from the Author

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ON THE

REPRODUCTION AND SUPPOSED EXISTENCE

OF

SEXUAL ORGANS

IN THE

HIGHER CRYPTOGAMOUS PLANTS.

BY

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On the Reproduction and supposed Existence of Sexual Organs in the Higher Cryptogamous Plants. By Arthur Henfrey, *F.L.S.*

Having been prevented by the pressure of other engagements from complying with the request which the Association did me the honour to make last year, that I should assist Prof. Lindley and Dr. Lankester in preparing a Report on Vegetable Physiology, I venture to present a fragmentary contribution on the subject, relating to a branch of the science to which my attention has been recently strongly attracted, in the pursuit of my own investigations. I was the more induced to devote the short time at my disposal to drawing up a summary of the state of knowledge of the reproduction of the higher flowerless plants, by the importance of the discoveries which have recently been made in this department, tending completely to change the general views which have hitherto been entertained by most botanists as to the extent to which sexuality exists in the vegetable kingdom, and in connexion with other new facts relating to the Thallophytes, to indicate that the existence of two sexes is universal.

Under the name of the higher Flowerless Plants, I include all those classes which are distinguished on the one hand from the Thallophytes or Cellular plants by the presence of a distinct stem bearing leaves, and on the other from the Monocotyledons and Dicotyledons by the absence of the organs constituting a true flower; they are, the Hepaticæ, Musci, Equisetaceæ, Filices, Lycopodiaceæ, Isoëtaceæ, and Marsileaceæ or Rhizocarpeæ.

On no subject has more discussion been maintained than on the existence of sexes among the Cryptogamous families. The discovery of the two kinds of organs, the *antheridia* and *pistillidia*, in the Mosses and Hepaticæ, and of the peculiar organs containing analogous spiral filaments in the Characeæ, were for a long time the chief facts brought forward by those who supported the sexual hypothesis; and in the endeavour to carry out the view into the other tribes, a similar nature to that of the *antheridia* was attributed to most varied structures in the Ferns and other plants. These attempts to find distinct sexual organs were in some instances pursued with so little judgement, that the opinion had of late years fallen in some degree into discredit, and two circumstances contributed still further to strengthen the doubts which were entertained. The first was the exact analogy, pointed out by Prof. von Mohl, between the mode of development of the spores of the Cryptogamia and the pollen-grains of the flowering plants, which interfered very importantly to prevent any comparison between the sporangia and ovaries, and apparently determined the analogy of the former to be with anthers. The second was the discovery by Prof. Nägeli, of organs producing spiral filaments, therefore analogous to the *antheridia* of the Mosses, on the germ frond, or *pro-embryo* developed from the spores of the Ferns.

At the same time, the facts observed in *Pilularia* were altogether equivocal. Mr. Valentine* traced the development of the larger spores, exhibiting in germination an evident analogy to ovules, from cells closely resembling the parent-cells of pollen and spores; while Prof. Schleiden stated that he had observed a fertilization of these supposed ovules by the smaller spores resembling pollen-grains, and thus seemed to remove the ground for attributing a fertilizing influence to the spiral filaments contained in the so-called *antheridia* of the Cryptogams.

In this state the question remained until 1848, when Count Suminski† published his observations on the germination of Ferns, showing that the researches of Nägeli had been imperfect, and that two kinds of organs are produced upon the pro-embryo of the Ferns, one kind analogous to the *antheridia*, and the other to the *pistillidia* of Mosses; from the latter of which the true Fern stem is produced, like the seta and capsule from the same organ in the Mosses; further stating that he had actually observed a process of fertilization. Soon after this M. G. Thuret‡ discovered *antheridia* like those of the Ferns in the Equisetaceæ; Nägeli § had previously

* Linnean Transactions, vol. xvii.

† Entwickelungsgeschichte der Farrenkräuter. Berlin, 1848.

‡ Ann. des Sci. Nat. ser. 3, vol. xi. 1849.

§ Zeitschrift für Wiss. Botanik, Heft 3. Zurich, 1846.

published, in opposition to Schleiden's observations, an account of the production of spiral filaments from the small spores of *Pilularia*, and finally M. Mettenius* discovered them in the small spores of *Isoëtes*. Thus they were shown to exist in all the families above enumerated, with the exception of the Lycopodiaceæ, in which they have recently been stated to exist by M. Hofmeister†. Before entering into a detailed account of their discoveries, it may be mentioned, that, besides their well-known occurrence in the Characeæ, which most authors consider as Thallophytes, antheridia are stated by Nägeli to exist on the Florideæ, among the Algæ; and peculiar bodies to which the same nature has been attributed, were recently discovered by M. Itzigsohn in the Lichens; a discovery confirmed by Messrs. Tulasne, who state that analogous bodies exist in many Fungi. Our knowledge of these latter points is, however, far less definite than that concerning the higher tribes, and I shall not include them in the following summary.

One of the most remarkable circumstances concerning the antheridia of the leaf-bearing Cryptogams, is the very varied nature of the time and place of their development; so great indeed is this, that it is only their essential structure, and the production of the moving spiral filaments in particular, which warrants the assumption of their identity of function in the different families. In order to make these variations clearly comprehensible, it will be necessary to describe the characters exhibited in the germination of the spores in each tribe, as it is only by this means that the important peculiarities of each case can be made evident. It will be most convenient to give a separate sketch of all that is known of the process of reproduction in each family, taking these separately and in succession; after this we shall be in a position to compare them together, and trace out their differences and analogies; the advantage of recalling all the essential facts to memory will, I trust, serve as an apology for the introduction of much that is already familiar to most botanists.

Mosses.—The antheridia of the Mosses occur in the axils of the leaves or collected into a head, enclosed by numerous variously modified leaves, at the summit of the stem. They are produced either on the same heads as the pistillidia, or in distinct heads on the same individuals, such Mossesbeing called monœcious; or the heads are found only on distinct individuals, such Mosses being termed diœcious. The structure of the antheridium is exceedingly simple; it consists of an elongate, cylindrical or club-shaped sac, the walls of which are composed of a single layer of cells, united to form a delicate membrane. Within this sac are developed vast numbers of minute cellules, completely filling it, and, the sac bursting at its apex at a certain period, these vesicles are extruded. When the nearly perfect sacs are placed in water, the vesicles within appear to absorb water, and swell so as to burst the sac of the antheridium, and often adhering together, they collectively appear to form masses larger than the cavity from which they have emerged. Through the transparent walls may be seen a delicate filament with a thickened extremity, coiled up in the interior of each vesicle. Often before the extrusion, but always shortly after, a movement of this filament is to be observed when the object is viewed in water under the microscope. The filament is seen to be wheeling round and round rapidly within the cellule, the motion being rendered very evident by the distinctness of the thickened extremity of the filament, which appears to be coursing round the walls of the cellule in a circle. According to Unger, this filament breaks

* Beiträge zur Botanik, Heft 1. Heidelberg, 1850.

† Flora, 1850, p. 700.

out of its parent cellule in Sphagnum, and then appears as a spiral filament moving freely in water, in fact, as one of the so-called spermatozoa.

The pistillidia of the Mosses are the rudiments of the fruit or capsules. When young, they appear as flask-shaped bodies with long necks, composed of a simple cellular membrane. The long neck presents an open canal like a style, leading to the enlarged cavity below, at the base of which, according to Mr. Valentine*, is found a single cell projecting free into the open space. This single cell is the germ of the future capsule; at a certain period it becomes divided into two by a horizontal partition, the upper one of these two again divides, and so on until the single cell is developed into a cellular filament, the young seta; the upper cells are subsequently developed into the urn and its appendages, and as this rises, it carries away with it, as the calyptra, the original membrane of the pistillidium, which separates by a circumscissile fissure from the lower part, the future vaginula. These observations of Valentine are not exactly borne out by those of Schimper† in some of the detail points. According to this author, the lower part of the pistillidium (the germen of Dr. Brown) begins to swell at a certain time, when a capsule is to be produced, becoming filled with a quantity of what he terms "green granulations." As soon as the thickness has become about that of the future seta, the cell-development in the horizontal direction ceases, and its activity is directed chiefly to the upper part, which begins to elongate rapidly in the direction of the main axis. This elongation causes a sudden tearing off at the base, or a little above it, of the cell-membrane enveloping the young fruit, and the upper part is carried onwards as the calyptra; the lower part, when any is left, remains as a little tubular process surrounding the seta. While the young fruit is being raised up by the growth of the seta, the portion of the receptacle upon which the pistillidium is borne, becomes developed into a kind of collar, and at length into a sheath (the vaginula) surrounding the base of the seta which is articulated into it there.

M. Hofmeister‡, again, describes the details much in the same way as Mr. Valentine. He states that there exists at the point where the 'style' and 'germen' of the pistillidium join, a cell, developed before the canal of the style has become opened. In those pistillidia which produce capsules this cell begins at a certain period to exhibit very active increase; it becomes rapidly divided and subdivided by alternately directed oblique partitions into a somewhat spindle-shaped body formed of a row of large cells. Meanwhile the cells at the base of the germen are also rapidly multiplied, and the lower part of the pistillidium is greatly increased in size. The spindle-shaped body continues to increase in length by the subdivision of its uppermost cell by oblique transverse walls, and the opposition which is offered by the upper concave surface of the cavity of the germen, causes the lower conical extremity of the spindle-shaped body to penetrate into the mass of cellular tissue at the base of the germen, a process which resembles the penetration of the embryo into the endosperm in the embryo-sac of certain flowering plants. The base of the spindle-shaped body, which is in fact the rudiment of the fruit, at length reaches the base of the pistillidium, and penetrates even some distance into the tissue of the stem upon which this is seated. The growth of the upper part going on unceasingly, the walls of the germen are torn by a circular fissure and the upper half is carried upwards,

* Linnean Transactions, vol. xvii.

† Recherches Anatomiques et Morphologiques sur les Mousses. Strasbourg, 1848.

‡ Botanische Zeitung, 1849, 798. Botanical Gazette, vol. ii. p. 70.

bearing the calyptra, the lower part forms the vaginule. The upper cell of the spindle-shaped body then becomes developed into the capsule, and the calyptra often becoming organically connected with this, as the base of the seta does with the end of the stem, it in such cases undergoes further development during the time it is being carried upwards by the growing fruit.

The view now entertained by Schimper, Hofmeister, and others of the reproduction of the Mosses is, that the antheridia are truly male organs, and that they exert, by means of the spiral filaments, a fertilizing influence upon the pistillidia, it being assumed that those bodies, or the fluid which they are bathed in, penetrate down the canal of the style or neck-like portion of the pistillidium to reach the minute cell, the supposed embryonal cell, situated in the globular portion or 'germen' of the pistillidium, and thus render it capable of becoming developed into a perfect fruit.

No such process of fertilization has actually been observed in the Mosses, and therefore all the evidence is at present merely circumstantial; but this is very strong. In the first place it is stated as an undoubted fact by Schimper and Bruch, that in the diœcious Mosses, those on which the antheridia and pistillidia occur in separate plants, fruit is never produced on the so-called male plants, and never on the so-called female unless the males occur in the vicinity; several examples are cited in the work of Schimper above referred to; when the sexes occur alone, the increase of the plant is wholly dependent on the propagation by gemmæ or innovations.

By the discovery of the antheridia and pistillidia in the other higher Cryptogams, the arguments from analogy greatly strengthen the hypothesis of the sexuality of Mosses.

Further observation is required, then, for the direct proof of the occurrence of a process of fertilization in the Mosses; but the facts now before us all tend to prove their sexuality if we argue from analogy, and the probabilities deduced from the negative evidence above referred to in regard to the diœcious species.

It is unnecessary to give any account of the well-known structure of the Moss capsules; yet in order to render the comparison with the phænomena of the life of Mosses with those of the other leafy Cryptogams complete, it may be worth while to allude to the germination of the spores. The spore is a single cell, with a double coat, like a pollen-grain; this germinates by the protrusion of the inner coat in the form of a filamentous or rather tubular process, which grows out and becomes subdivided by septa so as to form a confervoid filament. The lateral branches bud out from some of the cells, some elongating into secondary filaments, others at once undergoing a more active development, and by the multiplication of their cells, assuming the condition of conical cellular masses, upon which the forms of Moss leaves may soon be detected; these cellular masses becoming buds from which the regular leafy stems arise.

Hepaticæ.—The genera comprehended in this family present a wonderful variety of structure in the reproductive organs, but in almost all of them the existence of the two kinds of organs called pistillidia and antheridia have long been demonstrated, and in most cases the development of the sporangia from the so-called pistillidia has been traced. In those genera in which the plants most resemble the Mosses in the vegetative portion, as in *Jungermanniæ*, the pistillidia are very like those of the Mosses; this is also the case in *Marchantia*; but in *Pellia*, *Anthoceros* and other genera, the rudiment of the sporangium bears a striking resemblance to the so-called ovules of the Ferns, Rhizocarpeæ, &c. occurring upon the expanded fronds very much in the same way as those bodies do upon the pro-embryos of the said families. It would occupy too much space to enter into a minute detail of the various conditions that are met with. It is sufficient to say that in all cases the physiological stages are analogous to those of the Mosses; since the pistillidia produced upon the fronds or leaf-bearing stems developed directly from the spores, go on to produce a *sporangium alone*, in which the new spores are developed, without the intervention of the stage of existence presented by the pro-embryo of the Ferns and Equisetacæ, where the pistillidia and antheridia occur upon a temporary frond, and the former give origin to the regular stem and leaves of the plant.

Ferns.—This class formed for a long time the great stumbling-block to those who sought to demonstrate the existence of sexuality in the Cryptogamous plants. The young capsules were generally considered to be the analogues of the pistillidia of the Mosses, and the young abortive capsules which frequently occur among the fertile ones were supposed by some authors to represent the antheridia. Mr. Griffith*, shortly before his death, noticed a structure which he was inclined to regard as the analogue of the antheridium in certain of the ramenta upon the petioles.

In the year 1844, Prof. Nägeli† published an account of his observations on the germination of certain Ferns, and announced the discovery of moving spiral filaments closely resembling those of the Charæ, on certain cellular structures developed upon the pro-embryo or cellular body first produced by the spore. It is not worth while to enter into an analysis of his observations, as they have since been clearly shown to have been very imperfect; it is sufficient to state that he only described *one* kind of organ, and from his description it is evident that he confounded the two kinds since discovered, regarding them as different stages of one structure. The announcement of this discovery seemed to destroy all grounds for the assumption of distinct sexes, not only in the Ferns but in the other Cryptogams, since it was argued that the existence of these cellular organs, producing moving spiral filaments, the so-called spermatozoa, upon the germinating fronds, proved that they were not to be regarded as in any way connected with the reproductive processes.

But an essay published by the Count Suminski‡ in 1848 totally changed the face of the question, and opened a wide field for speculation and investigation on this subject, just as it was beginning to fall into disfavour. Count Suminski's paper gives a minute history of the course of development of the Ferns from the germination of the spore to the production of the regular fronds, and he found this development to exhibit phænomena as curious as they were unexpected. The cellular organs seen by Nägeli were shown to be of two perfectly distinct kinds, and moreover to present characters which gave great plausibility to the hypothesis that they represented reproductive organs; moreover, this author expressly stated that he had obtained absolute proof of sexuality by observing an actual process of fertilization to take place in the so-called ovules, through the agency of the spiral filaments or spermatozoa.

The main points of his paper may be briefly summed up as follows. The Fern spore at first produces a filamentous process, in the end of which cell-development goes on until it is converted into a Marchantia-like frond of small size and exceedingly delicate texture, possessing hair-like radicle hairs on its under side. On this under side become developed, in variable num-

* Posthumous Papers, Journal of Travels, 444.

† Zeitschrift für Wiss. Botanik, Heft 1. Zurich, 1844.

‡ Zur Entwickelungsgeschichte der Farrenkräuter. Berlin, 1848.

bers, certain cellular organs of two distinct kinds. The first, which he terms antheridia, are the more numerous, and consist of somewhat globular cells, seated on and arising from single cells of the cellular Marchantia-like frond. The globular cell produces in its interior a number of minute vesicles, in each of which is developed a spiral filament, coiled up in the interior. At a certain epoch the globular cell bursts and discharges the vesicles, and the spiral filaments moving within the vesicles at length make their way out of them and swim about in the water, displaying a spiral or heliacal form, and consisting of a delicate filament with a thickened clavate extremity ; this, the so-called head, being said by Count Suminski to be a hollow vesicle, and to be furnished with six or eight cilia, by means of which the apparently voluntary movement of the filament is supposed to be effected.

The second kind of organ, the so-called 'ovules,' are fewer in number and present different characters in different stages. At first they appear as little round cavities in the cellular tissue of the pro-embryo, lying near its centre and opening on the under side. In the bottom of the cavity is seen a little globular cell, the so-called embryo-sac. It is stated by Count Suminski that while the ovule is in this state one or more of the spiral filaments make their way into the cavity, coming in contact with the central globular cell. The four cells bounding the mouth of the orifice grow out from the general surface into a blunt cone-like process, formed of four parallel cells arranged in a squarish form and leaving an intercellular canal leading down to the cavity below. These four cells become divided by cross septa, and grow out until the so-called ovule exhibits externally a cylindrical form, composed of four tiers of cells, the uppermost of which gradually converge and close up the orifice of the canal leading down between them. Meanwhile the vesicular head of one of the spiral filaments has penetrated into the globular cellule or embryo-sac, enlarged in size and undergone multiplication, and in the course of time displays itself as the embryo, producing the first frond and the terminal bud whence the regular Fern stem is developed. In considering the import of these phænomena, the author assumes the analogy here to be with the process of fertilization in flowering plants, as described by Schleiden, regarding the production of the embryo from the vesicular head of the spermatozoa as representing the production of the phanerogamous embryo from the end of the pollen tube after it has penetrated into the embryo-sac.

The promulgation of these statements naturally attracted great attention, and since they appeared we have received several contributions to the history of these remarkable structures, some confirmatory, to a certain degree, of Suminski's views, others altogether opposed to them.

In the early part of 1849 Dr. Wigand* published a series of researches on this subject, in which he subjected the assertions of Suminski to a strict practical criticism ; the conclusions he arrived at were altogether opposed to that author's views respecting the supposed formation of the organs, and he never observed the entrance of the spiral filaments into the cavity of the so-called ovule.

About the same time M. Thuret† published an account of some observations on the antheridia of Ferns. In these he merely confirmed and corrected the statements of Nägeli respecting the antheridia, and did not notice the so-called ovules.

Towards the close of the same year, Hofmeister‡ confirmed part of

* Botanische Zeitung, vol. vii. 1849.

† Ann. des Sc. Nat. Jan. 1849. ser. 3. vol. xi. Botanique. ‡ Botanische Zeitung, 1849.

Suminski's statements and opposed others. He stated that he had observed distinctly the production of the young plant (or rather the terminal bud for the new axis), in the interior of the so-called 'ovule,' but believed the supposed origin of it from the end of the spiral filament to be a delusion. He regards the globular cell at the base of the canal of the 'ovule' as itself the rudiment of the stem, or embryonal vesicle (the embryo originating from a *free* cell produced in this), analogous to that produced in the pistillidia of the Mosses. He also describes the development of the ovule differently, saying that the canal and orifice are opened only at a late period by the separation of the contiguous walls of the four rows of cells.

About the same time appeared an elaborate paper on the same subject by Dr. Hermann Schacht*, whose results were almost identical. He found the young terminal bud to be developed in the cavity of one of the so-called 'ovules,' which were developed exactly in the same way as the pistillidia of the Mosses. He stated also that the cavity of the 'ovule' is not open at first, and he declares against the probability of the entrance of a spiral filament into it, never having observed this, much less a conversion of one into an embryo.

In the essay of Dr. Mettenius already referred to†, an account of the development of the so-called ovules is given. His observations did not decide whether the canal of the 'ovule,' which he regards as an intercellular space, exists at first, or only subsequently, when it is entirely closed above. Some important points occur in reference to the contents of the canal.

The contents of the canal in a mature condition consist of a continuous mass of homogeneous, tough substance, in which fine granules, and here and there large corpuscles, are imbedded. It reaches down to the globular cell or 'embryo-sac,' and is in contact with this. This mass either fills the canal or diminishes in diameter from the blind end of the canal down to the 'embryo-sac;' in other cases it possesses the form represented by Suminski, having a clavate enlargement at the blind end of the canal, and passing into a twisted filament below. In this latter shape it may frequently be pressed out of isolated 'ovules' under the microscope, and then a thin transparent membrane-like layer was several times observed on its surface. In other cases the contents consisted of nucleated vesicles, which emerged separately or connected together.

The embryo-sac consists of a globular cell containing a nucleus, and this author believes that the commencement of the development of the embryo consists in the division of this into two, which go on dividing to produce the cellular structure of the first frond.

With regard to the contents of the canal the author says,—

"Although I can give no information on many points, as in regard to the origin of the contents of the canal of the 'ovule,' yet my observations on the development of the 'ovule' do not allow me to consider them, with Suminski, as spiral filaments in course of solution; just as little have I been able to convince myself of the existence of the process of impregnation described by that author. It rather appears to me that the possibility of the entrance of the spiral filaments and the impregnation cannot exist until the tearing open of the blind end of the canal in the perfectly-formed ovule, as after the opening of the so-called 'canal of the style' in the pistillidia in the Mosses."

Another contribution has been furnished by Dr. Mercklin‡, the original of

* Linnæa, vol. xxii. 1849.

† Beiträge zur Botanik, 1. Heidelberg, 1850. Zur Fortpflanzung der Gefäss-Cryptogamen.

‡ Beobachtungen aus dem Prothallium der Farrenkräuter. St. Petersburg, 1850.

which I have not seen, but depend on analyses of it published in the 'Botanische Zeitung*,' and the 'Flora' for 1851†, and further in a letter from Dr. Mercklin to M. Schacht‡, which appeared in the 'Linnæa' at the close of last year.

He differs in a few subordinate particulars from M. Schacht in reference to the development and structure of the *prothallium* or pro-embryo, and of the antheridia and spiral filaments; but these do not require especial mention, except in reference to the vesicular end of the spiral filament described by Schacht, which Mercklin regards as a remnant of the parent vesicle, from which the filament had not become quite freed. The observations referring to the so-called ovule and the supposed process of impregnation are very important; they are as follows:—

"1. The spiral filaments swarm round the 'ovule' in numbers, frequently returning to one and the same organ.

"2. They can penetrate into the 'ovule.' This was seen only three times in the course of a whole year, and under different circumstances; twice a spiral filament was seen to enter a still widely open young 'ovule,' then come to a state of rest, and after some time assume the appearance of a shapeless mass of mucilage; the third case of penetration occurred in a fully-developed 'ovule,' through its canal; it therefore does not seem to afford evidence of the import of the spiral filament, but certainly of the possibility of the penetration.

"3. In the tubular portion of the 'ovule,' almost in every case, peculiar club-shaped, granular mucilaginous filaments occur at a definite epoch, these filaments, like the spiral filaments, acquiring a brown colour with iodine. These mucilaginous bodies sometimes exhibit a twisted aspect, an opake nucleus, or a membranous layer, peculiarities which seem to indicate the existence of an organization.

"4. These club-shaped filaments are swollen at the lower capitate extremity, and have been found in contact with the 'embryo-sac' or globular cell which forms the rudiment of the future frond.

"5. The spiral filaments, which cease to move and fall upon the prothallium, are metamorphosed, become granular and swell up."

Hence the author deduces the following conclusions:—

"That these clavate filiform masses in the interior of the 'ovule' are transformed spiral filaments, which at an early period, while the ovule was open, have penetrated into it; which leads to the probability that—

"1. The spiral filaments must regularly penetrate into the 'ovules,' and

"2. They probably contribute to the origin or development of the young fruit frond (or embryo). In what way this happens the author knows not, and the details on this point given by Count Suminski remain unconfirmed facts."

An important point in this essay is the view the author takes of the whole process of development in this case. He regards it as not analogous to the impregnation in the Phanerogamia, since the essential fact is merely the development of a *frond* from one cell of the *prothallium*, which he considers to be merely one of the changes of the individual plant; while all the other authors who have written on the subject, with the exception of Wigand, call the first frond, with its bud and root, an *embryo*, and regard it as a new individual, or at all events a distinct member of a series of forms constituting collectively the representatives of the species.

* Botanische Zeitung, vol. xxxiii. 1850. † Flora, vol. xxxiii. p. 696. 1850.
‡ Linnæa, vol. xxiii. p. 723. 1850.

Finally, Hofmeister, in his notice of this essay in the 'Flora *,' declares that the development of the so-called 'embryo' or first frond commences, not by the subdivision of the globular cell or 'embryo-sac,' but by the development of a free cell or 'embryo vesicle' in this, like what occurs in the embryo-sac of the Phanerogamia; and he asserts that this is the first stage of development from the globular cell in all the vascular Cryptogams, including that found in the pistillidia of the Mosses.

Equisetaceæ.—The first discovery of the analogy between the developments from the spore in germination, in the Ferns and Equisetaceæ, is due to M. G. Thuret †, who saw the spores of the latter produce a cellular pro-embryo somewhat like that of the Ferns, and in this were developed antheridia of analogous structure, emitting cellules containing many spiral filaments.

This announcement was confirmed by M. Milde ‡, whose observations extended over some months, during which time no 'ovule' was produced, but he saw what appeared to be the rudiment of one. Dr. Mettenius § states that he has met with decaying 'ovules' precisely like those of the Ferns, upon the pro-embryo of an Equisetum, and thus the evidence is completed, so far as the occurrence of the two kinds of organs is concerned.

Lycopodiaceæ.—The fructification of this family consists, as is well known, of spikes clothed with fruit-leaves, bearing on their inner faces sporangia containing spores. These spores are of two kinds. One sort occur in large numbers in their sporangium, and are very small; the others are much larger, and only four are met with in a sporangium. Spring ‖, who has devoted great attention to the general characters of the Lycopodiaceæ, has given especial names to the two kinds of sporangia; those with the four large spores he calls oophoridia, those with the small spores antheridia; yet he did not mean to attribute a sexual antithesis, merely a morphological one, as he expressly states.

The general impression however with regard to the import of the two kinds of spores has long been, that the large spores alone are capable of producing new plants, and five years ago Dr. C. Müller published an elaborate account of the development of the Lycopodiaceæ ¶, in which the germination of the large spores was described at length. The following are the essential results of his investigations.

The large spores are more or less globular bodies, usually flattened on the surfaces by which they are in contact in the oophoridium; thus, while the outer side has a spherical surface, the inner side has three or four triangular surfaces, as in *L. selaginoides*, and *L. denticulatum*. They possess two coats, the outer very thick and composed of numerous cells, the cavities of which are almost completely filled up by deposits of secondary layers. This outer coat exhibits various forms of raised markings on its outer surface, and in some cases these seem to form a distinct layer, a kind of cuticle, capable of being separated from the subjacent cells. The inner coat of the spore is *usually* perfectly structureless, and not very firmly attached to the outer coat. In *L. gracillimum* Dr. Müller observed below the outer coat a structure composed of a layer of rather large parenchymatous cells, which could be easily isolated; and as there was no structureless membrane within this, he regarded the layer as the proper inner coat. This observation is important in relation to the discrepancies between Dr. Müller's statements and those of Mettenius,

* 1850, p. 700. † Ann. des Sc. Nat. 1849, vol. xi. 5. ‡ Linnæa, 1850.
§ Beiträge zur Botanik, 1850, p. 22. ‖ Flor. Brasiliensis, 106–108.
¶ Botanische Zeitung, July 31, 1846, *et seq. num.* Ann. of Nat. History, vol. xix. 1847.

to be spoken of presently. The cavity of the spore is filled with granular mucilage.

When the spore is placed in favourable circumstances for germination it begins to swell up, and if the contents be examined with the microscope, a few minute cells will soon be found to have become developed in the mucilage. This cell-formation commences at a determinate spot upon the inner coat of the spore, the cells being so firmly applied that they appear blended with this inner membrane. The cell-formation goes on till an obtuse conical process is developed, which breaks through the outer tough coat of the spore, and this process is recognized as the germinal body or *keim-körper*, corresponding to the pro-embryo of the other Cryptogams. From this, which at this period does not by any means fill the cavity of the spore with its lower portion, an ovate process is produced, at first obliquely directed upwards, the bud of the future stem, and a conical process taking the opposite direction representing the radicle. On the ascending process a distinction can soon be observed between the terminal bud, a little oval body, and a short thread-like stem on which it is supported; as the bud opens, the leaves appear in pairs.

At the conclusion of the paper Dr. Müller offers some remarks on the evidence with respect to the import of the spores, the substance of which may be transcribed. "Up to the present time it remains doubtful what purpose is served by the antheridium-spore. Some persons maintain one opinion, others another. One author declares he has seen it germinate, another that he has never been able to do so. Kaulfuss* relates that Fox sowed *Lyc. Selago*, and Lindsay *L. cernuum* with success, and that *L. clavatum* sprung up abundantly with Willdenow. With himself it did not succeed; but the garden-inspector, Otto of Berlin, raised *L. pygmæum* several years in succession from seed. The last case however is readily explicable, since *L. pygmæum* possesses oophoridia."

Göppert† however states that he has seen the development of young plants from antheridium-spores in *L. denticulatum*. Dr. Müller expresses some doubt as to whether the observation was absolutely exact, since Göppert never mentions seeing a young plant actually adherent to an antheridium-spore, neither does he give the structure of the leaf, and the young plant he figures closely resembles a *Fissidens*, frequently springing up in flower-pots in green-houses. In his own attempts to raise plants from antheridium-spores, Dr. Müller in every case failed. He does not deny, however, that they may be capable of germination, especially as some Lycopodiaceæ appear to be devoid of oophoridia.

In 1849 appeared M. Hofmeister's notice on the fructification and germination of the higher Cryptogamia‡, in which he indicated the existence on the pro-embryo of *Selaginella*, of a number of peculiar organs, composed of four papilliform cells, enclosing a large globular cell in the centre. In one of these large spherical cells the young plant is produced. The nature of the structure was only briefly described in this paper for the purpose of showing its analogy with what occurs in *Salvinia*.

In 1850 Dr. Mettenius§ published an essay on the Propagation of the Vascular Cryptogams, and in this is to be found a full description of the organs mentioned by Hofmeister and altogether overlooked by Dr. C. Müller.

* Das Wesen der Farrenkräuter. Leipzig, 1827.

† Uebers. der Arbeiten und Veränd. der schlesischen Gesellsch. für vaterl. Kultur, 1841 und 1845.

‡ Bot. Zeitung, Nov. 9, 1849.

§ Beiträge zur Botanik. Heidelberg, 1850.

According to this author, the large spores of *Selaginella involvens* possess two coats, each composed of two layers; and in an early stage of the germination, the inner layer of the outer coat, together with the inner coat, form the walls of a globular body which does not wholly fill the cavity enclosed by the outermost membrane. This globular body is firmly attached to the outer membrane immediately under the point of junction of the three ridges separating the flattened surfaces of the inner side of the spore. The globule enlarges until its walls come to be applied closely to the outer layer, completely filling up the large cavity. Then between the two layers of the inner coat, at a point immediately beneath the point of junction of the three external ridges, a process of cell-formation commences, producing a flattened plate of tissue interposed between the two layers; this structure is the pro-embryo. The cells are at first in a single layer, but the central ones soon become divided by horizontal septa so as to produce a double layer, and finally four or more tiers of cells one above another. The outline of the pro-embryo, seen from above, is circular, spreading over the upper part of the spore. On its surface appear the so-called ovules. The first is produced at the apex of the pro-embryo, the rest, to the number of twenty or thirty, arranged upon its surface in three lines corresponding to the slits by which the outer coat of the spore bursts. These ovules, closely resembling those of *Salvinia*, *Pilularia*, the Ferns, &c., consist of a globular cell surmounted by four cells, which rise up into four papillæ, and leave a canal or intercellular passage between them, leading down to the globular cell or embryo-sac. The four cells are usually developed into four or five cells, one above the other, by the production of horizontal septa; sometimes they are developed unequally and to a considerable extent so as to form papillæ, presenting an orifice between them at some point on the outer surface, indicating the canal leading down to the embryo-sac.

During the development of the ovules, a delicate parenchyma is produced in the great cavity of the spore, finally entirely filling up this spore. Before it has completely filled it, the embryo makes its appearance in the embryo-sac of one of the ovules.

The first change in this sac is the appearance of a nucleus; from this cells are developed representing the suspensor of the embryo. The cells of the suspensor multiply and form the process which penetrates down into the parenchyma of the cavity of the spore; at the lower end may be detected the embryo, a minutely cellular body. Dr. Mettenius never saw the embryo produced in the embryo-sac before the suspensor had broken through the bottom of it to penetrate the parenchyma of the spore-cell; it was always within this parenchyma and attached to the end of the suspensor. In this point he is decidedly opposed to Hofmeister, who states that the embryo originates in the embryo-sac, whence a young embryo attached to its suspensor may easily be extracted from the spore.

The part of the embryo opposite to the point of attachment of the suspensor corresponds to the first axis of the Rhizocarpeæ, which never breaks out from the spore-cell in *Selaginella*; it pushes back the loose parenchyma of the spore-cell as it becomes developed, and when completely formed, is surrounded by a thin coat composed of several layers of the parenchymatous cells much compressed, enclosed in the still existing inner coat of the spore. On one side of the point of attachment of the suspensor the embryo grows out towards the point where the spore-cell has been ruptured, thus apparently in a direction completely opposite to the end of the axis. As it enlarges it produces in this situation the leafy stem growing upwards, and the adventitious root turning downwards. The pro-embryo is at first distended like a sac, and finally broken through on the one side by the first leaf, on the other by the adventitious root; upon it may be observed the numerous abortive ovules, with their embryo-sacs filled with yellow contents; part of its cells grow out into radical hairs. Dr. Mettenius several times saw two young plants produced from one spore; the ends of their axes lay close together, and separated inside the cavity of the spore. No account is here given of the characters exhibited by the small spores, or of anything like a process of fertilization; yet we have indicated in the foregoing description of the so-called ovules, a clear analogy between these bodies and the so-called ovules of the Ferns and Rhizocarpeæ. These points will be referred to again at the close of the report.

In a review of Dr. Mercklin's essay on the reproduction of the Ferns, in the Flora*, Hofmeister states that spiral filaments are produced from the small spores of *Selaginella*, but does not state that he has seen them or give any authority.

Isoëtaceæ.—The spores of the *Isoëtes lacustris* are of two kinds, analogous to those of the Lycopodiaceæ; both kinds being produced in sporangia imbedded in the bases of the leaves, but the large spores are found in great numbers, not merely four in a sporangium as in the Lycopodiaceæ. The development of the spores was little known until the publication of an essay on the subject in 1848, by Dr. C. Müller†, forming a sequel to his researches on the Lycopodiaceæ. Here, as in the other case, his observations on the earlier stages were imperfect; but he indicated the existence of the structures which have since been recognized as the so-called ovules; as also did Mr. Valentine‡ in his essay on *Pilularia*.

In his essay Dr. C. Müller compares the complete large spore, as discharged from the sporangium, to the ovule of flowering plants; and he describes it as a globular sac enclosed by three coats, which he names the primine, secundine, and the nucleus. The outermost coat, or primine, is stated to be composed of a thick cellular membrane exhibiting a raised network of lines, which give it the aspect of a cellular structure, but are in reality analogous to the markings on pollen-grains. The outer surface exhibits the lines indicating the tetrahedral arrangement of the spores in the parent cell, as in *Selaginella*, and it is at the point of intersection of these that the membrane gives way in germination. The next coat, or secundine, is another simple membrane lining the first. The nucleus is a coat composed of delicate parenchymatous cells, but among these are found groups of peculiar character. These are described as consisting of a large cell divided by two septa crossing each other at right angles, projecting from the general surface, being either oval in the general outline, or having four indentations opposite the cross septa, so as to give the appearance of the structure being composed of four spherical cells. The cells surrounding them are of irregular form, different from the generally six-sided cells of the rest of the nucleus. Many of these groups occur on the nucleus, always at the surface of the coat where the primine and secundine afterwards give way, scattered without apparent order over it, but one always near the point of the opening. To these structures Dr. Müller did not attribute any important function, explaining them merely as produced

* Flora, 1850, p. 700.

† Botanische Zeitung, April and May, 1848; Annals of Nat. History, 2nd ser. vol. ii. 1848.

‡ Linnæan Transactions, vol. xvii.

by peculiar thickenings of the tissue to protect the pro-embryo during germination. The contents of the nucleus were stated to resemble those of the cavity of the spores of *Selaginella*.

In these contents, which become dense and mucilaginous, a *free* cell is developed near the upper part of the cavity; this is the rudiment of the embryo, and by cell-multiplication becomes a cellular mass, which soon begins to exhibit growth in two directions, producing the first leaf and the first rootlet, projecting from a lateral cellular mass, which the author calls the "reservoir of nutriment." The embryo then breaks through the coats; the first leaf above and the first root below, the coats remaining attached over the central mass of the embryo. The subsequent changes need not be mentioned here, further than to state that the leaves succeed each other alternately, and are not opposite as in the Lycopodiaceæ; moreover no internodes are developed between them, so that the stem is represented by a flat rhizome, like the base of the bulb of many Monocotyledons.

In the paper by Dr. Mettenius*, already alluded to, we find some very important modifications of and additions to this history of development of the spores of *Isoëtes*, bringing them into more immediate relation with the other vascular Cryptogams.

This author describes the spore-cell as a thick structure composed of several layers; in some cases he counted four. It completely invests the pro-embryo, which is a globular cellular body filling the spore-cell. Among the cells of the outermost layer of the pro-embryo (which layer forms the *nucleus* of Dr. Müller), on the upper part, are produced the ovules, fewer in number than in *Selaginella*, arranged in three rows converging upon the summit of the spore, these rows corresponding to the slits between the lobes of the outer coat of the spore. The four superficial cells of the ovules (which are evidently the peculiar groups mentioned by Müller and previously noticed by Valentine†) grow much in the same way as in the Rhizocarpeæ and in *Selaginella*, into short papillæ. The embryo is developed in the substance of the pro-embryo, displacing and destroying its cells, and a globular portion (corresponding to the "reservoir of nutrition" of Müller) remains within the spore after the first leaf and rootlet have made their way out. This body is the analogue of that portion of the embryo of *Selaginella* which penetrates into the cavity of the spore, and to the end of the first axis in the Rhizocarpeæ.

The most important point, however, of Dr. Mettenius's researches relates to the phænomenon exhibited by the small spores. In the water in which the spores were sown he observed moving spiral filaments resembling those of the Ferns. He was not able to trace all the stages of development of these spiral filaments from the small spores, but he obtained nearly all the evidence relating to their origin which Nägeli has done in reference to the similar organs in the *Pilularia*‡. In the small spores minute vesicles are produced of varying size and number, seen through the outer coat. The inner coat or spore-cell breaks through the outer coat either in the middle or at both ends at the projecting ridges, by which they are originally in contact with the other spore-cells. Its contents are expelled, as is proved by finding numerous empty membranes. The expelled vesicles are met with in considerable number in the water, and contain one large or several small granules, and in them the spiral filaments are apparently produced; but the actual course of development was not observed. In one case a spiral filament was seen halt

* Beiträge zur Botanik. Heidelberg, 1850. † Linnæan Transactions, vol. xvii.
‡ Zeitschrift für Wiss. Botanik, Heft 3. Zurich, 1846.

way out of the spore-cell in active rotation, finally emerging completely, so that the moving spiral filaments are probably developed in the vesicles, while these are still contained within the spore-cell.

No actual connexion of these moving spiral filaments or spermatozoa with the so-called ovules has yet been traced.

Rhizocarpeæ.—Almost from the earliest period of the study of Cryptogamous plants, attempts have been made to prove the existence of distinct sexes in the Rhizocarpeæ, various parts of the structure being regarded by different authors as analogues of the stamens and pistils of flowering plants. Bernard de Jussieu* went so far as to class them (*Pilularia glob.* and *Marsilea quad.*) with the Monocotyledons, with *Lemna*, considering the large spore-sacs as pistils and the small ones as stamens.

Others have sought the male organs in the hairs upon the leaves or receptacles†; but the rest of the numerous authors who have written on the subject, have either denied the distinction of sexuality altogether, or are agreed in considering the large spores as either ovaries or ovules, the small spores as pollen-grains. Experiments have frequently been made upon the generative powers of the two kinds of spores. Paolo Savi‡ found that the large spores of *Salvinia* would not germinate alone, and therefore he regarded the small ones as anthers. Duvernoy§, on the contrary, states that he saw the large spores of *Salvinia* germinate when separated from the small ones, and therefore he did not regard the latter as anthers, but only rudiments. Bischoff||, who minutely described the structure of the European species, said that in his experiments the large spores of *Salvinia* germinated as well without the small granules as with them. Agardh¶ saw the large spores of *Pilularia* germinate separately, but later than those united with the anthers. Pietro Savi** made careful observations on the germination of the separated large spores of *Salvinia*, and found them to produce a green mamilla which underwent no further development; he therefore regarded the small spores as necessary for impregnation. Esprit Fabre†† carefully experimented on *Marsilea Fabri.* The separated large spores did not germinate; they did not even produce the stationary green papilla observed in *Salvinia* by Pietro Savi. Dr. C. Müller‡‡ found that the large spores of *Pilularia* would not germinate when separate from the small ones.

The development of the spores and the germination of the larger kind in *Pilularia* appear to have been first accurately described by Mr. Valentine§§, in a paper read before the Linnæan Society in March 1839. It is unnecessary to enter into the particulars of this paper, which gives accurate statements in most points, and mentions for the first time the occurrence of the cellular papilla upon the pro-embryo which has since been regarded as the "ovule," analogous to that found on the pro-embryo of the other vascular Cryptogams.

Dr. C. Muller's|||| essay appeared in 1840, and agrees in some points; but he appears to have mistaken the mode of origin of the pro-embryo. In 1843 Schleiden¶¶ announced that he had observed a process of impregnation in *Pilularia*, in which the small spores acted the part of pollen-grains, producing tubes which entered into a cavity on the surface of the large spore or "ovule," and, in accordance with his views of impregnation in general, became the embryo.

* Hist. de l'Acad. Roy. des Sc. 1739 and 1740.
† Micheli, Linnæus and Hedwig
‡ Biblioth. Italian. xx.
§ Diss. de *Salv. nat.* &c., 1825.
|| Nova Acta xiv. and Cryptogam Gew. part 2. 1828.
¶ De *Pilularia* diss. 1835.
** Ann. des Sc. Nat. 1837.
†† Ann. des Sc. Nat. 1837.
‡‡ Flora, 1840.
§§ Linnæan Transactions, vol. xvii.
|||| Flora, 1840.
¶¶ Grundz. der Wiss. Botanik, 1843.

The next paper on the subject was an essay published by Dr. Mettenius* in 1846, in which the anatomy and development of *Salvinia* is treated at length; that of *Pilularia* and *Marsilea* less perfectly. He did not observe the process of impregnation described by Schleiden, yet from the want of organic continuity between the embryo and the "ovule," he inclined to adopt the theory of fertilization propounded by Schleiden, both for the Phanerogamia and the Rhizocarpeæ, namely, that the end of the pollen-tube penetrated into the so-called ovule and became the embryo; nevertheless he had some doubts, since he could not reconcile the production of "pollen-tubes" from the small spores of *Salvinia* with the facts he had observed, and never saw the "tube" penetrate the "ovule" in *Pilularia*.

In 1846 Prof. Nägeli published some new and important observations on *Pilularia*†, in which he stated that the observations of Schleiden were altogether incorrect, and that the bodies which that author had described as three or four "pollen-tubes," produced by the small spores and adherent to the summit of the large spore, were in fact parts of this, constituting a papilliform structure, forming a part of the pro-embryo developed by the large spore itself. Moreover he discovered a totally unexpected fact in regard to the small spore or "pollen-grains." He found that these, without coming in contact with the large spores at all, became elongated by the inner coat protruding like a short pouch-like process through the outer. This contained starch-granules; and some he found burst and surrounded by starch-grains exactly like those inside the others; and in addition to these, minute cellules which seem to have been expelled from the small spores. In these cellules were developed spiral filaments exhibiting active movement, just like those of *Chara*, the Mosses, &c. These filaments finally make their way out and swim about freely in the water. They were constantly met with in the gelatinous mass in which the spores were enveloped.

In 1849 M. Hofmeister‡ published the essay on the higher Cryptogams already alluded to, and there briefly described his own critical observations, referring to the points of difference from his predecessors. His statements are as follows:—

"The publications of Mettenius and Nägeli, as also those of Schleiden himself, sufficiently show that the large spores of the Rhizocarpeæ (the organs called by Schleiden 'seed-buds' (ovules)) originate essentially in the same way as the spores of the Cryptogamia generally, and as the small spores of the Rhizocarpeæ ('pollen-grains' of Schleiden) in particular. One young spore in each *sporangium* becomes developed more rapidly than the others, and finally usurps the whole cavity. At the time when the spores are ripe, a large spore does not differ from a small one in any respect except in dimensions (the size of the organs allows of the structure of the outer secreted layer being very distinctly observed; in *Pilularia* five layers can be clearly detected). The large spore is a simple tough-walled cell filled with starch or oil-drops and albuminous matter, enclosed by a thick *exine*, which, at the point when the 'sister-spores' were in contact with the developed spore in the earlier stages, exhibits peculiar conditions of form, displaying, according to the generic differences, a splitting into thin lobes or a considerable thinning of the mass. Not the least trace of the cellular body (the pro-embryo, *papilla of the nucleus* of Schleiden) is to be seen at this point at the time when the spores are just ripe.

* Beiträge zur Kenntniss der Rhizocarpeæ. Frankfort, 1846.

† Zeitschrift für Wiss. Botanik. Heft 3, 4. 188, 1846.

‡ Botanische Zeitung, vol. vii. 1849; Botanical Gazette, vol. ii. 1850.

"After the ripe spores have lain a longer or shorter time in water, a process of cell-formation commences at that point of the spore, *within* the proper, internal spore-cell, whence results the formation of a cellular body occupying only a small portion of the internal cavity of the spore. The cells multiply rapidly, and break through the *exine*, appearing externally as the green cellular papilla called the '*keim-wulst*' by Bischoff, the 'papilla of the nucleus' by Schleiden. I see no ground why this should be named otherwise than as the *pro-embryo*. In *Pilularia* it is very soon seen, where the pro-embryo consists of only about thirty cells, completely enveloped by the *exine*, and where the only external evidence of its existence is a little protuberance,—that the pro-embryo consists of a large central cell surrounded by a simple layer of smaller ones. The smaller cells covering the apex of this large cell, four in number, elongate into a papilla before the pro-embryo bursts through the *exine*, which splits regularly into twelve to sixteen teeth;—subsequently they become divided by horizontal walls, and then appear as the organ which Schleiden, and after him Mettenius, supposed to be 'pollen-tubes' produced from some of the small spores. These papilliform cells most certainly originate from the pro-embryo, a fact which takes away all material ground from Schleiden's theory.

"The four papilliform cells separate from each other and leave a passage leading to the large central cell. In this cell the young plant originates shortly after the smaller spores, which *never* produce 'pollen-tubes,' begin to emit the cellules containing spiral filaments discovered by Nägeli. I observed and dissected out an embryo consisting of only four cells. It completely filled the large central cell, and there was not the least trace of a pollen-tube attached to it.

"The organization of *Salvinia* is somewhat different from this. On every pro-embryo several, as many as eight cells of the outer surface of the cellular layer next but two to the obtuse triangular cellular body, acquire a considerable size, a spherical form, and become filled with protoplasm; the four cells covering each of these larger cells lose the greater part of their chlorophyll and separate from each other to leave a passage leading down to the large central cell. In this large cell the young plant originates. The number of these organs in *Salvinia* allows the possibility of the occurrence of poly-embryony in this genus; I observed two embryos on one pro-embryo in one case.

"It is out of the question to talk of a 'larger pollen-tube' in *Salvinia*. Mettenius has already shown that the structure of the small spores renders such a product from them impossible."

Dr. Mettenius's Essay on the Vascular Cryptogams*, already frequently referred to, confirms the preceding account in all essential points, some slight criticisms relating only to the structure of the coats of the spore; and it adds a description of the development of the "ovules" in the pro-embryo of *Marsilea Fabri*, which agrees closely with that in *Pilularia*. Hofmeister† has recently announced the discovery of the production of cellules containing spiral filaments from the small spores in *Salvinia*, just as Nägeli saw them in *Pilularia*.

General Conclusions.

In the facts of which I have given confessedly a very imperfect *resumé* in the preceding pages, we have two important points to consider. In the first place, we have to determine how far they suffice to warrant the belief in the

* Beiträge zur Botanik. Heidelberg, 1850.

† Flora, 1850. p. 700 (in a note to a review of Mercklin's Essay on the Reproduction of Ferns).

existence of a distinction of sexes in these families. In the second place, we have to endeavour to trace the analogies which exist between the different conditions presented by the supposed sexual organs in the different families. These considerations, if we adopt the hypothesis of sexuality, lead to some very interesting questions in reference to the process of reproduction generally.

In regard to the first question, that of the existence of two sexes and the necessity of a process of fertilization, we have several kinds of evidence.

1. The inferences to be deduced from the universality of the existence of two kinds of organs in connexion with the reproductive process. We have seen that these exist in all the families at some period or other of the life of the representative of the species. In the Mosses and the Hepaticæ they occur in the fully developed plant. In the Ferns and Equisetaceæ they occur upon cellular structures of frondose character developed from all the spores, which frondose bodies or pro-embryos have an existence of some permanence, especially in the Equisetaceæ. In the Lycopodiaceæ, the Isoëtaceæ and Rhizocarpeæ, the pistillidia occur upon very transitory cellular structures produced from one kind of spore, the larger, while the smaller spores at once develope in their interior cellules containing moving spiral filaments such as occur in the antheridia of the other families.

2. The inferences to be deduced from the observations on the development of those plants in which the two kinds of organs, occurring in distinct places, can be separated. Strong evidence has been brought forward that the diœcious Mosses, as they are called, do not produce sporangia when the pistillidia are kept apart from the antheridia by natural accident. The majority of observers state that the large spores of the Rhizocarpeæ do not germinate if the small spores are all removed from contact with them ; a few counter-statements however do exist. Again, the majority of authors, and all the recent ones, state that only the large spores of the Lycopodiaceæ and Isoëtaceæ produce new plants ; while some older writers believed that they had seen the small spores do so.

3. The direct observation of a process of fertilization, of which we have only testimony from two authors, Suminski and Mercklin, in reference to the Ferns alone ; since the assertions of Schleiden in regard to the Rhizocarpeæ have been demonstrated by Nägeli, Hofmeister, and Mettenius to have been based on very imperfect observation.

The circumstantial evidence furnished under the first head seems to me very strong, so much so that I am inclined to adopt the idea of sexuality on this ground as the legitimate provisional hypothesis arising out of our present knowledge, especially when supported so strongly as it is by the negative evidence indicated under the second head.

The positive evidence of the third head is certainly very insufficient as yet, considering the extreme delicacy of the investigation. Suminski's other observations on the details have been contested in many particulars ; and Mercklin, the only other observer who asserts that he has seen the spiral filaments within the so-called ovules, describes the conditions differently, and states that he has only been able to observe them positively there three times. At the same time the difficulty of the investigation should make us hesitate in attaching too much weight to the failure of the other observers in tracing a process of fertilization ; moreover it is quite possible that actual entry of the spiral filaments into the canal of the ovules or pistillidia is not always, if ever, necessary.

The facts before us, then, appear to me strong enough to warrant the adoption of the views propounded by the latest authors on this subject, and the acceptance of the hypothesis of sexuality in the Vascular Cryptogams as the most satisfactory explanation of the phænomena as yet observed. The question lies now much in the same condition as that of the sexuality of flowering plants before the actual contact of the pollen-tubes with the ovules had been satisfactorily demonstrated.

Further arguments may be adduced from grounds lying out of the preceding statements, viz. 1. The late discovery of two forms of organs in the Algæ, Lichens and Fungi, which, although imperfect at present, lead to the expectation that the analogues of the antheridia and pistillidia of the Mosses, so long known, will be found in all Cryptogamous plants. 2. The analogies between the processes of animal and vegetable reproduction which appear to be offered by these new views of the nature of the phænomena in the Vascular Cryptogams. To this last argument I shall merely allude, as it may be considered to lie beyond the special province of the vegetable physiologist; yet when we recollect the imperceptible character of the gradations of the lower forms of the two kingdoms, there seems far sounder ground than is allowed by Schleiden for arguing from apparent analogies between the phænomena occurring in the two great kingdoms of nature.

Under the second point of view mentioned above, the facts of structure may soon be disposed of, so far as the analogies of form are concerned; the antheridia of the Mosses, Hepaticæ, Ferns, and Equisetaceæ agree with the small spores of *Isoëtes*, *Selaginella*, *Pilularia*, and *Salvinia* in producing the cellules in which are developed the moving spiral filaments which constitute the essential character of the organs of the one kind; while the pistillidia of the Mosses and Hepaticæ agree with the so-called "ovules" of the Ferns, Equisetaceæ, Lycopodiaceæ, Isoëtaceæ, and Rhizocarpeæ, in general structure and in the presence of the central large cell from which the new form of structure originates.

The great differences depend on the position in time and space of the organs, in the different classes, and the nature of the immediate product of the so-called "embryo-sac," the large central cell of the pistillidia and "ovules."

In the Mosses and Hepaticæ the pistillidia occur upon the plant when the vegetative structure is perfect,—and the immediate product of the great cell is a sporangium. If a process of fertilization take place here, we may regard the antheridia and pistillidia as analogues of the anthers and pistils of flowering plants, the sporangia of their fruits; or with Hofmeister we may regard the phænomenon as an instance of an "alternation of generations," where the pistillidium would be looked upon as an ovule, producing (in the sporangium) a new individual of totally different character from that developed from the spore (the leafy Moss plant in the usual acceptation of the term).

In the Ferns and Equisetaceæ, we find the spores producing a frondose structure of definite form, upon which are developed antheridia and pistillidia, or "ovules." Here then we seem to have one generation complete, and the new development from the pistillidium or "ovule" appears in a totally new form, producing stem and leaves which have a distinct individual form and existence, and produce the spores after a long period upon temporary parts of the structure, on the leaves; and by no means cease to exist when those are matured. Here we seem to have a real "alternation of generations," and Hofmeister compares the whole permanent plant of the Fern or *Equisetum* to the sporangium of the Mosses and Hepaticæ. In all the other families, the Lycopodiaceæ, Isoëtaceæ, the Rhizocarpeæ, the pro embryo is a very transitory production, and is developed from a differen spore from the spiral filaments. This pro-embryo is clearly analogous to that of the Ferns and Equisetaceæ; and if the existence of sexes be a fact, we have here a diœcious condition as contrasted with a monœcious condition in the two last-named families. Hofmeister here again assumes that the pro-embryo developed from the large spore is an intermediate generation between the two perfect forms of the plant.

It is rather difficult to decide upon the real analogies of these structures with those of the flowering plants. The resemblance of structure is so close between the pistillidia of the Mosses and Hepaticæ, and the "ovules" of the other Vascular Cryptogams, that they must be regarded as analogues, and then the former could not well be conceived to be analogous to the pistils of flowering plants, but rather to ovules; if this be the case, the sporangium must be considered the analogue of the perfect plant in the Fern, &c., and the leafy stem as the analogue of the pro-embryo of the Ferns, &c. The pistillidium of the Mosses can indeed hardly be regarded as analogous to the fruit of a flowering plant, as in that case the spores would be ovules produced long after fertilization; and on the other hand, if we consider the pistillidia of the Moss as an ovule, which it might be, analogous to that of the Coniferæ,—in which a large number of embryonal vesicles or rudiments of embryos are produced after fertilization on the branched extremities of the suspensors,—then we seem to lose the analogy between the product of the pistillidium of the Moss and that of the ovule of the Fern, unless we would regard the entire plant of a perfect Fern as analogous to the ovule of a Conifer.

Perhaps the time has hardly come for us to arrive at any conclusion on these points. The phænomena in the Ferns and Equisetaceæ, as well as in the Rhizocarpeæ, Lycopodiaceæ, and Isoëtaceæ less strikingly, seem to present a series of conditions analogous to those which have been described under the name of "alternation of generations" in the animal kingdom, and seeing the resemblance which the pistillidia of the Mosses have to the ovules of the other families, we can hardly help extending the same views to them; in which case we should have the remarkable phænomenon of a compound organism, in which a new individual forming a second generation, developed after a process of fertilization, remains attached organically to the parent, from which it differs totally in all anatomical and physiological characters. It is almost needless to advert to the essential difference between such a case and that of the occurrence of flower-buds and leaf-buds on one stem in the Phanerogamia, as parts of a single plant, yet possessing a certain amount of independent individuality. These are produced from each other by simple extension, a kind of gemmation; while the Moss capsule, if the sexual theory be correct, is the result of a true *reproductive* process*.

In conclusion, I may remark, that these anomalous conditions lose their remarkable character to a great extent if we refuse to accept the evidence of sexuality which has been brought forward here. If the structures are all products of mere extension or gemmation, the analogies which have been supposed to exist between them and the organs of flowering plants all fall to the ground. But believing that the hypothesis of sexuality is based on solid grounds, I am by no means inclined to allow the difficulty of the ex-

* Moreover we have an analogy to the increase by buds in the *innovations* by which the leafy stems of the Mosses are multiplied, both in the earliest condition, where a number of stems are developed from the byssoid mass produced by the spore, and afterwards by gemmæ on the stems and leaves, as in the Liverworts also. The byssoid mass produced by the Moss-spore has usually been called the *pro-embryo*, but it is evidently not analogous to the bodies termed pro-embryos in the Ferns, Lycopodiaceæ, &c. &c. It would almost seem to constitute a third member of a series of generations.

planation of these relations to be urged as a valid argument against their existence, and I trust that this imperfect report may be the means of attracting new investigators to a subject which presents so many points of interest and importance.—*July 3rd*, 1851.

Postscript.—Since the above Report has been in print Dr. W. Hofmeister has published his promised work upon the higher Cryptogams*, which contains an elaborate series of researches upon this subject. He there confirms all his previous statements, and all the essential particulars given by Suminski, Nägeli, Mettenius, &c., excepting the *facts* of the impregnation by means of the spiral filaments or spermatozoids, which however he considers it warrantable to *assume*. His speculations as to the relation of the Conifers to the Lycopodiaceæ, as shown by the development of the embryo, are very interesting. We can only claim space to indicate the general results of his work as given in the concluding summary:—"The comparison of the course of development of the Mosses and Liverworts on the one hand, with the Ferns, Equisetaceæ, Rhizocarpeæ and Lycopodiaceæ on the other, reveals the most complete agreement between the development of the fruit of the former and the development of the embryo of the others. The archegonium of the Mosses, the organ within which the rudiment of its fruit is formed, resembles perfectly in structure the archegonium of the Filicoids (in the widest sense), that part of the prothallium in the interior of which the embryo of the frondescent plant originates. In the two great groups of the higher Cryptogams, one large central cell originating free in the archegonium, gives origin by repeated subdivision to the fruit in the Mosses, and to the leafy plant in the Filicoids. In neither of them does the subdivision of this cell go on, in both does the archegonium become abortive, if spermatic filaments do not reach it at the epoch when it bursts open at the apex.

"Mosses and Filicoids thus afford one of the most striking examples of a regular alternation of two generations widely different in their organization. The first of these, produced by the germinating spore, developes antheridia and archegonia, sometimes few, sometimes many. In the central cell of the archegonium, in consequence of a fertilization through the spermatozoids emitted from the antheridia, becomes developed the second generation, destined to produce spores, which are always formed in a number much greater than that of the rudimentary fruits of the first generation.

"In the Mosses the vegetative life is exclusively committed to the first, the production of fruit to the second generation. Only the leafy stem possesses roots; the spore-producing generation draws its sustenance from the foregoing. The fruit is usually of shorter duration than the leaf-bearing plant. In the Filicoids the opposite condition obtains. It is true the prothallia send out capillary rootlets; those of the Polypodiaceæ and Equisetaceæ under all circumstances, those of the Rhizocarpeæ and Selaginellæ frequently. But the prothallium has a much briefer existence than the frondescent plant, which in most cases must vegetate for several years before it comes to bear fruit. Yet the contrast is not so strong as it appears to be at first sight. The seemingly unlimited duration of the leaf-bearing Moss-plant depends upon constant renovation (*verjüngung*). Phænomena essentially similar occur in proliferous prothallia of the Polypodiaceæ and Equisetaceæ. The structure of the lowest Mosses (*Anthoceros, Pellia*) is

* *Vergleichende Untersuchungen der Keimung, Entfaltung und Fruchtbildung höherer Kryptogamen* (*Moose, Farrn, Equisetaceen, Rhizocarpeen und Lycopodiaceen*) *und der Samenbildung der Coniferen.* 1851, Leipsic, Hofmeister, 4to, pp. 180, *tt.* 33.

less complex, and the duration of the fruit-bearing shoots is little longer than that of the fruit itself. On the other hand, the ramification of the prothallium of the Equisetaceæ is exceedingly complicated; its duration is even equal to that of a single shoot.

"It is a circumstance worthy of notice, that in the second generation of Mosses, as of the Filicoids, destined to produce spores, more complex thickenings of the cell-walls regularly occur (teeth of the peristome of Mosses, wall of capsule and elaters of Liverworts, vessels of Filicoids, &c.), while in the first generation, springing from the spores, such structures are found only rarely and as exceptions.

"The manner in which the second generation arises from the first, varies much more in the Filicoids than in the Mosses. The Polypodiaceæ and Equisetaceæ are hermaphrodite; the Rhizocarpeæ and Selaginellæ monœcious. All the Filicoids agree in the fact that the first axis of their embryo possesses but a very limited longitudinal development; that it is an axis of the second rank which breaks through the prothallium and becomes the main axis; further, in the end of the axis of the first rank never becoming elongated in the direction opposite to the summit. All Filicoids are devoid of a tap-root, and possess only adventitious roots.

"In more than one respect does the course of development of the embryo of the Conifers stand intermediately between those of the higher Cryptogams and the Phanerogams. Like the primary parent-cell of the spores of the Rhizocarpeæ and Selaginellæ, the embryo-sac is an axile cell of the shoot, which in the former is converted into a sporangium, in the latter into an ovule. In the Conifers the embryo-sac also very early becomes detached from the cellular tissue surrounding it. The filling-up of the embryo-sac with the albumen may be compared with the origin of the prothallium in the Rhizocarpeæ and Selaginellæ. The structure of the 'corpuscula' bears the most striking resemblance to that of the archegonia of *Salvinia*, still more to that of the Selaginellæ. If we leave out of view the different nature of the impregnation, in the Rhizocarpeæ and Selaginellæ by free-swimming spermatic filaments, in the Coniferæ by a pollen-tube (which *perhaps* developes spermatic filaments in its interior), the metamorphosis of the embryonal vesicle into the primary parent-cell of the new plant in the Conifers and Filicoids is solely distinguished, by the latter possessing only a single embryonal vesicle which completely fills the cavity of the central cell of the archegonium, while the former exhibits very numerous embryonal vesicles swimming in it, of which only one pressed into the lower end of the 'corpusculum' becomes impregnated. The embryo-sac of the Conifers may be regarded as a spore which remains enclosed in its sporangium; the prothallium which it forms never comes to light. The fertilizing matter must make a way for itself through the tissue of the sporangium, to reach the archegonia of this prothallium.

"Two of the phænomena which led me to compare the embryo-sac of the Conifers with the large spores of the higher Cryptogams, are common also to the embryo-sac of the Phanerogams: the origin from an axile cell of the shoot, and the independence of the surrounding cellular tissue (so striking, for example, in the Rhinanthaceæ, through the independent growth of the embryo-sac). By their pollen-grains producing tubes the Conifers are closely connected with the Phanerogams, from which they differ so much in the course of development of their embryo-sac and the embryonal vesicles. The separation of the prothallium of the Conifers into a number of independent suspensors, is a phænomenon of a most peculiar kind, having no analogue throughout the vegetable kingdom."—(*Loc. cit.* pp. 139–41.)—A. H. Dec. 16, 1851.

[illegible] complex and the duration of the fruit-bearing phase is little longer than that of the first [illegible]. On the other hand, the [illegible] of the [illegible] [illegible] is exceedingly complicated; its duration is even equal to life of a single shoot.

It is a circumstance worthy of notice, that in the sexual generation of [illegible], as of the [illegible], destined to [illegible] [illegible], many [illegible] [illegible] of the [illegible] [illegible] [illegible] [illegible] of the [illegible] of [illegible], wall of [illegible] and [illegible] of [illegible] [illegible], &c.; while in the first generation, [illegible] from the spores, such [illegible] are found only [illegible] and as exceptions.

The manner in which the second generation arises from the first varies much more in the [illegible] than in the [illegible]. The [illegible] and [illegible] are [illegible] the [illegible] and [illegible] [illegible] [illegible]. All the [illegible] agree in the fact that the first axis of their embryo possesses only a very limited longitudinal development; that it is no axis of the [illegible] which breaks through the prothallium and becomes the main axis; further, in the [illegible] the axis of the [illegible] never [illegible] [illegible] in the direction opposite to the [illegible]. All [illegible] are [illegible] of a [illegible]-root, [illegible] possess only a [illegible] [illegible].

In more than one respect does the course of development of the embryo of the Conifers stand intermediately between those of the higher Cryptogams and the Phanerogams. Like the primary [illegible] of the spores of the [illegible] and [illegible], the embryo-sac is an axile cell of the shoot, which in the former is converted into a [illegible], in the latter into an ovule. In the Conifers the embryo-sac also very early becomes detached from the cellular tissue surrounding it. The [illegible] of the embryo-sac with the [illegible] may be compared with the origin of the prothallium in the [illegible] and [illegible]. The structure of the 'corpuscula' bears the most striking resemblance to that of the archegonia of [illegible], still more to that of the Selaginellae. If we leave out of view the different nature of the impregnation, in the [illegible] and [illegible] by free-swimming spermatozoids, in the Conifers by a pollen-tube (which [illegible] [illegible] spermatic filaments in its interior), the [illegible] of the [illegible] vesicle into the primary [illegible] of the new plant in the Conifers and [illegible] is [illegible] distinguished, by the latter possessing only a single embryonal vesicle which completely fills the cavity of the central cell of the archegonium, while the former exhibits very numerous embryonal vesicles [illegible], of which only one [illegible] into the lower end of the [illegible] becomes impregnated. The embryo-sac of the Conifers may be regarded as a spore which remains enclosed in its sporangium; the prothallium which it forms never comes to light. The fertilizing matter must make a way for itself through the tissue of the sporangium, to reach the archegonia of this prothallium.

"Two of the phenomena which led me to compare the embryo-sac of the Conifers with the large spore of the higher Cryptogams, are common also to the embryo-sac of the Phanerogams: the origin from an axile cell of the [illegible], and the independence of the surrounding cellular tissue (so striking, for example, in the [illegible], through the [illegible] growth of the embryo-sac). By their [illegible] [illegible] [illegible] the Conifers are closely connected with the [illegible], and [illegible] they differ so much as the course of development of their embryo-sac and the embryonal vesicles. The separation of the [illegible] [illegible] of the Conifers [illegible] [illegible] [illegible] [illegible] [illegible], is [illegible] of a more [illegible] and [illegible] [illegible] throughout the vegetable kingdom."—(Loc. cit. pp. [illegible])—A. H. [illegible]