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THE PLANT CELL:

ITS MODIFICATIONS AND VITAL PROCESSES.

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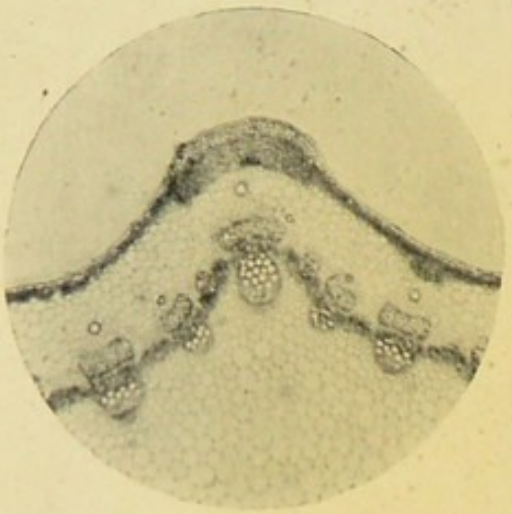

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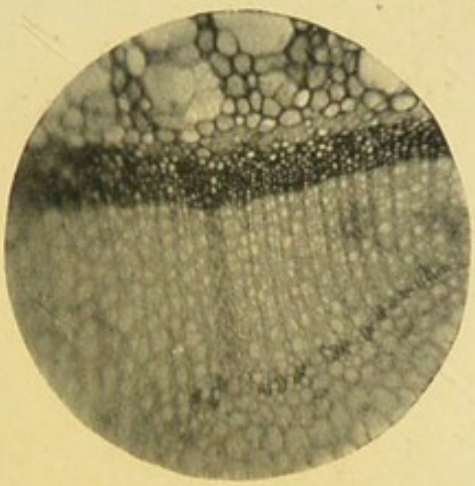

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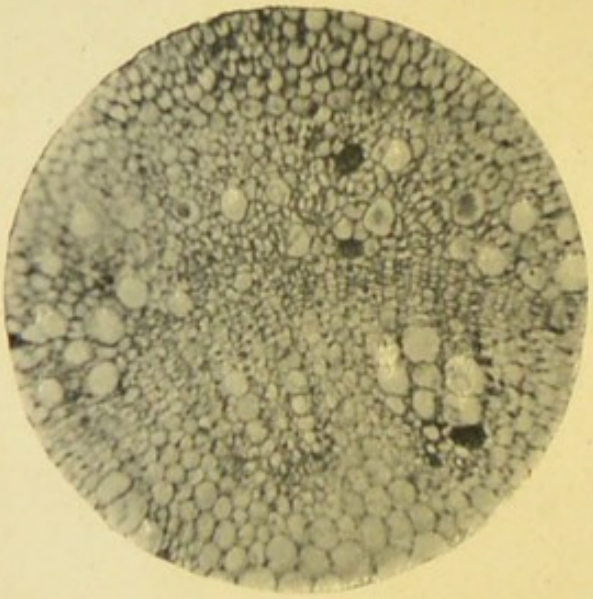

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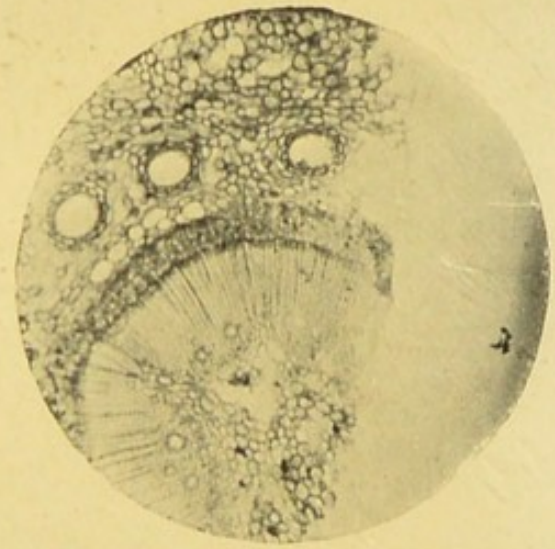

PLATE II

1. Portion of a transverse section of *Sambucus* stem of one year's growth. Note the primary bundles, and between them the interfascicular cambium and evidences of secondary xylem and phloem. Resin-canals are scattered throughout the cortex. Note also patches of sclerenchyma at the outer margin of cortex.

2. Portion of a transverse section of a dicotyledonous stem, showing arrangement of the xylem, cambium, phloem, and bast-fibres.

3. Portion of a transverse section of the young stem of *Lupulus*, showing the cambial region and young xylem and phloem elements.

4. Part of a transverse section of the stem of *Pinus*, showing the characteristic dicotyledonous arrangement; large resin-canals are seen in the cortex.

(See Chaps. iv. and v.)

THE PLANT CELL:

ITS MODIFICATIONS AND VITAL PROCESSES.

A MANUAL FOR STUDENTS

BY

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PREFACE.

In the following pages the Author's aim has been to deal with the Study of Structural and Physiological Botany from a biological standpoint, in which the working substance of a cell,—viz., the protoplasm—is given the first place in importance; the subsequent changes which are produced in form, function, &c., being looked upon as being due to the sole agency of the protoplasm, influenced by the various physical and chemical stimuli which may be brought to bear upon it. This method of dealing with the cell, whether animal or vegetable, has been found, in the writer's experience, to be a rational and useful one when such a wide subject as Biology is first approached by the student. The section on Cell-division has been presented in rather full detail, on account of the great importance attached nowadays to cytological phenomena in which the nucleus is involved. With regard to the illustrations, a few photo-micrographs have been inserted, and these, it is hoped, will give a rather more realistic aspect to one or two of the more difficult sections, such as those on Embryology and Nuclear Division.

The Author's thanks are due to Professor Oliver (University College, London) for several valuable suggestions, and for the help afforded whilst the Author was a student at University College.

H. A. H.

Hendon, 1909.

CONTENTS.

ERRATA.

Frontispiece, line 1, for *Sambucus* read *Lupulus.*

,, line 7, for *Lupulus* read *Sambucus.*

Page 12, lines 13 to 15 should read thus:—

"is meant a condition of *tension* inside a cell resulting from the intake of water by osmosis (see Chap. x.) until an equilibrium is set up between the sap inside the cell and the fluid outside."

Page 127, line 37, after "oospore" insert "elongates into a structure known as the *proembryo* which has a cell cut off from its lower end, and this," &c. The remainder of the proembryo forms the *suspensor.*

Page 128, line 4, omit the words "and, in some cases, the *foot* (an absorbent organ)."

LIST OF PLATES AND PHOTOMICROGRAPHS.

THE PLANT CELL.

INTRODUCTION.

In order to study the life-phenomena of any organism, and to arrive at a definite explanation of them, it is often found necessary to enquire into its minute structure; and, in the case of the plant, the study of the cell, including its form, growth, component parts, and the varied conditions under which it can exist, is an essential part of the science of Botany, as a branch of Biology. The facts and features brought to light by the microscope, coupled with those pertaining to Chemistry and Physics, have long afforded proofs of statements and observations which were formerly only regarded in the light of speculation.

In the following pages the object will be to give a concise and correct idea of the principal structural elements of plant-tissues; stress has been laid upon practical microscopical observations and reactions with various reagents, for these, although generally simple to perform, sometimes afford a very clear demonstration of important life-factors. A brief account has also been given of the most important chemical and physical phenomena occurring in a cell.

Cells; Types met with in the Plant.—From a purely biological standpoint a **cell** or **protoplast** is defined as "a mass of **protoplasm**, sometimes with and sometimes without a definite limiting membrane, having situated in its substance (except in a few cases) a **nucleus** and often accessory portions, such as plastids, chloroplasts, vacuoles, and food-granules of various kinds." The cases between which this definition distinguishes are :—

i. **The Amœboid Cell** (plasmodia).—Here the protoplasm is not, during at least the greater part of its existence, limited by any

firm cell-boundary, but is motile and creeps about, and also ingests food by means of protrusions (pseudopodia) pushed out from its clear outer portion, or ectoplasm (see Chap. i.).

ii. **Cells possessing Definite Cell-walls during their whole Existence.**—Here a firm limiting membrane is present, and the protoplasm although capable of moving within these limits, cannot move freely from one position to another. Further on, it will nevertheless be seen that "pits" or perforations may exist in the cell-wall, by means of which the protoplasmic contents of adjacent cells are put into communication with one another; and at times the protoplasm may pass slowly through these "pits" so as to vacate one cell-cavity for another, leaving its former casing quite empty.

iii. **Motile cells,** often possessing no differentiated cell-wall, but the outermost portion of the protoplasm is much firmer than the inner portion, thus forming a more or less resistant boundary. These cells have one or more protrusions of the firm outer protoplasm (ectoplasm), known as **cilia,** which are active in producing movements of translation or rotation (swarmspores).

We shall notice more especially the second of these subdivisions.

Tissues and their Arrangement: Function: Classification of Plants according to Evolution.—Before proceeding to the detailed study of the various cells of which a plant is made up, it is necessary to examine, briefly, the manner in which cells are grouped into **tissues,** and the nomenclature, general arrangement, and function of these as they occur in such organs of a plant as stem, root, and leaf; and it will also be convenient to have an outline of the main groups and subdivisions into which the vegetable kingdom is divided, from the point of view of evolution.

In **lower plants,** such as the Algæ, there are often found cells living as **single organisms** during their whole existence, and yet others are joined together so as to form a **colony,** such as a filament, or a flat, or round mass of cells, which live together forming what is known as a cell-community. Occasionally plants of a low order are observed, which are to all external appearances somewhat highly differentiated (*Fucus*, *Laminaria*), but which, nevertheless, when their internal structure is examined, are found to be of comparatively simple organisation.

On passing upwards through the Fungi to the Liverworts and Mosses, and so on to the Higher Plants, it is noticed first, that the external configuration of a plant becomes, as a rule, more complex, there being a subdivision of the whole into various **organs**; and secondly, that this subdivision coincides with a correspondingly complex internal organisation; it is found, in fact, that where in the lower plants all the vital functions take place in the one or perhaps a very few cells, in the higher plants a division of labour obtains whereby separate functions are relegated to as many separate tissues.

In the higher plants in which well-marked organs, such as stem, leaf, and root, are found, it will be seen that the cells composing these organs may be grouped into **tissues,** which have the following nomenclature and general arrangement from without inwards:—

Stem or Root.

External Tissues: (*a*) Epidermis.

(*b*) Cortex;* at times continuous with (*c*).

Internal Tissues: (*c*) A general **fundamental tissue** in which lie the vascular bundles, or,

(*d*) A well-marked **central cylinder** (bounded by a tissue known as **endodermis**), which comprises the vascular system, and the **pith** or **medulla.**

Besides these main tissues, there occur in various positions in the cortex, fundamental tissue, or central cylinder, certain other tissues, which, as a rule, have a supporting or protective function; such are **cork, collenchyma,** and **sclerenchyma,** the occurrence and features of which will be examined in due course (Chap. iii.).

In *leaf-structures,* the tissue arrangement may be of two kinds—viz., (*a*) the **bifacial,** or (*b*) the **centric.** In the former is found externally the **epidermis** on both upper and under surfaces of the leaf, and internally a tissue known as **mesophyll,** in which lie vascular elements and at times other tissues of a subsidiary nature. In the latter or centric type there is present a general arrangement not unlike that found in the stem of the same plant—viz., externally, epidermis and mesophyll; internally, a **central cylinder** in which are to be seen the vascular bundles.

*The cortex is only external with regard to the central cylinder. It is, however, convenient to deal with it among the external tissues.

(The leaves of *Pinus* and *Hakea* belong to the centric type.) In some leaf-structures, such as those of mosses, a much simpler arrangement obtains, the leaf being, perhaps, only two or three cells thick, and the vascular system quite rudimentary.

The subdivision of the tissues of stem or root-structures in plants into epidermis, cortex, and central cylinder, occurs typically in the Dicotyledons and Coniferæ, and these tissues are set apart early in the young stem or root; in the Monocotyledons and the Higher Pteridophyta (ferns) is found the arrangement noted in (*c*) (see *supra*)—viz., an external epidermis, and internally a ground-tissue in which lie several separate vascular bundles, no well-marked central cylinder existing, although in the young shoot a central cylinder may be detected.

In plants below the Pteridophyta the main grouping of tissues into external and internal may often hold good, but the differentiation is not so marked as it is in the higher types, and, finally, when the Fungi and Algæ are considered, the vascular tissues cease to exist *per se*, and the plant becomes a structure known as a **Thallus** (Thallophyta) the component tissues of which conform to one or at most a few simple types, and are not always to be differentiated into internal and external groups.

With regard to the general nomenclature of tissues, those in which the component cells have equal, or nearly equal, dimensions whichever way they are measured, are termed **parenchyma**; whilst those where the cells have an elongated shape, one dimension being possibly ten or twenty times the other, are known as **prosenchyma.** Amongst the latter are sclerenchyma, bast fibres, cambial elements, and elements of the xylem and phloem, all of which will be examined in detail (Chaps. iv. and v.).

The **functions** of the cells in the various tissues will be to a certain extent studied together with their structural details, but broadly speaking it may be here stated that the following tissues—viz., epidermis, cortex, and the mesophyll of leaves—function in assimilation, transpiration, and elaboration of food materials, the epidermis being also often protective in nature; the cork, collenchyma and sclerenchyma are mainly protective, and confer elasticity and rigidity upon an organ in which they are present; whilst the wood and bast confer rigidity, and are essentially concerned in the conduction of sap (the phloem

possessing the special functions of conducting and storing the constituents of elaborated sap).

There are, moreover, certain **isolated tissues*** in plants, such as *glands* and *resin-canals*, which have special functions, and these will be examined in due course (Chap. vi.).

In lower plants, such as the Algæ, all functions,—viz., **assimilation, respiration, nutrition as a whole,** and **reproduction**—may be carried on in the one or perhaps the few cells of which the plant is made up; and thus, the **division of labour** which obtains in a plant composed of many tissues, is absent in the lower forms.

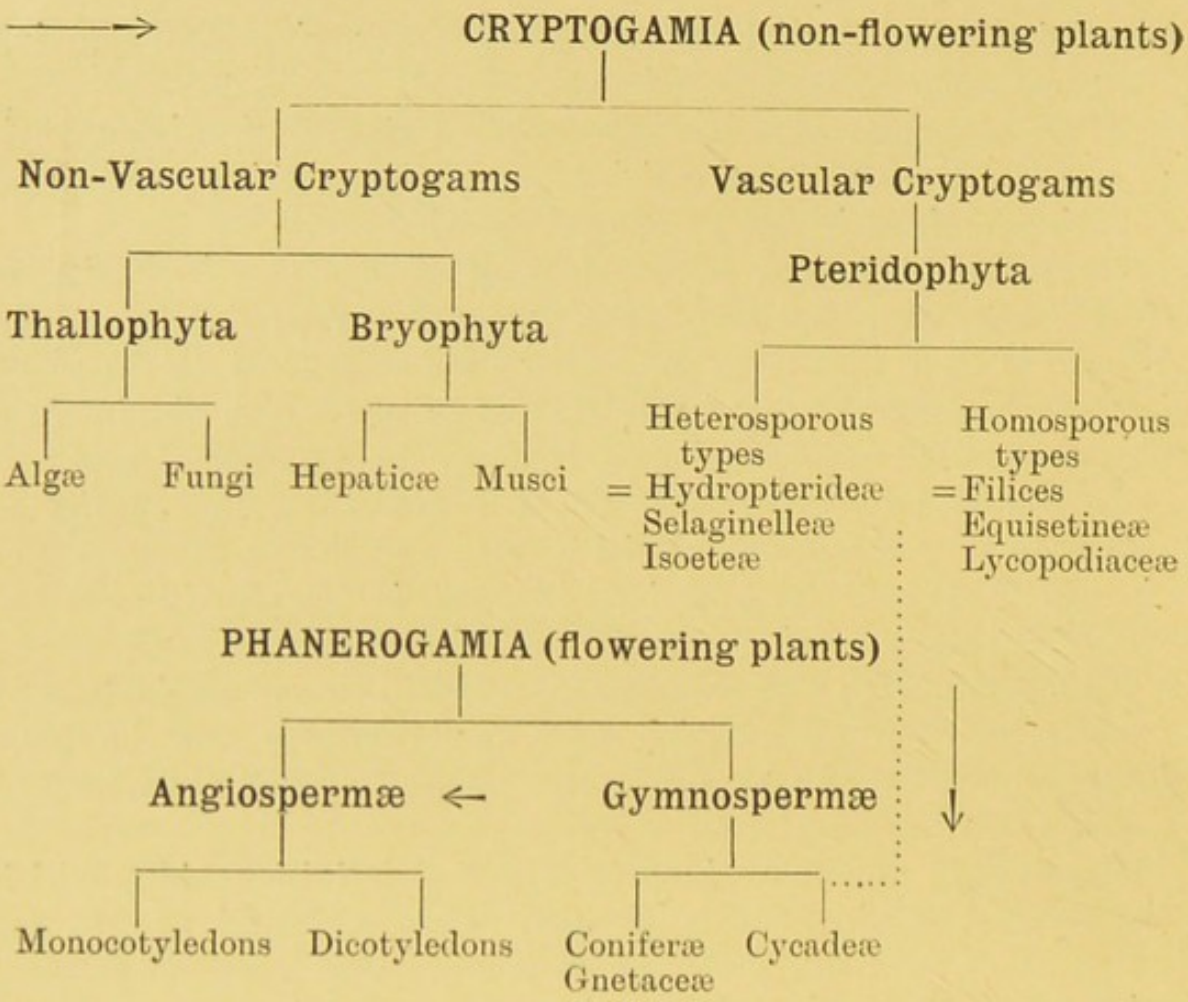
In higher plants the function of **reproducing the species** is relegated to well-marked special organs, and the processes occurring in these will be examined in detail in Chapter ix.; certain well-defined types being selected for this purpose.

In Chapter vii.; the phenomena involved in the production of fresh cells from pre-existing ones (cell-division) will be gone into, and, finally, in Chapter x. the physiology and chemistry of the cell will be considered.

An outline of the main groups and subdivisions into which the vegetable kingdom is divided will be found of use for purposes of reference, although it is not here intended to deal with botany from the point of view of classification.

Such an outline as the following will indicate the main genealogical relationships of members of the plant kingdom :—

* Not isolated in the strict sense of the term (see Chap. vi.).



The arrows show the order in which the table should be read; it indicates that the line of evolution of the Higher Plants has been by way of the Heterosporous Pteridophyta and the Cycadeæ, certain **fossil types** probably intervening.

The dotted line shows the homological connection between the Heterosporous Pteridophyta and the Gymnosperms (the subject of homology will be referred to in detail at the end of Chap. ix.). The chief variations in the structure, etc., of the cell, will be found amongst the Higher Plants—viz., higher ferns, Monocotyledons, Dicotyledons, and Gymnosperms (Coniferæ), and these will be the main groups used in dealing with plant histology.

CHAPTER I.

THE NATURE AND REACTIONS OF PROTOPLASM.

THE vital or working substance in every living cell is the **protoplasm,*** a material which has a very complex chemical and physical composition and constitution. Resolved into its elementary components, dead or "fixed" protoplasm may be said to be made up of **Carbon, Hydrogen, Oxygen, Nitrogen,** and **Sulphur**, and, in the case of the nucleus, in addition, **Phosphorus**; these elements are united in certain definite proportions and aggregated into complex molecules or groups of molecules. Certain **mineral substances** are also always found in close connection with the protoplasm, but not, however, in chemical combination (metaplasm). On the other hand, living protoplasm has probably a very different constitution as compared with the dead substance, and since it has been found impossible to correctly analyse the living material, its true composition still remains hypothetical; but chemists have from time to time constructed formulæ which have been assumed to represent the composition of dead protoplasm, and which have shown it to be made up mainly of a combination of **proteid, amine,** and **carbohydrate** molecules.

On examining a **young living cell** microscopically, the **protoplasm** appears as a nearly transparent substance, with here and there highly refractive granules; in the middle of the cell is the **nucleus,** a specialised portion of the protoplasm, and sometimes there are one or more **vacuoles,** or fluid-filled spaces, which resemble oil-drops in appearance (see Fig. 1).

It is probable, as will be seen later, that in many plant-cells the protoplasm is made up of two main portions—viz., a firmer, clearer external part, known as **ectoplasm,** and a more granular fluid inner part, known as **endoplasm**; in cells "fixed" and

* Termed by Huxley "the physical basis of life" (*Method and Results*).

stained in a special manner this distinction can sometimes be made out, but in the living cell it is not easy to do so, except in such cases as *Aethalium* * or *Amœba* (an animal organism not unlike *Aethalium*), where the demarcation is very distinct (see Fig. 2). In such a cell, which is a naked mass of protoplasm, the ectoplasm is capable of responding to **stimuli**, protrusions known as **pseudopodia** being pushed out in all directions; it is

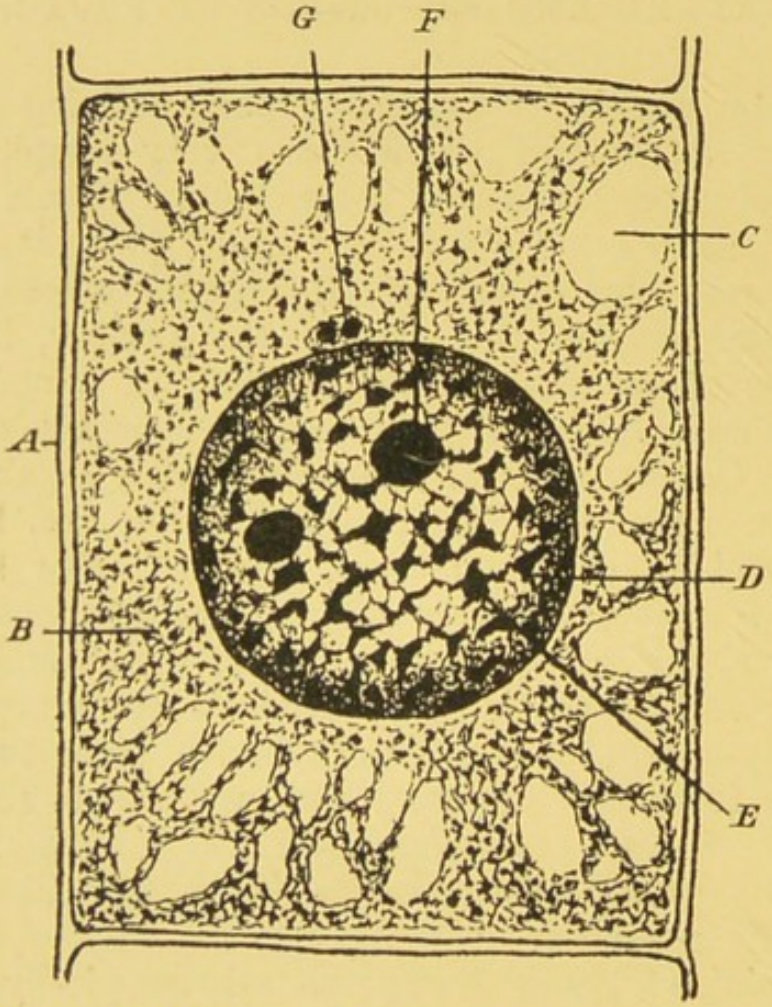


Fig. 1.—A Single Cell from a Root-Tip, fixed, and stained to show the various parts.—A, Cell wall; B, protoplasm, here granular, owing to coagulation, and partly to the presence of microsomata; C, vacuoles filled with cell sap; D, the nucleus: the clear part just outside the nuclear membrane may be taken to represent the kinoplasm; E, chromatin particles arranged upon a network of linin, the latter being faintly represented; F, nucleoli (plasmosomes); G, the centrosomes (probably absent in higher plants).

probable, however, that it is the endoplasm which receives the stimulus, which, after it has passed into the cell by way of

* One of the Myxomycetes.

the ectoplasm, causes the more fluid internal part to push out the ectoplasm, as it were. **Ciliary action** may possibly be explained on this hypothesis; and in the case of the absorptive cells (root-hairs) of roots the ectoplasm is able to exercise a

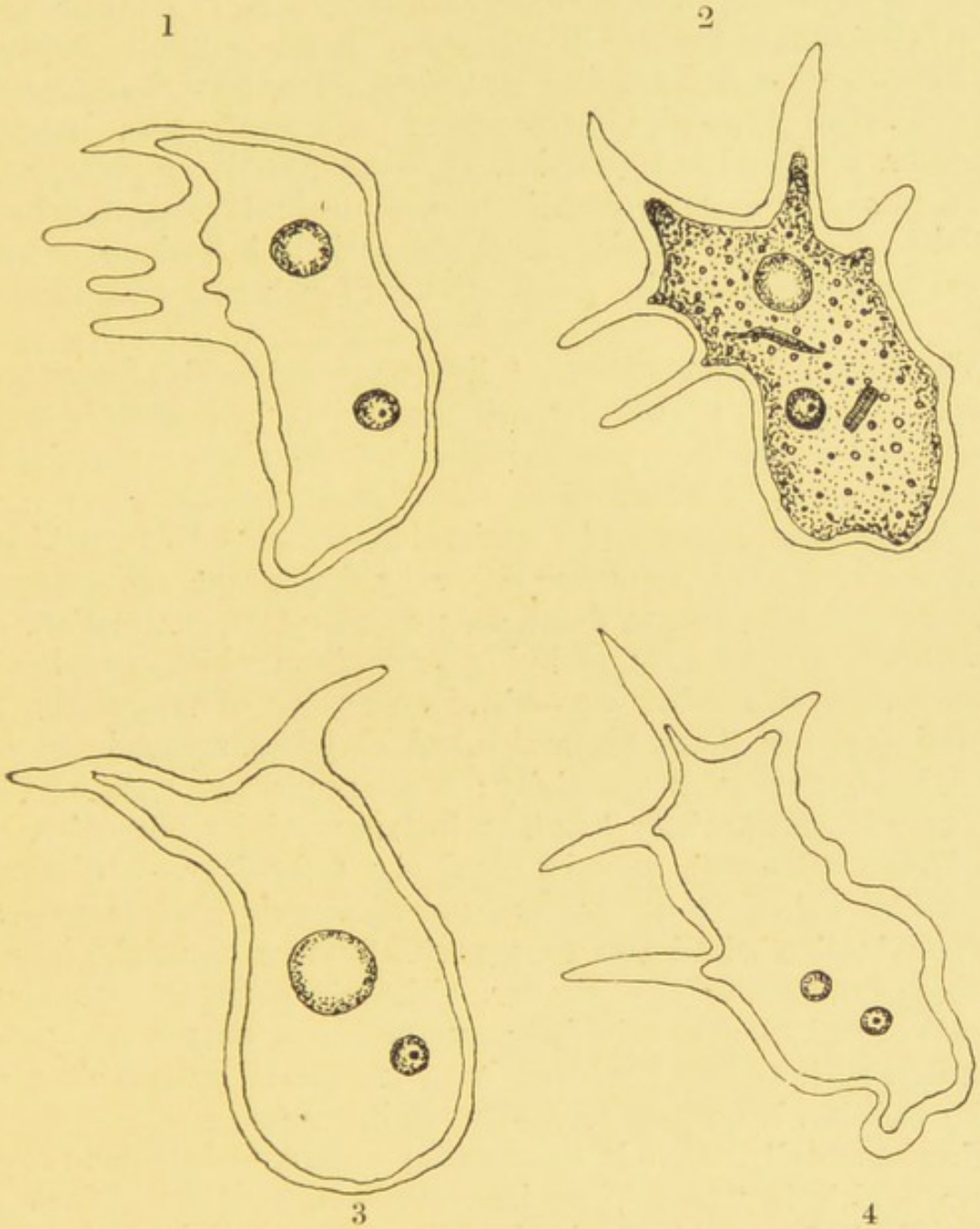


Fig. 2.—Amœba Princeps.—The figures show demarcation into clear ectoplasm and granular endoplasm, and change in shape of an organism at intervals of one minute. The nucleus and the "contractile vacuole" (an excretory structure) are seen in the endoplasm.

marked selective capacity over the absorption of food materials (salts in solution in the soil).

Apart from these two main portions, the protoplasm has been supposed to have a somewhat complex **physical constitution**; some cytologists produce evidence to show that it has a spongy basis, or **spongioplasm**, which is firm in consistency, and forms a sort of network, in the meshes of which a more fluid portion, or **hyaloplasm**, exists. On the other hand, Bütschli supposes that it possesses a foam-like structure not unlike that seen in emulsions of clove-oil, bicarbonate of soda, and water; latterly, however, the idea has been gaining ground that living protoplasm has a quite homogeneous constitution, as careful investigators have failed to detect any special structural basis in it,* whatever may have been observed in preparations of "fixed" and stained protoplasm.

The **chemical composition** of living protoplasm is also, as was stated above, somewhat hypothetical; but one fact is well-established—viz., that the living substance always contains a certain amount of **water of constitution**. Protoplasm, even of the driest seeds capable of germination, contains this combined water, and once it is removed, either by desiccation or treatment with dehydrating agents, death occurs owing to its extraction.

There is one property of living protoplasm which completely characterises this substance—viz., its capacity of responding to stimuli, whether these be mechanical, chemical, or produced by light, heat, gravity, or electricity; a comprehensive term for this property is "**irritability**," and, as instances of its possession by the living substance, may be cited the following:—*Aethalium*, a mass of naked motile protoplasm, when subjected to powerful illumination withdraws to a position where the light is less intense; and *Amœba*, a similar, although, correctly speaking, animal organism, draws in its pseudopodia at once if a harmful stimulus, such as that produced by a crystal of sodium chloride in its vicinity, is brought to bear upon it.

Fundamentally, there is no essential difference between protoplasm which is "naked," as in *Aethalium*, and that which is enclosed within a cell-wall; in the latter case the living substance may be, and often is, endowed with the power of movement round the enclosing membrane, and light, heat, electricity, and other physical and chemical agencies are found to produce measurable effects when brought to bear upon it.

* Wilson, *The Cell in Inheritance and Development.*

With regard to the influence of **heat**, it has been determined that a certain temperature, which varies for different cells, is required, in order that the protoplasm may carry on to the best of its ability the complex processes involved in the manufacture of nitrogenous and carbohydrate food; and it is a well-established fact that chloroplasts in the cells of green parts of plants are markedly affected by **light** (see Chap. x.), these chloroplasts being in the main protoplasmic in nature (*i.e.*, specialised portions of the protoplasm).

Other physical agencies, such as **gravity** and **moisture**, have a powerful "directive action" upon the protoplasm of cells of the growing-point of roots and stems; while certain chemical substances (enzymes and malic acid) have a marked influence in causing the attraction of swarmspores and the growth of pollen-tubes. This attraction is known as "**positive chemotaxis.**" With regard to the movement of the protoplasm round a cell (so-called "**streaming**" or "**rotation,**" see Chap. ii.), Hofmeister regarded this as depending upon variations in the absorptive capacity for water shown by the living substance at different points of a cell; in this case also, it is necessary to take into account the influence of temperature, and possibly differences in electrical potential at various points in a cell. The phenomena of **surface tension** may, however, account for some of these protoplasmic movements.

Experimenting upon the vitality of seeds, one investigator * discovered that those capable of germination were, when stimulated by an electric current, also capable of producing a so-called "**blaze-reaction**"—viz., an electric response-current in a definite direction when included in circuit with a sensitive galvanometer—and he showed that this current was evidence of the vitality of the protoplasm of the seeds experimented upon. The reaction was in all probability due to chemical changes set up by stimulation in the living substance, of the nature of slow oxidations, giving rise to changes in electrical potential. In the above experiments it was found, moreover, that if the "water of constitution" in the protoplasm were first of all removed by drying at high temperatures, or alcohol, no blaze-reaction resulted, pointing definitely to the fact that this loosely combined water was essential to the maintenance of vitality. Another factor which is also

* Prof. Waller.

essential to the continued activity of protoplasm in plant-cells is the presence of **oxygen**, either as a gas or in a compound, whereby, just as in the animal cell, the protoplasm is **oxidised**, giving rise to the evolution of heat; many of the bye-products formed in cells are the result of oxidation processes, whereby, finally, complex compounds are broken down into carbon dioxide and water (see also Chap x.). In addition to the water of constitution mentioned above, protoplasm requires an extra supply of **water** (in which certain essential salts are dissolved) for vital processes, and this it derives from the soil, air, or water surrounding the cells of a plant; and here a very important point arises—viz., the question of "**turgidity**,"—by which term is meant an equilibrium between the sap inside a cell and the fluids outside, this balance being known physically as **osmotic equilibrium.** Turgidity has been shown to favour **growth**, and it is a common experience that slack or withering parts of a plant soon cease to live (see Plasmolysis, Chap. ii.).

To recapitulate then, it may be said that the following conditions are necessary to the continued activity of protoplasm :—

(*a*) A certain **temperature**, which, in most plants, is something above zero Centigrade.
(*b*) Access to **moisture.**
(*c*) The presence of **oxygen.**
(*d*) A requisite degree of **turgidity** in the case of an enclosed protoplast, and, in addition,
(*e*) Protoplasmic **continuity** in the case of a cell-community between the living cells of the same plant. This factor is important, and will be considered more fully later ; and
(*f*) The presence of certain **assimilable food-materials** and **mineral salts** (see Chap. x.).

Note.— Protoplasm is soluble in dilute caustic potash and also in solutions of sodium or potassium hypochlorite: the nucleus also being dissolved. The living substance (cytoplasm) is also dissolved by solutions of pepsin or trypsin ; the nucleus (chromatin) resists pepsin, but dissolves in trypsin solution. At a certain temperature (between 70° and 80° C.) protoplasm passes into a condition known as "heat-rigor," when all functions cease, the living substance being killed (coagulation).

CHAPTER II.

THE STUDY OF A LIVING ASSIMILATING CELL.

A. The fully Differentiated Assimilating Cell.

BEFORE passing on to the consideration of the various modifications which are met with in plant cells, it is advisable to examine a typical living cell in which some of the more well-defined vital processes may be easily demonstrated. Such cells are to be found in the green assimilating tissues of plants, such as the mesophyll of leaves, and the outer part of the cortex of herbaceous stems.

Vallisneria spiralis, a water-plant, affords very good material to work with in this respect, as the cells of the leaf of this plant are typical **assimilating cells**, the term assimilation being understood in its true botanical sense, as, for example, in the taking in of carbon dioxide and water, and the elaboration of these into carbon-compounds in the chlorophyll bodies, oxygen being evolved during the process.

If a leaf of *Vallisneria* be taken, and a small portion of it mounted in water and examined under the half-inch power of the microscope, the following details may be made out by focussing into various planes :—

i. The outermost layer of the leaf, composed of elongated cells rectangular in shape, and forming the epidermis.

ii. Internally as regards these, somewhat elongated cells rounded off at the angles : it is with these cells for the most part that the leaf carries on the process of assimilation.

iii. Smaller cubical cells, which occur near the edges of the leaf.

Using a higher power of the microscope ($\frac{1}{6}''$ objective) it is possible to distinguish in any of these cells (i. or ii.) the following features (see Fig. 3) :—

(*a*) The **cell-wall,** a delicate membrane enclosing the other parts of the cell or cell-contents.

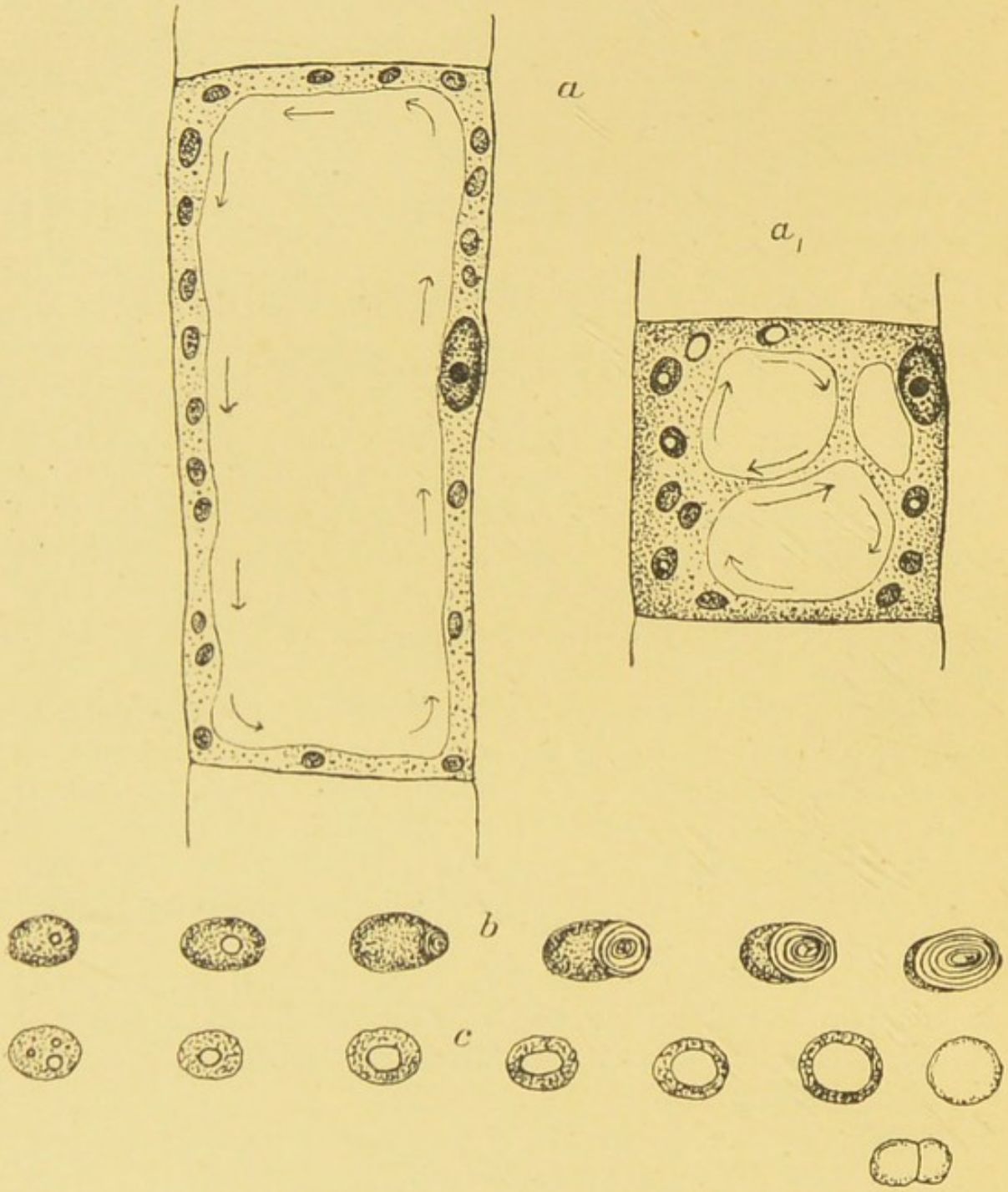


Fig. 3.—*a*, Two cells from the leaf of *Vallisneria:* the left-hand one shows cell-walls and the peripheral layer of protoplasm in which are seen the nucleus and chloroplasts. The arrows show the direction of rotation of the protoplasm; the central clear space is the "central vacuole." The right-hand cell shows the younger cell and chloroplasts containing granules of starch in their interior in process of formation. *b*, Formation of starch-granules in chloroplasts in a cell of *Begonia* leaf. *c*, Formation of starch-granules in chloroplasts of a cell of *Vallisneria* leaf.

(*b*) A layer of **protoplasm,** lining the inner surface of the cell-wall.*
(*c*) The **nucleus,** lying somewhere in this layer.
(*d*) Numerous oval green **chloroplasts,** also lying embedded in the protoplasm.
(*e*) The **central vacuole,** filled with **cell-sap,** enclosed by the protoplasmic sac; in the smaller cells several vacuoles may be present.

These several parts should now be examined in detail; and for this purpose it is as well to use a small "stop" on the sub-stage diaphragm of the microscope (or on the iris-diaphragm often fitted to the condenser) in order to cut off the peripheral illuminating rays, and thus obtain a very much sharper definition of each object examined.

With these precautions it is possible to make out that the cell-wall is a delicate membrane of a transparent homogeneous material: in this case it is not always possible to make out that the boundary-wall of adjacent cells is in reality double, unless very careful focussing is made, but that this is so will be readily seen in many other tissues which will be examined further on.

The inner edge of the layer of protoplasm is now more distinct, and the protoplasm itself is seen to be composed of a clear substance in which are suspended the chloroplasts, and some small granules, these latter being either of a protoplasmic nature† or **food-granules** (**starch,** etc.).

Lying in the protoplasm, and, as a rule, close to the cell-wall, is the **nucleus,** an ellipsoidal body with a centrally situated round spot, the **nucleolus**; the main substance of the nucleus in the living cell appears to be nearly homogeneous, but certain reagents, such as acetic acid, show up a distinct **reticulum,** and some stains, notably safranin and hæmatoxylin bring out other features, which will be examined in Chap. viii.

By the time these observations have been completed, there will probably have occurred a phenomenon which first appears in the more internal rectangular cells. If closely watched the protoplasm of some of these cells will be seen to be moving slowly round the cell, carrying with it granules, nucleus and chloroplasts. This movement is known as "**rotation**" or "**streaming,**" and up to a certain point its rate increases with the temperature; it is the **endoplasm** which really moves, the

* This layer is the "primordial utricle" (*primordialschlauch*) of von Mohl.
† So-called "microsomata."

ectoplasm forming a very delicate firmer layer next the cell-wall, which certainly moves slowly, but not so fast as the more fluid endoplasm. It is, however, hardly possible to distinguish optically between ectoplasm and endoplasm in the living cells of *Vallisneria* leaf; but in root-hairs these two portions may be made out as distinct from one another, when the protoplasm is observed under a high power.

The **chloroplasts** are most conveniently examined in the smaller cubical cells near the edge of the leaf. Each chloroplast is ellipsoidal in shape, small when compared with the nucleus, and of a light greenish-yellow colour, the latter being due to the presence of **chlorophyll**, a pigment which permeates the substance of the chloroplast; the ground-substance of each chloroplast is, however, protoplasmic in nature.

The effect of certain simple **reagents** upon the living cell must next be studied; and for this purpose it is usual to employ:—

(*a*) A solution of **acetic acid** in water, 20 per cent. strength.
(*b*) A solution of **iodine** in a dilute solution of potassium iodide, until the whole is of a dark sherry-red colour.
(*c*) **Schulze's solution.** This is a solution of iodine and potassium iodide in chloride of zinc solution.*
(*d*) **Iodine solution,** followed by a drop of concentrated **sulphuric acid.**

The reaction of the cell and its parts to these reagents will now be described.

(*a*) **Acetic acid,** 20 per cent. solution in water, will, if added (one drop under the cover-slip of the preparation) to the water in which the portion of Vallisneria leaf is mounted, produce the following effects:—

i. The protoplasm shrinks away from the walls of the cell observed, and retracts towards the middle of the cell-cavity, strands or "**bridles**" of protoplasm being observed which at first connect the main mass with the cell-wall.
ii. The whole cell will shrink somewhat, the walls becoming convex inwards.
iii. The nucleus takes on after a short time a punctate appearance, probably due to coagulation of certain substances in its interior.

The retraction of the protoplasm is known as "**plasmolysis,**" and is dependent upon the disturbance of the osmotic equilibrium

* The exact quantities are as follows:—0·2 grm. iodine added to a solution of 70 c.c. conc. zinc chloride and 10 grms. of potassium iodide.

of the cell, whereby water is extracted from the cell-sap contained in the central vacuole; the substance causing this disturbance, here acetic acid, is known as the **plasmolyte.** The reaction shows that the protoplasm lines the cell-wall in the form of a **sac,** which encloses the central vacuole; concentrated solutions of any salt (for instance, sodium chloride) act as plasmolytes, the osmotic balance being so delicate that any but the most dilute solutions will upset this balance causing plasmolysis. Certain solutions of a definite strength and known as **isotonic solutions** do not cause plasmolysis (see section on *Osmosis*, Chap. x.).

(*b*) *Iodine solution* added to a fresh preparation causes at first a partial plasmolysis, which, however, does not obscure the following important effects:—

i. A darkening of some of the granules in the protoplasm; these are **starch-granules** fully formed.

ii. A darkening of portions of the chloroplasts, this being due to the effect of the iodine upon granules of reserve **starch** undergoing formation in the substance of these bodies.

iii. The nucleus and nucleolus are coloured brown (reaction for proteid).

(*c*) *Schulze's solution,* added to a fresh preparation, acts first upon the **cell-wall,** which turns blue; the other effects noticed are similar to those of (*b*), except that the starch-granules turn a somewhat brilliant blue colour in contradistinction to the rather deeper blue caused by iodine solution alone.

(*d*) *Iodine solution followed by a drop of pure sulphuric acid* turns the cell-wall blue. This reaction shows that the cell-wall, more especially that of the young cell, is composed of **cellulose;** the first action of Schulze's solution shows the same thing. *Pure sulphuric acid* alone will cause the protoplasm to assume at first a pink colour (when sugar is present) owing to its action upon the sugar, furfuraldehyde being produced. *Cellulose* is dissolved by strong sulphuric acid with the formation of *dextrose.*

The presence of **granules of starch** in the interior of the chloroplasts, a point brought out by reaction (*b*), indicates that these bodies are active starch manufacturers and storers. In *Vallisneria* and *Begonia* leaves all stages in the production of starch-granules may be traced in the chloroplasts, from the minutest particle shown up by the iodine solution, to the fully-formed

granule, where only the thinnest film of the substance of the chloroplast remains (see Fig. 3).

In *Begonia* leaf (cells of the mesophyll) starch-granules are formed at first in the interior of chloroplasts, but subsequent growth proceeds at the side of these structures; in *Vallisneria*, on the other hand, the granules are seen to be centrally situated from beginning to end. Moreover, even in the apparently fully-formed grains, a delicate film of chloroplast substance is always to be detected, stretched over the grain.

In this formation of starch in the chloroplasts of cells from the green parts of plants is to be found a partial demonstration of **assimilation**; for a chloroplast is able, by means of its chlorophyll, to utilise during the daytime certain of the rays of white light falling upon the leaves, these rays being turned to account in the decomposition of the carbon dioxide which enters the cells after having gained admission through certain pores (**stomata**) existing in the epidermis (photosynthesis). In the substance of the chloroplast certain somewhat complex chemical reactions take place which result in the formation of carbon compounds, such as **starch, sugar,** or **cellulose** from the carbon dioxide and water supplied; and in this process **oxygen** is evolved and passes out again through the stomata.

The whole process above described is, correctly speaking, only part of the assimilatory reactions taking place in the cell; for, as will be pointed out more fully later on, nitrogenous substances are also elaborated and assimilated in the leaf-cells, and the materials resulting from this elaboration (amido-acids) are made use of by the protoplasm in the complex processes involved in formation of fresh protoplasm and nutrition of the cell as a whole. Nevertheless, this preliminary study of the assimilation of carbon dioxide and water in the chloroplasts, with the optical demonstration of the final result—viz., formation of starch granules—is a useful introduction to the investigation of other and possibly more complex vital processes taking place in the cell (see Chap. x.).

B. The Young Undifferentiated Cell.

A cell, such as the assimilating cell of *Vallisneria* leaf, does not present the same features throughout its whole existence—viz., peripheral protoplasm, chloroplasts, and the phenomenon of

"rotation." In fact, it is only in the adult cell that these are to be seen. The cells of a very young leaf or a rudimentary organ of any kind present very different features; in the first place, the protoplasm almost entirely fills the cell-cavity, and the nucleus is situated in the geometrical centre of the cell. Moreover, chloroplasts do not, as a rule, appear as such in the cells of organs which will ultimately become green until those organs have been exposed to light (there are a few exceptions to this statement—*e.g.*, the seed leaves of Pinus and the green layer in the cortex of stems just internal to the cork), but are replaced by structures known as **plastids** or **leucoplasts,** which are, so to speak, chloroplasts in which as yet no chlorophyll has been formed (see Fig. 4).

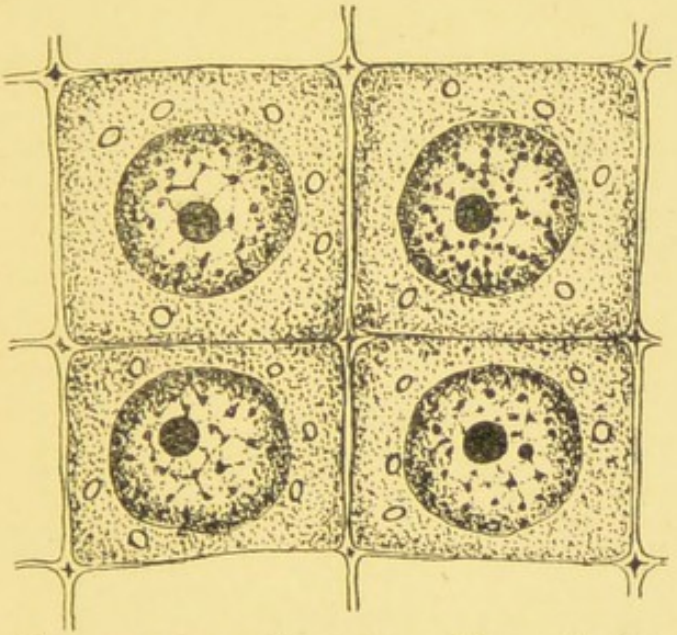


Fig. 4.—Young Cells from a Root-tip.—The cytoplasm fills the cell-cavity, and the nucleus is a relatively large structure. The small oval bodies are plastids.

The protoplasm of such a young cell does not show the "streaming" movement seen in some older cells, and the cell-sap is small in amount, does not at first form vacuoles in the protoplasm, but exists in it somewhat as water does in the meshes of a sponge. The cell-wall is very thin, and gives the characteristic "blue" reaction for cellulose when treated with iodine and sulphuric acid; acetic acid will cause a shrinking away of the protoplasm from the wall, but not to the same extent as in older cells, and the nucleus will, under these conditions, show the punctate appearance before mentioned. The plastids are turned

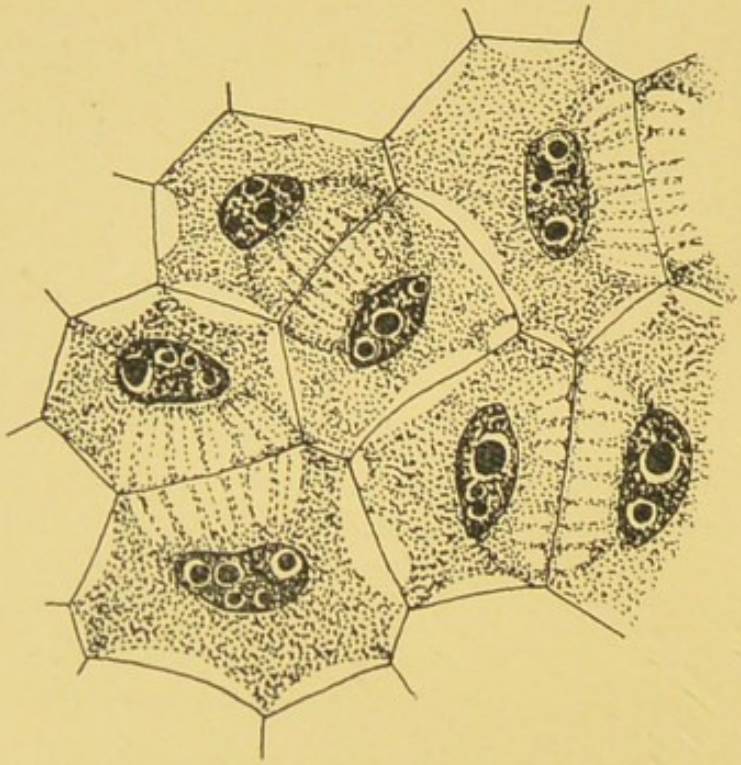


Fig. 5.—Young Cells from the developing Endosperm of *Caltha palustris*.—The cells have been recently dividing, and the nuclei show numerous nucleoli. The cytoplasm has shrunk away from the cell-wall somewhat.

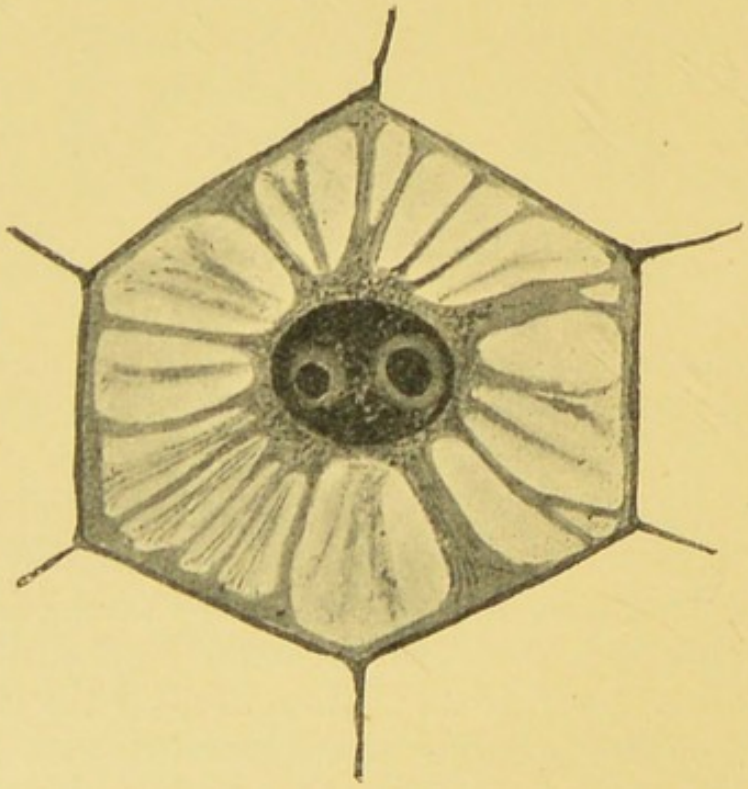


Fig. 6.—A slightly older Cell than those of Fig. 5 from the Endosperm of *Caltha*.—Vacuoles have formed and the protoplasm has been thrown into "bridles" passing from a central mass in which lies the nucleus to the peripheral layer.

brown by iodine solution, since no starch has as yet been formed in them; at times, however, starch may be formed in them by a different process to that which takes place in chloroplasts, the available energy for this being derived not from light rays, but some other source.

The **general shape** of the young cell is in section often oval, or, if there is much lateral pressure due to other cells, polyhedral; thus, if the pressures are equal in every direction, and the cells of equal size, the geometrical shape of a cell is that of the *regular*

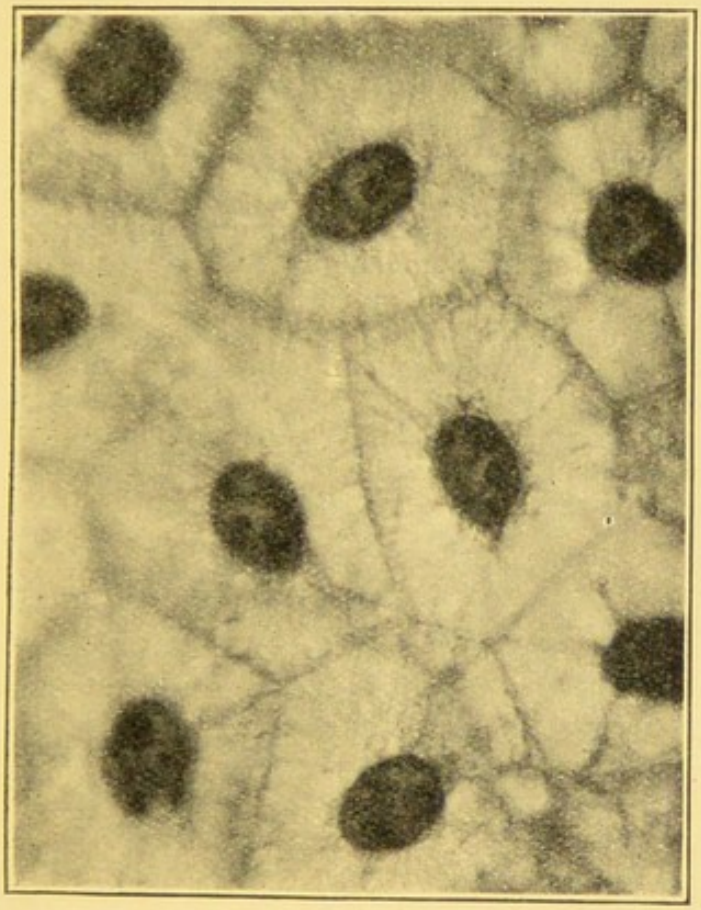


Fig. 6*a*.—A Photomicrograph showing Young Cells of the Endosperm of *Caltha palustris*.—Bridles of protoplasm are to be seen passing between adjacent cells.

dodecahedron; but, as a rule, the pressures are not always equal, and since the cells are not always of the same size, the shapes met with are often irregular (see Fig. 5).

As growth proceeds, the cell-sap which exists in the meshes of the protoplasm gradually collects into **vacuoles,** this being due to the relatively unequal growth in volume of the cell-cavity and in

mass of the protoplasm, the former preponderating; at this stage the nucleus is usually embedded in a central mass of protoplasm, whilst "**bridles**" of varying breadth pass from this mass to a layer of protoplasm lining the cell-wall internally. In still older cells the protoplasm forms a layer lining the wall, and encloses a central vacuole, the nucleus lying somewhere in this peripheral layer.

Starting from the young undifferentiated cell as the simplest type many subsequent modifications are to be found, and in the following pages the main object will be to study in detail the changes in **structure, size,** and **function** which occur in cells of different parts of plants, according to the position they occupy and the conditions brought to bear upon them.

Note.—The permanent microscopical preparation of the young cell is readily carried out by first "fixing" a root-tip or other embryonic tissue in Flemming's solution (see note at end of Chap. viii.), washing, after fixing, in distilled water for some hours, and then hardening in alcohol, and transferring to methylated spirit; sections, either longitudinal or transverse, should then be made from this, and these stained with hæmatoxylin (Delafield's) and fuchsin, using the stains in dilute solution, and staining with each separately. The section is then dehydrated with alcohol and spirit, cleared with clove-oil, and mounted in xylol balsam (Canada balsam thinned with a little xylol). Very beautiful preparations may be made by this method.

CHAPTER III.

CELLS OF THE EXTERNAL TISSUES AND CERTAIN SUPPORTING AND PROTECTIVE TISSUES IN PLANTS.

A. CELLS ARISING FROM THE DERMATOGEN.

1. The Epidermis and Structures in connection with it.

THE **epidermis** forms the outermost layer of cells occurring in such of the higher, and also lower, plants as possess differentiated organs; the layer forms, as a rule, a protective covering to the more delicate tissues beneath, and, moreover, is intimately concerned in the function of transpiration and the admission and means of exit of the gases of respiration and assimilation, matters which will be examined more fully when the stomata are studied.

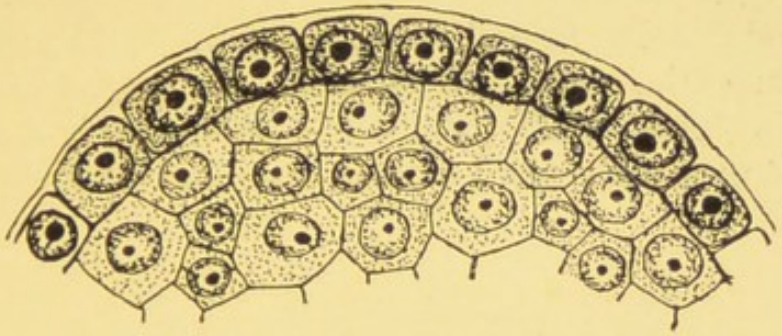


Fig. 7.—THE DERMATOGEN FROM THE APEX OF A BUD.—The outer layer of young cells represents the dermatogen, the deeper cells belonging to the "periblem."

Every epidermal cell is at first, like all young cells, a thin-walled undifferentiated structure; the **developing epidermis** is best examined in thin longitudinal sections taken through the apex of a young shoot of *Abies* or *Pinus*. In such a section the following features may be noted (see Figs. 7 and 34):—

(*a*) An outer layer of small cubical cells, filled with protoplasm, and possessing relatively large nuclei.

(*b*) A tissue composed of more oval or polyhedral cells with large nuclei lying internal to (*a*); this is the **periblem,** from which arise laterally the cortex and mesophyll of leaves.

(*c*) An axial portion, the central cylinder.

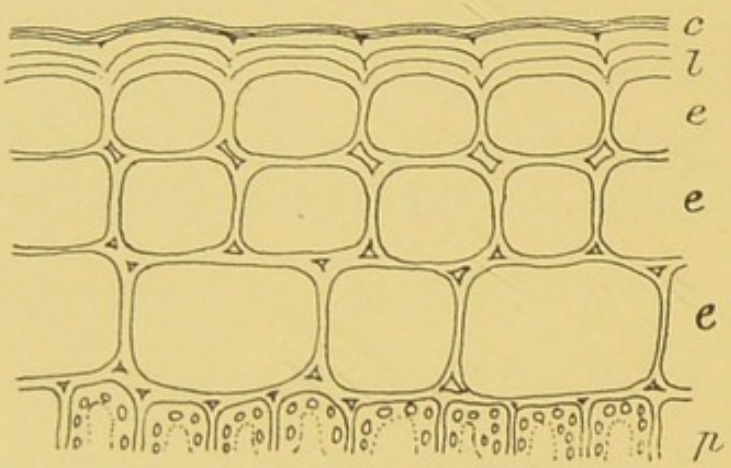


Fig. 8.—Portion of a Transverse Section of the Leaf of *Ficus elastica*.—*c*, Cuticle; *l*, lamellæ of the outer walls; *e*, epidermal cells; *p*, "Palisade" parenchyma. (In this case the epidermis is three-layered, a somewhat uncommon occurrence.)

The outermost layer of cells (*a*) is the **dermatogen,** and from it the epidermis is derived. Every cell of this layer is capable of dividing, and fresh cell-walls are formed during these divisions at right angles to the surface of the bud. The layer thus, as a rule, remains only one cell thick, since no walls parallel to the surface (tangential walls) are formed. An exception to this is seen in *Ficus elastica* (leaf), where the epidermis is three-layered. The dermatogen cells are, however, soon modified, so as to form

b

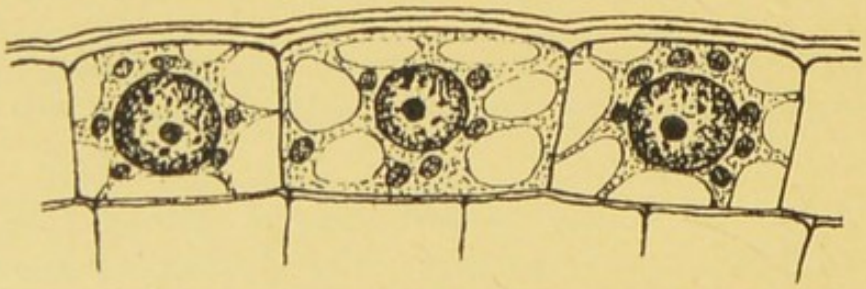


Fig. 9.—Epidermal Cells from the Leaf of *Hippuris*, showing the persistence in them of cytoplasm and nucleus and the presence of chloroplasts.

permanent epidermal cells, which may or may not possess protoplasmic contents; in the majority of instances these latter are

absent, but in a few cases, such as *Hippuris* and *Vallisneria*, they possess not only protoplasm and nucleus, but also chloroplasts or plastids (see Fig. 9).

The walls of the cells forming the dermatogen are composed of unaltered **cellulose.*** When, however, the permanent stage is reached, the outer walls no longer consist of pure cellulose, but are considerably modified with regard to their chemical composition. In fact, the **external wall** becomes often greatly **thickened**, and, in addition, the outermost layers of the external wall become converted into a substance known as **cutin** (see Fig. 10), which, when certain reagents are added, may be made

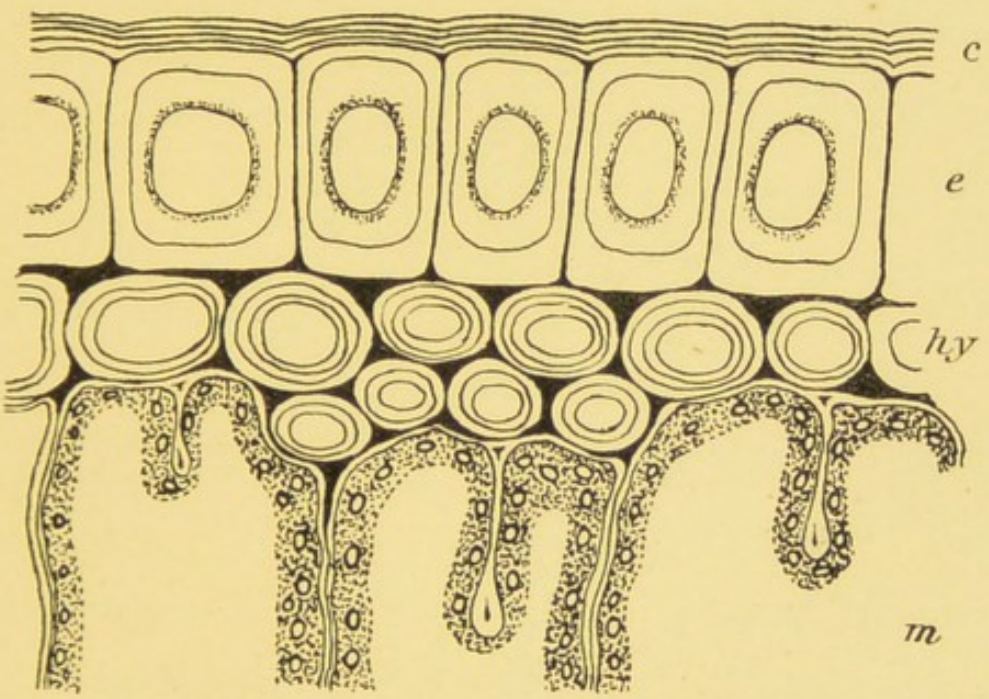


Fig. 10.—Portion of a Transverse Section of the Leaf of *Pinus sylvestris*.—*c*, Cuticle; *e*, epidermal cells, the walls being made up of two distinct layers; *hy*, hypodermis; *m*, cells of the mesophyll containing chloroplasts.

to swell and separate from the wall. It will be noticed that it is, in general, only the outer wall which becomes modified in this manner; the side and internal walls are, as a matter of fact, often thickened, but not to such an extent as the external one. But just internal to the epidermis there occurs in some stems and leaves (*Pinus*) a layer of cells known as the **hypodermis**, the component elements of which possess very thick walls which

* In which a form known as pectose occurs in large amount.

make up for any deficiency in strength of the epidermis (see Figs. 8 and 10).

In *surface view* epidermal cells present a variety of shapes; thus they may be rectangular, polyhedral, or sinuous in contour (see Fig. 11). In all cases, however, a regular pattern is preserved, the component cells fitting close so as to leave no intercellular spaces, except where stomata occur.

In section, some epidermal cells may show minute perforations or "**pits**" in their inner walls. These pits have been functional in permitting of the passage of the protoplasm from the epidermis into the deeper cells just internal to it when the work of the living substance has been completed; they may be seen in the epidermal cells of *Smilax*.

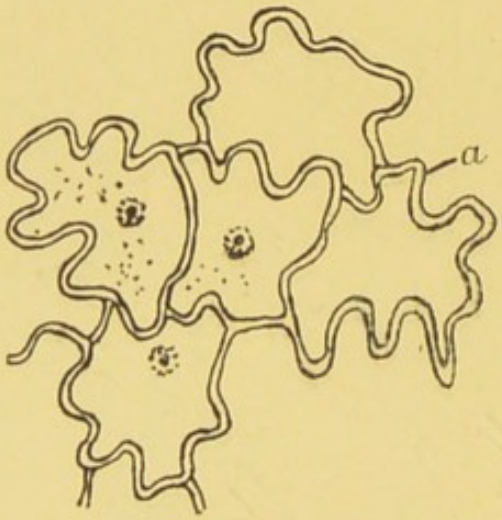


Fig. 11.—Epidermal Cells of *Sedum*, seen in surface view.

Note.—Epidermis may be studied in any of the higher plants. Great thickening of the outer wall may be seen in the epidermal cells of the Holly leaf, and of *Viscum album*, leaf of *Pinus sylvestris*, and *Ficus elastica*. The cuticle may be caused to separate by the use of caustic potash; and by the use of Schulze's solution, the part of the wall which still remains unaltered cellulose may be distinguished from the rest.

2. Structures to be observed in connection with the Epidermis.

These are:—

(*a*) **Stomata** (occurring in leaves, petioles, petals, and some stems).
(*b*) **Hairs,** of varied shape, size, and function.

(*a*) **Stomata** are apertures or intercellular spaces occurring at certain points in the epidermis, which permit of the passage of the gases of the atmosphere into spaces surrounded by the

mesophyll cells of a leaf, or cortical cells of a stem; they also allow of the exit of aqueous vapour during transpiration, a most important function, and also of oxygen during assimilation.

A single **stoma** arises by the division of a young epidermal cell into two, and these separate slightly along the line of junction known as the middle lamella, leaving an opening which leads into the afore-mentioned space (see Fig. 15, *a*). The walls of these cells become greatly thickened, but the cell-contents persist; and a certain amount of apparent subsidence may take place, as in *Pinus*, so that ultimately the cells, which are known **guard-cells**, come to lie somewhat below the general level of the epidermis (see Fig. 15, *b*).

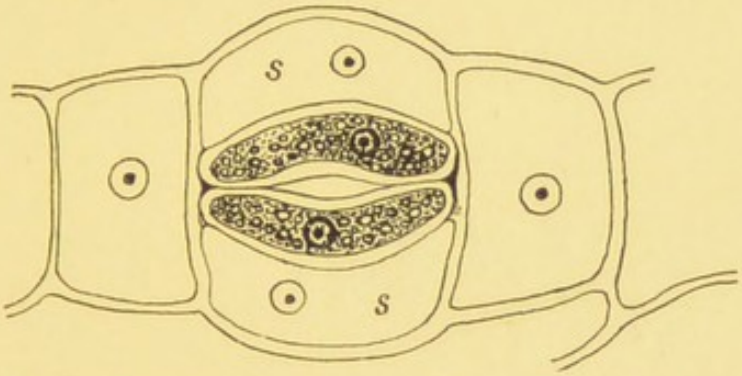


Fig. 12.—A Stoma from the Leaf of *Smilax*, seen in surface view. The two crescentic guard-cells possess cytoplasmic contents and chloroplasts.

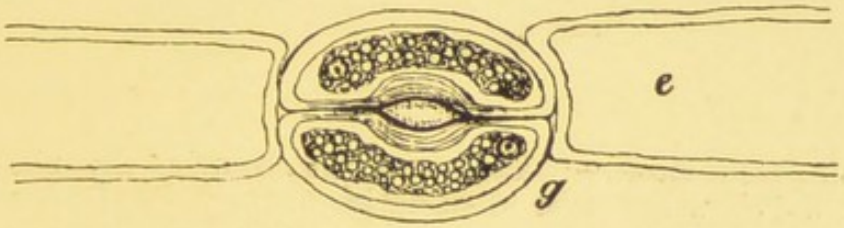


Fig. 13.—A Stoma from the Leaf of *Iris*, in surface view (from a photomicrograph).

The primary cells may divide more than once, the last division of all resulting in the formation of guard-cells; the first-formed cells are then termed "**subsidiary**." Subsidiary cells are well seen in the leaf of *Sedum* (see Figs. 12 to 14). In surface view guard-cells are usually crescentic in shape.

A section across a stoma will show the following features:—

i. An outer passage, the "**vestibule,**" bounded, as a rule, by epidermal cells, or at times by subsidiary cells. The guard-cells lie at the inner end of the vestibule, and are very close together, leaving only a very narrow entrance into

ii. The **respiratory cavity,** which lies deeper than the guard-cells, and is surrounded by the thin-walled cells of the mesophyll, or, in the case of herbaceous stems, by the outermost cortical cells (see Fig. 15, *b*).

From this preliminary examination of the structure of a stoma, it is possible to deduce its function. If the **mesophyll cells*** of a leaf are studied, it will be found that they conform in structural characters to the type of thin-walled assimilating-cell which was examined in Chapter i. In each cell there is seen a layer of peripheral protoplasm, in which are suspended chloroplasts and nucleus; moreover, a large amount of **watery cell-sap** is present in the central vacuole, and during the daytime aqueous vapour is being constantly given off through the thin walls into

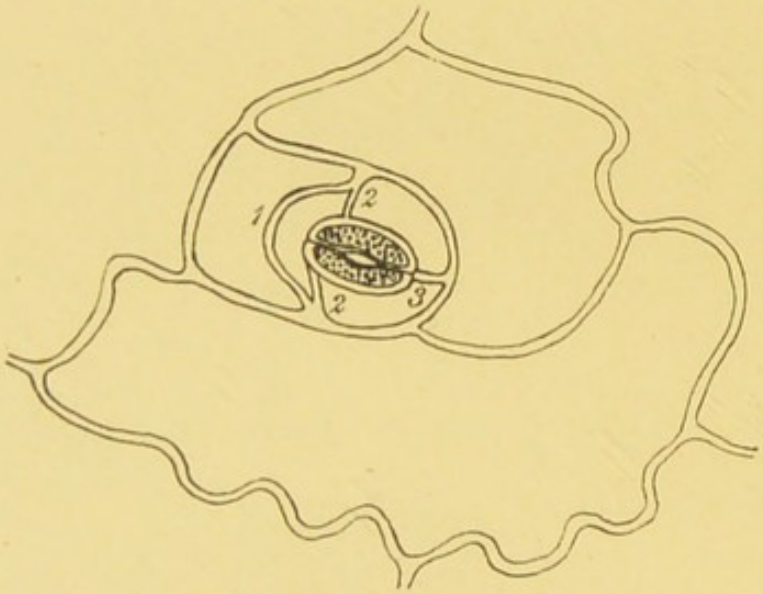


Fig. 14.—A Stoma from the Leaf of *Sedum*, showing the subsidiary cells (1, 2, and 3 show the order of formation of the walls of these latter).

the respiratory cavity of the stoma. This process is known as **transpiration,** and a current, the **transpiration current,** is kept up by the evaporation of moisture through the stomata, so that water is drawn up from the stem and root to replace that evaporated from the mesophyll cells. Transpiration is readily demonstrated by placing a leafy plant under a bell-jar, in the sunlight, when the moisture evaporated through the stomata will condense upon the inner surface of the bell-jar. (For further details of transpiration see Chap. x.).

In some plants there are contrivances (**hairs**) in connection

* Sometimes called the spongy parenchyma.

with stomata whereby transpiration may be regulated, in order to cope with such conditions as draught; otherwise certain plants would wither in a few hours. Stomata are usually more numerous on the under surface of a leaf than on the upper aspect, and in some leaves may be greatly reduced in number, in order to prevent excessive loss of water (leaves of plants in the Canary Islands, belonging to the genus *Cactus*).*

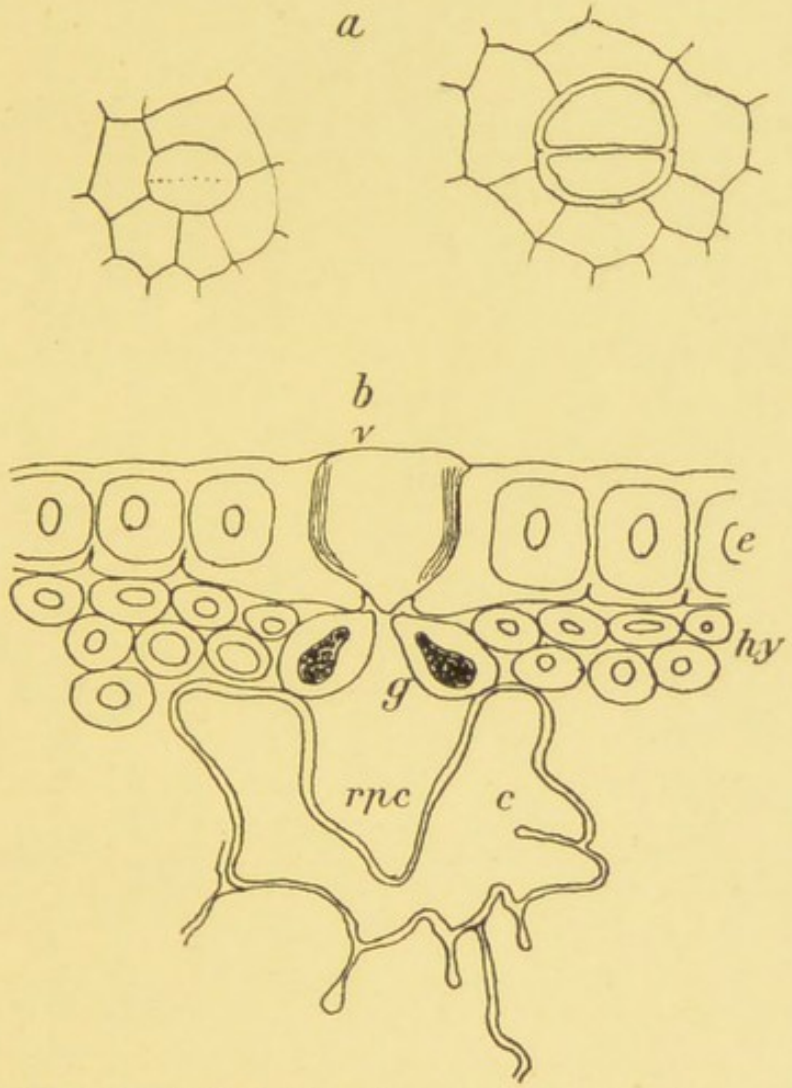


Fig. 15.—*a*, THE FORMATION OF A STOMA (two stages) IN THE LEAF OF *Prunus laurocerasus*. *b*, A STOMA FROM THE LEAF OF *Pinus*, seen in section.—*v*, Vestibule; *e*, epidermal-cells; *g*, guard-cells; *hy*, hypodermis; *rpc*, respiratory cavity; *c*, mesophyll cells.

The stomata have, however, another and most important function—viz., that of admitting the gases of the atmosphere

* The stomata also undergo certain changes whereby the aperture, or stoma proper, is closed at times, by variations in the turgidity of the guard-cells; this occurs at night time.

to the mesophyll cells, generally in a state of solution in aqueous vapour, these gases (CO_2 and O_2) being required for purposes of **respiration** and **assimilation**; and besides admitting these gases, the stomata also permit of exit to the gases produced and evolved during respiration and assimilation—viz., CO_2 and O_2 respectively. During the daytime, whilst light is impinging on

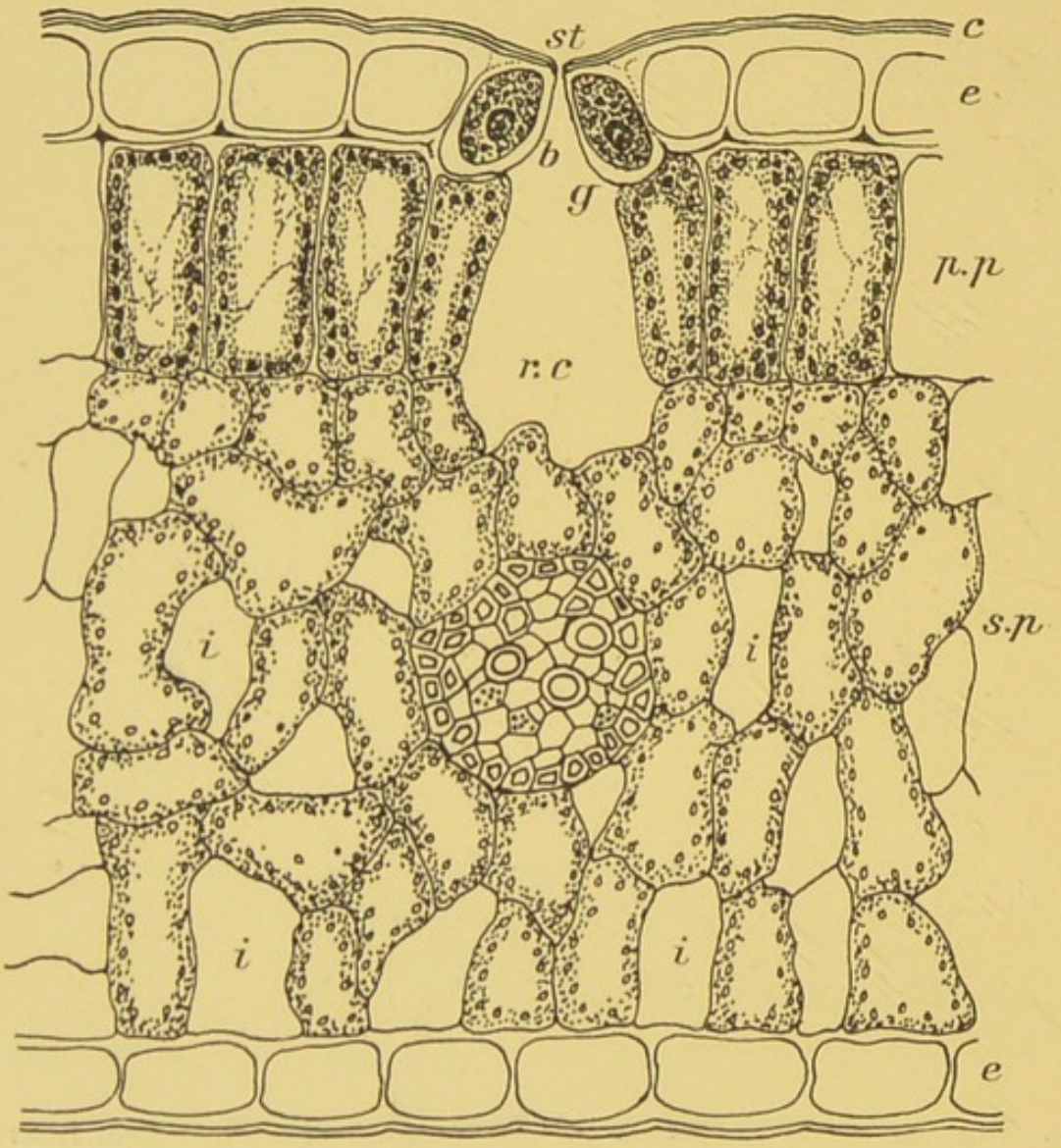


Fig. 15*a*.—Transverse Section of a Bifacial Leaf (semi-diagrammatic).—*e*, Epidermis of upper and under surfaces; *c*, cuticle; *st*, stoma; *b*, vestibule of stoma; *g*, guard-cells; *r.c*, respiratory cavity; *p.p*, palisade parenchemya; *s.p*, spongy parenchyma; *i*, intercellular spaces. A section of the leaf-trace (bundle) is seen in the spongy parenchyma.

a plant, transpiration and assimilation proceed to the greatest extent in the green parts of the plant, respiration being over-

shadowed by the former. At night, however, respiration is more apparent, whereas transpiration and assimilation of CO_2 are at a minimum, although growth as a whole is probably going on at an increased rate.

Some of the experiments demonstrating these vital processes will be described in detail in Chapter x.; but it was necessary to make brief mention of them here, since it seems more rational to study the function of a given structure, or cell, in connection with its histological details.

Note.—Stomata are best studied by examining thin strips or sections of the epidermis of such leaves as Holly, *Pinus*, *Hakea*, and *Iris*. Guard-cells may be stained with methyl-green, which picks out these cells to the exclusion of others. Subsidiary cells are seen in the epidermis of *Sedum* leaf, and developing stomata in the young leaf of *Prunus laurocerasus* (see Fig. 15, *a*).

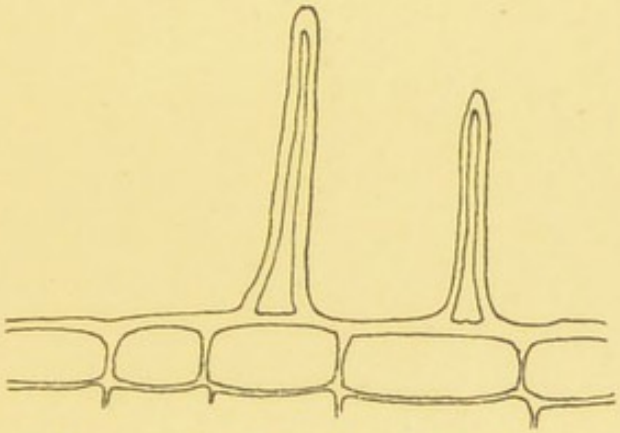


Fig. 16.—Simple Hairs from the Petiole of *Rhododendron* (Leaf).

(*b*) **Hairs** are structures which arise from epidermal cells, and are either *simple* or *compound*; thus they may be:—

i. Simple unbranched or branched **unicellular** hairs.
ii. **Multicellular** hairs.
iii. **Secretory** hairs, which are often multicellular, but at times unicellular.

Simple unbranched hairs may occur on leaves, petioles, or bud-scales. They originate from epidermal cells, the outer walls of which are pushed out at an early stage, the protoplasm flowing into the protrusion. Soon, however, in most cases, the protoplasm leaves the hair and passes into the deeper cells, after its work has been done in connection with the growth of the hair (see Fig. 16). Some simple hairs retain their protoplasmic contents throughout their whole existence, as, for instance,

root-hairs (trichomes), where the **ectoplasm** forms a distinct layer which exercises a marked **selective capacity** over the absorption of salts in the soil (see Fig. 21); but the function of most simple hairs is in the main one of **protection** either from excessive cold, heat, or mechanical injury. Occasionally a large number of hairs are aggregated together to form one variety of *emergence*;* and in the case of the long felt-like hairs which cover buds (Hazel and Alder), these are mainly useful in protecting the latter from the effects of frost. Simple hairs may at times be **branched** (stellate hairs).

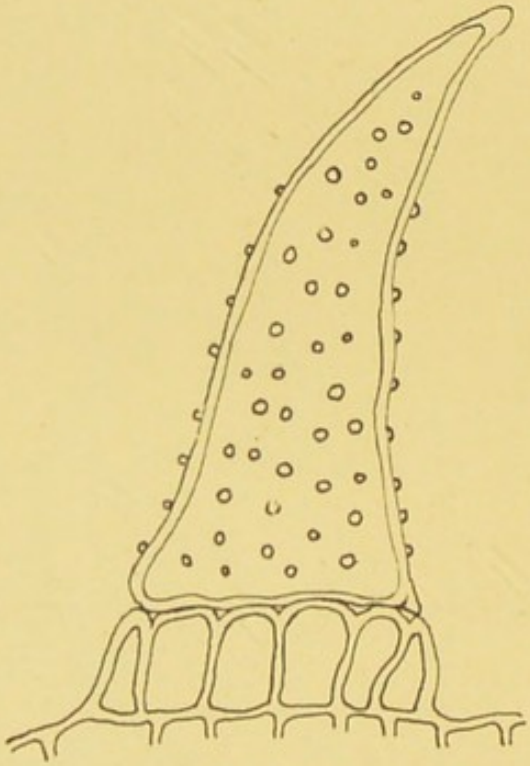


Fig. 17.—A Compound Hair from *Rhododendron*—at the base are six small cells. The small projections on the wall of the large upper cell are composed of carbonate of lime.

Multicellular hairs are those which, having retained their protoplasm, divide and form several cells lying in one or more planes (see Figs. 17 and 19); such hairs may be stellate, sickle-shaped, or shield-shaped. Stellate hairs may, however, be a variety of branched unicellular hair; and in the case of the long simple hairs, a wall may arise which cuts off the elongated portion from the original epidermal cell (see Fig. 16).

* These emergences may also have cells from the deeper layers in their structure; some of them are glandular and possess an internal secretory layer.

Secretory hairs are occasionally composed of one or, at most, a few cells, the apical one of which forms the glandular portion (*Pelargonium*).

In the leaf of *Pelargonium* (see Fig. 18) the hair consists of three distinct cells—viz., a basal cell and two upper ones—the apical one being spheroidal in shape and possessing protoplasmic contents which manufacture a sticky secretion. Such a hair is known as a **capitate glandular hair,** and occasionally these hairs serve as organs of absorption for ammonia and nitric acid existing in the atmosphere.*

Another type of secretory hair is seen in the stinging nettle (*Urtica urens*); each hair is here an elongated cell which arises from an epidermal cell of the stem or leaf, having a broad base surrounded by a cup-shaped receptacle formed by a large number

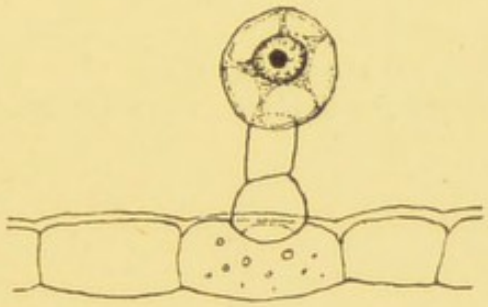


Fig. 18.—A Capitate Glandular Hair from the Leaf of *Pelargonium*.

of small cells which have been produced by the divisions, in an early stage, of adjacent epidermal cells. The whole hair tapers towards the apex, which is extremely delicate and surmounted by a small knob; internally are seen protoplasm and nucleus. **Formic acid** (strictly speaking, an excretion, and not a secretion) is formed in the hair, and it is this substance which produces the stinging sensation and rash when the fine broken apex of the hair penetrates the skin (see Fig. 20). The hair of the nettle is thus seen to be mainly protective in function.

In *Rhododendron* secretory hairs arise which are composed of many cells, each of these possessing protoplasm, and secreting a sticky substance (see Fig. 19).

* Kerner and Oliver, *Natural History of Plants*, vol. i.

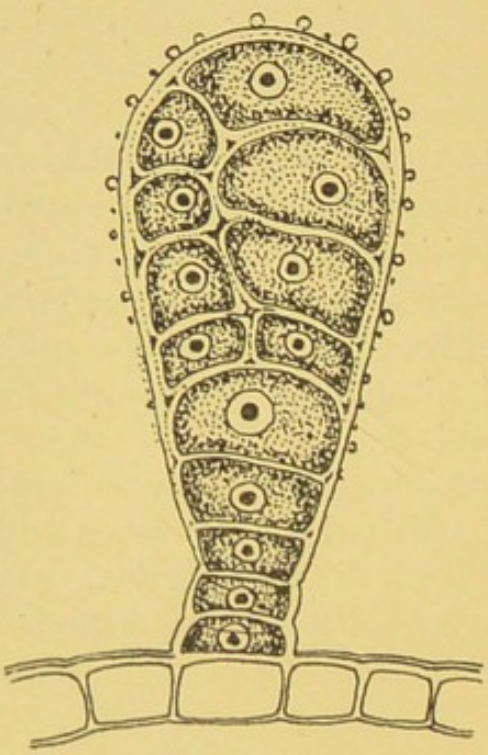


Fig. 19.—A Compound Glandular Hair from *Rhododendron*. The small projections on the surface are globules of oily secretion.

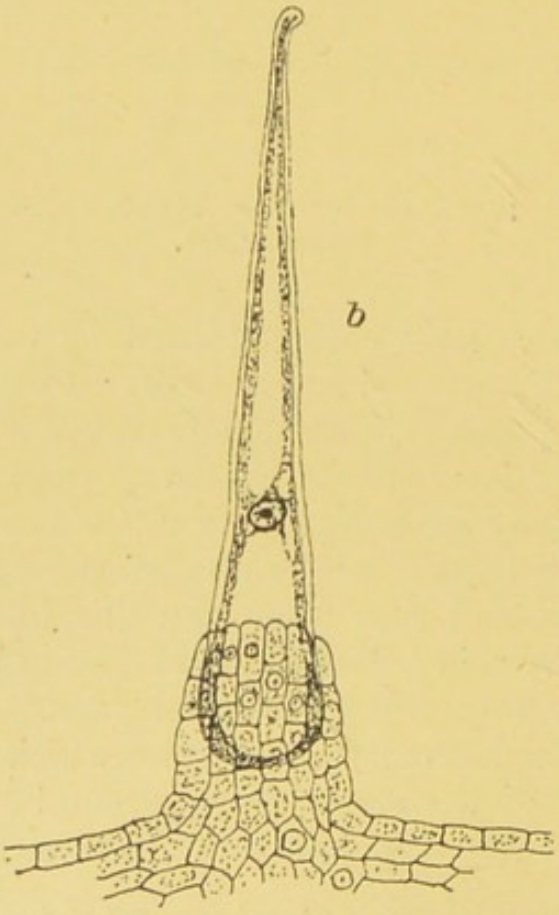


Fig. 20.—A Glandular Hair of the Nettle (*Urtica urens*).—The broad base of the hair is embedded in a cushion of small cells.

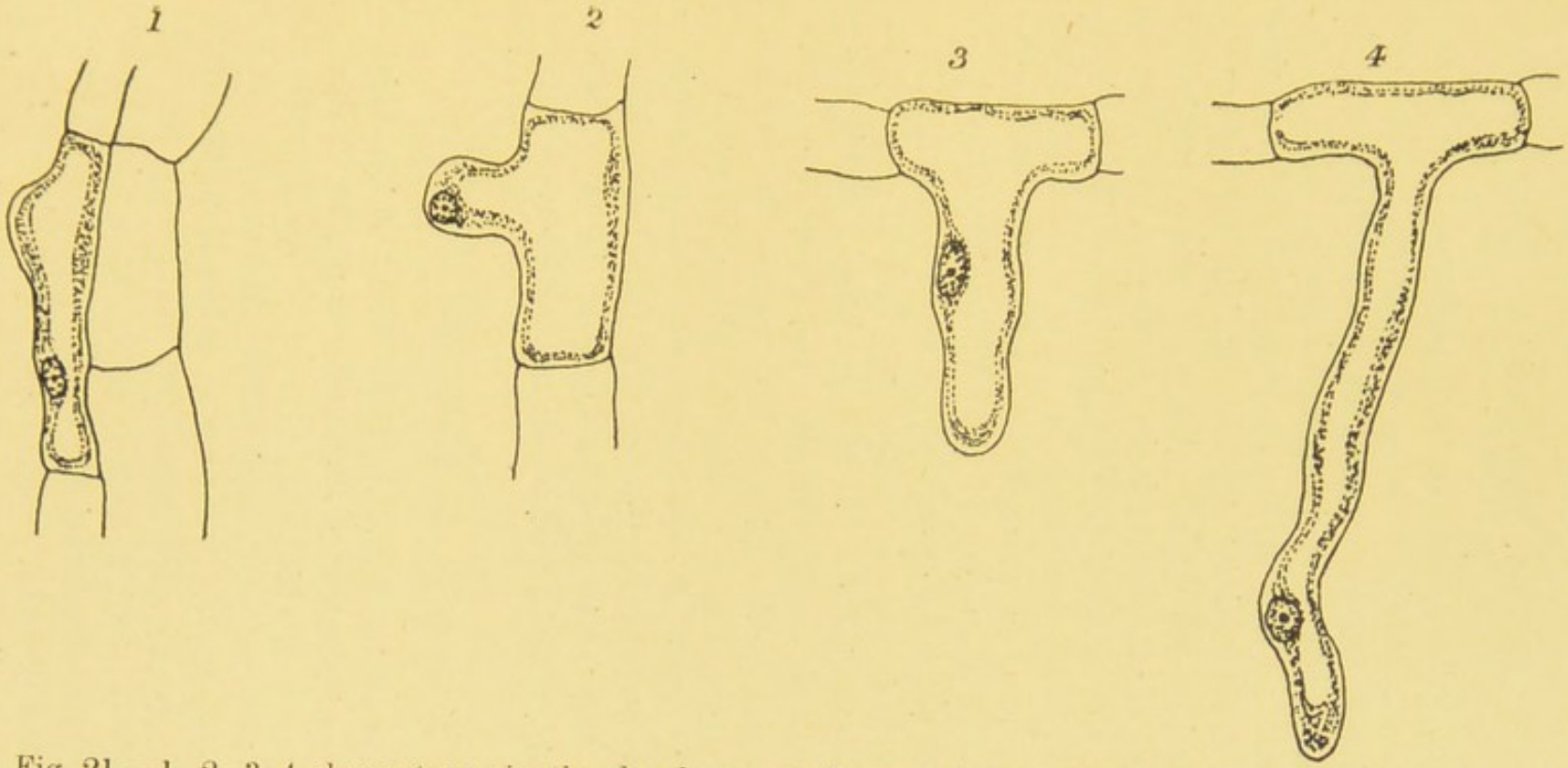


Fig. 21.—1, 2, 3, 4 show stages in the development of a root-hair (trichome) from an epiblemal cell near the root-tip of a seedling. The division of the cytoplasm into clear ectoplasm and granular endoplasm is indicated.

B. CELLS ARISING FROM THE PERIBLEM.

1. The Cortex.

The **cortex** will be described here under the external tissues, but, strictly speaking, it is only an external tissue when considered relatively to the central cylinder (where the latter is present); nevertheless, it is convenient to class it with the external tissues. Cortical cells are formed by the subsequent growth and modification of cells of the **periblem**—viz., that layer which is just internal to the epidermis in the young shoot. Each adult cell of the cortex is, in most cases, a typical assimilating cell, with the exception that cortical cells in roots do not contain chloroplasts, but plastids. As a rule, the shape of a cortical cell is oval, or more often rectangular or polyhedral in section, and such a cell would be termed parenchymatous, since no diameter is much in excess of the others.

In stems which possess a well-marked central cylinder the cortex extends radially from the epidermis (or hypodermis) to the endodermis or starch-sheath. In herbaceous stems all the cells may possess chloroplasts, but where the layer is of any extent only the outermost cells possess chlorophyll. At times a well-defined layer of cells possessing chlorophyll is met with at the outer margin of the cortex, this being known as the **phelloderm**; but it is formed from a tissue known as cork-cambium, and, as such, will be examined later.

2. Cells of the Mesophyll of Leaves.

The **mesophyll** in leaves is that tissue which exists between the epidermis of the upper and under surfaces, in the case of the bifacial leaf, and in the centric type is the mass of cells which intervenes between the epidermis and the central cylinder. A layer of columnar cells known as **palisade parenchyma** is often present between the true mesophyll or spongy parenchyma and the epidermis of the upper surface of a bifacial leaf, and these palisade cells are characterised by the presence of large numbers of chloroplasts (see Fig. 15*a*). Each cell of the **spongy parenchyma** is thin-walled and possesses protoplasm and chloroplasts, and is chiefly concerned in the processes of transpiration, and

the assimilation of carbon dioxide (during the daytime); but the palisade cells are far more powerful than those of the spongy parenchyma as assimilators of carbon dioxide, and this by reason of the large amount of chlorophyll they possess.

In the centric leaf of *Pinus* each cell of the spongy parenchyma has curious infoldings of the cell-wall, which, in the adult cell, are known as **trabeculæ**. These increase the available transpiring surface of the cell (see Fig. 10, *m*).

In bifacial leaves the palisade cells are arranged in groups which converge by their bases on to single cells of the spongy parenchyma, known as **collecting cells**; this arrangement facilitates the diffusion of **sugar** formed in the palisade parenchyma into the other cells of the mesophyll (see also Chap. x.).

C. CELLS OF CERTAIN SUPPORTING AND PROTECTIVE TISSUES OCCURRING IN PLANTS IN VARIOUS POSITIONS.

Under this heading will be described:—

(*a*) Cork.
(*b*) Collenchyma.
(*c*) Sclerenchyma.

These tissues are found in varied positions in the stem, root, or leaf of higher plants, chiefly the Dicotyledons, Monocotyledons, Coniferæ, and higher Ferns; and in all cases their function is to confer **elasticity** and **rigidity**,* and act as a means of protection to more delicate tissues.

(*a*) **Cork** is found in the form of layers of varying thickness in the stem or root; in the latter it is produced from a zone of actively dividing cells known as the **pericycle**, which occur just internal to the endodermis in those roots which possess a well-marked central cylinder.

Cork-cells may arise from **epidermal-cells**, in stems, and in this case are cut off in the first instance from the inner portions of these cells; but, as a rule, the first division going to produce the cork-forming layer occurs in the first layer of cortical cells just below the epidermis.

If a longitudinal section be taken of a young stem of *Sambucus*

* Rigidity in succulent plants is greatly aided by turgidity of the living cells.

the **cork** is distinguished as a layer of cells some five or six deep, lying just internal to the epidermis; one or two lines of these cells may be seen to possess protoplasmic contents, the outer cells being empty and often pressed together (see Figs. 22 and 23).

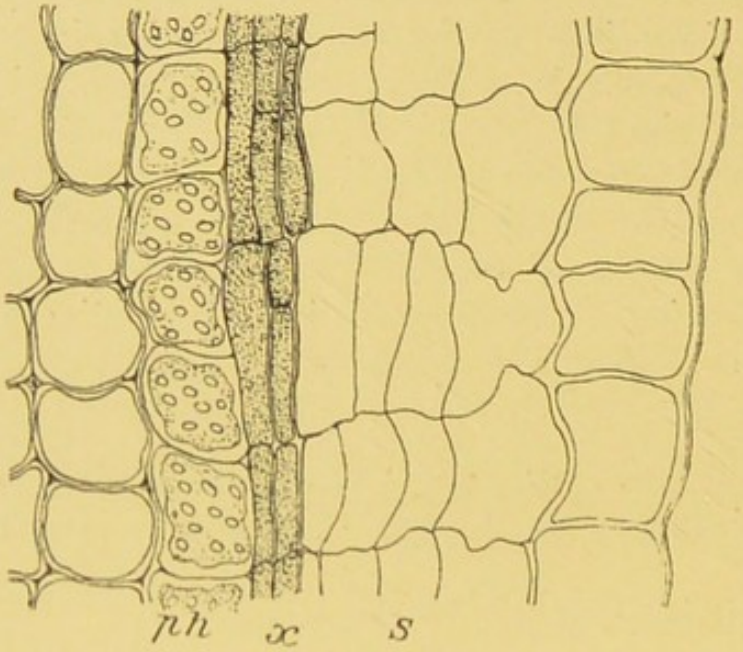


Fig. 22.—A Portion of a Longitudinal Section through the Young Stem of *Sambucus* to show the Cork.—*s*, Cork-cells; *x*, cork-cambium; *ph*, phelloderm.

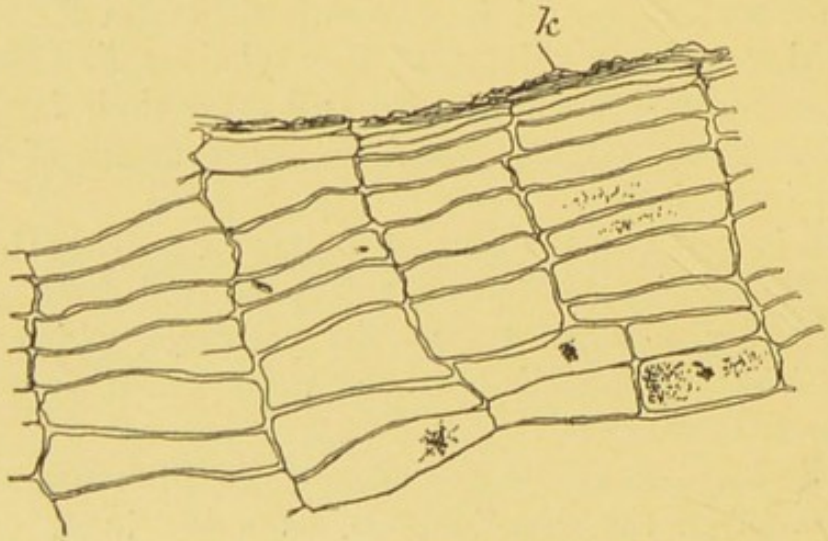


Fig. 23.—Older Cork-Cells from the Potato Tuber.—*k*, Compound cork-cells being cast off.

The cells containing protoplasm are known collectively as the **cork-cambium** * or **phellogen**, and, strictly speaking, should come

* A similar layer occurs in leaf-petioles at the time of separation of the leaf in the autumn; it is known as the absciss-layer, and separation takes place along the middle lamellæ.

under the heading of meristem, to be considered later. The cork-cambium produces on its outer aspect fresh cork-cells, and on its inner aspect, at times, a layer of cells possessing chloroplasts, known as the **phelloderm** (see *supra*). In some plants—*e.g.*, *Quercus sessiliflora*—several separate zones of cork may be found at different depths in the cortex. Cork forms, at times, a layer of considerable thickness, which affords no mean protection to the cortical tissues of the stem; the walls of the freshly-formed cork-cells are composed of pure cellulose and pectose, but they soon become toughened and rendered more elastic by the deposit in them of a substance known as **suberin**. Older cells of

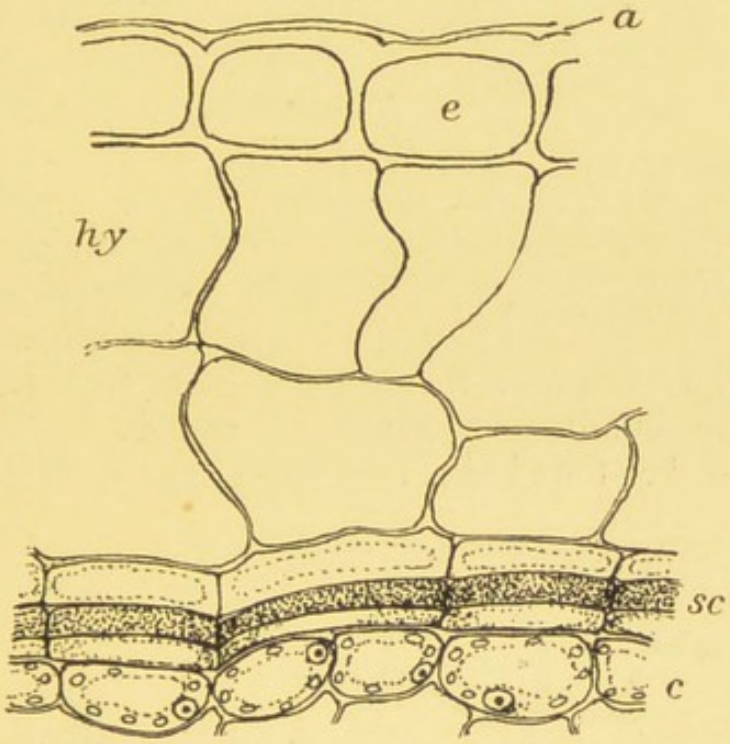


Fig. 24.—Portion of a Transverse Section of the Young Stem of *Pinus* to show the formation of Cork.—*e*, Epidermis; *a*, cuticle; *hy*, hypodermis; *sc*, cork-cambium; *c*, cortical cells.

the cork contain air only, so that cork-tissue is of low specific gravity and very elastic in nature. In some stems openings are formed in the "bark," through which the more superficial of the cork-cells are continually shed; these apertures are known as **lenticels**, and are caused by the thinning of the epidermis at certain points and subsequent rupture, leading to an aperture which is of value in admitting air into the intercellular spaces of the cortex.

(*b*) **Collenchyma.**—This tissue usually occurs just internal to the epidermis, in such stems as that of *Cucurbita;* the cells composing it are in reality the outermost cortical cells, at the angles of junction of which the **intercellular substance** becomes converted into a material, highly refractile in appearance, which when dry is not unlike dried mucilage. On the addition of water or caustic potash solution it swells up to many times its original bulk, and it may be stained with methylene blue (see Fig. 26). Collenchyma confers **elasticity** upon the outer layers of the cortex, and, as a protective layer against mechanical shock, must be of great service to the plant.

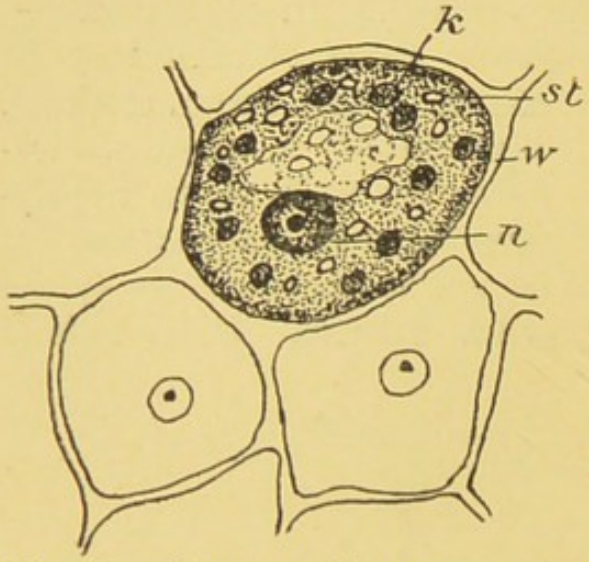


Fig. 25.—Cortical Cells from the Young Stem of *Pinus.*—*w*, Cell-wall; *k*, chloroplasts lying in the granular cytoplasm; *n*, nucleus; *st*, starch-granules.

(*c*) **Sclerenchyma.**—In various parts of a plant there occur **elongated fibres,** massed together into bundles or zones of greater or lesser extent; they are to be found in the outer parts of the rhizome

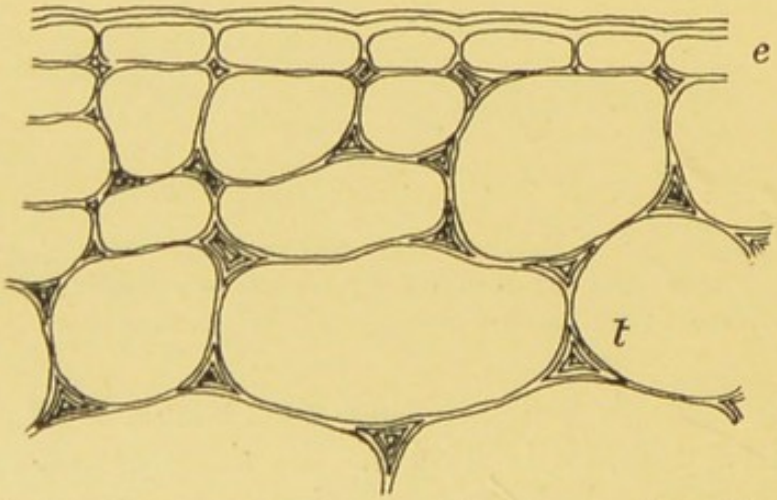


Fig. 26.—Collenchyma from the Stem of *Cucurbita* (transverse section).—On treatment with dilute caustic potash the intercellular substance at the angles of the cells swells up to twice or three times its original volume.

or petioles of Ferns, and also surrounding the vascular bundles in these plants. Each fibre arises at an early stage from

elongated cells (prosenchyma), the walls of which become greatly thickened (**sclerised**), and at times deeply pigmented, usually a brown colour; as soon as the thickening is completed the protoplasm leaves the cell-cavity and passes through "**pits**" in the walls into other cells. A transverse section across a patch of sclerenchyma shows rather irregular rounded or **polyhedral** elements with very thick walls, the latter being perforated here and there by narrow "**pits**" joining the cavities of adjacent fibres. The walls also show **concentric striations**, pointing to the fact that the various thickening layers have been laid down at different times (*cf.* growth of the cell-wall by accretion, Chap. iv.). On treatment with **iodine solution** the fibres stain a **yellowish-brown**. In longitudinal sections of stems or roots the fibres are seen to be elongated fusiform elements, not composed, as would appear, of single cells, but of several which have united end to end, the intermediate end-walls becoming absorbed. The fibres join one another obliquely, and have tapering ends.

Note.—Sclerenchyma may be studied in transverse and longitudinal sections of the stems of *Zea mais*, *Pinus*, and the rhizome or petiole of *Pteris aquilina*. *Tilia* and *Euphorbia* stems are also good. In *Zea mais* the fibres are arranged round the fibro-vascular bundles; the "pits" in the walls are well seen in transverse sections of the leaf of *Sansevieria* and of the stem of *Euphorbia*. In the stem of *Pinus* the sclerised elements are the bast-fibres; they are of an oval, flattened shape in transverse section.

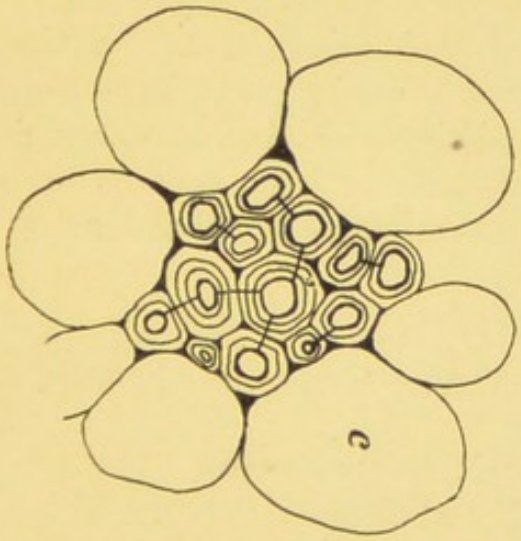


Fig. 27.—A Small Patch of Sclerenchyma from the Leaf of *Sansevieria*, seen in Transverse Section.—Note the laminated structure of the walls of the fibres and the "pits" connecting their cavities. The large cells surrounding the patch are cells of the mesophyll.

CHAPTER IV.

MERISTEM.

THE various organs and adult tissues of which a plant is made up arise from young undifferentiated tissue which occurs in certain positions, notably at the apices of young shoots and roots, and in the form of zones of dividing cells in stems and roots, and at times in other positions; this rudimentary tissue is known as **meristem,** and the first few cells of this tissue as **promeristem.** A meristematic tissue from which the primary tissues arise (viz., that producing the first wood and bast, and the epidermis, pith, and cortex) is known as a **primary meristem,** whereas that arising from previously differentiated cells (viz., that producing cork, secondary wood and bast) is known as **secondary meristem.** Amongst the latter would be classed the various **cambiums** met with (cambium proper, cork-cambium, pericycle) and certain layers known as **intercalary meristem,** which arise in such organs as young leaves towards the base, and which, in this case, function in the transverse growth of the leaf.

Meristem may thus be defined as "a tissue which, during some part of the existence of a plant, is, as regards its component cells, either in a condition of active cell-formation or else remains capable of renewed activity after periods of quiescence." The cambiums may be described as **zonal meristem.**

A. DIVIDING CELLS OF ANY RUDIMENTARY TISSUE AND THEIR MODE OF GROWTH.

Cells of embryonic tissues are in structural details similar to the type of young undifferentiated cell which was examined in Chapter ii., B., where it was seen that protoplasm almost filling the cell-cavity, large nucleus, cell-sap, and plastids were the main cell-contents.

In a tissue where **rapid cell-formation** is in progress (meristem),

it is possible to detect here and there cells in which typical division-figures (**mitosis**) can be made out, especially where a thin section is cut and stained as directed in the note at the end of Chapter ii. (see Fig. 28). In these young cells the cell-walls are very thin, and on account of turgidity are a good deal on the stretch; the polyhedral shape so often observed in the cells of young tissues is due partly to mutual cohesion and pressure; and, moreover, a certain amount of **intercellular matrix** (which forms the middle-lamella) is soon secreted which tends to make the cells cohere. If the intercellular substance is dissolved by certain reagents,* the cells may be made to separate from one another, and

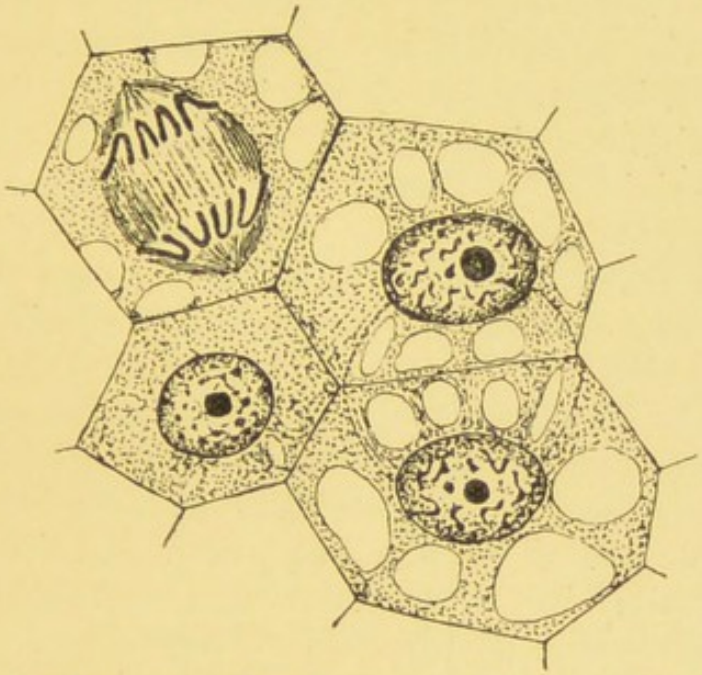


Fig. 28.—Young Dividing Cells from a Rudimentary Tissue.—In one cell the nucleus is undergoing division (mitosis).

they then tend to resume the spheroidal shape. The directions in which fresh cell-walls are formed is determined to a certain extent by the directive action of the protoplasm, and by the relative position of the cells in the young tissue. In buds or root-tips it is possible to make out two main modes of wall-formation with regard to their direction in space, and these are known by the terms **synclinal** and **anticlinal.** The synclinal walls are formed more or less parallel to the external contour of the bud, or the contour of the central cylinder, whilst anticlinal walls are those formed at right angles to these. The

* Schulze's Macerating Mixture (see *infra*).

general shape of the synclinal and anticlinal surfaces, when cut by a plane passing through the longitudinal axis of the bud, would thus be parabolic, the two sets of parabolæ cutting one another at right angles, and the foci of both sets of curves would be within the area of the growing point of the shoot.

The **contents** of the young cells consist, as has been mentioned, of protoplasm, nucleus, sometimes plastids, and cell-sap, in which latter certain salts are held in solution. The plastids (when present) manufacture starch, not quite in the same manner as the chloroplasts, but from certain elaborated materials (sugar) brought to the cells from the leaves, and from the starch thus built up the protoplasm is able to manufacture **cellulose,** for the purpose of wall formation. The production of cellulose is, however, not a simple matter, since it has been shown that in the production of the **cell-plate,** or partition wall dividing a cell into two during the later phases of cell-division (see Chap. viii.), the protoplasm undergoes an almost direct transformation into cellulose by the splitting off of its carbohydrate molecule, the remaining proteid and amine portions being then free to combine with carbohydrate derived from other sources in the cell. Moreover, it has been found that many stages ordinarily exist between protoplasm and cellulose, and that starch before it can be utilised must first be converted into dextrins and sugar by the agency of enzymes, and it is probably this sugar which is made use of by the protoplasm. In the latter process oxidation possibly has a large share. The unlignified cell-wall has a large amount of **pectose** in its composition, pectose having the same generic formula as cellulose; the middle-lamella, in fact, consists of calcium pectate.

Physically speaking, **growth of the cell-wall** takes place in two ways, viz.:—

(*a*) Growth by **intussusception,** fresh particles of cellulose being intercalated between those already existing.

(*b*) Growth by **accretion**—*i.e.*, fresh layers of cellulose are laid down one after the other, somewhat after the manner in which crystals increase in size.

Both these processes are going on together in the cell; growth of the wall in surface-area being effected by intussusception, whilst growth in thickness of the cell-wall proceeds by accretion.

In this connection it is necessary to give a few instances of the **secondary thickening** of the cell-wall by accretion. The

walls of **endosperm cells** in some plants (Date, *Sagus taedigera*, *Phytelephas*) become after a time enormously thick, the cell-cavities being still connected by means of "pits" which traverse the walls of adjacent cells. The thickening takes place mainly by the deposition of layer after layer of cellulose, but, as a rule, other substances are also deposited which confer upon the walls great toughness (*Phytelephas*).

The cells of the **pith** of some plants (*Hoya carnosa*) have extremely thick walls, through which pass "pits," usually simple in nature. As a rule, however, adult pith-cells are thin-walled (*Sambucus*) and contain nothing but air.

Epidermal cells often possess, as has been seen (see *supra*) very thick outer walls (*Viscum album*, Holly), and at times layer after layer can be distinguished; in such cases treatment of the walls with caustic potash usually results in a separation and swelling of the **cuticle**, followed by a swelling of the layers of the outer wall. The thickening of the walls of **sclerenchymatous fibres** and **wood elements** also takes place mainly by accretion.

The wall of the young cell is not, however, devoid of interstices; indeed the fact that salt molecules of different sizes can penetrate into the cell through the wall, points definitely to the existence of such interstices. Naegeli looked upon the cell-wall as being constituted somewhat as follows:—

i. The ultimate molecules (micellæ) of cellulose have spaces between them. Each micella is supposed to be surrounded by a watery envelope.

ii. These molecules are again grouped into larger particles (tagmata) between which larger spaces exist. Thus a sort of complex meshwork is produced, which permits of the passage of certain substances.

It is highly probable that some such structure is present in the cell-wall of a young cell, and that molecules of salts can pass through. In this connection, however, the study of **root-hairs** offers an explanation of the absorption of salts into the interior of the cell, which cannot be arrived at by simply considering the structure of the cell-wall. It is, in fact, highly probable that the **ectoplasm** lining the inner aspect of the wall of the root-hair exercises a **selective capacity** upon the absorption of salts in solution from the soil, some salts being admitted to the exclusion of others; and as in the root-hairs, so in the young thin-walled cells of a rudimentary tissue, although in this case the materials supplied to the cell are, as a rule, not raw, but elaborated, the mole-

cules being larger than those of salts. Later on, during the life of the cell, the walls are generally too thick to allow of the above-mentioned process of absorption, and then the presence of "**pits**," or perforations in the walls, becomes a factor of great importance in the transference of food materials and water from cell to cell; and it has already been seen that the cytoplasm also passes slowly from cell to cell by means of the same "pits."

Note.—Cells of young developing tissues (meristem) may be studied in the young endosperm of *Caltha palustris* (see Fig. 5), or in sections of root-tips or apices of stems. The same method of fixing, hardening, and staining may be used as in the preparation of the young undifferentiated cell. (Note at end of Chapter ii.). *Caltha* is the marsh marigold, and the endosperm starts developing from the beginning to the middle of June, after the petals have fallen, and the carpels have just started to ripen. Transverse sections of the carpels will cut the ovules longitudinally, and a large number of sections may be rapidly examined, the thinnest and best being selected for mounting.

B. ZONAL MERISTEMATIC TISSUES.

Under this heading are included :—

i. The **Cambium** (stem and root).
ii. **Cork-cambium** (stems).
iii. **Pericycle** (roots).

The second of these has been already examined under cork-tissues. The pericycle will be examined in Chap. v.

In cambium wall-formation during cell-division takes place in only two directions, generally speaking—viz., the radial and the tangential directions in a stem or root; thus the walls produced in such a tissue have always a fixed orientation, being either situated along a radius, or perpendicular to radii of the organ in which they occur. In rudimentary tissues other than cambium it was pointed out above that the main directions of wall-formation were either synclinal or anticlinal with regard to certain fixed planes in the bud, and that walls might be formed at times in almost any direction in space. In the tissue now to be studied, however, a marked regularity in the directions of wall-formation is preserved. The planes in which walls are formed are always parallel to either a fixed perpendicular, or transverse plane in the organ.

The statements made with regard to thickening and growth

of the cell-wall and the absorption of food materials apply equally to cambium as to other rapidly-dividing young tissues; and it will be seen that the change from the typical thin-walled cambial cell to the modified elements met with in the wood and bast is often a very rapid one.

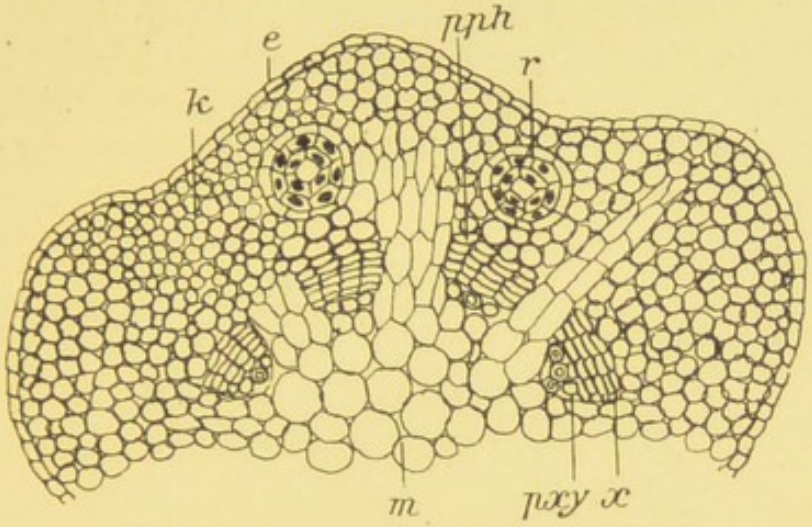


Fig. 29.—Portion of a Transverse Section near the Apex of a Young Shoot of *Pinus*.—*e*, Epidermis; *k*, periblem (rudimentary cortex); *x*, rudimentary cambium; *pxy*, protoxylem; *pph*, protophloem; *m*, medulla; *r*, resin-canals.

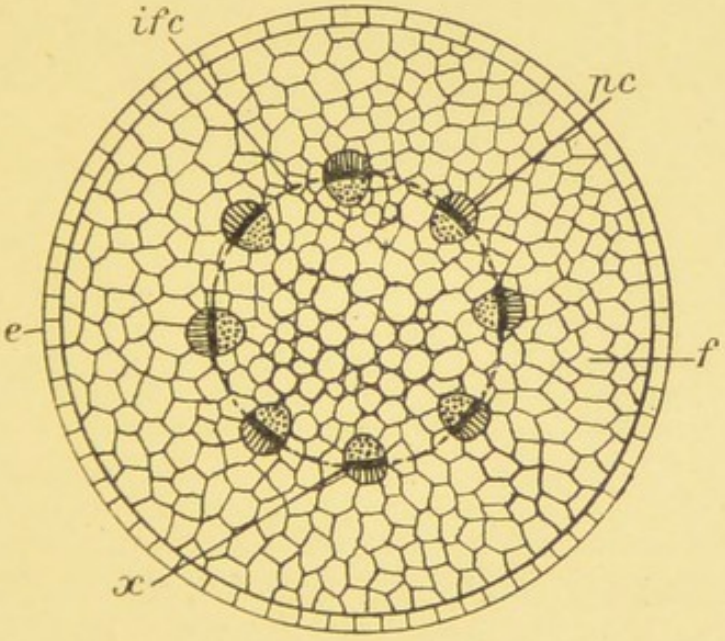


Fig. 30.—Diagram illustrating the Arrangement of Primary and Secondary Vascular Tissues in a Dicotyledonous (or Coniferous) Stem. (A transverse section near the apex of a young stem.)—*e*, Epidermis; *f*, fundamental or ground-tissue; *pc*, procambial strands, inner parts protoxylem, outer parts protophloem; *x*, meristem zone (cambium) of a procambial strand; *ifc*, dotted circle indicating the position where the interfascicular cambium will arise.

I. **The Cambium** (found as a distinct layer of meristem in the stem and root of Dicotyledons and Coniferæ).—Before passing on to the detailed description of the cambium, it is necessary to examine briefly the **arrangement of the tissues** in the vascular region of a dicotyledonous stem, together with the early origin of the cambial layer, and its subsequent history.

The **vascular region** proper is that part which lies internal to the **endodermis** or starch-sheath, a ring of cells which is found immediately internal to the cortex in dicotyledonous or coniferous

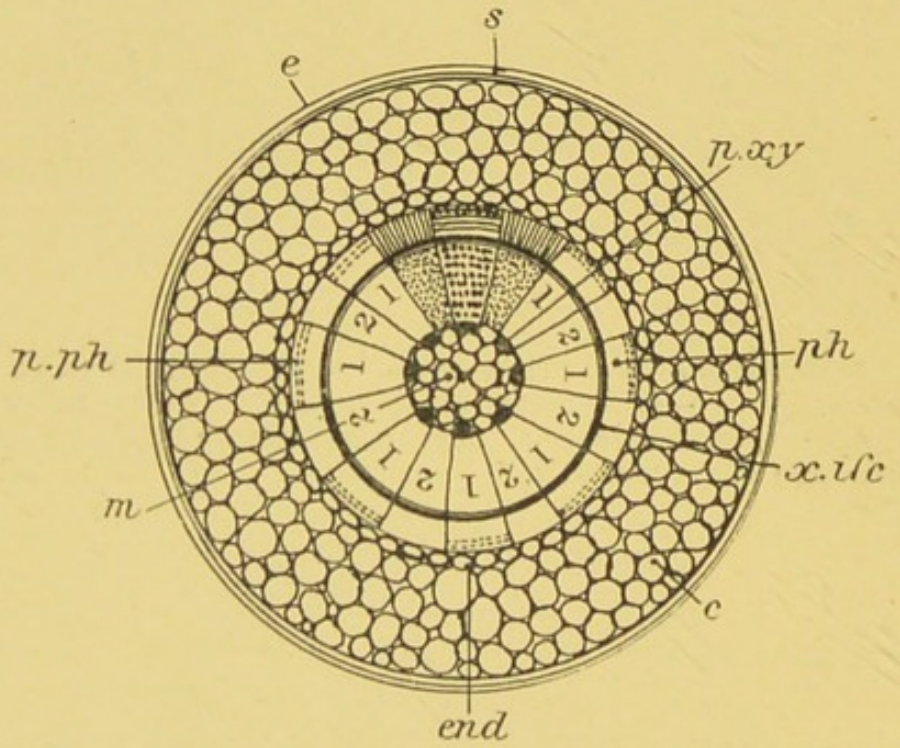


Fig. 31.—A Transverse Section across an older Stem.—*e*, Epidermis; *s*, cork-layer; *c*, cortex; *end*, endodermis; *x*, cambium ring (the line points to an interfascicular portion, *ifc*); *ph*, phloem ring; *p.ph*, remnants of the original protophloem; *1*, *2*, *1*, *2*, etc., the ring of xylem, made up of xylem elements derived from the fascicular and interfascicular cambium respectively; *p.xy*, protoxylem; *m*, medulla or pith.

stems; all the tissues internal to the endodermis are included in the term "**central cylinder**,"* and comprise, from without inwards, the bast and phloem, the cambium, the wood, and, in the centre, the pith or medulla (see Figs. 31, 32, 33, and 34). All the tissues, however, contained in this central cylinder are not, in the true

* A central cylinder or "plerome" is also to be found in the young monocotyledonous stem, but the primary cortex appears to merge into it, there being no endodermis proper.

sense of the term, vascular—the vascular tissues proper being the **wood** and **soft-bast**, and possibly the cambium—these tissues being functional in the **conduction of sap**, raw and elaborated, to and from the leaves respectively. The other tissues of the stem, such as cortex, young pith, &c., derive their supply of elaborated sap more by **osmosis** through the phloem than by direct conduction.

The term **cambium** is applied, in stems and roots of Dicotyledons and Conifers, to a narrow zone of meristem situated between the woody portions of the fibro-vascular bundles and

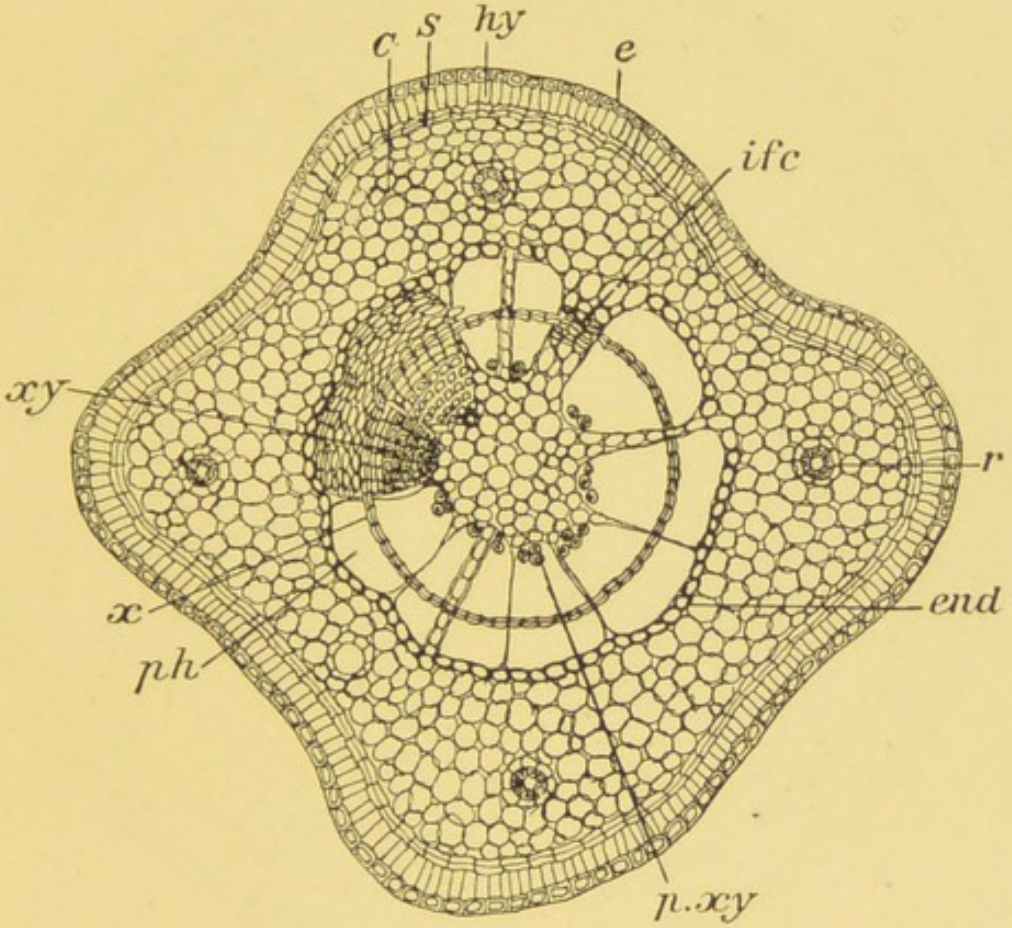


Fig. 32 (semi-diagrammatic).—A TRANSVERSE SECTION THROUGH a FIRST YEAR'S STEM OF *Pinus*.—*e*, Epidermis; *hy*, hypodermis; *s*, cork-layer; *c*, cortex; *r*, resin-canals; *end*, endodermis; *ph*, phloem; *x*, cambium layers; *ifc*, interfascicular cambium; *xy*, xylem; *p.xy*, protoxylem.

that portion known as the phloem or bast; it is functional in producing on its **inner aspect** fresh elements of the wood or **xylem**, and on the **outer aspect** fresh **phloem** elements. The **origin** of the cambial layer can be traced back to an early period in the growth of stem or root; a transverse section, for example, just

below the apex of a young shoot of a Dicotyledon (or Conifer) will show, when examined under a low power of the microscope, the following details :—

(*a*) A general fundamental or **ground-tissue.**

(*b*) A few patches, circularly arranged, towards the centre of the section, which are, in reality, sections across the rudimentary primary vascular bundles, or, as they are sometimes called, the **procambial strands** (see Figs. 29, 31, and 32).

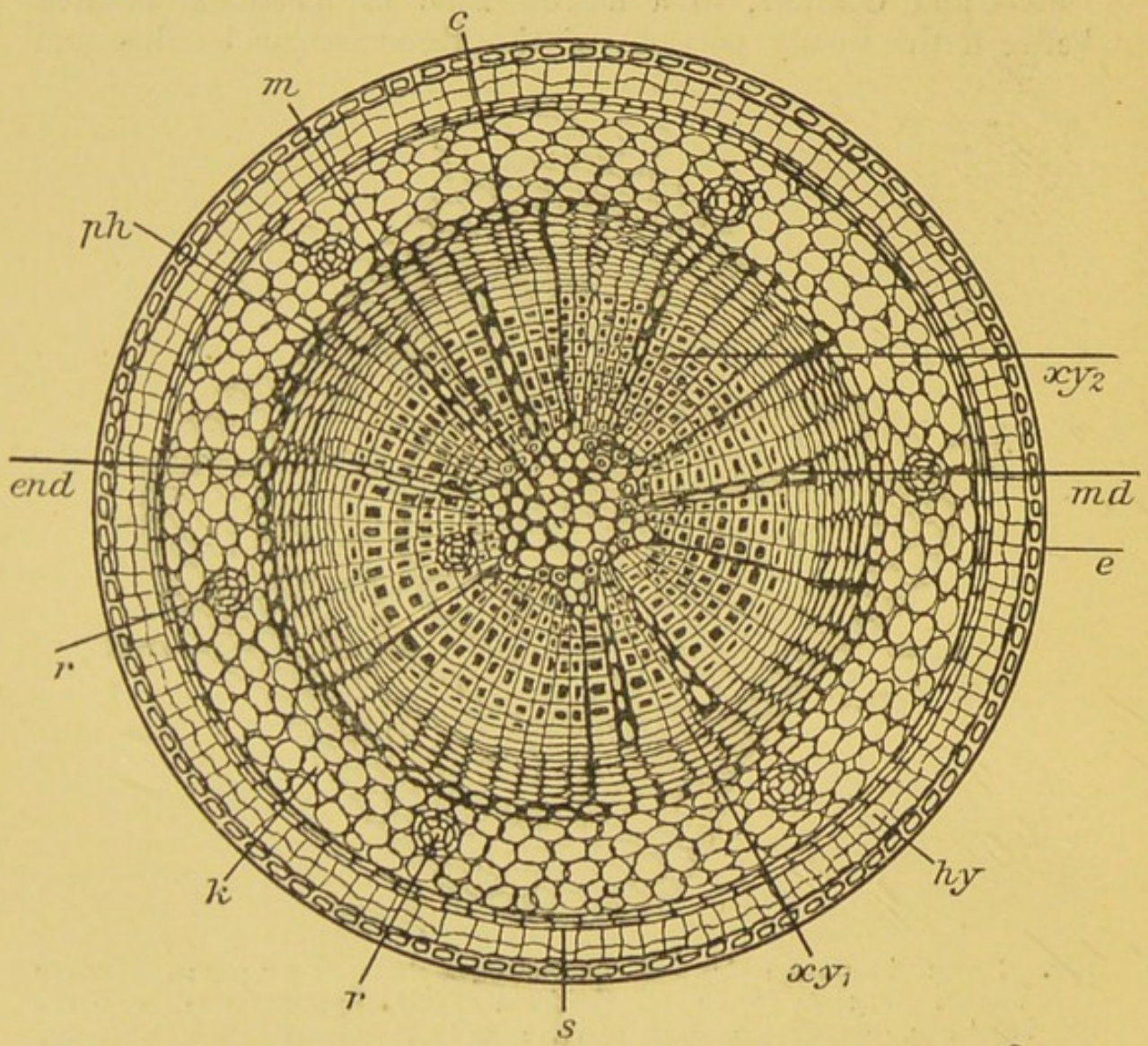


Fig. 33 (diagrammatic).—A TRANSVERSE SECTION THROUGH AN OLDER STEM OF *Pinus*, showing the complete Ring of Wood and Bast.—*k*, Cortex; *md*, medullary rays (secondary, see *infra*); *m*, pith. Other letters the same as in Fig. 32.

Each **primary vascular bundle** is composed of three portions, viz.:—

(i.) An inner part made up of a few embryonic wood-elements having spiral or annular thickenings on their walls, and known as **protoxylem.**

(ii.) An outer part made up of thin-walled elements, the rudimentary phloem, or **protophloem.**

(iii.) An intermediate part composed of thin-walled meristematic cells, the rudimentary **cambium** of the primary vascular bundles (fascicular cambium).

Further down the stem the primary bundles are differentiated into typical **xylem, cambium,** and **phloem,** and between the primary bundles it is found that certain cells of the ground-tissue have remained or have subsequently become meristematic; these

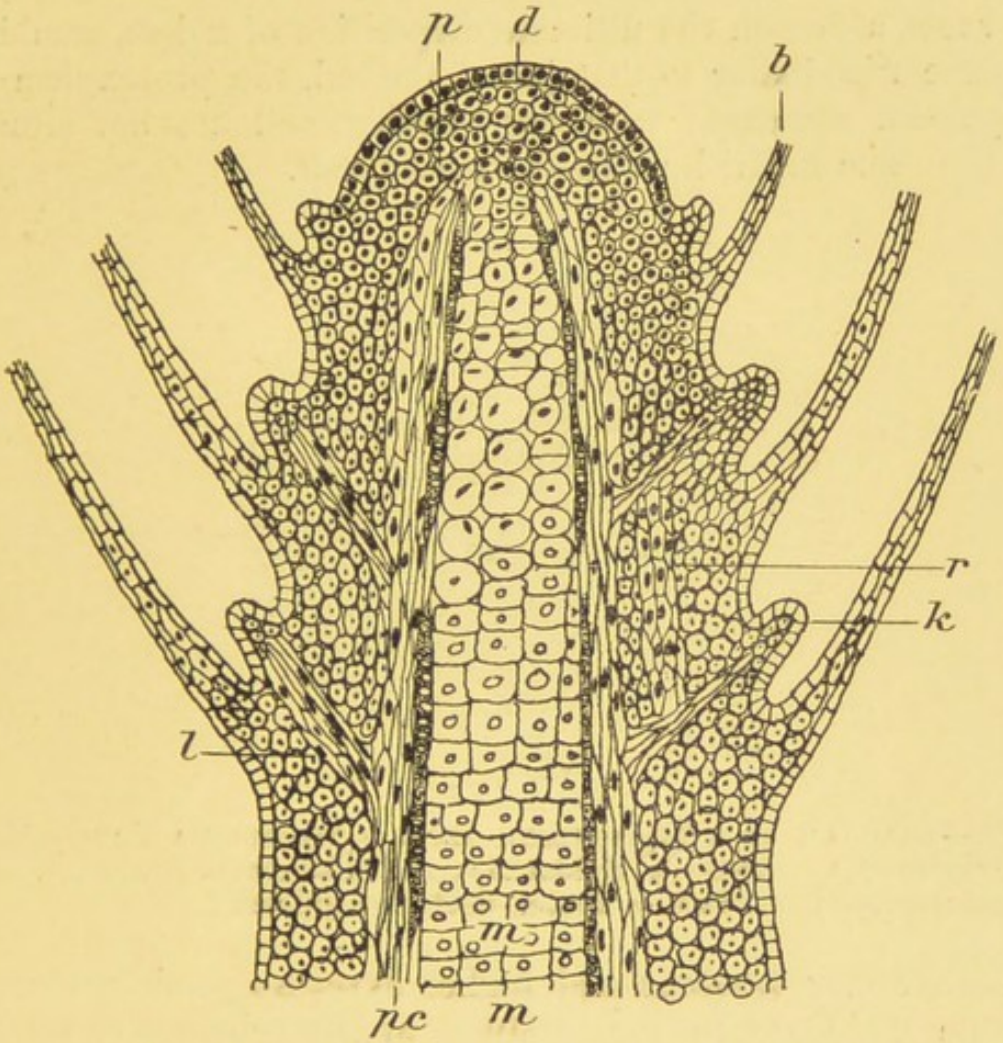


Fig. 34.—A Longitudinal Section through the Apex of a Young Shoot (Dicotyledon or *Pinus*).—*d*, Dermatogen; *p*, periblem; *pc*, procambial strands; *m*, medulla; *b*, bracts; *k*, leaf-buds; *l*, lateral offshoots from procambial strands. The portion included between the procambial strands (*pc*) is the "central cylinder."

cells, in fact, will give rise to intermediate patches of cambium, the so-called **interfascicular cambium.** The interfascicular cambium produces, in like manner to the cambium of the primary

bundles, xylem upon its inner aspect and phloem upon its outer aspect, but, as will be readily understood, there is no protoxylem or protophloem to be seen in these portions, as they are secondary formations (see Figs. 30, 31, and 32, *ifc*).

The fascicular and interfascicular cambium unite during the first year's growth, and thus is produced **a complete ring of meristem** in stem (or root) which gives rise to fresh annual rings of xylem and phloem (see Figs. 31, 32, 33). The whole process is known as **secondary thickening.**

In **roots**, although the ultimate disposition of xylem, cambium, and phloem is similar to that just described, the protoxylem and protophloem **alternate** with one another, and are not situated upon the same radial lines in the young root.

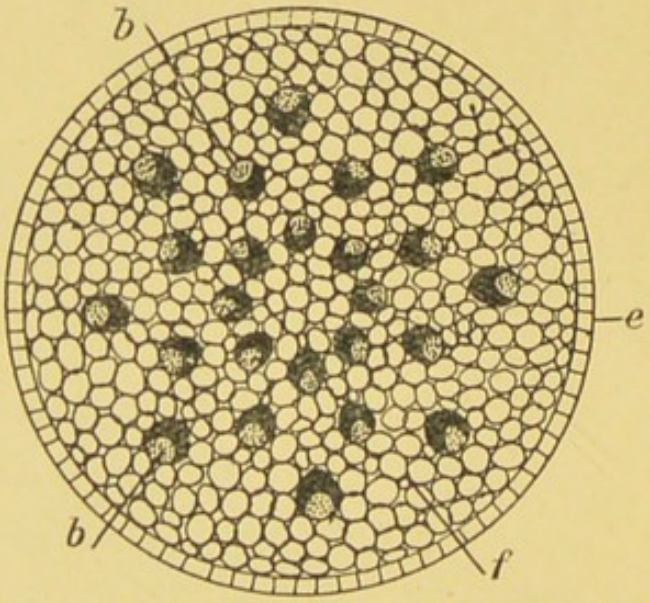


Fig. 35.—Diagram of a Transverse Section through a Young Monocotyledonous Stem—*e*, Epidermis; *f*, fundamental tissue; *b*, fibro-vascular bundles (black = xylem, dotted = phloem).

In the Monocotyledons and higher Ferns no persistent ring of meristem analogous to the cambium of Dicotyledons exists, and the fibro-vascular bundles are made up of xylem and phloem formed early from certain rudimentary elements; generally speaking, in Monocotyledons, the phloem is found between the arms of a **V**-shaped mass of xylem (see Fig. 35); whilst in the higher Ferns the phloem surrounds a centrally situated mass of xylem in each separate bundle. Thus the bundles of Monocotyledons and Ferns are termed "**closed**" bundles, in contradistinction to those of Dicotyledons and Conifers, which are known as

"**open**" bundles—viz., bundles capable of receiving fresh annual rings of xylem and phloem by the activity of the cambial layer. In a few instances, however (*Dracæna*), the stems of certain Monocotyledons possess **zones of meristem** from which fresh annual rings of fibro-vascular bundles are produced, these bundles being, however, always of the closed variety; and it may be here mentioned that **petioles of bifacial leaves** in Dicotyledons possess only scattered closed bundles, there being no cambial layer in

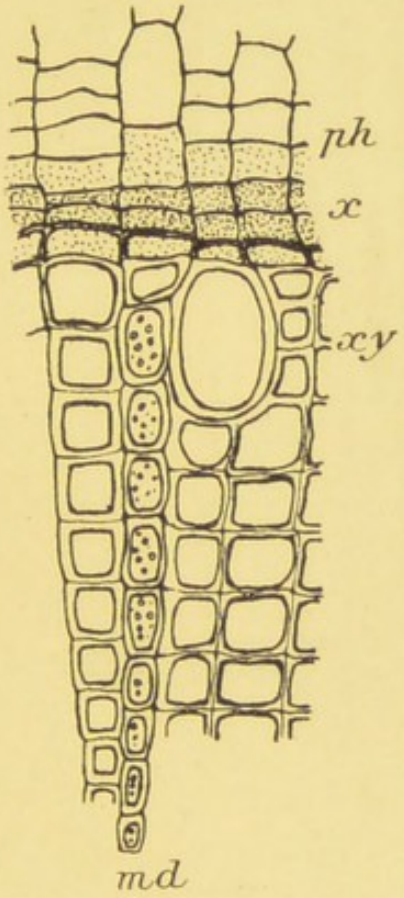


Fig. 36.—Portion of a Transverse Section through the Stem of *Ricinus communis*.—*x*, Cambium; *ph*, phloem; *xy*, xylem (one large vessel is seen amongst the tracheides); *md*, medullary ray.

each bundle, and thus no possibility of secondary thickening. In **centric leaves** (*Pinus*), on the other hand, where a central cylinder is present, there may be, for a short time, a narrow zone of cambium between the xylem and phloem portions of the fibro-vascular bundles. In some dicotyledonous stems (*Podophyllum peltatum*) scattered vascular bundles occur instead of a well-defined ring of wood and bast; this is known as **anomalous stem-structure.** Other instances also occur.

For the purpose of studying the structural details of the **cambium** both transverse and longitudinal sections should be taken of the stems and roots selected. In *transverse section* the layer has much the same appearance as the cork-cambium, each cambial element having a somewhat flattened rectangular shape,

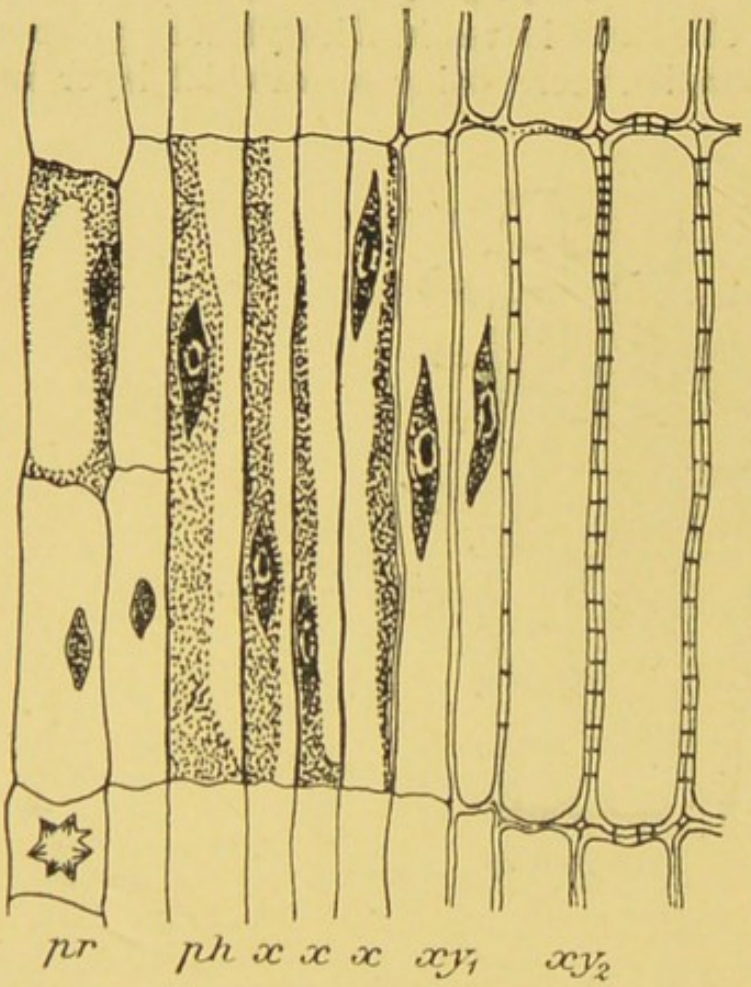


Fig. 37.—A LONGITUDINAL SECTION THROUGH THE CAMBIAL REGION OF *Vinca major* (stem).—*x x x*, Cambial cells; *ph*, young sieve-tubes of the phloem; *pr*, phloem-parenchyma; xy_1, young wood elements (pitted tracheides); $x\,y_2$, older wood-elements.

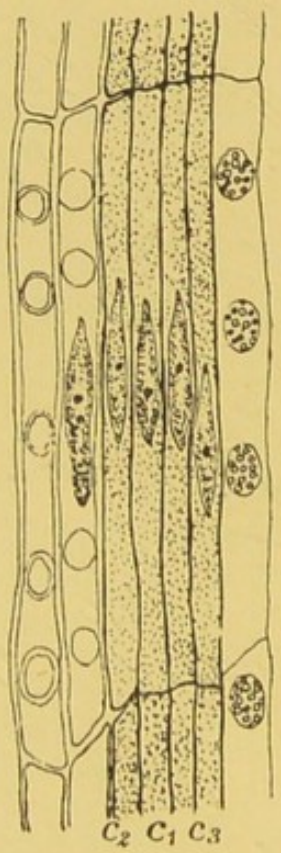


Fig. 38 (semi-diagrammatic).—A LONGITUDINAL SECTION THROUGH THE CAMBIAL REGION OF *Pinus*.—c_1, c_2, c_3, Cambial elements; c_1 remains active, c_2 and c_3 going to form xylem and phloem elements respectively.

and in careful preparations the protoplasm is seen to fill the cell-cavity almost entirely (see Figs. 36 and 36*a*). In *longitudinal sections* (see Figs. 37, 38, and 39) each cambial cell is observed

[*To face p.* 54.

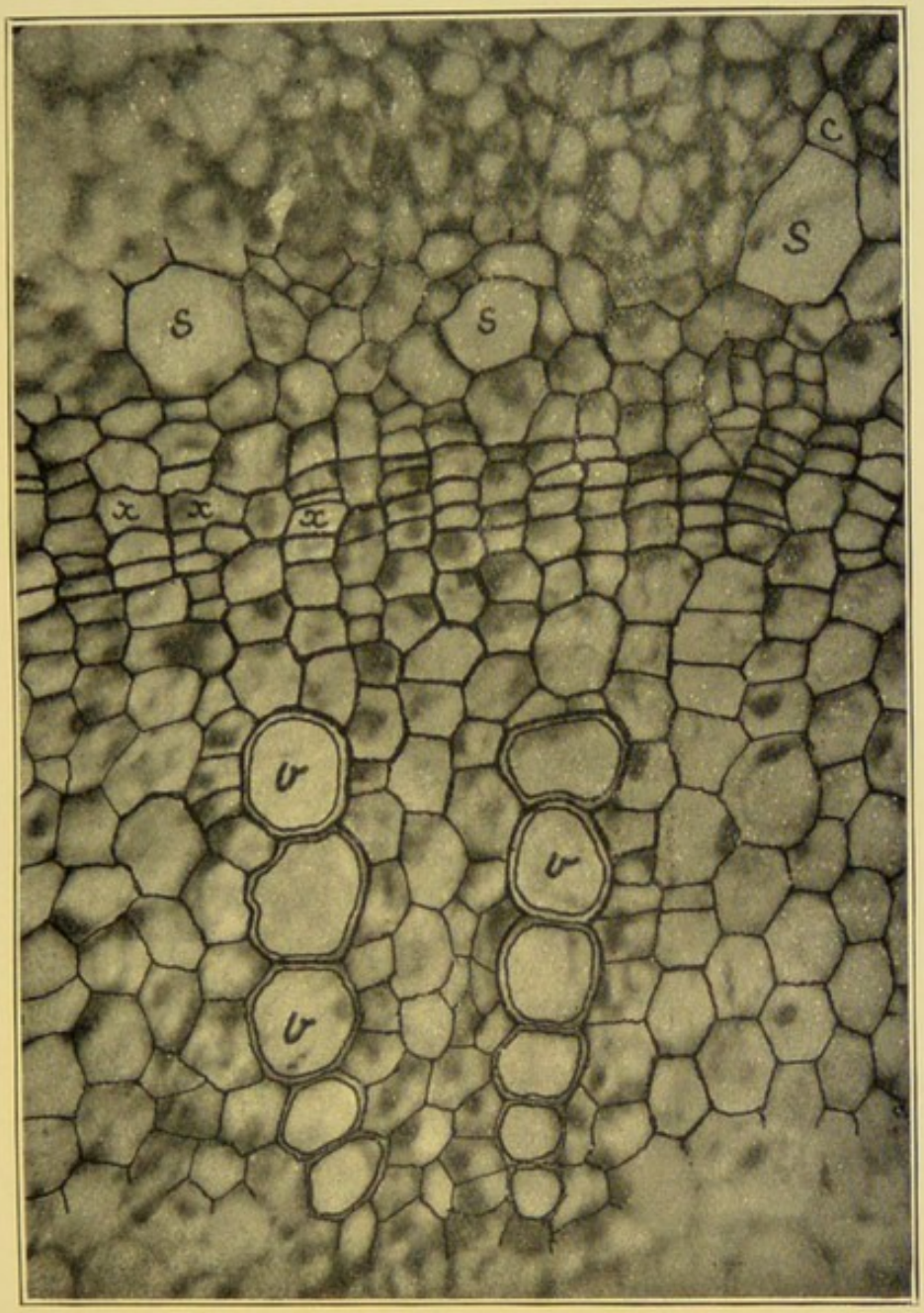


Fig. 36*a*.—A Photomicrograph showing the Cambial Region Xylem and Phloem in Transverse Section, from the Young Stem of *Sambucus*.—*x*, Cambial cells; *s*, sieve-tubes in the phloem; *v*, large vessels (annular) in the xylem.

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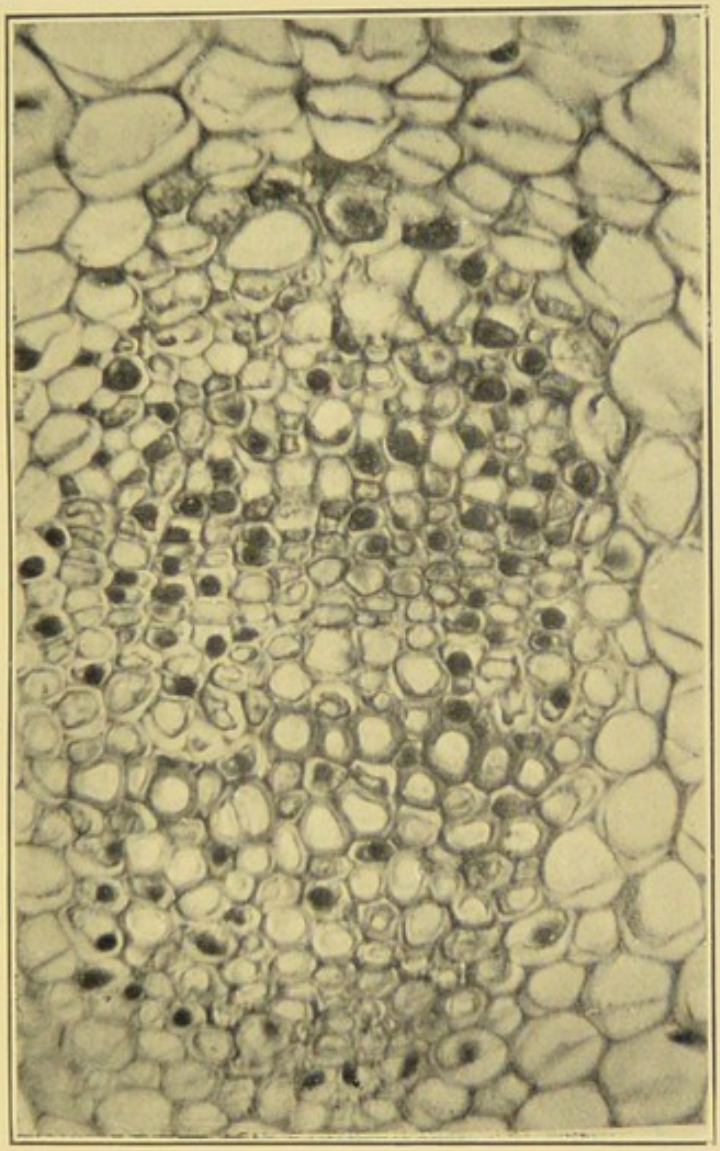

Fig. 36*b*.—Photomicrograph showing a Transverse Section of a Primary Bundle (Dicotyledon). Note the central cambium, the phloem at the top, and the xylem at the bottom.

to be an elongated (prosenchymatous) element possessing granular protoplasm in which lies a very elongated fusiform nucleus. The wall of the element is very thin at first, but a cell which has just been formed on either side by the division of a cambial element soon undergoes modification into a xylem or a phloem element, the wall being then thickened and otherwise altered (see Chap. v.). In dividing, there are usually only one

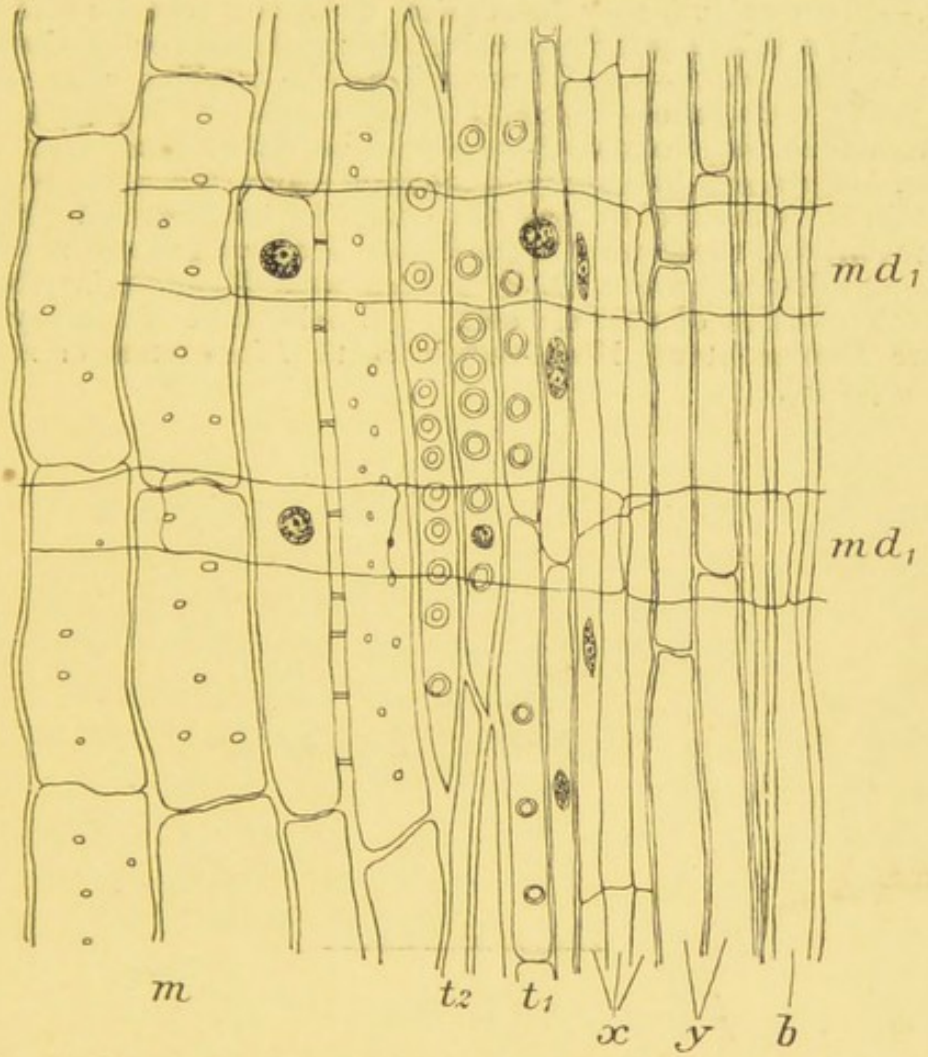

Fig. 39.—A Longitudinal Section in the Region of the Inter-fascicular Cambium of the Stem of *Pinus*.—x, Cambial cells; y, young sieve-tubes; b, bast-fibres; t_1, t_2, young wood-elements (tracheides with "bordered pits"); m, medulla; md_1, ground-tissue rays.

or two lines of cells forming active cambial elements. Supposing (see Fig. 38) that there is one such line of cells, c_1, and that this line of cells has already produced the elements c_2 and c_3, then it is found that the original line c_1 remains active, c_2 and c_3

going to form permanent elements of the xylem and phloem. Occasionally, however, several lines of cells may be active.

In the division of a cambial cell the nucleus probably divides *en masse* (amitosis), and does not undergo mitotic division, a process which would take too long a time for its completion. The elongated fusiform shape of the nucleus is also further evidence of its mass-division.

Note.—The cambium may be studied by taking transverse and longitudinal sections of any quickly-growing dicotyledonous or coniferous stem or root; in some roots—*e.g.*, Horse-radish—the cambium may appear to form a rather wide zone on account of the absence of any great amount of thickening in the elements just cut off on either side. For staining cambium, fuchsin and hæmatoxylin are good stains to use, the protoplasm being stained by the fuchsin and the nuclei by the logwood. The tissue used for studying cambium should, if good preparations are required for keeping and demonstration, be first fixed with Flemming's solution or 2 per cent. solution of chromic acid. Suitable plants for studying this layer are *Ricinus* (stem), Horse-radish (root), *Pinus* (stem or root), and *Cucurbita* (stem).

CHAPTER V.

THE VASCULAR TISSUES.

In describing the elements composing the **conducting tissues** of plants it must be remembered that similar elements may occur in all of the four great groups, Dicotyledons, Conifers, Monocotyledons, and Pteridophyta; but it is convenient, when considering the vascular tissues, to take those groups in which the greatest variety of conducting elements occur, and in this respect, the Dicotyledons and Conifers afford much the widest scope for investigation. Moreover, by doing this a more rational sequence will be preserved, seeing that it has just been shown in the preceding Chapter how the **xylem** and **phloem** arise in Dicotyledons and Coniferæ from the cambial layer; and, in addition, certain other important tissues occur in Dicotyledons and Conifers, such as the **medullary rays, endodermis,** and **pericycle,** which, although not strictly speaking vascular tissues, are nevertheless included in the central cylinder, and have important functions.* In some instances the other groups—viz., Monocotyledons and Ferns—possess conducting elements which are important to study, and these will be incidentally described; but, in the majority of cases, it will be found that Dicotyledons and Coniferæ possess in their vascular system a sufficient variety of conducting-element to enable the student to gain a very fair idea of the more important of these.

Therefore, in the following description of the component elements of the vascular tissues, the order of examination set forth below will be found convenient:—

(A) The **Phloem** [produced by the cambium (Dicotyledons and Coniferæ) upon its outer aspect].

(B) The **Xylem** [produced by the cambium (Dicotyledons and Coniferæ) upon its inner aspect].

* The endodermis and pericycle occur also in Monocotyledons and Pteridophyta, both being present in the roots of either group; and an endodermis is to be found round each of the separate bundles in the rhizomes of Pteridophyta.

(C) The **Medullary rays** (produced in part by certain cells of the cambium).

In addition, the endodermis, pericycle, and medulla or pith will be briefly described as component tissues of the central cylinder. It should, however, be remembered that in those plants which do not possess a strictly limited central cylinder, or a well-defined zone of cambium, phloem and xylem elements may be met with in the so-called closed vascular bundles, similar in many respects to those occurring in the xylem and the phloem of the more highly differentiated groups—viz., Dicotyledons and Coniferæ.

(A) The Phloem or Bast.

The cells produced by the cambium on its outer or cortical aspect go to form a tissue consisting almost entirely of elements known as **sieve-tubes.** The undifferentiated cells originating from the cambium are at first quite thin-walled, but soon changes take place which result in :—

(i.) Thickening of the lateral and end-walls.

(ii.) The formation of special areas known as **sieve-plates** upon the end-walls.

These sieve-plates are formed as follows :—thin areas are left in the end-walls during the development of the sieve-tube, and after a time these thin areas, which coincide with one another in adjacent end-walls, unite, the intermediate middle-lamella becoming absorbed. The other portions of the end-walls become much thickened ; and in some cases several such sieve-areas may be present in the end-walls of tubes (*Tilia*), the number of actual perforations, or pits, which may be present in each sieve-area being perhaps twenty, thirty, or more.

Sieve-tubes may be readily examined by taking transverse and longitudinal sections of such a stem as that of *Cucurbita.* In transverse section each sieve-tube is seen to be of a somewhat irregular shape ; lying just outside the cambial layer, and close to the tube—being, in fact, cut off from the main cell—is to be seen a smaller cell, known as the **companion-cell,** which appears full of granular contents. In such a section the tubes are usually recognised by their sieve-areas, which may be made more evident by staining the section with eosin (see Fig. 40).

In longitudinal sections each sieve-tube is seen to be an elongated element, with its narrow companion-cell lying next to it along its whole extent. Towards the middle line of the tube are to be seen the contracted **protoplasmic contents**—that is to say, if ordinary spirit-preserved material is being used for the

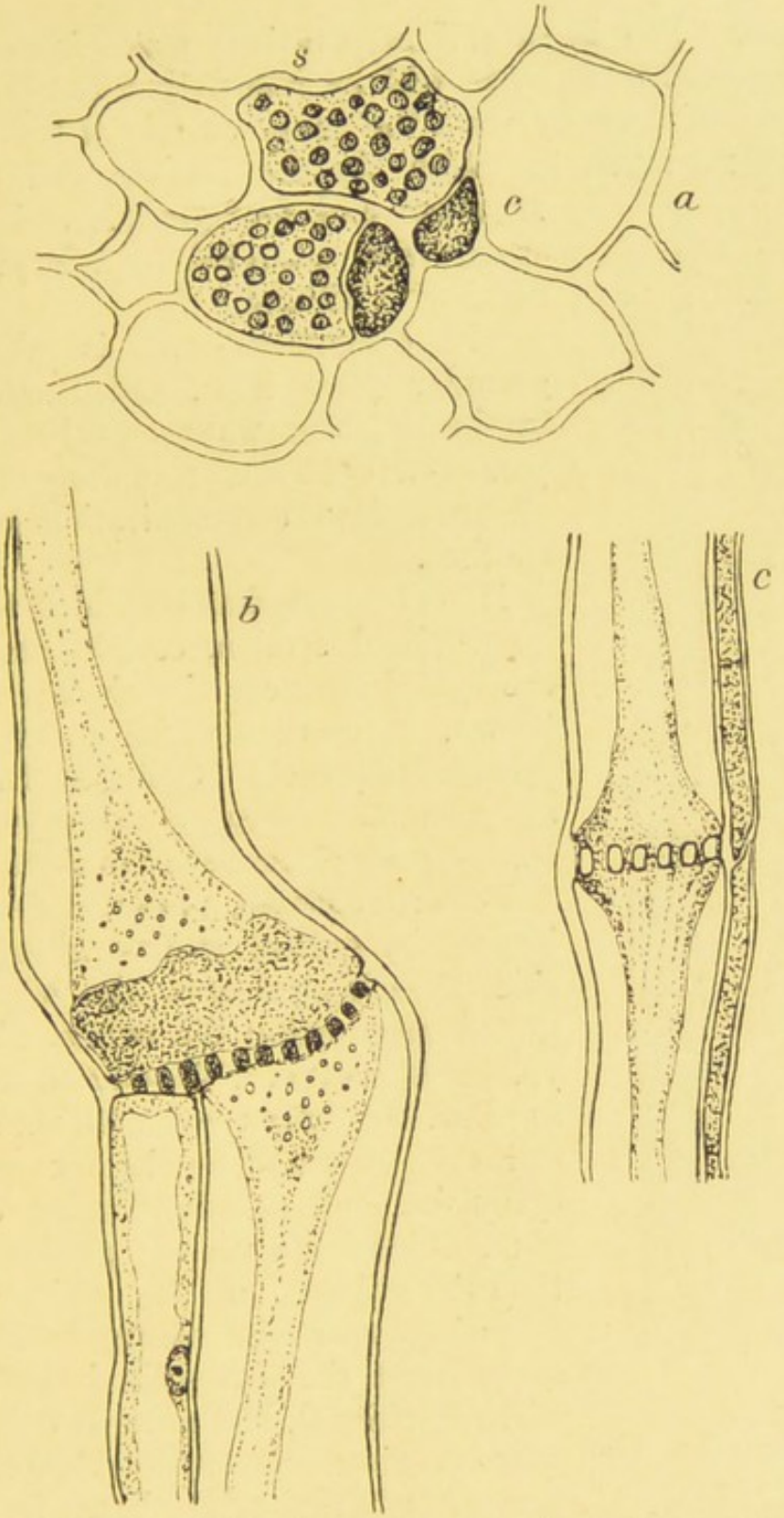

Fig. 40.—*a*, Two sieve-tubes in transverse section, showing sieve-plates, *s*, and companion-cells, *c* (*Cucurbita*). *b*, Portions of two adjacent sieve-tubes seen in longitudinal section. Note the sieve-plate, its perforations being plugged by callose. The granular mass on the upper surface of the sieve-plate is the callus. The cytoplasm is contracted towards the centre of the tubes. *c*, Portions of two sieve-tubes showing a pervious sieve-plate.

examination. But in careful preparations made from material fixed in a special manner, it will be found that the protoplasm of each sieve-tube really lines the inner surface of the wall as a thin **peripheral layer**, in which lie the nucleus and drops of **mucilage** and **food-granules**, the central space being occupied by a large vacuole filled with cell-sap.

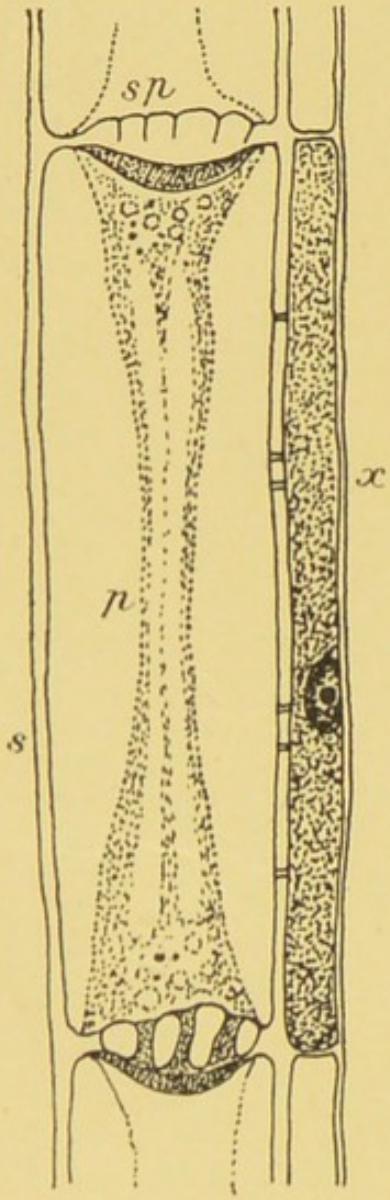

Fig. 41. — A COMPLETE SIEVE-TUBE FROM *Cucurbita* STEM. — *p*, Cytoplasm (contracted); *sp*, sieve-plate; *c*, callus; *x*, companion-cell.

The companion-cell is filled with granular protoplasm, and small "**pits**" in the adjacent walls of tube and companion-cell put the protoplasts of the two elements into communication with one another.

If iodine solution be added to a fresh longitudinal section, certain granules in the cytoplasm near the sieve-plates turn brown, a reaction which points to the presence of proteid. Globules of mucilage are also to be seen in the mass of contracted protoplasm near the sieve-plate.

Towards autumn, a mass of a substance known as **callose** is formed on either side of each sieve-area, the whole completed mass being the **callus**. It stains yellow if treated with solution of *aniline sulphate*, and bright red with *eosin*. The callus is deposited by the agency of the cytoplasm, and functions as an effectual plug, which stops up the perforations in the sieve-plate. In the spring of the following year the callus becomes absorbed, and the sieve-tube becomes once more functional, but after two or three years a given sieve-tube becomes obliterated, others having been formed in the meantime.

Closely connected with the phloem is a tissue which occurs typically in the leaves of some plants, notably the centric leaf of *Pinus*. This tissue is known as **transfusion-tissue**, and its component cells are

characterised by the presence in their walls of small **bordered-pits** (for the structure of bordered-pits see pp. 67 and 68 on

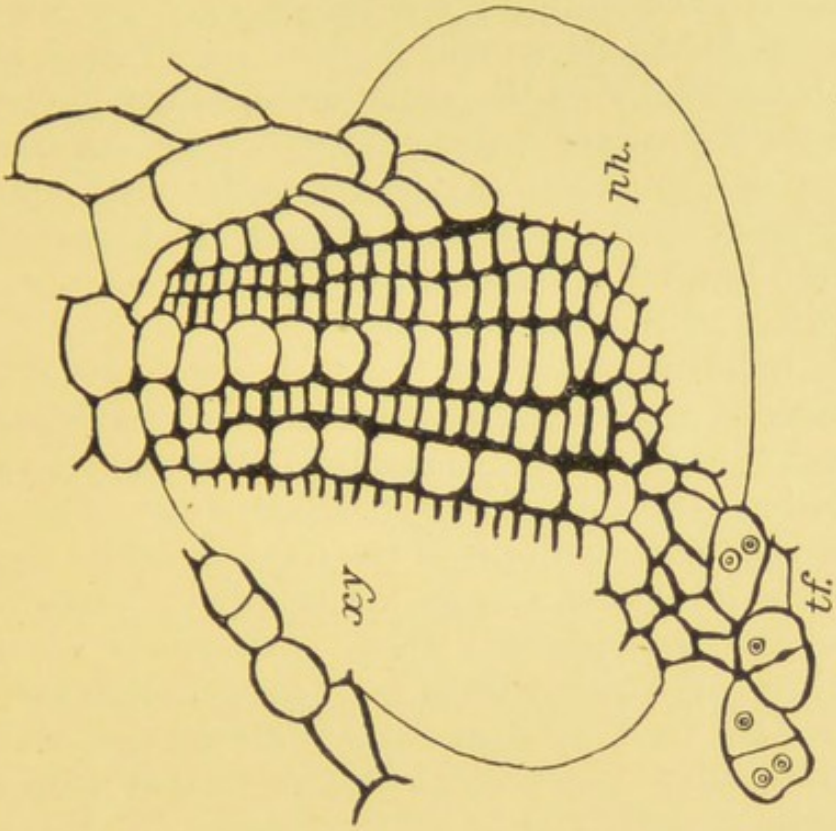

Fig. 41*b*.—Portion of a Transverse Section across a Fibro-vascular Bundle in the Leaf of *Pinus*, to show the manner in which phloem (*ph*) communicates with the transfusion-tissue (*tf*) ; *xy* is the xylem of the bundle.

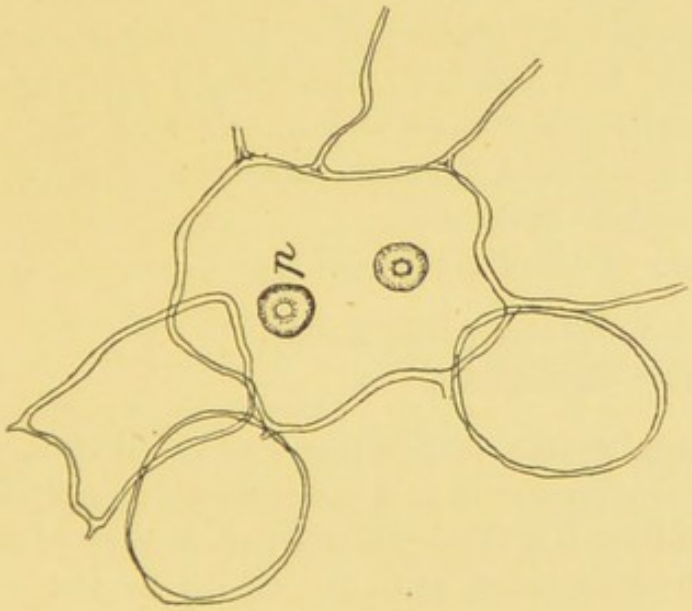

Fig. 41*a*.—A Transfusion-Cell from the Central Cylinder of the Leaf of *Pinus*.—*p*, Small bordered-pits in the wall.

the xylem), and are known as **transfusion-cells** (see Figs. 41*a*, 41*b*). The tissue lies outside the bundles, internal to the endodermis, and its communication with the phloem of each bundle may be

readily traced (see Fig. 41*b*). The function of this tissue is to aid in the downward **translocation** of elaborated food-material, which passes in from the mesophyll through the endodermis into the transfusion-cell, and so into the phloem.*

The sieve-areas in the sieve-tube of *Pinus* are situated, not on the end-wall, but laterally on the **radial walls**, so that this would seem to facilitate the inward diffusion of elaborated sap from the mesophyll into the phloem. In bifacial leaves elaborated sap passes directly from the cells of the palisade layer and spongy parenchyma into thin-walled phloem cells, situated on the under side of the endings of the leaf-bundles.

In ultimate **function** sieve-tubes and their companion-cells act in the **translocation and storing of elaborated food-materials**, and in addition each tube is possibly concerned in the manufacture or further elaboration of certain of these food-materials. The elaborated sap from the mesophyll cells of the leaves finds its way into the phloem of the leaf-traces, and so downwards by means of the perforations in the sieve-plates. These perforations are large, and through them large quantities of sap, food-granules, and cytoplasm can pass at a time. All the way down the stem and root elaborated sap can, after being perhaps further changed in the sieve-tubes and companion-cells, find its way by osmosis into the cortex externally, and the cambium internally; and in the spring the stored nitrogenous and carbohydrate food in the tubes is converted, by means of **enzymes**, into soluble proteids and carbohydrates, which pass out laterally by means of osmosis into the tissues requiring fresh elaborated food for the purposes of growth and general nutrition (see also Chap. x.).

Subsidiary Elements of the Phloem.—These are :—

(*a*) **Phloem-parenchyma.**
(*b*) **Bast-fibres.**

(*a*) The **phloem-parenchyma** is composed of small thin-walled cells lying between the sieve-tubes, and possessing protoplasm and **reserve starch.** Functionally these cells form a sort of supplementary tissue to the sieve-tubes, and are useful in the storage of carbohydrates.

* Transfusion-cells exist also in the endodermis of the roots of *Iris ;* and in *Pinus* leaf the transfusion-cells on the xylem side of the bundles permit of the passage of water from the wood into the mesophyll.

(*b*) The **bast-fibres** are situated outside the phloem proper, and are individually elongated **sclerenchymatous elements,** which form a layer of varying thickness; in the stem of *Pinus* they are oval and compressed when examined in transverse section, and possess minute "**pits**" in their thick walls. Bast-fibres are not formed as such, annually by the cambium, but result from the modification of elements formed in previous years. Functionally they serve as a **protective** and **supporting layer** to the more delicate phloem lying internal to them (see Fig. 53, ph_2).

B. The Xylem.

The elements formed by the cambium in Dicotyledons and Conifers upon its inner aspect—viz., the rudimentary xylem—are at first elongated thin-walled cells (prosenchyma), which, however, soon undergo the following modifications :—

1. A general **thickening** and **chemical change** in the cell-wall, known as **lignification** (deposit of **lignin**).
2. The production of **localised areas of thickening,** the intermediate portions remaining thin (thin wall-areas).
3. The **thin wall-areas** later on often became absorbed in adjacent portions of cell-wall, leading to the formation of actual **perforations** or "**pits.**" At times, however, a thin partition remains unabsorbed, this being usually formed by the **middle lamella,** which is, in reality, an intercellular substance.

During these changes the cell undergoes an **elongation,** but, as a rule, not much increase in its other dimensions. At times the adjacent end-walls of elements may become absorbed, leading to the formation of **vessels** of relatively great length; or the elements may remain single, the end-walls persisting, when they are known as **tracheides.**

The best method of classifying wood-elements is by means of the various thickenings and "pits" occurring on their walls, and in this manner it is possible to distinguish the following varieties :—

(*a*) **Tracheides or vessels with simple "pits" in their walls.**—The pits are at first only thin wall-areas, but subsequently the middle lamella may become absorbed, leading to definite perforations (see Fig. 42, *a*).

(*b*) **Tracheides or vessels with reticulate* thickenings** on their walls, the reticulate markings consisting of localised thickened areas, the intermediate parts remaining thin (see Fig. 44, *c*).

(*c*) Elements possessing both the modifications (*a*) and (*b*)—viz., **reticulo-pitted vessels or tracheides** (see Fig. 42, *b*); in this case the **pits** occur in the areas enclosed by the reticulations, and are often of the "bordered" variety (see next heading, *d*).

(*d*) **Tracheides or vessels possessing "bordered-pits."**—These "pits" occur in two main varieties—viz., the **simple bordered-pit,**

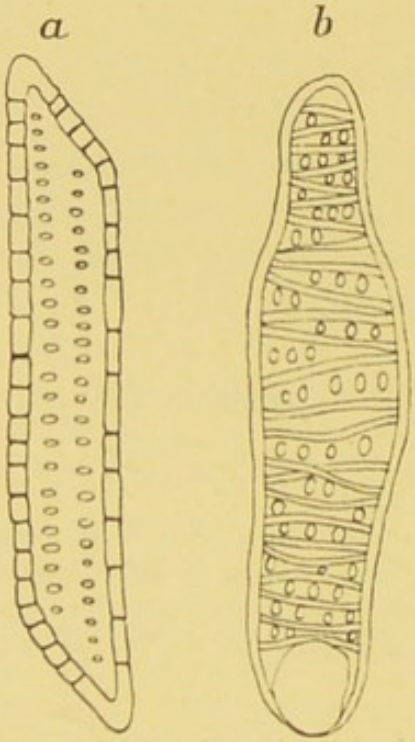

Fig. 42.—*a*, A Pitted Tracheide from Xylem of *Quercus*. *b*, A Pitted and Reticulate Tracheide (*Quercus*).

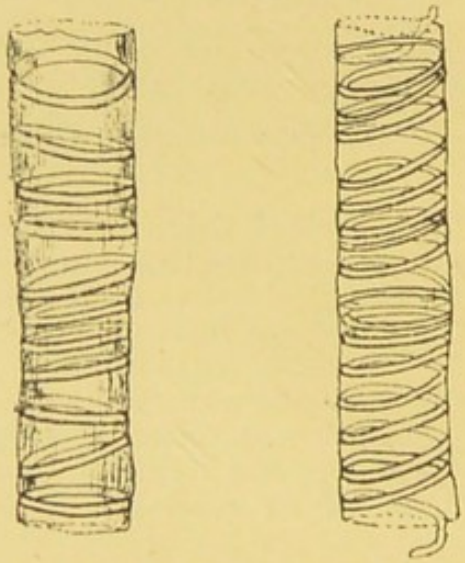

Fig. 43.—Portions of Annular and Spiral Vessels from the Protoxylem of Dicotyledonous Stems.

where an upraised thickened margin occurs round a simple circular or oval pit, and the "bordered-pit," which is met with in the tracheides of such a plant as *Pinus*—almost to the exclusion of other elements. These pits occur only on the **radial walls** of tracheides, and have the following structure:—

i. In surface view each "pit" is circular in contour, the diameter occupying almost the entire breadth of a tracheide. The central part, or

* The scalariform vessel met with in the xylem of Ferns is one form of reticulate element (see Fig. 44, *c*).

lumen of the pit, is surrounded by a raised **thickened border** (see Figs. 47 and 48).

ii. In **tangential sections** of the stem of *Pinus* bordered-pits may be studied in section. It is found that the raised borders coincide in position on corresponding parts of the cell-wall in two adjacent tracheides (see Fig. 48), and that these thickened parts enclose between them a space, the **pit - chamber,** into which the lumina of the two halves lead. Stretching across this chamber is the **middle lamella,** in the centre of which occurs a thickening, fusiform in section, and known as the **torus.** By this arrangement the lumina of the "pit" may

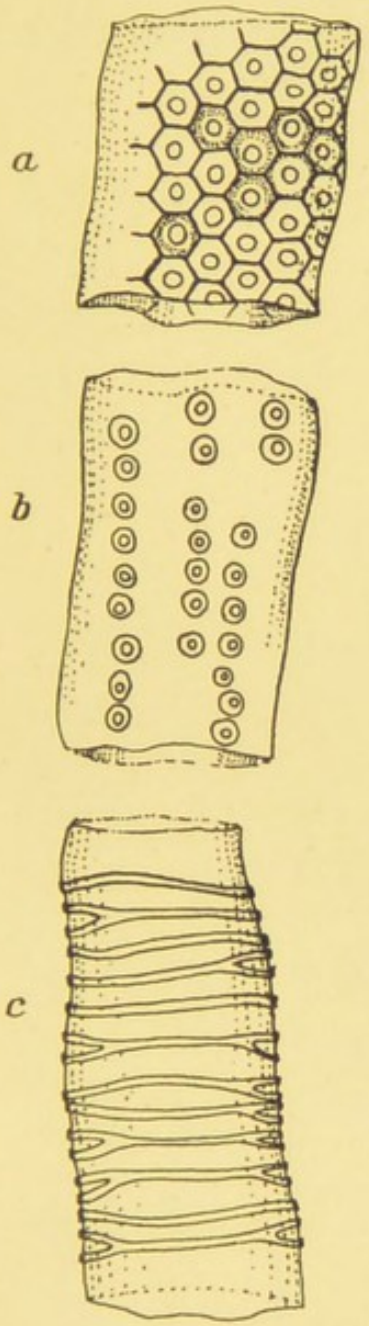

Fig. 44.—*a*, Portion of a Reticulo-pitted Vessel (Bog-oak).

b, Portion of a Vessel with Small Bordered Pits, different in structure to those of *Pinus* (Bog-oak).

c, Portion of a Scalariform Vessel (*Pteris*).

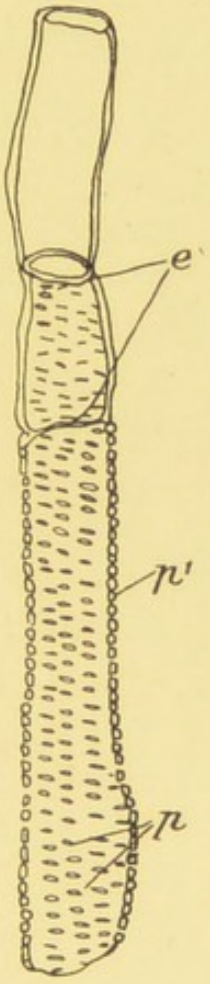

Fig. 45.—A Pitted Vessel (recently-formed).—*e*, End-walls which become absorbed; *p*, pits in surface view; p^1, pits in section.

be closed at times, owing to the forcing up of the torus against either of them.

The development of bordered-pits may be observed in longitudinal sections of the young stem. The tracheides which have been just formed by the cambium show thin circular wall-areas, round which the first indication of the border soon appears (see Fig. 50).

(*e*) **Tracheides or vessels with annular or spiral thickenings** are to be seen in the **protoxylem** of Dicotyledons and Coniferæ, and also in the **xylem** of fibro-vascular bundles of Monocotyledons and Ferns (see Fig. 43). The endings of the leaf-bundles also show these elements.

(*f*) **Wood-fibres** are also seen at times,

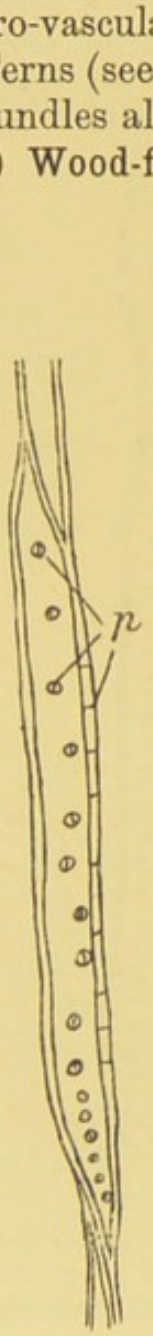

Fig. 46.—A Wood Fibre. —*p*, Small pits; these are slit-like, with a thickened border.

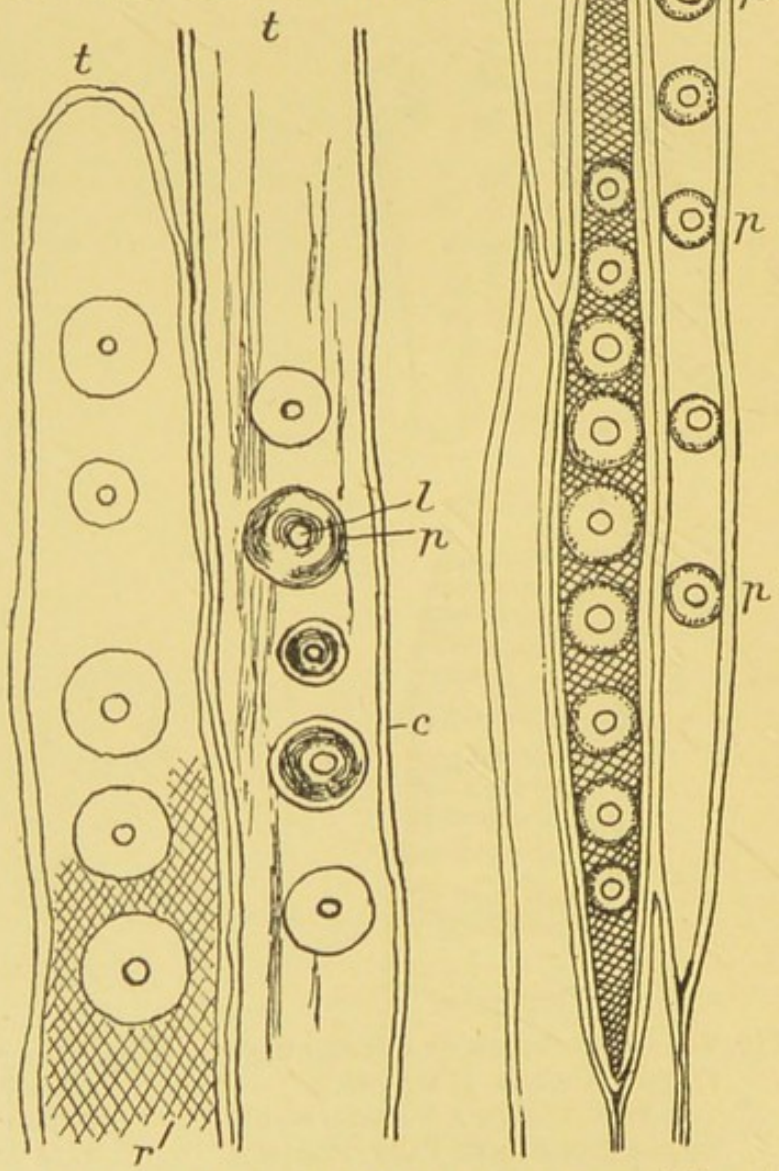

Fig. 47.—Details of Xylem Elements (*Pinus*). —Tracheides with bordered-pits (*p*) on the radial walls. *t t*, tracheides; *l*, lumen of pit; *c*, tangential wall; *r*, reticulations.

although more rarely than the other above-mentioned elements. They are formed by the junction end to end of several tracheides, and they have thick walls in which occur slit-like pits surrounded by a narrow thickened border (see Fig. 46).

(*g*) Lying amongst the other elements a few cells occur in some stems, which are termed **wood-parenchyma**. Each cell is thick-walled, with simple pits in the walls, and internally are to

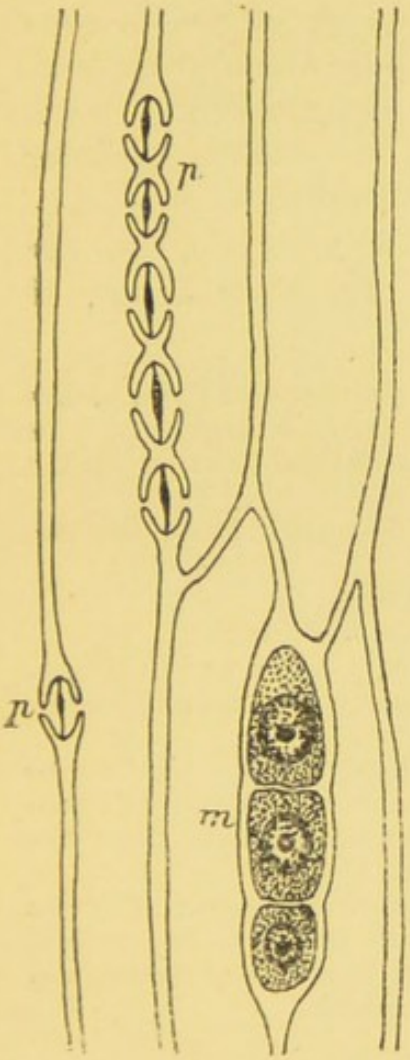

Fig. 48. — Bordered-pits (*p*) in Tangential Section.—The middle lamella is seen in section, and the torus appears as a central thickening on this; *m*, medullary ray.

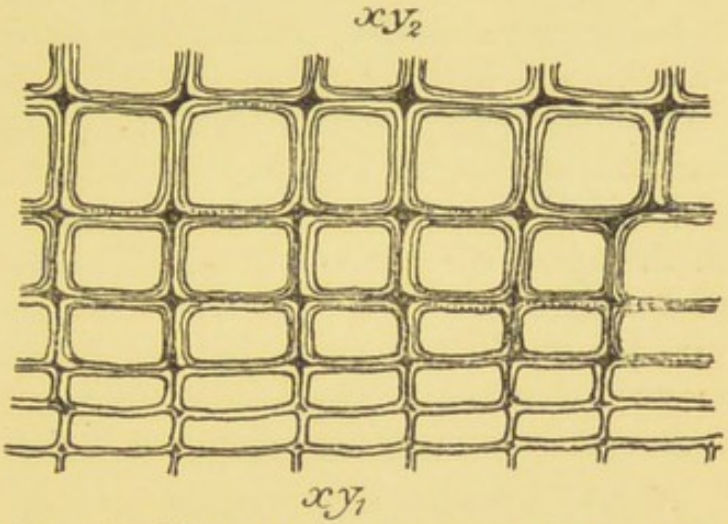

Fig. 49.—Tracheides seen in Transverse Section.—xy_1, Young tracheides; xy_2, older elements.

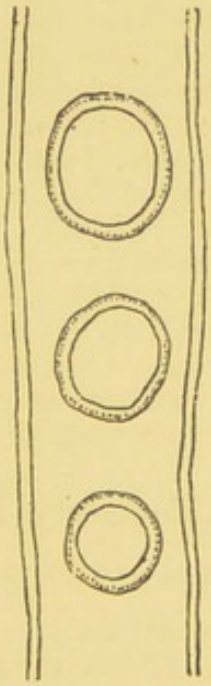

Fig. 50.—Portion of a Tracheide showing Bordered-pits in course of Formation (*Pinus*).

be seen protoplasmic contents and **starch**. Wood-parenchyma is, in fact, a tissue set apart for the supplementary storing of carbohydrates, and is analogous to the phloem-parenchyma.

All these elements of the xylem, with the exception of the wood-parenchyma, are functional in the **upward conduction of raw unelaborated sap** from the root to the leaves, the moving forces being the **transpiration current** and **root-pressure** (see Chap. x.). The tracheides are especially useful in this process, it being probable that the sap passes partly by means of the cell-cavities and partly through the cell-walls. The various forms of "pits" occurring in the walls may possibly be of use in sap-conduction, but, as a matter of fact, these pits function more as a means of exit for the protoplasm after it has finished its work in the xylem-elements. Those elements of the central cylinder of Dicotyledons and Conifers which now remain to be studied—viz., the medullary rays, the endodermis, the pericycle, and the medulla—are not conducting tissues, but are, nevertheless, of importance from several points of view.

Note.—To facilitate the practical examination of the xylem those plants in which the various elements may be studied will now be mentioned. In all cases both longitudinal and transverse sections should be made of the stems or roots :—

Pitted and reticulate vessels and tracheides, Bog-oak, Hazel, *Ricinus*, and Lime (stems of all these).

Tracheides with bordered-pits : *Pinus* (stem or root).

Scalariform (reticulate) vessels : *Pteris* and other Filicineæ.

Spiral and annular elements : protoxylem of Dicotyledons and Coniferæ, and xylem of Monocotyledons and Ferns. Also the bundles in many leaves.

Wood-parenchyma : Hazel (stem).

In showing up wood-elements either solution of *aniline sulphate* or *iodine solution* may be used. The latter reagent also shows up the endodermis (starch-sheath) wood-parenchyma and medullary rays, since the starch in the cells of these tissues turns dark blue.

In the examination of individual separate elements wood may be macerated in *Schulze's macerating mixture*,* which dissolves the middle lamellæ, and the resulting mass teased out, washed in distilled water, and the separate elements stained with *methyl-green* solution.

C. The Medullary Rays (see Figs. 52, 53, and 54).

Medullary rays are of two kinds, viz. :—

(*a*) Primary or **ground-tissue rays.**
(*b*) Secondary or **true medullary rays.**

* Dilute nitric acid (20 per cent.), to which 2 to 3 per cent. of a saturated solution of chlorate of potash has been added.

[*To face p.* 68.

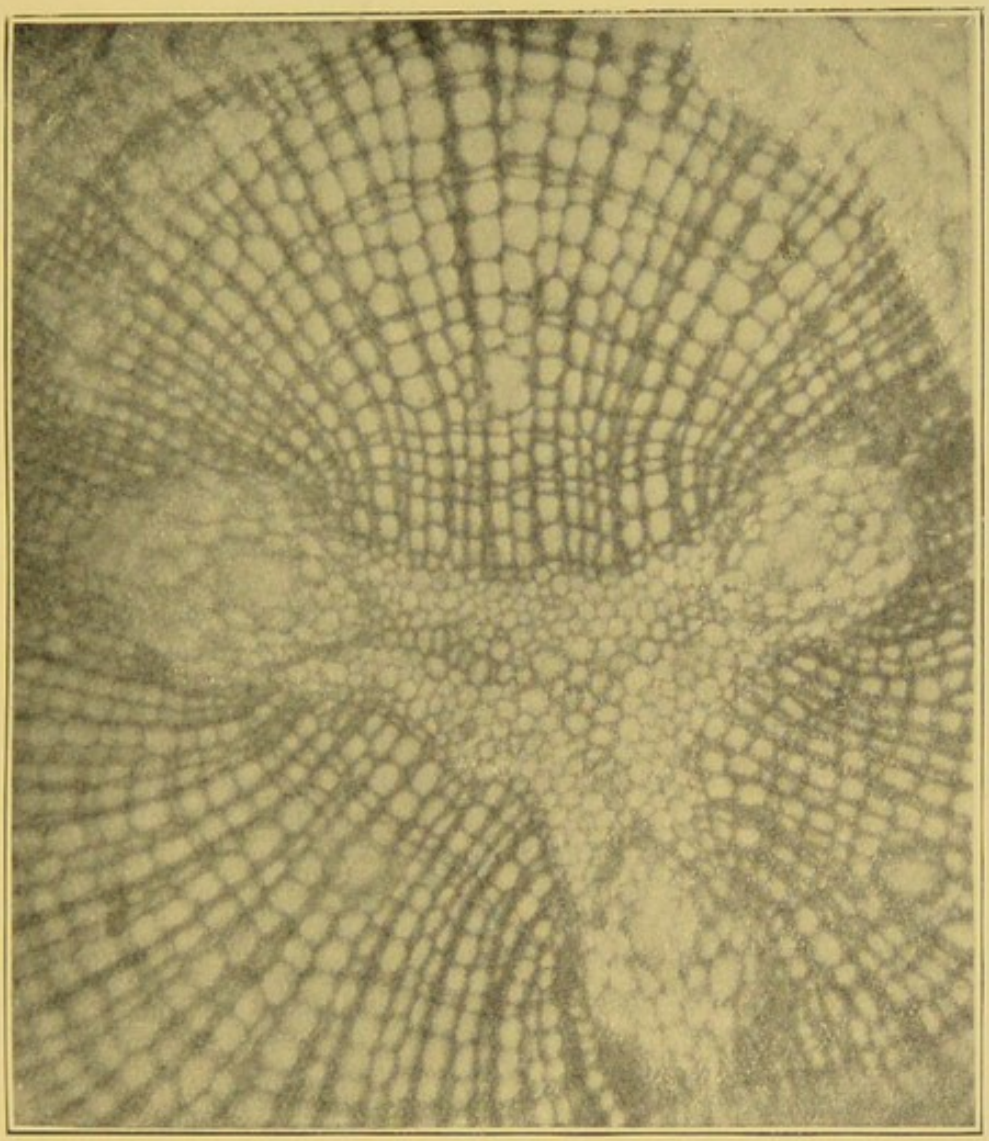

Fig. 51.—A Photomicrograph of Portion of a Transverse Section across a Root of *Pinus* to show the tracheides of the xylem in section.—In the centre is seen the tri-radiate protoxylem, and enclosed between the Y-shaped arms of this three large resin-canals.

(*a*) **Ground-tissue rays** are those portions of the fundamental or ground-tissue in the stem or root of Dicotyledons and Coniferæ which exist between the primary vascular bundles before the interfascicular cambium has arisen. When the secondary bundles are formed by the activity of this cambium the cells of these columns of tissue become, at first, compressed, and, finally, almost

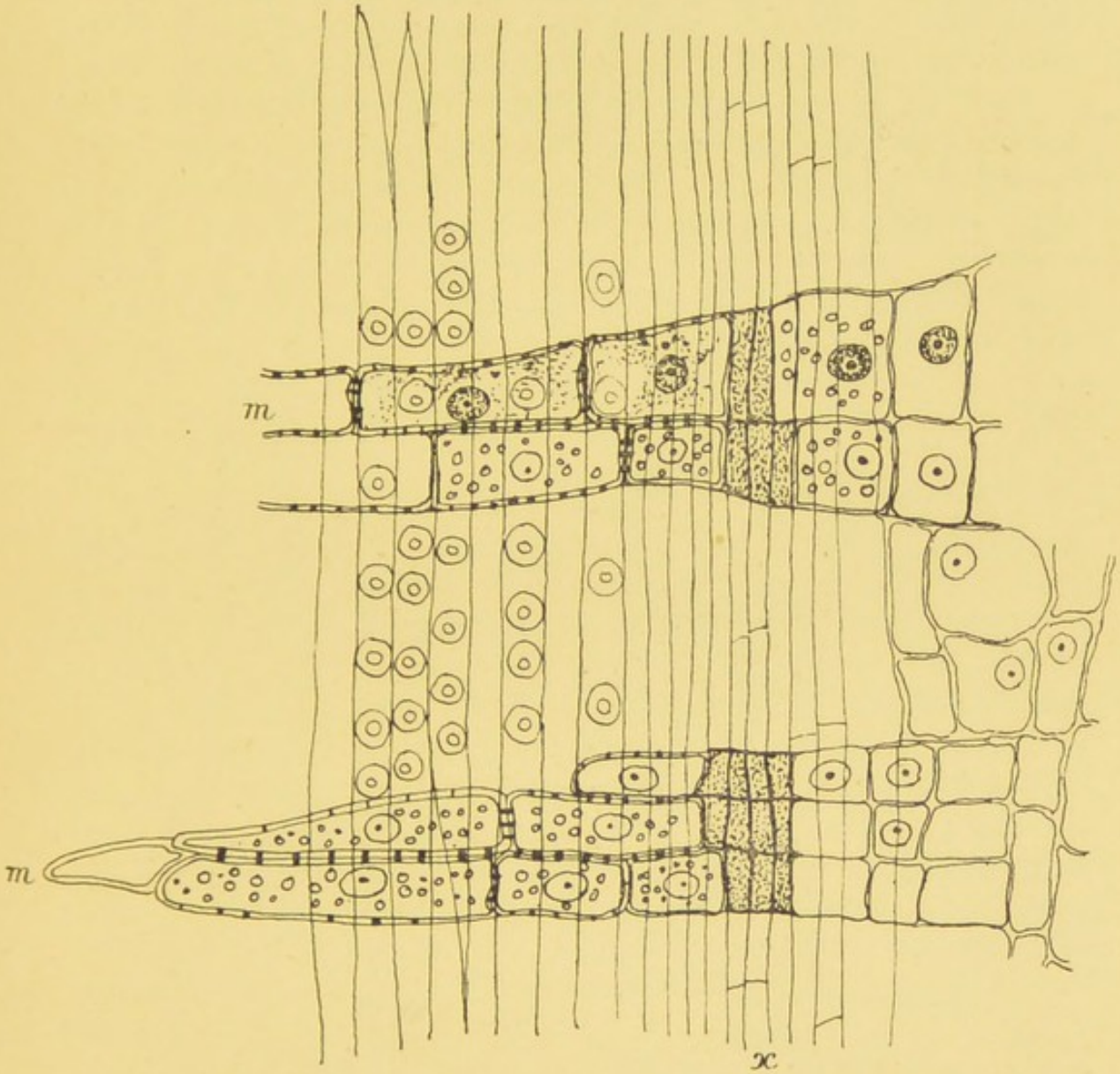

Fig. 52.—A Longitudinal Radial Section of the Stem of *Pinus* to show the true medullary rays.—*m*, *m*, Medullary rays arising from cells of the cambium (*x*, dotted in fig.).

obliterated. The component cells of the rays are similar in structure to those of the cortex or ground-tissue, and the centrally-situated mass of fundamental tissue, which is at first

connected to the cortex by means of the rays, becomes, later on, the pith or medulla.

(*b*) **True or secondary medullary rays** are, on the other hand, formed from **special cells of the cambium**, and stretch out from this both ways into the xylem and phloem. At times a ray may pass right through both, so as to connect pith and cortex; but, as a rule, the rays end in the xylem and phloem (see Fig. 52).

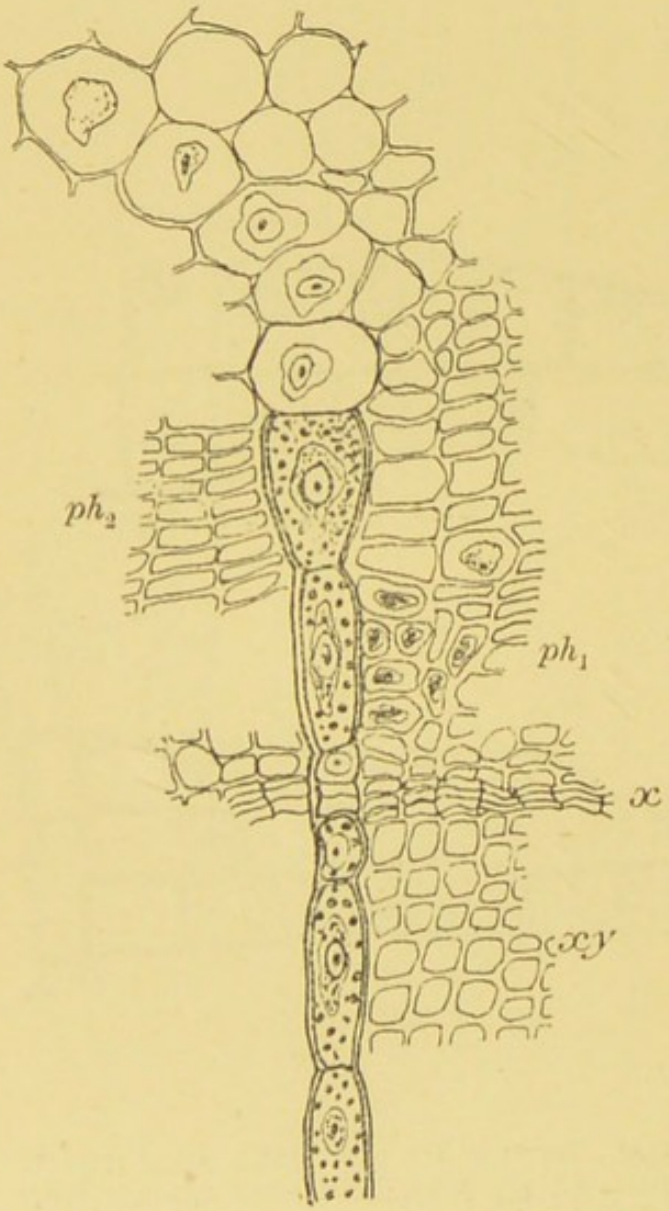

Fig. 53.—Portion of a Transverse Section of the Stem of *Pinus* to show the course of a medullary ray through the xylem and phloem and into the cortex. — x, Cambium; xy, xylem; ph_1, phloem; ph_2, bast-fibres.

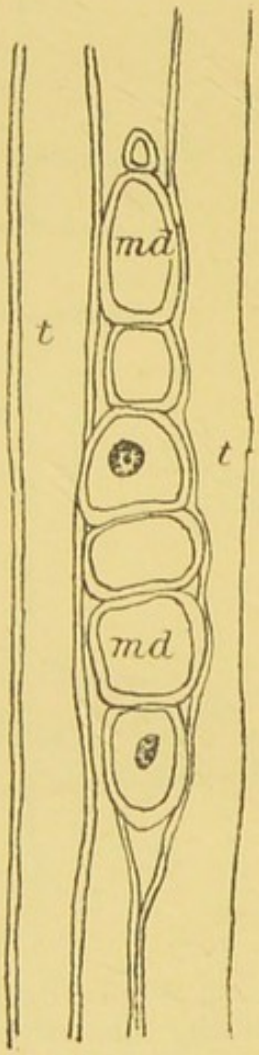

Fig. 54.—Medullary Ray seen in a Tangential Longitudinal Section of a Stem of *Pinus*.—t, Tracheides; md, medullary ray cells.

In transverse sections of such a stem as *Pinus* (first or second year's growth) these rays may be seen as single lines of oval elements which show up well by treating the section with iodine or Schulze's solutions, the reaction being due to the darkening of the **starch-granules** in the component cells of the ray by the reagent (see Fig. 53).

To examine the origin and relations of the true medullary rays it is necessary to make longitudinal sections in directions parallel to, and at right angles to, radii of the stem—viz., *radial longitudinal* and *tangential longitudinal* sections.

In *radial* sections, which include the cambium, each ray is seen to originate from certain cells of the cambial layer. Usually more than one cambial cell is active, and often as many as five or six may be the forerunners of the same number of radial lines of ray-cells. As observed in such a section, the shape of each component cell of the ray is rectangular, and numerous **simple pits** may be detected in the rather thick cell-walls. The contents of each cell consist of protoplasm and **starch-granules** (see Fig. 52).

In *tangential* sections of the xylem, each ray appears as a spindle-shaped perpendicular line of cells, ranged one above the other (see Fig. 54). The number of cells in the tier depends, of course, upon the relative position of the plane of section.

In function the true medullary rays act as **reservoirs of carbohydrate food-material**, being supplemented to a certain extent by the wood-parenchyma. In the early spring, when the sap is beginning its upward movement in the xylem, the starch in the ray-cells is converted by the agency of the enzyme **diastase** into **dextrins** and **sugar**, of great value to the cambium and young xylem and phloem elements, before the sap has started to be elaborated in the leaves in quantity sufficient for the needs of the plant.

Note.—The true medullary rays are best studied in the stems of *Pinus*, or the Lime. In the latter, the rays are, in transverse section, seen to be very broad towards the cortical ends and narrow towards the pith, the increased breadth at the outer extremity being due to the occurrence of radial, as well as tangential, divisions in the component-cells of the ray. Sections of stems should be treated with Schulze's solution or iodine to show up the rays.

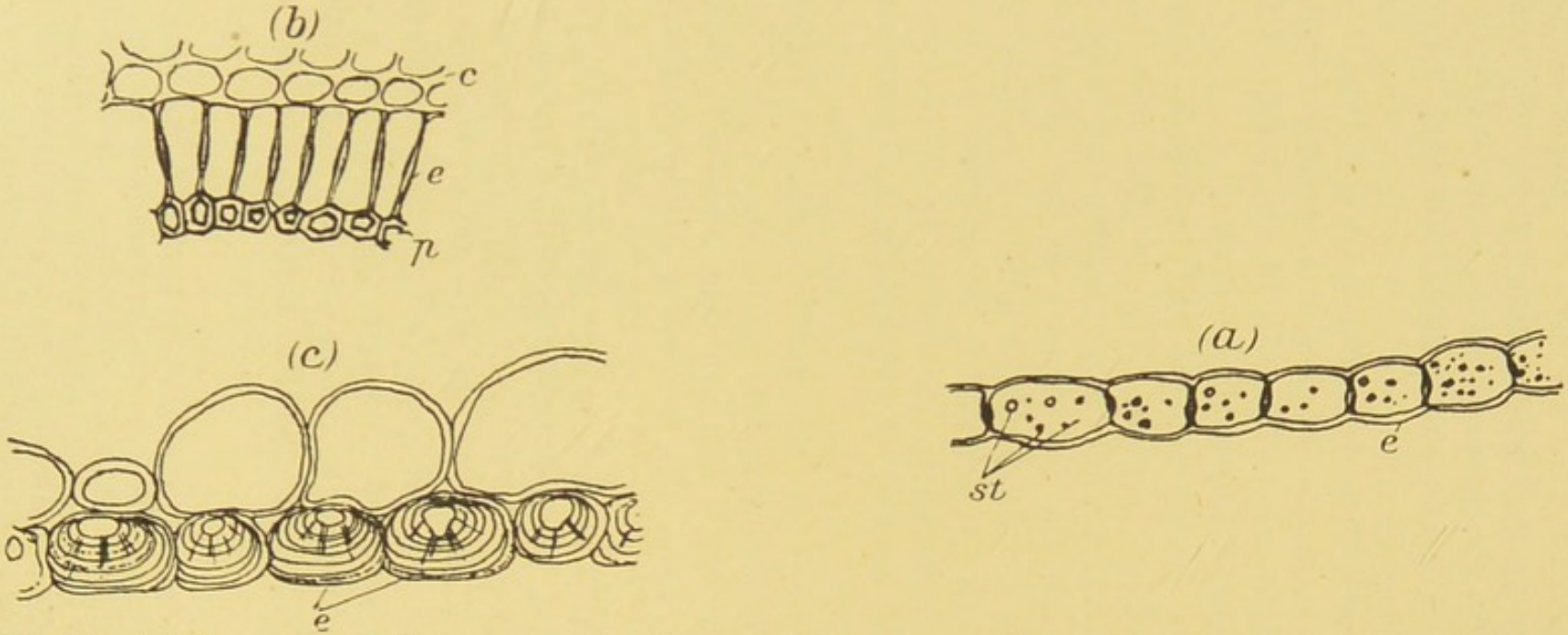

Fig. 55.—(*a*) Endodermis Cells from the Stem of *Hippuris* (note the spindle-shaped thickenings on the radial walls).—*st*, Starch granules.

(*b*) Portion of the Endodermis of the Root of *Iris*.—*e*, Endodermis cell; *c*, cortical cells; *p*, pericyclic fibres (sclerenchyma).

(*c*) Endodermis of an Aerial Root (*Orchis*).—*e*, Thick-walled cells showing lamellation and radiating striæ.

Subsidiary tissues occurring in the Central Cylinder of Dicotyledonous and Coniferous Stems and Roots.

These are :—

i. The **endodermis** or **starch-sheath** (occurring in both stem and root).
ii. The **pericycle** (roots only). This tissue is meristematic.
iii. The **medulla** or **pith,** with its **medullary sheath.**

i. The **endodermis, bundle-sheath,** or **starch-sheath** is a ring of cells, only one cell thick, which marks the limits of the central cylinder in a stem or root of more than one year's growth (Dicotyledons, Coniferæ).* Its component cells at times contain

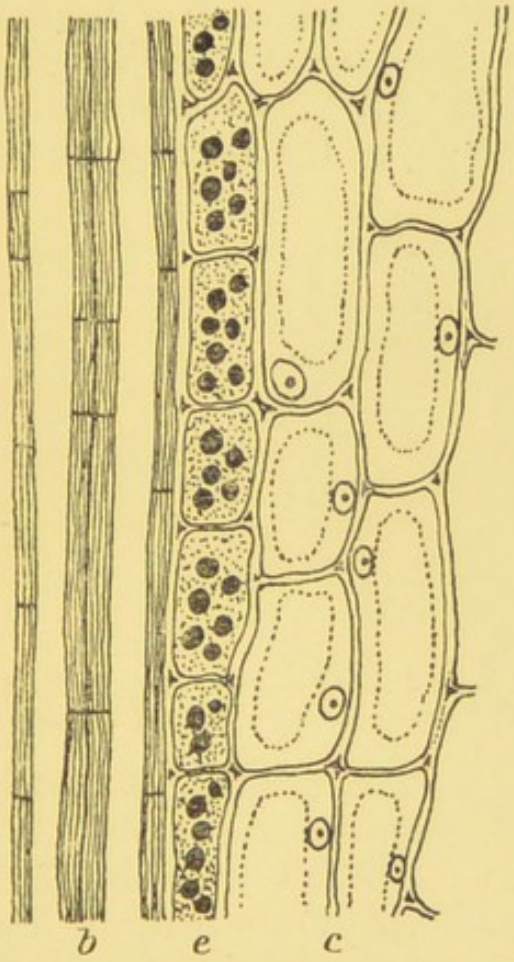

Fig. 56.—Endodermis Cells in a Longitudinal Section of the young Stem of *Corylus avellana* (Hazel).—*e*, Endodermal cells with starch-granules (stained with iodine) ; *b*, bast-fibres ; *c*, cortical cells.

starch-granules, and in many cases a distinctive feature is the presence of peculiar fusiform thickenings on their **radial** walls. Functionally this layer forms a **starch reservoir,** but in many

* The separate bundles or schizosteles in the rhizomes of certain Pteridophyta (*Pteris*) are also surrounded by an endodermis.

stems and roots may be protective in nature, since the outer walls are often very thick (see Figs. 55, 56). The endodermal cells do not always contain starch, as the latter is being constantly used up by the cambium, &c.

ii. The **pericycle** is a **meristematic zone** of cells occurring in the root, just internal to the endodermis; it may be several cells in thickness, and from it are produced, (*a*) the secondary or lateral roots, (*b*) a ring of cork, and (*c*) the pericyclic fibres; the latter being elongated thick-walled sclerenchymatous fibres, not unlike bast-fibres, and often taking the place of these. The pericycle may consist of one layer of cells only, and may even be absent altogether in some roots, and at times it may arise from the outermost cells of the central cylinder.

iii. The **medulla** or **pith** is formed in stems and roots of more than one year's growth by the remains of the central **ground-**

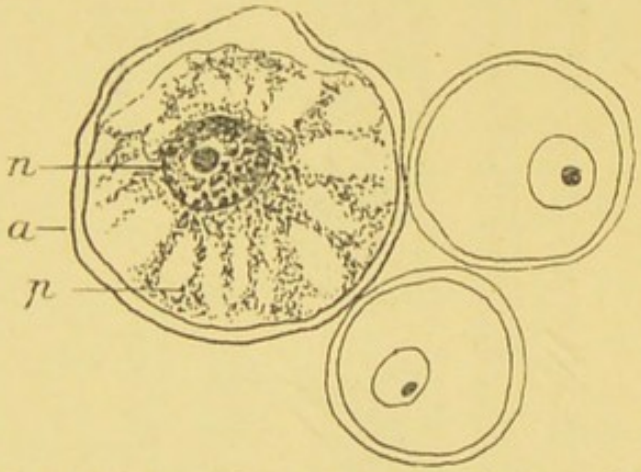

Fig. 57.—Young Cells of the Rudimentary Pith of *Lupulus humulus*.—*a*, Cell-wall; *p*, cytoplasm; *n*, nucleus.

tissue of the younger stem. Near the apex of the shoot the cells of the centrally situated portion of the ground-tissue are young undifferentiated elements possessing protoplasmic contents (see Fig. 57). Older cells of the medulla are, except in some succulent herbaceous stems, devoid of protoplasm, and contain only air; and their walls are at times very thick, and perforated by numerous simple **pits** (see Figs. 58, 59). A **medullary sheath** formed of somewhat rectangular thick-walled elements, in the walls of which either simple or small bordered-pits are sometimes seen, may occasionally be present. This so-called sheath is only a slightly modified layer of the outermost cells of the medulla.

The **function** of the pith is to form a highly elastic tissue which reduces the weight of the stem, and acts as a sort of "cushion" to the central cylinder. At times, however, the pith-

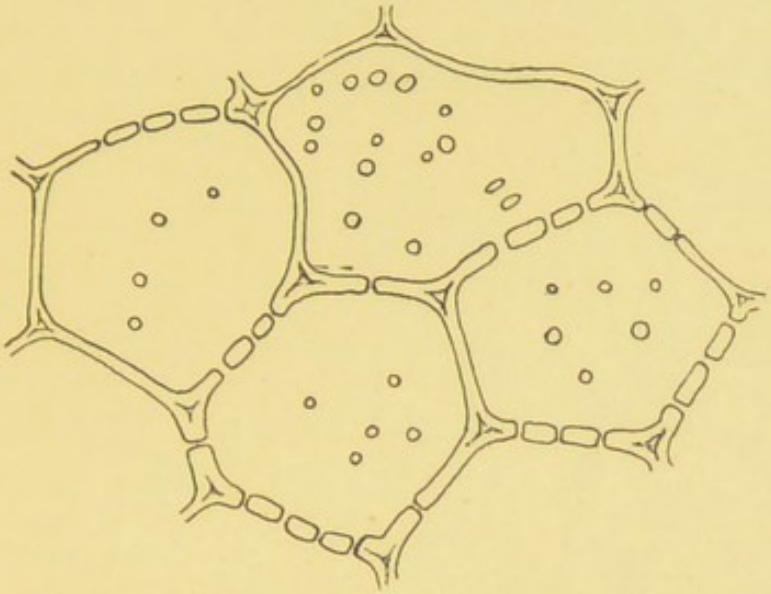

Fig. 58.—Older Cells of the Pith of *Corylus avellana*. Note the simple "pit" both in surface view and in section.

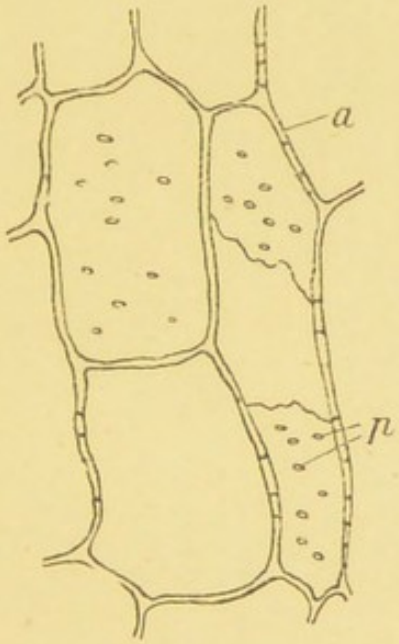

Fig. 59.—Pith-elements from the Stem of *Vinca major*.—*a*, Cell-wall; *p*, simple pits.

cells break down, leaving the centre of the stem hollow (*Bambusa*), except at the "nodes." The pith is in no sense of the term a conducting tissue.

APPENDIX TO CHAPTER V.

Origin of the first Wood-Elements of the Procambial Strands.

The origin of the **first wood-elements** may be studied in longitudinal sections of the apex of a young shoot (*Pinus*). Here they take the form of fusiform cells, characterised by the presence of large oval thin wall-

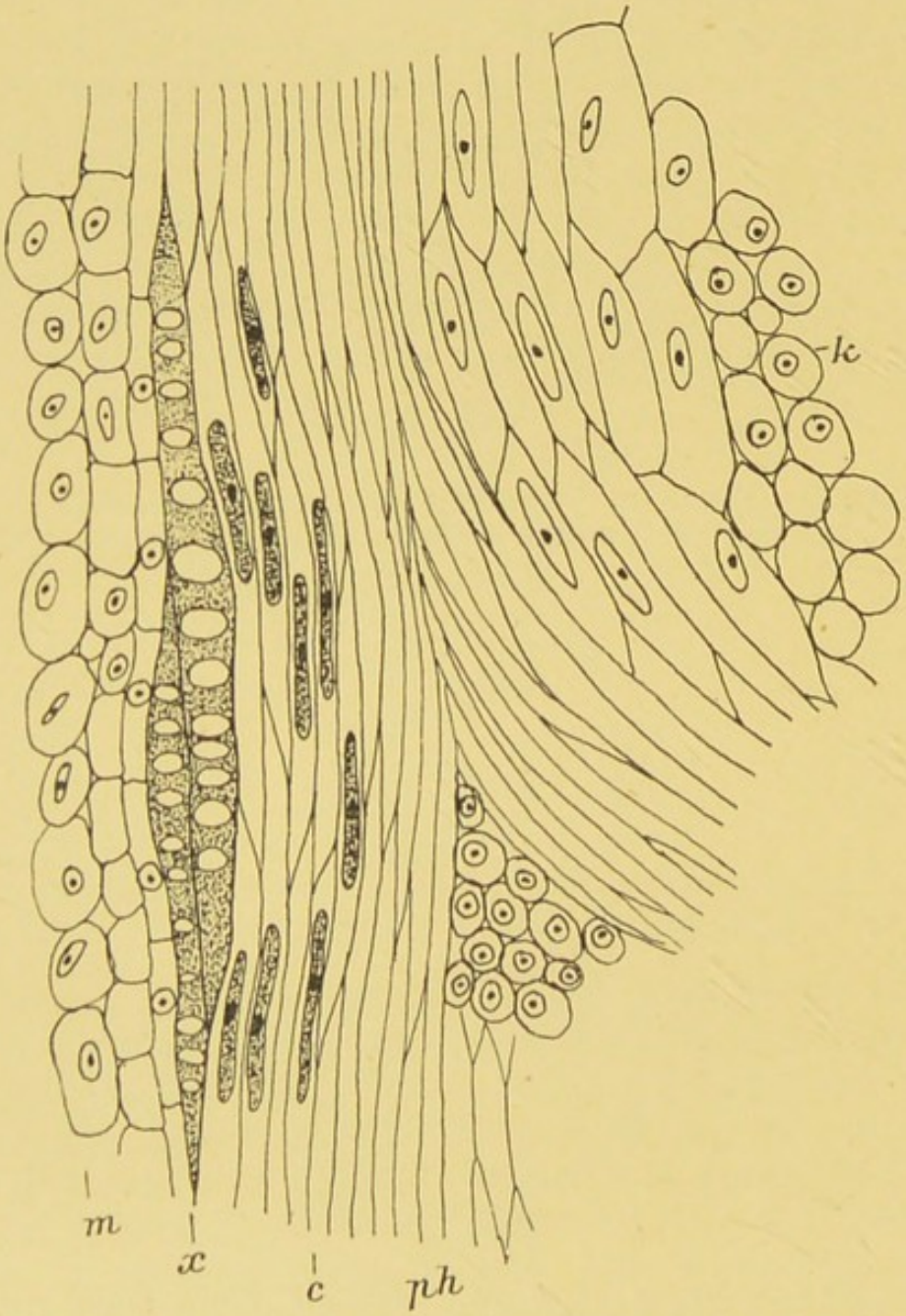

Fig. 60.—Portion of a Longitudinal Section near the Apex of a Young Shoot of *Pinus*, to show the origin of the first wood-elements.—*c*, Meristematic cells which soon undergo modification to produce (*x*) the young wood-cells (note the oval thin wall-area, so-called "pits"); *ph*, rudimentary phloem elements (protophloem); *m*, ground-tissue; *k*, cortex (periblem).

areas separated by bars of thickened wall; these thickenings become, further down, the **annular** and **spiral** bands of the elements of the protoxylem (see Fig. 60). External to these fusiform cells are to be seen somewhat elongated cells filled with protoplasm and with long spindle-shaped nuclei. These cells form the rudimentary meristem and phloem elements, which, further down the shoot, are differentiated into young cambium and protophloem.

In this connection it is interesting to note that **spiral vessels** occur in such plants as the Mosses and Liverworts. In the simple leaf of *Funaria*

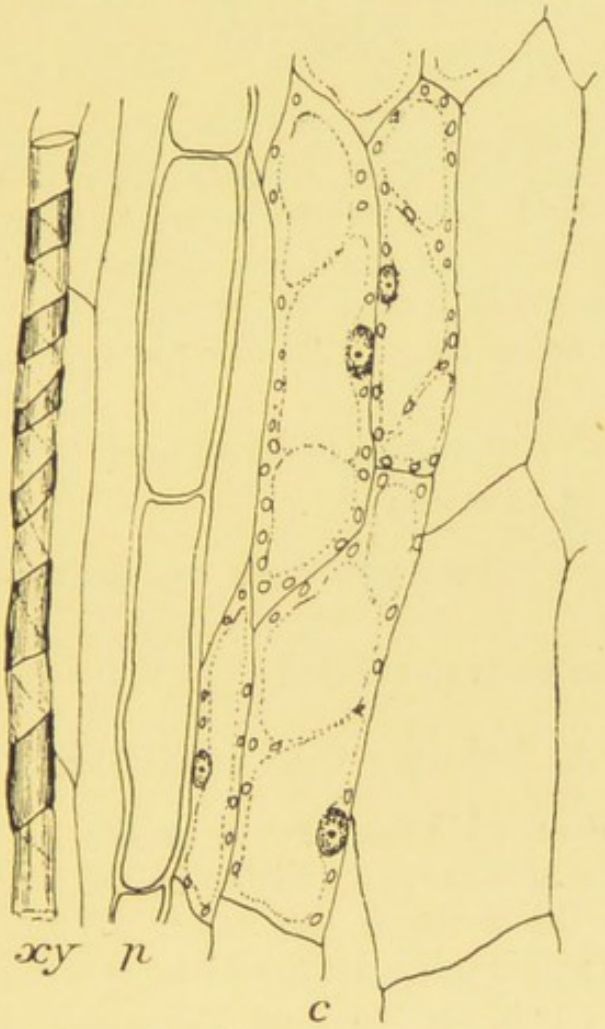

Fig. 61.—Portion of a Moss-leaf, showing (in optical section) indications of a simple vascular system.—*xy*, Spiral vessel; *p*, protective cells just outside the vessels; *c*, cells of the green assimilating tissue of the leaf (mesophyll).

a few elements having the characteristics of the spiral vessels, with rather broad thickening spirals, are to be seen towards the central axis of the leaf (see Fig. 61). These are surrounded by a few elements of a thick-walled nature, and outside these latter comes the green assimilating tissue of the leaf. Nevertheless the Bryophyta are not included amongst the vascular Cryptogams.

CHAPTER VI.

ISOLATED TISSUES OR CELLS HAVING A SPECIFIC FUNCTION.

THE tissues and cells which will now be described are, so to speak, only isolated in so far as they have special functions to perform. It should, however, be clearly understood that their protoplasmic contents communicate with those of the cells of surrounding tissues, and that no living cell in a plant can be looked upon as being completely isolated from the other cells of the community.

Under the above heading will be studied :—

(*a*) **Secretory cells** of oil-glands.
(*b*) **Resin-canals.**
(*c*) Cells in which **mineral matters** may separate out under certain conditions.
(*d*) **Idioblasts.**
(*e*) **Laticiferous cells** and vessels.

A. Secretory Cells of Oil-Glands.

Oil-glands are of wide occurrence in the higher plants, and may be found in almost any position in the stems, leaves, or in connection with the parts of the flower. The essential cells of any gland are the **secretory cells**, which, as a rule, line a **central cavity** as a layer one or two cells thick, into which cavity a special oily secretion is poured, or freed by the breaking down of the secretory cells.

One type of such a gland occurs in the outer layers of the cortex of fruits belonging to the genus *Citrus* (*Citrus aurantii*). If a thin section be taken of the cortex in a direction perpendicular to the surface, the following structure may be made out, using a low power of the microscope :—

i. Externally, the **epidermis** of the fruit.
ii. Internally, cells of the **cortex** (pericarp).
iii. The **oil-glands** lying quite near the surface.

Each **gland** is made up of the following parts (see Fig. 62) :—

(α) An external layer of rather thick-walled cells, arranged concentrically.

(β) An internal layer of thin-walled cells full of granular contents. This is the so-called **endothelial layer.**

(γ) A **central cavity,** in which may be seen globules of **oil** and a small quantity of cell-debris.

The cells of the endothelial secretory layer break down and disorganise, thus setting free the oily secretion. Mixed with this oil is a certain amount of cell-sap, which confers considerable

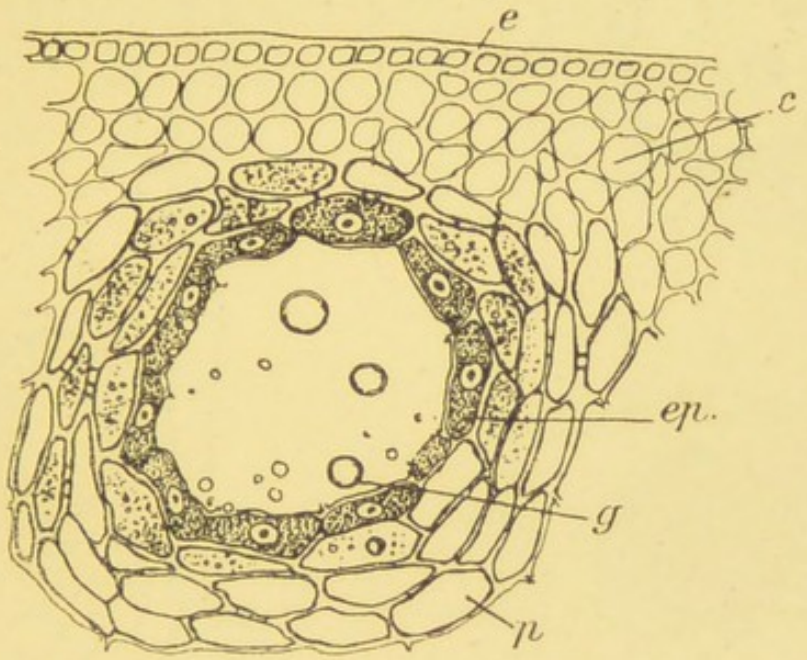

Fig. 62.—A Section across an Oil-gland in the Outer Cortical Tissue (pericarp) of *Citrus Aurantii*.—*e*, Epidermis; *c*, cortex; *ep*, endothelial secreting layer; *g*, oil-globules lying in the central cavity; *p*, thick-walled cells just outside the gland.

turgidity upon the gland. At times the gland may burst through the cortex and epidermis, setting free the secretion on the external surface.

B. Resin-canals.

These structures occur typically in the cortex and xylem of stem and root of *Pinus*, and also in the leaves, where they are surrounded by the cells of the spongy parenchyma.

In a transverse section of the stem or leaf each **resin-canal** is seen to possess the following parts (see Figs. 63, 64, 65, 65*a*) :—

i. An outer layer of thick-walled elements one or two deep. This layer forms the **guard-ring** of the canal.

ii. An internal layer of very thin-walled cells **(endothelial layer)** which are full of a granular protoplasm.

iii. A **central cavity,** the section across the "**duct,**" in which may be seen globules of liquid **resinous material.** This is set free into the duct by the breaking down of the endothelial cells.

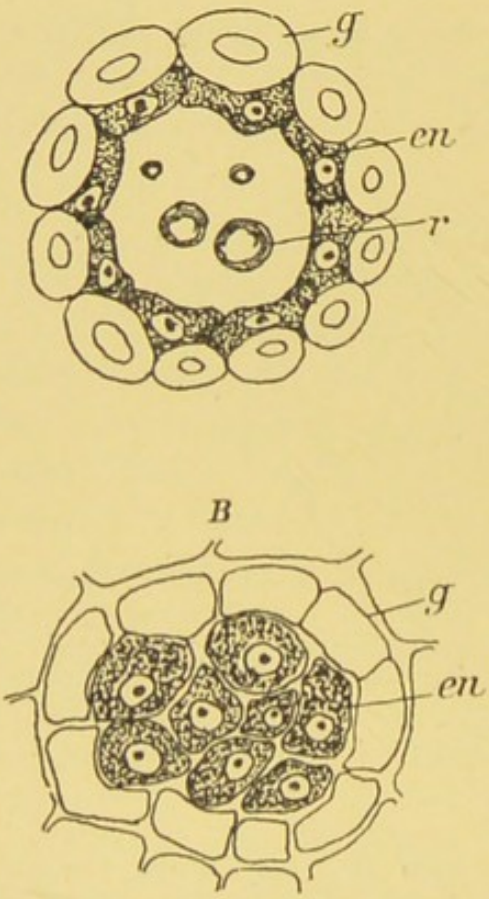

Fig. 63.—A. A Fully-formed Resin-canal in Transverse Section.—*en*, Endothelial layer; *g*, protective fibres; *r*, resin-globules.

B. A Young Resin-canal, showing an internal mass of granular secretory cells (*en*), with as yet no central cavity or duct.—*g*, Protective-cells.

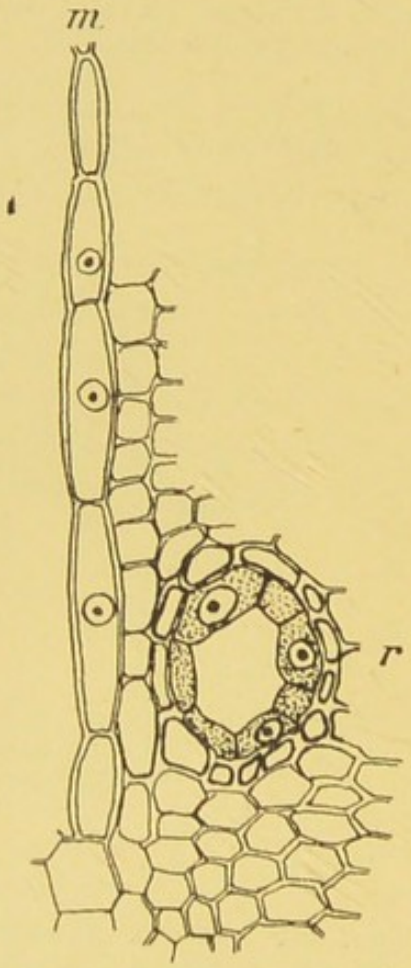

Fig. 64.—A Resin-canal (*r*) in the Xylem of *Pinus*.—*m*, Medullary ray.

In longitudinal section (see Fig. 66) the elements composing the guard-ring are seen to be a variety of **sclerenchymatous fibre,** and are very thick-walled, with small cell-cavities. The endothelial layer is made out internal to the guard-ring, forming on either side of the central duct a line of parenchymatous cells with granular contents. The **development of resin-canals** may

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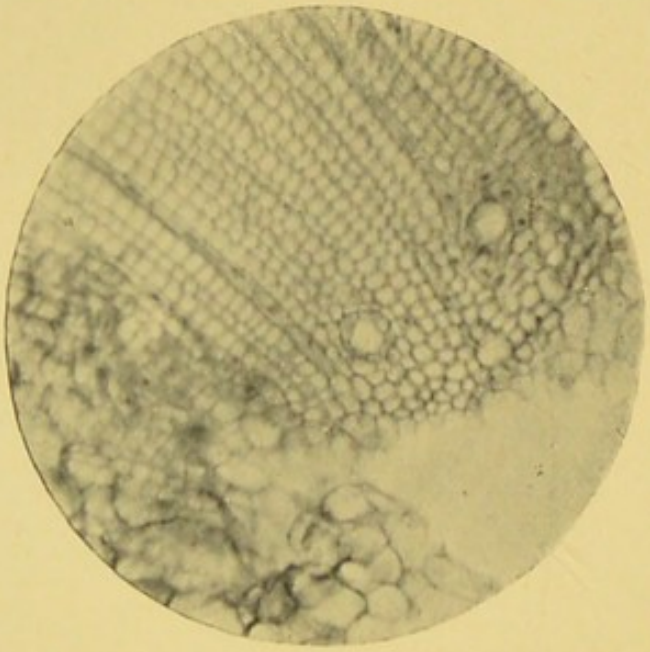


Fig. 65*a*.—A Photomicrograph showing two Resin-canals in the Wood of *Pinus*. Note also the shape of the tracheides in transverse section, and the medullary rays lying close to both canals.

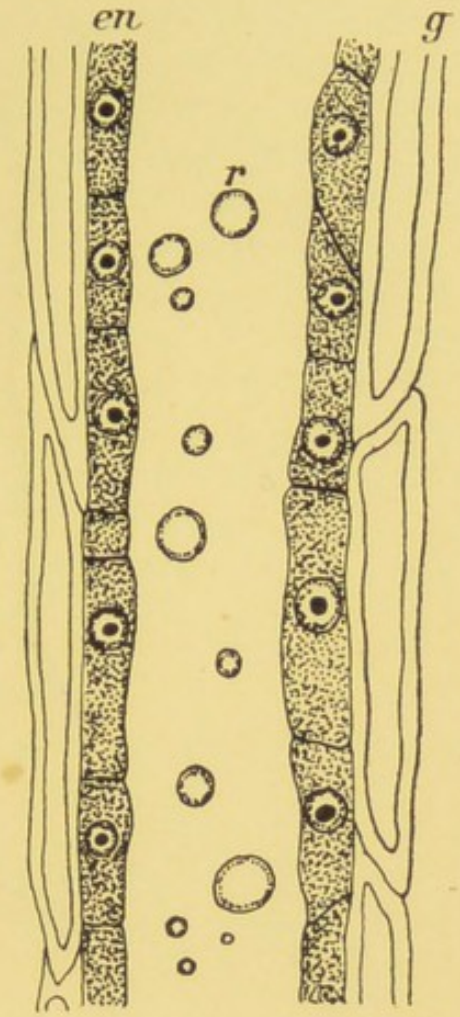


Fig. 65.—A RESIN-CANAL FROM *Pinus* STEM, in longitudinal section.—*en*, Endothelial layer; *g*, thick-walled protective cells (fibres); *r*, globules of resinous material lying in the duct.

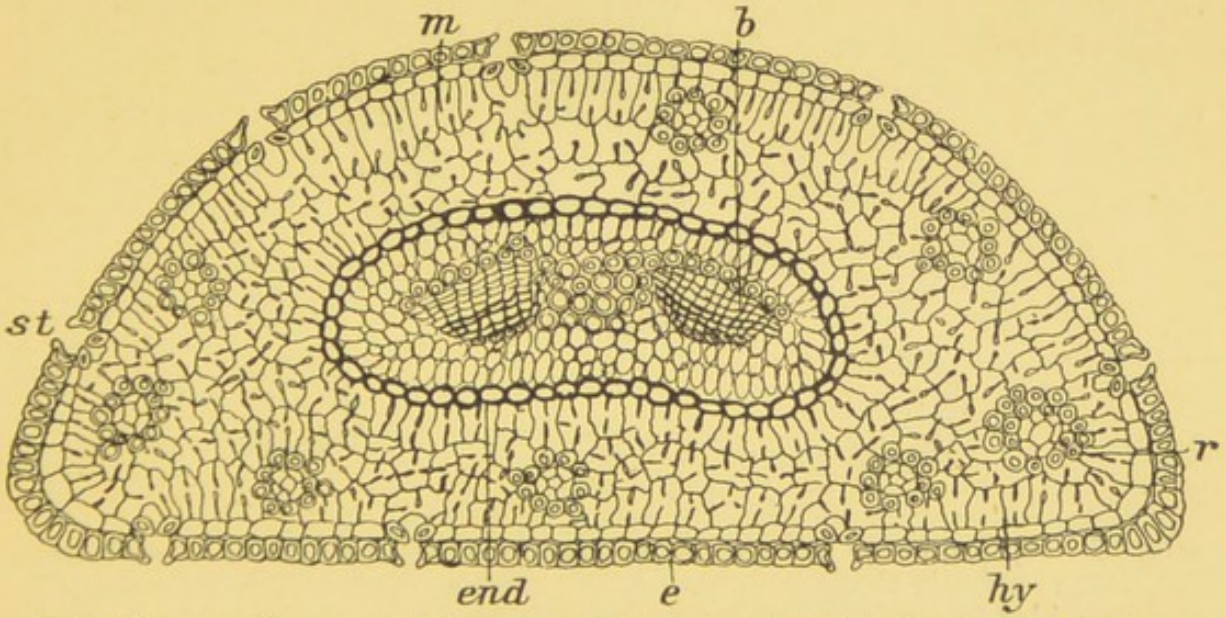


Fig. 66.—A DRAWING (from a photomicrograph) OF A TRANSVERSE SECTION OF THE CENTRIC LEAF OF *Pinus* to show distribution of resin-canals.—*e*, Epidermis; *hy*, hypodermis; *st*, stoma; *m*, mesophyll; *r*, resin-canals lying in the mesophyll; *end*, endodermis; *b*, fibro-vascular bundles.

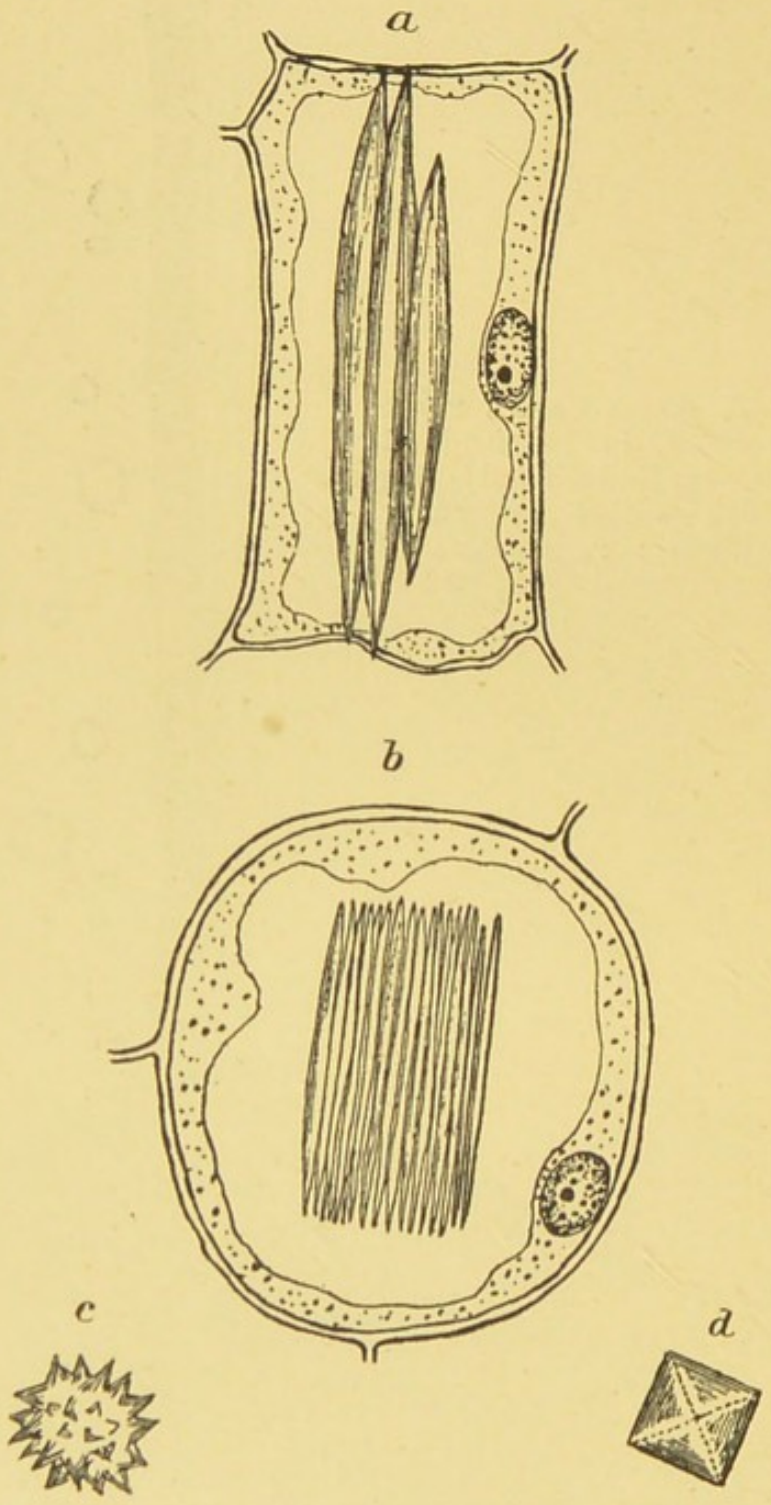


Fig. 67.—*a*, Raphides in a cell of the stem of *Dracæna*; these crystals are large spindle-shaped ones. *b*, A bundle of small needle-shaped raphides in a cell of *Dracæna*. *c*, Clustered crystals from the leaf of *Begonia*. *d*, A quadratic crystal from *Begonia* leaf. All these crystals are composed of calcium oxalate, $Ca(CO_2)_2$.

be observed in transverse and longitudinal sections of the young shoot or leaf of *Pinus*. The first stage seen is one where a small column of young cells possessing granular contents is set off from the surrounding cortical or mesophyll cells, and invested by a ring of rather thick-walled elements, which ultimately form the guard-ring. The latter soon become differentiated, whilst the central cells of the internal mass break down to form the duct, the remaining granular cells persisting as the endothelial layer (see Fig. 63, B). This mode of origin of a resin-duct is known as **lysigenous origin,** in contradistinction to the **schizogenous** method, in which the central cells of a future canal become merely separated from one another along the middle lamellæ. It is probable that the resin is formed as a product of disintegration of the cell-walls of the endothelium, and is thus not a direct secretion of the cytoplasm.

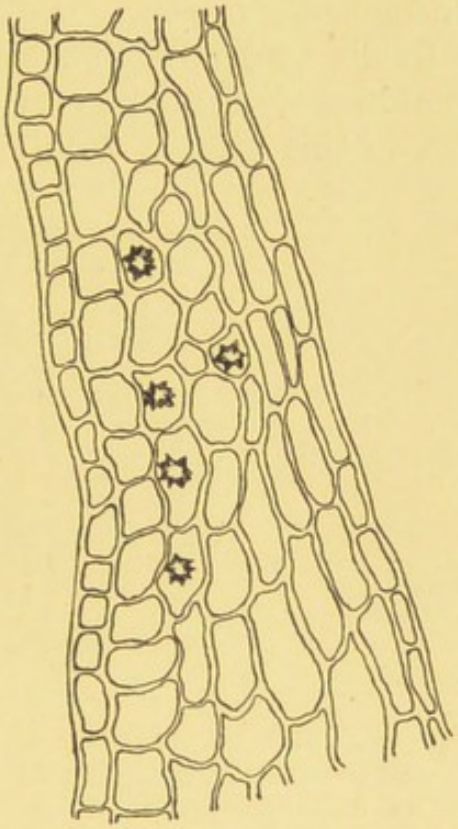


Fig. 68.—Clustered Crystals in some of the Cells of a Bud-scale of *Prunus laurocerasus*.

C. Cells in which Mineral or Organic Matters may separate out under certain conditions.

The materials which separate out in these cells are not always, strictly speaking, secretions, but more often of the nature of **excretions**, to be got rid of later on by oxidative processes, removal to other parts, or other reactions in the cell; and the substances thrown out of solution, such as **crystals,** etc., would often remain in solution in the cell-sap were it not for the fact that in order to examine them sections of the tissue have to be made, the mere process of cutting and exposure to the air causing, in many instances, spontaneous crystallisation. Sometimes, however, mineral matters separate out in the living cell. In this connection it is convenient to examine here the following structures :—

1. **Crystals** occurring in certain cells.
2. **Crystalloids.**
3. **Cystoliths.**

1. **Crystals of oxalate of lime,** $Ca(CO_2)_2$, may occur in the following forms:—

α. **Raphides,** or elongated acicular crystals, found singly or in sheaves in the cells of the cortex in the stem of *Dracæna* (see Fig. 67). They also occur in the root of *Hyacinthus* and many other plants.

β. **Quadratic crystals** occurring singly in cells of the leaf of *Begonia.*

γ. **Clustered crystals,** also occurring in leaf-cells of *Begonia*, and in other tissues (see Fig. 68).

These crystals are distinguished from those of other salts by the fact that, on addition of dilute *hydrochloric acid*, they dissolve without effervescence, whilst they are insoluble in *acetic acid.*

Oxalic acid is a bye-product of metabolism in the cell, and it combines with calcium to form calcium oxalate, which separates out, in this case, in the living cell.*

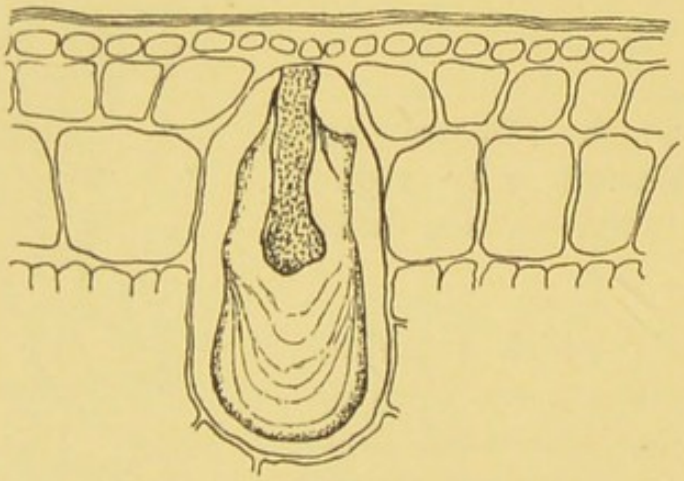


Fig. 69.—A Cystolith of Carbonate of Lime ($CaCO_3$) formed in an Epidermal Cell of the Leaf of *Ficus elastica.* Note the "core" of cellulose upon which numerous layers of carbonate of lime are deposited.

2. **Crystalloids**, or, as they are often called, **spheroids**, of a substance known as **inulin** (a carbohydrate), separate out in the cells of the tubers or petiole of *Dahlia* when these are treated with alcohol. Inulin takes the place of **starch** or sugar in these cells. The spheroids have a peculiar concentric and radiating structure (see Fig. 71, *a*) which is very characteristic. Large spheroids of

* Occasionally crystals of oxalate of lime are found in the walls of cells (mesophyll cells of *Wellingtonia*).

inulin occur in the Artichoke, which extend through many cells. Crystalloids of a proteid nature are also found at times in the cell (*cf.* "Aleurone grains," Chap. x.).

3. **Cystoliths** are structures in certain of the deeper epidermal cells of the leaf of *Ficus elastica* (see Fig. 69). The main mass

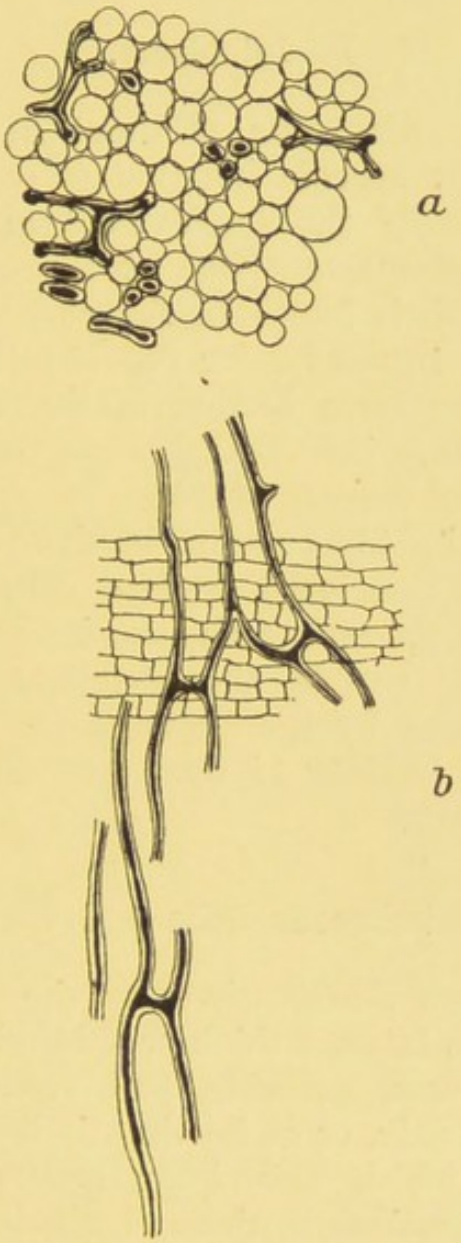


Fig. 70.—*a*, LATICIFEROUS VESSELS in transverse section of *Euphorbia* stem. *b*, LATICIFEROUS VESSELS in a longitudinal section (*Euphorbia*). Note the branching and union of vessels by short side branches.

of the cystolith is composed of amorphous carbonate of lime [$CaCO_3$], which is deposited in the form of concentric layers or small clusters upon an axial core of cellulose which projects into

the cell-cavity from the outer cell-wall. On the addition of *acetic acid* the carbonate of lime dissolves with effervescence, leaving the core of cellulose intact. It is worthy of note in this connection that the epidermis of the leaf of *Ficus* is three-layered, a somewhat unusual occurrence.

D. Idioblasts.

Certain isolated cells occur at times in various parts of a plant which have the specific function of secreting or excreting substances detectible by the employment of special tests; such cells are known as **idioblasts.** One of the commonest forms is the **tannin-cell**, which is found in the cortex of such plants as *Pinus* and *Quercus.* In the former tannin-cells are recognised by treating a fresh transverse section of the stem with a dilute solution of *perchloride of iron* ($FeCl_3$), when these cells turn black, owing to formation of tannate of iron.

Another form of idioblast occurs in the petiole of the leaf of *Nymphæa.* In this case **large stellate cells** are found at the points of junction of the numerous strands of cells composing the ground-tissue of the petiole, these stellate cells having walls which are characterised by the presence on them of small projections formed of oxalate of lime (see Fig. 71, *c*). Their function is not obvious.

E. Laticiferous Cells and Vessels.

These elements are characterised by the presence in them of a secretion known as **latex,** a thick or thin milky fluid composed of a mixture of **gums, proteids,** and **resins,** which at times coagulates spontaneously, or on heating (india-rubber).

The **vessels** in which this latex occurs may be seen in transverse and longitudinal sections of *Euphorbia* stem, or in the stem of *Ficus elastica;* in longitudinal sections the vessels are seen to be branched, and communicate here and there by means of short lateral passages. They are formed by the early development of elongated passages which arise by the lengthening and branching of **prosenchymatous cells,** and these, by their further differentiation, give rise to a system of branched canals in the cortex of the stem. The latex is formed from the protoplasm

lining the vessel; numerous dumb-bell shaped starch-grains are also often present lying in the latex.

Laticiferous cells are, strictly speaking, a form of idioblast. They are large oval cells, the protoplasm of which manufactures the milky secretion, the process being probably of the nature of an oxidation or breaking-down of the cytoplasm.

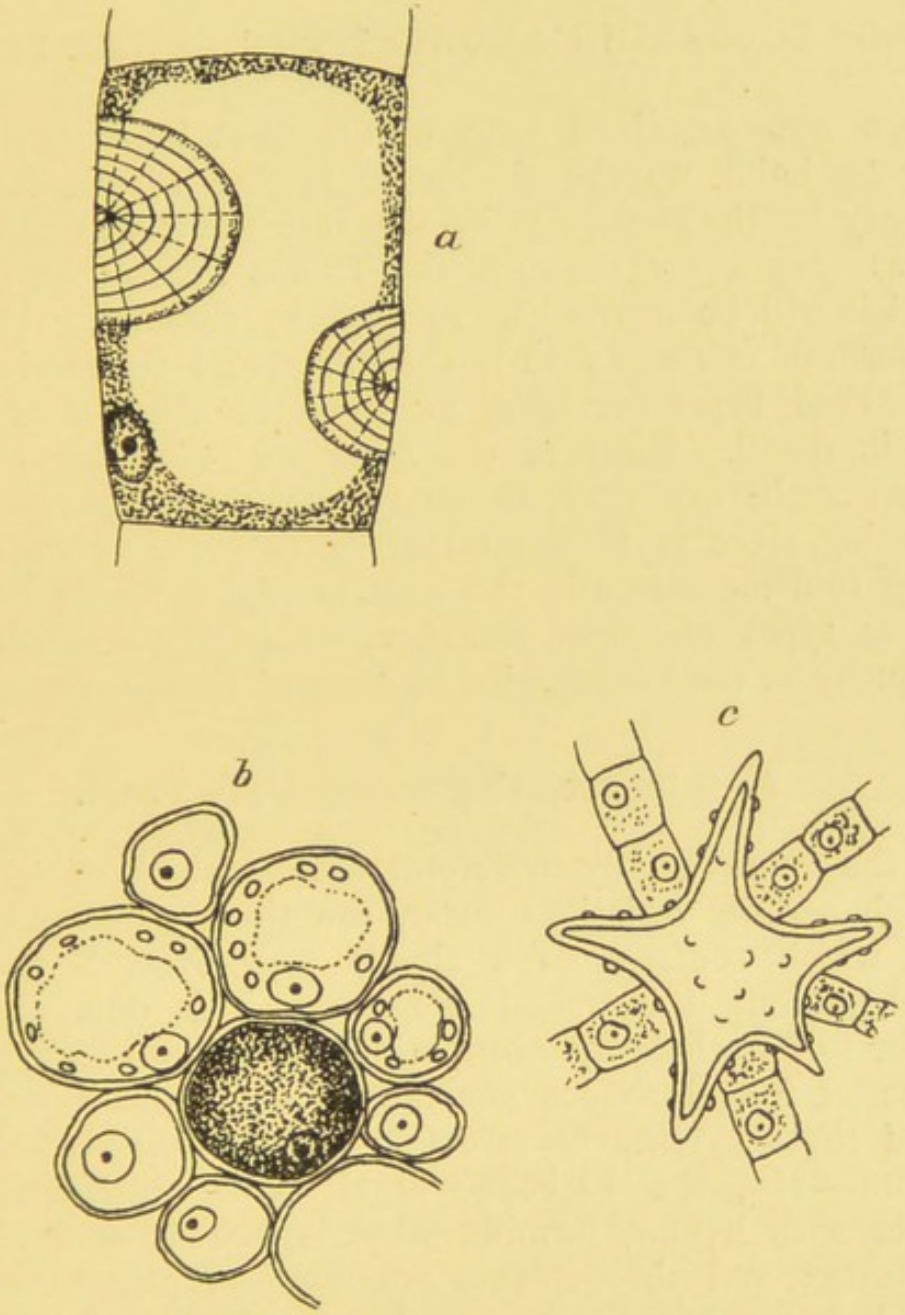


Fig. 71.—*a*, SPHEROIDS OF INULIN in a cell of *Dahlia* tuber. *b*, A TANNIN-CELL lying amongst the cortical cells of *Pinus* stem. *c*, A STELLATE IDIOBLAST formed at the junction of several strands of "tubular" cells in the flower-stalk of *Nymphæa*. The nodules on the wall are composed of oxalate of lime.

CHAPTER VII.

CELLS OCCURRING AMONGST THE LOWER PLANTS.

HAVING now examined some of the most important elements going to build up the tissues of Higher Plants, it becomes necessary for the student to inquire into the structural details of cells as they occur amongst the Lower Plants; and in this respect it will be convenient to start by examining briefly the chief form of cell met with in the Fungi, and then to take a few well-marked types occurring amongst the Algæ, and examine these in detail. Many of the Algæ are unicellular organisms, and, as such, are easy to study; they are, moreover, very interesting, since in them vital processes occur which are often difficult to demonstrate in the cells of higher plants, but which, in these types of lower organism, escape the confusion often consequent on the examination of complex tissues.

A. Cells occurring amongst the Fungi.

In the more highly differentiated members of the Fungi, although certain variations occur, the tissues are composed of cells* which conform to a simple type—viz., a tubular or parenchymatous thin-walled element. The cells are joined together to form long filaments, which are known as **hyphæ**, and sections of fungal tissues generally show a dense interwoven mass of these hyphæ, cut across in many directions. In a few members—viz., the Lichens—**algal cells** are found living together with hyphæ, forming what is known as a **symbiotic community**; and these plants are often propagated by small masses known as **soredia**, composed of a certain number of hyphæ, amongst which are embedded a few algoid cells.

* Each of these so-called cells is in reality a "cœnocyte"—viz., it possesses many small nuclei—and is thus composed of many potential protoplasts.

In the lowest members of the Fungi—*i.e.*, *Schizomycetes*, or fission Fungi, as they are sometimes called—unicellular organisms either rod-shaped (Bacilli), or in the form of small spheroidal cells (cocci), are found, which may be joined together into chains, or occur in the form of masses of varied shapes (*streptococci*, *staphylococci*). Many of these forms are **motile cells**, such as the *Bacillus typhosus*, *Bacillus subtilis*, *Proteus vulgaris*, etc. Occasionally, as in the *Streptothrix* group, long branching filaments are formed, composed of large numbers of rod-like cells (*Actinomyces*, *Bacillus mycoides*); but the life-histories and vital processes of the *Schizomycetes* are, nowadays, considered to belong to the domain of bacteriology rather than that of botany pure and simple, and it is not here intended to give more than a brief survey of the general characters of the group.

In the higher Fungi, although, as was above stated, the chief type of tissue met with is that composed of hyphal filaments, there occur, nevertheless, variations in this tissue, more especially in connection with the processes of reproduction; thus, in the propagation by **spores**, the ends of hyphal filaments are modified so as to become divided up into large numbers of **spores** or **gonidia**, (exogenous spore-formation), and in yet other instances spores may be formed inside special organs, the **asci** (**ascospores**) in the process of endogenous spore-formation. No tissues corresponding to the vascular tissues of Higher Plants occur in Fungi, and even the highest members are only to be distinguished by the variety and form of their fructifications, the vegetative part of the plant being nearly always small and insignificant, and known as a **mycelium.**

The cells composing the hyphal filaments possess protoplasm, many nuclei, and cell-sap, but no chlorophyll ever appears in them; and in place of starch, **oil-globules** are found in the cell.* Moreover, the fungi are able to absorb, by means of their mycelia, **organic materials** direct from the substratum on which they grow, so that the processes of elaboration of nitrogenous and carbohydrate material from salts and other raw material supplied are not necessary in the members of this great group. In those plants next above the Fungi—viz., the Bryophyta (*Hepaticæ* and *Musci*)—vascular tissues of a rudimentary type

* Glycogen in Fungi seems also at times to take the place of sugar or starch in the higher plants.

may be met with, and the cells composing the other tissues of these plants, although, as a rule, simple in type, have some resemblance to those met with in Higher Plants. It will, however, be seen that in plants below the Fungi—viz., the Algæ—cells are often met with which in all respects agree with the typical assimilating cell, which was studied in Chapter ii.

It is not intended here to pursue the study of the cells of Fungi any further, but to proceed to the examination of a few of the more well-defined types of lower plant organism met with amongst that group of the Thallophyta known as the Algæ.

B. Cells occurring amongst the Algæ.

The types here selected for study will be :—

a. **Spirogyra** (belonging to the *Conjugatæ*).
b. **Vaucheria** (belonging to the *Siphoneæ*).
c. **Sphærella** (belonging to the *Volvocineæ*).
d. **Melosira** (belonging to the *Diatomaceæ*).

a. **Spirogyra.**—This plant is one of the filamentous Algæ, in which a large number of cylindrical cells are united end to end to form a **colony**. It is found at the bottom of ponds in the form of large interwoven masses of a light green colour. Each of the cells composing a filament is relatively a large one, and, when examined microscopically, may be seen to be composed of the following parts (see Fig. 72, 1) :—

i. Externally, a delicate **cell-wall.**
ii. An internal layer of **cytoplasm,** lining the inner surface of the cell-wall and enclosing a **central vacuole;** from this layer bridles pass to a central mass in which lies
iii. The **nucleus.** This body possesses a well-defined central spot, the **nucleolus.**
iv. A spirally wound ribbon-shaped **chlorophyll band,** which lies next the cell-wall embedded in the peripheral cytoplasm. The edges of the band have a sinuous appearance, and the axial portion seems to be rather thicker and more refractile than the lateral parts. Arranged at regular intervals along the axial portion of the band are to be seen rounded refringent structures, which are known as the **pyrenoids;** these, as will soon be seen, are active **starch-formers** and **storers,** and require special examination. For this purpose a fresh preparation of a filament may be treated with a drop of weak *iodine solution*, when the following effects may be noted :—

α. Each cell will undergo a partial **plasmolysis** (see Fig. 72, 3).
β. The **nucleus,** and especially the **nucleolus,** will turn **brown** (reaction for proteid).
γ. The **pyrenoids** are acted upon as follows:—The central portions may stain a *yellowish-brown*, whilst the outer parts turn *blue*. This reaction shows that **starch** is present at the periphery of the pyrenoid.

Under a high power of the microscope it is possible to study the pyrenoids more closely. It will then be found that some of these bodies are completely surrounded by a ring of starch, whilst others have only a few separate granules arranged round them in the form of a circle (see Fig. 72, 2).

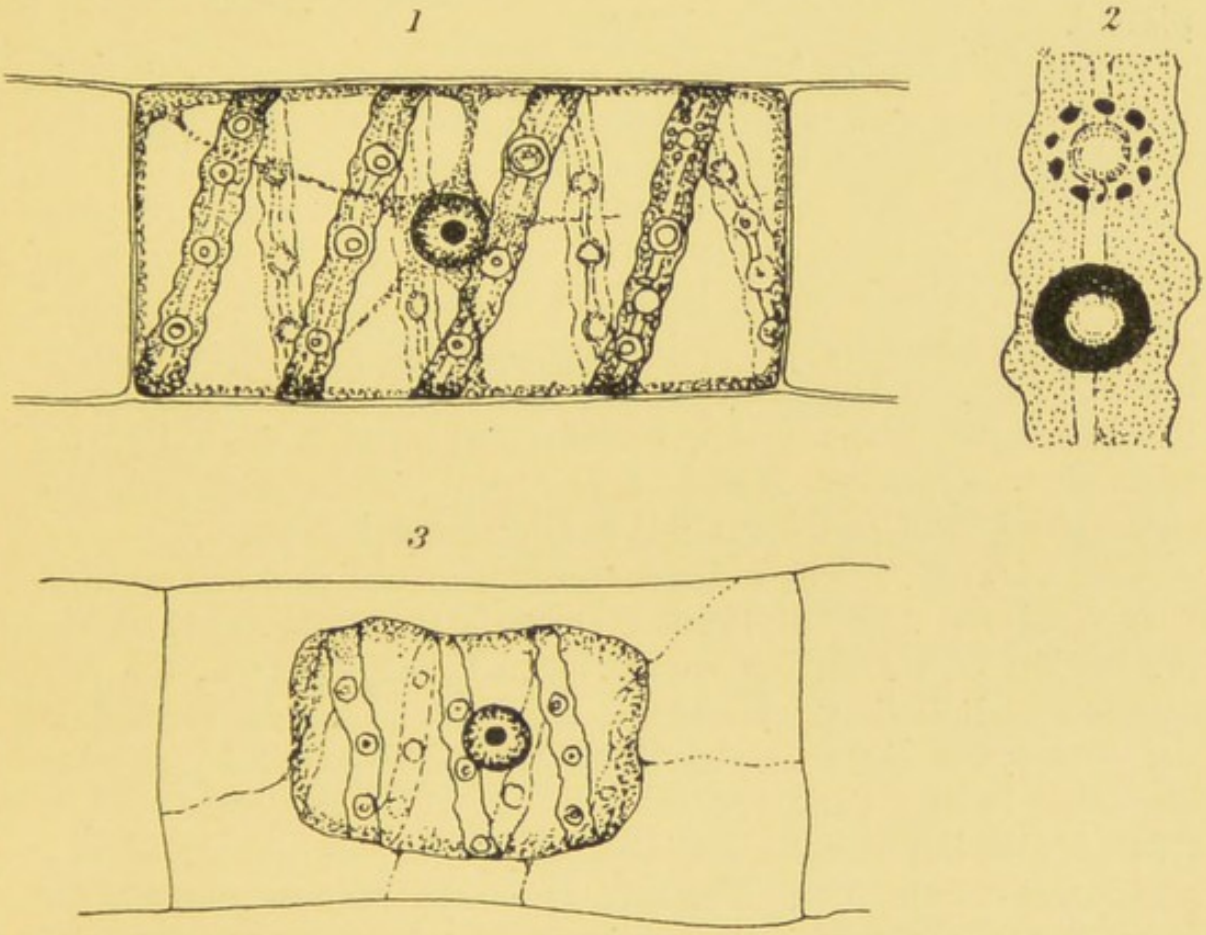


Fig. 72.—1. A Single Cell from a Filament of *Spirogyra*. Note the delicate layer of peripheral cytoplasm, the nucleus held in the middle of the cell by strands or bridles of protoplasm. The spirally wound chlorophyll band has numerous pyrenoids arranged in line along its axial portion.

2. Portion of the Chlorophyll Band after the cell has been treated with iodine solution. The uppermost pyrenoid has a ring of small separate starch-granules round it; the lower one is completely surrounded by a ring of starch.

3. Plasmolysis in a Cell of *Spirogyra*. Bridles of protoplasm pass at first from the plasmolysed portion to the cell-wall.

In a living *Spirogyra* cell it is often possible to detect small granules in the cytoplasm in the vicinity of the pyrenoids, and, by carefully focussing these, and cutting off the peripheral rays of illumination to render them sharper in definition, it will be seen that they are vibrating rapidly to and fro. It is probable that this is not quite the same sort of movement as the well-known **Brownian vibration** of small particles in the protoplasm, which is a physical phenomenon, but is evidence of protoplasmic activity, since the vibrating particles are situated chiefly over the pyrenoids, and the bulk of these latter bodies is protoplasmic in nature, each pyrenoid in fact being looked upon as a plastid.

If *Schulze's solution* be used as a reagent the cell-wall will stain **blue**, showing that it is composed of pure **cellulose**. The other reactions are the same as those noticed in α, β, and γ.

For the complete study of *Spirogyra* very instructive preparations may be made by first fixing filaments in very dilute Flemming's solution or chromic acid ($\frac{1}{2}$ per cent.). The filaments are then washed in distilled water, treated with alcohol for a few minutes, and stained with the *Ehrlich-Biondi* triple stain (composed of methyl-green, fuchsin, and orange G). By this method the cytoplasm is stained pink, the nucleus green, and the chlorophyll band and pyrenoids reds of different shades.

The cells of which a filament of *Spirogyra* is made up form very good examples of **typical assimilating cells**, in which the production of **starch** (or sugar) forms a large part of the processes of assimilation. Moreover, this starch is only formed in the presence of light, as may be easily demonstrated by growing filaments in the dark for some days, when the cells will, if treated with iodine solution, show the pyrenoids devoid of any peripheral starch-rings. The **nitrogenous substances** requisite for formation of the proteid and amine parts of the cytoplasm molecule are derived from the dilute solution of **nitrites** and **nitrates** in the surrounding water, these being, together with water itself and other salts, assimilated mostly during the absence of light. The **oxygen** necessary for respiration is also derived from the surrounding water, in which traces of oxygen are dissolved; and, possibly, some of the oxygen evolved from the cell during the assimilation of carbon dioxide is dissolved in the water and used again for purposes of respiration. **Carbon dioxide** exists in the

water of ponds, dissolved to a slight extent,* but quite sufficient for the needs of *Spirogyra* and other algal plants.

A filament grows in length only by the **division of its terminal cells**, and this division involves, as a rule, the **mitotic** division of the nucleus (see Chap. viii.); but by suitably altering the composition of the medium in which the filaments are growing, one observer has succeeded in changing the type of nuclear division in *Spirogyra* from the "mitotic" into the "**amitotic**" form, in the latter of which the nucleus divides *en masse*. This experiment is one of great interest, as it shows that adaptation to altered conditions may take place even in these low forms of vegetable life.

Conjugation in *Spirogyra* will be considered later under "Reproduction" (Chap. ix.).

b. **Vaucheria.**—In this plant, which is also a filamentous Alga growing under conditions similar to those which obtain in the case of *Spirogyra*, the filament is composed of **one long tubular cell**, and not of a colony of separate cells joined end to end.

Preparations of the fresh living filament may be first examined. On mounting a filament, including its free-growing end, in water, the following features will be noticed under a medium power of the microscope:—

i. A delicate **cell-wall** forming the outer boundary of the filament.
ii. A narrow layer of **cytoplasm** lining the inner surface of the cell-wall; in this layer are to be seen (see Fig. 73, 1)—
iii. Large numbers of small oval **chloroplasts,** and
iv. Numerous small **nuclei.** These are usually only to be detected by first fixing a filament in weak Flemming's solution, washing, and staining with *carmine* or *hæmatoxylin*, with or without preliminary treatment of the cell with alcohol to extract the chlorophyll. The nuclei lie close to the cell-wall, and arise by repeated divisions of pre-existing nuclei.

The above structure—viz., peripheral protoplasm—in which lie numerous nuclei, determines *Vaucheria* to be a **cœnocyte**, a term which denotes that a large number of "potential" cell-units are present, enclosed by a common cell-wall (*cf.* Cells of fungal hyphæ).

v. **Oil-globules** are to be seen in the central space enclosed by the protoplasm (**central vacuole**). Oil is manufactured by the chloroplasts of *Vaucheria* in the place of **starch** (or sugar). On the addition of *iodine solution* the nuclei turn a brownish colour, but no starch-granules show up.

* The dissolved CO_2 is present in the form of $CO_2 . H_2O$, or carbonic acid.

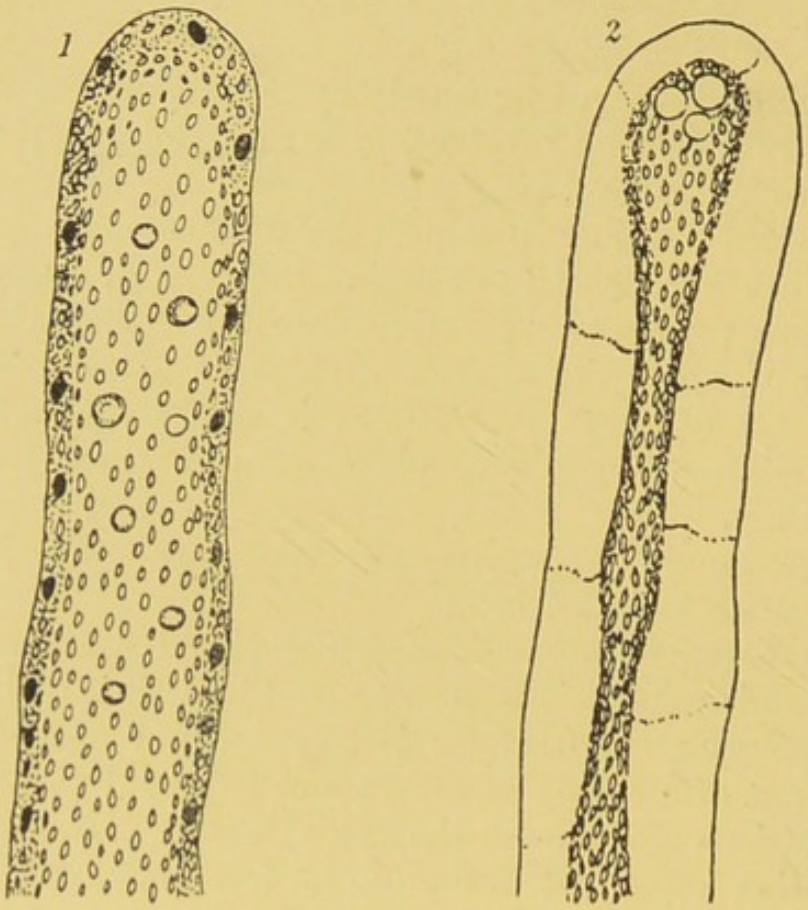


Fig. 73.—1. The end of a Filament of *Vaucheria*, stained so as to show the nuclei and represented as seen in optical section. Note the peripheral cytoplasm, in which lie numerous chloroplasts and the nuclei (shown black in the figure). The larger round bodies are oil-globules which float in the cell-sap in the central cavity.

2. Plasmolysis in *Vaucheria*.

3. Formation of a swarmspore (see text).

4. Freeing of the swarmspore by splitting of the apex of the terminal cell-wall.

The **cytoplasm** in a fresh *Vaucheria* filament will, if watched, and especially if the slide be warmed, be found to exhibit the phenomenon of "**rotation**" or **streaming**, similar to that which was observed in the cells of *Vallisneria* (Chapter ii.).

Plasmolysis is very striking in *Vaucheria*. On the addition of a drop of 20 per cent. acetic acid or strong salt solution, the cytoplasm retracts from the wall, bridles at first connecting the retracted portion with the cell-wall; ultimately the protoplasm forms a retracted axial cord, the oil-globules being often forced out of it and lying between it and the wall of the filament (see Fig. 73, 2).

Vaucheria is often reproduced by an **asexual** method—viz., by means of **swarmspores**—which may be described at this point. A portion of the cytoplasm with several nuclei and chloroplasts is cut off from the free end of the filament by the formation of a thin **partition wall**. This mass of cytoplasm soon acquires a delicate external layer of **ectoplasm**, and from this latter numerous short **vibratile cilia** arise.* The cellulose wall at the free end of the filament then ruptures and sets free this **swarmspore**, which at once begins to move rapidly through the water by means of its cilia. At a certain period, however, it becomes fixed by one extremity to an object, the cilia vanish, and the cytoplasm develops a wall of **cellulose**. After a period of quiescence this "**encysted**" spore becomes active and produces a fresh *Vaucheria* filament, the thick wall bursting and the cytoplasm growing out into an elongated mass which is soon coated by a thin wall of cellulose. The nuclei and chloroplasts also undergo division, and soon a typical filament is reproduced.

The **sexual** method of reproduction will be described in Chapter ix.

c. **Sphærella.**—This organism occurs in several forms, and the one which will be described here is known as *Sphærella pluvialis*, occurring in pools of rain-water which have lain a few hours.

Sphærella, in its free-swimming stage, is a **motile cell**, the motility being consequent on the possession of two **vibratile**

* Pairs of these cilia arise just opposite each of the numerous nuclei, which latter are arranged in line all round, immediately internal to the outer firm boundary.

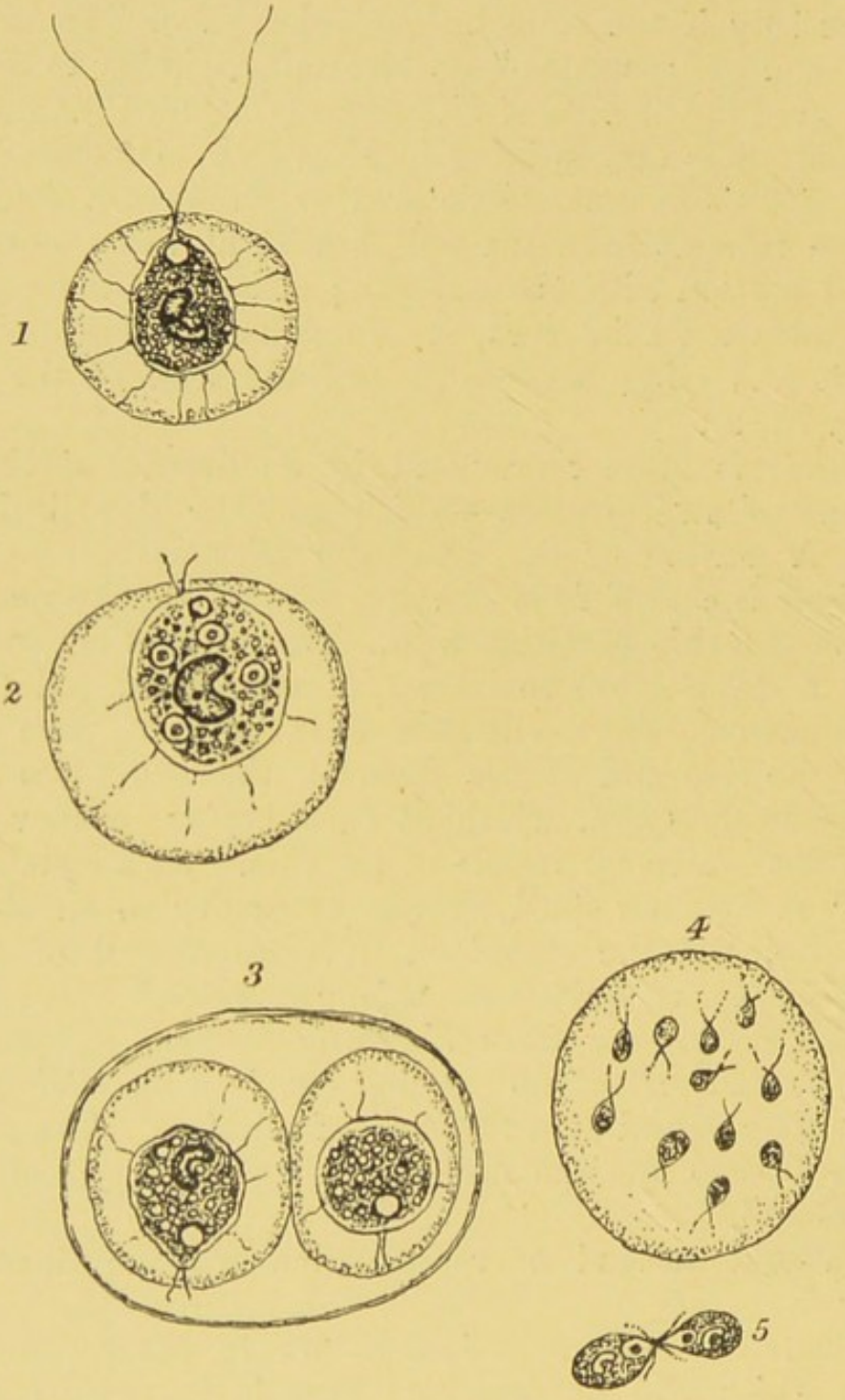


Fig. 74.—1. A SINGLE FREE-SWIMMING INDIVIDUAL OF *Sphærella* (see text).
2. THE SAME TREATED WITH ALCOHOL AND IODINE SOLUTION.
3. THE PALMELLA STAGE, where two individuals have been formed by division, the whole being surrounded by a gelatinous capsule.
4. THE FIRST STAGE IN THE REPRODUCTION OF *Sphærella* by conjugation.
5. FUSION OF TWO OF THE RESULTING SWARMSPORES by their anterior ends.

cilia. The movements are of two kinds—viz., **rotatory** and **translatory**, and these are so rapid as to make examination of the living organism somewhat difficult. If a single organism be examined microscopically, the following structure will become apparent (see Fig. 74):—

i. A very delicate **outer membrane** of cellulose, giving the "blue" reaction with Schulze's solution.

ii. Internal to this, and separated from it by a considerable space, a pear-shaped mass of **cytoplasm**, which may be seen to be composed of a very thin layer of **ectoplasm**, and an internal **endoplasm**, in which many **chlorophyll** bodies are present.

iii. Somewhere in the endoplasm the **nucleus**, a crescentic structure, may possibly be detected; but in the living cell this is not easy.

iv. At the anterior end of the cell may be seen the **two vibratile cilia**, which spring from the ectoplasm and pass through the outer membrane of cellulose.

v. Near the point of origin of the cilia, the **red eye-spot** can be distinguished; the function of this body is not obvious, but that it can be affected by light is not improbable.

Delicate "**bridles**" of cytoplasm stretch from the inner mass to the internal surface of the outer membrane.

If such a cell be treated with *alcohol*, and then *iodine solution* be added, the **pyrenoids** will show up, a **starch-ring** being present round each of these; only three or four pyrenoids are, as a rule, present; the chlorophyll exists in the small chloroplasts in the endoplasm, and is extracted by the alcohol.

The **cilia** are in reality hollow protrusions of the **ectoplasm**, into which the endoplasm suddenly flows, only to withdraw again with equal rapidity. During this process each cilium is quickly bent in one direction, and straightened again, the supposition being that a cilium is thinner on one aspect than on the opposite side. These sudden movements of the cilia have the effect of moving the whole organism through the water, or of producing rotatory movements.

With the exception of *Æthalium* (or the protozoan *Amœba*) *Sphærella* is the lowest form of plant cell which has been studied; in the case of such organisms, moreover, the animal kingdom is closely approached, *Sphærella* being very similar in structure to *Noctiluca* (Protozoa). With regard to the distinction between a lower plant and a lower animal organism the possession of **chlorophyll** does not afford much help, as both plant and animal may possess this pigment (*cf. Hydra*). The **assimilation of carbon dioxide** is, however, a distinctive feature, **starch** being formed by plants,

while no analagous process takes place in animals, with the exception, perhaps, of the Tunicata, which are able to manufacture **cellulose** for their outer casings.

Reproduction in *Sphærella* takes place in two ways, viz., an **asexual** method and a **sexual** one, in the latter of which the conjugation of two similar individuals takes place. In the former, or **asexual** process, a single cell divides into two, which become encapsuled by a gelatinous cyst, secreted by the cell, and common to both individuals: further divisions arise, resulting in the production of a number of cells, pairs of these being enclosed in cysts, and the whole enclosed by a gelatinous mass similar in structure to that enclosing the daughter cysts. In this stage the whole mass is said to be in the **palmella phase** (see

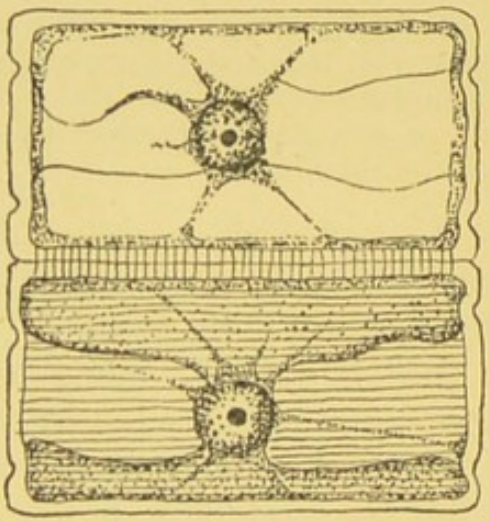


Fig. 75.—Two Cells of a Chain of Diatoms (*Melosira*). Note the peripheral protoplasm, the central nucleus held in position by "bridles," and the two somewhat irregularly shaped chlorophyll bodies. The frustule of the Diatom is seen to be striated in a longitudinal direction: the double nature of each frustule is not shown in the figure (see text).

Fig. 74, 3), and, later on, the separate cells may be freed from their cysts and become free-swimming organisms once more. At certain times, however, reproduction takes place by the **conjugation** of two similar small ciliated motile cells which have arisen by the division of the original cell into a large number of equal ciliated individuals (see Fig. 74, 4 and 5). These become freed by the bursting of the original cell-membrane of parent-cell, and, whilst swimming freely, two of these bodies approach one another, and meet by their **anterior ciliated ex-**

tremities. After a short period they fuse, and the resulting mass develops a delicate membrane like the original parent-cell, and two vibratile cilia.

d. **Melosira** (*Diatomaceæ*).—**Diatoms** are members of the Algæ, characterised by the possession of **silicified cell-walls,** which are often beautifully marked. The various markings met with serve in many cases to distinguish the different genera, as also does the enormous variety of shapes which these organisms can assume.

The cell-wall of a diatom is known as the **frustule**, and contains enough **silica** in its composition to enable it to retain its form and markings, even after it has been heated to a white heat. *Melosira* is here chosen for examination, as this genus shows the structure of the cell very clearly.

The living cell has the following structure (see Fig. 75) :—

(*a*) An external case or **cell-wall**, composed in reality of two parts, one of which fits into the other, pill-box fashion. The wall is marked longitudinally by closely-set parallel lines, which are only apparent under a high power.

(*b*) An inner peripheral layer of **cytoplasm** lining the inner surfaces of the two halves of the frustule; from this layer "**bridles**" of protoplasm pass to a central mass, in which is suspended the **nucleus.**

(*c*) Two laterally situated masses of a brownish-green colour are to be seen in the cell. These are the **chlorophyll bodies** or **chromatophores.** They are semi-fluid in consistency, and internally have sinuous borders.

Melosira occurs in **chains** of varying length, there being often one hundred or more individuals in a chain. The isolated cell is capable of protruding a portion of its cytoplasm between the two halves of the frustule, and uses this as a **pseudopodium** for purposes of locomotion. Occasionally, however, diatoms are able to move by causing currents of water to pass through their interior and out again.

Cell-division in Diatoms takes place lengthwise between the two halves, and the cell-wall of the new individual is enclosed within the ruin of that of the mother-cell, so that repeated divisions lead to a progressive decrease in the size of individuals. At times, however, large forms known as **auxospores** arise, and these by their divisions go to produce a smaller series. Auxospores arise by the conjugation of two smaller individuals, the resulting cells subsequently decreasing in size on division.

CHAPTER VIII.

CELL-DIVISION.

HAVING now examined some of the chief modifications of the plant-cell, and gained an outline of the more important vital processes to be demonstrated in it, attention may now be directed to the manner in which fresh cells may arise from pre-existing ones; and in this respect it is found that, in the majority of instances, the **nucleus** is the structure in a cell which undergoes the most marked changes. In the higher plants, in fact, cell-division is always preceded by division of the nucleus.

Of the types of cell-division met with there are two main varieties—viz., the **amitotic** and the **mitotic**. In the former the nucleus divides *en masse*, the cytoplasm becoming aggregated round the resulting nuclei, after a process of redistribution; whilst in the latter, or mitotic type, certain changes take place in the structure of the nucleus which lead to the development of a well-marked **karyokinetic** or **division-figure**, followed by the formation of a **partition-wall** dividing the original cell into two.

A. Amitotic Cell-division.

This type is comparatively rare in the Higher Plants; it occurs, however, in **cambial cells**, and it is also seen in old internodal cells of *Tradescantia virginica*. In the lower plants it may occur at times, as in the case of the nuclei of *Vaucheria*, and in internodal cells of *Chara fragilis*.

In **amitosis**, the nucleus becomes constricted in the middle, and this constricted part becomes narrower, until finally the original nucleus has split into two **daughter-nuclei**. This type of nuclear division is looked upon by many as an evidence of **degeneration** (more especially in animal cells); but in a few cases it is a sign of the need of rapid division, where time and space will not allow of the more highly differentiated mitotic type.

In some cases of **free cell-formation** the nuclei may divide amitotically, the cytoplasm of the original cell becoming distributed round the several nuclei resulting from the division. Cell-walls may be subsequently formed cutting off separate cells from one another. The formation of *endosperm* in Phanerogams takes place in a somewhat similar manner, although mitosis is here the usual type of division of the nuclei.*

B. Mitotic Nuclear Division, followed by division of the cell.

1. This process almost always precedes division of the cell in Higher Plants and most of the lower plants, although in the latter case differences may be seen during some of the phases.

In order to properly understand mitosis, it is necessary first of all to examine more fully than has been done hitherto the structure of the **quiescent nucleus.** To do this, powers of the microscope, ranging from the $\frac{1}{6}$ inch to the $\frac{1}{12}$ inch oil immersion, should be employed, and preparations of the cell for the purpose of examining the nucleus should preferably be made in the manner described in the *Note* at the end of Chapter ii., young growing tissues, such as a **root-tip** of *Allium* or *Hyacinthus* serving very well for material to work with. The preparation having been made, a cell should be selected for examination in which the nucleus is still intact, and as yet shows no signs of karyokinesis. Such a nucleus will, under the $\frac{1}{12}$ inch objective and a suitable eyepiece of the microscope, be magnified about 800 or 900 diameters, and will show the following structure (see Fig. 76, 1, Fig. 81A, and Fig. 1) :—

(*a*) An external boundary, the **nuclear membrane**, which is probably the innermost firmer portion of the **kinoplasm**, or layer of the cytoplasm just outside the nucleus. The nucleus may, in fact, be looked upon as a **space** filled with fluid and bounded by the kinoplasm, in which space certain other structures are suspended

(*b*) Internal to the nuclear membrane, a clear portion, of a fluid nature, the so-called **nuclear plasm**, in which are suspended :

(*c*) A **network** of a material known as **linin**. This is not easy to detect, except by very careful focussing.

(*d*) Granules of a substance known as **chromatin**, arranged at somewhat irregular intervals upon the linin network ; here and there rather

* Such a formation of cells is sometimes known as "multicellular formation." Free cell-formation results in the production of distinct isolated cells, as in the case of the production of ascospores in the Fungi.

larger masses of chromatin occur, termed **net-knots** or **karyosomes** (see Fig. 1, Chap. i.). The chromatin is so-called on account of its capacity to take up stains like *hæmatoxylin* and *safranin*.

(*e*) Other structures which, like the chromatin, are able to take up certain stains, are the **nucleoli** or **plasmosomes.** These lie in the spaces between the linin network. There may be only one large nucleolus present situated centrally.

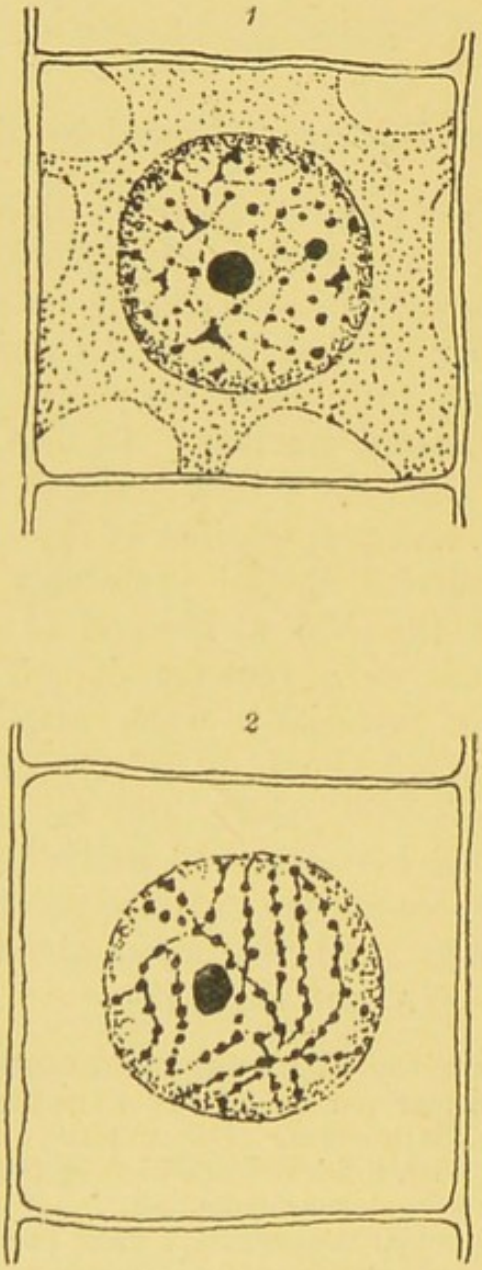
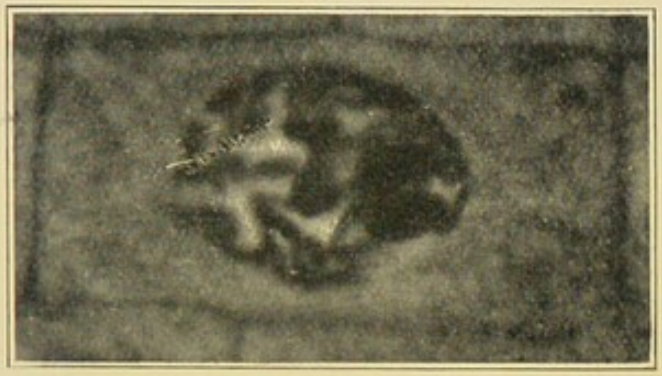
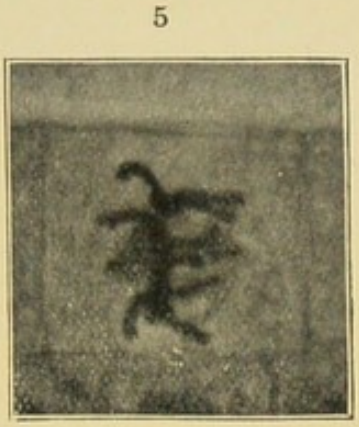


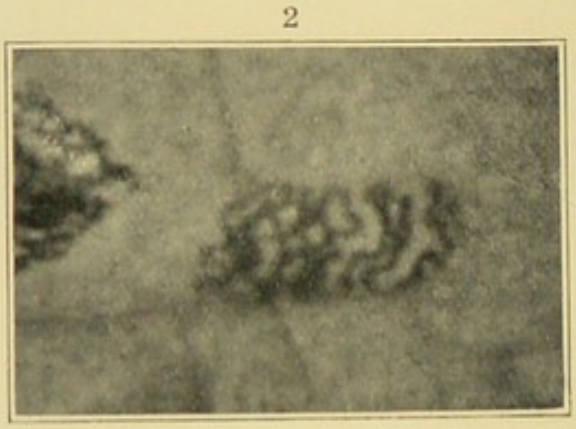
Fig. 76.—1. A Quiescent Cell from a Growing Root-tip. The nucleus is situated centrally in the granular cytoplasm, and shows externally the nuclear membrane, and internally the clear nuclear plasm, the linin network upon which are seen at intervals the chromatin granules and a few karyosomes ; two nucleoli are present.

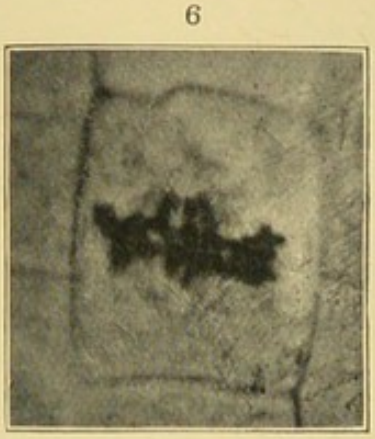
2. The Initial Phase of Mitosis (early prophase). The chromatin granules have increased in size, and are becoming arranged in the form of a definite chain upon the linin thread.

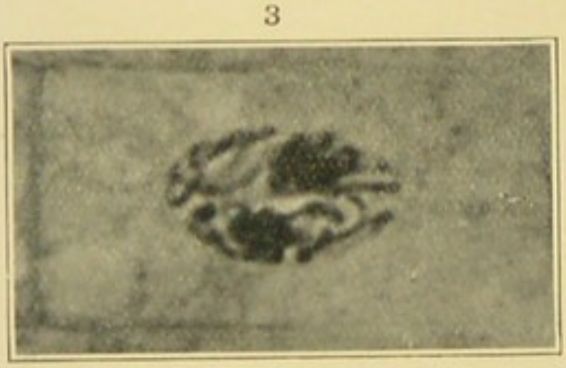
PLATE I.

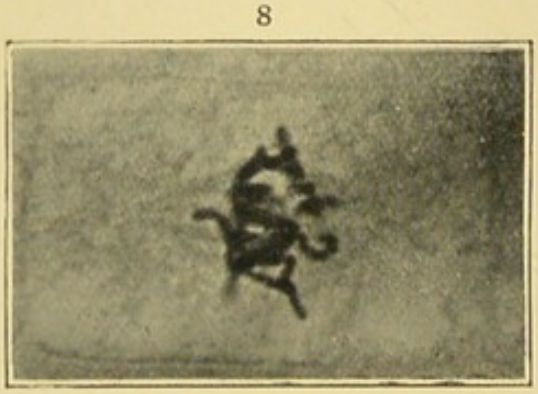












PLATES I. and II. (Photomicrographs showing Various Phases in Mitosis).

1, 2, 3, and 4 show the spireme stage;
5, 6, and 7, the monaster stage seen from the side;
8 and 9, the secondary chromosomes separating;
10, 11, and 12, later stages of the metaphase;
13 (right-hand cell), 14, 15, and 16, end-stages (telophase).

Mostly from longitudinal sections of root-tips of *Allium* and *Hyacinthus*. 16. From the endosperm of *Caltha*. 15. From a cortical cell of *Larix* cone. 14. From endosperm of *Caltha*.

To face p. 103.]

PLATE II.

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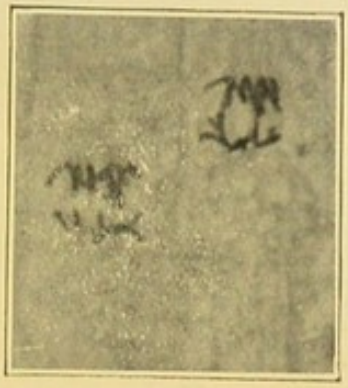

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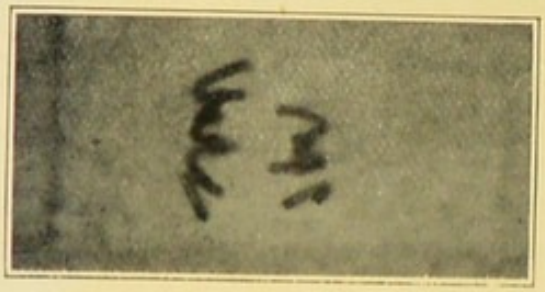

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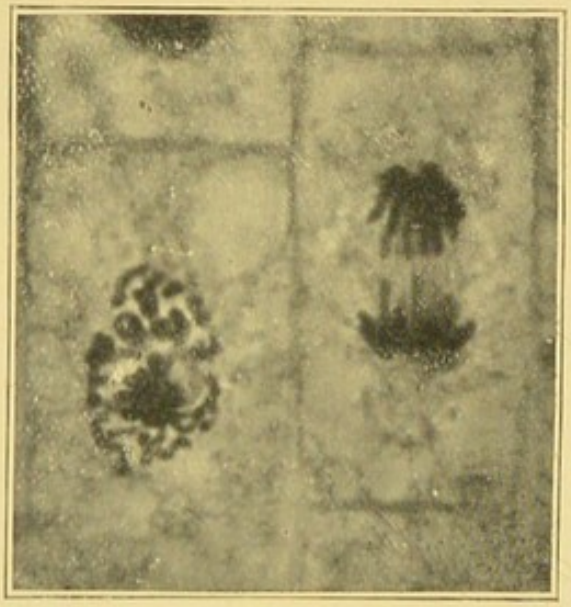

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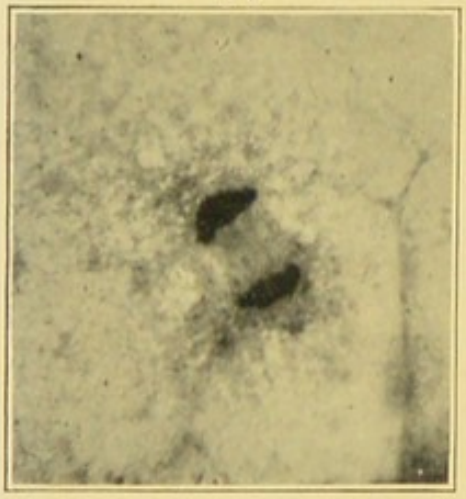

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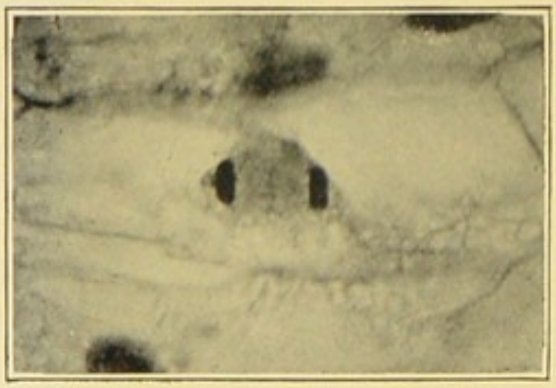

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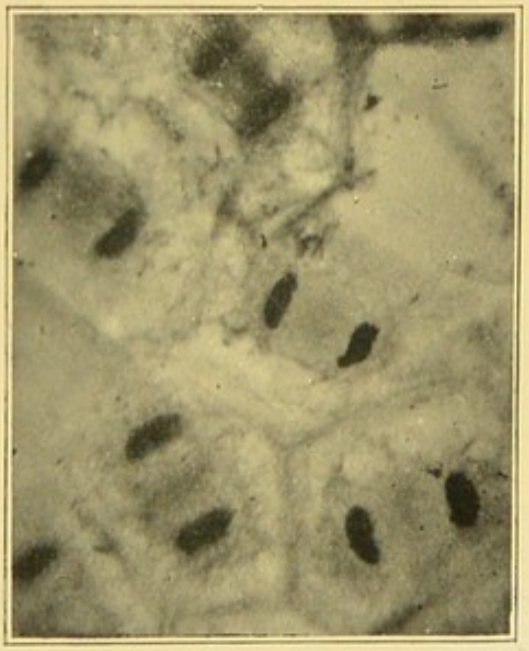


The **chromatin** is the essential substance in the nucleus, and in chemical composition is identical with **nuclein**, a material which contains phosphorus in its molecule. The **nucleolus** is composed of a substance known as **paranuclein**, or **parachromatin**, and, during mitosis, may possibly be partly converted into chromatin, or a body from which chromatin may subsequently be formed.

In the cells of most plants below the mosses, and also in certain cells during the reproductive cycle, in some of the higher plants (Cycads) two peculiar structures are to be seen lying close to the nucleus in the kinoplasm. These are the **centrosomes**, and in lower plants and most animal cells, even during vegetative divisions, they appear to possess an important *rôle*. In the following description of mitosis the centrosomes will be omitted, as in Higher Plants they are in all probability absent, at least during ordinary vegetative divisions.

2. **The Details and Mechanism of Mitotic Nuclear Division, or Karyokinesis*** (see Plate I., Diagrams 76 to 80, and Figs. 81A to 90 inclusive).

The **mitotic process** is most conveniently divided into five stages, the first four being termed **phases**, while the last involves the formation of the **cell-plate**, or rudimentary partition wall which divides the parent-cell into two. Thus it is possible to distinguish between (α) **Prophase,** (β) **Metaphase,** (γ) **Anaphase**, and (δ) **Telophase,** in each of which certain changes take place in the nuclear structures. It will be best to study each of these phases separately and in order.

(α) **The Prophase,** in which the nucleus prepares for division. —At the beginning of mitosis certain conditions must be present in a cell in order that the nucleus may be provided with adequate powers to complete the process. These conditions are :

(a) The presence of an adequate supply of **soluble nitrogenous food** and **carbohydrates** (elaborated food-materials from the leaves).
(b) The maintenance of an **optimum temperature**.
(c) The presence of **oxygen** for the purposes of oxidation of waste products arising during mitosis.
(d) **Protoplasmic continuity** between adjacent cells of a dividing tissue.

* See an article by the author in *Knowledge and Scientific News*, Feb., 1909, on "The Mechanism of Nuclear Division." Also one in same magazine, Aug., Sep., 1909, on "Mitosis in Higher Plants."

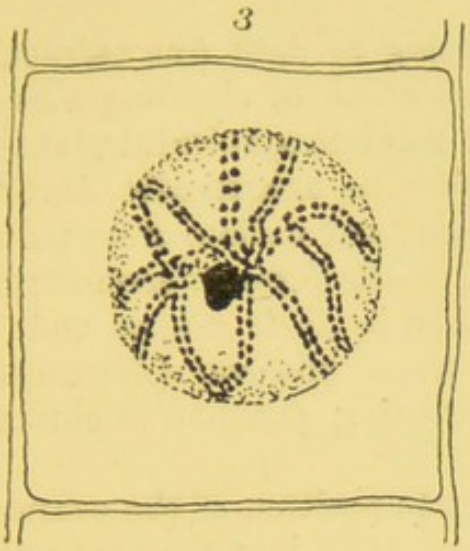
There are possibly other factors, especially in connection with the increase in mass of the chromatin, which must require a supply of phosphorus-containing food material, but these cannot be gone into fully, the chemistry of the process being somewhat obscure.

Microscopically, the **first change** to be noticed in the nucleus is the **increased capacity which this structure shows in the taking up of such stains as hæmatoxylin or safranin.** In this respect it is the **chromatin-granules** which show this increased staining capacity, the nucleoli not showing much difference at first (early prophase). Next, the chromatin-granules become more regularly arranged upon the linin network, and soon the appearance is presented of a definite **chain of granules** set at equal or nearly equal intervals apart upon a continuous coiled thread of linin (see Fig. 76, 2). At a slightly later stage, careful observation has shown that each chromatin-granule **becomes divided into two,** so that there are then two parallel rows of granules arranged regularly upon two threads of linin, the latter structure also having undergone a similar fission to the granules.* During this process, the chromatin-granules have increased in size, and approached one another, so that, finally, there seem to be **two parallel threads** coiled with the limits of the nuclear membrane (see Fig. 76, 2, and Fig. 77, 3). A good resolving power of the microscope is necessary to make out the dual nature of the chromatin band. In the **endosperm** of *Fritillaria*, and **root-tip** of *Hyacinthus*, during mitoses, it is, however, fairly obvious.

These changes complete the early prophase, and the coiled chromatin-band is now known as the **spireme** or **skein** (see Fig. 77, 4). Traces of the nucleoli may still be seen at this stage, but the nuclear membrane has already become indistinct.

The phenomenon now occurs of the **breaking up of the spireme into a number of equal lengths of chromatin,** known as the **primary chromosomes**: this is effected by either mechanical rupture or chemical absorption occurring in the linin-thread at several equidistant points (see Fig. 78, 5). The number of the primary chromosomes varies in different plants, and may be as many as twenty-four (*Lilium*); and it is obvious that each primary chromosome is a **double structure.**

* This was definitely shown to occur in *Helleborus foetidus*, by Mottier, and it can be observed in most cases.



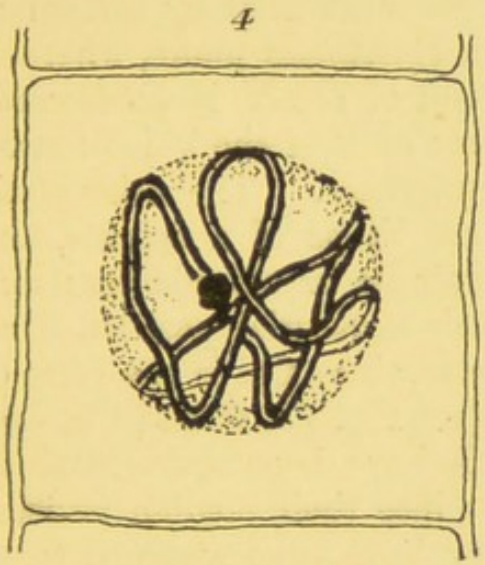
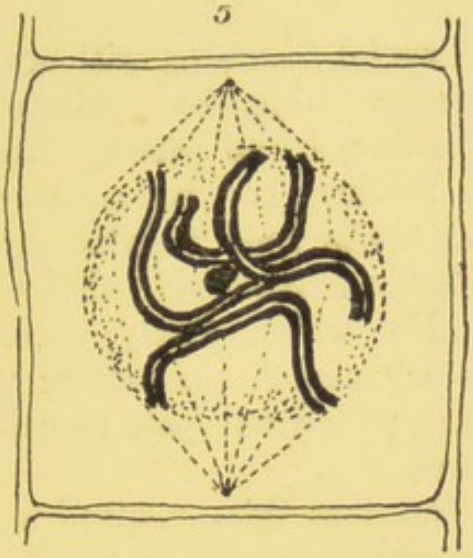


Fig. 77.—3. A Later Prophase. The chromatin-granules have each undergone fission into two.

4. A Complete Spireme. The chromatin-granules have increased in size, and lie so close together as to produce the appearance of a double thread.



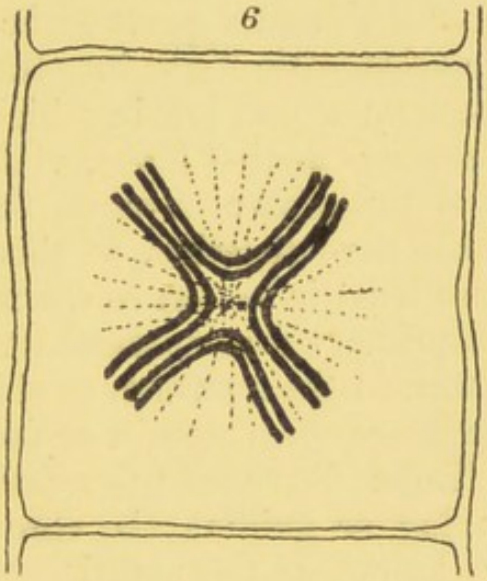


Fig. 78.—5. A Later Prophase. The double band of chromatin has been split up into four primary chromosomes, each of these preserving its double nature. The achromatic spindle is now beginning to appear, the fibrils of the spindle converging to two poles which are at opposite ends of the cell.

6. A Final Prophase (monaster stage) seen in surface view. The primary chromosomes have been guided into the median equatorial plane of the spindle, so as to form a star-shaped figure. Each chromosome lies with its bend towards the centre of the median plane. The prophase is now completed.

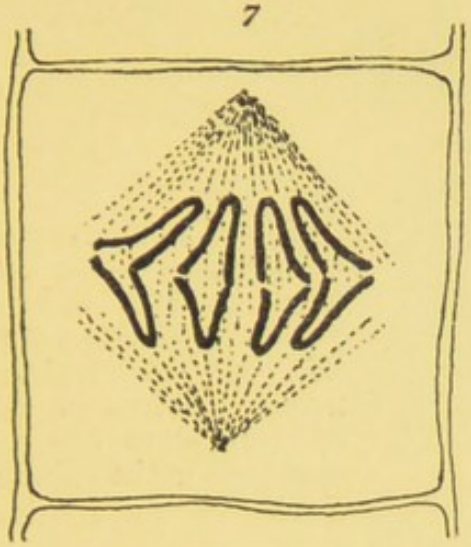
Careful focussing will now often bring to light **fine refractile lines** radiating from points near either end of the long axis of the nucleus, and passing towards the **median equatorial plane** of the nucleus and cell; these lines are the **achromatic fibrils.*** The fibrils soon become more obvious, and radiate from points (**poles**) on either side of the nucleus, in the form of cone-shaped bundles, which (partly) become attached by their central ends to the primary chromosomes; some of them, however (the central ones), pass from pole to pole without being attached to chromosomes.

The next thing noticed is a **change in position of the primary chromosomes.** Each of these becomes bent into the shape of a U or a V, and appears to be dragged (or guided) by certain of the achromatic fibrils into the **median equatorial plane,** where it takes up a position in which the bend of the V looks towards the centre of that plane, whilst the free ends of the V look away from the centre towards the circumference. The achromatic fibrils have together, at this stage, the shape of a **spindle,** and form what is known as the **nuclear spindle** or **amphiaster;** and the primary chromosomes form in their equatorial position what is termed the **monaster** or single **rosette,** since this is the form of the figure when seen in surface view (see Fig. 78, 6, and Fig. 85).

Those fibrils of the spindle which have been influential in pulling or guiding the chromosomes into their median position are known as the **mantle-fibres;** they have been assumed to be **contractile,** and they lie on the outer surface of the spindle in the form of cone-shaped bundles radiating from the poles at each end of the cell. This assumption is, however, partly hypothetical, since some observers will not allow of any of the fibrils being contractile, but bring forward evidence to show that **chemotaxis** plays a *rôle* in the movements of the chromosomes, especially during the **metaphase.** It is, however, quite possible in some cases to make out the cone-shaped masses of fibrils at the beginning of the metaphase (see Plate I., 6 and 8).

The prophase is completed by the time the primary chromosomes have assumed the equatorial position: no trace of nucleoli can be detected at the completion of this phase, and the nuclear membrane has vanished.

* So-called because they do not stain with those dyes which the chromatin takes up.



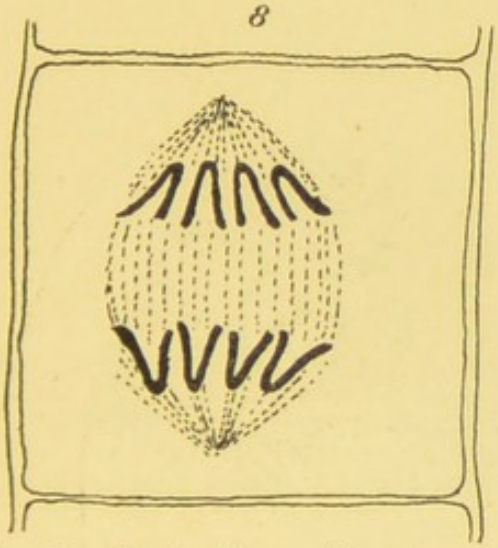


Fig. 79.—7. An Early Metaphase. The two halves of each chromosome are separating from one another in the form of V-shaped secondary chromosomes; the achromatic spindle is now quite a marked feature.

8. A Later Metaphase, showing the two systems of secondary chromosomes travelling away from one another towards the poles of the spindle.

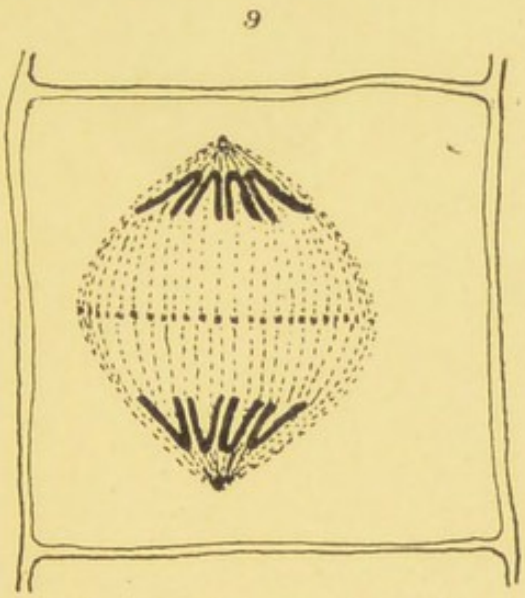


Fig. 80.—9. A stage where the two systems of daughter-chromosomes here almost reached the poles of the spindle (late metaphase). The line of dots along the middle of the spindle indicates the line along which the cell-plate will form.

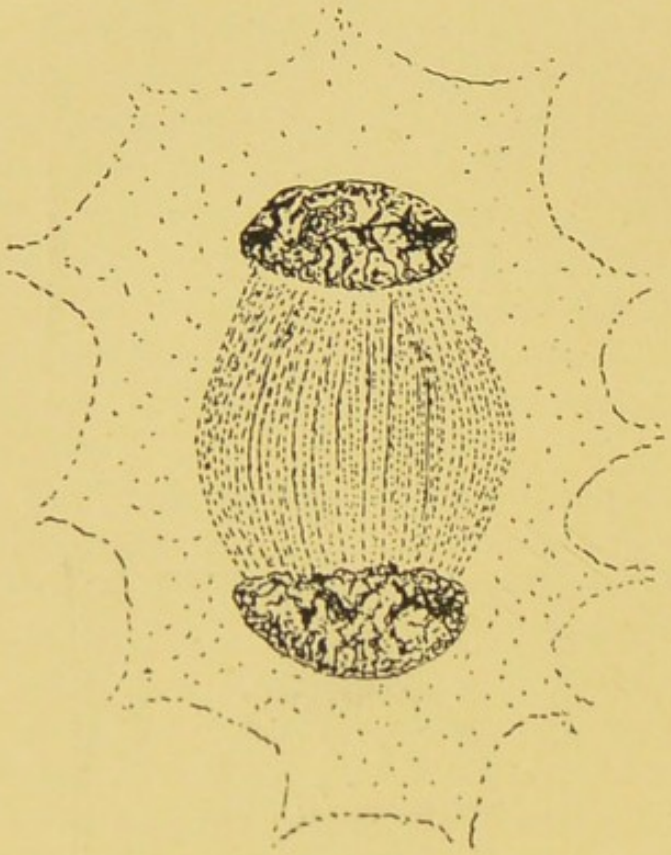


Fig. 81.—An End-stage (Anaphase) from the Developing Endosperm of *Caltha palustris*. The two daughter-nuclei are formed, but no cell-plate has yet appeared in the spindle.

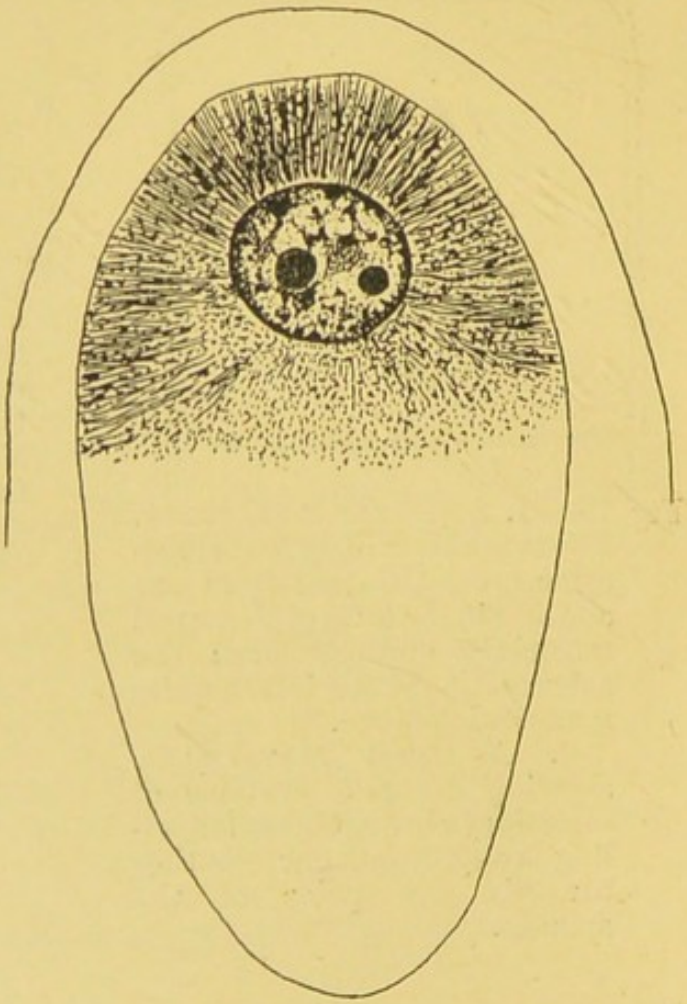


Fig. 81A.—A Quiescent Nucleus lying in the Cytoplasm at the Apex of the Embryo-sac of *Lilium* (four-nuclei stage).

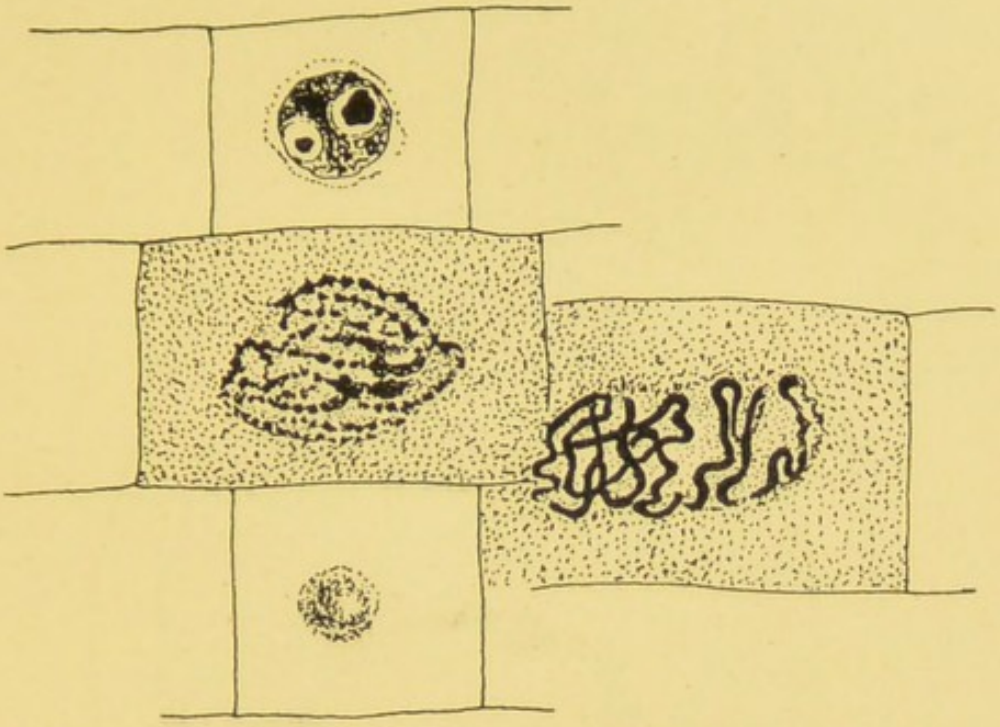


Fig. 82.—Early and Late Spireme Stages (from a photomicrograph, *Hyacinthus* root-tip).

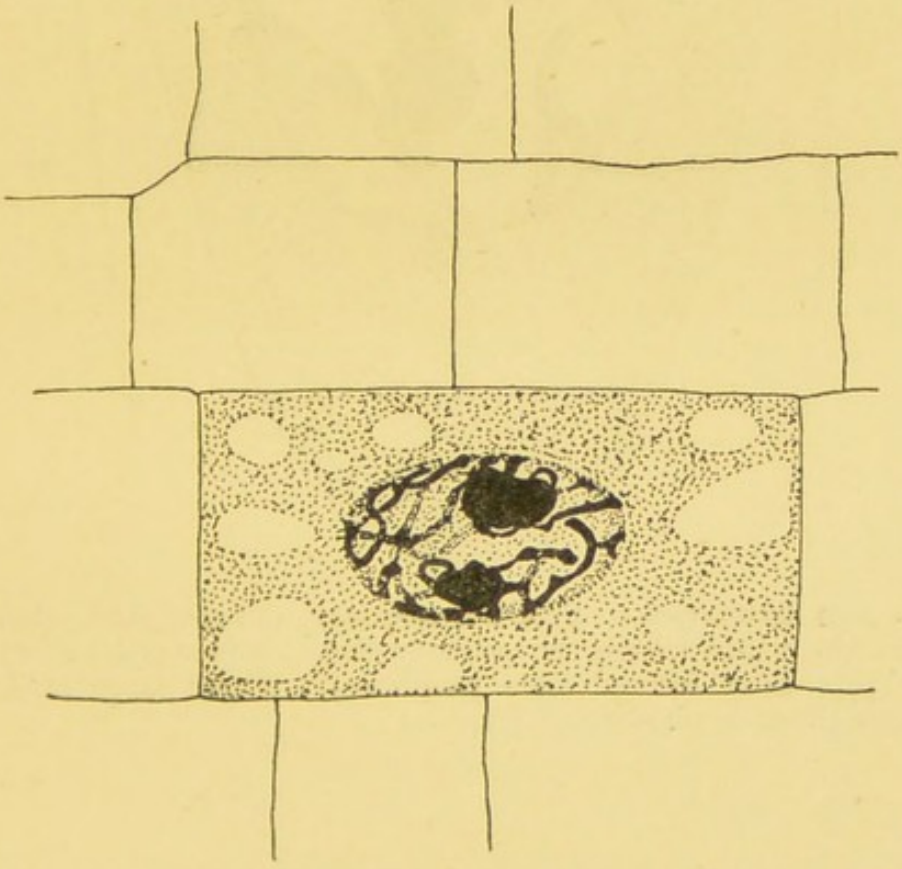


Fig. 83.—A Complete Spireme (from a photomicrograph, *Allium* root-tip).

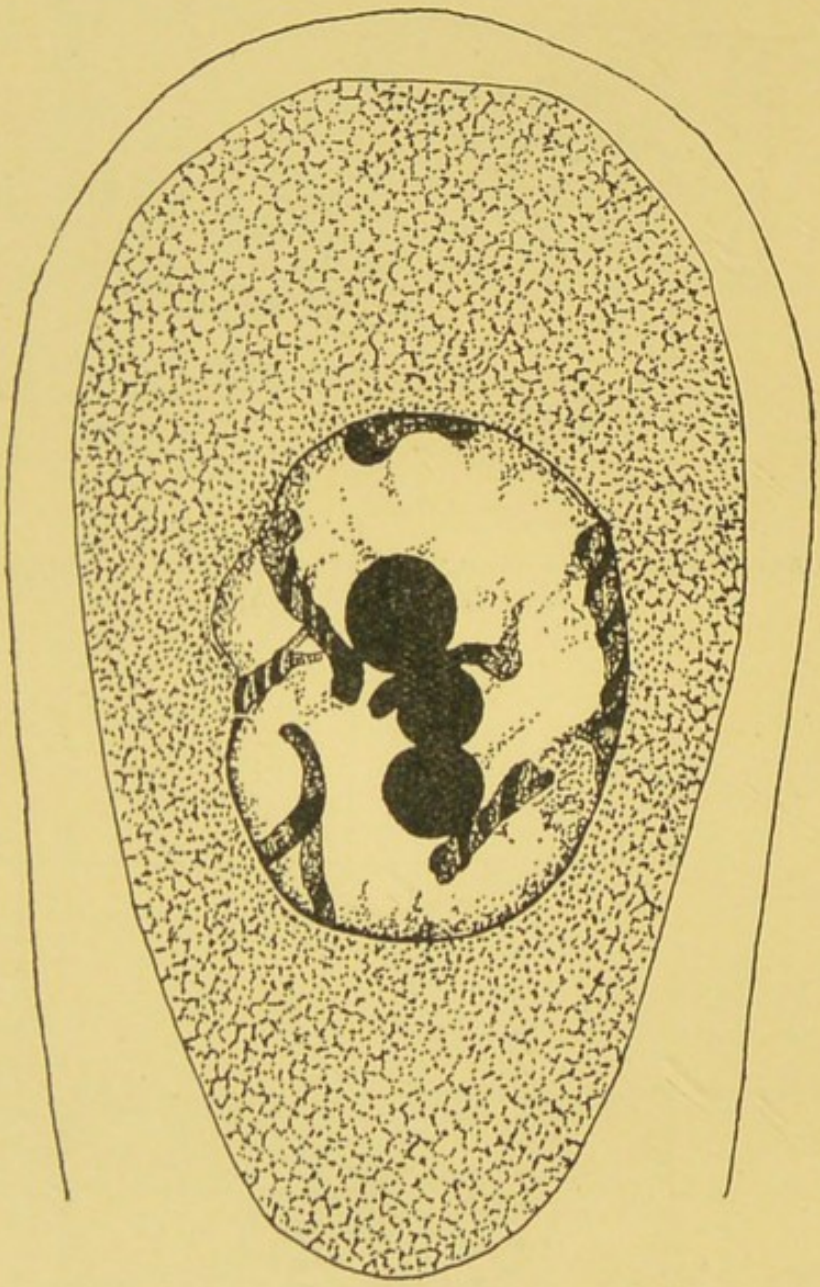


Fig. 84.—The Embryo-sac of *Lilium martagon* showing the nucleus of the sac at the phase where the primary chromosomes (split and twisted) have just been formed (late prophase). Three large nucleoli are present (from a photomicrograph).

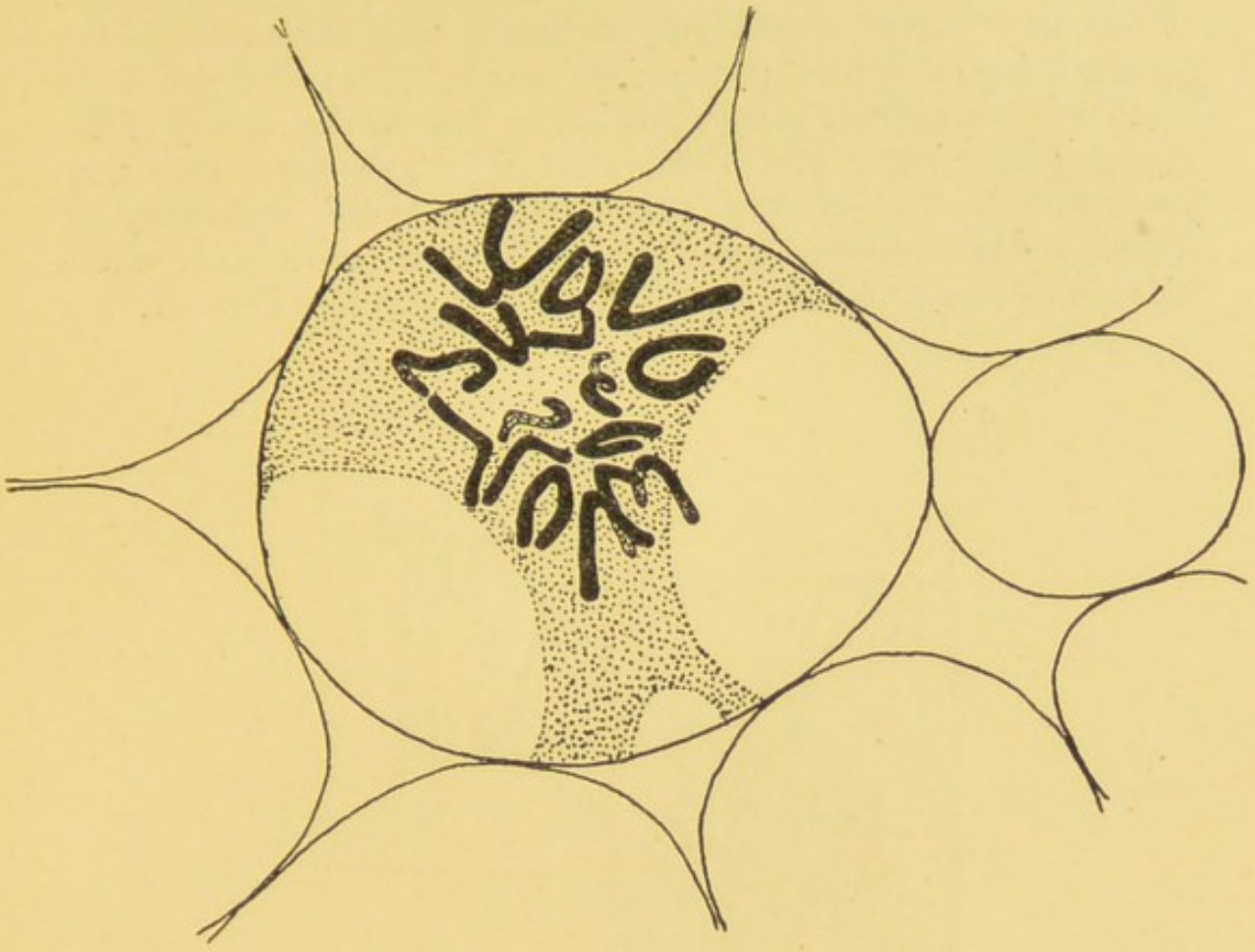


Fig. 85.—The Monaster Stage in a Cell of the Root-tip of *Hyacinthus*. The chromosomes are in reality double, but the duplication cannot be seen when the loops are seen in surface view (from a photomicrograph).

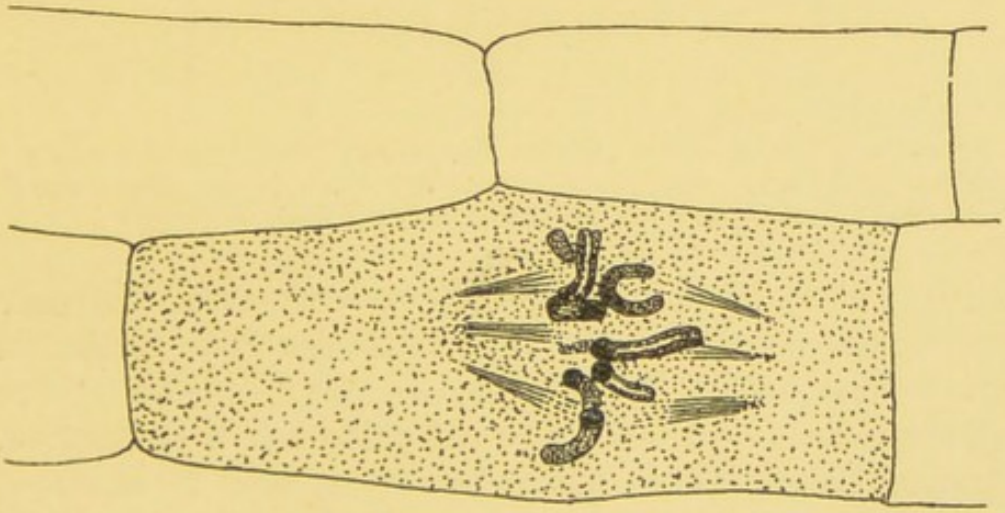


Fig. 86.—The Monaster Stage seen from the side (root-tip of *Allium*).

(β) **The Metaphase.**—This phase commences by the **separation of the two halves of each longitudinally split chromosome,** the bends being the first portions to come apart; the free-ends remain in contact for some time, but at last, by the agency of the mantle-fibres, these are drawn asunder. The appearance now presented is that of **two systems** of so-called **secondary** or **daughter-chromosomes** travelling away from one another, there being an equal number of loops in each system (see Figs. 87, 88).

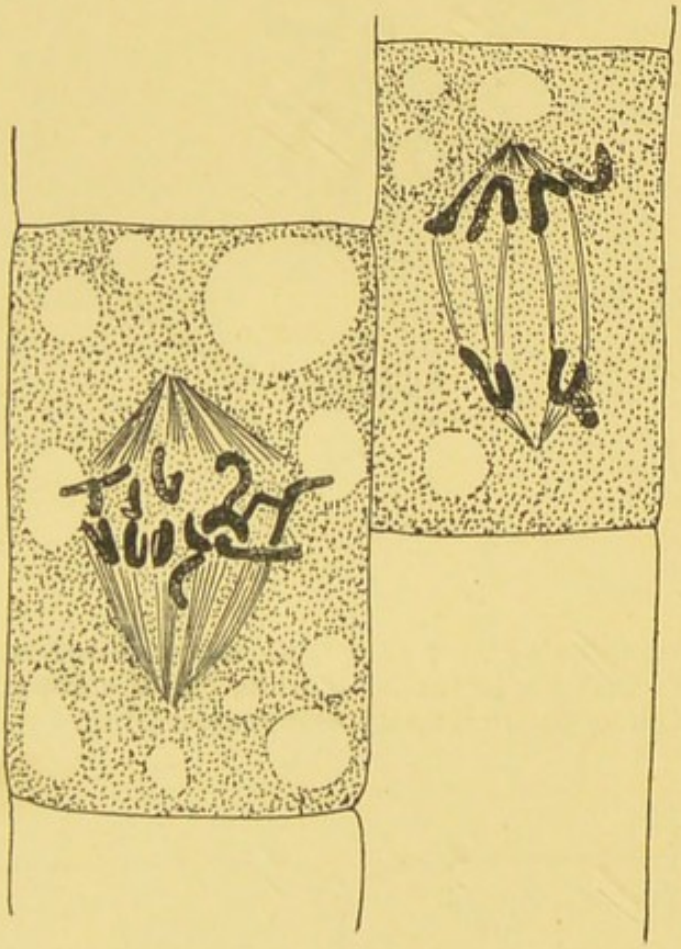


Fig. 87.—Two Cells from *Allium* Root-tip, showing the early metaphase and late metaphase respectively. Note the cone-shaped bundles of mantle-fibres in the left-hand cell.

In surface view, or in slightly oblique sections of the cell, it is now possible to make out two "**rosettes**" of chromosomes; between these are to be seen certain fibres of the achromatic spindle which persist until the cell-plate has been formed, and even after this. These fibrils are composed of the so-called **interzonal fibres,** and are not contractile in nature.

The **later metaphase** shows the two systems of secondary

chromosomes close to the poles of the spindle ; this stage is also known by the terms—**double-rosette** or **diaster-stage** (see Fig. 79, 8, Fig. 80, 9, and Fig. 88). On the lines of the chemotactic theory, the passage of the two systems of chromosomes is effected, not by the agency of the mantle-fibres of the achromatic spindle, but by the **attractive influence** of certain substances in the vicinity of the poles of the spindle (**enzymes**) upon the chromosomes ; nevertheless, distinct cone-shaped bundles of the spindle

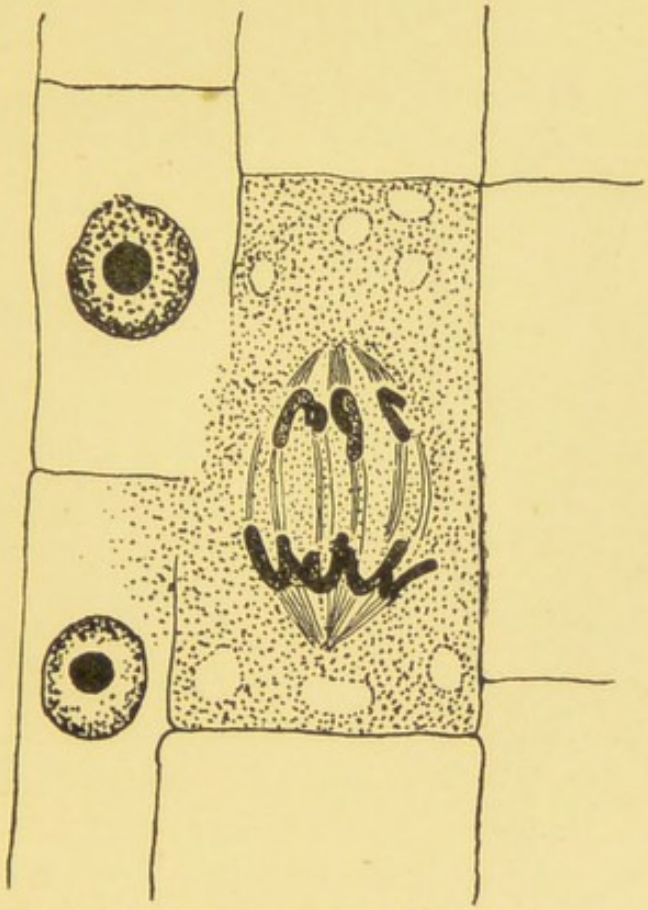


Fig. 88.—A METAPHASE STAGE FROM *Allium* ROOT-TIP, showing two systems of loops widely separated (from a photomicrograph).

fibres can be seen attached in many cases to separate chromosomes along their whole length, so that the theory of the pulling action of the mantle-fibres cannot be lightly dismissed. It is possible that a compromise must be made, both chemotaxis and the action of the mantle-fibres being taken into account.

(γ) and (δ) **The Anaphase** and **Telophase** ; formation of the **cell-plate.**—The final or end-stages in mitosis comprise (*a*) **Involution of the secondary chromosomes,** and (*b*) **The formation of the cell-plate.**

(*a*) After the daughter-chromosomes have reached opposite poles of the achromatic spindle, a short period of quiescence supervenes; then the chromosomes become joined end to end so as to form a typical **spireme** at each pole (**dispireme stage**), the band of chromatin being of a single and not a double nature. Each spireme is then broken up into **chromatin-granules** arranged upon a linin thread, and **nucleoli** once more make their appearance (see Figs. 81, 89).

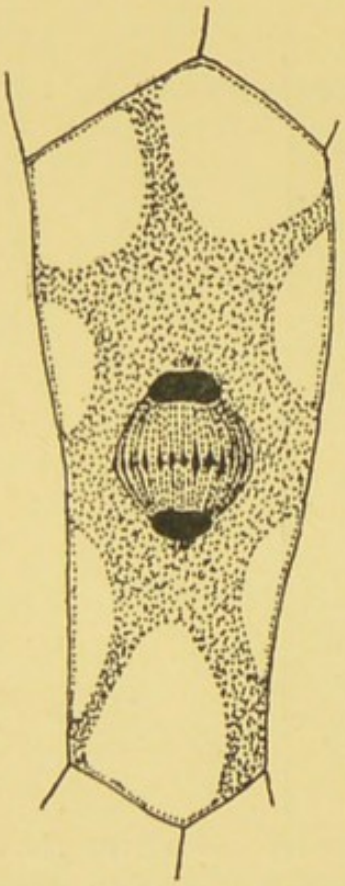


Fig. 89.—An End-stage from a Cell of the Young Female Cone of *Larix Europæa*. The cell-plate is just beginning to form.

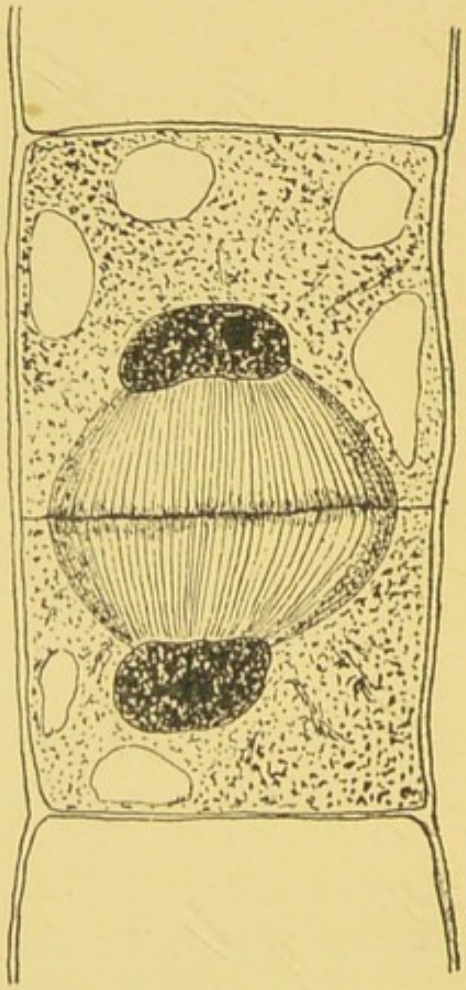


Fig. 90.—Formation of the Cell-plate (complete partition wall between two daughter-cells). The daughter-nuclei are complete (from *Hyacinthus* root-tip).

(*b*) Whilst these changes have been going on in the daughter-nuclei at each pole of the spindle, small **thickenings** appear on the fibrils of this structure in the **median equatorial plane**: these are the first indications of the **cell-plate**. Gradually these thickenings enlarge, and at last join one another all round, so

that a delicate **film** or plate is produced, separating the two halves of the spindle from one another; concomitantly with this change, the whole spindle **contracts** somewhat towards the median plane, and this contraction has the result of bulging out the circumference of the spindle, so that ultimately it touches the side walls of the cell. In this manner the cell-plate comes to extend right across the cell and constitutes the **rudimentary partition-wall** separating the two resulting cells from one another (see Fig. 90). The cell-plate is in its later stages composed of chemically pure **Cellulose**, and it has been shown that during its formation the protoplasm (or kinoplasm) becomes directly converted into cellulose by the splitting off of its proteid and amine portions.

The two halves of the spindle lying on either side of the cell-plate persist, and the achromatic fibrils become ultimately converted into **bridles of cytoplasm**, which communicate with one another through minute "**pits**" in the partition-wall.

The **origin of the achromatic spindle** is somewhat hypothetical; thus it has been supposed to arise from the **kinoplasm**, just outside the nuclear membrane, but at times it seems that it takes its origin from the **nuclear plasm**. Some observers state that the spindle-fibres arise early and lie as a sort of feltwork just outside the nucleus, which, as mitosis proceeds, pushes its way into the interior of the nucleus towards the chromosomes. In *Stypocaulon* and *Erysiphe*, according to Harper, the spindle is an **intra-nuclear** formation, so that here it would appear to arise from the nuclear-plasm.

In those cases where, as in lower plants, **centrosomes** are formed in the cell, the achromatic spindle is an early formation, and arises between the centrosomes, close to the nucleus, during the early prophase. Moreover, fibrils, known as the "**astral rays**," stretch out in all directions from the poles or centrosomes, and not only into the interpolar region.

With regard to **variation in form** of the chromosomes, it may be mentioned that at times the chromosomes may take on the form of **rings** instead of loops, the free ends of the loops remaining united for some time. This is known as **heterotypic mitosis**, the process above described being normal or **homotypic mitosis**. Moreover, it is an interesting fact, that during the reproductive divisions in the microspore and embryo-sac of

Higher Plants, the number of the primary chromosomes is "**reduced**" to half of what it is during the vegetative division of the same plant. This is known as **cell-division with reduction.** It occurs, for example, in *Osmunda regalis* in the mitoses occurring in cells of the prothallus (gametophyte).

Note.—Some of the various "fixing" reagents used for the preparation of material for the study of mitosis, and also a list of plants and organs suitable for this study, will be mentioned here.

(*a*) *Flemming's Solution.*—This is a very useful reagent for the rapid fixation of quickly-growing tissues, such as root-tips, one modification of it being as follows:—

5 per cent. chromic acid, - -	10 c.c.
2 per cent. osmic acid, - - -	5 c.c
Glacial acetic acid, - - - -	1 c.c.
Distilled water up to - - -	50 c.c.

This solution may be used more dilute if required. Root-tips fix in it in about 12 hours, and, after fixing, should be well washed in distilled water and transferred progressively to the following strengths of alcohol: —50 per cent., 70 per cent., 90 per cent., and, finally, absolute alcohol. By this method the tissue is hardened. For preserving after hardening, the root-tips or other tissue should be kept in pure methylated spirit.

(*b*) *Chromic Acid.*—This may be used in 5 per cent., or 2 per cent., or ½ per cent. solutions in distilled water. It is not so good as Flemming's solution as a fixing reagent. It may be made more useful by the addition of acetic acid.

(*c*) *Absolute Alcohol.*—This both fixes and hardens tissues, but is not suitable for delicate organs.

(*d*) *A Mixture of Acetic Acid and Alcohol* (about 55 per cent. strength) is sometimes used as a fixing agent.

(*e*) *A Solution of Corrosive Sublimate in Alcohol* (2 to 5 per cent.) is at times a useful fixing reagent. It is used mostly for animal tissues, more especially for the fixing and hardening of larval tissues.

The most serviceable reagents for the fixation of plant-tissues, particularly for those in which it is desired to study mitosis, are *Flemming's solution* and *Chromic acid solution*, since these, if used dilute, will not cause much preliminary shrinking of the cytoplasm.

Plants suitable for the study of cell-division are the following:—*Hyacinthus* (root-tips of water-cultures), *Allium* (root-tips of water-cultures), *Fritillaria* (endosperm, root-tips of water-cultures), *Lilium* maturation stages in the embryo-sac, pollen mother-cells), *Larix* (cortex and medulla of young ♀ cone).

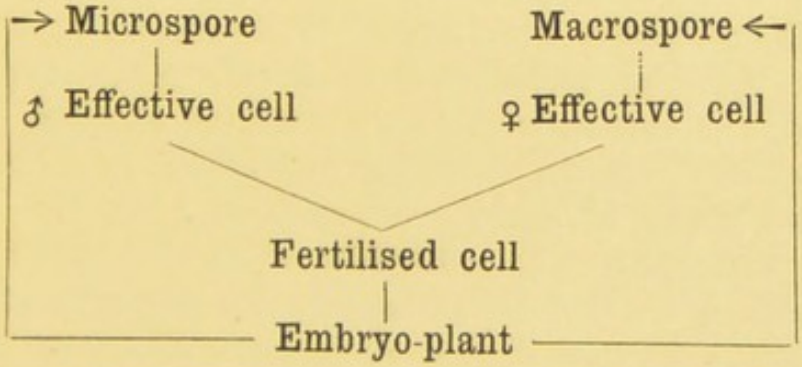
Longitudinal and transverse sections should be made by cutting with a flat razor in split pith, or tissues may be hardened and embedded in *celloidin* or *paraffin*, and microtome sections made, a somewhat more lengthy process.

CHAPTER IX.

CELLS HAVING THE FUNCTION OF REPRODUCING THE SPECIES.

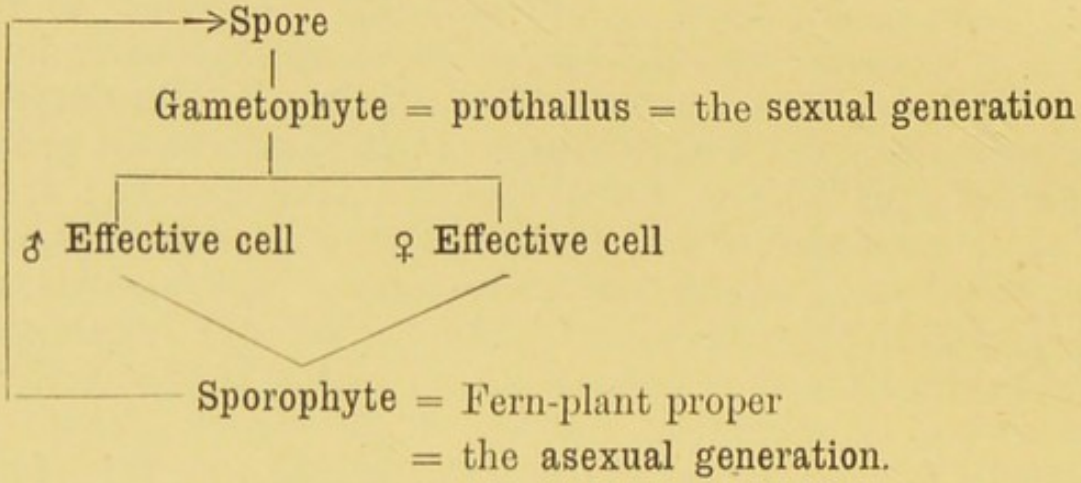
In this chapter a very important subject will be dealt with—viz., **reproduction**—and it will be found convenient, to start with, to examine the reproductive cycles as they occur in the three great groups of the Higher Plants—*i.e.*, **Angiosperms**, **Gymnosperms**, and **Pteridophyta**. In all these, certain primary **essential cells** arise in special organs, the reproductive organs. Thus, in Angiosperms and Gymnosperms, the **male cells**, or, as they are usually termed, the **microspores** or pollen-grains, arise in the anthers of the stamens of a flower; and the **female cell**—viz., the **macrospore** or **embryo-sac**—is formed in the nucellus of the ovule, or sporangial portion of the flower. These two elements, the microspore and macrospore, undergo, first of all, a process known as **maturation**, in which certain cells are formed in each structure; one of these cells, in each of the fully matured sexual elements (microspores and macrospores) being the **effective cell**, which, by fusion with its counterpart, results in the production of a **fully-fertilised cell**, from which the **embryo-plant** is reproduced.

Thus, to put the process into tabular form, the following stages are noted:—



= spore-forming or asexual generation.

In the Higher Pteridophyta (Ferns), the reproductive cycle is somewhat more complicated, inasmuch as **two separate generations** are produced. One of these—the **sexual form**—is known as the **gametophyte,** and is the product of the germination of the **spore**, the latter arising in a special organ, the sporangium, which occurs on the fern-plant proper. The other, or **asexual generation,** is the **sporophyte,** and is the result of the fusion of two effective cells produced in special organs, which arise on the under surface of the gametophyte, or **prothallus**, as it is sometimes called. Thus, tabulating as before, the following sequence is noted :—



The arrows indicate in both tables the completion of the cycle.

This reproductive cycle, then, includes two distinct generations, and, for this reason, the Higher Pteridophyta are said to exhibit the phenomenon of an **alternation of generations.**

With these few introductory remarks, it is possible to proceed to the study of the formation and maturation of the essential cells in Angiosperms, Gymnosperms, and Pteridophyta, and, in all, the process of **fertilisation** and formation of the embryo-plant will be shortly described. With regard to the **Pteridophyta**, it may be mentioned that **two main types** can be recognised, viz., one in which only **one kind of spore** is produced by the sporophyte, or spore-bearing plant, and the other in which **two kinds of spore** are produced. In the latter, **two separate gametophytes or prothallia** are formed, and the effective cells thus arise on two separate sexual generations, there being in this case a sort of **double alternation of generations.** The two types are known respectively as **Homosporous** (one spore

only) and **Heterosporous** (two kinds of spore), and both will be studied on account of the valuable comparisons which can be made between their reproductive cycles and those which occur in the Angiosperms and Gymnosperms.

After reproduction in the higher types of plant has been studied, a brief description will be given of the process as it occurs in the **Bryophyta, Fungi,** and **Algæ.** It is not intended to examine very fully reproduction in the Fungi, so that only an outline of this will be given. The important point is to gain a clear idea of the reproductive cycles met with in the three great groups mentioned above.

A. Reproduction in Angiosperms.

In the **Angiosperms** the essential primary sexual elements are the following:—

a. The **microspore** or pollen-grain.
b. The **macrospore** or embryo-sac.

Each of these undergoes a process of **maturation**, and at the completion of this **fertilisation** takes place.

a. **The Microspore: its Origin and Maturation.**—The **pollen-grains** are produced in certain parts of the anthers of a flower; usually four rudimentary masses of cells are set off in the young anther, and these are the **archesporial cells**. These cells arise by the division of a **primary archesporial cell,** and of the resulting mass the outermost cells give rise by further divisions to a sheathing layer known as the **tapetum**; the remaining inner mass form the **pollen mother-cells**, from which the **microspores** are ultimately produced (see Fig. 91, *a*).

At a somewhat later period each **mother-cell** undergoes division into **two** cells, the resulting cells dividing again (see Fig. 91, *b*, *c*, *d*), so that ultimately there are **four** nucleated masses of cytoplasm enclosed within the original wall of the parent-cell. Each of the four masses is a **potential microspore,** and soon assumes a thin wall of cellulose which, later on, becomes modified in a manner which will be described. A large number of mother-cells are often present, and it will be seen that the number of microspores ultimately formed is four times as great as that of the mother-cells.

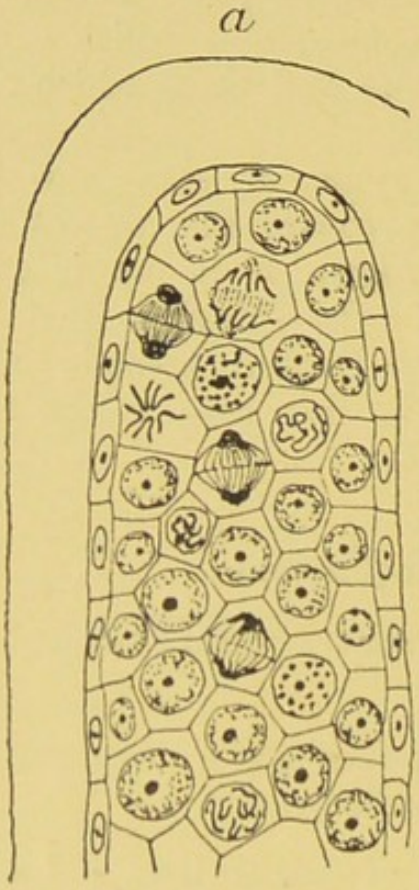
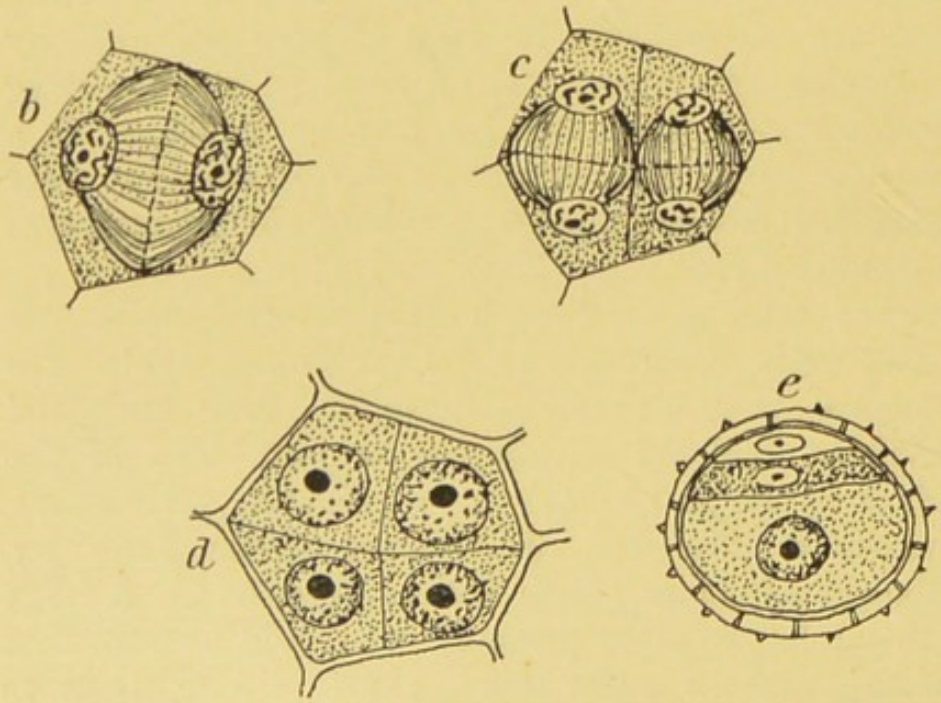


Fig. 91.—*a*, A portion of a longitudinal section through a young anther of *Polygonatum*, showing part of the pollen-sac, filled with pollen mother-cells in all stages of division. *b*, A single mother-cell which has divided into two, the cell-plate having just been formed. *c*, The same after the second division, walls being formed at right angles to the first wall. *d*, Four complete daughter-cells (young microspores) still enclosed by the wall of the original mother-cell. *e*, A mature microspore. Three cells are present, the uppermost one being the prothallial cell, the middle one the antheridial or generative cell, and the lowest the vegetative cell, from which ultimately the pollen-tube is formed.



After a time the wall of the parent-cell is ruptured or becomes absorbed, and the young microspores come to lie free in the **pollen-chambers** or sacs (microsporangia), which are lined by the remains of the tapetum. The immature **microspore** presents the following features:—

i. A thin **cell-wall** externally.
ii. Internally, granular **cytoplasm,** in which are a large nucleus and food-granules (starch, &c.).

The wall soon becomes modified so as to consist of two distinct layers (see Fig. 91, *e*)—viz., an outer one, the **extine,** which is thick, and often beautifully marked by reticulations, projections of various shapes, or thin-wall areas; and an inner one, the **intine**, which encloses the cytoplasm. From the markings on the extine it is often possible to distinguish the genus or species from which the pollen was derived.

Maturation of the microspore consists in the formation of certain cells by the division of the cytoplasm and nucleus of the main cell. At first a small cell is occasionally cut off, which is known as the **prothallial cell,** the significance of which will be pointed out when the Heterosporous Ferns are considered. Next, a cell is cut off from the remaining larger cell; this is the so-called "**generative**" **cell,** and is the effective *male* cell in fertilisation. Thus, in the mature microspore there are present **three cells** enclosed within the intine (see Fig. 91, *e*), viz.:—

α. The prothallial cell; this cell is generally absent. It may, however, e seen in the microspore of *Sparganium*.
β. The **generative cell.**
γ. The **vegetative cell,** this being the large cell left after the formation of *α* and *β*. It is this cell which forms the **pollen-tube** during fertilisation.

All these maturation changes in the microspore may take place whilst it is resting on the stigma of the ovary. The further changes which take place—viz, formation of the pollen-tube and division of the generative nucleus—are best considered under fertilisation.

b. **The Macrospore: its Origin and Maturation.**—The **macrospore** or **embryo-sac** is contained at the apex of the nucellus of the ovule (macrosporangium) in Angiosperms, and has the following origin:—The terminal hypodermal cell of the axial row of cells in the young nucellus is the so-called **archesporial cell** or

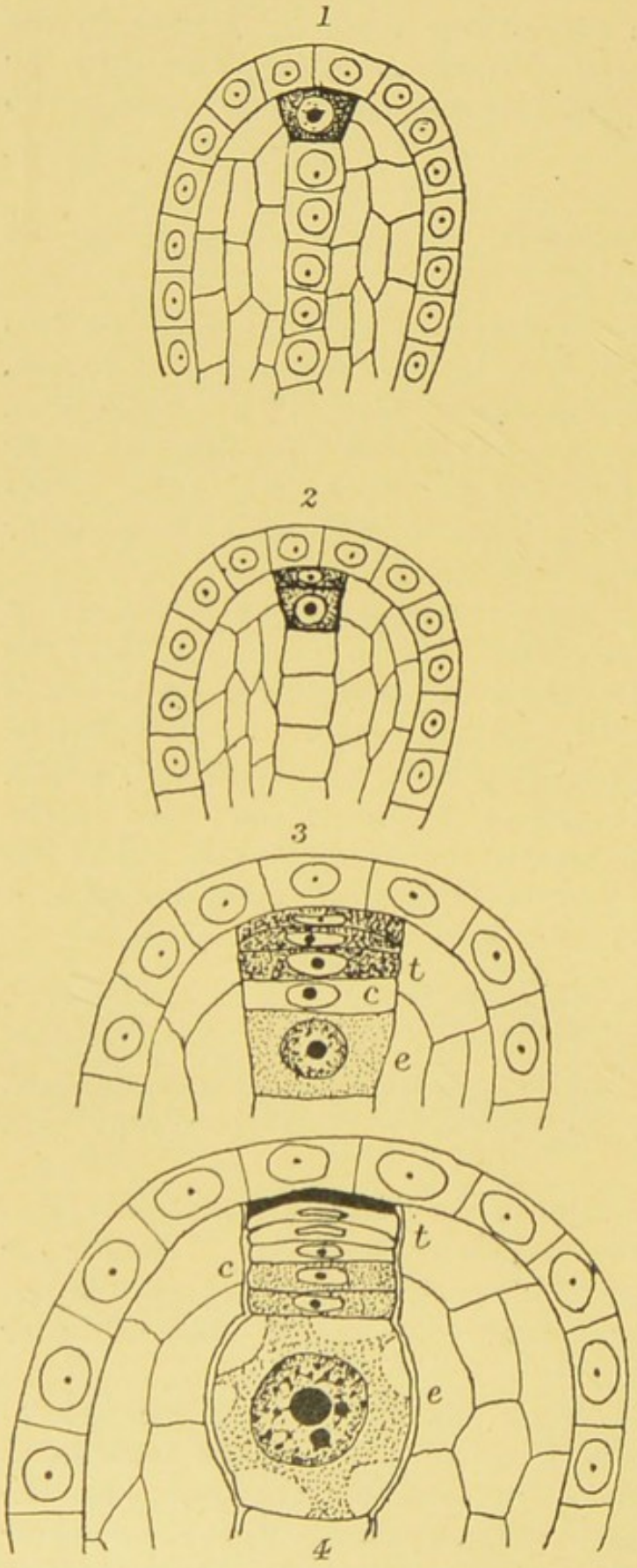


Fig. 92. — 1. The Young Nucellus of an Angiosperm (*Lilium*). The dark cell is the hypodermal terminal cell of the axial row of cells, and is the mother-cell of the embryo-sac (archesporial cell).

2. The archesporial cell has divided into two—viz., an upper or tapetal cell, and a lower larger cell.

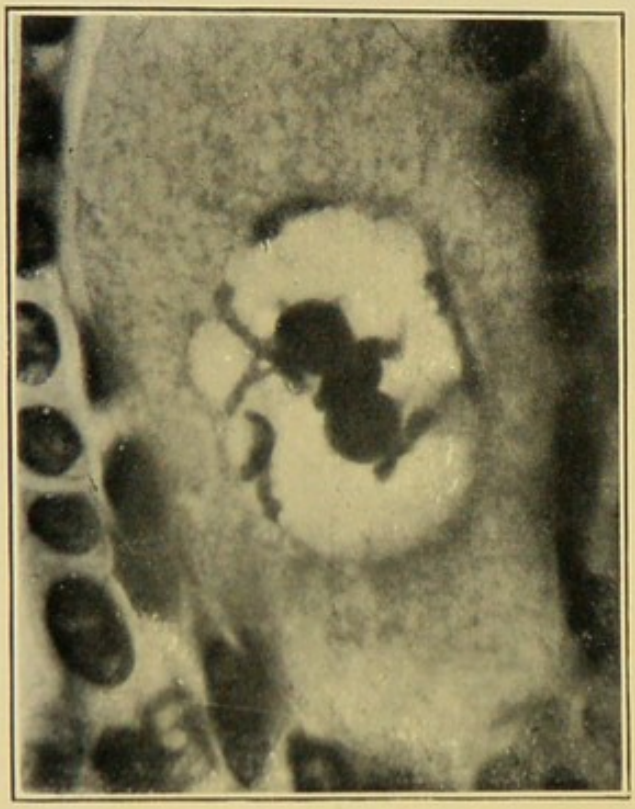
3. The tapetal cell has divided into three secondary tapetal cells, and the lower one has had a small cell — the cap-cell—split off from its upper end. The lowest cell, *e*, is the young embryo-sac.

4. The cap-cell has divided into two, and the embryo-sac (macrospore) is enlarging.

To face p. 123.]

PLATE III.

1



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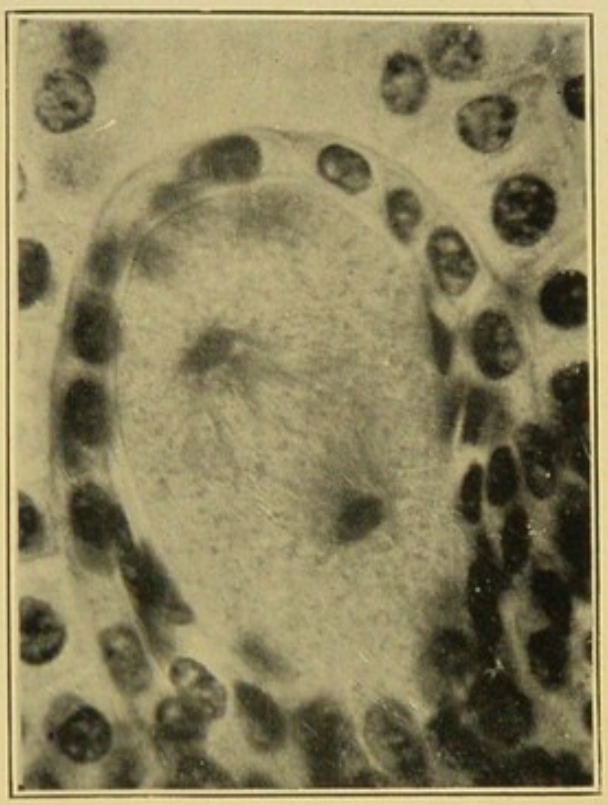

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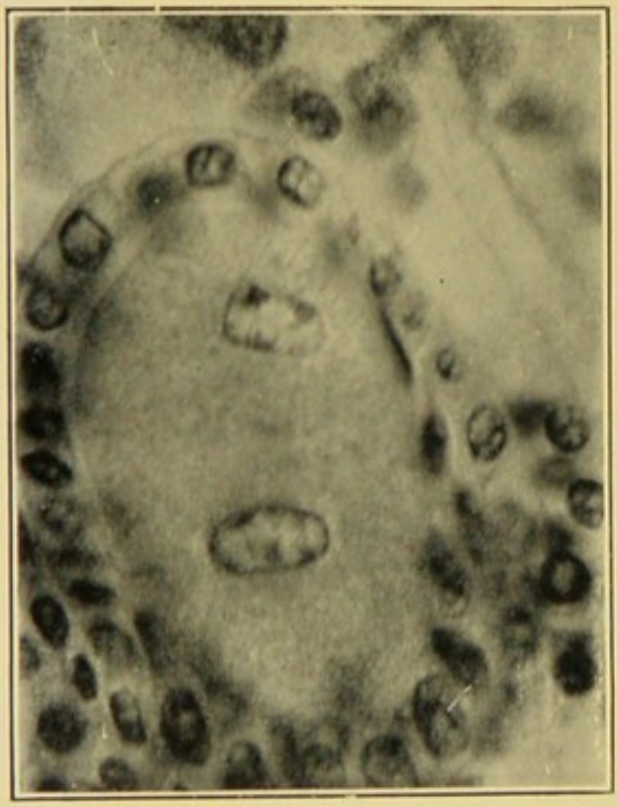

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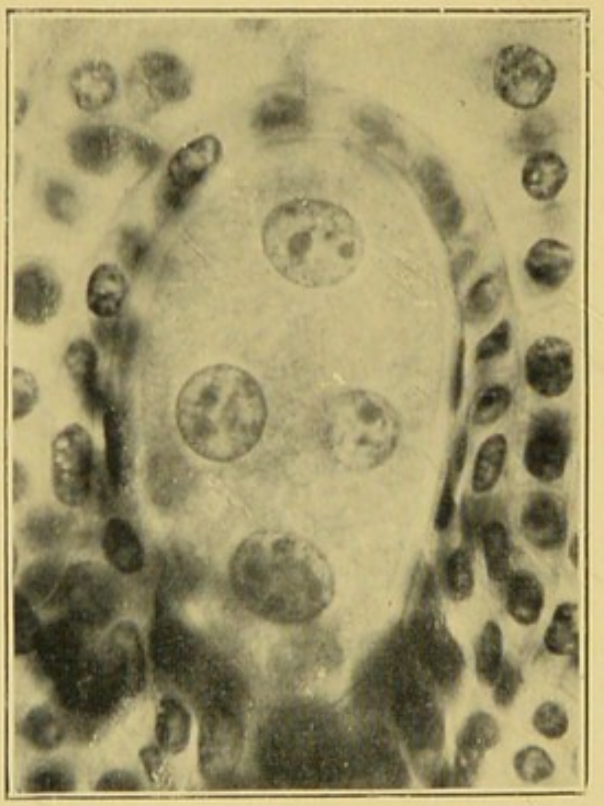

PLATE III. (Stages in the Maturation of the Embryo-sac).

1. A photomicrograph of the embryo-sac and its nucleus at the stage where the latter is about to undergo its first mitotic division (*Lilium*).
2. A photomicrograph showing the completed first division (*Lilium*).
3. A slightly later stage than 2, showing the completed daughter-nuclei.
4. End of the second division, four nuclei being now present.

The next stage would be that where each of the nuclei in 4 have divided again, leading to the presence of eight nuclei, four at each end of the embryo-sac.

mother-cell of the embryo-sac (see Fig. 92, 1). This cell divides into an upper or **primary tapetal cell**, and a lower larger cell; the primary tapetal cell gives rise to three or more **secondary tapetal cells**, which, later on, become obliterated by pressure.

The lower larger cell has cut off from its upper end a cell which soon divides into two (so-called cap-cells), one of the resulting cells dividing again; so that, finally, there are present in a typical case seven cells (see Fig. 92, 2, 3, and 4), viz.:—

i. The three **tapetal cells.**
ii. An intermediate tier of three cells, so-called **cap-cells**; and
iii. A large lower cell, which is the **rudimentary embryo-sac**; the cap-cells (ii.) become obliterated as well as the tapetal cells (i.) by the pressure caused by further growth of the embryo-sac.*

The young **embryo-sac** (**macrospore**) is a large cell possessing **cytoplasm** and a relatively large **nucleus**. In the latter are, as a rule, several nucleoli and an open chromatin reticulum. The embryo-sac increases in size enormously, and soon comes to be one of the largest cells present in the plant.

Maturation of the macrospore consists in the occurrence of certain changes in the cytoplasm and nucleus of this cell which result in the production of the **essential female cell** or **egg-cell**, and certain other accessory cells or nuclei, which will now be described (see Plate iii.). The first change noticed is the **division of the nucleus of the embryo-sac into two** by the mitotic method of nuclear division; another division then takes place in each of these nuclei, so that there are now **four nuclei** present in the cytoplasm, situated usually at the angles of regular figure (see Plate iii., 4, and Fig. 93). A further division of each of these four nuclei results in the production of **eight nuclei**, four of which become massed together at the upper pole of the embryo-sac and four at the lower pole. Of these eight nuclei, one from each end passes to the middle of the embryo-sac, and these remain for a time close together; they are the so-called **polar nuclei** (see Fig. 94), and in a short time they fuse to produce the **definitive nucleus** (see Figs. 95, 96, and 97). At this stage there are then present in the embryo-sac **seven** nuclei, three at each end and

* See Goebel, *Outlines of Classification and Morphology.*

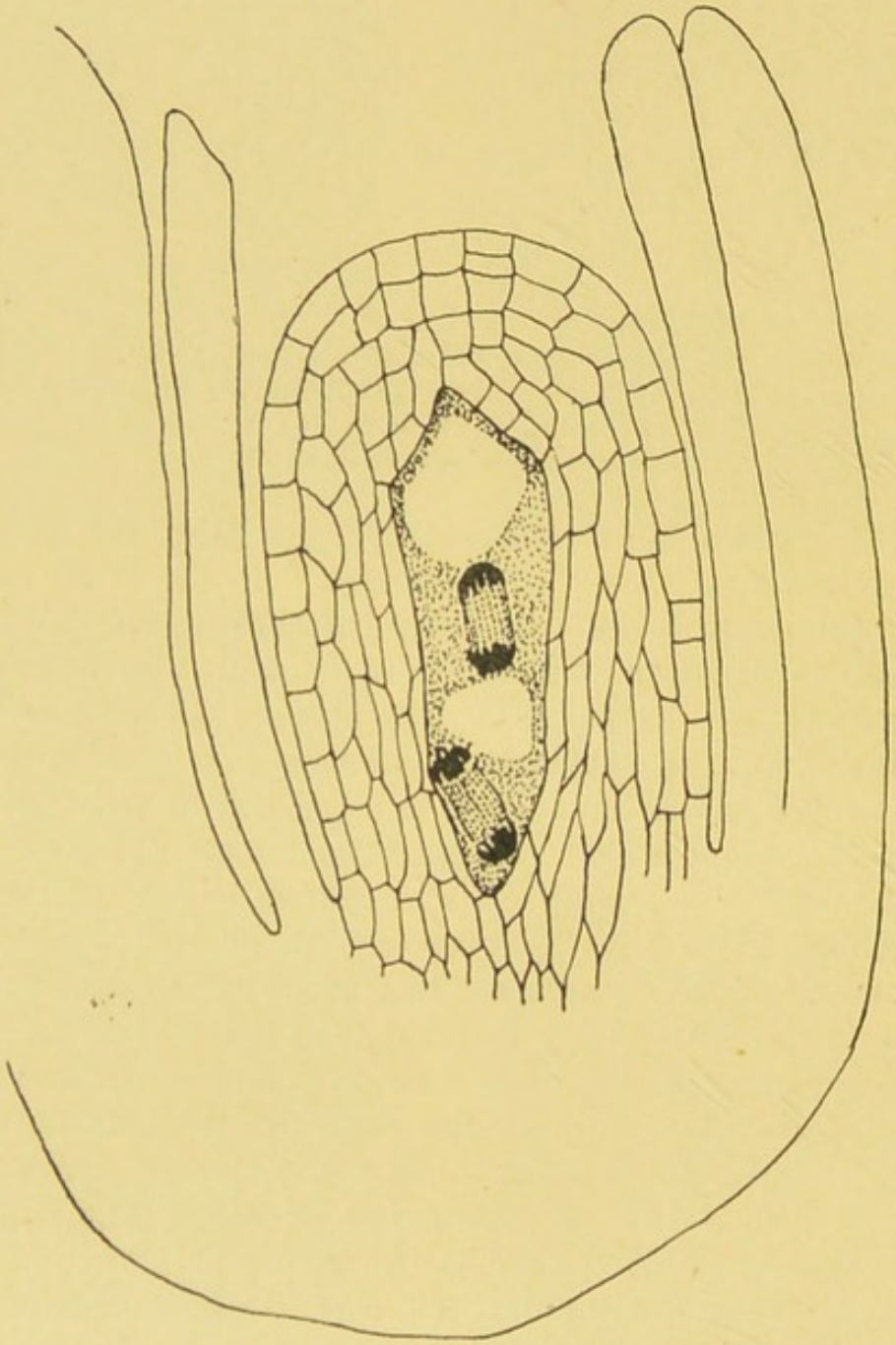

Fig. 93.—The Young Ovule of *Caltha palustris*, showing the embryo-sac at the stage where two mitotic figures are present, end of the second division (from a photomicrograph).

one larger one in or near the centre. The cytoplasm becomes distributed round them in such a way as to lead to the presence of three cells at each end, and the central definitive nucleus is usually held in a central mass by "bridles" of protoplasm. Of the six cellular structures present the three at the upper end constitute the **two synergidæ** (lying uppermost) and the **egg-cell**, the latter of which is the effective female cell (also termed the **oosphere**),

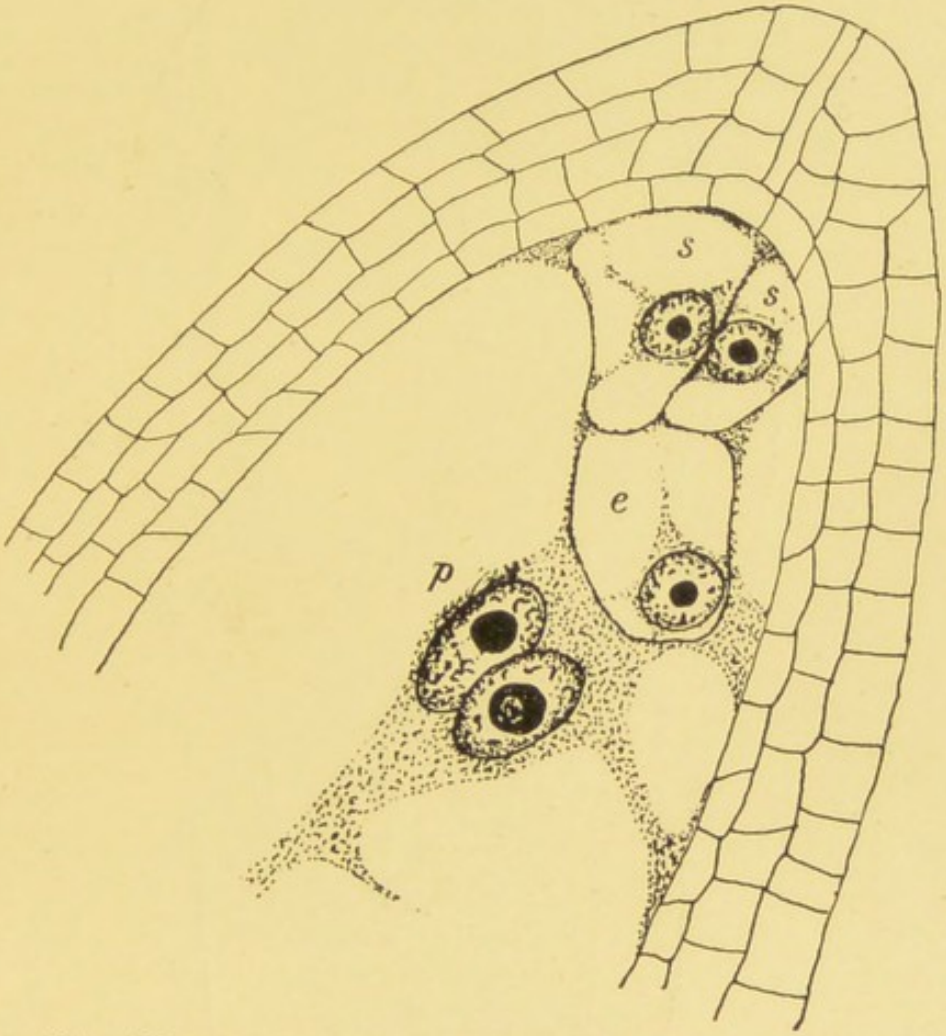

Fig. 94.—The Upper End of the Embryo-sac of *Helleborus niger*, showing fusion of the "polar" nuclei. The two synergidæ (*s*) and the egg-cell (*e*) are also seen lying above the polar nuclei (from a photomicrograph).

whilst the three at the lower end are the **antipodal cells**. At this stage the macrospore is completely matured and ready for fertilisation.

[Most of the preceding stages described may be seen in Plate iii. and Figs. 93 to 97 inclusive.]

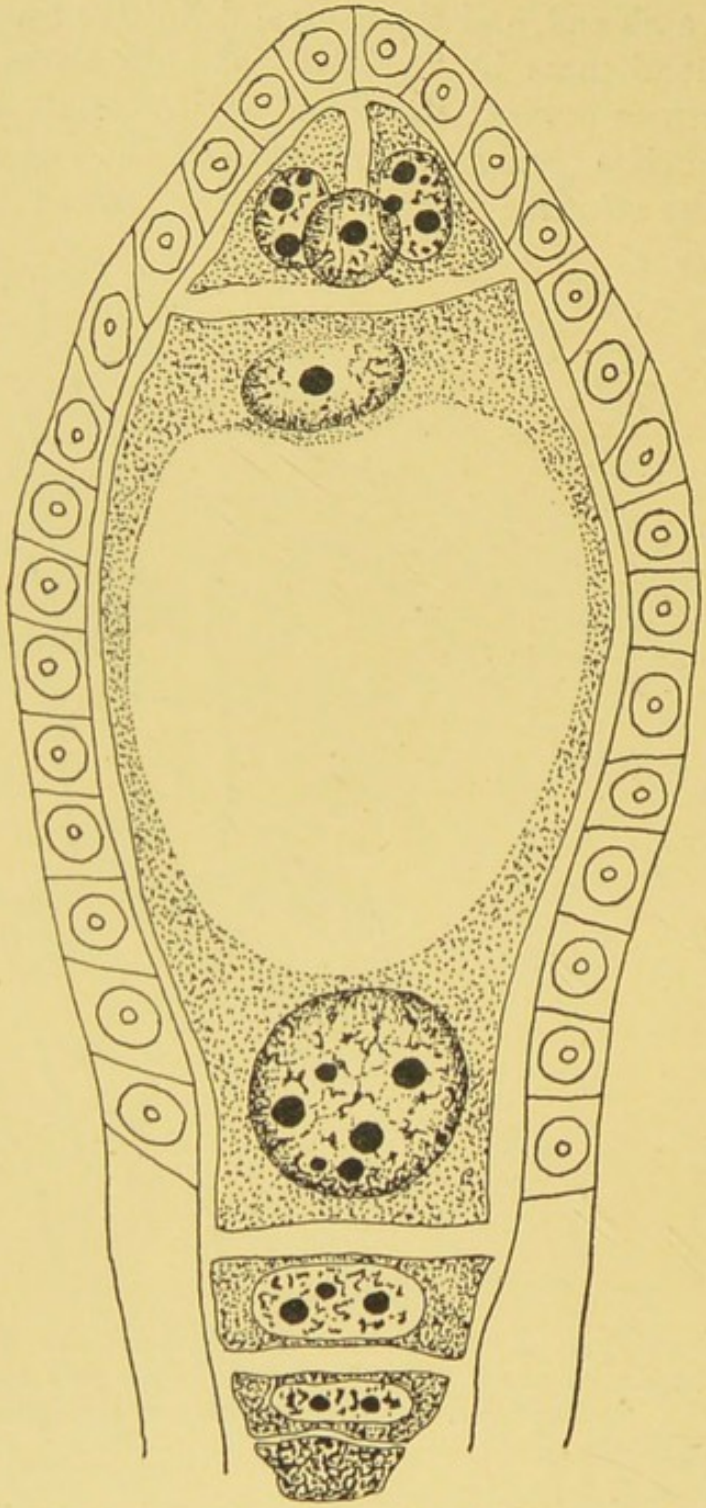

Fig. 95.—The Completely Matured Embryo-sac of *Lilium*.—It shows at the upper end the synergidæ, one of the generative nuclei, and the egg-cell nucleus, and, at the lower end, the large spheroidal definitive nucleus and three antipodal cells.

[*To face p.* 126.

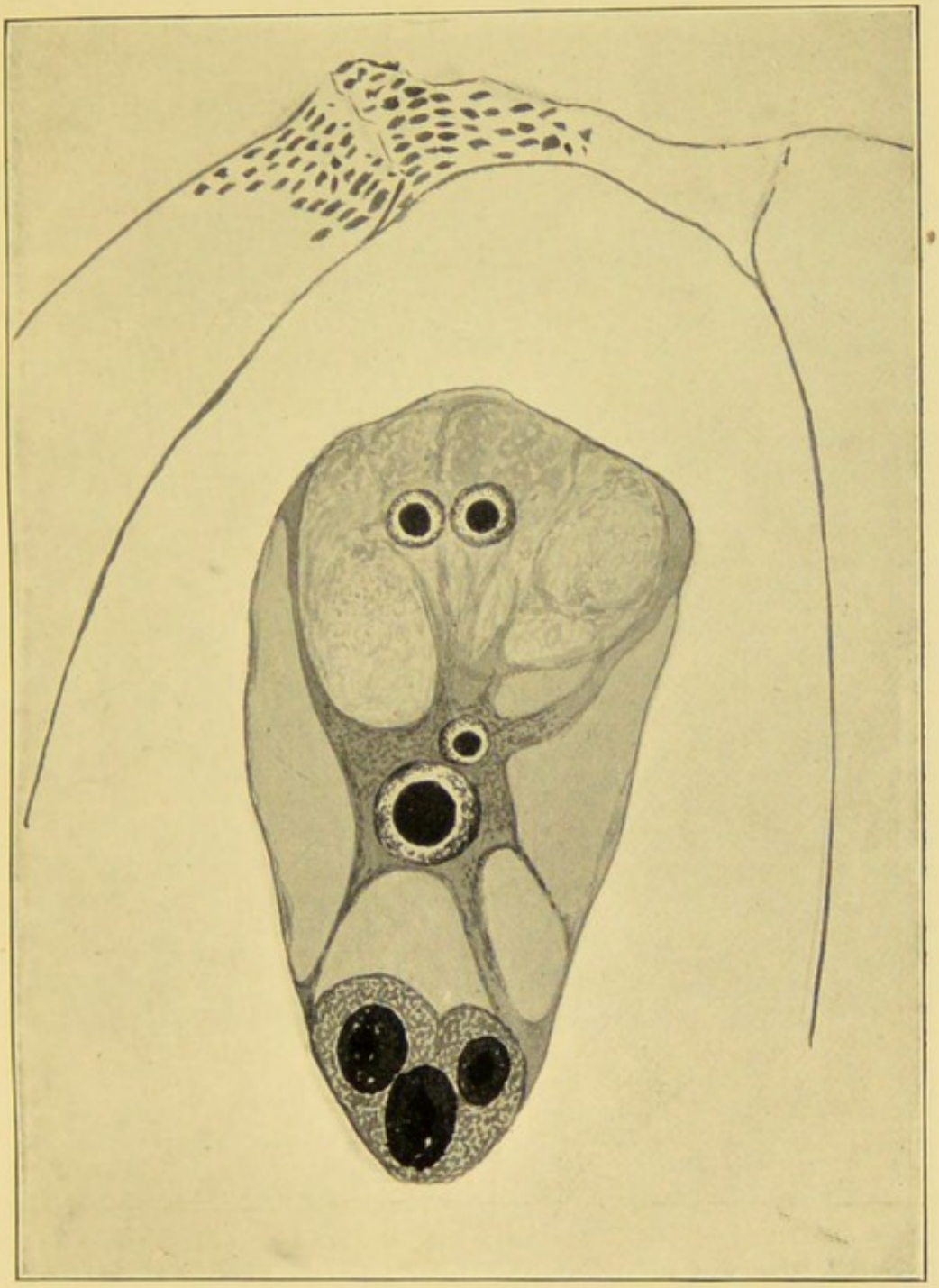

Fig. 96.—The Completely Matured Embryo-sac of *Helleborus niger*. Note the relatively large nucleoli. (From a photomicrograph.)

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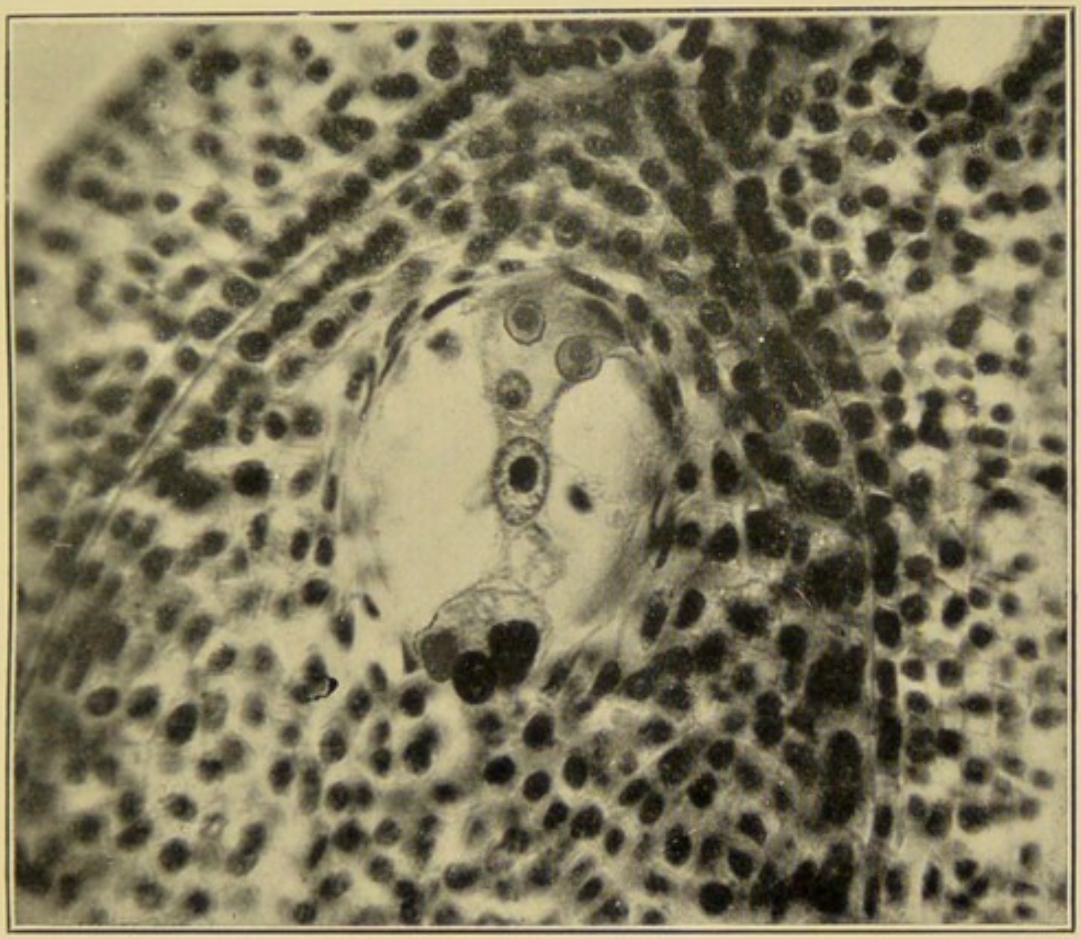

Fig. 97.—A Photomicrograph showing the Completely Matured Embryo-sac of *Helleborus*. The structures to be made out are the central definitive nucleus, the synergidæ and egg-cell at the upper end, and three antipodal-cells at the lower end of the sac.

c. **Fertilisation and Subsequent Changes.**—The matured **microspore** lying on the stigma of the pistil of an Angiospermous plant now undergoes the following further changes:—First, the large **vegetative cell** of the microspore (see p. 121) grows down into the conducting tissue (the central loose tissue) of the style in the form of an elongated cell, the **pollen-tube**. This process is brought about by the action of **enzymes** in the tube, which dissolve the cellulose walls of the cells of the conducting tissue; a further action of these enzymes being the conversion of the **starch** in the cells into **dextrins** and **sugar**, which furnish nutriment to the tube during its progress. Having reached the cavity of the ovary, the pollen-tube is attracted towards the micropyle of an ovule, the tip penetrates the micropyle, and grows through the nucellar tissue to the upper pole of the embryo-sac (the attraction of the tube being probably of the nature of **positive chemotaxis**). The next change which occurs is the passage of the **nucleus of the generative cell** (see p. 121) to the apex of the pollen-tube, where it divides into two. One of the resulting nuclei then passes between the synergidæ, which are situated at the upper pole of the embryo-sac, and, having reached the **egg-cell** or **oosphere**, penetrates into this cell, and, after a short time, **fuses with the egg-cell nucleus**, the cytoplasm also fusing with that of the egg-cell. This process completes the fertilisation of the oosphere, which now becomes the **oospore**. The other nucleus resulting from the division of the generative nucleus also passes between the synergidæ, and **fuses with the definitive nucleus**, which now becomes the **endosperm nucleus**. Round this latter the remaining cytoplasm of the embryo-sac soon collects, and divisions occur, resulting in the formation of the early endosperm nuclei, which lie free in the cytoplasm in the middle of the embryo-sac. This cytoplasm, with its nuclei, later on, lines the wall of the sac.

The fusion of the second generative nucleus with the definitive nucleus completes the process known as **double fertilisation**, a phenomenon which has recently been shown to occur in the majority, if not all, of the Angiosperms.

The fertilised egg-cell, or oospore, divides, after a short period of quiesence, into two cells, viz.—an upper or **epibasal cell**, and a lower or **hypobasal cell**, which bear an important relation to the position of the rudimentary tissues to be shortly formed from

them. Thus, from the **epibasal cell** are subsequently produced the **young stem, first leaf,** and the **cotyledons** (or cotyledon, in the case of monocotyledons); whilst from the **hypobasal cell,** the **root,** and, in some cases, the **foot** (an absorbent organ), and the so-called **hypocotyledonary portion of the stem** arise. The manner in which these tissues arise is, briefly, by the formation of **octants** of cells, from which, by subsequent synclinal and anticlinal divisions, the rudimentary tissues are developed.

Before the embryo-plant (spore-forming or asexual generation) thus formed is completed, the **endosperm** (or **secondary prothallium,** so-called: see section on "Homology") has increased to a great extent, and cells with definite cell-walls have arisen. At first the endosperm nuclei lie free in the shell of cytoplasm lining the embryo-sac, and no walls are formed until

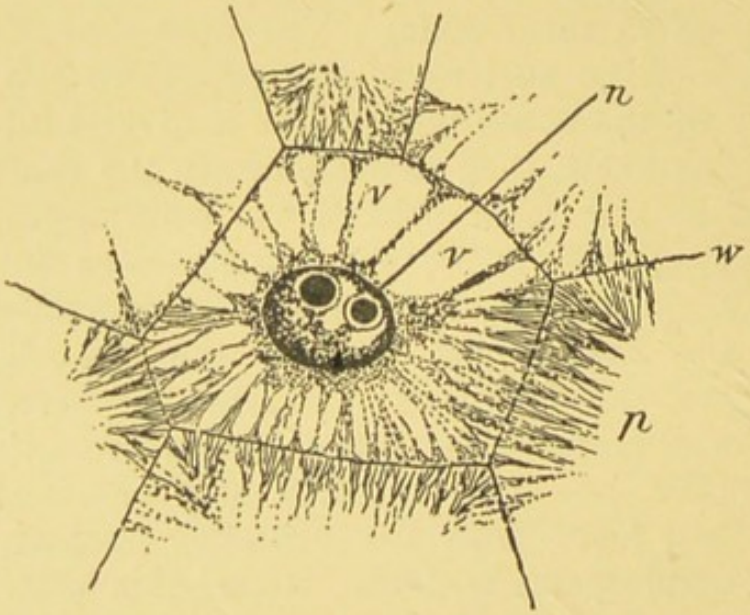

Fig. 97*a*.—A SINGLE CELL FROM THE ENDOSPERM OF *Caltha palustris*, showing:—*w*, cell-wall; *n*, nucleus; *p*, protoplasmic "bridles" passing through the cell-wall; *v*, vacuoles.

a considerable number of nuclei have been produced. After a time, however, the cytoplasm grows in thickness, and fresh nuclei are produced centripetally. Ultimately cell-walls are formed simultaneously between a large number of nuclei, there being a peculiar formation of radiating inter-nuclear achromatic spindles, across which walls are formed. (In *Caltha palustris*, very beautiful preparations of the developing endosperm may be made, which show this internuclear wall-

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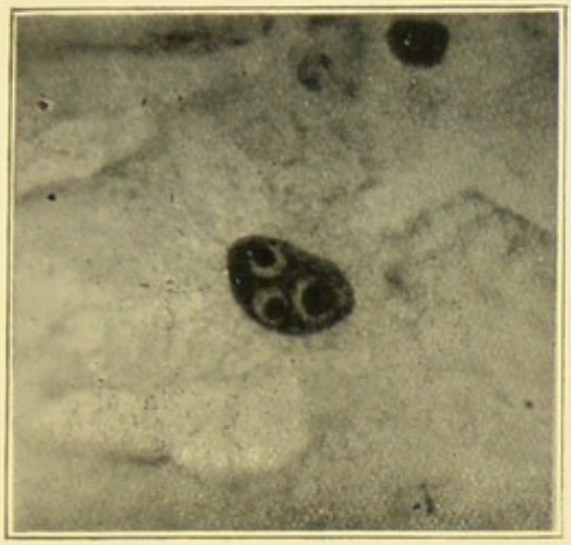

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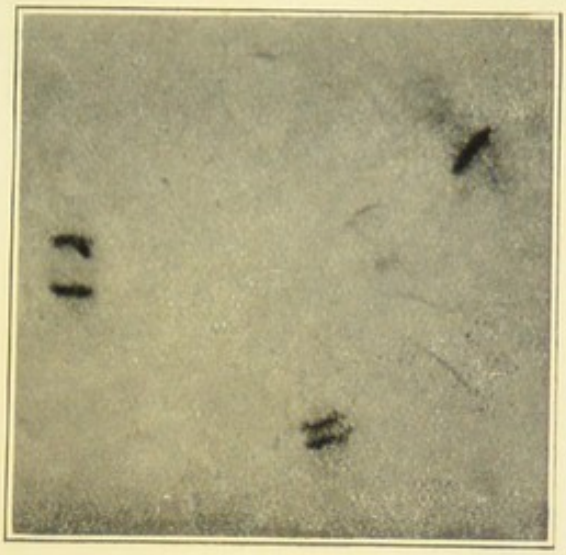

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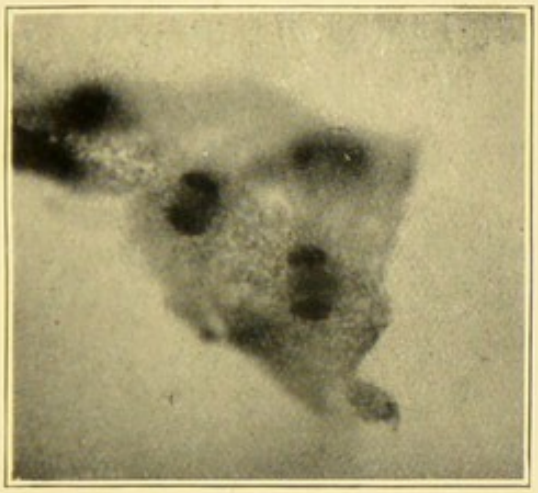

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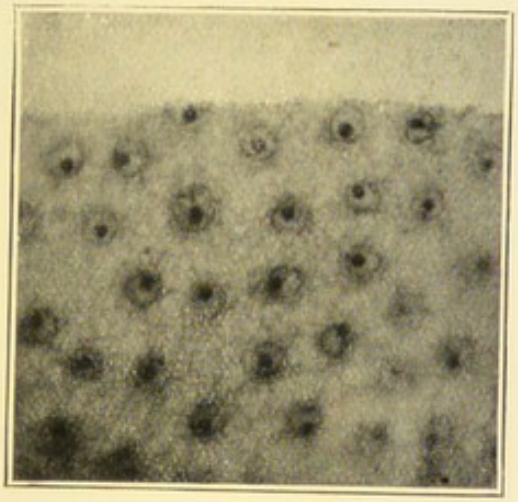

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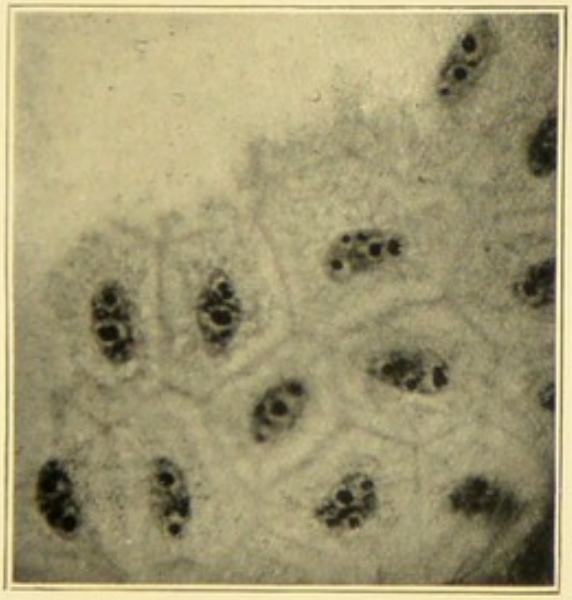

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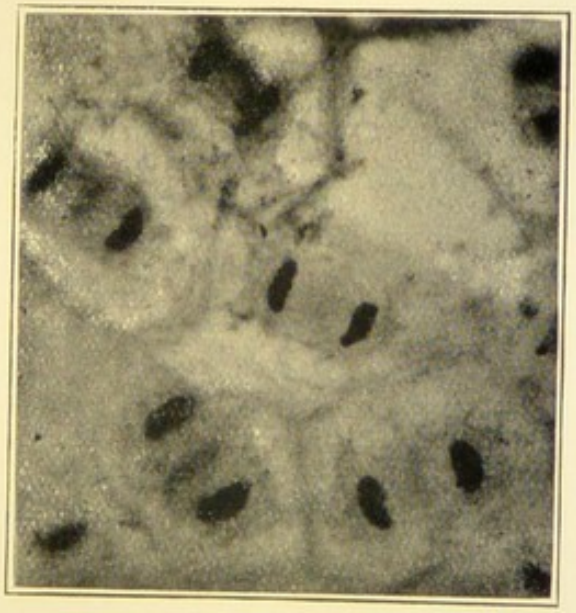

PLATE IV. (Stages in Endosperm-formation).

1. Nucleus resulting from third division of the endosperm nucleus (*Caltha*).
2. Three stages in the mitoses of nuclei lying free in the cytoplasm of the embryo-sac.
3. End-stages in the mitoses of two nuclei of the early endosperm of *Caltha*. Note the oval daughter-nuclei.
4. Portion of the sheet of endosperm of *Caltha*, showing a large number of free nuclei just previous to multicellular formation.
5. Young endosperm cells just subsequent to wall-formation. Note the large number of nucleoli in each nucleus (*Caltha*).
6. Somewhat older cells of *Caltha* endosperm, showing in each cell two daughter-nuclei and a well-marked achromatic spindle. Partition walls not yet formed.

formation [see Plate iv.]). Endosperm is thus produced after the method known as *multicellular formation* (see p. 101). In the later endosperm cells of *Caltha* the intercommunicating cytoplasmic fibrils may be readily made out (see Fig. 97*a*).

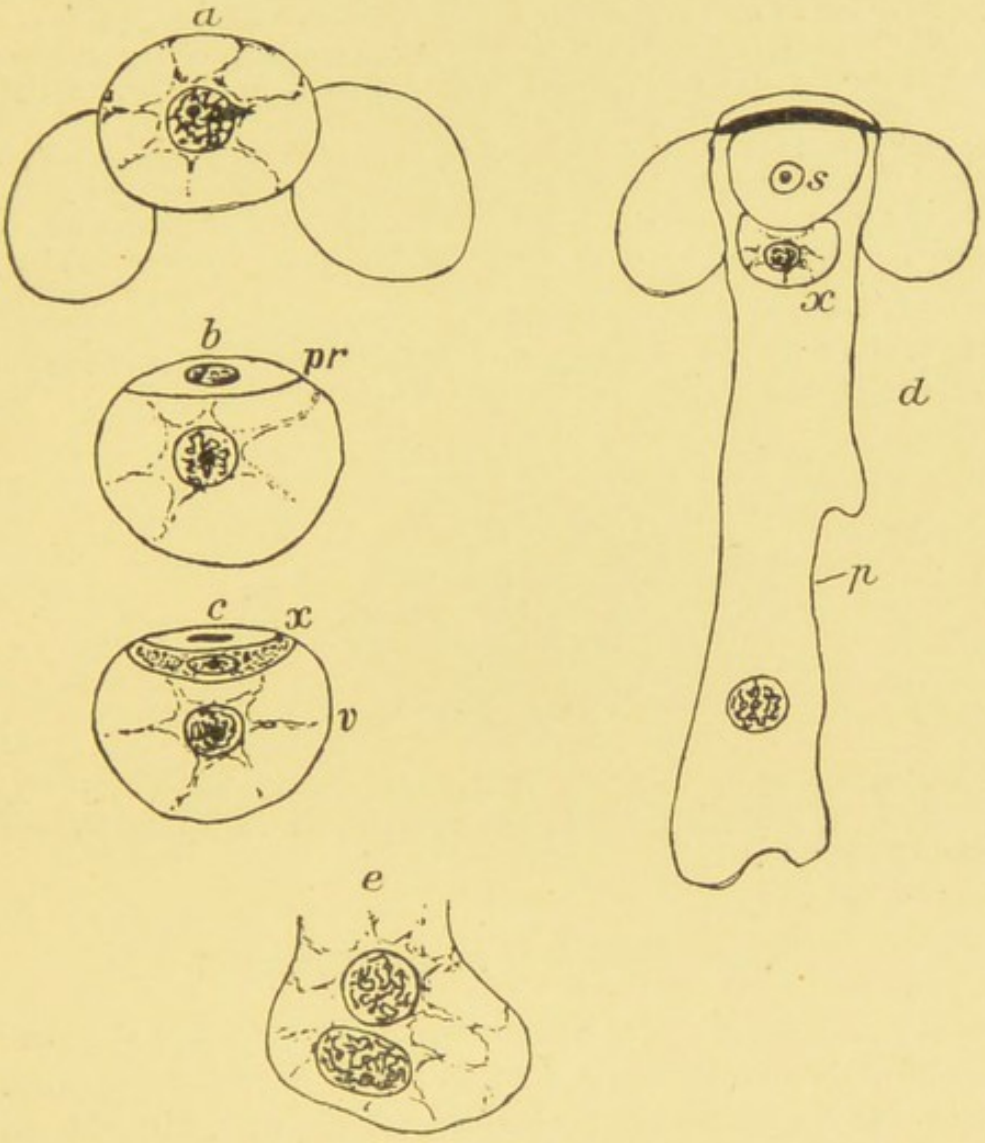

Fig. 98 (Diagrammatic).—THE MICROSPORE OF *Pinus* AND THE STAGES TAKING PLACE DURING ITS MATURATION.—*a*, The young unmatured microspore. *b*, A prothallial cell has been cut off. *c*, The larger cell in *b* has had another cell cut off from it: this is the antheridial cell; *v*, the vegetative cell. *d*, The antheridial cell has divided into a "stalk" cell, *s*, and the true generative cell, *x*, *p*, is the pollen-tube formed by the elongation of the vegetative cell. *e*, The nucleus of the generative cell has divided into two, which travel towards the apex of the pollen-tube and lie there in a mass of cytoplasm. (Drawings made from figures at the British Museum of Natural History.)

Note.—The study of the development of the microspore may be readily carried out in sections of the young flower of *Polygonatum*. Longitudinal sections of the fixed and hardened flower buds will cut across the young anthers. Sections should be stained with safranin and hæmatoxylin to show up the mitotic figures in the divisions of the pollen mother-cells. The study of the maturation of the microspore is difficult to carry out, and rather beyond the scope of the practical work noted in these pages.

The development of the embryo-sac and its maturation stages can, however, be readily studied in *Lilium martagon*, using young flower-buds. *Helleborus niger* is also a useful plant for the later stages, as also is *Caltha palustris*. Transverse sections of the young ovary of *Lilium* will cut across the ovules and embryo-sac longitudinally, and often in the same section three different stages may be recognised.

The development of the embryo is best observed in *Capsella bursa-pastoris*. In this plant the early growth of the embryo may be made out by selecting ovaries of various sizes, placing them in glycerine and water, and gently squeezing them, in order to flatten the ovules and force out the embryos. Development of endosperm can be studied by taking transverse sections of the ripening carpels of *Caltha* (fixed and hardened), and staining to show up the nuclei, lying free in the cytoplasm of the embryo-sac. *Helleborus niger* may also be used for this purpose.

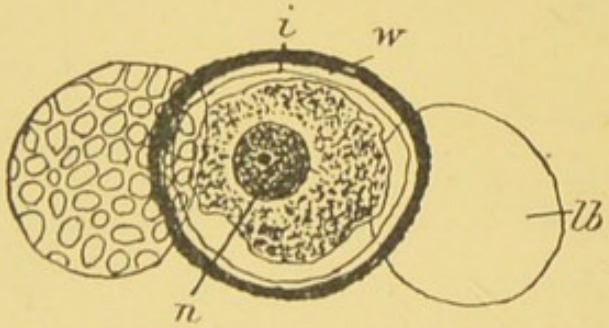

Fig. 99. — Structure of the Immature Microspore. — *w*, Extine; *i*, intine; *n*, nucleus lying in the cytoplasm; *lb*, lateral lobes formed from the extine.

B. Reproduction in Gymnosperms.

The Gymnosperms are interesting from the fact that in them the reproductive cycle forms a sort of link between the process as it occurs in Angiosperms and that taking place in the heterosporous Pteridophyta. The Cycadeæ show perhaps the most resemblance in this respect, but the type here selected will be *Pinus*, in which genus all the more important details may be readily made out.

As in the Angiosperms, the microspore (pollen-grain) and the macrospore (embryo-sac) form the primary sexual cells, and in each of these certain processes of maturation take place, which lead to the formation of the effective cells in reproduction.

a. **The Microspore: its Origin and Maturation** (*Pinus*).—The origin of the **microspore** takes place, as in the Angiosperms, by the setting apart of an **archesporium** in the anther, from which are produced an outer sheathing layer, the **tapetum**, and an inner mass of **pollen mother-cells**; each of the latter gives rise to **four rudimentary microspores**, which are set free later on into the cavity of the **pollen-sac** or **microsporangium** (see Fig. 100)

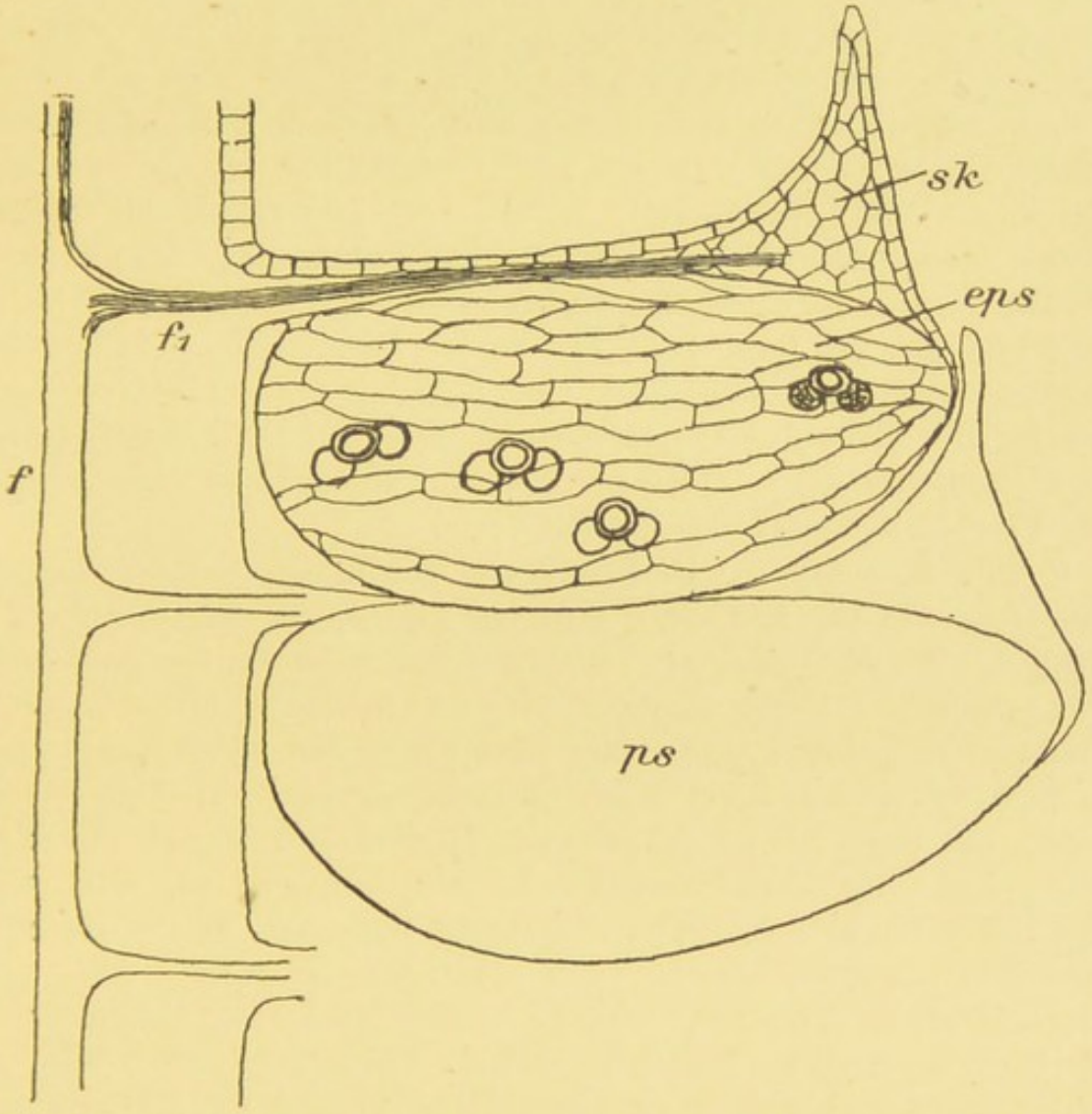

Fig. 100.—A Section (Longitudinal) of two Pollen-sacs (Microsporangia) of *Pinus*.—*sk*, Microsporophyll; *ps*, pollen-sac; *eps*, wall of the pollen-sac: several pollen-grains are seen inside; *f*, f_1, fibro-vascular bundles.

The tapetal cells in this case may give rise to a secondary tapetum. The young **unmatured microspore** (pollen-grain) has the following structure:—

i. An outer wall, which soon becomes thickened, the **extine**, from which are produced two **lateral lobes**; these possess reticulations, and are useful in buoying up the microspores during dispersion by the wind (see Fig. 99).

ii. An inner and thinner wall, the **intine.**

iii. Internally, **cytoplasm** and a large **nucleus.**

Maturation of the microspore takes place either in the pollen-sac or whilst it is lying upon the apex of the nucellus in the ovule, and consists in the cutting off of certain cells from the main mass; thus, the first cell to arise is the **prothallial cell**, which may divide again. The second division, which cuts off a cell from the larger remaining cell, gives rise to the **antheridial** or **generative cell**; whilst the large cell now left is the **vegetative cell**, from which the **pollen-tube** is produced. Later on the generative cell divides into a **stalk-cell** and the **generative cell proper** (see Fig. 98), this usually occurring after the pollen-tube has been formed. The later changes are best described under fertilisation. It is noteworthy that in *Ginkgo* and the *Cycadeæ* the generative cells are further differentiated into *antherozooids* (ciliated motile cells) of a peculiar type.* This process thus links these groups with the Pteridophyta (Heterosporous type).

b. **The Macrospore: its Origin and Maturation.**—The **embryo-sac** (macrospore) has an origin similar to that of the Angiosperms. An **archesporial cell** arises just beneath the epidermis (or oftener rather deeper) of the nucellus of the ovule (macrosporangium), this latter being situated upon the upper surface of a carpellary leaf (**macrosporophyll**) of the female cone (see Fig. 101). A **primary tapetal cell** is cut off from the apical end of the archesporial cell, and also **cap-cells** from the lower larger cell. The remaining large cell is the **embryo-sac** (macrospore), which soon enlarges to many times its original size. The next change which occurs is the division of the cytoplasm and nucleus of this macrospore into a number of free cells which soon develop cell-walls and undergo further division, and the tissue which is ultimately formed by this process fills the embryo-sac, and is known as a **prothallium** (incorrectly termed endosperm).

At the upper (micropylar) end of this prothallium now arise

* For a very good account of the formation of the antherozooids of Ginkgo, see *The Journal of Applied Microscopy and Laboratory Methods* for May, 1902.

several peculiar flask-shaped structures, the **archegonia,*** and the early formation of an archegonium (see Fig. 102) is as follows:—

One of the **apical cells** of the prothallium divides into two, and the lower of these divides again. The lowest or larger cell is the **archegonium proper**, and contains an **oosphere** composed of cytoplasm and large nucleus. The upper cells, by further divisions at right angles to the former ones, give rise to cells which separate in the centre and leave a space, the canal of the archegonium (see Figs. 102 and 103). A few cells are soon cut off from the upper part of the oosphere, the lowest

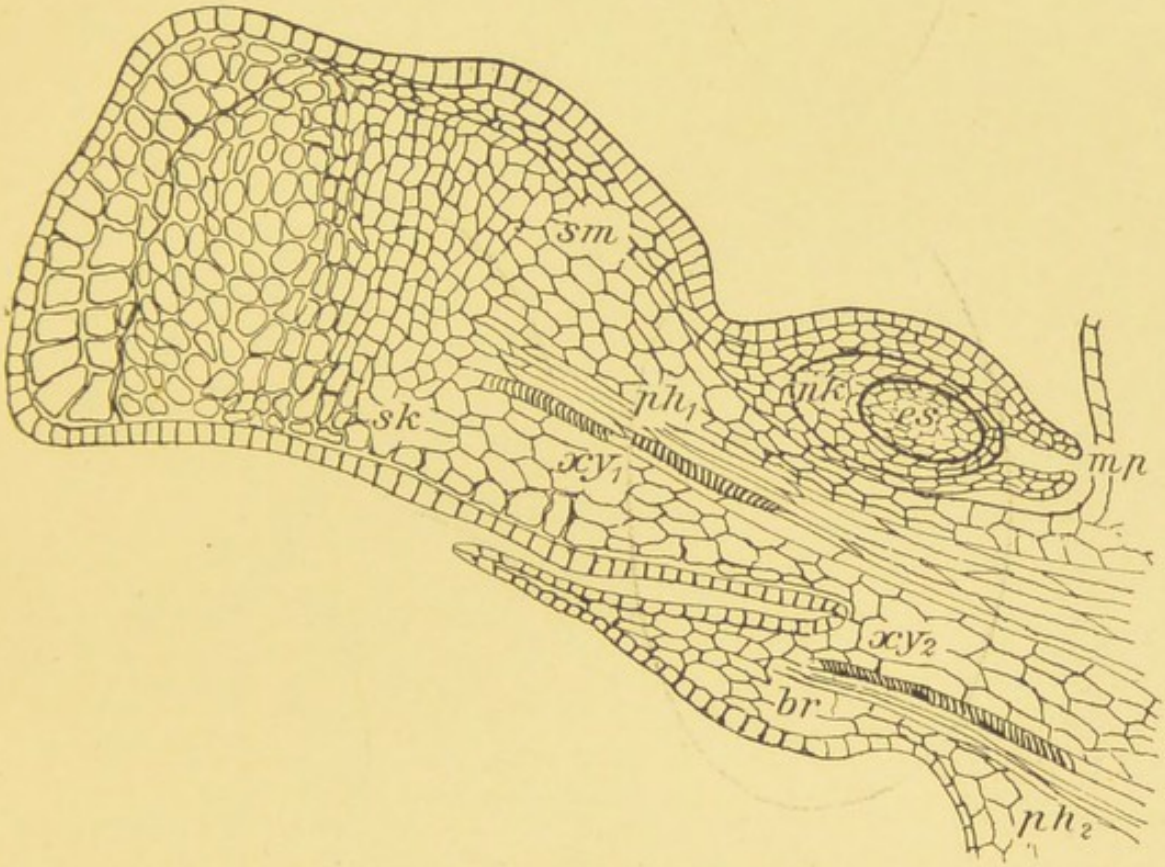

Fig. 101.—A Longitudinal Section of the Fruit-scale (Macrosporophyll) and Bract of *Pinus*, to show relations of the embryo-sac and nucellus.—*sk*, Fruit-scale; *br*, bract; *nk*, nucellus; *mp*, micropyle; *es*, embryo-sac (prothallium or "endosperm" already formed); *sm*, the "samara" or wing of the ovule; xy_1, ph_1, xy_2, ph_2, the xylem and phloem of the scale and bract respectively: note that the relative positions of these are reversed in the fruit-scale, the phloem being uppermost.

*The "corpuscula" of earlier writers. Each archegonium was formerly erroneously looked upon as a separate embryo-sac, but, strictly speaking, the corpuscula = oospheres.

being the so-called **ventral canal-cell**, the other two being the **neck canal cells.**

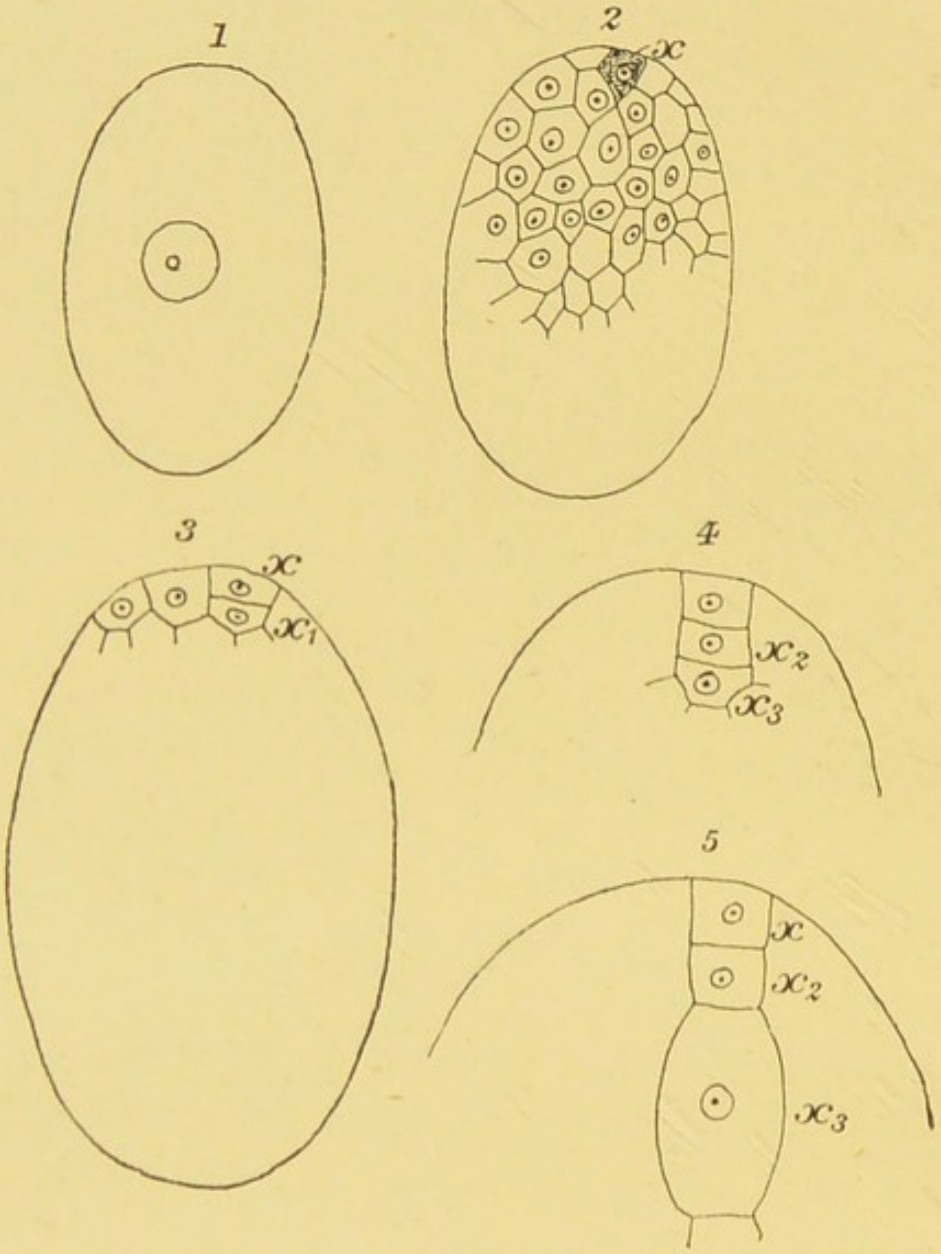

Fig. 102.—Diagrams showing the formation of the Archegonia in the Embryo-sac (Macrospore) of *Pinus*.—1. The young embryo-sac with its nucleus. 2. The cytoplasm and nucleus have divided to form a tissue the prothallium ("endosperm") in the sac; x is the cell from which an archegonium will arise. 3. The cell x has had a cell, x_1, cut off from it. 4. The cell x_1 has divided into cells x_2 and x_3; x_3 is the rudimentary "body" of the archegonium. 5. The cells x and x_2 are later divided by walls at right angles to the previous ones, and a space arises, the canal, which is lined by the cells so formed. The cytoplasm of x_3 usually has a few cells cut off from its upper portion, these being the so-called ventral and neck canal-cells; the remainder forms the oosphere.

To face p. 135.]

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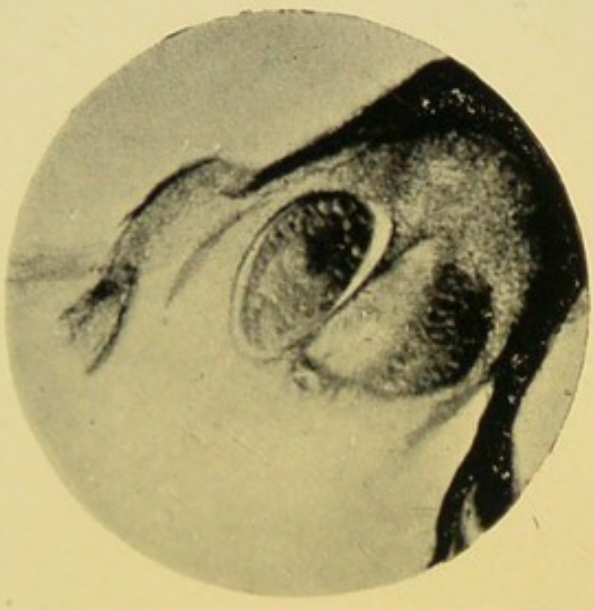

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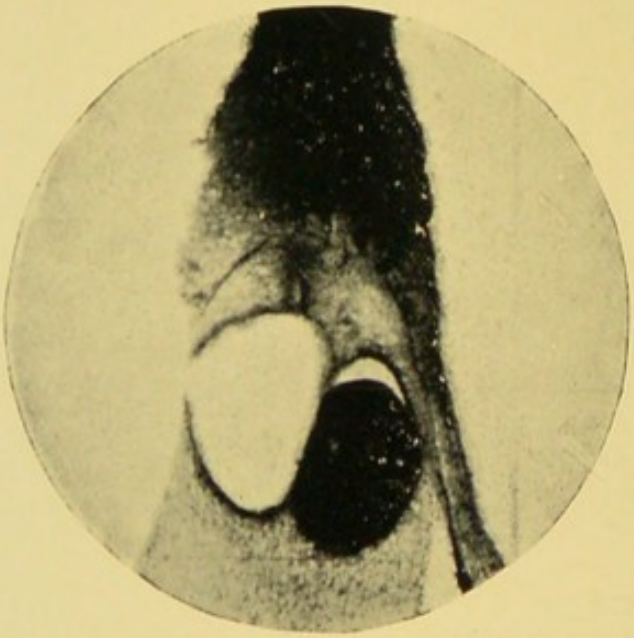

Fig. 104.—*a*, Photomicrograph showing three archegonia. *b*, Photomicrograph showing to the left the canal of an archegonium leading into the archegonium proper. A pollen-tube is seen just penetrating the upper end of the embryo-sac; the generative nucleus is to be seen close to the upper end of the right-hand archegonium.

[This process of maturation resembles that occurring in the macrospore of the heterosporous Pteridophyta (*Marsilea, Salvinia*), *qua vide* where oogonia (= archegonia) arise upon a special female prothallium produced in that spore: see, however, "Homology," at end of chapter.]

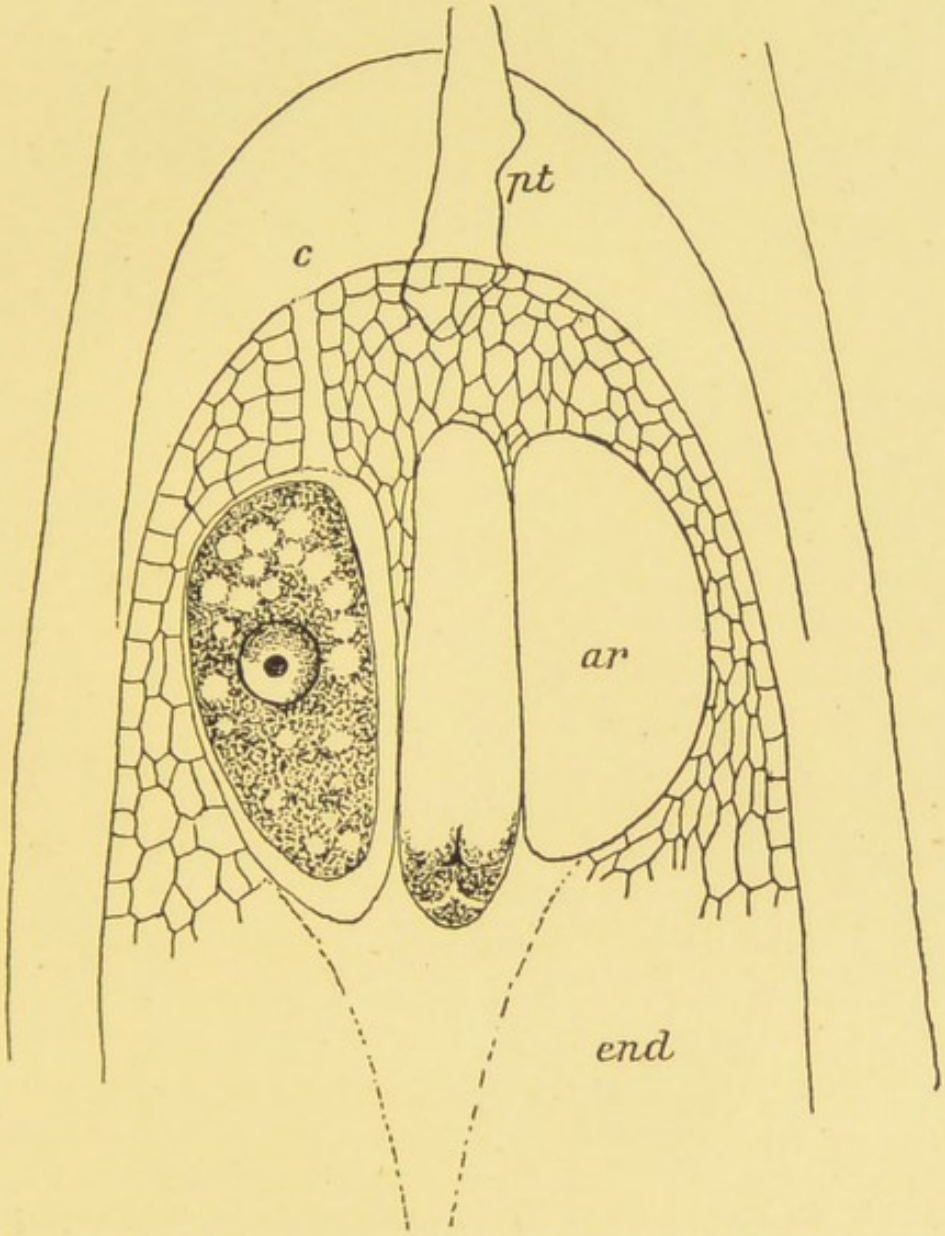

Fig. 103.—Three Archegonia at the Apex of the Embryo-sac of *Pinus*.—*ar*, Archegonium; in the left-hand one an oosphere with its nucleus is present: the middle one shows at its lower end signs of division; *end*, endosperm (prothallium); *c*, canal of an archegonium; *pt*, pollen-tube.

c. **Fertilisation and Subsequent Changes** (*Pinus*).—The process of **fertilisation** consists essentially in the fusion of a **generative**

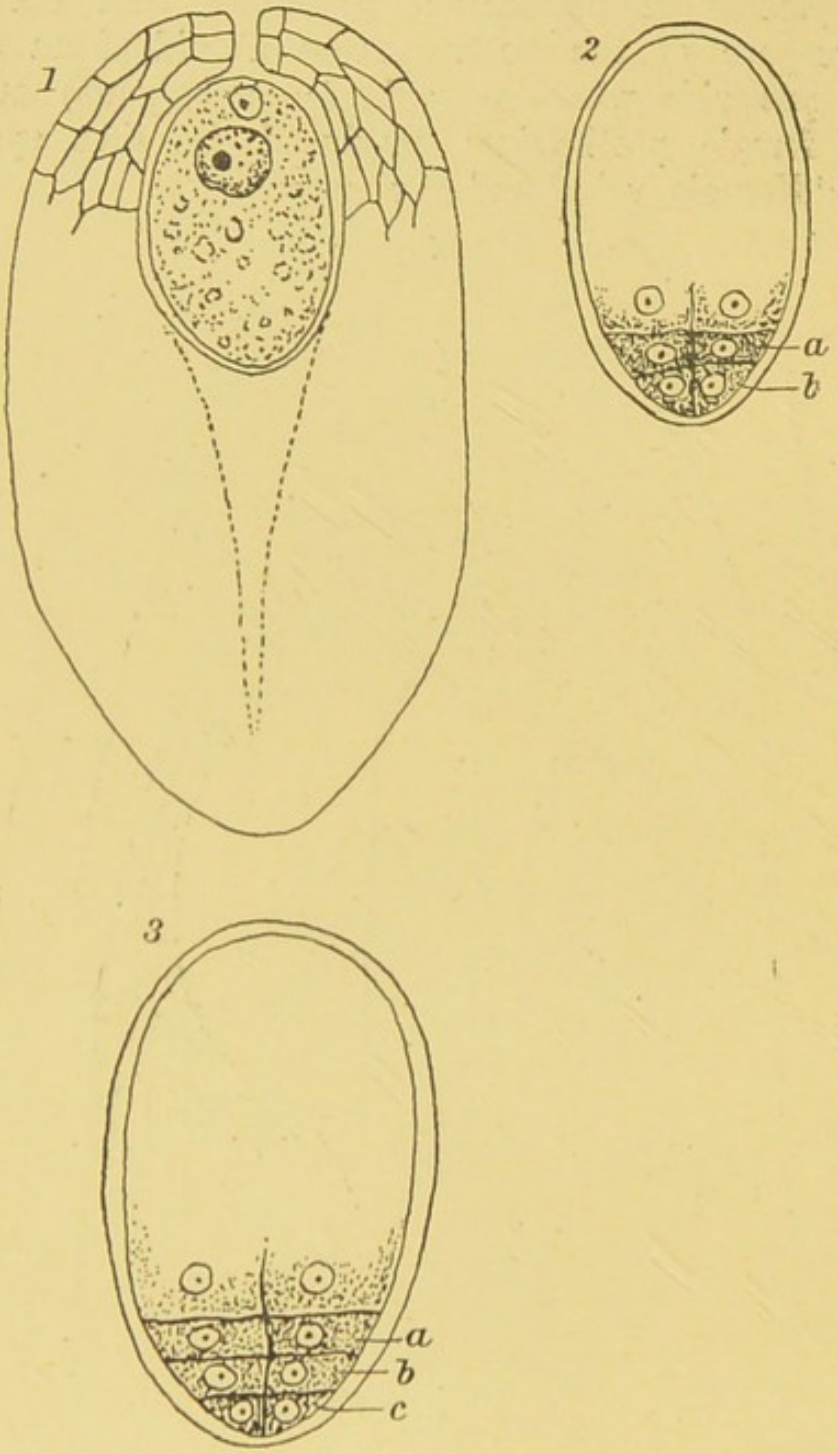

Fig. 105.—1. An archegonium at the apex of the embryo-sac of *Pinus*, containing an oosphere which has just received a generative nucleus from the microspore (small nucleus just above the larger one of the oosphere).

2. The first two divisions at the lower pole of the oospore, subsequent to fertilisation.

3. Shows the appearance at the end of the third division. The lowest cells are the embryonal cells; the lowest but one (*b*) are the cells from which the suspensors are produced.

nucleus derived from the **microspore** (see p. 132) with one of the **oospheres** contained in the archegonium at the upper pole of the prothallium in the macrospore (embryo-sac). The **pollen-tube**, derived from the further growth of the **vegetative cell** of the microspore, grows through the tissue at the apex of the nucellus of the ovule until its tip rests upon the upper cells of the prothallium at the top of the embryo-sac in the vicinity of the canal of an archegonium. The nucleus of the generative cell now travels to the tip of the pollen-tube, and, lying in a mass of cytoplasm existing there, **divides into two** (see Fig. 98, *e*). One of these nuclei (the so-called **male pro-nucleus**) penetrates the canal of an archegonium, being probably attracted by a substance (enzymic in nature) secreted by the neck canal-cells, and enters the oosphere, where it lies for a short time close to the nucleus of the oosphere (the so-called **female pro-nucleus**). **Fusion** of these two nuclei now occurs, and the resulting nucleus travels to the lower end of the fertilised oosphere, or **oospore**, as it is now called.

This nucleus, and the cytoplasm at the lower end, now divide, giving rise to **two cells** devoid of cell-walls. In each of the resulting cells a division at right angles to the direction of the former one arises, so that **four cells** lying in the same plane are produced. Each of these four cells divides again twice, so that, finally, there are present at the lower pole of the oospore **four rows of cells,** there being three cells in each vertical row. The lowest cell of each of these tiers is a **potential embryonal cell** (**pro-embryo**), the middle cell in each row is the **suspensor-cell**, and the upper cell later on disappears, or forms, with the remains of the oospore above, pabulum for the lower cells (see Fig. 105).

The **suspensor - cells** soon elongate greatly and push the embryonal cells before them deep into the prothallium. Each of the **embryonal cells** then divides into two cells by a somewhat oblique wall, the uppermost being the **epibasal cell** and the lower one the **hypobasal cell**. These two cells are divided again by a wall at right angles to the first, and the next division results in the formation of an **octant**, from the segments of which the rudimentary organs are produced somewhat after the same manner as in Angiosperms, subsequent growth proceeding from a primary apical cell, which forms the apical tissues.

In the above process, then, **four embryonal cells** are formed, but in reality only **one** becomes a fully developed embryo.

This is an instance of **polyembryony**, a phenomenon which occurs in some Angiosperms, notably *Funkia cordata*. The other embryonal cells, as a rule, form embryos which are later

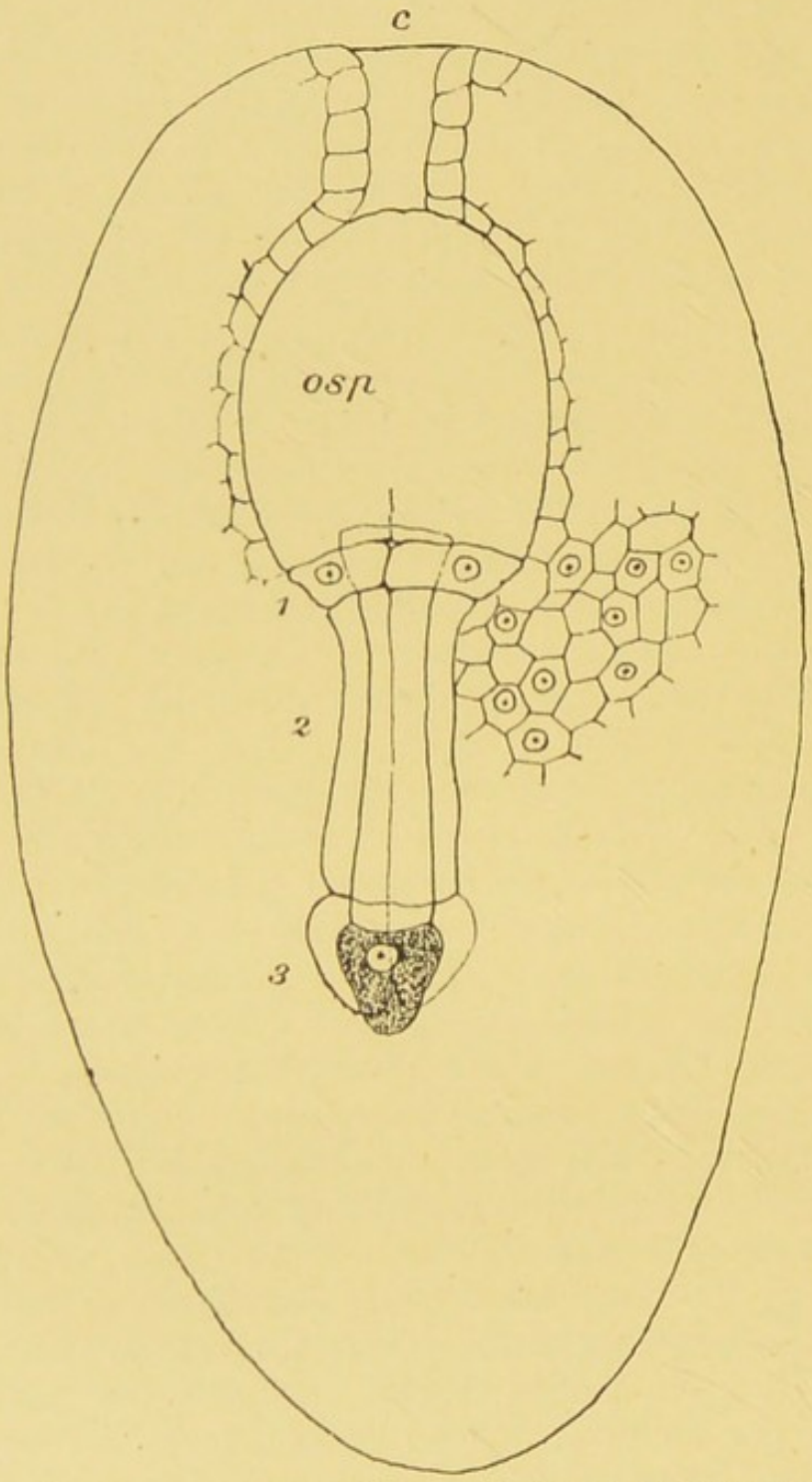

Fig. 106. — Embryo-sac of *Pinus*, showing Elongation of the Suspensors.—1, Basal cells, which probably form pabulum for the others, or else abort; 2, the suspensor cells, greatly elongated; 3, the pro-embryonal cells, one of which will become an embryo-plant by subsequent division; *osp*, remains of the oospore in the archegonium.

on absorbed, whilst the final developing embryo grows at the expense of the **prothallium** contained in the macrospore; more than one oosphere is usually fertilised, but the embryos formed from these do not get beyond a certain stage.

Note.—The practical examination of the reproductive cycle in the Gymnosperms is readily carried out by taking longitudinal sections of male and female cones of *Pinus* at various stages of their growth. The development of the microspore can be made out by this method, and the maturation is often to be observed when the pollen-grain is lying at the apex of the nucellus of an ovule in the female cone.

The formation of the embryo-sac and its prothallium may be studied by taking sections of very early female cones of *Pinus* from the time when they are about 4 mm. in length onwards. Archegonia are soon formed after the prothallium is complete, but some care is necessary in selecting cones for this examination.

Fertilisation and subsequent changes are best seen in sections of ovules of cones gathered from June 1st to the end of that month, although, in some Conifers, fertilisation takes a long time. The later changes, just previous to and after the elongation of the suspensors, are more readily obtained than the earlier ones. In *Pinus* fertilisation takes two years to accomplish.

C. Reproduction in the Pteridophyta.

In this great group of plants, as was pointed out above, an **alternation of generations** is met with—that is, a **sexual** generation formed from the **spore** alternates with an **asexual** generation which arises as the result of the fusion of the two **effective cells** produced in special organs upon the sexual plant or **gametophyte**. Moreover, two main types of reproduction are met with in Pteridophyta. In the one, or **Homosporous** type, only one kind of spore is produced, and this, by its germination, produces the gametophyte or **prothallus**; whilst in the other, or **Heterosporous** type, two kinds of spore are found—viz., **microspore** and **macrospore**—in each of which a **separate prothallium** is formed. Thus, the microspore in the latter case produces a **male prothallium** upon which organs comparable to antheridia arise in which the **male** effective cells are formed, and the macrospore produces a **female prothallium** upon which an organ arises in which the **female** effective cell originates.

The Homosporous type is exemplified in *Pteris* or *Aspidium*, which belong to the order Filicineæ; and the Heterosporous type is seen in *Marsilea* or *Salvinia*, members of the order Hydropterideæ. Each of these types will be examined in order.

I. Reproduction in the Homosporous Pteridophyta (*Aspidium*).—The stages and structures to be examined here are:—

a. The **spore** and **sexual generation** (gametophyte or prothallus).

b. The **sexual organs** arising on the sexual generation, and the **essential cells** formed in these organs.

c. **Fertilisation** and the origin of the **sporophyte** or **asexual generation.**

These will be considered in detail.

a. **The Spore and Sexual Generation** (Gametophyte).—The **spores** are formed in certain well-defined structures known as the **sporangia**. These arise either from *one* epidermal cell or a *group* of cells upon small cushions of tissue, the **sori**, which are formed upon the under surfaces of the **sporophylls** or spore-bearing fronds of the fern. Usually these sori are found at the endings of the lateral branches of the leaf-traces of the frond, and their position varies according to the genus. A sheath of cells known as the **indusium** often covers over each sorus, but in some cases the sori are naked. Each **sporangium** is composed of three parts (see Fig. 107), viz.:—

i. The **stalk,** which grows from the sorus.*

ii. The **spore-chamber** or **sporangium proper,** which is thin-walled, and composed of small translucent cells. Inside the chamber are seen the **spores,** which are produced at an early stage by the divisions of an archesporial cell which forms the **spore mother-cells,** each of these latter going to produce **four** spores.

iii. The **annulus,** a curved portion at the back of the sporangium. This is composed of peculiar cells, each having thick walls perpendicular to the surface, and thinner very elastic outer walls. The annulus acts as an elastic layer which helps to stretch open the spore-chamber when the thin front wall ruptures† and sets free the spores.

A single mature **spore** is a simple spheroidal cell which possesses two walls, an **outer** thick wall and an **inner** thin one. Internally are cytoplasm, large nucleus, and a few food-granules (starch). (See Fig. 107, 2.) At a certain period, determined by the relative humidity of the atmosphere, rupture of the thin anterior wall of the sporangium occurs, and the spores are freed,

* A stalked gland arises in some cases from the stalk close to the sporangium proper, and is characteristic of the species *Aspidium filix-mas.* It is not represented in Fig. 107.

† In connection with the rupturing of the anterior wall two peculiarly-shaped cells are found, between which the rupture occurs along the middle lamella. The two cells constitute the so-called "stomium."

being, in fact, shot out by the effect of the elastic recoil of the annulus, and, after falling upon a suitable substratum, each spore germinates. The outer wall of a mature spore is much wrinkled in the genus *Aspidium* (in the figure this is not represented).

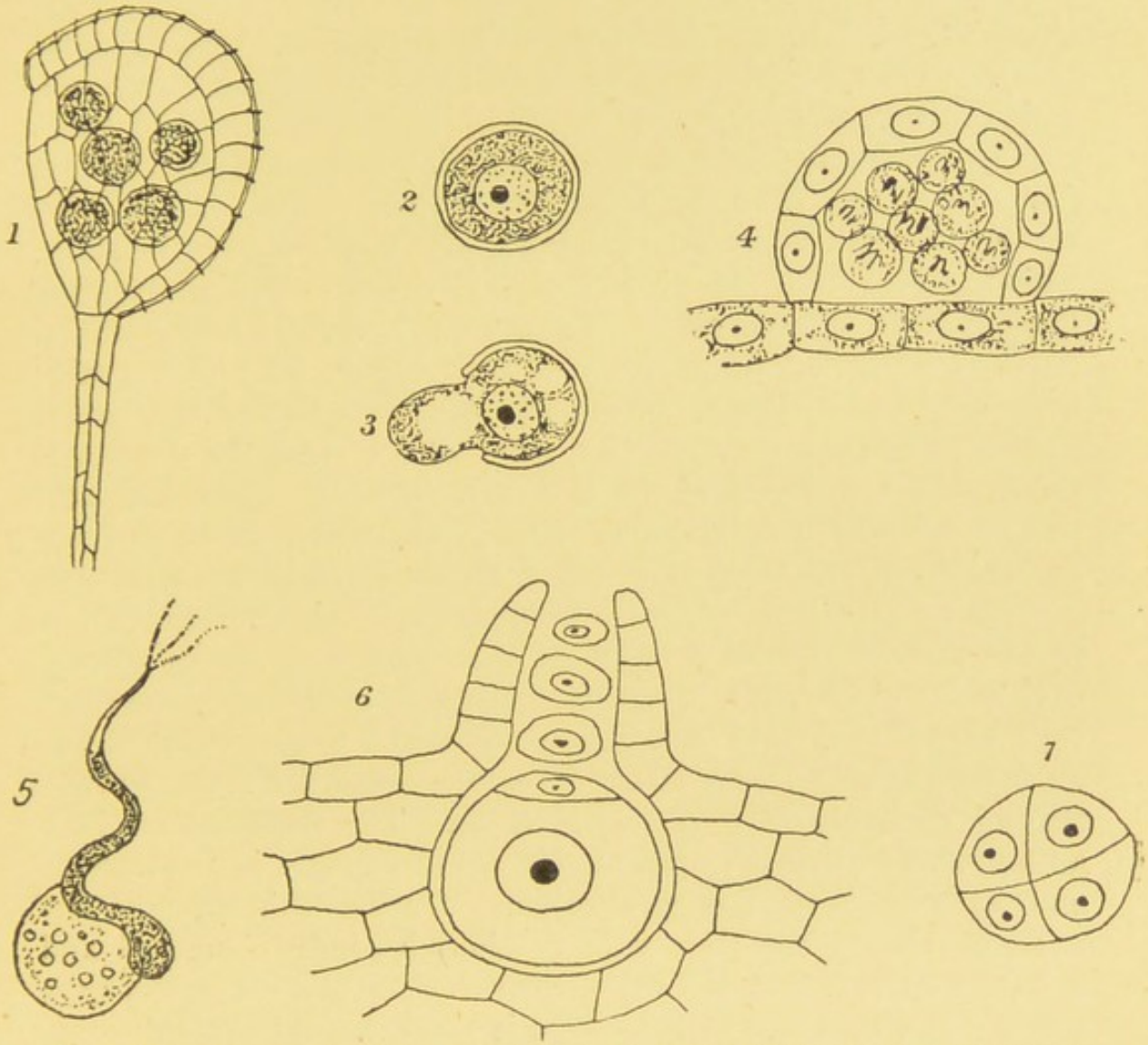

Fig. 107.—Details (Diagrammatic) of the Reproductive Cycle in *Aspidium* (Homosporous Ferns).—1. A mature sporangium, showing the spore-chamber with spores inside, the stalk, and the curved annulus. 2. A single spore. 3. Germination of the spore by the splitting of the thick outer wall and protrusion of the cytoplasm contained in the thin inner wall. 4. An antheridium from the under surface of a mature prothallus; a few mother-cells of the antherozooids are seen in the central cavity. 5. A single antherozooid, showing the rounded head with vesicle attached, and the tail, at the end of which are the cilia. 6. An oogonium sunk in the under surface of the prothallus. Note the oogonium proper containing the oosphere, and the canal, in which are the canal-cells. 7. The first two divisions of the oospore.

Germination of a spore consists in the swelling and ultimate rupture of its outer wall, and protrusion of the inner thin-walled cell in the form of a tubular growth. This protrusion is soon divided into two cells by the formation of a wall, and subsequently a large number of cells are formed, the whole mass being the **rudimentary gametophyte** or **prothallus** (sexual generation). **Chloroplasts** soon appear in the cells of this structure, which ultimately takes on the form of a small cordate mass, notched or bilobed at the broader end. It is flat, and only a few cells thick. The upper surface is smooth, and on the under surface are found towards the apex—(i) A number of **rhizoids**, which serve both as organs of attachment and absorption. Each rhizoid is somewhat like a long root-hair, only thicker. (ii) The **sexual organs**. These are the **antheridia** and **oogonia**; their origin and subsequent changes will be described separately.

b. **The Sexual Organs, with their Origin, and the Essential Cells.**—As mentioned above, the male organ (**antheridium**) and the female organ (**oogonium**) arise in the under surface of the gametophyte, or prothallus. Each **antheridium** is, when mature, a rounded structure, which is formed from a single cell of the under surface of the prothallus, this cell undergoing certain divisions which result in the formation of an external layer of cells, enclosing a mass of cells known as the **mother-cells of the antherozooids**. These latter form the essential **male**, or fertilising elements (see Fig. 107, 4, 5). The maturation of an **antherozooid** consists in the occurrence of changes in the nucleus and cytoplasm of the mother-cell. During this process the **nucleus** (chiefly the chromatin portion) becomes elongated and **specially curved**, one end being thicker than the other, and over the whole a thin film of cytoplasm is present. At the thin end, or **tail**, are two or three long **vibratile cilia**, formed, in all probability of ectoplasm, or **kinoplasm**; whilst at the thicker end, or **head**, is a **vesicle**, which is cytoplasmic in nature, and contains a few vacuoles and granules of food-material (probably starch).

Each antherozooid is, by virtue of the possession of vibratile cilia, a **motile cell**, and swims about in the droplets of moisture on the under surface of the prothallus. Its further history is perhaps better postponed until after the study of the oogonia.

The **oogonia** are also formed on the under surface of the

prothallus, and, as a rule, are sunk in the tissues of that structure. Each mature oogonium is a flask-shaped organ, composed of two portions—viz., the **oogonium proper**, or **venter**, a spherical receptacle sunk in the prothallus, and a **canal** leading from this to the surface. These two parts arise from a single cell of the under surface of the prothallus, this undergoing division into two, the lower cell being again divided into two. The lowest, or rather the deepest of these, becomes the **oogonium proper**, whilst the two upper ones undergo divisions at right angles to the former plane, lateral cells being formed, and a passage —the **canal**—arises between them, along the point of union of the planes of division which contains the axial cells. The protoplasmic contents of three small central cells cut off early from the cytoplasm in the venter of the oogonium form the **ventral** and **neck canal-cells**, whilst the remaining large mass in the cavity of the oogonium is the **oosphere** (see Fig. 107, 6), this being the essential **female** cell. The neck canal-cells are later on converted into a **gelatinous plug**, which contains a substance (malic acid) capable of attracting the antherozooids (**positive chemotaxis**).

c. **Fertilisation and the Formation of the Embryo-sporophyte (Asexual Generation).**—**Fertilisation** is accomplished by the passage of **one antherozooid** into the **oosphere** by way of the canal of the oogonium. At a certain period the neck canal-cells secrete a substance (**malic acid** or an **enzyme**) which has a powerful attraction for the antherozooids, and one of these bodies finds its way down the canal, passing through the mucilaginous plug which now fills that space.

After penetrating the oosphere, the antherozooid fuses with the nucleus of the oosphere, and this body, being thus fertilised, becomes the **oospore.**

The oospore is soon divided by an **oblique wall** into an **epibasal** and a **hypobasal cell.** A second wall at right angles to the first is then formed, and of the four cells now present, the **two upper ones** go to produce the **stem** (rhizome) and **first leaf of the sporophyte**, whilst the **lower two** give rise to the **root**, and an **absorbing organ, the foot.** The foot remains sunk in the prothallus whilst the first leaf grows upwards, usually through the notch of the prothallus, the rhizome and root growing horizontally and downwards respectively. In con-

nection with the formation of the embryo-sporophyte, it should be mentioned that the young tissues are produced by the divisions arising in what is known as an **apical cell.** This cell is **pyramidal** in shape, with the base outwards, and walls are produced in it, parallel to the three sides of the pyramid. Fresh tissues, even lateral buds, all have this form of cell at their apices, and growth is thus entirely apical at first, the subsequent walls arising in other planes. The apical cell is found not only in the Pteridophyta, but also in the Bryophyta, and is typical of both these groups of plants.

Note.—The study of the reproductive cycle in the Homosporous Pteridophyta may be carried out in *Pteris* or *Aspidium* (Filicineæ). The spores are readily examined by brushing off a number of sporangia into a drop of water on a slide, and observing rapidly under the microscope, when the annuli will stretch open, and the spore-chambers rupture, freeing the spores.

The prothalli are best examined by growing spores on moist humus, so prepared as to exclude moulds, and watching the stages of growth, in order to pick out prothalli showing the various phases in the formation of the antheridia and oogonia, and, later on, of the embryo-sporophyte. Fresh gametophytes may be examined in glycerine and water, or the structures may be fixed and hardened and sections taken in split pith, or, after embedding in celloidin, by means of a special microtome.

II. **Reproduction in the Heterosporous Pteridophyta** (types *Marsilea, Salvinia*).—A brief description of this type of reproduction in Pteridophyta is necessary on account of the important comparisons to be made between it and that occurring in Angiosperms and Gymnosperms.

In *Marsilea,* one of the Hydropterideæ, two kinds of **sporangia** are found—viz., **microsporangia** and **macrosporangia,** in special organs, the **sporocarps.** In the former, a number of small spores, or **microspores,** are produced; and in the latter, a few large spores, or **macrospores,** arise.

A **microspore,** on being freed by the rupture of its sporangium, **germinates,** and produces a small **male prothallium,** which is enclosed within the limits of the thick outer coat or **exospore** of the microspore. Upon this prothallium, **antheridial cells** are formed, in which **antherozooids** arise, somewhat after the same manner as those of *Aspidium.* A **macrospore,** when freed from its sporangium, also **germinates,** and gives rise to a somewhat larger **female prothallium,** upon, or in, which an **oogonium** is formed, containing, after the cutting off of certain canal-cells, the **oosphere.** There are thus two separate **gametophytes**

(sexual generation) or prothallia, and the process occurring in the Homosporous type—viz., formation of the prothallus from the one spore—might be looked upon as the fusion of two prothallia, produced by the germination of a potentially double (male and female) spore.

The further history of the cycle in *Marsilea* consists in the freeing of the motile antherozooids, and the **fusion** of one of these with the **oosphere** nucleus, the oosphere being then known as the **oospore**. From the oospore the **embryo-sporophyte** (asexual generation) is again produced. Other Heterosporous Pteridophyta are the **Selaginelleæ** and **Isoeteæ**. *Equisetum* gives rise to spores all of the same size, but the sexual organs arise on *separate* prothallia (dioecism). The determination of the sex of the prothallium in this case is largely a question of nutrition.

Reproduction in the Bryophyta, Fungi, and Algæ.

In order to complete the survey of the reproductive processes occurring in plants it is necessary to examine briefly the main variations occurring in the reproduction of **Mosses, Liverworts, Fungi,** and **Algæ**. It is not intended here to give an exhaustive account of these, as this would involve the consideration of many subsidiary groups, and would, moreover, lead to inevitable confusion. For a full account of many of these the student may be referred to Goebel's *Outlines of Classification and Special Morphology*, or any of the larger text-books.

1. **Reproduction in the Musci (Bryophyta).**—In these plants an **alternation of generations** exists, the plant arising from the **oospore**—viz., the **sporophyte**—nevertheless, remaining in a special organ found in connection with the fructification of the moss-plant. Thus, **antheridia** and **oogonia** arise on the moss-plant, which is here the **gametophyte**, or sexual generation, in special fertile shoots, and the result of fusion of an **antherozooid** with the **oosphere** (the product being the **oospore**) is the formation of a mass of cells known as **sporogenous cells**, inside a special organ, the **sporogonium**. The sporogonium and sporogenous cells are thus comparable to the **sporophyte**, or asexual generation, and the ripe **spore**, on germination, gives rise to a rudimentary cellular structure, the **protonema**, from which the moss-plant or **gametophyte**, is produced. The moss-plant proper

is thus homologous with the **prothallus** of Homosporous Pteridophyta; but, as has just been seen, both gametophyte and sporophyte are **united** in the same plant. The musci are also propagated by a vegetative method—viz., by means of **gemmæ**, which are small cellular offshoots of the gametophyte.

2. **Reproduction in Hepaticæ (Bryophyta).**—Here there is also an alternation of generations, and the reproductive organs, **antheridia** and **oogonia**, are found on the gametophyte, or sexual generation (which has often the form of a simple flattened structure), upon the under surfaces of special fructifications. At times a type of **vegetative propagation** occurs, in that **gemmæ**, or buds, composed of a few cells, are formed, usually at the bottom of small cup-shaped receptacles (*Marchantia*). The result of the fusion of an **antherozooid** with the **oosphere** in an oogonium is the **oospore**, which divides and forms a **sporogonium**, which is the sporophyte, or **asexual generation**. In the sporogonium the **spores** are produced, and germination of a spore results in the production of the **thallus**, **gametophyte**, or sexual generation once more. In *Riccia*, the sporogonium is quite a simple structure, whilst in *Anthoceros* it forms a more complicated growth.*

3. **Reproduction in the Fungi (Thallophyta).**—Two main methods of reproduction occur, viz., an **asexual**, by means of **spores**, and a **sexual** type (*Phycomycetes*), often of the nature of **conjugation**. In the former, or asexual method, **spores** are often formed at the ends of special hyphal branches or **gonidiophores**, the spores being here known as **gonidia** (*Mucor*). At times, on the other hand, the ends of certain hyphæ develop into special strutures known as **asci**, which are enclosed in an **ascocarp**, and spores (**ascospores**), to the number of eight, are formed in these in rows, being, later on, freed by rupture of the asci. Spores may also be formed in **sporangia** (endospores).

In the more highly differentiated Fungi (*Agaricus*, &c.), large fructifications are formed, and on the under surfaces of the terminal parts of these—viz., the **hymenium**—delicate **lamellæ** are produced, from the two surfaces of which **spores** arise upon hyphal structures known as *basidia*, there being four spores to

* The sporogonium at times develops a "foot," which attaches it to the gametophyte. In *Anthoceros* (*Hepaticæ*) and *Funaria* (*Musci*) the foot is well marked.

each basidium ; the fructification may be a closed structure, as in the Truffle, or Puff-ball, and the spores here originate in special hyphal filaments or asci (*Gasteromycetes*).

In the lower fungi (*Zygomycetes* and *Oomycetes*), at times, a **sexual** mode of reproduction occurs, in that **two similar hyphæ** approach one another and meet by their somewhat club-shaped extremities. **Fusion** of the adjacent cells then occurs, and the resulting body puts on a thick pigmented wall, and is known as a **zygospore**. In a few cases (*Eurotium*) two somewhat dissimilar organs may be produced from adjacent filaments. Thus, a large globular organ containing cytoplasm may arise, corresponding to an **oogonium**, and this is fertilised by the content of a smaller organ (= **antheridium**) which has arisen close by or from the same hyphal filament just below. The resulting mass then becomes an **oospore**, and can reproduce the fungus, the fertilised mass often forming swarmspores, which are freed later ou by the rupture of the oogonium, each being capable of forming a hyphal filament, the **promycelium**.

In the **Schizomycetes**, or fission-fungi (**Bacteria**), the only methods of reproduction are the **vegetative**, by simple fission, and the reproduction by **spores**. The spores may arise either by the development of large forms (**arthrospores**) on a main chain of organisms, or by **endogenous** formation, the spore being formed by the aggregation of the cytoplasm in certain of the members of a colony, and the production of a thick wall round the resulting mass. Rupture of the original wall of the parent-cell then frees the **spore** thus formed (*Bacillus mycoides, Tetanus bacillus, B. anthracis*). These few instances will serve to show the great variety of methods of reproduction in the Fungi.

4. **Reproduction in the Algæ (Thallophyta).**—It is necessary here to take a few well-defined types for study : thus **Spirogyra, Fucus,** and **Vaucheria** afford three distinct varieties of **sexual** reproduction in this group of plants.

(*a*) **Conjugation in Spirogyra** (see Fig. 108, 1, 2, and 3).—This alga has already been seen to possess the ordinary vegetative mode of reproduction, but, in addition, a method known as **conjugation** sometimes occurs, especially when the surrounding conditions do not favour vegetative reproduction (towards autumn or in colder weather). In **conjugation**, two similar filaments, adjacent and parallel to one another, undergo with regard

to certain cells of these filaments, a change, which results first of all in the pushing out of small **protrusions** from the cell-walls of adjacent cells (see Fig. 108). These protrusions grow out laterally from the main cells until they meet, and then the partitions between them become dissolved, thus leading to the formation of a **tubular passage** joining the two cells; the cytoplasm, chlorophyll band and nucleus of one cell then passes along this passage into the other cell and **fuses** (with the exception of the chloroplasts) with the cytoplasm and other structures of the latter. The resulting mass is known as a **zygote** (each of the original masses being the **gamates**), and soon takes on a thick wall of **cellulose**; the chlorophyll band of the receiving cell persists, whilst that of the other aborts. It is usual to look upon the

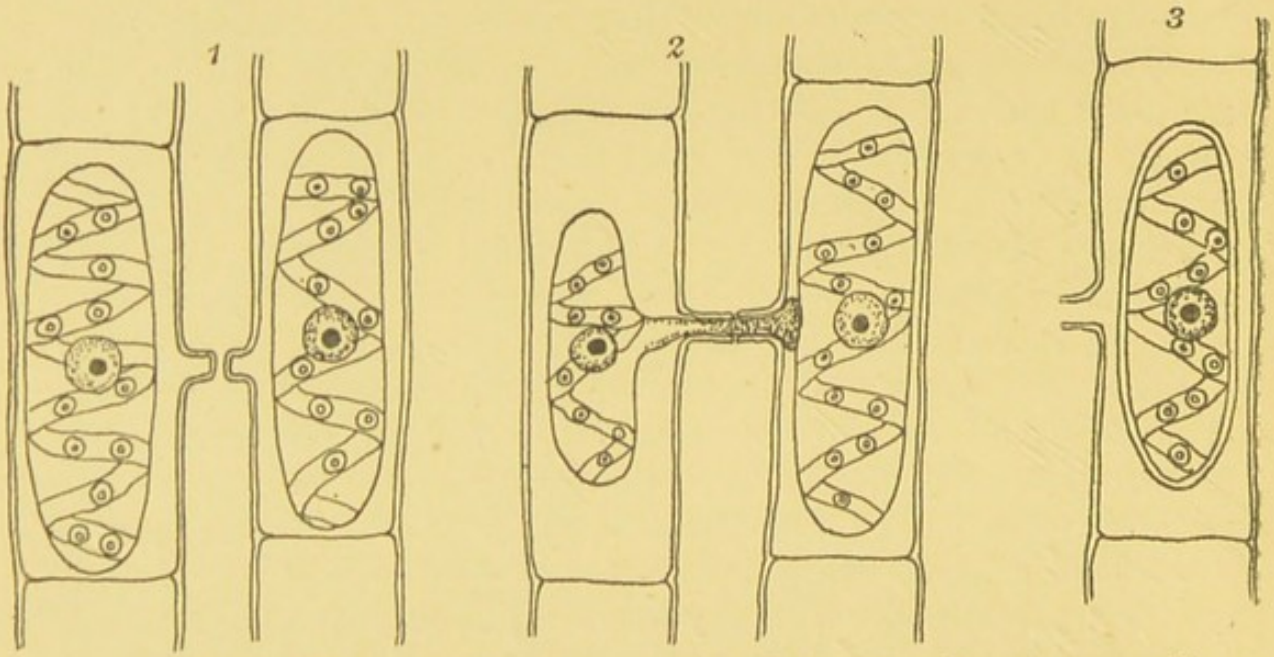

Fig. 108.—Conjugation in *Spirogyra*.—1. The protoplasm in two adjacent cells has contracted, and a protrusion from each cell has already been formed. 2. The protrusions have met, the intermediate wall has been dissolved, and the protoplasmic contents of one cell are passing into the cavity of the other. 3. Fusion (conjugation) of the two masses has occurred, and the resulting "zygote" has assumed a wall of cellulose.

"fertilising" gamete as the **male** cell, and the other or receiving gamete as the **female** element. At a later date the encapsuled mass is set free from the cavity of the original cell, by bursting of the wall of the latter, and soon **germinates**; germination results in the formation of an elongated cylindrical cell which divides into two and so on, so as to produce ultimately a filamen-

tous **colony.** In one species (*Spirogyra quinina*) five adjacent cells conjugate with five others of a parallel filament at the same time.

(*b*) **Reproduction in Fucus vesiculosus.**—**Fucus** is an alga which to all external appearances seems highly differentiated, there being a system of branching organs which give a false aspect of stem and leaf structures; internally, however, the histology is seen to be of a simple type, the main tissue being composed of elongated **tubular cells** joined end to end so as to form an open network. Externally there is, however, a simple type of **epidermis,** immediately underneath which is a zone of small "**cortical**" elements. The whole plant conforms, however, to the type known as a **thallus.**

The **organs of reproduction** are situated in special parts of the thallus, and consist of **antheridia** and **oogonia** which arise in spaces known as **conceptacles** (male and female) found sunk in the tissue of the thallus at the ends of somewhat club-shaped branches. An **oogonium** arises first of all from a single cell at the bottom of a **female conceptacle,** and this cell divides into two. The lowest of these is the **basal cell,** the upper one being the **oogonium proper.** The contents of the oogonium form the **oosphere,** and this is a simple mass of nucleated cytoplasm (see Fig. 109, 1, 2, 3). The male organ or **antheridium** arises in the form of a special branching system of tubular cells from the bottom or sides of a **male conceptacle.** The terminal and a few of the lateral cells of this branch contain cytoplasm and nuclei which divide to form the **mother-cells of the antherozooids.** The antherozooids when mature are set free by the bursting of the wall of the parent-cell as free-swimming **motile cells.** Each **antherozooid** is a small nucleated pear-shaped body, possessing an **eye-spot,** and two laterally situated **vibratile cilia** (see Fig. 109, 5).

The **oosphere** now undergoes a process of **maturation.** In this process the original cell divides into **eight equal-sized egg-cells,** each of which is a **potential sexual cell.** At a certain period the egg-cells are set free by the rupture of the wall of the oogonium, and lie in the conceptacle or in the sea-water in the vicinity of the main plant. Some hair-like structures, the **paraphyses,** which arise from cells at the bottom and sides of the conceptacle, possibly serve to retain the egg-cells in the chamber, so that occasionally fertilisation may take place in the conceptacle itself.

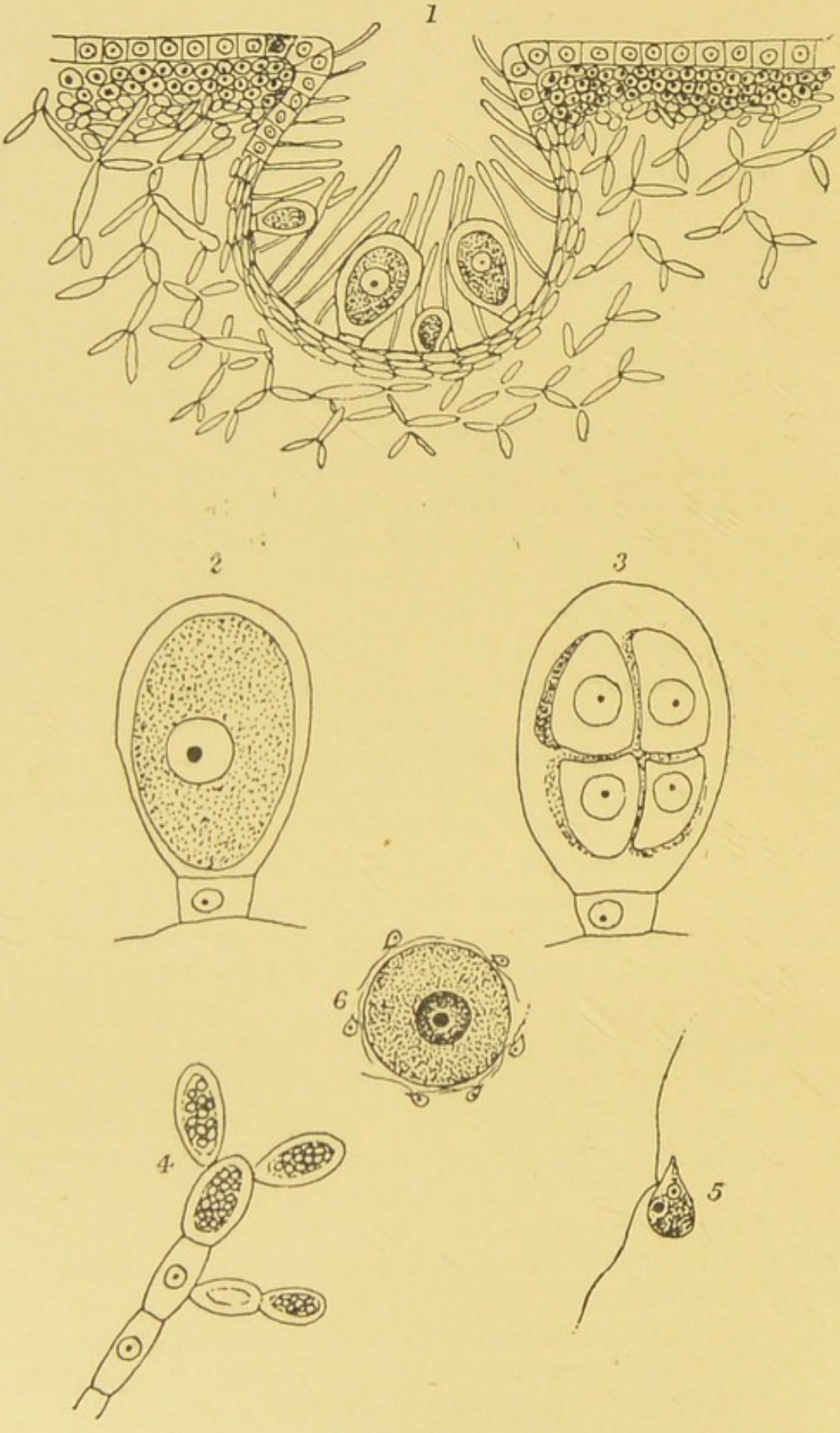

Fig. 109.

Fertilisation consists in the **fusion** of an **antherozooid** with an **egg-cell**, the nuclei of both participating in this fusion; as a rule, a large number of antherozooids may be seen swimming round one of the spheroidal egg-cells, but only one motile cell is needed for the purpose of fertilisation (see Fig. 109, 6).

After fusion, the **fertilised egg-cell** (**oospore proper**) is divided by two walls into four cells, and subsequent divisions result in the formation of a pear-shaped structure which, after a time, becomes fixed by a branching "**foot**" at one extremity to a suitable support. The foot does not function as a root, or absorbing organ, but only as a means of attachment.

(*c*) **Reproduction in Vaucheria** (see Fig. 110, 1, 2, 3, and 4).

The reproduction of *Vaucheria* by means of **swarmspores** has already been studied. The other method is a **sexual** one in

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Fig. 109.—Reproduction in *Fucus vesiculosus* (Diagrammatic).—1. Section across a female conceptacle showing oogonia springing from the bottom of it and numerous paraphyses. 2. A single oogonium, composed of a basal cell and an oogonium proper, which contains the oosphere. 3. Division of the oosphere into eight egg-cells previous to fertilisation. 4. An antheridial "branch" from a male conceptacle; the antheridia spring from the end and sides near the top of the "branch." The antheridia contain the mother-cells of the antherozooids. 5. A single antherozooid, with lateral eye-spot and two vibratile cilia situated laterally. 6. An egg-cell, freed from the oogonium and surrounded by antherozooids; one of these will ultimately fuse with the cytoplasm of the egg-cell, the nuclei also fusing.

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which the **antherozooid** and the **oosphere** form the **effective cells.** An **antheridium** and an **oogonium** arise on the same filament close to one another, by the formation of protrusions of the cell-wall into which a certain amount of cytoplasm flows with nuclei and chloroplasts. The **antheridium** is a small curved structure, and the **apical part** becomes cut off from the lower portion by a thin partition-wall. In this apical part the cytoplasm and nuclei are soon differentiated into a number of **ciliated antherozooids**, these being somewhat similar in structure to the antherozooids of *Fucus*. The **oogonium** arises close to an antheridium, in a similar manner to the latter, by the cutting off of the protrusion from the main filament by a thin partition-wall; the cytoplasmic contents of this protrusion form the **oosphere.**

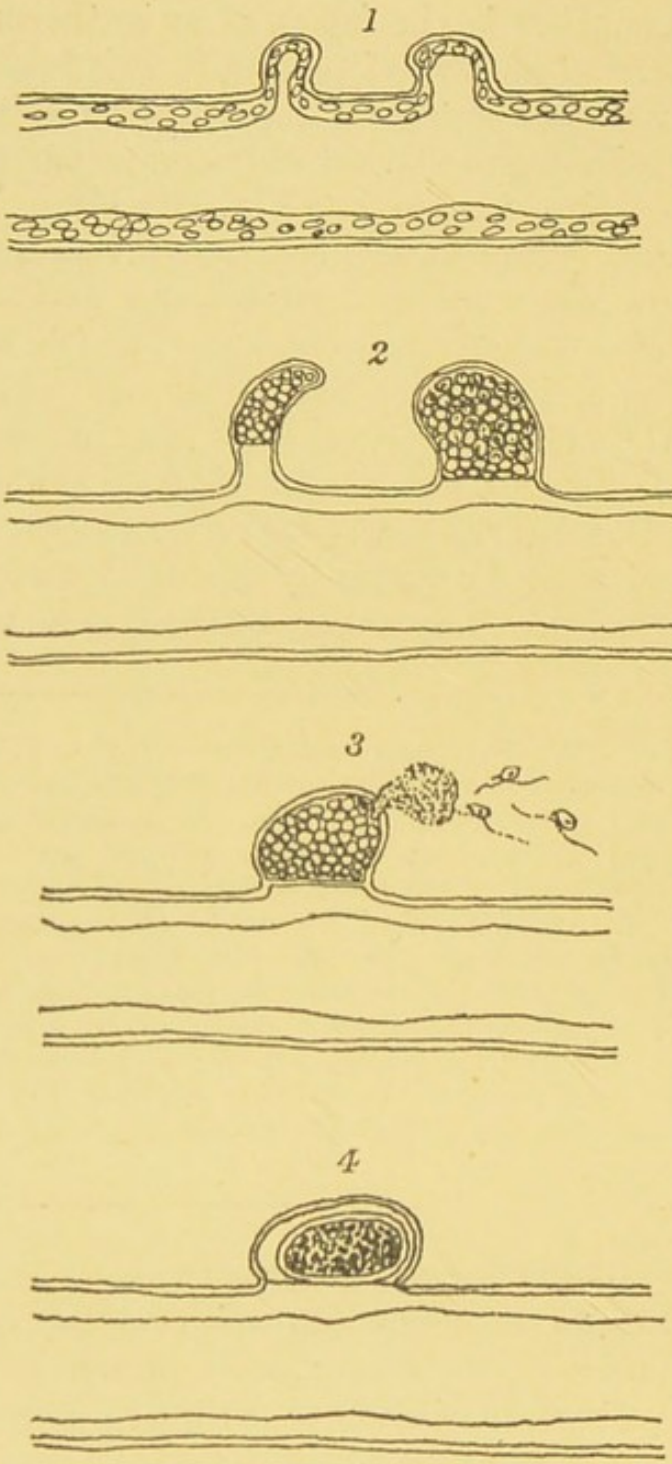


Fig. 110.—Reproduction in *Vaucheria* (Diagrammatic).—1. Portion of a filament of *Vaucheria*, with two protrusions arising near one another. 2. One of these protrusions has been converted into an antheridium (the smaller one), the other into an oogonium, both being shut off from the main filament by their walls. 3. The oosphere in the oogonium has secreted a plug of mucilage, and antherozooids are being attracted by this. 4. The result of fusion of one of the antherozooids with the oosphere; the oospore has assumed a wall of cellulose, and later will be freed from the oogonium by rupture of the wall of the latter.

Fertilisation takes place by the passage of an antherozooid into the oosphere, a plug of mucilage containing a chemical substance secreted by the latter acting as a means of attraction for the antherozooids (**positive chemotaxis**); **fusion** then occurs, and the result of this is an **oospore**, which soon assumes a thick wall of **cellulose**. After a period of quiescence the wall of the oogonium ruptures and frees the spore, which **germinates**, forming a typical *Vaucheria* filament.

Note.—The study of the reproductive processes in the Algæ is often best carried out by first growing filaments, &c., in an aquarium, so that plants may be gathered and examined at frequent short intervals. *Spirogyra* "conjugates" towards autumn as the water is getting colder, and so is unfavourable for vegetative reproduction. The same applies to *Vaucheria*.

In *Fucus*, the conceptacles are found in the club-shaped swollen ends of certain fertile branches of the thallus, and externally look like small "pits" or dimples in the surface of these. Sections may be taken in the transverse direction, and these will often cut the conceptacles at the sides of the branch in a direction perpendicular to the surface.

Antheridia and oogonia in *Fucus* arise in separate conceptacles.

The Homology of the Various Types of Reproduction.

By the term **Homology**, used in connection with reproduction, is meant a comparison of the various stages in the reproductive cycles of different groups of plants, and is interesting from the fact that there may often be traced in the higher types studied, **remnants of phases** which are more or less marked and of importance in the cycles occurring in **lower types**. The study of Homology is thus the only reliable method of placing a plant in its correct position in the scale of **evolution**, and as such, should be given due consideration in the study of Botany.

The comparison of the various reproductive cycles which have been examined is best made by drawing up a **table**, showing, in each group, the successive stages met with during maturation of the primary sexual elements, up to the time when fertilisation is completed by the union of the effective cells produced during the maturation process in each element. Such a table would be somewhat as is seen in the table of Homologies, facing p. 154, the **male** and **female** elements being distinguished by the symbols ♂ and ♀ respectively.

From this table it may be seen that in **Angiosperms**, the **antipodal cells**, formed during the maturation of the embryo-sac

(**macrospore**) are to be regarded as a remnant of a former **female prothallium**, which is represented in the **Gymnosperms** by the **prothallium** formed early in the embryo-sac, and which is existent in the **macrospore** of the Heterosporous Pteridophyta. The **synergidæ**, in like manner, have been looked upon as remnants of **archegonia**, or **oogonia**, occurring in **Gymnosperms**, or **Pteridophyta**, as special organs growing upon the female prothallium or **gametophyte** (sexual generation). The **prothallus** of Homosporous Pteridophyta is in reality a double structure, homologically, although the **spore** from which it is produced shows no signs of a mixed or hermaphrodite nature. It is not homologous to the **prothallium** of Gymnosperms alone, but to the combined **prothallial cell** of the microspore, and the **prothallium** of the embryo-sac or macrospore. The **antherozooids** of the Pteridophyta and lower types are homologous, not with the whole microspore of Angiosperms and Gymnosperms, but with the **generative cells** only in that structure.

In the Heterosporous Pteridophyta, the **male prothallium** formed in the microspore is homologous with the **prothallial cell** formed early during the maturation of the microspore in some Angiosperms (*Sparganium*) and Gymnosperms, and the **female prothallium** formed in the macrospore is homologous with the prothallium formed early in the embryo-sac of Gymnosperms, and, as was above stated, probably with the antipodal ells produced during the maturation of the macrospore in the Angiosperms.

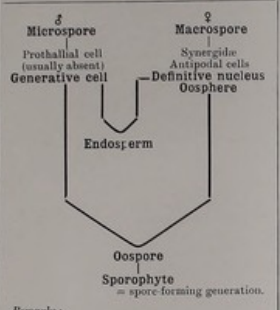
In the **Cycadeæ** (Gymnosperms) **antherozooids** or spermatozooids are met with which are produced in the **microspore**, and the **prothallial cells** cut off early in this microspore somewhat recall the **male prothallium** formed in the microspore of Heterosporous Pteridophyta. The Cycads probably form the nearest existing link between the Angiosperms and the Pteridophyta, more especially with the Heterosporous members of that group.

The phenomenon of **double fertilisation** in the Angiosperms has no parallel in the lower groups. By this method a **secondary prothallium** is produced in the macrospore (embryo sac), by means of which the embryo is nourished during the period which precedes germination, and for a short time after it. In the lower groups, however, the embryo-sporophyte depends partly for its first nutriment upon the cells of the **prothallus**

TABLE OF HOMOLOGIES.

(To face p. 154.

ANGIOSPERMS.



Remarks:

Antipodal cells = Rudiments of a **primary prothallium** or gametophyte (female prothallium of Macrospore, Heterosporous Pteridophyta).

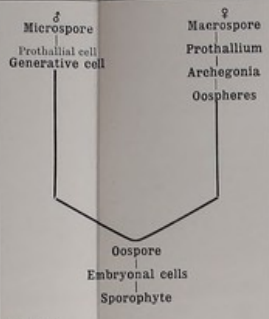
Synergidæ = Rudiments of **former Archegonia**, or **Oogonia** of Pteridophyta.

Endosperm is the result of **double fertilisation** and = **a secondary prothallium.**

Prothallial cell in Microspore (when present) = Rudiment of **Male prothallium** homologous with **Male prothallium in Microspore of Marsilea** (Heterosporous Pteridophyta).

Generative cell = Antherozooids of lower types.

GYMNOSPERMS.



Remarks:

Prothallium in Macrospore = **Female prothallium** produced in **Macrospore** of Marsilea (Heterosporous Pteridophyta).

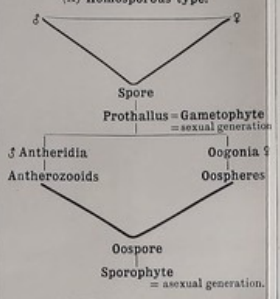
Archegonia = **Oogonia** of either Homosporous or Heterosporous Pteridophyta.

Generative cell = Antherozooids of lower types.

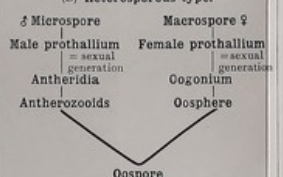
In *Ginkyo* and *Cycadeæ* (*Zamia*) *Antherozooids* are produced in the Microspore in the place of non-motile generative cells.

PTERIDOPHYTA.

(A) **Homosporous type.**



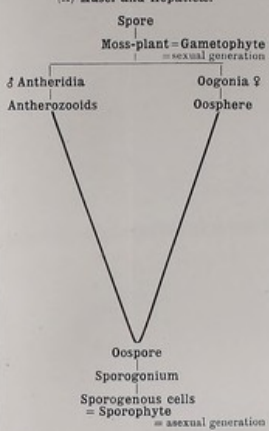
(B) **Heterosporous type.**



Alternation of Generations occurs in these Groups.

BRYOPHYTA.

(A) **Musci and Hepaticæ.**



Alternation of Generations occurs here, the **Sporophyte and Gametophyte being united in the same plant,** the Sporogonium producing a "foot" which attaches it to the Gametophyte.

Vegetative propagation by *Gemmæ* in both Groups.

FUNGI.

(A) **Asexual** reproduction by means of **spores,** viz.:—

Gonidia (*exogenous*).
Ascospores (*endogenous*).
Uredospores.
Teleutospores (*exogenous*).
&c., &c.

(B) Reproduction by **conjugation** of two similar hyphal cells: the product = a **Zygospore.**

(C) Reproduction by means of the **essential cells** in—

i. A structure resembling an **Oogonium,** together with

ii. A structure resembling an **Antheridium,**

the product being an **Oospore.**

Type = *Eurotium.*

(D) Vegetative propagation by means of—

i. **Soredia** (Lichens).

ALGÆ.

(A) **Asexual** reproduction by means of **swarmspores.**

Types = *Vaucheria.*
Œdogonium.

(B) Reproduction by **conjugation** of two similar protoplasts (Gametes): the product of union of two **Gametes** = a **Zygote.**

Type = *Spirogyra.*

(C) Reproduction by means of the **essential cells** in—

i. **Antheridia,** together with

ii. **Oogonia,**

the product being an **Oospore.**

Types = *Vaucheria.*
Fucus.
Œdogonium.
Chara.

in Homosporous Pteridophyta, and those of the **female prothallium** in the macrospore of Heterosporous Pteridophyta.

In the **Bryophyta** an apparent anomaly is encountered, for it is not, as would at first appear, the moss-plant (Musci) which is the **sporophyte**, but a rudimentary mass of cells, the **sporogonium** and **sporogenous cells**. The **gametophyte**, or product of germination of the **spore** is here a much more highly differentiated plant than the sporophyte, and in Musci forms the **moss-plant proper**. In the **Hepaticæ**, the **sporophyte** and **gametophyte** are, as in the **Musci, fused** in the one plant, a sporogonium being produced, which corresponds to the sporophyte, or **asexual generation**. Germination of a spore produced in the sporogonium results in the formation once more of the protonema, from which arises the moss-plant or Liverwort proper (**gametophyte**, or **sexual generation**).

In the **Thallophyta**, the homologies become somewhat limited. The **antheridia** and **oogonia** are, of course, homologous structures to those found in the Bryophyta and Pteridophyta, but beyond this it becomes very difficult to trace their reproductive relations, although attempts have been made to do so.

Certain divergencies from the main type of maturation of the embryo-sac in Angiosperms are sometimes met with. Thus, in *Peperomia*, **the primary nucleus** of the embryo-sac divides into sixteen, instead of eight nuclei, and these are uniformly distributed through the cytoplasm, instead of forming an egg-apparatus (synergidæ and egg-cell) and antipodal cells. No **polar nuclei** are met with in this case.

In *Sparganium simplex*, the antipodal cells divide many times, and give rise to a mass of one hundred and fifty, or even more, cells; in this plant also a prothallial cell is met with in the microspore. These instances are interesting, as they point to a sort of reversion to ancestral processes.

Parthenogenesis, or the development of an **unfertilised egg-cell**, is known only in the case of *Chara crinita* (Algæ). The development of parthenogenetic eggs is more common in the animal kingdom, notably in the case of *Daphnia* (water-fleas).

CHAPTER X.

CHEMICAL AND PHYSIOLOGICAL STUDIES IN CONNECTION WITH THE CELL.

It is now necessary to direct attention to some of the more important chemical and physiological processes to be observed in the living plant, processes which are, moreover, to be looked upon as the reflection on a large scale of what is going on in each living cell.

Some of these processes may be demonstrated in the **cell** itself by the use of suitable reagents, and yet others are only to be detected by the employment of experimental methods involving the use of the whole, or, at any rate, a large part of a plant. It was, moreover, seen in Chapter i. that the vitality of the protoplasm depends upon the maintenance of certain conditions, such as an adequate supply of water and oxygen and the co-existence of a suitable temperature, and also that **protoplasmic continuity** between the living cells in a cell-community was a necessary factor. Therefore, in the performance of laboratory experiments upon plants, or parts of plants, it is often essential to ensure the presence of those conditions under which the plant investigated exists in nature; otherwise the results of experiment will be inaccurate and hardly expressions of natural processes.

A. The General Chemistry and Physiology of the Cell.

Before proceeding to the detailed study of some of the more readily demonstrable chemical processes taking place in the cell, it is advisable to have an outline of the chemistry and physiology of that structure, looked at from a general point of view. The protoplasmic contents of a typical assimilating cell may be looked upon as a very efficient **energy-transformer** and **utiliser**, in which the principle of the conservation of energy holds good, just as it does whatever the working substance may be.

The vital processes involved in the building up during deoxidation and subsequent breaking down of the protoplasm during oxidation are included under the comprehensive term **metabolism**, the building up process being known as **anabolism**, and the breaking down **katabolism**. Thus, it is usual to speak of the nitrogenous and carbohydrate metabolism of a cell, these two being, in fact, the main vital phenomena in assimilation. Moreover, wherever metabolic activity is proceeding, **water** must always be present, since every chemical reaction in the cell involves this substance. In this respect, then, it would be quite as correct to use the term **assimilation** in connection with water as it is in the case of the formation of carbon-compounds from the CO_2 derived from the medium surrounding a plant, or the manufacture of proteids from the nitrogenous raw materials supplied; for in both these latter cases water is assimilated quite as much as carbon and nitrogen.

For **growth** to proceed satisfactorily in a green plant there are certain elements, in addition to those already mentioned (see p. 7), which have been found to be absolutely indispensable. These are **Potassium**, **Phosphorus**, **Calcium**, **Magnesium**, and **Iron**. Sodium does not appear to have the same importance as Potassium in metabolism, and most plants can do without it; in Fungi, on the other hand, **Calcium** may be dispensed with, but **Iron** is necessary to the normal growth of these plants. Certain elements—viz., **Ca**, **Mg**, **K**, and **Fe**—are always found in the ash produced by the combustion of protoplasm, but it is probable that salts of these metals exist in the living substance not in any chemical combination, but rather as substances which it is extremely difficult to get rid of during analysis. They are thus termed **metaplasm**. The ash of plants contains in its composition many more elements than the four mentioned above, but, as in the case of **Iodine** and **Bromine** in sea-plants, **Silica** in cereals, and, at times, **Aluminium**, such elements are not absolutely essential to growth. Nearly every element, including some of the rarer ones (rubidium, thallium, &c.), has been found in the ash of various plants, but it appears that only Potassium, Magnesium, Calcium, Iron, Sulphur, Nitrogen, Phosphorus, Oxygen, Carbon, and Hydrogen (with, perhaps, sodium and silicon) have any real metabolic value. As will be shortly seen, **Iron** is essential for the formation of chlorophyll.

There is another very important consideration to be taken into account in many of the vital processes which go on in a cell, and that is the formation and action of those peculiar bodies known as the **enzymes** (**unorganised ferments**). The chief feature about these substances is the fact that very small quantities of them will produce very marked and extensive chemical changes in other substances. Their action may be expressed by the term **catalytic**, somewhat after the mode of operation seen in the reaction between oxide of manganese and chlorate of potash in the manufacture of oxygen.

Of these enzymes the best known (in plants) are **diastase**, which converts **starch** into **dextrine** and **sugar**,* and certain **peptic ferments** which are present in the leaf-cells of such plants as *Drosera* and *Carica papaya*. The process which takes place when an enzyme acts is known as **hydrolysis**.

In the plant-cell, just as in certain animal cells (cells of glands), the enzymes are probably formed by protoplasmic activity, a precursor known as a **zymogen**, being first of all produced, and, subsequently, by the action of water or an acid upon the zymogen the enzyme is formed (see p. 159). The importance of enzymes in a cell is undoubted, as upon their action depend most of the chemical changes involved in the **conversion of reserve carbohydrate and proteid** into forms more suited for direct use by the cytoplasm.† The **anabolic** processes taking place in a cell are in many instances very complex, and it is only in a few cases that distinct **intermediate stages** can be recognised, when such substances as **starch** and **proteid** are converted into **protoplasm**. Recently the views concerning **nitrogenous metabolism** have undergone a certain amount of revision, particularly when it was shown that some plants (*Bacteria*) were able to utilise the **free nitrogen** of the air, and convert it into substances which were of further value to plants as sources of nitrogenous food-material (see *infra*). A similar instance is that where filaments of *Beggiatoa* are able to utilise **sulphuretted hydrogen** existing in solution in natural springs, converting it into sulphur and sulphuric acid by a process of oxidation. The **katabolic** side of

* Some forms of diastase (cytase) can dissolve cellulose.

† The action of enzymes increases up to an *optimum* temperature ranging from 30° to 45° C. Enzymes are destroyed at a temperature of from 60° to 70° C. Darkness or subdued light appears to favour their action.

metabolism is often quite as complex as the anabolic. The **oxygen** required by the cell for the purposes of oxidation is obtained either from the air or water surrounding it or from easily reducible substances in the cell itself. Most of the oxygen produced during the **assimilation of CO_2** and **H_2O** is, as will be shortly proved, evolved from the cell as free oxygen, and is not utilised for the purposes of oxidation, although, in the case of water-plants, some of it may be dissolved in the water and re-utilised. As will be pointed out a little further on, the intermediate reactions involved in nitrogenous katabolism occasionally result in the formation of such bodies as **alkaloids** or **glucosides**; and many of the bye-products of both carbohydrate and nitrogenous metabolism consist of **organic acids**, such as oxalic, tannic, meconic, ulmic, &c., which combine with bases present in the cell-sap to form definite **salts** which at times separate out in the sap (*vide* **raphides**). These bodies—viz., the alkaloids, glucosides, and organic acids—are, as a rule, removed to those cells of a plant where they will have no further action upon metabolism.

Constructive processes in the cell are partly **anabolic**, and partly **katabolic**; thus, the building up of fresh **protoplasm** from proteids, carbohydrates and amido-acids (see *infra*) is an **anabolic** process, whilst the formation of **cellulose, wood,** and **cork** are instances of **katabolic** construction, cytoplasm being broken down again in these latter.

The Enzymes (ferments), which have been mentioned above, are formed by the protoplasm by a sort of double process—viz., anabolic to start with, and the substances so produced (zymogens) are broken down again (katabolism) to form the ferment.

Oils and **fats** arise in the cell during metabolism by a breaking down of the cytoplasm during oxidation; and many of the non-nitrogenous vegetable acids met with are products of katabolism, but in a few instances they may be formed as bye-products during anabolic processes (**oxalic acid**).

The formation of the **cell-wall** by the cytoplasm has been shown to be connected with the deposition of **microsomata** upon the wall, and the conversion of these into cellulose (or pectose) by a process of self-decomposition (**secretion**). The **cell-plate** (*vide* Chap. viii.) is formed in much the same manner.

In a few cases the formation of oils and fats has been shown

to take place in the substance of small structures comparable to plastids, known as **elaioplasts**; in these bodies **glycerine** and a **fatty acid** are combined to form the oil or fat.

The deposition of **starch** in the plastids and chloroplasts is in the main a process of secretion; the **sugar**, which is first formed during photosynthesis (see *infra*), being utilised for the purpose of starch-formation (storage); this process is thus **katabolic** in nature.

The cell obtains **energy** for the purposes of elaboration of food from several sources, viz.:—

a. **Light.**
b. **External heat.**
c. **Internal heat** liberated during oxidation.*

The influence of **heat** upon vital activity in a cell increases up to a certain point, the so-called **optimum temperature**, after which it again decreases.

With regard to the relation between **heat** and **chemical action**, the following reservations must be made:—Some reactions require for their completion heat from outside or from the cell itself, and these are known as **exothermic** reactions, whilst others evolve heat during their progress, and are called **endothermic** reactions. In the former case the cell loses a certain amount of energy, whilst in the latter energy is gained. Occasionally reactions occur which may be exothermic or endothermic according to circumstances, and these are known as **reversible** reactions. In the case of the energy of **light rays** (radiant energy) it will be seen further on that the **chloroplasts** are able to transform the radiant energy into energy of chemical action (**actinic**), and in this manner the chloroplast is enabled to form **starch** (or sugar) from the raw materials CO_2 and H_2O supplied to it.

Occasionally the energy of chemical action (oxidation) is intense enough in plant-cells to cause **luminosity** (certain Bacteria). This phenomenon is, however, not so frequent in plants as in animals (see *infra*).

The **absorption of water** by germinating seeds is often attended with a considerable evolution of **heat**, due partly to

* A large part of the energy of a plant is derived from the oxidation of carbohydrates during respiration.

actual combination of the water with protoplasm (comparable to the formation of $H_2SO_4 : xH_2O$ when water is added to sulphuric acid). This is an endothermic reaction, and is a source of energy to the cell. In this case, also, the heat evolved during **respiration** must be taken into account. On the other hand, the action of **enzymes** mentioned above is in the main one of breaking down of complex compounds into simpler bodies (hydrolysis), and, as such, often requires heat from outside—viz., it is an exothermic reaction, and involves a loss of energy to the cell. The cellulose and woody framework of a plant represent a store of *potential energy*, whilst the oxidative processes in the cell liberate an amount of *kinetic energy*, which appears in the form of *heat*.

B. Details of Vital Processes.

Having now obtained an outline of the main vital processes to be considered in the cell, it is necessary to examine in detail a few of the more important of these, and, where possible, try to elucidate some of the intermediate stages in the formation of the essential food-substances elaborated by a cell from the raw-material supplied.

In this respect the following will be described :—

i. **Starch** and starch-formation.

ii. The relation existing between **chlorophyll, light,** and the **assimilation of CO_2 and H_2O.**

iii. The formation of **elaborated nitrogenous food.**

iv. The **cell-sap** and the **mechanics of sap-conduction.**

v. The evolution of **oxygen** during assimilation, and of **carbon dioxide** and **water** during respiration.

vi. The **assimilation of carbon dioxide** and **water** from the surrounding medium.

vii. **Variations of protoplasmic activity** under different conditions, especially those concerned with growth in **light of varying refrangibility,** and the effect of **gravity** and other **physical agencies** upon growth.

viii. The production of **heat, light,** and **changes in electrical potential** in cells of plants; action of **electric currents** upon cytoplasm.

Each of these must be considered in detail; v. and vi. include experiments which demonstrate the processes mentioned.

i. Starch and Starch-formation.

Starch, which has a composition represented by the general formula $C_6H_{10}O_5$,* is a **carbohydrate** belonging to the group of polysaccharides. It occurs in plant-cells, either alone, or in chloroplasts or plastids, in the form of **granules** and grains of various sizes and shapes. In order to examine starch, a small portion of a thin slice of a potato-tuber should be placed in a small drop of water on a slide, and gently squeezed. The slice is then removed, and the now somewhat opalescent drop covered with a cover-slip and examined under a low power. Numerous **starch-granules** are then seen, which, when examined by transmitted light, have a semi-translucent refractile appearance, but by reflected light are white and opaque. The size of the individual granules varies from a small circular particle to the large oval grains many times the size of the former; and, by using the $\frac{1}{6}$-in. objective, cutting off the peripheral illuminating rays, and using somewhat oblique illumination, one of the larger granules may be seen to possess the following structure (see Fig. 111):—

a. A dark spot situated somewhat eccentrically: this is the **hilum** of the grain.

b. Outside this alternating layers of **light and dark lamellæ**, arranged round the hilum, but, as a rule, thicker on one side of the hilum than the other (see 4, Fig. 111).

c. If the plane mirror of the microscope be used for illuminating, the rays will be partially polarised; and if, after these rays have passed through the starch-granule, they be again passed through a **Nicol's prism** (analyser) in the eye-piece of the microscope, they can be **analysed** by rotating the prism (contained in the eye-piece) so that its axis assumes different inclinations. The result of this analysis shows that a granule of starch is made up of alternating zones of two substances which **rotate the plane of polarisation** in different directions, and that one of these substances contains more **water** in its composition than the other. The starch-grain is thus **anisotropic.**

In form, the larger granules in cells of potato-tubers are **oval**, whilst the smallest are **circular**, no hilum being present in these latter. In the cells of maize **endosperm**, the granules are **polyhedral**, and in the rhizome of *Iris*, **dumb-bell shaped.**

In potato, much of the reserve starch in the tuber-cells is

* Usually found together with a certain amount of water of constitution. Cellulose is represented by the formula $n(C_6H_{10}O_5)$.

formed at first in plastids,* and by the time the tuber is full grown, all the plastids have been converted into starch. During the examination of the chloroplasts in the cells of *Vallisneria*

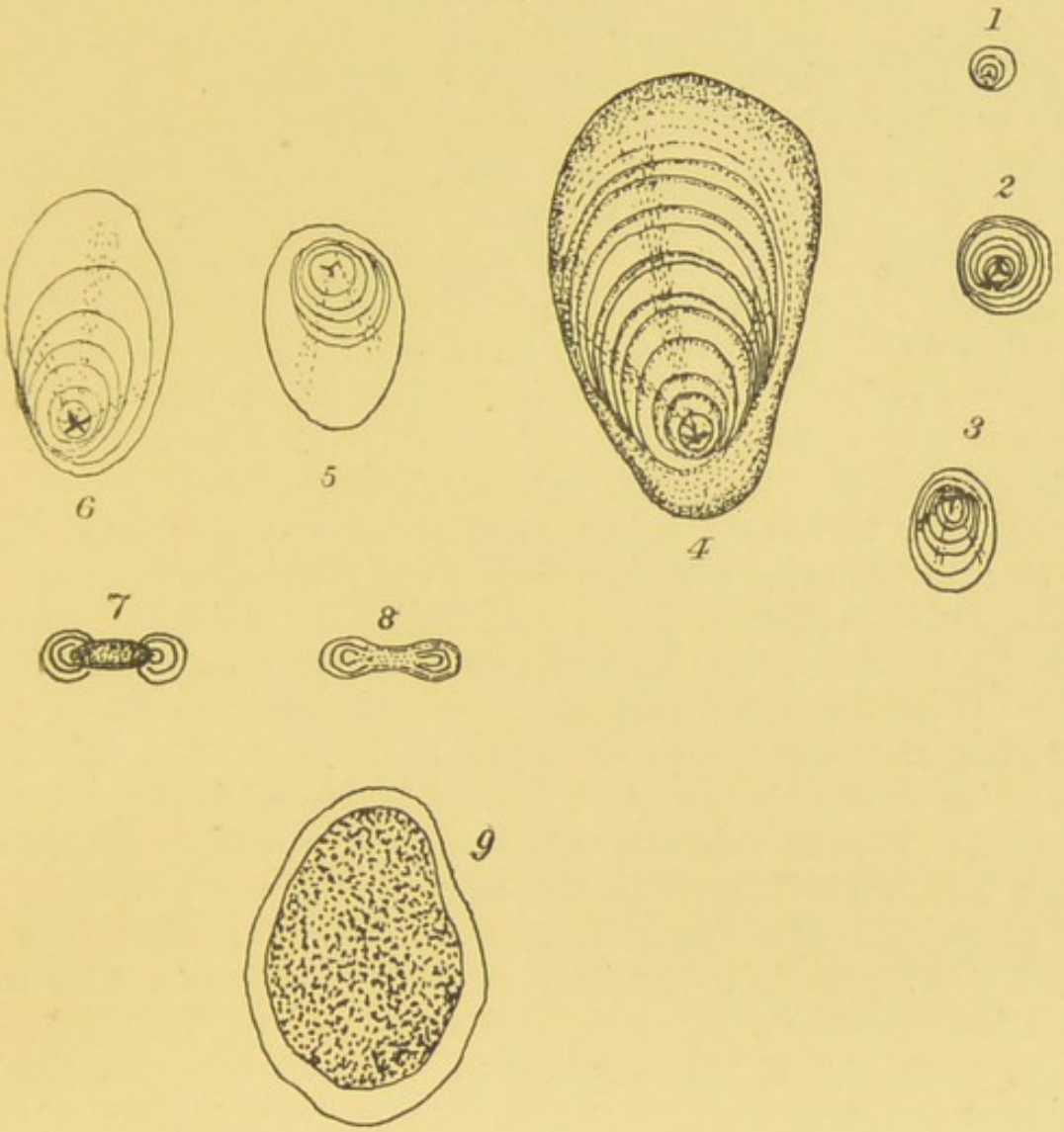


Fig. 111.—Various Starch-grains from Cells of the Potato-tuber. 1. Small granules in which the first signs of a hilum and concentric laminæ can be detected. 2, 3, 4. Grains of various shapes and sizes in which the hilum and lamination are well marked. 5, 6. Grains in which the starch is deposited regularly at first, and subsequently somewhat irregularly. 7. A plastid from the rhizome of *Iris germanica*, showing the formation of starch at both ends. 8. The resulting dumb-bell shaped granules formed from 7. 9. Effect of boiling water upon a starch-grain: the outer envelope is the farinose, the inner granular portion (stained with iodine) is the granulose.

* Some of the starch is, however, formed in the tuber by the translocation of carbohydrate from the cells of remote parts, and starch is then reformed by the plastids from sugar, &c.

leaf (Chap. ii.), it was seen that the starch-granules formed in them were produced (or rather stored) during the daytime in the presence of **light**, but in the formation of starch in the plastids in the absence of light a somewhat different process goes on, although the ultimate product is the same. Thus, in plastids it is highly probable that **elaborated food (sugar)** from the leaves is used, and gradually worked up by the protoplasm, each plastid being, as has been pointed out, a specialised portion of the cytoplasm of a cell, and as such, capable of acting as a **"plastic"** body. After the plastid or chloroplast has been completely converted into starch, the further growth of each granule goes on by a process of **accretion**, the main cytoplasm of the cell forming successive layers. The **hilum** in the larger granules may at times indicate the position of a former plastid, but is more often produced by splitting of the centre of the granule, producing a tri-radiate figure. Compound and semi-compound starch-grains are also found in the cells of the potato-tuber.

The **blue reaction** of starch with **iodine** indicates the formation of a definite but rather unstable **chemical compound**, which is readily destroyed by **heating** or treatment with **alcohol**.

Boiling in water causes the granules to swell, and finally a sort of sac or shell is produced, formed by an external substance known as **farinose**, enclosing a granular substance, or **granulose** which takes up iodine. **Caustic potash** also causes a swelling of the granules, and a **dilute acid** or a solution of **diastase** will dissolve the granules, especially on gently warming, with the formation of dextrin.

The **chemistry of starch-formation** is rather complex. It is not intended here to give more than a brief outline of the process, which is, as yet, somewhat undetermined. It may, however, be mentioned, that a good deal of the starch in plants is the result of **anabolic** processes, and not of **katabolic**. The main feature in these processes seems to be the **elimination of oxygen**. Experimental evidence points to the fact that there are many stages between CO_2, H_2O, and starch in the anabolism of these substances by the chloroplasts, and between protoplasm and starch during the katabolism of the living substance.

It has been thought that **formaldehyde** is an intermediate product during the formation of starch (or sugar) in chloroplasts or plastids, and that this, by elimination of **water**, is converted

into starch, thus:—$CO_2 + H_2O = CH_2O + O_2$ (the O_2 being evolved during assimilation), then $6CH_2O - H_2O = C_6H_{10}O_5$ (starch).* At times it appears that cane-sugar may be formed by the polymerisation of formaldehyde.

The above equations, however, are by no means a complete representation of starch-formation, it being probable that other intermediate stages occur. Moreover, it appears that sugar is the carbon-compound formed as the final product, the starch being produced subsequently by a process of secretion and stored in the chloroplast, and the sugar first formed may be either *cane-sugar* or a *hexose* (*i.e.*, dextrose). Some of the sugar is used up at once for formative purposes, and it is the remainder that is stored. In some cases, it seems that the protoplasm may be converted into starch by oxidation and splitting off of the proteid and amine parts of the molecule (katabolic). In the formation of the **cell-plate** (cellulose), some such process as this appears to take place, **starch** or **sugar** being here used for reconstructive purposes. The **synthesis of cellulose** is, however, a rather more complex process than would appear from the molecular composition of that substance, and the **ectoplasm** next the cell-wall is probably here the working substance, a process analogous to *secretion* taking place.

The initial process, in which the chlorophyll synthesises CO_2 and H_2O to form sugar, is termed **photosynthesis.** The later reactions involved in the production of reserve starch in the chloroplasts are more the result of **chemosynthesis.**

ii. (*a*) **The Relation existing between Chlorophyll, Light, and the Assimilation of Carbon Dioxide.** (*b*) Pigments other than chlorophyll. (*c*) The conditions governing chlorophyll formation.

(*a*) **Chlorophyll** is the green colouring matter which, as has been seen, exists in the chloroplasts, probably dissolved in an **oily substance,** which permeates the substance of these structures. In reality, in alcoholic solution chlorophyll is made up of a mixture of **two pigments**—viz., a greenish one known as **phyllocyanin,** and a yellow one, **phylloxanthin.**† If a leaf or other

* See Vines, *Physiology of Plants.*

† Recent researches seem to point to the fact that chlorophyll is a single pigment which is readily decomposed (by alcohol or boiling water) into the above-mentioned two pigments.

green part of a plant be placed in **alcohol** for some hours, the **chlorophyll** is extracted, and, on adding **benzine** in equal volume to this alcoholic extract, and shaking up the mixture, the benzene separates the **phyllocyanin** and floats on the top of the alcohol, the latter liquid retaining the **phylloxanthin.**

By making an alcoholic extract of chlorophyll **alkaline** with caustic potash, and examining the extract by means of the **spectroscope** (the tube or special vessel containing the chlorophyll solution being placed in the path of rays of white light before they reach the prism), some characteristic **absorption bands** may be seen in the spectrum of white light which has passed through the tube containing the chlorophyll. In all, **seven** such bands occur in various parts of the spectrum, and they indicate that chlorophyll **absorbs** certain of the rays of sunlight and allows others to pass. The absorption bands are situated as follows in the spectrum (see Fig. 112):—

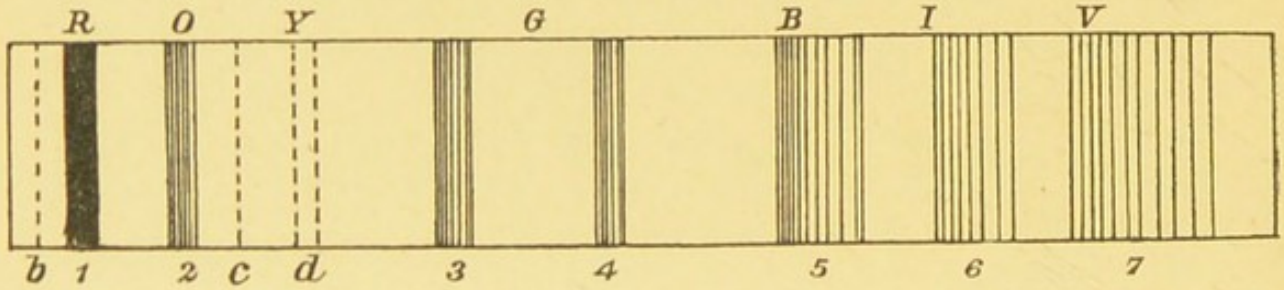


Fig. 112.—The Absorption Spectrum of Chlorophyll (see text).—*b*, *c*, Fraunhofer lines in the red. *d*, The sodium band in the yellow portion of the spectrum. 1, 2, 3, 4, 5, 6, and 7 are the bands in the spectrum formed by the absorption of certain rays by the chlorophyll (alcoholic slightly alkaline solution).

One band (the I band) occurs in the **red**, between the **Fraunhofer lines B** and **C**, another in the **orange** whilst a **third and fourth** are in the **green** portion of the spectrum. There are also **three broad bands** in the **blue and violet** at the other end (**chemical rays**).

The significance of these bands is as follows:—Of the **white light** which reaches a chloroplast, only those rays which are indicated by the position of the **absorption bands** in the spectrum are made use of for the purposes of the assimilation of CO_2 and water, the other rays passing through. The **chloroplast** is a specialised portion of the cytoplasm of a cell, and as such is able to **transform the energy** derived by the sifting out by

chlorophyll of certain light-rays into **energy of chemical action** during the processes of starch-formation; and in this process, as has been seen, CO_2 and water are assimilated, and certain intermediate **carbon compounds** are formed, to be quickly broken down or synthesised again (photosynthesis). It is probable that the **red rays** (the least refrangible) are the ones most utilised in these reactions, and since the more refrangible violet and blue rays are also absorbed to a certain extent, it seems likely that they are also used to further the process. Possibly these rays are converted into others of a lower refrangibility, or, as is more rational to suppose, the red rays may be converted into those which are known to further certain chemical actions (*cf. infra*, Timiriazeff's experiment).

If green parts of plants are kept in the dark for some time they become **etiolated**—that is, the chlorophyll disappears (or **etiolin** is formed), and the chloroplasts are unable to assimilate carbon dioxide and water and produce sugar to the same extent as before. In the case of plastids, in parts of plants which are not green, formation of starch probably takes place by the conversion by these structures of elaborated material (sugar) from the leaves into other carbon-compounds, and finally into starch (chemosynthesis). In some cases, also, it is probable that the cytoplasm undergoes a gradual conversion into starch by the splitting off of the proteid and amine portions of its molecule.

Chlorophyll has been found in those parts of plants **which have never been exposed to the light**, such as the **seed-leaves** of *Pinus*, and in the **phelloderm** formed from the cork-cambium in certain stems (see Chap. iii.). In such cases it is probable that chlorophyll is formed in a somewhat different manner to that in which it arises in parts exposed to the light, or else that just enough light penetrates to these tissues for the pigment to be formed.*

(*b*) **Pigments other than Chlorophyll occurring in Plant-cells.**—**Red, blue,** and **yellow** colouring matters may exist in cells, singly or combined, either in the form of **chromoplasts** containing the pigment, or dissolved in the **cell-sap.** In the cells of the petals of *Tropæolum*, angular **chromoplasts** are to be

* It can be demonstrated that the light needed for chlorophyll-formation need not necessarily be so intense as that needed for CO_2 assimilation (see Darwin and Acton, *Practical Plant Physiology*).

found in the cytoplasm, each of these containing an orange-red pigment. The basis of each chromoplast is protoplasmic in nature.

In the carrot, the cells of the **cortex** possess reddish **crystalloid** bodies of a proteid nature, which contain *carotin*. This pigment has some chlorophyll in its composition. Such pigments are usually formed **in the presence of light, oxygen** and **Fe-salts,** much as chlorophyll is in the chloroplasts (see *infra*). It is probable that the chemical composition of many of them is not far removed from that of chlorophyll, particularly in the case of yellow or greenish-yellow pigments, some of which bear a definite relationship to **phylloxanthin.** In many instances the colouring substances exist in a cell **dissolved in the cell-sap,** as in the **Beet-root** and **pericarp** of many fruits. The **red** pigments belonging to this group are changed to **green** or **blue** on the addition of an **alkali,** and when **acid** is added to such an alkaline solution, the red colour returns when neutralisation is complete (*cf.* action of acids and alkalies upon **litmus,** a vegetable pigment). The blue colouring matter in many cells is known as *anthocyanin*.

The **whiteness** of many petals is due to the presence in the cells of **chromoplasts** (**leucoplasts**), which **reflect** the rays of white light falling upon them almost entirely. Intercellular spaces and the convexity of the outer walls of the epidermal cells may also contribute towards this result.

The **function** of many of these pigments is often, as in the case of the petals of flowers, of the nature of an **adjuvant to fertilisation,** insects being attracted by brilliantly-coloured petals; but where a greenish-yellow pigment is present in definite chromoplasts, the assimilation of carbon-dioxide may at times occur. The majority of the pigments existing in chromoplasts may be extracted from them by **alcohol;** where the colouring matter is in solution in the cell-sap, as in the Beet-root, boiling kills the cytoplasm, and upsets the osmotic balance of the sap in the cells, leading to an outward diffusion of the pigment. The colouring matter of such **permanent elements** as those of wood and sclerenchyma exists in the **cell-walls,** and is the product of the decomposition of substances deposited in the walls at various times. Such pigments have, of course, no vital significance once they have been deposited.

(c) **The Conditions Governing the Formation of Chlorophyll**

in the Chloroplasts have been determined to be the following:—

i. The action of *light*. In darkness, green plants become *etiolated*—that is, the chloroplasts lose their green tint, a yellowish one being substituted, which is due to the formation of *etiolin*.
ii. The presence of *oxygen*.
iii. The presence of traces of an *iron-salt* in the soil. Without this iron, the chlorophyll is not formed. The influence of iron upon the colouring of petals of *Hydrangea* is well known, and seems to point to the necessity of the same conditions for the formation of other pigments than chlorophyll.

Etiolated plants will, when again exposed to light, develop chlorophyll, provided the other conditions of its formation be present; and it has been shown that photosynthesis can proceed to a limited extent in chloroplasts in which only etiolin is present.

iii. The Formation of Elaborated Nitrogenous Food (*Proteids*).

The assimilation of **nitrogen** which takes place chiefly in the leaf-cells and other green parts of a plant is a subject which is difficult to deal with from an elementary point of view, seeing that it involves complicated **synthetic** and **analytic** reactions between organic and inorganic compounds in a cell. The **nitrogen** is obtained from **nitrites** (or **nitric acid**) and **nitrates**, as well as **ammonia** at times (*cf.* absorption of ammonia by capitate hairs). In many cases **reserve proteids** are present in the cell-sap, which, when acted upon by **enzymes**, are converted into **albumoses** and **peptones**, and these are then gradually built up into protoplasm by the further agency of the living substance. The conversion of proteids into albumoses and peptones is mainly a process of **hydrolysis**, the elements of **water** entering into the reactions, a fresh compound being then formed by the splitting up or reconstitution of the previous one. The formation of proteids in a cell involves synthesis of a high order. During this process various waste-products are formed, notably **oxalic acid**, and in some cases this acts upon **calcium nitrate** in the cell-sap, forming **calcium oxalate**, the released **nitric acid** being again assimilated. Speaking generally, in the **synthesis of protein**, the following substances are involved in the reactions:—

Nitrites, nitrates, phosphates, sulphates, and chlorides of K, Ca, Mg, Fe, and at times other metals; water, carbon-compounds (starch, &c.), ammonia, asparagin, and nitric acid. The actual chemistry of the process is a subject

which is as yet somewhat undecided, and beyond the scope of an elementary text-book. It may, however, be mentioned, that the synthetic processes involve the interaction of substances known as **amido-acids** (asparagin), and a **carbohydrate**, together with a **sulphur-containing** compound. The assimilation of nitrogen is thus a process of **chemo-synthesis** as opposed to **photosynthesis**, and can proceed in the absence of light.

With regard to the ultimate fate of **carbohydrate** and **nitrogenous materials** in the cell, it is important to remember that of these essential food-substances, there are two main parts—viz., that which is at once utilised by the cell-protoplasm, and known as **circulating** proteid, or carbohydrate, and that which forms **stored** or **reserve** food. As has been seen, the various **enzymes** are constantly at work converting reserve starch and proteid into soluble substances, which can pass from cell to cell, from the parts where they are manufactured or stored to remoter cells of a plant. If a leaf in which starch has been actively formed during the daytime be examined early, before the next day's assimilation has started, it will be found that during the night-time all the starch has been used up, in fact, has been converted into sugar, which has been transported to other parts as circulating food-material. The same may be said of the **asparagin** (an amido-acid), formed in the leaves: this substance quickly passes away from the leaf-cells, and is, together with carbohydrates and sulphur-compounds, constructed into proteid and protoplasm in remoter parts. It has been shown that **hydrocyanic acid** can at times be used for proteid construction in the place of an amido-acid.

iv.—The Cell-sap and the Mechanics of Sap-conduction.

The **cell-sap** is a fluid which varies somewhat in composition according to the part of a plant from which it is taken. Thus, the **watery sap** which is present in the root-hairs of a root, and is conducted upwards by the woody portions of root or stem, contains far less solid matters in solution than the **sap of the elaborating cells** of the leaf, or of the downward-conducting elements of the **phloem**. Nevertheless, from a general point of view, it may be said that the cell-sap is made up of the following substances :—

a. **Water.**—In some cases 98 per cent. of the sap is composed of water.
b. **Mineral matters** in solution—viz., salts of **sodium, potassium,**

lithium, magnesium, calcium, and at times **silicon.** Of these, the **nitrates** and **nitrites** of sodium and potassium, the **phosphates** and **chlorides** of the same metals, and the salts of **calcium** and **silicon,** occur in the sap of most plants, silica being present in the sap of cereals to a considerable extent. In sea-weeds and shore-plants, **iodides** and **bromides** of sodium and potassium are also found. **Sulphates** of the above metals also occur.

c. **Dissolved Carbohydrates (sugars**—viz., glucose, cane-sugar, and mannite, inulin), and **amides** (asparagin). **Dextrins** also occur as intermediate products between starch and sugar; **gums,** such as arabinose, tragacanth, &c., may also be present. **Proteids, albumoses,** and **peptones** are also present at times. Some of the proteids—*e.g.*, **gluten**—are insoluble.

d. **Soluble Alkaloids and Glucosides.**—These are bodies which are intermediate products in the katabolism of nitrogenous substances and protoplasm in plant-cells. The **alkaloids** are amides—viz., are NH_3, in which one or more H atoms are replaced by a radicle. The **glucosides** are nitrogenous bodies composed of **amines** combined with **glucose.** Both of these bodies separate out sooner or later in the cell, and are rendered harmless .

Examples of the alkaloids are: quinine (*Cinchona*), nicotine (a liquid alkaloid contained in the leaves of *Nicotiana tabaca*), atropine (in the berries of *Atropa belladonna*), strychnine (in the seeds of *Strychnos nux vomica*); and, as instances of glucosides, may be given, digitoxin (*Digitalis purpurea*), picrotoxin, and many others. In the case of the leaves of *Prunus Laurocerasus*, a glucoside **amygdalin** is present, which, when acted upon by **emulsin** (an enzyme), breaks up into **hydrocyanic acid, glucose,** and benzoic aldehyde, this being one way in which the glucosides are split up in plants (**hydrolysis**).* The glucosides may be confounded at times with **tannin,** with which substance glucose often exists in loose combination.

e. **Ferments.**—These are the unorganised ferments or **enzymes,** such as **diastase, papain,** and the **peptic ferment** in the leaf-cells of *Drosera*. They are very important bodies. **Diastase** converts **starch** into **dextrins** (achroodextrin, erythrodextrin) and **sugar** (glucose), and the peptic ferments convert the **proteids** into **albumoses** and **peptones,** bodies more suitable for assimilation than the proteids. [The **organised ferments** belong to the Fungi, and one of the best known is *Saccharomyces*, the yeast-fungus.] Other ferments are **invertase,** which inverts cane-sugar, **cytase, lipase** (a fat-splitting ferment), and **synaptase.**

f. **Organic Acids.**†—These may be present as acids, or in combination with **mineral** or organic **bases** in the cell. The acids found may be **oxalic, malic, citric, racemic,** and **tartaric. Tannic** and **gallic** acids are often present, and **salicylic acid** is found in the cells of *Gaultheria procumbens* as methyl-salicylate. The acids are in many cases bye-products of cell-metabolism—viz., oxalic acid. **Calcium**

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* Another such instance is where salicin is split up by means of synaptase into saligenol and glucose.

† Inorganic acids (viz., HNO_3) may also be present at times, and NH_3 (ammonia) may occasionally be found. In the latter case, however, amido-acids are soon formed.

oxalate has been shown to be formed by the decomposition of **calcium nitrate** in leaves, the calcium combining with oxalic acid, and the **nitric acid** being subsequently assimilated.

g. **Fats** and **waxes** occur at times in the cell, and should be mentioned here, although they can hardly be looked upon as being soluble in the cell-sap. They are formed by the decomposition of **protoplasm**, and, possibly, at times, by other methods. The waxes are excreted by the epidermal cells of some leaves, and form short rods set at right angles to the surface on the outer aspect of the external walls. In this manner a layer of wax is formed which prevents water from collecting on the leaf.

The cell-sap, then, contains many substances of the nature of **raw food-materials**, some **elaborated food-substances** (such as sugar, inulin, amido-acids, and proteids), **ferments**, and a good many **excretory products**, or bye-products of the breaking down of the cytoplasm. Other materials are also present, such as **resins** and **gums**, **oils**, &c., which are not soluble in the cell-sap, but which are products removed as soon as they are formed. In many cases the resins, &c., may be looked upon as products of the degradation of the cell-wall, and form striking instances of substances thrown out of a cell which may nevertheless be of great value to the plant. The manner in which raw food-materials, such as salts of potash, sodium, silica, &c., enter the plant, has been partly considered already during the examination of **root-hairs** and the young cell (Chap. iv.). It was there pointed out that the **ectoplasm** of the root-hair exercised a **selective capacity** over the absorption of salts in dilute solution in the soil; in the one case, perhaps, salts of sodium and potassium being taken in to the exclusion of others; and in the other case, possibly salts of silica being admitted as well.

A closer consideration of the phenomena of **osmosis** is not inappropriate at this point; the absorption of the dilute solution of earthy salts by the **root-hairs** is dependent upon the presence in the central vacuole of the hair of substances which are osmotically active—that is, which exert a distinct attraction upon the molecules of water and salts outside the cell. At a certain stage the so-called **osmotic pressure** inside the cell reaches a limit at which internal diffusion or endosmosis ceases and equilibrium exists. But the water in the vacuole of the root-hair is being constantly withdrawn by reason of the suction action of the transpiration current (see p. 174), and also by further osmosis all

the way up the root, and, consequently, the osmotic balance of the hair is being as constantly disturbed, so that fresh water and salts are drawn in again from the soil. The turgid condition of a cell when the upper limit of osmosis has been reached determines a certain stretching of the cell-wall (**turgidity**), and this stretching is a great aid to the growth of the wall in area.

Solutions may be prepared which are said to be **isotonic**—that is, when a cell is placed in them neither influx nor exit of water takes place. But a cell, such as a root-hair, when placed in a solution which is ever so slightly greater in concentration than the sap in the hair, will suffer a certain amount of exosmosis—that is, water will pass out, and the hair will shrink (see Plasmolysis, Chap. ii.).

In speaking of selective absorption by the root-hairs, it was shown that certain salts may be taken in to the exclusion of others in the soil; this is quite true, but, nevertheless, the factors determining this selective absorption, depend not only upon the regulating influence of the ectoplasm, but also upon the physical nature of the salt in solution in the sap inside the hair—that is, the osmotic activity of the substances in the cell must be considered in addition to the selective influence of the ectoplasm.

In addition to these few statements with regard to osmosis and turgidity, it must be mentioned that during the distribution of the assimilable food in a plant, the question of the osmotic nature of the substances in the cells to which this food passes, is a highly important one, and is, moreover, one which chiefly determines whether or no such a substance as sugar, for instance, shall be taken into any given cell. The fact that the surplus of the circulating food is converted into reserve food, leads to a constant movement of the diffusible materials towards the storing cells (see also *Appendix* at end of Chap x.).

With regard to the **absorption of nitrites and nitrates** by the root-hairs, it is an interesting fact that certain **Bacteria** exist in the soil which are capable of converting **ammonia and free nitrogen** into **nitrites** and **nitrates.** Several species of Bacteria probably exist, each one taking on a single stage in this process. In the Leguminosæ there are certain **tubercles** to be found on the rootlets, and these tubercles have been shown to be composed of dense masses of Bacteria (*B. radicicola*) belonging to a species which is able to convert the free nitrogen of the

ground-air into **ammonia, nitrites,** and **nitrates.** The latter salts are then absorbed by the roots.* The bacteria are known as "**nitrifying bacteria,**" one of the forms being *Closterium Pasteurianum.*

In Chap. iii. it was mentioned that certain **glandular capitate hairs** were able to absorb **ammonia** from the atmosphere. It should be understood, however, that it is most probably **ammonium nitrite** which is absorbed, since this substance exists at times in the air (*cf.* Thorpe's *Inorganic Chemistry*, vol. i.). The capacity of working up nitrogen possessed by the different species of soil bacteria has been put to practical test of recent years in connection with the raising of cereals.

The manner in which the dilute solution of salts, or **raw sap,** is drawn up through the vascular tissues of the root and stem until it finally reaches the leaves of a plant must next be examined, and in this connection it is necessary to consider two phenomena. The first of these is the **transpiration current,** and the second **root-pressure.**

The **transpiration current** is an upward flow of sap through the wood of root and stem, caused primarily by the suction action produced by the **evaporation of water from the leaves.** It has been found that about 98 per cent. of the radiant energy absorbed by a plant is utilised in evaporating the water of transpiration. This evaporation takes place through the **stomata,** the mesophyll cells surrounding the **respiratory cavity** of each stoma, constantly giving off, during the daytime, moisture, which collects in and is subsequently evaporated from the respiratory chamber. The effect of this loss of water from some of the mesophyll cells is to draw in water by osmosis from cells of the spongy parenchyma, which are more remote, and ultimately from the **annular** and **spiral** elements of the leaf-traces, which, as has been seen, lie in the mesophyll of a bifacial leaf; and since these elements are the terminations of the fibrovascular bundles of the petioles and ultimately of the stem, water is being constantly sucked up from elements containing sap of progressively decreasing concentration (see Fig. 113).

In this manner a current—the so-called **transpiration current**

* See Muir and Ritchie, *Manual of Bacteriology*, 1907; also Detmer and Moore, *Practical Plant Physiology.*

—is put into action, and during the daytime, for the most part, water is evaporated from the leaves, and as constantly replaced by raw sap drawn up from the roots, and, ultimately, the soil.

In **direct sunlight** and in **hot dry weather,** the transpiration current is much more rapid than in diffuse daylight, or colder weather; also, the **relative humidity** of the atmosphere influences the rate of evaporation of water from the leaves, so that, in moist weather, the current may be greatly diminished.

With regard to the **elements of the xylem** which function most in this upward conduction of sap, it has been found that the **tracheides** exercise by far the greatest influence. At times **air-bubbles** in the tracheides may act, either by reason of **capillarity,** or a sort of pumping action, as distinct aids to the flow. It was formerly thought that the **cell-walls** formed the most important paths of self-conduction; but although the walls, when saturated, may form conducting strands, the sap passes mostly by way of the **cavities** of the tracheides. In trees the only wood which conducts sap is the *alburnum* or young wood; the heart-wood or *duramen* is always dry.

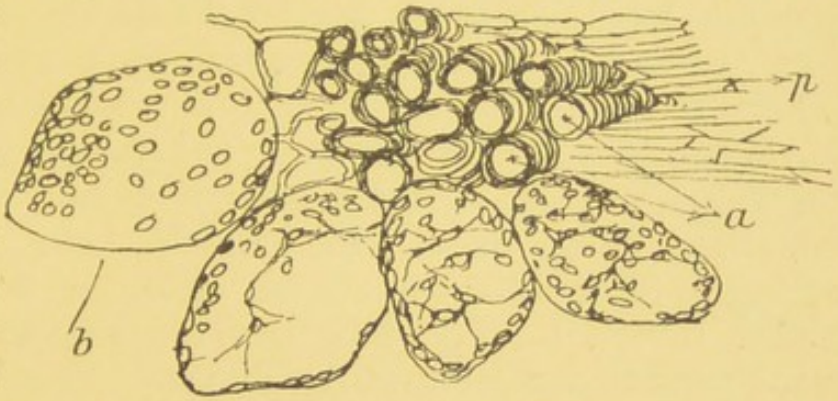

Fig. 113.—Drawing showing the Mode of Termination of the Vascular Bundles in the Mesophyll of a Bifacial Leaf (*Begonia*).—*a*, Spiral and annular vessels; *p*, phloem portion of the bundle; *b*, cells of the mesophyll.

In tracheides with **bordered-pits,** the flow of sap may at times be prevented from passing in the transverse direction by reason of the forcing of the **torus** on to the lumen of either side of the pit.

That the transpiration current is not the only factor at work in producing the upward flow of sap in a plant is shown by cutting across a stem below all the leafy parts, when it will be found that sap constantly exudes through the cut xylem; by connecting up the cut surface with a **manometer** (a mercurial pressure-gauge) the **force** producing this exudation may be measured, and is sometimes found to be considerable. This

force is known as **root-pressure**, and is the result both of turgidity and of the damming up of the sap at certain levels in the root and stem until a considerable rise of pressure has been produced. As a result, when transpiration is at a minimum root-pressure is at a maximum, and *vice versâ*.*

By these two methods, then, the dilute solution of salts (raw sap) is either sucked up or forced up through the xylem to the leaves, in the cells of which active assimilation of CO_2, H_2O, and nitrogen is proceeding. After the **raw sap** has been **elaborated** and added to during photo- and chemo-synthesis it becomes the **elaborated sap**, and, as such, passes into the thin-walled **phloem** elements lying on the under surfaces of the leaf-traces in bifacial leaves. It then passes down by means of the large perforations in the sieve-plates of the sieve-tubes, and also laterally by **osmosis**, and is finally distributed by osmosis into the **cortex, young shoots, cambium, medullary rays**, and other tissues needing elaborated food-material. Some of this food-material is used at once, but towards the end of the "growing" months a good deal of it is converted into **reserve-material** for use during the early months of the succeeding spring. Such reserve-material exists in large quantities in **bulbs, tubers, corms, fruits** and the **phloem, medullary rays, wood-parenchyma**, and **starch-sheath.** The conversion of this stored starch, proteid, &c., during the early spring is due in most cases to the action of **enzymes** (diastase, synaptase, &c.). Occasionally carbohydrates (*i.e.*, starch-grains) "**wander**" from cell to cell, being first dissolved by enzymes, and then reconstructed in more remote parts.

Other forms of reserve food occur, the chief amongst them being:—

a. **Oils** and **fats** in many seeds.

b. **Cellulose** (in endosperm). This is dissolved by the enzyme **cytase.**

c. **Inulin** (a carbohydrate) occurring as the spheroids in *Dahlia.*

d. **Aleurone grains.** These are found typically in the endosperm-cells of *Ricinus*, and are composed of two parts—viz., a **crystalloid** of a proteid nature, and a **globoid**—the latter being a double phosphate of magnesium and calcium. Smaller aleurone grains are also found in *Zea mais* in the starch-containing cells just outside the endosperm.

* Both root-pressure and transpiration exhibit periodic diurnal fluctuations, which are dependent upon a property of the protoplasm known as rhythm or periodicity.

e. **Glucosides.** The **glucose** formed by the action upon these bodies of various enzymes is useful as circulating food-material.

f. **Protein** reserve, such as **gluten, zein,** and, at times, the amido-acid **asparagin,** although the latter is usually more a form of **circulating** than reserve food.

The various processes, both physical and chemical, which take place in a green plant, from the absorption of **raw** food-materials to the manufacture, utilisation, and storing of **elaborated** food in the leaves and other parts, may, for greater convenience of reference, be put into tabular form as follows:—

A. **Absorption of Raw Materials by the Roots.**

Substances absorbed = *a.* Water.
b. Salts in solution (chiefly salts of Ca, Mg, K, and Fe).

B. **Upward Conduction of Raw Sap by the Wood.**

Moving forces = *c.* Transpiration current.
d. Root-pressure.

C. **Elaboration of Raw Sap in Leaves and other Green Parts.**

Processes involved = *e.* Intake of CO_2, H_2O, and O_2; outgo of O_2.
f. Photosynthesis: CO_2 and H_2O being synthesised in the chloroplasts to form (i.) Formaldehyde; (ii.) Sugar.
g. Starch stored in the chloroplasts, and gradually transformed into sugar by enzymes, and used for cellulose formation and circulating food.
h. Formation of amido-compounds, some being used at once to form protoplasm.

D. **Translocation, Utilisation, and Storage of Elaborated Compounds.**

Processes involved = *i.* The sugar and amido-compounds conducted by means of phloem and osmosis to tissues requiring elaborated food (circulating carbohydrates and proteids).
k. Manufacture of **proteids** from sugar, amido-compounds, and a sulphur-compound, some being used at once, and some stored. Manufacture of wood and cellulose.
l. Storage of surplus proteid and carbohydrate in various tissues; subsequent conversion of these by enzymes into more assimilable food = digestion.

Of the processes above noted, *f*, *l*, and *k*, are mainly anabolic, whilst *g* and *l* are mainly katabolic; wood and cellulose (*k*) are, however, katabolic formations.

Certain Experiments Demonstrating Life-processes in the Cells of Plants.

Three experiments for the demonstration of important vital processes may be considered at this point (v. and vi.), viz.:—

a. The evolution of **oxygen** during assimilation.
b. The evolution of **CO_2** during respiration.
c. The retention in the plant of **carbon dioxide** during assimilation (this being used during the formation of **sugar** preparatory to starch-formation).

a. **The evolution of oxygen during assimilation** is readily demonstrated in the case of some water-plants (*Vallisneria*, *Elodea*, *Potamogeton*). If such plants are grown in an aquarium, **bubbles of gas** will often be seen to rise from the leaves to the surface during the action of sunlight. These bubbles, if collected in a test-tube (filled with water and inverted over the water in the aquarium) and tested, will be found to consist of pure **oxygen.**

In **land-plants** more care is required to demonstrate the same process. A plant is taken and enclosed in a large vessel containing atmospheric air to which a known extra volume of **CO_2** has been added, the whole being placed in sunlight. After some hours the gas in the vessel is tested, and is found to contain **less CO_2** and **more O_2** in proportion than was originally the case. Here the CO_2 evolved during respiration may be neglected, as it is relatively small in the daytime during assimilation.

b. **The Evolution of CO_2 during Respiration** (see Fig. 114).—A plant is taken and placed in a vessel (bell-jar) of 10 litres capacity (A, Fig. 114). Connected with this vessel are (i.) two bulbs, C, containing sticks of caustic potash, and (ii.) an aspirator, B. By means of the latter a slow current of air (**freed from CO_2** by the absorbing action of C) is drawn through the apparatus. In the vessel A is placed, previous to the starting of the experiment, a small dish, D, which contains a saturated solution of **caustic potash.** The aspirator is then stopped, the bulbs shut off, and the whole apparatus placed in a dark place for some hours. Under these conditions **no assimilation of CO_2** can take place, for as fast as it is given off during respiration it is absorbed by the potash in the dish D.

The experiment is stopped after about twelve hours, and the CO_2 absorbed is estimated by precipitating with baryta water,

and the resulting barium carbonate collected, washed, dried, and weighed. From the weight thus obtained **the volume of CO_2 evolved** may be readily calculated. If, in the above experiment, the gas remaining in the vessel A be tested, it will be found to contain **less O_2** in proportion to **N** than atmospheric air, thus proving that oxygen has been used for the purposes of **internal oxidation** of carbon compounds or protoplasm, and an equivalent volume (or nearly so) of CO_2 evolved. During respiration in the plant-cell **water** is formed as well as carbon dioxide.*

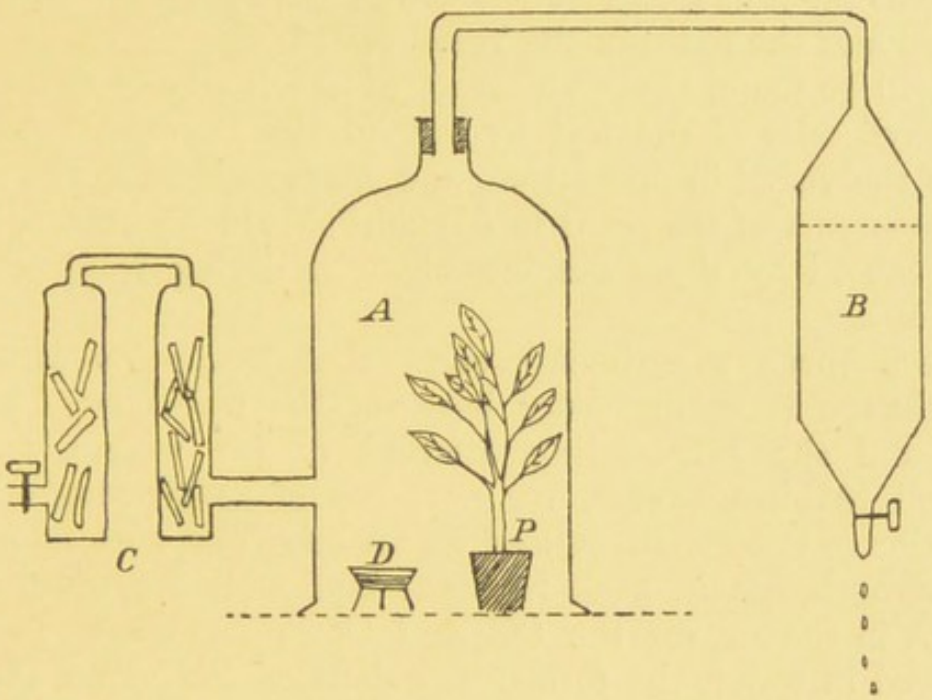

Fig. 114.—Apparatus for Demonstrating the Evolution of CO_2 from a Plant during Respiration.—A, Large bell-jar; P, plant; D, small dish containing a saturated solution of caustic potash; C, tubes containing sticks of caustic potash to absorb the CO_2 of the atmosphere before it is drawn into the jar A; B, aspirator.

In connection with respiration it is necessary to mention that many plants possess amongst their internal tissues **air-spaces** and **intercellular spaces** which are filled with oxygen or atmospheric air. These spaces form at times channels of aëration of considerable extent, more especially in such plants as *Nymphæa*, *Nuphar*, and *Equisetum*. The value of such aëration is manifest, in that the oxygen needed for respiration surrounds masses of

* Some plants (anærobic bacteria) are able to exist in the absence of free oxygen, and in them a process known as intramolecular respiration goes on.

internal tissue, and is thus directly available. The system of spaces lying amongst the spongy-parenchyma of a bifacial leaf is an instance of a similar provision for adequate aëration.

c. **The assimilation of CO_2 or rather the intake of $CO_2 . H_2O$ (= carbonic acid) into plant-cells for the purposes of sugar-formation** is demonstrated by placing a quickly-growing plant in a vessel, which is then filled with a mixture of **air moisture and CO_2** in known proportions, the CO_2 being in excess of what it is in atmospheric air. This vessel is then placed in sunlight for about six hours, and at the end of that time the experiment stopped and the gases in the vessel tested.

It will be found that as a result of the intake of CO_2 into the mesophyll cells of the leaf by way of the stomata, there is **less CO_2** in the vessel in proportion, and **more oxygen.** The respiratory constants of the plant in daylight should be known, but the error caused by the gases interchanged during respiration is a small one.

These three experiments show that a continuous **gaseous interchange** is taking place between the leaf-cells of a living plant and the surrounding atmosphere (or water), and that the cell requires **oxygen** for purposes of **respiration** or tissue-oxidation. Plants surrounded by an **inert gas**, such as **nitrogen** or **hydrogen**, die in a short time; and **moisture** must also be present in the air, for the CO_2 and O_2 gain entrance into a cell dissolved in water, the former as a definite compound, **$CO_2 . H_2O$**, or **carbonic acid.**

vii. Variations of Protoplasmic Activity under Different Conditions.

Under this heading will be considered:—

a. The influence of **light** upon the **direction of growth** of organs.
b. The influence upon **metabolism** of **light rays of varying refrangibility.**
c. The action of **gravity** or a **centripetal force** in any direction upon the direction of growth.
d. The influence of **mechanical** and **chemical stimuli** upon protoplasm.

a. **The influence of light-rays** (direct sunlight especially) upon growing organs is usually referred to under the comprehensive

term **heliotropism**. Organs which grow towards a source of light are said to be **positively heliotropic**, whilst those which grow away from it are **negatively heliotropic**. In this sense stems and flowers are **positive**, whilst roots are **negative**, and most leaves are **transversely** heliotropic, setting at right angles to the rays of light. In most instances there is a **certain position** with regard to the direction of the incident rays of light which an organ takes up in preference to others, and this is known as the **optimum** position; thus, to refer to the lower plants, **Æthalium**, a mass of naked protoplasm, if subjected to powerful illumination, will withdraw to a position where the light is not so powerful. Many leaves assume a position which permits not of the **maximum** amount of light falling upon their upper surfaces, but of just that amount which is found to coincide with the requisite intensity of assimilation in these organs. Light has thus a kind of **tonic** effect (phototonus) upon the growth and position of organs. The explanation of the **movements** of an organ caused by **light** is to be found in the fact that those cells of the organ which are nearest the source of illumination **transpire** most freely, and are not so turgid as the opposite parts; and since **turgidity** favours **growth**, it follows that the remoter parts will grow more strongly than those nearest the source of light, and, by so doing, will cause a **curve** in the organ **concave towards the light incidence**. In this manner arise the curvatures produced in some stems and flower stalks. It is well known that **roots** grow much faster in the dark than in the light; this can readily be shown by growing water-cultures of *Hyacinthus* in transparent white vases and in opaque ones respectively, when it will be found that the roots springing from the bulb in the dark jar are, after some days' growth, much longer than those from the bulb in the transparent one. In this connection it may be mentioned that the violet and ultra-violet rays of the spectrum have most influence upon the formative action of protoplasm.

It is an interesting fact that the **chloroplasts** in the palisade-cells of a leaf take up positions which vary according to the **intensity of illumination** of the upper surface of the leaf; thus, in very intense illumination they become arranged along the **side-walls**, presenting only their edges to the incident rays (apostrophe), whilst in medium illumination they are situated

along the **upper and under walls**, presenting their broader surfaces to the light (epistrophe). This is an instance of adaptation so as to ensure an "**optimum**" intensity of assimilation.* In *Mougeotia* (one of the Conjugatæ) the chloroplast is in the form of a band in each cell of the filament, and this band **rotates** into a position which enables it to receive the optimum intensity of illumination; in strong illumination it presents its edge to the incident rays.

b. **The Influence upon Metabolism of Light Rays of Varying Refrangibility.**—An experiment devised by Engelmann (described in the *Botanische Zeitung* for 1881, p. 447) illustrates in a striking manner the influence of the **red**, **yellow**, and **violet** portions of the spectrum upon the **intensity of assimilation of CO_2**. A filament of *Spirogyra* is mounted in water along the middle of an opaque microscope slide, so as to traverse three transparent circular portions of the slide (see *a*, Fig. 115). These three spaces are illuminated by **red**, **yellow**, and **violet light**, **R**, **Y**, and **V** respectively (see Fig. 115). A small culture of *Proteus vulgaris* (a motile organism which is markedly attracted by **oxygen**) is now introduced under the cover-slip of the preparation, and, the filament being carefully focussed under the microscope, the following observations may be made:—

i. In the vicinity of those cells of the filament illuminated by the **red rays**, a **vast swarm** of motile bacteria become aggregated.
ii. **Fewer bacteria** exist in the region of the cells illuminated by the **yellow rays.**
iii. **Very few organisms** are to be seen near the cells lighted by the **violet portion** of the spectrum. Engelmann employed a substage prism in order to produce a spectrum, the red, yellow, and violet portion of which thus illuminated the spaces in the slide from beneath.

This shows that **more oxygen** is being evolved from those cells of the filament illuminated by the **red** rays than from those under the influence of the **yellow** or **violet** rays, and that, therefore, **assimilation is more intense in red than in other illumination.**

Another experiment, due to Timiriazeff, and depending upon the formation of **starch** in the leaf-cells, is as follows (see Fig. 115):—

A given leaf of a plant is selected on a certain day, and, **before any light has fallen upon it**, is covered, with the exception of a

* The small leaves of *Lemna trisulca* are excellent organs for the observation of this phenomenon.

small strip, with an opaque sheath of tinfoil. Upon the uncovered strip a small **spectrum** of sunlight is thrown by means of a suitably arranged prism, and the whole left for some hours. The leaf is then cut off and immersed in **alcohol**, to dissolve out the chlorophyll, and subsequently washed in distilled water and transferred for a time to a vessel containing a solution of **iodine** in potassium iodide. It will then be found upon examining the leaf after again washing, that in the part which was illuminated by the spectrum a band of "stained" starch is present, the staining

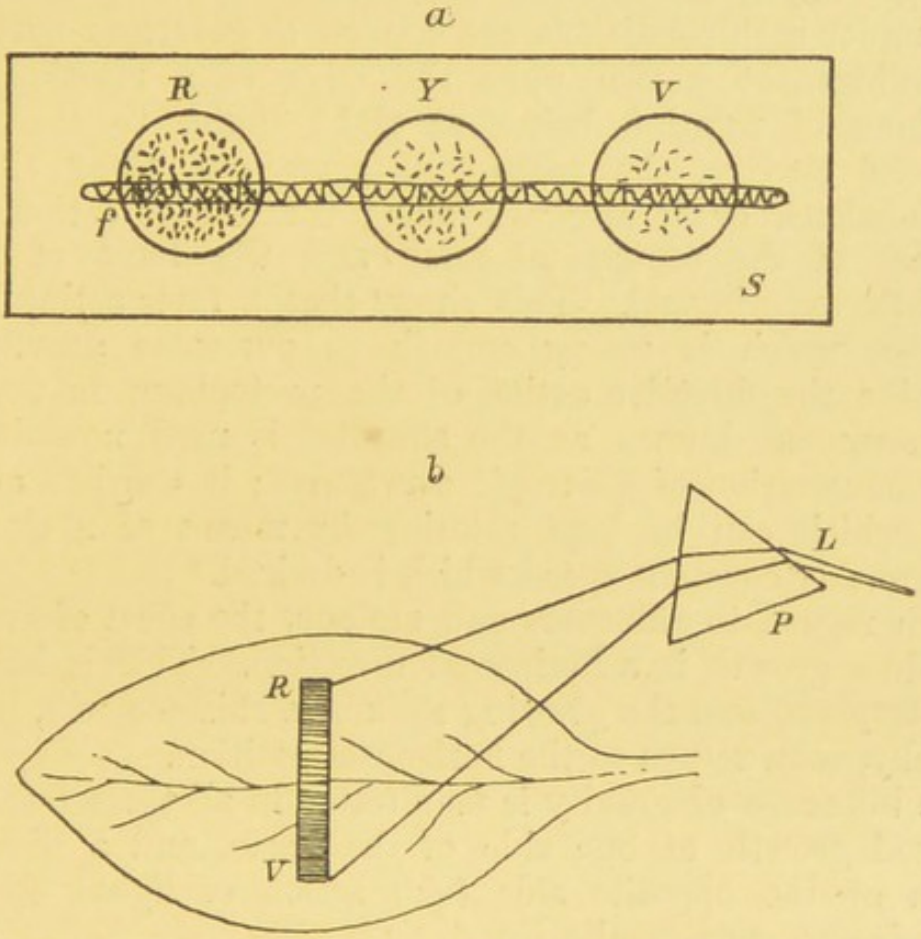

Fig. 115.—(*a*) ENGELMANN'S BACTERIA EXPERIMENT.—S, Glass slide (opaque); R, Y, V, three spaces left clear, which are illuminated by red, yellow, and violet rays respectively; *f*, filament of Spirogyra.
(*b*) TIMIRIAZEFF'S EXPERIMENT.—L, Beam of white light; P, prism; R, V, spectrum thrown upon a leaf.

being **deepest** in that part which was previously illuminated by the **red rays**, and weakest at the opposite or **violet end.** Photosynthesis (followed by storing of starch) is thus more intense under the influence of rays of low refrangibility.

These two experiments show conclusively that **assimilation** of

CO_2 proceeds most actively under the influence of the rays of the spectrum which are of low refrangibility.

c and *d*. **The Action of Physical, Tactile, and Chemical Stimuli upon Protoplasm.**—The effect of **gravity** (**geotropism**), or a **centripetal force**, upon protoplasm, is very marked at times. Thus, there arises a directive action which causes **root-tips** to curve **downwards** into the soil, even when seedlings are placed horizontally; and **stem-structures** will, on the contrary, curve **upwards.** Roots are thus said to be **positively geotropic**, whilst stems are **negatively geotropic**, and the curves shown by these structures under such conditions are known as **geotropic curvatures.** If seedlings are grown upon the edge of a rotating wheel, the plane of rotation being **at right angles** to the line of action of gravity, the roots will grow out **along the radii** of this wheel, or at any rate along the line of action of the **resultant of the centripetal force and the force of gravity** (**Knight's** experiment). This shows that a force acting in any direction, which is strong enough to overcome gravity, will determine the **directive action** of the protoplasm in root-cells. An instrument known as the **clinostat** is used nowadays for the demonstration of geotropic curvatures; it consists of a flat wheel which can be kept rotating by means of a clockwork device at any constant speed which is desired.*

With regard to **rhizomes** and **stolons**, the effect of gravity is to produce growth in a horizontal direction. This is known as **diageotropism**, and the growing apex of a rhizome will, if placed vertically, soon return to the horizontal position.

The influence of gravity is manifested in all these cases by an increased growth of one side of the organ, and a diminished growth of the opposite side (*vide* action of light), so that a geotropic curvature results.

If the cells upon one side of the apex of a quickly-growing stem be more turgid than those on the other, increased growth will take place on that side, and a corresponding curvature of the apex away from that side will be produced; this curvature is known as a **nutation.** At times a periodic alteration in the turgidity of the cells all round the apex takes place in succession, and the curve thus produced is a circle, or since growth in

* See Detmer and Moore, *Practical Plant Physiology.*

length is also proceeding an ellipse or spiral; this is then known as a **circumnutation.**

In flat (dorsiventral) organs an upward or downward or side to side movement will be produced by the same variations in growth, and the phenomenon is here known as **epinasty** or **hyponasty** as the case may be. These movements are known as *movements of variation.*

So-called *nyctitropic movements* are due to curvatures in organs (leaves) owing to the periodic variations in turgidity of certain cells, which are determined by the altered conditions of growth as night approaches. The cells which cause these movements are usually situated at the bases of the petioles (in leaves), so that a drooping of the organ occurs, or if the organ is a flower, a closing of this.

The twining or revolving movements of **stem-climbers** are due to the action of gravity, which causes an increased growth on either the right or left side of the growing internodes of the apex of a shoot. In this manner, either right-handed (dextrorse) or left-handed (sinistrorse) curves may be produced, which serve to twine the stem round a support.

In the case of the **nodes** of grass-haulms, the resting tissue of these parts may be stimulated by the action of gravity, so that the lower aspect of the node exhibits increased growth; this causes an upward bending of the haulm.

Tactile stimuli produce measurable effects upon certain growing organs. At times, especially in certain **climbing plants** (tendril-climbers), the contact of a resisting body, such as a wall, or stick, causes **increased growth** in those cells of the plant-organ which are **remote from the stimulus,** and this has the result of producing a curvature which enables the organ (tendril, &c.) to entwine the support. In *Drosera*, contact stimuli will cause the **glandular hairs** of the leaf to curve over and enclose a small particle which has fallen upon them; and if this particle happens to be of an **organic nature** (albumen, small fly, &c.), a further action results—viz., secretion of a **peptic ferment** in certain cells of the leaf.

In *Mimosa pudica*, tactile stimuli applied to one of the small pinnæ of the bi-compound leaf, causes first of all a **drooping of the pinna, then of the lateral leaflet, and finally of the whole leaf.** This result depends upon the disturbance of the **osmotic**

balance (turgidity) in the cells of the **pulvini** (small cellular cushions), situated at the bases of the leaves and leaflets, **whereby turgidity is lessened.** The stimulus in this case passes along certain cells surrounding the vascular bundles, and travels by means of cytoplasmic connecting "bridles" between adjacent cells.

Chemical substances exert at times a powerful **attractive influence** upon protoplasm; and, on the other hand, they may **repel** the living substance. The **growth of pollen-tubes** is brought about by such stimuli, as also is the **attraction of anther-ozooids** towards the oospheres of Pteridophyta (see *supra*). In the latter instance, **enzymes** often seem to be the chemical substance producing the attraction, the process being known as **positive chemotaxis. Negative chemotaxis** is seen in the repulsion of *Æthalium*, produced by strong salt solution or acetic acid. The **selective action** exercised by the ectoplasm of root-hairs is also of a kindred nature.

The influence of moisture (**hydrotropism**) is sufficient at times to determine the direction of growth of an organ (root). The stimulus is in the main of a **chemical nature.**

These few remarks on the chemistry and physiology of the cell may serve to emphasise the fact that the cytoplasm is, as was incidentally mentioned in Chapter i., capable of responding to a variety of stimuli; or, as is often said, possesses the property of **irritability.** It has also been seen that protoplasm is capable of **transmitting stimuli** from one cell to the cells of remote parts; and, finally, evidence has been put forward showing **that growth, as a whole, is the result of the action upon the cytoplasm of the various physical and chemical agencies which are from time to time brought to bear upon it.***

viii.—The Production of Heat, Light, and Changes of Electrical Potential in a Cell, and the Action of Electric Currents upon the Cytoplasm.

The subject of **heat-production** in the cells of plants is one which, from the experimental point of view, is often beset with difficulties, owing to the inability to measure such small changes

* Huxley long ago maintained that the vital properties of the protoplasm were the result of the disposition of the molecules of which it is composed, and that no such term as "inherent vitality" was necessary in escribing the attributes of the living substance. (*Method and Results*, 1893.)

in temperature as may at times arise; but occasionally a considerable rise may be observed, more especially in the case of **germinating seeds.** If the bulb of a delicate thermometer be surrounded in a vessel by some seeds of *Pisum sativum*, and water added, after a time a rise of some **4° C.** will be observed, this being due partly to the **absorption of water by the cells of the cotyledons,** but mostly to **respiration.**

The **internal tissues** of quickly-growing stems will sometimes indicate a slightly higher temperature than the **outer tissues.*** In this case, a **thermo-electric needle** in circuit with a sensitive galvanometer must be used, the needle being so arranged as to be **non-polarisable** (that is, coated with a substance which is not acted upon by the acid sap).

In the **growing spadix** of Aroideæ, also, a considerable elevation of temperature has been noted (10° to 12° C.); and certain **bacteria** (*B. subtilis*) also cause a great rise of temperature during growth (*cf.* firing of hayricks).

The **evolution of radiant energy** takes place in some of the lower plants, as in the case of the *Bacterium phosphoreum*, one of the Schizomycetes.† So intense is the radiation in this instance, that pea-seedlings will grow towards a vessel in which a culture of these organisms is growing. Other bacteria, such as those producing the "phosphorescence" of decaying fish, are also capable of evincing light-rays.

The luminosity in such cases as these is dependent upon the **oxidation** going on in the cells.

Differences of electrical potential have been observed to be present between the upper and under surfaces of certain leaves (leaves of *Victoria regia*, &c.), and it has been shown that if the internal and external tissues of some stems are connected through a circuit in which a sensitive galvanometer is included, a current will flow from the internal to the external parts (*Becquerel*). Here, also, non-polarisable electrodes are essential.

In Chapter i., the **blaze-reaction** mentioned in connection with experiments upon the capacity of germination possessed by seeds, was adduced as evidence of **changes in electrical potential produced by oxidative changes of low intensity** proceeding in the dormant cytoplasm of the cells composing the seeds; in fact,

* See Becquerel, *Physiologie Vegetale.*
† See *Knowledge and Scientific News*, Feb., 1909.

wherever **chemical actions** are proceeding, however small these may be, there will **variations** in **electrical potential** be produced, a current flowing from the regions of greater activity to those of less.

Strong electric currents have the effect of causing an immediate **contraction** of the cytoplasm of a cell (*Spirogyra*, or *Elodea Canadensis*), from which recovery is impossible. Currents of a less intense nature cause either a **partial retraction** from the cell-wall, with, later on, after the current has been stopped, resumption of function. Upon **swarmspores** and **antherozooids** swimming in water, a strong current has the peculiar effect of **polarising** these bodies, so that they set with either one or the other extremity facing in a definite direction—viz., either with or against the direction of flow of the current.

APPENDIX.

THE PHYSICS OF THE ABSORPTION OF WATER, SALTS, AND GASES BY THE CELL.

The question of the absorption of raw food-materials by the living cell is a most important one, and involves, as has been seen on p. 172, the consideration of **osmosis.** This process, which must be studied a little more in detail, is partly vital and partly physico-chemical, and concerns not only the absorption into the cell of water and salts, but also of the gases CO_2 and O_2, which are used during assimilation and respiration respectively. If a bladder composed of moistened vegetable parchment be filled with a solution of sodium chloride in water and immersed in distilled water, water will pass into the bladder, and a certain small amount of salt will also escape in the opposite direction. The inward diffusion of water is known by the term **endosmosis,** whilst the exit of salt is known as **exosmosis.** After a certain time a condition of equilibrium is reached, when neither endosmose nor exosmose occur, and this state is known as **osmotic equilibrium,** the bladder being turgid.

If the concentration of two solutions of a salt separated by a permeable membrane is the same, no permanent interchange of water and salt occurs, but if the dilution of one of the solutions be altered ever so little by the addition of more solvent, then osmosis occurs. Nevertheless, even when the state of balance has been reached, it is assumed that a constant interchange of equal quantities of salt is taking place, so that a condition of rest never obtains.

In the case of the living plant-cell (root-hair, &c.), the state of things is somewhat modified by the fact that the membrane separating the two solutions (which are here on one side, the

cell-sap, and on the other side, either a dilute solution of earthy salts, or of a gas) is by no means an inert one like parchment, but is composed of several parts—viz., a layer of cellulose, then a layer of ectoplasm, then a layer of endoplasm, and, finally, lining the central vacuole, another very delicate pellicle of ectoplasm (hyaloplasm); consequently, the osmotic phenomena observed in the case of the cell are not quite equivalent to the purely physical processes observed to take place when experimenting with the parchment membrane.

The endosmosis of earthy salts into a root-hair is, as has been seen, governed to a certain extent by the osmotic properties of substances in the cell-sap; during the metabolism of the cell, bye-products are formed, which it is found exert an attraction upon the salts and water outside in the soil, and consequently, these are drawn in by endosmosis, whilst a small amount of the above bye-products (chiefly organic acids) escapes by exosmosis. The condition of **turgidity** thus set up is always present in such a cell as a root-hair, and, in fact, in any cell which is growing to any extent, this condition being, indeed, essential to the growth in extent of the cell-wall.

A state of absolute equilibrium is, of course, rarely reached, since the salts absorbed are as constantly removed by diffusion into adjacent cells, and by the osmotic effect of the transpiration of water from the leaves which leads to a progressively decreasing concentration of the sap in the cells below, and in the tracheides of the wood in stem and root (*cf. Transpiraton*). The passage of the soluble elaborated foods (sugar, amido-acids), from the leaf-cells to other parts of a plant is effected mainly by osmosis; the elaborated food is being constantly used up either for formative processes or storage, and this removal of soluble foods from the cell-sap leads to a corresponding intake of these substances from adjacent and remote cells. The bye-products of metabolism are also, as was noted above, useful aids in promoting osmosis in this respect.

The gases CO_2 and O_2 must, before they are taken into a cell, be dissolved in water; the cell-walls of the mesophyll cells in a leaf are saturated with moisture, and the gases, entering by means of the stomata are led to intercellular spaces surrounded by the cells of the mesophyll (spongy parenchyma). If, for instance, the percentage of CO_2 in a cell is smaller than that

in the intercellular space, this gas will pass into the cell by endosmosis, and the same may be said of oxygen; during the assimilation of CO_2 and water during the day-time in the cells of the mesophyll, oxygen is one of the bye-products, and this, since its osmotic pressure and percentage in the cell-sap are greater than those of the same gas in the intercellular spaces, will escape to a certain extent by exosmosis, leading to the evolution of oxygen from the surface of the leaf through the stomata.

A given solution of either salts or a gas is said to be **isotonic** with another solution, when no permanent interchange takes place between their saline or gaseous constituents when they are separated from one another by a permeable membrane. In the plant cell, although for a short space of time, the condition of osmotic balance may be present, this condition rarely lasts any length of time, since the absorbed substances are being constantly used up. The main conditions for adequate osmosis in the plant-cell are:—

a. The stability of the cell-wall and ectoplasmic membrane.
b. The presence of **dilute** solutions of salts, &c., in the soil or cell-sap; adequate dilution is necessary, since, before molecules of salt can pass through the membrane by osmosis, they must be **ionised,** that is to say, the atoms or atomic groups must be separated from one another by the solvent.

In the plant-cell, however, the ectoplasm exerts a regulating action (selective capacity), which, to a certain extent, modifies osmosis; and the membrane of separation becomes, in a measure, comparable to the semi-permeable membrane—viz., that which permits of the entrance or exit of certain molecules (salts, acids), but not of others (colloids). Moreover, in many instances, salts may be absorbed which do not appear to have any influence upon metabolism, but gain an entrance on account of the smallness of their molecules, or atomic groups into which they are split up.

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