still enclosing the solid copper chloride which dissolves gradually from the permeation of the water. These cells manifest active growth and a variety of differences not easy to explain and dependent on secondary circumstances; some have very thin pellicles, are roundish, and exhibit a slight tendency to grow upwards; they usually form a number of small wart-like outgrowths and attain very considerable dimensions (from 1 to 2 cm. in diameter). They appear to be formed chiefly by the solution of large pieces of the copper chloride. Others have thick reddish brown pellicles, grow quickly upwards in the form of irregular cylinders, rarely branch, and attain a diameter of from 2 to 4 mm. and often a height of several centimetres. Combinations of the two forms also occur which sometimes form a kind of horizontal tuberous rhizome-like structure from which long stalk-like outgrowths arise upwards, and root-like protuberances downwards.

It is impossible, in the space at our disposal here, to give a detailed description of these phenomena; one only may be specially mentioned:—that these pellicles of copper ferrocyanide do not grow, as Traube supposes, entirely by intussusception, but also in quite a different way (by eruption). When a brown pellicle has been formed round the green drops, water penetrates quickly from without through the pellicle to the copper chloride; this becomes rapidly stretched, and, as may be clearly seen, at length ruptured. The green solution immediately escapes through the fissure, but becomes at once coated with a pellicular precipitate which appears either as an intercalated piece of the previous one, or as an excrescence or branch of it, a process which is repeated as long as any copper chloride remains inside the cell. We cannot therefore in this case conclude that deposition of fresh molecules of the pellicle takes place between those already in existence. These cells cannot, so to speak, be injured; if they are pricked, then at the moment when the point which pricks them is withdrawn an outgrowth follows immediately, which is easily to be explained from what has been said. In consequence of the rapid flowing in of water through the perforation, the dissolved or the still solid copper chloride has no time to form a homogeneous solution; a stratification arises which begins in the lower part of the cell with a very concentrated solution, and passes in the upper part into almost pure water when the cell has already grown to some height. Since the dilute upper fluid is lighter than the surrounding solution, it exerts an upward pressure upon the membrane—just as a cork held down under water attempts to rise—till it is ruptured below or at the apex (in the second form of cell). But the lighter fluid, when on the point of ascending, becomes at once surrounded by a pellicle which remains attached to the walls of the fissure of the old one; and thus apical growth takes place in cells of this description in the form of eruptions, just like the formation of branches and excrescences in the round ones. If the fluid in the upper part of the cell is pure water, large pieces of the pellicle break off

and rise up into the surrounding solution like air-balloons open below. If the copper chloride is entirely consumed in the formation of the pellicle, the opening caused by the tearing off of the upper cap does not close, or the whole cell ascends like an air-balloon. If rapidly growing cells of the second form are placed in a horizontal position, an outgrowth takes place at the extreme apex as the least solid point, which is directed vertically upwards, and then grows in this direction like the earlier apex of the cell. This process, even though it calls to mind distantly the bending upwards of growing stems which are placed horizontally (geotropism), bears in fact not the least actual resemblance to this phenomenon, as will be shown in Chap. IV; and this is at once evident if it is remembered that in these cells there is no such thing as growth by intussusception.

Sect. 2. **Movement of Water in Plants**[1]. The growth of the cells of plants is always connected with the absorption of water, and not only as regards the increase of size of the cell-cavity; the growth of the cell-wall and of other organised structures is also accompanied by the intercalation of particles of water between the solid molecules. Water must therefore be conducted to the growing cells and tissues; and when the organs which absorb the water lie at a distance from those which require it for their growth, the movement which results is necessarily considerable. Water is in the same manner required by the organs of assimilation, since it furnishes the hydrogen required for organic compounds. The reservoirs of food-material in which the assimilated compounds are for a time accumulated also require water for the purpose of again dissolving these substances, in order that they may be carried as formative materials to the leaves and the growing apices of roots and stems. All these movements of water, which are necessarily connected with nutrition and growth, proceed slowly like growth itself; their direction is in general determined by the relative positions of the organs which absorb the water from without and of those which make use of it.

In plants which grow under water or beneath the ground where no loss of water takes place or only to a very inconsiderable extent, there is no need for these processes. The case is nearly the same also with some land-plants which are almost completely protected by a peculiar organisation from loss of water by evaporation when it has once been absorbed, as the Cactus-like Euphorbias, Stapelias, &c., which are by this means enabled to live in the most arid localities. But the great majority of plants have foliage with a very large superficial development; when the leaves are also delicate, as in most plants with a rapid growth, a very considerable portion of the water of their cell-sap is removed by evaporation within a short time, so that in the course of a single period of vegetation the quantity of water which has been withdrawn by evaporation may exceed many times the weight and volume of the plant itself. It is easy to understand that this is possible only when the loss is compensated by the absorption of corresponding quantities of water through the roots, and that the water withdrawn from the leaves is replaced in this way. As long as the tissue of plants in which transpiration

[1] See Sachs, Handbuch der Experimental-Physiologie, the section on the movement of water, p. 196, where the literature up to 1865 is mentioned; the most important of the more recent publications are quoted in the sequel.

takes place remains turgid, the addition must nearly equal the loss by evaporation; so long therefore as evaporation proceeds continuously from the leaves or other surfaces, a constant current of water exists from the roots to the leaves. When evaporation ceases, as in very moist air when the leaves are wetted by dew or rain or after the falling of the leaves, the current of water also ceases as soon as the tissues which have become somewhat flaccid are again turgescent. Since evaporation is accelerated by a high temperature of the air, by its dryness, and above all by sunshine, and as these conditions are constantly changing, the rapidity of the current of water is also subject to continual change.

The current of water occasioned by evaporation has, as will be seen, no immediate connection with the processes of growth and nutriment; the horse-chestnut and other trees and shrubs which put out in spring only a definite number of leaves, and during the summer do not any further increase their foliage, transpire the most rapidly during this time; and at this time also the current of water is most considerable in them. In winter both growth and evaporation, and with this last the amount of water also in the tissues, remain stationary; when the buds are put out, the water is first of all only set in motion to the extent required by the increase of the growing organs; but as the development of the organs increases their surface, the amount of evaporation again rises, and the current begins afresh.

While the movement of water required for purposes of growth and nutrition must take place in the most different forms of tissue—in the parenchyma and even in the primary meristem of buds and of the apices of roots—it is nevertheless certain that the current of water caused by evaporation passes exclusively through the woody portion of the fibro-vascular bundles; all the rest of the tissue may be destroyed at any place without the current of water ceasing, if only the wood remains entire. In Conifers and Dicotyledons a strong current passes through the root and stem, dividing in the branches and leaves into constantly narrower channels; while in Ferns and Monocotyledons the current of water passes, even in the primary stem, through isolated narrower channels corresponding to the course of the isolated woody bundles. That the lignified elements of the xylem of the fibro-vascular bundles determine the channel of the current, is seen not only from direct observation, but also from the fact that the formation of wood proceeds the more rapidly the more considerable is the evaporation and the stronger the current of water in a plant. In submerged and underground parts of plants from which no evaporation takes place the xylem remains entirely or nearly unlignified; in Dicotyledons and Conifers, where the evaporating surface increases with age, the channel taken by the current is also annually widened by the increase of the wood. The crown of leaves of palm-trees remains after a certain time of nearly the same size, and the stem and the channels of the current (woody bundles) which traverse it consequently retain their diameter unchanged.

The movements of water caused by growth as well as those induced by evaporation have this in common, that their direction is towards the places where they are required. If the growth or the evaporation begins at a certain time at a definite spot, the nearest portions of the tissue give up their water first of all, then the more distant ones, until at length the organs at the greatest distance, generally the roots, are compelled to absorb water from without. The movement

therefore propagates itself continually further and further from the point to which it tends, and finally over the whole plant to the medium which surrounds the root. The kind of motion may therefore—without considering for the moment its actual causes—be described as a process of suction. This is especially evident in leafy stems and branches which, having been cut off and placed with their cut surface in water, suck up as much water through their woody bundles as is required for transpiration and for the unfolding of fresh leaves, unassisted in this case by any pressure from below.

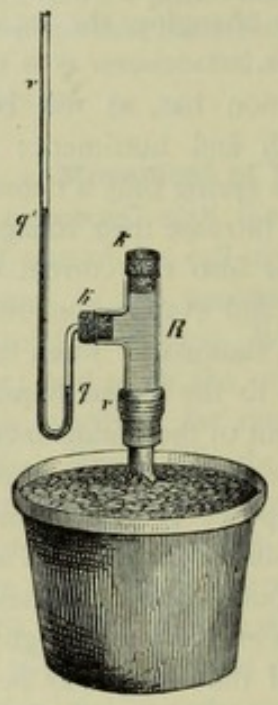

FIG. 438.—Apparatus for observing the force with which water escapes under root-pressure from the transverse section of a stem *r*. The glass tube *R* is first of all firmly fastened to the stem, and the tube *r* then fixed into it by the cork *k*. *R* is completely filled with water, the upper cork *k* then fixed in it, and mercury poured into the tube *r* so as to stand from the first higher at *q'* than at *q*, the level *q'* rising above *q* according to the intensity of the root-pressure. The apparatus is much more convenient to handle than that hitherto in use.

Another kind of motion of water in the plant, depending not on suction but on pressure from below, is caused by the roots, and is altogether independent of the use of the water for the purpose of growth or of evaporation. If the woody stem of a land-plant is cut through above the root, the root being attached to the ground in the ordinary manner, and if the ground is damp and sufficiently warm, water exudes from the transverse section of the stem either at once or after some time, the current continuing for days, and the quantity of water which flows out amounting sometimes to many times the volume of the root. This current of water, which rises in wood as well as in glass tubes, can only be induced by a pressure exerted on the lower parts of the root. If a manometer of a proper form is fixed in the section (Fig. 438), it shows that even in smaller plants with but little wood (as tobacco, maize, the stinging nettle, &c.) the water which exudes stands at a pressure which holds in equilibrium a column of mercury several centimetres in height; while in some woody plants, as for instance the vine, this pressure may amount to 76 cm. (or one atmospheric pressure).

In many plants of small height this root-pressure is observable from the fact that water exudes at particular points of the leaves in the form of drops, provided that the internal supply of water is nowhere diminished by powerful evaporation, and the pressure thus removed. Thus drops of water appear abundantly and repeatedly on the margins and apices of the leaves of many Grasses (especially striking in the maize), Aroideæ, Alchemilla[1] &c., when transpiration is diminished

[1] According to Duchartre, De la Rue, and Rosanoff, the exudation usually takes place through the stomata, which are either developed in a peculiar manner, or are very large, or, possessing the ordinary form, are accumulated at these places. De Bary remarks in connection with this:—'If water is forced into the wood of a branch of a plant adapted to the purpose, *e.g. Fuchsia*

by the absence of light and the cooling of the air, and the activity of the roots increased by warm damp earth. In some plants, as Nepenthes, Cephalotus &c., curious pitcher-like structures occur at the ends of the leaves, at the bottom of which water exudes, and in which it collects[1]. Even in unicellular plants, or those which consist only of rows of cells, as the Mucorini (*e. g. Pilobolus crystallinus*), *Penicillium glaucum*, and the large Fungi (as *Merulius lacrymans*), the water is forced out in drops from the upper part, it having been absorbed by the lower parts which perform the function of roots and press it upwards.

Fluid however not unfrequently appears in drops in places where there can be no pressure directed upwards from the root. Thus the nectaries of flowers, as those of *Fritillaria imperialis*, exude drops of nectar even when the stem is cut off from the root and merely placed in water. In this case the forces which cause the pressure must arise in the upper masses of tissue, perhaps even in the flower, for the water is conveyed to the cut stem not by pressure but by suction.

The phenomenon known as the Bleeding of wood cut in the winter must not be confounded with this. This bleeding occurs when the cut branch or piece of stem, previously cold and saturated with water, is rapidly warmed; the air which is enclosed with the water in the cells and vessels of the wood expands, and forces the water out where it can find an opening. If the piece of wood is again cooled, the air contracts, and the water in contact with the section is again sucked in. It is evident that these expansions and contractions of air in the wood must also take place when the woody substance of the tree is uninjured; and hence currents are set up from the parts which are becoming warmer to those which are becoming cooler, and tensions are brought about. All this however happens only so long as air as well as water is found in the cavities of the wood, as is the case in the winter and spring before the leaves unfold and evaporation begins.

Although the movements of water in plants have been copiously investigated and discussed for nearly 200 years, it is nevertheless still impossible to give a satisfactory and deductive account of the mode of operation of these movements in detail[2]. This much appears certain, that the ultimate forces concerned are always capillarity and diffusion (in the broadest sense of the term). But since in the living plant these forces

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globosa, by the moderate pressure of a column of mercury, drops of water at once exude from the large stomata' (Bot. Zeit. 1869, No. 52, p. 882).

[1] [The liquid contained in the pitcher-like organs of Sarracenia, Nepenthes, Cephalotus, &c., is not pure water. Dr. Völcker (Ann. and Mag. of Nat. Hist. Vol. IV, p. 128, and Phil. Mag. Vol. XXXV, p 192) states that it is generally clear and colourless, rarely yellowish, and reddens litmus. The proportion of residue left on evaporation varies from 0·27 to 0·92 p. c. This residue consists of 38·61 p. c. organic matter, chiefly malic acid with a little citric acid, 50·02 p. c. potassium chloride, 6·36 p. c. soda, 2·59 p. c. lime, and 2·59 p. c. magnesia. Dr. Buckton (Nature Vol. III, p. 34) found that the liquid contained in the pitcher-like labellum of Coryanthes consists of 98·51 p. c. water and volatile oils, and 1·49 p. c. non-volatile residue. It is clear and somewhat glutinous in consistence, with a high refractive power, and a sp. gr. 1·062; neutral to test-paper; on evaporation it becomes milky, finally yielding a transparent gum insoluble in alcohol.—Ed.]

[2] Although Dr. Müller, in the second part of his 'Botanische Untersuchungen (Heidelberg 1872) assumes that he has actually accomplished this, those only will believe this who are entirely ignorant of vegetable physiology.

act under conditions widely different from those in operation in artificial apparatus, we are compelled on all essential points to draw our conclusions as to the internal processes from the careful study of the external phenomena in the plants themselves. Our space will however only permit us to refer to these in general terms. The main result of the investigations hitherto made is to maintain the distinction between the different causes of motion in the fluids of the plant to which we have already alluded, until a more thorough knowledge justifies some other interpretation. What follows is less for the purpose of explaining the phenomena than of illustrating by examples what has already been said.

(*a*) The slow movement of water caused merely by *Growth and Assimilation* is seen in its simplest form in unicellular Fungi and Algæ and in those in which the cells are arranged in rows and plates, and in germinating spores and pollen-grains; since in these cases the growing and assimilating cells absorb the water which they require immediately from their moist environment. That this is caused by the imbibing power of the cell-wall and of the protoplasm as well as by endosmose (*i. e.* the attraction of the dissolved substances within the cell for water), is certain, although we have not yet sufficient knowledge of the exact mode in which these processes go on. On the other hand, in plants which consist of masses of tissue the young growing parts withdraw the water of vegetation from the older mature parts, and these latter become in consequence empty if they receive no fresh supply from without. This is seen clearly when tubers, bulbs, trunks of trees which have been cut down, &c., put out buds in ordinary moderately dry air, and thus gradually lose the water they have contained[1].

(*b*) *Transpiration*[2]—*i. e.* the evaporation of water from cells and masses of tissue—is produced and modified by external and internal conditions and causes. Among external causes those must first be noted which produce evaporation from moist surfaces, such as the relative temperature and dryness of the air and that of the transpiring tissue itself. Evaporation will generally increase as the temperature of the surrounding air rises and its degree of saturation consequently decreases; and this must for our purpose be considered the most direct measure of the greater or less tendency to evaporation. It must not however be expected that the amount of evaporation from plants is simply in proportion to any one of these conditions. It is still doubtful whether light, *i. e.* radiation as such, independently of the elevation of temperature caused by it, influences transpiration[3]. The stomata of most plants open more widely in light than in the dark[4]; that is, the openings which allow of the escape of the aqueous vapour formed in the interior of the tissue become larger, and this must have the effect of promoting further evaporation within. It is not yet decided whether light acts on the stomata as such, or by means of the heat which accompanies it, or the chemical changes which it causes.

Among the conditions connected with the organisation of the plant itself which determine the amount of transpiration must be noticed the nature of the cortical tissue, the size and number of the intercellular spaces, and the character of the substances dissolved in the cell-sap. When the cortical tissue is a continuous and thick layer of periderm as in many woody branches, potato-tubers, &c., or even a thick layer of bark as in older trunks of trees, the evaporation of water from the succulent tissues which lie beneath is rendered difficult in the extreme. The cuticularised outer wall of the epidermis of

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[1] For further details see Nägeli, Berichte der kön. bayer. Akad.; Botanische Mittheilungen, Vol. II, p. 40.

[2] Sachs, Experimental-Physiologie, p. 221.—Müller, Jahrb. für wiss. Bot., Vol. VII; 1868. —Baranetzky, Bot. Zeit., 1872, Nos. 5-7.

[3] Dehérain's recent researches (Ann. des sci. nat. 1869, pl. XII, p. 1) do not decide the question.

[4] Von Mohl, Bot. Zeit. 1836, p. 697.

young leaves and internodes is less efficacious in this respect; if it is very thin as in many quickly growing leaves, especially those of water-plants, or altogether imperceptible as in roots, these parts dry up very quickly in ordinary air; while an intermediate condition is presented by the cuticularised outer layer of the epidermis of leaves and young internodes. In contradistinction to this the evaporation is very small from hard evergreen leaves, Cactus-stems &c., which are covered by a thick cuticular coating. It may be assumed that in plants provided with a thick cuticle transpiration takes place principally through the stomata, and is therefore dependent on their smaller or larger number and size. The evaporation does not in this case proceed from the surface of the organ (or only to an imperceptible extent) but in its interior, *viz.* at the places where the cells of the parenchyma bound the intercellular spaces. These spaces may be supposed to be always at least nearly saturated with aqueous vapour; but the vapour will escape through the stomata with every increase of its tension or decrease of the tension of the vapour without, and will thus give rise to the production of more vapour in the inside. The production of vapour in the intercellular spaces is moreover the more abundant the larger they are themselves, or in other words the larger the superficies of cell-wall which bounds them. This circumstance, and the much larger number of stomata on the under side of the leaves, are clearly the reason why evaporation is generally so much more copious from it than from the upper side. Since water containing any substance in solution evaporates more slowly than pure water, and the more slowly the more concentrated and denser the solution, this force must also be considered among the conditions which limit the transpiration of water from the sap of plants. It must not however be forgotten that evaporation takes place only on the external surfaces of the cell-walls of tissues, which on their part remove the water by imbibition from the cell-sap.

The conditions now named which regulate transpiration are combined in the most various ways, and not only cause different plants to show different amounts of transpiration, but also the amount to be very different in the same plant at different times. A definite statement cannot however be made of the total amount of transpiration, *i. e.* of the quantity of water required by a plant during its period of vegetation, although certain very variable limits can always be assigned to each species in this respect. Two plants of the same species may, as any one may see, thrive equally well if one grows in damp soil and dry air, the other in dry soil and damp air, the former thus using up a large, the latter a small amount of water. In general the conditions of transpiration which have been mentioned exhibit periodic variations related to the meteorological distinction of day and night; the temperature, the moisture of the air, and light, are usually favourable to evaporation by day, unfavourable by night; but under certain circumstances this condition may even be reversed.

(*c*) *Currents of Water in the Wood.* Superficial cells or those which bound intercellular spaces and lose water directly by evaporation, would very soon collapse and dry up if they were not able again to replace that which they have lost. This can only take place by the flow of water from the adjoining cellular tissue from which no evaporation occurs; but when this tissue is placed in the same condition as the former, it must also compensate its loss from more distant layers of tissue, and these again from those which are connected with the conducting organs or woody bundles which convey the water from the roots. The question here presents itself whether this movement of water within the succulent tissue (especially in the parenchyma of the leaves) is caused by endosmose from cell to cell, or whether it does not occur at least principally along the cell-walls, these latter forming the channels of communication between the woody bundles and the surfaces where the evaporation takes place, the contents of the cells being only incidentally carried along with the transmitted fluid.

The chief evidence of the fact that the currents of water in the roots, stem, and branches caused by transpiration take place only in the wood, *i. e.* in the lignified xylem, has already been stated. It can be demonstrated in a more conspicuous manner

by placing a cut stem or branch with its cut surface in a coloured solution[1] while the leaves are transpiring. If the stem or branch is cut through at various heights after a few hours, or according to circumstances after a longer period, the colouring of the wood will show how high the solution has been sucked up in it, and will be seen only in the woody bundles and not in the cortex or pith. If branches with pure white flowers are employed in this experiment (according to Hanstein's process), such as a white-flowered Iris or Deutzia, and if they are placed in a dark aqueous solution of aniline, the white petals are found, after from ten to fifteen hours, to be permeated by dark blue veins corresponding to the fine woody bundles of the venation. This beautiful appearance however soon vanishes, the poisonous colouring material subsequently killing the adjoining layers of parenchyma, and colouring the spaces between the veins blue by diffusion, and the corolla thus becomes flaccid[2].

The difference in the amount of transpiration under different external conditions must also correspond to a difference in the rapidity of the current of the water in the wood. In rainy weather, when there is no evaporation or but very little from the leaves, the movement of the water in the stem will be very slow; but when the transpiration increases with sunshine and wind, the current of water in the woody bundles is also accelerated. Under the hypothesis that the water moves only in the woody substance of the walls of the wood-cells themselves and not in their cavities, I have calculated the rapidity of the ascending current of water in a branch of the silver poplar in which there was strong evaporation, and obtained a rate of 23 cm. per hour. McNab placed branches of *Prunus Laurocerasus*[3] from which evaporation was taking

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[1] I must take this opportunity of making the remark that I still entertain, and in a high degree, the doubt previously expressed, whether it is not a purely pathological phenomenon that is produced in this manner.

[2] [This is a method of experimentation which has been practised by numerous observers since the commencement of the last century, when it was apparently first tried by Magnol. Sarrabat (otherwise Delabaisse) coloured the veins of the flowers of the Tuberose (*Polyanthes tuberosa*) and Snapdragon (*Antirrhinum majus*) by watering the plants with the juice of the berries of Phytolacca. (Dissert. sur la circul. de la Sève, Bordeaux, 1733.)

Van Tieghem (in the French edition of this work, p. 791) quotes Reichel as having plunged the roots of a flowering plant of *Datura Stramonium* into a decoction of the wood of Fernambouc; the liquid followed the course of the vessels, and after eight days veined the corolla with red, and made its appearance also in the stamens, the walls of the fruit, and even in the style. (De vasis plantarum spiralibus, Leipzig, 1748.) For other old authorities see De Candolle, Phys. Veg. i. 82.

De Saussure found that the stem of a bean became coloured by a decoction of Brazil-wood; and this was one of the facts upon which he based the conclusion that organic matters were capable of being taken up by the roots of plants (Ann. des Chem. u. Phys. xlii. p. 275). Biot noticed that the red colouring matter of Phytolacca was absorbed by white hyacinths when poured upon the soil in which they were grown; after two or three days, however, the red colour disappeared from the flowers. (Comptes Rendus, 1837, i. 12.) Unger also made the same experiment (Botanical Letters, p. 38). Hallier immersed the ends of cuttings of plants in solution of indigo or black cherry juice. (Phytopathologie, 1868, p. 67). Persoz states (Introd. à l'étude de la Chimie moléculaire, p. 553) that plants of *Impatiens parviflora*, the roots of which are immersed in a solution of sulphindigotic acid, absorb that fluid in a reduced or colourless state due to the action of the roots upon it; in the petals it again undergoes oxidation and becomes blue. The experiments of Herbert Spencer (Principles of Biology, i. p. 538) may also be referred to.—Ed.]

[3] McNab, Transactions of the Botanical Society of Edinburgh, 1871. [Dr. Pfitzer has suggested that the result may be arrived at by the much simpler mode of allowing the plant grown in a pot to become so flaccid from want of water that the leaves droop perceptibly, and then, after supplying the root with water, to observe the length of time that elapses before the leaves at various heights from the ground recover their normal position. Pfitzer found by this means a much more rapid rate of ascent indicated than that stated by McNab; and believes that there is a serious source of error in McNab's experiments, from the saline solution not rising so fast as pure water.—Ed.]

place in a solution of lithium citrate, and then examined the ashes of successive internodes by the spectroscope. The solution was found to rise from 42 to 46 cm. in one hour. But neither method of calculation is exact or probably of much value.

The current of water in the woody substance which replaces the loss occasioned in the leaves by transpiration is not caused by osmose, since at the time when the evaporation is strongest and therefore the current in the wood quickest, the cavities of the conducting wood-cells do not contain sap but air, or at the most are only partially filled with fluid. If the rising of the water took place by endosmose from cell to cell, the cells would themselves possess closed cell-walls and be full of sap, the concentration of which would constantly increase from below upwards in the wood. But the conducting cells are at this time not closed, but partially or altogether (as in Coniferæ) connected with one another by open bordered pits. In the spring, before strong transpiration sets in, and therefore at a time when the water in the wood is comparatively at rest, the wood-cells also, it is true, contain sap, flowing in quantities out of their communicating cell-cavities when holes are bored in the trunks (as in the birch, maple, &c.)[1]. But this sap does not, as is proved by analysis[2], show a concentration increasing from below upwards. The fact also that water rises in cut leafy branches placed with their upper end in water or planted and taking root, and flows therefore in a direction opposite to the ordinary one in the branch, shows that endosmose depending on a definite distribution of the concentration of the sap cannot be the cause of the current of water. Since vessels and wood-cells communicating with one another through their open pores form narrow cavities which sometimes become wider as they proceed, sometimes narrower, the woody substance may be represented by a bundle of narrow glass tubes alternately bulging and contracting, in which the water which fills them rises by capillary attraction. But how little efficacious a contrivance of this kind would be is seen at once from the width of the capillary tubes, which is much too great to raise water to a height of 100 feet or more. It must also be pointed out that in the summer, when the current of water is strongest, it is principally air and not fluid that is conveyed through the cavities of the cells.

Since it is evident from what has been said that the movement of the water takes place in the woody substance and not in the cell-cavities filled with water, there remain only two hypotheses; viz. (1) that the movement takes place in the water contained in the lignified cell-walls (or in other words imbibed by them); and (2) that it is caused by a very thin stratum of water which overspreads the inner surface of the wood-cells and vessels[3]. In both cases it must be assumed that the transpiration in the tissue of the leaves causes the upper parts of the wood to contain less water, and therefore to draw up the water from the parts which lie lower. The woody bundles of the roots are surrounded by succulent parenchyma, from which they remove the water; and these again absorb it from the soil by endosmose. It may however be imagined that both the kinds of motion mentioned proceed along the surface as well as in the substance of the cell-walls (the contents not participating in it) to the surface of the root, where the water contained in the soil is sucked up. The question whether the attraction of the cell-walls for water,—putting aside the question whether it moves in their substance or only on their surface,—is sufficiently powerful to sustain the weight of a column of water of the height of 100 or even 300 feet or more attained by some trees,

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[1] The older statements of Unger are referred to in my 'Experimental-Physiologie'; others will be found in Schröder, Jahrb. für wiss. Bot. vol. VII, p. 266 *et seq.*

[2] The conduction is however by no means so considerable in the reversed as in the ordinary direction, as Baranetzky found in the laboratory at Würzburg; but this may be connected with other peculiarities of the organisation.

[3] This hypothesis follows from the discoveries of Quincke on capillarity, and has been communicated to me by him.

may be answered without hesitation in the affirmative, since we have to do here with molecular forces in opposition to which the action of gravity altogether disappears. But it is another question whether the rapidity of the molecular movements of water of this nature is sufficient to cover the requirements of the foliage of a tree which amounts on a hot day to hundreds of pounds[1].

The hypothesis finally that the water is forced up into the stem and even into the leaves by root-pressure must be abandoned, since this could only operate in the cavities of the wood; and these are always empty in energetically transpiring plants. In the case of tall trees the pressure would also not be sufficient; and if I at one time assumed that this might be a cooperative cause at least in shrubs and annual plants, I must retract this after my observations made in the year 1870; since these show that the root-stock of such plants as the sun-flower, gourd, &c., is even subject to a negative pressure when they are transpiring strongly; *i. e.* does not press water up, but greedily sucks it in at a cut surface above the ground (*vide infra*).

The insufficiency of all attempts hitherto made to explain the movement of water in the wood due to transpiration is especally noticeable from the fact that it is only under certain internal conditions which cannot be more accurately ascertained that wood is capable of conducting water with the force and rapidity required by the evaporation from the leaves. Woody but air-dry branches with a lower cut surface placed in water are never able to raise up as much water as is necessary to replace the evaporation even from an upper cut surface; while the same branch in a fresh state conducts water fast enough to replace the much greater amount of evaporation from the numerous leaves. A change is thus caused in wood simply by drying up which deprives it of the power of conducting water rapidly. The natural alteration which takes place in wood, by which it is transformed as it increases in age into 'duramen'—the cell-walls becoming harder and of a deeper colour—also deprives it of this power. If a tree is deprived not only of the bark but also of the 'alburnum' (the light-coloured younger wood on the outside), in an annular zone, the foliage of the tree, according to the statement of different writers, dries up, because the water is not conducted sufficiently rapidly through the duramen.

Among the most remarkable of the phenomena related to this is the fact that the younger terminal portions of the stems of large-leaved plants partially lose the power of conducting water when cut off in air. If the cut leafy end of the stem of *Helianthus annuus*, *H. tuberosus*, *Aristolochia Sipho*, &c., be placed with the cut section in water, the suction is not sufficient to compensate the evaporation from the leaves, which therefore wither after a shorter or longer time. As I have already shown in the second edition of this book, the withered shoot may in a short time be revived by forcing in water by means of the contrivance represented in Fig. 439. I did not discover till afterwards that the shoot remains turgid even when the pressure is reduced to zero, and even when the mercury is raised up by the suction of the shoot in the same arm of the tube (*q*), when therefore a force acts on the section of the shoot in the opposite direction. This shows that the forcing in of water is only necessary at first, but that the revived shoot has itself sufficient power of suction even to raise up a column of mercury several centimetres in height, and thus to replace the loss by transpiration from the leaves. Thus much was known about the phenomenon of the withering of cut shoots placed in water, when Dr. Hugo de Vries took up the further investigation of it in the laboratory of the Würzburg Institute. The results obtained by him I will now quote:—

'If rapidly-growing shoots of large-leaved plants are cut off at their lower part which has become completely lignified, and are placed with the cut surface in water, they remain for some time perfectly fresh. But if they are cut through at the younger parts of their stem and are then placed in water, they soon begin to wither, and the

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[1] See Nägeli u. Schwendener, Das Mikroskop. vol. II, p. 364 *et seq.*

more rapidly and completely the younger and less lignified the part where the section is made. This withering can be easily prevented by making the section under water, and taking care that the cut surface does not come into contact with the air, the conduction of water through the stem thus suffering no interruption. If care is taken that while the section is being made in the air the leaves and upper parts of the stem lose only a very small quantity of water by evaporation, withering does not begin till later and increases only slowly after the cut surface is placed in water and the leaves again transpire.'

It results from these experiments that the cause of withering is the interruption in the conduction of water from below; and this interruption produces withering not only from the conduction of the water ceasing for a short time, but chiefly also from the power of conducting water in the stem being diminished by the loss of water above the cut surface, which loss cannot be restored simply by placing the cut surface in contact with water.

If the cut surface does not remain too long in contact with the air, the diminution

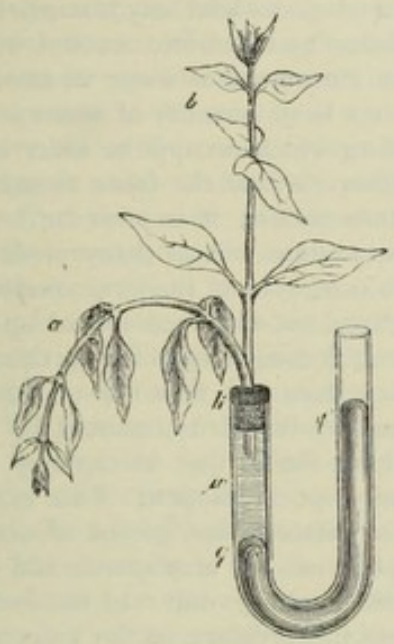

FIG. 439.—Apparatus for showing the revival of withered shoots by forcing water into them. The U-shaped glass tube is first filled with water, and the perforated stopper of caoutchouc *b* in which the stalk of the plant is inserted, is then fixed in. When the shoot is withered, as represented by *a*, mercury is poured into the other arm of the tube, so as to stand at q' some 8 or 10 cm. above q, and the shoot then revives, as represented by *b*, even when the level q becomes subsequently higher than q'.

of the capacity for conduction takes place in only a short piece of the stem above the cut. When placing in water ends of shoots which have begun to wither after being cut off, it is only necessary to remove by a new cut a sufficiently long piece above the first cut, but this time beneath the water, for the shoot to revive. In the case of shoots 20 centimetres or more in length which at this distance from the apex are not lignified, the removal of a piece 6 cm. long is usually sufficient to revive the withered shoot (*e.g.* in *Helianthus tuberosus*, *Sambucus nigra*, *Xanthium echinatum*, &c. This experiment proves beyond question that the change, whatever its nature may be, takes place only in this relatively short piece above the cut. That it consists in a diminution of the power of conducting water is shown by the following experiment:—When a sufficient number of the lowest and largest leaves have been removed from a stem of *Helianthus tuberosus* cut off in the air and placed in water, and which has begun to wither, the leaves that are left and the terminal bud will after some time begin to revive even without again cutting the stem. The water which is required for the transpiration of a great number of leaves can therefore no longer be conducted through the stem after

it has been cut off in air, although that which is wanted for the transpiration of a few leaves can be.

The cause of this phenomenon is therefore a diminution in the power of conducting water in a short piece above the cut surface of the stem. This is evidently occasioned by the loss of water from the cells caused by the suction of the higher parts not being compensated by absorption from below. All circumstances which favour this loss of water increase also the loss of power of conducting it, and cause the shoot which is placed in water to wither more rapidly and completely. It must therefore be assumed that the conducting power of the cells depends on the quantity of water they contain. The probability of this hypothesis is increased by the fact that by artificially increasing the amount of water in the cells of this piece, its conducting capacity can also be increased, as is proved by forcing in water from below. If the modified portion is dipped in water of from 35° to 40° C., the withered shoots soon revive, and if then placed in water of 20 C°. remain fresh for days (as in the case of the elder), or at least wither more slowly (*e. g.* the artichoke).

(*d*) *Water retained in the wood by Capillary Attraction.* If the capillarity of the cavities in the wood must be considered as without any immediate action on the currents of water, this force must nevertheless be taken into account with respect to other processes connected indirectly with the movement of water in the plant. In winter and after long-continued rain in summer a large quantity of water is found in the cavities of the wood together with bubbles of air which occupy the wider spaces. It is not known how this water has reached the higher parts of the trees, though it is possibly by the formation of dew as the temperature varies; it is however to a great extent retained by capillarity. A part of the water flows out in many cases through holes bored in the stem if they are not placed too high, as in the birch, maple, vine, &c. It may be supposed that the water which flows out has been forced up by the root-pressure which must also be taken into account; though how far up this pressure extends is not yet ascertained. The water which does not flow out of the cavities when there is less transpiration is clearly retained by capillarity, assisted by the air in the cell-cavities; for Montgolfier and Jamin have shown that in capillary spaces which contain water and air the water is not easily set in motion. This explains also the phenomenon already mentioned, that water escapes when pieces of wood which have been cut off in cold weather are warmed, because the air expands and forces out the water. Subsequent cooling causes on the contrary water to be sucked in at the cut surface, because the air contracts, and the pressure of the external air forces in water from without.

(*e*) *The ascent of water from the root into the stem*[1]. The most important features of this phenomenon have already been briefly mentioned. It is to be observed in the open air in plants of the most different kind, if they possess vigorous root-systems and well-developed wood; as, for instance, in the birch, maple, and vine, and among annual plants, in the sunflower, Dahlia, Ricinus, tobacco, gourd, maize, stinging nettle, &c. In order to study the phenomenon accurately, it is best to grow the plants for some time previously in large flower-pots until they have developed a strong root-system. Land-plants such as maize grown in water and artificially fed by nutrient substances, are also well adapted for the investigation. If the stem of such a plant is cut across smoothly 5 or 6 cm. from the ground, and a glass tube fixed to the stump by means of an india-rubber tube, the result will be seen as follows. If the plant was in a condition to transpire freely before it was cut, the cut surface of the root-stump remains at first quite dry, and if water is poured into the glass tube it is at once sucked up[2]. The

[1] See in particular Hofmeister, On the tension and the quantity and rapidity of the flow of the juices of living plants; Flora 1862, p. 97.

[2] This fact is sufficient to prove that the root-pressure has no share in the ascent of the water at the time when transpiration is active.

woody substance of the root-stump has evidently been exhausted by transpiration before the operation, and contains but very little water; not only are its cavities empty, but even the cell-walls of the wood may not be saturated. After a shorter or longer time however the exudation of water at the cut surface begins—rising higher and higher in the tube—and continues from six to ten days if the plant is properly treated, becoming during the earlier part of the time continually more copious, attaining a maximum, and finally diminishing until it ceases with the death of the root-stock. If the cut section is repeatedly dried with blotting paper during the time that the water is flowing, it is clearly seen that the water exudes from the woody tissue—in Monocotyledons from the xylem of the separate bundles—and that it comes principally from the openings of the larger vessels. That the water which flows out had previously been absorbed by the roots out of the ground, and not merely from the store in the root-stock, is at once evident from the fact that the quantity which exudes at the cut section is after a few days greater in volume than the whole of the stock. Under the conditions here described, the water which flows out contains only traces of organic substances in solution; but the presence of mineral constituents can be easily proved, especially lime, sulphuric acid, phosphoric acid, and chlorine, which the plant has absorbed out of the ground. The water which flows in the spring from holes bored in trees such as the birch and maple, contains however considerable quantities of sugar and albuminous substances; since the longer stagnation in the cavities of the wood gives it the opportunity of absorbing these substances out of the closed living cells of the wood and out of the surrounding parenchyma, a result which cannot be expected, or only in a smaller degree, in the case of the rapid flow from the smaller root-stocks of quickly-growing plants.

In order to determine the quantity of the outflow, a narrow burette may be used instead of the tube, in which the amount can be read off hourly in cubic centimetres when the outflow is at all considerable. The root-pressure which acts upon the cut surface is however then considerably altered. In order to avoid this, a tube of the form shown in Fig. 438 *R* (p. 600) is fixed to the stump, and to it is attached a narrow tube instead of the manometer; the free end of this tube is bent downwards into a graduated burette. If the reservoir is from the first filled with water, as much runs into the burette as flows out from the cut section, and the pressure therefore remains constant. This experiment shows that the flow of water varies from day to day, from one time of the day to another, and even from hour to hour; but the causes of these variations in the outflow, which must depend on the activity of the roots, are not yet known; it would even seem as if a periodicity were established independent of the temperature and of the moisture of the ground[1].

The measurement of the lowest pressure at which the outflow can take place at the cut surface can be effected by the apparatus figured in Fig. 438, where it is expressed by the difference of level of the mercury in the two arms of the tube, or by $q-q'$. This will however only afford a measurement of the pressure which the outflowing water may still have to overcome at the cut surface; but it has obviously had also to overcome other resistances of unknown magnitude in the interior of the root-stock. With respect to this point I was interested in ascertaining how great is the difference in the outflow if one of two equal root-stocks has no pressure to overcome at the cut surface, the other a considerable but constant pressure. If, in Fig. 440, *a* indicates the cut stem of a sunflower or similar plant grown in a pot, *c*, *d*, *e* the tube which is attached to it by the india-rubber tube *b*, and *f* a glass tube bent downwards, which (not as in the figure) reaches beyond the rim of the pot and terminates in a burette, while the opening of *f* lies exactly on the level of the cut surface of the stem; then, when the tube *c*, *d*, *e*, *f* has been filled with water, we have an apparatus for observing the outflow when the

[1] Very detailed observations on this point have just been made by Baranetzky in the Würzburg laboratory, in the summer of 1872.

pressure at the cut surface is at zero. A second root-stock from a plant of exactly the same age and vigour and grown in a pot of the same size is provided with the apparatus figured in Fig. 440, where the tube *f* through which the outflow takes place reaches the vessel *b* through the cork *g*. This vessel contains water above, mercury below. A tube *k* rises from the cork *i* to a certain height and is bent round at the free end *o* where it dips into a graduated tube. If the apparatus is so contrived that, for example, the opening for the outflow *o* stands about 15 cm. above the level *n*, then the column of mercury *o n* exercises a pressure of 15 cms. on the water *b*, and through it on the cut surface at *b*. When the water begins to flow out from the cut surface at *b*, the quantity of water in *b* will be increased, and an equal volume of mercury will flow out at *o*. The mercury collects in the burette, and its level enables

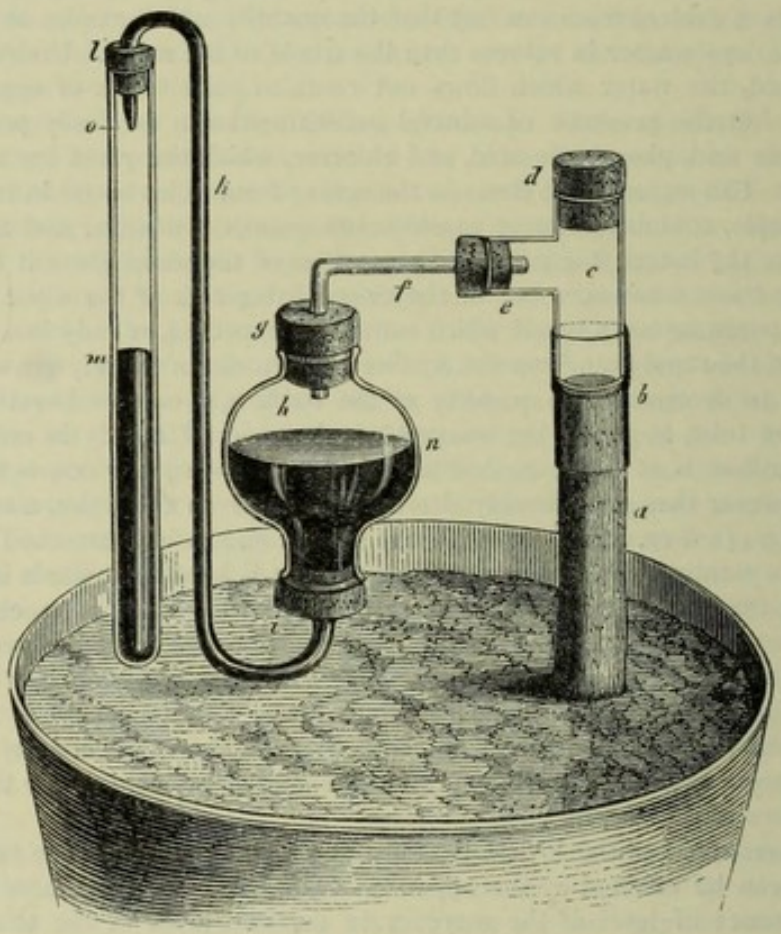

FIG. 440.—Apparatus for measuring the root-pressure when considerable and constant. The cork *i* has a lateral incision in order to allow of the escape of the air when the mercury is dropped in.

the quantity of water which has flowed from the cut surface to be read off from hour to hour, and to be compared in the other apparatus where there is no pressure. After a longer period of observation, the level *n* falls sensibly and the pressure *on* augments a little. But it is easy to bring it again to the original amount if a fresh quantity of mercury is poured in every twelve hours.

I observed in this manner in the summer of 1870 for five days two equally strong root-stocks of the sunflower[1]; and the result was that the difference of the outflow was but small, although the amount of pressure in one case was zero, in the other case 17 cm. of mercury. In the first thirty-three hours the outflow where there was no pressure at the cut surface amounted to 26·45 cubic cm.; when the pressure was 17 cm.

[1] I cannot here describe the whole series of minute observations.

of mercury it was 20·9 cubic cm. A sudden change in the pressure of the mercury of 1 or 2 cm. also caused no considerable alteration in the rapidity of the outflow.

It is necessary then to make some conjecture as to the cause of this powerful ascent of water in the wood of the root-stock; how it happens that the water sucked up at the surfaces of the roots not only passes into the cavities of the wood, but is pressed upwards with so great a force as to be able to overcome a considerable resistance at the cut surface; for it is obvious that the water which flows out above must have been sucked in below at the surfaces of the roots. This suction can only be induced by the endosmotic action of the parenchymatous cells of the cortex of the root. If we suppose that this endosmotic force is very considerable, these cells will swell greatly; and as much water will filter through the cell-walls to the cavities of the wood as is sucked up from without by endosmose. The parenchymatous cells which are gorged by endosmose drive into the vessels the water which presses into them in consequence of the endosmose, and with such force that in flowing out above from the vessels it is still able to overcome a considerable pressure. It follows from this explanation that the pressure which acts at the cut surface must, in accordance with the laws of hydrostatics, be exerted also against the inside of the vessels which receive the water from the turgid parenchymatous cells. But the water which enters them has also to overcome the resistance to filtration exercised by the cell-walls. The endosmose of the cortical cells of the root must overcome these resistances. Although we do not know the magnitude of the endosmotic force, yet we have ground for supposing that it is much greater than that given by Dutrochet's experiments on animal membranes; and this explanation would therefore be very probable. But a difficulty occurs in answering the question why the turgescent cortical cells of the root expel their water only inwards into the woody tissues and not also through their outer walls. We may however here be helped by the supposition that the molecular structure of the cells is different on their outer and inner sides, and that those facing the exterior of the root are best adapted to allow endosmose, while those facing the interior of the root are best adapted for permitting filtration under high endosmotic pressure. It must however be observed that this supposition is at present only a hypothesis for the purpose of explaining to a certain extent the processes which take place in the root. The exudation of drops of water from the upper cell of the Fungus *Pilobolus crystallinus*, from the root-hairs of a Marchantia grown in damp air, &c., shows moreover that cells distended by endosmotic tension can in fact exude water at certain spots. It is difficult to give any other explanation of the exudation of nectar in flowers; the excreting cells must evidently absorb the water or the sap with great force on one side, and then exude it on the other side. That in this case pressure from the root does not directly cooperate is shown by the fact that this exudation of nectar, which is often very copious, as in the flowers of *Fritillaria imperialis*, takes place even when cut flowers are simply placed in water. In this respect these exudations of fluid differ from the exudation of drops on the leaves of many plants, which only takes place when they are still in connection with the root, and which is clearly caused by the forcing power of the root (as in Aroideæ, &c.). It also happens however sometimes that drops of water are exuded from cut surfaces of the tissue, while another cut surface of the organ sucks up water. This I found, for instance, to be the case with pieces of the young stems of different Grasses, cut off from 6 to 10 cm. in length, which were placed with the lower end in damp soil; the free upper end then repeatedly and continuously exuded drops of water in darkness and in an atmosphere saturated with moisture. Here the parenchymatous cells of the lower cut surface clearly acted as the cortical cells of the root, sucked up by endosmotic action, and probably pressed the water thus sucked up into the vessels, from which it then escaped to the upper cut surface.

(*f*) *The combined action of transpiration, conduction, and absorption of water through the roots* takes place under ordinary and favourable conditions in such a manner that nearly as much water is absorbed through the roots and conducted upwards through the

wood as is transpired from the leaves. As long as this equilibrium lasts, the plant is turgid and tense in all its parts; and conversely it may be concluded from the unaltered turgidity and tenseness of the leaves and internodes, that the conduction of water is compensated by the evaporation from the leaves. Hence, under these conditions, the quantity of water evaporated may be taken as the measure of the suction of the root (or of a cut surface), and conversely the suction observed as the measure of the evaporation from the leaves. Since however the tissues can be more or less turgid without its being immediately perceptible, evaporation and suction are not usually exactly equal. But for most observations the small occasional difference may be neglected so long as no actually perceptible amount of flaccidity, *i. e.* of withering, caused by the collapse of the cells, takes place when the evaporation is stronger and the suction weaker; or so long as, in the opposite case, no exudation of drops of water results on the leaves of rooted plants. It is only when longer observations are made on growing plants that the comparatively small quantities of water have to be taken into account which are needed for the increase in size of growing organs.

Without going more minutely into the various cases which present themselves[1], it need only be pointed out in addition that withering is the consequence of the quantity of water evaporated being greater than that absorbed through the roots or through a cut surface of the stem. This only occurs in general when the amount of transpiration is very considerable, or when the ground is very dry, or when in cut shoots the power of the stem to conduct water has ceased. The exudation of drops of water already mentioned is, on the other hand, the consequence of a smaller quantity of water evaporating from the leaves than is absorbed by the roots and forced up into the upper organs. If a branch of a potato-plant, a leaf of an Aroid, a cut stem of maize, or the like, is fixed in the cork *k* in Fig. 439, and if, when the evaporation is weak a pressure of mercury of 10 or 12 cm. is allowed to act for some time, drops of water appear at the same spots on the apices or margins of the leaves, where they would appear in plants with roots in the evening or night or in damp weather. In the same manner the exudation of drops from plants with roots can be produced or increased by warming the ground and covering the leaves with a bell-glass in order to hinder evaporation[2].

The pressure due to the root which is so conspicuous in stems when cut across and when the amount of evaporation is very small, can scarcely be of any considerable use in promoting the current of water in the wood caused by strong transpiration. The fact already mentioned that strongly transpiring plants suck up water at the cut surface of their stems immediately after the upper part has been cut off, shows that the propelling force of the root does not act sufficiently quickly to protect even the vessels of the root-stock of strongly transpiring plants from complete exhaustion; that is, although the force which drives the water into the root-stock is great, as we have seen, it acts too slowly to be taken into account when the evaporation is rapid.

The same conclusion is reached if the quantity of water which exudes in the same time from the cut stem of a plant above the root is compared with that which is absorbed at the lower cut surface by the upper part of the same plant. The absorption of the upper part is always much more considerable in amount than the outflow from the root-stock, even when the withering of the upper part indicates that the capacity of its wood for conduction has diminished, and that it absorbs less than it would absorb in the normal condition. Thus, for example, the water absorbed by the cut leafy top of

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[1] See Rauwenhoff, Phytophysiologische Bijdraden in Versagen en Mededeelingen der kon. Akad. van Wetens, Afdeeling Natuurkunde, 2de Reeks, Deel III, 1868, where however the indispensable thermometric observations are wanting.

[2] The exudation of drops on the margins of the leaves of plants, the roots of which are surrounded by damp warm earth, their foliage rising into moist air, is an altogether different phenomenon, as I know from the experience of many years.

a tobacco-plant amounted in five days to 200 cubic cm., while the root-stock exuded only 15·7 cubic cm. In the same manner in *Cucurbita Pepo* (when much withered) the amount absorbed was 14 cubic cm., the exudation from the root-stock only 11·4 cubic cm. The withered upper part of a sunflower absorbed in a few days 95 cubic cm., while the root-stock exuded only 52·9 cubic cm. The result is also the same when the relative amounts which extend over a shorter time are compared.

It follows from these facts that, with the exception of times when the amount of transpiration is small or when drops of water exude from the leaves, no root-pressure at all exists when the plant is uninjured; and that this pressure is exerted only after evaporation and absorption have ceased or when they are very small. The exhaustion of the root-stock of a strongly transpiring plant (as after it has been cut off) proves rather that a plant with roots behaves in exactly the same way as a cut shoot. Just as the latter absorbs water from a receiver, so the wood of the root-stock which has lost water in consequence of evaporation above absorbs water from the cortical cells of the root which obtain it by endosmose. From all this it still remains in doubt whether in such cases the contents of the cortical cells of the root must not be left altogether out of consideration, since it is possible that the suction of the cell-walls merely, due to imbibition or surface-action, reaches as far as the surface of the roots.

(*g*) The parts of land-plants which are covered with a cuticle and which serve for transpiration appear to have no power of absorbing in any considerable quantity the water by which they are moistened, such as the rain and dew which is deposited on the leaves. As long as the tissues and leaves of uninjured plants with roots become turgid and are supplied with water from below, any considerable absorption through the surfaces of the leaves themselves, if they are already quite moist, is not to be expected, since it is not easy to see where the water can go in cells that are already gorged[1]. But even when a plant has withered, it is still doubtful whether its revival depends on the absorption of water by the leaves, since it is not impossible for an upward pressure to take place subsequently. Greatly withered shoots do not under such circumstances become turgid or do so only very slowly unless the cut surface is placed in water, and even in this case there is doubt as to the absorption of water through the surfaces of the leaves.

In harmony with this Duchartre found also[2] that rooting plants (Hortensia, *Helianthus annuus*), which wither in the evening in consequence of the dryness of the earth in the pot, did not recover or become turgid if copiously moistened by dew during a whole night, the pots in which the roots spread being provided with a closed cover. Epidendral Orchids, Tillandsias, &c., behave in the same way in this respect; they also absorb neither water nor aqueous vapour through their leaves, nor even in any considerable quantity through the roots. The water which they require for their transpiration and growth must be conveyed to them in the form of rain or dew which moistens the root-envelopes or wounded surfaces[3].

When land-plants wither on a hot day and revive again in the evening, this is the result of diminished transpiration with the decrease of heat and increase of the moisture in the air in the evening, the activity of the roots continuing—not of any absorption of aqueous vapour or dew through the leaves. Rain again revives withered plants not by penetrating the leaves, but by moistening them and thus hindering further transpiration, and conveying water to the roots, which they then conduct to the leaves.

A simple experiment will afford much instruction to the student in these matters. The pot in which a leafy plant is growing is enclosed in a glass or metal vessel provided

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[1] Duchartre has neglected this obvious reflection in his researches (Bulletin de la Soc Bot. de France, Feb. 24, 1860); in other respects also these experiments are very defective.

[2] Duchartre, *l. c.* 1857, pp. 940–946.

[3] Duchartre, Expériences sur la végétation des plantes epiphytes (Soc. Imp. et centrale d'horticulture, Jan. 1856, p. 67; and Comptes Rendus, 1868, vol. LXVII, p. 775).

above with a lid in two portions, and surrounding the stem so as completely to cover the earth in the pot. If the soil is dry the plant withers. If a bell-glass is placed over it the plant revives, and again withers if it is removed. This shows that the withering is the result of increased, the revival the result of diminished evaporation from the leaves when the roots convey but very little water to the plant. If cut shoots are allowed to wither and are then suspended in air nearly saturated with aqueous vapour, the leaves and younger internodes again revive, although the whole shoot continues to lose weight from evaporation. This phenomenon results from the water passing from the older parts of the stem to the younger withered parts, as must be concluded from Prillieux's experiments[1].

Sect. 3.—**Movements of Gases in Plants**[2]. All growing cells of a plant, or all that are otherwise in a condition of vital activity, are continually absorbing atmospheric oxygen and giving back in its place a nearly equal volume of carbon dioxide. The cells which contain chlorophyll have in addition the property, under the influence of sunlight, of absorbing carbon dioxide from without, exhaling at the same time a nearly equal volume of oxygen mixed with nitrogen. In proportion to the activity of the chemical processes which take place within the cells, the movements of gases occasioned by them vary greatly in rapidity. The formation of carbon dioxide at the expense of the atmospheric oxygen takes place continuously and in all the cells; but the quantities concerned are small in proportion to the large amount of carbon dioxide which is decomposed in the green tissues, and in exchange for which equal volumes of oxygen are exhaled. Some idea of the activity of this last-named process is obtained by reflecting that about one-half the (dry) weight of the plants consists of carbon which has been obtained by the decomposition of atmospheric carbon dioxide in tissues containing chlorophyll under the assistance of light.

Oxygen and nitrogen are permanent gases, as also is carbon dioxide within the limits of the temperature of vegetation, and indeed far below it. Aqueous vapour, on the contrary, is only produced from water within these limits, and under certain conditions even returns to the liquid state. In other respects aqueous vapour behaves just like oxygen and nitrogen in reference to the processes to be considered here.

When the gases with which we have to do are traversing closed cell-walls, expanding when diffusing themselves through the cell-sap, or permeating or escaping from the protoplasm, chlorophyll-grains, &c., their motion is a molecular one of diffusion. When they fill in their elastic condition the intercellular spaces, vessels, cells destitute of sap, or the large air-cavities among the tissues, it is a movement of the mass depending exclusively on expansive force. The movements of diffusion tend to bring about conditions of equilibrium which depend on the coëfficients of absorption of the gas by a particular cell-fluid, on the molecular condition of the cell-wall, &c., on temperature, and on the pressure of the air. But these conditions are continually varying; and the equilibrium which is aimed at is being still more

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[1] Prillieux, Comptes Rendus, 1870, vol. II, p. 80.

[2] Sachs, Handbuch der Experimental-Physiologie, p. 243. — Müller, Jahrb. für wiss. Bot. vol. VII, p. 145.

continually disturbed by chemical transpositions on which depend the metamorphosis of substances in the plant, assimilation, and growth; so that a state of rest can very seldom occur. The ordinary condition of the gases which are diffused through the cells of plants is that of movement.

But even the masses of gas found in the cavities of plants are not generally at rest. By the setting free or absorption of carbon dioxide or oxygen in the cells, the equilibrium is disturbed also in the neighbouring cavities; and changes in the pressure of the air or in temperature also exert an influence. The flexions again of the stem and leaf-stalk produced by the wind cause pressures and dilatations of the gases which fill the cavities, and these again give rise to currents of gas in the interior. The rapidity of the movement in the cavities varies greatly in proportion to their size; within the very narrow intercellular spaces of ordinary parenchyma the motion is slow and inconsiderable even under considerable pressure, as contrasted with the rapid currents which are possible in the large intercellular spaces of most foliage-leaves and similar organs, or in the wide air-canals of hollow stems, or in the lacunæ of the tissue of water-plants.

In attempting to collect the most common phenomena into a more definite arrangement from this general point of view, the following appear to be the more important points.

(*a*) *Unicellular plants*, as well as those which consist merely of strings or plates of cells such as occur in Algæ, Fungi, and Mosses, are in immediate contact with the air or with the surrounding water which contains gas in solution. The only essential condition here is that the gases shall be able to enter and escape from the cells by the movements of diffusion. If, for example, a cell of this kind containing chlorophyll is placed in sunlight, the carbon dioxide absorbed by it is decomposed; a fresh supply of the gas is therefore continually penetrating into it from without, because it is prevented from saturating the cell-sap; oxygen, on the contrary, is being constantly disengaged, the cell-sap receives more than it can contain, and gives off the excess by outward diffusion. Under these conditions therefore two molecular currents are set up in opposite directions which permeate the cell-wall, the protoplasm, and the cell-sap; and since carbonised products are formed in the cell at the expense of the decomposed carbon dioxide, this decomposition is the simultaneous cause of fresh quantities of the gas perpetually diffusing into the cell. The quicker the decomposition of the carbon dioxide, the more quickly it is replaced. The behaviour in the dark of cells containing chlorophyll is exactly the reverse, as is also always the case with cells destitute of chlorophyll; they absorb oxygen and produce carbon dioxide; only the process is much slower and less active. The cell acts as a centre of attraction for the gas which is decomposed in it, and as a centre of repulsion for the gas which is produced in it. This rule holds good also for the individual cells of a tissue, only that in this case the processes are more complicated, inasmuch as the diffusion currents of the gases do not take place between the cells and an unlimited external volume of gas, but between cells and cells on the one hand, between cells and internal air-cavities of limited size on the other hand.

(*b*) Among plants consisting of complicated aggregates of cells, submerged *Water-plants* are of peculiar interest, because their intercellular spaces do not open outwardly through numerous stomata, but communicate with large cavities which are formed in the interior of the tissues by the disjunction of cells or by their union with one another by the rupture of their walls. The underground stems of Equisetum and of many bog-plants show similar phenomena. Uninjured plants of this kind are closed and air-tight outwardly; the gases which collect in the cavities can originate only from the surrounding tissues, which absorb oxygen, nitrogen, and carbon dioxide by diffusion from the surrounding water. These gases cannot at once diffuse through the surrounding tissues,

but undergo change within them, and when once collected in the spaces, they are still further influenced by the chemical processes that go on in the surrounding tissues. A submerged water-plant, for example, which contains chlorophyll absorbs carbon dioxide from without under the influence of sunlight; and at least a portion of the disengaged oxygen collects in the cavities. When it becomes dark this process ceases; the collected oxygen is now absorbed by the fluids of the tissue and gradually transformed into carbon dioxide, which can again diffuse back into the cavities, but partially also through the layers of tissue into the surrounding water. This, as well as the different coëfficients of diffusion of the gases, causes the air contained in the cavities to have an altogether different composition from that in solution in the surrounding water, and this composition to be subject to continual change. But it is not only the chemical composition of the gas in the cavities that is altered in this way; the pressure is also subject to variation. When the oxygen which is liberated from the green tissues collects rapidly in the cavities under the influence of bright light, the gas is then subject to high pressure, and escapes with force, injuring the surrounding layers of tissue. The greater rapidity of diffusion of carbon dioxide, and its slower production in the tissue in darkness, do not, on the other hand, allow an increase of tension of the gas to arise easily in the cavities of the dark plant.

The nitrogen of the atmosphere takes a more subordinate and secondary part in all these processes. It is indeed never absent from the air contained in the cavities, but is generally present in large quantities in it, together with oxygen and carbon dioxide. It is not however subject to such rapid and considerable variations, being neither used up nor disengaged in the changes connected with the assimilation of food in the tissues.

(*c*) *Land-plants* differ from water-plants in their inner cavities, when present[1], communicating directly with the atmosphere through the stomata. The anatomical conditions show at once that these organs are only the channels of exit from the intercellular spaces which are in connection with one another through the whole plant; and we know from experiment that these are in their turn in complete connection here and there with the cavities of the vessels and with the wood-cells. The large air-cavities which are abundant even in land-plants (in hollow stems, leaves, fruits, &c.), the woody tubes (or vessels) and wood-cells, and the usually extremely narrow capillary intercellular spaces of the parenchyma, form therefore a system of cavities full of air and in communication with one another, which are all closed below at the root, but which open outwardly above in the leaves, internodes, &c., through numberless extremely narrow capillary openings.

What was said in paragraph *b* on the changes which take place in the air contained in the cavities of water-plants, applies in general also to that of land-plants; but the equalising of the difference in the pressure at the various parts of a large plant is facilitated by the occurrence of ducts, that of the difference between the internal and external air by the stomata. This equalisation however proceeds in general extremely slowly, because the stomata, in consequence of their small diameter, can allow only small volumes of gas to pass through them in a short time. Notwithstanding their uninterrupted connection, there may therefore be considerable differences of pressure and great variations in the composition of the internal and external gas, as in water-plants. It must also not be forgotten that those layers of tissue in which a rapid interchange of gas is proceeding are covered with an epidermis containing a greater number of stomata than those which require a less active interchange in consequence of slower growth and assimilation. In addition to this, organs with a thin cuticle are better adapted to bring about

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[1] Large Fungi and Algæ have indeed no stomata; but their internal air (among the hyphæ) is certainly in communication at least in places with the surrounding air by cavities among the superficial hyphæ. The stems of Mosses possess neither internal cavities nor stomata, while their sporecapsules possess both.

interchange of gas by diffusion than those whose epidermis is provided with a thicker cuticle which hinders the diffusion-current. This is clearly the reason why roots require no stomata, since, in consequence of their slow increase in size and their thin-walled slightly cuticularised epidermis, they can accomplish the interchange of oxygen and carbon dioxide by diffusion alone; while the leaves, in consequence of their thick cuticle, require a large number of stomata in order rapidly to interchange large volumes of carbon dioxide with as large volumes of oxygen in sunshine. Even flowers and rapidly growing parasites which contain no chlorophyll possess stomata, though in smaller numbers, because they absorb a quantity of oxygen and exhale carbon dioxide. When the epidermis is replaced in the older parts of stems and roots by cork-periderm, the parts are not only externally impervious to air (with the exception of occasional fissures) in the ordinary sense, but even the interchange of gas by external diffusion practically ceases. But this case occurs only in those parts of plants where the fibro-vascular bundles form air-conducting vessels and usually also air-conducting wood-cells, by means of which an interchange of gas is brought about internally with that contained in the parenchyma enveloped by the cork. This is especially the case with woody Dicotyledons and Conifers.

These considerations apply also to a great extent to aqueous vapour. The evaporation of the water of vegetation, resulting, as we have seen in the previous paragraph, in the production of currents in the plant, is almost entirely prevented by cork-periderm and bark, and at least very much hindered by cuticularised epidermal cells. Since the parts of plants exposed to the air are covered with one or other of these epidermal structures, evaporation can in general only take place to a subsidiary extent from their surface; the greater part of the aqueous vapour which these parts of the plant lose is evidently given off from the moist cell-walls in the interior of the tissue where they adjoin intercellular spaces and larger air-cavities. If these spaces are saturated with aqueous vapour, evaporation ceases; but if the external air is comparatively dry the vapour escapes through the stomata, and evaporation into the intercellular spaces recommences. If the transpiring tissue is heated, as by sunshine, the formation of vapour proceeds more rapidly in the interior, and the greater tension of the vapour causes its more rapid passage through the intercellular spaces and stomata.

Those surfaces of the organs of plants which are constantly in contact with water cannot exhale aqueous vapour through such fine openings as the stomata under existing conditions of temperature; stomata are therefore wanting in submerged plants, or occur only occasionally. The leaves, for instance, of water-lilies, which float on the water, are especially instructive in this respect; on the side in contact with the water they have no or very few stomata, on the upper side exposed to the air a large number. This is the more striking since leaves entirely exposed to the air have generally a larger number of stomata on the under than on the upper side, where they are sometimes entirely wanting.

CHAPTER II.

CHEMICAL PROCESSES IN THE PLANT.

SECT. 4.—**The Elementary Constituents of the Food of Plants**[1]. If we dry at a temperature of 100° or 110° C. any fresh vegetable structure so as to expel all the water which it contains, a friable residue will be left which no longer loses weight. In ripe seeds this usually amounts to about $\frac{8}{9}$ of the weight; in seedlings after the supply of reserve-material has been consumed, to generally less than $\frac{1}{10}$, increasing in subsequent stages of vegetation to $\frac{1}{5}$ or $\frac{1}{3}$; in submerged water-plants and Fungi it often amounts to less than $\frac{1}{10}$, and sometimes even to only $\frac{1}{20}$. These proportions, which are only roughly estimated, vary within wide limits according to the nature and age of the plant and of the particular organ.

If the dried residue of the plant is further exposed to a red heat in the presence of oxygen, by far the greater part of it is consumed and disappears in the form of products of combustion, chiefly carbon dioxide and aqueous vapour. The residue which now remains behind, usually a fine white powder, is the *Ash*, comprising generally only a small percentage of the dried substance, a proportion which is again subject to great variations with the specific nature of the plant and the kind and age of the particular organ.

Chemical analysis of the combustible part of the dried substance shows that it consists in all plants of Carbon, Hydrogen, Oxygen, Nitrogen, and Sulphur; the latter remains behind after combustion in the form of sulphuric acid in combination with the bases of the ash.

In the ash are invariably found in addition Potassium, Calcium, Magnesium, Iron, and Phosphorus, and generally Sodium (Lithium?), Manganese, Silicon, and Chlorine; in marine plants also Iodine and Bromine. With these constituents there are sometimes associated, in rare cases and under special circumstances, very small quantities of Aluminium, Copper, Zinc, Cobalt, Nickel, Strontium, and Barium. The presence of very small quantities of Fluorine in plants is also

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[1] For a preliminary acquaintance with the very copious literature, my Handbuch der Experimental-Physiologie (Sects. 5 and 6) will be sufficient. A study of Th. de Saussure's Recherches chimique sur la végétation, Paris 1804, is also indispensable to any one who wishes to form an independent judgment for himself. A detailed description of the theory of nutrition is contained in, among other works, Meyer's Lehrbuch der Agriculturchemie 1870, 71. A variety of fundamental researches will also be found in Boussingault's Agronomie et Physiologie végétale. E. Wolff's Aschenanalyse für landwirthschaftliche Prod. &c., Berlin 1871, is also very valuable; as well as his Vegetationsversuche in wässerigen Lösungen ihrer Nährstoffe (Hohenheimer Jubiläuumsschrift 1862).

inferred from the presence of calcium fluoride in the bones of animals which obtain the whole of their food directly or indirectly from plants.

It is self-evident that we have only to consider as elementary food-substances those which are indispensably necessary for the process of nutrition; while those the existence of which in the plant is proved by analysis, but which may also be absent without their nutritive power being impaired, may be considered as accidental admixtures.

Of the first importance however among the indispensable food-materials are the elements of the combustible substance which are present in all plants without exception, viz. Carbon, Hydrogen, Oxygen, Nitrogen, and Sulphur; because they are included in the chemical formula of cellulose and of the albuminoids which constitute protoplasm, and because therefore without these substances the plant-cell itself could not exist. It may be inferred also from the invariable presence of Potassium, Calcium, Magnesium, Iron, and Phosphorus in plants, that they are indispensable constituents of their food, and still more from the fact established by experiments on vegetation, that the nutrition and growth of all plants hitherto examined for this purpose is impossible or abnormal if any one of these elements is wanting. In the case of Sodium, Manganese, and Silicon this has not yet been proved; it would appear rather that they may be dispensed with in the chemical process of nutrition. That Chlorine is necessary for the perfect nutrition of *Polygonum Fagopyrum* has been shown by Nobbe[1]. Whether Iodine and Bromine play the part of true food-materials in the marine plants in which they are found has not yet been ascertained; and these two elements may, from the mode of their occurrence, be for the present neglected as unimportant in this respect.

In the more general considerations as to the nutrition of plants we have therefore chiefly to do with the following elements:—

Carbon, Hydrogen, Oxygen, Nitrogen, Sulphur;
Potassium, Calcium, Magnesium, Iron;
Phosphorus, Chlorine;

to which are to be added, under certain circumstances, Sodium and Silicon.

The physiological importance of these elementary substances is however very different. Those placed in the first line compose, as already mentioned, the greater part of the substance of the plant; they mainly form the organised and organisable part of the plant and of every individual cell; their importance therefore lies in the fact that they furnish the chief materials for the construction of the plant. The constituents of the ash, on the other hand, are of less importance in this respect, if only in consequence of their much smaller quantity; they appear to promote chemical decompositions and combinations in plants, in consequence of which the far more abundant combustible principles are constructed out of the first-named five elements.

Carbon is a necessary constituent of every organic compound in varying proportion; usually about one-half the weight of the entire dried substance of the plant consists of this element. If the large quantity of vegetable matter which is annually produced

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[1] Landwirthschaftliche Versuchsstationen, vol. VII, 1865.

is taken into account, the fact becomes the more remarkable that this enormous quantity of carbon is derived from the carbon dioxide of the atmosphere of which it forms on the average only about 0·04 per cent. It is only the cells which contain chlorophyll—and only under the influence of sunlight—that have the power of decomposing the carbon dioxide taken up by them, and at the same time of setting free an equal volume of oxygen, in order to produce organic compounds out of the elements of carbon dioxide and water, or in other words to assimilate. It is very probable that under these circumstances carbon dioxide loses only one-half its oxygen, while the other half of the oxygen which is exhaled is derived from the decomposition of water.

The fact is unquestionable—partly established by direct researches on vegetation, partly inferred from the circumstances under which many plants live in a natural condition—that most plants which contain chlorophyll (*e.g.* our cereal crops, beans, tobacco, sunflower, many saxicolous Lichens, Algæ, and other water plants) obtain the entire quantity of their carbon by the decomposition of atmospheric carbon dioxide, and require for their nutrition no other compound of carbon from without. But there are also plants which possess no chlorophyll and in which therefore the means of decomposing carbon dioxide is wanting; these must absorb the carbon necessary for their constitution in the form of other compounds. But since plants destitute of chlorophyll are either parasites or saprophytes, they absorb their carbon in the form of organic compounds which have been produced by other plants that contain chlorophyll with decomposition of carbon dioxide. Parasites draw these products of assimilation directly from their hosts, while saprophytes (as *Neottia Nidus-avis*, *Epipogium Gmelini*, *Corallorhiza innata*, Monotropa, many Fungi, &c.), make use for the same purpose of the materials of other plants which are already in a state of decomposition. Even the food of Fungi which are parasitic in and on animals is derived from the products of assimilation of plants containing chlorophyll, inasmuch as the whole animal kingdom is dependent on them for its nutrition. The compound of carbon originally present on the earth is the dioxide, and the only abundantly active cause of its decomposition and of the combination of carbon with the elements of water is the cell containing chlorophyll. Hence all compounds of carbon of this kind, whether found in animals or in plants or in the products of their decomposition, are derived indirectly from the organs of plants which contain chlorophyll.

Hydrogen is present, equally with carbon, in every organic compound; in consequence however of the smallness of its combining equivalent, it falls far below it as a percentage constituent of the weight of the dried substance of plants. As has already been mentioned, the hydrogen of the plant is probably derived from the decomposition of water in cells containing chlorophyll in the presence of sunlight. It enters into combination with the carbon oxide (CO) simultaneously presented to it by the reduction of the carbon dioxide[1]. Only a very small

[1] [The abstract of Adolph Baeyer's paper on the Chemistry of Vegetable Life in Journ. Chem. Soc. 1871, pp. 331–341, should be consulted. It is shown to be probable that chlorophyll fixes carbon oxide just as hæmoglobin does. When sunlight falls upon chlorophyll which is surrounded by carbon dioxide, that compound seems to suffer the same dissociation as at high temperatures,

portion of the hydrogen contained in nitrogenous vegetable substances can be carried into the plant in the form of ammonia.

Oxygen is always present in organic compounds in smaller quantities than would be sufficient to oxidise the hydrogen and carbon present in them into water and carbon dioxide, because organic compounds are produced from carbon dioxide and water with the elimination of a part of their oxygen. The proportion of oxygen in vegetable substances is moreover very variable; and some even contain none at all of this element. But the total quantity of oxygen forms, next to carbon, the largest proportion of the weight of the dried substance. Oxygen is introduced into the plant in the form of water, carbon dioxide, and oxygen salts in larger quantities than any other element; while extraordinarily large quantities of oxygen are set free into the air by the process of assimilation in the green organs. All the other organs of the plant also absorb atmospheric oxygen, and thus slowly reproduce carbon dioxide and water at the expense of the assimilated substances. Together with the process of deoxidation which is very active in the cells containing chlorophyll, another process of oxidation is proceeding comparable to that of the respiration of animals, but not generally very active, by which a part of the assimilated substance is again decomposed.

Nitrogen, an essential constituent of the albuminoids which form protoplasm, of vegetable alkaloids, and of asparagine, always forms only a small fraction of the weight of the dried substance of plants, — often less than 1, seldom more than 3 p. c. The nitrogen contained in the chemical compounds just mentioned is obtained from compounds of ammonia and nitric acid; parasites and saprophytes perhaps also absorb organic nitrogen-compounds from without. It is on the other hand certain from a great number of experiments on vegetation, especially those of Boussingault, that plants have no power of using the free nitrogen of the atmosphere for the production of their nitrogenous compounds[1]. If plants are artificially supplied with all other food-materials, but it is rendered impossible for them to absorb ammonia or compounds of nitric acid as their source of nitrogen, no increase takes place of the albuminoids or of the nitrogenous substances generally, although the nitrogen of the atmosphere is at the command of the plant in so great quantities, filling up the intercellular spaces and diffusing through the fluids of the tissue[2].

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oxygen is liberated and carbon oxide remains combined with the chlorophyll. The simplest reduction of carbon oxide is to formic aldehyde; it need only take up hydrogen, $CO + H_2 = COH_2$, and under the influence of the cell-contents, just as by the action of alkalies (which Butlerow has shown to be the case), the aldehyde is transformed into sugar.—Ed.]

[1] [The important researches of Lawes, Gilbert, and Pugh on the sources of the nitrogen of vegetation (Phil. Trans. 1861, pt. 2, and Journ. Chem. Soc. 1863. p. 100) should be carefully studied on this point.—Ed.]

[2] [Adolf Mayer of Wiesbaden has recently carried out a number of experiments to determine whether the aërial parts of plants have the power of absorbing ammonia or not. Preventing access of ammonia through the roots, he subjected the leaves to the influence of ammonium carbonate both in the gaseous and dissolved state, and found that it was absorbed in appreciable quantities, although the plants did not appear to thrive when access of ammonia through the roots was entirely prevented. Similar results have also been obtained by T. Schlœsing (see Comptes Rendus, vol LXXVIII, p. 1700).—Ed.]

Sulphur, a constituent of albuminoids, of allyl, and of the essential oil of mustard, is taken up in the form of soluble salts of sulphuric acid, and chiefly (or perhaps always) of calcium sulphate. This salt is probably, as Holzner first pointed out[1], decomposed by the oxalic acid which is formed in the plant itself, and the insoluble calcium oxalate is thus formed, while the sulphuric acid parts with its sulphur to the organic compounds which have been mentioned.

Iron[2] (often accompanied by very variable quantities of Manganese) is indispensable for the production of the green colouring substance of chlorophyll, as is shown by experiments on vegetation; and since the green organs which contain chlorophyll assimilate organic substances out of water and carbon dioxide, the importance of this element for the life of the plant is very evident, although extraordinarily small quantities of it are sufficient for this purpose. It may be taken up by the plant in the form of the chloride or sulphate or of some other compound. If larger quantities of solutions of iron become distributed through the tissues, the cells quickly die. Although small quantities of iron are essential for producing the green colour of chlorophyll, it is nevertheless uncertain whether the green colouring substance itself contains iron as an integral constituent of its chemical formula.

Potassium is as essential for the assimilating activity of chlorophyll as iron for its production. Nobbe[3] has recently shown that if food-materials otherwise complete but possessing no potassium are supplied to plants (as buckwheat), they behave as if they were absorbing only pure water instead of the solution of food-material. They do not assimilate and show no increase in weight, because no starch can be formed in the grains of chlorophyll without the assistance of potassium. The chloride is the most efficacious form in which potassium can be offered to buckwheat; the nitrate comes next to it. If the potassium is offered only in the form of sulphate or phosphate, a very evident want of health is apparent sooner or later, which results from the starch which is formed in the grains of chlorophyll not passing into the growing organs and thus becoming available for purposes of vegetation. Sodium and Lithium cannot replace potassium physiologically, because the former is simply useless to the plant, while the presence of the latter in the cell-sap is injurious to the tissues.

Phosphorus, *Chlorine*, *Sodium*, *Calcium*, and *Magnesium*, have, as far as is yet known, no definite relation to special physiological purposes. The constant occurrence however of compounds of phosphoric acid in company with albuminoids, as well as of potassium salts in organs containing starch and sugar, points towards definite relations which they may possess to those chemical processes that immediately precede the processes of construction in plants. A large part of the calcium taken up by plants is, as has been mentioned, precipitated by oxalic acid, and

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[1] Holzner, Ueber die Bedeutung des oxalsauren Kalkes, Flora 1867.—Hilgers, Jahrb. für wiss. Bot. vol. VI, p. 1.

[2] For special proof of the importance of iron see my Handbuch der Experimental-Physiologie, p. 142.

[3] Nobbe, Schröder, and Erdmann, Ueber die Organische Leistung des Kaliums in der Pflanze; Chemnitz, 1871.

remains inactive. The importance of calcium must therefore be sought partly in its serving as a vehicle for sulphuric and phosphoric acid in the absorption of food-material, and partly in its fixing the oxalic acid which is even poisonous to the plant, and rendering it harmless. The elements just named are taken up by the plant when they are offered to it in the form of phosphates, sulphates, nitrates, or chlorides.

Silicon finally is taken up by a very large number of plants in the form of a very dilute aqueous solution of silicic acid; by some in larger quantities than all the other constituents of the ash. By far the larger part of the silicic acid passes into the insoluble state within the cell-walls, and remains behind after the destruction of its organic substance together with calcium (magnesium and potassium?) as a skeleton possessing the structure of the cell-wall. In land-plants it accumulates chiefly, though not exclusively, in the tissues exposed to evaporation, and especially in the cuticularised walls of the epidermis. In Diatoms, the cell-wall of which is very strongly silicified, this arrangement of course does not exist. Since it is possible to cause, by artificial feeding, plants which usually contain abundance of silica (like maize) to grow almost entirely without it, and without any obvious departure from their normal structure, silicic acid appears to be of very subordinate importance for the chemical and organic processes; and its deposition in the cell-walls does not take place to any great extent until they are already fully developed.

The combinations of food-material must be subject within the tissues to progressive changes of position in addition to and in consequence of their chemical transformations. The equilibrium of diffusion is disturbed by the decomposition of a salt; immediately round the spot where this takes place the fluid of the tissue contains fewer molecules of the compound; and the more distant molecules of the same salt in a state of solution move therefore towards the spot where they are wanted. Every cell therefore which decomposes any particular salt acts as a centre of attraction upon the fluids of the tissue surrounding it, and the salt in question is drawn towards this centre. But this process is the same in the case of every other salt dissolved in the same fluid. If, for example, calcium sulphate is decomposed in a cell and crystals of calcium oxalate formed, this itself supplies a cause for the more distant molecules of sulphate to be drawn towards that cell; but it affords no reason for the molecules of potassium nitrate which are also present to move in the same direction. Every substance dissolved in the cell-sap is set in motion only in so far as the equilibrium of diffusion and the uniform distribution of its own molecules is disturbed. It follows therefore clearly that there can be in general no such thing as a continuous uniform motion of a so-called 'nutritive sap.' It is only when a number of compounds which supply food-material are taken up at one spot such as the root, and are transplanted to another spot as the buds and green leaves, that the direction of movement is nearly the same for all; but even in this case the rapidity with which the molecules of each particular salt move will vary, because this depends on the rapidity of consumption at the point towards which the movement is directed, and on the special rate of diffusion of each compound. Only when the force of the pressure drives the whole of the cell-sap to one side is the motion uniform for different substances, provided that the fluid moves in open channels such as the laticiferous vessels or sieve-tubes; but if the pressure causes filtration through closed cell-walls, then in this case also the molecules of different salts are urged forward with a different rate, because the rapidity of filtration of different solutions varies with their composition and degree of concentration.

The same principles hold good also for the absorption of combinations of food-material from without into the absorbing organ. It has already been shown in the previous paragraph how the decompositon of carbon dioxide in the light in a cell containing chlorophyll induces new quantities of the dioxide at once to enter this cell, whether the gas be at the time dissolved in water or present in the atmosphere. If no carbon dioxide were decomposed in the cell, its contents would become saturated with the gas in proportion to the pressure and the temperature, and every cause for further motion would be removed. But the decomposition is constantly providing more space for the entrance of fresh molecules of carbon dioxide; and this gas, although present in such small quantities in the atmosphere, collects here and supplies the material for the production of compact masses of carbon-compounds.

A water-plant acts in the same manner on the salts dissolved in the surrounding water. The external water and the internal cell-sap are in continuous connection through the fluid imbibed in the cell-walls. If the chemical processes within the plant are supposed to be at rest, an equilibrium of diffusion will tend to become established between the external and internal fluid according to the prevailing conditions. But the chemical processes in the interior are continually disturbing this equilibrium, the molecules of the salt in question continually streaming from without to the places in the interior where they are to be used. If the molecules of calcium phosphate are even very sparingly distributed through the surrounding water, a dense accumulation will gradually arise in the plant, not of calcium phosphate, but of some other compounds of phosphoric acid and of calcium, because the molecular equilibrium is being continually disturbed by the separation of the phosphoric acid from the calcium, that is, by the chemical process. If the calcium phosphate remained as such within the plant, the movement would cease so soon as the equilibrium of diffusion was established. It will be at once clear from a consideration of these facts that the accumulation of certain substances in the interior of plants depends in the first place on whether the compound of them which is present in the surrounding water is decomposed in the plant; that moreover the constituents of the different compounds must accumulate in the plant in different quantities according to the extent to which they are needed; and that finally the quantitative composition of the substances in question within the plant usually bears no resemblance to that of the surrounding water. Substances which are present in the water in the form of extremely dilute solutions occur in the plant in great quantities; while others which are abundant in the water are much less so in the plant. Thus, for instance, marine plants take up a much larger quantity of potassium and a smaller quantity of sodium than corresponds to the composition of sea-water; species of Fucus again collect considerable quantities of iodine which is present in sea-water only in extremely small quantities. Since moreover different plants decompose the same compounds with different degrees of rapidity, it is obvious that different plants which draw their food-materials from the same water must exhibit an entirely different composition of their ash.

The processes are more complicated when a land-plant has to take up the saline compounds of its food-material from the soil which contains but little water. By far the greater number of land-plants thrive in soil which usually contains a quantity of water much below its full capacity of absorption, its pores being almost entirely filled with air. The small quantity of water present adheres completely to the minute particles of soil, and for this reason does not flow away; and this adherent water often covers the surface of the particles of earth in the form of a fine stratum. The roots can only absorb this water when they are in the closest contact with the particles of soil; hence plants freshly planted wither even in moderately moist ground until a sufficiently large number of particles of earth become attached by means of new root-hairs to the newly formed rootlets. At these points of intimate connection between the root-hairs and the soil the adhering water of the latter is directly continuous with

the cell-sap of the root by means of the water imbibed by the cell-walls of the root-hairs. In this manner it is possible for the root to suck up the water of the soil; as this water enters the points of contact, the equilibrium of the strata of water that cover contiguous particles of earth is disturbed, and the water of the soil retained by capillary attraction is set in motion towards the points of contact. This process spreads centrifugally from every root, and thus gradually makes the most distant parts of the soil subserve the nutrition of the plant. If salts, such as calcium sulphate, are present in solution in the enveloping strata of water, these salts follow the movements of the water, and finally enter at the points of contact with the root-hairs.

But a large portion of the food-material, especially compounds of ammonia, potassium, and phosphoric acid, occur in the ground in a fixed condition, or, as it is generally termed, absorbed; they are not extracted from the soil even by very large quantities of water; the roots nevertheless take them up out of it with ease. It may be supposed in these cases that the absorbed food-materials occur as an extremely fine coating over the particles of soil, and can therefore only be taken up together with them by the root-hairs at the points of contact; and they are there rendered soluble by the carbon dioxide exhaled by the roots. This action of the root is limited to the points of contact; only those absorbed particles of substance which come directly into contact with the root-hairs are dissolved and sucked up. But since the number and length of the roots is very considerable in all growing land-plants, and since also they are continually lengthening and forming new root-hairs, the root-system comes gradually into contact with innumerable particles of earth, and can thus take up the necessary quantity of the substance in question. This power of the roots of taking up, by means of the acid sap which permeates the walls of even their superficial cells, substances which are insoluble in pure water, presents itself in an extremely evident manner, as I was the first to show, when polished plates of marble, dolomite, or osteolite (calcium phosphate) are covered with sand to the depth of a few inches, and seeds are then sown in the sand. The roots which strike downwards soon meet the polished surface of the mineral and grow upon and in close contact with it. After a few days an impression of the root-system is found corroded in rough lines into the smooth surface; every root has dissolved at the points of contact a small portion of the mineral by means of the acid water which permeates its outer cell-walls.

In taking up both the soluble constituents of the soil as well as those insoluble in pure water, the absorption is therefore first of all accomplished by the plant itself; and it is at the point where solution takes place at the surface of the root that absorption inwards is also effected by endosmose. But in spite of this complication the same principles hold good for the absorption of material from the soil as have been explained in the case of absorption from a solution. Here also it is the consumption, the decomposition of the compounds in the plant, that regulates the absorption of the material. The quantitative composition of the ash has therefore no resemblance to that of the soil; and the ash of plants of different kinds growing side by side and deriving their nutriment from the same soil may be altogether different[1]. But the composition of the soil is important to the plant in a secondary degree; since plants of the same kind, if they grow for example on a soil rich in lime, will take up a greater quantity of lime than if the soil contained but little of it. This is obviously not in contra-

[1] [Messrs. Lawes and Gilbert's long series of experiments on this subject are of especial value. (See Journ. Roy. Agric. Soc. vol. VIII, p. 496 *et seq.*, 1847; Journ. Chem. Soc. vol. X, p. 1, 1857; Report Brit. Assoc. 1861 and 1867.) Their latest publication, 'Report of Experiments on the growth of Barley for twenty years in succession on the same land' (Journ. Roy. Agric. Soc. second series, vol. IX) contains much information as to the power possessed by plants of extracting different substances from the soil.—Ed.]

diction to the principle laid down, but only shows that the decomposition of a salt in the plant will take place more largely the more easily it is enabled to take it up.

Sect. 5.—**Assimilation and Metastasis** (Stoffwechsel)[1]. The food-materials absorbed by the plant are, with a few exceptions, compounds of oxygen containing the highest possible proportion of that element. The assimilated substances, on the contrary, which form the greater part of the dried substance contain but little oxygen, some even none at all. It follows from this that assimilation must be a process of deoxidation. The transformation of food-materials containing a large proportion into the substance of plants containing but little oxygen must necessarily be accompanied by elimination of that element; and since we already know that this takes place only in cells containing chlorophyll and under the influence of sunlight, we have at once the locality, the conditions, and the time of the assimilation thus determined. No organs which are destitute of chlorophyll can assimilate; and in the dark or when the amount of light is small, even those assimilating organs which contain chlorophyll lose the power of producing organic substances out of water and carbon dioxide with the assistance of other food-materials,—a process to which we shall henceforward exclusively apply the term *Assimilation*.

The products of assimilation of the cells containing chlorophyll may undergo various kinds of chemical metamorphosis either in these cells themselves or after passing into other organs; and the aggregate of these processes may be distinguished from assimilation as *Metastasis*. It is important to bear clearly in mind the difference between these two processes, both in respect to their external conditions and to their results, the following being the chief points:—(1) Assimilation takes place only in those organs that contain chlorophyll; metastasis in all alike. (2) Assimilation occurs only under the influence of light; metastasis equally well in the dark. (3) Assimilation is necessarily accompanied by the elimination of a large quantity of oxygen; metastasis is usually connected with the absorption of small quantities of oxygen and the exhalation of small quantities of carbon dioxide. (4) Assimilation increases the dry weight of a plant; metastasis only alters the nature of the assimilated materials, and these usually suffer a diminution of their mass, the destruction of a part of the assimilated organic compounds being necessarily associated with the inhalation of oxygen and exhalation of carbon dioxide necessary for metastasis. (5) The increase in weight of a plant which contains chlorophyll depends on the accession of assimilated substance in the organs that contain the chlorophyll being greater during the time that they are exposed to light than the loss in the dry weight connected with the exhalation of carbon dioxide during metastasis in all the organs and at all times of vegetation. (6) Organs containing chlorophyll and plants entirely destitute of it (parasites and saprophytes) do not assimilate but absorb substances already assimilated; no process takes place in them except metastasis; and since this is associated with

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[1] See Sachs, Handbuch der Experimental-Physiologie, the section on the Transformation of Food-material.

inhalation of oxygen and exhalation of carbon dioxide, they decrease the entire store of assimilated substances.

Growth, *i.e.* the formation and multiplication of cells, always takes place at the expense of substances already assimilated; and these therefore must be subject to continual chemical change.

Growth is only possible as a result of assimilation; but the two processes do not usually concur either in time or locality. The assimilated substances may remain in the plant for a longer or shorter time without becoming employed in the growth of cell-walls or in the production of protoplasmic substances (protoplasm or grains of chlorophyll); and in this case they are termed *Reserve-materials*. Every cell, tissue, or organ in which assimilated substances are stored up for subsequent use is called a *Reservoir of Reserve-material*. The assimilating cell may itself serve as a reservoir for reserve-material (as unicellular Algæ or the leaves of evergreen plants); but usually a physiological division of labour is effected in the plant of such a nature as to transfer the products of assimilation from the organs that contain chlorophyll to other organs or masses of tissue which serve as reservoirs of the reserve-material and give it up to the parts destined for the formation of new organs (buds, the rudiments of the roots, or cambium). In Mosses, Vascular Cryptogams, and woody Phanerogams, the tissue of the stem is usually also the reservoir for this purpose; in perennial herbs and shrubs it is more often the persistent bulbs, tubers, and rhizomes that perform this function. The spores of Cryptogams which have the power of germination always contain a small quantity of reserve-material, at the expense of which the first processes of germination take place; in Rhizocarpeæ and Lycopodiaceæ the whole of the prothallium and embryo is produced in this manner. The seeds of Phanerogams remove a much greater quantity from the mother-plant, which accumulates either in the endosperm or in the cotyledons; the greater the quantity of this reserve-material the more numerous and the larger are the stems, roots, and leaves which the seedling can produce before it begins to assimilate. The minute seedlings, for instance, of Nicotiana and Campanula may be contrasted with the strong ones of the bean, almond, oak, &c. Since no assimilation takes place in the dark, it is only necessary to allow seeds, tubers, bulbs, rhizomes, &c., to germinate and develope in the dark in order to form an idea of the number and size of the organs which can be formed from the reserve-material.

The organs of assimilation which contain chlorophyll stand at a distance from the reservoirs of reserve-material and from the growing buds and roots; the products of assimilation must therefore be conveyed to the localities where they are required and where they are temporarily deposited. Growth and the deposition of reserve-material are therefore necessarily associated with corresponding movements of the products of assimilation and of those undergoing metastasis.

All these facts may be proved without any more accurate knowledge of the substances themselves which are produced by assimilation in the cells that contain chlorophyll and which undergo metastasis. But before entering on this question, we may first of all discuss the other:—whether all the products of metastasis are immediately applicable to the building up of new organs; and if not,

what substances furnish the material for the production of cell-walls, protoplasm, and grains of chlorophyll. Among the extraordinarily large number of the products of metastasis which are proved by chemical analysis to exist in various plants, there are a comparatively small number of substances the behaviour of which in the growth of the organs and whose universal distribution through the vegetable kingdom clearly show that they furnish the material for the growth of cell-walls and of other organised structures. These substances may be termed, without reference to their chemical nature, *Formative Materials*. Starch, the different kinds of sugar, inuline, and the fats must be considered the formative materials of the cell-wall; the albuminoids the formative materials of protoplasm and of the grains of chlorophyll.

Among the remaining products of metastasis are some which stand in genetic relation to the production of sugar; the glucosides, to which also belong certain tannin-substances. Asparagin is formed at the expense of the albuminoids contained in the reservoirs of reserve-materials, and is afterwards again consumed in the formation of albuminoids in the young organs.

All those organic compounds may be termed *Degradation-Products* which are produced by subsequent change in the substance of the organised structures of plants, and which have no further use in the building up of new cell-walls or protoplasmic structures. Thus bassorin is a degradation-product of cell-walls, as also is the mucilage of quince and linseed; the substances which cause lignification, suberisation, or cuticularisation are also probably the result of a partial degradation of the cellulose of the cell-walls. A residue of the protoplasm of older parenchymatous cells often remains until they entirely die away, and may also be considered a degradation-product. In the same manner a small residue of the chlorophyll-grains of leaves which die in the autumn remains over in the form of minute yellow granules which have no further use. The red and yellow granules also which cause the colour of ripe fruits and of the antheridia of Characeæ and Mosses, result from the degradation of chlorophyll-grains, and have no further physiologico-chemical use.

Those substances may be termed *Secondary Products of Metastasis* which are formed during this change, but have no further use in the building up of new cells, remaining inactive at the place where they are produced. Thus in the germination of many seeds (the date, Ricinus, Phaseolus, Faba, &c.) tannin-like compounds are formed in particular cells, and in many cases red colouring substances which, without undergoing any perceptible change, remain in these cells, while the rest of the substances of the seedling go through the most various chemical transformations and changes of place in the course of its growth. The same is the function of the essential oils in the glands of leaves, of caoutchouc in the laticiferous vessels, of resin and resin-forming substances in the resin-passages, and of the gummy compounds contained in the gum-passages of many plants. In this category may also be included the greater number of vegetable acids and many alkaloids. No interpretation has yet been given of the function of these substances in the internal economy of the plant; in the case of calcium oxalate Holzner's theory has already been mentioned that it is formed as a secondary product when the sulphuric acid combined with the calcium is replaced by oxalic acid; and that the

free sulphuric acid then undergoes various further decompositions, while the base of the salt remains unused and inactive in combination with the oxalic acid produced as a secondary product, or as calcium oxalate in the crystalline form. Among colouring substances no relation to the chemical processes which proceed in the plant has been traced except in the case of the green colouring substance of chlorophyll; it is only in the presence of this substance that elimination of oxygen, and therefore assimilation, can take place. In the case of a long series of other substances, many colouring matters, acids, alkaloids, wax, tannin, pectinaceous substances, &c., no relation to the other processes of metastasis is known, nor any physiological signification which they possess in the life of the plant.

In some cases substances which have ceased to take part in the processes of growth and of metastasis are nevertheless important or even indispensable for other purposes of vegetation. Of this class are the saccharine juices secreted by nectaries, which are of service to the plant only so far as they attract insects which thus bring about the conveyance of the pollen to the stigma. For a similar purpose a portion of the tissue of the anthers of Orchids is transformed into a viscid glutinous substance by which the pollinia become attached to the proboscis of insects. Thus again the sapid and nutritious substances which constitute the pericarps of some fruits are of no direct use for the growth of the seeds, but cause their dissemination by animals which feed on the fruits and thus disperse the seeds.

We must now again turn, after this preliminary explanation of the various parts played by the products of metastasis in the life of the plant, to the most important group of organic compounds, those which have been distinguished above as formative materials.

The determination whether any chemical compound belongs to the class of formative materials of the cell-wall and protoplasmic substances, depends on its behaviour during growth, on its chemical composition, on its appearance and disappearance in growing cells and tissues, and on its chemical relations to other substances, especially to cellulose and to protoplasmic substances. Spores, seeds, bulbs, tubers, rhizomes, the persistent parts of woody plants, and other reservoirs of reserve-material, always contain chemical compounds belonging to two different groups. On the one hand nitrogenous substances are always present in the form of albuminoids (often several different ones as in the grains of cereals) which scarcely differ chemically from protoplasm, and when contained in the succulent reservoirs of reserve-materials preserve even the form of protoplasm. From this coincidence, and still more when the movements of these substances and other phenomena are kept in view, the conclusion must be drawn that we have in them the material for the formation of protoplasm in the newly-formed organs. On the other hand all these reservoirs of reserve-material contain one or more non-nitrogenous substances belonging to the series of carbo-hydrates and oils. In seeds and spores there is generally a great deal of oily matter and little or no starch; but many seeds contain on the other hand a great deal of starch with but little oily matter. In tubers, many bulbs, rhizomes, and stems, there is usually much starch stored up with but little oily matter; while in some tubers (as the dahlia, artichoke, &c.), the starch is replaced by inuline; in the bulbs of *Allium Cepa* by a substance resembling grape-sugar; in the root of the beet by crystallisable cane-sugar.

Small admixtures of oily matter appear to be never absent, and in some cases, especially in many seeds, this alone is present without any carbo-hydrate (as the almond, gourd, castor-oil plant, &c.).

Together with albuminoids, carbo-hydrates, and oils, a variety of other compounds may also occur in the reservoirs of reserve-material; but the limitation of substances of this kind to particular species of plants shows that they are not of the same significance as the former. They may be of great importance for the growth of the species; but more accurate knowledge is still wanted in all cases.

Since seeds, tubers, and other parts of plants that are filled with reserve-material can be made to unfold buds, to put out roots, and even to form flowers and the rudiments of fruits by supplying them with pure water and oxygenated air when the conditions for assimilation (chlorophyll and sunlight) are absent, it follows that the substances stored up in these reservoirs furnish the material for the growth of the new leaves, roots, and flowers. The reservoirs are therefore emptied in proportion as the growth of the new organs progresses; and when finally they become completely empty, all further growth ceases, if sunlight and chlorophyll do not cooperate to produce new formative material by assimilation. It is moreover easy to follow the reserve-materials in their course from the reservoirs through the conducting tissues to the growing organs, and to recognise their relation to the growth of particular tissues. A close study leads first of all to the conclusion that the albuminoids contained in the reservoirs of reserve-material reappear as such in the protoplasm of the newly-formed organs, having, independently of temporary qualitative changes, only altered their position. On the other hand it shows that the oily matter and the carbo-hydrates which had accumulated in the reservoirs finally entirely disappear as such or leave only a small residue (oil); while in their place a mass of new cell-walls is formed which were not in existence before; and the material for the construction of these can only have been derived, under the given conditions, from the carbo-hydrates, or, when these are absent, from the oily matter which has now disappeared. If we thus come to the conclusion that starch, sugar, inuline, and oil are the substances from which are formed the cell-walls of plants, at all events in so far as they are nourished from a reservoir of reserve-material, it by no means follows from this that the whole of the store is used up entirely in the production of cellulose; on the contrary a variety of other substances are formed during growth, such as vegetable acids, tannin, colouring matters, &c., which are probably also derived from the same non-nitrogenous reserve-materials. A part of the non-nitrogenous substance is also entirely destroyed and converted into carbon dioxide and water, a process which may cause a loss of 40 or even 50 per cent. of the weight of the organic substance of those seeds which germinate in the dark.

If the reserve-materials stored up in different seeds, tubers, bulbs, &c. are compared, it is seen that starch, the various kinds of sugar, inuline, and oil, are of the same physiological value with regard to their most important purpose, viz. the formation of new organs; inasmuch as these substances can replace one another. Thus the cell-walls of the embryo of *Allium Cepa* are formed at the expense of the oily matter of the endosperm; but the cell-walls of the leaves and roots which grow from the bulbs evidently obtain their formative material from the glucose-like substance which fills the bulb-scales in a state of solution. In the beet however

cane-sugar is stored up for the same purpose, inuline in the tubers of the dahlia, and starch in the tubers of the potato, the bulbs of the tulip, &c.; and these are subsequently consumed. But in most seeds all these carbo-hydrates are replaced by oily matter; and it cannot be doubted that this furnishes the material for the growth of the cell-walls when the new organs are being formed.

To the series of these substances of the same physiological value belongs finally *Cellulose* itself, which may also be deposited in considerable quantities as a reserve-material, as in the endosperm of the date, the greater part of the hard kernel of which consists of cellulose in the form of dotted thickening-masses of the cell-walls. These are dissolved during germination, and the products of their solution conveyed to the growing parts of the embryo, where they finally supply the material for the growth of the new cell-walls.

If on the other hand the substances which occur in dormant seeds, bulbs, tubers, and other reservoirs of reserve-material, are compared with those which are found in the conducting tissues and growing organs of seedlings and young roots—which we already know must necessarily be produced from the former, because there is no other material which can produce them—it is seen that these reserve-materials must undergo repeated *Metamorphosis* while they are being conveyed to the growing organs and are being consumed in the process of growth, and before the permanent form of cellulose has been attained. Thus sugar and starch are found temporarily in all oily seeds during germination, and are often accumulated in great quantities, disappearing when germination is completed. In proportion as they are formed the amount of the original oil decreases; and in proportion as they again disappear the quantity of cellulose in the cell-walls increases. In other cases starch is conveyed from reservoirs of reserve-material to the growing organs, sugar being at the same time formed; and fine-grained starch is again temporarily formed in the growing tissues themselves, disappearing once more with the growth of the cell-walls. This temporary formation of starch in the growing tissues themselves is an extremely common phenomenon, whether the reservoirs of reserve-material were filled with oily matter, inuline, sugar, starch, or cellulose. This transitory starch appears in the cells of the parenchyma and epidermis of young organs (only rarely in those of the fibro-vascular bundles) after they have become differentiated from the primary meristem; and disappears when the final elongation of the organs is completed, generally becoming transformed into sugar (glucose), which in its turn speedily disappears.

Transitory metamorphoses appear to take place also when the albuminoids stored up in the reservoirs of reserve-materials are being transported and consumed; although these metamorphoses cannot be followed by micro-chemical observations, as in the case of the oils and carbo-hydrates. Thus a portion of the caseine in the cotyledons of Leguminosæ passes over into albumen during germination; the insoluble protein in the endosperm of wheat is dissolved and carried up into the seedling plant. The albuminoids contained in seeds appear to be subject during germination to still more complete decompositions. The asparagin which occurs temporarily in parts of the embryo can only be formed by partial decomposition of the albuminoids[1]. It appears however that these products of

[1] According to Hosæus, ammonia is also formed during germination; and Borscow maintains

the decomposition of the albuminoids under the influence of the energetic oxidation which takes place in the germinating seed, *i. e.* in the growing parts of the embryo, are again consumed in the formation of albuminoids.

The preceding remarks refer to the processes of growth which are associated with the consumption of the substances stored up in the reservoirs of reserve-material. If those plants are now examined in a similar manner whose reserve food-material has been consumed, whose green leaves have begun to assimilate under the influence of light, and which are forming the substances necessary for the growth of their buds, roots, &c., the same substances are found similarly distributed through the conducting tissues of the internodes and the petioles and veins of the leaves as far as the buds and apices of the roots, and subject to the same metamorphoses as in the seedlings. It follows that the assimilating organs which contain chlorophyll perform the same function for the growing parts of the plant that the reservoirs of reserve-material do for the seedling; but with this difference, that the former produce the formative materials afresh, while in the latter they are not formed but only stored up.

The organic compounds originally formed in the cells containing chlorophyll by the decomposition of carbon dioxide and water under the influence of light are generally carbo-hydrates. The most common of these is starch; sugar occurs less often; oily matter perhaps occasionally. It has been shown (p. 46) that the starch which so commonly occurs in the chlorophyll-grains of plants that vegetate under normal conditions, can only be produced when the plant is subject to the well-known conditions of assimilation, *i. e.* when it decomposes carbon dioxide and water under the influence of sunlight. Seedlings which have completely exhausted their supply of reserve-materials by growth in the dark, and are afterwards exposed to the action of light, do not till then develope their chlorophyll. The first grains of starch which are found a little later in the plant are those enclosed in the chlorophyll, and these are at first small, but gradually grow larger. It is only afterwards that starch is found also in the conducting tissues of the internodes and leaf-stalks up to the buds, which then begin to grow anew. It has been shown further that this starch which is formed in the grains of chlorophyll disappears in the dark; *i. e.* becomes dissolved and transferred to the conducting tissues. In *Allium Cepa* the chlorophyll forms no starch; but a substance similar to grape-sugar is found in large quantities in the green leaves, and is distributed through all the tissues of the plant. Where drops of oil are found in the chlorophyll, they appear to be first of all formed at the expense of the starch which has been produced there; this conclusion being derived especially from the observation of what takes place in Spirogyra.

The result of tracing by micro-chemical observation the products of assimilation in the conducting tissues leads once more to the conclusion that the starch which is formed in the cells containing chlorophyll is subject to a variety of chemical metamorphoses before it reaches the growing tissues and the reservoirs of reserve-material. Even during the period of vegetation the substances which are

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that ammonia is set free during the vegetation of Fungi (Mélanges biol. tirés du Bullet. de l'Acad. imp. des Sci. Nat., Petersbourg, vol. VII, 1868). This is however denied by Wolf and Zimmermann (Bot. Zeitg. 1871, nos. 18, 19).

conducted to the young parenchyma of growing parts as soon as this has been differentiated from the primary tissue, give rise to the formation of fine-grained starch which accumulates there temporarily, and disappears with the final and rapid increase in size of the cells. Starch and other substances are then produced afresh by assimilation in the fully developed leaves; and starch and the products of its transformation again appear in the conducting tissues, not to be consumed there, but only to be conducted to the still younger parts. The metamorphoses of the formative materials which are conveyed from the assimilating organs to the reservoirs of reserve-material, generally show a reversed order of succession to that which takes place during germination; the starch produced in the leaves is transformed in the leaf-stalks of growing beet into glucose, from which crystallisable cane-sugar is formed in the swollen tuberous roots; in the artichoke the starch is converted into inuline which is conducted through the stem to the underground tubers; in the potato, the mature leaves of which form starch, a substance similar to glucose is chiefly found in the conducting tissues, which is conveyed to the growing tubers, and there evidently forms the material from which the large masses of starch are formed. In ripening fruits and seeds a large quantity of glucose is generally found which disappears from the seeds when they become ripe, starch being formed in the reservoirs of reserve-material; in Ricinus the oil of the endosperm is evidently formed at the expense of the saccharine substance which is conveyed to the seed; in the embryo of the same plant, as well as in that of Crucifers, fine-grained starch is formed temporarily, which disappears when the seeds are ripe, and is replaced by oily matter.

Whether the albuminoids also are first formed in the assimilating cells which contain chlorophyll and whether they can be formed only in them, is still an undecided point. It is certain that they are formed in the chlorophyll-containing cells of Algæ; but it cannot be concluded from this that they can only be produced in the corresponding cells of plants with differentiated tissues; at all events experiments on the artificial production of the yeast-fungus show that it is able to form out of sugar and an ammonium-salt or nitrate (with the assistance of the constituents of the ash) not only cellulose but also albuminoids, as may be inferred from the increase of the protoplasm in the rapidly multiplying cells. If the colourless cells of yeast are able to do this, it may be inferred, until the contrary is proved, that those cells of other plants which do not contain chlorophyll can also produce albuminoids, if only a carbo-hydrate or oil (or both) is conveyed to them from the leaves, and an ammonium-salt or nitrate from the roots. That the formation of albuminoids probably takes place in this way within the conducting tissues of internodes and petioles may be concluded from the deposition of calcium oxalate in these tissues; since in the formation of this salt sulphuric acid becomes separated from the calcium, and its sulphur enters into the chemical formula of albuminoids[1].

When the cells of the leaves become emptied of their contents at the close of the period of vegetation, and the deciduous parts fall, not only the starch which was formed latest in the latter, but also the material of the grains of chlorophyll, is itself absorbed and conveyed through the leaf-stalks to the reservoirs of

[1] See Sachs, Handbuch der Experimental-Physiologie, p. 345.

reserve-material; all the serviceable substances contained in the leaves become incorporated in the permanent organs. The leaves change colour; a small quantity of very small shining yellow granules usually remain behind in the cells of the mesophyll as a residue of the absorbed chlorophyll-grains; and the leaves which are emptied in the autumn are therefore yellow. If they are red this is in consequence of a red sap which fills the cells in addition to the chlorophyll-grains[1]. Enormous quantities of crystals of calcium oxalate often remain behind in the deciduous leaves; the constituents of the ash which are serviceable to the plant, especially phosphoric acid and potassa, are conveyed with the starch and the protoplasmic structures to the permanent parts; so that the falling leaves thus consist only of a skeleton of cell-walls and of the subsidiary products of metastasis which are of no value to the plant.

The direction of the *Transport* of the assimilated substances in the plant is determined by the fact that it must take place from the assimilating organs to the growing parts and to the reservoirs of reserve-material; while at the commencement of every new period of vegetation its direction must be from these reservoirs to the growing organs; and since new organs are usually formed above as well as below these reservoirs and the assimilating leaves, it is obvious that the movements of the assimilated substances must take place at the same time in opposite directions.

The *Conducting Tissue* for the transport of the formative materials consists, in plants with differentiated systems of tissue, of the parenchyma and the thin-walled cells of the phloëm of the fibro-vascular bundles. By the parenchyma of the fundamental tissue, which always has an acid reaction, are conveyed the carbo-hydrates and oils; by the soft bast the mucilaginous albuminoids which have an alkaline reaction. Only when the conduction is very rapid, as when the leaves are emptied in autumn, and in plants with very rapid growth (as the castor-oil plant and gourd) are small quantities of starch found also in the sieve-tubes. Where there are laticiferous vessels, they furnish an open communication between all the organs of the plant; they contain albuminoids, carbo-hydrates, and oils, as well as the secondary products of metastasis, as caoutchouc and poisonous substances.

The mode of motion of the assimilated substances is usually molecular; *i. e.* it is a movement of diffusion, especially where the transport takes place through closed cells. The pressure caused by the tension and turgescence of the tissues has in addition a tendency to propel the fluids in the direction of least resistance, which is also that in which they are consumed. In the system of communicating sieve-tubes and laticiferous vessels the movement of the substances is necessarily one of the entire mass, caused by inequalities of pressure, and by the distortions and curvatures which the wind produces.

As far as concerns the movements of diffusion, it is a general rule that every cell which decomposes any substance, renders it insoluble, or uses it for its growth, acts upon the dissolved molecules of this substance in the neighbourhood

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[1] [On the colouring matter of the leaves in autumn, see Sorby, Quart. Journ. of Science 1871, p. 64; and 1873, p. 215.—Ed.]

as a centre of attraction; the molecules stream to the parts where they are wanted because the molecular equilibrium of the solution is disturbed by its consumption. On the other hand every cell which produces a new soluble compound acts on the dissolved molecules as a centre of repulsion, because the continually increasing concentration occasions at the point of production a streaming of the molecules away from it towards the point of less concentration, the concentration continually decreasing towards the points where the substances are consumed. When the movement of diffusion is caused by the production and consumption of definite compounds of this nature, the proximate cause of the molecular movement of the dissolved substances must be the chemical processes involved in their metamorphoses. These metamorphoses take place, as we have seen, not only at the points where the substances are consumed in the process of growth, but also in the conducting tissues; and this production of transitory compounds must therefore favour movement towards the points of deposition and of growth. The formation of insoluble starch is in this sense a fact of peculiar importance. If for instance the starch produced in the leaves of the potato is required to be transported to the tubers, it must necessarily be conveyed in a soluble form, such as we find in the conducting tissues of the stem in the form of glucose. But if this glucose had to undergo no further change in the tubers, a solution of glucose of constantly increasing concentration would be uniformly distributed through the conducting tissues and the tubers; and the accumulation of the whole of the reserve-material in the tubers would be impossible. The glucose is used up in the tubers in the formation of starch-grains; and a fresh quantity therefore continually streams in that direction; the whole mass of the material produced in the leaves is therefore gradually transferred to the reservoirs of reserve-material. The starch is first transformed into glucose, and then back into starch; and it is in this chemical process that the vehicle for the movement consists. Starch is even produced temporarily in the conducting parenchyma, but of course cannot be transported as such from cell to cell; its movement being effected by the grains being dissolved in one cell, the product of solution diffusing into the adjoining cell, and being there employed in the formation of starch-grains which are then again dissolved, and so on. When again cane-sugar is formed in the tuberous roots of the beet, the movement towards the root of the glucose which is produced from the starch assimilated in the chlorophyll is brought about in this way,—every particle of glucose undergoes chemical transformation when it reaches the root, and the molecular equilibrium of the solution of glucose is thus disturbed; the root acting like a centre of attraction on the glucose in the leaf-stalks. But the continual formation of the solution of glucose in the leaves at the expense of the starch causes in them an increase of concentration and a streaming of molecules towards the root, where the concentration of the solution of glucose is continually decreasing, while that of the solution of cane-sugar increases. The same is evidently the interpretation of the formation of inuline in the tuberous roots of the dahlia and the tubers of the artichoke, and of that of oil in ripening seeds at the expense of the sugar which is conveyed to them.

The co-operation in the movement towards the parts where the substances are consumed of the tissues of the pressure exercised on the cell-sap by the tension

I infer, even where we have to do with closed cells, from the fact that considerable quantities of the cell-sap appear on the surface of a transverse section of succulent organs, both from the parenchyma and from the cambiform cells, and this is clearly forced up by internal pressure. Since the tension and turgescence of the tissue are always less in the buds and apices of the roots than in the older parts, there must always be a tendency for the filtration of the sap towards the latter, which must act in the same way as diffusion.

That the contents of the perforated sieve-tubes and laticiferous vessels are also subject to considerable pressure from the surrounding tissue is shown by the extent to which these fluids flow out when the organ is cut through. The fluid which is subject to pressure will have a tendency to escape from these tubes to parts of the plant where the lateral pressure is less, which is the case in the buds and apices of the roots. The flexions and distortions occasioned in the organ by the wind will at the same time cause the fluid contents of the sieve-tubes and laticiferous vessels to be pressed away from the older bent parts towards the buds where the tension is less.

The statements here compressed into a very brief space rest on a series of detailed micro-chemical and experimental researches which I have described in the Botanische Zeitung, 1859 and 1862–1865; Pringsheim's Jahrbücher für wissenschaftliche Botanik, Vol. III. p. 183 *et seq.*; Flora, 1862, pp. 129 and 289, and 1863, pp. 33 and 193; and have presented in a connected form in the section on the Transformation of Food-materials in my Handbook of Experimental Physiology[1]. The reader will there find the reasons for the views here given; and a few examples will now be sufficient to render somewhat clearer the general statements with regard to metastasis and the migration of the assimilated substances. In the outset it must be stated that by grape-sugar or simply sugar I understand a substance soluble in the cell-sap, easily reducing copper oxide, and readily soluble in strong alcohol, although it may not always exactly correspond to the grape-sugar of chemists, a point which is of but little importance for our present purpose.

The parenchyma of the bulb-scales of the tulip — *i. e.* the four or five thick colourless leaves which serve as reservoirs of reserve-material—contains, as long as the plant is dormant, in addition to considerable quantities of mucilaginous albuminoids, a very large quantity of coarse-grained starch. The presence of sugar cannot be determined at this time by micro-chemical processes. As soon as the bud of the leaf- and flower-stem which is concealed within the bulb, but had already been formed with all the parts of the flower during the previous summer, begins to elongate in February, and roots make their appearance from the base of the bulb, small quantities of sugar are found with the starch in the parenchyma of the bulb-scales. The whole of the parenchyma and of the epidermis of the leafy stem, of the young foliage-leaves, of the perianth, of the stamens, and of the carpels, becomes filled with fine-grained starch, the substance of which has already been derived from the bulb-scales, where the starch-grains have become transformed into sugar, which diffuses into the growing organs, and there, as far as it is not directly consumed, again supplies material for the formation of starch-grains.

Together with its consumption in the growth, at first slow, of the cell-walls, this temporary re-formation of starch at the expense of that contained in the bulb-scales

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[1] The recent researches of Schröder (Jahrb. für wiss. Bot. Vol. VII, p. 261), Sorauer, Siewert, Rœstell &c., (collected in Hoffmann and Peters' Annual Report on the Progress of Agricultural Chemistry for 1868 and 1869, Berlin 1871) contain fresh confirmations of the account here given.

continues at first in the young internodes, leaves, and flowers. The cells enlarge and become continually more filled up with fine-grained starch till the time when the bud comes above ground (Fig. 441). Then follows the rapid extension of the stem; the leaves expand, and the flower unfolds. With the considerable and rapid increase in size of the cells caused by this unfolding, the fine-grained starch disappears in all these parts, sugar being temporarily produced which furnishes the material for the growth of the cell-wall. When all the parts above ground are fully unfolded, the cells, although much larger, are now devoid of starch. The corresponding loss which the bulb-scales have experienced up to this time is clearly seen from the decrease of their starch-grains; they may be found in all stages of absorption. The turgescence of the bulb-scales at the same time decreases, and they become wrinkled; but the formation of sugar in them still continues at the expense of the starch, even when the parts above ground have already done growing. The starch stored up in the bulb-scales finds in fact still another use; while the flower-stalk is extending, the bud in the axil of the uppermost bud-scale begins to develop rapidly (it had already been formed in the previous summer); its cataphyllary leaves swell and become filled with starch; and the residue of the starch not consumed in the growth of the flower-stalk is transported from the scales of the mother-bulb through its base into the young bulb (Fig. 441, 2). These scales become gradually entirely emptied of starch, and while the green foliage-leaves exposed to light are assimilating and contributing their share to the growth of the new bulb, they finally wither and dry up from the simultaneous loss of water and of assimilated matters. The reserve-materials which accumulate in the daughter-bulbs are partly derived from those of the mother-bulb; but are completed by the products of assimilation of the green leaves of the flower-stalk. When the flower-stalk has also died down, nothing remains of the whole plant but the bud which has developed into a new bulb. For a time it does not put out any new organs, but is apparently dormant; but in the interior the end of the stem continues to grow slowly, and produces new rudiments of leaves and the flower-bud for the next year; when the process now described is repeated.

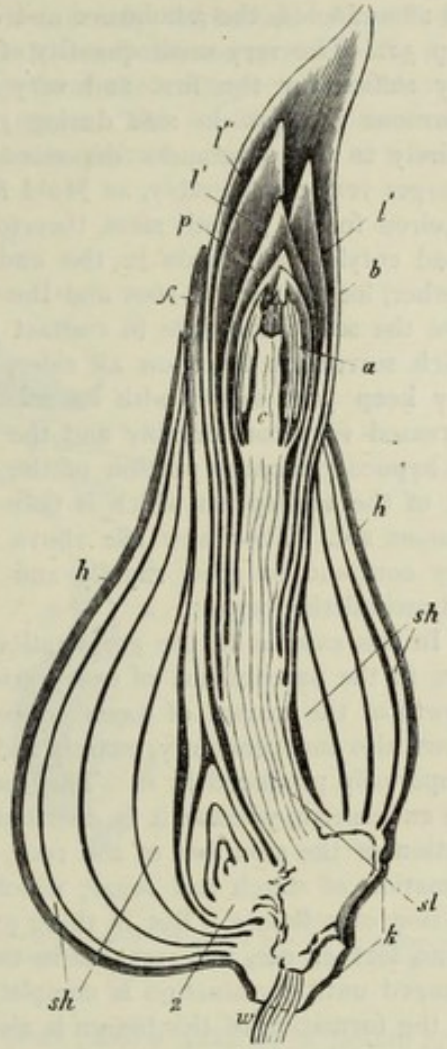

FIG. 441.—Longitudinal section through a germinating bulb of *Tulipa praecox*: *h* the brown enveloping membrane, *k* the flattened stem which forms the base of the bulb and bears the bulb-scales *sh*; *sl* the elongated part of the stem which bears the foliage-leaves *l'l''*, and terminates in the flower; *c* the ovary, *p* perianth, *a* anthers; 2 a lateral bulb in the axil of the youngest bud-scale, which developes into the bud of next year's bulb; *w* the roots which spring from the fibro-vascular bundles of the base of the bulb.

So far we have only pointed out the relation of the starch and of the sugar produced from it to the growth of the plant; there are formed however along with it, and probably likewise at the expense of these carbo-hydrates, other substances, such as the colouring matter of flowers, the oil in the pollen-grains &c. The albuminoids at first contained in the bulb-scales become transported to a distance from them,

and furnish the material for the formation of the protoplasm in the young cells of the growing flower-stalk; a large part is evidently employed in producing the grains of chlorophyll in the foliage-leaves as they become green. Its function is now to produce at least as much formative material by assimilation as is required to build up the transitory flower-stalk, and to supply it to the bulb.

The ripe seed of *Ricinus communis* contains a very small embryo in the middle of a very large endosperm; neither contains starch, sugar, nor any other carbo-hydrate, if we exclude the very small amount in weight of the cellulose of the thin cell-walls. The reserve food-material consists of a great quantity of oil (as much as 60 per cent.) and albuminoids, the admixture and composition of which have already been described on p. 52. The very small quantity of these substances contained in the embryo would only suffice for the first and very inconsiderable development of the seedling; its enormous increase in size during germination must therefore be attributed almost entirely to the substances deposited in the endosperm. The endosperm of Ricinus enlarges very considerably, as Mohl first showed, during germination, and the material required for its growth must therefore be diverted from the embryo. The two thin broad cotyledons remain in the endosperm, with their surfaces in contact with one another, long after the root and the hypocotyledonary part of the stem have emerged from the seed; they are in contact by their backs with the tissue of the endosperm which surrounds them on all sides, and absorb the reserve-materials from it, while they keep pace slowly with its enlargement. When the parts of the seedling have increased very considerably and the root has developed a number of lateral roots, the hypocotyledonary portion of the stem elongates so that the cotyledons are drawn out of the endosperm which is then completely emptied and reduced to a thin membranous sac. They now rise above the ground, become expanded to the light where they continue to grow rapidly and become green, to serve from this period as the first assimilating organs.

In this case, as in the germination of all oily seeds, sugar and starch are produced here in the parenchyma of every growing part, disappearing from them only when the growth of the masses of tissue concerned has been completed. Since the endosperm grows also independently, starch and sugar are, in accordance with the general rule, temporarily produced in it. The cotyledons apparently absorb the oil as such out of the endosperm, whence it is distributed into the parenchyma of the hypocotyledonary portion of the stem and of the root, serving in the growing tissues as material for the formation of starch and sugar, which on their part are only precursors in the production of cellulose. But in these processes of growth tannin is also formed which is of no further use, but remains in the separate cells, where it collects apparently unchanged until germination is completed. It can scarcely be doubted that the material for the formation of this tannin is also derived from the oil of the endosperm, although perhaps only after a series of metamorphoses. The absorption of oxygen, which is an essential accompaniment of every process of growth and especially of germination, has in this case, as in that of all oily seeds, an additional significance, inasmuch as the formation of carbo-hydrates at the expense of the oil involves the appropriation of oxygen.

Since the metamorphoses of material proceed *pari passu* with the growth of the separate parts, the distribution of the products of metastasis through the tissues is continually changing, and can only be understood by a consideration of all the surrounding circumstances. The micro-chemical investigation of seedlings in the state represented in Fig. 442 *II*, gives, for instance, the following result: — in the endosperm is found a great deal of oil and a little starch, with sugar at the outside; the epidermis and parenchyma of the slowly growing cotyledons are filled with drops of oil; a large number of the epidermal cells contain tannin; starch-granules are found only in the parenchyma of the leaf-veins; the parenchyma of the hypocotyledonary portion of the stem, which is at present growing the most rapidly, contains only

comparatively little oil but much starch and sugar; and a number of the cells of the epidermis and parenchyma are filled with tannin. The primary root has first of all completed its growth in length and thickness (after germination it begins afresh); in its lower part it contains neither starch nor sugar (the former is present in the root-cap); in its upper part from which the lateral roots spring and in the lateral roots themselves sugar is also present, which is conveyed into the growing apices of the latter. When the hypocotyledonary portion of the stem has subsequently taken a direction straight upwards and ceases to grow, the oil, starch, and sugar have almost entirely disappeared from it, and in their place the cell-walls have become thick, and the vessels and first cells of the wood and bast are already thickened. After the stem of the young plant has become upright, the cotyledons expand and grow rapidly, and the remainder of the oil which they had taken up from the endosperm now also disappears from them together with the starch and sugar. The seedling has now entered on a state in which the non-nitrogenous reserve-materials are consumed; a framework

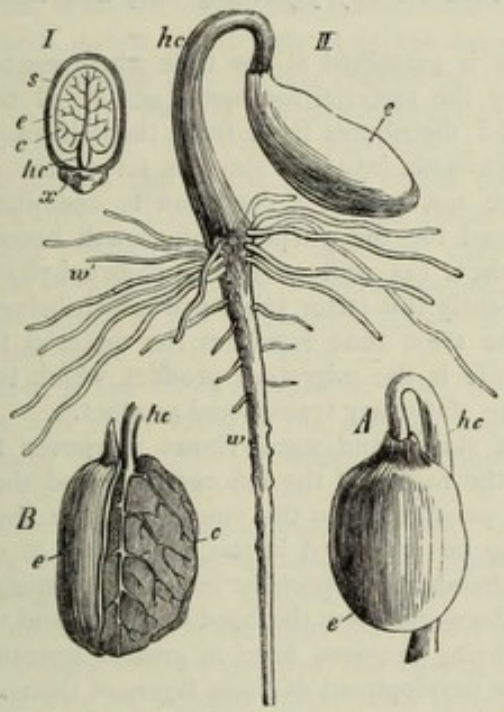

FIG. 442.—*Ricinus communis*: *I* longitudinal section of the ripe seed; *II* germinating seed with the cotyledons still in the endosperm (shown more distinctly in *A* and *B*), *s* testa, *e* endosperm, *c* cotyledon, *hc* hypocotyledonary portion of the stem, *w* primary root, *w'* secondary roots, *x* the caruncle.

of large and solid cell-walls is produced in their place; and a quantity of tannin remains behind in some of the cells as a secondary product, as well as various other substances not present in the seed.

The albuminoids which form so peculiar and intimate a mixture with the oil in the ripe seed, and which are partially contained in the aleurone-grains of the endosperm in the form of crystalloids, are, during the processes which have been described, transferred to the embryo, where they produce the protoplasm. During the whole of the period of germination the cells of the fibro-vascular bundles are found to be densely filled with albuminous mucilage, subsequently only those of the phloëm; these substances are evidently in motion towards the apices of the roots where new cells are continually being formed. Every young rudiment of a lateral root behaves to reagents as an accumulation of albuminous substance in contact with the fibro-vascular bundles of the primary root. But a very considerable portion of this material remains in the upper part of the stem of the seedling where new leaves are formed, and a still larger portion in the cotyledons themselves, where it furnishes the material for the formation of the numerous grains of chlorophyll.

After the consumption of the reserve-material at the end of the period of germination, the cells—with the exception of the youngest parts of the buds and the apices of the roots—are destitute of any formative material; although it has grown to a large size and contains a great quantity of water, the dried weight of the plant is very small and even less than that of the seed, because a portion of the substance has been destroyed in the process of respiration. But active organs are formed from the earlier inactive store of material; the roots absorb water and dissolved food-material; the green cotyledons begin to assimilate; they produce starch in their chlorophyll; and the same substance is subsequently found also in the parenchyma of the petioles and in the stem as far as the bud, the young leaves of which grow from the products of the assimilation of the chlorophyll. At first the unfolding of new leaves and the increase in length and thickness of the stem and roots are very slow; but the capacity for work possessed by the plant increases with every freshly developed leaf and every new absorbing root; on each successive day it can produce a larger quantity of formative material than on any preceding one, and thus the rate of growth also increases.

If a castor-oil plant is examined at the time when vegetation is most active, when the green leaves supply the material for metastasis in all the organs, starch is found in their chlorophyll and distributes itself from them through the parenchyma of the veins and petioles downwards into the stem as far as the root, and upwards to the young leaves which are not yet in a condition to assimilate. The excess which is not immediately required for the purposes of growth becomes deposited in the pith and medullary rays, where (as well as in the chlorophyll) it is always accompanied by sugar; and it is evidently this latter substance which brings about the diffusion from cell to cell, and at the same time furnishes the material for the formation of new starch-grains. The sugar is the migratory product which takes part in the diffusion; the starch-grains are the stationary transitional product.

The distribution of starch and sugar shows moreover that they move from the primary stem through the rachis of the inflorescence and the pedicels into the parenchymatous tissues, and penetrate into the young tissue of the flower, the growing fruit, and the ovules, there to be employed in the production of cellulose. The distributed starch collects more abundantly especially in the immediate neighbourhood of those layers of cells which afterwards form the hard endocarp and the solid testa of the seed, in consequence of its being required here in greater quantity, disappearing also from them after the complete development of these layers of tissue.

The sugar and starch are conveyed through the funiculus to the ovules; they are distributed through the integuments and the parts surrounding the nucleus; and a large quantity of sugar enters the growing endosperm, which supplies the material for the formation of the oil which gradually accumulates, while fresh supplies of sugar are constantly entering from without. In the growing embryo the cells are filled at a certain period with fine-grained starch, which then entirely disappears and is replaced by oil. All this indicates that the oil of the ripe seed of Ricinus is produced from the starch and sugar which were transported to it from the assimilating organs during the period of repose; and even the hard woody pericarp and the testa obtain their formative material from those substances. The albuminoids which collect also in the young leaves and from which the chlorophyll-grains are formed, as well as that portion of these substances which accumulates in the seed as reserve food-material, are transported from the stem by the sieve-tubes and the cambiform cells of the fibro-vascular bundles.

'In the Leguminosæ[1] a very important part in the transport of the reserve proteinaceous substances is played by *Asparagin*. To demonstrate this, moderately thin sections are placed in alcohol, and the saturation assisted by shaking. This mode

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[1] What follows is taken from a letter from Dr. Pfeffer. (Compare Book I, Sect. 8, p. 51).

is however applicable only when the asparagin is abundant; when it is present in small quantities it can still be demonstrated by placing a thin cover-glass on the sections, and running in underneath a little absolute alcohol. In this case the asparagin crystallises out round the section; while in the former case it is precipitated in the cells in the form of crystals. These can easily be recognised; they are comparatively large, and cannot be mistaken for other crystals which are formed in all plants on treatment with alcohol, even where no asparagin is present, since these—which belong to various salts, among others to nitrates—always remain very small and have an entirely different appearance.

'*Lupinus luteus* is a good object for examination, and possesses the great advantage that we have in its case an analytical investigation of Beyer's[1] in which the organic constituents and especially the asparagin have been determined in the root, hypocotyledonary portion of the stem, and cotyledons, at two stages of germination, the last shortly before the cotyledons have thrown off the testa.

'The following is what is known respecting the movements of the non-nitrogenous reserve-substances. Starch is first of all formed in the hypocotyledonary portion and root, then disappears and remains only in the endoderm, the rest being transformed into sugar. Asparagin is first formed in the hypocotyledonary portion and root when they are about 10 mm. long, but then rapidly increases in quantity while these parts elongate; and it is now formed also in the petiole of the cotyledons, and in the cotyledons themselves before they have become green and thrown off their testa, especially in their lower part. The conditions remain the same during the whole of the time that the reserve albuminous substances are being consumed. Asparagin is now found in large quantities in the petiole of the cotyledons, almost to the extent of a saturated solution (1 part dissolves in 58 parts of water at 13° C.), as well as in the hypocotyledonary portion and in the stem as soon as it begins to grow. The asparagin extends from the root and stem towards the *punctum vegetationis* almost exactly as far as the sugar, becoming finally, like the latter, less abundant. Beneath the cotyledons it is wanting in the pith, while in the stem it is as abundant there as in the cortical tissue; it is never found in the vascular bundles. The asparagin also extends into the petiole of young leaves as far as the base of the unfolding pinnæ, as well as into the lateral roots. As long as asparagin is formed out of the albuminous substances in the cotyledons, it may also be found in the plant distributed as has been described; but when the cotyledons have been entirely emptied, the asparagin also disappears; but this does not happen in the case of *Lupinus luteus* until several leaves have completely unfolded.

'The process is quite analogous in *Tetragonobolus purpureus* and *Medicago tuberculata*; in *Vicia sativa* and *Pisum sativum* the presence of asparagin in the cotyledons themselves cannot be proved with certainty, but is found at their base and usually also in their petiole, although these plants produce decidedly less of it than *Lupinus luteus*. Since moreover chemical analysis has established the production of great quantities of asparagin on germination in the case of a large number of other species of the order, we may regard this substance as the form of transport for the albuminous substances characteristic of all Leguminosæ. Albuminous substances are moreover found in these plants also in the thin-walled elongated cells of the vascular bundles; and it is quite possible that they are at the same time also transported by these structures. It is evident that the source of the asparagin must be the albuminous substances, because the absolute amount of nitrogen remains the same during germination; and the nitrogen of seeds is all or nearly all contained in their albuminous ingredients.

'As to the influence of darkness on the formation of asparagin, we have diametrically opposite statements from Piria and Pasteur. The only certain point is that

[1] Landwirthschaftliche Versuchsstationen, vol. IX.

light has no influence at all on the formation of asparagin, but has upon its transformation into albuminous substances; it therefore accumulates in plants germinating in the dark, and remains unaltered till their death. The influence of light can however only be indirect, as is shown by the fact that in Tropæolum asparagin is formed temporarily in the dark during the first stages of germination, and then again disappears; and even in Leguminosæ appears to undergo subsequent metamorphosis into albuminous substances. The explanation is now quite simple.

'The following numbers show the percentage composition of asparagin, and the composition of an amount of legumin, containing an equivalent quantity of nitrogen.

Asparagin.	*Legumin.*
C = 36·4	C = 64·9
H = 6·1	H = 8·8
N = 21·2	N = 21·2
O = 36·4	O = 30·6

'It is seen at once that in the formation of asparagin out of legumin a large quantity of carbon becomes available. The exact mode in which this comes to pass must be left in doubt, like the fixation of carbon in the re-formation from asparagin of albuminous substances (albumin is probably formed, and not legumin; their composition does not vary greatly, but the latter gradually disappears almost entirely in growing plants). But when a plant growing in the dark uses up its non-nitrogenous reserve-material, and even the carbon and hydrogen set at liberty by the conversion of legumin into asparagin, the material which would be produced in the light by assimilation is wanting for the re-formation of the albuminous substances out of asparagin. In Tropæolum, where asparagin occurs only in the first stage of germination, it may completely disappear in the dark. The amount of asparagin formed is however only moderate, and it disappears before the reservoir of reserve-material is exhausted; it therefore at most always plays only a subsidiary part, as is also the case in *Silybum Marianum*, *Helianthus tuberosus*, and *Zea Mais*. In Ricinus on the other hand I could not find, either in the dark or in the light, any asparagin at all; and Dessaignes and Chautard looked for it in vain in the seeds of the gourd, buckwheat, and oat, germinating in the dark. Its physiological significance remains therefore at present limited to the Leguminosæ; and in them it is confined to the consumption of the reserve albuminous substances, since it is, according to Pasteur, never present in the flowers. When the lateral buds are put out, this substance is not formed in Leguminosæ any more than in other plants. Hartig maintains that the production of asparagin, or at least of a trace of a substance identical with it, is a general phenomenon; but I think that he had before him the small crystals mentioned above which he mistook for true asparagin. He has moreover not contributed any evidence as to the physiological significance of this substance.

'The existence of asparagin has also been proved in the leaves and stems of some plants (see Husemann, Pflanzenstoffe); and its presence in the underground perennial parts of *Stigmaphyllon jatrophæfolium* almost gives the impression of its being there also a reserve-material.'

The absorption of assimilated substances into the plant from without takes place in seedlings, the reserve-materials of which are contained in the endosperm, in parasites[1], and in saprophytes which contain no chlorophyll. Seedlings, which

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[1] Parasites which contain chlorophyll, like the Loranthaceæ, can themselves assimilate, and only require therefore to draw water and mineral substances from their host (see Pitra in Bot. Zeitg.

are best known in this respect, show how the reserve-materials of the endosperm may pass into the absorbing organs (in this case almost always foliar structures) without there being any actual cohesion of the absorbing organ with the endosperm; they only lie in close apposition, and can be separated without any injury (as in Ricinus, Fig. 442). It cannot be doubted that the metamorphoses which take place in the nutrient endosperm are brought about by the absorbing organ, that is by the embryo itself; the behaviour of the endosperm of the germinating date, which is absorbed by the delicate tissue of the absorbing organ belonging to the cotyledon, shows clearly that the hard thickening-layers of the cell-walls of the endosperm are first of all transformed into sugar under the influence of this organ, and then absorbed. A substance evidently passes out of the absorbing organ into the endosperm which causes this metamorphosis of the cellulose. The oil and albuminoids of the endosperm are at the same time taken up into the embryo, where all the conducting parts of the parenchyma are filled with sugar and starch as long as the endosperm is not entirely absorbed. In the same manner also in Grasses substances possibly pass out of the embryo into the endosperm, and there bring about the chemical metamorphosis and solution of the starch and albuminoids before they are absorbed by the scutellum which is applied to the surface of the endosperm. It is possible however that in this case there may be agents capable of bringing about the solution of the starch and gluten in the presence of water independently of any chemical action of the embryo.

The absorbing roots of parasites penetrate into the tissue of the host, and often grow into it in the most intimate manner. It is certain that the exciting cause of the transport of the products of assimilation from the host to the parasite resides in the latter; the parasite acts on the conducting masses of tissue of the host like a growing bud of the host itself; the food-materials penetrate into it because it consumes and changes them.

The influence exerted by the absorbing organ of the embryo on the substances in the endosperm, dissolving and chemically changing them, points to the way in which the absorption of food-material is effected by saprophytes which possess no chlorophyll, their absorbing organs probably first causing the solution and chemical transformation of the decaying organic constituents of the humus. The decaying foliage in which Monotropa, Epipogium, and Corallorhiza grow, does not give up to water the serviceable materials which are still present in it, any more than the cellulose of the endosperm of the date, or the starch of the endosperm of Grasses, or the oil of the seed of Ricinus, can be extracted by water; but these saprophytes nevertheless obtain their nutriment from them. The fact that the roots of plants of this kind are so few in number and so diminutive in length, as in Neottia, or are entirely wanting, as in Epipogium and Corallorhiza, is very remarkable in connection with this. These plants are concealed in the nutrient substratum till the time of flowering, and may act upon it by their whole surface; and it is important to note that the absorbing surface of seedlings is very small in proportion to the great

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1861, p. 3). Those parasites which are apparently destitute of chlorophyll (like Orobanche), and saprophytes (as Neottia) contain, according to Wiesner (Bot. Zeitg. 1871, p. 37), traces of chlorophyll, which however can hardly be taken into account in assimilation.

amount of work done, as is also the case with the absorbing roots of Cuscuta, Orobanche, &c.

Sect. 6. — **The Respiration of Plants**[1] consists, as in animals, in the continual absorption of atmospheric oxygen into the tissues, where it causes oxidation of the assimilated substances and other chemical changes resulting from this. The formation and exhalation of carbon dioxide — the carbon resulting from the decomposition of organic compounds—may always be directly observed; the production of water at the expense of the organic substance in consequence of the process of respiration is inferred from a comparison of the analysis of germinating seeds with the composition of those which have not yet germinated. Experiments on vegetation show that growth and the metastasis in the tissues necessarily connected with it only take place so long as oxygen can penetrate from without into the plant. In an atmosphere devoid of oxygen no growth takes place; and if the plant remains for any time in such an atmosphere it finally perishes. The more energetic the growth and the chemical changes in the tissues, the larger is the quantity of oxygen absorbed and of carbon dioxide exhaled; hence it is especially in quickly germinating seeds and in unfolding leaf- and flower-buds that energetic respiration has been observed; such organs consume in a short time many times their own volume of oxygen in the production of carbon dioxide. But in all the other organs also—in every individual cell—respiration is constantly going on; and it is not merely the chemical changes connected with growth that are dependent on the presence of free oxygen in the tissues; the movements of the protoplasm also cease if the surrounding air is deprived of this gas; and the power of motion possessed by periodically motile and irritable organs is lost if oxygen is withheld from them; but if this happens only for a short time the motility returns when the oxygen is again restored.

The respiration of plants is, like that of animals, associated with a loss of assimilated substance, this loss being always a great deal smaller in assimilating plants than the gain of substance by the activity under the influence of light of the cells which contain chlorophyll; but when, as in the germination of seeds, an energetic growth is combined with powerful respiration, no new products of assimilation replacing the loss, the loss in weight of the growing plant may be very considerable. Seeds which germinate in the dark may in this way lose almost one-half of their weight when dry, and it would seem that this loss is occasioned exclusively by the decomposition of the non-nitrogenous reserve-material and its combustion into carbon dioxide and water. If the rest of the non-nitrogenous reserve-material consists of oil, *i. e.* of a substance containing very little oxygen, a portion of the inhaled oxygen remains in the germinating plant, carbo-hydrates containing a large quantity of oxygen such as starch and sugar being formed at the expense of the oil.

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[1] The special references for what is said on this subject will be found in my work on Experimental Physiology, sect. 9, On the action of atmospheric oxygen. Of more recent works may be mentioned especially, Borscow, On the behaviour of plants in nitrogen (Mélanges biologiques tirés du Bulletin de l'Acad. Imp. des Sci. Nat. de St. Petersbourg, vol. VI, 1867); also Wiesner Sitzungsber. der Wiener Akad. vol. LXVIII, 1871.

The loss of assimilated substance caused by respiration would appear purposeless if we had only to do with the accumulation of assimilated products; but these are themselves produced only for the purposes of growth and of all the changes connected with life; the whole life of the plant consists in complicated movements of the molecules and atoms; and the forces necessary for these movements are set free by respiration. The oxygen, while decomposing part of the assimilated substance, sets up important chemical changes in the remaining portion, which on their part give rise to diffusion-currents, and these bring into contact substances which again act chemically on one another, and so on. The dependence on respiration of the movements in protoplasm and motile leaves is very evident, since, as has been mentioned, they lose their motility when oxygen is withheld from them. These considerations lead to the conclusion that the respiration of plants has the same essential significance as that of animals; the chemical equilibrium of the substances is being continually disturbed by it, and the internal movements maintained which make up the life of the plant. Respiration is, it is true, a source of loss of substance; but it is also in addition the perpetual source from which flow the forces necessary to the internal movements[1].

The combination into carbon dioxide of the inhaled oxygen with a portion of the carbon of the assimilated substance is, like all combustion, accompanied by the production of a corresponding amount of heat; but this only rarely leads to a sensible increase of temperature of the masses of tissue, because respiration, and in consequence the production of heat, is not in general very copious, while the circumstances are very favourable to the loss of heat by the plant. In this respect also plants may be compared with cold-blooded animals. When an amount of heat is set free in the cells by the process of respiration, it first of all distributes itself over the large mass of water which permeates the cells and the adjoining tissue. In the case of a water-plant the least excess of temperature is at once equalised by the surrounding water; while in the case of a land-plant evaporation has a powerful cooling effect on the aërial parts, quite independently of the action of the radiation of heat which is favoured by the large superficial development of most plants, and especially by their hairiness. With these causes of a rapid loss of heat, it is not surprising that the parts of a plant which are expanded in the air are even colder than it, although their respiration is continually producing small quantities of heat. But if the causes of the loss of heat are removed, it is possible to observe with the thermometer the increase of temperature caused by respiration. This can be done by accumulating rapidly germinating seeds, as is shown in the

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[1] [M. Corenwinder, from a series of observations on the maple and lilac, has confirmed the view to a certain extent held by Mohl, that the process of respiration is always going on in a plant even when concealed by the greater activity of the decomposition of the carbon dioxide by the parts containing chlorophyll. He distinguishes two periods in the vegetative season of the plant:—the first period, when nitrogenous constituents predominate, is that during which respiration is most active; the second, when the proportion of carbonaceous substance is relatively larger, is the period when respiration is comparatively feeble, the carbon dioxide evolved being again almost entirely taken up by the chlorophyll, decomposed, and the carbon fixed in the process of assimilation. He found that the proportion of nitrogenous matter in leaves gradually diminishes, while that of carbonaceous matter increases, between autumn and spring. (See Révue scientifique, Aug. 1, 1874.—Ed.]

considerable elevation of temperature of grains of barley in the manufacture of malt; and this elevation can also be proved in the case of other germinating seeds, or growing bulbs and tubers. The proof is more difficult in plants with green leaves.

In some flowers and inflorescences the production of carbon dioxide which accompanies the inhalation of oxygen is very energetic, the radiation of the heat produced being at the same time diminished by the small superficial extent of the organ and by protecting envelopes; and in such cases a very considerable elevation of temperature of the masses of tissue has been observed. The best illustration of this is the spadix of Aroideæ at the time of fertilisation, where (especially in warm air) an excess of temperature of from 4° to 5° or even of 10° C. or more has been detected. Less considerable elevations of temperature have also been observed in the separate flowers of Cucurbita, *Bignonia radicans*, *Victoria regia*, &c.

In the few cases in which up to the present time the development of light or *Phosphorescence* has been observed in living plants, this phenomenon is also dependent on the respiration of oxygen. In *Agaricus olearius* (of Provence) this has been definitely proved by Fabre. This Fungus emits light only so long as it is alive, and ceases to do so at once when it is deprived of oxygen; the respiration is in this case also very copious. Besides this Fungus, *Agaricus igneus* (of Amboyna), *A. noctilucens* (of Manilla), *A. Gardneri* (of Brazil), and the Rhizomorphs are known to emit light spontaneously; the statements with respect to the light emitted from various flowers are of extremely doubtful value[1].

The apparatus described in my Handbook of Experimental Physiology, p. 271, may be easily employed, with the necessary modifications, for the observation of the production of carbon dioxide and the elevation of temperature of germinating seeds. The following experiment is also adapted for the demonstration of these points in a lecture. One-third of a glass cylinder of 2 litres capacity is filled with soaked peas or some other seeds or with flowers in the act of unfolding (*e.g.* small flower-heads of Compositæ, as Matricaria or Pyrethrum), and closed with a well-fitting glass stopper. If the vessel is opened carefully after several hours, the air contained will be found to extinguish a burning taper let down into it, as if it had been filled with carbon dioxide.

In order to observe the development of heat also in small quantities of seeds and even in single flowers of larger size, I use various forms of the apparatus represented in Fig. 443. The flask *f* contains a strong solution of potash or soda *l* which absorbs the carbon dioxide set free from the plants. In the opening of the flask is placed a funnel *r*, containing a small filter-paper perforated with a needle. The funnel is filled with soaked seeds or with cut flower-buds in the act of opening; and a bell-glass *g* is now placed over it, through the tube of which a thermometer graduated to tenths of degrees is let in so that the bulb is surrounded on all sides by the plants. A loose pad of cotton-wool *w* closes the tube. In order to compare the temperature, a similar apparatus is placed close beside, in which the seeds or flowers as the case may be are or are not replaced by pieces of moist paper or green leaves. It is convenient to place both apparatuses in a large glass case in order still more completely to shield them from slow changes of temperature in the air of the room. If the isolation is not complete, the access of fresh oxygenated air to the plants is not hindered, and the continuance of respiration is therefore not prevented; the arrangement is on the other hand sufficient to reduce to a minimum the loss of heat by radiation and evaporation. The thermo-

[1] [For a collection of recorded instances of phosphorescence in plants see Hardwicke's Science Gossip, 1871, p. 121.—Ed.]

meters of both apparatuses, previously compared, must be frequently read off in order to detect the variations of temperature. If the bulbs are small enough, the elevation of temperature in the funnel may be observed even with single flowers. In order to reduce still further the amount of evaporation and radiation, it is convenient, before the bell-glass *g* is placed over, to cover the funnel with a perforated glass plate, the thermometer being inserted through its perforation.

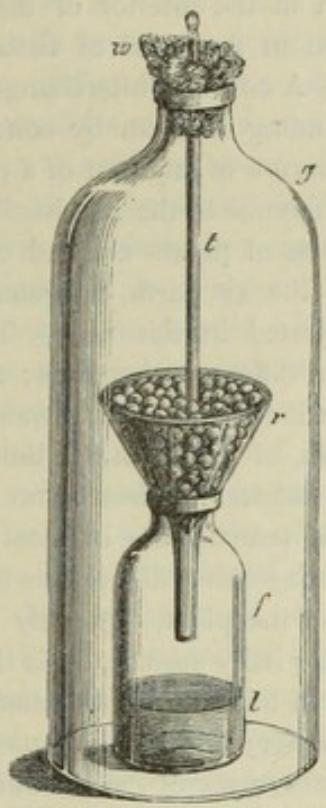

FIG. 443.—Apparatus for observing the rise of temperature in flowers and germinating seeds.

It is possible under favourable circumstances to observe by means of this contrivance a rise of temperature of 1·5° C. with 100 or 200 peas, while the roots are developing; the anthers of a flower of the gourd caused a rise of about 0·8° C. in a tolerably large thermometer with the bulb of which they were in contact on only one side. A single capitulum of *Onopordon Acanthium* produced an elevation of 0·72° C; the stamens of a single flower of *Nymphæa stellata* one of about 0·6° C. A number of flower-buds of *Anthemis chrysoleuca* heaped round the thermometer rose as they unfolded about 1·6° C.

It will be readily understood that flowers must not be used for these experiments as soon as they have been gathered; but that it is necessary to wait for some hours till they have acquired the temperature of the room. (Further details will be given elsewhere.)

CHAPTER III.

GENERAL CONDITIONS OF PLANT-LIFE.

SECT. 8. **The Influence of Temperature on Vegetation**[1] can only be investigated scientifically by observing the influence of definite and different degrees of temperature on the separate vital phenomena of plants, *i. e.* on the various processes of assimilation and metastasis, of diffusion, growth, the variations in the turgidity of the cells and tension of the tissues, on the movements of protoplasm and irritable organs and of those endowed with periodic motion, &c.

The determination of the facts which have here to be investigated depends on an accurate knowledge of the temperature of the plant in any given case, or rather on that of the part of the plant in question on which the experiment is to be made.

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[1] For more detailed proofs see my Handbook of Experimental Physiology, p. 48 *et seq.*

This is often attended with great difficulties, and is sometimes almost impossible. Independently of the changes of temperature, usually inconsiderable, caused by respiration in the interior of the plant, the temperature of each cell depends on its position in the mass of tissue and on the variations of the surrounding temperature. A constant interchange of temperature is going on between the plant and its surrounding medium by conduction and radiation which essentially determines the temperature of any part of a plant at any particular time.

In reference to the conduction of heat, it must be mentioned in the first place that all parts of plants are bad conductors; the differences of temperature between them and the air, earth, or water that is in contact with them become only very slowly adjusted in this way. The conductivity for heat is probably also always different in different directions; that in the longitudinal direction in dry wood bears the proportion to that in the transverse direction of *e.g.* 1·25 : 1 in the acacia, box, and cypress, of 1·8 : 1 in the lime, alder, and pine.

The radiation of heat is on the other hand a very frequent and rapid cause of changes of temperature in most parts of plants; the chief effect of these changes being to bring about differences between the temperature of the surrounding medium and that of the plant, especially when the parts of the plant are of small size but have a large hairy surface, as is the case with many leaves and internodes. It must be noted in this connection that the radiating power of a body is equal to its absorptive power; and that radiation depends not merely on the temperature, but also on the diathermacy of the surrounding medium.

In the aërial parts of plants, transpiration is an energetic additional cause of loss of temperature; inasmuch as water in the act of evaporation withdraws from the plant the amount of heat necessary for its vaporisation, and hence makes it colder.

In investigations of the influence of temperature on the various processes of vegetation, the phenomena noticed above must always be carefully considered It may be assumed in general that the result of their united agency is that small water-plants and the underground parts of plants have usually nearly the same temperature as that of the surrounding medium when this temperature is not subject to too great variations; but that on the other hand leaves and slender stems exposed to air are generally colder than the air; while the thick stems of woody plants are sometimes warmer, sometimes colder, in consequence of their slow conducting power. How greatly the temperature of parts of plants of considerable superficial extent may be depressed by radiation below that of the air is shown by the fact that a thermometer placed on the grass and exposed to radiation indicates on clear nights a temperature several degrees lower than one placed in the air. If the latter is only a few degrees above the freezing-point, the foliage of plants may in this manner fall below zero and suffer the effects of frost. The formation of dew on summer nights, and of the hoar-frost which is deposited in such large quantities on plants especially in the late autumn, are striking proofs of the effect of radiation in lowering their temperature. The relation of the temperature of plants to that of their surrounding medium is however very complicated when we have to do with solid bodies like trunks of trees, because the different powers of conduction in the longitudinal and transverse directions of the wood, and other causes, then cooperate with the action of radiation and of absorption of heat through the bark. In general, as has been

shown by Krutsch's beautiful experiments, the trunk is cooler during the day than the surrounding air, but warmer in the evening and night[1].

With respect to the changes of volume in masses of tissue and in individual cells as the temperature varies, nothing is known with certainty except as regards dry wood. The numbers given by Caspary as the coëfficients of the expansion of wood caused by heat depend on untrustworthy observations and on a complete misunderstanding of the phenomena which take place in the objects observed[2]. When leaf-stalks and the branches of trees become bent at temperatures far below the freezing-point, this is obviously not altogether (even if principally) caused by the different layers of tissue having different coëfficients of heat-expansion; but is mainly a consequence of the fact that the water of vegetation freezes, while the cell-walls lose water and in consequence contract more or less according to their state of imbibition and of lignification. The phenomenon depends therefore in the first place on a change in the state of imbibition and turgidity produced by different temperatures. Villari has carefully measured[3] the coëfficients of heat-expansion for different dry woods. Like the expansion caused by the absorption of water, that caused by heat is much less in the direction of the fibres than in the radial direction across the fibres; but with the difference that the coëfficients of expansion for absorption are reckoned by hundredths in the radial and thousandths in the longitudinal direction, those for heat by hundred-thousandths and millionths; so that the alterations of the dimensions of dry wood in the two directions caused by changes of temperature are about 1000 times smaller than those caused by the absorption of water. The following table is from Villari for temperatures between 2° and 34° C.:—

COËFFICIENTS OF HEAT-EXPANSION FOR 1° C.

Wood.	In radial direction.	In longitudinal direction.	Proportion.
Box-wood . .	0·0000614	0·00000257	25 : 1
Fir	0·0000584	0·00000371	16 : 1
Oak	0·0000544	0·00000492	12 : 1
Poplar . . .	0·0000365	0·00000385	9 : 1
Maple . . .	0·0000484	0·00000368	8 : 1
Pine	0·0000341	0·00000511	6 : 1

Since these numbers only hold good for dry wood, while wood as a constituent of the living plant can be observed only in the moist state, they cannot be applied directly to the explanation of the physiological phenomena due to changes of temperature; but they are nevertheless of great interest, since they give us an insight into the molecular structure of wood, especially as to its elasticity in different directions.

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[1] [According to Becquerel, trees warm surrounding layers of air during the day and a good part of the night; they begin to cool them as soon as they have attained the same temperature. The maximum temperature is reached by the air two or three hours after midday; in the tree it is reached after sunset, in summer towards 9 p.m. See Mémoire sur les fôrets et leur influence climaterique: Mém. de l'Inst. vol. XXXV, pp. 460-470.—ED.]

[2] Proceedings of the International Horticultural Exhibition and Botanical Congress held in London, 1866, p. 116.

[3] Poggendorff's Annalen 1868, vol. 133, p. 412.

Something more is known as to the influence of different degrees of temperature on the vital phenomena of plants. On this subject the important fact must first be noted that the exercise of every function is restricted to certain definite limits of temperature within which alone it can take place; *i.e.* all functions are brought into play only when the temperature of the plant, or of the particular part of the plant, rises to a certain height above the freezing-point of the sap, and cease when a definite maximum of temperature is attained, which can apparently never be permanently higher than 50° C[1]. Hence the life of the plant, *i.e.* the course of its vital processes, appears to be confined in general within the limits zero and 50° C. It must however be noted that the same functions may have very different limits between 0° and 50° C. in different plants; as is also the case with different functions in the same plant. A few examples will serve to explain this.

Since the cell-fluids, consisting of aqueous solutions often in a state of high concentration, do not usually freeze at zero, it is always possible for certain processes of growth to take place when the temperature of the surrounding air is as low as this, although this fact has not yet been sufficiently established. Uloth (Flora 1871, no. 12) observed the remarkable fact that seeds of *Acer platanoides* and of wheat which had fallen between pieces of ice in an ice-house germinated there and pushed a number of roots several inches deep into the fissureless pieces of ice. From this observation he concluded that these seeds had the power of germinating at or even below the freezing-point of water; and that the penetration of the roots into the ice is caused by the development of warmth in the seed and by the pressure of the growing roots. It seems to me however that another explanation is possible. The ice was evidently surrounded by warmer substances, such as the walls of the house, which emitted to it rays of heat. Now it is a well-known fact that rays of heat, when they strike upon bubbles of air or bodies firmly frozen into a piece of ice, warm them and melt the surrounding ice. In this way not only the seeds but also their roots were warmed by the radiation of heat which passed through the ice, and thus the particles of ice in contact with them were melted. This experiment gives us therefore no certain knowledge of the actual temperature of the germinating seeds. The statements of different observers as to the highest temperature of the water in which some of the lower Algæ grow vary greatly; and Regel's assertion is perhaps the most probable that water must be below 40° C. for plants to grow in it. I have convinced myself that a considerable number of plants are killed by an immersion for only ten minutes in water of 45 or 46° C., while flowering plants endure for a longer period an air-temperature of 48° or 49° C.; but at 51° C. lose their vitality after from ten to thirty minutes (any possible injury by drying up being of course prevented)[2]. As to the high temperatures which the spores of Fungi can endure without losing their power of germination, very different statements, some of them altogether incredible, have been made, according to which temperatures of more than 100°, even as high as 200° C.,

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[1] Sachs, Ueber die obere Temperaturgrenze der Vegetation, Flora 1864, p. 5.

[2] H. de Vries, Matériaux pour la connaissance de l'influence de la temperature, in Archives Néerlandaises, vol. V, 1870, arrived at the same results from a number of experiments on Cryptogamia and flowering water and land-plants.

would seem not to be injurious. Of ninety-four experiments which were made by Tarnowsky with all possible precautions[1], the result was that the spores of *Penicillium glaucum* and *Rhizopus nigricans* exposed for from one to two hours to air of a temperature between 70° and 80° C. germinated only very rarely, while a temperature of 82° or 84° C. altogether killed them. Spores heated in their proper nutrient fluids nevertheless entirely lose their power of germination at 54° or 55° C.[2]

The growth of parts of the embryo at the expense of the reserve-materials begins, as my experiments show[3], in the case of wheat and barley even below 50° C.; in *Phaseolus multiflorus* and *Zea Mais* at 9°·4 C.; in *Cucurbita Pepo* at 13°·7 C. But when the reserve-materials of the seed have been consumed, a higher temperature is apparently always necessary to enable growth to proceed at the expense of freshly assimilated material. The highest temperatures at which my observations indicate that germination can take place were about 42° C. in the case of *Phaseolus multiflorus*, *Zea Mais*, and *Cucurbita Pepo;* in wheat, barley, and peas about 37° or 38° C.

The lowest temperature at which the grains of chlorophyll turn green was determined for *Phaseolus multiflorus* and *Zea Mais* at above 6°, and probably below 15° C.; for *Brassica Napus* above 6° C.; for *Pinus Pinea* between 7° and 11° C. The highest temperature at which leaves already formed and still yellow turn green was for the first-named plants above 33°; for *Allium Cepa* above 36° C.

The exhalation of oxygen and the corresponding assimilation begin, according to Cloëz and Gratiolet, in the case of Potamogeton between 10° and 15° C.; in Vallisneria above 6° C. In many Mosses, Algæ, and Lichens, assimilation may possibly take place at still lower temperatures; according to Boussingault (Compt. rend. vol. 68, p. 410), carbon dioxide is decomposed by the leaves of the larch at 0°·5 to 2°·5 C., and by those of meadow-grasses at 1°·5 to 3°·5 C. The upper limit of temperature for this function has not been ascertained.

The sensitiveness and periodical movement of the leaves of Mimosa do not begin till the temperature of the surrounding air exceeds 15° C.; the periodical movements of the lateral leaflets of the leaf of *Desmodium gyrans* only at temperatures above 22° C. The upper limit of temperature for the sensitiveness of the leaves of Mimosa depends on the continuance of the warmth; in air of 40° C. they become rigid within an hour; at 45° C. within half an hour; at 48° to 50° within a few minutes, but may again become sensitive when the temperature falls. A temperature of 52° C. causes permanent loss of the power of motion, and death.

The lower limit of temperature for the motility of the protoplasm in *Nitella syncarpa* is stated by Nägeli to be zero; for the hairs of Cucurbita my observations place it at a temperature of 10° or 11° C. The upper limit is 37° C. in the case of *Nitella syncarpa* according to Nägeli; in the hairs of Cucurbita, when immersed in water of 46° or 47° C., the current is arrested within two minutes; in the air exposure

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[1] One of the most important of these precautions is to prevent with certainty the entrance of spores after the temperature has been raised in the apparatus to the required point.

[2] For further details see pt. III of the Proceedings of the Botanical Institute of Würzburg.

[3] Sachs, Abhängigkeit der Keimung von der Temperatur, Jahrb. für wissensch. Bot. vol. II, 338, 1860.—A. De Candolle in Bibliothèque universelle de Genève 1865, vol. XXIV, p. 243 *et seq.*—Köppen, Wärme und Pflanzenwachsthum, eine Dissertation, Moscow 1870.—See also further under chap. IV.

to a temperature of 49° or 50° C. for ten minutes does not stop the current. The current in the hairs on the filaments of Tradescantia ceases within three minutes in air of 49° C., beginning again when the temperature is reduced.

The absorption of water through the roots is also subject to certain limits of temperature. Thus I found that the roots of the tobacco-plant and gourd no longer absorb sufficient water to replace a small loss by evaporation in a moist soil of from 3° to 5° C.; the heating of the soil to from 12° to 18° C. suffices to raise their activity to the needful extent. The roots of the turnip and cabbage on the contrary absorb a sufficient quantity of water from soil reduced nearly to the freezing-point to replace a moderate loss by transpiration.

A second result of the observations hitherto made may be stated as follows:— The functions of a plant are assisted and accelerated in their intensity when the temperature rises above the lower limit for that function; on reaching a definite higher degree, a maximum of intensity is attained; the activity then decreasing with a further increase of temperature, until it entirely ceases at the upper limit. There is therefore no proportionality between a rise in the temperature and in the intensity of the function. Thus, according to my observations, the rate of growth of the roots of a seedling of *Zea Mais* attains its maximum at 27°·2 C., of the pea, wheat, and barley at 22°·8 C.; while an increase of the temperature of the soil beyond these points causes in each case a decrease in the rapidity of growth[1].

The sensitiveness of the leaves of Mimosa is rather sluggish between 16° and 18° C., and appears to reach its maximum at 30° C. The periodically motile lateral leaflets of the leaf of *Desmodium gyrans* oscillate, according to Kabsch, in from eighty-five to ninety seconds at 35° C., in from 180 to 190 seconds between 28° and 30° C.; at lower temperatures the oscillations are imperfect, and at 23° or 24° C. they become almost imperceptible.

The rapidity of the movement of the protoplasm in *Nitella syncarpa* attains its maximum, according to Nägeli, at 37° C.; at a higher temperature the movement ceases. In the hairs of Cucurbita, *Solanum Lycopersicum*, and Tradescantia, as well as in the leaves of Vallisneria, I found the motion of the protoplasm slow between 12° and 16° C., very rapid between 30° and 40°, slower again between 40° and 50° C.

Very great and rapid variations of temperature between zero and 50° C. have been shown by experiments made by De Vries on a number of different growing plants not to be attended with danger to life, inasmuch as no injury could be detected either at the time or afterwards. It does not however follow from this that more severe changes of temperature are without effect. It would appear rather that when a plant is generally exposed to a favourable temperature, its functions are carried on the more energetically the more constant this favourable temperature remains. This is shown by ordinary experience in horticulture, and still more by the experiments of Hofmeister (Pflanzenzelle, p. 53), and De Vries (*l. c.*) on the movement of protoplasm, and of Köppen (*l. c.*) on the growth of roots. The influence of sudden variations of temperature in producing an injurious effect

[1] Further details of this subject will be found in my treatise already named, and in De Vries and Köppen (*l. c.*). Compare also what is said in Chap. IV, on the influence of temperature on the rapidity of growth.

on the plant is however very complicated, and has not yet been thoroughly investigated. I have shown that any rapid increase or decrease of temperature is accompanied by an increase or decrease of the rapidity of growth; although, according to Köppen, the increase of growth during a long period is less when the temperature is variable than when it is constant, the mean temperature being the same in both cases.

If the upper and lower limits mentioned above are exceeded, the functions of the plant may, according to circumstances, simply come to rest, again to become active on the return of a favourable temperature, or permanent changes are brought about, resulting in injury and finally in the destruction of the cells.

Cells killed by too high a temperature or by freezing show in general the same changes as if they had been killed by poison, electricity, &c.; the protoplasm becomes stationary, turgidity ceases because the resistance of the cell-walls together with that of the primordial utricle diminishes, and allows the sap to filter out; the tissues become flaccid; secondary chemical changes of the sap produce the same dark colour as in the expressed juices; and rapid evaporation soon causes a complete drying up of the dead tissue.

The injury resulting from too high or too low a temperature may, under certain circumstances, be indirect and slow in its manifestation; this will be the case when a particular function is too highly excited or too much depressed, and thus the harmonious co-operation of the various vital processes is disturbed. Thus growth may be so excited by too high a temperature that assimilation, especially when the light is deficient, is not sufficient to supply the necessary formative material; and the transpiration of the leaves may in addition be so much increased that the activity of the roots is insufficient to replace the loss. On the other hand too low a ground-temperature may so depress the activity of the roots that even small losses by transpiration from the leaves can no longer be replaced. We shall refer in the sequel to the injuries caused immediately to the cells by too high a temperature and by the freezing and thawing of the tissues.

The destruction of the life of cells by too high a temperature depends, like freezing, on their containing water. While succulent tissues are killed below or at 50° C., air-dry seeds of *Pisum sativum* can resist a temperature of over 70° C. for an hour without losing their power of germination; of grains of wheat and maize heated to 65° for an hour, 25 p. c. germinated in one case, 98 p. c. in another case. Peas soaked in water for an hour and exposed to a temperature of 54° or 55° C. were all killed; rye, barley, wheat, and maize at 53° or 54° C. Spores of Fungi showed similar phenomena, as is seen from Tarnowsky's experiments. The cause of death appears to be the coagulation of the albuminoids of which the protoplasm is composed, and this again depends on their containing water and on other circumstances, since these render a different temperature necessary for coagulation in different cases. The decomposition of the cell-wall is perceptible only at higher temperatures; and that of starch, which only takes place between 55° and 60° C., need not be taken into consideration here, since cells which contain no starch are also killed by a higher temperature than 50° C.[1]

Freezing, or the destruction of cells by the solidifying of the water contained in them into ice and by the subsequent thawing of the latter, depends also mainly on the quantity of water in the cells. Air-dry seeds appear to be able to withstand any degree of cold without injury to their power of germination; the winter-buds of woody plants the cells of which contain a great quantity of assimilated substances but only a

[1] The statements of Wiesner (Sitzungsber. der Wien. Akad. 1821, Oct., vol. LXIV, pp. 14, 15) I am unable to understand. A variety of recent statements as to the high temperatures which the spores of Fungi are said to be able to resist without losing their power of germination are so incredible and require such critical sifting that I pass them by altogether.

small quantity of water, stand the cold of winter and frequent rapid thawing; while the young leaves at the time of their unfolding in the spring succumb to a slight night-frost. An at least equally important condition lies however in the specific organisation of the plant; varieties of the same species frequently differing in their power of resistance to cold and thawing. Some plants, like Mosses, Hepaticæ, Lichens, some Fungi of a leathery texture, the mistletoe, &c., appear in particular never to freeze; Pfitzer states that the Naviculeæ freeze between —12° and —25° C. and continue to live after thawing; while many flowering plants from a southern climate are killed by rapid changes of temperature near the freezing-point[1].

Whether the tissue of a plant can be killed simply by the solidifying of the water contained in its cells into crystals of ice is uncertain; while on the other hand it is unquestionable that in a great number of plants death is caused only by the mode in which the thawing takes place. The same tissue which retains its vitality if thawed slowly after the freezing of the water of its cell-sap, becomes decomposed if thawed rapidly after exposure to the same degree of cold. Death is therefore caused in these plants not by the freezing but by the thawing[2].

When ice is formed in the tissues of a plant, two points must be taken into consideration. The water, when about to freeze, is on the one hand contained in a mixed solution, the cell-sap; on the other hand it is retained by the force of cohesion as water of imbibition in the molecular pores of the cell-wall and of the protoplasmic bodies. Now it is an established fact in physics that a solution when freezing separates into pure water which solidifies into ice and a concentrated solution with a lower freezing-point[3]. A portion of the cell-sap-water becomes therefore by freezing more concentrated than the part which is not frozen; and chemical changes may possibly be induced, as Rüdorff has shown, by new combinations actually arising in a freezing solution. How far this circumstance must be considered in the destruction of cells by freezing and thawing is not yet decided.

What takes place in the freezing of a moistened and woollen organised body is somewhat similar to that which occurs in a freezing solution. In this case also, when the temperature falls to a certain point, only a portion of the imbibed water freezes; the rest remains as water of imbibition between the molecules of the body, which contracts, while the freezing portion of the water of imbibition separates to form ice-crystals. This phenomenon happens in a striking manner in starch-paste; a homogeneous mass before freezing, it has the appearance after thawing of a spongy coarsely porous structure, the water running off clear from its large cavities. The behaviour of coagulated albumen on thawing is exactly the same. In these cases a permanent change has clearly been brought about by the freezing of a portion of the imbibed water; the molecules of the substance which group themselves into a network containing but little water when ice is formed in paste or coagulated albumen, on thawing no longer combine with the portions of the water which separated from them on freezing into a homogeneous whole; the thawed paste is in fact no longer paste.

Even when living succulent tissue freezes, a portion of the imbibed water separates and freezes as pure water, the rest remaining as water of imbibition in the protoplasm and the cell-walls, at least as long as the temperature does not sink very low. In leaves

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[1] On the maximum of temperature which vegetation can in general bear see Göppert, Bot. Zeitg., 1871, nos. 4 and 5.

[2] The correctness of this statement is supported by a careful series of observations which I communicated to the königl. sächs. Gesellsch. der Wissensch. 1860, On the formation of crystals, &c., and which will be found also in the Landwirthschaftlische Versuchsstationen 1860, Heft V, p. 167, and in my Handbook of Experimental Physiology. I do not find that Göppert's objections (Bot. Zeitg., 1871, no. 24) affect my results; to his experiment on *Calanthe veratrifolia* quite a different explanation can be given from that suggested by him.

[3] Rüdorff, Pogg. Ann 1861, vol. CXIV, p. 63; and 1862, vol. CXVI, p. 55.

and succulent stems frozen at a temperature between $-5°$ and $-10°$ C. it is easily seen that only a portion of the water is present in the form of crystals of ice; another portion permeates the cell-walls which are not rigid but still flexible. If the congelation takes place slowly, the water assumes on the surface of the succulent tissue the form of a coating of ice consisting of densely crowded small crystals. These crystals stand at right angles to the surface of the tissue, and increase by growth at their base. A very large portion of the water of a tissue may in this way take the form of a coating of ice, while the tissue, becoming less watery, contracts in proportion[1], and loses its turgidity. This phenomenon is seen with remarkable clearness in the large leaf-stalks of *Cynara Scolymus* when they freeze slowly. The succulent parenchyma separates from the epidermis, which surrounds the former like a loose sack; the parenchyma itself splits apart in the interior so that each fibro-vascular bundle is enclosed in an envelope of parenchyma. Fig. 444 shows how the coatings of ice project from the masses of parenchyma. From pieces of the leaf-stalk which weighed 396 grammes I have collected 99 gr. of ice, which, when evaporated to dryness after thawing, left only slight traces (about 1 p. c.) of solid substance. I have often observed similar phenomena in other plants; the formation of ice is however not so regular as here. In the cavities of the

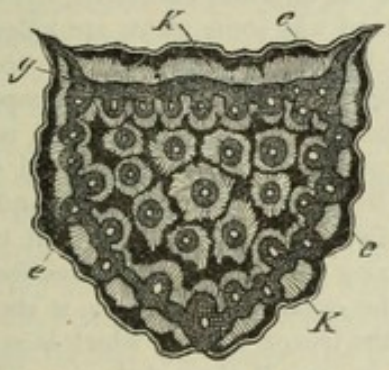

FIG. 444.—Transverse section of a slowly frozen leaf-stalk of *Cynara Scolymus*: *e* the detached epidermis; *g* the parenchyma in which lie the transverse sections of the fibro-vascular bundles (left white). It forms a tough but pliant mass, which is ruptured during the process of freezing; a peripheral layer has become separated from the inner parts which surround the bundles; the surface of each portion of the parenchyma is covered with a crust of ice *K K* consisting of densely crowded prisms (the cavities of the ruptured tissue are left black in the figure).

ruptured tissue (as in the succulent stems of the cabbage) small irregular flakes of ice are formed; sometimes the ice splits the epidermis and projects in the form of combs above the surface of succulent stems (Caspary). I have already shown elsewhere[2] that when sections of succulent parts of plants (such as the beet) are protected from evaporation and allowed to freeze slowly, continuous coatings of ice are produced on the surfaces of the section, consisting of prisms growing at the base. The formation and growth of these ice-crystals may be explained in this way. The temperature of the tissue falls to a certain point, thereby causing the freezing of an extremely thin stratum of water which overspreads the outside of the uninjured cell-walls. A new very thin stratum of water then immediately passes from the thickness of the cell-wall to its surface and also freezes, thickening the stratum of ice already formed; and thus it goes on. The cell-wall is constantly absorbing cell-sap-water from within, and at the same time allows the outermost molecular stratum of its water of imbibition to freeze. The first thin layers of

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[1] When this contraction operates unequally on different sides of a leaf or branch, it is easy to see that curvatures must result which are indeed actually frequently observed. The splitting of the trunks of trees in consequence of frost is probably only the result of changes of this nature.

[2] Sachs, Formation of Crystals in the Freezing, and change of the Cell-walls in the Thawing of Succulent Parts of Plants (Bericht der kön. sächs. Ges. der Wiss. 1860). I have already mentioned in the first edition of this work the formation of crystals in the interior of frozen plants described above, and applied it to the explanation of freezing. Prillieux (Ann. des Sci. Nat. vol. XII, p. 128) afterwards, in 1869, also described similar phenomena in a variety of plants.

ice on the exterior of the uninjured cells form polygonal plates in contact with one another; each plate becomes a prism by growth on its lower side; and the closely crowded prisms form a coating of ice which easily crumbles. These processes cause the cell-sap to become a more and more concentrated solution, while the cell-wall and the protoplasm contain a gradually diminishing quantity of water. It can now be to a certain extent understood why a rapid thawing kills the cells, while a slow thawing does not; for if the thawing take place slowly, the ice-crystals melt at their base where they touch the cell; the water as it becomes fluid is at once absorbed into the cell; and the original conditions of the cell-sap, cell-wall, and protoplasm may be re-established, if they have not been permanently impaired during the freezing. If on the contrary the coating of ice melt off very quickly, a portion of the water runs into the interstices of the tissue before it can be absorbed; the original normal degree of concentration of the cell-sap and degree of imbibition of the cell-wall and protoplasm cannot be re-established in the cells; and this may be fatal. It is evident, on the view here taken, that the danger of freezing increases with the amount of water in the tissue; for the less watery the tissue the more concentrated is the cell-sap and the larger is the proportion of water retained by the force of imbibition; only a small portion of the water can therefore form ice-crystals, and when they thaw the injurious effects are not so great.

We can now also understand why some plants are killed by being thawed too quickly when they have been frozen by very severe cold, while freezing by a moderate amount of cold is not injurious to them; for the lower the temperature falls the larger is the proportion of the cell-sap and water of imbibition that is converted into ice; the disturbance of the degree of concentration of the sap and of the imbibition of the cell-wall is always greater with the increase of the cold; and therefore the restoration of the normal condition on thawing more difficult. That the splitting asunder of whole masses of tissue during freezing such as has been described has but little effect on the continuance of the life of the organ after thawing, is shown by the fact that even the leaf-stalks of the artichoke, the frozen state of which is represented in Fig. 444, remain uninjured till the following summer if thawed slowly. These internal rupturings have as little to do with the sudden destruction of the life of the cells from cold as the splitting of the trunks of trees caused by frost, which, when the temperature falls very low, is produced by the contraction of the bark and outer layers of wood, the crevices again closing when the temperature rises.

The idea that growing plants, especially those which require a high temperature for their growth, can be directly killed by the cooling of their tissues for a short time nearly to the freezing-point is shown by H. de Vries' experiments (*l. c.*) to be fallacious. The older observations of Bierkander and Hardy that some plants of this description (*e. g.* Cucurbitaceæ, Impatiens, the potato, *Bixa Orellana*, *Crescentia Cujete*, &c.) freeze when exposed to the air at low temperatures above the freezing-point, may nevertheless be explained if it is recollected that the temperature of their tissues may fall below the freezing-point from radiation, even when that of the air is 2° or 3° or even 5° C. above it. But there is another way in which low temperatures above zero are injurious to plants from southern climates, *viz.* when the soil about the roots remains for a considerable time at this low temperature while the leaves continue to transpire. In this case the absorption of water through the roots becomes so slow that they are no longer able to replace the loss caused by evaporation from the leaves, which in consequence wither, and at length altogether dry up. It is then sufficient to warm the soil about the roots in order to revive the withered leaves; as I found in the case of plants of Nicotiana, Cucurbita, and Phaseolus grown in pots[1]. In England the branches of a vine which were made to grow into a hothouse, while the roots stood in the ground outside, withered in winter, evidently only from the low temperature of the ground; for when this was watered with warm water, the branches in the hothouse recovered.

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[1] Sachs, in Landwirthschaftliche Versuchsstationen, 1865, Heft 1, p. 195.

Among the changes caused in plants by long-continued depression of temperature, one of the most striking is the change in colour of leaves which persist through the winter, originally observed by Mohl[1], and recently more minutely studied by Kraus[2]. This change is of two kinds; the leaves either merely lose their colour and become brownish, yellowish, or rusty brown, as in Taxus, Abies, Pinus, Juniperus, and Buxus; or turn a decided red on the upper surface, as in Sedum, Sempervivum, Ledum, Mahonia, Vaccinium, &c. The loss of colour of the first group depends, according to Kraus, on a change in the grains of chlorophyll, which lose their form and definition, a cloudy mass of protoplasm of a reddish brown or brownish yellow colour being formed, while the nucleus remains colourless. These changes are usually more complete in the 'pallissade-cells' on the upper side than in the parenchyma which lies deeper. A spectroscopic examination shows that of the two pigments, a mixture of which forms, according to Kraus, the colouring substance of chlorophyll, the golden-yellow one remains unchanged, while the spectrum of the blueish-green substance undergoes a slight change.

The winter-leaves of the second group, which are coloured red or purplish-brown on the upper side, owe this colour to a rounded hyaline strongly refractive mass lying in the upper part of the pallissade-cells, which appears of a beautiful carmine-red where the leaves are red, but elsewhere of a pale yellow, and consists mainly of tannin. The grains of chlorophyll, intact and of a beautiful green, are all crowded together in the inner end of these cells. In the spongy parenchyma of the mesophyll a colourless or red mass of tannin occurs in the centre of each cell, while the chlorophyll-grains, also intact, are collected in roundish or irregular lumps, sometimes in one place sometimes in several, but always on the sides towards the adjoining cells. In these cases the colouring matter of the chlorophyll is unchanged with regard to either of its constituent pigments. The red colouring matter is soluble in water, and cannot be distinguished by spectrum-analysis from the red colouring substances of flowers.

In all leaves which persist through the winter, and in the green parts of bark, Kraus found that the grains of chlorophyll had removed from the walls to the interior of the cell, and had collected there in lumps (see Sect. 8). When the weather has become sufficiently warm in the spring, the normal condition is restored; the red colouring substance disappears, and the grains of chlorophyll again take up their normal position on the cell-walls. Kraus shows that the winter change of the leaves depends on the fall of the temperature, since it is restored to the normal state by a simple rise in the temperature, whether in the dark or the light. By taking cut branches of box into a warm room when the cold was severe and placing them in water, he found that the protoplasm of the cells, which had become homogeneous after one or two days, collected on the walls, and then divided into grains (as in the formation of grains of chlorophyll in the dark); the red colouring matter being changed first to a yellowish-green and finally to pure green. After the lapse of three, five, or at most eight days, the walls of the cells became lined with bright green sharply-defined grains of chlorophyll. In Thuja the process required two to three weeks (with me however only a few days). The restoration is therefore rather a slow process; while, according to Kraus, a single frosty night suffices to bring about the change in the form and colour of the chlorophyll-grains in the case of Buxus, Sabina, and Thuja. That light has no share in the restoration of the normal condition of the chlorophyll, is shown by the fact that it takes place also in branches which are kept in a dark room. On the other hand the fact that the parts protected by being covered by other leaves show no change of colour would seem to indicate that the whole phenomenon has less to do with the low temperature of the air than with the cooling produced by radiation.

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[1] Mohl, Vermischte Schriften; Tübingen, 1845, p. 375.

[2] Kraus, Observations on the winter colouring of evergreen plants; in the Sitzungsber. der phys.-med. Societät zu Erlangen, Dec 19, 1871, and March 11, 1872.

Convenient contrivances for observing the action of particular higher or lower temperatures on plants or parts of plants of considerable size are easily arranged[1]. It is more difficult to expose microscopic objects to a particular higher or lower temperature in such a manner that it can easily and certainly be observed, and that the temperature of the object is also that indicated by the thermometer, or nearly so. All these requirements are fulfilled by the very cheap heating apparatus for the microscope represented in Fig. 445. Since I have not only made great use myself of this apparatus for three

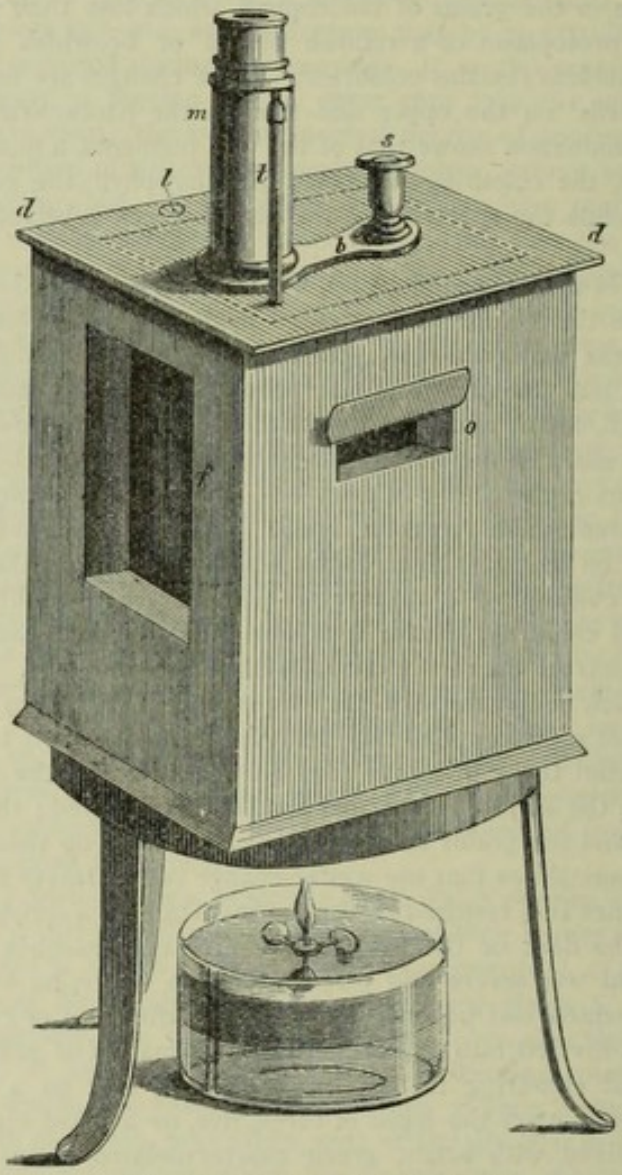

FIG. 445.—Heating apparatus for the microscope.

years, but have also recommended it to others, a description is the more in place here as it is well adapted for demonstrations in lecture rooms.

The size of the heating apparatus must vary with that of the microscope; mine is constructed for one of Hartnack's ordinary instruments. The box is nearly cubical, and has double walls of sheet-zinc at the bottom and sides, enclosing a space 25 mm. thick, which is filled with water through the hole *l*. It is quite open above; but in the front side-wall is an opening *f*, which is closed by a glass plate well fitted but not otherwise fixed. This window is sufficiently large, and is so placed that it allows enough light to fall on the mirror of the microscope which stands in the box. The height of the

[1] See Sachs, Handb. der Exp.-Phys. pp. 64, 66.

box is so arranged that the upper rim of the double wall is on a level with the arm *b* of the microscope. The opening of the box is closed by a thick cardboard cover *d d*, in which an opening is cut exactly to fit the arm *b*. By the side of the tube of the microscope a round hole is cut in the cover through which a closely fitted small thermometer *t* is passed, so that its bulb hangs near the object. The box is painted on the inside with black varnish, and a piece of cardboard moistened with water lies beneath the foot of the microscope in order to prevent its moving and to keep the air within moist. The focus is easily adjusted to the object by means of the fine adjustment *s* which projects above the cover; two openings in the side, one of which is shown at *o*, enable the slide bearing the object to be moved, when necessary, by a pair of forceps. It is still more convenient to fix the slide on a wire which goes through a cork fitted to the opening *o*.

If observations are required at a higher temperature, the water in the box is heated by a spirit-lamp placed underneath. When the temperature has reached nearly the desired point, the spirit-lamp is replaced by an oil-lamp with a floating light; the temperature will after a time become constant. In order to obtain higher or lower constant temperatures, one two or three floating night-lights are placed in the lamp. If care is taken that the combustion be uniform, the temperature in the box remains for several hours so constant that it will vary only about 1° C. This constancy of temperature ensures that the temperature of the object itself is that indicated by the thermometer.

It is easy by means of this heating apparatus to observe and demonstrate the influence of temperature on protoplasm-currents. To take observations at lower temperatures it is sufficient to enlarge the hole *l*, in order from time to time to place pieces of ice in the cold water[1].

Sect. 8.—**Action of Light on Vegetation**[2]. A. General. The entire life of the plant depends on the action of light on the cells that contain chlorophyll, this being the essential condition under which new organic compounds are formed out of the elements of carbon dioxide and water. The amount of oxygen evolved in this process is nearly the same as that required for the combustion of the substance of the plant; and the amount of work equivalent to the heat produced by this combustion gives a measure for the amount of work performed by light in the chlorophyll-containing cells of the plant.

After a certain quantity of assimilated substance has been produced under the influence of light, a long series of vegetative processes may be carried on at its expense without any further direct action of light. The growth of new organs and the metastasis connected with it kept up in the organs by means of respiration is entirely or to a certain extent independent of light, and can even be carried on in absolute darkness. This is the case in the germination of seeds, bulbs, and tubers, the development of buds from woody branches and underground rhizomes, &c. Even leafy plants which have accumulated a sufficient quantity of reserve-material in the light, put out shoots and even flowers and fruits when placed in the dark.

As the parts of chlorophyll-containing plants which are underground or other-

[1] [For further arrangements for maintaining a constant temperature under the microscope, see Stricker and Burdon-Sanderson, Quart. Journ. Micr. Sci. 1870; Schafer, ibid. 1874.—Ed.]

[2] A. P. De Candolle, Physiologie végétale, 1832.—Sachs, Ueber den Einfluss des Tages-lichtes auf Neubildung u. Entfaltung verschiedener Pflanzenorgane; Bot. Zeit. 1863, Supplement.—Sachs, Wirkung des Lichtes auf die Blüthenbildung u. Vermittlung der Laubblätter; Bot. Zeit. 1865, p. 117. —Sachs, Handb. der Exp.-Phys. 1865, p. 1.

wise excluded from light are nourished by the products of assimilation produced in the light, so also parasites and saprophytes destitute of chlorophyll live, as has already been explained, on the work performed by plants that contain chlorophyll, and are therefore dependent indirectly on light, even though the whole of their development may be completed in darkness, as in the truffle; in other instances they only emerge to unfold in the air the flowers already formed underground, and disseminate their seeds, as is the case with *Limodorum abortivum*, Epipogium, Corallorhiza, Monotropa, Lathræa, Orobanche, &c. Even many plants which do contain chlorophyll and which live on inorganic food complete their growth and the processes connected with it in complete darkness, only putting forth their green leaves at certain times for the purpose of again accumulating beneath the ground fresh formative material. This is the case with the autumn crocus, tulip, crown imperial, terrestrial orchids, and many others, and especially with plants which form bulbs, tubers, and rhizomes. If the growing end of a stem of a green-leaved plant (*e. g.* Cucurbita, Tropæolum, Ipomæa, or Hedera) is secluded from all light while the green leaves remain exposed to it, the buds develope in the dark; leaves and flowers are produced, which latter attain their full size and beauty of colour, are capable of fertilisation, and produce fruits and even fertile seeds at the expense of the substance assimilated in the light in the green leaves and carried to them by the stem.

These and a number of other facts show that growth, *i. e.* the processes by which the form of the plant is attained, and metastasis are not necessarily dependent, or only to a subordinate extent, on the influence of light, if only the necessary quantity of assimilated material has previously been accumulated.

This is a general statement of the case. If however the various separate processes of vegetation are observed—the behaviour of protoplasm, the formation, arrangement, activity, and destruction of chlorophyll, the growth of the younger and older parts, the movements resulting from the tension of the tissues, &c.—a long series of very varied facts presents itself which requires detailed consideration, because the rays of different refrangibility which are mingled in white daylight affect vegetation in a manner altogether different; certain functions are induced only by the strongly refrangible rays, others only or chiefly by those of less refrangibility. These effects moreover vary not only with the temperature but also with the intensity of the particular rays. Finally it must be observed that light affects plants only when its rays penetrate into their organs; this however modifies them in intensity and to a certain extent also in refrangibility. In every investigation of the action of light these points must therefore be kept in view. The following summarises what is at present known as to the general facts.

(1) *Action of rays of different refrangibility.* The rays of different refrangibility commingled in white sunlight which appear as variously coloured bands in the spectrum, vary in their physiological action on the processes of vegetation. Chemical changes, so far as they are in the main dependent on light, are produced chiefly or solely by rays of medium or low refrangibility (*viz.* the red, orange, yellow, or green). This is the case for instance with the production of the green colour of chlorophyll, the decomposition of carbon dioxide, and the formation in chlorophyll of starch, sugar, or oil.

On the other hand the rays of high refrangibility (the blue or violet, as well as the invisible ultra-violet rays) are the principal or the only ones which produce mechanical changes so far as these are dependent on light. It is these rays which influence the rapidity of growth, alter the movements of the protoplasm, compel swarm-spores to adopt a definite direction in their motion, and change the tension of the tissues of the motile organs of many leaves and hence affect their position.

These two laws, the result of careful observation, are only in apparent contradiction to the division of the rays of light which is current in chemistry and physics into those called chemically active, including the highly refrangible blue, violet, and ultra-violet, and the chemically inactive, or at least less active, including the less refrangible red, orange, and yellow, and partly also the green rays. This division has long been familiar; silver-salts, nitrogen terchloride, and other inorganic compounds, are powerfully acted on by the former, scarcely at all by the latter. But when it was shown that the organico-chemical processes in plants were caused mainly or solely by the latter kind of rays, it was seen that this classification into chemical and non-chemical rays resulted from an imperfect induction, and that the correct statement of the fact is rather that there are chemical processes (generally dependent on light) which are related to rays of particular refrangibility. As far as concerns the mechanical effect on the plant of the highly refrangible rays, it is at present uncertain whether they are not ultimately due to chemical changes. In any case the action is visible to the observer only in the form of mechanical effect (movements, tensions, &c.); and this is in harmony with the classification given above.

If sunlight is made to pass through sufficiently thick strata of solutions of potassium bi-chromate and ammoniacal copper oxide[1], the first only permits the passage of light consisting of the less refrangible half of the spectrum (red, orange, yellow, and some green), while the blue solution allows, in addition to some green, only the blue, violet, and ultra-violet rays to pass through. The sunlight is therefore in each case halved by the absorption in such a way that the spectrum beneath the orange solution extends from the red to the green, that beneath the blue solution from the green to the ultra-violet. If the light after passing through these fluids is directed on plants capable of decomposing carbon dioxide, and pieces of very sensitive photographic paper are at the same time exposed by their side, it is seen that the less refrangible rays of light (transmitted through the potassium bichromate) effect the decomposition of carbon dioxide and the colouring of the chlorophyll almost as energetically as white daylight, while they produce only a very slight effect on the photographic paper. The growth of seedlings, on the contrary, proceeds in this light exactly as in the dark, although the leaves turn green. Conversely the light which had passed through the ammoniacal copper oxide had very little effect in decomposing carbon dioxide, although the action on photographic paper was very vigorous. The growth of seedlings was on the contrary the same as in white light; and the mechanical process of heliotropic curvature was

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[1] Sachs, Bot. Zeit. 1864, p. 253 *et seq.*, where the labours of previous observers are referred to in detail.

very manifest. A number of more recent observations have confirmed and extended the results previously obtained[1].

(2) *Variation in the action of light on plants in proportion to its intensity*[2]. That the action of light on vegetation varies with its intensity, as that of temperature with its elevation, does not admit of a doubt, and agrees with the observed facts of vegetative physiology. There can scarcely be said, however, to be any exact investigations on this point; and the great obstacle to their accomplishment is that we have at present no method of measuring the intensity of rays of light of any particular refrangibility in terms of a fixed unit which can be applied to plants. As far as concerns the highly refrangible rays, *i.e.* those which have the greatest mechanical effect, we are compelled to adopt the photo-chemical method of Bunsen and Roscoe[3], which however gives no information respecting the different intensity of the red, orange, and yellow light, and can only be applied with great difficulty to experiments on vegetation. In the photometry of the less refrangible rays, on the contrary, we can always have recourse, according to the ordinary method, to the sensitiveness of the eye, *i.e.* to brightness, which cannot be considered in itself an actual objective measure of the intensity of the light, though it must under certain circumstances depend upon it. In describing the relation between the intensity of light and vegetation, we have therefore at present, with a few exceptions, to employ the ordinary expressions dark, dull, bright, dazzlingly bright, &c. There is one case in which this relation between the subjective sensitiveness of the eye and the action upon vegetation of the light which causes it can be very strikingly proved; Pfeffer has shown that the curve of the subjective sensitiveness of the eye for the colours of the solar spectrum coincides exactly with the curve expressing the power of different regions of the spectrum in decomposing carbon dioxide[4]. This coincidence must however at present be considered purely accidental[5], and cannot be extended to other phenomena. If the sunlight or diffused daylight which reaches the observer were always of the same intensity, it would be easy to regulate artificially, according to definite gradations, the intensity of the light that acts on the plant. But since the light of incandescent bodies (such as the Drummond's light[6]) contains the same rays as sunlight and acts similarly on the functions of plants, constant sources of light of a definite intensity can in this way be arranged, which will admit of gradual adjustment, in order to study the influence on vegetation of light of different intensities.

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[1] I have replied, in the second part of the 'Arbeiten des botan. Inst. in Würzburg,' 1872, to the objections urged by Prillieux to this statement, which rest on an entire confusion of the ideas Intensity of Light (objective), Brightness (subjective), Refrangibility (an objective), and Colour (a subjective property of light).

[2] With respect to the distinction which must here be borne in mind between the objective intensity of light and its brightness to the eye, see the paper quoted above and the literature there referred to.

[3] See the admirable paper by Wolkoff in the Jahrb. für wiss. Bot. vol. V, p. 1.

[4] Pfeffer in Sitzungsber. der Ges. zur Beförderung der ges. Naturwiss. für Marburg, 1872, May 16.

[5] See note on p. 669.

[6] See Hervé Mangon, Comp. rend. 1861, p. 243.—Prillieux, ibid. 1869, p. 408.

If we now turn to the observations on record, those of Wolkoff are the only ones in which actual measurements have been made. With the assistance of the photometric method contrived by Bunsen and Roscoe[1], he showed first of all that changes in the intensity of the highly refrangible light do not stand in any appreciable relation to the exhalation of gas by water-plants. This is an additional proof that these rays play only an extremely small part in this process, so small indeed that in the experiments the actual effect might be concealed by other causes (see p. 667). He next used as the source of light a dull glass plate illuminated by daylight, at different distances from which he exposed the plants (Ceratophyllum, Potamogeton, *Ranunculus fluitans*) in a dark room; and he ascertained that the exhalation of gas was, within certain limits, nearly proportional to the intensity of the light[2]. There is probably however some particular intensity of the efficient rays at which a maximum of gas is exhaled, and above which the rapidity of the process again decreases and the plant suffers injury; but whether this maximum intensity of light is attained or exceeded by the sunlight as it falls on the surface of the earth cannot at present be determined. In reference to the smallest degree of intensity of light at which exhalation of gas can still take place, we have only the statement of Boussingault that a leaf of oleander ceased to exhale oxygen after sunset[3].

The green colour of the chlorophyll of Monocotyledons and Dicotyledons is not produced in the dark, as may be seen by enclosing plants in closely shutting boxes of wood or metal, or in a dark cellar. The colouration begins however when the amount of light is barely sufficient to read a book by; and when it increases to the ordinary brightness of a sunny summer day, the rapidity of the change increases, and the colour becomes a deeper green than that produced when plants are placed for a longer time in places not so strongly illuminated. Famintzin nevertheless showed[4], in the case of *Lepidium sativum* and *Zea Mais*, that bleached seedlings become green more slowly in direct sunlight than in diffused daylight.

The small intensity of light which suffices for the formation of chlorophyll is not sufficient for assimilation or for the formation of starch in the chlorophyll. Plants (such as Dahlia, Faba, Phaseolus, Cucurbita, &c.), which rapidly become green in the normal condition of full daylight, as well as in the diffused light of the back of a room, still form no starch in their chlorophyll. They do however produce chlorophyll in a window where, at the most, they enjoy but half the direct sunlight and diffused daylight; but, in harmony with this, the assimilation of these plants is much less active in the window than in full daylight in the open air[5]. The following experiment gives a somewhat more precise result. Four plants of *Tropæolum majus* grown from seed in the back of a room, all gave, when dried at 110°C., a smaller weight than the seed; they had not assimilated, and died after

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[1] Bunsen and Roscoe: Pogg. Ann. vol. 108.

[2] See also Pfeffer: Arbeiten des botan. Inst. in Würzburg, Heft 1, p. 41.

[3] Comp. rend. vol. 68, p. 410.

[4] Famintzin, Mélanges biologiques; Petersburg. vol. VI, p. 94, 1866.

[5] Sachs, Bot. Zeit. 1862, No. 47; and 1864, p. 289 *et seq.*

consuming the reserve-material, although in the shade of the room they all produced green leaves. Four other plants of the same species which germinated at the same time grew for three months, exposed for only seven hours each day to the diffused light of a west window in the forenoon; they weighed when dry nearly 5 grammes. Four other plants which were exposed in a west window from 1 p.m. till the following morning, and therefore to the afternoon sunshine, weighed also only 5 grammes; while four other plants which stood in the window during the same time day and night produced nearly 20 grammes each of dry substance[1]. It is a necessary conclusion from the increase in weight of these plants, that in the diffused daylight of the window of a room carbon dioxide is decomposed by the cells which contain chlorophyll; although this does not take place with great activity. The same conclusion is drawn from the observation that *Vallisneria spiralis* and *Elodea canadensis* give off bubbles of gas when the light falls on them for only a rather short time from the northern sky on a clear day, although the exhalation is much more rapid in direct sunlight. In the case of most plants which grow in full daylight, especially our cultivated plants, the increase of weight by assimilation is greatly diminished when they are grown in a window. Within a room itself they usually become exhausted by their own growth in consequence of the defective assimilation, which is not sufficient to replace the material consumed in growth and in respiration; and the plant ultimately dies. Many Mosses on the other hand, and wood-plants of various kinds which grow in the deep shade (as the wood-sorrel), are killed by constant exposure to broad daylight; but whether in these cases it is the intensity of the light or the transpiration that is too great, and which of the two is the direct cause of injury, is unknown. Stems which attain an enormous length in complete darkness remain perceptibly shorter in the shade of a room; in a window their growth is still less, and least of all in the open air in full daylight. The reverse is the case with the leaves of Dicotyledons and Ferns; in the dark they are often very small; in deep shade they are considerably larger, and still more so in a light window; in this position they even appear in many plants (Phaseolus, Begonia, &c.) to attain their maximum of superficial development, remaining smaller in the open air[2].

(3) *Penetration of the rays of light into the plant.* In order to determine the dependence on light of certain phenomena of vegetation, it is of special interest to know the depth to which rays of a given refrangibility can penetrate any tissue of a plant, and the intensity with which the different elements of daylight act on particular internal layers. With the exception of the underground parts of plants, stems enveloped in bark, young organs enclosed in leaf-buds, and the like, which are in complete darkness, the assimilating and growing organs are penetrated by

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[1] Sachs, Exp.-Phys. p. 21. It must however be observed that the shorter the duration of the light in these cases, the longer was the time of their exposure to the dark in which they again lost a portion of the assimilated substance by respiration.

[2] The statement made by Famintzin (Mél. biol. vol. VI, p. 73, 1866) that the motile Algæ, *Chlamydomonas pulvisculus*, *Euglena viridis*, and *Oscillatoria insignis* turn both from direct sunlight and deep shade to a light of medium intensity, is contradicted by Schmidt (quoted *infra*), who found that they always turn to light of greater intensity, and even to direct sunlight. The method of observation of both authors was however very imperfect.

light. The deeper the light penetrates, the more does it lose in intensity by absorption, reflexion, and dispersion. This loss however affects the different elements of white light in very different degrees, as was shown by my investigations made in 1859[1], at present the only ones on this subject. The rays of greatest refrangibility are in general almost entirely absorbed by the superficial layers of tissue, while the red light penetrates most deeply. Of successive layers of an apple, gourd, succulent stems, &c. only the outermost receives the light that falls on it unchanged (independently of the reflexion from the surface); each deeper layer is penetrated by light less intense than the preceding one, and of a different composition. This change in the light which penetrates the tissue is principally caused by colouring materials, especially chlorophyll, which have an absorptive power for particular groups of rays, allowing others to pass through, and producing in addition rays by fluorescence which were not contained in the incident light. But the relations of these changes of light in the tissues to the changes which the light causes are not yet accurately known; not even in reference to chlorophyll, to which we shall again recur. What we have now said is intended only to draw the attention of the student to the subject; more exact investigations must be made in working out the different questions which arise.

B. Special. (1) *Chemical Action of Light on Plants.* (*a*) *Formation of Chlorophyll*[2]. By the formation of the grains of chlorophyll the protoplasm becomes differentiated into a colourless homogeneous part which forms the proper motile or protoplasmic body of the cell, and into smaller distinct green portions which remain imbedded in the former, the grains of chlorophyll. This process, as far as concerns the differentiation, is independent of light, at least in flowering plants, where the chlorophyll-grains are formed in the cells of the leaves even in the dark. The chemical process, on the contrary, by which the green colour is produced has a complicated dependence on light. If, for instance, the temperature is sufficiently high, the green colouring substance is formed in the cotyledons of Conifers and in the leaves of Ferns in complete darkness as well as under the influence of light[3]. In Monocotyledons and Dicotyledons, on the contrary, the grains of chlorophyll which are formed in the dark remain yellow, until they are exposed to light even of small intensity, when they become green if only the temperature is sufficiently high; and the nearer, as I have shown, the temperature approaches a definite maximum (25 to 30° C.) the quicker does the chlorophyll of Angiosperms become green in the light. Provided therefore that the temperature is favourable, the chlorophyll in the cotyledons of Conifers and the leaves of Ferns does not require light in order to assume its green colour; while that in Angio-

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[1] Sachs, Ueber die Durchleuchtung der Pflanzentheile; Sitzungsber. der Wien. Acad. 1860, Vol. 43; and Handb. der Exp.-Phys. p. 6.

[2] Sachs, Bot. Zeitg. 1862, p. 365, and Exp.-Phys. pp. 10 and 318.—Sachs, Flora 1862, p. 213, and 1864, no. 32.—Mohl, Bot. Zeitg. 1861, p. 238.—Böhm, Sitzungsber. der Wiener Akad. vol. II. Compare also Book I. sect. 6 of this work.

[3] P. Schmidt (Ueber einige Wirkungen des Lichts auf Pflanzen; Dissertation, Breslau 1870, p. 22) believes that these facts can be at least partially combated; but his experiments only prove that the chlorophyll which is formed in the dark is again destroyed by long exposure to dark at a high temperature (33°·7 C.), as is also the case with other plants.

sperms does require it; and in both cases the change does not take place at low temperatures (see p. 651).

It may be concluded from such observations as have been made that all the visible parts of the solar spectrum have the power of turning the etiolated grains of chlorophyll of Angiosperms green; but that the yellow rays and those nearest to them on each side are the most powerful; and that this is also the case with the exhalation of oxygen from cells containing chlorophyll [1].

(*b*) *The Decomposition of carbon dioxide* in cells containing chlorophyll, on which depends the assimilation of plants, and which is perceptible externally by the exhalation of a volume of oxygen nearly equal to that of the carbon dioxide absorbed, is brought about under favourable circumstances (see p. 651) by rays of light. In submerged water-plants the gas (always mixed with a larger or smaller quantity of nitrogen) escapes in the form of bubbles from wounds, especially transverse cuts of the stem; and it has been shown by Pfeffer and myself that when their size is constant the rapidity of these bubbles, *i. e.* the number of them formed in a unit of time, may even be used to give an exact measurement. In observations on land-plants it is on the other hand necessary to expose the leaves to light together with air containing carbon dioxide in glass vessels of a suitable size and form, and to measure the quantity of gas by a eudiometer.

The smallest intensity of light necessary for the evolution of oxygen is—judged by the subjective measure of its brightness to our eye—rather considerable (see p. 664). This evolution is always taking place with considerable energy in diffused daylight, even when the rays reach the plant only from a small portion of the sky; but it is much stronger in direct sunlight.

The specific effect on the evolution of oxygen of the variously refrangible elements of sunlight, in other words of the different coloured bands of the solar spectrum, has been carefully investigated by Draper and very recently again by Pfeffer [2]. The observations were made partly with the solar spectrum, partly with solutions of different colours which transmitted light of a particular refrangibility. The amount of gas exhaled was measured partly by the eudiometer, partly by the number of bubbles. Pfeffer showed first of all 'that each portion of the spectrum exercises a specific quantitative influence on the power of assimilation; and that this remains unchanged whether the particular rays act separately on the parts of plants that contain chlorophyll, or combined with some or with all the other rays of the spectrum.'

The following additional result was also obtained from Draper's and Pfeffer's observations, and from mine already quoted:—'Only those rays of the spectrum which are visible to our eye have the power of decomposing carbon dioxide; and indeed those which appear brightest to the eye, the yellow rays, are alone as

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[1] See in particular Guillemin, Ann. des Sci. Nat. 1857, vol. VII, p. 160.

[2] Draper, Annales de chimie et de physique 1844, p. 214 *et seq.*—Pfeffer, Arbeiten des Botanischen Instituts in Würzburg, Heft I, p. 48, where reference is also made to the whole of the rest of the literature.—Pfeffer, Sitzungsber. der Gesellsch. zur Beförderung der gesammt. Naturwiss. zu Marburg 1872, May 16; and Bot. Zeitg. 1872, no. 23 *et seq.*, where the paper by Müller, Botanische Untersuchungen, Heft I, Heidelberg 1871, is also discussed.

efficacious in this process as all the others put together. The most refrangible rays of the visible spectrum, and those which act most energetically on silver chloride &c., play a very subordinate part in the process of assimilation.'

Draper placed glass tubes filled with water saturated with carbon dioxide in which he had placed green parts of plants, in the different coloured portions of a solar spectrum. Seven of these tubes were exposed simultaneously in the same spectrum. The following table gives the result of two experiments of this kind:—

Part of the Spectrum.	Gas evolved.	
	Experiment I.	Experiment II.
Dark-red	0·33	0·0
Red-orange	20·00	24·75
Yellow-green	36·00	43·75
Green-blue	0·10	4·10
Blue	0·0	1·00
Indigo	0·0	0·0
Violet	0·0	0·0

Pfeffer experimented chiefly on leaves of the cherry-laurel and oleander, which were placed in air containing carbon dioxide (shut off by mercury) in suitable glass vessels, and received the sunlight through coloured solutions (tested by the spectroscope). The following was the result of sixty-four experiments:—If the amount of gas evolved in light which has passed through a stratum of water of standard thickness is represented by 100, the numbers here given are the corresponding quantities of carbon dioxide decomposed in light which has passed through equal thicknesses of the solutions named.

Solution.	Colour of light.	Amount of carbon dioxide decomposed.
Potassium bichromate	Red, orange, yellow, green	88·6
Ammoniacal copper oxide	Green, blue, violet	7·6
Orcin	Red, orange-green, blue, violet	53·9
Aniline-violet	Red, orange-blue, violet	38·9
Aniline-red	Red, orange	32·1
Chlorophyll	Red-orange, yellow, green	15·9
Iodine solution	Quite dark	14·1 (carbon dioxide produced).

From a comparison of these numbers Pfeffer deduced the following values for the decomposing power of the different regions of the spectrum, the action of white light being again placed at 100:—

For Red-orange	32·1
Yellow	46·1
Green	15·0
Blue-violet	7·6
	100·8

and from these is deduced the first statement of Pfeffer given above.

If these values are erected as ordinates upon the solar spectrum, taking its corresponding parts as abscissæ, the result, as shown in Fig. 446, is that the curve of the different powers of light for causing evolution of gas corresponds in the main with the curve of subjective brightness of the same regions of the spectrum; but has no relation to the curve of heating power.

Pfeffer's experiments had shown that the method first employed by me for determining the intensity of the action of light on water-plants, *viz.* counting the number of the bubbles of gas given off in a unit of time, gave nearly the same results as actual measurement of the gas, the result being in fact somewhat too great, and inexact in inverse proportion to the amount of gas given off. I then applied this method to determine the amount of oxygen given off from a small-water-plant (*Elodea canadensis*) when exposed to a portion 13 mm. in breadth of a

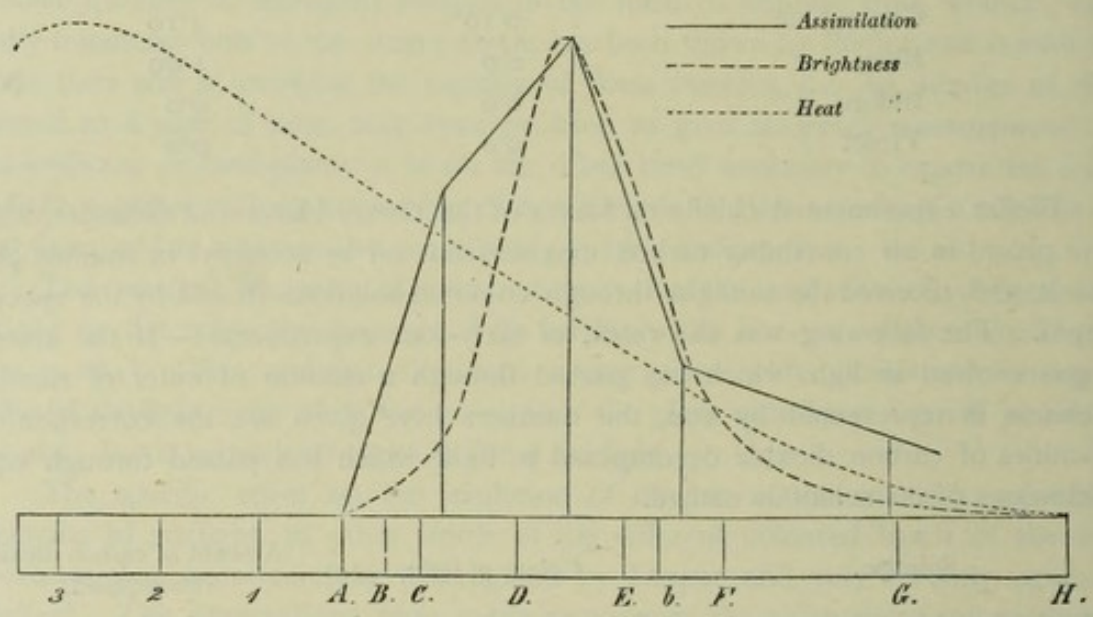

FIG. 446.—Graphic representation of the efficacy of rays of different refrangibility in causing the evolution of oxygen, compared with their brightness and heating power. The solar spectrum *A*—*H* serves as a base, on which lines to represent the three different effects are erected as ordinates; the three curves are thus obtained which represent assimilation, brightness, and heat.

very intense solar spectrum 23 cm. long. In this experiment I had the advantage of being able to determine the amount of gas given off by the same plant in all the regions of the spectrum in successive very short spaces of time, and thus avoiding various errors of observation which inevitably accompany eudiometric observations, or at least are very difficult to get rid of. A number of observations conducted in this manner gave the following result as the mean capacities for decomposition possessed by the different regions of the solar spectrum, yellow being placed at 100:—

Red	25·4
Orange	63·0
Yellow	100·0
Green	37·2
Blue	22·1
Indigo	13·5
Violet	7·1

If allowance is made for the small error mentioned above incident to the method of counting the number of bubbles, we find that the curve of capacity for exhaling oxygen agrees still more exactly with the curve of brightness than is represented in Fig. 446, which was drawn from only a few data obtained with difficulty.

Since a comparison of the curve of brightness with that of the evolution of oxygen, otherwise convenient, has turned the attention of observers in a wrong path, and has led to many erroneous theories, it will be convenient to state the only relation between the two with which we have to do here, in the following terms: — The evolution of oxygen caused by chlorophyll is a function of the length of the waves of light; only those wave-lengths which are not greater than 0·0006866 mm. and not less than 0·0003968 mm. being able to produce this effect. Starting from the two extremes, the capacity of light for causing evolution of oxygen rises till it reaches its maximum at a wave-length of 0·0005889 mm. It will be at once seen that we have here a similar phenomenon to that of the relation of vegetation to temperature; for we found (see p. 652) that this function also rises with the rise of temperature, attains a maximum at a definite temperature, and again decreases as the temperature rises still higher[1].

(*c*) *Formation of Starch in the Chlorophyll*[2]. The yellow chlorophyll-grains formed in the dark are small; after turning green on exposure to light they become considerably larger, corresponding to the increase in size of the cells in which they are contained. It is only after they have assumed their green colour and under the continued action of more intense light, in other words under conditions favourable to assimilation, that the formation commences of the starch which is enclosed within the chlorophyll-grains (see p. 46). When cells whose chlorophyll has already produced starch on exposure to light are again placed in the dark, the starch is absorbed and disappears completely from the chlorophyll-grains, and does so the quicker the higher the temperature. If light is again allowed access starch is again formed in the same chlorophyll-grains; and the formation of starch is therefore a function of chlorophyll exposed to light, its absorption a function of chlorophyll not exposed to light. If complete or partial darkness is continued for a length of time, the chlorophyll is usually itself destroyed; it first loses its form, is then absorbed, and finally disappears from the cells together with the colourless protoplasm; in the case of leaves of rapidly growing Angiosperms this takes place after a few days when the temperature is high. Cactus-stems with slow growth and the shoots of Selaginella on the contrary remain green for months in the dark.

The absorption and re-formation of starch in the chlorophyll—a process which I was the first to demonstrate in the leaves of Phanerogams—can be seen more readily in Algæ of simple structure like Spirogyra, which may therefore serve for purposes of investigation. I had already shown that the formation of starch in

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[1] The same law of dependence is also evidently applicable to the sensitiveness of the eye to brightness; and this is the cause of the curve of the brightness of light running nearly parallel to that of the evolution of oxygen.

[2] Sachs, Ueber die Auflösung und Wiederbildung des Amylums in den Chlorophyll-körnern bei wechselnder Beleuchtung: Bot. Zeitg. 1864, p. 289.

chlorophyll depends on conditions which favour assimilation, and that assimilation proceeds vigorously in light transmitted through potassium bichromate, and consists therefore of red, orange, yellow, and to a certain extent green rays; while the more strongly refrangible half of the spectrum, consisting of green, blue, violet, and ultra-violet rays, obtained by passing the light through ammoniacal copper oxide, has only a very slight effect. The conclusion at once followed from this, that the formation of starch must take place in the set of rays first named to the same extent that it does in full sunlight, but only to a very small extent in the latter set. This was confirmed by Famintzin's experiments[1], in which he found that in Spirogyra the formation of starch in the chlorophyll took place only in the mixed yellow light (that had passed through potassium bi-chromate), and not in the mixed blue light (that had passed through ammoniacal copper oxide), in which the starch already formed even disappears. Since however a small exhalation of oxygen takes place even in the mixed blue light, it must be supposed that a small production of starch occurs in it. Kraus's experiments[2] with Spirogyra, Funaria, and Elodea, confirm this. He also found that in plants of Spirogyra which had lost their starch from exposure to dark, the formation of this substance in the grains of chlorophyll recommenced in five minutes in direct sunlight, in two hours in diffused daylight. In funaria the formation of starch recommenced in the same manner within two hours in direct sunlight, within six hours in diffused daylight; and similar results were obtained from leaves of Elodea, Lepidium, and Betula[3].

(2) *Mechanical Action of Light on Plants.* (*d*) *The influence of light on the movement of protoplasm* varies according to the nature of the motion. Those movements which are the cause of the formation of new cells are not in general directly dependent on light (see p. 673); since they take place, in the great majority of cases, in partial or complete darkness. The 'streaming' motion of the protoplasm in older cells, or rotation and circulation, also goes on in continuous darkness as well as in alternate daylight and night; and even in the hairs of etiolated

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[1] Famintzin, Action of Light on Spirogyra; Mélanges biologiques, Petersburg 1865, Dec.; and 1867, p. 277.

[2] Kraus, Jahrb. für wissensch. Bot. vol. VII, p. 511.

[3] In accordance with the theory propounded by me that the starch formed in the chlorophyll-grains under the influence of light is the first product of assimilation produced by the decomposition of carbon dioxide, Godlewski has found (Flora, 1873, p. 383), as the result of experiments as simple as ingenious, that in an atmosphere devoid of carbon dioxide no starch is produced in the chlorophyll-grains even in the dark; that the starch contained in the chlorophyll disappears when the carbon dioxide is removed from the surrounding atmosphere, not only in the dark, but even in bright light. It may be inferred from this that the starch which is at any time found in the chlorophyll is only the excess of the whole product of assimilation which has not yet been taken up. Of especial importance is his observation, which agrees with his eudiometrical experiments, that an increase in the proportion of carbon dioxide in the atmosphere to 8 p.c. in a bright light increases the rapidity of the formation of starch four or five fold, while in a diffused light the action is much less. A very large quantity of carbon dioxide in the atmosphere, on the contrary, retards the formation of starch in inverse proportion to the intensity of the light. Godlewski's experiments, made on the cotyledons of seedlings of *Raphanus sativus*, are also opposed to the statement of Böhm (Sitzungsber. der Wien. Akad. March 6, 1873), that the starch contained in the chlorophyll is not a product of assimilation, a view which has already been sufficiently refuted by my earlier investigations.

shoots which are developed in darkness[1]. It has not been ascertained whether in these cases the rapidity and direction of the movement, the mode of distribution of the currents, and the accumulation of the protoplasm at particular spots, are influenced by the direction of the rays of light. An influence of this kind is apparently exercised by light on the plasmodia of Aethalium. As long as the plasmodia are still in motion and not ripe for the production of spores, they appear on the surface of the tan when it is dark; but in the light, as in a sunny window, they again conceal themselves in the dark parts of the tan,—a process which the plant may be made to repeat two or three times in a day. It is not till the plasmodium has collected into a thick firm mass, and is preparing for the production of spores, that it comes to the surface in places exposed to light, but apparently only in the night or early morning.

The protoplasm which envelopes the grains of chlorophyll in the green leaves of Mosses and Phanerogams and in the prothallia of Ferns, is induced, by the varying intensity of the light, to accumulate to a greater or less degree at different parts of the cell-walls, carrying the grains of chlorophyll along with it, and thus altering their distribution in the cell. It is still uncertain whether in this case the light affects the protoplasm only, the grains of chlorophyll being carried passively along with it; or whether the influence of the light is not first of all on the latter, which then give the impulse to the protoplasm. In either case it appears certain that the grains of chlorophyll do not of themselves possess any power of free motion, but are carried about by the motile protoplasm. Famintzin and Borodin[2] found that under the influence of continued partial darkness the chlorophyll-grains in various Mosses and in the prothallia of Ferns collect on the side-walls of the cells (those at right angles to the surface of the organ); and that when these parts are exposed to light they leave them and distribute themselves over the parts of the cell-walls which are parallel to the surface of the organ. Prillieux[3] and Schmidt have confirmed these statements. The view which I adopted long ago (see the first and second editions of this work), that these changes of position in the chlorophyll-grains are caused by the protoplasm, is confirmed by Frank's recent researches[4]. He shows that when the light falls only from one side, the protoplasm and the grains of chlorophyll collect mostly on those parts of the cell-walls on which the strongest rays fall, if the cells are sufficiently large to allow the light to be so arranged, and these changes to take place in the position of their contents (as in the prothallia of Ferns and leaves of Sagittaria). Frank brought under a general point of view the changes in position of the grains of chlorophyll described by Famintzin and Borodin; he shows that the protoplasm in these cells is capable, according to circumstances, of adopting two different modes of distribution. In one mode, which he calls Epistrophe, the protoplasm and chlorophyll-grains collect on the free cell-walls, *i. e.* those which do not immediately adjoin other cells; for

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[1] Sachs, Bot. Zeitg., 1863, Supplement.

[2] Bohm, Sitzungsber. der Wien. Akad. 1857, p. 510.—Famintzin, Jahrb. für wissensch. Bot. vol. IV, p. 49.—Borodin, Mélanges biologiques; Petersburg, vol. VI, 1867.

[3] Prillieux, Compt. rend. 1870, vol. LXX, p. 60.—Schmidt *l. c.*

[4] Frank, Bot. Zeitg. 1872, Nos. 14, 15; and Jahrb. für wissensch. Bot. vol. VIII, p. 216 *et seq.*

instance, next the surface in the superficial cells of organs consisting of several layers (the leaves of Sagittaria, Vallisneria, and Elodea); on the upper and under walls in organs consisting of only one layer of cells (leaves of Mosses, prothallia of Ferns); and on the parts that bound the intercellular spaces in internal cells. This is the position assumed in the normal conditions of vegetation and the mature state of the cells, but before they become too old. The second mode, or Apostrophe, takes place under unfavourable external conditions; as for instance in small fragments of tissue, when respiration is defective, turgidity diminished, the temperature too low, the cells too old, or—what is of most interest here—when light is cut off for a considerable time. Under these circumstances the protoplasm and chlorophyll-grains collect chiefly on the walls that are not free, *i. e.* on those adjacent to other cells. The occurrence of apostrophe under direct sunlight which Borodin asserts[1] (in various Phanerogams as Lemna, Callitriche, and Stellaria), is denied by Frank, who maintains that what takes place in these cases is rather a collection of the protoplasm at the spots where the light is strongest, which may happen to be at the sides.

It is evidently these aggregations of chlorophyll-grains on the side-walls of the cells caused by sunlight which were observed by Borodin that produced the phenomenon pointed out by Marquard and more exactly described by myself[2], *viz.* that green leaves (*e. g.* those of Zea, Pelargonium, Oxalis, Nicotiana, &c.) when exposed to sunlight assumed a bright green colour in a shorter time than in diffused light or in deep shadow. This can be made very evident by shading particular parts by pressing closely on them a strip of lead or tinfoil; if this strip is removed after five or ten minutes, the parts that were shaded show a dull green, those exposed to the sun a bright green colour. It is obvious that the tissue will appear to the eye a deeper green in proportion as the green grains are distributed uniformly over the surfaces facing the eye, a less deep green in proportion as they collect on the side-walls. Borodin's observations directly confirm this hypothesis. This alteration in the grouping of the grains of chlorophyll which accompanies a change in the intensity of the light is caused only by the highly refrangible rays; the less refrangible rays (the bright and red ones) have the same effect as darkness[3]. It results therefore, as I showed in 1859, that if a strip of blue glass is laid on a leaf exposed to sunshine, it will produce no change of colour, while one will be caused by a strip of red glass.

Since these movements of the grains of chlorophyll are produced by the colourless protoplasm in which they are imbedded, it might be expected that the protoplasm of hairs which contain no chlorophyll or only a small quantity would be similarly influenced by the colour and intensity of the light. But the statements of Borscow and Luerssen[4] which might be interpreted in this direction at least to some extent have not been confirmed by the observations of Reinke[5].

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[1] Borodin, Mélanges biol., Petersburg, 1869, vol. VII, p. 50.

[2] Sachs, Berichte der math.-physik. Klasse der k. sächs. Ges. der Wiss. 1859.

[3] Borodin, *l. c.*; Frank, Bot. Zeitg. 1871, p. 238.

[4] Borscow, Mélanges biol., Petersburg 1867, vol. VI, p. 312.—Luerssen, Ueber den Einfluss des rothen u. blauen Lichts u. s. w., Dissertation, Bremen, 1868.

[5] Reinke, Bot. Zeitg., 1871, Nos. 46, 47.

The swarming of zoospores is also connected with protoplasmic movements. Their motile organs, the cilia, are supposed to be themselves only slender threads of protoplasm, by the vibration of which both the rotatory and the advancing movement of the zoospores is caused. The axis of rotation becomes subsequently the axis of growth; the anterior end in the advancing motion (where the zoospore is usually narrower, hyaline, and provided with cilia), becomes the base of the germinating plant when the zoospore has come to rest. These movements of zoospores and the very similar ones of Volvox are affected by light to this extent, that when the light comes from one side they either tend towards or away from the source of light, this depending apparently partly on the species and partly on the age of the individual. Here also Cohn states that the less refrangible rays have the same effect as darkness, while the direction of the motion is determined by the blue and therefore more highly refrangible rays[1].

(*e*) *Cell-Division and Growth*[2]. The first formation and early growth of the new organs in the higher plants consisting of masses of tissue is the result of a great number of cell-divisions, which usually take place in complete darkness; as, for example, in the roots of land and marsh-plants, the buds on underground rhizomes, and leaves and flowers which are produced within the dense envelopes of the bud. Cell-formation of the same kind may however take place under the influence of light which may even be intense, as is shown by the growth of the roots of land-plants in water exposed to light, or that of the aërial roots of Aroideæ (which are highly transparent at their cell-forming apex). The formation of stomata and hairs which is the result of cell-division may take place either in the light or in complete darkness within the bud, without any essential difference being observable in the two cases. In the same manner the cambium of the trunks of trees is covered by completely opaque envelopes, such as bark; while that of many annual stems (as Impatiens) is exposed to the light which penetrates the thin succulent cortex. Similar phenomena are presented in the formation and ripening of ovules within transparent or completely opaque ovaries. They are most obvious when shoots or even flowers which under ordinary circumstances are developed in the light are made to grow in complete darkness from bulbs, tubers, or seeds. The small variations from the normal condition which occur in such cases do not affect the early development of the organs; but their later growth which does not depend on cell-division is necessarily interfered with, as well as the development of chlorophyll. An obvious and necessary condition of these processes of growth, whether in the dark or the light, is the presence of a supply of assimilated reserve-materials, at the expense of which the formation of new cells can take place. In the case of the buds of the higher plants their reservoirs of reserve-material are the bulbs, tubers, rhizomes, parts of the stem, cotyledons, and endosperm; after the complete exhaustion of these growth ceases in the dark but

[1] Cohn, Schles. Ges. für vaterl. Cultur, Oct. 19, 1865. The facts have however recently been questioned by Schmidt.

[2] Sachs, Ueber den Einfluss des Tageslichtes auf Neubildung u. Entfaltung verschiedener Pflanzen-organe, Bot. Zeitg. 1863, Supplement. If I here consider cell-division and growth as essentially mechanical processes, this does not imply that chemical changes do not also accompany every process of growth.

continues in the light, because the assimilating organs can then produce new material. This relation of growth which is dependent on cell-division to assimilation, is especially clear in Algæ of simple structure (as Spirogyra, Vaucheria, Hydrodictyon, Ulothrix, &c.), which assimilate in the day-time under the influence of light, while cell-division proceeds exclusively or at least chiefly at night. The swarmspores are also formed in the night, but swarm only with access of daylight. In some Fungi also, as *Pilobolus crystallinus*, the splitting up of the protoplasm in the sporangium into a number of spores takes place only in the night, the spores being thrown out on access of light. While therefore in the larger and more highly organised plants assimilation and the construction of new cells out of the assimilated substances is carried on in different parts but at the same time, in small transparent plants in which the parts where these functions are effected are not surrounded by dark envelopes, they take place at different times. We have here a case of division of physiological work which shows us that the cells which have to do with chemical work (assimilation) cannot at the same time perform the mechanical labour of cell-division; the two kinds of labour are distributed in the higher plants in space; in very simple plants in time. Provided there is a supply of assimilated reserve-material, cell-division can therefore take place either in the light or the dark. Whether there are special cases in which light promotes or hinders cell-division is not known with certainty. We might suppose we have such a case when Fern-spores and the gemmæ of Marchantia[1] germinate in the light but not in the dark; but Borodin has shown that the less refrangible rays are alone active in this process of growth, mixed blue light (passed through ammoniacal copper oxide) acting like complete darkness. But since the less refrangible rays, as we have seen, have exactly the same effect on growth as the absence of light, but on the other hand are the efficient agent in assimilation, it may be supposed that these spores and gemmæ do not contain certain substances necessary for germination, which must therefore be produced by assimilation. On the other hand it has not yet been explained on what depends the formation in long-continued darkness from many stems (as those of Cactus, Tropæolum, Hedera, &c.), of roots which are not produced under the ordinary amount of light. Whether the degree of humidity is an element in this is uncertain but not improbable.

When the young organs emerge from the bud-condition, an active growth commences, which is chiefly occasioned by the absorption of water into the cells and by a corresponding superficial extension of the cell-walls, cell-division still taking place only occasionally or not at all. This process of elongation takes place, in the case of aërial stems and foliar structures, in the daylight which penetrates deep into the transparent succulent tissues. In order to estimate the amount of its influence on these processes, it is best to grow seedlings or shoots of the same species of plant in continuous complete darkness, and others under an alternation of day and night, especially in the height of summer. Independently of the fact that chlorophyll (with the exceptions already named) does not assume its green colour in the dark but remains yellow, differences of form which are often

[1] Borodin, Mélanges biol., Petersburg, 1867, vol. VI; Pfeffer, Arbeiten des bot. Inst. in Würzburg, vol I, 1871, p. 80.

very striking are exhibited by plants grown in the dark, and constitute the bleached or etiolated condition. The internodes of etiolated plants are in general much longer than those of plants of normal growth; and the long narrow leaves of Monocotyledons are subject to the same change. On the other hand the leaves of Dicotyledons and Ferns usually (but not always) remain very small and do not completely outgrow their bud-condition, or exhibit peculiar abnormalities in their expansion. These peculiarities will be explained more in detail in Chap. IV. It is not necessary however to contrast etiolated plants with those of the normal green colour, in order to establish the influence of light on their growth. If plants of the same species are compared when grown in more or less deep shade with others grown in full daylight, these differences are still more conspicuous, varying according to the intensity of the light. Different species are however affected to a different extent by etiolation; the internodes of climbing plants, which are very long even under normal conditions, become much longer still in the dark; and some leaves of Dicotyledons, as for instance those of the beet, become tolerably large under the same circumstances, while on the other hand the abnormally elongated internodes of etiolated potato plants put out leaves of only a very small size. It is remarkable that etiolation, as I have already shown[1], does not extend to the flowers[2]. As long as sufficient quantities of assimilated material have been previously accumulated, or are produced by green leaves exposed to the light, flowers are developed even in continuous deep darkness which are of normal size, form, and colour, with perfect pollen and fertile ovules, ripening their fruits and producing seeds capable of germination. The calyx however, which is ordinarily green, remains yellow or colourless. In order to observe this it is only necessary to allow tulip-bulbs, the rhizomes of Iris, or the like planted in a pot, to put up shoots in complete darkness, when perfectly normal flowers are obtained with completely etiolated leaves. Or a growing bud on a stem of Cucurbita, Tropæolum, Ipomæa, &c., with several leaves, is made to pass through a small hole into a dark box, the leaves which remain outside being exposed to as strong light as possible. The bud developes in the dark a long colourless shoot with small yellow leaves and a number of flowers, which, except in the colour of the calyx, are in every respect normal[3]. The extremely singular appearance of these abnormal shoots with normal flowers shows in a striking manner the difference in the influence of light on the growth of different organs of the same plant.

The retarding effect of light on the growth of the shoot is evident even in a short time; and, as I have already briefly shown[4], a periodical oscillation in the rapidity of growth is caused by the alternation of day and night (when the temperature is nearly constant). This variation is shown by the growing internode

[1] Sachs, in Bot. Zeitg. 1863, Supplement; and 1865, p. 117.

[2] [An exception to this rule is afforded by the coloured kinds of lilac which are forced during the months of February and March by the market-gardeners of Paris, at a temperature of from 33° to 35° C., and in almost complete darkness. The flowers expanded under these conditions are completely white. See Duchartre, Journ. de la Soc Imp. et cent. d'hort. de France, 1860, pp. 272–280.—Ed.]

[3] Sometimes however abnormal flowers appear in the dark as well as the normal ones. See Sachs, Exp.-Phys. p 35.

[4] Sachs in Heft II of the Arbeiten des Bot. Inst. in Würzburg, 1872.

exhibiting a maximum of hourly growth towards sunrise, decreasing gradually from the advent of daylight till mid-day or afternoon, when it reaches its minimum, and increasing from this time till morning, when it again attains its maximum.

Since the leaves of etiolated plants are much smaller than in the normal state, it might be expected that they would grow much more quickly in the day than in the night, or that the mechanical laws of their growth would be opposed to those of the internodes with respect to the influence of light. But it would be too hasty to come to this conclusion; for the objection might be made that normal leaves assimilate in the day, while they grow chiefly in the night[1].

One of the best-known phenomena occasioned in plants by light is the fact that growing stems and leaf-stalks, when the amount of light which they receive is very different on different sides, bend or become concave towards the side exposed to the most intense light. This curvature is caused by the slower growth in length of the illuminated than of the shaded side; and parts of plants which show this behaviour to light are called *heliotropic*[2]. From the fact of heliotropic curvature towards the side which receives the most light, it is obvious that the plant would grow more quickly if shaded on all sides than if the light were more intense. The observation that leaves, some roots, Fungi, filamentous Algæ (like Vaucheria), &c., curve heliotropically, indicates that their growth is retarded by light. That the chlorophyll has no share in causing this heliotropism is shown by the fact that organs which contain none, like some roots, or Fungi, as the perithecia of *Sordaria fimiseda* (according to Woronin), the stipes of the pileus of Claviceps (according to Duchartre[3]), and colourless etiolated stems, bend towards a stronger light. Since most heliotropic parts of plants are highly transparent, the light which falls on one side must penetrate more or less to the other side, on which also some light falls; it follows therefore that even inconsiderable differences in the intensity of the light which falls on the two sides must cause heliotropic curvature; *i. e.* difference in the rate of growth[4]. If plants which show heliotropic properties are grown in a box which receives light from one side that has passed in one case through a solution of potassium bichromate, in another case through one of ammoniacal copper oxide, the internodes of the first remain quite straight and lengthen considerably as if they were in the dark, while those exposed to the mixed blue light grow less and at the same time bend strongly towards the light. It follows from this that only rays of high refrangibility, the blue, violet, and ultra-violet, cause the curvature by retarding growth[5].

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[1] Compare *infra*, Chap. IV. Sect. 20.

[2] Further details on heliotropism will be given in Chap. IV. [See also p. 190.]

[3] Duchartre, Compt. rend. 1870; vol. LXX, p 779.

[4] It must however be noted that in the case of parts containing chlorophyll the light in penetrating the tissues loses its more refrangible rays which are the only ones that produce the effect; as has been already shown, only the less refrangible rays pass through the superficial layers (see p. 665).

[5] See Sachs, Bot. Zeitg. 1865, On the action of coloured light on plants, where the literature is also quoted. I consider experiments with absorbent fluids more decisive than those with the spectrum; in this latter Guillemin states that not only do all the rays act heliotropically, but that there is even a lateral curvature towards the blue end of the spectrum. When the light is sufficiently strong the spectrum is certainly never free from diffused white light, which will cause heliotropism even when its intensity is very small.

In addition to the large number of the parts of plants which, when illuminated unequally bend so as to make the more strongly illuminated side concave, there are a much smaller number which bend in the opposite direction, *i. e.* become concave on the shaded side. In order to distinguish between them the former are termed *positively*, the latter *negatively heliotropic*.

Both positive and negative heliotropism occur not only in organs containing chlorophyll, but also in those that are colourless; among the former in the green tendrils of Vitis and Ampelopsis[1]; among the latter in the colourless root-hairs of Marchantia[2], the aërial roots of Aroideæ, Orchideæ, and *Chlorophytum Gayanum*, and the rootlets of some Dicotyledons, as *Brassica Napus* and *Sinapis alba*[3]. From the fact that positive heliotropism depends on a retardation of the growth of the organ exposed to the stronger light, it might be inferred that negative heliotropism is occasioned conversely by a more vigorous growth of the side exposed to the stronger light. This conclusion would be confirmed by a superficial examination of the phenomena; but if the attendant circumstances are observed more closely, some considerations arise which I shall examine in detail in Chap. IV. It need only be mentioned here that according to a theory started by Wolkoff, two different explanations are possible:—Very transparent organs, like the apices of the roots of Aroideæ and of Chlorophytum refract the light which falls upon them in such a manner, that the shaded side of the organ may actually be more strongly illuminated than the other; and its negative heliotropism is then only a special case of positive heliotropism. But in other cases, as in the ivy and *Tropæolum majus*, the internodes are positively heliotropic when young, but negatively when old before growth ceases; and Wolkoff supposes that the curvature which is in these cases convex on the illuminated side is caused by the more vigorous assimilation and consequent longer duration of growth. It depends therefore upon nutrition which only affects the mechanism of growth in a secondary degree.

(*f*) *Action of Light on the tension of the tissue of the contractile organs of leaves endowed with motion*[4]. The leaf-blades of Leguminosæ, Oxalideæ, Marantaceæ, Marsileaceæ &c., are borne on modified petioles which serve as contractile organs, bending upwards or downwards under various external and internal influences, and thus giving a variety of positions to the leaf-blades. If these plants are placed in permanent darkness, the curvatures due to internal changes alternate upwards and downwards. Light exercises an immediate influence on these periodically contractile organs; any increase of its intensity tends to give the blade an expanded position, such as it occupies in the day-time; any diminution tends to cause it to assume a closed position upwards or downwards such as it has in the night. This sensitiveness, which I previously termed 'paratonic,' is not the cause of the periodic movements; but rather counteracts the periodicity caused by the internal forces. In most leaves endowed with periodic movements the paratonic

[1] Knight, Phil. Trans. 1812, Pt. I, p. 314.

[2] Pfeffer, Arbeiten des bot. Inst. in Würzburg 1871, Heft I, Div. 2.

[3] For the literature on this subject see Sachs, Exp.-Phys. p. 41.

[4] See Sachs, Ueber vorhergehende Starrezustände, &c., Flora, 1863. — Further details will be given in Chap. IV.

influence of light is so strong that it neutralises them, and induces in their place a periodicity dependent on the alternation of day and night. In the lateral leaflets of the leaves of *Desmodium gyrans* on the contrary the internal causes of the rapid periodic oscillations are so powerful as to overcome the paratonic sensitiveness; and these leaflets move upwards and downwards when the temperature is high even in spite of changes in the amount of light. My earlier researches[1] show that it is only the more refrangible rays that excite paratonic sensitiveness, while red rays act like darkness.

The influence of light on the position of the contractile organs is not however only of this direct character; the motile condition is also indirectly dependent on it. Both the periodic and paratonic movement, as well as that of Mimosa when mechanically irritated—in fact, the power of movement in plants—is lost when they have remained in the dark for a considerable time, such as a whole day; in other words, they become rigid by long exposure to darkness. From this rigid condition they do not immediately recover when again exposed to light; the exposure to light must continue for a considerable time, some hours or even days, before the motile condition which I have termed 'Phototonus' is restored. It is only in this condition that the leaves are motile and sensitive to changes in the intensity of the light or to mechanical irritation. The paratonic curvatures of fully developed contractile organs caused by sensitiveness to light are distinguished from the heliotropic curvings of growing organs by the fact that, firstly, they are connected with phototonus, while the latter are not; and secondly, that they always take place in a plane determined by the bilateral structure, while the plane of heliotropic curvature depends only on the direction of the rays of light.

Optical Properties of the Colouring matter of Chlorophyll. If the parts of plants that contain chlorophyll are repeatedly boiled in water and then quickly dried at a temperature not too high and pulverised, a substance is obtained which is easily examined and can be preserved for a long time unchanged. From this powder the green colouring matter can be extracted by alcohol, ether, or oil. The green solution is speedily changed by the action of light in proportion to its intensity, the less refrangible rays of the spectrum acting most actively and rapidly. It then assumes a dirty brownish yellow-green colour, the green colouring matter having become modified or lost its colour.

If sunlight that has passed through a stratum of the pure green solution not too thick or too dark is decomposed by a prism, an extremely characteristic spectrum is obtained in which rays of very various refrangibility appear to have been more strongly absorbed the darker the solution or the thicker the stratum. This chlorophyll-spectrum has been the subject of much research; the most recent and comprehensive being that of Kraus, from whose description I borrow the following[2]:—

The spectrum of an unchanged alcoholic solution of chlorophyll shows seven absorption-bands, four of which are narrow (Fig. 447 *A*, *I*, *II*, *III*, *IV*), and are situated in the less refrangible half; while three (*V*, *VI*, *VII*) are broad and are situated in the more refrangible half. The latter, distinguishable as distinct bands only in very dilute solutions, coalesce, even in the solutions of medium concentration which are

[1] Sachs, Ueber die Bewegungsorgane von Phaseolus und Oxalis, Bot. Zeit. 1857, p. 811 *et seq.*

[2] Kraus. Sitzungsb. der phys.-med. Soc. in Erlangen, June 7 and July 10, 1871. See also Askenasy, Bot. Zeit. 1867, p. 225; Gerland und Rauwenhoff, Archives néerlandaises, vol. VI 1871; and Gerland, Pogg. Ann. 1871, p. 585. [Kraus, Zur Kenntniss der Chlorophyllfarbstoffe u. ihrer Verwandten; Stuttgart, 1872. For reference to Mr. Sorby's papers see Sect. 8 *a*.]

ordinarily examined, into a single continuous absorption-band occupying the whole of the more refrangible half of the spectrum.

The bands *I*, *II*, *III*, and *IV* are situated in the red, orange, yellow, and yellow-green. The deep black band *I*, sharply defined on both sides, lies between Fraunhofer's lines *B* and *C*; the three others, shaded off on both sides, diminish in strength in the order of their numbers. Between these bands the illumination is dim, and progressively in the order of the numbers; *i. e.* is less dim between *II* and *III* than between *I* and *II*, &c. To the left of *I* the light is undiminished.

The bands *V*, *VI*, and *VII* in the more refrangible half of the spectrum are shaded on both sides; *V* is situated to the right of Fraunhofer's line *F*; *VI*, which is dark in the

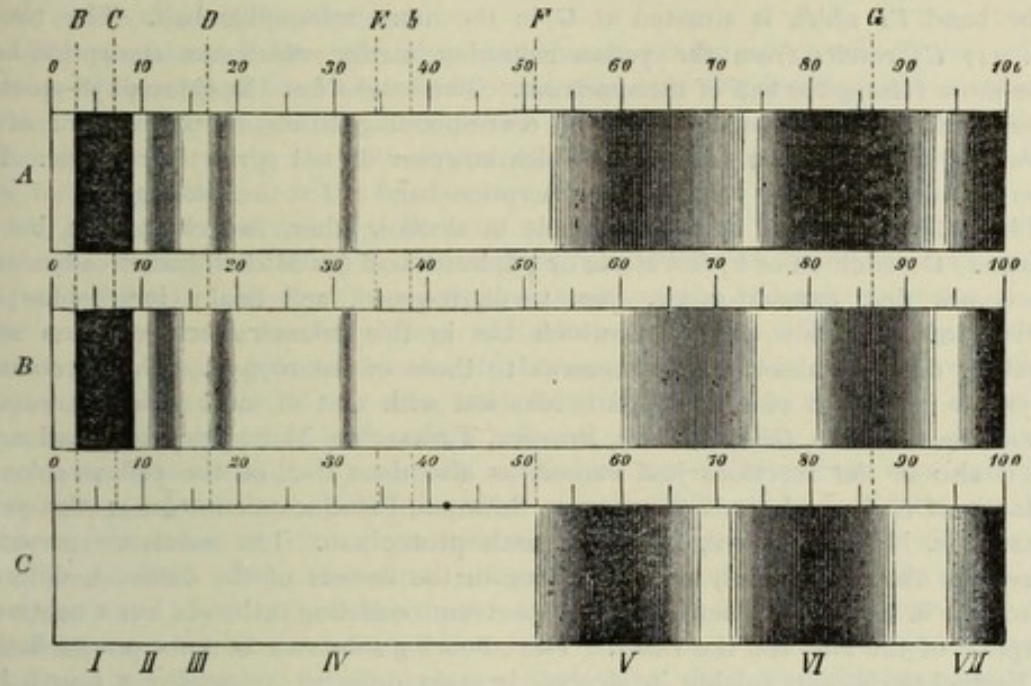

FIG. 447.—Absorption-spectra of the colouring matter of chlororophyll (after Kraus). *A* the spectrum of the alcoholic extract of green leaves; *B* that of the blue-green constituent soluble in benzol; *C* that of the yellow constituent. The absorption-bands of *A* and *B* are indicated in the less refrangible (left-hand) portion as they would be produced by a more concentrated, in the more refrangible (right-hand) portion of the spectrum as they would be produced by a less concentrated solution; the letters *B*—*G* indicate the well-known Fraunhofer lines of the spectrum; the figs. *I*—*VII* Kraus's absorption-bands in succession from the red to the violet end; the spectra are divided into twenty equal parts.

middle, to the left of and on the line *G*; *VII* may be regarded as the total absorption of the violet end.

The Spectrum of living leaves agrees with that of the solution in its main characteristics[1]. The bands *I*—*V* are, according to Kraus, easily made out in all ordinary leaves of Dicotyledons, Monocotyledons, and Ferns. But this spectrum differs constantly from that of the solution in all its bands being always nearer the red end; a point which was determined by Kraus by the use of Browning's micro-spectroscopic apparatus. This difference in position of the absorption-bands of the spectrum is, as he shows, an illustration of the universal rule that the absorption-bands approach nearer to the red end in proportion to the specific gravity of the solvent of the colouring substance. It follows from this that the green colouring matter is distributed in such a manner in the colourless matrix of the chlorophyll-grains that it must be considered in a state of solution. In no case can the colouring matter of chlorophyll in living cells be in a solid state, or equivalent to the residue left behind when the solution is evaporated.

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[1] For further evidence of this very remarkable fact see Gerland und Rauwenhoff, *l.c.*, p. 604. It is not easy to understand how any physicist could maintain the contrary.

If an alcoholic solution of chlorophyll (according to Conrad it must be very dilute[1]) is agitated with any quantity of benzol (say double its volume) two very sharply separated strata are formed after the fluid comes to rest, a lower alcoholic stratum of a pure yellow colour, and an upper blue-green stratum of benzol. Kraus considers this process to be a dialytic one; there are, according to him, two colouring substances in the ordinary chlorophyll-solution, a blue-green and a yellow one, soluble in very different degrees in alcohol and benzol[2].

Kraus therefore holds the spectrum of chlorophyll to be a combination-spectrum, *i. e.* that it arises from the superposition of the two spectra of the blue-green and the yellow colouring-matter. The blue-green substance gives the four narrow absorption-bands in the less refrangible half of the spectrum (Fig. 447, *B*), and part of the band *VI* which is situated at *G* in the more refrangible half. The band *F* (Fig. 447 *C*) results from the yellow colouring matter which has absorption-bands in the more refrangible half of the spectrum. The band *VI* of the chlorophyll-spectrum is the result of partial superposition of corresponding bands in the spectra of the yellow and the blue-green substances, which however do not perfectly coincide. Both colouring substances alike produce the absorption-band *VII* at the violet end.

The yellow colouring matter is soluble in alcohol, ether, and chloroform, but not in water. On addition of hydrochloric or sulphuric acid (as Micheli had already shown) it becomes first emerald-green, then verdigris-green, and finally indigo-blue; the spectrum of the yellow substance which has in this manner become green shows altogether different absorption-phenomena to those of chlorophyll. The spectrum of the yellow ingredient of chlorophyll is identical with that of most yellow flowers (as Ranunculus, Mimulus, *Gentiana lutea*, Brassica, Taraxacum, Matricaria, &c.), and agrees with it also in the reactions just named, as also does that of the yellow colouring substance of fruits and seeds (Euonymus, Solanum, Pseudocapsicum &c.); this yellow substance is, like chlorophyll, combined with protoplasm. The substance present in the cells in the liquid form, as for instance in the flowers of the dahlia, is different; it is soluble in water, and does not give a spectrum consisting of bands, but a continuous absorption of the blue and the violet. The colouring substance of some orange flowers, *e.g.* Eschscholtzia, also soluble in alcohol, is again different, possessing a fourth band in the blue-green to the left of the three bands of the ordinary yellow substance. The colouring matters of bright-coloured lower organisms which are soluble in alcohol are not identical with either of the two which constitute chlorophyll, but are related to them.

According to Kraus, the yellow substance of etiolated leaves also exactly resembles the yellow constituent of chlorophyll; he considers the green colour produced by exposure to light to be the result of the formation of the blue-green constituent.

The *Fluorescence* of the colouring-matter of chlorophyll is seen from the fact that a sufficiently dark concentrated solution appears dark-red by reflected but green by transmitted light. The fluorescence is much more decided if the pencil of converging rays of the sun is made to fall on the green fluid through a condensing lens. If the solar spectrum is thrown upon the surface of a solution of chlorophyll[3], it may be

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[1] Kraus obtained a solution of chlorophyll by pouring alcohol upon boiled leaves which have contained water. Conrad shows that it is only such dilute solutions of chlorophyll (alcohol of 65 p.c. or less) that show Kraus's reactions; and that on the contrary a solution obtained from dried leaves by absolute alcohol and then mixed with benzol does not separate into yellow and blue-green strata.

[2] This is however rendered doubtful by Conrad's more recent researches. If a solution of chlorophyll in absolute alcohol is evaporated, the residue extracted with water does not contain a yellow constituent as it does when the solution is prepared with dilute alcohol. It is therefore not improbable that chlorophyll-green is decomposed by dilute alcohol, and that the two constituents of which Kraus supposes chlorophyll to consist did not exist before the operation any more than those imagined by Frémy.

[3] Hagenbach, Pogg. Ann. vol. 141, p. 245; Lommel, *ib.* vol. 143, p. 572.

ascertained which rays of the sunlight cause the fluorescence; the red begins a little to the left of the line *B* of the solar spectrum, and stretches, although varying in intensity, over the violet end. On the dark-red ground are seen seven intensely red bands, each corresponding exactly both in position and in strength to an absorption-band in the spectrum of chlorophyll. If the fluorescence caused by the solution of chlorophyll is itself observed through a prism, it is seen to consist only of red rays, the refrangibility of which coincides with the strongest absorption-band of chlorophyll between *B* and *C*. Every ray produces by fluorescence only such as correspond in their refrangibility to the absorption-band *I*. Whether the chlorophyll contained in living cells is subject to the same fluorescence is not certain, from the imperfect observations at present made; but it is probable, from the absorption-phenomena and their connection with fluorescence.

The question whether the absorption-bands of the spectrum of the colouring-matter of chlorophyll have any causal connection with the function of the chlorophyll-grains in decomposing carbon dioxide has recently been answered by Lommel in the affirmative, on purely theoretical grounds, in support of which he brings forward the following facts[1]:—

'The most efficacious rays in promoting assimilation in plants are those which are most strongly absorbed by chlorophyll, and which at the same time possess a high mechanical intensity (heat-action); these are the red rays between *B* and *C*.' But a glance at the carefully prepared tables given at pp. 667, 668, shows that this theoretical reasoning is incorrect. If Lommel's hypothesis were correct, the evolution of oxygen would be seen, on observing the solar spectrum, to attain its maximum between *B* and *C*[2], which however, as Pfeffer has shown, is by no means the case. The second of Lommel's statements is:—'The yellow rays can produce only a small effect notwithstanding their considerable mechanical intensity, because they are absorbed only to a small extent; and the same is the case with the orange and green rays.' This statement is again entirely opposed to observation; for it is these very rays that are the most efficacious in promoting evolution of oxygen. Lommel says indeed (*l. c.* p. 584) that 'this inference is incorrect'; it is however no inference, but the result of actual observation. That the light which has passed through a solution of chlorophyll causes only an inconsiderable evolution of oxygen is easily explained when it is recollected that even the yellow is considerably weakened in the spectrum of chlorophyll. But according to Lommel's theory there ought to be no evolution of oxygen at all when light has passed through a solution of this kind if it shows the absorption-bands very dark, since those rays which according to him are alone efficacious are wanting.

There is however no need for this direct contradiction; for a correct estimate of known facts leads to the conclusion that it cannot be those rays which are absorbed by the colouring matter of chlorophyll that cause the evolution of oxygen; for the rays absorbed in such a solution are the same as those absorbed in a green leaf (see p. 679). In the former there is however no evolution of oxygen (and apparently also no oxidation); and there is nothing to justify the supposition that the same rays which the colouring matter of chlorophyll absorbs in solution without causing evolution of oxygen should cause it in the living leaf. It must certainly be right to suppose, as a necessary result of the principle of the conservation of energy[3], that the rays which are efficacious in causing evolution of oxygen must be absorbed,

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[1] Lommel, Pogg. Ann. Vol. 143, p. 581 *et seq.*

[2] Müller, (Botan. Beobachtungen; Heidelberg 1871, Heft I) has adduced a great array of figures in support of this conclusion. But any one who knows how such observations should be made knows also what value is to be attached to these. See also Pfeffer, Bot. Zeit. 1872, No. 23 *et seq.*

[3] See also what I said on this subject seven years ago in my Experimental Physiology, p. 287.

inasmuch as they perform chemical work; but observation shows that it is not the rays absorbed by the green colouring matter that perform this work either in the solution or the living plant[1].

The Relation of Cell-division to Light has, as I have already explained, been completely misunderstood by Famintzin. In my paper 'On the influence of daylight on the formation and unfolding of various organs of plants' (Bot. Zeit. 1863, Supplement), I described in detail a long series of processes which show that the fresh formation of parts connected with cell-division is in general independent of light as long as there is a supply of reserve food-material to support growth. The main results were again collected in my 'Handbook of Experimental Physiology,' p. 31, referring also to that paper. Notwithstanding this, Famintzin[2] commences his paper quoted above (three years later than one, and five than the other of my works) with the words:—'The action of light on cell-division has not yet been carefully examined by any one. All that I have been able to find on this subject is limited to a remark of A. Braun's on Spirogyra and a statement of Sachs relating to cell-division in general.' He then quotes a passage from Braun cited also by me, and continues:—'Basing his remarks on these statements, Sachs expresses himself as follows,' and then quotes some passage from my Handbook, p. 31, no reference being made to the earlier paper or its conclusions. He then maintains that his own observations lead to entirely different results; but it is easy to show that they rather lead to the same as mine. At the end of his memoir (p. 28) he says:—'The cell-division of Spirogyra is not prevented by light, as has hitherto been supposed, but on the contrary is promoted by it' (which is incorrect). According to Famintzin's observations, this acceleration of cell-division by light depends on the fact that light induces the assimilation of food-material; which is obviously a different question from that argued by me and opposed by him; since, presupposing the presence of a supply of food-material, I only argued the question whether light exerts any influence on the physical fact of cell-division.

'The cell-division of Spirogyra,' continues Famintzin 'has been proved to be dependent on light to the same extent as the formation of starch; but the relationship in the former case differs from that in the latter in the following respect:—the formation of starch is induced by a very brief exposure to light (about half an hour) and requires that its action be direct; starch is formed only under the influence of light; in its absence the formation at once ceases. Cell-division, on the other hand, is induced only after light has acted for some hours; it then commences in the cells whether these have been exposed to light for some time or have been removed into the dark.' This shows therefore that when food-materials are formed cell-division takes place in the light as in the dark; a fact which I had proved five years before by a great number of observations.

Better in more than one respect is Batalin's treatise 'On the action of light on the development of leaves' (1871)[3]. Starting from the facts discovered by himself and by Kraus that cells have the same size in small etiolated leaves as in large leaves of the same species grown in light, he concludes with justice that the number of cells is larger in the normal than in the etiolated leaf, and that the size of leaves is proportional to the number of cells in them. But from this he draws the following erroneous conclusion:—'The leaf grows so long as it produces new cells; and the growth of the leaf does not depend on the increase in size of the cells.' It should rather be,—'The growth of the leaf depends firstly and directly solely on the increase in size of the cells, and is proportional to this; but the cells, when they have grown larger, divide so that they are actually of about the same size in the small etiolated

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[1] Gerland (*l. c.* p. 609) has also arrived at a similar conclusion.

[2] Famintzin, Mélanges phys. et chim., Petersbourg 1868, vol. VII, On the action of light on the cell-division of Spirogyra.

[3] Batalin, Bot. Zeit. 1871, p. 670.

as in the large green leaf.' He continues:—'Leaves do not grow in the dark because their cells cannot divide without the assistance of light;' while the exact converse is the fact,—they do not divide because they do not grow. This error prevails throughout the whole treatise, which in other respects contains a number of instructive observations.

It must be observed in addition that the very small growth of leaves in the dark is not a universal phenomenon even amongst Dicotyledons. The leaves produced from the tuberous roots of the dahlia and beet grown in the dark, and even those of Phaseolus attain very considerable dimensions, and sometimes, especially when the temperature is high, almost the size of those developed in the light[1].

Contrivances for observing plants in light of different colours (or of different refrangibility). In order to allow light of different degrees of refrangibility to act upon plants, three methods may be adopted:—(1) The use of the spectrum; (2) The removal of particular rays by absorbent media (glass or fluids); and (3) Coloured flames.

(1) If a ray of light is decomposed by passing it through a prism, it is possible to expose small plants or parts of plants to the action of narrow zones of the spectrum; and hence to allow light of approximately equal refrangibility to act upon them. Draper, Gardner[2], Guillemin, and Pfeffer, have worked in this manner. In using the spectrum it must however be observed that the intensity of the light in its different parts is less than that of the light that passes through the slit in proportion to the length of the spectrum. If the spectrum at the distance from the prism where the observation is made is, for instance, 200 mm. long, but the slit only 1 mm. broad, the mean intensity of light of the whole spectrum is only $^1/_{200}$ of that which passes through the even slit, if no light is otherwise lost, which is seldom the case. Only a small luminous intensity must therefore be expected in the spectrum. In order to obviate this difficulty, it is necessary that very intense light pass through the slit, which may be effected by the use of condensing lenses. If, as is usually the case, sunlight is employed, the ray to be decomposed must be kept in a fixed position by a heliostat, or at least by a moveable mirror.

(2) *Absorbent media.* The defects which have been mentioned in observations with the spectrum, as well as the considerable cost of a heliostat, are avoided when coloured light is obtained by means of absorbent media. For this purpose discs of coloured glass or strata of fluids enclosed between colourless glass plates may be used. These last possess the advantage that almost any required amount of space may be illuminated by the light in question, and that the transmitted light only loses so much in intensity as is due to the small amount of absorption of the transmitted rays by the coloured medium. It is a mistake, though a very common one, to think that observations made with coloured screens are less exact than those made with the spectrum; in general it is just the reverse; and which method should have the preference must be decided in each case.

The use of absorbent media is always subject to the disadvantage that they do not generally transmit light of a single colour, but several different kinds of rays. This disadvantage is especially the case with coloured glass plates; and, with the exception of the deep red ruby and the very dark blue cobalt glass, there are scarcely any kinds which answer our purpose. It is more practicable to obtain coloured fluids of the desired quality, although here also the number that can be used is small. The two which have been already mentioned are particularly useful, *viz.* a saturated solution of potassium bichromate, and a dark solution of ammoniacal copper oxide; by means of these, with the right concentration and thickness of the stratum, experiments can be contrived so as to split white daylight exactly into two halves, the first solution transmitting the less refrangible rays from the red to the green, the

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[1] See *infra*, Sect. 20.

[2] Gardner, Froriep's Notizen 1844, vol. 30, No. 11.—Guillemin, Ann. des Sci. Nat. 1857, vol. VII, p. 160.

blue solution all the more refrangible rays from the green to the ultra-violet. Those fluids also are of great use which transmit the whole spectrum with the exception of a few groups of rays as sharply limited as possible. If certain phenomena occur when plants are exposed to light transmitted through these solutions, it is certain that they are not caused by rays of that particular refrangibility which are absent, and *vice versâ*. It is obvious that absorbent media are of use in experiments only when the spectrum of the light that passes through them is accurately known. Glass plates are employed as windows in dark boxes closed on all sides in which plants are placed; coloured fluids can also be employed for the same purpose by enclosing them between parallel plates of glass and using these as a window. When it is not necessary to allow light to fall in parallel rays upon the plant, the most convenient use of coloured fluids is to fill with them the space between the two walls of a double glass bell which is then placed like an ordinary bell-glass over the plants to be observed.

For microscopic observations in coloured light I employ boxes like that represented in Fig. 445 (p. 658); only that instead of the colourless plate of glass, a double window is used, the space between the two panes being filled with coloured fluids.

(3) *Coloured Flames—i.e.* the light of bodies in a finely divided state heated to incandescence in a flame which is itself non-luminous—have not hitherto been employed for accurate observations on plants. I know only of one statement by Wolkoff[1]; that etiolated seedlings of *Lepidium sativum* became green when placed for seven or eight hours at eight inches distance from a non-luminous gas flame in which sodium carbonate had volatilised and become incandescent. This light, as is well known, consists only of rays which correspond to Fraunhofer's line *D*. The red light of the flame of lithium or the blue light of that of indium &c., may be employed in the same manner as this yellow flame, if sufficient intensity and the necessary permanence can be attained with these flames[2].

[The foregoing account would be incomplete without some statement of the results attained on this subject by Mr. H. C. Sorby. The following is a brief abstract, supplied by him, of investigations which will be found reported in detail in his published papers[3]:—

Vegetable colouring-matters may be divided into two principal classes, *fundamental* and *accidental*. The fundamental are those which are essential to the healthy growth of the plant; and by carefully studying the position of the absorption-bands in living leaves these substances are often found in a free and solid state, even when they are soluble in water, or could easily combine with the closely associated oils or wax. When set free by boiling in water or by decomposition, they dissolve according to their properties in this respect in water, or combine with oil or wax if these be present. The petals and other portions of the organs of reproduction often contain some of the fundamental colouring-matters of the leaves, but frequently others are developed.

Accidental colouring-matters are those which may be present or absent without apparently interfering with the healthy growth of the individual plant, and are often so conspicuous as to make mere *colour* of very little importance if it depend upon them, and not on the difference in the kind or relative proportion of the fundamental colouring-matters. These non-essential substances are far more common in the petals than in the leaves, and if of any use to the plant, are only indirectly advantageous, as, for instance, in attracting insects. It is doubtful to which of these two divisions certain

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[1] Wolkoff, Jahrb. für wiss. Bot. 1866, vol. V, p. 11.

[2] [The most recent researches on the spectrum-analysis of the green colouring matter of plants is by Chautard in Ann. de Chim. et de Physique, Sept. 1874.—Ed.]

[3] [Proceedings of the Royal Society, vol. XV. 1867, p. 433.—Quarterly Journal of Microscopical Science, vol. IX, 1869, p. 358; vol. XI, 1871, p. 215.—Monthly Microscopical Journal, vol III, 1870, p. 229; vol. VI, 1871, p. 124.—Proceedings of the Royal Society, vol. XXI, 1875, p. 442.]

substances should be referred, and perhaps some may not be essential for the healthy performance of vital functions, but merely necessary products; and some may be essential to one plant and not to others.

It has been found convenient to arrange the colouring-matters of plants in the following groups, which are as it were of generic value, and include several different species.

Chlorophyll group.—The green substance described as chlorophyll by many writers must often have contained two perfectly distinct green substances, and the product of the action of acids on one of them, mixed with one, and in some cases with three, different species of xanthophyll, and one or two of lichnoxanthine. These two green substances are *blue chlorophyll* and *yellow chlorophyll*[1]. *Blue chlorophyll* dissolved in alcohol is of a splendid blue-green colour, the whole of the green part of the spectrum and a considerable part of the contiguous blue being readily transmitted. *Yellow chlorophyll* absorbs the whole of the blue and the blue end of the green, so that the general colour is a bright yellow-green. *Chlorofucine* is of a clear yellow-green colour. It has many properties in common with the above-named two kinds of chlorophyll, being, like both of them, highly fluorescent and easily decomposed into another modification by acids. All three are insoluble in water and soluble in absolute alcohol, but not always in carbon bisulphide.

The difference between their spectra will be better understood by means of the following figure, 447 *b*, which represents the absorption-bands as seen in solutions diluted so as to show those at the blue end, and only the darkest and most characteristic of those in the red.

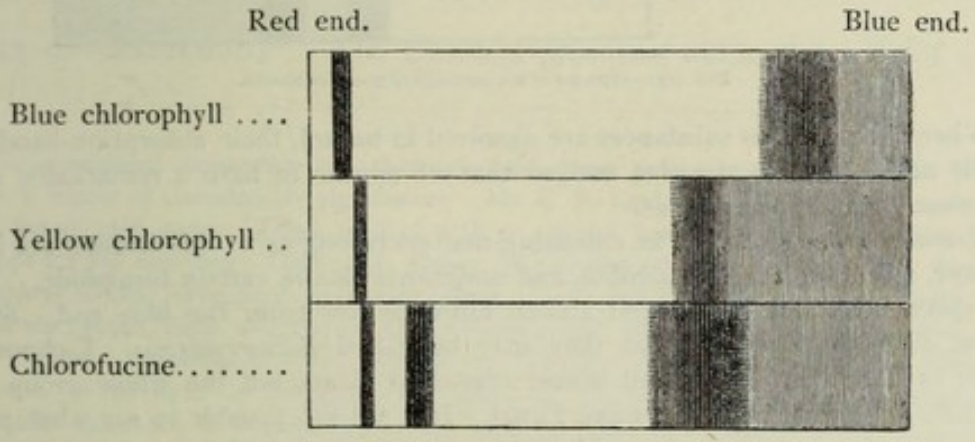

FIG. 447 *b*.—Spectra of the chlorophyll group compared.

Xanthophyll group.—This group includes a number of yellow or orange-coloured substances, insoluble in water but soluble in carbon bisulphide, giving spectra with two more or less well-marked absorption-bands in different positions, according to the particular species. They are not fluorescent, and when dissolved in absolute alcohol, after addition of a little hydrochloric acid, they all gradually become colourless, but two of them are first changed into a blue substance. Nearly all green leaves contain three perfectly distinct fundamental species, which Mr. Sorby has named *orange-xanthophyll*, *xanthophyll*, and *yellow xanthophyll*. The spectrum given in Fig. 447 (p. 679), copied from Kraus, must have been due to a mixture of the latter two. Olive Algæ contain another fundamental species, *fucoxanthine*. In many Fungi, and in the petals of flowers, occur other more orange-coloured species, of which that in *Peziza aurantiaca* is a good example. Sorby adopted the name proposed by Kraus[2] for a still more red orange-

[1] [The spectrum given by Kraus (Fig. 447 *B*, p. 679), is due to a mixture of these with some of the products of the action of acids.—ED.]

[2] Chlorophyllfarbstoffe, p. 109.

coloured species; but what Kraus describes as *phycoxanthine* must have been a mixture of this substance with fucoxanthine and lichnoxanthine. The difference between the spectra of some of the above-named species will be better understood by means of the following figure (447 *c*), which represents those of the solutions in carbon bisulphide.

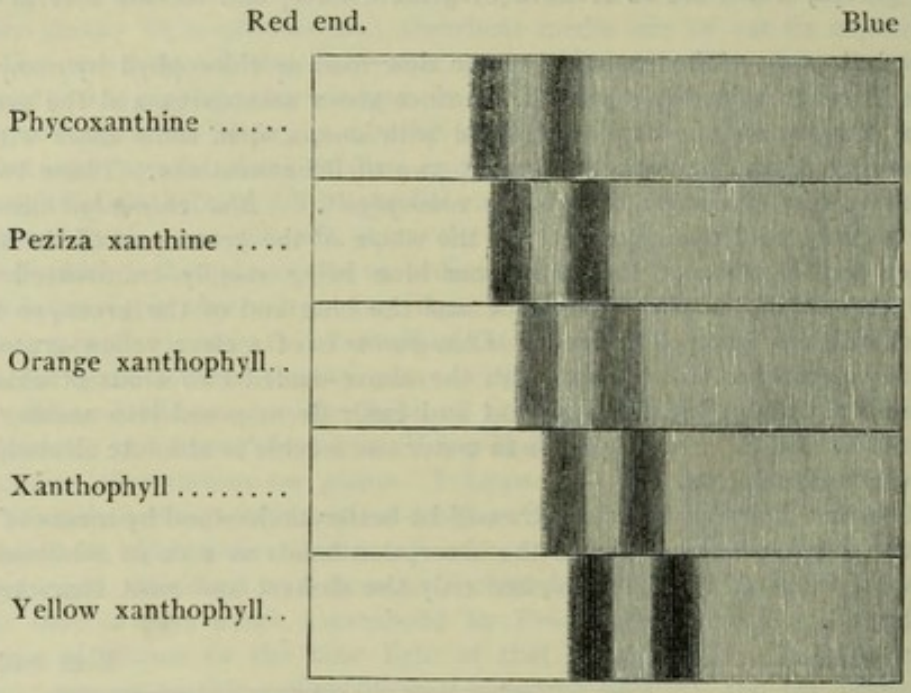

FIG. 447 *c*.—Spectra of the xanthophyll group compared.

When these various substances are dissolved in benzol, their absorption-bands are all equally raised towards the blue end, so that we appear to have a remarkable series of very closely related substances.

Lichnoxanthine group.—The colouring-matters belonging to this division are insoluble in water, soluble in absolute alcohol, and sometimes also in carbon bisulphide. They all give spectra without bands, and absorb more or less from the blue end. Some are yellow, and others so red that they may be called *lichnoerythrines*. Lichnoxanthine occurs in both the highest and lowest classes of plants, but the whole group is more especially developed in Lichens and Fungi. It is not yet possible to say what part they play in the economy of plants, and in some cases they are probably only products of the oxidisation of chlorophyll and resins, from which they may be prepared artificially.

We now come to a number of different groups, soluble in water but insoluble in carbon bisulphide.

Phycocyan and *Phycoerythrine groups.*—There are at least five distinct colouring-matters included in these two groups, which differ from one another in many well-marked particulars. The phycocyans are highly fluorescent, but the phycoerythrines little if at all. They give remarkable spectra with one main absorption-band. Some are connected with albuminous substances in much the same manner as the hæmoglobin of blood, being like it decomposed at exactly the same temperature as that at which albumen coagulates, whilst the others appear to be associated with some different but related substance. They are especially characteristic of red Algæ, but also occur in a few Lichens.

Erythrophyll group.—The colouring-matters belonging to this group are very numerous, and their production often depends upon obscure and accidental causes, easily modified by slight variations in the internal or external conditions. They may be divided into three well-marked sub-groups, according as they are changed by the action of sodium sulphite. They are soluble in water, and are usually, if not always, dissolved in the juices of the plant, and disseminated in cells of various kinds. A greater number

of different species occur in the petals than in the leaves. They are usually indicative of low constructive energy, but yet are not products of merely chemical decomposition.

Chrysotannin group.—Much remains to be learned with respect to these more or less pale yellow or even colourless substances, and the part they play in plant-life. The most striking fact connected with them is that when oxidised they give rise to the various brown substances which are the cause of many of the characteristic tints of autumnal foliage. These changes are mainly, if not entirely, due to chemical action, and can easily be imitated artificially.

Exposure to a greater or less degree of light may produce a great quantitative or even qualitative difference in the colouring matters. Rudimentary petals and rudimentary leaves correspond closely, but subsequently development takes place in two different directions; and very often when the petals of the more highly developed varieties are only partially grown, the constituent colouring-matters are both qualitatively and quantitatively the same as those in some other variety, as though this were due simply to a natural arrest of development. By growing almost in the dark flowers coloured by more or less of the orange species of the xanthophyll group, the petals are obtained of the full size, but only yellow and corresponding exactly to the normally yellow variety; and there is this remarkable peculiarity, that the relative proportion between the different colouring-matters approximates more or less closely to what is obtained by exposing to light a solution of those found in the normal petals; that is to say, absence of light tends to prevent the formation in the petals of those more orange-coloured substances which are the most readily decomposed by exposure to light when they are dissolved out from the petals.][1]

Sect. 9.—**Electricity**[2]. The chemical processes within the cells of a plant,

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[1] [The occasional occurrence of 'chlorophylloid green colouring-matters' in the tissues of animals is a matter of considerable significance. Mr. E. R. Lankester has obligingly drawn up the following list of such cases. Those marked with an asterisk have been observed by him with the spectroscope for the first time:—Infusoria; *Stentor Mulleri* and others. Foraminifera. Radiolaria; *Rhaphidiophrys viridis*, *Heterophrys myriapoda* (Quart. Journ. Micr. Sc. 1869). Cœlenterata; **Spongilla fluviatilis* (Journ. Anat. and Phys. 1869), **Hydra viridis*, *Anthea cereus* var. *smaragdina* (chlorofucine). Vermes; *Mesostomum viride* (Planariae), **Bonellia viridis* (in the skin), **Chætopterus Valenciennesii* (in the walls of the alimentary canal). Crustacea; **Idotea viridis* (Isopoda). The chlorophylloid substance is not present in the same physical or chemical condition in all these cases. In Rhaphidiophrys, Heterophrys, Spongilla, and Hydra, it is localised in granules imbedded in the protoplasm: this is also the case in Bonellia, but the granules are finer. In Idotea it is not in granules but diffused in the chitino-calcareous integument. In all cases the chlorophylloid substance agrees in having a strong absorption-band in the red—a little to the right or left; and, except in Idotea, in being soluble in alcohol; and in having strong red fluorescence and in finally losing its colour when dissolved. In Bonellia, Chætopterus, and Spongilla, the absorption-spectrum presents differences in other respects in each case, and the green tint is itself different—being black olive-green in Chætopterus, bluer but equally dark in Bonellia, and apple-green in Spongilla and Idotea. In Spongilla the green colour is not developed if the animal grows in the dark. But like etiolated vegetable tissues, Spongilla, when immersed in strong sulphuric acid, gradually developes a strong leaf-green colour, fully as intense as that of the naturally green specimens (Quart. Journ. Micr. Sc. 1874, p. 400). Bonellia, on the other hand, always lives in a dark hole excavated by it in calcareous rock, and Chætopterus lives in a thick opaque tube.—Ed.]

[2] Villari, Pogg. Ann. 1868, vol. 133, p. 425.—Jürgensen, Studien des phys. Inst. zu Breslau, 1861; Heft 1, p. 38 *et seq.*—Heidenhain, ditto 1863, Heft 2, p. 65.—Brücke, Sitzungsb. der Wien. Akad. 1862, vol. 46, p. 1.—Max Schultze, Das Protoplasma der Rhizopoden; Leipzig, 1863, p. 44.—Kühne, Untersuchungen über das Protoplasma, 1864, p. 96.—Cohn, Jahresber. der schles. Ges. für vaterlandische Cultur 1861; Heft 1, p. 24.—Kabsch, Bot. Zeit. 1861, p. 358.—Riess, Pogg. Ann. vol. 69, p. 288.—Buff, Ann. der Chem. u. Pharm. 1854, vol. 89, p. 80 *et seq.*—[J. Ranke, Untersuchungen über Pflanzenelektricität, Akad. der Wissen. München, Math.-Phys. Klasse, July 6, 1872.]

the molecular movements connected with the growth of the cell-wall and protoplasm, and the internal changes on which the activity of the protoplasm depends—whether exhibited in the formation of new cells or in movements of rotation—are probably connected with disturbances of the electrical equilibrium, although no actual empirical proof of this has yet been obtained. The fluids with different chemical properties in adjoining cells, the diffusion of salts and of assimilated compounds from cell to cell, and their decomposition, must also bring electromotive forces into play; but even this has not yet been observed directly. Even the electrical currents which must no doubt be set up by the evolution of oxygen from cells containing chlorophyll, by the formation of carbon dioxide in growing organs (as in seedlings), and by the transpiration of land-plants — although investigated by a few physicists—has not yet been actually established or accurately determined. According to Buff's careful observations, which have been confirmed by Jürgensen and Heidenhain, the internal tissue of land-plants is always electro-negative to its strongly cuticularised surface; the surface of roots, saturated with sap (like a transverse section of the tissue), is also electro-negative to the surface of the stems and leaves. If a plant or a cut part of a plant is placed, with the necessary precautions, in the circuit of a very sensitive galvanometer, a current passes from the external surface to the cut surface or to the surface of the root; this is in consequence of the contact of the cell-sap of the surface of the root or of a cut surface with the pure water employed to complete the circuit. The alkaline fluids of the thin-walled phloëm of the fibro-vascular bundles are surrounded by the acid fluids of the parenchyma, and become completely mixed by diffusion-currents. This behaviour, which must certainly produce electromotive effects, has not hitherto been investigated with this object[1].

The leaves and branches of plants present a large surface to the air; and the tissue of the whole plant is permeated with electrolytic fluids. These phenomena appear to adapt plants to be the medium for equalising electrical differences between the earth and air by means of currents traversing the plant. Since therefore the electrical tension of the air is generally different from that of the earth, and the relationship of the two is constantly varying with changes of weather, it may be assumed that in all probability constant electrical interchanges are going on through the agency of plants[2]. Whether these have a favourable effect on the processes of vegetation has at present, like the whole subject, not been investigated scientifically. The destructive discharges of atmospheric electricity which are effected through trees by means of flashes of lightning[3], at least show that smaller differences of electrical equilibrium between the air and earth may also be equalised by means of plants[4].

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[1] Sachs, Ueber saure, alkalinische, und neutrale Reaction der Säfte lebender Pflanzen; Bot. Zeit. 1862, No. 33.

[2] [Becquerel thought that the evaporation from leaves forms an upward current of vapour which acted as a conductor to electricity. In this way, by destroying the necessary electrical conditions, he thought forests tended to dissipate hail-clouds. Mém. de l'Inst. vol. XXXV, pp. 806, 807.—Ed.]

[3] [The disruptive effect of lightning upon trees is probably due to the sudden conversion of moisture into steam. See Osborne Reynolds, Proc. Phil. Soc. Manch. 1874, p. 15.—Ed.]

[4] [Edwin Smith (Chemical News, Dec. 17, 1869) has detected constant currents of electricity passing in certain directions in plants, as follows:—In a cut piece of leaf-stalk (rhubarb) from the

The researches on the action of the electric stimulus on the movements of protoplasm and of leaves the motion of which is caused by tension of the tissues, have not at present led to any important result from a physiological point of view, although distinguished observers have paid attention to this subject. It can only be said in a general way that very weak constant currents or induction-shocks (for a short time) produce no perceptible effect; that sufficiently strong electromotive force produces effects on the protoplasm and in the contractile tissues similar to those produced by a high temperature and by mechanical means; and that finally, when the strength of the current is still further increased, the protoplasm is killed and the motility of the leaves permanently destroyed, but sometimes in the latter case without causing death.

Jürgensen allowed the current from a battery of small Grove's elements, the force of which was regulated by a rheochord, to act under the microscope on the tissue of a leaf of *Vallisneria spiralis*. A constant current from one element produced no perceptible action; two or four elements caused a retardation of the protoplasmic movement, and when continued for a longer time completely stopped it. When the current was interrupted, the movement, if it had only been retarded, was restored to its original rapidity after the lapse of a short time; if it had entirely ceased, it was not recommenced even if the current was at once stopped. When the movement is thus arrested, the grains of chlorophyll which are carried along by the very watery protoplasm accumulate at different spots. A current from thirty elements causes permanent cessation of the movement even if the connection is only momentary. Induced currents act like constant ones; but the number of induction-shocks which pass through the cells in a unit of time appears to have no considerable influence on the action.

The changes of form of protoplasm under the influence of a sufficiently strong electric current are, according to the observations of Heidenhain, Brücke, Max Schultze, and Kühne, similar to those caused by a high temperature near the extreme limit or beyond it. From those of Kühne it appears to result that protoplasm is a very bad conductor of electricity, and that the excitement caused by a current at particular spots in the protoplasm is not easily transferred to other spots.

Cohn, Kabsch, and others, state that weak induction-currents act on the sensitive parts of the leaves of Mimosa, the stamens of Berberis, Mahonia, and *Centaurea Scabiosa*, and the gynostemium of *Stylidium graminifolium* like concussion or contact, the parts moving as if under the influence of these agencies. According to Kabsch, stronger induction-currents, which permeate the whole plant, destroy the sensitiveness of the gynostemium of Stylidium even for mechanical excitation; but after half an hour the sensitiveness again returns. The statement of Kabsch is noteworthy that the movement of the leaflets of *Desmodium gyrans* are permanently prevented by stronger induction-currents, which however do not kill them.

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end nearest the root to the end nearest the blade of the leaf; from the outer side of the leaf-stalk nearest the cuticle to the inner axis; from the lower end of the flower-stalk (pæony) to the bract or petal; from the upper to the under surface of the leaf; in the stem (hawthorn) from the cambium to the outer cuticle; in the root (several plants) from the outside to the axis, and from the root-stock towards the apex; in the hollow stems of monocotyledonous plants (grass) from the inner to the outer surface; in the potato from the centre to the outside; but in the lemon, pear, gooseberry, and turnip from the outside to the centre; in a living plant (Tropæolum) from the plant itself to the soil.

Dr. Burdon-Sanderson has made a remarkable series of observations on the electric currents in *Dionæa muscipula* (see Report of British Association for 1873; also Nature, vol. VIII, p. 479 and Proc. Roy. Soc. vol. XXI, p. 495). By the aid of Thomson's galvanometer he has shown that these currents are subject, in all respects in which they have been as yet investigated, to the same laws as those of animal muscle and nerve.—Ed.]

SECT. 10. — **Action of Gravitation on the Processes of Vegetation**[1]. Since the attraction of the earth acts uninterruptedly on all parts of the plant, the entire vegetable organisation must be so contrived that the weight of the separate parts of the plant is serviceable, or at least not injurious to the various purposes of the life of the plant.

In observing these relationships the first thing is to distinguish between those contrivances which have for their object to bring the weight of the parts of the plant into harmony with the purposes of its life—gravitation itself not taking any direct recognisable part in the attainment of these objects—and those phenomena of vegetation on the other hand which are brought into existence by the direct influence of gravitation on the mechanism of growth.

To the first of these groups belongs the fact that the branches and foliage of upright stems are distributed nearly equally on all sides, and that in larger plants the firmness and elasticity of the masses of tissue in the stem is promoted by the formation of wood, or is brought about by other means, as for instance in the trunk of Musa. But since it is very common in the organic world for the same purpose to be attained by very different means, slender delicate stems with but little wood can protect themselves from sinking down and can expose their foliage to the light by twining round firm supports, or by climbing with the help of tendrils, hooks, spines, &c. The same purpose is evidently served by the various floating contrivances of water-plants and those of fruits and seeds ; in all these cases the structure is obviously adapted to make the weight of the part of the plant serviceable or at least not injurious to its life ; although it cannot be maintained that gravitation takes any part in the formation of wood, in the sensitiveness of tendrils, or in the production of a floating apparatus. The only explanation of these arrangements lies in Darwin's Theory of Descent ; *viz.* that, under the influence of long-continued natural selection, only those structures are finally able to maintain their existence which, while sufficient for the other requirements of life, are so arranged that the weight of the part is not injurious or is even useful. It must not be inferred from this, nor does observation render it probable, that gravitation takes any direct part in these phenomena.

Gravitation however exerts a direct influence on the growth of young parts of plants as soon as the longitudinal axis of the growing organ is inclined obliquely to the perpendicular and therefore to the action of gravitation. In this case the growth in length of the oblique organ is different on the upper and under sides, and the more so the more nearly horizontal the axis of growth. According to the nature of the organ and its purpose in the economy of the plant, either the upper side grows more strongly than the under side, or the reverse. A curvature concave either downwards or upwards is thus caused by the influence of gravitation and growth, and this curvature increases until the free-growing end is directed vertically either downwards or upwards ; the former, for example, in primary roots, the latter in many primary stems. In lateral branches, leaves, and secondary roots,

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[1] These statements are intended in the first place to draw the attention of students to the processes of vegetation which are especially influenced by gravitation. Its action on the mechanism of growth will be fully described in Chap. IV, where also the literature is quoted.

similar phenomena occur, though not so strongly. Internal processes of vegetation, the weight of the upper parts, or the influence of light, act in opposition to that of gravitation, so that conditions of equilibrium arise which cause the organs to stand horizontally or obliquely to the perpendicular.

Thus the vertical direction of primary roots and stems, and the oblique direction of their lateral branches, are determined solely by gravitation, or at any rate to some extent, so long as these parts are still growing; when they subsequently become lignified or cease to grow, they maintain the position once acquired. If therefore a growing plant rooting in the ground (inside a pot) is placed horizontally, the mature parts remain in this position; but the apex of the primary root turns downwards, and the growing internodes of the end of the stem turn upwards, the leaves, branches, and secondary roots also bend until they make about the same angle with the horizon that they did before the change in their position. The parts which were actually growing when the change was made are shown by the curvatures caused by the influence of gravitation.

Although we must defer till the fourth chapter the consideration of the internal changes which accompany these curvatures, the proofs that they are really caused by gravitation may be presented in the two following forms:—

(1) Individuals of the same species have everywhere on the earth's surface the same position with respect to the horizon, and therefore also with respect to the earth's radius. Upright stems therefore, such as pines, grow in South America in totally different directions from what they do with us; if their axes of growth were elongated downwards, they would intersect in the centre of the earth, and coincide with its radii. It follows therefore that their direction of growth must be determined by a force which stands in a perfectly definite relation to the position of the earth's centre of gravity. But there is only one such force, *viz.* gravitation or the attraction of the mass of the earth. The same argument holds for horizontal or oblique branches, leaves, and roots, since these form a constant angle with the primary stem.

(2) Gravitation differs from other forces in acting independently of the chemical or other properties of the body, being regulated only by its mass; but the same property is also possessed by centrifugal force. If, as Knight[1] first showed, a growing seedling is made to rotate with a rapidity sufficient to bring centrifugal force into play, this force acts on the different parts like gravitation; *i. e.* the parts which would otherwise be influenced by gravitation (as the primary root), now follow the direction of the centrifugal force and grow outwards from the centre of rotation, while the stem, which would otherwise grow upwards contrary to the direction of gravitation, now assumes a direction towards the centre of rotation, *i. e.* in a direction opposite to that of the acting force. This law is strikingly illustrated when seedlings, the roots and stems of which had previously grown in one straight line, are fixed upon a rotating disc (protected from evaporation by a bell-glass) in such a manner that the axis of growth has a tangential direction. The mature parts maintain this direction during the rotation, while those which are still growing bend so that the apices of the roots point

[1] Knight, Phil. Trans. 1806, part I, p. 99.

outwards and the apices of the stem inwards (towards the centre of rotation). If the rotation takes place in a horizontal plane, gravitation acts, in addition to centrifugal force, on the growing parts, and the direction of the stem and root becomes oblique. But when the rotation is very rapid, it is possible to increase the centrifugal force to such an extent that the axis of growth remains nearly horizontal. If, on the contrary, the seedlings are fixed to a disc rotating in a vertical plane, each side of the growing part is in turn directed for a short time upwards, downwards, to the right, and to the left. The action of gravitation therefore affects all sides equally; *i. e.* the growth of the organ is practically independent of gravitation. Centrifugal force is therefore the only force that acts on the growing parts; and the root takes an outward radial direction even when the disc is not rapidly turned, the stem an inward radial direction. If however the disc is made to turn very slowly in a vertical plane (round a horizontal axis), so that there is in fact no centrifugal force (as by intermittent turns, one revolution in ten to twenty minutes with a radius of from 5 to 10 cm.), I have shown[1] that the organs then grow neither in the direction of gravitation nor in that of the centrifugal force, but just in those directions in which they had happened to be placed when fixed in the vessel. Under such conditions parts which normally grow straight often curve in a plane quite independently of external forces, and this can only be due to internal causes of growth which are distributed unequally round the axis of growth. Thus, for example, primary roots and stems of germinating seeds (Faba, Pisum, Fagopyrum, Brassica), will not lie in a straight line, but their respective axes of growth will intersect at any angle up to a right angle, the anterior side of the base of the stem growing more rapidly than the posterior side, and thus causing a curvature. It is clear that the direction of the secondary roots which spring from the primary root, as well as that of the leaves on the stem, is also, under these conditions, affected only by internal causes of growth. It is only in this way that we can explain the directions and forms assumed by parts of plants when uninfluenced by gravitation, centrifugal force, or heliotropic curvatures, which could not occur in these experiments.

CHAPTER IV.

THE MECHANICAL LAWS OF GROWTH.

Sect. 11. **Definition.** The growth of crystals consists in an increase of their volume by the apposition of homogeneous particles in definite directions. In plants the process which we call growth is much more complicated; and the term is employed in different senses, according as we are speaking of the growth of a grain of starch or of chlorophyll, of part of a cell-wall, of a whole cell, or of a multi-

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[1] Würzburger Med.-Phys. Gesellschaft, March 16, 1872.

cellular organ. The common point in all these processes is that they depend at last on the intercalation of new molecules between those already in existence, in other words on intussusception, as has already been explained in the first section of Book III. But even in structures so simple as grains of starch or parts of cell-walls, we are met with insurmountable difficulties when we attempt to explain the mechanical process of growth in all its details; and the present state of our knowledge by no means enables us to propound a connected theory of the growth of the entire cell or of a multicellular organ. We are in fact at present able only to follow empirically the processes of growth in detail, their causes and results. After this we may attempt to form definite ideas of the separate processes, taking for granted at the outset the purely formal phenomena of morphology, and regarding as the ultimate object of the enquiry the obtaining an insight into the mechanism of growth. If the solution of this difficult problem must be deferred to a distant future, it at any rate lies within the scope of this work to collect together the ascertained phenomena. But even here we meet with the difficulty that no one has as yet undertaken to limit the term Growth to a definitely circumscribed idea. The term is however always employed in the case of plants and animals to designate changes in form or volume or both brought about by internal causes, themselves the result of organisation, and in their turn excited and maintained by definite external causes, as heat, light, gravitation, the supply of food-materials, water, &c. Changes in the form or volume of parts of plants that remain quite passive to external forces, and in which changes no organic process cooperates, ought not to be included in the term Growth. Thus, for example, there is no growth when the form or length of an internode or root is altered by simple stretching, pressure, twisting, or bending (it may be by the hands). It is quite possible however that under certain circumstances internal changes might be brought about by external influences to which the part of the plant is at first altogether passive, but which, combined with organic processes, cause true growth or changes of growth. By organic processes I understand those internal changes which fulfil the two following conditions:—firstly, they are caused by the specific organisation of the part of the plant, which is of such a nature that any external influence can only effect changes in accordance with it; secondly, they result in a permanent change of the organised part which is not at once reversed by opposite external influences. If, for example, the elevation of the temperature above the inferior limit (see Sect. 7, p. 651) has caused an increase in volume of the embryonic structures already saturated with water, the parts will not contract to their previous volume when the temperature again falls below this point, but will retain the increase acquired during the higher temperature; in other words the process is not reversed, it only ceases. Microscopic as well as other kinds of examination also show that the internal organisation has undergone permanent change varying with the specific properties of the plant. If on the contrary a stem is allowed to wither from want of water, it becomes shorter and ceases to grow; when it again absorbs water it becomes longer and thicker and begins to grow. The contraction on withering and the lengthening on the absorption of water are mere physical phenomena; but the lengthening and thickening of a part resulting from continued turgescence may actually depend upon growth, the organisation of the

plant being altered permanently and to an amount varying with the species by the operation of the turgescence. It is again the result of permanent and specific change of organisation when a tendril, in consequence of the light pressure of the body to which it clings, lengthens less on the side in contact, more on the opposite exposed side; the curvature thus caused does not disappear if the pressure has lasted long enough; the whole phenomenon is therefore one of growth. When, on the contrary, the motile organ of a Mimosa-leaf bends downwards in consequence of irritation, and afterwards again bends upwards, this is, it is true, caused by the peculiar organisation of the plant; but the movement induces no change in the organisation itself, and its effects are not permanent, the leaf soon returning to its original condition. The sensitiveness of the leaves of Mimosa does not therefore depend on a change of growth caused by the irritation; while the power of tendrils to curl round supports depends, it is true, on sensitiveness, but of such a character as to cause a change in the processes of growth.

If increase in volume is included in the idea of growth, as is the case in ordinary language, the rigorously scientific use of the word would require special care; for if we simply say that a plant or a part of a plant of considerable size grows, this may be accompanied actually by a decrease of the whole volume. Thus, for example, when bulbs sprout or seeds germinate in the air, the whole does not grow, but only the younger parts develope at the expense of the older, which in addition give off aqueous vapour and carbon dioxide. It is therefore necessary to distinguish accurately the growing parts from those which do not grow.

There are however changes of form in the parts of plants which are not associated with increase, and which may even be attended with decrease in volume, but which nevertheless depend on a permanent and irreversible change of organisation. Thus, for instance, the pith, after removal from the internodes, increases in length for days even while it loses water by evaporation in air that is not saturated. It would scarcely seem convenient to exclude these and similar phenomena from the idea of growth; and it is therefore necessary to distinguish between growth with and growth without increase in volume; in the latter case growth consists in a mere change of form which again depends on an alteration of position of the smallest particles. Every case of increase in volume of a grain of starch or of a cell must not be regarded as growth, inasmuch as it may be caused by absorption, and may be reversed by loss of water; nor is it necessary that growth in a single cell should be associated with increase in volume, since particular parts of the cell may furnish material for the increase of other parts. In this case the cell considered as a whole only changes its form; and if this change is caused by internal organic forces, it must be considered as a kind of growth. Those changes in the form and volume of cells must, on the other hand, be excluded from the idea of growth which occur only occasionally and admit of being completely reversed, as is the case with the contractile organs of sensitive and periodically motile leaves.

An error which is constantly made by those who are unacquainted with physiology is to confuse the ideas Growth and Nutrition, or to consider them identical. It is no doubt true that all growth must be associated with the conveyance of food-materials to the growing parts; but these food-materials are usually withdrawn from older parts where they were previously inactive; the whole organism, consisting of both growing

and non-growing parts (as a bulb suspended and putting out leaves in the air), is not nourished as such from without. The growth of certain parts is therefore no indication of nutrition of the whole. Still less necessary is the connection between growth and nutrition from without; the special organs of nutrition, the green leaves, do not grow after they are mature, although they carry on the process of nutrition. The two processes may coincide both in place and time, *i. e.* in the same cell; but may also be separated in both space and time; and this is indeed usually the case, as has been sufficiently shown in Sect. 5.

Sect. 12. **Various causes of Growth.** Growth, like vital activity, takes place only when certain favourable external conditions coexist. These are the presence of assimilated food-material, water, oxygen, and a sufficiently high temperature. Under these conditions individual cells or masses of tissue may grow, provided that their organisation permits it. But independently of these conditions there are others, as we have seen in the last chapter, which, without absolutely causing or arresting growth, nevertheless influence it; as light, gravitation, and pressure. The first-named may be called the necessary, the last the secondary conditions of growth. In all growth all the necessary conditions must concur while the secondary conditions intervene only in certain cases, and exert their modifying influence very differently on the corresponding parts of different plants.

The conditions spoken of as Necessary and Secondary Conditions depend upon the environment of the plant, and act upon it from without. They may therefore be described as *External Conditions* or causes of growth, in contradistinction to the *Internal Conditions* dependent on the organisation of the plant. The existence of the latter conditions is most strikingly manifested in the fact that all parts of plants are able to grow only during a certain time; when this time—the period of youth and development — is past, they no longer grow, even when all the favourable conditions concur. This shows that the internal organisation undergoes changes, which at length render the continuance of growth impossible. But even in organs which are still growing a certain independence of external circumstances may be perceived; an oak-leaf invariably grows differently from an elm-leaf, an oak-fruit from an oak-root. The differences of these processes of growth is at once manifest in the difference of form and of the other properties of the organ; and no combination of external circumstances has the power of giving to a root, by change in its growth, the form of a leaf, or to an oak-leaf the structure of an elm-leaf. There are also certain internal conditions of growth which do not decide, like the age of an organ and the necessary external conditions, whether growth shall take place, or at what rate; but determine how it shall proceed, and what specific and determinate organisation shall be attained by it. This latter circumstance depends only on the parent plants, or in other words on the species or variety to which it belongs. Descent determines the specific character of the growth; all the other conditions determine only whether growth shall take place at all, and with what rapidity and energy. The *innate* internal conditions that regulate the nature of the growth of the plant, when once present cannot again be destroyed or reversed; while the external conditions may be at one time brought into action, at another time set aside. The internal and external conditions of growth may therefore be distinguished as the historical and the physical; but those properties of a plant which have been

obtained historically are generally termed *hereditary*. The term is not open to objection unless heredity be considered, as has recently been done by many, as a kind of natural force requiring no further analysis. For in distinguishing hereditary conditions of growth—*i. e.* those that have been acquired historically—from physical ones, it is not meant that the former do not also owe their existence to physical phenomena, but only that besides the accidental concurrence of physical conditions, it is also necessary to take into account certain characters which the plant has acquired when in the embryonic condition (in the broadest sense of the term) in the form of definite specialities of organisation through the influence of its parents.

These remarks must suffice here. The extremely difficult question which has been raised may be illustrated by protracted and elaborate explanations, but cannot be satisfactorily answered.

The external or physical causes of growth are the only ones that can be submitted to direct experimental investigation; the internal hereditary causes must be considered simply as something that exists and that is in the main unalterable; for if it were possible to change some of the mechanical and chemical properties of a tissue by means of external influences, this could not affect the true kernel of the hereditary characteristics; and again conversely changes in these hereditary peculiarities, or *variations*, are never brought about by direct external influences, but only by unknown internal changes. Since therefore the specific peculiarities in the organisation of a plant are something in its nature that is entirely unknown, any investigation of the processes of growth must rest satisfied with showing the mode in which they are always associated with constant internal conditions, and what visible changes are produced in the processes of growth by physical influences. We cannot therefore be astonished if in the action of known external causes—light, gravitation &c.—on plants, effects are produced which appear altogether strange to one accustomed to examine purely physical processes; but this astonishment disappears when it is borne in mind that the specific organisation of a plant itself represents a complexity of causes which we cannot analyse, and therefore are unable to estimate. It is in the constant recognition of this unknown factor—which causes physiological effects to turn out so entirely different from purely physical ones—that the difference between physiology and physics consists. The most striking mode however in which the aggregate of conditions of growth manifests itself in the inherited organisation, is when the same external causes produce entirely opposite effects on plants belonging to different species and even on different parts of the same plant.

To understand correctly the phenomena of vegetation, it is also necessary to distinguish between the direct and indirect action of external causes on growth. For since growth is always dependent primarily on the presence of assimilated food-materials, light, temperature, or other external conditions may indirectly influence growth by affecting the formation and transport of the food-materials. But it is also possible and even probable that the mechanical process of intussusception itself on which growth is directly dependent, may be modified by those and other causes the influence of which on growth is therefore in that case a direct one. The growth of one part may also be indirectly promoted or retarded by the growth or the removal of another part.

The unknown factor which exists in the inherited properties of organisms is by no means without analogy in inorganic nature. Chemists and physicists have also to assume peculiar properties of elementary substances. The aggregate of properties by which a particle of iron is absolutely distinguished from a particle of oxygen is as unknown and much more invariable than the aggregate of physiological causes which distinguish the inherited properties of an oak from those of a pine.

So far as the definition given above of historical properties concerns the inherited specific peculiarities of plants, the term is not metaphorical from the point of view of the Theory of Descent, but must be taken in its literal signification. The specific properties which determine qualitatively the growth of each organ have sprung up successively in the course of time, *i. e.* in a series of generations. The chief evidence in favour of this view will be given in the last chapter of this work. It need only be mentioned now that this theory of the genesis of specific properties indicates the only possibility of arriving at an understanding of them in accordance with the laws of causality. At the present time this is possible only in the most general outline.

The use here made of the terms 'historical' and 'physical' may also be illustrated from another subject in the following manner. The nature of the geological formations of which the crust of the earth consists can be understood only from a historical point of view, because it is only at particular spots and at particular times that the conditions have concurred which produced, for example, the Chalk or Old Red Sandstone. The formation of these rocks was dependent on chemical and physical processes, which must however have been preceded by other physical changes in the crust of the earth, in order that these rocks should be formed exactly at particular spots and particular periods. A crystal of sodium chloride can, on the contrary, be produced at any time if the necessary conditions are artificially brought together. Pseudomorphosis of crystals can again be explained only from a historical point of view, although it is certain that the chemical and physical properties of the substances are alone concerned in the process. We see therefore—and this is the object of these remarks—that the historical explanation of a natural phenomenon does not exclude its explanation from a physical point of view, but on the contrary includes it where we have to do with natural phenomena; and this principle is equally applicable to those properties of vegetable species which have been acquired hereditarily or historically, even when the application is practically much more difficult than in the case of inorganic nature.

Sect. 13. **General Properties of the Growing Parts of Plants**[1]. From the consideration of this subject the true crystals which are found in cells may be entirely excluded, since they do not differ in their general properties from those which occur elsewhere. The organised elementary structures on the contrary, the protoplasm, the nucleus, chlorophyll- and starch-grains, and the cell-walls, exhibit properties which distinguish them from all inorganic bodies.

These organised bodies are, in the first place, all *capable of swelling; i. e.* they have the power of absorbing water or aqueous solutions between their solid

[1] See Nägeli u. Schwendener, Das Mikroskop, p. 402 *et seq.*

particles with such force that the particles are forced apart; the whole structure increases in size, and can thus exercise considerable pressure on the surrounding parts. If water is by any means withdrawn from the body which has thus swollen up, its particles again approach one another, and with such force that considerable strains may be exerted on the adjoining parts connected with it; as, for example, is shown in the bursting of dry capsules. The swelling and dessication of organised parts may therefore cause change of form in the surrounding parts, *i.e.* in other organised parts. This power of swelling is of still greater importance, since it is this process that renders possible the interchange of sap between the individual cells as well as between whole masses of tissue. In order that growth by intussusception may take place, the dissolved food-materials must be able to enter by imbibition between the particles of the growing structure, and the chemical processes must take place there which construct from the dissolved food-materials solid particles to be intercalated between those already in existence, and in consequence of which the organic mass alters its volume and form (see Book III, Sect. 1).

A second general property of the organised parts of plants is that they *change their form* when the external conditions remain perfectly unaltered, internal changes being the only efficient cause. Almost every process of growth is associated with change of form. These facts may be more briefly described by ascribing to organised structures endowed with the power of growth internal forces or plastic tendencies, if it is clearly understood that the term is only used to express a still unresolved aggregate of causes. As a result of these internal forces, organised structures have the power of overcoming resistance. Thus, for example, plasmodia which are constantly altering their form, are able, notwithstanding their gelatinous and very soft nature, to overcome their own weight, and to creep up solid bodies. In the same manner the growth of wood takes place with such force as to overcome the very considerable pressure of the surrounding bark.

But although the internal causes of these plastic tendencies are able to overcome certain obstacles, it is on the other hand certain that growth is also influenced by external forces, such as pressure, traction, stretching, bending, &c., which are able to alter the form of solid bodies. The observations which have been made on this subject will be collected in the following sections; but it is in the first place necessary to define certain terms which will frequently be employed.

Like unorganised solid bodies, those which are organised oppose a greater or less resistance to the external forces which tend to alter their form; and are hence divided into hard and soft bodies. A *hard* body is one which offers considerable resistance, like many lignified or silicified cell-walls; a *soft* body is one which offers very little resistance, like protoplasm, chlorophyll-grains, or swollen cell-walls which have ceased growing, as gum-tragacanth. Structures which become disintegrated under pressure and traction rather than undergo any considerable change of form, are *brittle*, like grains of starch or crystalloids of aleurone. If, on the contrary, they are capable of undergoing considerable changes of form, whether this take place by pressure or traction, they are *extensible*. It is clear that flexibility depends to a certain extent on extensibility, since the side of the bent part which becomes concave is compressed, the convex side stretched. All these properties are relative, and the same body may exhibit different phenomena according to the

nature of the external forces which act upon it. Thus, for example, under a sudden blow the apex of a root behaves like a brittle body, and breaks easily, while it is flexible if slowly bent.

If the form of an extensible body has been changed by pressure, traction, or bending, and if, when then left to itself, it retains the form to which it has been forced, it is called *inelastic*; if, on the other hand, it resumes its original form, it is *elastic*. If the changes of form produced by external causes are small, they are usually completely reversed when the body is left to itself, and within these limits the body is perfectly elastic; but if the change of form exceeds certain limits dependent on the nature of the body and the length of time during which the force has been acting, it does not again assume exactly its previous form. The greatest amount of change which yet permits a complete restoration of the original form determines the *Limit of Elasticity* of the body; when this is exceeded, the stretched substance partially retains the form which it has been made to assume, and the less complete the return to its primitive shape the more imperfect is its elasticity. It would appear as if all organised bodies were imperfectly elastic to any long-continued stretching or alteration of form, and as if there were no limit of elasticity in the case of very long-continued but weak external influence. In all these points organised bodies, especially the growing parts of plants, exhibit the same phenomena as inorganic bodies. It must however be remembered that the terms explained above have reference only to effects visible externally; the internal changes which bring about the external effect may be very different in different bodies. Rigidity, *i. e.* resistance to bending, depends, for example, evidently on very different internal conditions in the case of a woody cylinder and of a succulent stem or root consisting mainly of parenchyma. This is at once experimentally proved by the woody cylinder becoming less flexible and even brittle from loss of water, while the flexibility of succulent parenchyma is thereby increased. This is readily understood on recollecting that the flexibility of the woody cylinder depends on that of the walls of the wood-cells, which are not closed cavities, and therefore cannot become turgid, while the flexibility of parenchymatous tissue depends on the change of form of the closed turgescent cells, the extensibility and elasticity of the cell-walls taking only a subordinate part. Changes of form take place however more easily the less the turgidity of the cells; a parenchymatous tissue may be compared to an aggregation of bladders each of which is full of water; if they are all turgid with water, each bladder is tense and rigid, as also is the whole; if, on the contrary, they contain only enough water to fill without distending them, each separate bladder is flaccid, as also is the whole, which can therefore be bent in any direction. A mass of parenchyma may therefore be stiff and rigid even if its cell-walls are thin and very flexible, if only they are firm enough not to give way from the pressure of the water which stretches them or to allow it to filter through. The flexibility and elasticity of the moist cell-wall cannot however be compared directly with these properties in a perfectly dry cell-wall or a strip of metal, as Nägeli and Schwendener (*l. c.* p. 405) have already shown. 'If we consider first of all,' they say, 'a fragment of moist cell-wall, say a lamella of the thallus of Caulerpa, a bast-fibre thickened so that the cell-cavity has disappeared, a spiral vessel, and so forth, it is proved by their behaviour to polarised light that stretchings, bendings, and other

similar forces do not perceptibly change the arrangement of the atoms in the crystalline molecules, but that only the distance of the molecules themselves from one another is increased or diminished. On the other hand it is known that water is retained in the moist cell-walls with great force; and microscopic examination has shown that it cannot be forced out by the bending compression of the part. No other hypothesis is therefore possible, except that the amount of water in a distended cell-wall is the same as in one in a neutral condition. The particles of water are therefore merely displaced by external forces, but are not forced out; they move, for example, with the bending of the part from the concave to the convex side, but afterwards fill up as completely as before the molecular interstices of the substance; and, since the sum of their tensions is but slightly altered, also occupy nearly the same space. If the same reasoning is applied to tissues without intercellular spaces and filled with sap, it is perfectly obvious that the cell-walls are not susceptible of change of volume any more than in the previous case. The same is the case also with the fluid contained in the cells. The only question now remaining is whether the changes of tension which are caused by external forces modify the permeability of the cell-walls at least in places. If this were the case, then when a tissue is compressed—since the hydrostatic pressure (turgidity) is in no case decreased by it, but the resistance of the cell-wall weakened[1]—a part of the cell-fluid must obviously be forced out, until the hydrostatic pressure has again reached an equilibrium with the diminished resistance of the cell-walls. In the same manner the effect of traction on a tissue must be to cause an influx of water through it, or, if this is prevented, the formation of an empty space[2]. If, on the other hand, the changes of tension which occur in plants have no perceptible influence on permeability, the tissues simply possess the properties of moist cell-walls; in any condition of tension[3] they always occupy the same space[4].'

In order to understand many of the phenomena now to be described, it is necessary to have a clear conception of the changes which a cell filled with sap undergoes in reference to its turgidity when it is compressed or stretched or simply bent by external forces. By *Turgidity* we understand the hydrostatic pressure which the water absorbed by endosmose exercises equally on all sides on the cell-wall, and which reacts on the contents in consequence of the elasticity of the cell-wall; so that in a turgid cell, while the cell-wall is stretched, the contents are compressed. A clear conception of this state of mutual tension of the cell-wall and cell-contents may be obtained by closing a short wide glass tube at one end with a firm fresh bladder free from holes, pouring in a concentrated solution of sugar or gum, and finally closing also the other end with a thick bladder. This artificial cell, placed in water, absorbs it by endosmose with great force; the pieces

[1] These words are not clearly intelligible. Turgidity or the tension of the cell-wall is always increased, as we shall see directly, by pressure from without on a turgid cell; its resistance to infiltration may in this manner be at length entirely overcome.

[2] Of course only when the cell-wall does not become folded.

[3] By tension is here clearly meant bending, stretching, or pressure from external forces.

[4] The discussion given on p. 373 of the work quoted with respect to the alteration of the molecular structure of cell-walls by violent mechanical and chemical forces is of no importance for our present purpose.

of bladder which were previously stiff and tense arch into a hemispherical form and offer great resistance to pressure. If a hole is punctured by a fine needle in the bladder, a jet of fluid several feet in height springs from it. The force which drives out the fluid with such violence is the elasticity of the stretched bladder; but the cause which brings this elasticity into play is the endosmotic attraction for water of the fluid contained in the cell.

If we suppose in the case of a vegetable cell enclosed on all sides a degree of turgidity sufficient to stretch the cell-wall perceptibly, but leaving it still capable of further tension without bursting, and if this cell-wall is supposed to be extensible and elastic—as is especially the nature of growing and non-lignified cell-walls—the question presents itself:—What changes does the turgidity of the cell undergo when it is stretched or compressed by external forces or otherwise altered in form? This question can be sufficiently answered for our purpose by the simple contrivance represented in Fig. 448. *K* is a wide and thick india-rubber tube to which the glass tube *S*, closed at *g*, acts as a stopper. After filling *K* with water, the glass-tube *R*, open below at *o*, is fixed in and firmly fastened, the level of the water standing somewhere about *n* in the thin drawn-out upper end of the tube. In order to give to the india-rubber tube, which here represents the cell-wall, a sufficient tension from the outset, it is convenient to make the thin end of the tube *R* from 20 to 30 cm. long, and to raise the level *n* in proportion. The wide part of *R* is fixed in a holder, so that the cell hangs down. A condition of equilibrium is thus established between the elasticity of the india-rubber tube and the hydrostatic pressure which can be compared with the turgidity of the vegetable cell; and in this condition the water-level stands at *n*. If the tube *S* is now pulled downwards, the elastic tube is lengthened and at the same time made narrower, but the amount of space enclosed by it is increased, as may be seen by the falling of the water-level *n* in the narrow glass tube. If on the other hand the glass tube *S* is pushed up and the india-rubber tube thus compressed without any bending or creasing taking place in *K*, the space enclosed by the tube *K* is diminished, as is shown by the rising of the water-level *n*. The same thing takes place when the tube *K* is bent in any way, or when it is compressed on any side.

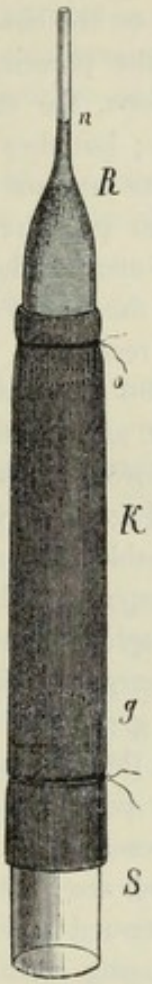

FIG. 448.—Apparatus for illustrating the change in the turgidity of cells caused by external distension or compression.

It is evident that if the upper glass tube *R* were closed at *n* so as to prevent a rise or fall of the water-level, any change which previously caused a rise of the level would now occasion an increase of the hydrostatic pressure, and *vice versâ*. It therefore be stated that in a closed and turgid cell any pressure acting from without or any curvature increases the turgidity, while any stretching of the cell

diminishes it. If we imagine a straight succulent stem or a growing root to be bent, the cells on the convex side will be stretched, those on the concave side compressed, and the turgidity will be diminished in proportion in the former and increased in the latter. This result is very clearly confirmed if a very succulent rapidly growing internode of the grape-vine is slowly but firmly bent till it describes about a semicircle. It will be observed that during the bending a number of small drops of water escape in rows from the epidermis on the concave compressed and shortened side. It is indifferent whether they escape through fissures or are forced out through the cell-walls; in either case they show that the cells display a higher degree of turgidity on the concave compressed side than when the internode was straight.

In the present state of our knowledge, if we would keep clear of uncertain speculations, the considerations now given must be considered as by no means complete; but they are sufficient to draw the attention to processes which must be taken into account in the interior of the growing parts of plants when they are subject to pressure, traction, bending, and so forth, from external forces. But if these internal changes are for the time left out of account, the purely external effect of the forces already mentioned is deserving of greater attention than it has hitherto received[1]. It would be of essential service, for instance, to ascertain at what point a growing internode, root, leaf, &c., possesses the greatest extensibility, flexibility, and elasticity, and whether this point coincides or not with that of the most vigorous growth, and how perfect is the elasticity of the part; and so forth. We shall see that even somewhat crude observations in this direction afford results which enable us to remove old errors and avoid new ones.

Compared with the extensibility of mature internodes and parts of internodes, that of rapidly growing parts is very considerable, but their elasticity, on the contrary, is very imperfect. But the greater the development of the wood of a growing part, the greater is its elasticity and the less its extensibility. In young non-lignified roots, on the contrary, the resistance to bending is greater in the youngest than in the older parts, especially those whose growth in length has long been completed. The extremities of roots, very young leaves, and the ends of stems still enclosed in the bud, are generally brittle under a blow or pressure, but pliable and plastic to long-continued action of this kind, a condition that gives place during growth to an increasing resistance to sudden blows, which is in the first place due to increase of extensibility, afterwards to increase of elasticity.

In rapidly growing stems, leaves, and roots, the limit of elasticity is easily overstepped even by momentary flexion; and they always retain afterwards a slight though distinct curvature. It is often even possible, especially with roots and slender internodes, to give them any desired form by repeated bending with the fingers in different directions, like a thread of wax or a red-hot iron wire, without the power of growth being at all injured by the process. This effect is attained with greater certainty by exerting on the growing structure a flexion which is prolonged although small in amount. Thus the pedicels of many flowers are bent downwards by their weight, and retain this curvature even when the weight is removed, until a new con-

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[1] See A. P. De Candolle, Physiologie Végétale, vol. I, p. 11.

dition of growth imparts greater elasticity and firmness to the tissues. Under the influence of gravitation they then grow more rapidly on the lower side, become upright, and raise up the still greater weight of the fruit; as is strikingly seen in *Fritillaria imperialis*, *Anemone pratensis*, and many other plants with pendent flowers and erect fruits. In other cases again the curvature, which was at first due merely to external causes, becomes permanent and fixed in the tissue itself by the processes of growth, as in the fruit-stalks of *Solanum Dulcamara*.

One of the most striking phenomena of this class is that a blow on the side of a rapidly growing internode causes it to assume a curvature which lasts for a considerable time. The same thing occurs when the upper part of a shoot is taken in the hand and a curvature imparted to it similar to that caused by the blow. The upper part acquires in consequence a pendent position which may however be again neutralised by subsequent growth.

There has been as yet no exact or detailed investigation of the elasticity of growing shoots, roots, and leaves; and the enquiry is, as I have convinced myself, attended with considerable difficulty. Observations sufficient to enable us to study some of the phenomena of vegetation to be described in this chapter can however be made with the simplest methods and apparatus.

(*a*) *Extensibility of growing Internodes.* The upper and lower end of an internode of a freshly cut fragment of a stem were marked with Indian ink. The shoot was held above and below the marks, laid on a micrometer graduated to millimetres, and stretched as strongly as possible without breaking[1]. The result is shown in the annexed table:—

Name.	Original length of internode.	Amount of temporary elongation.	Amount of permanent elongation.
1. *Cimicifuga racemosa*	296 mm.	6·8 p.c.	3·5 p.c.
2. *Sambucus nigra*	26	18·0	5·4
The next older internode	65	3·1	1·1
A still older internode	115	·8	·0
3. *Aristolochia Sipho*	102·5	4·4	1·0
The next older internode	242	2·2	·4
4. *Aristolochia Sipho*	33·5	10·4	1·5
The next older internode	252·5	1·8	·4
5. *Aristolochia Sipho*	71·5	6·3	3·5
The next older internode	226	2·6	·8

Imperfect as was the method of observation, these figures nevertheless show (1) that growing internodes are highly extensible, (2) that extensibility decreases with age, (3) that elasticity increases with age.

(*b*) *Elasticity to flexion of growing Internodes.* Internodes of fresh turgescent shoots were cut off, and bent on a card on which concentric circles were drawn; the axis of the internode was made to coincide as nearly as posssible with one of

[1] This somewhat primitive method of stretching, which of course does not furnish an exact measure of the extensibility of different internodes, was employed because stretching by means of weights necessitates fastening the shoot, which is attended with great inconveniences.

the circles; the radius of this circle is recorded in the following table as the *radius of curvature*. The internode was then left to itself, and its permanent curvature determined in the same manner. The branch was then bent on the other side, and so on, as shown by the table. The internode was finally laid with its concave side on the measuring rod and pressed straight on to it.

Name.	Length of the internode.	Radius of curvature when bent.	Radius of curvature when left to itself.	Thickness of the middle part of the internode.
Valeriana officinalis; stalk of young inflorescence.				
Before bending . . .	200 mm.	cm.	cm.	6 mm.
1. Bent	—	4	13	
2. Bent in opposite direct.	—	4	21	
3. Bent as in (1) . .	—	4	23	
4. Bent as in (2) . .	—	4	24	
Straightened . . .	201·5	—	—	
Cimicifuga racemosa. Before bending	165	—	—	5
1. Bent		5	19	
2. Bent in opposite direct.		5	22	
Straightened . . .	165·5	—	—	
Heracleum sibiricum; stalk of umbel. Before bending .	165·5	—	—	5
1. Bent		5	18	
2. Bent in opposite direct.		5	23	
3. Bent as in (1) . .		5	25	
4. Bent as in (2) . .		5	22	
Straightened . . .	167·0	—	—	
Vitis vinifera; young internode.				
Before bending . . .	47·5	—	—	5·8
1. Bent		2	4	
2. Bent in opposite direct.		2	6	
3. Bent as in (1) . .		2	6	
4. Bent as in (2) . .		2	9	
Straightened . . .	47·5	—	—	
Vitis vinifera; older internode.				
Before bending . . .	133·8	—	—	7
1. Bent		4	8	
2. Bent in opposite direct.		4	17	
3. Bent as in (1) . .		4	11	
4. Bent as in (2) . .		4	25	
Straightened . . .	133·0	—	—	

These examples, selected from a long series of observations, show:—(1) that growing internodes are very flexible, (2) that after bending they do not altogether recover their straightness, or that the elasticity of curvature is imperfect; (3) that

repeated bendings constantly in opposite directions leave progressively smaller curvatures[1]; (4) that one vigorous bending, and to a still greater extent repeated ones in opposite directions, leave the internode flaccid, or deprive it of its rigidity (of which no special account is taken in the table); and (5) in the case of the three first examples, that an internode bent first in one and then in another direction lengthens slightly, while in the case of the two last there was no lengthening, but in one even a perceptible contraction.

(*c*) *Change of length of the concave and convex sides of a bent internode.* Here again, as in paragraph *b*, the bending was done by the hands, and measured by the radius of curvature on a card on which concentric circles were drawn. The original length, as well as those of the sides which remain concave and convex after the object is left to itself, were measured by means of a carefully applied strip of card divided into millimetres. In order to get a great difference between the concave and convex sides, very thick internodes were selected, and their thickness measured in the middle.

Name.	Length of internode.	Radius of curvature when bent.	Radius of curvature when left to itself.	Contraction of the concave side.	Lengthening of the convex side.
Silphium perfoliatum 13·2 mm. thick.					
Before bending . .	185 mm.				
Bent		14 cm.	26 cm.	1 mm.	2 mm.
Bent in opposite direct. .		14	30	1	1·5
Straightened . . .	185				
Ligularia macrophylla 7·5 mm. thick.					
Before bending . .	199				
Bent		6	17	3·5	4
Bent again . . .		5	13	3·5	4·5
Bent in opposite direct. .		6	30	·5	1·5

These observations show, as was to be expected, that the permanent curvature of an internode is connected with a permanent contraction of the concave and lengthening of the convex side.

(*d*) *The region of greatest flexibility*, and at the same time of least elasticity in growing shoots, appears to coincide with the spot where the maximum rapidity of growth exists (*vide infra*, Sect. 17) or is just past; more exact determinations are however wanting on this point. If a number of rapidly growing shoots are cut off at a point where there is no longer any growth in length, and if this place is taken in one hand and the terminal bud in the other hand (after the removal perhaps of the older leaves), and the shoot is then bent tolerably vigorously by a pull at the bud, it may be seen, with the aid of a card on which a number of concentric circles have been drawn, that the strongest curvature (with the smallest radius of curvature) takes place at a point at a great distance, often as much as 10 or 20 cm., from the bud,

[1] The curvature is less the greater the radius of curvature.

and where (so long as direct observations are wanting) the most vigorous growth in length or at least the commencement of its decrease may, from other indications, be inferred. Both above and below, *i. e.* on older as well as younger parts of the shoot (or of the single internode), the curvature is less, the radius of curvature greater, and the regions of least pass insensibly into those of greatest curvature. It follows that a long portion of a curved internode cannot in these cases be considered as an arc of a circle, and must not be treated as such in measurements of length. It follows also that the radii of curvature spoken of in paragraphs *b* and *c* represent only approximate values which can give but a rough idea of the curvature observed in those cases.

In the primary roots of seedlings of Vicia, Faba, Pisum, Zea, &c. from 5 to 15 cm. in length, I convinced myself by a similar series of experiments that the most flexible and least elastic regions lay far below those where growth in length had already completely ceased[1].

(*e*) *Sudden curvature of growing shoots from a blow or concussion.* If upright growing shoots[2] are suddenly and violently struck below at a point where growth has ceased, the curvature thus caused advances upwards in the form of a wave, so that immediately after the blow which has been given to the lower part the apex of the shoot is strongly bent, the concavity of the curvature lying on the side from which the blow was received. The elasticity of the bent part causes the apex to spring back immediately; but when, as we have seen, the elasticity is very imperfect, the shoot retains a part of its curvature. As soon as the shoot has come to rest after some oscillations, it may be observed that below the apex, where the shoot is most flexible to an ordinary passive curvature, a permanent curvature is established, the apex bending over, and always on that side from which the blow was received. In many cases this phenomenon is produced by a single blow from a stick, as *e. g.* in Fagopyrum, Lythrum, and Senecio, flower-stalks of Digitalis, Cimicifuga, Aconitum, &c.; in more rigid stems and the parts of those that are less flexible and elastic, the bending over of the apex does not take place till after three or four or even from twenty to fifty blows have been given to the lower woody part; the amount of curvature also varies in different plants. If shoots are cut off low down so that a woody piece the growth of which has ceased can be taken in the hand, and the shoot made to oscillate rapidly backwards and forwards, it assumes, when it comes to rest, a distinct curvature below the apex in the region of greatest flexibility. The plane of curvature coincides with that in which the oscillations take place, and the apex may bend to either side; but the permanent curvature will always be concave on the side on which the oscillations were strongest. If finally a rooting shoot or one firmly held in the hand receives repeated lateral blows at its summit, that is, above the most flexible part, a perma-

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[1] Further details will be found in the Arbeiten des Bot. Inst. in Würzburg, Heft 3.

[2] The phenomenon here described was first observed and studied by Hofmeister (Jahrb. für wissensch. Bot. vol. II, 1860); and a few important corrections of his description were given by Prillieux (Ann. des Sci. Nat. vol. IX, sheet 2). The statements here made, which confirm the previous observations in all essential points, while differing from them in a few others, are entirely based on my most recent observations.

nent curvature is produced in this region, but it is in this case convex to the side from which the blows came.

In all the cases which I have described the position of the permanent curvature is the same as that of the strongest curvature, even if acquired only momentarily by the shoot. The appearance is precisely the same as if the shoot were taken in the hand and then strongly bent once, or as if it were repeatedly bent backwards and forwards, but more strongly in one direction. Mere concussions which produce no strong flexion of the shoot cause no permanent curvature; if shoots are enclosed in glass tubes and violent impulses repeatedly imparted to them by jerking the tubes upwards or swinging them from side to side no change is visible when the shoots are removed from the tube.

If the part of a shoot susceptible of curvature is marked with ink in equidistant divisions, and then made to oscillate by blows below this part, the convex side of the permanent curvature is then found to have become longer, the concave side shorter, precisely in accordance with the phenomena described in Sects. *b* and *c*[1]. For the measurements in the following table as thick shoots as possible were used, since they give considerable differences in length between the convex and concave sides even when the curvature is slight. The measurements were made with strips of card graduated in millimetres, and which I applied closely to the concave and convex sides.

Name.	Original length.	Approximate radius of curvature.	Lengthening of the convex side.	Contraction of the concave side.
Silphium perfoliatum .	152 mm.	18 cm.	3·4 p. c.	·0 p. c.
do. do. . .	120	—	1·7	·6
Macleya cordata . .	87·5	7	2.3	1·7
do. do. . .	104	24	·5	1·5
Polygonum Fagopyrum	63	8	2·1	1·6
Helianthus tuberosus .	98	—	2·0	1·4
Valeriana exaltata .	150	32	·8	·7
do. do. . .	110	—	·7	2·1
Vitis vinifera . .	149	6–10	1·3	2·0

The permanent curvature which remains after violent oscillations of a shoot, or the *Curvature of Concussion*, is the result of a lengthening of the convex and a simultaneous contraction of the concave side. A proof is thus afforded that the whole phenomenon is dependent on the very imperfect elasticity and the great flexibility of the region that is capable of flexion[2]. A shoot bent in this way shows the same changes as one that is simply bent between the hands. This result

[1] According to Hofmeister all the sides of the shoot become longer. He calculated the length of the curve which he took for an arc of a circle; and Prillieux measured only the concave side, which he found to be always shorter; the contraction of the whole shoot, *i. e.* of its neutral axis, cannot however be inferred from that of the concave side. The thickening which, according to Hofmeister, should take place, if the shoot becomes longer on all sides, I consider cannot be demonstrated, in consequence of the extremely small change in diameter which takes place in such cases.

[2] Compare the different description given by Hofmeister in his paper On the Bending of the Succulent Parts of Plants, in the Berichte der kön. sächs. Ges. der Wiss., 1859.

would not be at all altered were it found, in harmony with what was said in paragraph *b*, that the concave side was also sometimes slightly lengthened, since it is stretched by the recoil of the oscillations; and this elongation is not always entirely neutralised. Prillieux has compared this curvature to that of a lead-wire fixed to an elastic support, when the support was struck; he was unable however to see the reason why the older and younger parts of the shoot did not exhibit the phenomenon. In the older parts this depends on their more perfect elasticity, in the younger on their smaller flexibility, and on the circumstance that they are not strongly bent, but are only thrown backwards and forwards by the oscillations of the lower and more flexible parts.

The subsequent neutralisation of the curvature by growth must depend first of all on the increase of turgidity in the concave and its diminution in the convex side, and on the growth being consequently promoted in the former. This may be assisted also by the secondary effect of elasticity, in consequence of which the stretched epidermis of the convex side contracts, while the compressed tissues of the concave side distend.

Sect. 14.—**Causes of the condition of Tension in Plants.** The elasticity of the organised parts of plants results in tension chiefly from the operation of three causes; *viz.* (1) the turgidity, in other words the hydrostatic pressure of the contents of the cell on the cell-wall; (2) the swelling and contraction of the cell-walls when they imbibe or lose water; and (3) the changes in volume and form caused by the growth of the cells.

1. *Turgidity.* The force by which water is drawn by endosmotic attraction to the cell from the parts that surround it, is not merely sufficient to fill the space enclosed by the cell-wall, but also to enlarge it, the increasing amount of sap distending the cell-wall until its elasticity is brought into equilibrium with the endosmotic absorption. In this condition the cell-wall is stretched to its full capacity, or the cell is *turgid.* If the cell loses a portion of its water by transpiration or by neighbouring cells withdrawing it, the tension of the cell-wall is decreased and the volume of the cell diminished. The hydrostatic pressure produced by the endosmotic action of the cell-wall acts from within and is the same at all points within the small cell-cavity; but this does not prevent different points of the cell-wall stretching and contracting in different degrees as the turgidity increases, in consequence of local variations in extensibility. Hence not only may the volume but also the form of the cell be changed by turgidity. The greater the tension between the cell-wall and its contents, in other words the greater its turgidity, the greater is the resistance offered by the cell to external forces which tend to alter its form by pressure, but the more readily does it burst in consequence. If the cell loses so much water that the space enclosed by the flaccid cell-wall is no longer filled, it may become folded inwards by the external pressure of the air or of the surrounding water, and in this case the cell is said to collapse; if the cell-wall is thick, firm, and inflexible, a tension of an opposite character to turgidity takes place in the cell. Since turgidity is nothing but the mutual tension of the cell-wall and contents, or a state of equilibrium between endosmotic absorption and the elasticity of the cell-wall, it is evident that only closed cells, *i. e.* such as have no orifices, can be

turgid. The molecular pores through which the water set in motion by endosmose forces its way into the cells are essentially different from orifices; the former are so small that their diameter is completely under the control of the molecular forces, while even the smallest orifice withdraws at least the middle portion of its space from the influence of the molecular action of the substance that bounds it. Microscopic openings, like the pores of bordered pits, are orifices of this latter kind, and are excessively large compared with the molecular pores through which endosmose acts. Cells with pits penetrating the cell-wall cannot therefore be turgid, because any tension however small between cell-wall and contents is at once neutralised by the superfluous sap becoming pressed out through the orifices. It is indeed possible for water to be forced out in this way even through closed cell-walls, but only when the turgidity is very great, and the hydrostatic pressure of the cell-sap on the perfectly tense cell-wall is sufficient to force out the water through the molecular pores[1]. The resistance offered by the cell-wall to this may be called resistance to filtration. It is very different in amount in cells of different kinds, and on it the degree of turgidity depends, when the intensity of the endosmotic force of the sap and the elasticity of the cell-wall are constant.

What follows with respect to the turgidity of the individual cell is equally true in general of masses of tissue; only that a much greater variety of phenomena may arise in this case according to circumstances. If, for example, a number of similar layers of tissue are united into a system, a curvature of the system may take place when one layer loses water by evaporation and thus becomes shorter, or when it absorbs more water than another layer and thus becomes longer. For instance the primary roots of seedlings which have become partially flaccid by evaporation and perceptibly shorter, quickly bend upwards concavely if placed with one side on water; if placed entirely in water they become straight and longer. Curvatures arise in the same manner when layers of different tissues are united with one another and subjected to a variable amount of turgidity. Stems of the dandelion for instance split lengthwise and placed in water roll up in a spiral manner, the outside being concave, because the medullary parenchyma absorbs much more water, and consequently, from the extensibility of its cell-walls, expands more than the epidermis or the cortex, which absorb water more slowly, and whose cell-walls are besides not so extensible.

As the cell, with increasing turgidity, opposes greater resistance to forces which tend to change its form, a mass of tissue becomes more rigid when all its cells are more strongly turgid, and *vice versâ*. If, for example, a cylinder of pith is cut out from a growing internode, it is flaccid and flexible; but if it is placed for a quarter or half an hour in water, it not only becomes considerably longer, but also very rigid and even brittle in consequence of all its cells becoming rapidly filled with water. This effect is still more visible when the pith is surrounded by other less elastic tissues, as in an uninjured internode. If this internode withers, *i. e.* becomes flaccid from transpiration, and is placed in water, the pith very soon begins to

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[1] That the water which filters through under such circumstances actually passes through molecular pores is clear from the fact that the amount of soluble substances contained in the water is altered by the filtration.

become turgid and to distend; but since it is surrounded by other tissues of different properties, it must stretch them in order to lengthen itself; this is only possible however until the elasticity of these layers is in equilibrium with the tendency of the pith to distend. In this case the elongation of the whole caused by the turgidity of the pith is much less than that of the pith alone would be; but on the other hand there is now a violent tension between the pith and the surrounding tissues, in consequence of which the whole internode appears very rigid or but slightly flexible. The whole internode may be compared to a cell the contents of which are represented by the pith, its cell-wall by the surrounding tissues. If the pith loses water the whole becomes smaller, the passively stretched tissues contracting elastically; and since the tension is thus decreased, the whole becomes more flaccid; the reverse when the change is in the opposite direction.

2. *Imbibition* is the term given, as we have already seen, to the capacity[1] of organised structures to absorb water between their molecules with such force that they are thus driven apart, their cohesion being partially or entirely overcome, and the whole thus increasing in volume. Loss of water, on the other hand, as by transpiration, causes approximation of the molecules and a corresponding decrease in volume of the whole. Both distension and contraction take place with such force as to overcome external resistances of considerable magnitude. While in closed and thin-walled cells the changes in form and volume are chiefly caused by turgidity, in very thick-walled cells on the contrary with a small cavity (as many bast-fibres and collenchymatous cells), they are brought about mainly by imbibition and desiccation of the cell-wall, and especially when it is to a high degree capable of swelling, in other words is in a state to absorb or give off large quantities of water. In cells with open pores, where there can be no hydrostatic pressure or turgidity, as in wood-cells and vessels with bordered pits, imbibition and the desiccation of the perforated cell-wall are the only means of changing the size and form of the cell.

If, as is usually the case with thick cell-walls, the different concentric layers of cellulose have different degrees of capacity for imbibition and swelling (see Book I, Sect. 4), tensions are caused between these layers by the absorption or loss of water, which may even end in the layers becoming detached from one another; as, for example, occurs in the transverse discs of thick-walled bast-cells and starch-grains. But it is not only the quantity of water absorbed and given off that varies in the different layers of a cell-wall, but also the direction in which the water is principally absorbed or allowed to escape between the molecules. Tensions are thus caused which may lead to the production of torsions and oblique fissures, to the rolling or unrolling of spiral bands of the cell-wall, and to a change in the obliquity of the spirals[2].

All these changes, which are necessarily associated with the tensions of layers that have become convex and concave, take place also in masses of tissue and organs the cells of which have lost their contents and consequently their turgidity, while their cell-walls have become capable of imbibition, or, as it is generally termed,

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[1] See Nägeli u. Schwendener, Das Mikroskop, p. 424 *et seq.*

[2] Compare Cramer, in Nägeli u. Cramer's Pflanzen-physiologische Untersuchungen 1855, Heft 3, p. 28 *et seq.*; and Sachs, Experimental-Physiologie, p. 429.

hygroscopic. The layers of cell-walls and the thin-walled masses of tissue which in the living state contain most water, contract most strongly after death and from desiccation; with change of form they become concave, or are ruptured by the contraction of the intermediate lignified tissue. Without entering at present into a detailed consideration of these extremely variable phenomena, which, though often of extreme importance in the life of the plant, do not influence growth, it need only be mentioned that on them depend the bursting of most sporangia, anthers, and capsular fruits, the remarkable movements of the awns of various species of Avena and Erodium, as well as those of the Rose of Jericho (*Anastatica hierochuntica*) and of the so-called asthygrometer[1]. Of direct importance on the other hand, as respects the mechanical laws of growth, are the changes in volume of the wood and bark of trees which accompany the variation in the quantity of water they contain, and the very powerful tension between them thus caused in woody plants, to which I shall again recur in detail. The attention of the student need now only be called to one point, *viz.* that when wood distends on imbibition or contracts on desiccation, this is caused entirely by the alteration in form and volume of the cell-walls, since turgidity cannot take place in wood as it does in a tissue consisting of closed cells. The distension and contraction of wood when it absorbs or loses water are very different in different directions, strongest in the tangential, weaker in the radial, weakest of all in the longitudinal direction[2]. This is the cause, for instance, of the longitudinal splits in woody stems when they become dry, which close again when water is absorbed; and the changes of dimension due to these phenomena take place with extraordinary force.

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[1] Compare Cramer's statements in Wolff's treatise, Die sogenannte Asthygrometer; Zürich, 1867.

[2] This is the case, according to Laves, in the changes of dimension. (See Sachs, Experimental-Physiologie, p. 431.)

	In the direction of the axis.	In the direction of the radius.	In the direction of the circumference.
Maple	0·072	3·35	6·59
Birch	0·222	3·86	6·59
Oak	0·400	3·90	7·55
Fir	0·076	2·41	6·18

The change in volume of wood was investigated by Weisbach (*l. c.* p. 412).

	Water absorbed by 100 parts by weight of dry wood.	Distension of 100 parts by volume of dry wood.
Maple	87 parts	9·4
do.	87	7·1
Birch	97	7·0
do.	91	8·8
Oak	60	7·2
do.	91	7·8
Fir	94	5·7
do.	130	5·1

In comparing the change in volume with the amount of water absorbed, it must be borne in mind that the numbers in which the latter is expressed do not give merely the amount of water imbibed by the cell-walls, which alone causes the distension, but also that retained in the cavities by capillary attraction. It may therefore happen that there appears a smaller increase in volume when a larger quantity of water is absorbed.

3. *Growth* itself must cause states of tension in the layers of a cell-wall or of the tissue of which an organ is composed, if the layers, although firmly united to one another, grow unequally. It is however much more difficult to understand the modifications of tension due to growth than those due to turgidity and imbibition, as the former cannot be altered artificially without a material change being caused also in the latter. Since the growth of every organised structure, such as a cell-wall, can only proceed so long as it is permeated with water, and since moreover the growth of the entire cell requires it to be in a turgid condition, and this condition itself has an influence on growth, it is extremely difficult to decide how far each of these phenomena is the cause of the other. If by growth we understand, according to the definition already given, only permanent and irreversible changes of organisation, affecting in the first place the molecular structure of the organism, it may be assumed, in accordance with the present state of our knowledge, that growth is always preceded by imbibition and turgidity, and that it is the tensions of the molecular forces caused by these conditions which render possible the intercalation of new solid particles among those already in existence. If, for example, a cell-wall is stretched by turgidity, the distance of its molecules increased, and possibly a different arrangement of them brought about, this state may be reversed on the cessation of the turgidity, by the elasticity of the cell-wall. But if, during the condition of tension, growth takes place by the intercalation of new solid molecules, the tension of the cell-wall is altered and in general diminished. If now the turgidity ceases as before, a new condition of equilibrium occurs in the cell-wall ; a permanent change is caused by growth, which was however rendered possible by hydrostatic pressure and imbibition.

The share taken by growth in the tension of the tissues amounts to this: new molecules are intercalated in the original substance, and the tension due to imbibition and turgidity is thereby partially neutralised. This is however only momentary; for after the intercalation of new molecules the turgidity again increases, the degree of imbibition is modified, new tensions are again caused, which on their part are partially neutralised by the intercalation of fresh solid molecules. It is probably near the truth to suppose that the limit of the elasticity of the growing cell-walls is constantly nearly reached by turgidity and imbibition as well as by the secondary tensions produced by them. But on the other hand the tension is constantly being diminished by the intercalation of new molecules. Growth may therefore be described as a constant overstepping of the limit of elasticity of the growing cell-wall constantly neutralised by intussusception.

It will of course be understood that in the brief description now given we do not mean to state a theory of growth, but only to indicate in general terms the mechanical effect exercised by growth on the tension of tissues, and conversely. It would be easy to deduce the explanation in particular cases. If, for example, a cell-wall is imagined distended by turgescence or by traction exerted by the surrounding tissue, the intercalation of solid particles between the layers of cellulose already in existence may take place to a greater or less extent, causing a differentiation in their extensibility, elasticity, and power of imbibition, and thus leading to mutual tensions of the layers, as may be seen almost invariably in thin transverse sections of the cells of plants, and especially in the outer walls of those of the epidermis. But

these differences in the mode of intussusception even in the different layers of the same passively distended cell-wall may depend on a variety of circumstances; as, for instance, on the degree of proximity of the layers to the protoplasm, on whether they are in contact externally with the air, &c. But growth by intussusception may also vary according to the nature of the tissue of which the cell forms a part, or the chemical properties of the cell-contents, and according as the cells are passively distended or compressed by other cells. All these considerations are however merely hypothetical, and simply indicate the nature of the relations between growth by intussusception and the tensions caused directly by imbibition and turgidity. It may in any case be regarded as certain that intussusception is only possible as the result of imbibition and turgidity; but that these properties, as well as extensibility and elasticity, must, or at least may be, in their turn modified by it. The volume of the growing part increases; and since this takes place in different degrees in different layers of the same cell-wall, and in different layers of the tissue of the same organ, tensions varying in degree must be produced between these different layers.

It may not be superfluous to add some explanatory observations relative to what we understand by *Tension*.

Corresponding to every tension is an opposite tension. If a tissue which has a tendency to become distended is prevented from doing so by its connection with surrounding tissues, both are in a state of tension, the one negative, the other positive. The tissues which are passively distended may be said to be in a state of *negative tension*, those which are compressed or hindered in their distension to be in a state of *positive tension*. In a turgid cell, the cell-wall is therefore in a state of negative, the contents in a state of positive tension.

As long as there is no movement or change of form, the two opposing tensions must be equal; *i. e.* the work which the part in a state of positive tension performs is equal to the work performed by means of its elasticity by the part in a state of negative tension; or the elastic forces set in action must perform the same amount of work in two layers with opposite tensions and in equilibrium with one another. If, for example, a steel cylinder 1000 mm. long is supposed to be placed in an india-rubber tube 500 mm. long and closed below, and if the tube is stretched so that it can be fastened above the upper end of the steel cylinder, we have a system in a state of tension, the india-rubber negative, the steel positive; and since the system is at rest, the opposing tensions must be equal; *i. e.* all the particles of the india-rubber tend to contract with the same force as that with which those of the steel, which are now compressed, tend to separate from one another.

This example shows at the same time that the amount or intensity of the tension can by no means be measured by the changes in dimension which the layers experience at the moment when they are set free from it. Let us, for example, suppose, in our system of steel and india-rubber, that the steel cylinder is shortened 0·1 mm. out of 1000 by the india-rubber, while the india-rubber tube must be stretched 500 mm. out of 1000 in order to produce an equilibrium. If the tube is now opened above, it at once contracts 500 mm. (supposing it to be perfectly elastic), while the steel cylinder elongates only 0·1 mm.; the change of dimension is therefore 5000 times greater in the case of the india-rubber than in that of the steel, although the actual tension of the two was the same. But the alteration of dimension

indicates only the amount of stretching to which the india-rubber, and of compression to which the steel was subjected. If therefore the layers of the tissue of an internode are separated from one another, the alterations of dimension which then ensue depend on the extensibility and compressibility of the layers as well as on the amount of tension. There is only one case in which the amount of tension can be inferred from the changes in dimension of the tissues when freed from a state of tension, *viz.* when their extensibility and compressibility are the same, and when perfect elasticity also exists in both. Under this condition in our system of steel and india-rubber, the tension would have been only half as great if the india-rubber tube had been at first 750 instead of 500 mm. long; it would only have been required in this case to be stretched 250 instead of 500 mm., and the alteration of dimension would show us that the tension was only half as intense as before. But the case is quite different with growing internodes; the extensibility of the tissues when in a state of tension is constantly changing in consequence of growth. In a young internode the epidermis and wood are very extensible; if they are separated from the pith this latter only lengthens slightly, because it was only slightly compressed, but the epidermis and the wood contract very considerably because they are very extensible and were stretched by the pith. On the other hand the alterations of dimension in layers of an older though not mature internode will be the reverse. The pith, when freed from the tension, elongates considerably, but the wood contracts only slightly, because its extensibility is now but small and it was but slightly stretched by the pith; the pith on the contrary being very compressible, was prevented from lengthening by the resistance of the wood. The intensity of the tension cannot by any means be determined in either case from the changes of dimension; these only show that there are tensions, and indicate also what parts are extensible and compressible, and which are in a state of positive and negative tension[1]. It may be laid down as a rule that when the separation of two tissues causes one of them to contract or expand, while the length of the other apparently does not change, both layers were nevertheless in a state of tension, only the one which remained unchanged in length was but slightly extensible or compressible, while the other possessed these properties in a higher degree. When, on the other hand, an internode consists of very extensible cortex and very compressible pith, both will alter very considerably in length when separated; and yet the tension is not necessarily as great as in another internode where the cortex is less extensible and the pith less compressible, and where both undergo smaller alterations of length when separated. Similarly in our system of steel and india-rubber, if the steel is supposed to be replaced by a cylinder of india-rubber, this cylinder would be very strongly

[1] In his treatise On the tension of the tissue of the stem and its results (Bot. Zeitg. 1867, No. 109) Kraus has employed the differences of length between the entire internode and its isolated layers of tissue as a general measure of the intensity of the tension; but this, it will be seen from what has here been said, is inaccurate. If, for example, the wood and pith of an older internode are isolated, the contraction of the former is scarcely perceptible, while the latter elongates considerably; the pith of the internode was therefore in a state of great tension, while the wood was not; although the degree of tension of the two was the same, differing only in sign (positive and negative). On p. 112 (*l. c.*), Kraus gives a correct account of the behaviour of the layers of tissue of growing internodes.

compressed by the tube of india-rubber which in its turn would be stretched by it; and when the system was broken up a smaller contraction would take place of the tube but a much greater elongation of the cylinder than in the case of the steel, even if the tension put into action had been the same in amount as in the system of steel and india-rubber.

Sect. 15.—**Phenomena due to the Tension of Tissues in the growing parts of Plants**[1]. A. *Tension of different layers of a cell-wall.* By cutting as large pieces as possible out of the walls of living cells and placing them in water, it is found that if the cell-wall consists of layers of which the outer ones have a less and the inner ones a greater capacity of imbibition, the piece of cell-wall will bend so that the outer side becomes concave, the inner side convex. If the greater part of the water of imbibition is withdrawn from the piece of cell-wall by placing it in a solution of sugar or in alcohol or thick glycerine, the bending diminishes or even changes into the opposite direction, the inner side becoming concave; this direction being again reversed by again placing the object in water. Narrow strips which may be cut at right angles to the surface out of pollen-grains of Cucurbita or Althæa or the cells of the internodes of Nitella, are well adapted for this experiment.

The concave curvature evidently depends on the inner layers of the cell-wall absorbing more water in the direction parallel to their surface than the outer layers, and thus stretching more and becoming the convex side of the system. When water is withdrawn the opposite result must ensue. Let us suppose the cell to be closed and entire and not at all or scarcely turgid, *i. e.* with no hydrostatic pressure between cell-wall and cell-contents. The inner face of the cell-wall will be in contact with the cell-sap, and will absorb more water than the outside; a tension will therefore be produced, the inner layers of the cell-wall having a tendency to stretch, and being partially prevented from so doing by the outer layers. This tension of the tissues will impart to the cell-wall a certain stiffness and rigidity which is quite unconnected with turgidity. But since in the normal state and especially when they are growing cells are always turgid, the whole system of tissues will be distended independently of this.

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[1] The phenomena here described were first observed, although somewhat superficially, by Dutrochet (Mém. pour servir à l'hist. des végét. et des. anim. 1837, vol. II). Hofmeister, in his treatise On the Bending of Succulent Parts of Plants (Berichte der kön. sächs. Gesells. der Wissensch. 1859), made some important corrections of the theory. On the direction of the parts of plants caused by gravitation, see ibid. 1860; on the Mechanical Laws of the Sensitive Motions of Parts of Plants, Flora 1862, No. 32 *et seq.* A connected account of the phenomena was given in my Experimental-Physiologie, p. 465 *et seq.* Very minute investigations were published by Kraus in Bot. Zeitg. 1867, No. 14 *et seq.*, where the transverse tension of wood caused by the increase of its diameter was also for the first time described. Nägeli and Schwendener also contributed to the development of the theory in their 'Microskop,' p 406 *et seq.* In other respects these phenomena require a much more exhaustive examination than has yet been given them; the account here given will only serve to introduce the student to facts which are easy of observation. In explaining the processes in the interior I differ greatly from the views of Hofmeister (Lehre von der Pflanzenzelle, p. 272 *et seq*). The difference in our views is so complete that it would be useless to point out particular points of difference. It is not surprising if in so difficult a subject and one so little worked, different investigators follow entirely different methods for arriving at the same end.

If narrow strips are cut out of large succulent cells, or very thin slices of tissue are made so as not to contain any perfect cells, a concave outward curvature is obtained at the moment of making the section. This is at once explained by recollecting that the outer layer, especially when cuticularised, was in a state of passive tension even before the section was made; while the inner layer, which was in an absorbent condition, was swelled up from contact with the cell-sap. At the moment of division this inner layer retains its water of imbibition; but the outer layer, which was in a state of greater tension, obeys its elasticity, and in consequence of its contraction becomes the concave, the former the convex surface of the section. It is clear however that these phenomena must also occur when water is removed or absorbed. It is only in this way that it seems to me possible for the cell-walls to take any part in the tension of the tissues, a part which however must always be subordinate in the closed living cell to the influence of turgidity, since this stretches both the inner and outer layers, and every change in the degree of turgidity must cause contraction or distension of the entire cell-wall.

It is a question not without importance in what relation the imbibition and swelling of the cell-wall stand to the turgidity of the whole cell. If we imagine a single turgid cell, and suppose that from any cause the cell-wall (whether the layers are in a state of tension or not) is able to absorb more water from its contents than it had before, the question arises whether the turgidity is thus increased or diminished. By the increased amount of water absorbed from the contents by the cell-wall, the former must be diminished, as also must the hydrostatic pressure on the cell-wall, and the more so when the size of the cell is increased by the imbibition. But since the cell-wall may also increase in thickness, the pressure on the contents may be supposed to increase from this cause. If however we take the simplest and least favourable case, *viz.* that the size of the cell remains unaltered but the thickness of the wall increases, and therefore that it distends inwardly, this will nevertheless not cause any increased pressure between cell-wall and contents, because the water which was the sole cause of the thickening of the cell-wall and diminution of the cell-cavity was withdrawn from the cavity. The swelling of the cell-wall can at the most diminish the size of the cell-cavity[1] by the volume occupied by the water withdrawn from it. No increase of turgidity can therefore take place in this case, and still less when the cell also increases in size. The same argument of course applies also to a multicellular mass of tissue. But the case is different when the water withdrawn from the cell-contents by the cell-wall is replaced by means of endosmose, and the turgidity thus again increased; in this case in proportion as water is absorbed by the cell-wall the turgidity and volume of the whole cell must also increase.

B. *Mutual Tension of the layers of tissue of an organ.* (1) *Tension in the direction of length; i.e. parallel to the axis of growth of the organ.* In the internodes of upright stems some idea may be obtained, if not of the intensity of the tension, at least of its kind (whether negative or positive), and of its variation in the different layers of tissue, by measuring the length of the internodes, separating the layers

[1] When an amount of water v penetrates into an organised body, and increases its volume, the increase of volume can never be greater than v, but at the most as large. The development of heat during imbibition indicates that a decrease of volume is taking place, and therefore that although v is the amount of water absorbed by imbibition, the increase of volume is only $v-d$.

of tissue by a sharp knife, and comparing their length with that of the entire internode. It is obvious that the length of the entire internode is the result of the mutual tensions of its layers, some being, in this experiment, shorter and some longer than the entire internode; and it results from what has already been said about opposite tensions that if any particular layers have not changed in length after being separated, this does not prove that they were not distended or compressed when forming a part of the system, but only that they opposed a strong resistance to the tension then in existence, which resistance rendered the alteration of their length imperceptibly small. But the opposite is also possible; *viz.* that a layer of tissue when separated will show no perceptible contraction because it was so extremely extensible and inelastic that it yielded with extremely little resistance to the traction of the layers which were in a state of positive tension, the limit of its elasticity being continually overstepped.

If this method is applied to rapidly growing internodes, it is generally found that the epidermis, the bark, or the wood (xylem), are shorter than the entire internode, while the isolated pith is considerably longer; the former therefore were in a state of negative, the latter was in one of positive tension. All isolated layers are flaccid, while the entire internode was rigid from the mutual tension.

If a median longitudinal lamella bounded by two strips of epidermis is cut out of a growing internode with its xylem still unlignified, and if its tissues are then isolated so as to lie side by side, then, indicating the epidermis by *E*, the cortical layer by *C*, the xylem by *X*, the pith by *P*, the respective lengths after isolation may be stated as follows :—

$$E < C < X < P > X > C > E.$$

It is at once evident from this that every layer was before the separation in a state of negative tension towards the next one inside, of positive tension towards the next one outside. The epidermis alone is in a state of passive tension; the pith alone is passively compressed, or rather prevented from extending.

The extensibility and elasticity of tissues are altered during the growth of an internode, as may be seen by comparing internodes of various ages; the extensibility of the wood decreases rapidly, that of the epidermis and cortex more slowly, as may be inferred from the decreasing rapidity with which these tissues contract on their isolation, and from the thickening of the cell-walls[1]. The pith from internodes of different ages shows on isolation at first an increasing, afterwards a decreasing amount of elongation. If the tendency of the pith to expand remained the same at all ages, it would, when isolated, elongate more in older than in younger internodes, in consequence of the increasing resistance of the tissues which are in a state of passive tension; but when the growth in length has ceased, or soon after, the pith loses its tendency to expand, as may be concluded from the fact that on isolation from such internodes it elongates less, and finally not at all[2], although the

[1] The decrease in the extensibility of the epidermis was determined by Kraus (*l. c.*, tables, p. 9), by attaching weights to strips of epidermis.

[2] The relation between the tension of tissues and the state of growth of the internode (*i. e.* the phase of its greatest period of growth) requires fresh and detailed investigation. Kraus's Table III (Bot. Zeitg. 1867), shows that the greatest difference of length between cortex and pith does not always occur at the time of the greatest growth; and that even after growth has ceased,

resistance of the wood has greatly increased; were the pith now as elastic as before, it would expand more rapidly when freed from the very great resistance of the wood.

The following table will now be understood; the length of the entire internode being always placed at 100, and the amount of contraction indicated by negative, of expansion by positive percentages.

	Number of the internode, counting from the youngest.	Change of length of the isolated tissue in percentage of the entire internode.		
		Cortex.	Xylem.	Pith.
Nicotiana Tabacum	I— IV	−5·9	−1·5	+ 2·9
	V—VII	−3·1	−1·1	+ 3·5
	VIII— IX	−3·5	−1·5	+ 0·9
	X— XI	−0·5	−0·5	+ 2·4
do.	I— II	−2·2		+ 2·3
	III— IV	−1·2		+ 4·2
	V—VII	−1·0		+ 2·8
	VIII— IX	−1·8		+ 2·7
Sambucus nigra	I	−2·6	−2·6	+ 4·0
	II	−2·0	−2·8	+ 5·5
	III	−1·5	−0·0	+ 1.5
do.	I	−0·6		+ 3·7
	II	−1·6		+ 5·1
	III	−0·0		+ 0·9
do.	I	−1·3		+ 6·5
	II	−1·5		+10·1
	III	−0·6		+ 2·3

These numbers, taken from my Handbook of Experimental Physiology, may be supplemented by some others, calculated from the statements of Kraus[1] (*l. c.* Table 1).

	Number of the internode, counting from the youngest.	Change of length of the isolated tissue in percentage of the entire internode.			
		Epidermis.	Cortex.	Xylem.	Pith.
Nicotiana Tabacum	III— IV	−2·9		−1·4	+3·5
	V— VI	−2·9	−1·3	−0·8	+2·7
	VII— IX	−2·7	−2·1	−0·0	+3·4
	X—XII	−1·4	−0·5	−0·0	+3·4
	XIII—XV	−1·05	−0·0	−0·8 (?)	+4·0
Vitis vinifera	I		−3·1	−1·6	+6·0
	II		−1·7	−0·0	+8·7
	III		−2·5 (?)	−1·0 (?)	+7·1
	IV		−0·0	−0·0	+6·0
	V		−0·0	−0·0	+2·7

tensions may still continue. It must however be remarked that the method by which these numbers have been obtained is liable to considerable suspicion.

[1] Kraus has only given the absolute numbers; but a correct notion can be obtained only by comparing them with the length of the internode.

	Number of the internode, counting from the youngest.	Change of length of the isolated tissue in percentage of the entire internode.			
		Epidermis.	Cortex.	Xylem.	Pith.
Sambucus nigra	I		−3·1	−0.0	+0·0
	II		−1·5	−1·0	+6·4
	III		−1·6		+6·5
	IV		−1·6	+0·3 (?)	+6·1
	V		−0·2	+0·2 (?)	+0·7
	VI		−0·5	−0·5	+0·1
Helianthus tuberosus	I— IV	−4·3	−1·7		+6·8
	V— VI	−1·7	−0·0		+6·6
	VI—VII	−0·9	−0·4		+4·4
	VIII	−0·5	−0·0		+3·2
	IX— XI	−0·0	+0·9 (?)		+2·0

It is easy to establish the existence of similar contractions of the outer tissues and elongations of the parenchyma in the case of growing leaf-stalks, as those of Beta, Rheum, Philodendron, &c.

If a growing internode or a leaf-stalk is split by two longitudinal sections at right angles to one another, the parts will bend concavely outwards, evidently in consequence of the lengthening of the pith and contraction of the outer tissue. This phenomenon is seen most clearly if a thin longitudinal slice is taken from the middle of the internode, laid flat, and the pith then halved lengthwise; as the knife advances the two halves will bend concavely outwards. If, instead of cutting it in two, thin strips of tissue are cut proceeding from without inwards, first one including the epidermis, next one including the cortical tissue, and finally one including the wood, they will all bend concavely outwards, because the adjacent layers are all in a state of negative tension on the outside, of positive tension on the inside, and when separated, the outer side always becomes shorter, the inner side longer.

That this bending is caused by simultaneous contraction of the outside and lengthening of the inside, is at once clear from the measurements already given, but may also be observed directly, as will be seen from the following table. Longitudinal slices of considerable thickness were cut from the middle of growing internodes, laid flat, and the pith then halved by a longitudinal cut; the radius of the curvature which each half at once assumed was determined, and the length of the convex inner and the concave outer side measured by means of a strip of card graduated in millimetres.

	Length of the entire internode.	Radius of curvature of the segment.	Contraction of the concave outer side.	Lengthening of the convex inner side.	Semidiameter of the internode.
Silphium perfoliatum.					
Left half	69·5 mm.	4 cm.	2·8 p.c.	9·3 p.c.	3 mm.
Right half	69·5	4	2·4	9·3	3
Silphium perfoliatum.					
Left half	190	3—4	2·8	9·5	3·5
Right half	190	3—4	2·6	10·8	4·5
Macleya cordata.					
Cavity.	134·5	5—6	0·74	7·1	3·3

As we have already seen from the measurements of the layers when entirely isolated, it was also evident from the curvature of the two halves of the longitudinal slice that the contraction of the epidermis is less than the elongation of the pith. Since this slice is somewhat longer than the entire internode, the proportionate contraction of the outside would be greater, the lengthening of the inside less.

A rapid rate of growth, united with a certain amount of physical differentiation of the different layers of tissue, such as occurs in erect leafy shoots, stout leaf-stalks, and tendrils, appears generally to be favourable to the production of the tensions in tissues of which we have been speaking, as they are not found in stems of very slow growth, like stout rhizomes, the thick stolons of Yucca and Dracæna, &c. That the existence of tension has more to do with a physical differentiation in the elasticity and extensibility of the layers than with a morphological one, is shown by the fact that very considerable tensions are found even between the outer and inner layers of the hyphal tissue of the stems of the larger Hymenomycetous Fungi, which are morphologically similar. Within the growing apical region of roots, on the contrary, where we have a combination of two layers of tissue sharply differentiated morphologically, *viz.* an axial fibro-vascular bundle surrounded by a parenchymatous cortex, we do not find any considarable tension when the part is split by two longitudinal cuts at right angles to one another, or when the layers are completely isolated. But since it is easy to prove that the cortex of the root grows more rapidly and for a longer time than the axial bundle[1], it may be assumed that in an uninjured growing root there is nevertheless a small tension between them, positive in the case of the cortex, negative in that of the axial bundle; but it is only rarely that this tension becomes strong enough to be perceptible by the parts bending inwards when cut lengthwise; probably because the axial bundle, although entirely composed of procambial tissue, is so extensible that it yields almost without resistance to the traction of the cortex. The case is different in the older parts of the root behind the growing end (which does not exceed 10 mm. in length). If this portion is split, the parts generally gape concavely outwards, although much less so than the growing part of erect stems. The curvature is however considerable in the aërial roots of Aroideæ, where the opposite curvature which takes place at the apex is also sometimes well-marked.

The description now given of the states of tension in the case of stems is also applicable to all expanded internodes and leaf-stalks. Within the bud itself, and especially at the *punctum vegetationis*, there appears to be no tension of the tissues, or only one as slight as in the apices of roots. It is only when the epidermis is becoming cuticularised and the walls of the bast-cells are beginning to thicken that the tensions become perceptible.

The individual parts of fully mature organs, especially leaves, not unfrequently retain the tensions acquired during growth, which are in such cases often particularly strong. This is the case, for instance, in the contractile organs of the sensitive or periodically motile leaves of Papilionaceæ, Mimoseæ, Oxalideæ, &c., to which we shall recur. While in these cases the true leaf-stalks and the internodes from which

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[1] The halves of roots split lengthwise continue to grow for days, and bend concavely on the cut surface.

they spring have long become rigid, and no longer show any considerable tension of the tissues, an extraordinary elongation of the parenchymatous cortex occurs in the contractile organs, if they are separated from the solid axial fibro-vascular bundles; and considerable flexion results when these organs are split lengthwise. The opposite to this occurs in the nodes of the stems of Grasses, *i. e.* in the annular thickenings at the base of the leaf-sheaths; no perceptible tension is observable in these. If a median longitudinal section is made and divided into its inner and outer layers, they exhibit none of the curvatures which are so striking in portions of the internodes. This flaccidity of the tissue, or at least the insignificance of the tension, must depend on the concurrence of two causes; on the one hand on the cessation of the growth of the parenchyma in the node (although it remains in a state capable of growing, and under certain circumstances begins to grow again), and on the other hand on the extensibility of the fibro-vascular bundles which do not become lignified within the node, or not till a late period when the cells of the same bundles, where they lie in the leaf-sheath and the internode, have long become lignified and rigid. While, therefore, the parenchyma of the node continues to grow, it stretches the unresisting fibro-vascular bundles, and when its growth ceases no perceptible tension remains. In the contractile organs of sensitive and periodically motile leaves, on the contrary, the axial fibro-vascular bundle becomes elastic and resistant before the growth of the surrounding parenchyma has ceased; and when this is the case a tension remains which is further increased by the extraordinary capacity of the parenchyma for becoming turgid.

If we now attempt to give an account of the causes which render the tension at first (when in the bud) imperceptible in the internodes of erect rapidly growing stems, and make it subsequently increase and finally altogether disappear when the internodes are fully mature, we find that we must content ourselves with probable conjectures rather than with fully demonstrated propositions.

The origin of tension between the layers must in any case be referred mainly to differences in the rate of growth of the cell-walls, it may arise from the intercalation of fresh material taking place less rapidly in one layer than in another; and it is especially manifest when the cell-walls in the one case subsequently undergo thickening. From the first of these causes the layers which lengthen more slowly are placed in a state of passive tension by those that grow more rapidly; while the second cause diminishes their extensibility to an increasing extent, especially when, as in the xylem of the fibro-vascular bundles, the cell-walls become lignified, which renders them capable of resisting extension. The more quickly, on the other hand, the thin cell-walls in the pith and parenchyma generally increase in size (especially in length) by superficial growth, the stronger becomes the tension of the passively distended layers of tissue. To this must be added the peculiar power of the medullary cells to absorb water from the older parts with great force and rapidity, and thus to maintain themselves in a state of the highest turgidity. This distends the pith independently of the superficial growth of its cell-walls, and besides influencing the more slowly growing layers of tissue, also contributes to increase the superficial growth of the cell-walls of the pith. If the woody bundles then become lignified as the tissues become more developed internally, and the resistance of the epidermis, which is constantly becoming more cuticularised, becomes too great, these tissues

oppose an insuperable resistance to the further distension of the pith by growth and turgidity, and no further elongation of the internode is possible. The tendency of the pith to expand ceases; its cells lose their turgidity, they give off their water to adjacent tissues, and become filled with air.

According to this view, which has been fully established in the main, the actual motive power of growth in internodes emerging from the bud-condition is the pith, and the thin-walled parenchyma generally. It is only the force thus exercised that causes the other tissues to increase in length as long as they are sufficiently extensible. The extraordinary absorbent power possessed by the pith enables it when growing to withdraw the water from the surrounding layers of tissue, and thus prevents its cells from becoming more strongly turgid, neutralising by this means one of the causes of the superficial growth of the cell-walls. It must also be remembered, as has already been shown in Fig. 448, that the turgidity of the cells of the dilated layers is even diminished, while that of the compressed cells (in the pith) is increased by the tension; and we consequently have here another cause of differences in the superficial growth of the cell-walls. Finally, it must be borne in mind that the internodes, at least of land-plants, are exposed to transpiration as soon as they emerge from the bud; but this cause of diminished turgidity will affect chiefly the epidermal cells and the subjacent layers, least of all the pith.

The great importance which is here attached to turgidity as a cause of growth is justified by the fact that the growth of the internodes is at once stopped by its decrease, *i. e.* by the withering of the shoot; while it is promoted by its increase, *i. e.* the growth of the shoot in water or damp air.

The first and most efficient cause of the tension of tissues in a growing internode is therefore the different capacity for turgidity of the different tissues; this depending partly on the nature of their fluids, partly on the structure of their cell-walls, and partly on their relative position in the internode. A more secondary place must be assigned to the swelling of the cell-walls caused by imbibition; since it may be assumed that even when the turgidity of the cell is slight, the cell-wall still obtains sufficient water to satisfy its capacity for imbibition. If it were *directly* dependent on this, all the layers of tissue would grow equally rapidly, even when the turgidity was small, or had entirely disappeared. I rather hold the state of the case to be that when the cell-wall is passively distended by turgidity or by the tension of the surrounding layers of tissues, it is only enabled to deposit fresh substance in the direction of its surface when perfectly saturated; this does not however imply that other causes do not cooperate in promoting the intercalation.

The importance of turgidity as a cause of growth may be very strikingly illustrated in the case of isolated cylinders of pith, as we shall show presently.

When, in consequence of their separation, the tissues which were in a state of passive tension become suddenly shorter, and the pith which was in a state of positive tension suddenly longer, this process must be connected with a corresponding change in the form of the cells[1]; the cells which contract must at the same time

[1] Any considerable change in the volume of the medullary cells when isolated must not indeed be expected, when it is recollected that neither the water contained in the cells nor the cell-walls

become wider in diameter, while those of the pith which lengthen must on the contrary become narrower. It is impossible however to measure directly these changes of diameter, which are so small that ordinary methods are inapplicable.

It is, however, a necessary consequence of what has been said that the passive lengthening of the epidermal cells, &c., in a growing internode makes them narrower; the young epidermis must therefore be too narrow, besides being too short for the inner masses of tissue. Similarly the pith, being prevented from elongating in the growing internode by the surrounding layers, must in consequence have a tendency to enlarge transversely; besides being too long for the elongated tissues, it will also be too thick for them, and must have a tendency to force them apart. It follows therefore from the longitudinal tension which has been observed in the layers of tissue of a growing organ, that a transverse tension must also exist in it of such a nature that the outer layers are in a state of passive tension, while the medullary cells which are prevented from lengthening have a tendency to dilate transversely.

If thin transverse segments[1] are cut radially from somewhat older growing stems, they gape open, evidently because the epidermis contracts in the peripheral direction, having been previously of too small circumference for the inner tissue, in other words, in a state of passive tension. The tendency of the medullary cells which are prevented from lengthening to become broader transversely, does not appear, on the other hand, to be always hindered by the surrounding wood and cortical tissue, but often to be even promoted by them; so that these layers of tissue which surround the pith grow more rapidly in the peripheral direction than does the pith itself, and therefore exercise a radial traction upon it. A striking proof of this phenomenon is afforded by the frequent formation of cavities in stems and leaf-stalks at the time and place where the growth in length is most rapid. The increase in thickness of the pith is not sufficient to fill up the space which is enclosed by the surrounding tissues, and which increases in size; its cells separate in the longitudinal direction, and the woody cylinder remains clothed on the inside by a layer of pith, the longitudinal tension of which still continues. The existence of an outward traction upon the pith can also be demonstrated in the case of internodes with solid cylinders of pith which are growing and at the same time increasing rapidly in diameter (*e.g.* Nicotiana, *Silphium perfoliatum*), by dividing a fresh transverse segment (laid on glass) through the centre. The two cut surfaces of the pith now become curved outwardly and separate from one another, while the cortical parts of the segment still touch. This is an indication of the outward traction of the pith, and of the tendency of the cortical envelope to dilate peripherally.

These statements rest however at present on but a small number of observations, and better results may be expected from their repetition. It may nevertheless be assumed that in young internodes, before the fibro-vascular system has begun to become lignified, the pith exerts an outward pressure. This is accompanied later,

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permeated with water alter their volume from the forces exerted in this case. An alteration in the volume of the entire pith could at most arise from a change in the size of the intercellular spaces in consequence of the change in form of the cells.

[1] Sachs, Experimental-Physiologie, p. 471.

when the tangential growth of the wood and cortex is more rapid, by an outward traction, which at length becomes so strong as to overcome the tendency of the pith to dilate transversely. The pith is therefore now actually in a state of passive tension transversely (and at the same time compressed longitudinally), until at length the cells in the centre of the pith become detached from one another, and a hollow is formed, if the whole does not lose its sap and become dried up, as for example in the elder. Kraus observed[1] that the medullary cells of an internode are very slightly longer when it is growing than when mature; but this may be explained, in accordance with what has been said, by the cells of the pith finally losing their power of elongating when isolated. In the internode they are certainly not at first longer, and are afterwards shorter; but the difference is only observable on isolation, and indicates that these cells at length lose the property of changing their form when isolated, or in other words have become rigid.

The views here brought forward respecting the tension of the tissues of growing internodes and leaf-stalks are, I think, supported by the fact that the sudden and very considerable lengthening of the pith at the moment of its separation from the surrounding layers of tissue is followed by a slow lengthening which lasts for some days, while, on the contrary, the cortex and epidermis, which are in a state of passive tension, scarcely experience afterwards any perceptible contraction (but, according to Kraus, do not become longer even when placed in water). This subsequent lengthening of the isolated pith takes place with extreme force when it absorbs water, as Kraus has already shown; but the lengthening also continues in dry air when the pith even loses small quantities of its water, a point which had been previously overlooked.

The isolated cylinder of pith of a growing internode is very flaccid, flexible, and extensible; but if placed in water it soon becomes tense, rigid, and elastic, longer and apparently also thicker. The lengthening may amount in a few hours to as much as 40 p. c., or even more. These phenomena are explained if we suppose the medullary cells to be very strongly endowed with endosmose[2], by which they become in a high degree turgid, and thus not only increase considerably in size, but also become more rigid. The considerable increase in size presupposes, however, from the rapidity with which it takes place, great extensibility in the cell-walls. Isolated prisms of pith exposed to the air become shorter even than the length they possessed in the internode[3]; the cell-walls which were previously in a state of tension evidently contract elastically, as the turgidity diminishes from loss of water.

But if care is taken that isolated cylinders of pith do not absorb any water, while at the same time they can only lose a very small quantity of it, by enclosing them in a glass tube containing about 1 litre of dry air, they nevertheless continue to lengthen perceptibly for some days, although not so considerably as when they absorb water; and this lengthening affects chiefly the older parts, while the

[1] Bot. Zeitg. 1867, p. 112.

[2] Notwithstanding this powerful endosmose, the amount of solid substance dissolved in the cell-sap of the parenchyma is very small, as is shown by the fact that in cylinders of pith of this kind I found the dry weight only from 2 to 5 p. c., a considerable portion of which belonged to the cell-walls and protoplasm.

[3] Kraus *l. c.*, Tables, p. 29.

youngest parts sometimes contract. The whole cylinder becomes dry and rigid on the surface. Out of a large number of observations the following may be chosen to elucidate this point.

A prism of pith from a part of a shoot of *Senecio umbrosus* 235·5 mm. long, lengthened about 5·7 p. c. when isolated, and weighed 5·3 grammes. It was divided into three parts by marks of indian ink; their lengths being:—i. (the oldest) 100 mm., ii. 100 mm., iii. (the youngest piece) 49 mm. The prism of pith was now fixed in a dry glass tube, which was then corked at both ends. After fourteen hours the parts had lengthened as follows:—part i. about 4·5 mm., part ii. about 6·5 mm., part iii. about 2 mm. or 4·1 p. c., while the pith had lost 0·15 grm. of water. After remaining for twenty-six hours more in the glass tube the following further changes had taken place; part i. had again lengthened about 2·5 mm., part ii. about 0·5 mm., while the length of part iii. had diminished about 0·5 mm. No further loss of water had taken place, because the glass tube had become covered with moisture. The pith was now placed in water, and after six hours the following increase of length had taken place:—in part i. about 18 mm. or 16·8 p. c., in part ii. about 23 mm. or 21·6 p. c., in part iii. about 11 mm. or 21·6 p. c. (as compared with the length before placing in water). The pith had also become considerably thicker, having absorbed 6 grammes of water. The estimation of the dry weight showed that the pith contained only 0·22 grm. of solid substance; this was combined, when the pith was isolated, with 5·08 grm. of water; it subsequently lost 0·15 grm., but by the end of the experiment had again absorbed 6 grm. At first therefore the pith contained 4·23 p. c., at last only 1·97 p. c. of solid substance. Experiments of this kind show that the pith of the youngest internodes loses its water most easily by evaporation, as is shown by its decrease in length. Kraus was led by other experiments to the same conclusions; and he also showed—not in contradiction, as he thought, but in harmony with these results (*l. c.* p. 123)—that the older pith of growing internodes attracts water more eagerly and expands more than that of younger internodes.

If the question is now asked how the lengthening of the pith can take place in spite of the loss of water (though this may be small), it must first of all be noted that its surface becomes remarkably dry under the circumstances described. It is scarcely possible to attribute this significant desiccation of the surface to the small loss of water indicated by the weight; it is probably rather caused by the inner cells of the pith withdrawing water from the outer cells, and thus lengthening; but the outer cells would become shorter if they were not stretched by the inner ones. That this is actually the case is shown by the rigidity of the pith under these circumstances, caused by the tension that subsists between the dry outer layer and the moister inner mass. If the prism of pith is divided lengthwise, the parts curve outwards; and sometimes the outer surface becomes even strongly concave. If the inner cells of the pith are able to withdraw water from the outer ones, it may be inferred that the outer cells are also able to withdraw it from the surrounding wood and especially from the peripheral tissues, preventing these from becoming strongly turgid; their growth being thus retarded in favour of that of the pith, by which they are now placed in a state of passive tension. It is noteworthy that the medullary cells which contain a minimum quantity of dissolved substances nevertheless absorb water

sufficiently powerfully to abstract it from the surrounding tissues which must evidently contain a much greater quantity of dissolved substances[1].

It is now clear from the observations which have been described, why portions of shoots cut lengthwise in half or in four and placed in water curve outward to such a remarkable extent; and why a curvature, which may be small but continues to increase for some time, takes place when such pieces are placed in a closed glass tube in dry air.

(2) *Transverse tension caused by subsequent thickening of the wood.* It has already been shown that transverse tensions also arise during growth caused by the longitudinal tension, a more exact knowledge of which is still a desideratum. With the commencement of the increase in thickness of the stem caused by the cambium-ring, a new cause of tension arises, acting in both a radial and peripheral direction; and this transverse tension generally continues as long as the cambium-ring remains active. The layers of tissue formed from the cambium-ring have at first a tendency to expand in the tangential direction to an extent greater than the space between the epidermis and the primary cortex permits. These outer tissues therefore become stretched in the peripheral direction; and, since they are elastic and have a tendency to contract, they exert a pressure in the radial direction on the cambium and the tissue formed from it, *viz.* the wood and the layers of secondary cortex. It happens however also that the rings of wood produced on the inside of the cambium grow more strongly in the tangential direction than the phloëm produced on the outside, which is therefore passively distended. A tension is hence set up in the transverse diameter of the stem during its increase in thickness of such a kind that each layer is stretched peripherally on its outside and compressed radially on its inside; in other words, is in a state of negative tension on its outside, of positive tension on its inside. If the separate layers of a transverse segment —epidermis, primary cortex, secondary cortex (phloëm) and xylem—are separated, and their peripheral length compared, we get the following expression for the transverse tension :—

$$E < C < Ph < X.$$

As the increase in thickness proceeds the transverse tension increases, as is shown by Kraus's very complete experiments; *i. e.* if the rings of tissue in a transverse segment of the stem or in a woody branch are separated from one another, by dividing it longitudinally and then separating the rings, they contract the more the nearer they lie to the circumference, and the contraction is the more considerable, compared with the original circumference of the whole, the older the original segment. The traction upon the cells of the epidermis and of the primary cortex caused by the transverse tension is easily observed by the microscope in the transverse segment, if young internodes of plants which increase rapidly in thickness, as Helianthus, Ricinus, or Ribes, are compared with those which have already been forming wood for some weeks or months. The form of the cells shows that they have been strained in the peripheral (see Fig. 56, p. 69), and have in consequence grown

[1] I must content myself here with this preliminary sketch, which I shall carry out more in detail in the Proceedings of the Würzburg Botanical Institute. Absorbent root-hairs and cortical cells behave in the same manner as the pith.

rapidly in the tangential direction; the cells which have been thus altered in form are divided by radial septa. But at length the epidermis and primary cortex are no longer able to obey the peripheral traction; longitudinal fissures occur in the cortical tissue, generally after the commencement of the formation of cork. When the periderm and cork have been formed on the older parts of stems, these secondary epidermal tissues undergo a continuous strain in the peripheral direction, and exert in turn a radial pressure on the living phloëm, cambium, and xylem. The first result of this pressure exerted by the growing inner tissues is the splitting of the layers of bark, especially longitudinally. The form of the fissures depends, however, on the course of the bundles of bast which take part in the formation of the bark, and on other relations of the tissues to one another. If a stem does not in its growth take the form of a cylinder or slender cone but of a spherical tuber, as in Beaucarnea and Testudinaria, the layers of periderm split apart in the form of tolerably regular polygons which cover the spherical surface of the stem like shields. These examples show at the same time that even in Monocotyledons tensions are produced by the subsequent increase of the stem in thickness similar to those caused by the activity of the true cambium-ring; for in this case it is replaced by a thickening-mantle, in which new layers of fibro-vascular bundles and intermediate parenchyma are constantly being produced. (See Fig. 91, p. 107.)

It is evident that before the bark splits or fissures already in existence become wider and penetrate inwards, the transverse tension must attain a certain intensity, which, from the great firmness of the bark, cannot be inconsiderable. At the moment when the splitting takes place at least a portion of the tension must, however, be destroyed. This is clearly the reason why the transverse tension attains its maximum (measured in the way described above), as Kraus has pointed out, above the part of the stem where the scaling-off of the bark begins. But even in annual stems which increase rapidly in thickness, as Helianthus, Dahlia, &c., the transverse tension does not progressively increase from the apex to the root, but attains its maximum at an intermediate height, below which it diminishes. An explanation of this phenomenon is afforded by the fact that the limit of the elasticity of the bark is gradually exceeded by the long-continued pressure to which it is subject from within, and that the cell-walls which are strained grow at the same time by intussusception, and thus a portion of their tension becomes neutralised.

While we may consider the turgidity of the pith and its enormous endosmotic power as the principal cause of the longitudinal tension of growing internodes and leaf-stalks before they become lignified, it is on the other hand probable that the imbibition and swelling of the cell-walls are the chief cause of the transverse tension. The wood, where the transverse tension chiefly originates, is, when mature, scarcely adapted for any distension by turgidity; while at all events in cells or vessels with bordered pits it is altogether impossible. Closed wood-cells, when turgidity is possible in them, cannot however distend greatly; since their own wall, and the woody substance which surround them are far too inextensible to stretch to any considerable extent under the influence of hydrostatic pressure. It has, on the other hand, been already shown (Sect. 13) what considerable alterations of dimension the wood experiences especially in the peripheral and radial direction simply by imbibition. Every layer of wood freshly formed on the inside of the cambium-ring has

a tendency to grow wider in the peripheral direction, as long as the supply of water is sufficient to cause a decided swelling of the cell-walls. But the cambial tissue is by this means stretched tangentially, and the enlargement of its cells thus caused is increased by turgidity; and from the thinness of their walls it may be assumed that it is their turgidity that protects them from becoming destroyed by compression between the wood and the bark. The elements of the secondary cortex—the bast-cells and the phloëm-parenchyma—can scarcely experience any great change of dimensions owing to the swelling of their cell-walls; the former are indeed thick-walled, but their position does not allow them to form a layer which increases in size from this cause. Finally, the periderm and the bark dry up and contract, if not to any great extent, yet with considerable force.

The experience of every year shows that the fissures in the bark—especially of thick trunks at the end of winter in February and March—become deeper and wider, evidently in consequence of the great swelling of the wood which at this time contains the greatest quantity of water; while the bark had time to dry up and contract during the dry weather in winter. If the fissures increase in width by the strong tension thus produced—which can be easily seen when fresh—the damp weather in spring causes the bark to swell; the tension between it and the wood becomes much less, and the production of wood now begins afresh in the cambium. While the wood is becoming thicker during the summer, the bark dries up and shrinks, and the tension between the outside and inside again increases, to cease once more in the following spring. Not only does an annual period of transverse tension thus arise, but this is also the cause, as we shall see presently, of the difference between the spring and autumn layers of wood.

The statements made in this section may be briefly summed up as follows:—The tissues, at first homogeneous, become first of all differentiated in such a manner that chemico-physical differences cause certain layers, especially the pith, to absorb the water in the tissues more strongly than the others, and consequently to grow more rapidly; and the layers which are less turgid and grow more slowly are exposed to a passive traction which promotes their growth. After growth has ceased it is principally the stronger imbibition and swelling of the wood that presses the surrounding layers of tissue outwards and promotes their peripheral growth.

The intensity of the longitudinal and transverse tensions consequently depends mainly on the addition of water to the turgescent pith and the swelling wood; any decrease of the turgidity of the pith must cause it to contract, and hence the whole shoot to become shorter and flaccid. This is in complete accord with observation, since withered shoots, *i. e.* such as have lost water by transpiration, have not only become shorter but also flaccid. Any diminution of the amount of water absorbed by the wood must in the same manner diminish the transverse tension and the diameter of the shoot. A small loss of water in the peripheral tissue when in a state of passive tension does not on the other hand usually cause directly any considerable increase in its tendency to contract; since the increase in its size from turgidity and imbibition are generally much less considerable than in the pith and wood.

If now there are circumstances which cause a daily periodic change in the quantity of water contained in the tissues, the result will be also a periodic increase and decrease in the intensity of the longitudinal and transverse tensions. Such a daily periodicity of the tension has been actually discovered by Kraus (*l. c.* p. 122), who has observed that the longitudinal tension estimated by the difference in length of the pith and the bark, as well as the transverse tension estimated by the contraction of the bark when detached

from woody stems, decrease, under the normal conditions of life, from early morning till midday or early in the afternoon, when they reach their minimum, and then again increase, attaining their maximum early the next morning. Millardet determined this periodicity in quite a different way; and since the objects on which he experimented permitted an exact measurement, he detected in addition an increase, usually small, of the tension in the afternoon. Notwithstanding the statements of Kraus—which are partly opposed to this conclusion, but on the whole confirm it—I am inclined to attribute this periodicity chiefly or altogether to the variation in the amount of water contained in the tissues of the plant at different periods of the day. When transpiration is greatly diminished during the night, the quantity of water in the plant must increase, and with this the tension; and conversely the increase of transpiration during the early part of the day must diminish the tension. Space does not permit me to give in detail the opposing statements of other observers; but this will be done in part further on. Here I need only point out that the periodicity, especially of the longitudinal tension, may possibly be also directly dependent on light, *i. e.* independent of the heat which accompanies the light and of the increase of transpiration caused by it (although this cannot be proved by Kraus's experiments, *l. c.* p. 125). As far as concerns a daily periodicity *independent* of temperature, light, and the amount of water contained in the tissues, I could only admit it when any other explanation of the phenomena was shown to be impossible. At present this is not the case. From the intimate dependence and correlation of growth and tension, from the fact discovered by me[1] that the daily periodicity of growth coincides in every particular with the daily periodicity of tension observed by Millardet and Kraus, and finally from the fact that the periodicity of growth is caused simply by changes in temperature and light, I consider it very probable that the daily periodicity of tension is also dependent on these agencies. On the one hand they influence growth and through it the tension, while on the other hand they affect the amount of water contained in the tissues by modifying transpiration and its conduction from the roots. Like all other periodic phenomena of vegetable life, that of tension requires a very careful investigation of its external causes before we resort to the last expedient of assuming internal periodic changes, of which no explanation can be given in the present state of our knowledge.

Sect. 16.—**Modification of Growth caused by Pressure and Traction.** Cells or whole masses of tissue may be subjected to pressure and traction in very different ways. On the one hand these forces may result, in a perfectly normal manner, from the tension of the tissues; on the other hand, external and more accidental circumstances may cause single cells or masses of tissue to be compressed or stretched in particular places by solid bodies, or tissues to become accidentally freed from the pressure and traction to which they are normally subject. The numerous phenomena which indicate or prove that growth is altered in this way have however at present been exactly investigated from this point of view in only a few cases. The following will therefore only serve to draw attention to a subject in which further discoveries must contribute to the establishment of a mechanical theory of growth.

1. Every cell-wall is subject to *Pressure from within*, by which it is distended, so long as the cell is turgid. But since the daily experience of microscopists teaches us that all growing cells are turgid; and that on the other hand no cell which is unable to become turgid in consequence of openings in its cell-walls has any power of growth; and that moreover withered internodes, leaves, and roots

[1] Arbeiten des Bot. Inst. in Würzburg 1872, Heft II, p. 168.

do not grow, while these organs grow more rapidly the more strongly turgid they are, it may be inferred that turgidity is an essential condition of the growth of the cell-wall. This appears to a certain extent intelligible if Nägeli's theory of growth and Traube's experiments on artificial cells described in Sect. 1 of Book III are accepted. It may then be assumed that the interstices between the solid particles of the cell-wall which are occupied by water increase slightly in consequence of the distension of the cell-wall caused by the hydrostatic pressure of the sap; and that space is thus obtained for the intercalation of fresh particles of solid substance; the distension caused by turgidity then begins afresh and produces the same effect.

The distension which takes place at any particular spot of the cell-wall and the consequent intercalation of fresh solid substance, depend however chiefly on the internal properties of the cell-wall itself. Not only do different parts of the cell-wall differ in their extensibility, but they may even vary at the same spot in this respect in the longitudinal and in the tangential or the oblique direction, as may be seen from the swelling of the cell-wall. But that there is actually such a general difference in the extensibility in different directions is at once shown by the fact that growing cells assume the most various forms,—cylindrical, stellate, &c.; while, if the extensibility of the cell-wall were the same in all directions, the cells must all become spherical as the result of turgidity, or polyhedral under that of mutual pressure. This little is nearly all that we know at present with reference to extensibility, turgidity, and growth by intussusception. It must be borne in mind that the rapidity of the growth of cells is in proportion to the thinness and therefore the extensibility of their walls. The growth in thickness of the cell-wall usually begins when the increase of the cell in volume begins to diminish or has altogether ceased.

If then the distension of the cell-wall caused by turgidity is the origin of its superficial growth, something similar must also occur when the cell-wall is stretched in some other way by external forces, the turgidity being less. This is the case with the epidermis and cortex of shoots as a result of the tension of the tissues. Since in long internodes and leaves these cells usually grow principally in the longitudinal direction, while in broad leaf-blades they assume the form of polygonal plates, this may be referred in the first case partly to the disturbance to which they are subject being chiefly in the longitudinal direction, in the second case to its being in all directions parallel with the surface[1]. It has already been stated that the cells of the primary cortex of shoots which are increasing rapidly in thickness are not merely stretched but also grow rapidly in the tangential direction[2].

2. *Pressure from without on the cell-wall which is distended by turgidity* occurs in a very simple form when the apices of growing cells come into contact with solid bodies; as the root-hairs of land-plants with the particles of the soil[3]. The very thin

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[1] For further details on the possible influence of tension on the formation of stomata, see pfitzer, Jahrb. für wiss. Bot. vol. VII, p. 542.

[2] On the connection of the radial and peripheral arrangement of rows of cells in a transverse segment with the increase in diameter, see the lucid description of Nägeli in his Dickenwachsthum des Stengels bei den Sapindaceen, Munich 1864, p. 13 *et seq.*

[3] Sachs, Experimental-Physiologie, p. 186.

and extensible cell-walls are in close contact with the irregular surface of the particles, just as when an elastic bladder filled with water is pressed externally by an angular body, only that they retain, after the pressure is removed, the form which has thus been given them, evidently in consequence of the intercalation of fresh particles of solid matter which perpetuates the form at first acquired only by distension. The reverse takes place when the external pressure on the cell-wall is removed. A very simple instance of this is afforded by the formation of the so-called 'Tüllen' in vessels[1]. These appearances are produced where the thin non-lignified wall of a cell of the wood-parenchyma, still capable of growth, adjoins the bordered pits of a vessel. The portion of wall which is stretched over the opening is forced through it by the pressure of the sap of the cell and swells out in the form of a papilla into the cavity of the vessel. As long as the vessel contained sap and was in a turgid state, its turgidity was in equilibrium with that of the adjoining cell; but as soon as the cell-sap of the vessel was absorbed, the portion of cell-wall which covers the bordered pit was subject to pressure on one side only, and was therefore forced in the opposite direction. These phenomena can be produced artificially by the removal of the pressure to which the cells are subject from the adjacent tissues; thus, for example, the cambium swells up on the cut surface of woody branches when placed in moist sand or air, in the form of a cushion between the bark and the wood. This 'Callus,' as it is termed, results from the growth of the uninjured cambial and adjoining cortical cells next the cut, where their growth was previously prevented by the cells which have now been removed. When once projecting beyond the cut, they grow more rapidly than before in a lateral direction in consequence of the turgidity, and become divided by transverse and longitudinal walls[2].

The further development of such a callus where branches have been cut off leads to the well-known overgrowth on the stumps. In internodes of seedlings of Phaseolus which had accidentally become hollow, I found the medullary cells which surrounded the cavity to have grown into it in the form of spherical or club-shaped papillæ; divisions ensued, and nuclei were formed in the cells thus produced. The medullary cells which exhibited this active growth on the free surfaces of their walls would have retained their polyhedral form had the pith remained solid, because every surface of the cell-wall would have been exposed to the pressure of the two adjoining cells; but in consequence of the formation of the hollow, the pressure was removed on one side, and the turgidity, being no longer neutralised, caused the cell-wall to swell out, and induced in it an active superficial growth[3]. These phenomena and others of the same kind show that it is often sufficient merely to remove the pressure to which tissues or individual cells are subject in order to bring about an active growth of the free surfaces of their cell-walls. The first cause at least of the new growth is the distension of the free surfaces of the cell-walls in consequence of the turgidity of their cells which was previously neutralised by that of the adjoining cells. But that a very small pressure from without is sufficient to prevent the growth of softer tissues at the points of contact is seen in the case of many large

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[1] See Book I, p. 27 [and references in foot-note].

[2] Further details on this point will be given in a yet unpublished memoir by Prantl.

[3] Prantl succeeded in artificially inducing similar phenomena in the tubers of Dahlia.

Fungi which develope among the vegetable mould of woods, and enclose in the margin of their pileus light loosely lying leaves, pieces of stick, and the like. The small pressure from without clearly prevents in these cases the superficial growth of the walls of the cells with which these bodies are in contact, while the adjoining cells extend laterally and enclose them.

But the most remarkable illustration of this law is seen in the effect produced by a slight pressure on the growth of tendrils, the longitudinal growth of the cells being thus greatly hindered and sometimes even stopped, while the cells of the opposite free side elongate rapidly, as is seen even at the first glance without measurement by making a longitudinal section of a tendril curling round a slender support. In what way the slight pressure which acts in a radial direction, and is generally combined with friction, exerts an influence on the longitudinal growth is however entirely unknown. Very similar phenomena are exhibited by the primary and secondary roots of seedlings (as Zea, Faba, and Pisum). If they are allowed to grow in a damp

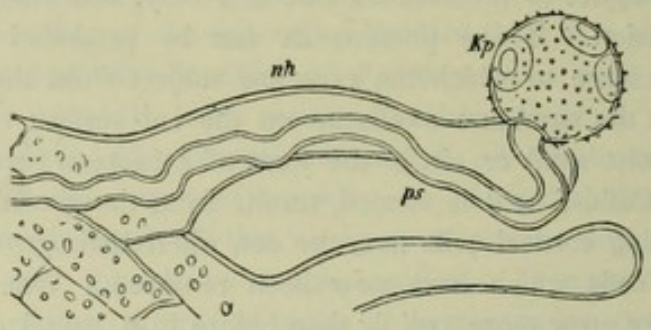

FIG. 449.—Growth of the pollen-tube of *Campanula rapunculoides*: *Kp* the pollen-grain; *ps* the pollen-tube closely applied to the stigmatic hair *nh*.

locality, and the growing parts are made to press on one side some solid body as a pin or another root, the root bends like a tendril round the body with which it is in contact, this side growing more slowly than the opposite one. It is evidently in consequence of a similar influence of pressure on growth that the aërial roots of Aroideæ and Orchideæ become closely attached to solid bodies, following exactly their inequalities. But even unicellular tubes, such as the hyphæ of Fungi and pollen-tubes (Fig. 449) are induced by contact with a solid body to grow closely applied to it. In this simplest case, where the hydrostatic pressure is uniform over the cell and distends the cell-wall, it does not admit of a doubt that the pressure from without impedes the growth of the cell, independently of turgidity, while the growth proceeds unhindered on the side which is not in contact.

But the mechanical processes by which pressure on an organ in the radial direction impedes its growth on that side are unknown. The solution of the question must depend in the first place on whether the pressure acts on the cell-wall directly or in some way or other through the protoplasm[1].

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[1] If the relation between protoplasm and the growth of the cell-wall were better known, stress might be laid on the fact that even a very slight pressure on the cell-wall disturbs the movement of the protoplasm, and may even cause it to become detached from the cell-wall (see Hofmeister, Lehre von der Pflanzenzelle, p. 51).

But in contrast to the phenomena which have now been described, external pressure also sometimes causes growth at places where otherwise there would be none. Thus Pfeffer has shown[1] that certain hyaline superficial cells on both of the flat sides of the gemmæ of Marchantia possess the power of growing out into tubular root-hairs when they remain in contact for some time with a moist solid body; while contact with water produces no effect of the kind. These cells usually develope into root-hairs only when their outer surface is directed downwards, while those on the upper side, not being in contact with a solid body, do not grow out. This, as we shall see presently, is an effect of gravitation, which is however overcome by the action of the slight continuous contact, since this causes the cells on the upper side of the gemmæ also to grow out into root-hairs. The 'haustoria' of Cuscuta and Cassytha and the adhesive discs on the tendrils of the Virginian Creeper are only formed, as was shown by v. Mohl, on the continuous contact of the surfaces of the tissue with a solid body; and this has been confirmed by recent experiments of Pfeffer's (*l. c.* p. 96)[2]. In these cases a growth combined with cell-division and differentiation of tissue is caused by contact or slight pressure on a part of the organ, and would not take place without this pressure. These haustoria and adhesive discs thus formed are altogether indispensable for the life of the plant; for Cuscuta is nourished exclusively by the haustoria which penetrate into the tissue of the host; and it is by the formation of adhesive discs on the tendrils that the Virginian Creeper is enabled to climb up walls. If the tendrils do not meet with any solid body to which they can attach themselves by means of these discs, they dry up and fall off, while those which have formed discs increase in thickness and become woody.

The injurious effect on growth of an external pressure on the cells is very evident in the formation of the annual rings in wood. In the earlier editions of this work I called attention to the fact that the larger radial diameter of the wood-cells in the portion of the rings formed in the spring, and their smaller radial diameter in the portion formed in the autumn, may possibly depend on a difference in the pressure from the surrounding bark to which the cambium and the wood are subject, this pressure being less, as we have shown, in the spring, and constantly increasing during the summer. This hypothesis has been fully confirmed by H. de Vries's recent investigations[3]. In branches two or three years old he increased the pressure of the bark in the spring by firmly winding strings round them at particular places. 'The experiment showed in all cases, firstly, that the absolute thickness of the annual ring was less beneath the ligature than the mean thickness of the same annual ring at some distance above or below that spot. In several instances the difference was so considerable that the spot where the experiment was made appeared of considerably less diameter even to the naked eye, and this effect was increased by the formation of cushions of wood immediately above and below the ligature. Secondly, the absolute thickness of the 'autumnal layer' of wood (up to the middle of August, when the increase in diameter of the tree on which the observations were made ceased), was always greater, and generally considerably so, than the normal thickness at the spot where the experiment was made. In the trees

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[1] Arbeiten des Bot. Inst. in Würzburg, Heft I, p. 22.

[2] [See also Darwin, On the Movements and Habits of Climbing Plants, London 1865, p. 84 *et seq.*—Ed.]

[3] H. de Vries, Flora 1872. No. 16.

examined (*Acer Pseudo-platanus*, *Salix cinerea*, *Populus alba*, Pavia) the autumnal wood was formed at this spot of fibres flattened radially, between which were a smaller number of vessels than in the normal wood; its composition was therefore the same as that of the normal 'autumnal wood.' The normal autumnal wood of *Ailanthus glandulosa* consists almost entirely of wood-parenchyma-cells flattened radially; while the autumnal wood beneath a ligature made in May consists of a thicker layer of flattened fibres, between which only a few vessels could be seen. These results show that when the pressure is increased, the formation of the autumnal wood begins at a time when, under normal pressure, a large-celled woody tissue is still being formed.

'A diminution of pressure is obtained by making radial longitudinal incisions into the bast-tissue. The strips of bast contract somewhat tangentially, since their tension ceases. Near the incisions the pressure of the bast upon the wood is entirely removed; but in the middle between two adjacent incisions a considerable pressure always remains. The fresh portions of tissue which are formed next to the wounds differ to the greatest extent in their composition from the ordinary structure of the wood. A layer of wood of the ordinary structure is formed, on the other hand, in the portions of the cambium at the greatest distance from the incisions, and afterwards also outside these abnormal portions of tissue. But it is only the tissue consisting of wood formed under artificially diminished pressure that we have at present to consider.' Incisions 4 to 6 cm. in circumference, and mostly 2 to 3 cm. long, were made in two- to three-year-old branches in the middle of June and the middle of July, and therefore after the formation of the normal autumnal wood had already begun. 'The effect of the decrease of pressure was first of all shown, after the branches had been cut off in the middle of August, by an increase in thickness considerably greater at the spots than above or below them. On the transverse sections the thickness of the annual ring was greatest near the incision and decreased gradually from there to the middle points between two incisions. The layer of wood formed after the commencement of the experiment was often more than twice as thick at the former as at the latter spots.' For a more exact investigation only those pieces were used in which a layer of distinctly flattened fibres of autumnal wood had been formed before the incision was made. 'But in all cases (the trees already named) the wood outside this layer of autumnal wood—and therefore all that formed after the decrease of pressure—consists of fibres which are not at all flattened radially, but have the same diameter, or even one somewhat greater, than those in the middle of the normal annual ring; it contains also as many vessels, or even more, than the normal wood. At the time therefore when autumnal wood is being formed in the normal parts of the branches, a woody tissue is produced, if the pressure is artificially diminished, agreeing in its structure with the ordinary wood formed in the middle part of the annual ring. For the normal production of autumnal wood it seems therefore necessary for the bark and the bast to exercise a considerably greater pressure on the cambium and the young wood.'

These results explain the older experiments of Knight in 1801. He fastened young apple-trees with a stem of about one inch diameter so that the lower part, about three feet long, was immoveable, while the upper part with the foliage could bend under the pressure of the wind. During the period of vegetation the upper moveable part of the stem increased considerably in diameter, the lower fixed part only slightly. This is easily explained if we bear in mind that the swaying of the upper parts of the stem in different directions by the wind must always stretch the bark on the convex side, and therefore eventually relax it; it must thus become looser, and therefore the pressure of the bark at these points is always somewhat less than at the lower and immoveable parts of the tree. This explanation is completely confirmed by the fact that in one of the trees which could be swayed by the wind only in a northerly and southerly direction, the diameter of the stem increased so much in this direction as to bear the proportion of 13 to 11 as compared with the diameter in the easterly and westerly direction. It is obvious that this explanation is much more probable

than that given by Knight himself, who thought the movement of the sap in the wood was promoted by the swaying of the stem caused by the wind.

The great assistance to the increase in diameter of trees afforded by the diminution of the pressure of the bark on the cambium was long ago employed in horticulture. The bark of young trees is split from above downwards in summer; cushions of wood are formed at the edges of the incisions, which soon close up the wounds. The use of this process is that from the more rapid increase of the wood in thickness, the conduction of water to the leaves becomes more copious and the loss by transpiration is more easily replaced. The development of the buds and hence the formation of the organs of assimilation will be promoted by the increase of turgidity in the young branches.

Sect. 17. **Course of the growth in length under constant external conditions**[1]. It has already been explained in the morphological portion of this work that the organs of a plant do not grow simultaneously and uniformly at all points; but that roots and stems always increase slowly in size at the apex, as leaves also do at least at first. The growing cells not only multiply by cell-divisions which take place regularly, but do not as a whole exceed a certain size, which is always small. Below this *punctum vegetationis*, consisting of primary meristem, not only does the differentiation of the homogeneous tissue into layers of different kinds begin, but also a more rapid increase in size of the cells, which do not now divide so often as before. In the parts of the organ which lie further from the *punctum vegetationis* cell-division ceases altogether (but at different periods in the different layers of tissue), while the growth of the cells still actively continues, until at length, when they have attained their ultimate form and size, the growth of the whole ceases. The cells are then several hundred or even thousand times larger than at the time of their formation beneath the *punctum vegetationis*. When the growth of stems, leaves, and roots has reached a sufficiently advanced stage of development, we are able therefore to divide their tissue into three regions:—(1) the *punctum vegetationis*, where new cells are chiefly formed and increase in size is slow; (2) the portion where the main part of the increase in size takes place, but where there is no longer any cell-division or only to a subordinate extent; this is the elongating portion of the organ; and (3) the portions which no longer grow, at least in length, *i. e.* the mature portions of the organ. When growth entirely ceases at the *punctum vegetationis*, as is usually the case with leaves, all the cells continue to enlarge until the whole is mature. If the stem produces a number of closely crowded leaves, as it usually does at its growing end, the whole of the region in which the chief part of the cell-division takes place is clothed with young leaves, which also themselves consist of cells undergoing division. But as soon as the leaves enter the second stage of development and begin to lengthen, they incline outwards; and when the stem is growing rapidly in length and forming evident internodes (which is by no means always the case) the lengthening begins at those points where it bears

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[1] Ohlert, Längenwachsthum der Wurzel, Linnæa 1837, vol XI, p 615.—Münter, Bot. Zeitg. 1843, p. 125, and Linnæa 1841, vol. XV, p. 209.—Griesebach in Wiegmann's Archiv. 1843, p. 267.—Sachs, Jahrb. für wissensch. Bot. 1860, vol. II. p. 339.—Müller, Bot. Zeitg. 1869, No. 24.—Sachs, Arbeit. des Bot. Inst. in Wurzburg 1872, Heft II p. 102; ditto, Heft III, 1873, and Flora 1873, No. 21.—Askenasy, Flora 1873, No. 15.

the leaves, which also begin to lengthen at the same time; the older mature leaves are generally placed on mature internodes. If the internodes are clearly marked out from one another, as is especially the case when the leaves are verticillate or sheathing at their base, each internode forms a more or less individualised whole as soon as it emerges from the bud, and different stages of growth may be distinguished in it, advancing from below upwards. This may take place in two different ways, according as the uppermost or lowermost part of an internode remains in an undeveloped condition, the other end being completely mature. This zone which continues for some time in an undeveloped state—cell-division taking place actively in it—is more commonly found at the lower than at the upper end of the internode (as in Phaseolus), especially when it is enveloped by closely adpressed leaf-sheaths or by a bulb, as *e. g.* in Equisetaceæ (especially *E. hyemale*), Umbelliferæ, the bulbous Liliaceæ, the haulms of Grasses, &c. If the internodes are not sharply distinguished, as in stems with small leaves and the floral axes of Dicotyledons, the various states of growth which have been described pass insensibly into one another on the stem; and this is always the case with roots. If leaves when once expanded continue to grow for some time, the process is the same as with flower-stalks or branches; while the lower portion of the leaf-stalk is fully mature, the upper parts present successively younger or less developed states. The formation of cells finally ceases at the apex and all the parts then become fully mature. This is strikingly the case in Ferns, less so in the pinnate leaves of Papilionaceæ or the incised leaves of Araliaceæ.

But very often the activity of the *punctum vegetationis* of the leaves lasts for only a short time and its tissue matures while cell-divisions still continue at the base of the leaf, and all the transitional states of growth are to be found between the base and the apex. This occurs, for instance, in the long leaves which grow from the bulbs of Liliaceæ and allied Monocotyledons. When a cell-producing zone of this kind occurs at the base of an internode or of a leaf, with more mature tissue lying above it, the whole organ behaves as if this zone were a *punctum vegetationis*; the states of growth succeeding one another in the reverse order. Such a zone, intercalated between mature portions of tissue may be called an Intercalary vegetative zone. The growth of the internode or leaf may be termed basipetal, in contrast to the acropetal development where the *punctum vegetationis* lies at the apex of the internode or leaf.

According as the conditions of growth — temperature, the supply of water, and light—are favourable, these phenomena proceed more or less rapidly and uniformly. Every young cell formed at the *punctum vegetationis* grows and matures more rapidly the more favourable these conditions are. But if the organs are observed under the most constant possible conditions as they emerge from the bud, it is seen that the growth of the organ both in length and thickness, dependent on the gradual development of the cells, does not advance by any means uniformly. The growing portion of a root, internode, or leaf does not lengthen to an equal amount in equal consecutive intervals of time; and the same is the case with stems consisting of a number of internodes, and with each zone, however small, of a growing organ. It is seen in fact that the growth of each part begins at first slowly, becomes gradually more rapid, and finally attains a maximum of

rapidity, after which the growth becomes again slower, and finally ceases when the organ is fully mature.

If successive equal intervals of time are represented by T_1, T_2 .. . T_n, and the increments during these intervals by I_1, I_2 .. . I_n, then it may be stated as a general rule that—

for $T_1 \quad T_2 \quad T_3 \quad T_4 \quad T_5 \quad T_6 \quad T_7$

we shall have $I_1 < I_2 < I_3 < I_4 > I_5 > I_6 >$ zero.

This rule holds good for the separate zones of roots, internodes, and leaves, as well as for the entire organs, and for whole stems from their first formation to the time of their full maturity. This course of growth I have termed *The Grand Period*[1], or Grand Curve of Growth; since it is at once evident that if the values I_1, I_2 .... I_n are drawn as ordinates with the intervals of time as abscissæ, a curve will be obtained which, starting from the axis of abscissæ, reaches a maximum of elevation, and returns again to the axis. The following examples will render this more clear.

Köppen[2] found the following increase of length attained in periods of twenty-four hours with a nearly uniform mean temperature:—

Roots[3] of *Lupinus albus*.

	Increase of length.	Mean temperature.
First three days: per diem	10 mm.	17·2° C.
Fourth day	18	16·6
Fifth day	44	17·1
Sixth day	32·6	16·9
Seventh day	27·9	17·1
Eighth day	28	16·4

In an internode of the flowering stem of *Fritillaria imperialis* I found the following increase of length in each period of twenty-four hours[4]:—

	Normal plant in the light.	Etiolated plant in the dark.	Mean temperature.
March 20	2·0 mm.		10·6° C.
21	5·3		10·5
22	6·1		11·4
23	6·8		12·2
24	9·3	7·5 mm.	13·4
25	13·4	12·5	13·9
26	12·2	12·5	14·6
27	8·5	11·5	15·0

[1] 'Grand periods,' in contrast to the small periodic oscillations of growth which, if represented graphically, would appear as smaller elevations and depressions on the grand curve.

[2] Köppen *l. c.* p. 48. I have calculated the daily growth from the lengths given in his tables.

[3] That is, the root together with the hypocotyledonary portion of the stem.

[4] A few irregularities in the course of the growth are explained by the temporary acceleration of the growth from the soaking of the ground. Compare the curve in pl. 1 of the Arbeiten des bot. Inst. in Würzburg, Heft II, p. 129.

	Normal plant in the light.	Etiolated plant in the dark.	Mean temperature.
March 28	10·6 mm.	14·2 mm.	14·3° C.
29	10·3	12·6	12·4
30	6·3	15·9	12·0
31	4·7	16·6	11·2
April 1	5·8	**18·2**	10·7
2	4·4	15·5	10·2
3	3·8	14·0	9·4
4	2·0	13·8	10·6
5	1·2	11·9	10·7
6	0·7	8·8	11·0
7	0·0	4·4	11·0
8		2·1	11·2
9		0·6	11·5
10		0·0	12·5

An internode of *Humulus Lupulus* gave—

	Increase of length in 24 hours.	Mean temperature.
April 22	19·0 mm.	14·9° C.
23	25·0	14·5
24	**26·0**	14·3
25	17·2	13·9
26	4·8	14·1

Harting found that a hop-stem consisting of a number of internodes which was 492 millimetres long on May 15th, had attained by the end of August a length of 7·263 metres, this growth being distributed as follows over the different months:—

0·492	metres in April.
2·230	May.
2·722	June.
1·767	July.
0·052	August.

These observations and a number of others show that the grand period of growth manifests itself even when the course of the changes of temperature acts in opposition to it; *i. e.* when the temperature rises while the rapidity of growth decreases owing to internal causes, and *vice versâ*. The course of growth may no doubt be so modified by great changes of temperature that the curve of the grand period can no longer be recognised in the measurements.

In order to determine the grand period of growth in a piece of a growing root, internode, or leaf-stalk, it is sufficient to mark a zone of the organ at the part where growth begins by two lines of indian ink, and to measure the daily (or half daily) growth of this piece until it ceases.

By applying this method to the primary root of *Vicia Faba*, the temperature varying each day between 18° and 21·5° C., I found the following increase to take

place in each period of twenty-four hours in a piece originally 1 mm. long situated immediately above the *punctum vegetationis* :—

1st day	1·8 mm.
2nd	3·7
3rd	17·5
4th	16·5
5th	17·0
6th	14·5
7th	7·0
8th	0·0

In the same way I found that a piece at first 3·5 mm. long of the first internode of *Phaseolus multiflorus* beneath the first pair of foliage-leaves, with a daily variation of temperature between 12·75° and 13·75° C., showed the following increase :—

1st day	1·2 mm.
2nd	1·5
3rd	2·5
4th	5·5
5th	7·0
6th	9·0
7th	14·0
8th	10·0
9th	7·0
10th	2·0

Since every organ that is growing in length consists of zones of different ages, which are produced in succession from the primary meristem of the *punctum vegetationis* (or of an intercalary vegetative zone), the successive zones of an internode or a root indicated by ink-marks must show different increments of growth in equal times. While the zone nearest the *punctum vegetationis* is beginning to grow, the next one has already entered on a later phase of its grand period, while one at a greater distance would have attained the maximum of its rapidity of growth, and a still further one would have ceased to grow. In other words, a number of zones below the cell-producing *punctum vegetationis* are in the ascending phase, while those lying further backwards are in the descending phase of their grand period; or again, each zone is in a later phase of its period of growth the greater its distance from the *punctum vegetationis*. If the successive zones of a growing organ are indicated by the figures I, II, III, &c., and the increments of growth observed at the same time in each of them by I_1, I_2, I_3, &c.; then we have the following relationship :—

I II III IV V VI VII VIII

$$I_1 < I_2 < I_3 < I_4 > I_5 > I_6 > I_7 > \text{zero}.$$

There is therefore in the organ a region of maximum rapidity of growth. Thus, for example, I found in the first internode of *Phaseolus multiflorus*, which was divided into twelve zones, each 3·5 mm. long, in the first forty hours :—

Zone.	Increment.
1st	2·0 mm.
2nd	2·5
3rd	4·5
4th	6·5
5th	5·5
6th	3·0
7th	1·8
8th	1·0
9th	1·0
10th	0·5
11th	0·5
12th	0·5

The maximum rapidity of growth lay therefore in the fourth zone, which was originally situated at a distance of about 10·5 mm. from the upper end of the internode.

As it is usual for several contiguous internodes of stems to be growing at the same time, and the maximum rapidity of growth occurs, according to circumstances, in the second, third, fourth, or fifth internode beneath the bud, the region of most rapid growth is at a considerable distance from the apex of the stem, and especially when the internodes attain a considerable length and several are growing at the same time. In roots, on the other hand, the maximum rapidity of growth occurs much nearer the *punctum vegetationis*, usually at a distance of only a few millimetres; and the portion of the root beneath its apex in which the chief part of the growth takes place is consequently only a few millimetres long, while in stems with long internodes it is often many centimetres in length. If therefore a root and stem with long internodes are divided into zones of equal lengths, *e. g.* 1 mm., commencing from the *punctum vegetationis*, the law of growth, as expressed by the general formula given above, is the same in both cases, but with this difference, that in the stem the number of zones that are increasing in length at the same time is much greater than in the root, in consequence of the fact that in the last case each zone completes its period of growth more quickly[1]; its curve is shorter and more abrupt.

Thus, for example, in a primary root of *Vicia Faba* which grew in damp air and which was divided, starting from the *punctum vegetationis*, into zones each 1 mm. in length, I found the following increments of growth in the first twenty-four hours at a temperature of 20·5° C.:—

Zone.	Increment.
10th	0·1 mm.
9th	0·2
8th	0·3
7th	0·5
6th	1·3

[1] It by no means however follows from this that the root grows more rapidly, *i. e.* attains in the same time a greater length than the stem.

Zone.	Increment.
5th	1·6
4th	3·5
3rd	**8·2**
2nd	5·8
apex	1·5

In this case, therefore, the third zone, where the maximum increase of growth took place, was at first at a distance of only 2 mm. from the apex.

It is clear that if an organ is divided into zones of small length, each zone will in general contain a larger number of cells the nearer it is to the *punctum vegetationis*, since the cells are longer the further they are from the apex. But from the point where growth ceases the number of cells in the successive zones of an organ of uniform structure will be the same. If therefore the zones are again designated by the numbers I, II, III, &c., the number of cells in them by N_1, N_2, $N_3 \ldots N_n$, then we have:—

$$\begin{array}{cccccccc} \text{I} & \text{II} & \text{III} & \text{IV} & \text{V} & \text{VI} & \text{VII} & \text{VIII} \\ N_1 > & N_2 > & N_3 > & N_4 > & N_5 > & N_6 > & N_7 = & N_8. \end{array}$$

But the difference in the number of cells in the zones is very far from being the cause of the difference in the rapidity of growth that prevails in them; as is seen at once if it is recollected that the number continually decreases from the apex throughout the growing region, while the rapidity of growth first increases and then decreases. This may be expressed by the following formula:—

$$\begin{array}{cccccccc} \text{I} & \text{II} & \text{III} & \text{IV} & \text{V} & \text{VI} & \text{VII} & \text{VIII} \\ N_1 > & N_2 > & N_3 > & N_4 > & N_5 > & N_6 > & N_7 = & N_8. \\ I_1 < & I_2 < & I_3 < & I_4 < & I_5 > & I_6 > & I_7 > & \text{zero.} \end{array}$$

If it were possible to divide in the same manner a filament of Vaucheria, a root-hair of Marchantia, or a similar unicellular organ, into small zones, it can scarcely be doubted (as we may conclude from other circumstances dependent on growth) that we should find the same law to regulate the distribution of the rate of growth in individual cells endowed with a power of apical growth. Since the same law applies to roots and stems—whether zones 1 or 2 millimetres or stems 1 or 2 centimetres in length are observed—it is to be expected that this formula would hold good also if zones of only a tenth or hundredth, or even thousandth of a millimetre could be marked out and measured. In other words, we should find that the law of the grand period holds good for each single minute particle of the surface of the wall of a young cell.

If the power of any particular zone to attain a definite length is called its *Energy of Growth*, then a zone which up to the time when its growth ceases reaches a length of 10 mm. would have a smaller energy than one which continues to grow until it has reached a length of 100 mm. Thus, for example, the successive internodes of most stems each of which was at one period 1 mm. long, differ very greatly in length when mature; the internodes first formed are short, the next longer, and finally we have one the longest of all, followed again towards the apex

by shorter ones. If we designate the energy of growth of the internodes I, II, III, &c., by E_1, E_2, E_3, &c., we get the series—

$$\begin{array}{cccccccc} \text{I} & \text{II} & \text{III} & \text{IV} & \text{V} & \text{VI} & \text{VII} & \text{VIII} \\ E_1 < & E_2 < & E_3 < & E_4 > & E_5 > & E_6 > & E_7 > & E_8. \end{array}$$

With this increase and decrease in the energy of growth of the various internodes of a stem is usually associated a similar relationship between the size of their leaves, the lower ones forming smaller, the upper ones larger leaves, and then a largest of all (or whorl of largest leaves), usually followed again by smaller ones[1]. The secondary roots also which spring from the same primary root show similar relationships, the first attaining a smaller length than those that follow, and these being again followed by a graduated succession of shorter ones. The same is the case also with the lateral branches of an annual stem, as well as of trees, especially when the order of development is distinctly monopodial.

It seems probable that an investigation of the zones of a root, stem, or leaf, would also show that the energy of growth of successive zones first increases, then reaches a maximum, and finally decreases. The cells in the zone in which the maximum energy of growth prevails would also be the largest, while their number would be least. This hypothesis is in harmony with Sanio's measurements[2] of the wood-cells of *Pinus sylvestris;* for he found that the final constant size of the wood-cells of the stem varies, increasing gradually from below upwards, till it attains a maximum at a definite height, and then again decreases towards the apex. The same is the case with the branches.

If it were possible to predicate the exact energy of growth of every separate zone of an organ, it would also be possible, from the fact that every zone has its separate period of growth, to determine a grand period for the whole organ itself. The maxima of rapidity of growth attained in the successive zones first rise and then fall; the duration of growth also of the zones probably at first increases and afterwards diminishes. Consequently the measurements of the whole organ represent the sum at first of only few and small partial increments, later of more numerous and larger ones; finally the sum of the partial increments diminishes, because the number of zones growing at any one time and the energy of their growth alike diminish. Further investigation will show whether this hypothesis, which is at least an approximate one, is correct.

If the increments of length of an internode, stem, or leaf, in short intervals of time such as half-an-hour or an hour, are compared, it is usually found that they do not increase and then decrease regularly, but irregularly, the growth being sometimes greater, sometimes smaller. If the grand curve of growth is constructed directly from them, it does not assume the form of a continuous curve, but shows a number of small zigzags, which however disappear, if, for example, the interval is extended

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[1] This phenomenon has not at present been sufficiently investigated. In many stems, especially creeping ones, when the leaves have reached a certain size, this size remains constant in a long series of leaves before any decrease occurs.

[2] Jahrb. für wissensch. Bot. 1872, vol. VII, p. 402. By a 'constant' size of the wood-cells I understand that which they possess in their later annual growths; in the inner annual rings they gradually increase, until in the following ones they attain a constant size.

from one to three hours or more. These phenomena I call irregular variations of growth[1]. They appear to result from the plant being subjected to continual small variations of temperature, air, light, and moisture of the soil, which alter the turgidity, and therefore the extensibility and elasticity of the growing cells. I come to this conclusion from observing that irregular variations of growth become less the more the plant is protected from variations in the surrounding conditions. Partial irregular neutralisations of the tension of the tissues may also cooperate to produce this result.

SECT. 18.—**Periodicity of Growth in length caused by the alternation of day and night.** The alternation of day and night implies varying combinations of the conditions of plant-life, especially of those that affect growth. Day and night are distinguished not only by the presence and absence of sunshine, but also by a consequent higher and lower temperature, which again causes variations in the moisture of the air. Independently of special meteorological phenomena, the temperature falls daily with the diminishing elevation of the sun till sunrise the next day, that of the air rapidly, that of the ground more slowly; at sunset the fall is sudden, as is the rise at sunrise. In general the atmosphere approaches a state of saturation as the temperature falls, *i. e.* the hygrometric difference decreases, as it increases with the rising temperature. But these general daily alternations act in a variety of ways, and even in opposite directions on the growth of plants; the increasing intensity of the light after sunrise retards growth, while the increasing temperature promotes it, as long as the other conditions remain the same; but the increase of the hygrometric difference caused by the increasing temperature of the air occasions also an increase of transpiration, which effects a diminution of the turgidity of the tissues, and this again retards growth.

It is uncertain which of these variable causes may have the greatest influence on growth; and it will depend on this whether the growth of the plant is most rapid by day or by night. On a cloudy but warm and damp day the weak light has only a slightly retarding effect, but the temperature and the great amount of moisture greatly promote growth; under these circumstances the growth may be greater than in the succeeding night (equal spaces of time being compared), when the total absence of light promotes growth, but the lower temperature is less favourable to it. But the proportion may be reversed; the plant may grow more slowly by day than by night when the difference in the temperature and moisture of the air during each is but small and very bright days intervene between dark nights, the intense light retarding growth by day more than the depression of the temperature by night.

The greatest variety of combinations may be imagined in this respect; and from the extreme changeableness of the weather the plant will, according to circumstances, sometimes grow more quickly by day, sometimes by night, without exhibiting any exactly recurrent periodicity. The numerous observations which have been made in this direction do not therefore point to any general law[2]. It has however

[1] For further details see Reinke, Verhandl. des bot. Vereins für die Provinz Brandenburg, Jahrg. VII; and Sachs, Arbeit. des bot. Inst. in Würzburg, Heft II, p. 103.

[2] These will be found described by me in detail in the Arbeiten des bot. Inst. in Würzburg, 1872, p. 170.

been ascertained that, especially when long spaces of time such as entire days are compared, all the other conditions of growth are outweighed by the effects of the variations of temperature, so that in general the rapidity of growth increases with a rising and decreases with a falling temperature. The result of a number of measurements made by Rauwenhoff during several months in the most changeable weather was that the mean growth was greater in twelve hours of the day than in twelve hours of the night; *viz.*—

	By day.	By night.
in Bryonia	59·0 p.c.	41·0 p.c.
Wistaria	57·8	42·2
Vitis	55·1	44·9
Cucurbita	56·7	43·3
do.	57·2	42·8
Dasylirion	55·3	44·7

A similar tabular statement shows that the favourable influence of a higher temperature by day outweighs the retarding influence of daylight. Rauwenhoff's measurements show accordingly that the mean growth during six hours of the forenoon is less than that during six hours of the afternoon; since, while the average amount of light is the same, the temperature is higher in the afternoon than in the forenoon. If the afternoon growth is placed at 100, then the morning growth is—

in Bryonia	86
Wistaria	71
Vitis	67
Cucurbita	79
do.	81

If however we calculate from Rauwenhoff's measurements the daily and nightly and the morning and afternoon values for shorter periods in which the changes of the weather do not neutralise one another, it will be found that the growth by night sometimes exceeds that by day, and that the afternoon is not always more favourable than the morning.

It is clear from what has been said that it is impossible to determine from observations in the open air, where the variations of temperature, light, and moisture are very great and are combined in a great variety of ways, in what manner each separate condition of growth affects the plant, and whether the alternation of day and night causes a similar alternation of growth, or whether there exist in the plant itself causes of daily periodicity independently of external changes. In order to decide this question, it is necessary first of all to make the observations independent of the accidents of weather, which is only possible by carrying them on in well-closed rooms where the temperature is kept constant or made to vary, and where the amount of light can be increased or decreased, and the moisture regulated in the air and in the soil of the flower-pot. Under these circumstances it is possible to study the action of an increasing or decreasing amount of light upon a plant exposed to constant conditions of humidity and temperature, and therefore exhibiting a constant degree of turgidity; it is sufficient to measure and compare the increments of growth during short periods of time.

A long series of observations of this kind on internodes has given me the following results[1]:—

(1) The more exactly a constant temperature is maintained in a constantly dark space, the amount of moisture being also constant, the more uniform is the course of growth at different periods of the day. There does not appear to be any daily periodicity of growth independent of external influences. The irregular variations of growth mentioned above were however observed.

(2) If great variations of temperature are allowed to act on a plant growing in darkness and with a constant amount of moisture, to such an extent that the temperature of the air round the plant alters some degrees C. from hour to hour, the rate of growth of the internodes rises and falls with the rising and falling temperature. If the hourly increments are taken as ordinates, and the intervals of time as abscissæ, the curve of growth follows all the elevations and depressions of the curve of temperature, without however any actual proportion being observable between the growth and temperature; the curves do not run parallel but are only of the same description.

(3) If care is taken that during the period of observation the temperature undergoes only slight and gradual changes, while (the temperature being sufficiently uniform) the amount of light changes in the ordinary manner, increasing from morning till midday and decreasing from midday till evening, to complete darkness at night, it will be found that the increments of growth are always greater from evening till sunrise, diminishing suddenly after sunrise, and then more slowly till evening. The alternation of day and night causes therefore under these circumstances a periodical rising and falling of the curve of growth of such a nature that a maximum occurs in the morning at sunrise and a minimum before sunset. A second rising of the curve of growth usually takes place also in the afternoon; but this, as I have shown, is a consequence of the higher temperature in the afternoon which overcomes the influence of light. The retarding influence of light is therefore strong enough to overbalance the favourable influence of the slight elevation of temperature in the forenoon, but not sufficient to overcome that of the stronger elevation of temperature in the afternoon.

The fact is of great interest that when a plant has been exposed to light during the day, its curve of growth after sunset, or if placed in the dark in the evening, does not immediately rise abruptly; *i. e.* that the most rapid growth which is independent of light is not at once attained when it is suddenly placed in the dark; but that—as is shown by the curve rising slowly till morning—the growth which has been retarded during the day only becomes gradually more rapid in the course of some hours, until the light to which the plant is again exposed in the morning causes a fresh retardation of growth, which again increases from hour to hour till the slowest rate is attained in the evening, if the temperature remains constant. In other words, the two internal conditions of the plant which correspond to darkness on the one hand and to daylight on the other hand pass over only gradually into one another. Light

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[1] Sachs, Arbeit. des bot. Inst. Würzburg, 1872, p. 168 *et seq.* The plants observed were chiefly *Fritillaria imperialis*, *Humulus Lupulus*, *Dahlia variabilis*, *Polemonium reptans*, and *Richardia æthiopica*.

requires a considerable time in order to overcome the nocturnal, darkness a considerable time to overcome the diurnal condition of the plant. If this were not the case, the curve of growth would at once rise abruptly in the evening when the room is suddenly darkened, would then continue at the same elevation till morning, fall abruptly when light is again let in, and continue at the same height till the evening. But this does not correspond to the observed phenomena.

In order to study more closely the changes of growth occasioned by internal causes, or the dependence of these changes on external conditions, it is necessary to measure

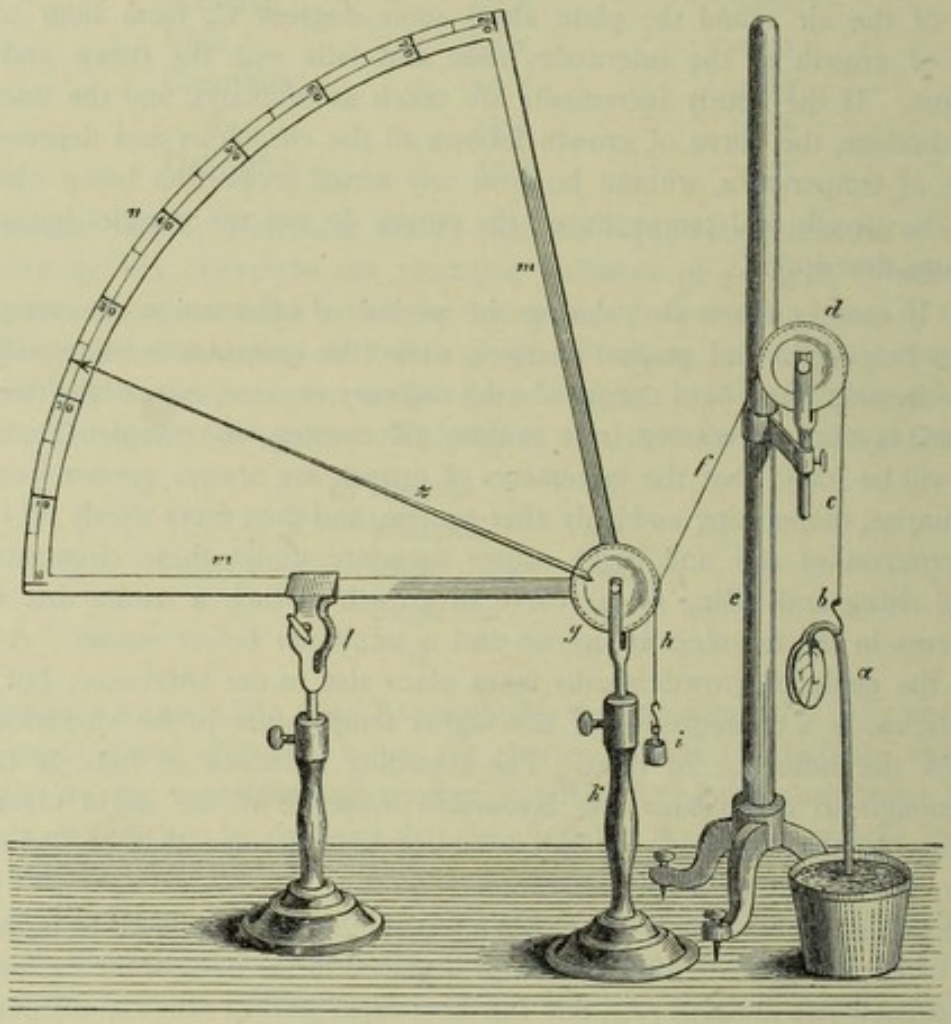

FIG. 450.—Arc-indicator, or apparatus for measuring the development of an internode of a growing plant *a* during short periods of time.

the increments in short spaces of time such as an hour or two or three hours. In the case of internodes or leaves of large plants which are growing very rapidly, as the flower-stems of Agave or the leaves of Musaceæ, this can be done with a certain degree of exactness by simple measurement with a measuring-rod. But for the purpose of more exact observations it is more convenient to make use of smaller plants which do not grow so rapidly, the growth during an hour not amounting to more than a millimetre, or even less. In such cases a simple measuring-rod is not sufficiently exact; and I have employed in its place three different methods. In each of them a thin but strong thread of silk is fixed to the upper end of the stem or internode of the plant growing in a pot, the thread passing vertically over an easily moveable pulley and moving an index fixed to the free end of the thread or to the pulley.

1. The *Thread-indicator* is a simple contrivance in which the free end of the thread which hangs down from the pulley and is kept tight by a weight of a few grammes, carries a horizontal needle which moves freely over a graduated scale as the end of the thread which is fixed to the plant rises with its growth.

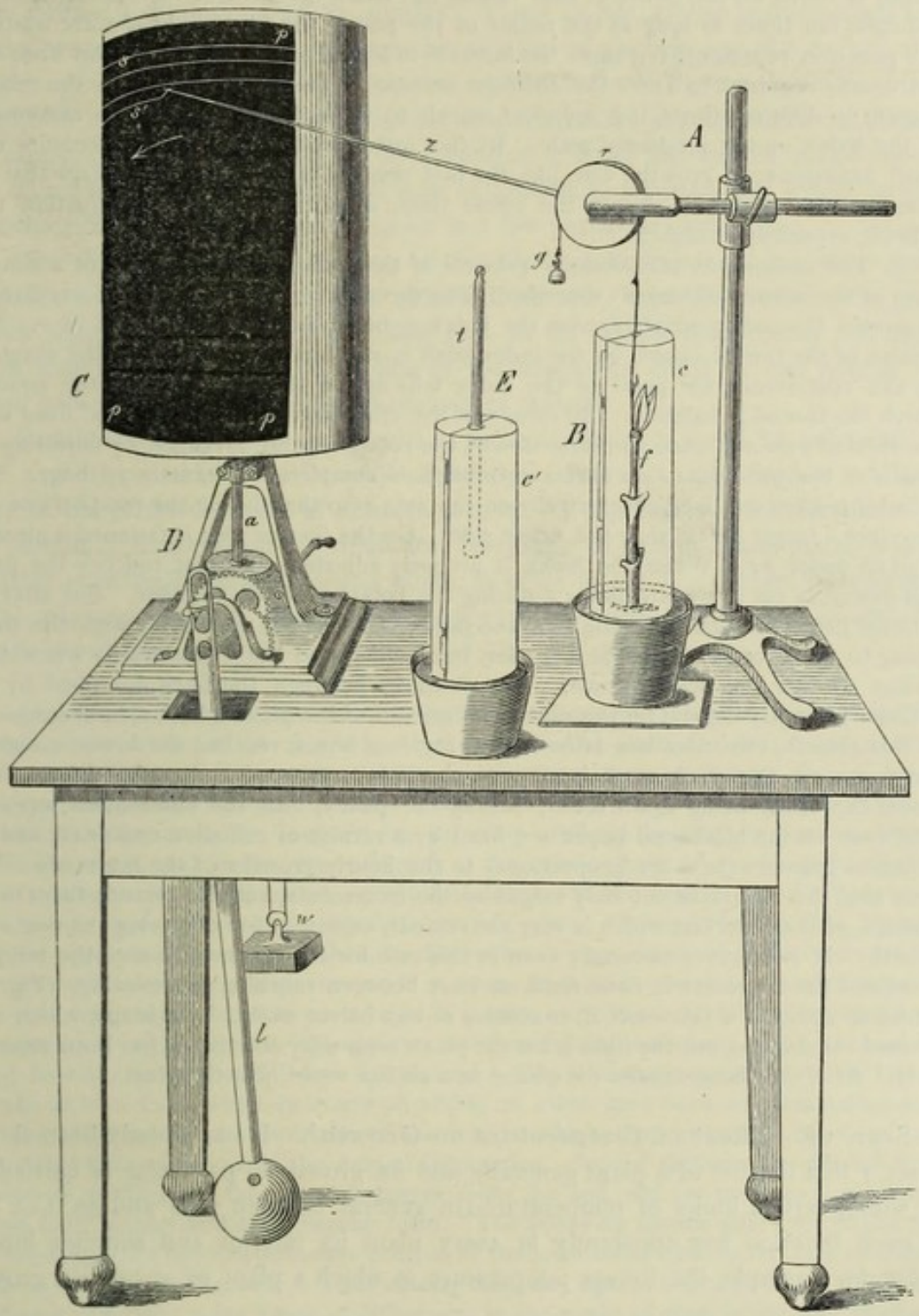

FIG. 451.—Autographic Auxanometer, for recording the development during short periods of an internode of a growing plant *f*; *s s'* the lines scored by the index *z* on the blackened paper *p* fixed to the cylinder *C* which is made to rotate eccentrically by means of the clock-work *D*.

2. In the *Arc-indicator* the thread *c f* (Fig. 450) fixed to the plant *a* is carried over the pulley *d* and fixed to a pin which is attached to a second pulley *g*. An index *z* made of a straight and firm straw is fastened to this second pulley in the radial direction, its

free end pointing to a graduated scale on the arc of a circle *m n*. The equilibrium of the index is secured by the small weight *i* which tends to turn the pulley in the opposite direction with a force which keeps the thread *c f* in a state of tension. As the internode below the hook *b* lengthens, the weight *i* sinks, and a piece of the thread *c f* of equal length is rolled off the pulley *g*, thus raising the index on the arc. If the index is, for example, ten times as long as the radius of the pulley, the portion of the arc which it will pass over represents ten times the increase in length of the internode. But since it is not usually required to know the absolute amount of the increase but only the relative amount in different times, it is sufficient merely to read off and compare the movements of the index on the graduated scale. By this instrument we are able to measure very small increments of growth; but, like the first process, it has the disadvantage that the observer must watch it during the whole time, which renders the investigation very difficult, especially at night.

3. The *Autographic Auxanometer* gets rid of this difficulty. It consists of a simpler form of the instrument already described. The thread *f* fastened to the plant sets directly in motion the pulley which carries the index *z*, being fixed to it by a pin at *r*. The tension of the thread caused by the index itself is still further increased by the weight *g*. By this contrivance the point of the index falls as the stem grows below the point to which the thread is fastened. By means of the clock-work *D* the cylinder *C* fixed upon the vertical axis *a* is made to rotate slowly, the rotation being arranged by adjusting the length of the pendulum *l* so that a revolution is completed in exactly an hour. The cylinder is however fixed eccentrically on the axis *a*, so that during the rotation one side describes a larger circle that the other side. On the former side is fastened a piece of smoked paper *p p*. When the index is properly adjusted, its point touches the paper and describes on it a white line *s s'* during the rotation of the cylinder. But after the rotation has continued for some time the index is no longer in contact with the paper owing to the eccentricity of the cylinder, but becomes so again afterwards when it inscribes another line lower down. The distances between the lines described by the cylinder evidently depend on the rapidity of growth of the plant[1]. When, in consequence of this growth, the index has, after say twenty-four hours, reached the lower margin of the paper *p p*, the clock-work is stopped, the paper removed and replaced by a fresh piece, the index being again set by raising the pulley, and the observation repeated. The lines on the blackened paper are fixed by a varnish of collodion and dried, and the distances between them are proportional to the hourly growths of the internode. It is clear that the apparatus not only magnifies the increments, but also records them in the absence of the observer, which is very convenient, especially for observing the nocturnal growth. It is however necessary even in this case for the observer to note the temperature and the hygrometric conditions, at least between morning and evening. Fig. 451 shows in addition a tin vessel *B*, consisting of two halves united by a hinge, which may be used for shutting out the light from the plant, even after the thread has been attached to it. At *E* the thermometer *t* is placed in a similar vessel near the plant.

Sect. 19.—**Effect of Temperature on Growth**[2]. It has already been shown in Sect. 7 that the life of a plant generally and its growth in particular is carried on only within certain limits of temperature (in general between zero and 50° C.), and that each function has apparently in every plant its inferior and superior limits; so that, for example, the lowest temperature at which a plant of wheat can grow is

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[1] See Arbeiten des Würzburg. bot. Inst., Heft II.

[2] F. Burkhardt in Verhandl. der naturf. Ges. in Basel, 1858, vol. II, 1, p. 67.—Sachs, Jahrb. für wissensch. Bot. 1860, Heft II, p. 338.—Alph. De Candolle in Biblioth. univ. et rev. Suisse, Nov. 1866. —H. de Vries, in Archiv. néerlandaises 1870, vol. V.—Köppen, Wärme und Pflanzen-Wachsthum, Dissertation, Moskow 1870.

different from the lowest at which a gourd can grow, &c. It has also been shown that growth, like other phenomena, is more active the higher the (constant) temperature above the inferior limit, but that there is a certain temperature at which growth reaches its maximum activity, and above which any further rise of temperature causes a diminution of its rapidity. There is not, in the mathematical sense of the term, any proportion between the rapidity of growth and the height of the temperature, and the more accurately the relation between the two has been investigated, the more difficult is it to express this relation by any mathematical formula. It cannot, on the other hand, be doubted that it is of the utmost importance for any future theory of the mechanical laws of growth to ascertain the extent to which growth depends on temperature, at least in a few particular cases.

The difficulties of investigations of this kind are however much greater than is generally thought; and the results obtained hitherto, valuable as they are, go no further than what is stated above, and give us no deeper insight into the way in which that particular mode of motion of the molecules which we call heat is connected with that mode of motion which causes growth.

Restricting ourselves to the results at present obtained, it will be seen that they have a great practical value in addition to their theoretical significance. A knowledge of the cardinal points of temperature, *viz.* its superior and inferior limits and the particular temperature at which the maximum of action takes place, is indispensable to investigations of various kinds, in order to get at a correct interpretation of the phenomena. On this account a few of the more trustworthy observations may be given here.

In order to determine the cardinal points of temperature to which allusion has been made, observations are of value only when conducted at a nearly constant temperature; the means deduced from very variable temperatures may, as I have shown, lead to very erroneous conclusions. It is however by no means easy to maintain a sufficiently constant temperature for a whole day even by artificial heating or cooling. Special difficulty is met with in the determination of the inferior limit or specific zero, since the observation must extend over a considerable time—in the case of germination, several weeks—to be certain that growth does not take place. It would be possible, by means of the apparatus already described, to determine in the course of a few hours whether growth still takes place in an internode at a very high or at a very low temperature, and at what temperature it is the most rapid, if it were not extremely difficult to regulate the temperature of the plant in the apparatus with sufficient exactness. The auxanometer will however be very useful even in this case. The observations on this point hitherto made, at least those which have any physiological value, have been on germinating seeds, as the temperature and moisture of the soil in which they grow can be more easily regulated than of the air in the case of internodes. Special facilities are offered by the roots of seedlings, as they do not emerge from the soil, and are more easily measured, from their simpler and more regular form. The following figures refer only to the roots of seedlings, the hypocotyledonary portion of the stem being also, in the case of Dicotyledons, included in the root. That exactly the same figures are not always obtained by different observers is the result of differences in the mode of observation, the amount of water, the nature of the soil, the inaccuracy of thermometers, &c.

The first point to determine is, whether germination—*i. e.* the growth of the embryo at the expense of the reserve materials in the seed—takes place only at certain temperatures, and at what temperature it takes place most quickly. Observations of my own gave the following results:—

	Inferior limit.	Most rapid growth.	Superior limit.
Triticum vulgare	5° C.	28·7° C.	42·5° C.
Hordeum vulgare	5	28·7	37·7
Cucurbita Pepo	13·7	33·7	46·2
Phaseolus multiflorus	9·5	33·7	46·2
Zea Mais	9·5	33·7	46·2

This table shews, if the ascertained temperatures are correct, that grains of wheat cannot germinate below 5° C, or seeds of the gourd below 13°·7, &c., however long they may lie in moist earth; and that they no longer germinate, but quickly perish at temperatures above those named in the third column; while at the temperatures named in the second column germination takes place in a shorter time than at either higher or lower temperatures. It may however be taken for granted, from the great difficulty of obtaining these numbers, that the result of further observations will not be identical, though probably approximate. It is clear that many series of experiments will be necessary in order to determine each of the cardinal points. The following figures, obtained by Köppen, agree moderately well with mine, as far as they relate to the same plants.

	Inferior limit.	Most rapid growth.
Triticum vulgare	7·5° C.	29·7° C.
Zea Mais	9·6	32·4
Lupinus albus	7·5	28·0
Pisum sativum	6·7	26·6

The following figures were obtained by H. de Vries:—

	Most rapid growth.	Superior limit.
Phaseolus vulgaris	31·5° C.	above 42·5
Helianthus annuus	31·5	below 42·5
Brassica Napus	31·5	„ 42·5
Cannabis sativa	31·5	above 42·5
Cucumis Melo	37·5	
Sinapis alba	27·4	above 37·2
Lepidium sativum	27·4	below 37·2
Linum usitatissimum	27·4	above 37·2

The following results[1], obtained by Alphonse de Candolle, are moderately trustworthy as far as relates to the inferior limit, but hardly so much so with respect to the superior limit and the temperature of most rapid growth, as may be concluded by comparing with those of other observers.

	Inferior limit.	Most rapid growth.	Superior limit.
Sinapis alba	0·0° C.	21° C.	28° C.
Lepidium sativum	1·8	21	28
Linum usitatissimum	1·8	21	28
Collomia coccinea	5·0	17	about 28
Nigella sativa	5·7	above 21 (?)	„ 28
Iberis amara	5·7		
Trifolium repens	5·7	21–25	below 28
Zea Mais	9·0	21–28	about 35[2]
Sesamum orientale	13·0	25–28	below 45

[1] I take the figures from the table of curves in De Candolle's treatise, with the assistance of the text.

[2] De Candolle remarks that the seeds of maize, melon, and Sesamum become brown, the first as if burnt at 40° C., a phenomenon which has not been noticed by others. These 'burnt' seeds however germinated afterwards at a lower temperature.

When De Candolle's inferior limits are below 5° C., they are most probably correct; his superior limits and temperatures of most rapid growth are, on the other hand, for the most part certainly too low.

Those figures deserve a more careful study which give the lengths attained by roots in the same periods of time at different temperatures, and express therefore the rate of the growth of the roots of seedlings at different constant temperatures. These numbers increase from the inferior limit to the temperature of most rapid growth, and fall again from it to the superior limit.

In *Zea Mais*, for example, I found—

	Temperature.	Length attained by the root.
in 2 × 48 hours	17·1° C.	2·5 mm.
48	26·2	24·5
48	33·2	39·0
48	34·0	55·0
48	38·2	25·2
48	42·5	5·9

Köppen obtained the following length of the roots in periods of forty-eight hours:—

Temperature.	*Lupinus albus.*	*Pisum sativum.*	*Zea Mais.*
14·1° C.	9·1 mm.	5·0° mm.	
18·0	11·6	8·3	1·1 mm.
23·5	31·0	30·0	10·8
26·6	**54·1**	**53·9**	29·6
28·5	50·1	40·4	26·5
30·2	43·8	38·5	64·6
33·5	14·2	23·0	**69·5**
36·5	12·6	8·7	20·7

The following are De Vries' results, also in periods of forty-eight hours:—

Temperature.	*Cucumis Melo.*	*Sinapis alba.*	*Lepidium sativum.*	*Linum usitatissimum.*
15·1° C.		3·8 mm.	5·9 mm.	1·1 mm.
21·6		24·9	38·9	20·5
27·4	18·2 mm.	**52·0**	**71·9**	**44·8**
30·6	27·1	44·1	44·6	39·9
33·9	38·6	30·2	26·9	28·1
37·2	**70·3**	10·0	0·0	9·2

The importance of maintaining a constant temperature during each experiment for the determination of these cardinal points is especially evident from the fact observed by Köppen, that the same part of a plant grows with very different degrees of rapidity even though the mean temperature be the same; if, for example, in one case the mean remains nearly constant, while in the other case it varies repeatedly above or below the mean. It is obvious therefore that if the mean temperature is that of most rapid growth, every oscillation either upwards or downwards must retard growth. Köppen shows however in addition (*l. c.* p. 17 *et seq.*) that growth is retarded by considerable oscillations even below this most favourable temperature. He found, for example, that after a seed of *Pisum sativum* had germinated for 144 hours at a constant temperature of 15·1° C., the root had attained a length of 110 mm.; when the temperature was variable, while the earth had twice been heated to 20° C. but had fallen between times to 15° C., the mean being 16° C., the roots grew only to 88 mm.; when the temperature varied between 15·0° and 30·0°, the mean being 18·0°, the length attained by the roots was only 56 mm. Although therefore the calculated mean temperatures were higher than 115° C., the growth was retarded, and the more so the greater the oscillations.

The following table of the lengths attained by the roots in ninety-six hours in each case is taken from a copious list of Köppen's.

Mean temperature.	Hourly change of temperature.	*Lupinus albus.*	*Vicia Faba.*
14·4° C.	0·06° C.	30·0 mm.	14·0 mm.
14·1	0·28	19·0	9·8
16·6	0·04	44·0	31·2
17·2	0·26	31·9	17·8

It appears therefore that the growing part of a plant must be subjected for a considerable time to any particular temperature in order that its growth may attain the greatest rapidity corresponding to this temperature.

Köppen's results are only in apparent contradiction to my own, according to which the curve of growth rises and falls with that of temperature; for it is possible that the entire growth in a given time may be greater when the temperature remains at a constant elevation than when it oscillates above and below it.

Sect. 20.— **Action of Light on Growth.—Heliotropism**[1]. Since we shall now pay exclusive attention to the questions whether and in what way light promotes or retards quantitatively the superficial growth of the cell-wall, we may for the time leave entirely out of consideration those cases where it changes or may possibly change qualitatively the physiological and morphological nature of the newly formed organs.

The dependence of growth on light has already been spoken of in general terms in Sect. 8; and it was there especially insisted on that, in order to avoid serious misconceptions, this must be distinctly separated from the question of the part taken by light in assimilation. Here also we are concerned only with the processes of growth itself, since we always start from the point at which the cells or organs concerned have already obtained a sufficient quantity, or even excess, of formative materials.

It has been already stated that the various parts of the flower grow as readily in permanent darkness as in light. Most internodes, on the contrary, as has been explained in Sect. 18, grow more slowly when exposed to light on all sides, and remain shorter than when growing in the dark; when the light reaches them from one side only, they curve concavely towards the source of light. Other organs however, as root-hairs, tendrils, and some internodes, become longer on the side exposed to light than on that left in the dark. We have seen also that the leaves of Ferns and Dicotyledons soon cease growing in the dark and remain small. These observations show clearly enough that different cells and organs are differently affected by light as respects their growth. Since the light itself remains the same and there is a supply of formative materials, any explanation of these differences must aim at showing how the inherited organisation of the plant must have been altered just in this way and no otherwise by the oscillations of the ether. It is however at present quite impossible to give such an explanation[2], since far too little is yet known

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[1] A. P. De Candolle, Physiologie végétale, Paris 1832, vol. III, p. 1079.—Sachs, Bot. Zeitg. 1863, Supplement, and 1865, p. 117.—Ditto, Experimental-Physiologie, Sect. 15.—Hofmeister, Lehre von der Pflanzenzelle, Sect. 36.—Kraus, Jahrb. für wissensch. Bot. vol. VII, p. 209 *et seq.*—Batalin, Bot. Zeitg. 1871, No. 40.

[2] If Müller, in the second part of his Botanische Untersuchungen (Heidelberg 1872), gives the impression of having achieved this with but little difficulty, this only shows how far he is from a true method of investigation.

of the phenomena themselves; the ascertained facts cannot yet even be reduced to a general law, especially in consequence of the obscurity which involves the action of light on leaves and on negatively heliotropic organs. If these difficulties, which were referred to in Sect. 8, were solved, the organs of plants might be divided in respect of their behaviour towards light into three kinds:—(1) those the growth of whose cells is in general independent of light; as petals, stamens, fruits, and seeds; (2) those whose growth is retarded by light; the positively heliotropic organs which become abnormally elongated by absence of light; and (3) those whose growth is promoted by light. To this last category would belong negatively heliotropic organs if we could be certain of the relation in which negative stands to positive heliotropism; whether, as has elsewhere been mentioned, it is not, at least in many cases, a modification of the positive form depending on the chemical action of light which is essential to growth; although recent researches render this very improbable.

The question in what manner light affects the mechanical laws of growth of the cell-wall can therefore, in the present state of our knowledge, have a definite meaning only in reference to positively heliotropic organs; inasmuch as it is in these cases certain that the growth of the cell-wall in the direction of the axis of growth of the organ is retarded and limited by light. But even in this case the question cannot at present be answered, since several others must first be solved. It must first of all be decided whether light acts in this manner on the cell-wall only when its incidence is oblique to the axis of growth. A similar problem, as we shall see, is presented in the action of gravitation on growth. The various phenomena of positive heliotropism allow in fact of the supposition that rays of light which penetrate the cell-wall in a direction parallel to the axis of growth of the organ do not hinder growth, while they do so more strongly the more nearly vertical they are to it, whether the organ be multicellular or a simple tube. Light therefore acts more intensely the more nearly the transverse vibrations of the ether are parallel to the surface of the cell-wall. But the solution of these questions would by no means explain the action of light on the growth of the cell-wall; in the first place we must know whether light acts directly on the cell-wall, or indirectly by means of the protoplasm, or by chemical changes in the cell-sap. But since we know that the cell-wall only grows so long as it is in contact on the inside with living protoplasm, and that the protoplasm itself is set in motion by light, in consequence of which it accumulates at particular parts of the cell-wall (see Sect. 8); and since this, like the growth of the cell-wall, is caused by the highly refrangible rays—the hypothesis must not at once be set aside. The question may moreover be asked whether light does not influence the growth of the cell-wall by means of chemical effects which it brings about in the cell-sap or the protoplasm, which however cannot be referred to assimilation, since they take place even in cells destitute of chlorophyll, as for instance in the positively heliotropic neck of the perithecium of *Sordaria fimiseda*, the stems of Claviceps, and in many roots of seedlings; and since the leaves of Dicotyledons exhibit relations to light (*vide infra*) which indicate a chemical action on assimilated substances, but not on the process of assimilation itself.

So long as we take into account multicellular organs alone, great weight might be allowed to the hypothesis of a change in the turgidity caused by light (brought about by some chemical alteration in the cell-sap and the consequent change in

diosmose[1]). But the fact that even unicellular tubes like those of Vaucheria and the internodal cells of Nitella are positively heliotropic, forbids this hypothesis, since in these cases the side exposed to light grows more slowly than the other, although all the parts of the cell-wall are subject to the same hydrostatic pressure from the sap.

The examples already given of positive heliotropism in submerged unicellular tubes, as well as the heliotropic curvings of multicellular internodes under water, show at once that they have nothing to do with a more rapid transpiration induced by light or its results.

The hypothesis would appear on the contrary to be worth more attention whether the reason why light retards the superficial growth of positively heliotropic cells is not because it first of all promotes increase of thickness, and therefore diminishes the extensibility of the cell-wall under the influence of the pressure of the sap on the side exposed to the strongest light. This hypothesis would be confirmed by Kraus's observations, according to which the cuticularising of the epidermis as well as the thickening of the walls of the cortical and bast-cells is in fact materially hindered in etiolated internodes, and the extensibility of these cell-walls consequently increased by the want of light. This explanation would apply not only in the case of the shaded side of a multicellular internode which curves towards the light, but also in that of a Vaucheria-tube or internode of Nitella; since it may be supposed that the wall is in the first place more strongly thickened on the side exposed to light and hence becomes less extensible, and therefore yields less to the pressure of the sap, and, in consequence, grows more slowly. We have at present no observations on heliotropic unicellular tubes.

If then it is proved, as the recent researches of Wolkoff give ground for believing, that the negative heliotropism of organs which contain chlorophyll depends as little as that of roots on the stronger power of assimilation possessed by the side exposed to the source of light, it must be assumed that all the actions which have been mentioned as possible in one direction may take place also in an opposite direction; and this will show the great difficulty of the investigation.

A complete account of the mode in which growth depends on light is scarcely possible at present; what has now been said will call the attention of the reader to the most important questions involved in the investigation. It may be desirable however to collect some of the more important facts at present known, and to add some critical remarks.

(a) *Organs whose growth is retarded by light.* To take first the case of those internodes (including, according to Hofmeister, the unicellular ones of Nitella) which, when the light is unequal on the two sides, curve so that the side facing the source of light is concave while the other side is convex, or in other words are positively heliotropic. These exhibit a periodicity in their longitudinal growth corresponding to the alternation of day and night, when the temperature is sufficiently constant. The growth is more rapid from evening to morning, and less so from morning to evening. Both these facts are however consistent with the phenomenon that the same internodes often grow longer, and even considerably so, in permanent darkness than they would under normal conditions. These three results lead naturally to the conclusion that it is the direct action of light (and only in fact of its more refrangible rays, see Sect. 8), which retards the growth of

[1] See Dutrochet, Mémoires pour servir, Paris 1837, vol. II, p. 60 *et seq.*

these internodes. In the case also of positively heliotropic roots (as those of *Zea Mais* Lemna, Cucurbita, Pistia, &c.), it may be supposed that if exposed to daylight they would exhibit the same alternation as internodes; but this is not yet fully established. Wolkoff has, on the other hand, already shown in the case of some roots that when they develope in water behind a transparent glass plate they grow more quickly in permanent darkness than under the alternation of day and night. Twelve primary roots of seedlings of *Pisum sativum* gave, for example, the following results:—

Day.	Successive increments.	
	In the dark.	In diffused light.
1st	195 mm.	161 mm.
2nd	239	153
3rd	250	210
4th	126	113
5th	113	78
In the 5 days.	923 mm.	715 mm.

The increments of growth of primary roots of seedlings of *Vicia Faba* were as follows:—

		In the dark.		In diffused light.
In 5 roots	as	309	to	272
11		743		612
9		612		416

In these cases a tendency of the roots was observed, though not a very decided one, to positive heliotropic curvature. The difference in the rapidity of growth would no doubt have been greater if the increments in the same time had been compared during the day only.

The long narrow leaves of many Monocotyledons exhibit the same phenomena as internodes and roots, becoming considerably longer in permanent darkness than under normal conditions, and showing positive heliotropic curvature when the light from the two sides is unequal. The plane of curvature may coincide with the plane of the leaf, so that one margin may be considerably longer than the other, and the whole leaf therefore unsymmetrical. I have observed this very evidently in a plant of *Fritillaria imperialis* grown in a window; those leaves only which sprung exactly from the side of the stem exposed to light being symmetrical like those growing in the open air. We have at present no observations on the daily periodicity in these leaves caused by light.

Observation of the broad netted-veined leaves of Dicotyledons is much more difficult. From the fact that in the dark they remain smaller, and often very much so, than under normal conditions, it might be concluded that their superficial growth presents exactly opposite phenomena to those of internodes and the long leaves of Monocotyledons. But Batalin has shown that it is sufficient to expose etiolated plants now and then to light—the time not being long enough for them to become green—for their growth in the dark to be afterwards considerably promoted. This leads to the supposition that light causes in etiolated leaves a change which does not consist in chemical assimilation, by which they are enabled to grow further in the dark. In any case this phenomenon shows that there is no real contradiction between the growth of these leaves and that of internodes, and that the reason why they become larger under the normal conditions of light than in permanent darkness is not because light has a directly favourable influence on the growth of the cells of these leaves. The recent experiments of Prantl[1] rather favour the hypothesis that green—and therefore healthy and normal—leaves exhibit the same diurnal periodicity of growth as positively heliotropic internodes. He succeeded, by a number of measurements both in breadth and length

[1] Compare also Sachs, Arbeit. des bot. Inst. in Würzburg, Heft II, p. 188.

of the leaves of *Cucurbita Pepo* and *Nicotiana Tabacum*, taken at intervals of three hours, to construct curves of growth, which in spite of adverse fluctuations of temperature, rose from evening to morning, attained a maximum after sunrise, and then fell during the day till evening; exactly what I showed to be the case with positively heliotropic internodes. If this general law is established, it results that the broad netted-veined leaves of Dicotyledons grow more quickly in the dark than in the light, and are therefore hindered in their growth by light. But when such leaves remain nevertheless smaller in permanent darkness because they cease growing earlier, this must be interpreted as an unhealthy condition depending on the suspension of certain processes of metastasis which must precede growth and which are induced by light. In conformity with this hypothesis we must suppose that in leaves which unfold under the alternate influence of day and night, growth is directly hindered by light; but that at the same time certain chemical changes take place which in general make growth possible, and enable it to continue in the succeeding darkness, if it does not last too long. That this has nothing to do with assimilation is shown by Batalin's experiments with leaves destitute of chlorophyll.

If we now enquire what are the mechanical changes which light causes in the organs we have been considering, and by which their growth is retarded, it is to be regretted that no experiments have yet been made as to their effect on unicellular organs which exhibit positive heliotropism, as Vaucheria-tubes and internodes of Nitella, since they present the most simple case from a mechanical point of view. In the case of the internodes of Phanerogams which consist of tense layers of tissue, Kraus found in the etiolated state a smaller tension between the medullary and cortical layers, and therefore that the cell-walls of the layers of tissue placed in a state of passive tension by the pith were less thickened, lignified, and cuticularised. It follows that these last are more extensible than in the normal internode, and therefore offer less resistance to the tendency of the pith to elongate. If we suppose that in unicellular tubes light also increases the cuticularisation and thickening of the cell-wall, the wall will offer greater resistance to the pressure of the cell-sap will become less stretched, and will therefore grow more slowly.

But little can be inferred as to the mechanical influence of light on growth from the changes in the tension of the tissues on the convex and concave sides of internodes with positive heliotropic curvature. If such an internode is split lengthwise so that the side exposed to light is separated from the other side, the former becomes more concave, while the latter becomes less convex or even somewhat concave towards the shaded side. In other words, the tension between the outer and inner layers is greater on the concave side exposed to light than on the convex shaded side. But the same phenomenon occurs also in internodes with an upward geotropic curvature, and with negatively heliotropic internodes, as well as with twining tendrils; and could not in fact be otherwise.

(b) *Of Negatively heliotropic organs*[1] only a comparatively small number are at present known. Among those which contain chlorophyll may be named the hypocotyledonary portion of the stem of the seedling of the mistletoe, the older nearly mature internodes of the ivy and *Tropæolum majus*, and the basal portions of the tendrils of the vine, Virginian creeper and *Bignonia capreolata*. I pass over at present the doubtful negative heliotropism, as I think, of the thallus of Marchantia and the prothallia of Ferns, as well as of other decidedly bilateral organs. Among organs which are not green must be especially mentioned the negatively heliotropic aërial roots of Aroideæ and epidendral Orchids[2]; but, beyond all others, the roots of *Chlorophytum guayanum*, which are extremely sensitive to light coming from one side. Negative heliotropism has, in addition, been stated to occur in the roots of seedlings of Cichoriaceæ, Cruciferæ, &c., and has recently been certainly determined by Wolkoff in the case of *Brassica Napus* and *Sinapis*

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[1] Knight, Phil. Trans. 1812, p. 314.—Dutrochet, Mémoires, &c., vol. II, p. 6 *et seq.*—Durand and Payer's statements.—Compare Sachs, Exper.-Phys., p. 41.

[2] According to a great number of observations of my own and statements of others.

alba. Among unicellular organs destitute of chlorophyll the only ones known at present with certainty to be negatively heliotropic are the root-hairs of Marchantia.

The remark that a number of organs destitute of chlorophyll and endowed with negative heliotropism, and in particular the highly sensitive roots of Chlorophytum, are very transparent, led Wolkoff to the hypothesis that the rays of light may be refracted by their cylindrico-conical shape, so as to produce a more intense illumination of the tissue on the side removed from the source of light than on that exposed to it; and that therefore the concave curvature on the former side is in fact a form of positive heliotropism. The apices of roots, when separated by a transverse section, if illuminated from one side and viewed from above, exhibit exactly such differences of luminosity as might be expected on this hypothesis. It must however not be forgotten that the apices of roots which are by no means negatively but at an earlier period even positively heliotropic, like those of *Vicia Faba*, manifest the same phenomenon, though perhaps to a lesser degree. Whether, on the other hand, it is possible to suppose a similar refraction of light in the case of the very thin-walled negatively heliotropic root-hairs of Marchantia, is still in doubt. Further researches must show whether Wolkoff's happy idea is tenable or not.

In the cases of the older internodes of the ivy which are only very slightly transparent, the older and lower parts of tendrils, &c., the existence of an actual focal line on the shaded side cannot be admitted, because this would evidently imply that they received more intense blue and violet light than, from the fact that the tissue which is penetrated by the light contains chlorophyll, it is probable they do. The negatively heliotropic curvature takes place however, at least in the ivy as well as in the roots of Chlorophytum, only in highly refrangible light (after passing through an ammoniacal solution of copper oxide), not in yellow light (which has passed through potassium bichromate). If, as Wolkoff at one time supposed, the more vigorous nourishment, *i. e.* accumulation of assimilated substances, were the cause of the more rapid growth on the side exposed to light in this class of negatively heliotropic organs, they ought to curve much more strongly in the less refrangible (red, orange, or yellow) than in the more refrangible rays. This hypothesis would moreover fail to explain why the same internodes which when young showed decided positive heliotropism, at a later period when their growth has almost ceased manifest the opposite behaviour towards light.

The experiments which Wolkoff is now carrying on in the botanical laboratory at Würzburg, and which are not yet completed, lead at present to the conclusion that there are two kinds of negatively heliotropic organs. In one kind are included roots, in which the negatively heliotropic curvature takes place near the apex at the spot where growth is most rapid; to the other kind belong internodes where the negatively heliotropic curvature takes place only at the older parts whose growth is completed, while the young quickly growing parts manifest positive heliotropism. In these latter cases the additional peculiarity occurs that the older parts, after being exposed to light on one side, will continue for some time to curve in the dark so that the side exposed to light becomes still more convex. This is a property which appears to be wanting in organs of the first kind as well as in those that are positively heliotropic.

It is evident that we are here confronted with an unsolved problem; and when all the facts have been taken into consideration, the theory that there are two kinds of cells, the growth of one of which (positively heliotropic) is retarded by light, whilst that of the other kind (negatively heliotropic) is promoted by it, may be the simplest and most in accordance with facts. This difference is the less remarkable since in the behaviour of growing cells with respect to gravitation we find a precisely similar difference, but much more strongly marked[1].

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[1] Schmitz, Linnæa, 1843, p. 513 *et seq.* If, as can scarcely be doubted, Schmitz's statements with regard to Rhizomorphs are confirmed, it results that no certain inference can be drawn as to the positive heliotropism of an organ from the fact that its growth is more rapid in the dark. We

Sect. 21.—**Influence of Gravitation on Growth :—Geotropism**[1]. It has already been shown in Sect. 10 that, when the access of light is equal on all sides or when heliotropism is prevented by the exclusion of light, gravitation is the cause of certain organs turning downwards, others upwards, and others again in a direction oblique to the horizon. At present we shall speak only of those which take a direction directly upwards or downwards, since other causes co-operate to bring about an oblique growth.

Just as organs, according to their internal nature, grow either more rapidly or less rapidly on the side which faces the source of light than on the other side, so also gravitation effects, in accordance with the nature of the organs, either an acceleration or a retardation of growth on the side which faces the earth. Those organs which are thus retarded in their growth are called *positively geotropic*, those which are accelerated *negatively geotropic* organs. Positively geotropic organs consequently become concave on the under side, and direct their growing apex downwards if their axis of growth is brought into a horizontal or oblique direction; negatively geotropic organs, on the contrary, become convex on the under side under similar conditions, and elevate their growing apex until it stands erect.

It has not yet been ascertained whether positively geotropic organs would manifest a different rapidity of growth if entirely withdrawn from the influence of gravitation (like positively heliotropic organs when withdrawn from the influence of light) from that displayed when gravitation acts in a direction parallel to the axis of growth. It would seem however as if gravitation only affects the rapidity of growth when its direction cuts that of the axis of growth at an angle, and the more so the nearer the angle approaches a right angle.

The positive or negative character of geotropism depends as little as that of heliotropism on the morphological nature of the organ. Not only, for example, are all the primary roots of the seedlings of Phanerogams positively geotropic, and most secondary roots which spring from underground stems, as tubers, bulbs, or rhizomes; but also many leafy lateral shoots, especially those which are destined to produce rhizomes or to form new bulbs (*e.g.* Tulipa, Physalis, Polygonum, &c.), and even foliar structures, like the cotyledonary sheaths of Allium, Phœnix, and many other Monocotyledons. Among positively geotropic organs must also be included the lamellæ and tubes of the hymenium of Hymenomycetous Fungi. All axes which grow upright (and are not bilateral), petioles, and the stipites of many Hymenomycetous Fungi, exhibit, on the other hand, decidedly negative geotropism.

The geotropism, like the heliotropism, of different organs varies in all degrees. It is, for example, manifested very strongly in the primary roots and upright

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could scarcely have a better proof of the necessity for a fresh and more accurate investigation of all the phenomena of heliotropism.

[1] Knight, Phil. Trans. 1806, vol. I, pp. 99–108.—Johnson, Edinburgh, Phil. Journ. 1828, p. 312.—Dutrochet, Ann. des Sci. Nat. 1833, p. 413.—Wigand, Botan. Untersuch. Braunschweig 1854, p. 133.—Hofmeister, Jahrb. für wissensch. Bot. vol. III, p. 77.—Ditto, Bot. Zeitg. 1868, Nos. 16, 17, and 1869, Nos. 3–6.—Frank, Beiträge zur Pflanzen-Phys. Leipzig 1868, p. 1.—Müller, Bot. Zeitg. 1869 and 1871.—Specheneff, Bot. Zeitg. 1870, p. 65.—Ciesielski, Untersuch. über die Abwärtskrümmung der Würzeln, Breslau 1871.—Sachs, Arbeit. des bot. Inst. in Würzburg 1872, Heft 2, Abh. 4 and 5.—Ditto, Exper.-Phys., p. 505.—Ditto, Flora, 1873, No. 21.

primary stems of seedlings; much less strongly in the secondary roots which spring from rhizomes, climbing stems, &c. The secondary roots of the first and of higher orders which spring from the primary roots of seedlings display this phenomenon in different degrees. It appears to be the general rule that when lateral shoots of the same kind spring from a vertical and therefore decidedly geotropic organ, the branches of the first order are less geotropic, and the further ramifications still less so the higher the order to which they belong; the exceptions to this rule may be caused by special circumstances. This gradation is very obvious in roots. From the primary root or a strong root springing from the stem with decidedly positive geotropism, proceed secondary roots of the first order which exhibit the phenomenon much less decidedly; and from these again secondary roots of the second order which apparently are not at all geotropic, and therefore grow in all directions as they may chance to originate. Geotropism, like heliotropism, does not depend on the organ containing or not containing chlorophyll, nor on whether it consists of masses of tissue or of a simple row of cells or of a single cell. To this last category belong, for example, the positively geotropic radical tubes of the Mucorini and the negatively geotropic sporangiophores of the same family and of numerous other Mould-fungi. In the same manner the rhizoids of Chara display positive, the stems negative geotropism, both consisting of unicellular segments, the former destitute of chlorophyll, the latter green. Whether and how strongly an organ is positively or negatively heliotropic or geotropic depends altogether on its importance in the economy of the plant, and hence on its physiological functions.

From the remarkable fact that there are organs endowed with positive and negative heliotropism and geotropism, and from many similarities exhibited by the two phenomena, the question presents itself whether all positively heliotropic organs must not possess one description of geotropism either positive or negative, or *vice versâ;* in other words, whether the two properties do not stand in some definite relation to one another. This does not however appear to be the case. Of primary roots, all of which are positively geotropic, some display positive, others negative heliotropism; and again, the aërial roots of Chlorophytum, Aroideæ, and Orchideæ, display very distinct negative heliotropism, but are scarcely at all geotropic. There appears therefore to be no necessary connection between the two phenomena.

It is clear that organs which are both heliotropic and geotropic, and on which, since they lie obliquely to the horizon, the light falls from above or from below, are subject to changes in their growth dependent both on light and on gravitation. Thus, for example, the bending upwards of a branch placed horizontally on which the light falls from above may be caused at the same time by positive heliotropism and by negative geotropism. An erect stem, on the other hand, which turns heliotropically towards a source of light at the side and thus makes a curvature which is concave below, will have a tendency to become erect in consequence of its negative geotropism, just as if there were no light falling on it from one side. Stems therefore which in the evening were bent by positive heliotropism, will stand upright in the morning. These considerations are evidently of the first importance in making observations on the two phenomena.

We have already seen that no clear idea has yet been obtained of the mode in which light acts in influencing growth in heliotropic organs. As little are we at

present in a condition to affirm how the acceleration or retardation of the growth of the cell-walls results from the action of gravitation. The hypotheses and considerations there stated may be repeated here *mutatis mutandis*. Particular stress must be laid on the fact that movements are induced in protoplasm by the action of gravitation just as by the action of light. Thus Rosanoff showed[1] that the plasmodia of *Æthalium septicum* are negatively geotropic, creeping, under the influence of gravitation, over steep moist walls, and turning, under the action of centrifugal force, towards the centre of rotation; they take therefore those directions which would be least expected from their apparently fluid condition. The question suggests itself whether there is not also protoplasm which behaves in this respect in an exactly opposite manner; and from the dependence of the growth of the cell-wall on the activity and probably also on the disposition of the protoplasm in the cell, the hypothesis must not be altogether set aside that all geotropic phenomena are in the first place caused by the protoplasm taking up definite positions in the cells under the

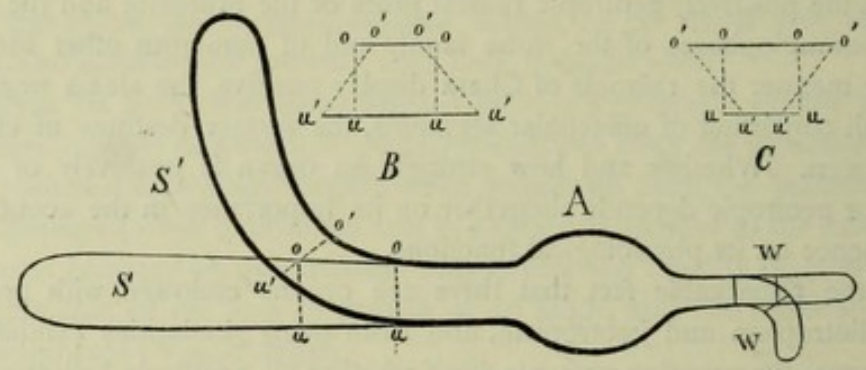

FIG. 452.—Diagram for illustrating geotropic upward and downward curvature.

influence of gravitation, and thus accelerating or retarding the growth of the cell-walls on the under sides. Since nothing is known on this subject, we must direct our attention solely to the growth of the cell-walls, leaving it undecided whether the effect of gravitation be direct or indirect.

In order to state clearly the problem how gravitation acts on the growth of the cell-wall[2], we may consider as the simplest example a unicellular tube, such as we find in Vaucheria, the posterior end of which developes as a positively geotropic root, the anterior end as a negatively geotropic stem. Fig. 452 *A* may represent this, assuming that the whole tube grew at first in a vertical direction either upwards or downwards, but was then placed in a horizontal position, as shown by the light outlines *S* and *W*. After some time the radical end would show a downward curvature, like *W'*, the part *S* on the contrary the upward curvature, as *S'*. It is self-evident that each of these curvatures can only result from the growth, equal on all sides when the organ is erect, having now become unequal on the upper and under sides, the convex growing in both cases more quickly than the concave side.

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[1] Rosanoff, De l'influence d'attraction terrestre sur la direction des plasmodia des Myxomycètes (Mémoires de la Société impériale des sciences de Cherbourg, vol. XIV).

[2] Duchartre's assertions on geotropism in his Observations sur le rétournement des champignons (Compt. rend. 1870, vol. LXX, p. 781), show that he has not clearly comprehended the question.

If we now apply the results of my experiments on internodes and nodes of Grasses which curve upwards to the simple tube, the growth is found to be more rapid on the convex under side, less rapid on the upper side of the upwardly curved part, than when it grew erect. It may be assumed, from Ciesielski's measurements of roots, that when the tube curves downwards the growth is more rapid on the convex upper side, less rapid on the concave under side, than when the curved part grew for a longer time in a vertical direction. In other words, when the tube is placed in a horizontal position the growth is accelerated on the upper side of the positively geotropic part and on the under side of the negatively geotropic part, but always retarded on the opposite sides.

If therefore we assume that in Fig. 452 *B* the two side walls of a transverse disc of the part *S* of the tube when in an upright position had lengthened in a definite time to the equal lengths *o o* and *u u*, it would have remained upright; and if the tube had been placed horizontal during this time, the lower side would have attained the greater length *u' u'*, the upper side the shorter length *o' o'*, and the piece must in consequence become curved. Exactly the opposite would be observed, as shown in Fig. 452 *C*, if the growing piece belonged to the part *W* of the tube.

If now the unicellular tube *A* were supposed divided by transverse and longitudinal divisions into a tissue consisting of a number of layers of cells; or if, what amounts to the same thing, a stem of a seedling were supposed substituted for the part *S* of the tube, and a root for the part *W*, the same phenomena would occur, as experiments have shown, in every cell of the growing part, as those previously observed in the tube. In the part *S* every cell would grow more rapidly on the under side, less rapidly on the upper side than if the part were upright, the reverse in the part *W*. We should find that in *S* both the upper and under sides of any cell (*i. e.* upper and under in relation to the radius of the earth) are longer than those of the cells situated above it, the reverse in *W*; in other words, that every individual cell of a part which shows geotropic curvature behaves in the same way as if the part previously straight were held firmly by the two ends and then bent. This will be made clearer to the student if in the portion of the curved part included in *A* lines are drawn parallel both to the straight and the curved outlines, and the septa of the cells are then indicated in the straight piece simply by parallel lines crossing the first at right angles, in the curved part by lines corresponding to the radii of curvature. The cells exposed by longitudinal sections through nodes of Grasses and roots endowed with geotropic curvature exhibit this phenomenon, although with many irregularities.

When the facts connected with the geotropism of the cell-wall have thus been made clear, we may proceed to the question, why or by what effect of gravitation these differences are occasioned in the growth on the upper and under sides of every cell of a geotropic organ when placed in a horizontal position. We have at present however no answer to this question, any more than in the case of heliotropism, the same diagram availing, *mutatis mutandis*, for the two phenomena.

The view brought forward by Hofmeister, and for some time adopted by me, that positive geotropism occurs only in those organs and in those parts of organs in which there is no tension in the tissues, while the organs in which there is strong tension are negatively geotropic, rested on imperfect induction. On the one hand

the parts of the roots of seedlings which curve downwards (as I have shown elsewhere), are not entirely without tension between the cortex and the axial bundle; while, on the other hand, in the nodes of Grasses, although they display a high degree of negative geotropism, there is no or very little such tension. Even in the negatively geotropic contractile organs of the petioles of Phaseolus[1] the tension between the cortex and the axial bundle is of a similar character to that which occurs in positively geotropic roots, but extremely intense. If therefore the tension of tissues and the alteration effected in it by the influence of gravitation cannot be considered as the cause of the upward curvature, it may still be admitted that it is only useful to upright organs by increasing their rigidity and elasticity, and thus making them more adapted for the erect condition; while this would be quite unnecessary in those that grow downwards.

A good illustration of the part played by rigidity and elasticity in producing the erect position of negatively geotropic organs, is afforded by the pendent pedicels of many flowers and flower-buds, in which the tendency to bend upwards is altogether obscured, the weight of the flower being sufficient to bend the pedicel downwards. If in such cases the flower-buds are cut off, the pedicel becomes erect[2] from the stronger growth of the under side, as *e.g.* in *Clematis integrifolia*, *Papaver pilosum* and *dubium*, *Geum rivale*, and *Anemone pratensis*. The tension in the tissue of such pedicels is not sufficient to give them the rigidity needful to overcome the weight of the flower by their geotropic curvature upwards; this weight, on the contrary, overcomes the tendency of the pedicel to curve convexly on the lower side, which tendency comes into play when the weight is removed. The same is the case in very long but not very rigid shoots, as those of the weeping willow, weeping ash, &c.

Since geotropic like heliotropic curvatures take place only during growth[3], the position of the parts that will curve in the various organs is known beforehand if the course of their growth is known (see Sect. 17); and conversely the part where growth is at any time taking place may be ascertained by this rule from the fact of its curving.

From causes which we cannot go into here more in detail, the curvature does not generally take place in the form of an arc of a circle; but there is in organs of considerable length—whether they curve upwards or downwards—a spot where the curvature is greatest, *i. e.* where the radius of curvature is least. It would appear, from all that is at present known, that when organs are laid in a horizontal position the strongest curvature is always found at the spot where growth is most rapid. But since in erect stems a piece of considerable length (often 20 cm. or more) is actually growing, a long and flat arc is formed when the stem erects itself from a horizontal position, the maximum curvature of which is at a considerable distance from the apex of the stem. In primary roots, on the contrary, growth exists only in a space of a few mm. from the apex, the maximum increment of growth taking place at

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[1] Sachs, Experimental-Physiologie, p. 105.

[2] See De Vries, in Arbeiten des Würzburg Bot. Inst., Heft II, p. 229.

[3] It must be noted that some organs, if grown in a normal position and then placed horizontal, begin then to grow like the nodes of Grasses and the contractile organs of Phaseolus.

the most from 2 to 3 mm. from the apex, and the strongest curvature is therefore at this spot, or very near the apex; and when the organ lies in a horizontal position the curvature is very strong, or the radius only very small (a few millimetres). It is easy to see that when a very strong curvature takes place near the apex of a root, it serves to fix it in the ground; while it is mechanically useful for the erection of stems that they curve in larger flatter curves. In the jointed haulms of Grasses the work of flexion is distributed over two or three nodes, a portion of the curvature taking place in each node until the haulm again stands erect.

Knight, the discoverer of the fact that gravitation is the cause of geotropic curvature, thought that the curving upwards of the stem was occasioned by the food-materials collecting in greater quantities on the under side and hence causing a more powerful growth. Hofmeister, who called attention to the relation of the tension of the tissues to the various curvatures of the parts of plants, explained the action of gravitation in causing an upward curving in the first place by an increase of the extensibility of the tissue on the under side, which is in a state of passive tension. I have, on my part, directed attention to the fact that the growth of the under side of organs placed horizontally which have a tendency to curve upwards is accelerated, while that of the upper side is retarded; but whether this is caused by a corresponding distribution of the food-materials, or by a change in the extensibility of the passive layers, or in any other way, I leave for the present undecided.

The curving downwards of the roots of seedlings was explained by Knight in an unsatisfactory way as a result of the softness and flexibility of the growing apex, a view which was adopted by Hofmeister in a less crude form, and for some time also by myself. It was assumed on this theory that the tissue of growing roots may be compared to a tough piece of dough, which tends, from the force of its own weight, to curve downwards at the free unsupported end. I thought that by the excess of weight of the free apex a traction was exerted on the growing cell-walls of the parts of the upper side which curve, by which growth or deposition of food-material is promoted on this side, while the reverse must be the case on the under side; and I think that Hofmeister explained the process in a similar manner. Frank therefore did not hit the nail on the head when he merely insisted that the downward curving of the apex of the root depends on growth being stronger on the upper side; this we had admitted. It would have been more to the purpose had he said why growth is more rapid on the upper than on the under side of the apex of a root placed horizontal. Frank, on the other hand, was right in maintaining that our explanation was untenable, because, as Johnson had already shown, the apex of a root turns downwards even when its own weight is counterbalanced by an equal or slightly greater one, and because the root, even when it rests on a horizontal solid support, shows the same phenomena of growth which cause its apex to point downwards. The statements of Frank and the subsequent ones of Müller were however inadequate on the points in question. If I relinquish Hofmeister's view, which I had previously in the main adopted, it is in consequence of more comprehensive experiments on the growth of roots, and especially on their geotropic curvature. It would carry us too far here to give the reasons for and against the theories which have been alluded to; and it would serve as little purpose to go into an explanation of particular phenomena, as for example the fact that roots penetrate to a depth of from 2 to 3 mm. into mercury, whether they impinge upon it vertically or obliquely[1].

It seems to me that any theory of geotropism can only be adequate if it is able to

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[1] See Pinot u. Mulder, Ann. des Sci. Nat. 1829, vol. XVII, p. 94, and Bydragen for de natuurkund. Wetensch. 1829, vol. VI, p. 429; also Speschenеff (Bot. Zeitg. 1870, No. 5), whose statements I am able to confirm in the main by a number of experiments of my own.

explain equally the positive and the negative descriptions, and to show why the same external cause produces opposite results in cells and organs of precisely similar structure, acceleration or retardation of growth on the under side and the reverse on the upper side.

If a number of organs grow in a horizontal or oblique direction without curving either upwards or downwards, this may result from their not being geotropic and growing straight forward in the direction of their first origin, as rootlets of a high order which grow downwards from the under side of their parent root, upwards from the upper side, horizontally from the sides, or continue to grow straight and oblique according to the direction of the primary root. To this must be referred, among other phenomena, the striking one described by me that plants which grow in uniformly moist soil emit a large number of fine roots out of it with their apices pointing upwards; there are even rootlets of the first or second order which spring from the upper side of

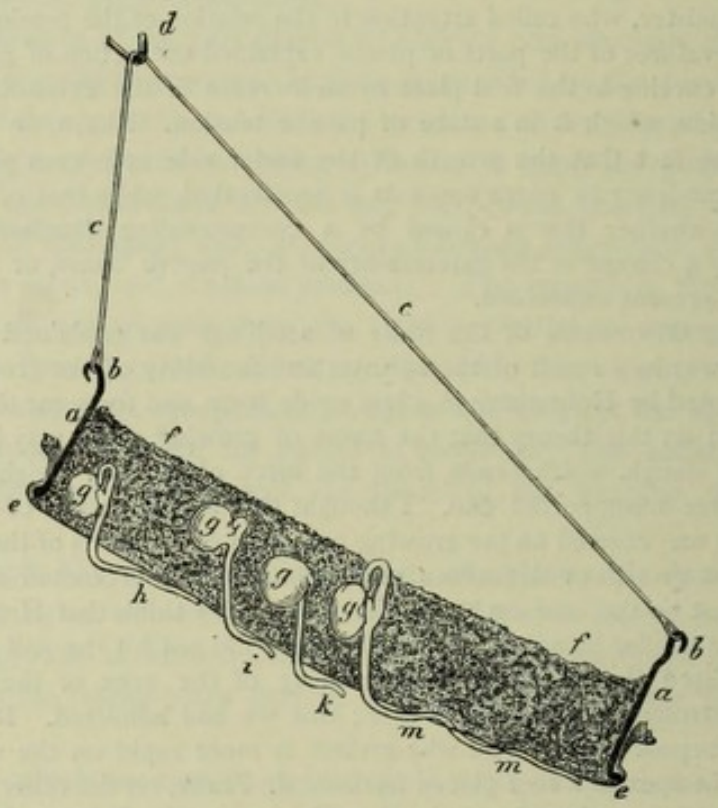

FIG. 453.—Apparatus to illustrate the mode in which the geotropism of the roots *h i k m* of seedlings *g g g* is overcome when they come into contact with a moist surface.

horizontal or oblique parent roots and grow straight upwards without being geotropic. If the air is able to enter the ground freely, its surface is often dry, and the fine roots which are directed upwards die off, as I have ascertained by growing plants in glass vessels filled with earth.

But even geotropic organs may grow obliquely or horizontally when other causes oppose or counterbalance their geotropism. One of the most common of these causes is the bilateral structure which makes an organ grow more strongly on one side from internal causes. Since I shall recur to this subject in the next section, only a single example need be given here. In the case of seedlings, rootlets of the first order not unfrequently appear above the surface of the soil obliquely when it is uniformly moist; and I have convinced myself that this is the result in cases which have been observed (*e. g. Vicia Faba*) of a stronger growth of their lower side altogether independent of geotropism, in consequence of which they always grow in a flat curve concave upwards. But external causes may also act in opposition to geotropism even when this is very strongly developed. Thus Knight and Johnson have shown, as I have recently described

more in detail, that primary roots with strong positive geotropism, as well as secondary rootlets, when growing in moderately damp air, deviate from their vertical or oblique direction when there is a moist surface near them. Under these circumstances a curvature concave to the moist surface takes place at the region below the apex where there would otherwise be a downward curvature, the apex being by this means conducted towards the moist surface so that it may penetrate into the moister soil or grow in contact with it. The apparatus represented in Fig. 453 is well adapted to exhibit this phenomenon. It consists of a zinc frame *a a* covered below with wide-meshed network, thus forming a sieve hanging obliquely and filled with moist sawdust *ff*. The seeds *g g g* germinate in the sawdust, their roots penetrating at first vertically downwards into it. When the apex of a root escapes through the network into air which is not too dry, it turns towards the moister surface *b–m*, its geotropism being thus evidently overcome[1].

Sect. 22. **Unequal Growth**[2]. Our observations have hitherto had reference almost exclusively to the growth of multilateral or polysymmetrical organs, such as erect stems and descending roots. Organs of this kind offer the simplest example of growth taking place equally on all sides. But they form only a small minority, since not only a large number of primary stems like those of Hepaticæ, Rhizocarpeæ, and Selaginelleæ, but also by far the greater number of erect stems, and all leaves, display a decidedly bilateral structure, *i. e.* two sides of their axis of growth exhibit different characters. With this bilateral organisation is also usually connected a difference in the growth of the two unequal sides, which causes curvatures and hence changes in the position of the apex. The two unequal sides of bilateral organs must also be acted on differently by external agencies which affect growth, such as light, gravitation, and pressure. We do not attempt here to solve the question of the causes which produce the bilateral structure in any particular case; it need only be shown incidentally that this structure of lateral organs (as we have already seen in Book I, Sect. 27) is probably always brought about by internal causes, and is independent of the action of external circumstances. This is in general at once evident from the fact that the median plane of bilateral appendicalar organs has always a perfectly definite geometrical relation to the axial structure which bears them, and that moreover in the dark and under the influence of slow rotation round a horizontal axis, which eliminates the effect of gravitation, the bilateral structure and relation to the axis remain unchanged.

But before we proceed to the consideration of the growth of bilateral organs, it must be premised that even in multilateral erect stems and vertically descending roots growth does not always proceed equally and with equal rapidity on all sides of the longitudinal axis; it is much more common for first one side and then another of the organ to grow more rapidly than the rest, curvatures being thus caused the convexity of which always indicates the side that is at the time growing most rapidly.

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[1] [For a further detailed series of experiments on the influence of gravitation on growth, see Sachs, Flora, 1873, No. 21, and Arb. des bot. Inst. Würzburg, 1873, Heft 3.—Ed.]

[2] A. B. Frank, Die natürliche wagerechte Richtung von Pflanzentheilen (Leipzig, 1870). The views propounded in Frank's treatise are opposed by H. de Vries in the second Heft of the Proceedings of the Würzburg Bot. Inst. 1871, p. 223 *et seq*—See also Hofmeister, Allgemeine Morphologie der Gewächse, Leipzig, 1868, Sect. 23, 24.

If another side then grows more rapidly, it becomes convex, and the curvature changes its direction. Curvatures of this kind caused by the unequal growth of different sides of an organ may be called *Nutations*. They occur most commonly and evidently when growth is very rapid, and consequently in organs of considerable length, and are produced under the influence of a high temperature either in darkness or when the amount of light is very small.

When two opposite sides of an organ grow alternately more and less rapidly, curvatures are caused first on one side and then on the other; it will, for example, bend first to the left, then become erect, and then bend to the right side; as occurs, *e.g.* in the long flower-scapes of *Allium Porum*, which finally take an erect position when their growth is ended. It is much more common for the apices of erect stems above the curved growing part to move round in a circle or ellipse, the region of most active growth moving gradually, as it were, round the axis. This kind of nutation may be termed a *Revolving Nutation*. Since the apex of the stem is constantly rising higher during the nutation owing to the elongation of the part below it, its revolving motion does not take place in a plane, but describes an ascending spiral line. This form of nutation occurs in many flower-stalks before the unfolding of the flowers, as in those of *Brassica Napus*, where the movement ceases when growth is completed, and the stem finally becomes erect. It is very general in climbing stems and in almost all erect stems that bear tendrils; but bilateral tendrils also revolve at the time when they are about to take hold of a support[1].

In bilateral appendicular organs nutation does not usually take the form of a revolving motion, or only to a subordinate extent, as in tendrils. The outer or dorsal side more often grows more rapidly so that the organ is curved concavely to the primary axis, and the inner side afterwards begins to grow more quickly, so that the organ finally becomes straight, or even concave on the dorsal side. This is the case in all strongly developed foliage-leaves, very strikingly in those of Ferns, which are at first rolled up towards the axis, and then unroll, often bending over backwards, becoming finally straight. The same phenomenon occurs in the tendrils of Cucurbitaceæ, which are also at first rolled up inwards, then become straight, and are finally rolled backwards. Other tendrils are at first straight or only slightly concave inwards like leaves in vernation, but are afterwards rolled backwards. Movements of nutation are very common and easily observed in stamens with long filaments, as *Tropæolum majus*, *Dictamnus Fraxinella* (Fig. 454), *Parnassia palustris*[2], &c., and in long styles like those of *Nigella sativa*, &c. They occur at the time of the maturity of the sexual organs, and serve to place the stigmas and anthers in the positions adapted for the conveyance of pollen by insects from one flower to another[3]. Most lateral shoots behave in the same manner as ordinary leaves, growing at first only quickly enough on the outer side to become adpressed to the primary axis in vernation, afterwards more rapidly on the inner side, by which they become straight and diverge at a greater angle from the primary shoot.

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[1] See Sect. 25, On the Twining of Tendrils.

[2] [On the stamens of Parnassia, where there is not properly any movement of nutation, see Gris, Comp. rend, Nov. 2, 1868; and A. W. Bennett, Journ. Linn. Soc. vol. XI, p. 24, 1869.—Ed.]

[3] *Vide infra* under Fertilisation, Chap. VI.

These movements of nutation of bilateral appendicular organs take place mostly in one plane which coincides with the median plane of the organ. As long as the organ grows most rapidly on the dorsal side, it may be termed, after de Vries, *hyponastic*; afterwards, when it grows most rapidly on the inner or upper side, *epinastic*. Since in the later stages of development of an organ growth ceases at certain places—while at different distances from these places it presents different stages of growth, until it finally ceases everywhere—it is clear that in the same organ, by the side of spots where growth is completed and nutation no longer takes place, others occur with hyponastic and others again with epinastic growth, until at length nutation and growth alike cease altogether, as in Fern-leaves.

Seedlings of Dicotyledons are a remarkable illustration of bilateral structures which nutate in one plane; although their stem and primary root become afterwards multilateral and grow vertically upwards and downwards. The stem terminates in a pendent or nodding bud; and the curvature, which is generally very great, exhibits



FIG. 454.—Nutation of the filaments of *Dictamnus Fraxinella*; the filaments of the stamens whose anthers have not yet opened are bent downwards; those with anthers already burst are bent upwards.

itself also in germination when it takes place out of the ground, in a vessel that rotates slowly round a horizontal axis; it is a true curvature of nutation independent of light and gravitation. But the older portions of the stem become straight as they develope from the curved portion; and in proportion as the stem increases in length, the straight part which bears the nodding bud also lengthens. When germination takes place in a feeble light, or better in a slowly rotating vessel, a more rapid growth occurs of the older portion of the stem which was at first concave, causing it to become convex on this side; and hence the older and younger parts of the stem form together a letter S, as in Phaseolus, *Vicia Faba*, *Polygonum Fagopyrum*, Cruciferæ, &c. But the primary roots of dicotyledonous seedlings also manifest a tendency to a bilateral structure; since, when they develope under slow rotation round a horizontal axis, they seldom continue to grow straight, but curve concavely either in front or behind, sometimes even becoming rolled up. These and other instances of nutation are not clearly seen when the development takes place under normal conditions, because the growth of the stem of the seedling is retarded by light, and the curvature both of stem and root prevented by geotropism.

A knowledge of the different capacity for growth possessed by the anterior and posterior sides of bilateral organs lies at the root of an understanding of the fact that leaves, lateral shoots, and many secondary roots, although they are heliotropic and geotropic, yet assume definite positions with respect to the horizon, but without growing vertically upwards or downwards. When multilateral primary stems and roots grow vertically, the essential cause is their growth being uniform on all sides of the axis of growth; the different sides of the organ are in equilibrium with one-another. Every deviation from the vertical position, to the right, left, front, or back, is counterbalanced by geotropism; the growing part continues to grow until the free apex stands erect, in which position the action of gravitation is again equal on all sides. In the same manner light acts equally strongly on all sides of such organs. If therefore one side is exposed to stronger light, a heliotropic curvature takes place which finally brings the free part into a position in which all sides receive equally strong light on all sides, and therefore grow uniformly without any further curvature. The case is different with bilateral organs the anterior and posterior sides of which possess independently different capacities for growth, and which therefore exhibit a tendency for their more rapidly growing side to become convex. If the growth is very strongly hyponastic or epinastic, the curvature thus caused may take place in spite of the opposing action of light and gravitation, supposing the organs to be actually heliotropic or geotropic. Organs which grow horizontally or obliquely to the horizon must not be assumed to be on that account wanting in heliotropism or geotropism; still less is it necessary to suppose in these cases any special or altogether abnormal relations to light and gravitation. It is sufficient, as de Vries has clearly shown, to suppose that light and gravitation act in the ordinary way on the growth of bilateral organs, in order to explain their directions of growth, if only it is borne in mind that their heliotropism and geotropism cooperate with their hyponastic and epinastic properties, and thus bring about positions of the organs which must be considered as the resultants of these different forces. The weight of the overhanging part must however also be taken into account, its tendency being always to change the lateral direction of the organ into a more horizontal or even pendulous one; and this must occur more decidedly the less the elasticity of the organ. When large leaves assume oblique or horizontal positions, it is because their epinasty tends to make them concave downwards as they unfold, while their positive heliotropism tends to make them concave upwards. The result is consequently a more or less flat expansion of the leaf, the position of which depends on the relation of the weight of the lamina to the flexibility of the petiole and mid-rib. The same phenomena are observable in horizontal or oblique lateral shoots, in which however the hyponasty of the axis often counterbalances the greater mass of the pendent parts (as in *Prunus avium*, *Ulmus campestris*, *Corylus Avellana*, *Picea nigra*, &c.). As soon as the position resulting from these forces is attained, it becomes permanent, from the mature parts becoming lignified, rigid, and hard, and thus in a condition to maintain the weight of the pendent parts.

If leaves which are unfolding or still growing have their under side turned upwards or towards the light, very strong curvatures take place, generally combined with torsions, by which the lamina finally resumes more or less completely its normal position; and the impression is given as if the under side were more

sensitive to the influence of light, and the upper side to that of gravitation than the reverse. But this hypothesis is superfluous if it is borne in mind that in this case epinasty works concurrently with heliotropism and geotropism, and hence much stronger curvatures must take place than in the normal position where the former acts in opposition to the two latter forces.

The results here described are derived from the experiments of de Vries, which have been already quoted. For the following I am also indebted to him.

(a) *Leaves.* If a strongly developed mid-rib is separated from a leaf in active growth, it curls up concavely on the under side, showing that a tension exists between it and the mesophyll. De Vries found this to be the case in nearly two hundred species, with only a few exceptions. This curvature does not take place equally strongly at all ages; in leaves which have but just emerged from the bud it does not occur at all; it increases with age, and attains its maximum when the leaf is nearly fully grown, then again decreases, and altogether disappears when the leaf has reached full maturity. This tendency to curve is at first apparent along the whole length of the mid-rib; it disappears first of all at the base, the part capable of curvature becoming constantly smaller and smaller towards the apex. If mid-ribs of leaves are separated in this last stage of growth and fixed upright in a damp and dark place (*e.g.* in wet sand in a spacious closed zinc box), they will continue to grow for some time; and since growth is more vigorous on the inner (anterior or upper) side, they will curve concavely on the posterior (or under) side, the curvature being however partially counteracted by geotropism. If separated mid-ribs of leaves are suspended horizontally in wet sand, so that the median plane lies horizontal, the epinastic curvature will take place without hindrance in a horizontal direction; but a geotropic curvature will at the same time ensue in a vertical plane, so that the two kinds combine to produce an obliquely ascending position. If, on the other hand, two similar mid-ribs are separated and placed horizontally in wet sand, with the posterior side in one case above, in the other case below, geotropism will act in the former in opposition to epinasty, while in the latter the two will cooperate; and the consequence will be that in the former case the epinastic curvature will be more or less neutralised, while in the latter a strong curvature will take place upwards, the two forces acting in unison.

Phenomena of the same kind are produced by a combination of epinasty with heliotropism, if the separated mid-rib is placed vertically in wet sand in a closed vessel into which light is admitted from one side through a glass plate. Heliotropism is generally but not always exhibited, and is then always positive; but in all the cases hitherto observed is too weak to overcome epinasty. It will be seen from what we have said that all these movements of the mid-rib will be much less considerable when it is still in connexion with the mesophyll. Petioles show in general the same phenomena as mid-ribs, but their motions which result from heliotropism, geotropism, and epinasty are unimpeded.

(b) *Bilateral secondary shoots*, such as branches of an inflorescence, horizontal or erect leaves, and stolons, would exhibit precisely similar phenomena. It may be proved also that the branches of the inflorescence of *Isatis tinctoria*, *Archangelica officinalis*, *Crambe cordifolia*, and all others that have been observed, the horizontal branches of *Pyrus Malus*, *Asperugo procumbens*, &c., as well as the runners of Fragaria, *Potentilla reptans*, *Ajuga reptans*, &c., are epinastic. When placed horizontally in wet sand, they all curl upwards, whether the side that normally faces downwards (the posterior side) was placed below or above, but in the latter case more strongly, because geotropism and epinasty then cooperate. In some species (as Tilia and Philadelphus) a branch, when stripped of leaves and placed in its normal position, did not curl upwards, while one placed in a reverse position did so, proving that there was in these cases an equilibrium between geotropism and epinasty. The horizontal branches of *Prunus avium*, *Ulmus campestris*,

Corylus Avellana, and some other plants were found on the other hand to be hyponastic; when laid horizontally in their natural position they curved upwards, but downwards if reversed, because their hyponasty was stronger than their geotropism.

Similar experiments to those made on petioles with respect to heliotropism, showed in many cases the absence of this phenomenon, especially in the case of stolons; and that in other cases it was always positive, but too feeble to overcome the influence of their epinasty. In the case of branches, especially such as are long and slender, more account must be taken of weight in modifying the direction of growth than in that of leaves. The removal of the leaves (*e. g.* in Corylus) is in this case followed by a sudden curving upward, the result of elasticity; but this is subsequently intensified by geotropism and in many cases (as in Abies) also by hyponasty.

It may be left to the ingenuity of the student to determine the directions of organs by his own observation in any particular case, from the points of view stated above.

SECT. 23.—**Torsion**[1]. Organs of any considerable length very commonly display torsions about their axis of growth; the striations on the surface of the organ are not parallel to its axis of growth, but run round it in the form of more or less oblique spiral lines, as if the organ were fastened at one end, and then twisted at the other. Torsions of this kind occur in the unicellular internodes of Nitella; they are common in the elongated multicellular internodes of the erect stems of Dicotyledons, universal in climbing internodes; the pedicels of the thecæ of Mosses are generally very strongly twisted. Even in flat leaves, as Wichura has shown, torsions of the lamina occur very commonly; they behave like strips of paper fastened at one end and twisted by the other round their median line. These torsions are particularly conspicuous in the leaves of many Grasses, of *Allium ursinum*, species of Alstrœmeria, &c., causing the under side of the lamina to lie uppermost towards the apex[2].

Since the striæ on a twisted organ run spirally round the axis, they must exceed the axis in length; if therefore the torsion is the result of growth, the growth of the outer layers of cylindrical, conical, or prismatic organs (internodes, roots, &c.) must be more rapid or must last longer than that of the inner layers; and in twisted leaves there must be the same difference as respects the growth of the mid-rib in comparison to that of the margins. The fact that at the time of most rapid growth the inner layers generally grow more rapidly than the outer ones (Sect. 13), thus preventing the possibility of torsion, the additional fact that torsion does not generally take place until growth is ceasing, and lastly, the circumstance that etiolated internodes, which in a normal state do not exhibit torsion, usually manifest this phenomenon at the close of their growth, lead to the conclusion that torsion is the result of growth continuing in the outer layers after it has ceased or begun to cease in the inner layers. In twisted leaves, especially those of Alstrœmeria, the torsion however begins earlier. If the growth of the outer layers, besides being greater,

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[1] H. de Vries in the second Heft of the Proceedings of the Würzburg Botanic Institute 1871, p. 272.—Wichura in Flora 1852, No. 3, and Jahrbuch für wissensch. Bot. vol. II, 1860.—Braun in Bot. Zeitg. 1870, p. 158.

[2] [Similar torsions occur in petals as Cyclamen, fruits as *Ailanthus malabarica*, and not unfrequently in pedicels or inferior ovaries as Orchideæ, causing the anterior part of the flower to become apparently posterior, and *vice versâ*.—ED.]

were also exactly parallel to the axis, and if the resistance to the strain thus caused of the outer against the inner layers were exactly in the direction of the axis, there would be no torsion, but only a longitudinal tension between them, which would be directly opposed to the tension of the layers already described. It is however evident that this would be possible only if all the parts were arranged with mathematical precision; but that any irregularity, however small, must give a lateral direction to the strain in the outer layers, and thus cause a torsion[1].

Torsions are also very often the result of an increase in diameter or are made more evident as the formation of wood advances, as is often seen in the bark of old stems of Dicotyledons and Conifers, and more clearly in the oblique course of the fibro-vascular bundles. It may be concluded with probability that the phenomenon is the result of the small but powerful increase in length of the young wood-cells; if these did not increase at all in length no torsion would take place.

The examples of torsion we have been considering so far are produced solely by internal causes; the direction in which the striæ run round the axis is usually constant in the same species; but other instances of torsion frequently occur which result from external and accidental circumstances. It is evident that when any weight is attached to the side of an organ growing in a horizontal or oblique direction, such as an internode, leaf, or tendril, the tendency will be to produce a twisting of the organ round its axis. If the organ which is twisted in this manner is very elastic, the torsion will disappear when the weight is removed; but if it is only very imperfectly elastic, the torsion will remain permanently, as in a twisted thread of wax; and this will be the case if the organ is in a growing state. This does in fact occur in growing internodes, petioles, the mid-ribs of leaves, &c. If an organ of this kind is laid horizontally in wet sand, after a pin slightly weighted on one side, as by a drop of sealing-wax, has been passed horizontally through its summit, the small twisting force is sufficient, as de Vries has shown, to cause a permanent torsion in the growing part. The same result will of course ensue if a leaf or branch instead of a pin is attached to the side of the organ. Branches which grow horizontally and bear decussate pairs of leaves usually exhibit alternate torsions of their internodes to the right and left, so that the leaves all stand in two rows along the branch instead of four. De Vries has shown that this is occasioned by the unequal twisting force of the leaves of each pair. If the young leaves are cut away no torsion results; if only one of each pair is removed, the torsion is determined by the weight of the remaining leaf.

Torsions of this kind also occur frequently when leafy shoots rise in consequence of geotropism from a horizontal position, and are caused by the unequal distribution of the weight of the leaves, and by their various geotropic and heliotropic curvatures twisting the stem as it becomes erect. Very clear instances are furnished by long petioles as those of Cucurbita, when the branch from which they spring is fixed in

[1] This can easily be made clear to the student in the following way. If an india-rubber tube is strongly stretched, and another tube only a little wider is drawn over it, and the first is then released, it contracts and is then too short for the outer tube. If the two tubes were perfectly uniform in structure in the longitudinal and transverse directions, the only result would be a longitudinal tension; but torsion takes place also because a transverse is combined with the longitudinal tension.

a reverse position. The effect of geotropism alone or combined with heliotropism would be simply to cause the petiole to curl upwards in a vertical plane; but the weight of the lamina is scarcely ever equally distributed on the two sides of the plane of curvature; one side is more heavily weighted, and causes the plane of curvature of the petiole to bend obliquely to that side, and other parts of the petiole to be thus exposed to the influence of gravitation and heliotropism. Complicated curvatures and torsions of the petiole and of the lamina itself are caused in this way, the final result being again to reverse the lamina, so as to bring its proper upper side uppermost and expose it to the light as much as possible.

It will be seen therefore that a distinction must be drawn between two kinds of torsion; firstly, that of erect organs; and secondly, that of organs which grow in a horizontal or oblique position. In the former case the torsion results from internal conditions of growth, and especially from the outer layers growing more rapidly than the inner ones; the arrangement of the internal parts—in the internodes of higher plants probably the course of the fibro-vascular bundles—determines the direction of the torsion.

Torsions of the second kind are caused in quite a different way. The outer layers of the growing organ are in a state of passive tension, and there is no internal tendency to torsion; but the weight of the parts attached to it causes a torsion of the growing organ, which is rendered permanent by growth and by the very imperfect elasticity of the organ.

Sect. 24. **The Twining of Climbing Plants**[1]. The stems of climbing plants, composed of long internodes, have the power of twining spirally round upright slender supports; and the long petioles of the Fern Lygodium possess the same property. This twining is a consequence of unequal growth, of a revolving nutation. It is not caused, as Mohl held, by an irritation exercised by the support on the growing internodes, and is therefore essentially distinct from the twining of tendrils round supports, which depends on the irritation caused by constant and permanent pressure[2].

Only a few plants twine to the right (*i. e.* from right to left as one looks at the support round which the plant twines), following the course of the sun or of the hands of a watch; among these are the hop, *Tamus elephantipes*, *Polygonum scandens*, and the honeysuckle; the greater number twine to the left, as *Aristolochia Sipho*, *Thunbergia fragrans*, *Jasminium gracile*, *Convolvolus sepium*, *Ipomæa purpurea*, *Asclepias carnosa*, *Menispermum canadense*, Phaseolus, &c.

The first internodes of twining stems, whether they are primary stems as in Phaseolus, lateral shoots from rhizomes as in Convolvulus, or from aërial organs as

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[1] L. Palm, Ueber das Winden der Pflanzen: Preisschrift, Stuttgart 1827.—Mohl, Ueber den Bau und das Winden der Ranken und Schlingpflanzen, Tübingen 1827.—Dutrochet, Comptes rendus 1844, vol. XIX, and Ann. des. Sci. Nat. 3rd ser. vol. II.—Darwin, On the Movements and Habits of Climbing Plants, Journal of the Linnean Soc. (Bot. vol. IX, London 1865).

[2] Darwin has already attempted to show that Mohl's view of the irritability of climbing internodes is untenable, without however bringing forward any convincing proof. But this proof has been afforded by H. de Vries in a series of investigations carried on in the Würzburg laboratory, which will be published in the third part of the Proceedings of the Würzburg Bot. Inst. The description here given of the mechanical principles is based principally on his results.

in Aristolochia, do not twine but grow erect without any support. The succeeding internodes of the same shoot twine; they first of all elongate considerably, while their leaves grow only slowly. The long young internodes incline to one side in consequence of their weight, and in this position the revolving movement of nutation begins; the overhanging part curves and executes a movement which causes the terminal bud to describe a circle or ellipse. This circular motion is caused entirely by the curving of nutation. If a black line is painted along the convex side of an internode of a plant that twines to the right, like the hop while the bud is pointing to the south, then, when the bud points to the north it will be found on the concave side; when to the west or east on the lateral surface between the convex and concave sides. Usually two or three of the younger internodes are in a state of revolving nutation at the same time; and, since they are in different stages of growth, the curvature of the older internode does not generally coincide with that of the younger one; the whole does not therefore form a simple arc, but often an elongated letter S, with the different parts lying in different planes. As new internodes develope from the bud, they begin to revolve, while the third or fourth internode ceases to do so, becomes erect, and manifests another form of movement, becoming twisted, until its growth ceases[1].

The direction of revolving nutation and of torsion is, in all climbing plants, the same as that in which they twine round their support[2]. If a point in the terminal region exhibiting nutation is prevented from moving by some external cause, as by being fixed, the revolving movement of the free part will continue for some time, but the free part will then grow in a spiral ascending in the direction of nutation. The revolving movement of nutation then combines with a new torsion of the lower parts which are already coiled spirally; but this torsion is opposed in its direction to the revolving nutation, and therefore also to the torsion previously mentioned. It is probably occasioned by the weight of the free overhanging apex of the shoot; at all events this causes the concave side of the part in a state of revolving nutation to face from that time the axis of the spiral which has been formed.

The most common case in which a revolving movement of nutation is averted in this way is when the apex of a shoot comes, in consequence of this motion, into contact with an erect support. If the support is not too thick, it forms the axis of the spiral curvatures which the climbing stem makes round it; when the support is very slender, the stem winds in such large coils that they do not touch the support at all, or only accidentally at a few places.

But the revolving nutation can also be artificially interfered with in various other ways; as, for example, by placing a support on the posterior side of the shoot as respects its revolution, and fastening it by means of gum to the apex, which would otherwise become detached from it. The first spiral coil is in this case formed in precisely the same manner as if the support were in its normal position, but the support stands outside the coil which does not embrace any support. Spiral coils

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[1] Torsion is therefore not the cause of the revolution of the apex of the shoot, as is seen at once from the fact that the number of revolutions of torsion in the same time is different from that of the revolutions of nutation.

[2] What follows is from de Vries.

of this kind, not embracing any support, are frequently produced when the stem rises above its support.

The youngest coils of a twining stem are not usually in contact with its support; they are wide and flat; while the older coils are in close contact with it, and are narrower and more oblique. This shows that the close clinging of climbing stems to their support is a subsequent result, the coils being at first looser and wider, and becoming afterwards closer and more oblique. This fact, which is of great importance in the interpretation of the phenomena of climbing plants, was placed beyond doubt by de Vries, who caused the summits of climbing plants to coil in this manner without having any support in the middle. In this case also the coils were at first wider and flatter, and became closer and more oblique with increasing age, until at length the piece became quite erect, a revolution of torsion being all that represented each spiral revolution. It is not improbable that geotropism is the cause of the coils—at first flatter and sometimes almost horizontal—becoming afterwards more oblique. It is clear that the stronger the force with which the coils become closer and more oblique, the more closely must they cling to their support. If there is a support in the axis of the coils, the younger parts of the summit will be constantly prevented by it from performing their normal revolution of nutation, and the apex will therefore continue to grow in a spiral, and will climb continually further up the support, the older coils always becoming more oblique and clinging to the support. If the support is removed soon after a few loose coils have been formed round it, the shoot will retain its spiral form for a time, but will then straighten itself and recommence the revolution at its apex.

A revolution of torsion of the twining internodes must, on purely mechanical grounds, accompany every revolution of twining; but torsions of the parts which had already coiled also occur, especially with round rough irregular supports; their direction is sometimes to the right, sometimes to the left.

During the course of the twining the leaves must sometimes stand on the outside, sometimes on the inside of the coils[1]; in the latter case the leaf-stalk will be pressed against the support on which it slips laterally under the pressure of the contracting coil, dragging the internode sideways with it, and thus causing a local torsion.

What has now been said contains almost all that we at present know on the mechanical laws of the twining of climbing stems. A few remarks, borrowed from Darwin, may be added.

The revolution of the free overhanging apex is often strikingly uniform in the same plant under the same external conditions (as *e.g.* in the hop, Micania, Phaseolus, &c.).

The following table of Darwin's gives some idea of the time required, under favourable conditions, for a revolution:—

Scyphanthus elegans	1 hour	17 min.
Akebia quinata	1	30
Convolvulus sepium	1	42
Phaseolus vulgaris	1	55
Adhatoda	48	

[1] I may take this opportunity of remarking that, according to Dutrochet, the genetic spiral of the phyllotaxis takes the same direction in climbing plants which have their leaves arranged spirally

The direction of the twining is usually constant in the same species; but it does sometimes happen, as in *Solanum Dulcamara* and *Loasa aurantiaca*, that different individuals twine in opposite directions. Darwin found, in these two species and in *Scyphanthus elegans* and *Hibbertia dentata*, that the same stem will sometimes twine first in one and then in the other direction.

The positive heliotropism of twining internodes is generally feeble; a powerful heliotropism would obviously be only a hindrance to the twining and especially to the revolution, by which an effort, so to speak, is made to reach the support. Heliotropism is however shown by the fact that when the light falls from one side only, revolution takes place more quickly towards the source of light than away from it; as *e. g.* in *Ipomœa jucunda*, *Lonicera brachypoda*, Phaseolus, and Humulus.

It may be concluded from what has been said on the mechanism of twining that there is for every species a certain maximum of thickness of the support at which the twining is possible. The support must not be much thicker than the diameter of the coils which the shoot can make without a support; if the support is too thick, the apex of the shoot attempts to make coils by its side, and these eventually become effaced. Darwin (*l. c.* p. 22) acknowledges his ignorance of the cause why the climbing plant cannot twine round supports which are too thick; de Vries's experiments however seem to give a sufficient explanation.

The movements of twining internodes are more energetic the more favourable the external conditions of growth, and the more rapid the growth itself; they are therefore vigorous when food is abundant, temperature high, and the plants contain abundance of sap. The direct action of light is not necessary for twining, since even etiolated plants (as *Ipomœa purpurea* and *Phaseolus multiflorus* cling closely to their support in the dark. The assertion of Duchartre that *Dioscorea Batatas*) does not twine in the dark reduces itself, according to de Vries's more recent observations, to the fact that while normal green shoots climb more loosely in the dark, they cease rotating and twining when they become etiolated.

Sect. 25. **The Twining of Tendrils**[1]. Under the term Tendril may be comprised all filiform or at least slender long and narrow parts of plants which possess the property of curving round slender solid supports with which they come in contact during their growth, clinging to them in consequence, and thus at length fixing the plant to them. Tendrils are therefore at once distinguished from climbing internodes by their irritability to contact or pressure.

Organs of the most various morphological description may assume this physiological property. Sometimes tendrils are metamorphosed branches, as in Vitis Ampelopsis, Passiflora, and *Cardiospermum Halicacabum*, where they may be considered more accurately as metamorphosed flower-stalks or inflorescences. In Cuscuta the whole stem may be regarded as a tendril rather than as a climbing stem. In other cases, as in Clematis, Tropæolum (Fig. 455) Maurandia, Lophospermum, *Solanum jasminoides*, &c., the petioles may serve as tendrils. In *Fumaria officinalis* and *Corydalis claviculata* the whole of the finely-divided leaf is sensitive to contact, and its separate parts have the power of twining round slender bodies. In *Gloriosa Plantii* and *Flagellaria indica* the mid-rib protruding beyond the leaf serves as a tendril. In many Leguminosæ and Bignoniaceæ and in *Cobæa*

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as the twining; and therefore also the same as the spontaneous torsion and the revolving nutation of the same plants.

[1] See the literature quoted in the preceding section.

scandens the anterior (upper) part of the pinnate leaf is transformed into slender filiform tendrils inclined forwards, while the basal part of the leaf is rigid and divided into leaflets; sometimes, as in *Lathyrus Aphaca*, the whole of the leaf is replaced by a filiform tendril. The morphological character of the tendrils of Cucurbitaceæ is still doubtful, though they must probably be regarded as metamorphosed branches.

The distinguishing properties of tendrils are more perfectly developed the more exclusively they serve as organs of attachment for the sole purpose of climbing, the less therefore they partake of the normal character of leaves or parts of the stem; in other words, the more perfectly the metamorphosis is carried out. To this category belong especially the simple or branched filiform tendrils of the Cucurbitaceæ, Ampelideæ, and Passifloreæ. A typically developed tendril of this kind is represented in the mature state in Fig. 456, after it has seized hold of a support by its apex and then coiled up. What is said here refers especially to true tendrils of this description.

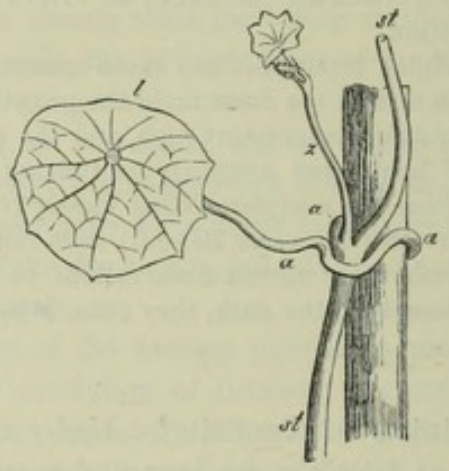

FIG. 455.—Mode of climbing of *Tropæolum minus*. The long petiole *a* of the leaf *l* is sensitive to long-continued contact, and has clung round a support and round the stem of the plant itself *st* so as to fix this stem firmly to the support; *z* the shoot from the axil of the leaf.

The characteristic properties of tendrils are developed when they have completely emerged from the bud-condition, and have attained about three-fourths of their ultimate size. In this state they are stretched straight; the apex of the shoot which bears them usually revolves, the tendril itself exhibiting the same phenomenon, curving along its whole length (with the exception usually of the oblique basal portion and the hooked apex) in such a manner that the upper side, the right side, the under side, and the left side become in turn convex. No torsion takes place. During this revolution the tendril is rapidly growing in length and is sensitive to contact; *i. e.* any contact of greater or less intensity on the sensitive side causes a concave curvature first of all at the point of contact, from which the curvature extends upwards and downwards. If the contact was only temporary, the tendril again straightens itself. The degree of sensitiveness[1] is very different in different species; in *Passiflora gracilis* a pressure of 1 milligram is sufficient to cause curvature in a very short time (25 sec.); in other species a pressure of 3 or 4 milligrams

[1] This and what follows is from Darwin, Movements and Habits of Climbing Plants, p. 100 *et seq.*

is required and the curvature does not take place so soon (30 sec. in Sicyos); the tendrils of other species curve, when slightly rubbed, in a few minutes; in the case of *Dicentra thalictrifolia* in half an hour; in Smilax only after more than an hour; in Ampelopsis still more slowly.

The curvature on the side in contact with the support increases for some time, then remains stationary, and finally (often after some hours) the tendril again straightens itself, in which state it is once more sensitive. A tendril the apex of which curves easily is sensitive only on the concave under surface; others, as those of Cobæa and *Cissus discolor*, are sensitive on all sides; in *Mutisia Clematis* the under and lateral surfaces are sensitive, but not the upper surface.

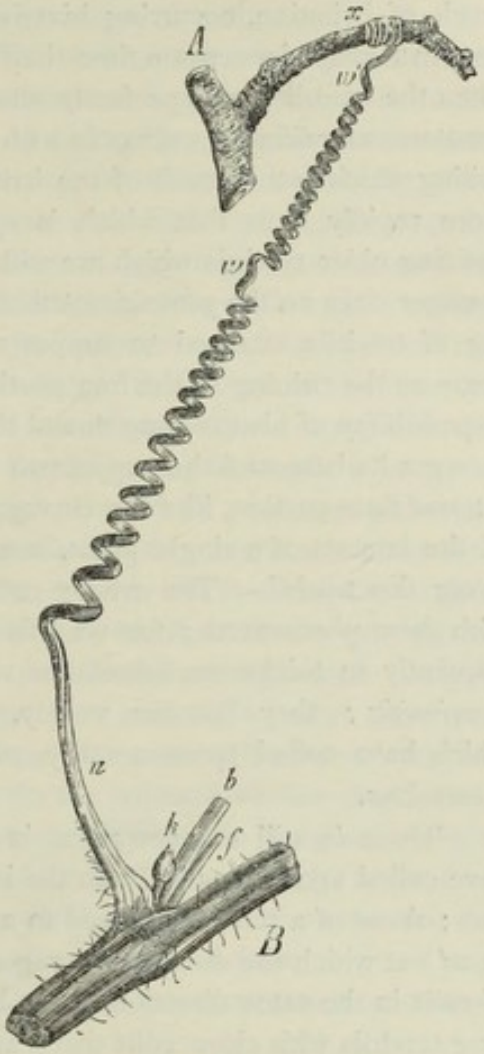

FIG. 456.—Coiling of a tendril of *Bryonia dioica*. *B* a portion of the branch from which the tendril springs by the side of the petiole *b* and the axillary bud *h*; the lower part of the tendril *u* is straight; the upper part *x* has coiled round a twig *A*; the long intermediate part between the rigid basal portion *u* and the point of attachment *x* has coiled spirally, and thus raised the branch *B*; *w w'* the two spots where the direction of the coil is reversed.

While the revolving nutation and sensitiveness last the tendril attains its full size in a few days; the revolving motion then ceases, and with it the sensitiveness; and further changes then follow, differing in different species. In some the tendrils remain straight after they have completely developed and become motionless; in others they become abortive and fall off, as *e. g.* in Bignonia, Vitis, and Ampelopsis. It is more common for the tendrils to roll up from the apex slowly to the base, when growth has ceased with the concave side undermost, so that they at length form a spiral (as in Cardiospermum and Mutisia) or more often a helix narrowing conically upwards (as in Cucurbitaceæ, Passifloreæ, &c.) in which state they then dry up and become woody.

These processes must however be considered as abnormal, the tendrils having failed of performing their purpose of coming into contact, by means of their revolution, with a support during the period that they are sensitive and still in a growing state. If this contact takes place on the sensitive side, a curvature arises at the spot, and the tendril clings to the support; fresh sensitive spots are thus constantly brought into contact with it, and the free apex twines firmly round the support in a larger or smaller number of coils (Fig. 456). The nearer the spot where contact first takes place to the base of the tendril the larger are the number of revolutions round the support, and the stronger the attachment; though even a small number of revolutions is sufficient to attach it with considerable force. The portion of the tendril between its base and the point of attachment is obviously unable to twine

round the support like the free apex; and therefore the irritation caused by the contact extending to the portion that is not in contact produces a different form of curvature consisting in a rolling up of this portion into the form of a corkscrew, as shown in Fig. 456 *u*, *w*, *w'*. This coiling is similar to that already mentioned as taking place of its own accord in many tendrils which do not take hold of a support, especially in the circumstance that the under or dorsal side of the tendril is always the concave one; but it differs from a spontaneous coiling in being always the result of irritation, occurring invariably when tendrils take hold of a support, and also in taking place some time (half a day to a day) after the attachment, at a time when the tendril is still perfectly sensitive and growing rapidly in length; while the spontaneous coiling occurs only with the cessation of growth and of irritability. The coiling which is the result of the irritation caused by contact also takes place much more rapidly than that which is spontaneous; both can be readily observed by noticing older tendrils which are still straight and have not attached themselves, and younger ones on the same shoot that are attached and already coiled up. The coiling of tendrils attached to supports is therefore a result of irritability in the same sense as the twining of the free portion round a support; and it is only the physical impossibility of also twining round the support that forces the portion of the tendril between its base and the support to coil up like a corkscrew. The coiling of this intermediate portion, like the curvature of a longer piece of a tendril in consequence of the contact of a single point, is a proof that the local irritation is communicated along the tendril. The whole consequence of irritation does not however end with these phenomena; for tendrils that are fixed to a support also increase subsequently in thickness, sometimes very considerably, like the petioles of *Solanum jasminoides;* they become woody, and have a longer term of life than those which have coiled spontaneously, or generally than those that have not attached themselves.

There is still another point in which attached tendrils differ from those that have coiled spontaneously. In the latter all the coils of the spiral run in one direction; those of a tendril attached to a support have, on the contrary, points (Fig. 456, *w*, *w'*) at which the direction changes; between any two of these points is a number of coils in the same direction, those beyond them being in the opposite direction; in long tendrils with close coils there are often as many as five or six of these points. Darwin has already shown that this is no special property of tendrils, and still less a specific result of irritation, but is rather a physical necessity; for if a body which coils up is fixed at both ends so that one end is totally unable to twist, the coils must necessarily be produced in opposite directions in order that the torsions which are unavoidably produced may counterbalance one another. This behaviour of fixed tendrils can be imitated by cementing a narrow stretched strip of india-rubber firmly along another strip which is not stretched, and then releasing the former; it contracts and forms the inside of a spiral, the outer side of which is formed by the strip that is not stretched. If the double strip is held at each end and first stretched out straight and then relaxed, coils will be produced, some to the right, others to the left, as in a tendril. If one end is now let go, the strip will twist itself anew into a spiral.

Since all the movements of tendrils that have been described are the result of

growth, they take place only when the external conditions of growth are favourable, and the more energetically the more favourable they are; this is the case when food is abundant, temperature high, and the plant contains abundance of sap, the result of a copious supply of water combined with small loss by transpiration. Under these conditions tendrils can, as I have shown, carry on their nutation and sensitive movements even in the dark, and can twine and coil round supports. An instance is afforded by plants of *Cucurbita Pepo*, the upper parts of which are grown in a dark vessel, and which are nourished by green leaves exposed to light.

As regards the mechanical conditions of the curvatures caused by contact, as well as the coiling of free tendrils, it cannot be doubted that we have here to do with processes of growth and of its alteration by transverse pressure on the side which is growing less rapidly. The tendrils are only sensitive to contact or pressure so long as they are in a growing state. A curvature due to irritation may be effaced during growth, as for instance the curvature of growing shoots caused by concussion; but if the irritation from the support lasts for a longer time and a coiling takes place, the difference in length between the convex and concave surfaces remains permanent. The cells of the convex are longer than those of the concave surface (as in roots turned downwards or nodes of Grasses turned upwards); in thick tendrils which coil round slender supports the difference in length is so great that it strikes the eye at once without measuring. De Vries's recent experiments on tendrils that have not yet coiled, which he marked with transverse streaks and measured after they had coiled, show that the growth of the convex surface is more considerable, that of the concave surface less so than in the portions of the same tendril above and below the curved part that have remained straight. A tendril of *Cucurbita Pepo* twined round a support 1·2 mm. thick; after the curvature was complete, the increment of the curved part for each millimetre of original length was 1·4 mm. on the convex surface, while on the concave surface it was only 0·1 mm.; the mean increment on both surfaces in the portion that remained straight amounted to 0·2 mm. If the growth which takes place in the entire tendril at the time of contact with a support is small, a considerable acceleration occurs on the convex surface, but in general there is no elongation on the concave surface, or there may even be a contraction; in the case of a tendril of Cucurbita this contraction amounted to nearly one-third of the original length.

Similar alterations in the length of the convex and concave surfaces are observable in the spontaneous coiling of free, as well as in the coiled portion of attached tendrils between the base and the point of attachment; and since in these cases the amount of growth which takes place in the entire tendril is usually small a short time previously, the contraction of the concave surface is, according to de Vries, a very common phenomenon.

The conclusion to be derived from these phenomena and from others not described here is that the growth of the surface not in contact is first of all increased by the pressure of the support; the support presses the surface that is in contact, and the pressure which the concave surface undergoes arrests its growth, or even causes a contraction in it. It seems probable that a relaxation of the parenchyma of the surface in contact (by giving off water to the parenchyma of the upper surface) and a consequent elastic contraction of its cell-walls, contribute to this result;

at least this seems the only explanation of the contraction of the surface in contact in the case of tendrils the growth of which has already become slow. We have however as yet no knowledge of the mode in which the slight pressure of a light thread or that of the revolving tendril on a support causes this alteration of growth not only at the point of contact, but along the entire tendril.

The only cause of the spontaneous coiling of tendrils when not fixed to a support is that the upper surface continues to lengthen for a considerable time after the growth of the under surface has ceased. The cells of the growing upper surface probably withdraw from those of the under surface a portion of their water (as the inner layers of the pith from the outer layers, see p. 725), which causes the latter to become shorter, and the former to become longer.

Without entering further into the numerous questions of a purely mechanical character connected with the curving of tendrils, it may at least be explained why thick tendrils are unable to twine round very slender supports. If two tendrils are compared one of which twines round a slender, the other round a thicker support, it will be seen that in the former the proportional difference in length of the outer and inner sides must be greater than in the latter. If a thick and a slender tendril twining round supports of equal thickness are compared, the proportionate difference in length of the outer and inner surfaces will be greater in the former than the latter case; and if the support is supposed to decrease constantly in thickness, the difference will increase more rapidly in the case of the thick than in that of the slender tendril, and the question arises whether the difference in growth of the two surfaces of the tendril can reach to any given amount or not. The difference in length between the two surfaces caused by unequal growth has, in fact, a limit, as is shown by experiment. The slender tendrils of *Passiflora gracilis* twine firmly round threads of silk; the thick tendrils of the vine on the other hand twine only round supports which are at least from 2 to 3 mm. thick. The most strongly curved tendril of a vine which I could find had twined firmly round a support 3·5 mm. thick, and in a nearly circular coil; the mean thickness of the tendril at this spot was 3 mm. The concave surface of a coil was nearly 11 mm., the convex outer surface nearly 29 mm. long, the proportionate length of the two surfaces therefore nearly as 1 : 2·6. If this tendril 3 mm. thick were forced to twine round a support only 0·5 mm. in thickness, an almost circular coil would have on the concave surface a length of 1·6 mm., on the convex surface a length of 20·4 mm.; the relative length of the two surfaces would therefore be as 1 : 13; and it does not seem possible for growth to cause so great a difference in length between the two surfaces of a tendril. If, on the other hand, the problem were to cause a tendril 0·5 mm. thick to twine firmly round a support of the same thickness in nearly circular coils, it would only be necessary that the inside of a coil should be 1·6 mm., the outside 4·7 mm. long, or that the proportion between the two surfaces should be as 1 : 3.

In order for a tendril to attach itself firmly to a support, it is not sufficient that its coils should merely be in contact with it; they must be firmly adpressed to it. That this is actually the case is seen when a tendril is made to twine round a smooth support, and the support is then withdrawn; when, as de Vries has shown, the coils become at once closer and increase in number. This fact shows also that a tendril which is irritated by contact with a support endeavours to form coils the radius of

whose curvature is less than that of the support, provided the support is not too slender nor the tendril too thick.

The cases are very instructive, in reference to the pressure which the coils of tendrils exercise on their supports, where leaves are embraced by strong tendrils, and folded and compressed by them.

What has now been said is merely intended to draw attention to the more important mechanical principles which must be taken into account in the twining of tendrils. The biology of climbing plants and of those furnished with tendrils, so fertile in extraordinary adaptations, cannot be gone into in detail. On this subject the reader will find in Darwin's treatise quoted above a mass of beautiful observations most admirably described.

Since the physiological function of tendrils is to take hold of supports (generally other plants) in order to allow the slender-stemmed plant which is furnished with them to climb up, the point of greatest importance is for the tendril to be brought into contact with a support. This is usually effected with extraordinary perfection by the revolving nutation not only of the tendril itself but also of the apex of the shoot that bears it at the time when it is sensitive, thus causing every object anywhere within reach of the tendril which could be used as a support to be brought almost inevitably into contact with it. The apex of the shoot which bears the tendril usually describes an ascending elliptic helix, the revolution being completed in from one to five hours. As in the case of twining stems, a strong positive heliotropism would be injurious, as it would often carry the tendril away from the supports. Some tendrils appear in fact to be not heliotropic (those of Pisum according to Darwin), in others a weak positive heliotropism is shown by the fact that the revolving nutation takes place more quickly towards the light than away from it. Some tendrils, strikingly those of the Virginian creeper and *Bignonia capreolata*, have the remarkable power of developing broad discs at the end of their branches when they remain in contact for some time with hard bodies, which attach themselves like cupping glasses to rough surfaces, and enable the plant to climb up vertical walls when it finds no slender support round which it can coil. In this case it is obviously necessary that the tendril should turn towards the wall which serves as its support in order to become attached to it, and this is effected by negative heliotropism, which causes the tendril to approach the wall shaded by foliage, where it now performs its revolving movements of nutation—one might almost say its groping movements—creeps along the surface, finds out the crevices and depressions, and developes its adhesive discs.

CHAPTER V.

PERIODIC MOVEMENTS OF THE MATURE PARTS OF PLANTS AND MOVEMENTS DEPENDENT ON IRRITATION.

Sect. 26. **Definition.** The logical arrangement of our subject requires us to devote a separate chapter to the little that we yet know on the mechanism of the periodic movements of leaves and foliar structures and those due to irritation, in order to call the attention of the reader to the fact that although these movements present many external resemblances to those described in the last chapter, they are nevertheless the result of altogether different causes, and have nothing to do with the phenomena of growth, a distinction to which sufficient attention has not at present been paid.

The movements now under consideration are distinguished most conspicuously from those described in the last chapter by the fact that they do not arise during growth and are not caused by it, but on the contrary are only manifested when the organs in question are perfectly mature[1], and when the peculiarity of their internal structure, which renders the phenomenon possible, is fully developed; while the movements we have hitherto been considering cease with the completion of the growth of the organ. The greater number of the movements which are brought into play during growth—as the curvatures caused by heliotropism or geotropism or by the pressure of supports on tendrils and climbing plants — produce new permanent conditions, since growth is modified. It is only when the action has been a very transitory one that heliotropic or geotropic curvature or that of tendrils due to irritability, can again be effaced by further growth. During these processes the organ is advancing towards maturity; the changes which have not been effaced are therefore, as it were, stereotyped.

The case is quite different with the changes now to be described. They take place in organs whose growth is completed, but whose structure allows the tissues

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[1] Some exception may be taken to this statement from the fact that the periodically motile and irritable parts of plants are also sometimes heliotropic and geotropic, as is the case with the leaves of Phaseolus and the filaments of Cynaraceæ. But this only proves that mature parts, when in abnormal conditions, commence growing afresh. These conditions here consist in the light falling unequally on the two sides, or on the upper side of contractile organs turning downwards (as in Phaseolus). In the same manner mature petioles of ivy begin growing afresh in the dark, or when the light is unequal on the two sides, and mature nodes of Grasses when placed in a horizontal position, the former on the shaded, the latter on the under side.

to assume different conditions which alternate under the influence of external or internal causes.

In those movements which occur during growth the tension of the tissue is concerned only so far as any change in it reacts on growth and modifies it. Periodic movements and those due to irritation, on the contrary, depend entirely on changes in the tension of the tissues which, in this case, is fully developed only when the organ has attained maturity. These alterations of the tension of the tissues do not however induce new permanent conditions, but can be effaced; every change is again reversed by internal forces, and the previous condition restored so long as there has been no structural injury.

The movements caused by growth occur in unicellular as well as in multicellular plants and organs; those we have now to consider would appear, on the contrary, to take place only when the organs consist of masses of tissue. The reason of this difference is probably that movements of the first kind are always caused by the growth of the cell-wall, those of the second kind by access or loss of water, *i. e.* by changes in the turgidity of the cells which form the tissue[1].

Sect. 27. **Review of the phenomena connected with periodically motile and irritable parts of plants.** It is remarkable that all organs at present known as coming under this category are, in a morphological sense, foliar structures, as green foliage-leaves, petals, stamens, or occasionally parts of the carpels (styles or stigmas). It is the more striking that no axial structures or parts of stems are contractile in this sense, because the contractile parts of leaves are usually cylindrical, or at least are not expanded flat, and therefore possess the ordinary form of an axis. There is this further agreement in the anatomical structure of all parts which exhibit these phenomena;—that a very succulent mass of parenchyma envelopes an axial fibro-vascular bundle or a few bundles running parallel to one another; the elemental structures of these bundles being only slightly or not at all lignified, and therefore remaining extensible and flexible, a fact of importance in reference to the possibility of the movement. With the exception of the leaves of Dionæa and Drosera, the movement always consists of flexions upwards and downwards, generally in the median plane of the organ, the fibro-vascular bundle thus forming the neutral axis of the curvature. The mass of parenchyma which envelopes the fibro-vascular bundle often has the form of a pulvinus, and does not contain in its outer layers any air-conducting intercellular spaces, or only very small ones, while in the inner layers they are larger, especially in the immediate vicinity of the bundle; these being, according to Morren and Unger, wanting only in the irritable stamens of Berberis and Mahonia. The tension of these layers of tissue which is generally very considerable, is caused by the stronger turgidity of the parenchymatous cells

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[1] The ultimate cause of the movements now under discussion is indeed the same as that of the growth of the tissues, namely, the turgidity of the individual cells. In either case an increase in the turgidity of the cells causes an increase in volume of the tissues; if the organ is still in a growing state, this increase remains permanent; if it is already mature, it causes only a temporary enlargement, which is effaced when the turgidity again diminishes; in other words, the variation in turgidity gives rise to complicated movements of various kinds.

on the one hand and the elasticity of the axial bundle and epidermis on the other hand. As far as observations go at present, especially those made on larger contractile organs, the tendency to extension is greatest in the middle layers of the parenchyma between the epidermis and the axial bundle, but the elastic resistance of the epidermis is less than that of the bundle.

If we now consider the nature of the movements in reference to the causes which directly operate to produce them, we may, in the present state of our knowledge, distinguish between three different kinds, *viz.*—

(1) Those *periodic movements* which are produced entirely by internal causes, without the cooperation of any considerable external impulse of any kind. Such movements may be termed *automatic* or *spontaneous*.

(2) The greater number of spontaneously motile foliage-leaves are also *sensitive to the influence of light*, and many petals to that of *warmth*, in such a way that within certain limits any increase in the intensity of the light or temperature causes such a curvature of the contractile organs as to place the leaves in an expanded and completely unfolded position; while any decrease in the intensity of the light or temperature produces the opposite curvature, causing the leaves to fold up. The expanded position is called that of growth or *the diurnal position*, the opposite one that of sleep or *the nocturnal position*. In consequence of this sensitiveness to fluctuations in the light and temperature, these organs make periodic movements depending on the alternation of day and night, which, being induced by external causes, must be clearly distinguished from the automatic or those brought about by internal causes; and the more so because both kinds usually occur in the same organ, and are combined in various ways[1].

(3) In a smaller number of instances periodically motile foliage-leaves, as well as some reproductive organs which do not exhibit periodical movements, are *irritable to touch or concussion*. If a particular spot of the organ is only lightly touched or subjected to a slight rubbing from a solid body, the side which is touched becomes concave or contracts[2]. The same effect is produced if a stronger impulse acts on any other part of the irritable organ, assisting to excite the property at the irritable part. If the motile part has curved in consequence of the mechanical irritability, it afterwards resumes its previous position, and is then again irritable. Usually, especially in the irritable filaments of the Cynaraceæ, the surface is covered with hairs by means of which any light touch, especially the contact of any solid body, as the foot of an insect, is communicated to the whole organ, and acts therefore as a stronger irritation.

The physiological function of these various forms of movement in the economy of the plant is known only in a few instances, as in the case of irritable stamens, where the insects that visit the flowers cause the irritation and consequent alteration in the position of the stamens, these movements being serviceable for the conveyance

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[1] This distinction, partly founded on facts that have long been known, is very necessary for a clear insight into the phenomena, and was first brought forward by me in the treatise on the various immobile conditions of the periodically motile and irritable parts of plants ('Flora,' 1863).

[2] This contraction has been actually proved in only a few cases, but must be assumed in the others.

of the pollen either to the stigma of the same flower (as in Berberis[1]) or to those of other flowers (as in Cynaraceæ). The movements of petals caused by variations in the light and temperature usually cause the flowers to open in the day, and therefore render them accessible to the visits of insects for the purpose of pollination; while the closing of the flowers in the evening or in damp cold weather in the daytime, —*i. e.* at times when insects would otherwise not visit them—protects the pollen-grains from moisture and decay[2]. We have no knowledge, on the other hand, of any purpose in the economy of the plant served by the periodic and irritable movements of foliage-leaves.

A *spontaneous periodic movement* is seen most conspicuously in the few cases where the period extends only over a few minutes, and the oscillation of the organ takes place by day and night under a sufficiently high temperature, as in the small lateral leaflets of the trifoliolate leaf of *Desmodium gyrans* (the Indian 'telegraph-plant'), and the labellum of the flowers of *Megaclinium falcatum* (an African orchid). The lateral leaflets of *Desmodium gyrans*[3] are attached to the common petiole by slender petiolules 4 to 5 mm. in length, the petiolules being the organs by the movements of which the leaflets are carried round, their apices describing nearly a circle. One revolution takes, when the temperature is above 22° C., from 2 to 5 minutes; the motion is often irregular, sometimes interrupted, and then recommencing suddenly in jerks. The labellum of *Megaclinium falcatum*[4] narrows below into a claw traversed by three slender fibro-vascular bundles, the curving of this portion imparting to the labellum a swinging motion up and down. In a much larger number of other foliage-leaves endowed with periodic motion the spontaneous periodicity is almost entirely concealed by the contractile parts being also very sensitive to light, so that a cursory observation detects only the daily period, or the different positions by day and night. If however these plants, or even cut branches placed in water, remain for some days in the dark or in artificial light of unvarying intensity, it is seen that the periodic movements do not cease, but continue even when the temperature is constant, *i. e.* independently of any irritation resulting from change of temperature. Under these circumstances the leaves are in a constant slow motion, indicated by the varying positions at short intervals (as *e. g.* in Mimosa, *Acacia lophantha*, *Trifolium incarnatum* and *pratense*, Phaseolus, various species of Oxalis, as *O. Acetosella*, &c.[5]). A. P. de Candolle has also shown that the leaves of Mimosa make periodic movements under a uniform artificial light. The behaviour of the lateral leaflets of *Desmodium gyrans* and of the labellum of *Megaclinium falcatum* on the one hand, and that of leaves which assume different positions by day and by night on the other hand, offer a contrast in the following respect; in the former the internal periodic causes of the movement are stronger than the irritation of the light to which they may happen to be exposed, while in the latter these internal causes are outweighed by the irritation caused by the varying amount of light under ordinary conditions. To this last category belong

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[1] [H. Müller (Befruchtung der Blumen durch Insekten; Leipzig, 1873) has shown that the irritability of the stamens of Berberis is a contrivance for cross-fertilisation rather than self-fertilisation.—Ed.]

[2] [On contrivances for the protection of pollen from the influence of the weather, &c., see Kerner, Die Schutzmittel des Pollens gegen die Nachtheile vorzeitiger Dislocation und gegen die Nachtheile vorzeitiger Befeuchtung; Innsbruck, 1873.—Ed.]

[3] For further illustrations see Meyen, Neues System der Pflanzen-Physiologie, 1839, vol. III, p. 553. [The first account of *Desmodium gyrans*, based on Lady Morison's observations, is by Broussonet, Mém. Acad. de Paris, 1784, p. 616.—Ed.]

[4] C. Morren, Ann. des sci. nat. 1843, 2nd series, vol. XIX, p. 91.

[5] For further proof see Sachs, Flora, 1863, p. 468, where the literature of the subject is quoted.

the movements of the compound leaves of Leguminosæ, of many species of Oxalis, and of Marsilea. In the Leguminosæ the common petiole is often attached to the stem by a larger contractile organ or '*pulvinus*'; and in all the cases just named the petiolule of each leaflet possesses a similar organ. If, as in the bipinnate leaves of Mimosa, there are secondary common petioles, these are also attached to the primary petiole by contractile organs. These organs always consist of an axial fibro-vascular bundle surrounded by a thick layer of turgid parenchyma. The other parts of the leaves, the petioles as well as the lamina, are not spontaneously contractile, but the alterations in their length are caused by the curvatures of the organs at their base. The movement is either a curving upwards and downwards, as in Phaseolus, Trifolium, Oxalis, and the common petioles of Mimosa, or is directed from behind and below in a forward and upward direction, as in the leaflets of Mimosa.

(2) The phenomena known as *Waking* and *Sleeping* are exhibited with peculiar distinctness in the leaves of Leguminosæ and Oxalideæ and of Marsilea, and are caused by the organs which also produce the spontaneous periodic movements[1]. They occur also in the leaves of many other plants as Scitamineæ, where the lamina is attached to the petiole by a similar cylindrical contractile organ, as well as in many leaves (especially also in green cotyledons) the petiole and lamina of which do not possess a sharply differentiated prominent contractile organ; in these cases the movements of sleeping and waking are occasioned by the basal and apical portions of the petiole. It is not known whether these leaves are also endowed with automatic periodic motion. In all these green leaves the movement is caused principally by the alternation in the intensity of the light, and especially by that of the strongly refrangible rays[2]; every increase of intensity causing a movement in the direction of the diurnal position, every decrease one in the direction of the nocturnal position.

In the diurnal position of these organs the leaves generally have their surfaces completely unfolded and expanded flat; in the nocturnal position they are on the contrary folded up in different ways, being turned upwards, downwards, or sideways. The leaflets of Lotus, Trifolium, Vicia, and Lathyrus are, for example, folded upwards at night, those of Lupinus, Robinia, Glycyrrhiza, Glycine, Phaseolus, and Oxalis downwards; the common petiole of Mimosa turns downwards at night, that of Phaseolus becomes erect; the leaflets of Mimosa and *Tamarindus indica*[3] turn laterally forwards and upwards in the dark, those of *Tephrosia carabica* backwards. When the petiole and other parts of the same leaf are contractile, the curvatures of the various motile parts may differ; thus, for example, the petiole of Phaseolus turns upwards in the evening, while the leaflets turn downwards; the petiole of Mimosa on the other hand turns downwards while the leaflets turn forwards and upwards, till they partially cover one another in an imbricate manner. As the periodic movement of leaves, and that of sleeping and waking must be distinguished from revolution caused by growth, which makes them unfold, so in flowers a distinction must be drawn—which is not always done[4]—between mere unfolding and the periodic movements of sleeping and waking. Petals which, after opening and remaining open for some time, simply fall off or wither (like those of Mirabilis, *Cereus grandiflorus*, *Helianthemum vulgare*, &c.) are not included in this category. There are others however[5] which last for some days and alternately open and close, usually in the evening and morning or on a change of weather, as *e.g.* those of Tulipa, Crocus, the potato, Oxalis, Mesembryanthemum, Ipomæa, Convolvulus, Hemerocallis, Portulaca, &c. The

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[1] [See Somnus Plantarum, P. Bremer, Linn. Amœn. Acad. iv. p. 333.—Ed.]

[2] See Sachs, Bot. Zeit., 1857, p. 813.

[3] See Meyen, Neues System der Pflanzen-Physiologie, vol. III, p. 476.

[4] Compare Dutrochet, Mémoires pour servir, 1837, vol. I, p. 469 *et seq.*

[5] [See Linnæus, Philosophia Botanica, ed. 1780, pp. 272–275; K. Fritzsch, On the Periodical Opening and Closing of Flowers, Journ. Hort. Soc. Lond. vol. VIII, 1853.—Ed.]

ligulate florets of the capitula of many Compositæ, as the dandelion, daisy, Tragopogon, and many other Cichoriaceæ, behave in reference to the whole inflorescence like single petals, alternately approaching and receding from one another.

(3) Many leaves endowed with periodic motility or sensitiveness to light are also *irritable to contact and concussion*, as those of *Oxalis Acetosella*, *stricta*, *corniculata*, *purpurea*, *carnosa*, and *Deppei*[1], *Robinia pseud-Acacia*[2], various species of Mimosa, as *sensitiva*, *prostrata*, *casta*, *viva*, *asperata*, *quadrivalvis*, *dormiens*, *pernambucina*, *pigra*, *humilis*, and *pellita*, *Æschinomene sensitiva*, *indica*, and *pumila*, *Smithia sensitiva*, *Desmanthus stolonifer*, *triquetrus*, and *lacustris*. In the greater number of these plants a rather violent or often repeated concussion is requisite to set the parts in motion, which then always assume the position of sleep; in other words, mechanical irritation acts in the same way as a diminution of light. This is the case also in *Oxalis* (Biophytum) *sensitiva* and *Mimosa pudica*, where however a very slight concussion or simple contact on the contractile organ suffices to cause immediate and considerable motion, which is then conveyed, when the plant is highly irritable, by conduction of the irritation to the parts not touched.

Among irritable stamens may be enumerated the various species of Berberis[3] (*e. g.* *vulgaris*, *emarginata*, *cretica*, and *cristata*, and of the sub-genus Mahonia. In contact with the corolla when at rest, they curve concavely inwards when the base of the inner side of the filament is lightly touched, so that the anther comes into contact with the stigma.

There is a greater diversity in the phenomena produced by a slight blow or friction on any part of the filaments of various Cynaraceæ (as Centaurea, Onopordon, Cnicus, Carduus, and Cynara) and Cichoriaceæ (as Cichorium and Hieracium). The filaments which spring from the tube of the corolla bear the five firmly attached (not coherent) anthers, which together form a tube through which the style grows up while the pollen is escaping. At this time the filaments are irritable; when at rest they are curved concavely outwards as far as the width of the corolla-tube will permit; on contact or concussion they contract, become straight, and hence come into close contact along their whole length with the style which they enclose, lengthening again after some minutes and resuming their curved form. Since each separate filament is independently irritable, touching a single filament or a blow on one side only of the capitulum will irritate, according to circumstances, only one, two, or three of the filaments, and by the contraction of one side the whole of the reproductive organs will be bent to one side. By the displacement connected with this or the pressure of the other filaments on the corolla, they are also irritated, and thus arises an irregular oscillating or twisting motion of the reproductive organs of the flower. If the whole capitulum is shaken, or if the hand is passed over the surface of the flower, or the flower is blown into, a 'creeping' motion ensues of all the flowers in the capitulum. This phenomenon occurs only while the style is growing through the anther-tube and the pollen is being emptied into the tube; the motion of the filaments effected by insects causes the anther-tube to be drawn downwards and a portion of the pollen thus to escape above it, which is then carried away by insects to other flowers and capitula where the stigmas are already unfolded[4].

Among irritable female reproductive organs are the lobes of the stigmas of Mimulus, Martynia, *Goldfussia anisophylla*, &c., which close when their inner side is touched, evidently in order to retain the pollen brought to them by insects. More striking are the movements which follow a light touch on the gynostemium of Stylidium, a genus

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[1] From Unger, Anatomie und Physiologie der Pflanzen, 1853, p. 417.

[2] Mohl, Flora, 1832, vol. II, No. 32, and his Vermischte Schriften.

[3] Goeppert, Linnaea, 1828, vol. III, p. 234 *et seq.*

[4] These phenomena were discovered as long ago as 1764 by Count Battista dal Covolo, and are well described by Kölreuter in his preliminary Nachrichten von einigen das Geschlecht der Pflanzen betreffenden Versuchen; 3rd Appendix, 1766, pp. 125, 126.

almost peculiar to Australia (*e. g. S. adnatum* and *graminifolium*). The cylindrical gynostemium which bears the stigma and close beside it two anthers, is, when at rest, turned sharply downwards; irritation causes a sudden elevation and even reversal of the flower.

A more detailed description of these and other contractile organs will be found in Morren's treatise named below[1].

Sect. 28. **Mobile and immobile condition of the motile parts of plants**[2]. The parts of plants endowed with periodic motion and irritability may present alternately two different conditions according to the external influences to which the plants are subjected. These properties may be suspended for a shorter or longer time, and may give place to a condition of immobility which again disappears if the external influences are favourable, provided the organ is not in the meantime killed. This immobile condition differs from that caused by death in the fact that it is transitory, and that the internal changes which cause it are reparable. It is very important, in order to understand the phenomena of movement, to make a clear distinction between the terms 'movement' and 'motility'; the causes which produce any particular movement must not be confounded with those on which motility or the power of moving depends. This distinction has, however, been neglected by more than one writer, and great obscurity has resulted. The following illustration may serve to explain the distinction. The theory of walking presupposes a condition of the muscles and sinews in which they are capable of motion—a proper arrangement of the bones, the activity of the nerves, and the nutrition of all the parts of the body by the blood. The question is a purely mechanical one when all the parts necessary to the act of walking are known to be present and in their normal position. But in attempting to show why the organs necessary for walking sometimes refuse their work—as after severe fatigue, when the extremities are paralysed, &c.—we have to do with altogether different questions. When once the mechanical laws which regulate the act of walking under normal conditions are known, it is only necessary to show why the power of motion is lost in the abnormal condition; but this may result from purely mechanical causes, from change in the molecular structure of the substance of the muscles or nerves, &c.—questions which have nothing to do with the mechanical phenomena of walking. It is easy to apply these observations to the motile parts of plants. Their anatomical and true experimental investigation in the normal motile condition lays the foundation of the mechanical explanation of every single movement of a leaf. On the other hand the question why leaves under certain circumstances are immobile, although it no doubt

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[1] C. Morren, On Stylidium, Mém. de l'Acad. roy. des sci. de Bruxelles, 1836; on Goldfussia, ditto, 1839; on *Sparmannia africana*, ditto, 1841; on Megaclinium, ditto, 1862. Also on Oxalis, Bull. de l'Acad. roy. des sci. de Bruxelles, vol. II, No. 7; on Cereus, ditto, vols. V and VI. [On the irritability of the stamens of Ruta, see Carlet, Comp. rend., August 25, 1873, and May, 18, 1874; Heckel in Comp. rend. July 6, 1874. On Sparmannia, Cistus, und Helianthemum, see Heckel, in Comp. rend. March 23 and April 6 and 20, 1874.—Ed.]

[2] Sachs, Die vorübergehende Starrezustände periodisch beweglicher und reizbarer Pflanzen-Organe, Flora, 1863, No. 29 *et seq.*—Dutrochet, Mém. pour servir, vol. I, p. 562.—Kabsch, Bot. Zeit. 1862, p. 342 *et seq.*

requires consideration from a mechanical point of view, will yet in general need for its answer a proof that chemical or molecular changes of the contents and walls of the cells have produced abnormal conditions, by which they have become immobile, or cease to be capable of the normal curving upwards and downwards. The mechanism of a watch which is going correctly may be accurately known to the watchmaker; but if it begins to go wrong or stops altogether a special examination is needed, not of the mechanism of the watch, but of the causes which have prevented the motive forces from acting. These causes may be of a purely chemical nature, as from injury to the spring by a drop of acid which has diminished its elasticity; or they may be of a purely mechanical nature, as when the watch has been exposed to too high or too low a temperature, or has lain within reach of a powerful magnet.

The investigation of the transitory condition of immobility and of its external causes does not therefore in the first place concern the mechanics of the arrangement of the motile part necessary for every separate movement, but leads to questions which concern the molecular structure and chemical nature of the tissue. The fact that poisonous substances destroy the motility of the tissue, teaches us nothing as to the mechanics of its movements in the normal condition. It may be assumed that transitory conditions of immobility are caused by chemical and molecular changes in the cells, which when they are strongly pronounced would kill them; it is only because the injurious influences are interrupted in time, and the internal changes have not reached the point at which they cause death, that they can be neutralised, and the normal internal condition of the tissue, and together with this its motility, be restored under favourable external conditions.

Transitory conditions of immobility ensue from a low temperature above the freezing point, and a high one below 50° C. if not lasting too long; in the case of leaves also from darkness lasting for two or more days, a deep shade for a longer time; with irritable leaves from want of water but not sufficient to cause withering. In the case apparently of all irritable organs a transitory condition of immobility is caused by placing the plant for a time *in vacuo* or in an atmosphere devoid of oxygen or strongly impregnated with carbon dioxide or certain vapours as that of chloroform. In all these cases death is the final result of a long continuance or increase of the injurious influence.

The following particulars are taken from the detailed illustrations in my work already quoted.

(1) *Transitory rigidity from cold* occurs in the leaves of *Mimosa pudica* when the influences are otherwise favourable if the temperature of the surrounding air remains for some hours below 15° C.; the lower the temperature falls below this point, the more quickly does the rigidity set in; the irritability to touch and concussion disappears first, then that to the action of light, and finally also the spontaneous periodic movement. The lateral leaflets of *Desmodium gyrans*, are, according to Kabsch, immotile when the temperature of the air is below 22° C.

(2) *Transitory rigidity from cold* occurs in Mimosa within an hour in damp air of 40° C., within half an hour in air of 45° C., in a few minutes in air of 49° to 50° C.; the sensitiveness returns after exposure for some hours to warmer air. In water the rigidity from cold of Mimosa sets in at a higher temperature, *viz.* in a quarter of an hour between 16° and 17° C., and the rigidity from heat at a lower temperature than in air, *viz.*

in a quarter of an hour between 36° and 40° C.[1] During the rigidity from heat, whether in air or water the leaflets are closed, as after irritation, but the petiole is erect, while when irritated it turns downwards.

(3) *Transitory rigidity from darkness.* If plants whose leaves are periodically motile and irritable to light and concussion, as Mimosa, Acacia, Trifolium, Phaseolus, and Oxalis, are placed in the dark, the spontaneous periodic movements take place without the changes in position caused by irritability to light, but all the more clearly, and the irritability to touch is also not at first injured. But this motile condition disappears completely when the darkness lasts for one day or more. If a plant rendered rigid by exposure to dark is again placed in the light, the motile condition is restored after some hours or even a day.

Perfect darkness is however by no means necessary in order to produce rigidity. It may be brought about by placing a plant that is very dependent on light, like Mimosa, for some days in a deficient light, as in an ordinary dwelling room, at some distance from the window.

In contrast to the rigidity caused by dark, I have applied the term *Phototonus* to the motile condition resulting from permanent exposure to light. A plant in this condition, if placed in the dark, will, as we have seen, remain for some time (hours or even days) in a state of phototonus, which then disappears gradually; the plant is therefore, under normal conditions, in a state of phototonus even in the dark. In the same manner a plant which has become rigid from the dark retains its rigidity for some time (hours or even days) after being exposed to light. The two conditions therefore pass over into one another only slowly.

In the case also of rigidity caused by dark, the irritability of Mimosa to concussion disappears first, and then the spontaneous periodic motion. In the same manner a plant which has thus become rigid reassumes first of all its periodic movement, then its irritability.

The position of the various parts of the leaves of Mimosa when in a state of rigidity caused by dark is different from that caused by darkness in phototonic plants, and also different from that under rigidity caused by heat. In the first case the leaves remain quite expanded, the petiolules directed downwards, the common petiole almost horizontal.

Changes in the intensity of the light produce the same effect as irritants, but only on healthy phototonic plants; leaves which have become rigid from exposure to the dark show no irritability to variations in its intensity until they have again become phototonic from long-continued exposure to light. A plant of *Acacia lophantha*, left for five days in the dark, was found to have lost during the last forty-eight hours every trace of its spontaneous movements. It was then placed in a window, where within two hours it directed its leaflets strongly downwards, the sky being cloudy, and other small changes of position took place in the petiolules. In this condition the plant was still rigid; when it was then placed about noon in the dark with another phototonic plant of the same species, the position of its leaves did not change, the leaflets remained expanded, while the other plant within an hour closed its leaflets and assumed the most complete nocturnal position. Both plants were then once more placed in the window, when the first again retained the position of its leaves unchanged, while the normal phototonic plant expanded its closed leaflets in an hour, the sky being still cloudy. By the evening the lowest six leaves still remained rigid and expanded, but the upper eight

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[1] A plant of Mimosa immersed in water of from 19 to 21·5°C. remains sensitive to impact and light for eighteen hours or more. Bert's statement (Recherches sur le mouvement de la sensitive; Paris, 1867, p. 20) that Mimosa remains irritable up to 56 or even 60°C. is not sufficiently confirmed, and is opposed to all that we know about the superior limits of temperature for vegetation.

or nine leaves closed; the next morning all the leaves again expanded into their normal diurnal position[1].

Trifolium incarnatum exhibited similar phenomena, with only immaterial differences.

It is worth noting that in the plants observed by me the positions of the leaves induced by the rigidity caused by dark resemble the diurnal more than the nocturnal position of phototonic plants.

(4) *Transitory rigidity from drought* I have observed only in *Mimosa pudica*. If the earth in the pot in which a plant is growing is left unwatered for a considerable time, the irritability of leaves perceptibly diminishes with the increasing dryness, and an almost complete rigidity ensues, causing the common petiole to assume a horizontal position, and the leaflets to expand. Leaves which have lost their irritability are not withered nor flaccid; but the watering of the soil causes a return of the irritability within two or three hours.

(5) *Transitory rigidity resulting from chemical influences*. In this category I include especially the condition termed by Dutrochet[2] Asphyxia, which occurs in Mimosa when placed in the receiver of an air-pump. While the air is being pumped out, the leaves fold up, no doubt in consequence of the concussion; but the leaflets then expand, the petiole becomes erect, and while the leaves assume the same position as after prolonged withdrawal of light, they now remain rigid and possess neither periodic motility nor irritability to concussion. When brought again into the air the plant again becomes motile. It can scarcely be doubted that the effect of the vacuum is essentially a result of the removal of the atmospheric oxygen, and therefore causes rigidity by suspending the respiration.

Kabsch[3] confirmed these statements, and showed that the stamens of Berberis, Mahonia, and Helianthemum also lose their irritability *in vacuo*, regaining it in the air.

The cessation of the irritability of the stamens of these plants which Kabsch states to take place when they are placed in nitrogen or hydrogen gas may also be ascribed to a simple suspension of respiration, the irritability returning on access of air. The destruction of the irritability which takes place, on the authority of the same observer, in the stamens of Berberis in pure carbon dioxide or in air containing more than 40 p. c. of this gas must, on the contrary, be considered a positively injurious chemical action of the nature of poisoning. If they remain from three to four hours in carbon dioxide, the irritability returns only after some hours on replacing them in air. Carbon protoxide mixed with air in the proportion of from 20 to 25 p. c. destroys irritability, while nitrous oxide produces no effect. The stamens, on the other hand, bend towards the pistil in nitrous oxide, and lose their irritability in $1\frac{1}{2}$ or 2 minutes. Ammoniacal gas appears to cause transitory rigidity after a few minutes.

Kabsch states that rigidity ensues after from $1\frac{1}{2}$ to 2 hours even in pure oxygen, the stamens again recovering in the air. The vapour of chloroform causes transitory rigidity in the leaves of Mimosa, either in the expanded or in the folded position caused by irritation[4].

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[1] [Bert (Bull. de la Soc. bot. de France, vol. XVII. 1871, p. 107) found that the irritability of the leaves of Mimosa was destroyed by placing them under bell-glasses of green glass almost to the same extent as if placed in the dark; the plants being entirely killed in twelve days under blackened, in sixteen days under green glass; plants placed in the same manner beneath white, red, yellow, violet, and blue glasses being still perfectly healthy and sensitive, though varying in the rapidity of their growth.—Ed.]

[2] Dutrochet, Mém. pour servir, vol. I, p. 562.

[3] Kabsch, Bot. Zeit. 1862, p. 342.

[4] [J. B. Schnetzler (Bull. de la Société vaudoise des Sciences naturelles, 1869) points out that the substances which destroy the contractility of animal 'sarcode' also destroy the irritability of the stamens of Berberis and the leaves of Mimosa. Curare has no prejudicial effect in either case; while nicotine, alcohol, and mineral acids destroy both. In the Comptes rendus for April 23rd,

(6) *Transitory rigidity caused by electrical agency*[1] was observed by Kabsch in the gynostemium of Stylidium. A weak current produced the same result as concussion; a stronger current destroyed the irritability, which however returned after half an hour. In *Desmodium gyrans*, on the other hand, the leaflets which had been rendered rigid by cold (22° C.) were again made motile by the action of an induction-current.

SECT. 29. **Mechanism of the Movements**[2]. We have now to explain in what manner the movements we have been describing are effected in any particular case in the normal and healthy condition of the organs. But we must first investigate the anatomical and mechanical contrivances which have the power, under the influence of certain forces, of causing those changes in the tissue that result in the movements in question; and we must then enquire whence the forces are derived which actually set in motion the contractile organs. That the forces which act when the organs are in a state of tension are set in motion by a small impulse, is evident from the fact that the movements are brought about by causes which could only produce the effect by special contrivances, the motive power of the movement being altogether out of proportion to the effect produced. The strong downward curving not only of the large contractile organ of a Mimosa-leaf by a slight touch on the under side, but the concurrent movement of other leaves, reminds one of the behaviour of a steam-engine, the powerful forces of which are set in action by a slight pressure on a valve. But the extraordinary transmutation of tension into active force effected by light in the periodically motile parts of plants, causing them to pass from the nocturnal to the diurnal position, cannot be made the subject of so exact a comparison. This phenomenon may rather be compared to the power of the rays of the sun to set fire to gunpowder placed in the focus of a burning-glass, which on its part sets a machine in motion by the expansion of its gases, or propels a cannon-ball in the barrel.

As far as observations have at present been made, two kinds of forces exist in the contractile organs of plants, which, by their mutual tension, cause both the irritable and the periodically motile conditions of plants: on the one hand the attraction of water by the substances contained in the parenchymatous cells of the tissue capable of expansion; on the other hand, the elasticity of the cell-walls. By the former the turgid parenchyma is strongly stretched until the elasticity of the cell-wall reaches an equilibrium with the endosmotic force. From the arrangement of the tense tissues (see Sect. 27) this state of equilibrium is necessarily transitory; every increase of the turgidity on one side must cause a curvature on the other side, every diminution on one side a curvature towards that side. Since it is impossible to suppose that the elasticity of the cell-walls undergoes periodical change, or is altered by variations in the amount of light or by slight concussion, the only alternative left is to ascribe the alterations in the tension of the con-

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1870, is a record of a series of experiments on the effect of chloroform on the irritability of the stamens of Mahonia.—ED.]

[1] Kabsch, Bot. Zeit., 1861, p. 358.

[2] The only general descriptions of these movements is Hofmeister's in Flora, 1862, No. 32 *et seq.*, from which mine differs in important points; but I cannot enter here into a discussion of the particulars of the difference in our interpretation of the phenomena.

tractile organs — and therefore the movements themselves — to changes in the turgidity of the parenchymatous cells, which can only be caused by water entering or escaping from them; and the problem is now essentially to show how this influx or efflux of water can be rendered possible by mechanical contrivances, and by what forces it can be brought about. When the phenomenon under consideration is the influx of water, in other words an increase in the turgidity of the parenchyma in the whole or in one side of the organ, the hypothesis may for the time suffice that the cells have a constant tendency to absorb more water by endosmose. Greater difficulties are presented in the solution of the question why a portion of this water which has been taken up with so much force is again given off on slight concussion or on an increase in the intensity of the light and in consequence of unknown internal causes (in the case of spontaneous periodic movements), and is again replaced subsequently by a like quantity. Some knowledge of the mechanism of these movements is essential to the answering of this question[1]; and we have now to describe the amount of such knowledge that we possess in the case of a few of the contractile organs which have been most carefully examined.

1. *The mechanism of movements caused by contact or concussion.*

(a) *The Sensitive Plant*[2] (*Mimosa pudica*). The leaf when fully developed is bipinnate, and consists of a petiole from 4 to 6 cm. long with two pairs of petiolules 4 to 5 cm. in length, and on each of these from fifteen to twenty-five pairs of leaflets 5 to 10 mm. long and 1·5 to 2 mm. broad. All these parts are connected by contractile organs; every leaflet is immediately attached to the rachis by such an organ from 0·4 to 0·6 mm. long, and this again to the primary petiole by another similar organ from 2 to 3 mm. long and about 1 mm. thick. The base of the petiole itself is transformed into a nearly cylindrical contractile organ 4 to 5 mm. long and 2 to 2·5 mm. thick, which is furnished, like those of the petiolules, with a number of long stiff hairs on the under side; the upper side being only slightly hairy or not at all.

Each of the contractile organs consists of a comparatively very thick layer of parenchyma with a feebly developed epidermis without stomata, and penetrated by an axial flexible but only very slightly extensible fibro-vascular bundle, which separates into several bundles where it emerges into the channeled petiole. The parenchyma consists of roundish cells enclosing, in the eight layers which surround the axial bundle, large air-conducting intercellular spaces which become much smaller in the eighteen or twenty outer layers of cells, and are entirely wanting in those immediately beneath the epidermis. These intercellular spaces are in communication with one another from the fibro-vascular bundle to the middle layers of tissue; the very small ones of the outer layers have the appearance of separated triangular internodes, and when cut (therefore in the irritated state) seem to be full of water. The cells of the under side of the 'pulvinus' are thin-walled, those of the upper side have much thicker walls (about three times as thick) of pure cellulose. Together with a moderate quantity of protoplasm (including a nucleus) and small grains of chlorophyll and starch, each of the cells contains in its cavity a large globular drop, consisting, according to Pfeffer,

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[1] This view is essentially that already adopted by Brücke in 1848 in the case of Mimosa, and supported by Unger (Anatomie und Physiologie der Pflanzen, p. 410).

[2] Dutrochet, Mém. pour servir, vol. I, p. 545.—Meyen, Neues System der Pflanz.-Phys., vol III, p. 516 *et seq.*—Brücke, in Müller's Archiv für Anat. und Phys., 1848, p. 434; ditto, in Sitzungsberichte der kais. Akad. de Wiss. Wien, vol. L, July 14, 1864.—Hofmeister, Flora, 1852, No. 32 *et seq.*—Sachs, Handb. der Exp.-Phys., 1866, p. 479 *et seq.*—P. Bert, Recherches sur les mouvements de la sensitive; Paris, 1867.

of a concentrated solution of tannin surrounded by a delicate pellicle[1]. The young organs however manifest sensitiveness when the cell-walls of the upper side are not thicker than those of the other side and the globular drop has not yet made its appearance.

A somewhat slight concussion of the whole plant causes the contractile organs of all the primary petioles to curve downwards, those of the petiolules forwards, those of the leaflets forwards and upwards. The primary petioles which were previously turned obliquely upwards then become horizontal or turn obliquely downwards, while the petiolules and leaflets close. This condition is identical externally with the nocturnal position of the leaves, but differs internally, a concussion still acting as an irritation in this position and causing especially a stronger depression of the primary petiole. The irritated contractile organ is also flaccid, as Brücke has shown, and is more flexible than before the irritation, the weight being the same; in the nocturnal position, on the contrary, the organ is more rigid and less flexible than in the diurnal. In the contractile organs of the primary petioles and petiolules a light touch on the hairs on the under side is sufficient to produce the movement, and in those of the leaflets the lightest touch on the glabrous upper side. When the temperature is high and the air very damp, the irritability is much greater, and any local irritation incites movements in the neighbouring organs, often in all the leaves of a plant, a phenomenon which has been termed Conduction of the irritation. If, for example, one of the anterior leaflets is cut off by a pair of scissors, or its contractile organ is touched, or if it is placed in the focus of a burning-glass, it takes the position which is normally the result of irritation, the next lower pair of leaflets then follows, and in succession those at a greater distance; after a short time the leaflets of an adjoining petiolule begin to fold together from above upwards, and the same with the other petiolules. Finally, often after a considerable time, the primary petiole bends downwards; the phenomenon is then transferred to the primary petiole of the next leaf below, and also probably to that of the next one above; their petiolules and leaflets taking also similar positions. Thus in the course of a few minutes all the leaves are set in motion; sometimes particular parts are passed by which only begin to move subsequently. The conduction of the irritation appears to take place more easily from above downwards than from below upwards, both in the leaves and the stem. If the plant is left to itself the leaflets and petiolules again expand after a few minutes, the primary petioles become erect, and the leaves are again irritable.

If the parenchyma of the upper side of the leaf is cut away as far as the central fibro-vascular bundle from the large contractile organ of a primary petiole, the petiole afterwards again becomes erect, and more so than would otherwise be the case; and the part thus treated retains a smaller degree of irritability. If, on the other hand, the parenchyma is removed from the under side, the petiole turns sharply downwards, and its irritability is destroyed. It follows from this that it is only the under side that is irritable; the parenchyma of the upper side takes only a subordinate part in the movement, as will be shown more clearly presently.

If one of the large contractile organs is cut away close to the stem, it curves downwards, and a drop of water escapes from it. If it is now split lengthwise through the central fibro-vascular bundle into an upper and lower half, the former bends still more strongly downwards, while the lower bends only slightly or becomes nearly straight. These curvatures are still more clearly seen if the two halves are again divided lengthwise by a cut at right angles to the previous one; the four pieces then also manifest a small lateral curvature inwards. If the upper and lower parenchyma are again separated from the central fibro-vascular bundle by two cuts lengthwise, the former bends strongly downwards, the latter slightly upwards; they also increase so much in length as considerably to exceed the central bundle. These and other experiments show that a considerable tension of the parenchyma exists with reference to the central bundle even

[1] Similar globular drops are stated by Unger to occur also in Glycyrrhiza and *Desmodium gyrans*.

when the contractile organ has been irritated and has lost its water, and that in this condition the tension is greater between the parenchyma of the upper side of the fibro-vascular bundle than between the parenchyma of the under side and the bundle.

If one of the contractile organs of the petiole which has been treated in this way is placed in water, in order to replace the loss of water which has taken place during the operation, and thus to produce a condition similar to the normal one, the downward curvature of the upper half becomes still stronger, but the under side also curves strongly upwards, and its tissue, previously flaccid, becomes very tense and almost cartilaginous, as in the other half. This shows that the turgidity of the parenchyma of the under side had decreased more than that of the upper side from the loss of water resulting from the operation, and that it increases also more rapidly when re-absorbing water. In other words, the irritable under side both gives off and re-absorbs water more readily than the upper side. The upper parenchyma always has a tendency to press the central bundle downwards; but the lower parenchyma tends to press it upwards only when it contains much water; when therefore the organ contains but little water, it must be bent downwards, and can only be bent upwards when the quantity of water in it is larger. Conversely, in the case of a leaf springing from the stem it may be concluded that when the contractile organ is erect it contains abundance of water, when it bends downwards in consequence of irritation but little. This conclusion is still further confirmed by the fact that if an incision is made with a very sharp knife in the stem of a very irritable plant at a distance from a leaf and without shaking it, a large drop of water escapes when the knife enters, and the large contractile organ of the next leaf bends downwards or takes the position caused by irritation, evidently in consequence of loss of water; the tension of the sap in the interior of the plant being suddenly diminished and the organ losing water[1]. This conclusion is also in harmony with the fact already mentioned and first established by Brücke, that the organ which bends downwards in consequence of irritation is more flaccid and flexible than before, the only cause of which, under the circumstances, can be diminished turgidity, or loss of water. This further conclusion may also be drawn from these experiments,—that the loss of water in the irritated organ takes place only or at least chiefly in the parenchyma of the under side; and this is again in harmony with the fact that an organ from which the upper parenchyma has been removed still remains sensitive, while the removal of the lower parenchyma destroys all irritability. Pfeffer obtained in his recent investigations a clearer insight into these processes: the following is the result communicated to me by letter.

Pfeffer first of all determined, by careful measurements of the same organ in the two conditions, that the *mass* of the lower parenchyma which contracts from the irritation decreases, while that of the upper parenchyma which lengthens increases; but the increase in mass of the upper half is much less than the decrease in mass of the lower. It follows that the whole organ decreases in mass, since irritation causes it to bend upwards. This decrease in mass of the lower parenchyma is the result of loss of water, as is shown by the following experiment. After cutting through the contractile organ at the base of the petiole where the central fibro-vascular bundle is still undivided, the organ is at first not sensitive (and bent downwards); but if the plant is placed in air saturated with moisture, it again becomes sensitive after a shorter or longer time; when irritated, water escapes each time very rapidly from the incision in considerable quantity when the tissues of the plant are abundantly supplied with water. This water (as Pfeffer has shown can be clearly demonstrated by experiment) comes from the parenchyma, and almost entirely from that portion which surrounds the central bundle and contains large intercellular spaces. It is apparent sometimes only beneath and at the sides of the fibro-vascular bundle, sometimes also above it. Sometimes Pfeffer observed also the section of the fibro-vascular bundle to exude moisture. When a powerful irritation

[1] For further observations on the result of this experiment see Sachs, Handbuch der Exp.-Phys. p. 481 *et seq.*

is applied to the under side of an organ from the upper side of which the parenchyma has been removed, water may sometimes be seen to escape also from the horizontal cut surface of the parenchyma; it is certain that during irritation water escapes from the lower parenchyma; it gives off a small portion of it to the upper parenchyma (as is shown by the measurements that have been quoted), a larger portion flows off at the sides through the intercellular spaces, and a smaller portion apparently enters the central fibro-vascular bundle. The whole amount of water that escapes to the lower parenchyma is so small that it is no doubt at once consumed at these spots at the moment of irritation.

Since water escapes from the parenchymatous cells of the under side when irritated, and passes into the intercellular spaces, the air must be at least partially expelled from the latter; and this is evidently the cause of the darker colour of the irritated parts already observed by Lindsay. Pfeffer fixed a petiole in the normal condition so that the contractile organ could not bend when irritated; when he touched a point of the irritable side he saw the darker colour spread instantaneously from the point of contact. No other explanation of this phenomenon is possible than that the air is expelled from the intercellular spaces and replaced by water, which would cause a smaller amount of light to be reflected from the interior. The expelled air will collect, in consequence of the laws of capillarity, in the larger intercellular spaces round the central fibro-vascular bundle, from which it will easily reach the petiole.

We do not however at present know how a light touch or concussion causes the strongly turgid cells of the under side to lose a portion of their water through their walls and then to take it up again with great energy.

In the diurnal position of the organ slight transverse folds are seen to run along both sides which after irritation become more shallow on the upper but deeper on the under side, showing that the consequent curvature causes a slight passive compression on the under side. This side first of all contracts in consequence of its loss of water and of the elasticity of its cell-walls, and then becomes still further compressed by the downward curvature of the upper side[1].

In the contractile organs of the leaflets of *Oxalis Acetosella*[2], where the anatomical and mechanical contrivances are similar to those of Mimosa, this compression is much stronger, and the folds make their appearance on the under side when the organ is irritated. Pfeffer states that a decrease in mass also takes place, and since a very considerable elongation of the upper parenchyma is required for the movements, there must be a more considerable transference of water from the under side. The organs of Oxalis differ from those of Mimosa in remaining irritable after the intercellular spaces have become filled with water; but when in this state they become flaccid on irritation; it is probable therefore that a portion of the water passes from the contractile organ into the tissue of the petiole and lamina. The depression of the leaves of *O. Acetosella* and *stricta* when sunlight falls suddenly upon them[3], is, like the irritable movements, attended with flaccidity, and has been determined by Pfeffer to be of the same nature.

(b) The anatomical and mechanical contrivances in the *Stamens* of Berberideæ[4], the *Gynostemium* of Stylidium, and the *Leaves* of *Dionæa muscipula* and Drosera[5] have at

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[1] [The most recent publication on the irritability of the leaves of *Mimosa pudica* is by Pfeffer in Pringsheim's Jahrb. für wiss. Bot. 1874.—Ed.]

[2] See Sachs, Bot. Zeit. 1857, pl. XIII.

[3] See Batalin, Flora, 1871, No. 16.

[4] The irritability of the stamens of Berberideæ differs from that of the same organs in Cynaraceæ, in being displayed on the inner surface only of the filament. The parenchyma of the irritable portion possesses also no intercellular spaces, these being replaced by a copious 'intercellular substance.'

[5] [The peculiar motion of the hairs on the surface and margin of the leaves of Drosera, by means of which, with the assistance of the viscid substance excreted by them, insects are captured and apparently devoured, was first observed by Roth in the eighteenth century (Von der Reizbarkeit der

present been too little investigated to allow of their being described here in a brief space[1].

(c) Closer attention has been paid to the phenomena connected with the stamens of Cynaraceæ[2]. Their external features in the normal condition have already been described. For a close examination of them it is necessary to remove single flowers from the capitulum, and to cut away the corolla from below as far as the point of insertion of the filaments, or to cut across the corolla-tube, stamens, and style above the insertion of the filaments, and to fix the reproductive organs which are thus isolated by means of a pin in damp air. When the filaments have recovered from the irritation caused by this operation, they are convex outwards. The filaments are flat and strap-shaped; they consist of three or four layers of long cylindrical parenchymatous cells, separated by thin straight septa, and surrounded by a layer of epidermal cells of similar form, strongly cuticularised and growing out in many places to hairs, each of which is cut off by a longitudinal wall. Unger states that intercellular spaces of considerable size lie between the parenchymatous cells; through the middle of the parenchyma passes a delicate fibro-vascular bundle, which, like the epidermis, is strongly stretched by the turgid parenchyma.

If the flower has been dissected according to the plan first described, and one of the filaments, curved convexly outwards and fixed below to the corolla, above to the anther-tube, is touched, it becomes straight and therefore shorter and in contact along its whole length with the style. If all the filaments are touched, it is seen that they have considerably decreased in length so as to draw down the anther-tube. After a few minutes they resume their original length and curvature, and are then again irritable. If the corolla has been dissected according to the second mode, where the filaments are cut away and can move freely below, it is easily to see that every time they are touched a curvature immediately ensues; if the outer side is touched, it becomes at first concave, then convex; if the inner side is touched, it becomes concave, and sometimes afterwards convex. The contraction of the irritated filament begins at the moment of contact, after some time reaches its maximum, and the organ then at once begins again to lengthen, at first quickly, then more slowly. The amount to which the irritated filaments contract was determined by Cohn from the mean of a number of measurements in the case of *Centaurea macrocephala* and *americana* at 12 p. c. of the maximum length; but he considers this estimate too low. Unger, whose measurements seem to be more exact, gives the proportion at 26 p. c.; he also observed that the filament does not increase in thickness, while he gives the increase in breadth at 18 p. c. from the original size; and concludes from this (but incorrectly) that no decrease in mass results from the irritation, but only a change in the shape of the filament. Pfeffer states in a letter that the increase in thickness of the filament is much less than this, and not nearly sufficient to prove that the irritation causes no decrease in mass. He supposes

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Blätter des sogenannten Sonnenthaues; Bremen, 1782). That the movement is due to some other cause than an irritability or contractility of the tissue is shown by the fact that the motion of the glands is excited by living insects, or dead organic substances as raw meat, but not by inorganic substances such as a piece of chalk. For further details see Grönland, Ann. des Sci. nat., 4th series, vol. III, 1855, p. 297; Trécul, Ann. des Sci nat. ditto, p. 303; A. W. Bennett in Quart. Journ. Micr. Sci. 1873, p. 428; Mrs. Treat in Amer. Nat. December, 1873, p. 705 *et seq.*; Canby in Amer. Nat. July, 1874, p. 396.—Ed.]

[1] See Unger, Anat. und Phys. p. 419.—Suringar, on Drosera, Vereeniging voor de Flora, van Neederland eng. July 15, 1853.—Nitschke, on Drosera, Bot. Zeit. 1860, No. 26 *et seq.*—Snetzler, on Berberis, Bull. de la soc. Vaudoise des sci. nat. vol X, 1869.—Kabsch, on Berberis, Mimulus, &c., Bot. Zeit. 1861, No. 4; on Stylidium, Bot. Zeit. 1861, No. 46.

[2] Cohn, Contractile Gewebe im Pflanzenreich, Breslau 1861; ditto, Zeitschrift für wiss. Zoologie, vol. XII, Heft 3; Kabsch, Bot. Zeit. 1861, No. 4; Unger, Bot. Zeit. 1862, No. 15, and 1863, No 46.

that in this case also water escapes from the cells into the intercellular spaces, especially because he was able to determine that a flaccidity of the tissue results from the irritation. In proportion as water escapes from the parenchymatous cells does the whole tissue contract from the elasticity of the cell-walls, of the stretched central bundle, and of the epidermis. That the contraction is in this case so considerable depends on the greater extensibility of the cell-walls and of the delicate central fibro-vascular bundle in Mimosa, which is stated by Pfeffer to be on the contrary but slightly extensible[1].

2. *Mechanism of the changes caused by variation in the temperature and in the intensity of the light.*

(a) *The Opening and Closing of Flowers.* With the exception of a few statements by Dutrochet, and the observation by Hofmeister[2] that the flowers of the tulip open with an elevation and close with a depression of temperature, scarcely anything is at present known regarding the mechanism of these movements. I can now only make a few general remarks which Pfeffer has placed at my disposal; they are based on a series of investigations which is not yet completed. The opening of the flowers is connected, in the crocus, tulip, and dandelion, with an increase in length of the inner side of the perianth-leaves; there is no considerable increase of the length of the outer side; the part where the curvature takes place is always below.

Under the ordinary conditions of vegetation these movements are not caused by a change in the amount of moisture in the air, since they take place even under water. In *Crocus vernus* and *Tulipa Gesneriana* and *sylvestris* small variations of temperature give rise to remarkable movements, every rise causing the flowers to open, every fall to close. The crocus is especially sensitive even to variations of half a degree C. The opening takes place whether the rise is rapid or slow, and both phenomena may be repeated many times in a short space. As in analogous phenomena, there are here also superior and inferior limits, and a temperature of greatest sensitiveness. The crocus, for instance, only opens above 8° C.; at a temperature above 28° C. any rise causes the flowers to close.

When the temperature is constant a sudden change in the amount of light causes movements in the crocus, tulip, and Compositæ, an increase making them open, a decrease making them close; but slight changes of temperature may reverse the movements in the case of the crocus and tulip. Spontaneous periodic movements also occur in the two latter plants, although not considerable in amount; more so in other species that will be named.

Ornithogalum umbellatum, *Anemone nemorosa* and *ranunculoides*, *Ranunculus Ficaria*, and *Malope trifida* also manifest similar phenomena resulting from changes of temperature at any time of the day, but not so strikingly as in the case of the crocus.

The phenomena are somewhat different in the dandelion and other Compositæ and in *Oxalis rosea;* in the evening a considerable rise of temperature (*e.g.* from 9° to 30° C.) does not cause the flowers to open, although a slight but scarcely perceptible curvature outwards results. In the morning, on the contrary, an increase of temperature accelerates the opening to a very remarkable degree. If flowers of the dandelion are kept in the dark in the day-time at a temperature below 10° C., they scarcely open at all; but in the evening open rapidly and entirely if the temperature is raised; the next morning they are again closed at the ordinary temperature; and when this is raised they do not open at all or only very slightly. The flowers of some other Compositæ and of Oxalis,

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[1] [The most recent experiments of Pfeffer on the stamens of *Cynara Scolymus* and *Centaurea Jacea* show that the filaments are irritable along their whole length. Irritation caused a contraction of from 8 to 22 p. c. in length, accompanied with but a very slight increase in thickness, the diminution in mass being caused by an escape of water into the intercellular spaces, which oozes out when the filament is cut through. If the intercellular spaces are filled with water by injection the stamens are no longer irritable.—Ed.]

[2] Hofmeister, Flora, 1862, p. 517; Boyer, Ann. des Sci. nat. 1868, vol. IX.

when kept for a whole day at a temperature of from 1° to 3° C. remain closed, and exhibit the same phenomena as the dandelion if the temperature is raised in the morning and evening. The flowers of the tulip and crocus also open in the morning when the temperature rises after they have been closed during the night more quickly than in the evening, or when they have been made to close again after first opening in the morning by lowering the temperature. While therefore in the crocus and tulip an alteration in the temperature always causes a movement of opening or closing, in the Compositæ it only assists the spontaneous movements.

An alteration in the amount of light also affects the flowers of Compositæ, but sudden darkening in the day-time only causes them to close slightly. The flowers of *Leontodon hastilis*, *Scorzonera hispanica*, and Hieracium, when placed in the dark for a whole day open spontaneously, but do not close so completely in the evening as when in the light; on the second day this is more striking. Flowers of *Oxalis rosea* which unfold in the dark open as fully as in the light, but close less completely. The spontaneous periodic movements pursue their course during the whole time of flowering as in the light. The flowers of the daisy, on the contrary, expand completely in the dark, their periodic movements being but very slight.

The curvature takes place, both in the Cynaraceæ and the Cichoriaceæ (*e.g.* Taraxacum) in the lower part of the flower or corolla-tube; the inner side elongates, the length of the outer side not changing.

We see therefore that light, like warmth, causes an elongation of the parenchymatous tissue of the inner side of the flower, this being directly opposed to the phenomena displayed by leaves, whose contractile organs exhibit, as Pfeffer has shown in the case of Phaseolus, Oxalis, and Trifolium, a contraction of their parenchymatous tissue in the light, and an elongation in the dark.

The elongation of the inner side of the petals when the flower opens appears intelligible only on the supposition of a change in shape of the cells or an increase in their size; but direct observation has not yet established either alternative. It may however be considered certain that the curvature which causes the opening of flowers takes place also in narrow strips of the petals when the air is damp. It is however obvious that the elongation of the inner side on a rise in temperature cannot be the result of the rarefaction of the air contained in the intercellular spaces, for the movements would then take place also when the air is artificially rarefied, which is not the case. Pfeffer considers that the opening of flowers is connected neither with flaccidity nor increase in rigidity of the tissue.

(b) *The opening and closing of leaves resulting from alternation in the amount of light and temperature* (*the Sleep of Plants*[1]). If plants with motile leaves, like Papilionaceæ and Oxalideæ, after having remained in the light, are suddenly placed in the dark, the leaves after some time take up their nocturnal position, closing upwards or downwards according to the species (Sect. 27). If light is now let in upon the plant in the state of sleep, the leaves again open and assume their diurnal position. Placing them in the shade has the same effect as complete darkness, but not so strongly.

These facts show that fluctuations in the intensity of the light cause curvatures of the motile parts of plants. If these parts are also irritable to concussion, as in Mimosa and *Oxalis acetosella*, darkness causes a similar position of the leaves to concussion. But the internal conditions are, as has been mentioned, very different in the two cases; for the folding up caused by dark is associated with an increase in the rigidity of the part, and therefore with an increase in its turgidity; while in that caused by irritation there is a decrease of all these, as Brücke was the first to show in the case of Mimosa. In the leaves of Phaseolus which are not irritable to concussion Pfeffer also found an increase of

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[1] Dutrochet, Mém. pour servir, vol. I, p. 509.—Meyen, Neues Syst. der Pflanz.-Phys. vol. III, p. 487.—Sachs, Bot. Zeit. 1857, Nos. 46, 47.—Bert, Recherches sur les mouvements de la sensitive, Paris 1867.—Millardet, Nouvelles recherches sur la périodicité de la sensitive, Marburg 1869.

rigidity in the nocturnal position. Conversely the diurnal position caused by the admission of light or an increase in its intensity is the result of a diminution of the rigidity or turgidity; but it is then the side of the organ which becomes concave by day (*i. e.* the upper side in the large organs of the petiole of Mimosa, the under side in Phaseolus) that loses water and contracts. The causes of this phenomena are however unknown. Increase of temperature, on the contrary, which affects the motile part directly, is, according to Pfeffer, associated, in Oxalis, and in a less degree in Phaseolus, with increase of rigidity, and therefore also of turgidity, and causes a movement towards the nocturnal position, and hence a stronger turgidity of the upper side.

When, on the other hand, an increase in the intensity of the light and a rise of temperature act on a contractile organ at the same time, its curvature is a resultant of the two changes; according as the one or the other preponderates, the leaf approaches more nearly the diurnal on the nocturnal position.

But the quantity of water contained in the whole plant, and therefore to a certain extent that contained in the motile part, depends in addition on the relation between transpiration and the activity of the roots. If, for example, the transpiration in the night is small but the roots very active in moist and warm soil, the quantity of water in the plant will gradually increase and its motile organs will be able to become more strongly turgid, but at the same time more rigid; and when one side of the organ (in the petiole of Mimosa the under side) thus becomes the longer one, a curvature results towards the opposite side (in Mimosa therefore upwards)[1]. Conversely the increase of transpiration when the roots are not sufficiently active will tend to diminish the quantity of water in the contractile organ, and therefore in general to induce the nocturnal position. These processes must act in combination with the direct effects of light and temperature on the contractile organs; and thus, under normal conditions, where these external agencies are subject to continual variation, the motile parts seldom come to rest, even independently of the internal causes which induce spontaneous periodic motion.

The movements of *Mimosa pudica* which take place under the combined conditions of the normal alternation of day and night have been more accurately investigated. Its leaflets remain closed during the whole night, but are usually open in the day; but the primary petioles are in perpetual motion day and night. To the exhaustive observations of Bert, and especially to those of Millardet, we are indebted for a knowledge of the fact that the contractile organ of the petiole, after it has bent strongly downwards in the evening, begins to become again erect before midnight, and continues to become more and more so until the most erect position has been reached before sunrise. At sunrise it begins to be suddenly depressed, while the other parts of the leaf assume their expanded diurnal position. This depression of the petiole continues to increase till evening, the lowest position being reached when complete darkness commences; and the other parts then also assume their nocturnal position. The depression of the primary petiole during the day, and the corresponding movements of the other parts of the leaf, are interrupted by a slight rise both in the forenoon and afternoon.

In this diurnal and nocturnal periodicity a depression of the petiole also follows the access of light, the same phenomenon taking place also in the middle of the day if the light is suddenly withdrawn. The rising of the petiole does not proceed with equal rapidity as the intensity of the light increases and diminishes, as might be expected from what takes place when light is admitted. Finally, we still need an explanation of the

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[1] Millardet (*l. c.* p. 46 *et seq.*) has already pointed out what has here to be especially kept in view, that in Mimosa any change in the tension of the tissues (*i. e.* every alteration of turgidity) in the contractile organ of the primary petiole takes place more strongly on the irritable under side than on the upper side, and that the periodic movements depend mainly on this. Where the position during sleep is erect, as in the leaflets of Mimosa and Trifolium, this must be supposed to be the case on the upper side.

fact that the petiole, which bends low down in the evening, should become erect in the night, and why two elevations should also take place in the day.

If we recall what has been said above as to the various combinations of the effects of temperature and light indirectly on the entire plant as well as immediately on the contractile organs, some such explanation as the following may be attempted of the diurnal periodicity observed by Bert and Millardet.

The strong depression of the petiole in the evening is caused by the effect of darkness on the contractile organ; it is doubtful whether the turgidity increases in it during the depression; but the amount of water in the plant increases during the night in consequence of the diminished transpiration from the leaves. The contractile organs also thus become more strongly charged with water, especially on their under side; and therefore gradually assume a more erect position. At sunrise, when the light should properly cause the petiole to become still more elevated, transpiration increases and the plant loses water, and the organs therefore also become more flaccid (again especially on the under side), perhaps also in consequence of the action of the increase of temperature directly on the contractile organ. But the roots, which at the end of the night had become colder and less active, have in the meantime again become warm, and the more powerful absorption fills the plant more completely with water, which causes the elevation of the petiole in the forenoon. But the gradual elevation of temperature causes a fresh decrease in the quantity of water in the plant and in the contractile organs, and perhaps directly causes the latter to assume the position of sleep. Hence a depression takes place about noon; but this is followed in the afternoon by a second elevation, perhaps in consequence of the smaller amount of transpiration which results from the fall in the temperature. Towards evening the light diminishes in intensity, inducing the nocturnal position of the organs. Further researches may show how far this tentative explanation, derived from a very defective knowledge of the causes of the movements, may be adequate.

3. With respect to the *Mechanism of spontaneous periodic movements*, on which something has been said in Sect. 27, still less is at present known than with respect to those connected with sleep. That we have here also to do with alternate elongation and contraction of the parenchyma of the upper and under sides of the organ is at once evident; and it is more than probable that this is also brought about essentially by increase and diminution in the amount of water. But by what means the turgidity, first of one and then of the other side of the organ, alternately increases and diminishes, while the temperature, intensity of light, and amount of water remain constant, is as completely unknown as why first one and then the other side of growing and revolving stems and tendrils grows for the time most rapidly.

CHAPTER VI.

THE PHENOMENA OF SEXUAL REPRODUCTION.

SECT. 30. **The essential element in the process of sexual reproduction** is the formation, in the course of development of the plant, of cells of two different kinds, which have no independent power of further development, but which, by their coalescence, give rise to a product which possesses that power.

It is only in a comparatively small number of cases, and in plants of very simple structure, like the Desmidieæ, Mesocarpeæ, and Volvocineæ, that the two uniting cells are alike in their mode of production, size, form, and behaviour when

coalescing[1]; and even in these cases they probably differ internally, since it is difficult to explain on any other hypothesis the necessity for their union into a product capable of development (the Zygospore). In some other Conjugatæ, as Spirogyra, this internal differentiation is exhibited at least to the extent that the contents of one of the conjugating cells pass over into the other which remains stationary. But usually, even in many Algæ (as Vaucheria, Œdogonium, Coleochæte, Fucus, &c.) and Fungi (Saprolegnia), and in all Characeæ, Muscineæ, Vascular Cryptogams, and Phanerogams, a great variety of differences are manifested between the sexual cells as to size, form, motility, mode of production, and the share they take in the formation of the product of the union. This differentiation presents, especially in the Algæ and Fungi, a most complete series of gradations between the conjugation of similar cells and the fertilisation of the oosphere by antherozoids, any boundary line between these two processes being unnatural and artificial. The difference also between the sexual cells is developed only gradually and step by step, like the external and internal differentiation of plants; and it is this that renders it probable that in the lowest forms of the vegetable kingdom, as in the Nostocaceæ, no process at all of this kind exists, or that at all events there are plants of extremely simple structure in which no such process occurs.

Wherever there is an evident external difference between the two sexual cells, one behaves actively in the union, and loses in the process its individual existence, the other behaves passively, absorbing into itself the substance of the active one, and furnishing by far the larger proportion of the first materials for the formation of the immediate product of the union. The former is termed the *male* or *sperm-cell*, the latter the *female* or *germ-cell* or *oosphere*.

These most essential features of the sexual process may also be recognised in the fertilisation of the Ascomycetes and Florideæ, although the external appearance of the sexual organs, the ascogonium and trichophore on the one hand and the antheridia on the other hand, are strikingly different from those which occur in any other class of plants[2].

The usual condition of the female cell during the sexual process (except in the Ascomycetes and Florideæ) is that of a naked primordial cell (oosphere), formed either by simple contraction of the protoplasm of a cell previously enclosed within a cell-wall (the oogonium of Vaucheria, Œdogonium, and Coleochæte, the central cell of the archegonium of Muscineæ and Vascular Cryptogams) or by the division of the protoplasm of a mother-cell combined with contraction and rounding off of the daughter-cells (as in Saprolegnia and Fucaceæ), or by free-cell-formation (as in the corpusculum of Coniferæ? and the embryo-sac of Angiosperms). In all these cases the germ-cell is spherical or ellipsoidal, except that in the Angiosperms it is sometimes elongated; in general its form is the simplest that the vegetable cell can assume. The rounding off is not connected with any internal differentiation; at

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[1] See De Bary, Die Familie der Conjugaten, Leipzig 1858, p. 57; Pringsheim, Monatsber. der Berlin. Akad. Oct. 1869, Paarung der Schwärmsporen [Ann. des sci. nat. 5th series, 1869, vol. XII, pp. 191 and 211; De Bary, ibid. p. 208]; Pfitzer, in Hanstein's Botanische Abhandlungen, 1871, Heft II, p. 70 *et seq.*

[2] De Bary, Beiträge zur Morphologie und Physiologie der Pilze, Frankfort, Heft III, at the end.

least where any internal differentiation is exhibited (as in the formation of chlorophyll and the granular contents in Œdogonium and other Algæ), the phenomenon is a secondary one in the process of fertilisation. The germ-cell (or its equivalent the ascogonium) is never actively motile, even when, as in the Fucaceæ, it is expelled and set in rotation by the attached spermatozoids; it usually remains enclosed in the mother-cell that produces it (the oogonium of Algæ and Fungi, the central cell of the archegonium of Muscineæ and Vascular Cryptogams, the corpusculum of Gymnosperms, and the embryo-sac of Angiosperms), where it awaits fertilisation by the male cell. While the latter loses during the union its character as an individual cell, the germ-cell is rendered capable of a more complete individual existence, which is first indicated by the invariable formation of a wall of cellulose, even when the germ-cell results simply from the contraction of the protoplasm of an oogonium and still remains enclosed in its cell-wall, as in Œdogonium and Vaucheria. In this respect the zygospore of Conjugatæ and Mucorini behaves also like a fertilised germ-cell or oospore.

The male cell is more variable in its form and in its behaviour in the process of fertilisation. It always moves to the germ-cell which remains at rest; in the Florideæ it is carried passively by the water; in the Fucaceæ, in Vaucheria, Œdogonium, and other Algæ, in some Saprolegnieæ, and in all Characeæ, Muscineæ, and Vascular Cryptogams, it swims actively; in other cases it becomes attached in its growth to the female cell, as in the antheridial branches of some Saprolegnieæ and the antheridium of Ascomycetes, or it is carried passively to the female organ, as the pollen-grain of Phanerogams and the spermatozoid of Florideæ. The great variety of form of the male cell becomes especially conspicuous if we compare the roundish swarm-spore-like spermatozoids of Œdogonium and Coleochæte with the filiform antherozoids of Characeæ, Muscineæ, and Vascular Cryptogams, and with the pollen-tube of Phanerogams. The form is in each case evidently adapted to produce the right kind of motion in order to convey the fertilising substance to the female cell in a manner in harmony with its structure; while in the fertilisation of the latter the quality of the substance only is concerned. According to the present state of our knowledge it may be assumed that fertilisation always consists in a union of the fertilising substance of the male cell with the protoplasm of the female cell. In conjugation this union is brought about by the coalescence of the two cells. In the fertilisation of Œdogonium and Vaucheria, the entrance of the spermatozoid into the protoplasm of the oosphere and its absorption in it has been observed by Pringsheim. The antherozoids of Muscineæ and Ferns were observed by Hofmeister, and those of Marsilea by Hanstein, to enter the archegonium, those of Ferns by Strasburger to penetrate to the oosphere itself. It must therefore be inferred from analogy that in Phanerogams a union by diffusion takes place of some substance contained in the pollen-tube with the germ-cell; and in Ascomycetes of the contents of the antheridium with those of the ascogonium. It would be impossible otherwise to explain how the mere contact of the often thick-walled pollen-tube with the embryo-sac, or of the antheridium with the ascogonium, can fertilise the latter, while in the former cases such a complete coalescence of the male and female cells is necessary for this purpose.

The product resulting from the sexual process is usually a new individual, which

has no longer any organic connexion with the mother-plant, and is not united with it in growth. This is the case even in the Muscineæ, where the sporogonium, and in Phanerogams, where the embryo is nourished by the mother-plant, but there is no actual continuity of tissue between it and the latter. The case is quite different in the Ascomycetes (*e. g.* Peziza, Eurotium, and Erysiphe) and Florideæ, in which the female organ itself or certain cells connected with it are stimulated by the act of impregnation to produce new shoots from which results a sporangium containing spores; and it is only after the completion of this complicated vegetative process brought about by the sexual union that the asexual spores are set free, and produce new individuals independent of the mother-plant.

The reproductive cells of the same plant do not differ merely externally; the inability of either to originate by itself a new course of development, while the two together produce an organism capable of germinating, shows that the properties of the two are complementary to one another. The sexual differentiation, or difference between the male and female cells, which is neutralised by the act of fertilisation, has been preparing for a longer or shorter time; the product which is the result of fertilisation owes its formation to the neutralising of the sexual difference. In the Conjugatæ and other families where the sexual difference is extremely small or even imperceptible, the preceding processes of development are also alike; the mother-cells of the two kinds of reproductive cells even to the earliest stage of development do not differ externally. But where the sexual difference is greater, it is foreshadowed in the preceding processes of development. Thus the mother-cell of the spermatozoids of the Œdogonium differs in form from that of the oosphere; and this is especially seen in the development of the Œdogonieæ with 'dwarf males.' In Vaucheria the branches which subsequently become antheridia differ at an early stage from those which produce the oogonium. The sexual differentiation of the Characeæ is inaugurated long beforehand in the great difference in the development of the globules and nucules, the position of the two organs on the leaf being also different. In the Muscineæ and Vascular Cryptogams again preparation is made for the production of the antherozoids and oospheres in different ways by the formation of antheridia and archegonia. In Phanerogams the pollen-cells and the embryonic vesicles are also produced in different structures, the anthers and ovules, the difference between these organs commencing long before the formation of the reproductive cells. But this preparation is not confined to the difference between the organs which immediately produce the reproductive cells; in many classes of plants it even goes back so far that the entire plant developes as a male or as a female plant, producing only male or only female reproductive organs, This occurs in some Algæ, Characeæ, Muscineæ, and prothallia of Vascular Cryptogams; in Phanerogams the flower is sometimes exclusively male or female (moncœcious plants), or the same plant produces nothing but male or nothing but female flowers (dicœcious plants).

This carrying back of the sexual difference to processes of development long anterior in time shows how great must be the internal differentiation that finally subsists between the properties of the male and female cells. The fact is very remarkable that this preparation may be carried back in the development of the individual even beyond the limit marked by the alternation of generations. In the

Algæ, Characeæ, Muscineæ, Ferns, and Equisetaceæ, the nature of the alternation of generations is such that the sexual differentiation is developed in one of the generations, while it is neutralised in the succeeding generation. In these cases therefore we have a sexual and an asexual generation in the course of development of the same individual; the asexual generation is the product of the neutralising of the sexual differentiation of the sexual generation. The two generations, especially in Muscineæ and Vascular Cryptogams, differ essentially from a morphological point of view; they follow altogether different laws of development; one of their limits always occurs in the fertilised oosphere. The prothallium developed from the asexual spore of Ferns and Equisetaceæ is, for example, morphologically a thallus without leaves or roots, while its physiological significance is determined by the production of antheridia and archegonia. From the fertilised oosphere on the other hand is produced the Fern or Horsetail, characterised morphologically by the differentiation of stem, root, and leaf; but sexually this differentiated plant is neuter, producing neither male nor female cells, but only asexual spores. If the process of development of Rhizocarpeæ and Selaginelleæ is compared with these phenomena, it will be seen that in these classes the two generations, the prothallium and the spore-forming leafy plant, stand essentially in the same relation to one another as in Ferns and Equisetaceæ, only that the sexual differentiation goes back to the spore itself; the spores are of two kinds, large female spores which produce the small female prothallium, and small male spores which produce only antherozoids. The preparation for this sexual difference is manifested even in the asexual generation, by the sporangia producing only female or only male spores according to their position. In Salvinia the preparation goes back still further, each entire capsule producing only female or only male sporangia. It has already been pointed out how in Phanerogams the embryo-sac corresponds to the large, the pollen-grain to the small spore of heterosporous Vascular Cryptogams, and the endosperm to the prothallium. The endosperm of Phanerogams no longer appears as an independent structure, but only as a constituent part of the preceding generation; in Angiosperms it is often from the first rudimentary and sometimes entirely absent, and the female sexual cell, the embryonic vesicle, is then the immediate product of the embryo-sac which corresponds to the large spore. The true sexual generation therefore becomes less and less important; as such it becomes devoid of significance, while the sexual differentiation is carried back to the spore-forming generation, in which it determines the formation of the sexual organs, *i. e.* the stamens and ovules; and, where the flowering plant is diœcious, the sexual differentiation affects the entire individual, which is either male or female. In all Cryptogams, on the other hand, diœcism can be displayed only in a single generation in the course of development of the individual[1].

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[1] [*Parthenogenesis*, or the production of a fertile embryo in the female organ without any preceding process of impregnation, is a phenomenon of very rare occurrence in the vegetable kingdom. The best-known instance among Phanerogams is that of *Cœlebogyne ilicifolia* (see Smith in Trans. Linn. Soc. vol. XVIII, p. 510), on which however some doubt still rests. Among Cryptogams, *Chara crinita* is stated to produce spores capable of germinating from female plants without any access of the male element. The best authenticated cases are recorded by Pringsheim in *Saprolegnia ferax* and

These general observations show that the sexual differentiation stands, in the various classes of plants, in a very different relationship to the morphological differentiation manifested in the alternation of generations. Hence it arises that the product of the fertilised oosphere has from a morphological point of view a very different value in different groups of plants. In the Conjugatæ it is a zygospore from which generations of cells are subsequently developed similar to the mother-cells of the zygospore; in Vaucheria, Œdogonium, and Coleochæte it is an oospore from which an asexual generation developes, proceeding from it in different ways; in the Muscineæ the asexual generation constitutes the so-called fruit of Mosses; in Vascular Cryptogams and Phanerogams it is the plant furnished with leaves and rooting in the soil.

The process of development brought about by fertilisation or the union of the reproductive cells is usually not confined to the resulting embryo, but shows itself also in a variety of changes in the mother-plant itself. In Coleochæte the oospore becomes invested with a cortical layer; in Characeæ the enveloping tubes of the nucule grow after fertilisation, their coils increase in number, and their membranes become lignified on the inside; in the Hepaticæ a variety of envelopes arise from the mother-plant; in the Mosses the vaginule and in all Muscineæ the calyptra becomes developed; the tissue of the prothallium which surrounds the growing embryo of Ferns grows at first rapidly along with it; in Phanerogams the entire development of the seed and fruit depends on the changes caused in the mother-plant by the fertilisation of the embryonic vesicles. The two most remarkable cases occur in Florideæ and Ascomycetes on the one hand, and in Orchideæ on the other hand. In the former fertilisation does not in general directly cause the formation of an embryo, but brings about processes of growth in the mother-plant, in consequence of which the cystocarp is produced in Florideæ and the fruit in Ascomycetes. In the Orchideæ the action of the pollen-tube is visible on the mother-plant even before fertilisation; Hildebrand has shown (Bot. Zeit. 1863, p. 341) that in all Orchids which he examined the ovules were not in a condition to be fertilised at the time of pollination; and in some (as *Dendrobium nobile*) they have not even begun to be formed; it is only during the growth of the pollen-tubes through the tissue of the stigma and style that the ovules become so far developed that fertilisation can at length be effected. In the Orchideæ the formation of the female cell is therefore a result of pollination; it is determined by the action of the male pollen-tube on the tissue of the mother-plant[1].

When the embryo is developed within the mother-plant, as in the Muscineæ and Vascular Cryptogams, it withdraws its food-material from the plant; this being connected in the Vascular Cryptogams with complete exhaustion and the dying off of the prothallium. In Phanerogams not only does the embryo usually acquire a considerable development, even within the fruit, but a great quantity of the products of assimilation is also withdrawn from the plant by the accumulation of reserve-material in the seed and by the development of the fruit; in many cases the plant itself is also completely exhausted, all its disposable formative substances are given up to the seed and the fruit, and it dies off (monocarpous plants). It is clear that all these changes, and the various movements of materials in the mother-plant connected with them are results of fertilisation, results of immense importance caused by the union of microscopic cells, imponderable by the best balance.

Achlya polyandra; the only difference between the parthenogenetic germ-cells and those produced by the ordinary process of fertilisation being that the former remain dormant for a longer period. (See Braun, Abhand. der Berlin. Akad. 1856; and Pringsheim, Jahrb. für wiss. Bot. vol. IX, p. 191). —Ed.]

[1] [For a summary of the instances in which pollen appears to have influenced the fruit of the mother-plant, see C. J. Maximowicz, Journ. Roy. Hort. Soc. new series, vol. III. p. 161; and Darwin, Animals and Plants under Domestication, vol. I, p. 397.—Ed.]

Sect. 31. **Influence of the origin of the reproductive cells on the product of fertilisation.** The male and female cells or the organs that produce them are formed at a greater or lesser distance from one another on the same plant, or on different individuals of the same species. The male and female cells of the same species may also be more or less nearly related to one another as immediately or more remotely derived from the same parent-cell. The question arises what influence this genetic relationship of the male and female cells exercises on the product of fertilisation. At present we are unable to lay down any general law in this respect; but the overwhelming weight of evidence points to the law that the sexual union of nearly related cells is detrimental to the propagation of the plant, and in general the more so the further the morphological and sexual differentiation of the species has advanced. Only in a few plants of low organisation does a fertile union take place between sister-cells, as in Rhynchonema among Conjugatæ. But in most Algæ and Fungi (as Spirogyra, Œdogonium, *Fucus platycarpus*, &c.) the reproductive cells of the same plant are not so closely related, and especially where fertilisation is caused by actively or passively motile spermatozoids, there being at least a possibility of their meeting with oospheres of more remote origin. Even in Vaucheria, where the antheridium is the sister-cell of the oogonium, the curving of the former, and the direction in which the spermatozoids escape, indicates that fertilisation does not usually take place between the contiguous organs, but between those more remote or even between those produced by different individuals. The tendency for fertilisation to occur only between reproductive cells of as remote relationship as possible within the same species is manifested in a great variety of contrivances, the simplest being that on each individual of the sexual generation only male or only female organs are produced. Between the two uniting reproductive cells lies also the entire course of development of the two plants when they are derived from the same mother-plant, and a still longer course of development when they are derived from different mother-plants. This distribution of the sexes, which is generally termed *Diœcism*, occurs in all classes and orders of the vegetable kingdom, showing that it is a useful contrivance for the maintenance of different species. Thus we find this phenomenon in many Algæ as in most Fucaceæ, in some Saprolegnieæ and Characeæ (*Nitella syncarpa*, &c.), in many Muscineæ, in the prothallium of many Ferns (*Osmunda regalis*) and of most Equisetaceæ, and in many Gymnosperms and Angiosperms.

If the plant which produces both kinds of sexual organs is large or at least strongly differentiated, distance in the relationship of the two kinds of reproductive cells is still attained by the male and female organs being produced on different branches; and this phenomenon, which is in general termed *Monœcism*, is also common in the vegetable kingdom, as in some Algæ, many Muscineæ, and a very large number of Gymnosperms and Angiosperms[1].

But another relationship which, according to the law just stated, should apparently be very unfavourable, is also of very common occurrence in the vegetable kingdom, —where the reproductive organs are in close contiguity, and the sexual cells therefore

[1] The arrangement of the reproductive organs termed Polygamy is also a contrivance intended to hinder perpetual self-fertilisation of a flower or of an individual.

of near even if not always of the closest affinity. Thus, for example, the same cellular filament of Œdogonium produces both male and female cells, the same Vaucheria-tube antheridia and oogonia in close proximity, the same conceptacle of *Fucus platycarpus* produces both oospheres and spermatozoids; the nucules of most Characeæ are produced close beside the globule on the same leaf; the archegonia and antheridia of some Mosses (species of Bryum) are collected together in hermaphrodite 'flowers'; the prothallia of many Ferns produce both kinds of reproductive organs side by side; in the flowers of Angiosperms hermaphroditism is the typical and most common arrangement. But in all these cases where the aim is apparently to favour the union of sexual cells nearly related to one another, there are at the same time contrivances which hinder the male cells from reaching the contiguous female cells; or at least to render it possible that this should not always happen. This fact was first recognised by Kölreuter (1761) and Karl Conrad Sprengel (1793), and has been further illustrated recently by Darwin, Hildebrand, and others[1]. In spite of the hermaphrodite flowers of Phanerogams and the similar sexual arrangements of Cryptogams, it appears very certain that the union of nearly related sexual cells must be unfavourable to the perpetuation of most plants, since such various and often astonishing means are provided in order to prevent self-fertilisation within a hermaphrodite flower.

One of the simplest and commonest means for ensuring cross-fertilisation is *Dichogamy*, *i. e.* the arrangement by which the two kinds of reproductive organs, even when contained within the same flower, are mature at different times, so that the sexual cells which are in close contiguity, and therefore nearly related, are not capable of performing their respective functions simultaneously. The male cell must in these cases unite with the female cell from a different flower. This is in fact usually the case with the hermaphrodite flowers of Angiosperms, as also with most prothallia of Ferns and the monœcious Characeæ, where the nucule is situated close to the globule but becomes mature only at a later period (this is very strikingly the case in *Nitella flexilis*). Insects are the main agent in the conveyance of the pollen to the stigma of other flowers of dichogamous Phanerogams, for which purpose the parts of the flower possess special adaptations which will be described presently. In the dichogamous species of Nitella and prothallia of Ferns the motility of the antherozoids is sufficient to enable them to reach the archegonia of neighbouring prothallia, or the nucules on other leaves of the same plant, or even on other plants of the same species. Whether the Algæ named above and some Muscineæ are dichogamous is doubtful; but the motility of the antherozoids renders it possible for them to reach the oospheres of other plants or those on other branches of the same plant.

Among Angiosperms, in addition to the common occurrence of dichogamy,

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[1] K. C. Sprengel (Das neu entdeckte Geheimniss der Natur im Bau und in der Befruchtung der Blumen, Berlin, 1793, p. 43) first gave expression to the pregnant idea, 'Since a large number of flowers are diclinous and probably at least as many hermaphrodite flowers are dichogamous, Nature appears to have designed that no flower shall be fertilised by its own pollen.' Darwin (On the Various Contrivances by which Orchids are Fertilised, London, 1862, p. 359) says, 'Nature tells us in the most emphatic manner that she abhors perpetual self-fertilisation;' and again, 'No hermaphrodite fertilises itself for a perpetuity of generations.' [This last observation was first made by Andrew Knight in 1799 (Phil. Trans. p. 202).—Ed.]

there are also other contrivances of a very different nature which have the sole purpose of transferring the pollen of hermaphrodite flowers, by the help of insects, to the stigma of another flower of the same or of a different plant. In most Orchideæ, Asclepiadeæ, Viola, &c., the reproductive organs of each individual flower are developed at the same time, but at the time of maturity mechanical contrivances exist which prevent the pollen falling on the stigma of the same flower; it must be carried by insects to other flowers.

In other cases, as Hildebrand has shown in the case of *Corydalis cava*[1], the pollen does actually fall on the stigma of the same flower, but is there impotent, having the power of fertilising only when it falls on the stigma of a different flower, and only perfectly when carried to the flower of a different individual of the same species. Such a plant is therefore only morphologically hermaphrodite, but is physiologically dicœcious. J. Scott states that *Oncidium michrochilum* exhibits the same phenomena, the pollen not being potent on the stigma of the same flower, while cross-pollination ensures fertilisation[2]; the pollen and stigma are therefore without function except to the stigma and pollen of a different flower. Similar phenomena have been described by Gärtner in the case of *Lobelia fulgens* and *Verbascum nigrum*, and in species of Begonia by Fritz Müller[3].

No less remarkable is another contrivance for the mutual fertilisation of different individuals of plants with hermaphrodite flowers,—*Dimorphism*[4] (or Heterostylism), consisting in a difference between different individuals of the same species with reference to their reproductive organs. In one individual the flowers all have a long style and short filaments, while in another individual all the flowers have a short style and long filaments, as in *Linum perenne*, *Primula sinensis*, and other species of Primula. It sometimes happens also, as in *Lythrum Salicaria* and many species of Oxalis[5], that the reproductive organs in the flowers of different specimens of the same species exhibit three different relative lengths (Trimorphism), there being an intermediate length of style between the long-styled and the short-styled forms. In these cases of dimorphism and trimorphism Darwin and Hildebrand have shown that fertilisation is possible only (in the case of *Linum perenne*) or at least has the best result when the pollen of the long-styled flower is carried to the short-styled stigma of another plant, and *vice versâ*[6]. Where there are three different lengths of style, fertilisation succeeds best when the pollen is carried to the stigma which stands at the same height in another flower as the anthers from which the pollen came. It will be seen that this is but an expansion of the same rule.

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[1] [Ueber die Befruchtung von *Corydalis cava*, Jahrb. für wiss. Bot. 1866.]

[2] According to Fritz Müller (Bot. Zeit. 1868, p. 114), in some species of Oncidium the pollen-masses and stigmas of the same individual have a positively poisonous effect on one another.

[3] Fritz Müller, Bot. Zeit. 1864, p. 629.

[4] [Darwin, On the Two Forms, or Dimorphic Condition, in the Species of Primula, Journ. Proc. Linn. Soc. Bot. 1862, p. 77; ditto, On the Existence of Two Forms, &c. of the Genus Linum, ibid., 1863, p. 69; ditto, On Trimorphism in *Lythrum Salicaria*, ibid. 1864, p. 169; ditto, On the Character and Hybrid-like Nature of the Offspring from the Illegitimate Unions of Dimorphic and Trimorphic Plants, Journ. Lin. Soc. 1868, p. 393.—Ed.]

[5] Hildebrand, Bot. Zeit. 1871, Nos. 25, 26.

[6] [Darwin has given the name of *legitimate* to the union of two distinct forms, *illegitimate* to the impregnation of long- or short-styled plants by their own form pollen.—Ed.]

While in the very numerous diclinous, dichogamous, dimorphic, and trimorphic flowers, insects carry pollen from one flower to another, it is comparatively rare for cross-pollination to take place without the help of insects. This occurs in some Urticaceæ, as Pilea and Broussonetia, where the anthers emerge suddenly from the bud and scatter their light pollen in the air like a fine cloud of dust, which is then blown to the female organs of other flowers. In the rye the arrangement is still simpler; the flowers open separately, usually in the morning; the filaments elongate rapidly and push the ripe anthers out of the pales; the anthers then hang down at the end of the long filaments, open, and allow the heavy pollen to fall down, thus reaching the stigmas of other flowers lower down in the same spike or in neighbouring spikes, being assisted in this by the oscillations of the haulm under the influence of the wind[1].

In connection with the tendency so clearly evidenced even among Cryptogams, and still more among Phanerogams, to prevent self-fertilisation within the same hermaphrodite flower, it is a very remarkable fact that there are a number of plants among Angiosperms which form two kinds of hermaphrodite flowers, *viz.* large flowers which can generally be fertilised by the pollen of other flowers, and small, more or less depauperated flowers, sometimes underground, which never open [*Cleistogamous* Flowers], the pollen emitting its tubes immediately from the anthers and thus fertilising the ovules. There occur therefore in these cases different kinds of flowers on the same individual, one kind being adapted for cross-, the other kind exclusively for self-fertilisation[2]. This occurs, for example, in *Oxalis Acetosella*, where the small flowers are formed close to the ground when the larger flowers have already ripened their fruit; in *Impatiens Noli-me-tangere*, *Lamium amplexicaule*, *Specularia perfoliata*, many species of Viola, as *V. odorata*, *elatior*, *canina*, *mirabilis*, &c., *Ruellia clandestina*, many Papilionaceæ, as Amphicarpæa, and Voandzeia, *Commelyna bengalensis*, &c. When in these cases the large typically developed flowers are fertile, cross-fertilisation with other flowers of the same species must happen occasionally in the course of generations, and the small depauperated self-fertilised flowers then seem to be a subsidiary contrivance whose purpose is altogether unknown. It is however remarkable, and apparently in contradiction to the general rule, that the large normal flowers sometimes exhibit a tendency to infertility (as in species of Viola) or are altogether unfruitful (as in Voandzeia), so that reproduction depends in such cases mainly or entirely on the cleistogamous self-fertilised flowers. But since there are many questions in connection with this subject that are not yet solved, these rare exceptions cannot overthrow the general law[3].

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[1] [For a detailed account of the very remarkable phenomena connected with the pollination of rye and other cereals, see Hildebrand in Gardener's Chronicle, March 15 and 22, and May 24, 1873; also A. S. Wilson, Trans. Bot. Soc. Edin. XI, 506 and XII, 84. Flowers the pollination of which is effected by the wind are termed *anemophilous*, in contradistinction to the *entomophilous*, or those pollinated by the agency of insects.—Ed.]

[2] H. v. Mohl, Einige Beobachtungen über dimorphe Blüthen, Bot. Zeit. 1863, Nos. 42, 43. [See also A. W. Bennett on the closed self-fertilised flowers of Impatiens in Journ. Linn. Soc. 1872, p. 147; ditto, Pop. Sci. Rev. 1873, p. 337. In *Juncus bufonius* the pollen-tubes are emitted while the pollen-grains are still enclosed in the anther, perforating the wall of the latter.—Ed.]

[3] [Herrmann Müller (Nature, vol. VIII, p. 433 *et seq.*) has pointed out the existence of another kind of dimorphism, in which a species presents two different forms of flowers, one adapted to self-

In other cases, as in most Fumariaceæ, *Canna indica*, *Salvia hirta*, *Linum usitatissimum*, *Draba verna*, *Brassica Rapa*, *Oxalis micrantha* and *sensitiva*, the pollen must also, according to Hildebrand, owing to the position of the sexual organs, fall on the stigma in the same flower, and is potent; but in such cases, since the flowers are visited by insects, an occasional crossing with other flowers is not impossible. Even among Orchideæ, where we find the most wonderful contrivances to prevent self-fertilisation, Darwin found an instance in *Cephalanthera grandiflora* in which the pollen-tubes are emitted from the pollen-grains on to the stigma while the former are still in the anthers; but according to Darwin's experiments the number of good seeds produced is smaller when the plant is allowed to fertilise itself than when pollination is effected by foreign pollen with the help of insects.

A clear comprehension of the phenomena of dichogamy, dimorphism, and the other contrivances for ensuring cross-fertilisation, can only be obtained by a careful study of numerous individual cases[1].

It is more clearly seen in the fertilisation of flowers than almost anywhere else how exactly the development of the organs is adapted to the fulfilment of a perfectly definite purpose. Each plant has its own peculiar contrivance for the conveyance of the pollen to the stigma of another flower. It is not possible to make many general remarks on this subject; the following may suffice here.

It must be noted in the first place that insects[2] carry pollen undesignedly while seeking the nectar of flowers which has been produced exclusively for their attraction. Flowers which are not visited by insects, and Cryptogams which do not require them, do not secrete any nectar. The position of the nectaries, usually concealed deep at the bottom of the flower, as well as the size, form, arrangement, and often also the movement of the parts of the flower during the time of pollination, are always of such a nature that the insect—sometimes of one particular species—must take up particular positions and make particular movements in obtaining the nectar, and thus cause the masses of pollen to

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fertilisation, smaller and less brightly-coloured, growing in situations where there are but few insects, the other adapted to cross-fertilisation, larger and more brightly-coloured, growing where insects abound. These two forms have occasionally been described as distinct varieties or even species. —Ed.]

[1] See especially K. C. Sprengel, Das neu entdeckte Geheimniss der Natur, &c., Berlin, 1793.—Darwin, On the Fertilisation of Orchids, London, 1862.—Hildebrand, Die Geschlechtervertheilung bei den Pflanzen, u. das Gesetz der vermiedenen u. unvortheilhaften stetigen Selbstbefruchtung, Leipzig, 1867.—Strasburger in Jenaische Zeitschrift, vol. VI, 1870, and Jahrb. für wiss. Bot. vol. VII, where the mode of fertilisation of Gymnosperms, Marchantieæ, and Ferns is described. [The most complete account of the phenomena of the reciprocal adaptation of flowers and insects to cross-fertilisation is contained in Herrmann Müller's Befruchtung der Blumen durch Insecten u. die gegenseitigen Anpassungen beider, Leipzig, 1873, where also is a *resumé* of the literature of the subject. See also Kölreuter, Vorläufige Nachricht von einigen das Geschlecht betreffenden Versuchen, Leipzig, 1761.—Delpino, Ulteriori osservazioni sulla dicogamia, Milan, 1868–1870.—Axell, Om Anordningarna for fanerogama växternas befruktning, 1869.—Darwin, On the Agency of Bees in the Fertilisation of Papilionaceous Flowers, Ann. and Mag. Nat. Hist. 3rd series, vol. II, p. 461. —Ogle in Pop. Sci. Rev. 1869, p. 261, and 1870, p. 45 (on Salvia).—Hildebrand in Leopoldina, 1869 (Compositæ); ditto, in Monatsber. der Berlin. Akad. 1872 (Grasses).—Farrer in Ann. and Mag. Nat. Hist. 1868; Nature, vol. VI, 1872, p. 478 *et seq.* (Papilionaceæ).—A. W. Bennett, in Pop. Sci. Rev. 1873, p. 337.—H. Müller, in Nature, vols. VIII, IX, and X.—Sir J. Lubbock, On British Wild Flowers considered in relation to Insects, London, 1875.—Ed.]

[2] J. G. Kölreuter first recognised the necessity of insect help, and described special contrivances for pollination, in his Vorläufige Nachricht von einigen das Geschlecht der Pflanzen betreffenden Versuchen, 1761.

become attached to its hairs, feet, or proboscis, and afterwards, when assuming similar positions, to be applied to the stigmas of other flowers. In dichogamous plants the movements of the stamens, styles, or arms of the stigmas assist this end, taking place frequently in such a way that at one time the open anthers occupy the same position in the flower that the receptive stigmas do at another time, so that the insect, when taking up the same position, touches the open anthers in one flower and the receptive stigmas in another flower with the same part of its body. The same result is also obtained in dimorphic flowers, the pollination being in these cases efficacious when anthers

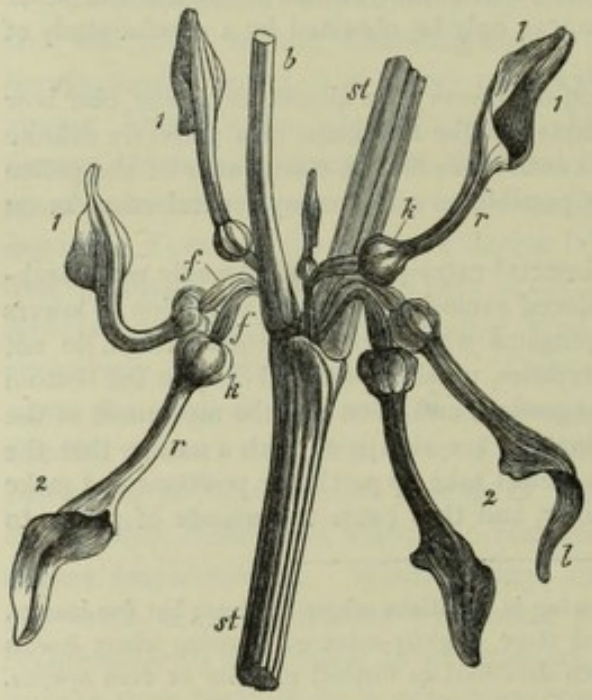

FIG. 457.—*Aristolochia Clematitis*: a piece of a stem *st* with petiole *b*; in the axil of this are flowers of different ages; 1, 1 young flowers not yet fertilised; 2, 2 fertilised flowers, the pedicels bent downwards; *k* swollen part of the tube of the perianth *r*; *f* the inferior ovary (natural size).

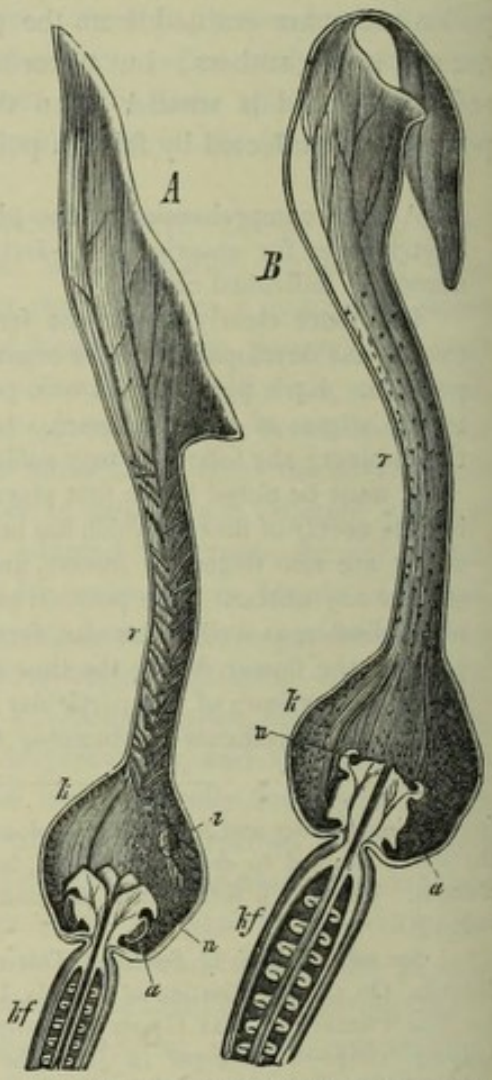

FIG. 458.—*Aristolochia Clematitis*: the perianth cut through longitudinally. *A* before, *B* after pollination (magnified).

and stigmas which occupy the same position in different flowers are made mutually to act on one another. But there are besides many other contrivances, most variable in their nature and often perfectly astonishing, for effecting the conveyance of pollen by insects. A few examples may suffice.

(1) Dichogamous Flowers[1] are either *protandrous* or *protogynous*[2]. In the former the stamens are developed first, their anthers opening at a time when the stigmas are still undeveloped and not yet receptive; the stigmatic surface is only developed later, and

[1] F. Delpino, Ulteriori osservazioni sulla dicogamia nel regno vegetabili, Atti della soc. Ital. di sci. nat. vol. XIII, 1869, and Bot. Zeit. 1871, No. 26 *et seq.*; ditto, in Bot. Zeit. 1869, p. 792.

[2] [For a list of British protandrous, protogynous, and 'synacmic' plants (or those in which the male and female organs are mature at nearly the same time), see A. W. Bennett in Journal of Botany, 1870, p. 315, and 1873, p. 329.—ED.]

usually not till the pollen has been carried away from the anthers by insects; they can then only be fertilised by the pollen of younger flowers. To this category belong the various species of Geranium, Pelargonium, Epilobium, Malva, Umbelliferæ, Compositæ, Campanulaceæ, Labiatæ, Digitalis, &c. The phenomena referred to, especially the movements of the stamens and stigmas, are so readily observed in these cases, *e. g.* in Geranium and Althæa, that no further description is necessary. In protogynous flowers the stigma is receptive before the anthers in the same flower are mature; when these subsequently open and allow the pollen to escape, the stigma has already been pollinated by foreign pollen or has even withered up and fallen off (as in *Parietaria diffusa*); and the pollen of these flowers can therefore only be applied to the fertilisation of younger flowers. To this class belong *Scrophularia nodosa*, *Mandragora vernalis*, *Scopolia atropoides*, *Plantago media*, *Luzula pilosa*, *Anthoxanthum odoratum*, &c. Among protogynous flowers *Aristolochia Clematitis* is characterised by striking and peculiar contrivances.

In Fig. 458 *A* is shown a young flower cut through lengthwise; the stigmatic surface *n* is already in a receptive condition, but the anthers are still closed; a small fly *i*, which has brought on its back a mass of pollen from an older flower, is forced in through the narrow throat of the perianth, and runs about in the globular swelling *k*; as many as from six to ten flies are not unfrequently found in one flower. They are shut up and cannot escape, because the throat of the perianth *r* is furnished with long hairs moving as on a hinge, which present no impediment to the entrance of the insect, but prevent its escape like a trap. While the insect is moving about in the cavity, its back laden with pollen comes into contact with the stigmatic surface and pollinates it, in consequence of which the lobes of the stigma curve upwards, as is shown in Fig. 458 *B*, *n*. As soon as this has taken place, the anthers, previously closed, open; they are laid bare by the change in the position of the stigmas, and are rendered accessible by the withering up of the hairs at the bottom of the cavity of the flower, which has now become wider. The flies which have now carried their pollen on to the stigmatic surface, can therefore creep down to the open anthers, where the pollen again becomes attached to them. By this time the throat of the perianth *r* has again become passable, the net-work of hairs in it having died and withered away after the pollination of the stigma. The insect, laden with the pollen of this flower, can now escape, and again performs the same work in another flower. But while the changes which have been described are taking place inside the flower, its position has also altered. As long as the stigma is still receptive, the pedicel is erect and the perianth open outwards (Fig. 457 *i i*), so that the visiting flies find a door hospitably open. But as soon as the pollination of the stigma has been effected, the pedicel bends sharply downwards just beneath the ovary, and when the flies, again laden with pollen, have flown out of the flower, the standard-like lobe of the perianth above the mouth of the tube (Fig. 458 *B*) closes, preventing the entrance of the flies, whose visits would now be useless.

(2) *Flowers in which the anthers and stigmas are mature at the same time, but self-fertilisation is hindered or prevented by the position of the organs and by mechanical contrivances.* The pollen is in these cases also usually carried to the stigma by insects, but generally in such a manner that the stigma can only be pollinated by the pollen from another flower, though sometimes, as in Asclepiadeæ, pollination from the same flower is not impossible in addition to cross-fertilisation. The contrivances for this purpose are astonishingly numerous, and sometimes so complicated that their purpose can only be detected by very careful investigation. To this category belong, for example, the various species of Iris, Crocus, and Pedicularis, many Labiatæ, Melastomaceæ, Passifloraceæ, and Papilionaceæ. Among the most interesting examples are the Asclepiadeæ, in which however the contrivances could be explained only by lengthy descriptions and a large number of illustrations[1]. In *Salvia pratensis* and some other species of this genus

[1] For a fuller description, see R. Brown, Observations on the Organs and Mode of Fecundation in Orchideæ and Asclepiadeæ; Trans. Linn. Soc. 1833, and Hildebrand in Bot. Zeit. 1867, No. 34.

the mechanical contrivance for preventing self-fertilisation and for ensuring crossing[1] is extremely beautiful and easy to understand. Fig. 459 represents a flower of *S. pratensis* seen from the side; at *n* is the two-lipped stigma in a receptive condition; and indicated by a dotted line inside the upper lip of the corolla is the position of one of the two stamens. If a pin is inserted into the tube of the corolla in the direction of the arrow, the two stamens spring out, as indicated at *a*; if a humble-bee inserts its proboscis in order to obtain the honey, the open anthers strike the back of the insect, and some of the pollen adheres to a particular part; when the bee places itself in the same position in

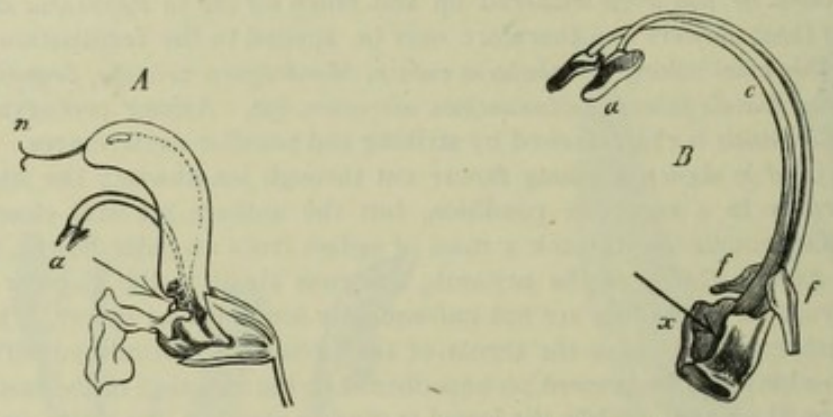

FIG. 459.—*Salvia pratensis*: a corolla with stigmas *n* and fertile anther-lobes *a*; *B* stamens removed from corolla.

another flower, the pollen is rubbed off its back on to the stigma. The cause of the stamen springing out in this way is made sufficiently clear in Fig. 459 *B*. This shows the short true filaments *ff* which adhere by their bases to the sides of the corolla-tube, and bear at their upper end the long connective *c x*, which oscillates readily about its point of attachment. Only the upper longer and slender arm of each connective *c* bears an anther-lobe *a*, the lower shorter arm *x* is without an anther, and is applied to that of the other stamen in such a manner that the two form together a kind of arm-chair. When the proboscis of the bee in search of honey penetrates the flower in the direction of

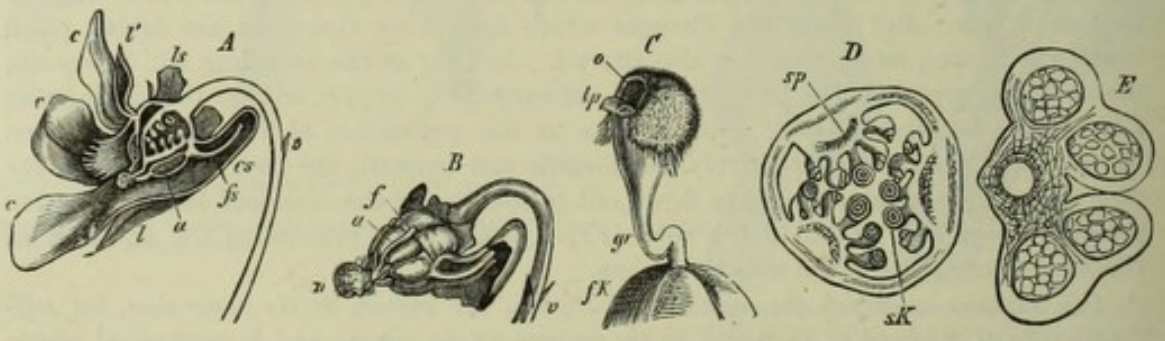

FIG. 460.—*Viola tricolor*: *A* longitudinal section through the flower (natural size); *B* the ovary fertilised and swollen; the filaments have been ruptured and the anthers drawn up by the growth of the ovary; *C* the stigma with its orifice *o* and lip *lp*, on the style *gr* (magnified); *l* sepals, *ls* prolonged base of the sepals, *c* petals, *cs* spur of the inferior petals or nectary; *fs* appendages of the two inferior stamens projecting into the spur, which secrete the nectar, *a* the anthers, *n* stigma, *v* bracts; *D* horizontal section through the ovary with the three placentæ *sp* and ovules *sK*; *E* horizontal section through an unripe anther.

the arrow, the lower arm of the connective is pressed down, and the upper arm *c* is made to move forward, and thus to strike the back of the insect.

In the pansy (*Viola tricolor*) we have quite a different contrivance for preventing the possibility of self-fertilisation. In Fig. 460, *A* and *B*, is shown the position and arrangement of the parts of the flower. The cavity of the flower enclosed by the petals is completely filled up by the anthers and ovary, with the exception of the tubular spur of

[1] For further details, see Hildebrand, Jahrb. für wiss. Bot. vol. IV, 1865, p. 1.

the inferior petal in which the nectar collects, secreted by the appendages of the two inferior stamens. The only entrance to this nectary, which therefore lies behind the reproductive organs, is through a deep channel in the inferior petal, lined with hairs. The upper and lateral petals incline towards one another in front of the ovary which is surrounded by the anthers, and above the channel in such a manner that the entrance to it is entirely filled up by the capitate stigma *B, n*. The stigma is seated on a flexible style (*C, gr*), is hollow and opens by an orifice which faces the hairy channel of the lower petal; the lower and posterior margin of this orifice has a lip-like appendage. The anthers open of their own accord, and the pollen in the form of a yellow powder collects below and behind the stigma among the hairs of the channel. An insect which has already brought pollen on its proboscis from another flower inserts its proboscis beneath the stigma through the channel into the nectary. The foreign pollen, which is attached to the proboscis, is thus rubbed off on to the lip of the stigma, it is detained by the viscid secretion which fills up the hollow of the latter, and subsequently emits its pollen-tubes through the canal of the style (see also Fig. 364, p. 499). While the insect is sucking the nectar in the spur, the pollen of this flower, which lies in the channel behind the stigma, becomes attached to the proboscis; when the proboscis is again drawn out, this pollen does not come into contact with the viscid stigma, the lip being drawn forward by the motion of the proboscis, and the orifice of the stigma protected. The pollen that is removed from this flower is now carried, in the manner described to the stigma of another flower. If the insect were to insert its proboscis again into the nectary of the same flower, the pollen would be detached into the cavity of its own stigma; but, as Hildebrand has remarked, insects do not usually do this, but suck up the nectar only once, and then visit another flower. The proceeding of the insect may be imitated by inserting a fine sharp pin beneath the stigma into the channel and again withdrawing it, and filling with the pollen thus removed the stigmatic cavity of another flower.

The contrivances for cross-pollination in Orchids, as numerous as they are complicated and ingenious, have been described in detail by Darwin in the work already named[1]. One of the simpler cases, and the most frequent in its main features, may be briefly described in the case of *Epipactis latifolia*. At the time when the reproductive organs are mature, the flower stands, in consequence of a torsion of its pedicel, so that the true posterior leaf of the six that form the perianth (the labellum) hangs in front and downward; it is hollowed out in its lower part, and is thus transformed into a receptacle for the nectar which it secretes (Fig. 461, *B, D, l*). The sexual organs, borne on the gynostemium *S* (in *C*) project obliquely above this nectary; the stigma forms a disc with several lips hollowed out and viscid in the centre, the surface of which is inclined obliquely above the nectary. The two gland-like staminodes *x x* stand right and left beside the stigma; above the stigma and covering it like a roof lies the single fertile anther, of considerable size, which is again on its part protected above by its cushion-like connective *cn*; the lateral walls of the two anther-lobes burst lengthwise right and left, so that their pollen-masses (pollinia) became partially exposed, the pollen-grains remaining attached to one another by a viscid substance. In front of the middle of the anther and above the stigmatic surface is the rostellum *b*, a peculiarly metamorphosed part of the stigma (see *A*); the tissue of the rostellum is transformed into a viscid substance covered only by a thin membrane. The flower of Epipactis is not fertilised if left to itself; the pollinia do not fall of their own accord out of the anther, and would even then not reach the stigmatic surface; they must be carried away by insects to the stigma of other flowers. The mode in which this is effected is explained by inserting the point of a black-lead pencil into the flower in a direction towards the bottom of the labellum and beneath the stigmatic surface; if it is then pressed

[1] See also Wolff, Beiträge zur Entwickelungsgeschichte der Orchideen-blüthe, in Jahrb. für wiss Bot. vol. IV, 1865.

slightly against the rostellum, and again withdrawn slowly in this position (*D*), the viscid mass of the rostellum or adhesive disc of the pollinia to which the pollen-masses are attached, remains sticking to the pencil. The pollinia are now completely removed from the two anther-lobes by the withdrawing of the pencil, as is shown in *E* and *F*. If the pencil with its pollinia attached is now again inserted into another flower in the direction of the bottom of the labellum, the pollinia necessarily come into contact with the viscid stigmatic surface and adhere firmly to it; when the pencil is again withdrawn they are left behind, being partially or entirely torn from the pencil. In consequence of the form and position of the parts of the flower, an insect which settles on the anterior part of the labellum would in the same manner be able to creep into the bottom of the nectary without disturbing the rostellum; but when it again crept out after obtaining the nectar, it

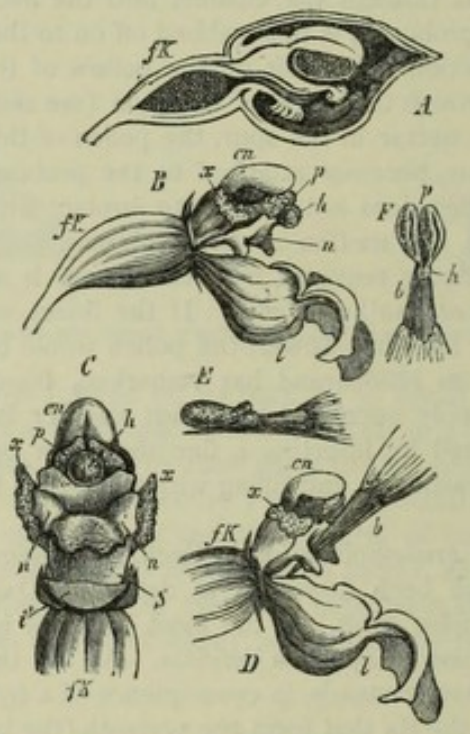

FIG. 461.—*Epipactis latifolia*: *A* longitudinal section through a flower-bud; *B* open flower after removal of the perianth with the exception of the labellum *l*; *C* the reproductive organs after removal of the perianth seen from below and in front; *D* as *B*, the point of a lead-pencil *b* inserted after the manner of the proboscis of an insect; *E* and *F* the lead-pencil with the pollinia attached; *fK* ovary, *l* labellum, its bag-like depression serving as a nectary, *n* the broad stigma, *cn* the connective of the single fertile anther, *p* pollinia, *h* the rostellum, *x x* the two lateral gland-like staminodes, *i* place where the labellum has been cut off, *s* the columnar style.

would strike against it and carry off the pollinia; and on crawling into a second flower, these would come into contact with the viscid stigma, and would remain attached to it. In some other Orchideæ the contrivances are much more complicated.

SECT. 32.—**Hybridisation**[1]. In the preceding paragraphs we have spoken only of the union of the reproductive cells of the same plant, or of two individuals of the same species. We learn however from experience that a fertile sexual union can

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[1] J. G. Kölreuter, Vorläufige Nachricht von einigen das Geschlecht der Pflanzen betreffenden Versuchen u. Beobachtungen, Leipzig, 1761; Appendices in 1763, 1764, and 1766. — W. Herbert, On Amaryllidaceæ, with a treatise on cross-bred vegetables; London, 1837.—Gärtner, Versuche u. Beobachtungen über die Bastarderzeugung im Pflanzenreich; Stuttgart, 1849. [See notice by Berkeley, Journ. Roy. Hort. Soc. vol. V, 1850, p. 156.]—Wichura, Die Bastardbefruchtung im Pflanzenreich, erläutert an den Bastarden der Weiden (with two nature-printed plates): Breslau, 1865. [See abstract by Berkeley, Journ. Roy. Hort. Soc. new series, vol. I, 1850, p. 57.]

take place between plants which are specifically distinct. A union of this kind is called *Hybridisation*, and its product a *Hybrid*. According as the union takes place between different varieties of one species, different species of one genus, or between two species belonging to different genera, the resulting hybrid may be termed a variety-hybrid, species-hybrid, or genus-hybrid.

Among Cryptogams only a few instances of hybridisation are known with certainty. Thuret (Ann. des sci. nat., 1855) obtained hybrid plants by bringing spermatozoids of *Fucus serratus* into contact with oospheres of *F. vesiculosus*. In some other families of Cryptogams forms have been found which have been supposed, from their characters, to have a hybrid origin. Thus A. Braun (Verjüngung, p. 329) adduces instances of hybrids between Mosses[1], *Physcomitrium pyriforme* and *Funaria hygrometrica*, and between *Physcomitrium fasciculare* and *Funaria hygrometrica*, and between the following species of Ferns—*Gymnogramme chrysophylla* and *G. calomelana*, *G. chrysophylla* and *G. distans*, and *Aspidium Filix-mas* and *A. spinulosum*[2].

The most important observations from a scientific point of view, which have given us the clearest insight into the nature of the difference of sex, are however those made on hybrids between flowering plants, resulting from the artificial conveyance of pollen from one species to another. Nägeli has collected the results of many thousand experiments on hybridisation made by Kölreuter in the last century, and more recently by Knight, Gärtner, Herbert, Wichura, and other observers. The following facts are taken chiefly from Nägeli's *resumé*[3].

Only those forms which are closely related genetically can produce hybrids. They are formed most easily between different varieties of the same species; with greater difficulty—but are still possible in a great number of cases—between two species of the same genus; of hybrids between species which belong to different genera only a very few instances are known, and it is probable that in these cases the species ought to be included in the same genus. The facility with which hybrids can be produced varies extremely in different orders, families, and genera of Angiosperms. The phenomenon is frequent among Liliaceæ, Irideæ, Nyctagineæ, Lobeliaceæ, Solanaceæ, Scrophulariaceæ, Gesneraceæ, Primulaceæ, Ericaceæ, Ranunculaceæ, Passifloraceæ, Cactaceæ, Caryophyllaceæ, Malvaceæ, Geraniaceæ, Œnothereæ, Rosaceæ, and Salicineæ. It does not occur at all, or only very exceptionally, in Gramineæ, Urticaceæ, Labiatæ[4], Convolvulaceæ, Polemoniaceæ, Grossulariaceæ, Papaveraceæ, Cruciferæ, Hypericineæ, and Papilionaceæ. Even genera of the same order or family differ in this respect. Among Caryophyllaceæ, the species of Dianthus hybridise easily, those of Silene only with difficulty; among Solanaceæ, the species of Nicotiana and Datura have a tendency to produce hybrids, while those of Solanum, Physalis, and Nycandra have not; among Scrophulariaceæ,

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[1] [See also H. Philibert, L'Hybridation dans les Mousses (Grimmia) Ann. des sci. nat. 1873, vol. XVII, p. 225.—Ed.]

[2] [See also T. Moore on *Adiantum farleyense*, Journ. Roy. Hort. Soc. new series, I, p. 83; Berkeley on *Asplenium ebenoides*, Scott, ibid. p. 137.—Ed.]

[3] Nägeli, Sitzungsber. der kais. bayer. Akad. der Wiss. in München, Dec. 23, 1865, and Jan. 13, 1866.

[4] [*Stachys ambigua* Sm. is considered to be a hybrid between *S. sylvatica* and *S. palustris*—Ed.]

Verbascum[1] and Digitalis, but not Pentstemon, Linaria, or Antirrhinum; among Rosaceæ, Geum, but not Potentilla.

Hybridisation between species belonging to different genera has been observed between Lychnis and Silene, Rhododendron and Azalea, Rhododendron and Rhodora, Azalea and Rhodora, Rhododendron and Kalmia, Rhododendron and Menziesia[2], Ægilops and Triticum, and between Echinocactus, Cereus, and Phyllocactus, to which must be added a few wild forms which appear to be genus-hybrids.

Besides the near genetic relationship, the possibility of the production of hybrids depends also on a certain relationship between the parent-plants, which is manifested only in the result of hybridisation, and which Nägeli calls 'Sexual Affinity.' This kind of affinity is not always concurrent with the external resemblance of the plants. Thus, for example, hybrids have never been obtained between the apple and pear[3], *Anagallis arvensis* and *cærulea*, *Primula officinalis* and *elatior*, or *Nigella damascena* and *sativa*, nor between many other pairs of species belonging to the same genus which are very nearly allied to one another; while in other cases very dissimilar forms unite, as *Ægilops ovata* with *Triticum vulgare*, *Lychnis diurna* with *L. Flos-cuculi*, *Cereus speciosissimus* with *Phyllocactus Phyllanthus*, the peach with the almond. A still more striking proof of the difference between sexual and genetic affinity is afforded by the fact that varieties of the same species will sometimes be partially or altogether infertile with one another, as *e.g. Silene inflata* var. *alpina* with var. *angustifolia*, var. *latifolia* with var. *littoralis*, &c.

When a sexual union is possible between two species A and B, A can usually produce hybrids when fertilised by the pollen of B, and B when fertilised by the pollen of A (reciprocal hybridisation). But there are cases in which A can only be the male and B only the female parent plant, the pollination of A by B yielding no result. Thus Thuret found, as has already been mentioned, that *Fucus vesiculosus* produces hybrids with the spermatozoids of *F. serratus*, while the oospheres of the latter species could not be fertilised by the spermatozoids of the former. Gärtner states that *Nicotiana paniculata* produces seeds when acted on by the pollen of *N. Langsdorfii*, while the latter does not under the influence of the pollen of the former. Kölreuter easily obtained seeds of *Mirabilis Jalappa* with the pollen of *M. longiflora*, while more than two hundred experiments on pollinating the latter by the former species extending over eight years produced no result.

Sexual Affinity presents a great variety of gradations. At one extreme we have complete infertility under the influence of the pollen of another variety or species, the pollen-tubes not even entering the stigma, and the pollinated flower behaving precisely as if no pollen had reached it; the other extreme is shown in the production

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[1] [On hybridity in the genus Verbascum, see Darwin, Journ. Linn. Soc. 1868, p. 437.—Ed.]

[2] [The history of the plant which is here intended is given in the Botanical Gazette, vol. III, p. 82. It was raised from seed of *Bryanthus* (*Menziesia*) *empetriformis*, supposed to be fertilised by the pollen of *Rhodothamnus* (*Rhododendron*) *Chamæcistus*. It is figured under the name of *Bryanthus erectus* in Paxton's Flower Garden, vol. I, t. 19; but it agrees well with specimens of its female parent from the Rocky Mountains, and is probably therefore not a hybrid at all.—Ed.]

[3] [An instance to the contrary is recorded in the Proc. Acad. Philadelphia, 1871, vol. I, p. 10. —Ed.]

of numerous hybrids, which not only grow vigorously, but are themselves fertile. The lowest degree of the action of pollen of a different kind consists in various changes taking place in the parts of the flower of the mother-plant, the ovary or even the ovules also growing, without any embryo being produced. A higher degree is manifested in the production of ripe normal fruits and seeds containing embryos, but these embryos having no power of germination. Further steps are indicated by the number of embryos which have the power of germination that are produced in the ovary[1].

When pollen from different species is applied simultaneously to the same stigma, only one kind is potent, *viz.* that from the species which has the greatest sexual affinity to the one that is pollinated. And since, as a general law, pollen is most efficacious on a different flower of the same species—in other words, the highest degree of sexual affinity occurs between different individuals of the same species—when a stigma is pollinated at the same time with pollen of the same and of another species, the first only is potent. But since, on the other hand, hybrids are sometimes more easily produced between varieties than between individuals of the same variety, in this case the foreign pollen may be prepotent over that of the same kind. When the pollen of different species reaches the stigma at the same time, and if that which reaches it later has a greater sexual affinity, it can only be potent when the first is not potent or acts injuriously. In Nicotiana the production of hybrids can no longer be prevented by its own pollen after two hours, in Malva and Hibiscus after three hours, in Dianthus after five or six hours.

The hybrid is possessed of external characters intermediate between those of its parent-forms, usually nearly half way between; less often it resembles one of the parent-forms more nearly than the other, and this is more often the case with variety-hybrids than with species-hybrids. It follows that in reciprocal hybrids from the species A and B, the hybrid A B is generally similar externally to the hybrid B A, though the two forms may differ somewhat internally. Thus, according to Gärtner, the hybrid *Nicotiana paniculato-rustica* is more fertile than the reciprocal hybrid *Nicotiana rustico-paniculata*[2]. An internal difference between reciprocal hybrids is also shown by the fact that one is more variable than the other; thus, according to Gärtner, the progeny of *Digitalis purpureo-lutea* is more variable than that of *D. luteo-purpurea*, the progeny of *Dianthus pulchello-arenarius* more variable than that of *D. arenario-pulchellus*.

When two species A and B hybridise, and the one species A exercises a greater influence on the form and properties of the hybrid than the other species B, the hybrid or its descendants, if fertilised by A, will revert more quickly to the parent-form A than it will to the parent form B if fertilised by it. Thus Gärtner states that the hybrid of *Dianthus chinensis* and *D. Caryophyllus* reverts to the latter form after three or four generations if repeatedly fertilised by it, while it requires fertilisation for five or six generations by *D. chinensis* in order to revert to that form.

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[1] See Hildebrand, Bastardirungsversuche an Orchideen, Bot. Zeit. 1865, No. 31.

[2] In this mode of designating hybrids, the name of the male parent-plant stands first; thus *Nicotiana rustico-paniculata* is the product of the fertilisation of *N. paniculata* by the pollen of *N. rustica*.

The characteristics of the parent-forms are as a rule so transmitted to the hybrid that the influence of both is manifested in all its characters, producing a fusion of the different peculiarities. This is more evident in the species- than in the variety-hybrids; in the latter some of the non-essential characters of the parents sometimes present themselves in the offspring uncombined side by side; *e.g.* various kinds of streaks and blotches instead of a mixing of the colours of the flowers. Thus a hybrid which Sageret obtained from *Cucumis Chate* (female) with *C. Melo Cantalupus* (which had a reticulated flesh) had a yellow flesh, a reticulate marking of the rind and moderately prominent ribs like the male parent, but white seeds and an acid flavour like the female parent. Another hybrid from the same species had, on the contrary, the sweet flavour and yellow flesh of the male, with the white seeds and smooth rind of the female parent. To this category belongs also the hybrid of *Cytisus Laburnum* and *purpureus* [known as *Cytisus Adami*], some of the branches of which partially or entirely resembled one and some of them the other parent-form. I have found what seemed to be a hybrid *Antirrhinum majus*, in which the inflorescence bore on one side of the axis only dark-red, on the other side only yellow flowers, while between the two halves stood a single flower which was half red and half yellow.

In addition to its inherited properties, the hybrid usually possesses characters of its own by which it is distinguished from both its parent-forms. One of these new characters, which occurs especially with variety-hybrids, is the tendency to vary more strongly than its parent-forms. Species-hybrids are usually weak in their sexual properties; those derived from nearly related parent-species are, on the other hand, more vigorous in their growth than their parent-forms, while hybrids resulting from the union of species less nearly related are generally feebler in their development. The luxuriant growth of the hybrids from nearly allied species is displayed in their taller and stouter stems, more copious root-system, and larger number of shoots (stolons, scions, &c.). Hybrids have also a tendency to a longer duration of life; those of annual or biennial parent-forms often live a number of years, probably in consequence of their producing a smaller number of seeds. Hybrids are also characterised by commencing to flower earlier, and continuing to do so longer and more abundantly, than the parent-forms; sometimes they produce an extraordinary number of flowers, which are also larger, more enduring, and of brighter colour and stronger odour. They have also a tendency to become double, their staminal and carpellary leaves to increase in number and develope into petals. Along with this luxuriant vegetative growth, the sexual organs are usually weak, and this in every possible degree. 'The stamens,' says Nägeli, 'are, it is true, in some cases perfect externally, but partially or altogether infertile, the pollen-grains not attaining their proper development; while in others the stamens are altogether abortive and reduced to rudiments. The pistils (gynæceum) of hybrids are in most cases not distinguishable externally from those of the parent species, but their ovules have no power, or only to a slight degree, of becoming fertilised; no embryonic vesicles are formed, or the embryo which begins to be developed from the embryonic vesicles perishes sooner or later. Under favourable circumstances, when fertile seeds are produced, their number is smaller, and they manifest a certain degree of feebleness in their slow germination and the short duration of this capacity.' The feebleness of the sexual

function is in some variety-hybrids scarcely perceptible, in others but small; in general it is the more marked the more distant the genetic and sexual affinity of the parent-forms. When species-hybrids have the power of producing seeds by self-pollination, and this is repeated in the progeny, their fertility generally diminishes from generation to generation; though this phenomenon probably depends less on the sexual feebleness of hybrids than on the circumstance that their flowers have probably been generally self-fertilised, instead of being pollinated by other flowers or other individuals of the same hybrid. Nägeli's rule holds true in the general way, that the male organs of species-hybrids are functionally weak to a higher degree than the female organs, although the rule is not without exceptions.

'Hybrids usually vary less in the first generation, the less the degree of affinity between their parent-forms; species-hybrids therefore less than variety-hybrids; the former are often characterised by a great uniformity, the latter by a great variability. When hybrids are self-fertilised, the variability increases in the second and succeeding generations the more completely it was absent from the first; and three different varieties arise more certainly the less the affinity between the parent-forms; *viz.* one corresponding to the original (hybrid) type, the two others bearing a greater resemblance to the two parent-forms. But these varieties show but little constancy, passing easily into one another, at least in the earlier generations. An actual reversion to one of the two parent-forms (with pure breeding-in) takes place especially when the parent-forms are very nearly related, as in variety-hybrids and those from species that approximate to varieties. When this reversion occurs in other species-hybrids, it appears to be limited to those cases where one of the parent-species exercised a preponderating influence in the hybridisation.' (Nägeli, *l. c.*)

When a hybrid is made to unite with one of its parent-forms, or with another parent-form, or with a hybrid of different origin, the product is termed a 'derivative hybrid'; and this may again on its part unite with one of the parent-forms or with a hybrid of different origin. When a union is effected between a hybrid and one of its own parent-forms, and the hybrid thus obtained unites again with the same parent-form, and so on through several generations, the derived progeny approach more and more nearly in their characters to those of this parent-form, until they come to resemble it in all respects. According as one or the other of the parent-forms is taken, a larger or smaller number of generations are required to effect the perfect reversion; and this behaviour has been reduced by Nägeli to a numerical expression (formula of heredity), which indicates in numbers the amount of influence exercised by a species in reference to the hereditary transmission of its qualities in hybridisation. In proportion as the derivative hybrid approaches one or the other of its parent-forms, its hybrid nature gradually decreases, and its fertility at the same time increases.

When a hybrid unites with a new parent-form or with a hybrid of another species, a derivative hybrid results in which three, four, or more species (or varieties) are combined; Wichura has even united six different species of willow in one such derivative hybrid. Hybrids of this kind, which may conveniently be termed 'combined hybrids,' usually follow the same rules with reference to their form and other characters as hold good in the case of simple hybrids. Combined hybrids become less fertile the larger the number of different parent-forms that are united in

them; and they are usually very variable. Wichura showed, from his own observations and those of Gärtner, that hybrid pollen produces a greater variety of forms in its progeny than does the pollen of true species.

The results of hybridisation are important with respect to the theory of sexuality, because there is no boundary-line or essential distinction between the self-fertilisation of pure species or varieties and their fertilisation by other species or varieties; and because in the latter case—in other words in hybridisation—certain peculiarities of sexual differentiation and union are rendered more evident. The two extremes of the conditions under which a fertile union of sexual cells is possible lie at a great distance from one another, but are connected by very numerous transitions. One extreme is presented in the genus Rhynchonema and in some Saprolegnieæ, where a fertile sexual union of sister-cells takes place regularly; the other extreme is furnished in genus-hybrids, where the uniting cells belong to very different forms of plants whose descent from a common ancestor dates back to a remote antiquity. But the great majority of phenomena in the vegetable kingdom show that sexual union is usually most productive when the cells stand neither in too close nor in too remote an affinity to one another; self-fertilisation is in the vast majority of cases as carefully avoided as the hybridisation of different species or genera. The phenomena may be comprised in the statement that the original form of sexual differentiation was probably the simultaneous formation of male and female organs in close juxtaposition on the same plant, but that sexual union is more potent and more favourable for the maintenance of the race when the closely contiguous cells do not unite, but those of different descent, a certain mean amount of difference of descent being established as the most favourable. This mean of the difference of descent associated with a maximum of sexual potency is obtained when the sexual cells belong to different individuals of the same species[1]. The phenomena of structure described in the preceding paragraphs which are manifested in polygamy, diclinism, dichogamy, dimorphism, the impotence of pollen on the stigma of the same flower (as in Corydalis and Oncidium), the mechanical contrivances for rendering self-fertilisation impossible (as in *Aristolochia Clematitis*, many Orchideæ, &c.), are different means for promoting the cross-fertilisation of individuals belonging to the same species or for rendering it alone possible.

CHAPTER VII.

THE ORIGIN OF SPECIES.

Sect. 33.—**Origin of Varieties.** The characters of plants are transmitted to their descendants, or, in other words, are hereditary. But, in addition to the inherited properties, new characters may arise in a smaller or larger number of the descendants of a plant which were not possessed by the parent-plants. Thus, for example, Descemet obtained in 1803[2], among the seedlings from *Robinia Pseud-acacia*, an

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[1] [See Darwin, Variation of Animals and Plants under Domestication, vol. II, chap. xvii, where several illustrations of the law are given.—Ed.]

[2] See Chevreul, Ann. des sci. nat. 1846, vol. VI, p. 157. [Journ. Roy. Hort. Soc. vol. VI, 1851, p. 61.]

individual without spines; Duchesne, in 1761[1], among seedlings of the strawberry, one with simple instead of trifoliolate leaves; and Godron[2], among seedlings of *Datura Tatula*, one with smooth instead of spiny capsules.

The characters which arise in single descendants are often only individual, *i. e.* they are not again transmitted to their descendants. Thus the seeds of the unarmed Robinia produced again spiny plants resembling, not their immediate ancestor, but more remote ones; while in other cases the new character is hereditary, though at first perhaps only partially so, the new form making its appearance only in a certain proportion of the descendants, while the others revert to the original form, as in Duchesne's unifoliolate strawberry.

When a new character is transmitted by inheritance to new generations, the number of individuals that revert to the primitive form often decreases from generation to generation, or the hereditary permanence of the new character increases; they become more and more constant, and sometimes even as much so as those of the primitive form. Such new constant forms are termed *Varieties*[3].

The same parent-form may produce a smaller or larger number either simultaneously or in succession, sometimes even hundreds of new forms; and this is especially the case with cultivated plants. The enormous number of varieties of the dahlia, differing in the colour, size, and form of the flowers and in their mode of growth, now cultivated in our gardens, have been derived since 1802 from the simple yellow-blossomed primitive form of *Dahlia variabilis*. The great variety of pansies, distinguished chiefly by the colour of their flowers, have resulted since 1687 from the cultivation of the *Viola tricolor* of our fields with small flowers almost uniform in colour[4]. Still more numerous are the varieties of *Cucurbita Pepo*, differing not only in the form of their fruit but also in all other characters; and the same is the case with the cabbage (*Brassica oleracea*) and a vast number of other cultivated plants.

Some plants have a special tendency to variation; among native species, for example, the fruticose Rubi, and those of Rosa and Hieracium; others, on the contrary, are distinguished by great constancy in their characters, as for example rye, which has as yet produced no hereditary varieties, notwithstanding long cultivation; while the nearly related species of wheat (especially *Triticum vulgare, amyleum* and *Spelta*) are distinguished by a number of old varieties and an ever-increasing number of new ones.

By far the greater number of hereditary varieties are the result of sexual reproduction; among Phanerogams the new characters appear suddenly in individual seedlings, which differ at once from the parent-plant in these respects. Sometimes however it happens that particular buds develope differently from the other shoots of the same stock; and of this *Bud-variation*[5] two different cases must be carefully

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[1] For further details, see Usteri, Annalen der Botanik, vol. V, p. 40.

[2] See Naudin, Compt. rend. 1867, vol. LXIV, p. 929.

[3] For examples, see Hofmeister, Allgemeine Morphologie, p. 565.

[4] Darwin, The Variation of Animals and Plants under Domestication, vol. I, p. 368 *et seq.*

[5] [T. Meehan adduces a number of remarkable instances of bud-variation in which hybridisation could not have taken any part;—in Rubus which rarely produces seeds in the wild state, *Convolvulus Batatas*, which seldom flowers in America, &c. See Proceedings of the Philadelphia Acad. of Nat. Sci. Nov. 29, 1870.—Ed.]

distinguished, since their significance is altogether different. In one case the abnormal shoot of a stock which itself belongs to a variety resembles or reverts to the primitive form; and this therefore is an instance not of the production but of the cessation of a new form. In the botanic garden at Munich there is, for example, a beech-tree with divided leaves, itself a variety, a single branch of which bears the ordinary undivided entire leaves, or has reverted to the primitive form. In the second case new characters not previously displayed arise on particular shoots of a stock. Thus, for instance, single shoots of the myrtle are sometimes found with leaves in alternating whorls of threes, instead of pairs; but these shoots again produce from the axils of their leaves the ordinary branches with decussate leaves. Knight (see Darwin, *l. c.* vol. I, p. 375) observed a cherry (the May Duke) with one branch bearing fruit of a larger shape which always ripened later. The common 'moss-rose' is considered by Darwin (*l. c.* p. 379) to have probably arisen by 'bud-variation' from *R. centifolia;* the white and striped moss-roses made their appearance in 1788 from a bud of the common red moss-rose; Rivers states that the seeds of the simple red moss-rose almost always again produce moss-roses[1].

Those changes which are produced in a plant by the nature of its food and other external conditions must not be confounded with variation. Specimens of the same plant often differ conspicuously in the size and number of their leaves, shoots, flowers, and fruits, according as their supply of food has been abundant or deficient; deep shade frequently occasions the most striking changes in the habits of plants that usually grow in sunshine; but these changes are not hereditary; the descendants of such individuals revert, under normal conditions of light and nutrition, to the original characters of the species.

Those characters, on the contrary, which may become hereditary or form the groundwork of varieties, arise independently of the direct influence of soil, locality, climate, or other external influences; they appear seemingly without any cause. We must therefore assume either that external impulses which are altogether imperceptible first cause an imperceptible deviation in the process of development, which is always extremely complicated, and that this variation gradually increases until it becomes perceptible, or that the processes in the interior of the plant itself react upon one another in such a manner as to cause sooner or later an external change.

The fact that wild plants, when cultivated, usually begin to produce hereditary varieties, shows that the change in the external conditions of life disturbs to a certain extent the ordinary process of development; but it does not show that particular external influences produce particular hereditary varieties corresponding to them; for under the same conditions of cultivation the most different varieties arise simultaneously or successively from the same parent-form. The same is the case also in nature with wild plants; in the same locality under precisely the same vital conditions a number of varieties are often found by the side of their parent-form, and the same variety is often found in the most diverse localities[2]. It is for this very

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[1] [See also M. J. Masters, On a pink sport of the Gloire de Dijon rose, Journ. Roy. Hort. Soc. new series, vol. IV, p. 153.—Ed.]

[2] Further details on this important subject are given by Nägeli in the Sitzungsberichte der kön. bayer. Akad. der Wiss. Dec. 15, 1865.

reason—because varieties are to so great an extent independent of external influences —that they are hereditary. A change produced in a plant by moisture, shade, or any similar cause, is for the same reason not hereditary, because its descendants, when placed under other vital conditions, acquire again other non-permanent characters. That hereditary characters, or those which may become so, are not produced by external influences, is proved most conclusively by the fact that seeds from the same fruit produce different varieties, either entirely so or together with the inherited parent-form.

Although the production of varieties and the form they assume are not the direct results of external influences, yet the continuance of the existence of a variety may be determined by these influences. When a variety has arisen, the question arises whether it will thrive best in damp or in dry ground, in sunny or shady places, and so forth; whether it can reproduce itself under these circumstances, or whether it will perish. The conclusion follows that hereditary varieties arise independently of direct external influences, but that the continuance of their existence depends on external causes. A variety which occurs only in a particular locality is not produced by the conditions of this particular locality; but it alone furnishes the peculiar vital conditions which this particular variety requires, while other varieties which have arisen at the same place disappear.

It has already been shown in Sect. 32 that hybrids show in general a tendency to the production of varieties. Two different sets of hereditary characters are combined in a hybrid, and there is hence a strong tendency towards the formation of new characters which may be more or less hereditary. Hybridisation is therefore one of the most important means at the command of the horticulturist for disturbing the constancy of inherited characters and producing a number of varieties from two distinct ancestral forms[1]. But even the ordinary sexual union of two individuals of a species, as in diœcious, dichogamous, or dimorphic plants, may be considered as a kind of hybridisation; in these cases also the individuals which unite must certainly be different, since otherwise their cross-fertilisation would be no more productive than self-fertilisation. In these cases therefore two sets of characters which differ, though it may be but slightly, also unite in the descendants; and if a hybrid from two different species exhibits a strong tendency to variation, the cross-fertilisation of two different individuals of one and the same species may at least give rise to a slight tendency in the same direction. It is therefore probable that in the cross-fertilisation of different individuals—towards which there is always a tendency in nature even in hermaphrodite flowers—we have a perpetual cause of variation in plants. But this is by no means the only cause of variation, as is shown by the existence of bud-variation, and by the reflection that there must always be a slight difference between individuals which produce a variable progeny.

A great number of facts point to the conclusion that almost every plant has a tendency to vary continually and in different directions, while every new character which is not produced directly by external agencies tends at the same time to become hereditary.

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[1] See also Naudin, Compt. rend. 1864, vol. LIX, p. 837. [Journ. Roy. Hort. Soc. new series, vol. I, p. 1.]

If notwithstanding this many wild plants and some cultivated ones are very constant and produce no varieties which can be distinguished externally, this is mainly the result of the fact that the newly produced varieties are unable to exist in the conditions by which they are surrounded, or at least soon disappear, a point to which I shall recur more in detail. The hereditary transmissibility of acquired characters exhibits itself in a most marked way when it does not affect the whole of the parent-plant, but only a particular branch. A still more remarkable case was observed by Bridgman. He noticed that the spores from the lower inner part of the lamina of the leaves of the varieties *Scolopendrium vulgare laceratum* and *S. vulgare Crista-galli*, which were of the normal form, uniformly produced plants of the normal parent-form, while those produced on the outer abnormal part of the leaf reproduced the special varieties[1].

Sect. 34.—**Accumulation of new characters in the reproduction of varieties.** The difference between a variety and its parent-form, or between the varieties of a common parent-form, is usually at first small and affects only a few characters. But the descendants of the variety may again vary, the new characters may thus become intensified, and other new characters of a different kind may be added to them. The amount of difference between parent-form and variety and between the various varieties of the same parent-form thus becomes greater; and if the tendency to become hereditary of the characters increases with the increase of their difference, the variety comes at length to differ so greatly from the parent-form that their genetic connection can only be proved historically or by the existence of transitional forms. This is the case with many of our cultivated plants, as *e.g.* the pear, which varies much even in the wild state, but in cultivation has altered its mode of growth, form of leaf, flower, and especially its fruit, to such an extent that it would be impossible to suppose the finest sorts of pears to be descendants of the wild *Pyrus communis*, if Decaisne had not proved their genetic connection by the study of the transitional forms (Darwin *l. c.* vol. I, p. 350). In the same manner it scarcely admits of a doubt that all the cultivated kinds of gooseberry are descended from the wild *Ribes Grossularia* of Central and Northern Europe; and Darwin brings forward historical evidence to show that the size of the fruit has been continually increased by cultivation since 1786, so that in 1852 it had attained the weight of 895 grs. Darwin found that a small apple $6\frac{1}{2}$ inches in circumference weighed as much (*l. c.* p. 356). The different varieties of cabbage are all descended from one parent-species, or, according to Alph. De Candolle, from two or three closely related ones still growing in the neighbourhood of the Mediterranean. In this case hybridisation has also cooperated; the varieties are for the most part hereditary but without any great constancy. The extent of the variation which has taken place under cultivation is shown by the existence on the one hand of shrubby forms with branching woody stems, 10 to 12 or even 16 feet high, on the other hand of the round cabbage with a short stem and a spherical, pointed, or broad head consisting of leaves closely packed one over another; and again of the savoy with its curled blistered leaves, the kohl-rabi with its stem swollen below, the cauliflower with its crowded monstrous flowers, &c.[2]

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[1] Ann. and Mag. Nat. Hist. third series, vol. VIII, 1861, p. 490; Darwin *l. c.* vol. II, p. 379.

[2] See Metzger, Landwirthschaftliche Pflanzenkunde, Frankfürt a. M. 1851, p. 1000; and Darwin *l. c.* vol. I, p. 323.

In the case of many cultivated plants the original wild form is unknown. It is possible that in a few cases it may have disappeared; but it is more probable that the varieties which have arisen in cultivation have gradually acquired such a number of new characters that their resemblance to the wild parent-form can no longer be traced. This is probably the case with the cultivated Cucurbitaceæ, gourds, bottle-gourds, melons, water-melons, &c., the hundreds of varieties of which were traced back by Naudin to three primitive forms, *Cucurbita Pepo*, *maxima*, and *moschata*, neither of which however is known in the wild state. These original forms have been as it were evolved from the resemblances and differences of the numberless varieties, and have only an ideal existence; it is doubtful whether either of them ever actually existed, or whether these ideal parent-forms do not merely correspond to three principal varieties which arose from a single primitive form which possibly still exists, or from the hybridisation of several. The characters of many of these varieties are perfectly hereditary, and all the organs show the greatest degree of variation; how great and various these differences are is seen from the fact that Naudin has divided the group of forms which he included under the name *Cucurbita Pepo* into seven sections, each of which again includes a number of subordinate varieties[1]. The fruit of one variety exceeds that of another variety more than two thousand fold in size; the original form of the fruit is probably ovoid, but in some varieties it is elongated into a cylinder, in others abbreviated into a flat plate; the colour of the rind varies almost infinitely in the different varieties; in some it is hard, in others soft; some have a sweet, others a bitter flesh; the seeds vary in length from 5 or 7 to 25 mm.; in some the tendrils are of enormous size, in others they are altogether wanting; in one variety they are transformed into branches which bear leaves, flowers, and fruits. Even characters which are normally constant throughout entire natural orders become extremely variable in the gourds; thus Naudin (Compt. rend. 1867, vol. LXIV, p. 929) describes a Chinese variety of *Cucurbita maxima* which has a perfectly free or superior ovary, whereas it is inferior elsewhere in the Cucurbitaceæ and in the nearly allied orders[2].

The varieties of melon (*Cucumis Melo*) Naudin divides into ten sections, which differ also not only in their fruit, but also in their leaves and their entire habit or mode of growth. Some melons are no larger than small plums, others weigh as much as 66 lbs.; one variety has a scarlet fruit; another is only 1 inch in diameter but 3 feet long, and is coiled in a serpentine manner in all directions, the other organs being also greatly elongated. The fruits of one variety can scarcely be distinguished externally or internally from cucumbers; one Algerian variety suddenly splits up into sections when ripe (Darwin, *l. c.* vol. I, p. 357).

The behaviour of the genus Zea is similar to that of Cucurbita. The cultivated varieties of maize are probably descended from a single primitive wild form which has been cultivated in America for a very long period; but it seems doubtful whether the native Brazilian species, the only one known in the wild state, with long glumes

[1] See Metzger, Landwirthschaftliche Pflanzenkunde, p. 692, and Darwin, *l. c.* vol. I, p. 358.

[2] Hooker states that a specimen of *Begonia frigida* at Kew produced, in addition to male and female flowers with inferior ovary, also hermaphrodite flowers with superior ovary. This variation was the product of seeds from a normal flower. (Darwin *l. c.* p. 365.)

enveloping the grains, is the primitive form; if it is not, then no plant is now known which can be considered as the ancestral form of our numerous and extremely diverse varieties of maize. In this case also continued cultivation has increased the amount of difference between the different varieties, as well as to a prodigious extent that between them and the primitive form; and the separate varieties are distinguished from one another by a number of different characters. Some are only 1½ feet high, others as much as 15 to 18 feet; the grains stand on the rachis in rows varying from six to twenty in number; they may be white, yellow, red, orange, violet, streaked with black, blue, or copper-red; their weight varies sevenfold; their form also varies extremely; there are varieties with three kinds of fruit of different form and colour on one rachis; and a great number of other differences also occur[1]. These instances may suffice to show to what an extent the amount of deviation of the varieties of a primitive form may increase under cultivation[2].

It is much more difficult, and to a great extent impossible, to prove directly to what extent the variation of wild forms can increase without cultivation, because historical evidence is in this case generally impossible, or can only be obtained indirectly or conjecturally. But since the laws of variation are unquestionably the same in the case of wild as of cultivated plants—although they operate in the two cases under different conditions—we may for the time at least assume as probable that plants vary as greatly in the wild as in the cultivated state. We shall however in the sequel have to examine a number of weighty considerations which lead to the conclusion that variation has produced infinitely greater effects in originating the various wild forms of plants than those which we perceive in cultivated varieties[3].

The variation of cultivated plants shows that there is only one cause for the internal and for the external hereditary resemblance between different plants, and that this cause is the common origin of similar forms from one and the same ancestral form. When we meet with corresponding phenomena in wild forms, and when we find that with them as with cultivated plants dissimilar forms are connected by a series of intermediate forms, just as we find to be the case between the primitive forms of cultivated plants and their most abnormal varieties, we are forced to the conclusion that in wild plants also a similar affinity is the only cause of resemblance. The extraordinarily numerous forms, for example, of the widely distributed genus Hieracium present phenomena similar in many respects to those of cultivated gourds, cabbages, &c. In addition to a number of forms which are considered to be species, there are a still greater number of intermediate forms, some of which only are hybrids, the greater part perfectly fertile varieties. Nägeli[4], who has made this genus

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[1] See Darwin *l. c.* vol. I, p. 365, and Metzger *l. c.* p. 207. No great value with reference to variation and the constancy of varieties must be set on the result of experiments on cultivated plants, since the possibility of hybridisation was not excluded. Some varieties of maize appear to hybridise with difficulty.

[2] Further material will be found collected in Darwin's and Metzger's works already quoted, and in De Candolle, Géographie botanique; Paris, 1855.

[3] [H. Hoffmann gives in the Bot. Zeit. for April 27 and May 1, 1874, an account of an interesting series of experiments on the extent to which the characters which distinguish the allied species *Papaver Rhœas* and *dubium* and *Phaseolus vulgaris* and *multiflorus* can be made to vary by cultivation, and on the tendency of the cultivated varieties to revert to the parent-form.—Ed.]

[4] Sitzungsberichte der kön. bayer. Akad. der Wiss. March 10, 1866.

the subject of close study, says:—'If an attempt is made to unite into a single species all the types which are connected by perfectly fertile transitional forms, we should find only three species of native Hieracia, which have been erected by some authors into distinct genera:—Pilosella (Piloselloideæ), Hieracium (Archieracium), and Chlorocrepis (*H. staticifolium*). Between these three groups we have, at least in Europe, no transitional forms; hybrids between Piloselloideæ and Archieracium have been erroneousiy stated to occur, but the alleged hybrids are either true Piloselloideæ or true Archieracia. . . . According to the present state of our knowledge, no other hypothesis is possible but that all the various species of Hieracium have sprung from the transmutation (descent with variation) of forms which have either disappeared or are still in existence; and a large number of the intermediate forms still occur which must have had their share in producing several new species by the splitting up of one original species, or which would have occurred in the transformation of a still living species into one derived from it. In the case of Hieracium the species have not become so completely separated by the suppression of the intermediate forms as is the case in most other genera.'

By the term *Species* is meant the aggregate of all the individual plants which have the same constant characters, these characters being different from those of other somewhat similar forms. It is clear from what has already been said that the only distinction between varieties of a known primitive form which have become constant, and the wild species comprised within a genus, is that in one case their descent is known, in the other it is not. The various cultivated varieties of a primitive form which have become constant are linked together by intermediate forms in which the progressive accumulation of new varietal characters may be perceived; but these intermediate forms may disappear, and then there is a more or less wide chasm between the various varieties themselves, as well as between them and the primitive form. Both of these cases occur also in wild plants. In some genera, like Hieracium, species the extreme forms of which differ greatly are connected together by a number of intermediate forms which occur along with them. The analogy of cultivated plants justifies us in considering these intermediate forms (so far as they are not hybrids) as varieties in a progressive state of development, some particular descendants of which have advanced furthest in the accumulation of new properties. But usually the intermediate forms, the connecting links so to speak between the ancestral and the derived forms, have disappeared; and the species of the same genus are then completely separated from one another, and their characters are at once distinguishable; while the different species of the same genus agree among one another in a number of inherited characters, and are distinguished only by single constant characters; the amount of resemblance is much greater than the amount of difference. The same relationship therefore exists, but in a greater degree, between the various species of one genus as between different varieties of the same primitive form. And since no other explanation is known of this relationship than common descent with variation and the heredity of the new characters, so we are entitled to consider the species of a genus as varieties of a common ancestral form which have developed further and become constant,—the original form having possibly actually disappeared or being no longer recognisable as such. There is therefore no natural boundary-line between variety and species; they differ only in the amount of divergence of the characters and in the degree of their constancy. Just as a number of varieties are included in the idea of a species — the varietal characters being neglected in the diagnosis of the species—so several species are united into a genus by including in the diagnosis of the genus a maximum of their common characters. But since it is impossible either to determine by measure or by weight which are the most important

characters of a plant, so it is difficult and to a certain extent impossible to define, *i.e.* to determine by comparison, what amount of differentiation is necessary in order to classify two different but similar forms as species rather than varieties. In the same manner it is left to a great degree to personal judgment to decide whether two different but similar groups of forms should be classed as varieties of two species or as species of two distinct genera. The only object actually presented to the eye is the individual (and even this not always as a whole); the ideas Variety, Species, Genus are abstract ideas, and indicate a progressive scale of the differences between individuals which is small in the variety, larger in the species, and still larger in the genus. But in all these cases points of difference are of less importance than the amount of resemblance; and since in the phenomena of variation we learn that forms which are similar but are constantly becoming more different are derived from the same ancestor by the continual accumulation of differences, so we assume that the higher degree of variation of similar forms which we express by the terms Species and Genus have resulted from the accumulation of new characters in the variation from one ancestral form.

Sect. 35.—**Causes of the progressive development of varieties.** The characters of the cultivated varieties of one parent-form show, as Darwin was the first to point out, a constant striking and remarkable relation to the purpose for which the plant was cultivated by man. The varieties of wheat differ from one another only slightly in the form of the haulm or leaves, which are of but small importance to mankind; but they show a great variety and extent of difference in the form and size of the grains, and the quantity of starch and proteine contained in them, *i. e.* in the characters of that part of the plant for the sake of which wheat is cultivated, and in those properties of this part which under various circumstances are especially useful to mankind. The varieties of the cabbage, on the other hand, scarcely differ at all in their seeds or even in their seed-vessels or flowers, the external properties of which are useless to man, and the internal properties only of value because the seed has to reproduce the variety; the varieties of cabbage differ exclusively in the development of those parts which are used as vegetables, and to which therefore cultivation is directed. The object of cultivation is therefore, retaining the taste and value as food for man, sometimes to increase the succulence of the tissues, sometimes to attain as large a size as possible, sometimes to alter the time of the year at which the vegetable can be used. These and a number of other properties are furnished by the different varieties. The varieties of beet differ only slightly in their flowers, more in their leaves, according as they are grown in the garden as ornamental foliage-plants or as agricultural crops; the varieties in the latter case differ from one another in the size and shape of the roots and the amount of sugar they contain, properties which make the plant valuable on the one hand as food for cattle, on the other hand for the manufacture of sugar. Fruit-trees of the same kind differ but little in general in their roots, leaves, flowers, or stems, but to an extraordinary extent in the size, shape, colour, smell, taste, period of maturity, and keeping-properties of the fruit, according to the special purpose or prevalent mode in which it is employed. In garden-flowers it is generally the flowers and especially the corolla and inflorescence that differs in the varieties of a species, because the greater number are cultivated only for the shape, size, colour, or odour of the flowers.

This relation of cultivated varieties to the requirements of man is explained if we suppose that only those varieties were cultivated, at first undesignedly afterwards

designedly, in which some character useful to man was more strongly manifested than in the others; those individuals were selected which best answered to a definite requirement; they alone were further cultivated; the particular character was again strongly displayed in some of their descendants, and only these individuals were again selected for reproduction; and the desired character was thus continually increased in strength. Other characters of the plant also varied at the same time, but they were disregarded, and the individuals in which they occurred were not preserved for reproduction, and no increase of these characters consequently took place from generation to generation.

The greatest service which Darwin has rendered to science is to have shown that wild plants are also subject to vital conditions the effect of which consists in this, that only some of the varieties of one primitive form maintain themselves and increase their peculiarities, while others perish. The relationship of the varying wild plant to its environment in the broadest sense of the word is however different from that of the cultivated plant to man; man protects his charges in order to preserve them; he places them under favourable conditions in order that those properties which are useful to him may become freely developed. Wild plants, on the contrary, have to protect themselves against all injury from without; their existence is continually threatened by other plants or animals or by the hostility of the elements; and in this *Struggle for Existence*, as Darwin has appropriately termed it, only those individuals are able to maintain themselves which are best able to resist the prejudicial influences to which they are exposed; and only those varieties which happen to be the best endowed in these respects will reproduce themselves and further develope their special properties. Hence the characters of wild plants, as far as they are not of a purely morphological nature, always show a perfectly definite relationship to the conditions in which they are placed; the form and other characters of the organs have essentially for their object to secure the existence of the plant under the local conditions of its habitat; varieties and species which are not endowed with qualities to endure the struggle for existence perish. The struggle for existence acts therefore in a certain sense similarly to the selection of the breeder; as the breeder developes only that which is suited to his own purposes, so in the struggle for existence only those varieties survive and reproduce their kind which are better adapted, through some property which they possess, to endure the struggle. Thus, finally, through imperceptible variation, through the destruction of those characters which are not beneficial, and through the further development of the useful ones—in one word, through what may be termed metaphorically *Natural Selection* in the struggle for existence,—forms are produced which are as well or even better adapted for the purpose of self-preservation than cultivated plants are for the purposes of man. By the undesigned reciprocal influences of plants and of their living and physical environment, specialities of organisation finally arise which could scarcely be better adapted for the preservation of the plant under its special local conditions, and which give the impression of being the result of the greatest ingenuity and foresight.

In order to understand clearly how the struggle for existence has caused the existing wild forms of plants to be so admirably adapted to their specific vital conditions, it must be borne in mind that all plants are continually varying to a very slight extent, and that the variation affects all their organs and all their characters,

although usually to an imperceptible amount. On the other hand, the struggle for existence in plants (as well as in animals) is a perpetual and never-ceasing one, in which the smallest advantage that the plant has obtained through variation in any one direction may be of the utmost importance for its perpetuation.

The struggle which the plant carries on by means of its capacity for variation has two different aspects. On the one hand its tendency is to adapt the organisation of the plant completely to the conditions of food and growth afforded by the climate and the soil. It is evident that the organisation of a submerged water-plant must be different from that of a land-plant; that the assimilating organs of a plant that grows in the deep shade of a wood must be differently constructed from those of a plant exposed daily to bright sunshine, and so forth. The vital conditions of all plants growing at a great elevation and in Arctic countries must be different from those growing in the lowlands of the Tropic and Temperate zones. If we had to do only with the general conditions of plant-life, the struggle for existence would be a comparatively simple process. It would be easy to imagine how, among the varieties of a primitive form which grew in water, there would be some which would be occasionally subjected to a subsidence of the water, and how these would give birth to descendants which would gradually assume the character of marsh- and finally of land-plants, as is well illustrated in the case of *Nasturtium amphibium*, *Polygonum amphibium*, &c.[1] It may also be supposed that some of the descendants of a plant exhibit a somewhat greater power of resisting frost, that this property increases in the course of generations, and that thus a form which can at first only bear a temperate climate gradually produces varieties which can endure a more and more severe climate; and so forth. But these comparatively simple relationships must lead to a great diversity in the varieties which claim descent from one ancestral form; for each adaptation to new conditions of climate or locality would act in different ways; *i.e.* varieties of different descriptions would take up and carry out in different ways the struggle against the influences of the elements.

But the struggle for existence and the changes occasioned by it in the organisation of plants are greatly complicated by the fact that every plant, while struggling to adapt itself to its special vital conditions, has also to protect itself at the same time against a number of other plants and against the attacks of animals; or, what is more to the point, its capacity for variation enables it to make use of particular favourable conditions which are offered to it by other plants and animals in order to take advantage of them; as parasites of their hosts, dichogamous and other flowering plants of the visits of insects, &c. These relationships are endless in their diversity, and can only be illustrated by examples.

But we must here call special attention to a remark of Darwin's; that the individuals of the same species or variety are competitors for position, food, light, &c. The fact that plants of the same species have the same requirements itself gives rise to a struggle for existence among them; and the same is the case, though to a somewhat smaller but still to a great extent between the different varieties of the same

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[1] A special interest attaches in this connection to Hildebrand's observations on Marsilea in Bot. Zeit. 1870, No. 1, and Askenasy's on *Ranunculus aquatilis* and *divaricatus* in Bot. Zeit. 1870, p. 193 *et seq.*

primitive form, to a less extent between different species and genera. The result of these relationships is seen on the one hand in the fact that with plants which live socially only the most vigorous seedlings arrive at full maturity, while the weaker ones are smothered, as may be seen in any young plantation; on the other hand, that species and genera which differ greatly from one another can thrive side by side, because their requirements are different and the competition between them is less.

From the fact that plants whose organisation differs can thrive better side by side on the same soil in consequence of the diminished competition between them, Darwin drew the important and pregnant conclusion that in the propagation of the varieties of one primitive form those new forms must be the best able to maintain themselves in the wild state which differ most from the primitive form and from one another, while the intermediate forms are gradually dispossessed. This is the reason why the connecting forms between the different species of a genus are so often wanting, although the conclusion cannot be avoided that the species arose by variation from a single ancestral form, and by the propagation of varieties.

In its larger features (but on that account more conspicuously) the struggle for existence between the various forms of plants, the competition for space, food, and light, are manifested in the luxuriant growth of what we term weeds in our gardens and fields. Our cultivated plants are able to bear our climate, and the soil supplies what they require for their vigorous growth. But a number of wild plants are still better adapted to the climate; and they grow still more vigorously, rapidly, and luxuriantly on cultivated soil, and their seeds or rhizomes are everywhere present in enormous quantities. If the cultivated plants are not carefully protected from the weeds, the latter soon dispossess them of the ground which was set apart for them. Every country and every soil has its own peculiar weeds; *i.e.* under any particular external conditions there are always certain forms of plants which thrive best and drive out the cultivated plants. To a certain extent we have a measure of the amount of advantage which weeds have over cultivated plants in the amount of labour bestowed by man on their destruction in order to preserve and maintain his nurselings. The primitive forms of our cultivated plants are mostly natives of other countries, where they are not only sufficiently adapted for the climate, but are able to sustain competition with their neighbours.

The number of species or of individuals of any species which we find in a meadow, a marsh, &c. is not a matter of chance; it does not depend merely on the number of seeds of one or another species produced or brought to the locality; every one of these species would, if it alone existed there or were protected by cultivation, of itself cover the space of ground in a short time; and yet there is a definite relationship between the numbers of individuals of the different species when left to themselves, a relationship which depends on the specific power of each particular species to maintain itself in the struggle with the rest[1].

How complicated may be this relationship in the cases of only two nearly related forms of plants in their struggle for existence in particular localities, has been described as exhaustively as clearly by Nägeli in the case of various Alpine plants. 'The internecine war,' he says[2], 'is obviously most severe between the species and races that are most nearly related, because they require the same conditions of existence. *Achillea*

[1] [How the relationship subsisting between the species in permanent pastures may be disturbed by the application of different manures, may be seen in Lawes and Gilbert's paper on this subject in Journ. Roy. Agric. Soc. vol. XXIV, 1863.—Ed.]

[2] Sitzungsber. der kön. bayer. Akad. der Wiss. Dec. 15, 1865.

moschata drives out *A. atrata*, or is driven out by it; they are seldom found side by side; while each grows along with *A. Millefolium*. It is clear that *Achillea moschata* and *atrata*, being extremely similar to one another externally, make similar demands on their environment, while *A. Millefolium*, which is less nearly allied to both, does not properly compete with them, because it requires other conditions of existence. Still less do plants of different genera or orders compete with one another . . . In the Bernina Heuthal (Upper Engadin) *Achillea moschata*, *atrata*, and *Millefolium* occur in profusion, *A. moschata* and *Millefolium* on slate, *A. atrata* and *Millefolium* on limestone; where the slate ends and limestone begins, *A. moschata* always ceases and *A. atrata* takes its place. Both species are therefore here strictly circumscribed as to soil, and this I have found to be the case also at various spots in Bündten, where both species occur together. But where one species is absent the other is widely distributed, and is then found indiscriminately on slate or limestone. Although *A. moschata* does not apparently grow so readily on limestone as *A. atrata* does on slate, yet in the neighbourhood of the primary rocks it is found on a distinctly calcareous formation along with the vegetation characteristic of it. In the Bernina-Heuthal I found in the midst of the slate which was thickly covered with *A. moschata* a large erratic block of limestone covered with a crust of soil scarcely an inch thick, upon which a patch of *A. moschata* had established itself, because it did not here meet with any competition from *A. atrata*. . . . A similar relationship was observed in certain districts between *Rhododendron hirsutum* and *ferrugineum*, *Saussurea alpina* and *discolor*, and between species of the genera Gentiana, Veronica, Erigeron, Hieracium, &c.' The obvious objection, that there cannot possibly be any struggle between two forms of plants as long as there is space for both in the area in question, rests on an incorrect basis, and is disposed of by Nägeli as follows:—'Upon a slate slope are a million plants of *A. moschata*; they obviously do not occupy the whole space, for a hundred millions or more could find room there; but the rest of the space is occupied by other plants. There is here a condition of equilibrium, which has been produced in reference to the nature of the soil and the preceding climatic influences. The number one million gives us also the proportion which *A. moschata* is able to maintain in relation to the rest of the vegetation; and the objection that there would still be plenty of room for *A. atrata* is an untenable one. If the space were accessible to species of Achillea generally, it would be occupied by the species which is already present, and which in any case has the advantage, *A. moschata*. If we now imagine that the two species happened for once to be intermixed on the slate slope, perhaps in consequence of artificial transplanting, in equal quantities, say 500,000 plants of each, *A. moschata* would thrive the better of the two, as the soil contains but little lime; *A. atrata* would become weaker and its tissue less matured, and would in consequence have less power to withstand external prejudicial influences, as summer frosts, long-continued rainy weather, or persistent drought, &c. If we suppose, for example, that every twentieth or fiftieth year a severe frost occurs at the time of flowering which destroys half the plants of *A. atrata*, while the more vigorous *A. moschata* resists it, the voids are again filled up by the dispersion of the seeds; but more plants of *A. moschata* spring up than of *A. atrata*, because the number of individuals of the latter was reduced by the frost to 250,000, while that of the former remains at 500,000. The million plants of Achillea on the slope will in consequence be composed of say 670,000 *A. moschata* and 330,000 *A. atrata*. After a second frost, which again destroys one half of the individuals of *A. atrata*, we should have about 800,000 of *A. moschata* to 200,000 of *A. atrata*. In this manner the number of the latter would decrease with every unusual summer frost, until at length it entirely disappeared, a nearly-allied hardier species becoming distributed over the locality in its place.' In conclusion, the following remark by the same author may be added:—'From such a course of reasoning the conclusion might perhaps be drawn that this result would always take place, and that one of two plants would always be crowded out, because the two could hardly be precisely equally hardy. But this conclusion would be unsound, because it would hold good only for

plants whose conditions of existence were as nearly as possible alike. We can imagine another case in which the two species suffer injury from altogether dissimilar external influences (one, *e. g.*, from spring frost, the other from dry heat), so that sometimes the number of individuals of one species, sometimes that of the other species diminishes, and where moreover the production and the germination of the seeds are affected by altogether dissimilar external influences, so that sometimes the one sometimes the other species increases most rapidly and occupies the vacant spots. The numerical proportion of the two species must in this case be variable, but neither is able to expel the other.'

Just as the struggle between two species is the result of their thriving more or less vigorously on a soil of a particular chemical nature, so also the need for more or less water, light, heat, &c. can determine also the nature of the struggle for existence. Nägeli gives some examples of the first case. When *Primula officinalis* and *elatior* occur together in a district, they are sometimes sharply separated from one another, *P. officinalis* preferring the dry, *P. elatior* the damp spots. Each is most vigorous in its own locality, and may expel the other. But when only one species occurs, it is not so particular; *P. officinalis* will choose damper, *P. elatior* drier situations, than if they were in company. *Prunella vulgaris* and *grandiflora* behave in the same manner in reference to poorer and more fertile soils; as also do *Rhinanthus Alectorolophus* and *minor*, *Hieracium Pilosella* and *hoppeanum*.

These examples may suffice to show what is meant by the Struggle for Existence. It must however be borne in mind that such a struggle must arise in reference to every vital phenomenon of a plant, and to each of its relationships to the external world, especially to the animal kingdom; and that its course must vary for the same plant in different localities. An understanding of the Theory of Descent, and especially na insight into the causes of the perfect structural contrivances adapted to the vital conditions of the plant which are often extremely local, depends essentially on a clear comprehension of the struggle for existence.

Sect. 36.—**Relationship of the morphological nature of the organ to its adaptation to the conditions of plant-life.** Every plant is very accurately adapted (though not absolutely so) to the conditions and circumstances in which it grows and is reproduced; its organs have the shape, size, mode of development, power of movement, chemical properties, &c. needful for this purpose. If this were not the case, the plant would inevitably perish in the struggle for existence. But the vital conditions are extremely various, and undergo, in the course of time, endless changes. The diversity in the characters of plants corresponds to this infinite variety in the conditions of life; and yet even in the more highly differentiated classes there are only three or four morphologically distinct forms of structure, axis (caulomes), leaves (phyllomes), roots, and trichomes, which suffice for these conditions, while maintaining a constant morphological character through numberless variations in their physiological properties. This relationship has already been described in chap. iii of Book I as the metamorphosis of the morphological members of a plant, understanding by metamorphosis the adaptation to various physiological purposes of morphologically equivalent members. The diversity in the physiological development is directed to the vital conditions of the plant; and to this extent Metamorphosis is synonymous with what we have here termed *Adaptation*, and which has also been described as Accommodation. When we speak of Purpose in the structure of a plant, we mean in fact nothing more than that the form or other characters of the organ are adapted to its conditions of life, which may be at once inferred from the

very survival of the plant in the struggle for existence. The terms Purpose, Adaptation, and Metamorphosis express therefore the same thing, and may be used as synonymous, as we have already repeatedly done.

For the purpose of the questions to be treated of in the following paragraphs it is important to have as clear a conception as possible of the relationship of adaptation to the morphological nature of the organs, and of the great constancy of morphological characters and the infinite diversity of metamorphosis; for such relationship can be explained by no other theory than that of descent.

In its most general features the relationship of adaptation to the morphological nature of organs is manifested in the fact that all the various morphological members perform the most different functions and in an infinite variety of ways; in other words, that the morphological nature of the parts of a plant is not directly determined by their function, nor is the function of an organ determined directly by its morphological nature. Thus, for example, trichomes sometimes take the form of a protective envelope (mostly in buds), sometimes of glands, sometimes of absorptive organs (as root-hairs), sometimes of asexual organs of reproduction (as the sporangia of Ferns), &c. The leaves again are usually organs of assimilation containing chlorophyll; but they may also be employed as protective envelopes to winter-buds (in most of our native woody plants), as reservoirs for reserve food-materials (in the seedlings of flowering plants and in bulbs); in Vascular Cryptogams they bear the sporangia. In flowering plants the organs of reproduction and their envelopes are peculiarly metamorphosed leaves; in many slender-stemmed Angiosperms the leaves are transformed into tendrils, in order to raise up the slender stem and fix it to neighbouring supports; the leaves of Nepenthes produce at their apex an appendage which forms a pitcher provided with a moveable lid and filled with the fluid which it itself secretes; some of the leaves contained in the flowers are developed into nectaries and then perform the function of glands; not unfrequently they are transformed into hard woody spines; in other cases they are sensitive to irritation, contractile, and so forth. The parts of the axis are scarcely less varied in their development; sometimes they cling round upright supports; sometimes they are woody and able to retain themselves in an erect position; sometimes they are slender swaying branches, or thick fleshy succulent masses (Cactus), or round tubers filled with food-materials (Arum, potato), or they become tendrils (the vine), or spines (Gleditschia); sometimes they assume the form of foliage-leaves (Ruscus, Xylophyllum, &c.). The adaptations of roots are less numerous; usually filiform, slender, cylindrical, and provided with root-hairs for absorbing water and dissolved mineral substances, they become tuberous reservoirs for reserve food-materials in the dahlia; their tissue is loose and contains air and they resemble swimming-bladders in Jussiæa; in the ivy, *Ficus repens*, &c., they are simple organs of attachment for the stem; in *Vanilla aromatica* they play the part of tendrils; but they never produce sporangia or sexual organs.

According to the definition already given of Purpose in the vegetable organisation, its relationship to the morphological nature of the organ can also be illustrated by keeping in view the purpose to be served, *i. e.* the character of the plant which is serviceable in the struggle for existence, and then observing the means employed for attaining this purpose, *i. e.* what members of the plant are

adapted for the purpose, and what metamorphosis they undergo. A few examples will explain this[1].

It is obviously useful for the greater number of flowering plants—in other words advantageous in the struggle for existence — that their stem should grow rapidly to a certain height, because the conditions of assimilation (light and warmth) are thus most perfectly fulfilled, and because—which is perhaps of greater importance —the flowers are more easily detected by insects on the wing, and the pollen transferred by them from one flower to another. Even where (as in many Coniferæ, &c.) the light pollen is carried by the wind to the female flowers, this is accomplished better when the flowers are at a greater height from the ground; and finally by this means the dissemination of the seeds by the wind or by frugivorous birds is promoted, or their scattering by the bursting of the fruits. That these arrangements for propagation are especially promoted by the upright growth of the stem is evident from the large number of plants which develope their leaves in a rosette close to the ground or on a stem that creeps along it, a rapidly ascending flower-stem being formed only just before the unfolding of the flower-buds. Still more strikingly is this the case in parasites and saprophytes (Orobanche, Neottia, &c.), which vegetate below and blossom above ground. If we concede these and other special purposes of upright growth, it is of interest to see in what various ways this one purpose is attained in different species of plants. In many shrubs the growing stem is endowed with sufficient firmness and elasticity to support in an upright position the weight of the leaves, flowers, and fruits; if it happen to be broken down, or if it must raise itself from a previously creeping position, advantage is taken of the property of geotropism. But the slender haulms of Grasses are not themselves endowed with this power; and in their case the basal portion of each leaf-sheath forms a thick ring the tissue of which retains for a long time its power of growth; and when the haulm is bent by the wind, or is in its early stage prostrate on the ground, the elevation into an erect position is brought about by the surface of the node which faces the ground growing rapidly and strongly; a knee-shaped bend is thus formed by which the upper part of the haulm is raised up. If, on the contrary, the stem is perennial, and has to bear a great weight of branches, leaves, and fruits, contrivances of this kind are not sufficient, and then the tissue becomes woody; if the weight of the crown increases year by year, the stem also becomes thicker each year, as in dicotyledonous trees and Conifers; if the weight of the foliage does not increase, as in Palms, the stem only retains the same thickness. In such cases a considerable quantity of assimilated food-material is necessary in order to produce the massive solid stem, while in many other cases the elevation is attained at the expense of a very small amount of organic substance, as in climbing and twining plants, such as are found in the most widely separated families of Angiosperms. Plants with a twining stem like the hop presuppose in general the existence and proximity of other plants which are able

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[1] In these examples I am compelled to confine myself to the most important points. Most of the adaptations are so complicated that a detailed description of them in even a single plant would require a great deal of space. What was said in the fourth chapter of this book on climbing plants and in the sixth on the adaptation of the foliar organs of a flower to the purpose of cross-fertilisation may be consulted.

themselves to grow upright and round which they twine; and in order that such a neighbouring support may be more easily and certainly taken hold of, the slender stem of climbing plants is endowed with a power of revolution by which the apex is carried round in a circle and occasionally pressed closely to the stem of an upright plant, up which it then climbs.

The greater number of plants provided with tendrils are also dependent on the proximity of erect plants round which they can climb; they are characterised by an extreme parsimony in the employment of organic substances for the purpose of an erect growth. Sometimes (as in the grape-vine) the tendrils are axial structures furnished with minute leaves and branching from the axils of these; but much more commonly (as in Clematis or Tropæolum) the petioles, or (as in Fumaria) the branched narrowly-divided lamina, or most often the metamorphosed apical parts of the foliage-leaves (*Cobæa scandens*, the pea and other Papilionaceæ) are developed in a filiform manner and perform the function of tendrils. The morphological significance of the tendrils of Cucurbitaceæ is not yet perfectly determined; but they are probably metamorphosed branches. Tendrils occur only in those plants whose stem is not able to bear in an erect position the weight of the foliage, flowers, and fruits; in the genus Vicia, for example, all the slender-stemmed species have leaf-tendrils; but in the thick-stemmed erect *V. Faba* they are rudimentary. The office of tendrils is to twine round the slender branches and the leaves of other neighbouring plants, and thus to fix the apex of the stem as with cords on various sides while it is growing upwards. The mode of development of tendrils, *i. e.* their endowment with useful properties corresponding to their purpose, is, as Darwin has shown, not only extremely diverse, but exhibits also very different grades of perfection, like climbing stems. Some tendrils are only of slight use; sometimes (as in some species of Bignonia) they are rather helps to an imperfectly climbing stem; but where they are perfectly adapted to their function, a variety of properties concur in a remarkable way to increase to a maximum the mode of adaptation to the use of the plant. The tendrils radiate in different directions from the growing apex of the shoot, which makes movements of revolving nutation by which the tendrils are brought into the greatest variety of positions, they themselves also revolving at the same time, so that within a certain area, often not a very small one, they assume an infinite number of positions, by which they must almost inevitably be brought into contact with some support, such as a branch or leaf, lying within this area. The supports are, so to speak, sought out in the most industrious manner; when one is touched by a tendril, the tendril bends and twines firmly round it; and when several tendrils do the same in different direction from the stem, it hangs suspended between the points of support. If this were all, the attachment would be a very weak one, and the elevation of the stem would only take place slowly; but the whole contrivance is perfected in the most ingenious way. When the tendrils have fixed themselves by their extremities, they draw the stem towards the support by twisting themselves spirally. When several tendrils do this in different directions, the stem which is suspended between them is tightly stretched, and the tenacity of the tendrils is at the same time considerably increased by the twisting. Many tendrils, while very tender at the time when they are sensitive, become afterwards hard and woody, and some become

much thicker; this is strikingly the case in *Clematis glandulosa* and *Solanum jasminoides*. But the most perfect adaptation is shown in the tendrils of the Virginian creeper, *Bignonia capreolata*, and some other plants. As in the grape-vine, the tendrils are here branched axial structures, and are to a much greater extent negatively heliotropic; their power of twining round slender supports is but slightly developed, but when, in consequence of their negative heliotropism, they come into contact with a wall, or in the wild state with a rock, trunk of a tree, &c., there is formed in the course of a few days on each branch of the tendril which touches the support with its curved and hooked apex, a cushion-like swelling which afterwards expands into a red flat disc, and becomes firmly attached by its surface to the support. The adhesion of this organ of attachment is probably at first occasioned by an exudation of viscid sap; but the attachment to the support is caused mainly by this organ of attachment forcing itself into all the depressions in the surface of the support and growing over the slight elevations. After this has taken place the whole tendril becomes thicker; it contracts spirally, the stem to which it belongs being thus drawn towards the wall, rock, &c.; then it becomes woody, and the firmness of its tissue and the power of retention of the disc are so considerable that, according to Darwin[1], a tendril ten years old and furnished with five of these discs can support a weight of 10lbs. without giving way and without the disc becoming detached from the wall. Since a shoot which is growing upwards forms a number of tendrils, this attachment to the flat support is a very effectual one, and enables the plant to endure the annually increasing weight of the stem which is gradually becoming thicker and more woody; and in this way it climbs over the walls and roofs of buildings more than 100 feet high. The fact is very interesting that those tendrils of the Virginian creeper which do not come into contact with the wall or rock die after some time, and wither up into slender threads which then fall off, no adhesive disc having been formed on them. But in order that these peculiar tendrils may more readily come into contact with the support, even the upright shoot is scarcely positively heliotropic, since this property would cause it and its tendrils to move further away from the supports; while the young shoots which exhibit such very slight heliotropism become erect under the influence of gravitation; otherwise the whole of the contrivances connected with the tendrils would be purposeless.

If looked at merely from the outside, the mode in which the Virginian creeper climbs up rocks, walls, and thick trees, presents a certain resemblance to the climbing of the ivy; but in fact the adaptations of the two are altogether different. It has already been shown how negative heliotropism causes the leafy branches of the ivy to become closely pressed to the support, and how the summit of the branch at first exhibits slight positive heliotropism, so that it is attached to the support with a slight convexity. At this point of pressure rows of aërial roots afterwards arise (not in consequence of pressure, for they make their appearance also on branches which hang free) which apply themselves to the inequalities of the bark of the tree or the rock which serves as a support, and thus fix the ivy-stem to it. Other weak-stemmed plants attain the same object (that of elevating their assimilating and flowering shoots) by apparently much simpler means, as the bramble, rose,

[1] [Movements and Habits of Climbing Plants; Journ. Linn. Soc. vol. IX, 1865, p. 87.]

and some climbing Palms like Calamus, &c., whose long shoots spread over neighbouring plants and are supported by them, their hooked prickles and other similar contrivances assisting in this.

It is of service to many plants in the struggle for existence that they should keep firm possession of the piece of ground they have once occupied, without forming for this purpose large woody masses, like trees and shrubs. The underground parts of such plants are perennial, and they send up separate shoots in each vegetative period to be exposed to the light and air where they will be able to assimilate, to produce flowers, and to scatter their seeds. This persistence of the underground parts has the advantage that the plant, although it assimilates and grows only at particular times of the year, is not compelled to seek each year, like annual plants, a new locality in which its seeds may germinate. The collection of reserve food-materials underground gives strength to the plant; it developes its buds beneath the soil to such an extent that at the right time they can grow up quickly at the expense of the rich supply of food. Every year very strong shoots are put forth, while in annual plants a number of feeble seedlings perish annually before some of them attain sufficient strength to protect themselves from the shade and humidity to which their neighbours subject them. Plants whose underground parts are perennial have in particular the power of resisting long and severe frost and the greatest variations of temperature, because these only penetrate slowly beneath the soil. It is for this reason that so large a number of Alpine and Arctic plants belong to this class. They are also able to grow in localities which are much too dry for the germination of the seeds of annual plants, because moisture is retained at a great depth for a longer period than near the surface. Numerous other advantages might also be mentioned which are of course secured to annual plants by other adaptations [1].

This permanence of the underground parts is attained in the greatest variety of ways. Sometimes the plant possesses slender creeping underground shoots in which the reserve food-materials are collected and which themselves rise above the surface at a particular time, as in many Grasses; or sometimes the leafy stems are developed from lateral buds, as in Equisetum; or there are thick stout stems from which shoots appear each year at the same place. In some cases the whole plant is annually renewed; all the parts which existed the previous year die off, and a complete rejuvenescence of the individual is accomplished underground. In the potato and artichoke only the apical parts of the underground lateral shoots swollen into tubers remain over till the next year, the whole of the rest of the plant having perished. In many of our native Orchids the rejuvenescence takes place in a similar way (see p. 199 and fig. 150); and one of the most interesting cases of annual rejuvenescence occurs in *Colchicum autumnale* (see fig. 391, p. 545). In these cases, with the exception of the Orchids, the reserve food materials accumulate in underground parts of the axis; in other cases this takes place in the swollen roots, which remain in connection with the underground part of the stem that bears the new buds, as

[1] [This subject—and especially the relation of peculiar habits of life to the power of resisting great cold—is very fully discussed in Kerner's treatise Die Abhängigkeit der Pflanzengestalt von Klima und Boden, Innsbruck, 1869.—Ed.]

in the hop, dahlia, and bryony. In bulbs again the reserve accumulates in the leaves (bulb-scales) which surround the bud that developes into the new plant. The reserve often collects in cataphyllary leaves of peculiar development; in *Allium Cepa* in the lower part of the leaf-sheaths, which persist through the winter, while the upper parts of the leaves die off.

We have already in the last chapter spoken of the immense variety of the contrivances which have for their object the partial or entire prevention of the self-fertilisation of plants, in order to produce a stronger and more numerous offspring by the sexual union of different individuals; and only a few examples need now be mentioned. Since the form, size, colour, position and movements of the parts of the flower are almost invariably adapted to facilitate the conveyance of pollen from one flower to another, generally by insects, and often even to render self-fertilisation impossible; and since a great diversity even of those forms of flowers which are constructed on the same morphological type results from this, so the properties of ripe seeds and fruits are no less adapted[1] to bring about the dissemination of the seeds. Fruits which are very similar from a morphological point of view may nevertheless assume physiological properties which are altogether different, and fruits which are very different morphologically may become extremely similar in consequence of their adaptation to the purposes of dissemination. The service rendered by insects in the fertilisation of diclinous, dichogamous, dimorphic, and many other flowers, is performed by birds in the dissemination of a number of seeds which are concealed beneath fleshy edible pericarps; in some cases, as the mistletoe, it is scarcely possible to imagine any other mode of dissemination than the eating of the berries by birds. Dry fruits or the seeds which are shed by dry fruits are often provided with an apparatus adapted for transport by the wind, the morphological value of which is as various as possible. The wings on the seeds of species of Abies are a superficial layer of the tissue of the scale (carpel), those on the seed of *Bignonia muricata* originate from the integument of the ovule; the wings of the indehiscent fruits (samaræ) of Acer, Ulmus, &c., are outgrowths of the pericarp; the crown of hairs on the seed of *Asclepias syriaca* evidently performs a similar service; as does the pappus of many Compositæ which is a metamorphosed calyx. In these cases it is obvious that the wind carries the seeds or fruits; in other cases animals of considerable size perform this office involuntarily, the hooked or rough fruits becoming attached to them and afterwards falling off[2].

In most of these adaptations, both their purpose and the mechanical contrivances for its attainment are easily recognised; but not unfrequently the latter require a closer examination and some reflection in order to understand them. Among many other cases of this kind one only may be mentioned here which any one can easily observe for himself. The fruit of *Erodium gruinum* and other Geraniaceæ[3] splits up into five mericarps each of which has the form of a cone with

[1] It is scarcely needful to mention again that this mode of expression has only a metaphorical meaning from the stand-point here assumed, and is only used for the sake of convenience.

[2] [A remarkable instance of this is recorded by Dr. Shaw (Journ. Linn. Soc. vol. XIV, 1874, p. 202), in the introduction into South Africa and enormously rapid distribution of a European plant, *Xanthium spinosum*, by the spiny achenes clinging to the wool of the Merino sheep.—Ed.]

[3] See Hanstein, Sitzungsber. der niederrheinischen Ges. in Bonn, 1868.

the apex pointing downwards, containing the seed and bearing above a long awn. When moist this awn is stretched out straight, but if it becomes dry while lying on the ground the outer side of the awn contracts strongly, causing the upper end to describe a sickle-shaped curve, which brings its point against the ground, the cone being thus placed with its apex downwards. The lower part of the awn now begins to contract into narrow spiral coils, causing the cone to turn on its axis and to penetrate the ground, and the erect hairs on it which point upwards retain it there like grappling-hooks. After the cone has penetrated the ground, the twisted part of the awn does the same, driving the part which contains the seed further and further into the soil. If the mericarp now becomes moistened, the coiled part attempts to straighten itself, but its coils are held by the hairs which stand on the convex surface; and thus this movement also contributes to drive the cone deeper into the soil. Whether therefore the moisture is greater or less, the mechanical contrivance produces the same effect, namely, to drive the part of the mericarp which contains the seed into the soil.

Some of the contrivances found in plants are extremely striking, from the concurrence of the most different qualities for the attainment of a perfectly definite purpose corresponding only to certain specific vital conditions, as the adaptation of the Virginian creeper to climbing up vertical walls, the contrivance to prevent self-fertilisation in the flowers of *Aristolochia Clematitis*, the bursting of the fruit of *Momordica Elaterium*, and a thousand similar structures. The most beautiful instances are generally connected with the ordinary structure, or even with other extreme cases, by a number of the most diverse intermediate or transitional forms. These transitional forms have been described in detail by Darwin in the case of climbing and twining plants, and the fertilisation of Orchids, in his works already mentioned, and by Hildebrand in the case of the fertilisation of Salvia[1].

Sect. 37.—**The Theory of Descent.** The facts and conclusions which have been indicated rather than described are the foundation of the Theory of Descent. This theory consists in the hypothesis that the most unlike forms of plants have a relationship to one another of the same kind as that which the varieties gradually developed from one ancestral form bear to it and to one another. It supposes that the different species of a genus are varieties derived from one progenitor which have undergone further development; and that in the same manner the various genera of an order owe their common characters to their descent from one and the same older ancestral form, and their differences to variation and to the accumulation by their descendants of new characters in the course of a long series of generations. The theory of descent goes still further, and assumes the same mutual relationship between the various orders of a class, and finally between the various groups. It considers variation with descent to be the cause of all the differences among plants; and the inheritance of these characters to be the cause of the agreement which subsists even between the most diverse forms of plants. What we call the common law of growth of a class, or in other words its *Type*, is the result of all the plants of this class being descended from one ancestral form or Archetype, as Darwin terms it. That which was long since termed in a merely metaphorical sense

[1] Jahrbuch für wiss. Bot. vol. IV, 1865.

the affinity between different forms of plants is, according to the theory of descent, an actual affinity or blood-relationship in various degrees. The differences have arisen in the course of a long series of generations, by the descendants of the same archetype continuing to vary; and the different individuals varying in different ways, the difference between them continually increases, and must continue to increase under diverse conditions of climate, and especially under those imposed by the struggle for existence, in order that they may still be capable of maintaining themselves. At the same time numberless varieties, species, and genera are constantly disappearing, because they are not sufficiently adapted for the struggle for existence under the new conditions caused by geological changes, and in consequence of the appearance of other forms which are better adapted to resist it.

The scientific basis for the theory of descent rests in the fact that it alone is able to explain in a simple manner all the mutual relationships of plants to one another, to the animal kingdom, and to the facts of geology and palæontology, their distribution at different times over the surface of the earth, &c.; since it requires no other hypothesis than descent with variation and the continued struggle for existence which permits those forms only to persist that are endowed with sufficiently useful properties, the others perishing sooner or later. But both these hypotheses are supported by an infinite number of facts. The theory of descent involves only one hypothesis that is not directly demonstrated by facts, namely that the amount of variation may increase to any given extent in a sufficiently long time. But since the theory which involves this hypothesis is sufficient to explain the facts of morphology and adaptation, and since these are explained by no other scientific theory, we are justified in making this assumption.

The theory of descent explains intelligibly how plants have obtained their extraordinarily perfect adaptations for resisting the struggle for existence; this struggle has itself been the means of their obtaining them by the 'Survival of the Fittest,' that is, by permitting the existence and propagation of those newly-formed varieties alone which are endowed with the various characters that render them best fitted to the climate and to resist the rivalry of competitors, the attacks of animals, &c. In this manner adaptations are gradually developed from a slight and imperceptible beginning by the accumulation of useful characters which have the appearance of being the result of the most careful and far-sighted calculation and deliberation, or sometimes even of the most cruel caprice (as in the fertilisation of *Apocynum androsæmifolium* by flies which are tortured to death in the process).

The fact that members which are morphologically similar are adapted for the most various functions is explained when we consider that the morphological features in the structure of plants are those which are most certainly transmitted unchanged to posterity, either because they are useless in the struggle for existence, or because they have proved useful in the various relations of life; as for example the differentiation into stem, root, leaves, &c., and into the different tissue-systems, by which the division of physiological labour and the acquisition of the most various properties useful for the struggle for existence are facilitated. The structure of Thallophytes, Characeæ, and Hepaticæ, shows that these morphological differentiations do not exist in the first or lowest forms of plants, but that they come gradually into existence; but when once fully developed they are preserved by

further variations, because they are never prejudicial, but often on the contrary advantageous for the purposes of adaptation.

The perfect mode in which morphological characters are inherited gives rise to a very remarkable phenomenon, the production of functionless members. It is obvious that hereditary peculiarities may have lost their use under the new vital conditions of the descendants, because the physiological requirements of the plant are supplied by other means, by fresh adaptations. Of this nature are, for example, the minute leaves on the root-like shoots of Psilotum, the formation of endosperm in the embryo-sac of many Dicotyledons whose embryo afterwards grows so vigorously as to supplant the endosperm, while it becomes itself filled with reserve food-materials which in other cases are stored up in the endosperm for the seedling. The most striking illustration however is the behaviour of parasites and saprophytes destitute of chlorophyll, which are found in various orders of plants, and the near allies of which form large green leaves containing chlorophyll, while these produce leaves similar in a morphological sense, but which are neither large nor green, and sometimes degenerated so as to have become obsolete. The explanation of this phenomenon is at once afforded by the theory of descent, viz. that the parasites and saprophytes which contain no chlorophyll are the transformed descendants of leafy ancestors which did form chlorophyll, but which gradually became accustomed to take up the assimilated food-materials of other plants or their available products of decomposition; and the more they did this the less needful did it become for the plants themselves to assimilate. The green leaves therefore became meaningless and ceased to form chlorophyll; but without chlorophyll the leaves were of little or no service to the new form, and therefore as little substance as possible was employed in their development, and they gradually degenerated.

Looked at from the point of view of the theory of descent, the natural system of the classification of plants represents their blood-relationship to one another. A species consists of all the varieties which are descended from a common ancestral form; a genus of all the species which were produced from an older progenitor, and became in the course of time further differentiated; an order includes all the genera which are descended with variation from a still older ancestral form; and the first primitive form of all the orders comprised in a group belongs to a still older past; and finally there must have been a time when a primordial plant originated the whole series of development; and this must have produced in its varying descendants the primitive types of all the later forms. The relationships of the various classes and groups described at length in Book II, might be represented by lines, which should express their actual affinity to one another; and the system of diverging lines which would thus be obtained might be compared to an irregular system of branching. In a plan of this kind we should proceed, starting from the lowest Algæ, along a number of lines of descent towards the various and more highly developed classes of Algæ. From the Siphoneæ a branch would shoot, beginning with the Phycomycetes, itself branching copiously, and leading to the various forms of Fungi. From a higher section of Algæ another line would branch out which would represent the Characeæ; and in its neighbourhood another would be given off which, splitting into two twigs, the Hepaticæ and Mosses, would represent the Muscineæ. From the same neighbourhood another line would start which would

represent the ancestors of the Vascular Cryptogams, and from this branch of the tree the Ferns, Equisetaceæ, Ophioglossaceæ, Rhizocarpeæ, and Lycopodiaceæ, would proceed as branches which themselves further ramify. Where the branch is given off for the heterosporous Vascular Cryptogams would be situated the primitive forms of Phanerogams, beginning with the Cycadeæ, and producing by further ramifications the Coniferæ, Monocotyledons, and Dicotyledons[1]. There is still much uncertainty in this plan, but the greater the progress made by a severe method of investigation and with the light of the theory of descent, the more nearly will it be possible to build up the family-tree and to give it a distinct form.

The theory of descent requires that the various forms of plants must have arisen at different times, that the primitive forms of the separate classes and groups existed at an earlier period than the derived ones; and palæontological research, although at present it has but a very small amount of material at its disposal, supports this view.

In the same manner it is a necessary consequence of the theory that each plant-form must have originated at a definite spot, that it must have spread gradually more widely from that spot, that its change of locality in the course of generations must have depended on climatic conditions, the competition of rivals, &c., and that its distribution must have been impeded by hindrances or assisted by means of transport[2]. The geographical distribution of plants has already determined in the case of many forms the spots on the surface of the earth or centres of distribution from which they gradually spread; it has shown how the distribution has been hindered sometimes by climate, sometimes by chains of mountains, sometimes by seas; how more recently formed islands have been peopled by the plants from the neighbouring continents which have become the ancestors of new species[3]; how some species when transported to a new soil (as European plants in America and *vice versâ*) have sometimes carried on a successful struggle for existence with the native plants and have increased enormously. In the distribution of plants at present existing, as for instance Alpine plants, it is possible to recognise the influences of the last great geological changes, of the entrance and disappearance of the glacial epoch and of earlier periods.

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[1] [In the fourth edition of his 'Lehrbuch,' recently published, Sachs has united Algæ and Fungi into one group (see Appendix, p. 847). He has also withdrawn the pedigree of the vegetable kingdom sketched in the text, and has substituted for it (p. 918) the following remarks:—

'Frequent attempts have been made to draw up such a so-called "genealogical tree" either for the whole or some part of the vegetable kingdom. Up to the present time these attempts have not proved very satisfactory. Our knowledge of the true relationships is still very imperfect; too much room is consequently left for fanciful speculation and the influence of subjective impressions. I shall content myself therefore with pointing out that in drawing out such a genealogical tree the closest attention must be paid to the simplest existing forms of the different types or classes; the relationship to the common primitive parent-forms will reveal itself most distinctly in these. From each of these simplest forms, however slightly different, a ramifying series may be derived; variation, proceeding independently in each series, will separate the series themselves still further; and the most perfect forms of the different types will therefore differ the most widely from one another.'—Ed.]

[2] Kerner has given an illustration of what can be accomplished in this direction in the relationships, geographical distribution, and history of the species of Cytisus from the primitive form Tubocytisus, in his pamphlet Die Abhängigkeit der Pflanzengestalt von Klima und Boden; Innsbruck, 1869.

[3] See Dr. Hooker, On Insular Floras, Gardener's Chronicle, Jan. 1867; Ann. des sci. nat. 5th series, vol. IV, p. 266.

When we reflect what a number of generations our cultivated plants must have passed through before any considerable amount of new properties were manifested in their varieties, and how long it takes for these new properties to become hereditary, and further how enormous is the diversity of hereditary properties, we are forced to the conclusion that an inconceivably long period must have elapsed since the appearance of the first plants on the earth. But geology and the physical nature of the globe require as great a space of time for the explanation of other facts; and a few millions of years more or less is a matter of but little consequence in the explanation of facts which require lapse of time in order to reach a given magnitude.

The first rudiments of the Theory of Descent, which holds good for the animal as for the vegetable kingdom, may be traced to Lamarck, at the commencement of the century, in his Zoologie Philosophique (Paris, 1801); it was afterwards advocated by Geoffroy St. Hilaire; but it is only since the publication of Darwin's work 'On the Origin of Species by means of Natural Selection' (London, 1859), that it has become an integral part of science. Darwin's great service to science is to have established as a fact the struggle for existence which all living beings have to fight, and to have proved its action in the maintenance or destruction of new forms. It is only in the struggle for existence that the motive principle is recognised, and that the theory of descent is enabled to solve the great problem why parts which are morphologically similar are adapted for such different functions; and conversely, to show how purpose in organisation can be explained, and at the same time the relations of affinity among plants. Darwin considers the Natural Selection which the struggle for existence brings about as the sole cause of the increasing differentiation of plants which are undergoing variation; he starts with the hypothesis that every plant varies in all directions without any definite tendency to become further developed in any one particular direction. He attributes to the struggle for existence alone the power of securing the perpetuation of one or more varieties among the countless numbers which are produced, and is convinced that in this way not only is a perfect adaptation of the new forms effected, but morphological differentiation is also carried further. Nägeli[1] assumes, on the contrary, that each plant has in itself a tendency to vary in a definite direction, to increase the morphological differentiation, or, as it is commonly expressed, to perfect itself. The great differences of a purely morphological nature between the classes and smaller divisions of the vegetable kingdom can then owe their existence to this internal tendency towards a higher and more varied differentiation; while the struggle for existence brings about the adaptation of the separate forms. Weighty arguments can be brought forward for and against this theory of Nägeli's; but in the present state of science I think it is impossible to decide either way; the great services of the theory of descent remain in either case; Nägeli's view does not exclude Darwin's; but the latter includes the former as a more special case.

The first and simplest plants had no ancestors; they arose by spontaneous generation or special creation. Whether this took place only once; whether only one or a number of primitive plants were produced simultaneously, giving origin in the latter case to different series of development, or whether, as Nägeli supposes, spontaneous generation has taken place at all times, and is now taking place, giving rise to new series of development, are questions which still await solution, and which we cannot follow out further here.

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[1] Nägeli, Entstehung und Begriff der naturhistorischen Art; Munich, 1865.

APPENDIX.

[In Hedwigia (1872, p. 18; see also Journ. of Bot. 1872, p. 114) Cohn has published a classification of Cryptogams in which, as respects Thallophytes, the distinction between Algæ and Fungi is abandoned. In the fourth edition (pp. 248–340) of the present work Sachs has however proposed and adopted a new classification which, except in this respect, has little in common with Cohn. In each class the names on the left hand belong to forms containing chlorophyll (so-called Algæ); those on the right to forms destitute of chlorophyll (so-called Fungi). The numbers refer to the pages in the present edition where the groups are described or mentioned.

CLASS I.

Protophyta.

Cyanophyceæ.
- Chroococcaceæ (216).
- Nostocaceæ (215).
- Oscillatorieæ (215).
- Rivularieæ (215).
- Scytonemeæ.

Palmellaceæ (in part).

Schizomycetes (214).
- Sphærobacteria.
- Microbacteria.
- Desmobacteria.
- Spirobacteria.

Saccharomyces (254).

CLASS II.

Zygosporeæ.

Conjugating cells locomotive.

Volvocineæ (217).
(Hydrodictyeæ) (217).

Myxomycetes (274).

Conjugating cells stationary.

Conjugatæ.
- Mesocarpeæ (220).
- Zygnemeæ (220).
- Desmidieæ (221).
- Diatomaceæ (222).

Zygomycetes.
- Mucorini (245).
- Piptocephalidæ (246).

CLASS III.

Oosporeæ.

Sphæroplea (231).

Cœloblastæ.

Vaucheria (223).

Œdogonieæ (229).
Fucaceæ (226).

{ Saprolegnieæ (242).
{ Peronosporeæ (244).

CLASS IV.

CARPOSPOREÆ.

Coleochætæ (231).
Florideæ (233).
Characeæ (278).

Ascomycetes (254).
Gymnoascus[1].
Discomycetes (259).
Erysipheæ (256).
Tuberaceæ (255).
Pyrenomycetes (256).
Lichenes (262).
Æcidiomycetes
(Uredineæ, 246).
Basidiomycetes (249).
Exobasidium (249).
Tremellini (249).
Hymenomycetes (249).
Gasteromycetes (251).—ED.]

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[1] [Baranetzky, Bot. Zeit. 1872.]

INDEX.

Abies, 448, 452.
Abietineæ, 452, 460.
Abortion, 198, 479, 563.
Absorption of assimilated substances, 642.
Acalypheæ, 583.
Acanthaceæ, 580.
Accumulation of characters, 826.
Acetabularia, 64, 226.
Achenium, 538.
Achillæa, 833.
Achlya, 12, 13.
Acorn, 536.
Acrocarpous Mosses, 319.
Acropetal order of development, 149.
Acrosticheæ, 361.
Actinostrobeæ, 460.
Acyclic, 523, 565.
Adaptation, 835.
Adhesion, 198, 479.
Adiantum, 161, 343, 344, 345.
Adventitious formations, 150, 152, 351, 563.
Aecidium, 241, 246.
Aesculineæ, 582.
Aesculus, 567.
Aethalium, 276, 760.
Agaricus, 249.
Aggregatæ, 581.
Aggregates of cells, 68.
Akebia, 467.
Albumen, 428.
Albuminoids, 629.
Albuminous, 513.
Aleurone, 51.
Algæ, 208.
Alisma, 514, 549.
Alismaceæ, 549, 554.
Allium, 17, 112, 546, 547.
Almond, 560.
Aloë, 171, 552.
Alpinia, 548.
Alsineæ, 583.
Alternate arrangement, 168, 524.
Alternation of generations, 202, 421, 805.
Althæa, 43, 86, 478, 483.
Amaranthaceæ, 569, 583.
Amentiferæ, 578.
Amœba-movement of protoplasm, 39, 276.
Amorphophallus, 162.
Ampelideæ, 568, 582.
Ampelopsis, 781, 839.
Amphigastria, 306.
Amygdaleæ, 585.
Amygdalus, 560.
Amyrideæ, 582.
Anacardiaceæ, 567, 582.
Anagallis, 496.
Ananasineæ, 555.
Anaptychia, 267, 270.
Anatropous, 427, 501.
Andreæa, 322.
Andreæaceæ, 329.
Androœcium, 426, 473.
Androspore, 229.
Aneimia, 89.
Anemophilous, 810.
Aneura, 296.
Angiocarpous Lichens, 268.
Angiosperms, 466.
Angle of divergence, 167, 181.
Anisocarpæ, 580.
Anisostemonous, 565.
Annonaceæ, 579.
Annual ring, 574.
Annular vessels, 23.
Annulus, 330, 356.
Anterior, 523.
Anthela, 521.
Anther, 427, 473.
Anther-lobes, 473.
Antheridium, 212, 258, 299, 321, 342, 363, 803.
Antherozoid, 203, 336, 384, 803.
Anthoceros, 302, 303.
Anthoceroteæ, 302.
Antipodal cells, 507.
Apetalous, 565.
Apex, 155, 182.
Aphanocyclæ, 579.
Apical cell, 118, 153, 348, 424.
Apical growth, 137, 410.
Apocynaceæ, 112, 580.
Apopetalous, 471.
Apophyllous, 471.
Apophysis, 334.
Aposepalous, 471.
Apostasiaceæ, 556.
Apostrophe, 672.
Apothecium, 268.
Apple, 537.
Aquifoliaceæ, 582.
Aquilegia, 500, 567.
Araliaceæ, 584.
Araucarieæ, 460.
Arbutus, 475.
Arc-indicator, 746.
Archegonium, 203, 336, 434.
Archetype, 843.
Archidium, 330.
Arcyria, 275.
Aril, 428, 501.
Aristolochia, 812.
Aristolochiaceæ, 578.
Aroideæ, 112, 549, 554, 646.
Arrangement of leaves, 173.
Artocarpeæ, 578.
Asarineæ, 578.
Asarum, 468.
Asclepiadeæ, 112, 580.
Ascobolus, 262.
Ascogonium, 257, 803.
Ascomycetes, 254.
Ascophorous hyphæ, 269.
Ascospore, 240, 254, 258.
Ascus, 240, 258.
Asexual generation, 203, 336, 423, 432, 805.
Asexual reproductive cells, 203.
Ashes, 36, 618.
Asparagin, 640.
Aspergillus, 257.
Aspidieæ, 361.
Aspidium, 351, 357, 359.
Asplenieæ, 361.
Asplenium, 123, 151, 358.
Assimilation, 626, 651, 666.
Aurantiaceæ, 569, 582.
Automatic periodic movements, 784, 801.

Autumnal layer of wood, 733.
Auxanometer, 748.
Auxospore, 223.
Axial fibrovascular bundle, 146, 418.
Axial longitudinal section, 182.
Axile placentation, 495.
Axillary branching, 155, 425.
Axis, 129, 166.
Axis of growth, 138, 182, 186.
Azolla, 398.

Bacillarieæ, 222.
Bacteria, 214.
Balanophora, 557.
Balanophoreæ, 505, 585.
Balsamia, 255.
Balsamineæ, 583.
Bambusa, 525.
Barbula, 316.
Bark, 20, 81, 717.
Base, 182.
Basidiomycetes, 249.
Basidiospore, 18, 240.
Basidium, 18, 240, 251.
Basifugal growth, 138, 350.
Bast, 94.
Bast-cells, 101, 592.
Batrachospermum, 235.
Begonia, 189, 563.
Begoniaceæ, 585.
Benthamia, 537.
Berberideæ, 570, 579, 787.
Berberis, 246, 570, 787.
Berry, 459, 539.
Betulaceæ, 578.
Bicornes, 581.
Bifurcation, 156, 161.
Bignoniaceæ, 580.
Bilateral structure, 183, 765.
Biscutella, 500.
Bisexual, 426.
Bixaceæ, 582
Blackberry, 537.
Blasia, 307.
Blastocolla, 115.
Bleeding of wood, 601.
Bloom on plants, 84.
Boletus, 81, 249.
Bordered pits, 20, 25, 464.
Borragineæ, 522, 580.
Bostrychoid cyme, 159.
Bostrychoid dichotomy, 157.
Botrychium, 378, 379, 380.
Botrydium, 225.
Bract, 519.
Bracteole, 291, 426, 519.
Branching, 148, 155.
Branching of leaves, 161.
Branching of roots, 160.
Branching of stem, 163.
Bromeliaceæ, 555.
Bryaceæ, 330.
Bryonia, 777.
Bryophyllum, 152, 563.
Bryopsis, 226.
Bryum, 81, 314.
Bud, 135.
Bud-rudiment, 282.
Bud-variation, 823.
Bulb, 196, 841.
Bulbil, 151, 282.
Bulbochæte, 230.
Bundle-sheath, 105, 106.
Burmanniaceæ, 556.
Burseraceæ, 582.
Butomus, 489, 549.
Büttneriaceæ, 583.
Buxineæ, 583.

Cabombeæ, 579.
Cactaceæ, 585.
Cæsalpineæ, 584.
Calamite, 374, 376.
Calanthe, 497.
Calcium, 622.
Calcium carbonate, 64.
Calcium oxalate, 52, 64, 112.
Callitrichaceæ, 585.
Callitris, 451.
Callus, 731.
Calothamnus, 476.
Calycanthaceæ, 584.
Calycereæ, 581.
Calycifloræ, 584.
Calyculus, 472.
Calypogeia, 309.
Calyptra, 300.
Calyx, 470.
Cambiform tissue, 100.
Cambium, 79, 93, 463.
Cambium-ring, 432, 573.
Camellia, 21.
Campanula, 566.
Campanulaceæ, 110, 566, 581.
Campylotropous, 427, 501.
Canal of the style, 498.
Canal-cell, 336, 344, 387.
Candollea, 569.
Canna, 548.
Cannabineæ, 578.
Cannaceæ, 556.
Cap-cell of root, 124.
Capillary attraction, 608.
Capillitium, 255, 275.
Capitulum, 520.
Capparideæ, 527, 579.
Caprifoliaceæ, 566, 581.
Capsella, 515.
Capsule, 294, 538.
Carbon, 619,
Carbon dioxide, 644, 666.
Carboniferous fossils, 376. 420.
Carcerulus, 537.
Carpellary leaf, 429.
Carpogonium, 257.
Carpophore, 537.
Caruncle, 540.
Caryophylleæ, 583.
Caryophyllineæ, 583.
Caryopsis, 538.
Casuarina, 473.
Casuarineæ, 585.
Cataphyllary leaves, 165, 193.
Caulerpa, 137, 226.
Cauline bundles, 134, 417, 575.
Caulome, 129, 136.
Cedreleæ, 582.
Celastrineæ, 582.
Celastrus, 524.
Cell, Primordial, 5.
Cell, Structure of, 1.
Cell-division, 8, 12, 673, 682.
Cell-families, 68, 209.
Cell-multiplication, 8.
Cell-nucleus, 2, 18, 37, 44.
Cell-sap, 2, 62.
Cell-tissue, 1, 8.
Cell-wall, 2, 19.
Cells, Formation of, 7.
Cells, Formation of the common wall of, 70.
Cells, Forms of, 5, 98, 576.
Cellulose, 2, 19, 631.
Celosia, 569.
Celtideæ, 578.
Centaurea, 797.
Centradenia, 475.
Central cell, 293, 336, 342, 434, 802.
Centranthus, 566.
Centrifugal force, action of, 691.
Centrifugal inflorescence, 520.
Centripetal inflorescence, 520.
Centrospermæ, 553, 583.
Ceramiaceæ, 237.
Ceratonia, 36.
Ceratophyllaceæ, 585.
Ceratozamia, 440.
Cercis, 187.
Cerorchideæ, 488.
Chalaza, 501.
Chara, 132, 279, 291.
Characeæ, 278
Characteristic forms of leaves and shoots, 190.
Chelidonium, 571.
Chemical processes, 618.
Chenopodiaceæ, 583.
Chenopodium, 469.
Chimonanthus, 557.
Chlænaceæ, 582.
Chlamydococcus, 218.
Chlamydomonas, 218.
Chlorantheæ, 578.
Chlorine, 622.

Chlorofucine, 685.
Chlorophyll, 6, 665, 678.
Chlorophyll-bodies, 45.
Chlorophytum, 756.
Chorisis, 528.
Chroococcaceæ, 216, 263, 273.
Chrysobalaneæ, 585.
Chrysotannin, 687.
Cichoriaceæ, 110, 787.
Cichorium, 23.
Cicinal cyme, 159, 522.
Cicinal dichotomy, 157.
Cicinus, 160.
Cilia, 211, 331, 334.
Cinnamomum, 566.
Circulation of protoplasm, 39.
Cistineæ, 582.
Citrus, 113, 569.
Cladonia, 265, 273.
Claviceps, 258, 259, 260.
Claw, 471.
Cleistogamous flowers, 810.
Clematis, 154.
Cleome, 527.
Climbing stems, 197, 772.
Clusiaceæ, 582.
Coalescence of cells, 73.
Cocoa-nut, 511.
Cœlebogyne, 805.
Cœnogonium, 268.
Coffee-berry, 512.
Coherence, 201, 471.
Colchicum, 545.
Coleochæte, 209, 231.
Coleorhiza, 143, 541.
Collema, 264.
Collenchyma, 24, 80, 83, 105, 576.
Colleter, 115.
Colloids, 594.
Colours of leaves in autumn, 657.
Columella, 275, 295, 303, 324, 331, 359.
Columnea, 534.
Columniferæ, 583.
Combined hybrids, 821.
Combretaceæ, 585.
Commelynaceæ, 112, 555.
Common bundles, 134, 369, 431, 463.
Compositæ, 115, 566, 581.
Compound spores, 241.
Conceptacle, 227, 271.
Concussion, Irritability to, 784.
Condition of aggregation of organised structures, 587.
Conducting tissue for the assimilated food-materials, 634.
Conducting tissue of style, 499.
Confervaceæ, 231.
Conidia, 244, 256.
Coniferæ, 115, 442.
Conjugatæ, 10, 220.
Conjugation, 8, 9, 203, 212, 221, 245, 261, 802.
Connective, 427, 473.
Contortæ, 580.
Contractile organs, 677, 783.
Convolvulaceæ, 580.
Corallorhiza, 194, 542, 643.
Coriaria, 166.
Cork, 80, 90.
Cork-cambium, 90.
Cormophytes, 130.
Cornaceæ, 584.
Corolla, 470.
Corollifloræ, 555, 584.
Corona, 471.
Corpuscula, 422, 434, 802.
Corrosion by roots, 625.
Cortex, 91, 280, 573.
Cortical sheath, 574.
Coryanthes, 601.
Cosmarium, 221.
Cotyledons, 435, 513, 557.
Crassulaceæ, 584.
Cremocarp, 537.
Crest, 540.
Crocus, 546.
Crown, 286.
Crozophora, 567.
Crucibulum, 69, 251.
Cruciferæ, 527, 570, 579.
Cruciforæ, 579.
Crustaceous Lichens, 263.
Crystalloids, 49, 596.
Crystals, 64.
Cucurbita, 24, 32, 33, 101, 477, 484, 779, 827.
Cucurbitaceæ, 566, 576, 581, 776, 838.
Cunninghamieæ, 460.
Cunoniaceæ, 584.
Cupressineæ, 451, 459.
Cupule. 473.
Cupuliferæ, 578.
Curvature of concussion, 707.
Cuscuta, 197, 241, 557, 561, 572, 733.
Cuscuteæ, 580.
Cuticle, 34, 83.
Cuticularisation of the cell-wall, 20, 34.
Cyatheaceæ, 360.
Cycadeæ, 436.
Cycas, 438.
Cyclantheæ, 554.
Cyclic, 523, 531, 565.
Cyclomyces, 249.
Cyme, 158, 160, 521.
Cymose branching, 158.
Cymose inflorescence, 520.
Cymose umbel, 158, 521.
Cynara, 655, 798.
Cynaraceæ, 787, 797.
Cyperaceæ, 548, 555.
Cypripedium, 479, 526.
Cystocarp, 213, 235.
Cystolith, 64.
Cystopus, 243, 244.
Cytineæ, 579.

Dahlia, 26, 63, 101, 823.
Daily periodicity of growth, 743.
Dammara, 453.
Davallieæ, 361.
Decussate, 168, 177.
Dédoublement, 481, 528, 568.
Definite inflorescence, 520.
Degradation-products, 48, 628.
Dehiscent fruits, 538, 539.
Delphinium, 531.
Deposition in the cell-wall, 31.
Derivative hybrid, 821.
Dermatogen, 126.
Descent, Theory of, 842.
Desmidieæ, 221.
Desmodium, 678, 785.
Development of the members of one branch-system, 155.
Diagonal plane, 523.
Diagram, Floral, 524.
Dialypetalæ, 581.
Diandræ, 580.
Dianthus, 472.
Diatomaceæ, 222.
Diatomine, 223.
Dichasium, 158, 159, 521.
Dichogamy, 808.
Dichotomy, 148, 156, 406.
Diclinous, 426.
Dicotyledons, 433, 556.
Dictamnus, 114, 154, 493, 528, 767.
Dictyota, 156.
Dictyoteæ, 237.
Didymium, 275.
Differentiation of cell-wall, 33.
Differentiation of tissues, 117.
Dilleniaceæ, 569, 579.
Dimorphism, 809.
Diœcious, 426, 804.
Diœcism, 807.
Dionæa, 689.
Dioscoreæ, 555.
Diosmeæ, 583.
Diosporineæ, 581.
Dipsacaceæ, 581.
Dipterocarpeæ, 582.
Directions of growth, 155, 182, 186.

Discomycetes, 259.
Discophoræ, 583.
Displacement, 198.
Diurnal and nocturnal positions of organs, 784.
Divergence, Angle of, 167, 181.
Dracæna, 107, 552.
Dried substance of plants, 618.
Drosera, 522, 796.
Drupe, 539.
Dryadeæ, 585.
Dudresnaya, 213, 237.
Dwarf males, 229.

Ebenaceæ, 581.
Elæagnaceæ, 584.
Elæagnus, 490.
Elaëis, 54.
Elaphomyces, 255.
Elasticity, 699.
Elater, 23, 294, 373.
Elatineæ, 585.
Electricity, 687.
Elementary constituents of the food of plants, 618.
Eleutheropetalæ, 581.
Eleutheropetalous, 471.
Eleutherophyllous, 471.
Eleutherosepalous, 471.
Elodea, 664.
Embryo, 203, 205, 421, 432, 434, 513.
Embryo, Cell-division in, 17, 511.
Embryo-sac, 422, 432, 454, 506, 802.
Embryonic vesicles, 422, 432, 458, 507, 803.
Emergences, 140.
Empetraceæ, 585.
Enantioblastæ, 555.
Endocarp, 518, 537.
Endogenous formations, 141, 149, 370.
Endosmotic force, 597.
Endosperm, 205, 421, 432, 434, 510, 805.
Endospore, 32, 294.
Endostome, 501.
Energy of growth, 741.
Entomophilous, 810.
Epacrideæ, 567, 581.
Epen, 103.
Epenchyma, 103.
Ephebe, 266.
Ephedra, 461.
Epicalyx, 472.
Epicarp, 518, 537.
Epidermal tissue, 78, 79.
Epidermis, 80, 81, 82, 717.
Epigynæ, 581.
Epigynous, 490.
Epilobium, 486.
Epimedium, 500, 570.
Epinasty, 767.
Epipactis, 814.
Epipetalous, 524.
Epiphragm, 253, 331.
Epipogium, 542, 620, 643.
Episepalous, 524.
Epistrophe, 671.
Equisetaceæ, 362.
Equisetum, 14, 122, 153, 363.
Equivalent members, 148.
Ergot, 258.
Ericaceæ, 567, 581.
Eriocauloneæ, 555.
Erodium, 841.
Eryngium, 490.
Erysiphe, 256.
Erythrophyll, 686.
Erythroxylaceæ, 582.
Escallonieæ, 584.
Eucyclæ, 581.
Eucyclic, 524.
Euphorbia, 168.
Euphorbiaceæ, 111, 567, 583.
Euphorbieæ, 583.
Eurotium, 257.
Everina, 272.
Exalbuminous, 513.
Excipulum, 268.
Exobasidium, 249.
Exogenous formations, 133, 149.
Exospore, 32, 294, 397.
Exostome, 501.
Extensibility, 698, 703.
Extension, 138.
Extine, 34, 485.
Extra-axillary branching, 562.

False dichotomy, 158.
Fascicular tissue, 79.
Female reproductive cell, 203, 802.
Ferments, 254.
Ferns, 340.
Fertilisation, 203, 430, 509, 803.
Fertilisation of hybrids, 821.
Fibrovascular bundles, 79, 92, 353, 431.
Ficus, 111, 200.
Fig, 200, 518, 537.
Filament, 427, 473.
Filices, 340.
Filiform apparatus, 507.
Fissidens, 313.
Flat pro-embryo, 318.
Flexibility of internodes, 703.
Floral diagram, 524.
Floral formulæ, 529, 565.
Florideæ, 233.
Flower, 319, 425, 523, 564.
Flowers of tan, 276.
Fluorescence of chlorophyll, 680.
Foliaceous Lichens, 264.
Foliage-leaves, 193.
Foliose Hepaticæ, 297.
Follicle, 538.
Fontinalis, 132, 331.
Food-materials, 619, 626.
Foot, 346, 389.
Foramen, 427.
Formative materials, 628.
Fossil Equisetaceæ, 376.
Fossil Lycopodiaceæ, 420.
Four-fold pollen-grains, 488.
Fovea, 408.
Foveola, 408.
Fovilla, 486.
Francoaceæ, 584.
Frangulineæ, 582.
Frankeniaceæ, 582.
Free cell-formation, 8, 11, 507.
Freezing, effects of, 653.
Frenela, 451.
Fritillaria, 172, 544.
Fruit, 430, 518, 536.
Fruticose lichens, 265.
Fucaceæ, 226.
Fucoxanthine, 685.
Fucus, 3, 227.
Fumariaceæ, 526, 535, 570, 579.
Funaria, 47, 82, 312, 320, 321, 331.
Fundamental tissue, 78, 102, 355.
Fungi, 238.
Funiculus, 427, 501.
Funkia, 15, 23, 482, 503, 508.

Gamopetalæ, 580.
Gamopetalous, 201, 471.
Gamophyllous, 471.
Gamosepalous, 201, 471.
Gases, movements of, 614.
Gasteromycetes, 251.
Gelatinous lichens, 265.
Gemmæ, 151, 298, 318.
General vital conditions of plants, 647.
Generating tissue, 79.
Generations, Alternation of, 202, 421, 805.
Genetic spiral, 169, 774.
Gentianaceæ, 580.
Genus, 829, 844.
Genus-hybrid, 817.
Geographical distribution of plants, 845.
Geotropism, 758.
Geraniaceæ, 583, 842.
Germ-cell, 203, 802.
Germinal vesicles, 203, 422, 507.

Germination of Phanerogams, 422, 541, 558, 638, 651.
Gesneraceæ, 580.
Geum, 201.
Glands, 110, 113.
Glandular hairs, 86, 139.
Glans, 538.
Gleba, 253.
Gleicheniaceæ, 360.
Globoids, 52.
Globulariaceæ, 580.
Globule, 284.
Glomerulus, 237.
Glume, 554.
Glumifloræ, 554.
Gnetaceæ, 460.
Gnetum, 461.
Gonidium, 263, 272.
Goodeniaceæ, 581.
Gramineæ, 525, 555.
Grand curve of growth, 737.
Granulose, 57, 60.
Graphis, 264.
Grass, flower of, 525.
Gravitation, action of, 187, 690, 758.
Grossulariaceæ, 584.
Growth, 692, 695, 712.
Growth, directions of, 182.
Growth in length, 735.
Growth in length of the root, 124.
Growth in thickness of the cell-wall, 22.
Growth in thickness of the stem, 107, 572.
Growth of starch-grains, 58.
Gruinales, 583.
Guard-cells of stomata, 75, 87.
Gum-passages, 77, 115.
Gum-resin, 116.
Guttiferæ, 582.
Gymnocarpous lichens, 268.
Gymnosperms, 423, 433.
Gymnostachys, 549.
Gymnostomum, 331.
Gynæceum, 426, 488, 491.
Gynandræ, 556.
Gynobasic style, 498.
Gynophore, 479.
Gynostemium, 479, 796.

Hæmodoraceæ, 555.
Hairs, 84, 130, 138.
Haloragideæ, 585.
Haplomycetes, 238.
Haustoria, 244, 733.
Head, 284.
Heat, Action of, 647.
Heat, Conduction of, 648.
Heat, Production of, 646.
Heat, Radiation of, 648.
Heat-expansion, Coëfficients of, 649.
Heating apparatus for the microscope, 658.
Hedera, 76, 859.
Hedychium, 548.
Helianthus, 42, 63, 69, 133, 497.
Helicoid cyme, 159, 521.
Helicoid dichotomy, 157.
Heliotropism, 190, 676, 752.
Helobiæ, 553.
Helvelleæ, 259.
Hemicyclic, 523, 565.
Hepaticæ, 295.
Heracleum, 533.
Hereditary characters, 696, 821, 822.
Hermaphrodite, 426.
Herminium, 198.
Herpothamnion, 236.
Hesperideæ, 582.
Hesperidium, 539.
Heterocyst, 215.
Heteræcism, 241, 246.
Heteromerous Lichens, 265.
Heterosporous Vascular Cryptogams, 339.
Heterostylism, 809.
Hieracium, 829.
Hilum, 540.
Hippocastaneæ, 567, 582.
Hippocrateaceæ, 582.
Hippurideæ, 585.
Hippuris, 133, 470.
Homoömerous Lichens, 265.
Hoya, 29, 592.
Humiriaceæ, 582.
Humulus, 111, 115.
Hyacinthus, 75, 87.
Hybrid, 817.
Hybridisation, 816.
Hydnora, 505.
Hydnoreæ, 579.
Hydnum, 249.
Hydrangeæ, 584.
Hydrilleæ, 554.
Hydrocharideæ, 554.
Hydrodictyeæ, 217.
Hydrodictyon, 217.
Hydrogen, 620.
Hydropeltidineæ, 579.
Hydrophyllaceæ, 580.
Hymenium, 240.
Hymenomycetes, 249.
Hymenophyllaceæ, 359.
Hymenophyllum, 341.
Hypericineæ, 582.
Hypericum, 476, 524.
Hyphæ, 238.
Hypoderma, 80, 83, 105.
Hypodermal tissue, 376.
Hypodermiæ, 246.
Hypogynæ, 580.
Hypogynous, 489.
Hyponasty 767.
Hypophysis, 515.
Hypothecium, 269.
Hypsophyllary leaves, 193, 519.

Ice, Formation of, 655.
Ilex, 35.
Imbibition, 710.
Incombustible deposits in cell-wall, 36.
Indefinite inflorescence, 520.
Indehiscent fruits, 538, 539.
Indusium, 356.
Inferior ovary, 497.
Inflorescence, 426, 431, 519.
Inherited characters, 822.
Innovation, 292.
Insect-agency in pollination, 429, 808.
Insertion, 167.
Insertion of leaves, 134.
Integument, 427, 501.
Intercalary growth of cell-wall, 22, 137.
Intercellular spaces, 71, 73.
Intercellular substance, 70, 74, 101.
Interfascicular cambium, 552, 573.
Intermediate tissue, 105.
Internodes, 135.
Internodes, Elongation of, 737.
Interposed members, 524, 568.
Intine, 32, 485.
Intrapetiolar buds, 562.
Intussusception, 31, 58, 590.
Inuline, 63.
Involucel, 520.
Involucre, 473, 520.
Irideæ, 548, 555.
Iron, 622.
Irritability, 776, 781.
Isatis, 155.
Isoëtes, 161, 401, 402, 407.
Isocarpæ, 581.
Isosporous Vascular Cryptogams, 338.
Isostemonous, 565.
Ivy, 76, 859.

Jasminiaceæ, 580.
Juglandeæ, 585.
Juliflorae, 578.
Juncaceæ, 555.
Juncagineæ, 549, 554.
Jungermannia, 310.
Jungermannieæ, 306.
Juniperineæ, 460.
Juniperus, 447, 451.

Knight's experiments on the influence of gravitation, 763.

Labiatæ, 580.
Labiatifloræ, 580.
Labium, 408.
Lamina, 191, 471, 564.
Lamium, 480.
Lateral arrangement, 184.
Lateral plane, 523.
Lateral roots, 144.
Lateral shoots, 152, 166.
Latex, 110.
Lathræa, 50, 572.
Laticiferous vessels, 74, 109.
Latticed cells, 101.
Lauraceæ, 566, 579.
Leaf, 109, 131, 136, 161, 173, 190.
Leaf-blade, 191, 564.
Leaf-forming axis, 131, 151.
Leaf-sheath, 365.
Leaf-stalk, 191, 564
Leaf-tendrils, 194, 775.
Leaf-thorns, 194.
Leaf-trace, 134, 431.
Leaf-veins, 192.
Leaflet, 191.
Legume, 538.
Legumin, 642.
Leguminosæ, 584, 640.
Lejolisia, 235.
Lemnaceæ, 553.
Lentibulariaceæ, 581.
Lenticels, 91.
Lepidodendron, 420
Lepidostrobus, 421.
Leptogium, 265.
Levisticum, 162.
Leycesteria, 566.
Libriform tissue, 35, 100.
Lichens, 262.
Lichina, 272.
Lichnoërythrine, 686.
Lichnoxanthine, 686.
Light, Action of, 659, 752, 784, 790.
Light, Intensity of, 662.
Light, Refrangibility of, 666.
Lignification of the cell-wall, 7, 20, 35.
Ligule, 192, 408, 547.
Liliaceæ, 524, 555.
Liliifloræ, 555.
Limnanthaceæ, 583.
Linaceæ, 583.
Loasaceæ, 582.
Lobelia, 566.
Lobeliaceæ, 111, 581.
Loculicidal dehiscence, 538.
Lodicule, 471.
Loganiaceæ, 580.
Lomentum, 537.
Lonicera, 566.
Loranthaceæ, 505, 513, 557, 585.
Lunularia, 298.
Lupinus, 52, 641.
Lychnis, 472.
Lycogala, 276.
Lycopodiaceæ, 400.
Lycopodieæ, 416.
Lycopodium, 70, 400, 404, 416.
Lygodium, 197, 360, 772.
Lythrarieæ, 585.

Macrosporangium, 393, 396.
Macrospore, 335, 396, 403, 432.
Magnesium, 622.
Magnoliaceæ, 579.
Mahonia, 475, 787.
Malaxis, 544.
Male reproductive cells, 203, 426, 802.
Malpighiaceæ, 582.
Malvaceæ, 583.
Manglesia, 478.
Manubrium, 284.
Marattia, 361.
Marattiaceæ, 361.
Marchantia, 23, 76, 89, 298, 301, 305.
Marchantieæ, 305.
Marcgraviaceæ, 582.
Marsilea, 140, 163, 384, 388, 393, 398, 399.
Mechanical laws of growth, 692.
Mechanical structure of irritable parts, 792.
Median plane, 167.
Medullary rays, 573.
Medullary sheath, 463, 574.
Megaclinium, 785.
Melanosporeæ, 229.
Melastomaceæ, 585.
Meliaceæ, 582.
Melobesiaceæ, 64, 234.
Members, 130.
Menispermaceæ, 566, 579.
Mericarp, 537, 538.
Merispore, 241.
Meristem, 79.
Mesembryanthemeæ, 585.
Mesocarp, 518, 537.
Mesocarpeæ, 220.
Mesophyll, 192, 356.
Metamorphosis, 631, 835.
Metamorphosis of organs, 128, 183, 194.
Metaplasm, 37, 41.
Metastasis, 626.
Metzgeria, 120, 160, 297.
Micranthæ, 554.
Microcyst, 277.
Microgonidia, 219.
Micropyle, 427, 501.
Microsporangium, 393, 396.
Microspore, 335, 396, 401, 432.
Mid-rib, 192.
Mimosa, 694, 793.
Mimoseæ, 584.
Mineral substances in food of plants, 622.
Mistletoe, 557.
Mnium, 151, 313.
Moist surfaces, Growth of roots in, 764.
Molecular forces, 587.
Molecular structure, destruction of, 591.
Molecules, 588.
Monoblepharidæ, 243.
Monocarpellary, 491.
Monocarpic, 519.
Monochlamydeæ, 578.
Monocleæ, 304.
Monocotyledons, 433, 541.
Monœcious, 426, 804.
Monœcism, 807.
Monopodial inflorescence, 520.
Monopodium, 156.
Monosymmetrical, 183, 533.
Monotropa, 194, 557, 620, 643.
Monotropeæ, 581.
Moreæ, 578.
Mosses, 295, 311.
Mother-cells of pollen, 32, 484.
Motility, 788.
Movement of food-materials, 623.
Movement of protoplasm, 39, 276, 651, 670.
Movement of water, 598, 652.
Movements of gases, 614.
Mucilage, conversion of the cell-wall into, 20, 36.
Mucor, 245, 246.
Mucorini, 245.
Mulberry, 518, 537.
Multilateral structure, 184.
Musaceæ, 548, 556.
Muscari, 154.
Muscineæ, 292.
Mushroom, 249.
Mycelium, 239, 249.
Myricaceæ, 585.
Myristica, 512.
Myristicaceæ, 579.
Myrsinaceæ, 581.
Myrtaceæ, 585.
Myrtifloræ, 585.
Myxoamœbæ, 10, 39.
Myxomycetes, 10, 274.

Naiadeæ, 504, 553.
Naias, 473, 495, 504.
Nardus, 525.
Natural Selection, 831,
Natural System, 844.
Nectar, 500.
Nectary, 430, 500.
Negative heliotropism, 677, 756.
Nelumbiaceæ, 579.
Nemalieæ, 237.
Neottia, 194, 620, 693.
Nepentheæ, 578.
Nepenthes, 601.
Nidularieæ, 251.
Nitella, 16, 285, 287, 288, 289.
Nitrogen, 621.
Node, 135.
Nostoc, 215.
Nostocaceæ, 215, 273.
Nostochineæ, 214.
Nucleoli, 38, 44.
Nucleus, 2, 18, 37, 44, 252, 422.
Nucule, 284, 289.
Nuphar, 539.
Nut, 538.
Nutation, 766.
Nutmeg, 512.
Nyctagineæ, 583.
Nymphæaceæ, 576, 579.

Ochnaceæ, 583.
Œdogonieæ, 229.
Œdogonium, 9, 22, 230.
Œnothereæ, 585.
Oil, 55, 115.
Oleaceæ, 566, 580.
Onygenaceæ, 256.
Oogonium, 3, 203, 212, 802.
Oosphere, 203, 212, 802.
Oospore, 213, 803.
Opening and closing of flowers, 798.
Operculum, 330.
Ophioglossaceæ, 378.
Ophioglossum, 379, 381.
Ophrydeæ, 488.
Orchideæ, 488, 505, 506, 526, 556, 814.
Orchis, 502, 536.
Order of development of roots, 143.
Order of succession of the parts of the flower, 530.
Organic centre, 182.
Organic processes, 693.
Organs of plants, 128.
Origin of species, 822.
Original forms of plants, 128.
Orobanche, 194, 241, 557.
Orobancheæ, 580.
Orthostichy, 167.
Orthotropous, 427, 501.
Oscillatoria, 215.
Oscillatorieæ, 215.
Osmunda, 341.
Osmundaceæ, 360.
Ovary, 429, 466, 488.
Ovule, 203, 427, 501, 504.
Oxalideæ, 583.
Oxalis, 787, 796.
Oxygen, 621.

Paleæ, 129, 347, 356, 554.
Pallisade-tissue, 465, 657.
Palmaceæ, 552, 554.
Palmellaceæ, 263.
Pandanaceæ, 554.
Pandorina, 219.
Panicle, 520.
Papaver, 571.
Papaveraceæ, 111, 571, 579.
Papayaceæ, 110, 582.
Papilionaceæ, 584.
Pappus, 471, 540, 841.
Paraphyses, 251, 293, 356.
Parasites, 194, 241, 557, 572, 620, 643, 844.
Parasitism of Lichens, 263, 273.
Parastichy, 173.
Paratonic condition, 677.
Parenchyma, 78, 100.
Parietales, 582.
Paris, 167.
Parnassia, 566, 766.
Paronychieæ, 569, 583.
Parthenogenesis, 805.
Passiflora, 776, 780.
Passifloraceæ, 582.
Pastinaca, 162.
Pediastrum, 68, 217.
Peduncle, 426.
Peltigera, 264.
Perianth, 293, 309, 426, 469.
Periblem, 126.
Pericambium, 144, 353.
Pericarp, 236, 518, 537.
Perichætium, 293, 309, 320.
Periderm, 81, 90.
Peridium, 239, 251, 253.
Perigonium, 320.
Perigynæ, 584.
Perigynous, 489.
Periodic movements of organs, 782.
Periodicity of growth in length, 743.
Perisperm, 428, 512.
Peristome, 331.
Perithecium, 256, 258.
Permanent tissue, 79.
Peronosporeæ, 244.
Pertusaria, 264, 271.
Petal, 470.
Petiole, 191, 564.
Peziza, 11, 261.
Phæosporeæ, 229.
Phalloideæ, 253.
Phallus, 254.
Phascaceæ, 329.
Phaseolus, 24, 126, 146, 492. 559.
Phelloderm, 91.
Phellogen, 90.
Philadelpheæ, 584.
Phloëm, 94, 100.
Phloëm-layers of fibrovascular bundles, 100.
Phloëm-sheath, 419.
Phlomis, 494.
Phœnix, 542.
Phosphorescence, 646.
Phosphorus, 622.
Phototonus, 790.
Phycocyanine, 216, 686.
Phycoërythrine, 234, 237, 686.
Phycomycetes, 240, 242.
Phycophæine, 226.
Phycoxanthine, 223, 226, 686.
Phyllanthaceæ, 583.
Phyllantheæ, 583.
Phyllocladus, 450.
Phyllode, 202, 408.
Phylloglossum, 407.
Phylloid, 211.
Phyllome, 130, 136.
Phyllopode, 420.
Phyllophyte, 130.
Phyllotaxis, 167, 173, 348.
Physarum, 275.
Physcia, 272.
Phytelephas, 512.
Phytolacca, 569, 576.
Phytolaccaceæ, 569, 583.
Pileus, 249, 254.
Pilularia, 32, 392, 395, 396, 397.
Pine-apple, 537.
Pineæ, 460.
Pinus, 25, 31, 70, 72, 89, 105, 442, 449, 465.
Piperaceæ, 495, 504, 578.
Piperineæ, 578.
Pisum, 52.
Pitcher-like organs, 601.
Pith, 108, 717.
Pitted vessels, 26.
Pittosporeæ, 582.
Placenta, 427, 488.
Plane of insertion, 167.
Plane of symmetry, 183.
Plantagineæ, 566, 580.
Plasmodium, 10, 39, 275, 760.
Platanaceæ, 578.
Platycerium, 347.

Plerome, 127.
Pleurocarpous Mosses, 319.
Plumbagineæ, 581.
Plumule, 518.
Podocarpeæ, 460.
Podocarpus, 450.
Podophyllum, 570.
Podostemoneæ, 585.
Point of insertion, 167.
Polarized light, 588.
Polemoniaceæ, 580.
Pollen, Formation of, 14, 15, 34, 440, 481.
Pollen-grain, 23, 203, 423, 426, 432, 449, 485.
Pollen-sac, 426, 440, 448, 482.
Pollen-tube, 33, 450, 485, 509.
Pollination, 429.
Pollinium, 488.
Pollinodium, 258.
Polycarpæ, 554, 579.
Polycarpellary, 492.
Polycarpic, 519.
Polyembryony, 459.
Polygala, 535.
Polygalaceæ, 582.
Polygamous, 467, 807.
Polygonatum, 165, 542.
Polygonaceæ, 495, 585.
Polypodiaceæ, 341, 360.
Polypodieæ, 361.
Polysymmetrical, 183, 533.
Polytrichum, 333.
Pomeæ, 584.
Pontaderiaceæ, 555.
Pore-capsule, 539.
Porphyreæ, 237.
Portulacaceæ, 583.
Posterior, 523.
Potamogeton, 548.
Potamogetoneæ, 554.
Potassium, 622.
Potato, 59.
Pressure, Effect of, on growth, 729.
Prickle, 85.
Primary cortex, 574.
Primary meristem, 79, 117.
Primary root, 142, 144.
Primary tissue, 78.
Primary wood, 574.
Primine, 501.
Primordial cell, 5.
Primordial epidermis, 126.
Primordial utricle, 42.
Primulaceæ, 495, 531, 568, 581.
Primulineæ, 581.
Procambium, 93.
Products of degradation, 48, 628.
Pro-embryo, 205, 279, 311, 432, 434, 458, 513.
Pro-embryonic branch, 282.
Prolification, 426, 439.
Promycelium, 239.
Prosenchyma, 78.
Protandrous, 812.
Proteaceæ, 584.
Proteine-grains, 51.
Proten, 103.
Protenchyma, 103.
Prothallium, 205, 335, 432.
Protogynous, 812.
Protomyces, 255.
Protonema, 205, 311, 341.
Protoplasm, 2, 37.
Prototaxites, 226.
Pseudaxis, 157, 159.
Pseudocarp, 201, 518.
Pseudopodia, 318, 329.
Psilotum, 406, 411.
Psoralea, 113.
Pteris, 24, 27, 28, 30, 35, 92, 96, 105, 123, 196, 343, 345, 347, 348, 350, 354.
Puccinia, 246.
Pulvinus, 783, 786.
Punctum vegetationis, 117.
Pycnidium, 256, 271.
Pyrenomycetes, 256.
Pyrola, 493, 557.
Pyrolaceæ, 581.
Pyxidium, 538.

Quercus, 559.

Raceme, 520.
Racemose branching, 158.
Racemose inflorescence, 520.
Radicle, 518, 558.
Radula, 309.
Rafflesiaceæ, 557, 579.
Ramondieæ, 580.
Ranunculaceæ, 567, 579.
Raphe, 427, 501.
Raphides, 65, 112.
Reaumuriaceæ, 582.
Receptacle, 239, 249, 426, 489.
Receptive spot, 344.
Reciprocal hybrids, 818.
Refrangibility, Action of rays of different, 666.
Regular flowers, 533.
Rejuvenescence of the cell, 8.
Reproductive cells, 202, 426, 802.
Reseda, 166.
Resedaceæ, 582.
Reserve-materials, 627.
Resin-passages, 77, 115, 465.
Respiration, 644.
Restiaceæ, 555.
Retardation of growth by light, 675, 754.
Revolving nutation, 766.
Rhamnaceæ, 582.
Rheum, 496, 507.
Rhizantheæ, 579.
Rhizine, 264.
Rhizocarpeæ, 383.
Rhizoid, 211, 282, 317.
Rhizome, 196.
Rhizophore, 147, 411.
Rhizopus, 245.
Rhodoraceæ, 581.
Rhus, 567.
Rhodospermine, 51.
Ribes, 91.
Riccia, 304.
Ricciеæ, 304.
Ricinus, 95, 97, 108, 161, 476, 558, 638.
Rivularia, 215.
Rivularieæ, 215.
Roccella, 272.
Root, 129, 140.
Root-cap, 123, 127, 140.
Root-hairs, 139.
Root-pressure, 600, 609.
Root-sheath, 143.
Root-system, 142.
Roots, Branching of, 160.
Roots, Growth of, 124, 740.
Rosa, 200.
Rosaceæ, 584.
Rose-hip, 201, 537.
Rosifloræ, 584.
Rotation of protoplasm, 39, 43.
Rubiaceæ, 566, 581.
Rutaceæ, 583.
Ruteæ, 583.

Sabal, 169.
Sabina, 451.
Saccharomyces, 254.
Sagittaria, 72.
Salicineæ, 582.
Salisburia, 446.
Salvia, 814.
Salvinia, 170, 384, 386, 387, 390, 391, 394.
Samara, 538.
Sambucus, 573.
Samydaceæ, 582.
Sanguisorbeæ, 585.
Santalaceæ, 505, 585.
Santalum, 507.
Sap, 62.
Sap-conducting intercellular passages, 76, 115, 464.
Sap-vesicles, 42.
Sapindaceæ, 575, 582.
Sapotaceæ, 581.
Saprolegnieæ, 242, 805.
Saprophytes, 194, 542, 557, 572, 620, 643, 844.
Sarcocarp, 537.
Saurureæ, 578.
Saxifraga, 492.

Saxifragaceæ, 566, 584.
Saxifragineæ, 584.
Scalariform vessels, 27, 98, 355.
Scale-leaves, 193.
Schizæaceæ, 341, 360.
Schizandreæ, 579.
Schizocarp, 537, 538.
Schizomycetes, 214.
Schizosporeæ, 214.
Schultz's solution, 67.
Schwendener's Lichen-theory, 262.
Scirpus, 548.
Scitamineæ, 555.
Scleranthеæ, 583.
Scleranthus, 569.
Sclerenchyma, 35, 104, 106.
Sclerotium, 239, 259, 277.
Scolecite, 262.
Scorpioid cyme, 160, 522.
Scorpioid dichotomy, 157.
Scorzonera, 111.
Scrophularia, 99.
Scrophulariaceæ, 580.
Scutellum, 144, 541.
Scutiform leaf, 389.
Secondary cortex, 573.
Secondary products of metastasis, 628.
Secondary roots, 142.
Secondary wood, 574.
Secundine, 501.
Seed, 423, 432, 518, 540.
Segmentation of the apical cell, 118.
Selagineæ, 580.
Selaginella, 47, 78, 104, 403, 405, 409, 410, 414, 415, 416, 417, 419.
Selaginelleæ, 416.
Sensitiveness, 651, 776, 781.
Sepal, 470.
Septicidal dehiscence, 538.
Septifragal dehiscence, 538.
Serpentarieæ, 578.
Seta, 294, 324, 330, 471.
Sexual affinity, 818.
Sexual generation, 203, 335, 400, 432, 805.
Sexual reproduction, Phenomena of, 801.
Sexual reproductive cells, 203, 426, 802.
Sheath-teeth, 370.
Shells, Formation of, in the cell-wall, 33.
Shield, 284.
Shoot, 136, 194.
Sieve-cells, 23.
Sieve-discs, 25, 101.
Sieve-tubes, 101, 418.
Sigillaria, 420.
Sileneæ, 583.
Silicon, 623.
Siliqua, 538.
Simarubeæ, 583.
Simultaneous whorls, 166.
Siphoneæ, 223.
Skeleton of cell-wall, 37.
Skeleton of starch-grain, 60, 589.
Skin of protoplasm, 38, 41.
Sleep of plants, 799.
Sodium, 622.
Soft bast, 101.
Solanaceæ, 198, 522, 580.
Solitary arrangement, 167.
Solorina, 271.
Solubility of starch-grains, 61.
Sorby's researches on chlorophyll, 684.
Soredial branch, 266.
Soredium, 271.
Sorus, 356.
Spadicifloræ, 554.
Spadix, 520.
Spathe, 473.
Special mother-cells, 32, 88, 485.
Species, 829, 844.
Species, Origin of, 822.
Species-hybrid, 817.
Spectrum of chlorophyll, 678.
Sperm-cell, 203, 802.
Spermogonium, 246, 256, 271.
Spermatia, 240, 246, 256.
Spermatozoid, 10, 203, 212, 803.
Sphacelia, 259.
Sphæroplea, 231.
Sphagnaceæ, 326.
Sphagnum, 326, 327, 328, 329.
Sphere-crystals, 63, 65.
Spicular cells, 66.
Spike, 520.
Spine, 197.
Spiræeæ, 585.
Spiral arrangement, 169.
Spiral flowers, 523, 531.
Spiral theory of phyllotaxis, 180.
Spiral vessels, 23, 97.
Spirogyra, 9, 10, 17, 220.
Splitting of the cell-wall, 71.
Spontaneous periodic movements, 784, 801.
Sporangium, 129, 252, 356.
Spore, 203, 240.
Spores, Mode of formation of, 14.
Sporidia, 248.
Sporocarp, 392.
Sporogonium, 292, 324, 338.
Spur, 500.
Stamen, 426, 473.
Staminode, 479.
Staphyleaceæ, 582.
Starch, 6, 57, 635, 669.
Starch-cellulose, 57.
Stem, 130, 136, 575.
Stem-tendrils, 196, 775.
Stephanosphæra, 218.
Sterculia, 478.
Sterculiaceæ, 583.
Sterigma, 257, 271.
Sticta, 264.
Stigeoclonium, 4, 8.
Stigma, 429, 488, 499.
Stigmaria, 421.
Stigmatic cells, 293, 323.
Stipule, 192, 281, 564.
Stolon, 196.
Stomata, 75, 86, 603.
Stone-fruit, 104, 106, 539.
Stratification of the cell-wall, 20, 29.
Stratioteæ, 554.
Strawberry, 518, 536.
Streaming of protoplasm, 38, 42.
Striation of the cell-wall, 20, 29.
Stroma, 256.
Strophiole, 540.
Struggle for existence, 831.
Strychnaceæ, 580.
Style, 488, 498.
Stylidieæ, 581.
Stylospore, 254, 256.
Stypocaulon, 118.
Styracaceæ, 581.
Subepidermal tissue, 80, 105.
Subhymenial layer, 269.
Successive whorls, 166, 170.
Sulphur, 622.
Superficial glands, 114.
Superior ovary, 491.
Surface-growth of the cell wall, 21.
Superposed members, 168, 524, 568.
Survival of the Fittest, 843.
Suspensor, 405, 424, 513.
Swarmspore, 5, 39, 211.
Swartzieæ, 584.
Swelling, 36, 698.
Swelling of starch-grains, 61, 592.
Swimming of swarmspores and spermatozoids, 39.
Symmetrical, 183, 469, 533.
Sympetalæ, 580.
Sympetalous, 201, 471.
Symphoricarpus, 566.
Symphyllous, 471.
Sympodial inflorescence, 521.
Sympodium, 157, 159.
Synandræ, 581.
Syncarp, 537.
Synsepalous, 201, 471.
System, Natural, 844.

Taccaceæ, 555.
Tamariscineæ, 582.
Tap-root, 561.
Targioneæ, 306.
Taxineæ, 460.
Taxodineæ, 460.
Taxodium, 446.
Taxus, 447, 450, 455.
Teeth, 331, 334.
Teleutospore, 248.
Temperature, Action of, 591, 651, 748, 784, 789.
Temperature, Dependence of vegetation on, 647.
Temperature, Limits of, 651.
Tendril, 194, 196, 766, 775.
Tension of tissues, 708, 713.
Terebinthaceæ, 116, 582.
Terebinthineæ, 582.
Terminal branching, 155.
Ternströmiaceæ, 582.
Testa, 421, 427, 512.
Tetracyclæ, 580.
Tetragonieæ, 585.
Tetraphis, 319.
Tetraspore, 234.
Thalloid Hepaticæ, 296.
Thallome, 130, 137.
Thallophytes, 130, 207.
Thallus, 130.
Theca, 294, 324.
Theory of descent, 842.
Thickening-ring, 107, 109, 575.
Thread-indicator, 747.
Thuja, 449.
Thujopsidæ, 460.
Thunbergia, 34.
Thymelæaceæ, 584.
Thymelæineæ, 584.
Tiliaceæ, 569, 583.
Tissues, Forms and Systems of, 77, 431.
Tissues, Morphology of, 68.
Torsion, 770.
Torus, 426, 489.
Trabeculæ, 413.
Tracheïdes, 73, 98.
Traction, Action of, on growth, 729.
Trama, 250.
Transfusion-tissue, 466.
Transpiration, 602.
Transport of assimilated substances, 634.
Trapa, 517, 557.
Traube's artificial cells, 594.
Tree-ferns, 355.
Tremellini, 249.
Trichia, 275.
Trichogyne, 212, 235.
Trichomanes, 341.
Trichome, 129, 138, 356.
Trichophore, 213, 236.
Tricoccæ, 583.
Triglochin, 549.
Tropæolaceæ, 582.
Tropæolum, 14, 776.
Tube connecteur, 237.
Tuber, 196, 255.
Tuberaceæ, 255.
Tubifloræ, 580.
Tulipa, 637.
Tüllen, 27.
Turgidity, 700, 708.
Turneraceæ, 582.
Twining of climbing plants, 772.
Twining of tendrils, 775.
Twining stems, 197, 772.
Type, 842.
Typha, 473, 495.
Typhaceæ, 504, 555.

Udotea, 226.
Ulmaceæ, 578.
Ulvaceæ, 231.
Umbel, 520.
Umbel, Cymose, 158.
Umbelliferæ, 584.
Umbellifloræ, 584.
Unequal growth, 765.
Unguis, 471.
Unicellular plants, 77, 209, 615.
Unilateral cicinal cyme, 522.
Unilateral helicoid cyme, 521.
Uredineæ, 246.
Uredo, 248.
Urn, 294, 324.
Urticaceæ, 111, 578.
Urticeæ, 578.
Urticineæ, 578.
Usnea, 264, 266, 272.

Vacciniaceæ, 581.
Vacuoli, 38, 41.
Vaginula, 309, 324.
Valeriana, 566.
Valerianaceæ, 566, 581.
Vallisneria, 664, 689.
Vallisnerieæ, 554.
Variation, 696.
Variation of hybrids, 820.
Variety, 823.
Variety-hybrid, 817.
Vasa propria, 101.
Vascular bundle-sheath, 355.
Vascular Cryptogams, 335.
Vascular portion of fibrovascular bundle, 98.
Vaucheria, 41, 223, 224, 225.
Vegetable ivory, 512.
Vegetative cone, 117.
Velum, 249, 408.
Venation, 103, 192, 547, 564.
Verbenaceæ, 580.
Verticillate flowers, 523.
Vesicular vessels, 110.
Vessels, 98.
Vicia, 558.
Viola, 499, 511, 814.
Violaceæ, 582.
Virginian creeper, 781, 839.
Viscum, 506, 557.
Vitis, 562, 780.
Volvocineæ, 217.
Volvox, 219.

Waking and sleeping of plants, 786.
Water, Ascent of, from the root, 608.
Water, Currents of, in the wood, 603.
Water, Exudation of, 600.
Water of crystallisation, 32.
Water of organisation, 32, 62.
Water, Movements of, 598. 652.
Watsonia, 507.
Wax, 84.
Welwitschia, 461.
Wendungszellen, 286, 289.
Whorl, 149, 166.
Whorl, Spurious, 149.
Wood, 98, 574, 717.

Xanthophyll, 685.
Xanthoxylaceæ, 583.
Xylem, 94, 717.
Xylem-portion of fibrovascular bundle, 98.
Xyrideæ, 555.

Yeast-fungi, 254.
Yucca, 552.

Zamia, 437.
Zea, 42, 61, 71, 94, 133, 141, 143, 144, 147, 827.
Zingiberaceæ, 548, 556.
Zoosporangium, 13.
Zoospore, 13, 211.
Zygnema, 46.
Zygnemeæ, 220.
Zygomorphic, 183, 533.
Zygophyllaceæ, 583.
Zygospore, 10, 212, 220, 245, 802.

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