VII.—*Studies in the Morphology of Spore-producing Members.—No. V. General Comparisons and Conclusion.*

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Contents.

Introduction.

In the series of Memoirs of which this is the fifth, and concluding part,* the spore-producing members of all the important types of living Pteridophyta have been

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* The preceding parts are as follows:—

I. "Equisetineæ and Lycopodineæ," 'Phil. Trans.,' B, vol. 185, 1894.
II. 'Ophioglossaceæ,' Dulau and Co., London, 1896.
III. "Marattiaceæ," 'Phil. Trans.,' B, vol. 189, 1897.
IV. "The Leptosporangiate Ferns," 'Phil. Trans.,' B, vol. 192, 1899.

In the following pages they will be referred to as 'Studies,' I., II., III., or IV.

examined.* But it will be well, before entering upon a full discussion of the results, to re-state the general problem of origin of the sporophyte generation, of which those members are so constant a feature. For since 1893, when the first Memoir of this series was written, many fresh facts bearing on the larger question have been disclosed, while a new face has been put upon the whole doctrine of alternation by the recognition of those differences of nuclear state, which have now been found in so many cases to accompany the alternating phases of the life history. Moreover, I am aware of having stated the problem in the first instance so that some of my expressions have been misunderstood, while others require amendment for other reasons. I therefore take the opportunity of first re-stating the general views upon which such data as have been acquired will have their bearing.

There are two broad facts which form the basis of the whole discussion: first, that spore-production is the end to which the life of all typical sporophytes tends; and, second, that the sporophyte in all typical cases arises from the unicellular zygote.† It is the generation thus initiated by the zygote, and tending uniformly to the production of spores, which is the subject of our present study, but especially the parts of it which produce the spores.

The materials for the general discussion are the facts as to form and structure of this sporophyte generation in living plants, together with those relating to fossil forms. It is easy to arrange these in apparent series, illustrating possible progressions from the simpler to the more complex, or conversely, possible retrogressions from the more complex to the simpler. But it is on broad lines of comparison and probability, checked by such knowledge of stratigraphical sequence of the fossils as can be obtained, that opinion must be based as to the true validity of such series as real exponents of any evolution in the past; it is only thus that it can be decided whether any particular series has actually been progressive or retrogressive.

I desire to repeat here with all emphasis, that the present is no mere attempt to trace homologies, or to define the actual relationships of the families of Archegoniatæ, though the new facts acquired will undoubtedly have their bearings on such questions. The first and main object has been *to obtain a knowledge of the methods of morphological change*: that is, to elicit the steps by which modification of internal structure and external form of the sporophyte actually has taken place. In such a study ample allowance is to be made for parallel developments in lines of descent which show no near relationship. In this connection I repeat with emphasis the view that, "it is even an open question whether the rudimentary sporophyte of certain Algæ be truly comparable with that of the Bryophyta; but in any case it

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* Excepting the Hydropterideæ, these plants have been so thoroughly investigated by others, that a special revision of their sporangial details seemed unnecessary.

† For reasons discussed elsewhere (Brit. Assn. Report, 1898, pp. 1036–1040), apogamy and apospory are regarded as abnormal developments.

occupies the same position in the life-cycle."[*] And again, "I do not suppose that any Bryophyte really represents the progenitors of vascular plants."[†] Nevertheless we are right in paying attention to the post-sexual cell-divisions in certain green Algæ, as throwing light on the probable origin of the sporophyte in the simplest Bryophyta, and use will be made of comparisons of the sporogonia of Bryophytes for elucidating points in the origin of the sporophyte of vascular plants, for it is the methods of advance which are really the first object of the investigation, and these may have been of the same nature, even in quite distinct evolutionary sequences. But naturally the best evidence is to be obtained from the comparative study of plants near akin: different specimens of the same species, or species of the same genus, or allied genera. From such materials short series can be constructed, from which, when suitably checked by wider comparison, and from considerations of general probability, more certain conclusions may be drawn as to the methods of morphological change.

After the several methods of change have been recognised and defined, it will then be possible to inquire which of them have been actually operative in any given case, and to what degree the various methods have been effective in the evolution of the plant as it is.

At the opening of the first Memoir,[‡] it was assumed for the purposes of the discussion that "whatever may have been the circumstances which led to it, antithetic alternation was brought about by elaboration of the zygote, so as to form a new generation, the sporophyte, interpolated between successive gametophytes, and that the neutral generation is not in any sense the result of modification or metamorphosis of the sexual, but a new product, having a distinct phylogenetic history of its own." Though not actually proved, that mode of origin seemed to me in 1893 to be highly probable, and I now see no reason to change that view. But as the question has since been raised afresh, whether this alternation did not arise by modification of homologous generations,[§] it has been found necessary to deal once more with alternation in the light of the many new facts which have been acquired bearing on the question; this was done in an Address to Section K of the British Association in 1898.[||] The most notable paper published on the subject since 1893 is that by STRASBURGER,[¶] who, following on the suggestion of OVERTON,[**] as to the importance of reduction of number of the chromosomes in the dividing nucleus as a differentiating character of the alternating generations, has drawn together many isolated observations of the

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[*] 'Studies,' I., p. 486.

[†] 'Studies,' I., p. 494.

[‡] 'Studies,' I., p. 473.

[§] SCOTT, Address to Section K, Brit. Assoc. Report, 1896, p. 996.

[||] Brit. Assoc. Report, 1898, p. 1031.

[¶] 'Annals of Botany,' vol. 8, p. 281; also 'Biol. Centrbl.,' 1894, p. 817.

[**] 'Jahresbr. Zürich Bot. Ges.,' Jan., 1892; 'Annals of Botany,' vol. 7, 1892, p. 139.

behaviour of nuclei in sexuality, and in spore-production. He first states the case for antithetic alternation, in terms very similar to those I had myself used some years previously, recognising, both in the ontogenetic and in the phylogenetic sense, the origin of the sporophyte from the fertilised ovum.* He correlated with these two generations a difference of chromosome-number, the nuclei of the post-sexual sporophyte having on division double that number of chromosomes which appears in the dividing nuclei of the sexual generation; he also located the point of reduction of number in the spore-mother-cells, regarding the tetrad division as the start of the new generation. Other evidence since acquired from Archegoniate plants, and from Phanerogams also, points consistently, and sometimes clearly to the justness of the conclusion, that a general difference of nuclear condition exists between those two generations which we describe as antithetic. Thus the theory of origin of the post-sexual sporophyte by intercalation of a phase between sexuality and spore-formation has been supported from a fresh quarter since my first Memoir was written.

The behaviour of the zygote on germination in certain Thallophytes is very suggestive; the nuclear divisions succeeding fertilisation are found to be more complicated than the numerical increase of the cells which follows would seem to demand;† these divisions point to a nuclear readjustment of the nature of a reduction. Various examples of this have now been described, which show evidence more or less conclusive that reduction does in these cases succeed sexuality; the process is commonly connected with the formation of small cell-groups, each cell of which is capable of supplying a new sexual individual. According to the hypothesis of antithetic alternation, such small cell-groups supplied the material upon which evolution could work: the following considerations show that there is a reasonable biological probability that it did so. In plants having an aquatic habit, sexuality by gametes motile through water could take place at any time, and sexual propagation would thus be an adequate means of numerical increase. But in those having a terrestrial habit, if they retain, as the Archegoniatæ have done, the motile spermatozoid, sexuality would only occur at those intervals when fluid water is present; thus in plants of aquatic ancestry passing to a terrestrial habit, in order to secure an adequate plant-population, a premium would be put upon the increase of individuals by vegetative means; increased spore-production would thus become a matter of importance in land-growing plants, while as the number of spores increased, their nutrition would demand an increasing vegetative system. Thus it is reasonable to think that from simple beginnings, such as those seen in the post-sexual stage of

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* STRASBURGER (*l.c.*, p. 820) uses the term "isogenic" in the sense in which we use "homologous" alternation, and "heterogenic" in the sense in which we use "antithetic" alternation. I see no advantage in thus superseding the earlier terms of CELAKOVSKY, and I shall retain those which have the priority.

† *E.g.*, Closterium, Spirogyra, &c. For an adequate digest of the facts, and citation of literature, see ZIMMERMANN, 'Morph. und Phys. d. pfl. Zellkernes,' Jena, 1896, p. 153, &c.

certain Thallophytes, the sporophyte as it is seen in the Archegoniatæ may have originated, as a matter of adaptation to life on dry land.*

But against this hypothesis, and apparently supporting the position of those who uphold PRINGSHEIM'S view of homologous alternation, is another line of evidence, which has since 1893 been strengthened by striking new facts, viz., the discovery of fresh cases of direct vegetative transition from the one generation to the other in Archegoniate plants.† Apogamy and apospory are both phenomena of more frequent occurrence, especially in Ferns, than had previously been anticipated, and many of the examples of it seem to obliterate any limits between the two generations. But though the upholders of the antithetic theory would hold the two generations to be distinct as regards origin, it is not essential for that theory that the distinction should always be maintained in individuals now living. These vegetative transitions, appearing as they do most frequently in plants which are highly specialised, such as the Leptosporangiate Ferns, or under the stress of special circumstances, do not appear to be incompatible with the antithetic theory as above sketched, for it seems probable that they were not of primary origin, but acquired more recently, as short cuts in the life-cycle; this suggestion accords well with the facts.

LANG remarks on the sharpness of the contrast between the tissues of the one generation and of the other.‡ Unfortunately attempts to trace the nuclear conditions which accompany these vegetative transitions in the Archegoniatæ have so far been without result, and a decisive opinion on nuclear grounds as to the validity of these cases as arguments against the antithetic theory must be held in suspense.§ Meanwhile, on grounds of general comparison, there is good reason to regard these developments as short cuts in the life-cycle, rather than as historical throw-backs, and that they arise under peculiar states of nutrition; on this view they would not be fitting material for far-reaching morphological argument as to the primary origin of normal forms.||

Taking into account the fresh facts and arguments issued since 1893, *I see no sufficient reason for changing the opinion then put forward: for the purposes of this discussion I shall continue to assume the antithetic view of alternation in Archegoniate Plants as a working hypothesis, though fully aware that it is not, and probably that it never can be, proved.*

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* 'Annals of Botany,' vol. 4, 1890, p. 362, where the attempt was made to put antithetic alternation on a basis of adaptation.

† HEIM, 'Flora,' 1896, p. 329; LANG, 'Roy. Soc. Proc.,' 1896, p. 250; 'Phil. Trans.,' B, 1898, vol. 190, p. 187.

‡ *L.c.*, p. 231.

§ STRASBURGER, *l.c.*, p. 300. [Since this was written cytological observations have been made on apogamy in Ferns (FARMER, 'Roy. Soc. Proc.,' vol. 71, p. 453). The results obtained thus far are favourable to the antithetic view here advanced.—F. O. B., July, 1903.]

|| BOWER, Brit. Assoc. Address, 1898, p. 1043; also 'Bot. Soc. Edin. Trans.,' 1894, p. 279.

Sterilisation.

The sterilisation of potentially sporogenous cells, that is, the conversion of cells of common origin with sporogenous cells, and which in other cases, or under other circumstances would form spores, into vegetative cells, is an essential feature in the antithetic theory. It is a fact illustrated in the sporophyte of the most various plants.* It should, however, be pointed out at once that the facts of sterilisation are compatible with either of the above views as to the origin of the sporophyte; the difference between the two views lies in the extent to which it is held that sterilisation has been operative in the past. The antithetic theory proceeds on the ground that all vegetative tissues of the sporophyte ultimately originated by sterilisation of potentially fertile cells. On the homologous view sterilisation has only played a secondary part. For the Bryophyta the balance of probability seems to be strongly in favour of an antithetic origin of the sporophyte, with sterilisation as a leading and essential factor in its evolution. In the Pteridophyta, owing to their extensive vegetative system, it is less obvious how the sporophyte originated; opinion must be based on detailed observation and comparison, such as it has been the object of these Memoirs to provide. It has recently been suggested that the alternation may have originated differently in these two phyla; that while the Bryophyta were of antithetic origin, the alternation in the Pteridophyta was possibly of homologous origin.† It seems to me highly improbable that there was any such difference of evolutionary history in these two series which show such unity in the general scheme of life. But whatever view be taken on this point, the facts of sterilisation are consistent with either side; the difference lies in the relative importance attributed to such processes in the remote past.

The facts bearing on views of sterilisation in the Bryophyta have been already touched upon in 1893,‡ but more recently the investigations of GOEBEL have filled in developmental details for certain of the Hepaticæ which are of special interest.§ The essential facts for the Bryophyta may be briefly summarised thus: that while in the Musci the whole mass of the sporogenous tissue is as a rule fertile, and all the cells undergo the tetrad division, in the Hepaticæ certain cells of the sporogenous tissue, isolated or in groups, may be either obliterated during the development of the rest, or may remain at maturity as sterile cells, constituting in some cases considerable tracts of tissue; conversely, cells normally sterile may occasionally become sporogenous. An old observation of LANIZIUS BENINGA|| records

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* 'Annals of Botany,' vol. 8, 1894, p. 345.

† COULTER, 'Bot. Gaz.,' vol. 27, p. 46, &c.

‡ 'Studies,' I., p. 484, &c.

§ "Archegoniatenstudien, 6, 'Flora,' vol. 80 (1895), p. 1; "Organographie," p. 317, &c., and especially pp. 326–329.

|| "Beiträge z. Kenntn. d. inn. Baues d. angew. Mooskapsels," 1847, tab. 58, figs. 9*, 9**.

how certain cells of the columella of a moss, *Syntrichia subulata*, were found to be undergoing the tetrad division, prior to forming spores. A similar condition has also been noted by KIENITZ GERLOFF* in a species of *Bryum*. Upon facts of this order, together with a general comparison of the sporogonia, a reasonable theory of the evolution of the more complex from more simple forms of sporogonia may be based, with progressive sterilisation as the leading feature.

It will be seen that these cases of sterilisation can be matched among the Pteridophyta: the facts regarding sterilisation in them, especially those acquired in this series of Memoirs, will now be briefly summarised.

In *Lycopodium* and *Phylloglossum*, and in the homosporous Ferns, after the sporogenous tissue is first defined, all its cells normally undergo the tetrad division, and develop into spores; occasional cells may become disorganised without full development, though as a rule all the potentialities are realised. But among the Marattiaceæ, where, as a rule, all the cells of the sporogenous groups are fertile, a number of exceptional cases have been noted: the most remarkable are those in *Danæa*,† in which it has been shown how certain cells of the larger sporogenous groups remain sterile, and may be developed as tapetum, or even as component cells of a partial septum. Somewhat similar conditions have been seen in *Kaulfussia*, *Marattia*, and *Angiopteris*. Such cases are shown to lead up to the formation of partial, or even complete septa.‡

In other cases it is the rule that only a portion of the cells of the sporogenous group are fertile: the remainder scattered through the mass become disorganised without forming tetrads. Among homosporous forms this was seen in *Equisetum*,§ *Tmesipteris*,‖ *Psilotum*,¶ *Ophioglossum*,** and *Helminthostachys*,†† and it occurs also occasionally in *Botrychium*.‡‡ In the sporangia of all these only a portion of the sporogenous cells is fertile, the remainder, scattered through the mass, become disorganised without forming tetrads. The substance of the cells thus disorganised is absorbed by the developing spores, and as the proportion of the sterile to the fertile cells is not fixed, an elastic arrangement exists which leads to the largest number of

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* 'Bot. Zeit.,' 1878, p. 47, taf. 2, fig. 52.

† 'Studies,' III., p. 40.

‡ 'Studies,' III., pp. 46, 50, 56.

§ 'Studies,' I., p. 500, Pl. 43, fig. 21.

‖ 'Studies,' I., p. 542.

¶ 'Studies,' I., p. 550, Pl. 51.

** 'Studies,' II., p. 27. See also ROSTOZEW, 'Recherches sur l'*Ophioglossum vulgatum*, L.,' 1891, p. 28.

†† 'Studies,' II., p. 35.

‡‡ In *Botrychium* the very large majority, if not all, of the sporogenous cells are fertile; in *B. Lunaria* all the spore-mother-cells showed the tetrad division; in *B. daucifolium* a few were seen to be in course of disorganisation. The tapetum is, however, very voluminous and granular, with many nuclei. It intrudes as finger-like processes between the blocks of spore-mother-cells, and finally forms a network embedding them.

spores being brought to maturity that the plant at the time can support. In function the cells thus absorbed resemble the nutritive cells of *Sphærocarpus* or *Riella*.*

In this connection it is to be remarked how difficult of definition the sporogenous groups are in certain cases while young. This is so in *Tmesipteris*† and *Psilotum*,‡ and appears to be due to the absence of a definite tapetum, and to the fact that the definitive sporogenous cells do not form a continuous mass. Again, in *Ophioglossum* the same difficulty arises in early stages; here again the groups of cells, first recognisable as the sporogenous masses by their denser contents, are not wholly devoted to spore-formation, for numerous isolated cells scattered through the mass are absorbed, but in addition to this, a broad, superficial band of cells, constituting a sort of ill-defined and broad tapetum round each of these groups, is disorganised.§ The frequently irregular outline of the sporogenous groups in *Ophioglossum*, *Tmesipteris*, and *Psilotum*, points to their not being the regular and exclusive product of segmentation of any single cell, or group of cells.

In heterosporous types sterile cells are commonly present in the female sporangium: it will be unnecessary to do more than mention *Selaginella*|| and the Hydropterideæ as examples. The arrest of potential spores in the fossil, *Calamostachys Binneyana*, has also been recorded: single members of a tetrad may remain small: "we may regard the latter as abortive spores, their suppression having allowed of the better nutrition of their surviving sister-cells."¶ This case throws a side light on a possible mode of origin of heterospory.

The case of *Isoetes* is more interesting still; the sterilisation which appears in both the mega-and micro-sporangia results in masses of permanent tissue in place of merely nutritive cells. The details for the microsporangium have been sufficiently discussed in the first of these Memoirs;** considerable tracts of a tissue-mass of a uniform origin, which may be designated a "potential sporogenous tissue," develop as vegetative trabeculæ and tapetum, while the remainder forms microspores; from the history of development, and from comparison, the conclusion seems justified, that the trabeculæ and tapetum represent sporogenous tissue which has been converted into sterile tissue, serving other purposes in the very large sporangium.

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* Similar cases are known in the anthers of Angiosperms.

† 'Studies,' I., p. 542, and fig. 126.

‡ 'Studies,' I., p. 550, and fig. 138.

§ 'Studies,' II., p. 20, and fig. 45.

|| GOEBEL ("Vergl. Entwickges.," SCHENK'S 'Handbuch,' vol. 3, p. 389) notes the fact that in the microsporangia of *S. helvetica* and *denticulata* he has observed some of the spore-mother-cells to be abortive, and suggests their function as nutritive cells.

¶ SCOTT, 'Studies in Fossil Botany,' 1900, p. 51.

** See GOEBEL. 'Bot. Zeit.,' 1880, p. 564; BOWER, 'Studies,' I., p. 530. See also WILSON SMITH, 'Bot. Gaz.,' vol. 29, 1900, p. 242, where the gradual distinction of the fertile from the sterile regions has been carefully described, and figured on Plates 17, 18.

Similarly in the megasporangium, carefully described by WILSON SMITH,[*] a similar sterilisation is carried much further, and it has been possible to show that "the megaspore-mother-cells are not morphologically predetermined, but are physiologically selected from among a large number of potentially sporogenous cells," and that "each archesporial cell gives rise to several magaspore-mother-cells, as well as to trabeculæ and tapetum." There has been a differentiation of tissues of uniform origin, and a large part has been diverted to functions as sterile vegetative tissue.

The case of *Lepidostrobus Brownii*, SCHPR., compares closely with that of *Isoetes*; the very large sporangia (microsporangia ?) are traversed by processes rising from the base of the cavity, and in some cases apparently extending through it to the upper wall. The origin of these processes is not certain, but their similarity in position and structure to those of *Isoetes* points to the probability of a similar origin.[†] Other *Lepidostrobi* show similar processes, with less certainty of detail.

Though in the microsporangium of *Isoetes* the sterile tracts are only trabeculæ, in the megasporangium they are actual partitions, or septa, in the young state; these may, however, be broken down at maturity,[‡] and the septate state be thus only transitory. With this may be compared the partial or complete septa in *Danæa*, and other Marattiaceæ.[§] Somewhat analogous conditions are found in the stamens of certain Angiosperms,[||] in which sometimes the septa may be narrow and transitory, and so appear as only partial septa in the mature stamen; or they may be broader, and be found to be complete partitions in the mature stamen. Study of the development has shown that the cells which form the septa in these cases are of similar origin to the sporogenous cells, and the conclusion follows that the septa owe their origin to sterile development of potentially sporogenous cells.

Upon the facts thus quoted, the general statement may be based, that among Vascular Plants *examples of sterilisation of potentially sporogenous cells are common, both in homosporous and in heterosporous forms, and that the sterile cells may be functional only as transitory "nourishing cells," or persist as permanent tissue, forming in some cases partial, in others even complete septa.*

Conversely, tissues which are normally sterile may sometimes contribute to the formation of spores, though this is less common. An example has been seen in *Danæa*,[¶] where a packet of fertile cells was found evidently derived from tissue outside the normal sporogenous group. In *Tmesipteris* the matter is clearer; for in certain non-septate synangia of small size, it was shown that the cells of the septum had become

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[*] See GOEBEL, 'Bot. Zeit.,' 1880, 1881, and WILSON SMITH, 'Bot. Gaz.,' vol. 29, p. 251, and Plates 19, 20.

[†] 'Studies,' I., p. 525, and Plate 48.

[‡] WILSON SMITH, *l.c.*, p. 256.

[§] 'Studies,' III., p. 40.

[||] 'Annals of Botany,' vol. 8, p. 343; also 'Studies,' II., pp. 1–9, Plate 4.

[¶] 'Studies,' III., p. 41, Plate 7, fig. 21.

sporogenous.* Thus, though examples are not common, it may be concluded that *among vascular plants, cells which are normally sterile may occasionally develop into spores.*

Comparing the results of our inquiry for Vascular Plants with those from Bryophyta, we find in both evidence of sterilisation, with, conversely, occasional reversion of cells normally sterile to spore-production. So that putting together the converse conclusions, and remembering at the same time the fact that in some cases the sporogenous groups are very ill-defined, *it may be stated generally for the sporophyte of Archegoniate plants, that spore-production is not in all cases strictly limited to, or defined by pre-ordained formative cells, or cell-groups.* This position, based as it is on the facts observed, is one which harmonises readily with a theory of sterilisation, as applied to the evolution of the sporophyte.

VOECHTING has formulated the proposition that "no living vegetative cell of the plant-body, which is capable of growth, has a specific and unalterable function."† This thesis in its most general sense should be extended so as to include also sporogenous cells; for, as we have seen, many cases can be cited of the conversion of cells which are sporogenous to a vegetative condition, and occasionally the converse. But both VOECHTING, and PFEFFER,‡ in discussing this equipotentiality of embryonic cells, and the influences which determine their development, have restricted the discussion chiefly to the vegetative organs. The facts before us show, however, that vegetative and sporogenous cells are not things apart, or essentially different, but that they are on occasions mutually convertible. The influences, external or internal, which act upon the embryonic cell, and determine whether it shall be vegetative or sporogenous, are still obscure; but clearly they act within restricted limits, for in vascular plants neither superficial cells of the plant-body, nor deeply seated cells have ever been found to develop as spore-mother-cells.

The conversion of potentially fertile cells into vegetative tissue was recognised by NÆGELI, and embodied by him in his fundamental law of organic development, as follows: "The phenomenon of reproduction of one stage becomes at a higher stage that of vegetation. The cells which in the simpler plant are set free as germs, and constitute the initials of new individuals, become in the next higher plant part of the individual organism, and lengthen the ontogeny to a corresponding extent."§ The sterilisation seen in the sporophyte of the Archegoniatæ is only one special case of that included in NÆGELI's general law. He points out that the law is realised in three different ways, and the case for the sporophyte generation, with which alone we are at present concerned, falls under his first head, expressed by him as follows: "The propagative cells which arise by division are converted into tissue-cells."‖ With this may be

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* 'Studies,' I., p. 546, Plate 52, figs. 161–165.

† 'Organbildung,' p. 241.

‡ 'Pflanzenphysiologie,' II., Aufl. 2, p. 163, &c.

§ 'Abstammungslehre,' p. 352.

‖ *Ibid.*

compared the following passage from HERTWIG : "In the histological differences of one organism I therefore see only different conditions of cells, which correspond in the constitution of their Idioplasm, and as descendents of a common mother-cell are equivalent in kind."[*]

It has been one of the objects of my observations on the Pteridophyta to ascertain the extent and the details of the conversion of propagative cells to sterile cells, and the result has been to show that such conversion occurs in a considerable number of cases, while mere obliteration of some cells, as nutritive for the rest, is a still more common feature.

The Archesporium.

This term was introduced by GOEBEL,[†] and defined as follows :—"In the vascular Cryptogams, as in the Phanerogams, the spore-producing tissue may be universally referred as regards its origin to a cell, a cell-row, or a cell-sheet—I designate these original parent cells of the sporogenous tissue—as the archesporium." To this he added (p. 569) "that in all vascular Cryptogams examined an hypodermal archesporium exists," thus definitely localising it in a position comparable to that in the Spermaphyta. He remarks, however, later,[‡] that he does not lay special stress upon the archesporium being always a cell-row or cell-sheet, and contemplates it as possible that sometimes the development may proceed otherwise than by the appearance of an archesporium of the form described.

In the course of these studies I have found this to be the fact : a considerable number of cases have been observed in which the archesporium is not hypodermal, in that it is not defined by a single periclinal wall of the parent cells involved. Thus in *Equisetum*,[§] after the first periclinal division of the cell which will form the essential parts of the sporangium, the outer cell contributes by further periclinal division considerable additions to the sporogenous mass; this is seen occasionally in *Lycopodium*,[||] while it is frequent in *Isoetes*,[¶] and conspicuously so in *Ophioglossum*,[**] the case was left open in *Tmesipteris*[††] and *Psilotum*.[‡‡] The existence of so many exceptions among Eusporangiate Pteridophytes suggests a reconsideration of the archesporium. What meaning is to be attached to the term, and is it of general application ?

The effect of GOEBEL's investigations on the sporangia of Pteridophytes was to extend downwards from the Phanerogams the demonstration of a formative cell or

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[*] 'Die Zelle und die Gewebe,' vol. 2, p. 62.

[†] 'Bot. Zeit.,' 1880, p. 545.

[‡] "Vergl. Entwick," SCHENK'S, 'Handbuch,' vol. 3, p. 384, footnote.

[§] 'Studies,' I., p. 497.

[||] 'Studies,' I., p. 519, 522.

[¶] 'Studies,' I., p. 531. See also WILSON SMITH, 'Bot. Gaz.,' vol. 29, p. 240. He finds many periclinal divisions of superficial cells which add to the sporogenous tissue.

[**] 'Studies,' II., p. 25.

[††] 'Studies,' I., p. 542, 550.

[‡‡] *Ibid.*

cells, to which the origin of the spores may be ascribed. Before 1880 it was held that a mass of cells within the young sporangium, showing irregular divisions, took upon them the character of a sporogenous tissue: GOEBEL'S results led him to the statement that "in the vascular Cryptogams, as in the Phanerogams, the spore-producing tissue can always be referred as regards its origin to a cell, a cell-row, or cell-sheet, which can be distinguished very early by the nature of its materials from the rest of the cell-tissue."* This archesporium was successfully recognised in certain cases, and the tendency of the time was to expect similar success in all cases. Thus a special significance came to be attached to these cells, quite apart from that of the surrounding tissues, as being predestined from the first to the important function of spore-production.

The location of the archesporium in Phanerogams was found to be consistently hypodermal; in a somewhat strained sense this was found to be the case in many of the Pteridophytes. But it was not sufficiently recognised that between the two lies all the difference between stratified and imperfectly stratified meristems. This point I brought forward in 1896,† in the proposition that "the study of sporangia or synangia of a plant should be carried out in the light of a knowledge of the segmentation of its apical meristems," and laid down the generalisation that "where the apical meristems are distinctly stratified, the structure of the young sporangium is stratified also; in those plants where there is a non-stratified structure, with one or more initial cells, and frequent periclinal division of superficial cells near the apex of stem leaf, or root, there the structure of the young sporangium is not distinctly stratified." The exceptions to the hypodermal position of the archesporium above enumerated all fall under this generalisation, and it may be added as a corollary *that in all vascular Cryptogams investigated, the sporogenous tissue is ultimately referable to the segmentation of a superficial cell or cells.* This has been noted by WILSON SMITH,‡ who has accordingly suggested that the term "archesporium" should be extended to these also, and he gives the definition as follows:—"The cell, or group of cells, whether superficial, or hypodermal, to which in a last analysis all the sporogenous portion of a sporangium can be traced, ought to be called the archesporium."

The use of the term "archesporium" has recently been discussed afresh by GOEBEL. He first describes the case for the anther of an Angiosperm, thus,§: "In each of the four angles of the anther a cell-row or cell-layer below the epidermis (hypodermal) divides by periclinal walls. Of the cells which thus arise the internal form the archespore, the outer the 'schichtzellen,' which now divide still further by periclinal walls." The archespore is thus defined as the inner product of the division of the

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* 'Bot. Zeit.,' 1880, p. 546.

† 'Studies,' II., pp. 6–9.

‡ 'Bot. Gaz.,' 1900, p. 325.

§ 'Organographie,' vol. 2, p. 771.

hypodermal layer, and it gives rise neither to any part of the sporangial wall, nor to the tapetum, though since these have a common origin with it from the hypodermal layer, it is not clear why the latter should not be styled the archesporium. Passing on to the Pteridophyta, after noting how superficial cells give rise to the essentials of the sporangium (sporogenous tissue and sporangial wall), and that the details are not uniform, he proceeds: "We may then designate that superficial cell or cell-layer as archespore, which sooner or later gives off sterile cells, while in the sporangia of Angiosperms the archesporium is a cell-layer lying below the epidermis, which is already differentiated; with this the above-noted differences in wall-structure of the Pteridophyta and Gymnosperms on the one hand, and of the Angiosperms on the other would correspond." This passage calls for the following remarks.

In the first place, Professor GOEBEL accepts the conclusion of WILSON SMITH, that since the sporogenous tissues of Pteridophytes are all referable in origin to superficial cells, therefore those cells are to be recognised as the archespore. By accepting this conclusion, he approves, I presume, the method by which it is arrived at; that is, the method of recognition of the archespore by "a last analysis" of cell-origin.

Secondly, Professor GOEBEL'S method of recognition of the archesporium is not consistent; he designates the inner product of the hypodermal layer in the Angiospermic stamen the archesporium, notwithstanding that the "schichtzellen" and tapetum are sister-cells with it. But in Pteridophyta, on the ground of common origin by segmentation, not only the tapetum but also the sporangial wall itself are described as derived from the superficial archesporium. If the recognition of the archesporium is to be based on "a last analysis" of the segmentations, then the hypodermal layer of the Angiospermic anther, and not merely its inner product of segmentation, is the archesporium.

Thirdly, the recognition of the archesporium by the method of "a last analysis" brings together under a common head, merely on the ground of early segmentations, things which are not really comparable, and ascribes a distinct origin to things which are indistinguishable when mature. The superficial archesporium of the Pteridophytes gives rise to part of the sporangial wall and tapetum; the archesporium of the Angiospermic anther, on GOEBEL'S definition, gives rise to neither. I find it impossible to conceive how by any known evolutionary progression the former type could pass into the latter, and the superficial cells be covered over; therefore I regard the two as not truely comparable. Further, the recognition of superficial cells as archesporial, draws a distinction between part of the sporangial wall which originates from them, and the rest which does not; thus in the Leptosporangiate Ferns, the apical part of the annulus would be archesporial, the lateral parts not.

With all respect for the opinion of the writer who introduced the term, I think that this last change in its application, as suggested by WILSON SMITH, and accepted by GOEBEL, makes more obscure the meaning of a word which has never been clear. The Bryophyta provide a *reductio ad absurdum* of the method of "a last analysis," for following this method in *Sphagnum* and some others, the amphithecium would be reckoned as the archesporium, while in the ordinary Bryineæ it would be the endothecium; or carrying the analysis in the latter case to its extreme limit, the first segments in the upper half of the zygote, or even the ovum itself, would be the archesporium.

The fact is that this sort of analysis of formative tissues has served its turn; it has led to much detailed investigation, and elicited facts, as regards segmentation, a knowledge of which is of value for comparison. But it has also shown *that the segmentations which lead up to the formation of spore-mother-cells are not comparable in all cases.* The time has come, in presence of so many divergent details, to frankly admit that *there is no general law of segmentation underlying the existence of that cell, or cells, which "a last analysis" may mark out as the "archesporium," and that, therefore, the general application of such a term to those cells which the analysis discloses, has no scientific meaning, beyond the statement of the histiogenic fact.** At the same time the value of the details that have been acquired by the pursuit of the archesporium, must not be underestimated for purposes of comparison. What is dangerous is the attachment to them of ulterior ideas; the assumption that because a definite "archesporium" is often found, it should by rights be always present, and the effort to trace in its appearance homologies which seem based on forced rather than on natural comparisons. The term has become so established in the literature of the subject that it cannot be summarily discarded; it may be retained merely in a descriptive sense in those cases where the cell (or cells) which gives rise to a sporogenous group is obvious, but in a descriptive sense only.

The discrepancies which thus become apparent in the course of development between different types of sporangia tend to justify the position already adopted on general grounds by STRASBURGER;† he remarks that the spore-mother-cell is to be regarded as the first term of the new generation, that the centre of gravity of the developmental processes does not lie in those cells, cell-rows, or cell aggregates which have been designated "archesporium" by GOEBEL; the archesporium still belongs to the asexual generation, and the presence or absence of a well-defined archesporium is not a matter of importance, for it is merely the merismatic tissue from which the spore-mother-cells are derived. From the point of view of a theory of sterilisation, these spore-mother-cells may be held to be, in the simpler cases at least, the residuum which progressive vegetative change has left, and there is no reason to expect that the demarcation of these islands of fertile tissue should have followed any definite system in plants at large, which should be reflected with any exact uniformity in the segmentations involved in their formation. On the other hand it would be only

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* How little value is to be attached to histiogenic limits has been shown by SCHOUTE ('Die Stelär-Theorie.' Groningen, 1902, pp. 81, 83, 90), who has concluded that HANSTEIN'S histiogenic regions do not coincide with VAN TIEGHEM'S definite regions of mature tissue.

† 'Annals of Botany,' 1894, p. 316; also 'Biologisches Centralblatt,' 1894.

natural to expect that, especially where the sporogenous cells form compact masses, those cells which give rise to them should be clearly defined at an early stage; GOEBEL points out[*] that the changes in the protoplasmic body of the sporogenous cells are gradual, not sudden, which would also lead to an early definition of the sporogenous masses such as is commonly to be observed.

The frequency of hypodermal origin of the sporogenous tissue in vascular plants is readily intelligible. In all except the very simplest sporophytes the spores are protected during development by tissues which surround them completely, for purposes of nutrition, and as a protective wall. In the Bryophyta the dissemination is secured by a dehiscence of that wall, which would be equally efficient whether the spores be produced close to the surface or deeply seated, since the dehiscence, whether by a terminal operculum or by longitudinal slits, gives free exit to the spores of the continuous spore-sac. And accordingly the spore-mother-cells in the Bryophyta may be central as in many Hepaticæ, or removed more or less from the centre by the columella, as in most Mosses. But in all vascular plants, where the spores are produced in separate pockets, or sporangia, the dehiscence leading to dissemination is referred to the several sporangia themselves; this necessitates for them a superficial position on the plant-body, or, better, a projecting of the sporangia beyond the surface. The hypodermal origin of the sporogenous tissue which is so frequent, may thus be recognised as a compromise between the two requirements of effective nutrition and ready dissemination. But the compromise may have been worked out differently in different lines of descent, and, indeed, it appears from the variety of the segmentations in the Pteridophyta that this has actually been the case. From this point of view no difficulty need be felt to arise from the absence of any general law of segmentation leading up to the formation of spore-mother-cells, but, on the other hand, similar and even definite types of segmentation, culminating in regularly segmented sporogenous groups resembling one another, may have been evolved along more than one line of descent.

The Tapetum.

The tapetum is not to be looked upon generally as a morphological constant, notwithstanding that it shows some constancy of character in certain circles of affinity. It originates from different sources: sometimes it is not differentiated at all, in other cases it may appear as a more or less definite band of cells, which originates from the tissues surrounding the sporogenous cell, or group of cells, sometimes from the sporogenous group itself.[†]

In *Psilotum*,[‡] *Tmesipteris*,[§] and *Ophioglossum*[||] there is no definite tapetum; it is

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[*] 'Organographie,' vol. 2, p. 770.

[†] GOEBEL, 'Organographie,' vol. 2, p. 768, &c.

[‡] 'Studies,' I., p. 550

[§] 'Studies,' I., p. 542.

[||] 'Studies,' II., p. 20.

true a broad irregular band of tabular cells, surrounding the sporogenous groups, becomes disorganised, but without assuming the glandular characters usual for a tapetum. On the other hand, a large number of cells of the sporogenous groups in these plants act like a diffused tapetum, becoming absorbed during the development of the spores; this fact may have its bearing on the absence of a definite tapetal layer outside. In *Equisetum*, however, both a diffused tapetum of this nature is found, and a definite single-layered tapetum, which originates outside the sporogenous group.* The large spores are thus amply provided for. A tapetum originating outside the sporogenous group is found in *Lycopodium*,† *Phylloglossum*,‡ the Marattiaceæ,§ and in *Helminthostachys*|| and *Botrychium*. In the two genera first named it is a definite layer; in the Marattiaceæ it is an indefinite band of cells of tabular form, not a single definite layer. But in *Selaginella*,¶ at any rate for the most part, the tapetum is cut off from the sporogenous group itself. The case of *Isoetes* is peculiar, and shows how indefinite the origin of a functional tapetum may be. In the microsporangia the tapetum "is organised out of that layer of the sterile cells, whether of wall or of trabeculæ, which is in contact with the fertile cells;"** it remains persistent till the maturity of the spores. In the megasporangium "the only difference is the greater abundance of the tapetum in the megasporangium. No doubt a considerable part of it is derived from the unsuccessful mother-cells.†† In the Leptosporangiate Ferns the tapetum is derived as a series of segments from the central (archesporial?) cell; this is the case even for the large sporangia of the Gleicheniaceæ and Osmundaceæ.‡‡

From these facts it appears that cells acting functionally as special nutritive cells—either disappearing by early disorganisation ("plasmodialtapete," of GOEBEL), or persisting till the spores are mature ("secretionstapete," of GOEBEL)—may be scattered through the sporogenous mass, or derived from the tissues lying outside it, or be cut off from the sporogenous cell or group of cells. Their similarity is in function, not in origin: the origin from the wall, or from the sporogenous group, may vary within the single sporangium, as in *Isoetes* or *Selaginella*. There is even good reason to recognise progressive changes of origin of the tapetum within certain circles of affinity; thus, in the *Lycopodium* sporangia the definite tapetum is derived from the sporangial wall, in the smaller sporangia of *Selaginella*, chiefly from the sporo-

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* 'Studies,' I., p. 500, Plate 43, figs. 20, 21.

† 'Studies,' I., p. 514, &c.

‡ 'Studies,' I., p. 508.

§ 'Studies,' III., p. 60.

|| 'Studies,' II., p. 35.

¶ 'Studies,' I., p. 524; also LYON, 'Bot. Gaz.,' 1901, vol. 32, p. 124.

** These words are quoted from WILSON SMITH, 'Bot. Gaz.,' 1900, p. 246. They accord with my own observations ('Studies,' I., Plate 49, figs. 110–113).

†† WILSON SMITH, *l.c.*, p. 256.

‡‡ 'Studies,' IV., pp. 35, 40.

genous group. Similarly, in the larger sporangia of the Marattiaceæ, it originates from the wall; in the smaller sporangia of the Leptosporangiate Ferns, from the central cell (archesporium ?). Again, in *Ophioglossum*, with its large sporangia, there is no definite tapetum, in *Helminthostachys* and *Botrychium* there is a tapetum derived outside the sporogenous group. These facts support the general statement that indefinite and nonspecialised nutritive arrangements are characteristic of larger sporangia, but more definite tapetal layers are found in the smaller; and further, that while in sporangia of relatively large size the tapetum may originate outside the sporogenous group, in smaller sporangia of the same affinity it may be cut off from the sporogenous cell or cell-group. A progressive change such as this last was suggested by LANG,* as a possible explanation of the results observed by him in the microsporangia of *Stangeria*; a functional tapetum is there derived from the sporogenous group; outside this two layers derived from the surrounding tissue resembles the tapetum of the Marattiaceæ in position, but do not take the tapetal characters; LANG suggests that these "may possibly represent a tapetum derived from cells surrounding the sporogenous group, an additional tapetal layer having arisen from the latter." In the microsporangia of the Gymnosperms there seems to be some want of uniformity in the origin of the tapetum,† while in the Angiosperms it is known to be derived from the tissues outside the sporogenous group, and to appear as a well-defined glandular band.

The result is then that the tapetum is inconstant both in occurrence and origin; that it may arise from different sources, even in the same sporangium; that in certain large groups of plants, in forms with larger sporangia the tapetum originates outside the sporogenous group, while in those with smaller sporangia it may be derived partially or wholly from the sporogenous group; and that there is good reason to think that a transition from one type to the other may have taken place in more than one phylum. Accordingly, it is not to be regarded as a general morphological constant.‡

The Sporangial Wall, and Opening Mechanisms.

In all the Archegoniatæ the spore-mother-cells are covered externally by a protective band of cells, which may be of variable thickness and structure; it serves the several purposes of protection, nutrition, and in many cases of dehiscence and mechanical ejection. The extent of the wall as such is closely related to the position of the sporogenous cells; where these are deeply sunk, the wall is a mere roof over them; where they are carried out by growth of the tissues surrounding them and a projecting sporangium is formed, there the wall envelopes them as a

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* 'Annals of Botany,' vol. 11, p. 436.

† GOEBEL, "Vergl. Entwick.," SCHENCK'S 'Handbuch,' vol. 3, p. 394; also 'Bot. Zeit.,' 1881, p. 701, &c.

‡ It should be remembered that the tapetum, as such, is absent in the Bryophyta.

tissue of greater extent. But in either case it is continuous with the tissue of the sporangium-bearing part, of which it is to be regarded as a specially developed region. This view of it accords well with the structure of the sunken sporangia, as seen, for instance, in the spike of *Ophioglossum*, in which the tissues of the wall are continuous with, and but little differentiated from, the cognate tissues of the whole spike. The superficial layer is rather deeper and more indurated, and there is along the future line of dehiscence a double row of narrow, and less indurated cells, which define the rupture; otherwise the superficial tissues of the spike and of the sporangial wall are alike. In the remaining Ophioglossaceæ, as also in the whole series of Lycopodineæ (including *Lepidostrobus*, but excluding *Isoetes*), the nature of the sporangial wall is the same, and shows little further specialisation, even where the sporangia project far, or are stalked. Much the same is also the case in the Equisetineæ.

In the Filicineæ more exact specialisation is the rule, and the mechanical annulus becomes a feature of the stalked sporagium. But a comparison of the sporangia of living Marattiaceæ among themselves, and with those of other Ferns, led to the statement,[*] that "the presence of an annulus, and its elaborateness, are to be correlated with the freedom of the sporangium from mutual relations with others:" where the sporangia, as in *Kaulfussia*, or *Danæa*, are so closely related that each sporangium is at most but slightly convex beyond the general level of the synangium, and so has no freedom for individual change of form on dehiscence, no indurated tissues are found, which can be held to act as an annulus, for mechanical widening of the slit of dehiscence. But in *Angiopteris*, where the sporangia are freely projecting bodies, a more elaborate mechanism is present;[†] when to these facts are added those relating to the Gleicheniaceæ, Schizaeaceæ, Osmundaceæ, and the remaining Leptosporangiate Ferns,[‡] the above statement seems well founded. The annulus is in fact only a specialised region of the tissue of the sporangial wall, and is not an essential part of the sporangium.

This conclusion accords with the facts of its inconstancy; for sporangia which open under water may have no mechanisms. That is the case in *Isoetes*, while the sporangia of the Hydropterideæ also are entirely without an annulus, nor is there any stomium, which would localise dehiscence. *Loxsoma* is a specially interesting case; the annulus though indicated by the cell-divisions as complete, is only partially indurated;[§] it is shown elsewhere[||] that the part which is not indurated could not be mechanically effective, owing to the mode of packing of the sporangia in the sorus.

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[*] 'Studies,' III., p. 59.

[†] In *Marattia* a mechanical system is present, which has the function of making the two-lipped sorus gape widely as a whole, while the individual sporangia are without any more individual mechanism than those of *Danæa* or *Kaulfussia*. See LUERSSEN, 'Beitr. z. Entw. d. Farnsporangien,' vol. 1, p. 21; also 'Studies,' III., p. 51.

[‡] 'Studies,' IV., p. 97.

[§] 'Studies,' IV., pp. 49, 102.

[||] *Ibid.*

The general conclusion to be drawn is, that these mechanical arrangements are not essential, or constant parts of the sporangium, however, constant they may seem to be in certain large groups; and that where they cannot be mechanically effective they are not formed.

The Individuality of the Sporangium.

It cannot escape notice that in some cases the individuality of the sporangium is not maintained. Certain synangial states are not uncommon, which can only be regarded, from the evolutionary point of view, as results of either septation or fusion; where the fusion or septation is incompletely carried out, and partial septa are present, it becomes a question whether the whole, or part of the complex body is to be termed correctly a sporangium. The mere application of a term is naturally a trivial matter, and the question which is really important is, how far our conception of the sporangium is to be modified by the existence of such cases.

The current conception of the sporangium is based upon those cases where it has a distinct individuality; in the Ferns and Lycopods, or even in the pollen-sacs of Angiosperms, such sporangia are seen; but it is a question how far the idea of the individualised sporangium derived from such cases is an enlightening one, from the point of view of descent. Similarly, the old conception of the cell as the structural unit of the plant-body was based on the study of the tissues of the higher plants, where the cells are for the most part individualised; it had to give way before the accumulated examples of cell-fusions, of polynucleate cells, and of non-cellular construction in plants. Just as by the comparison of such structures as these the idea of the cell has undergone modification, notwithstanding that cells are commonly definite bodies in the ordinary tissues of the higher plants, so may the existence of sporangial septations and fusions modify the conception of the sporangium.

The fact of septation of originally simple sporangia having taken place has only been proved in comparatively few of those cases where sporangia show that close relation to one another known as the synangium. The best cases of septation are those from the anthers of certain Angiosperms, such as the Onagraceæ, Mimoseæ, Loranthaceæ, Rhizophoreæ, &c. In these the comparative argument is made valid by the numerous allied genera, which give ground for close comparison. While many plants of these orders show the ordinary quadrilocular anthers, in others the loculi may be subdivided by further septa, and thus a number of sacs take the place of each original one. The development shows that the septation results from conversion of sporogenous tissue into sterile septa.* Similarly an argument for fusion of sporangia can also be supported on comparison among Angiosperms, though it is a less frequent change. Examples are to be found in the coalescent ovules of certain Loranthaceæ,† or in the confluent pollen-sacs of certain Guttiferæ, &c.

Among the Pteridophyta the genera are so isolated as a rule that the comparative

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* 'Studies,' II., p. 1–6, figs. 53–56.

† Treub, 'Buit. Ann.,' vol. 3, p. 1.

argument is difficult to apply; and in each case of a synangium it is a question for discussion whether the structure results from septation or fusion. But without at the moment entering on such discussions, it is plain that either way the individuality of the sporangium is lost in such cases. A good example of this has been shown in the sorus of *Danœa*, where, as also in other Marattiaceæ, partial septa are found.*

Definition of the Sporangium.

It may then be asserted for sporangia at large, that the individuality of the sporangium is not always maintained; that the elevation of sporangia relatively to the surface which bears them is variable; that while the sporangial wall is always present, the opening mechanisms are inconstant; that the tapetum is inconstant in occurrence, and in origin; and that there is no general law underlying the segmentation of the sporogenous cell or group of cells, so as to give it a constant hypodermal, or other origin. What then remains as the fundamental conception of the sporangium in vascular plants? Simply the spore-mother-cell, or cells, with the protective tissue; the definition of a sporangium will accordingly be this:—*Wherever we find in vascular plants a single spore-mother-cell, or a connected group of them, or their products, this with its protective tissues constitutes the essential of an individual sporangium*; this is indeed a simple translation of the word.

This definition is open to criticism, as indeed are all definitions of bodies represented in large series of variable organisms. Still it brings out the point that the essential feature of a sporangium is the presence of one or more spore-mother-cells, but without reference to the detail of their production, or the structure of the wall which covers them. It has its value in ridding the idea of the sporangium of its accidental accessories, and fixing the prominence upon what is really essential. *From the point of view of the hypothesis of sterilisation such sporangia may, at least in the simplest cases, be regarded as islands of fertile tissue which have retained their spore-producing character. It will be seen later how far this view will have to be modified in the more complex cases.*

Lastly, it will perhaps be objected that a sporangium may still be a sporangium, though it may contain no fertile cells. Many abortive sporangia may be quoted which have the form, position, and other details characteristic for the plant to which they belong, and are thus to be ranked as sporangia. That is true, but as such bodies as a rule do not serve any useful purpose, it may be asserted that they would never have existed independently of the fully formed sporangia, of which they are the abortive representatives. Such vestigial parts need not disturb the conception above defined, so long as attention is sufficiently given to the physiological condition of the plants in which these vestigial sporangia occur.†

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* 'Studies,' I., p. 40, figs. 26–30.

† 'Annals of Botany,' vol. 15, p. 225.

MATERIALS FOR A THEORY OF STERILISATION, AS APPLIED TO THE ORIGIN OF THE SPOROPHYTE.

A.—General.

It remains to draw together the results which have been acquired into some general statement. It is accepted as a working hypothesis that alternation of generations in the Archegoniatæ is of the antithetic type, and that Apogamy and Apospory are abnormal phenomena, probably of relatively recent origin, and produced under special conditions. Such alternation has been correlated with the establishment upon land-surfaces of a rising series of green plants of algal origin. Alternation has indeed been regarded as a natural consequence of the migration from water to land, and it has been pointed out in connection with this that sexuality would be restricted by the change, since external fluid water for the passage of the motile gametes is not constantly available on land; a premium was thus put upon spore-production, instead of a repetition of the sexual method, as a means of propagation of the race, and on these grounds an enlargement of the sporophyte is to be regarded as a probable feature in the early land-growing plants of algal origin.*

The green Algæ, in their post-sexual complications, supplied the material for a starting point, from which a more complicated sporophyte might arise. From such beginnings, though not necessarily as lineal descendants of any living type of Algæ, the simplest Bryophyte sporogonia may have been derived. The lines of modification would be, an increased number of the post-sexual divisions, with delay of the reduction of chromosomes till the tetrad division of the spore-mother-cells, and the sterilisation of the superficial cells to form a vegetative protection for those lying more centrally; there is a physiological probability underlying these steps of advance, and they find their embodiment in the simplest sporogonia of the Bryophytes.

The attempt will now be made to form a general view of the *methods of advance of the sporophyte* to more elaborate types. Some of the main points which are material features in those methods may be formulated, on the basis of the observations and comparisons stated above, as follows:—

(1). Spore-producing cells form a part of the tissue of all sporophytes which complete their part in the normal ontogenetic cycle; from this it is concluded that spore-production was normally a constant event in their evolution.

(2). There is a general biological probability of increase of spore-production in homosporous, land-living plants, since those with the largest spore-output are most likely to maintain and spread their race, while the numerical question is not complicated by the sexuality of the spores. As a matter of fact the number of cell-divisions in the sporogenous tissue preceding the tetrad division is usually indefinite in homosporous forms; the capacity of increase is thus structurally evident in them.

(3). The Archegoniate sporophytes illustrate by numerous examples the sterilisation of spore-producing cells, so as to form temporary nutritive cells, or permanent

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* 'Ann. of Bot.,' vol. 4, p. 364.

vegetative tissues. The converse, *i.e.*, the transformation of normally sterile into fertile cells, exists, but it is of rare occurrence. These facts indicate a prevalence of progressive increase of sporogenous tissue, coupled with progressive sterilisation.

(4). An increase in spore-output demands an increased vegetative system for protection and nutrition, and for mechanisms of dissemination; the tissues which result from progressive sterilisation contribute to meet this demand.

The above theses apply to all homosporous Archegoniatæ.

In addition to the features above noted there are four further primary factors, which may be recognised as involved in the structural advance of the sporophyte from simpler beginnings to such conditions as we see in its more elaborate forms, viz. :—

(5). Distinction of a vegetative basal region from a reproductive upper region.
(6). Relegation of sporogenous cells towards a superficial position in the plant-body.
(7). Segregation of sporogenous cells in separate pockets (sporangia).
(8). Formation of appendicular organs.

The first two only of these are illustrated, and indeed their first effects indicated in the Bryophytes; but all have been involved in the origin of the Pteridophytes; they will now be briefly discussed.

(5). With the exception of the very simplest sporogonia (*Riccia*) there is a structural and functional distinction of apex and base. In certain sporogonia the similarity of structure of the young seta and capsule suggests that the former is a sterilised region of the same nature as the head. In the Pteridophyta such indications are naturally less clear, though the structural similarity of the vegetative and fertile regions of *Lycopodium Selago* point to a similar conclusion. The facts, inconclusive as they are, coincide with a theory of sterilisation as the source of the basal vegetative region.

(6). In all Archegoniate plants the spores are produced internally, being covered by at least one layer of protective cells; but the depth within the plant-body at which they are produced is chiefly determined by the facilities for nutrition, and by the method of dissemination, while it is also closely dependent upon the bulk of the sporogenous tissue itself. In a small sporogonium the conveyance of nutriment throughout the sporogenous group is easily effected, though this may be a solid mass of cells occupying a central position, as in *Riccia*. But in the sporogonia of most Bryophytes (which probably took origin along several distinct lines of descent) a central columella is present; this columella serves the function of nutrition and water-supply, and in some cases of mechanical dispersion.* Goebel notes† how the columella varies in bulk

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* For a comparative account, based upon views of progressive sterilisation in sporogonia of Bryophytes, see GOEBEL, 'Organographie,' pp. 326-329 for Liverworts, and pp. 373–376 for Mosses. I see no reason why a comparison which gives such useful results in Bryophytes should not be extended to Pteridophytes also. The fact that the vegetative development has gone further in the latter is no sufficient reason for neglecting the lines of analogy between the two series of the Archegoniatæ.

† 'Organographie,' p. 376.

in proportion to the number of spores, being largest where the spores are most numerous; this indicates its importance in supply. But the other factor, necessity for dispersion of the spores, does not in any way determine the position of the fertile cells in the Bryophytes, for all the more elaborate sporogonia dehisce by longitudinal slits, or by an operculum, either of which methods would give freedom even to spores produced at considerable depths in the tissue. Accordingly in the Bryophyte sporogonia the sporogenous cells lie relatively deeply seated, and in the Mosses (with the exception of *Sphagnum*) they are segmented from the endothecium, and constitute at a certain period a definite and continuous archesporium.

In the Pteridophyta the sporogenous cells are of more superficial origin, being uniformly derived by segmentation from superficial cells, a condition not altogether different from that in the sporogonium of *Sphagnum*. In the progenitors of the strobiloid Pteridophytes it seems probable that the nutritive question should present itself in the same way as in the Bryophytes, and that after distinction of a vegetative base from a fertile upper region (the latter being thus functionally comparable to a sporogonial head), increasing spore-production should raise the same nutritive needs as in the Bryophytes, with a central mass of sterile tissue as the result; the sporogenous tissue lying between this and the outer protective wall would remain as an archesporium, as in the Bryophytes. Two influences would operate in determining the position of this archesporium; first the nutritive requirements, with some such proportion of the sterile conducting tract to the spore-output, and the consequent quantity of the supplies to be transmitted, as has been noted in the Bryophytes. But a second, and more potent influence in leading to a superficial position has doubtless been the need for dissemination; in the Pteridophytes this is by multiple dehiscence, which depends for its success more closely upon superficial position of the spores than is the case in the Bryophytes, with their terminal slits, or separating operculum. *Thus the Pteridophytes may be regarded as showing, in higher degree than the Bryophytes, the adaptive relegation of spore-production towards the surface of the sporophyte.*

(7). The *segregation of the sporogenous cells in pockets* (Sporangia) is one of the distinctive features of the Pteridophytes from the Bryophytes; in the latter, though an approach to a partitioning of the archesporium is seen in the Anthoceroteæ, it is never completely carried out. There is no definite indication how the polysporangiate state came into existence in the Pteridophytes; in the absence of demonstration we can only fall back upon hypothesis, based on comparative and physiological considerations. It has frequently been assumed that the polysporangiate state originated by branching of sporogonial heads,* but a process of septation would account equally well for the initiation of the structures as we see them. It has been shown elsewhere ('Studies' II.) that progressive septation has occurred in vascular plants; the question then is how far it is answerable for that plurality of sporangia which marks off the Pteridophyta so sharply from the Bryophyta. That such septation has actually taken

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* For instance, NÆGELI, 'Abstammungslehre,' p. 476–7.

place is directly proved in the case of certain Angiospermic anthers, where closely related genera and species allow of strict comparison; in the Pteridophyta, owing to the greater isolation of genera and relative paucity of species, conclusive comparisons are less readily made; but the close structural analogy between those anthers and a number of spore-producing parts of homosporous Pteridophytes suggests that a similar septation, by tracts of tissue rendered sterile, has actually occurred in them also (*e.g.*, *Danæa*, *Ophioglossum*); physiological considerations make this seem probable in homosporous plants, where high spore-output is specially important. Septation of sporangia, as a consequence of sterilisation, is therefore to be recognised as a factor in evolution of vascular plants as we see them; the question is how far it is answerable for that plurality of sporangia which marks off the Pteridophyta from the Bryophyta.

(8.) As to the *origin of appendicular organs*, it must be freely admitted that nothing is positively known; there is, however, one guide to which in such questions special weight is usually accorded; viz., the development of the individual. The origin of the individual leaf as an outgrowth laterally, below the apex of the axis, and in acropetal succession, may be held to be an indication of its origin in the race; this is the view which will be adopted below (p. 219). It must not be assumed, however, that all appendicular organs are of the same nature; it is possible that parts arising laterally and exogenously, in acropetal order, may have had in the first instance different offices, and a different evolutionary history; this will be pointed out below to have probably been the case, and that sporangiophores, though they also may arise on the axis itself, are not on that account alone to be held as leaves (p. 221).

In addition to the above, which may be held to be factors of *primary* importance, there are also others which may be held to be *secondary not only in importance, but also in time*; they have certainly produced effects which have modified the more elaborate types in more or less degree; they are as follows:—

(9). Fusion of sporangia.
(10). Abortion.
(11). Interpolation.
(12). Growth of parts bearing sporangia.
(13). Branching of parts bearing sporangia.

(9). A number of synangial conditions in Pteridophytes would be open, as far as their structure is concerned, to being regarded as the result of *fusion, and such fusion of sporangia has certainly occurred in some Angiosperms, so that its existence as a modifying factor cannot be denied.* The proof that it has taken place in any specific case in Pteridophytes is open to the same difficulties as the proof of septation; but the general physiological probability is in some measure a guide, in cases where the structure would be conformable with either fusion or septation; the general principle being, that in homosporous forms a large spore-output is an advantage, and enlargement of the sporangia, with consequent septation, would be one of the ways of carrying this into effect.

(10). Another factor which has contributed materially to the condition of the Pteridophytes as we see them is *abortion* :—that is indeed a form of sterilisation of whole sporangia ; the part which bore them may at the same time undergo a correlative enlargement. Thus while there is a reduction in number of sporangia, abortion may lead to an increase of the vegetative system, and an increase of the ultimate spore-producing capacity. This is seen in its simplest form in the Lycopodinæ, but it has probably occurred frequently also elsewhere.

(11). On the other hand, a factor which has played an important part in some lines of descent, but not in all, is *interpolation* of new sporangia in addition to those present in the fundamental type. It is in the Ferns that this has been a prominent factor, and it is looked upon as an example of that indefiniteness of number of primordia which is a frequent feature where the number of parts is large. The view is here entertained that the number of sporangia formed by primary hereditary initiative is apt to be supplemented by subsequent less regular modes of origin in certain circles of affinity, but this is not found in certain of those which there is reason to regard as primitive.

(12). *Growth* of parts bearing sporangia, whether non-localised, or specially localised as apical or intercalary growth, is a very fertile source of modification, not only of size, but also of form and proportion of the sporophyte as a whole ; the greater the growth of the parts which bear the sporangia, the larger is the accommodation for them. Arrest of growth has the contrary effect.

(13). *Branching*, whether of axes, leaves, pinnæ, or sori, acts similarly in increasing the accommodation for sporangia, or spore-bearing organs. The effect may be more direct, where the region in which it occurs bears sporangia, or indirect, where the branching is in the vegetative region.

These are then the factors of advance, or retrogression, which have been recognised as being represented in the spore-bearing generation of the Archegoniatæ. In estimating the probable effect of any or all of them in any individual case, general considerations of biological probability must be used as a control. The fundamental point as regards homosporous forms is the general probability of increase rather than decrease of complexity of the spore-producing parts ; the living types of them would then naturally range themselves in ascending rather than in descending series, as regards their complexity. The contrary view has commonly been entertained in dealing with the Pteridophyta, especially by those who have held the Leptosporangiate Ferns to be relatively primitive types, and many or even all other Pteridophytes to be derivatives from them. But such a view is not supported by the fossil record, while comparative and physiological probability are also against it. A theory of reduction is a ready weapon in comparative morphology, and indeed a necessary one for those who start by assuming the most complex and specialised organisms to be primitive; but the *onus probandi* lies with those who issue these blank drafts on morphological faith. To the evolutionist it seems unscientific to assume a high degree of complexity as a starting point, while no theory of reduction should be entertained unless a reasonable physiological explanation can be given for it, or a cogent comparative sequence demonstrates that reduction has taken place. *The general method put in practise here is to regard homosporous forms as in the upgrade of their evolution, as regard their spore-producing organs, unless there is clear evidence to the contrary.*

Naturally the reply will be made that the fossil Pteridophyta were giant forms, and the living representatives mere pigmies compared with them; and reference will specially be made to the *Lepidodendra*, as compared with living Lycopods. The answer to this is that small Lycopodinous forms are also among the early fossils, and that there is no sufficient evidence that the living Lycopods are descendants of the larger, rather than the smaller types of the coal; the comparative evidence as regards external form distinctly favours their relation to the smaller of the coal-types. A somewhat similar argument applies in the case of the Equisetineæ; small forms not unlike our modern *Equisetum* existed as early fossils, while as regards the strobilus, the *Equisetum* of the present day is fairly matched by certain allied fossils. Among the Ferns, a large living *Angiopteris* will probably compare favourably in size with any Fern which has been found as a fossil, while the sori are almost identical with those of some fossils. It is not denied that reduction has taken place sometimes, for instance, the Hymenophyllaceæ are probably reduced types, a view which accords well with the peculiar specialisation which the Leptosporangiate Ferns, and they in particular, show. The protest is against any wholesale assumption that reduction has been general among homosporous Pteridophytes.

The fact seems to have been that the giant forms of Pteridophyta themselves died out, though the smaller related forms survived; accordingly our living homosporous forms are not to be regarded as themselves reduced on the mere ground that larger forms akin to them existed in the past. The giant forms are chiefly the result of vegetative amplification: comparing the spore-producing parts of living homosporous Pteridophytes with those of their fossil correlatives, the present types, with few exceptions, hold their own in point of complexity, and do not show evidence of any general reduction. These considerations seem to me to justify the position that, unless good evidence of reduction be brought forward in any given case, the spore-producing members of the homosporous Archegoniatæ should be regarded as in the up-grade of evolution.*

Notwithstanding the great difference in general form between the sporophytes of the Bryophyta and Pteridophyta, the two offer certain lines of analogy which are important in the study of the methods of advance of the sporophyte; these will now

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* The physiological problems relating to the heterosporous condition, and especially those in seed plants, have purposely been left out of account, so as to avoid unnecessary complication; facts relating to them have been brought forward occasionally in formal comparison only in this Memoir.

be considered. The sporogonia of Bryophytes may be naturally arranged as illustrating progressive sterilisation of tissues; this has led on the one hand to the distinction of a basal vegetative region (Seta) from a fertile apical region (Capsule); but however complex the structure, the radial symmetry is maintained as the fundamental type of construction. The growth of the simpler sporogonia shows no definite localisation, but distinct apical and intercalary growth is seen in the more complex sporogonia. The former is most marked in the true Mosses, where it may be long continued. Intercalary growth is more widespread, the intercalary activity is often located in the sterile region, where it may lead to considerable vegetative extension, without disturbing the fertile region above it.

In the simplest sporogonia the sporogenous cells form a central solid tissue, but in certain Hepaticæ there are various indications of decentralisation of the fertile tissues, and formation of a sterile columella, while in the Anthoceroteæ, and most of the Mosses, a cylindrical fertile layer (archesporium) is clearly defined round it. In *Sphagnum* and *Anthoceros* the archesporium forms a complete dome; in the true Mosses the dome is commonly incomplete at the apex, and the archesporium is a cylinder. But the archesporium of Mosses is not sharply limited above or below; the same layer of cells is continued beyond the limit of actual fertility as a well-defined band.* *This indicates that the fertile zone is a residual region of an elongated potentially fertile tract, which has been limited by progressive sterilisation of its tissues.*

In all Bryophyte sporogonia the proportion of sporogenous to vegetative tissue is considerable: the assimilative function, as evidenced by the structure, is never raised to the position of a primary interest, and the sporogonium is throughout dependent in great measure for its nutrition on the activity of the sexual plant. But in the Pteridophyta self-nutrition is a primary interest of the sporophyte at an early age, and the dependence on the sexual plant is only a temporary phase; there is thus a greater preponderance of vegetative tissue, and the production of spores takes place later in the ontogeny. The fossil evidence shows that this must have been so for untold ages, thus the two Archegoniate series diverged early on the important ground of vicarious, as against self-nutrition. The consequence has naturally been to obliterate, especially in the vegetative region, such structural similarities as might have served to indicate some common origin. So far has this been the case, that exact comparisons between the two are little better than guesses, while some writers have even been led to doubt the essential correspondence of the sporophyte in Bryophytes and Pteridophytes. This latter view is not entertained here, however, and it is held that homologies may properly be traced between them, at least so far as the recognition of essential correspondence of their spore-mother-cells, and spores.

Since we believe sterilisation to have taken so prominent a place in the advance of

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* See CAMPBELL, 'Mosses and Ferns,' figs. 97, 98; also KIENITZ GERLOFF, 'Bot. Zeit.,' 1878, taf. 2, figs. 28, 31, 41.

the sporogonium of Bryophytes, it has been desirable to see how far this is a factor also in the Pteridophytes.* Examination has shown that sterilisation occurs in the sporangia of many of them; it may affect only individual cells of the sporogenous tissue, which then serve as transitory nutritive cells; in certain cases, however, it involves tissue-tracts, or even whole sporangia. *It is thus seen that there is in the Pteridophyta the essential basis of fact necessary for a theory of sterilisation in them also.*

Theory of the Strobilus.

The fertile zone of a strobilus may, like the fertile zone of a Moss-sporogonium, be regarded as a residuum from sterilisation, since it has a similar relation to the vegetative system. This makes it desirable to inquire whether the Bryophyte analogy will suggest how the strobilus of the simplest Pteridophyta may have come into existence, and this may legitimately be done without assuming near community of ancestry between these two essentially different types. For our study relates to the methods of advance, and is not bound by the restrictions of exact homology.

The modes of increase in number of sporangia, now operative in vascular plants, are seen to be septation and interpolation, while continued growth and branching of the parts which bear them are also contributory features. It may legitimately be held that such means of increase as are seen active at the present day, for instance septation, were probably active in the past also, though some of them (*e.g.*, interpolation) have probably been of more recent origin. This may be applied to the simplest examples of the polysporangiate state, viz., the Lycopods: in these there is a more strict relation of number and position of the sporangia to the sporophylls than in any other type, one sporangium is associated with each sporophyll, and interpolation of sporangia is unknown. It is true that branching of the fertile, or sterile axes may occur, but this does not complicate the fundamental simplicity of the strobilus.†

The topographical and functional correspondence of the strobilus of *Lycopodium* with the capsule of the Bryophytes has been above pointed out, both being regarded as residual fertile zones.‡ Our hypothesis, already suggested elsewhere,§ is, that similar causes would lead to the decentralisation of the fertile tissue in the primitive

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* 'Studies,' I., p. 495.

† It is to be noted that NÆGELI ('Abstammungslehre,' p. 477) selected *Lycopodium Selago* as a primitive type of sporophyte.

‡ This comparison was suggested in the first Memoir of this series ('Studies,' I., p. 495), and was more fully treated elsewhere ('Annals of Botany,' vol. 8, p. 343). An opinion against the view of the strobilus as comparable with a sporogonial head has already been expressed by Dr. GLÜCK ('Flora,' vol. 80, p. 303). In reply to this I showed ('Flora,' vol. 80, p. 487) not only that Dr. GLÜCK had misunderstood my views, but that he did not quote from them with verbal accuracy. I do not therefore think that I am called upon to meet his objections in detail. It may be noted, however, that the question is now stated in more moderate terms than in my former Memoir.

§ 'Annals of Botany,' vol. 8, p. 360.

Pteridophytes as in the Bryophytes, and result in the formation of a central sterile tract, with an archesporium at its periphery; that such an archesporium, instead of remaining a concrete layer as it is in the larger Musci, became discrete in the Lycopods, sterile tracts intervening between the residual fertile cell-groups; that these fertile cell-groups formed the centres of sporangia, which grew so as to project beyond the general surface, and that they were associated regularly with outgrowths, perhaps of correlative vegetative origin, from the intervening tracts of sterile tissue: these are the sporophylls. The primary origin of the sporophylls was, on this hypothesis, precisely in accordance with their development as it may be observed in any bud; the axis pre-existed the appendages, and the apex of the axis remained constant throughout: the development was in no sense a form of branching of the axis itself, but a formation of appendages laterally upon it.* Where the strobilus is a simple one, this segregation involves only one of the factors of increase above mentioned, viz., septation. But in actual living Lycopods branching is common, both in the strobilus, and in the vegetative region, also the apical growth of the strobilus may be continued, and the production of the sporophylls and sporangia be unlimited, while progressive sterilisation of sporophylls, as above noted, accounts for the increasing vegetative system required for their nutrition. The vegetative system of the sporophyte is thus here also largely, perhaps even wholly, the product of sterilisation, the effect of which is sometimes intermittent, as in the type of *L. Selago*, but more frequently it is regularly progressive from below. The result in the Lycopods is a more extensive vegetative system than in the Bryophytes, though the general relations are the same. The strobilus, like the fertile region of the Bryophyte capsule, may be regarded as a residual fertile zone, lying between the results of sterilisation below, and imperfect development above;† the chief differences from the Bryophyta lie in the segregation of the sporangia as distinct bodies, and the presence of foliar appendages. With modifications of detail a similar theory is applicable to other strobiloid types, while as is shown elsewhere (p. 250) all known Pteridophytes may be referred to some modification of a strobiloid type, with radial symmetry.‡

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* An hypothesis of a kindred nature was suggested by NÆGELI ('Abstammungslehre,' pp. 475–479). The chief difference between NÆGELI'S hypothesis and my own lies in the point that, while NÆGELI would regard each Lycopod sporangium as a sporogonial head, and the whole strobilus as a result of elaborate branching, in my suggestion in the text the strobilus would be the result of elaboration of one sporogonial head, and each sporangium would be only a fraction of the whole. It is clear, however, that NÆGELI contemplated in the primitive sporophyte an organism in which all the leaves were sporophylls, and that the vegetative system was increased by deferring the spore-production to later stages in the individual. In these respects his view is in accordance with my own.

† GOEBEL, 'Organographie,' pp. 689, 690.

‡ The above theory of the origin of the strobilus is not essentially connected with the comparisons which follow. Any one who disagrees with it should not on that account give less attention to those comparisons, which it is hoped will throw light upon the modifications of the strobiloid type: these will hold, even though the account given of the origin of the strobilus may not be the correct one.

Theory of the Sporangiophore.[*]

Whether or not this hypothesis of the origin of a Lycopod strobilus approaches the actual truth, comparison points out the genus *Lycopodium* as a primitive one; but other forms more or less closely related to them are characterised by more complex sporangial arrangements; the increase of the individual sporangium, as in *Lepidodendron* and *Isoetes*, has been noted elsewhere,[†] and evidence has been brought forward of the probability of septation of the sporangium in the case of *Tmesipteris*, and less clearly of *Psilotum*,[‡] while a somewhat similar origin seems not improbable for the plurality of sporangia borne on the sporangiophores of some Sphenophylleæ.[§] Again, the view put forward for the spike of *Ophioglossum* involves similar questions of increase,[||] as also that for the still more complex spike of *Helminthostachys*, with its lateral ranks of sporangiophores; lastly, the sporangiophore of *Equisetum* shows a near analogy in form to these several sporangium-bearing bodies, while the sori of certain Ferns have a somewhat similar conformation.[¶] These facts make it necessary to consider what is the real nature of those bodies which are designated by the non-committing term "sporangiophore"?

In taking up a question of this nature it is necessary to have an open mind as to "morphological dignity," and especially so as the organisms involved are all low in the scale of vascular plants; their morphology must not be dominated by ideas derived from Phanerogamic plants. In treating them, their evolutionary position should be constantly borne in mind; their chief types were laid down before Angiosperms appeared, and accordingly their morphology should be studied with the same freedom as if the higher organisms had never existed. The practice of referring every part of the shoot to some modification of axis or leaf, emergence or hair, has already been broken down in the case of sporangia,[**] and there is just reason to be prepared for its being broken down also as regards the parts which bear the sporangia. It is only a provisional convention, for convenience of description, which designates as "leaves" all structures which arise laterally, and exogenously upon an axis, and are derived in acropetal order from the primary meristem.[††] It is obvious that under this

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[*] My first suggestion of the non-phyllome theory of the sporangiophore was contained in a preliminary statement, "On the Morphology of Spore-producing Members" ('Roy. Soc. Proc.,' vol. 50, p. 265, 1891). This was stated in more general terms in "A Theory of the Strobilus in Archegoniate Plants" ('Annals of Botany,' vol. 8, p. 343).

[†] 'Studies,' I., p. 538.

[‡] 'Studies,' I., pp. 541–548.

[§] See below, p. 227.

[||] 'Studies,' II., and see below, p. 233.

[¶] It seems hardly necesary to state that there is here no suggestion of the origin of all these various types from any Lycopod ancestry; the comparison is made of their sporangial condition, with a view to some general conception of the nature and origin of the sporangiophore.

[**] GOEBEL, 'Bot. Zeit.,' 1881, p. 701.

[††] SACHS, 'Text-book,' Engl. ed., 1883, p. 135, &c.

definition are included structures which must have had a distinct evolutionary history.* If this be so in distinct organisms, it would appear possible also in an individual organism, that members of different evolutionary history may be produced upon the same axis, and even be associated together.

On the other hand it is seen that emergences and hairs are produced indiscriminately upon axes and leaves, but they are not regarded as the result of modification of any other part. Certain emergences even contain vascular tissue, and may perform important functions, and yet they are not recognised as results of any "metamorphosis" of other parts. It is essential for the free discussion of the sporangiophore that these points should be borne in mind.

Sporangiophores such as those above named have the following characters in common: they are outgrowths of varying length, which bear one, or more sporangia; these are when numerous more or less closely related one to another, and frequently synangial: they are usually disposed in a circle round the periphery of a disc-like expansion at the distal end of the sporangiophore, but other arrangements may be found. A vascular strand runs usually through the stalk to the distal end, where it may divide into branches which terminate in close relation with the sporangia. The position of the sporangiophores may vary, being sometimes upon the axis (*Calamostachys*, *Equisetum*), sometimes single, upon a leaf (Psilotaceæ) or more numerous (most Sphenophylleæ, and occasionally in Psilotaceæ) along the margin of the spike (*Helminthostachys*), or very numerous on the surface or margins of the leaf (Ferns). In all these cases the main structural features of the sporangiophores are the same, and the question arises whether these similar structures do not owe their origin to similar evolutionary response to similar requirements, carried out in the various positions in which we see them; *it is in fact suggested that the sporangiophores are simply placental growths, and not the result of any "metamorphosis" of parts, or appendages of prior existence.*

The biological advantages gained by the formation of such placental growths are as follows:—Indefinite increase of the simple sac is attended with practical disadvantages, which would be met by sub-division of sporangia into separate pockets; the difficulty of dissemination from the sporangia thus produced would be met by their projection, and still more fully by the separation of the sporangia, and is further helped when the sporangia are lifted distinctly above the surface of the part which bears them; this is specially so in those cases where foliar or other appendages protect the sporangia while young. But this raising of the sporangia upon an elongated stalk increases the

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* The most prominent case is that of the foliar developments in Pteridophytes, as parts of the neutral generation, and in Bryophytes, as parts of the sexual generation (BOWER, 'Annals of Botany,' vol. 1, p. 133). But further, GOEBEL has recently shown ('Organographie,' p. 261, &c.) that "leaf-formation has arisen in the Liverworts in quite a number of series, independently of one another." And if this be so for the Liverworts, are we sure that even the foliage leaves of all vascular plants have really had a common origin by descent? It would seem possible that the foliar development may have originated in them also in a number of separate evolutionary series; but of this there is as yet no clear evidence.

difficulty of nutrition; this is met by the vascular supply, which is so constantly a feature in the sporangiophores.

If some such formation of placental growths took place, it will be a natural consequence that they may be seated at any point where in the ancestry increase of spore-production has been actively proceeding; there will thus be a probability of their not occupying in all cases a fixed or uniform position. This is precisely what comparison discloses. The various positions which the sporangiophores take have always raised a difficulty for the formal morphologist; a frequent way of meeting the difficulty has been to refer them nominally to some category of vegetative parts.* But to those who hold the antithetic theory of alternation, it will seem highly undesirable to obscure the view by reference of the sporangiophores to "metamorphosis" of any vegetative part; on the other hand, when, as sometimes happens, they become sterile, with correlative vegetative growth, then those vegetative parts might more correctly be described as "metamorphosed" sporangiophores.

A comparison of Fern-sori is very instructive in its bearing on this theory of the sporangiophore as a placental growth, and more especially as regards its vascular supply; my own opinion is that the sori are of the nature of sporangiophores, but the bearing of this comparison of their vascular supply is equally valid whether or not the sori themselves be held as the equivalents of sporangiophores elsewhere.† The following examples suggest how such a vascular supply may originate; in *Danæa*, in which the sorus is sometimes even sunk in the surface-tissue of the leaf, it has no special vascular supply of its own; the bundle over which it is seated pursues an even course below it; the same is the case for *Angiopteris*; but for most *Marattias*, and especially in *M. Kaulfussii*, a vascular extension roughly in proportion to the more elevated position is found, while in *Kaulfussia*, where also the sorus is raised above the leaf-surface, the vascular supply may reach considerable dimensions.‡ The same is the case also in *Gleichenia*. The vascular extension is more marked among the

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* As recent examples of this, it may be noted how GOEBEL ('Organographie,' p. 665) describes the sporangiophores of *Helminthostachys* as "laubblattabschnitte," and (p. 666), speaking of the Ophioglossaceæ generally, says: "Wir können also auch hier das Sphorophyll auf eine besonders tiefgreifende Umbildung des vegetativen Blattes zurückführen."

SCOTT ('Studies in Fossil Botany,' p. 113) writes: "In *Cheirostrobus* it is evident that the sporangiophores are ventral, or superior segments of the same leaf of which the sterile tracts are the dorsal, or inferior, segments." But later, after discussing comparatively the Sphenophylleæ, *Cheirostrobus*, and *Calamostachys*, he remarks, "The difficulty is perhaps best met by regarding the sporangiophore (like the sporangium itself) as an organ *sui generis*, which often occupies the position of a ventral lobe of a bract, but may also arise independently, and may so far resemble an entire leaf." If the view of them as organs *sui generis* be consistently held, there is no need to speak of them as lobes or segments at all. Dr. SCOTT's view is substantially similar to my own, so far as the sporangiophores are held to be organs *sui generis*; but he does not recognise their derivation from single sporangia by septation and placental growth, as I have suggested in the case of *Tmesipteris*. His view was based on comparison of sporangiophores already formed.

† For a full statement on comparison of receptacles, see 'Studies,' IV., pp. 91–95.

‡ 'Studies,' III., p. 46, and fig. 42.

Gradatæ, and reaches its greatest length in the peculiarly specialised series of the Hymenophyllaceæ. On the lines of such general comparisons as these, disclosed in detail in former Memoirs,* it would seem probable that there has been a progressive extension of the vascular supply into the sorus, and that it has followed either the simple elevation of the sporangia beyond the surface, as in certain Simplices, or the elongation of the receptacle to accommodate an increased basipetal sequence of them, as in the Gradatæ.†

But, on the other hand, certain of the Mixtæ illustrate a recession of the receptacle, and of the vascular extension within it;‡ this has been shown in the *Dennstædtia—Davallia* series to follow the adoption of the mixed type of sorus. We thus see that there is in Fern-sori a considerable play of adaptability of the receptacle, and of its vascular supply; whether or not readers accept the sori of Ferns as essentially comparable to other sporangiophores, they at least illustrate just such an origin and variability of a special vascular supply as has been theoretically presumed to have taken place in the evolution of sporangiophores elsewhere.

Sporangiophores are also variable in the number of sporangia which they bear; in some degree this may have been due to initial differences in the race, though on this point there is little that can be said with certainty. On the other hand, the differences may be due to subsequent changes, and comparative evidence shows that modifications both of increase and of decrease in number of sporangia on the sporangiophore have occurred. In the Sphenophylleæ,§ where the number of the sporangiophores is larger, the number of the sporangia which they bear individually is commonly smaller, though there is no strict numerical relation. *S. majus* has been recognised on grounds of general comparison as a connecting link with the Psilotaceæ and Lycopods, but in that species the leaf-subtended sporangiophores bear 4–6 sporangia; in other species, in which the sporangiophores are twice or three times as numerous as the subtending leaves, the number of the sporangia may be two, or only one. Probably this indicates a decrease of sporangia by abortion, with a rough inverse proportion to the larger number of the sporangiophores. Such a reduction is seen also in the sori of many *Gleichenias*, where towards the apex of a pinnule the sorus may frequently be represented by a single sporangium; this condition is doubtless the result of reduction from the ordinary type, though it became the typical state for the Schizaeaceæ. Somewhat similar reductions of number from the normal are also found on the small sporangiophores near the apex of the strobilus of *Equisetum*, or of the spike of *Helminthostachys*, and at the limits of the fertile region in the Psilotaceæ. *Reduction in number of the sporangia on the single sporangiophore is thus a frequent feature.*

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* 'Studies,' III., p. 79; IV., pp. 123–4.

† 'Studies,' IV., p. 94, *b*.

‡ 'Studies,' IV., p. 94, *c*.

§ See below, p. 227.

Increase of size of the sporangiophore, and of the number of sporangia which it may bear, appears to have taken place in various ways ; (*a*) *by lateral extension*, which is seen in *Danæa*, and the details, with strong evidence of increase of number of the sporangia by septation, have been described elsewhere ;* such increase has probably also been effective among other Ferns. (*b*) *By longitudinal extension* ; this is, in my view, exemplified in the highest degree by the spike of the Ophioglossaceæ, accompanied by septation in *Ophioglossum*, and by continued apical growth and branching in this and other genera.† In a less degree longitudinal extension is seen in all the sori of the Gradatæ, being accompanied by a basipetal succession of interpolated sporangia. (*c*) A third type of increase is associated with that *irregular interpolation of sporangia* which is characteristic of the Mixtæ; there is every reason to believe that this method was of relatively late origin.

It is difficult, even after making allowance for such modifications as these, to form an idea of what were the original numbers of sporangia on each sporangiophore. Probably they were from the first variable, and there was no fixed type for all Pteridophytes. A good case has, however, been made out, on developmental grounds, for so low a number as two for *Tmesipteris*, though the number of sporangia was usually larger. *It seems probable, however, that at least a plurality of sporangia existed on primitive sporangiophores, and where only one exists, that condition has been the result of reductions such as those suggested for certain Sphenophylls, or for the "monangial" sori of Gleichenia and Schizæa.*

But a warning is necessary that mere form is not a sufficient characterisation of any given part as a non-foliar sporangiophore; for in some cases a clear line of evidence shows that certain parts which have the form of stalk with vascular supply, enlarged distal end, and pendent sporangia common for sporangiophores, are truly of foliar nature; I mean the female sporophylls of the Cycads. The argument for reduction from some more elaborate sporophyll is for them firmly established on a comparative basis,‡ and it seems hardly open to doubt that they are foliar structures reduced from some more elaborote Cycado-Filicinean leaves. But though this may be true for the Cycads, it does not invalidate our hypothesis for sporangiophores generally ; it merely suggests again that similar results, of which the biological advantages are obvious, may be arrived at along different evolutionary routes. It will also make caution especially necessary in treating similar cases among seed plants.

B.—Special.

The application of the above theories will now be made to the several groups of the Pteridophytes. Five more or less distinct types of disposition of the sporangia

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* 'Studies,' III., p. 40.

† 'Studies,' II., p. 11.

‡ ENGLER and PRANTL, 'Nat. Pflanzenfamilien,' vol. 2, abth. 1, pp. 14, 15 ; GOEBEL, 'Organographie,' p. 692; SCOTT, 'Studies,' p. 514; LANG, 'Annals of Botany,' vol. 14, p. 298, &c.

relatively to the axis and appendicular organs are known among the Pteridophytes, viz. :—

(1). The Lycopod type.
(2). The type of the Psilotaceæ and Sphenopylleæ.
(3). The type of the Ophioglossaceæ.
(4). The type of the Equisetaceæ.
(5). The type of the Filicineæ.

The theoretical position which may be arrived at on the basis of detailed investigation of their spore-producing members will now be briefly summarised for each of these types.

(1). The Lycopod Type.

The strobilus may be held to represent a residual fertile zone, or many interrupted zones in the primitive *Selago* type;* this residuum, from progressive sterilisation, is comparable as regards its relation to the vegetative system with the fertile zone in a Bryophyte sporogonium. Like this the ancestral type may have had a concrete and continuous archesporium, but of this there is no direct evidence; such an archesporium becoming interrupted, as is indeed foreshadowed in some Bryophytes, the discrete archesporia would then form the centres of sporangia; the origin of these as outgrowths of the surface tissues would thus be similar in descent to that which they show in the ontogeny. They are borne in strict numerical relation to the subtending sporophylls, which are also believed to have originated in descent as outgrowths laterally below the apex of the strobilus, just as they do in the individual ontogeny. This relation is maintained constantly in all Lycopods, but differences occur in position—distal, basal, or even cauline—of the insertion of the sporangium relatively to the sporophyll.

There are two ways in which, without departing from this stereotyped plan, an

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* I wish particularly to point out that the *Selago* condition, that is, the imperfect differentiation of the fertile from the sterile regions, was not unknown in the Palæozoic period. SCOTT remarks ('Studies in Fossil Botany,' p. 501) that "all the well-known Palæozoic Lycopods had perfectly definite strobili." It is true that the best known types had definite strobili, but some of the smaller forms had not. KIDSTON has described in his new species *Lycopodites ciliatus* how "the sporangia seem to have been borne at the base of the leaves on an ordinary branch, which does not appear to have been much modified, or to form a distinct cone." He further remarks that the genus *Lycopodites*, though it seems rare, is perhaps commoner than suspected, through being overlooked (KIDSTON, 'Trans. Nat. Hist. Soc. Glasgow,' vol. 6, part 1, p. 36). It is also the fact that the *Selago* condition occurs in the Sphenophylleæ, in *S. majus* (KIDSTON, *l.c.*, p. 128). This is also very beautifully seen in a photograph of a specimen from the Brussels Museum, shown me by Mr. KIDSTON.

The fact that this undifferentiated state existed in early fossils is important, as showing that it is not merely a character acquired in recent times. It may, therefore, be legitimately used in arguments as to the families of plants represented in the Palæozoic period. On its general morphological bearings, compare 'Annals of Botany,' vol. 15, 1901, p. 225.

increased spore-output is possible, and they are both exemplified in Homosporous Lycopods, viz., by continued apical growth and branching of the whole strobilus, which lead to increase in number of sporophylls and sporangia, and by increase in size of the individual sporangia.* The former is accompanied, in the *Selago* type of *Lycopodium*, by abortion of certain sporangia, while the subtending sporophylls develop as foliage leaves, and the vegetative system is thereby increased. The sterile regions may then alternate irregularly with the fertile zones, or in other species the plant may show varying degrees of specialisation, the fertile regions being commonly defined as terminal strobili; this is the commonest type for the genus. Clearly the increase of the vegetative system will facilitate the nutrition of an increased number of spores.

The second mode of increase is exemplified among living species, but more clearly among the fossils. Examination of the sporangia of the genus *Lycopodium* shows that in living species there is variation, the type of *L. Selago* being the simpler, and that of *L. clavatum* the more complex.† In the former a radial section discloses only one archesporial cell, in the latter three, and this difference makes itself apparent in the latter in the greater capacity of the mature sporangium; the other dimensions may also vary in a similar degree. Differences such as these, carried to an extreme, would give the enormous sporangium of *Lepidodendron*, which is essentially a Lycopod sporangium showing the result of great radial extension. A rough, though not by any means exact proportion, may be traced between the elaborateness of the vegetative system and the sporangial size, as shown in such forms as those named. Of living Lycopods, the large-leaved *Isoetes* shows the largest of these radially extended sporangia. But mechanical and nutritive difficulties impose a limit upon indefinite extension along these lines, and *Lepidodendron* and *Isoetes* are extreme examples of sporangial enlargement; in both of them structural modifications are apparent, which show that the limit of size of the non-septate sac has been approached; these consist in sterile tracts of tissue, forming trabeculæ, or even partial or complete septa; they suggest that the progression from a simple to a septate sac may be a consequence of partial sterilisation, and that it may arise as an adaptation to meet mechanical and nutritive difficulties.

In *Isoetes*, and in some at least of the cones of *Lepidodendron*, heterospory has been initiated, as also in *Selaginella*; in all of these there are indications of that reduction of the numerical output of spores which so commonly follows on their sexual differentiation, and this has probably been an additional factor in producing those sterile tracts referred to in *Isoetes*, and less completely in *Lepidodendron*; in *Selaginella*, however, the sporangium being of smaller size, no such sterile tracts are found.

It is thus seen that the Lycopodinæ, living and fossil, may be regarded as

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* 'Studies,' I., p. 534.

† 'Studies,' I., pp. 504–539.

illustrating a progression from a simple, slightly differentiated state, with small sporangia, to a more complete distinction of a sterile from a fertile region, frequently with larger sporangia, and from the homosporous, non-septate condition to the heterosporous state, with indications of a partial, or in the megasporangia of *Isoetes* even a temporarily complete septation. If this view be correct, it would be only a slight step further back to refer the whole series, as regards its origin, to the condition of a simple strobilus, in which all the leaves would be fertile; this condition is at least approached in *L. Selago,* in which the sporangia appear at an exceptionally early stage on the seedling plant. This fact, together with the undifferentiated shoot and simple sporangium, mark off the sporophyte of *L. Selago* as a relatively primitive type of Lycopod.

Phylloglossum has been commonly regarded as the most primitive type of Lycopod, and its strobilus certainly seems to be the simplest. The question has been discussed elsewhere as to the nature of the protocorm and protophylls, which are such prominent features in its vegetative system, and the view entertained that they show specially adaptive, rather than general Lycopodinous characters.*

The original Lycopodinous type may then be pictured as an unbranched upright strobilus, in which all the leaves were sporophylls, and the sporangia of moderate size; from this, along the lines above indicated, all known Lycopodinous forms can be derived. Sterilisation, whether of cells, or of cell-tracts, or of whole sporangia, has been an active factor, and vegetative amplification its consequence; branching either in the fertile or the sterile regions is frequent; septation is absent, or only imperfectly represented in *Isoetes*, while of interpolation or fusion of sporangia there is no evidence whatever in any of the Lycopods.

(2). THE TYPE OF THE PSILOTACEÆ AND SPHENOPHYLLEÆ.

In view of recent observations on these plants, and especially of the better knowledge now available of the Sphenophylleæ, it seems desirable to deal with these families together, and apart from the Lycopodinæ, notwithstanding that they have palpable affinity with the latter.

In the Psilotaceæ the axis bears sterile leaves and sporophylls,† which originate similarly on the axis, though they differ in mature form; they are disposed in irregularly alternating zones, as in the *Selago* type of *Lycopodium,* and accordingly the same argument will apply here as to the origin of the shoot by differentiation of a uniformly fertile strobilus.‡

Though the large sporangia of *Lepidostrobus* and *Isoetes* did not achieve actual

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* 'Annals of Botany,' 1901, p. 245, &c.

† It seems better to drop the term "sporangiophore" as applied to the whole appendicular organ, which may be better designated the sporophyll, and to retain the term sporangiophore for the process which arises from its adaxial side. *Cf.* THOMAS, 'Roy. Soc. Proc.,' vol. 19, p. 343.

‡ 'Annals of Botany,' 1901, p. 254.

septation, evidence of that septation is believed to have been found in the development of the synangium of *Tmesipteris*, where normally the sporangium-bearing part holds the same position relatively to the sporophyll as in the Lycopods.* The sporangiophore of *Tmesipteris* would thus be the equivalent of a septate sporangium, with a vascular supply into its stalk. If this be so for *Tmesipteris*, it should hold also for *Psilotum*, and the number of loculi may thus be variable, as is indeed found to be the case in individuals of both genera. The strobili of the Psilotaceæ are thus regarded as an advance in complexity on the Lycopod type, the sporangiophore replacing the simple sporangium.

But variations in the direction of still higher branching of the leaves, and formation of a plurality of sporangiophores also occur. These are usually found in the middle of the fertile zones, and especially in plants grown under favourable circumstances. A less complexity, even below the normal, is found about the limit of the fertile zones, where presumably the nutrition is less favourable; there is thus to be recognised a dependence of complexity upon determining factors, such as, *inter alia*, nutrition.† If such variations of detail as those seen in the individual, species, or genus in the Psilotaceæ had been prevalent in past times, it is reasonable to suppose that some of the results should have become fixed, either as types with greater or with less complexity of the spore-producing parts. In so far as favourable nutrition is one of the determining factors, such progressive sterilisation of sporophylls as has been recognised in the non-strobiloid Lycopods and the Psilotaceæ to be the most probable explanation of their state, will have played an important part, since it provides an increasing vegetative system, with better nutrition as a consequence.

But it may be urged, on the other hand, that the Psilotaceæ show mycorhiza, which is evidence of saprophytic nutrition, and that this in other cases leads to reduction of morphological complexity. It is true that saprophytism is often accompanied by reduction of the vegetative system, but it is not so with the reproductive organs. Ordinary green mycorhizic plants do not show any general reduction of the reproductive system, and even in extreme cases, such as *Sarcodes*, *Monotropa*, or *Neottia*, the stamens are developed as in the non-saprophytic forms. Similarly in the Psilotaceæ their mycorhizic habit, together with their epiphytism, may account for the simplicity of the vegetative organs, as seen especially in *Psilotum*; but it cannot be justly assumed, on account of the mycorhizic habit of the Psilotaceæ, that their spore-producing organs are as a whole on the down-grade of evolution. There seems, on the other hand, a reasonable probability that those sporangiophores in the Psilotaceæ, which are simpler than the normal, are reduced types, consequent on less intense influence of the determining factors of spore-production.

On these grounds I should regard the spore-producing organs in the Psilotaceæ as

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* 'Studies,' I., pp. 539–555.

† 'Studies,' I., p. 544; GOEBEL, 'Organographie,' p. 684, fig. 459; THOMAS, 'Roy. Soc. Proc.,' vol. 69, p. 345; SOLMS LAUBACH, 'Ann. Jard. Buitenzorg,' vol. 4, p. 174.

being not generally reduced, but rudimentary types, related in character to those of the Lycopods, though broken loose from their stereotyped sporangial state, and finding in the vascular supply of their sporangiophores the possibility of producing that latitude of structure to which on occasions their sporangiophores actually do attain. Within the living Psilotaceæ, however, the higher possibilities have not been realised in the form of permanently increased complexity; such branchings of sporophylls, and formation of extra sporangiophores as those described by THOMAS, do not appear normally perpetuated in any known race of plants. The family may be regarded as having in these respects unrealised morphological possibilities of further amplification, rather than reminiscences of a more extensive development in the past.

The fact that such variations as those above discussed exist in the spore-bearing organs of the Psilotaceæ, throws a fresh interest over the variability of number of sporangiophores and sporangia borne by the Sphenophylleæ. One of the most remarkable features of these fossils is the difference in number and character of the spore-bearing organs inserted on the apparently superposed leaf-verticils.*

The Psilotaceæ and Sphenophylleæ resemble one another in certain anatomical features. There can be no doubt of their being naturally related to one another, but differences exist between them in leaf-arrangement, which is verticillate in the Sphenophylleæ, and alternate in the Psilotaceæ; the form of the leaf shows no very near similarity, while in the Sphenophylleæ the fructification is more or less definitely strobiloid and differentiated from the vegetative region. The general plan of the strobilus in the Sphenophylleæ is, like that of the Psilotaceæ, referable to the Lycopod type, but it diverges even more strongly. In the simplest types the relation of each sporangiophore to its subtending leaf is maintained. On such grounds as these I think that the recent suggestion of THOMAS, that the Psilotaceæ should be included, with the Sphenophylleæ, in the Sphenophyllales, is to be upheld.† The two series, though related, should be regarded as illustrating two distinct evolutionary lines,‡ and from this point of view the similarity of the variation in the spore-producing members in the two series gains a special interest.

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* The subjoined statement is derived chiefly from the following sources:—WILLIAMSON and SCOTT, "Organisation of Fossil Plants," 'Phil. Trans.,' 1894, p. 919; SCOTT, 'Studies in Fossil Botany,' p. 92, &c.; KIDSTON, 'Trans. Nat. Hist. Soc. Glasgow,' vol. 6, p. 123; also KIDSTON, 'Roy. Phys. Soc. Edin. Proc.,' vol. 9, 1891, Plate 1; ZEILLER, "L'Appareil fructificateur des Sphenophyllum," 'Mém. Soc. Pal. de France,' No. II., 1893; SOLMS LAUBACH, 'Jahr. d. K. Geol. Reichsanstalt,' Vienna, 1895, vol. 43, p. 2.

† THOMAS, *l.c.*, p. 350.

‡ This is substantially the view of SCOTT, who was the first to compare the sporangial morphology of the Psilotaceæ and Sphenophylleæ ("On Cheirostrobus," 'Phil. Trans.,' vol. 189, 1897, p. 27), and to suggest an affinity between these families ('Studies in Fossil Botany,' p. 499). He, however, qualifies the nearness of the affinity suggested by the remark that "The Psilotaceæ are undoubtedly highly modified plants, very remote from the ancient Sphenophyllineæ, but anatomically they have much in common with them, while they diverge very widely from the typical Lycopods."

In *Sphenophyllum trichomatosum* STUR, the sporangia appear to be solitary near the axils of the bracts, and to be sessile, one (?) on each sporophyll (KIDSTON). It is uncertain whether they had any separate vascular supply. ZEILLER describes how in *S. angustifolium*, and perhaps in *S. tenerrimun*, only one whorl of sporangiophores is borne on each whorl of sporophylls. In *S. cuneifolium*, STERNB (*S. Dawsoni*, WILLIAMSON and SCOTT), the sporangia are borne on elongated pedicels,—the sporangiophores—traversed by a vascular strand, and inserted close to the base of the leaf-verticil, to which they adhere for varying distances upwards. The vascular supply of the sporangiophores is derived by branching from that of the leaf, of which they thus seem to be appendages. Each sporangiophore bears but one sporangium, and the sporangiophores are usually twice as many as the bracts of each verticil; but the number seems not always strictly maintained (KIDSTON). In *S.* (*Bowmanites*) *Roemeri*, SOLMS LAUBACH, two sporangia are borne on each sporangiophore, while the latter are disposed in three concentric verticils on each whorl of bracts, and attached by short stalks. In *S. majus* BRONGN, a species only known as yet in the form of impressions, four sporangia are borne by each sporangiophore, but apparently sometimes six; the sporangiophores seem to have been sessile, or at most very shortly stalked. Mr. KIDSTON says, "I am inclined to think they have been placed in two concentric circles, though on the specimen from which the figure was taken only one group was present." This points to a probability of variation within the species or individual. It is further important to note that in this species the cone is little modified in form from the ordinary foliage branch; the internodes are not shortened, and the bracts not more reduced in the limb than is seen in the segmented leaves of the ordinary foliage branches; the bracts stood out from the axis like the ordinary foliage leaves, and were united at the base into only a narrow collar or sheath. These characters are seen with special distinctness in a specimen of *S. majus* in the Museum at Brussels (KIDSTON).

In *Cheirostrobus*, which SCOTT places in relation with *Sphenophyllum*, while recognising also its affinity with the Equisetales and Lycopodales, the sporangia are grouped in fours upon the sporangiophores, while these are so distributed that three arise from the upper surface of each of the three-lobed bracts; so far as the vascular supply is a guide, it may be concluded that the sporangiophores are appendages of the sporophyll, and especially of its middle segment, since the vascular supply, which later divides into three strands for the three sporangiophores, originates from the bundle which runs on into the middle segment of the sporophyll. It is possible, however, that each sporangiophore should be more correctly regarded as the appendage of its subtending lobe of the sporophylls; in that case the correspondence with the abnormally branched sporophylls of *Tmesipteris* described by THOMAS would be nearer than if they were the special appendages of the central lobe only.

It is thus seen that in the plants above noted there are differences in number of the sporangia produced on each sporangiophore, in the number of the sporangiophores in relation to the subtending leaves, and in the position of their insertion; there are also differences in the number of the leaves in the verticils, and in the extent to which they are coalescent at the base to form a cup-like sheath. Further, the observations are based on comparatively few specimens, sometimes on a single, or even a fragmentary specimen. The case of the Psilotaceæ, plants which have obvious affinities with the Sphenophylleæ, is a warning not to take the number of parts stated for the different species as absolute or invariable. Thus there is reason to look upon the Sphenophylleæ as a group in which the spore-bearing parts are variable in a high degree.

The strobilus of *Sphenophyllum* is in most species sharply marked off from the vegetative region by shorter internodes, by the form of the verticillate leaves, and by their coherence at the base to form a cup, which, owing to the knee-like angle of the lower with the upper region, is widened out so as to include the sporangiophores, while the appressed upper region covers them in. This more differentiated state is, however, linked with that seen in the non-strobiloid Psilotaceæ by *S. majus* on the ground of the characters above noted; in fact, as regards forms, *S. majus* might almost rank as a verticillate representative of the Psilotaceæ.* In other species the strobilus is more clearly differentiated from the foliage region; the verticils are more webbed below, and the sporophylls, which are crowded on the shortened axis, differ widely from the foliage leaves. This condition may be compared with the definite strobilus in most Lycopods, as against the "*Selago*" condition, and it seems reasonable to suppose that here, as in *Lycopodium*, there has been a progression from the less differentiated to the more differentiated state. With this increasing definition of the strobilus there is associated a larger number of the sporangiophores; but it is to be noted that where the number of the sporangiophores is larger, the number of the sporangia which they individually bear is commonly smaller, though there is no strict numerical relation.

How this larger number of the sporangiophores originated it is impossible to say with certainty, but it is significant that where the number of the sporangiophores is the same as that of the sporophylls (as appears to be the case at least sometimes in *S. majus*), the sporangiophore is subtended by the sporophyll, as in the Lycopods and the Psilotaceæ; where the number is double that of the sporophylls, as in *S. Dawsoni*, the vascular bundles of each pair come off as branches from the corresponding foliar bundle. In certain cases also the pedicels are coalescent at the base. Such facts as these would be compatible with fission of sporangiophores, similar to that process which has led not uncommonly to an increase in number of stamens in the flowers of Angiosperms.† But lateral fission, if it did occur, cannot account for all cases of more numerous sporangiophores; in *S. Roemeri* they appear, from the description of

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* It may be noted that the alternate and verticillate arrangements of leaves are both represented in the genus *Lycopodium*, while some species show intermediate conditions between the two.

† Chorisis of the pedicels has already been suggested by SCOTT in the case of *S. Dawsoni*, "On *Cheirostrobus*," p. 27.

SOLMS LAUBACH, to have been arranged in three concentric verticils on each whorl of bracts; in the present uncertain state of the facts for this species, it is useless to surmise how this condition may have come about, but it is to be remembered that antero-posterior fission and interpolation, which are both seen in the Angiospermic flower, might either of them result in the condition observed.

Taking all the facts together, and reading them in the light of those relating to the Lycopods and Psilotaceæ, with which the Sphenophylleæ have undeniable relations, the following seems a reasonable view of their spore-producing members: that the fundamental type is that of the Lycopods and Psilotaceæ, viz., that each spore-producing organ was subtended by a sporophyll. This type appears to hold for *S. trichomatosum*; also, though perhaps without constancy, in *S. majus*, which shows besides in its "*Selago*" condition, and ill-defined strobilus, what may be regarded as a more primitive state than that in the strobiloid species; the sporangiophore in this species is comparable with that in the Psilotaceæ, but it has four to six sporangia.

With the more definite strobilus appears a shortening of the internodes, deeper webbing of the whorls, and an increase in number of the sporangiophores which they individually bear. This may reasonably be regarded as an evolutionary progression, all the features of it conducing to the better protection of the sporangia while young, together with more perfect arrangements for nutrition and dissemination: for the shortened internodes and webbed sporophylls give greater protection during development, but the difficulties of dissemination are increased thereby. To correct this the longer pedicel would be efficient, so as to give the sporangium greater freedom at maturity, but the longer the stalk the greater the difficulties of nutrition; the latter would be met by diminution of the number of sporangia on each pedicel, while the total spore-output would be maintained by the increase in number of the pedicels. In view of these considerations the suggested progression from less specialised to the more specialised types seems probable.

The Sphenophylleæ may then be regarded as a series of ascending complexity; I see in them no indication of general reduction, either in the vegetative or in the spore-producing organs. Compared with the Psilotaceæ the elaborateness of the spore-producing parts stands on a higher scale, and even shows some analogy with the arrangement of parts in certain Angiospermic flowers. Such relation as exists between the Psilotaceæ and Sphenophylleæ is to be traced with the less specialised types such as *S. majus*, and the relation of the two seems to be that the Psilotaceæ have remained on a more primitive footing, with some indication even of reduction of the vegetative organs in connection with their mycorhizic habit, while the Sphenophylleæ progressed to a more complex and definite state of the strobilus.

But the most complex condition of all is that of *Cheirostrobus*.* Without in any sense constructing an evolutionary sequence, which would be highly improbable among these fragmentary remains of past development, it is, I think, just to interpret

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* SCOTT, "On *Cheirostrobus*," 'Phil. Trans.' vol. 189, 1897.

the complex cone of *Cheirostrobus* in terms of those we have been considering, for the fundamental type of the strobilus is comparable with that of the definitely strobiloid Sphenophylls. Adopting then this position, it appears that the departure from the primitive type above sketched for the Sphenophylleæ is carried further in *Cheirostrobus*, but along similar general lines: the vascular supply of the three sporangiophores of each leaf unites below into a single strand, an indication of their common origin by branching, and this strand is inserted on the middle strand of the subtending leaf. A theory of fission of the spore-bearing organ is thus indicated structurally, which is analogous to that suggested for the more complex of the Sphenophylls. It may be noted that such branching of the spore-producing organs occurs also in the spike of *Ophioglossum*, and the specimens represented in my Plates 8 and 9 ('Studies,' II.), show how nearly the supposed branchings in *Cheirostrobus* may be matched. A certain degree of parallelism is also seen between the complexity of the sporophylls and the appendages, which comes out more plainly still in the next series, viz., the Ophioglossaceæ.

(3). THE TYPE OF THE OPHIOGLOSSACEÆ.

There seems good reason to believe that the Sphenophylleæ were homosporous, though this is not decisively proved. The Ophioglossaceæ are also homosporous, with their spore-bearing organs occupying typically the same position, higher or lower, on the adaxial face of the sporophyll as that in the Lycopods, Psilotaceæ, and Sphenophylleæ. The facts have been stated, and their bearings discussed at length elsewhere; a short summary will therefore suffice, with a reference to the former Memoir.*

The whole question of the relations of this family turns upon whether they be regarded as an ascending or a descending series. Those who look upon them as a series of reduction will naturally ascribe to them a Filicineous affinity; those who look upon them as an ascending series of increasing complexity, will be disposed to give them a place in relation to the Lycopodinæ and Sphenophylleæ. The former view is entertained by many botanists, but without, as far as I am aware, any full and detailed statement of the grounds for their opinion. SCOTT gives to the comparison a physiological and anatomical basis; he says, "Personally, I should incline to regard them rather as a specialised family, modified in consequence of saprophytic habit, though probably derived from a very ancient Fern-stock, possibly the same as that from which the Cycadofilices took their origin. This last suggestion is based on a number of points, chiefly anatomical."† The anatomical comparison has not yet been stated, but on the saprophytic habit the following considerations may be advanced: mycorhiza has been observed in *Ophioglossum vulgatum*‡ and in

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* 'Studies,' II., "Ophioglossaceæ," Dulau and Co., 1896.

† 'Studies in Fossil Botany,' p. 511.

‡ RUSSOW, 'Vergl. Unters.,' p. 122. Dr. LANG has verified this fact.

O. pendulum;[*] it has also been seen in twelve species of *Botrychium*, by GREVILLIUS,[†] but in varying abundance, and KÜHN had previously described it for *B. Lunaria*.[‡] In *Helminthostachys* the fungus is present in the first three or four roots of the young plant, but absent in the roots produced later.[§] It is thus seen that mycorhiza is not distributed with constancy in the family; in none of them does it take so prominent a part in the nutrition as to lead to their discarding, or even in marked degree reducing their dependence on the chlorophyll function. The facts will hardly justify the use of the term "saprophytic habit," as applied to them collectively, since the adult *Helminthostachys* is normally free from mycorhiza. But supposing that they all showed mycorhiza, it does not follow that general reduction would be the consequence; a very large number of plants having mycorhiza show no sign of reduction. Further, if reduction did take place, as has been pointed out in connection with the Psilotaceæ, it would primarily affect the vegetative organs, whose functions would thus be disturbed; but it would probably not alter the sporangial conditions, except as a secondary consequence, in case the mycorhiza-nutrition were less effective than the original autotrophic method. How little the occurrence of mycorhiza may be found to affect the morphological characters of Pteridophytes is shown in the Marattiaceæ. According to KÜHN[||] the fungus is found in the roots of *Kaulfussia*, of *Angiopteris*, and of *Marattia alata*, but not in those of *Marattia fraxinea*; but no reduction is to be noted as the result in the former Ferns as compared with the latter. Again, *Cyathea* is stated to have mycorhiza, while *Asplenium nidus* has not.[¶] Such facts as these make me think that it cannot be justly assumed that the mycorhizic habit in the Ophioglossaceæ has been a source of general reduction in the family. The argument in favour of their being a reduction series will have to be based on other evidence.

Pending the statement of that evidence, I may say that the view of them as an ascending series appears to me the more probable.[**] Some grounds for this are as follows: they are not nearly allied in characters to any living Ferns; they are homosporous, and share the general advantage among homosporous forms of an

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[*] JANSE, 'Ann. Jard. Buit.,' vol. 14, p. 64.

[†] 'Flora,' 1895, p. 445.

[‡] 'Flora,' 1889, p. 494. KÜHN failed to find it in *B. ternatum*, but GREVILLIUS showed (*l.c.*, p. 450) that this is probably due to its being isolated in small groups, which may have escaped his observation.

[§] LANG, 'Annals of Botany,' vol. 16, p. 42; FARMER, 'Annals of Botany,' vol. 13, p. 421; see also KÜHN, 'Flora,' 1889, p. 494.

[||] 'Flora,' 1889, pp. 491–497.

[¶] JANSE, *l.c.*, p. 64.

[**] It is a current view that the Ophioglossaceæ date from a remote past, though there is no actual evidence of their great antiquity. But even if they were very ancient forms, it does not follow that they are reduced; they may, like the Marattiaceæ (many of which are mycorhizic) have persisted for long ages in the type once laid down. The view advanced below of their derivation from a strobiloid source is compatible with either an early or a relatively late origin.

enlarging output of spores; the representatives of the family lend themselves to a natural arrangement in sequences leading from simpler to more complex types, while the simpler link themselves as regards the morphological character of their spore-producing members readily with one another, and also with other strobiloid types of Pteridophytes. Behind the comparisons with strobiloid types there is the line of biological probability that such advances as we contemplate should take place: these may be briefly stated as follows:—

The monophyllous character is a leading feature of most Ophioglossaceæ, but certain species of *Ophioglossum*, which are among the simplest of them, develop a number of leaves simultaneously (*O. Bergianum, Lusitanicum, bulbosum, nudicaule*), approaching in this respect the strobiloid type, and the approach is most marked in those species in which the fertile spike is simplest and smallest. The biological advantage of the monophyllous habit lies in the protection of the stock underground, where it perennates during adverse seasonal periods, while the leaves take advantage of favourable periods for assimilation and spore-production. But the soil presents an obstacle to the upgrowth of the leaf, and this difficulty would be minimised by the production of only one leaf annually, and that a large one, rather than a number, which will have each to encounter the same difficulty. Comparison of the species of *Ophioglossum* shows that as the number of the leaves decreases, their elaborateness increases, which is exactly what would be expected, if they represent a series of specialisation derived from a strobiloid source. Such elaboration is seen in a minor degree in the subäerial strobili of the Psilotaceæ, Sphenophylleæ and Cheirostrobus. The prothalli of the Ophioglossaceæ are buried in the soil;* it seems, therefore, reasonable to suggest, that in some such buried habit of the prothallus the buried habit of the upright stock should have originated; this, by an obvious adaptation as above explained, would at least offer opportunity for the acquisition of the monophyllous habit, with the elaboration of the assimilatory and spore-producing parts, as seen in the Ophioglossaceæ.† The size and branching of the subtending leaf has been seen in the Lycopods, Psilotaceæ, Sphenophylleæ and *Cheirostrobus*, to show a parallelism with that of the spore-producing member; this parallelism has been traced in the Ophioglossaceæ also,‡ but especially in the genus *Ophioglossum*, and it may be here again briefly summarised as follows:—

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* Jeffrey, 'Trans. Canadian Inst.,' 1896–7, p. 265; Lang, 'Annals of Botany,' vol. 16, p. 23.

† Some of the chief difficulties in recognising this origin of the Ophioglossaceæ from a strobiloid source are presented on the side of comparative anatomy (compare Boodle, 'Annals of Botany,' vol. 13, p. 377). Though, on the other hand, some of the anatomical details observed in *Helminthostachys* in a measure favour the Lycopodinous affinity (Farmer and Freeman, 'Annals of Botany,' vol. 13, p. 421). Other difficulties are in the sexual organs (Lang, 'Annals of Botany,' vol. 16, p. 50, &c.). But while considering these difficulties, it is to be remembered that no affinity of a very close nature is suggested with the Lycopodiaceæ, not even so close as that with the Psilotaceæ or Sphenophylleæ. The view that is advanced is that these sporophytes are all variants on the same fundamental strobiloid type.

‡ 'Studies,' II., pp. 29 and 42. The peculiar case of *O. simplex*, briefly described in 1901 (Brit.

Starting from a simple type such as *O. Bergianum* or *Lusitanicum*, with a small spike and few loculi, the genus may be laid out so as to illustrate gradual steps of enlargement of the spike, with increase of the number of loculi; the arrangement of these loculi has been shown to be consistent with a theory of septation.* Thus, with intermediate steps such as *O. vulgatum* and *reticulatum*, a type such as the large and often simple spike of *O. pendulum* is reached. But the branching of the spike is another step of increasing complexity; it occurs occasionally in *O. vulgatum* or *reticulatum*; it is frequent in *O. pendulum*, extending sometimes to the sterile stalk of the spike;† in *O. palmatum* a plurality of spikes is the rule, and they are attached mostly upon the upper surface of the leaf, but sometimes on its margin; they frequently show branching in various degrees, which, when compared with similar conditions in other species, is a clear index of their origin.‡ These branchings can hardly be looked upon as mere abnormalities, since they are distinct characters of the species.

Comparison of the sterile leaf in these same species discloses a parallelism in its enlargement and branching.§ In *O. Bergianum* and *Lusitanicum* a small and narrow leaf accompanies the small spike; in *O. vulgatum* and *reticulatum* the leaf is broad in proportion to the larger spike, while in *O. pendulum* the occasional branching of the long strap-shaped leaf nearly matches that of the branching of the large spike. But it is in *O. palmatum* that the parallelism is most clearly shown, for here there is even a near numerical balance between the spikes and the lobes of the very large sterile leaf; these results show, though on a larger scale, a peculiarly close analogy with what is seen in the Sphenophylleæ and in *Cheirostrobus*.

The species of *Botrychium* may be so arranged as to illustrate a similar progression, but along different lines of detail; the simplest beginnings are very similar in outline to the smaller species of *Ophioglossum*, but with the sporangia more individualised as projecting rounded bodies. These sporangia may be enlarged, and intermediate steps are seen leading to two in place of one.‖ The branching of the spike, which becomes so marked a feature in the larger species, is closely connected in the smaller species with this condition of the sporangia. The spike of *Botrychium* would thus be regarded as similar in origin to that of *Ophioglossum*, but showing branching in a higher degree. Here again the branching in the sterile leaf shows parallelism with that in the fertile spike.

Assoc. Report, Glasgow, p. 842) is an exception. Here the sporophyll seems to be absent, though the spike is of large size. I hope to give shortly a more detailed account of this peculiar plant, which was found by Mr. RIDLEY on the island of Sumatra, and handed over to me by Mr. GROOM.

* 'Studies,' II., pp. 52–55.

† It is to be remembered that *O. pendulum* is an epiphyte, and therefore subject to other conditions than ground-growing species. Probably the epiphytic habit was acquired after the main characters were already established.

‡ 'Studies,' II., Plates 8 and 9.

§ 'Studies,' II., p. 30.

‖ 'Studies,' II., Plate 5, figs. 82, 84; also Plate 6, figs. 91–95.

Helminthostachys exists as a solitary species, so that no clues are given by comparison within the genus, but its normal spike is evidently similar in plan to that in *Ophioglossum*, with the marginal rows of sunk sporangia replaced by serried ranks of sporangiophores. If the more elaborate type of *Helminthostachys* were derived from the simpler type of *Ophioglossum*, it would be by the subdivision of the deeply sunk sporangia, and their elevation beyond the surface upon projecting sporangiophores. A double advantage would thus be gained, that of more ready nutrition of the subdivided sacs, and more easy dissemination of the spores when mature. The extension of the vascular supply into them is an additional provision for adequate nourishment. This would involve a repetition of steps similar to those which on our view gave origin to the sporangiophores of the Psilotaceæ and Sphenophylleæ. But here the emergence of the sporangiophores took place in large numbers, on the margins of an Ophioglossaceous spike, while there the origin of the sporangiophores was carried out singly, or in small numbers, on the leaves or leaf-sheaths.

This view of the Ophioglossaceæ as an ascending series of increasing complexity accords thus throughout with the observations on structure and development of the spore-producing parts; it is also on the face of it a physiologically probable one. Clear analogies may be drawn between the spore-producing members which result and those seen in the Sphenophylleæ and *Cheirostrobus*. It is justifiable to trace those analogies, and even to use them as arguments, notwithstanding that the groups are not all closely allied anatomically, since they are believed to illustrate a parallelism in method of advance from smaller to a larger power of spore-production; the parent form for them all is believed to be a strobilus of a Lycopodinous type, with each spore-producing member subtended by a sporophyll; the factors of the advance from the simple sporangium to the more complex sporangiophore are septation, upgrowth of the placenta, extension of vascular supply into it, and branching, with apical growth also, in the Ophioglossaceæ. But even in the most complex forms the sporangiophore may still be regarded as a placental growth, and not the result of transformation of any other member, such as a vegetative leaf-segment.

(4). THE TYPE OF THE EQUISETINEÆ.

This heading includes typically strobiloid forms, but they show considerable diversity in the constituents of the strobilus, and in their arrangement. There are two categories of appendages, the sterile and the fertile. In order to prevent any misunderstanding, the latter will be termed sporangiophores, and their foliar nature will not be assumed; the sterile parts, which are not represented within the strobilus of *Equisetum* or *Equisetites,* though present in that of *Calamostachys*, will be deemed foliar, and comparable with the leaves or leaf-teeth of the vegetative region.

In *Equisetum* the strobilus is limited below by the annulus, which is usually assumed to be an intermediate step of transition between the vegetative leaves and the sporangiophores, the latter being regarded as the result of metamorphosis of the former; this conclusion was arrived at without considering the Calamarian strobili, which have a different constitution. The following is a brief statement of the facts essential for the comparison of the fossils with the modern *Equisetum.*

Of the Palæozoic Equisetineæ that are known, the nearest to the *Equisetum* type is the ancient *Archæocalamites* (*Bornia*);* the leaves were repeatedly branched; the furrows of successive internodes did not alternate as they do in *Equisetum*, but the cone was for the most part like that of *Equisetum* in having no sterile leaves intervening between the whorls of eight or ten sporangiophores; these whorls did not alternate. There is also evidence of the existence of plants with strobili of the *Equisetum* type in the Mesozoic period; thus the *Equisetum* type of strobilus was no recent departure.

But the most prevalent type of strobilus among the early Equisetineæ was that in which the sterile leaf-whorls were interspersed between the series of sporangiophores. Of these the best known type is that of *Calamostachys*, well shown in *C. Binneyana.*† Here sterile leaves and sporangiophores succeed one another in successive whorls; the sterile whorls are commonly composed of twelve coherent leaves, but thirteen have been counted; the sporangiophores are usually six, that is, half the usual number of the leaves of the sterile whorls, but seven and eight have been seen in a single whorl of them, while no whorl of sixteen bracts has been seen. Hence it is clear that the sporangiophores bear no strict numerical relation to the sterile bracts. The position of the bracts in successive whorls of them alternates, the successive whorls of sporangiophores on the other hand do not alternate, "but are placed one above the other in vertical rows. Hence it is evident that their position can bear no constant relation to that of the bracts." (*L.c.* p. 903.)

This absence of a strict relation of the sporangiophores to the bracts comes out also in *C. Ludwigi*, described in detail by WEISS.‡ He remarks of this species (p. 40), that the number of leaves in the sterile whorl is evidently variable; he made several countings, and concludes, "accordingly it may be accepted that there were sixteen leaves in the whorl, but that they might be reduced to twelve (or thirteen ?) by abortion of some of them." The leaves of the neighbouring whorls certainly alternated. Of the sporangiophores he says, the number in each whorl is six, and the successive whorls of sporangiophores stand vertically above one another; but he notes slight deviations from this, perhaps due to torsion. Here, again, there is no strict relation either of number, or of radial position, between the bracts and the sporangiophores; their independence was probably a character of the genus.

But the relation of the two as regards vertical position is also variable within the

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* RENAULT, 'Bassin Houiller et Permien d'Autun et d'Épinac,' vol. 2, p. 80, Plates 42, 43.

† WILLIAMSON and SCOTT, "Further Observations on the Organisation of the Fossil Plants, &c., Part I.," 'Phil. Trans.,' 1894, B, pp. 902–3; SCOTT, 'Studies in Fossil Botany,' p. 47, &c.

‡ 'Abhandl. z. Geol. Specialkarte,' vol. 2, part 1, p. 38.

fossil Equisetineæ; for, as is well known, the sporangiophores occupy in *Palæostachya* a position at the base of the internode, in *Calamostachys* in the middle of the internode, and in *Cingularia* (of which the true relations must be considered still uncertain) at the upper limit of the internode.* Such facts as these, here only briefly sketched, must be taken into account in discussing the morphology of the strobilus of the Equisetineæ, and in deciding the true character of the sporangiophores.

The current view of the strobilus of *Equisetum* is that it is a product of metamorphosis of the sterile shoot, and that the sporangiophore is an altered sterile leaf. This has been re-stated lately by GOEBEL,† on the basis of development of the individual, but without bringing the fossil Calamarian strobili into the comparison. It may, however, be safely asserted that if *Equisetum* and *Equisetites* had never existed, a comparison of the Calamarian strobili with those of other Pteridophytes would have led to a different view; it will be necessary therefore to examine this natural group of the Equisetineæ as a whole, and not only one isolated genus, even though that type be the well-known one now living.

Taking first the developmental evidence derived from *Equisetum*, as given by GOEBEL,‡ it is found that, notwithstanding the difference in mature form (which GOEBEL notes, and from which he concludes that the distinction arose at an early date), the origin of the two bodies is alike; but the sporangiophore, which is the more bulky, soon adopts a mode of growth which leads to a shield-like form. He concludes that the simpler development of the sterile leaf was the more primitive type, and that the stronger growth of the lower surface of the sporangiophore, so as to give it the hypo-peltate form, is a new development. He also alludes to the transitional forms between the two types, such as have been described by GLÜCK and others.§

Before the homology of the leaf-teeth with the sporangiophores is accepted, the grounds upon which it is based are to be examined; they appear to be these:—

(1). Similarity of the cell-structure on first origin.
(2). Similarity of position relatively to the axis.
(3). Transitions, through the annulus and its malformations, from the one type to the other.

The similarity of structure of the two as shown in vertical sections was pointed out by GLÜCK, though, as he himself remarks (p. 362), it holds only for the very earliest stages. But the similarity of segmentation has long ago been shown to be no proof of morphological identity in the case of embryos and hairs; but without going so far afield as this, a comparison of a vertical section through the leaf-margin

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* See SCOTT, 'Studies in Fossil Botany,' pp. 56–67, where the literature is quoted.

† 'Organographie,' pp. 679–682.

‡ 'Organographie,' p. 680.

§ GLÜCK, "Die Sporophyll-Metamorphose," 'Flora,' vol. 80, 1895, p. 364, and Plate 5. References are there given also to MILDE and other writers.

of *Angiopteris*,[*] with a vertical section through its sorus,[†] shows a near similarity of the cell-net: yet this does not suggest any homology of the leaf-margin with the lip of the sorus; and no more can the similarity of segmentation at the outset be held to prove the foliar nature of the sporangiophore.

Both sporangiophores and sterile leaves are lateral appendages of the axis, but this does not of itself prove the point; for instance, in plants which bear prickles, the prickles and the leaves occur together on the shoot; and the former arise not much later than the latter, while similar tissues take part in the formation of both. If both arose simultaneously close to the apex, the early distinction of them would be a matter of difficulty, though they are parts of different morphological character. It is possible thus to contemplate the origin of parts of similar cellular structure, but not morphologically comparable with one another, laterally upon the same axis.

The occurrence of middle forms between the teeth of the normal annulus and sporangiophores appears at first sight important evidence; but, as is well known, intermediate forms occur between ovules and foliage leaves, and, nevertheless, the opinion is widely accepted that the ovule, like other sporangia, is an organ *sui generis*, and not the result of modification of a leaf or leaf-segment.

The strength of the view stated by GOEBEL lies in the fact that it is supported by all three lines of argument above noted, and if it were not for the fossils it would probably not be called in question. But comparison with them suggests an alternative view, viz., that the sporangiophores are not of the nature of phyllomes, but are comparable rather with the sporangiophores of the Psilotaceæ or Sphenophylleæ; these they certainly resemble in form and function, though they differ from most of them in maintaining no strict relation of position to the true leaves. This suggestion must now be examined.

It is based primarily upon those Calamarian strobili in which each leaf-whorl is regularly succeeded by a whorl of sporangiophores. In the strobili the leaves of successive whorls show a radial alternation, as in the vegetative shoot, and it seems natural to suppose that they accordingly correspond to the ordinary succession of them in the vegetative region. But in addition to the sterile leaves, and not disturbing their succession, are the sporangiophores; if these were rightly regarded as leaves, it might be anticipated that the alternate succession of the sterile leaves would be disturbed where the sporangiophores intervene between their whorls, but it is not. Again, the number of the sporangiophores is usually half that of the sterile leaves, but the number is not strictly maintained, while their disposition in vertical, non-alternating series is on a plan quite apart from that of the alternating whorls of sterile leaves. Their position on the internode also, sometimes at the base, sometimes at the upper limit, often in the middle, again shows their independence of the sterile leaves. These facts together point to their being independent structures.

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[*] 'Annals of Botany,' vol. 3, Plate 23, fig. 71.

[†] 'Phil. Trans.,' B, 1897, Plate 10, fig. 66.

In considering the probability of this view, the condition of the spore-bearing parts in other homosporous Pteridophytes should be brought into comparison. Spore-bearing parts of a similar form to the sporangiophores of the Equisetineæ, bearing like them sporangia radially disposed, with a central vascular supply, occur in various positions in other homosporous Pteridophytes; for instance, irregularly disposed in a broad band on either margin of the spike in *Helminthostachys*, related definitely to the leaf in the Psilotaceæ and Sphenophylleæ, or on the leaf-surface in the Marattiaceæ (sori). All these are doubtless the morphological expressions of an advantage in the production of sporangia in groups, projecting beyond the surface, each group having its central vascular supply, while by their close relation to one another, or to the parts which bear them, the sporangia are adequately protected while young. Such sporangiophores would on this view be the result of a similar method of advance taking place at points not morphologically comparable. The resulting sporangiophores, however similar in form, would not be homogeneous, but only comparable in the manner of their production (homoplastic). In none of these cases is it probable that they are of the nature of leaves.*

It may be asked how this non-phyllome theory of the sporangiophores is compatible with the facts in *Equisetum*, in which the annulus has usually been accepted as a transition from the foliage-whorls to the sporangiophores. It is true the annulus lies at the boundary between the sterile and fertile regions, and that in *Equisetum* no vestiges of leaf-whorls are found higher up among the sporangiophores. GOEBEL has pointed out an obvious protective use for the annulus, which would sufficiently account for its constancy and limited size in the genus.† A comparison of other types of Equisetineous strobili affords the following explanation of the *Equisetum* strobilus in terms of the fossils. In the genus *Archæocalamites* (*Bornia*) RENAULT describes‡ for *B. radiata*, BRONGN., how the male fructifications are simple, or interrupted in their length by verticils of leaves, which render the spike itself, so to speak, articulated and of very variable length. The condition of these spikes is then different in proportion, rather than in essential points from that described for *Phyllotheca*,§ and this again differs from *Calamostachys* mainly in the number of the sporangiophores which intervene between the successive leaf-whorls. The tracts which bear the sporangia being thus variable, it would appear that the *Equisetum*-type is merely an extreme case, in which the whole series of sporangiophores which form the terminal strobilus are collectively above the last leaf-sheath, and that last leaf-sheath is of a reduced type, and appears as the annulus.

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* It is not contended that structures similar in form to these sporangiophores never originated from phyllomes; for instance, the foliar nature of the carpels of certain Cycads are clearly of phyllome nature.

† 'Organographie,' p. 681.

‡ 'Bassin Houiller D'Autun et d'Epinac,' p. 81.

§ Reference may also be made to the *Phyllotheca*-like abnormalities of *Equisetum* described and figured by MILDE, 'Nova Acta,' vol. 26, Plate 34, figs. 40, 46.

My own opinion is that in the present state of our knowledge the case is not proved either for the phyllome theory, which is out of harmony with the known facts in the fossils, or for the non-phyllome theory, which certainly is a less obvious explanation of the *Equisetum* strobilus. But the balance of evidence seems in favour of the latter, as without undue pressure it covers the whole area of facts, while it harmonises also with what is seen in other groups of Pteridophytes.

(5). THE TYPE OF THE FILICINEÆ.

In view of the difference in construction of the sporophyte in Ferns from that of the strobiloid Pteridophyta, it is necessary first to inquire what are the probable relations of these series. In point of time the distinction of habit dates back as far as the earliest known fossils, and accordingly it is only by comparison that any opinion can be formed as to their origin by descent, and then only as a probability, not a demonstration. The similarity of life-history shows, however, that the sporophyte of the Fern as a whole corresponds to that of the strobiloid types ; the further question will then be as to the correspondence of the parts, especially the axis and leaf.

The chief difference lies in the proportion of leaf to axis, and in the branching of the leaf, not in the fundamental relations of those parts as regards origin or position ; this is specially obvious in upright growing species, with radial symmetry of the shoot. But the size and complexity of the leaf varies greatly within many genera of Ferns, while in almost all genera some simple-leaved species are found ; thus within the Ferns, and even within the limits of a single genus, differences of leaf-form occur of the same nature, though not of the same extent, as those which mark off the Ferns from other Pteridophytes.

On the other hand, among the strobiloid types, and especially among their fossil representatives, the leaf is not always small, or simple ; the leaves of certain living Lycopods (*e.g.*, *Lycopodium serratum*, THUNB, and *Isoetes*) are relatively large, as were also those of some of the fossils, notably of *Sigillaria* ; the branched leaves of the Psilotaceæ and Sphenophylleæ, and even of some Calamarian forms, such as *Archæocalamites*, are instances of branching of leaves in strobiloid forms ; again, in our view great leaf-enlargement in a Lycopodinous type has resulted in the Ophioglossaceous condition ; thus variety of size and complexity of leaves existed in other Pteridophytes besides the Ferns. Even the dichotomy seen in the relatively small leaves of certain other Pteridophytes (*Archæocalamites*, Psilotaceæ, Sphenophylleæ) may perhaps find its counterpart in the dichotomy which is so frequent in the first leaves of young Ferns.*

Again, the Leptosporangiate Ferns show a very distinctive mode of segmentation, both of apex and margin of the leaf ; but I have shown elsewhere that in this character the Osmundaceæ form an intermediate step from them to the Marattiaceæ, while

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* Compare POTONIÉ, 'Lehrbuch d. Pflanzenpalæontologie,' p. 120.

the latter diverge clearly from the Leptosporangiate type, and show that in detail those definite cell-nets of the Leptosporangiate type are not essential characters of Fern-leaves at large.* These facts point to the justness of the conclusion that the Fern-leaf, however different in size, continued apical growth, and even in its segmentation is essentially comparable to the smaller and simpler leaves of the strobiloid forms. It would appear *à priori* reasonable to assume that in the first instance the larger-leaved were derived from a smaller-leaved ancestry.

On the other hand, there is a chain of evidence to show that certain of the Gymnosperms originated from a larger-leaved Cycado-filicinean ancestry.† It must not, therefore, be assumed that all small-leaved forms were so derived, or that all large-leaved forms were of prior origin, though morphological argument has frequently proceeded on this assumption.‡ The middle position is probably nearest to the truth, viz., that while in the first instance smaller-leaved forms gave rise to the larger-leaved plants which we call "Ferns," conversely, certain of the latter may, along lines of reduction, have eventuated in smaller-leaved Gymnospermic types. We shall, therefore, start from the position that *in the evolution of the Ferns some such leaf-enlargment as is faintly indicated in certain other Pteridophyta was carried out here to a higher degree than in any other Archegoniate plants ; in fact, that the Ferns are essentially strobiloid types which have attained to large and complex leaves.*§

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* 'Annals of Botany,' vol. 3, p. 359, where the results of study of the wings of various Fern-leaves are summarised. It is shown that while a definite marginal series of cells, with definite segmentation, is found in the Polypodiaceæ, the Marattiaceæ and Osmundaceæ (excluding filmy Todeas) have no single marginal series, but the wings when young are composed of cells showing the (T) division, such as are found in the leaves of other Pteridophytes (compare, *l.c.*, Plate 23, figs. 60 and 70–73, with GLÜCK'S figs. 20–29, 'Flora,' 1895). It is evident that the same method of segmentation is found in the leaves of Eusporangiate Ferns as in those of *Selaginella* or *Equisetum*. Similarly (*l.c.*, p. 339), notwithstanding the regularity of segmentation of the two-sided initial cell at the apex of the leaves of the Leptosporangiate Ferns, in the Osmundaceæ there is a single three-sided initial cell, and in the Marattiaceæ there may be a plurality of initials. The conclusion to be drawn from these facts will then be that the regularity of segmentation of apex and wings seen in the Leptosporangiate Ferns is not an essential character of the Fern-leaf at large ; it has probably been acquired in the course of the specialisation of these Ferns, and is not represented in those types which the fossil evidence points out as the most primitive forms.

† See SCOTT, 'Studies in Fossil Botany,' pp. 513–520.

‡ It was a common position, some twenty-five years ago, to regard the Leptosporangiate Ferns as the most primitive Pteridophytes, and to look upon all the rest as the results of reduction, not only of the sporangia and sori, but also of the sporophylls (see STRASBURGER, 'Bot. Zeit.,' 1873, p. 81, &c., as an example of this). It is to me impossible to harmonise such a position with any rational evolutionary view. It is doubtless possible, after assuming the largest developments, to construct the necessary sequences out of known forms, and to arrange them so as to give some appearance of reasonableness ; but the unsatisfactory point is the assumption itself ; it seems quite improbable that the most elaborate leaves can have been the most primitive.

§ This conclusion differs from the views of POTONIÉ ('Lehrbuch der Pflanzenpalæontologie,' 1899, pp. 156–159) and of Dr. HALLIER ('Beiträge z. Morph. d. Sporophylle u. Trophophylle,' Hamburg, 1902). These writers base their arguments upon homologous alternation, regarding the sporophyte as an un-sexed gametophyte. I shall hope on a future occasion to discuss their views in detail.

Among the Ferns, both radial and dorsiventral forms of the shoot occur, and often both may be seen in the same genus, or closely related group of genera. For instance, *Marattia* and *Angiopteris* have upright stocks; *Danæa** and *Kaulfussia* are oblique, or creeping; *Schizaea* and *Mohria* have upright, or oblique axes; *Lygodium* creeping. The Osmundaceæ are all upright, but, among the Gleicheniaceæ, *S. moniliformis* is upright, while all the rest are creeping. *Alsophila blechnoides* has a creeping rhizome in a typically upright genus; *Onoclea sensibilis* has a creeping stock, while *O. Struthiopteris* is upright. In the creeping genera of Hymenophyllaceæ, *H. pulcherrimum* and *H. fuciforme*, and *Trichomanes spicatum* and *H. javanicum* have upright stems. It is thus clear that the two types are not fundamentally distinct; the question may be raised which is the more primitive type.

The results of GOEBEL regarding the dorsiventral state in plants at large will have their bearing here.† He found in a number of instances that the dorsiventral is the derivative form, and the radial the type which, under certain external influences, especially that of unequal incidence of light, undergoes modification. It is not to be assumed that all dorsiventral structures are therefore derivative, but there seems a reasonable probability that in the sporophyte generation the primitive shoot was of the radial type.

The embryonic evidence bearing on this question is rather mixed; doubtless the form of the embryo in Ferns has been strongly affected by the flattened form of the prothallus. In the Marattiaceæ, which represent the prevalent Palæozoic type, the axis of the embryo is from the first vertical; this is even so in *Danæa*, and thus in the development of the individual of this genus that transition is illustrated which we presume to have happened in the race.‡ But in many of the Leptosporangiates a converse change is seen in the individual life; starting with an embryo, in which the axis is from the first oblique, the adult plant may still have an upright axis.§ It is to be remarked that, beyond the influence which the flattened form of the prothallus may have upon the young stages of the embryo, dorsiventrality would be a natural concomitant of leaf-enlargement in cases where the axis is not of strong construction, and the internodes long: while the dorsiventral axis has the advantage, especially when underground as in *Pteris* or *Lygodium*, of being less exposed to conditions of physiological stress; in climbing also the dorsiventral shoot is

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* The mature axis of *Danæa* is often upright, or very slightly oblique, but the axis of the embryo is upright, like that of other Marattiaceæ (BREBNER, 'Annals of Botany,' vol. 10, Plate 9). KUNZE'S drawing of the young plant of *D. simplicifolia* with six leaves, shows the axis still an upright one (SCHKUHR'S 'Farrnkräuter,' Suppl., vol. 1, p. 107).

† 'Organographie,' pp. 71–98.

‡ On embryos of Marattiaceæ, see BREBNER, 'Annals of Botany,' vol. 10, Plate 9; FARMER, 'Annals of Bottany,' vol. 6, Plate 15; CAMPBELL, 'Annals of Botany,' vol. 8, Plate 1.

§ A good example of this is seen in *Osmunda*. The embryo is dorsiventral, but the mature plant upright and radial (CAMPBELL, 'Annals of Botany,' vol. 6, Plate 6).

physiologically successful; it is, therefore, natural not only that dorsiventral types should have originated commonly among the large-leaved Ferns, but also that they should have been perpetuated when formed, and the consequence of that perpetuation would be a large proportion of dorsiventral species, though that may not have been the original type.*

So far as anatomy of the axis bears upon the question of priority of the dorsiventral, or of the radial type, it would seem to point to the creeping axis as the more primitive; the protostelic and solenostelic arrangements are now generally believed to be earlier types than the dialystelic, but the former are found most obviously in the creeping axes, and the latter in the upright. A good example of this, within a natural group, is seen in *Mohria*, as compared with *Lygodium*. But it is to be borne in mind that the upright forms have for the most part their leaves crowded upon a dialystelic stock, though they all start from a protostelic structure in the embryo; the necessary dilation of the stock to accommodate the crowded leaves would demand a distributed vascular supply, while mechanical requirements may also have played their part, for the strains upon the axis from a tufted series of leaves will be better met by a distended, than by a strictly central, vascular arrangement. Such a change from the protostelic to the dialystelic type might well be found as a direct adaptation in plants which retained otherwise relatively primitive conditions of leaf and sorus. Taking all these facts and physiological considerations together, it seems reasonable to hold *that the Fern-shoot was primitively radial, and that the dorsiventral has been a derivative condition, which originated at many points, while its advantages led to its perpetuation in a large number of living Ferns.*

The slight differentiation of the sporophylls from the foliage leaves is a marked feature in Ferns, and the same question arises here as in other Pteridophyta, as to their relations. Such differences as do occur are readily recognised as due to correlative growth, but, in addition to this, middle forms are common between the two;† and these, together with developmental evidence, support the just conclusion that sterile leaves and sporophylls are truly comparable parts. There are those who maintain that sporophylls are, from the point of view of descent, foliage leaves altered by the addition of sporangia; in fact, that the foliage leaf was the prior type, and the sporangium an accessory. I find it impossible to harmonise this position with the facts that sporangia are constant features in all normal Pteridophytes, and that in all normal Archegoniates spore-production is an essential stage in the life-history. The position which appears better to meet the facts for Ferns is, that the

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* According to the views put forward above as to the relationships of the Ophioglossaceæ, they would show an analogy only with the true Ferns, which, however, deserves notice. On the view that *Ophioglossum* is the more primitive type, with its upright stock, and *Helminthostachys* a derivative, there would have been a progression from the upright radial type to the dorsiventral of the same nature as is suggested for various series of the true Ferns.

† GLÜCK, 'Flora,' 1895, p. 233, &c.

two foliar types had a common origin, from a primitive leaf-type which was potentially fertile; certain of these leaves became by abortion of the sporangia sterile, and performed exclusively the assimilating function, while others—or parts of them—remained fertile. *The progressive sterilisation thus contemplated for Ferns is similar in its main features to that which may be traced in the Lycopods.* The fact that in certain Ferns all the leaves, even the primordial leaves, are actually fertile has a very definite bearing on this question.*

Turning now to the sporophylls, there is a prevalent type which underlies the various modes of arrangement of the sori on the leaves of Ferns; a comparative study of the species, even in those genera which, like *Polypodium*, include forms with sori apparently scattered irregularly over the leaf-surface, shows that the arrangement is referable back to that in which the sori form a single superficial or marginal series on either side of the midrib. Where there has been enlargement of the leaf-area this type may be greatly obscured, but even in such genera, when the species are numerous, the reference to this simple type is usually clear. Now, this was the prevalent type of the sori in the early Eusporangiate Ferns, and, with the exception of *Kaulfussia* (where the leaf-area is widely expanded), it is maintained by all the living Marattiaceæ. The genus *Dipteris* may be quoted as a good example, where the narrow-leaved *D. bifurcatum* conforms to the simple type, while the other broad-leaved species show how the sori spread over the surface. The simple type is obscured by enlargement of the leaf-area, and by branching of the parts bearing the sporangia, whether leaves, pinnæ, or sori. The most obvious of these modifications is the branching of the sori which is closely related to the enlargement of the leaf-area, and may, indeed, be looked upon as a consequence of it. Examples have been quoted and figured in numerous cases, and there is hardly any large-leaved type of Ferns which does not show frequent instances of sori which will bear the interpretation of enlargement and fission;† the result is clearly an increased accommodation for sporangia. *We recognise, then, a fundamental prevalent type of arrangement of the sori in two lateral longitudinal rows, on the surface, or the margin of the sporophyll, but that the type may be greatly obscured.*‡

The comparison has been drawn above between the sori of Ferns and the sporangiophores of other Pteridophyta; the structural correspondence is closest in the case of the simplest Fern sori.

Three types of sori have been recognised in Ferns, which may be designated the Simple (*Simplices*), Successive (*Gradatæ*), and the Mixed (*Mixtæ*); they are distinguished by the arrangement and order of appearance of the sporangia, as well as by other characters.§ Of these three the simple type is found characteristic of the

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* PRANTL ('Schizæaceæ,' p. 14) describes this for *Lygodium subulatum*.

† 'Studies,' III., figs. 1 and 3; also 'Studies,' IV., figs. 2, 74, 75, 146.

‡ I hope to return to this subject later as a separate investigation.

§ 'Studies,' IV., p. 122.

Ferns of the primary rocks; the Gradatæ were prevalent in the secondary period, and both of them survive to the present time, but, nevertheless, in point of numbers of living species, the Mixtae are now the prevalent forms, while palæontological evidence points to the relatively recent origin of these forms. There is a great body of evidence, comparative as well as palæontological, which indicates the Simplices as being the most primitive, in which all the sporangia of a sorus are formed simultaneously, while the common disposition of them is in a single series, arranged radially around a central point, or elongated line.

It may well be that no single primitive type for all Ferns existed, and the class as a whole may have originated along a multiplicity of lines, but on the considerations contained in the above paragraphs, *a primitive type, which was probably a prevalent one, may be sketched as having an upright, radial shoot, simple leaves, all of which were potentially fertile, and circular sori, of the radiate uniseriate type, arranged in two lateral rows, on the surface or the margin of the sporophyll.* An upright plant of *Danæa simplicifolia*, with circular sori such as are found in some species of the genus, would not be far removed from such a primitive type.

From such a type the following lines of elaboration of the spore-producing members may be traced, and since they lead to increasing advantages in the nutrition, and dissemination of the spores, there is a biological probability to support the suggestion of them. Preserving the simple type of sorus, a superficial extension of it would accommodate more sporangia than the circular form; this is exemplified in the oblong sori of many species of *Danæa*, in which the irregular size of the sporangia, and frequent partial septa, are evidence in favour of the extension.* Elongation and branching of the leaf would give room for an increased number of sori, as in the larger species of *Danæa*. In *Kaulfussia*, while the circular form of the sori is maintained, their number was increased, probably by fission, of which indications are frequently seen in this Fern, such fissions being probably connected with the increase of area of the leaf surface. An increase in number of the sori has been secured in *Marattia* and *Angiopteris* by elongation and elaborate branching of the leaf, which thus forms the base for a vast series of them. On grounds stated at length elsewhere, the synangial state is regarded as the more primitive, and the sorus with separate sporangia, as in *Angiopteris*, the derivative. Clearly the separation of the sporangia is a biological advantage, in so far as it gives opportunity for better dissemination of the spores.†

The increase of accommodation, by continued apical growth and branching of the

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* 'Studies,' III., p. 67, &c.

† 'Studies,' III., pp. 58 and 76–77. It seems undesirable to apply as a systematic name a word which assumes a view open to discussion. The authors who gave the name *Archangiopteris* to the new genus of Marattiaceæ, held the view that this Fern is a more primitive type than *Angiopteris*; but this opinion may not be shared by others. I should hold its elongated sorus and separate sporangia to indicate a derivative rather than a primitive type as compared with *Angiopteris*, and in its soral characters *Archangiopteris* would thus be the most modern type of the living Marattiaceæ (see 'Flora,' 1899, p. 72).

leaves, is unlimited in *Lygodium* and *Gleichenia,* and the spore-output is unlimited also, though the dimensions of the individual sorus are small; the sorus is often represented in *Gleichenia* by a single sporangium, while that is the constant condition in the Schizæaceæ. This state is regarded as the result of reduction from the circular type of sorus, balanced as regards spore-output by the unlimited increase in number of the sori.

The Osmundaceæ are non-soral, a condition which appears to have existed in certain fossils, and is also seen in *Acrostichum* and some others; there is no clear evidence how this condition arose, possibly it was primitive, but it seems more reasonable to regard it as a form of that variability which is a character of multiple structures.

From the type of sorus seen in the Simplices, it is no great transition to the type of the Gradatæ, where the sporangia are borne in a basipetal succession upon the elongated receptacle. But there is no conclusive proof along what line the transition actually occurred; it is, however, a physiologically probable one, since the nutritive drain of spore-production would thus be spread over a considerable period.* From such a type of sorus as that in the Gleicheniaceæ, where there is a raised receptacle (*Gl. dichotoma*), but simultaneous origin of the sporangia, to *Alsophila,* where there is a basipetal sequence of the sporangia, would be but a slight transition as regards soral characters. The succession once established, its continuance would be assured by the physiological advantage gained, while growth of the receptacle in length, and continued succession of the sporangia, would result in the soral conditions seen in various extreme types of the Gradatæ, where it appears not only in superficial (Cyatheaceæ), but also in marginal sori (Dicksonieæ, Hymenophyllaceæ).†

From the Gradatæ transitional steps have been observed, through the Dennstædtiinæ, to the mixed sorus, where the sporangia of various ages are in juxtaposition.‡ These facts, together with comparison of living forms, and the evidence of palæontology and comparative anatomy, sufficiently demonstrate that the Mixtæ are relatively late derivative Ferns. They are the prevalent Ferns of the present day in point of number of species. They may have arisen by a similar progression from a number of points, and thus represent a brush of parallel or divergent lines. The physiological drain of spore production is here still further spread over a continued period, while their mechanisms for dispersal show a high degree of precision; thus their derivative position is supported on physiological grounds; I regard them as a series of blind branches of descent.

It may be briefly stated that the type of sorus in the Hydropterideæ resembles most nearly that of the Gradatæ, allowance being made for the reducing effect of their heterospory, and their peculiar habit.

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* 'Studies,' IV., p. 115.

† For a general discussion of this, see 'Studies,' IV., pp. 122–132.

‡ 'Studies,' IV., pp. 71–74.

The above sketch shows how the main types of living Ferns may be referred in origin to the type with the radiate uniseriate sorus.* It may be a question whether all types of Ferns were so derived, and the non-soral forms present peculiar difficulties. There are also certain fossils which cannot be readily included within the lines of the above sketch; for instance, *Botryopteris* and *Crossotheca.* I mention this in order to show that the above views are not put forward as any complete account of the sporophyll-morphology of all Ferns.

It is thus seen that the Ferns, notwithstanding their apparent divergence of character from other Pteridophytes, may be regarded as essentially strobiloid forms which have undergone great elaboration of their appendicular organs; also that the more primitive soral conditions resemble in a measure those groups of sporangia borne on sporangiophores in certain other Pteridophytes, the more complicated soral conditions were probably derived from these, as a result of later evolution, the chief feature of which was the interpolation of new sporangia; and, lastly, that the suggested steps are in accordance with biological probability, as well as with the palæontological record.

The position at which we have arrived then is this: that though the mode of origin of the various forms of Pteridophyta cannot in the nature of the case be proved, it has been shown that the structural facts for their sporophyte are compatible with a theory of progressive sterilisation of the tissues; that from comparison with Algæ and Bryophytes a suggestion is given how the earlier steps may have been taken in producing a vegetative system by sterilisation of an enlarging sporophyte, and that in the case of single cells, tissue-tracts, sporangia, and even whole sporophylls and their appendages, facts are numerous in the Pteridophyta which are readily explained as instances of such sterilisation. Correlatively increased vegetative growth is seen in many cases, and as a result spore-production may be indefinitely delayed.

But the vegetative system, which thus takes its place first in the ontogeny, is naturally liable to great modification, in accordance with its function, indeed it seems not improbable that the vegetative and sporogenous systems, when once differentiated, may vary independently of one another; this comes out with special clearness in the Phanerogams, and particularly so in the case of parasites, this independent variation of the vegatative and sporogenous regions has probably held, though in less degree, in the Pteridophytes also. Comparative evidence of a common origin of the vegetative and sporogenous systems would thus tend to be obliterated. So far is this the case that in vascular plants the embryology and early vegetative development of the sporophyte do not give direct or consistent support to a theory of sterilisation. This, together with the lateness of the spore-formation in the individual life, have obscured the evolutionary history. Still in certain cases spore formation does appear early; interesting examples are seen in *Lycopodium Selago*, where sporangia may be formed

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* 'Studies IV.,' p. 87, &c.

soon after the first branching of the young plant, a fact of special interest in so primitive a form: in *Phylloglossum* and in *Lygodium subalatum*, in which PRANTL notes that sporangia are formed on all the leaves, even of the young plant.

The primitive sporophyte was probably of a radial type of construction, as are also sporogonia, and microphyllous, with simple spore-bearing organs. The megaphyllous state was probably of derivative origin. The more elaborate sporangial arrangements arose by amplifications of simpler arrangements, by branching and repetition of them, by placental upgrowths, and in more specialised cases by interpolation. On this view the Leptosporangiate Ferns are the extreme examples of specialisation of the megaphyllous habit, they show not only interpolation of new sporangia in the sporophyte, but also as frequent characters those peculiar signs of instability which are associated with apogamy and apospory; these irregular developments are regarded as additional marks of a series which has departed far from the primitive type. The primitive regularity is more nearly maintained in the smaller-leaved Pteridophyta, and probably with the greatest fidelity in the Lycopods.

EFFECT OF THESE RESULTS ON SYSTEMATIC GROUPING OF THE PTERIDOPHYTA.

The results from the study of the spore-producing members thus summarised on the systematic grouping of the Pteridophyta do not introduce any great change from the grouping at present current. But any arrangement based on comparative study of the spore-producing members must be checked by consideration of other characters, anatomical and embryogical, as well as those of the gametophyte and sexual organs, though, as explained elsewhere,* the spore-producing members are to be accorded prior importance over the vegetative organs in sporophyte, on the ground of evolutionary history. This method has, in fact, been the practice in classification by systematists at large.

The general comparison points to a radial strobiloid type underlying the construction of the neutral generation in all the Pteridophytes; but this type has been subject to modification by megaphyllous, and by dorsiventral development. The latter is characteristic throughout of no great group, but appears to have originated sporadically, it is therefore of only small account for systematic purposes. But the enlargement of the leaf appears general in some groups, such as the Ferns and Ophioglossaceæ, and, in a less degree, in the Sphenophylleæ and Psilotaceæ. The comparisons given above show, moreover, that the complexity of the spore-producing members in the homosporous Pteridophytes goes hand in hand with the complexity of the leaves, a fact which readily finds its explanation on a basis of nutrition. Accordingly, if the size and complexity of the leaf be the basis, the groups would then be arranged according to the characters of the most essential parts of the sporophyte.

Following this method, the Ferns take their place at one extreme; the small-leaved types, as exemplified by the Equiseta and Lycopods, will occupy the other extreme

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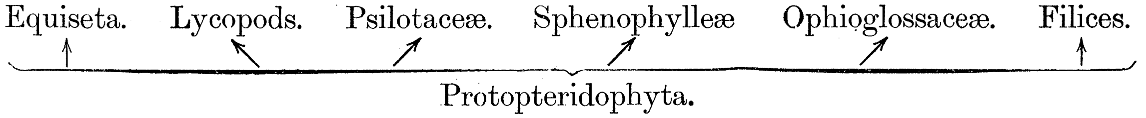
* 'Studies,' I., p. 475.

of the series, and between these will be ranked, according to the prevalent size and complexity of their leaves and spore-bearing members, the Psilotaceæ, Sphenophylleæ, and the Ophioglossaceæ. It must be clearly apprehended that the groups thus disposed are not held to be a simple evolutionary sequence, their relations to one another and to primitive forms (Protopteridophyta), which in my view were probably strobiloid and microphyllous, is suggested roughly by the following scheme :—



The view that the strobiloid type is the fundamental one harmonises with the anatomical facts. The non-medullated protostele is generally accepted by anatomists as the primitive arrangement in the axis ; it is found still among the Lycopods, persistent in the mature individual. But even large-leaved Ferns of most complex mature structure, such as the Marattiaceæ, show a single solid protostele in the young plant.[*] The same is the case generally in the young state of Leptosporangiate Ferns,[†] and even in the mature condition of some of them. It is so sometimes in the young plant of *Helminthostachys*, but " more usually a few parenchymatous cells are present in it."[‡] This is the case also in *Botrychium virginianum*,[§] and in *Equisetum*.[||] The medullated monostele is usually regarded as an advance upon the protostele, though in the cases quoted the difference is a very slight one. Other more complex arrangements, which it is unnecessary to follow into detail here, may arise later in the individual lives, and will appear to be natural consequences of leaf-enlargement in individual or race ; *the point for us is that in all the great groups of Pteridophytes either the protostele, or the medullated monostele, is found in the young plants ; such an anatomical structure is at least in accordance with the theory of a small-leaved strobiloid origin.*

Turning to the mature condition, the vascular systems show great diversity of detail. Founding his distinctions on vascular characters, Dr. JEFFREY has proposed the division of the Pteridophytes into two " great primitive stocks," viz., the Lycopsida, which are cladosiphonic and small-leaved, and the Pteropsida, which are phyllosiphonic and large-leaved ;[¶] this division may be upheld as a useful descriptive distinction on anatomical characters ; the relation of this grouping to our series may be shown thus :—

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[*] FARMER and HILL ('Annals of Botany,' vol. 16, p. 399), and BREBNER ('Annals of Botany,' vol. 16, p. 550). I prefer the results of these writers to those of Dr. JEFFREY ('Phil. Trans.,' B, vol. 195, p. 120, 1902), who had evidently based his conclusions on the observation of older specimens.

[†] This is shown in a statement referring primarily to *Alsophila excelsa*, but also to other Leptosporangiate Ferns, by Mr. GWYNNE VAUGHAN, in the 'Annals of Botany,' vol. 17, p. 710.

[‡] LANG, 'Annals of Botany,' vol. 16, p. 42.

[§] JEFFREY, 'The Gametophyte of *Botrychium virginianum*,' Toronto, 1898, p. 22 and fig. 61, *m*.

[||] JEFFREY, 'Boston Soc. Nat. Hist. Mem.,' vol. 5, No. 5, p. 171.

[¶] 'Phil. Trans.,' B, vol. 195, p. 144.

- Lycopsida
  - Equiseta.
  - Lycopods.
  - Psilotaceæ.
  - Sphenophylleæ.
- Pteropsida
  - Ophioglossaceæ.
  - Filices.

In speaking of his Pteropsida, Dr. JEFFREY remarks (p. 144), that they "had from the earliest times large leaves." It is quite true that large-leaved types existed at the very earliest period of which there is any fossil record. But comparative morphology looks beyond this. That large-leaved forms were throughout descent large-leaved, seems as incredible to those who hold to a theory of antithetic alternation, as that Minerva sprang fully armed from the head of Jove. It is open to us to inquire whether comparison gives any suggestion how the large-leaved types, with foliar gaps, may have originated.

There are two lines of such comparison: from external forms, and internal structure. Differences of size of the leaf exist within near circles of affinity; in the genus *Lycopodium* such differences between species are very marked; in the Psilotaceæ there is a palpable advance by branching from the general Lycopodinous plan. Among the fossils, *Archæocalamites* shows a branched Calamitian leaf, and some Sphenophylls show more branched leaves than others. Instances might be indefinitely extended among the Ophioglossaceæ and Ferns to show that leaf-complexity and size are very variable within near limits of relationship. These suggest that the megaphyllous character was probably derived from some simpler source, being an extreme and permanent condition of such variability as we see exemplified in the various phyla.

Similarly with the phyllosiphonic arrangement of the vascular tissue, it is open to any one to hold that this is nothing more than the internal structural expression of the accomplished fact of a larger leaf-development, and confirmed as a constant in those plants where large leaf-development is the type. A race originating from a small-leaved stock, and becoming large-leaved, would in the process undergo conversion from the one anatomical type to the other. Something of this nature is actually the case in the young Leptosporangiate Fern, where the stem is protostelic at first, and only becomes phyllosiphonic at a later stage.*

If such changes did take place during descent, the distinction of Dr. JEFFREY would not rank as defining phylogenetically distinct races, but rather as a register of such leaf development in the mature plants as differentiated them from some common source. This is the view of the facts which I adopt, and consequently the Pteropsida and Lycopsida are, in my view, not to be regarded as without any phylogenetic relation, but two phases of development of a strobiloid type, separated at a very early period on the ground of external form, and consequent anatomical difference.

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* See GWYNNE VAUGHAN, *l.c.*

But the question remains whether this megaphyllous development happened only once, or more than once among the Pteridophyta; in other words, whether all Dr. JEFFREY'S Pteropsida are really akin, so far as to represent one primitive stock. They include the Filices and the Ophioglossaceæ; the doubt will be as to the phylogenetic relation of the latter to the other Pteridophyta, and especially to the Filices.

In the second Memoir of this series (*l.c.*, p. 77) I upheld the view of CELAKOVSKY, which was thus expressed: "That both the Lycopodiaceæ and Ophioglossaceæ sprang from a common stock, which had the simple sporophylls of the Lycopodiaceæ. The Lycopods are probably of living plants, the nearest prototypes of the Ophioglossaceæ." Their affinity by descent was thus recognised with the strobiloid types rather than with the Filices. Since that Memoir was published, important facts have been disclosed by JEFFREY* and by LANG,† which add greatly to the knowledge of the sexual generation and embryology of the family; the knowledge of the gametophyte of the Lycopods has also been greatly extended by BRUCHMANN‡ and by LANG.§ The latter has written a clear statement of the bearing of the new facts upon the relation of the Ophioglossaceæ to other Pteridophyta, pointing out that they favour a more intimate Filicineous affinity. The chief points brought forward by him as regards the comparison of the gametophyte of the Ophioglossaceæ with the homosporous Lycopodiales, are summed up as follows: "There are no characters, the morphological value of which is attested by constancy throughout obviously allied groups, indicating affinity between the two; on the other hand, important points of difference exist in type of symmetry, in the sexual organs, and in embryogeny." Comparing them with the Filicales he sums up thus: "The form of the prothallus, structure of the sexual organs, and, though less clearly, the embryogeny of the Ophioglossaceæ, are such as might be expected in saprophytic forms derived from prothalli of the general type found in the Filicales. On the other hand, there appear to be no fundamental points of difference." He suggests especially comparison with forms not unlike the existing Marattiaceæ, though possibly belonging to a more primitive group, and remarks that evidence from the sporophyte "would require to be sufficiently clear to override the indications of a Filicineous affinity afforded by the prothallus. In the author's opinion such preponderating evidence has not been advanced."

The main points on which this conclusion is based are that in the Ophioglossaceæ the growth of the prothallus is apical, the spermatozoids are multiciliate, a basal cell is present in the archegonium, and a suspensor is absent, all which characters they share with the Filicineæ. In the homosporous Lycopods, however, the growth of the prothallus is essentially intercalary, the spermatozoids biciliate, the archegonium

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* 'Canadian Institute Trans.,' 1896–7, p. 265.

† 'Annals of Botany,' vol. 16 (1902), p. 23.

‡ 'Ueber die Prothallien und die Keimpflanzen mehrerer Europ. Lycopodien,' Gotha, 1898.

§ 'Annals of Botany,' vol. 13, p. 278, &c.

has no basal cell, and the suspensor is present. In face of these facts the position of the Ophioglossaceæ requires reconsideration.

It is necessary to note that CELAKOVSKY'S thesis does not specify the genus *Lycopodium*, nor even the homosporous forms, but simply the "Lycopods," a term which then included the Psilotaceæ and also the heterosporous *Isoetes*; on the other hand, it leaves out of account the Sphenophylleæ as being an extinct group. But these all take their place between the homosporous Lycopods and the Ophioglossaceæ, in our present view, on grounds of comparison of the sporophyte. The details of the gametophyte of the Psilotaceæ and Sphenophylleæ are unfortunately not available for comparison,* so that we are thrown back for comparison of the sexual generation upon *Isoetes* only, a genus which, on grounds of its heterospory, some may be disposed to discount.† It is a remarkable fact that two of the Filicineous characters above noted by LANG for the Ophioglossaceæ, are shared by *Isoetes*, viz., the multiciliate spermatozoids and the absence of a suspensor. These facts, taken together with the characters of the sporophyte, which show clearly Lycopodinous qualities, with a leaning towards megaphylly, and a corresponding extension of the sporangium, indicate in its case a singular parallelism of these apparently independent characters, and a tendency in them all towards those characteristic of Ferns. So much is this so, that various writers have, notwithstanding the palpable Lycopodinous type of its sporophyte, ranked *Isoetes* with the Ferns.‡

From Isoetes then we learn that a combination of cross-characters is found in a megaphyllous Lycopod type. What we find in the Ophioglossaceæ is that in conjunction with their more pronounced megaphyllous form, still retaining, however, the Lycopodinous plan of the sporophyte, they show more pronounced "Filicinean" characters of the gametophyte and of the sexual organs. With a view to bringing out more clearly the parallelism of the megaphyllous character with the "Filicinean" characters of the sexual generation in these Pteridophytes, they may be tabulated as follows :—

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* See 'Roy. Soc. Proc.,' 1901, p. 408, where LANG describes a prothallus found in close association with plants of *Psilotum*, which he inclines to ascribe to *Psilotum*, though the positive evidence is wanting. It is a prothallus of Lycopodinous type, and bears antheridia.

† It is to be noted that while *Isoetes* has multiciliate spermatozoids, and no suspensor, *Selaginella* has a suspensor and biciliate spermatozoids. Thus, these characters do not appear to be determined by the heterosporous condition.

‡ VINES, 'Annals of Botany,' vol. 2, p. 117) suggested a relation of *Isoetes* to the Ophioglossaceæ and Marattiaceæ. CAMPBELL ('Mosses and Ferns,' p. 274) places them with the Eusporangiate Filicineæ, but the consensus of later opinion is decidedly in favour of a Lycopodinous affinity, whether from the side of anatomy (SCOTT and HILL, 'Annals of Botany,' vol. 14, p. 413, &c.) or sporangia (WILSON SMITH, 'Bot. Gaz.,' vol. 29, p. 337, and myself); or from the comparison of fossils (SCOTT, 'Studies in Fossil Botany,' p. 502, and POTONIE, ENGLER, and PRANTL, I., vol. 4, p. 752). In ENGLER'S 'Syllabus' they stand as a third sub-series, Isoetineæ, under the Lycopodiales Ligulatæ. GOEBEL, on the other hand ('Organographie,' p. 387), thinks they are better ranked near to the Ferns as a special group, which shows unmistakable relations also to the Lycopodineæ.

	Growth of the prothallus.	Spermatozoids.	Archegonium.	Suspensor.	Habit.	Spore-producing members.
Lycopodiaceæ .	Mainly intercalary.	Biciliate	No basal cell	Suspensor	Leaves small	Solitary sporangium on sphorophyll.
Isoetaceæ . .	Reduced, no apical growth.	Multiciliate	No basal cell	No suspensor	Leaves enlarged	Solitary, trabecular sporangium on sporophyll.
Psilotaceæ . .	?	?	?	?	Leaves branched	Sporangiophore replaces the Lycopod sporangium.
Sphenophylleæ .	?	?	?	?	Leaves often branched	One or more sporangiophores on each sporophyll
Ophioglossaceæ	Apical	Multiciliate	Basal cell	No suspensor	Megaphyllous	Complex spike (one or more) replaces sporangium of Lycopods.
Filices . . .	Apical	Multiciliate	Basal cell	No suspensor	Megaphyllous	Complex sori distributed over leaf-surface.

It thus appears that between the extremes of the microphyllous Lycopods and the megaphyllous Filices lie certain families which take a middle position; of these the Isoetaceæ and Ophioglossaceæ show cross characters; their sporophytes are constructed on the Lycopod type, modified in the direction of megaphylly, while their gametophytes are more definitely "Filicinean." The relation of these to the Lycopods is strengthened by comparisons with the Psilotaceæ and Sphenophylleæ, in which unfortunately the details of the gametophytes are not known, though their sporophytes are referable to an amplification of a strobiloid plan, akin to that of the Lycopods.

The parallelism thus recognised between enlargement of the leaf of the sporophyte and "Filicinean" characters of the gametophyte may be compared with other parallelisms of characters in the two generations of Pteridophyta; for instance, that which has already been noted between the sporangia and the sexual organs in the Filices, in respect of their bulk and position. It has been shown that where the sporangia are large and broad-based, or even sunk in the tissue of the sporophyte, the antheridia are also large, and are often sunk in the tissue of the prothallus, while the venter of the archegonium is also immersed; this is so in the Eusporangiate Ferns. But where the sporangia are smaller, and project, being borne on thin stalks, as in the Leptosporangiate Ferns, there the sexual organs also project, and the antheridia are of smaller size. The probable evolutionary progression in our view would be from the larger and deeper-seated condition of the parts named, in the Eusporangiate Ferns, to the smaller, projecting or stalked parts in the Leptosporangiate Ferns, the latter being the more specialised.

To a certain extent a similar parallelism may be traced in other phyla, for instance, the homosporous Lycopods, the Equiseta, and the Ophioglossaceæ, which are Eusporangiate, have also sunken antheridia; and it would seem probable that the broad-based, or sunken type for both sexual organs and sporangia was the primitive type for the Pteridophyta. The Leptosporangiate state was acquired in the Ferns only, and therefore it is only within the Ferns that this parallelism is of comparative value.

Another parallelism, again within the Ferns, which it is difficult to refer to any common external influence, is that pointed out between the mode of dehiscence of the antheridium and the position of the annulus of the sporangium.* It is found that, with the exception of *Mohria* and *Aneimia*, all Ferns with an oblique annulus have a dehiscence of the antheridium with a cap-cell, which breaks away; all those with a vertical annulus have a star-like dehiscence of the antheridium. *In such cases as these, where there is an obvious affinity of all the plants compared, it may be held as probable that there has been a progression from one type to the other within the group, the progression affecting the parts of both the generations.*

But the case becomes more difficult to understand when the parallelism involves representatives of distinct phyla, as in the case tabulated above; and the interpretation becomes still more obscure when it is remembered that for the Equiseta the parallelism does not hold; there the gametophyte has the obvious "Filicinean" characters of apical growth, and of the sexual organs, while a suspensor is absent;† these characters are combined with an entirely non-Filicinean sporophyte, which certainly shows nearer analogy to the Lycopods than to the Ferns. *Such cross characters are difficult to harmonise with any phylogenetic theory; on account of them the Equisetineæ are placed in an isolated position, and in the same way, though with less pressing grounds, a separate position should be accorded to those types which lie in the above table between the extreme types of Lycopods and Ferns, in proportion as the crossing of the characters is more or less pronounced.*

On this basis the Isoetaceæ would probably take their place as a sub-series of the Lycopodiales, Ligulatæ.‡ *The Psilotaceæ and Sphenophylleæ would constitute a series of Sphenophyllales, separate from, but related to, the Lycopodiales.*§ *The Ophioglossaceæ would form an independent series of Ophioglossales,*‖ *more aloof than the latter from the Lycopodiales, but not included in the Filicales, though having a relation to them.* The actual connection of these series by descent must remain open, and it is quite possible that some or all of them may have originated along distinct

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* 'Studies,' IV., p. 127–8.

† Considerable importance is attached by JEFFREY and by LANG to the presence or absence of the basal cell of the archegonium as a comparative feature, and their view is based on the constancy of this character in Lycopods and Ferns; but in *Equisetum* (CAMPBELL, 'Mosses and Ferns,' p. 430) "usually, but not always, no basal cell is formed." Again, in *Lycopodium* the biciliate form of spermatozoid is not constant: there may be three cilia. (BRUCHMANN, *l.c.*, p. 32; GOEBEL, 'Organographie,' p. 387.) These facts may in some degree affect the comparative value of such characters.

‡ Compare ENGLER'S 'Syllabus,' p. 65, where this position is assigned to them, though others may prefer to give them a still more isolated position, as approximating more towards the Filicinean series.

§ The Psilotaceæ are placed in the Lycopodiales Eligulatæ in ENGLER'S 'Syllabus' (p. 64).

‖ Compare ENGLER'S 'Syllabus,' p. 63, where they are placed as a third series of the Filicales. I prefer to give them a position independent of the Ferns altogether. This independence of the Ophioglossales will harmonise with the anatomical results (FARMER and FREEMAN, 'Annals of Botany,' vol. 13, p. 421–444).

lines from a general primitive group, which may provisionally be designated the Protopteridophyta. These were probably small-leaved strobiloid forms, of radial type of construction, and with the sporangia disposed on some simple plan. The grouping thus arrived at may be tabulated* as follows.

PTERIDOPHYTA—
- i. EQUISETALES.
    - Equisetaceæ.
    - Calamariaceæ.
- ii. LYCOPODIALES.
    - *a.* Eligulatæ.
        - Lycopodiaceæ.
    - *b.* Ligulatæ.
        - Selaginellaceæ.
        - Lepidodendraceæ.
        - Sigillariaceæ.
        - Isoetaceæ.
- iii. SPHENOPHYLLALES.
    - Psilotaceæ.
    - Sphenophyllaceæ.
- iv. OPHIOGLOSSALES.
    - Ophioglossaceæ.
- v. FILICALES.
    - *a.* Simplices.
        - Marattiaceæ.
        - Osmundaceæ.
        - Schizæaceæ.
        - Gleicheniaceæ.
        - Matonineæ.
    - *b.* Gradatæ.
        - Loxsomaceæ.
        - Hymenophyllaceæ.
        - Cyatheaceæ.
        - Dicksonieæ.
        - Dennstaedtiinæ.
        - Hydropterideæ (?).
    - *c.* Mixtæ.
        - Davallieæ.
        - Lindsayeæ.
        - Pterideæ and other Polypodiaceæ.

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* It should be clearly understood that this tabulation is not intended to convey the idea of an evolutionary sequence.