Is the Eusporangiate or the Leptosporangiate the more primitive type in the Ferns[1]?

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With Plate VII.

IN my paper on 'The comparative examination of the Meristems of Ferns as a phylogenetic study,' published in the Annals of Botany, vol. III, p. 305, &c., a very considerable number of facts were passed in review, relating to the embryonic tissues of root, stem, leaf, wing, and sporangium; the observations were made upon representatives of various divisions of the Filicineous series, viz. the Hymenophyllaceae, Polypodiaceae, Cyatheaceae (in part), Schizaeaceae, Osmundaceae, and Marattiaceae. The main result was to show that there is a singular parallelism in character of all the meristems in these several divisions; it was demonstrated that, in the divisions first named, the meristems of each of the constituent parts of the plant are relatively simple in construction, and exhibit a definite regularity of segmentation, one initial cell (or in the wings a row of initial cells) of definite form being present in each. Passing onwards through the series, this simplicity and regularity is departed from; the structure be-

[1] This question was discussed by the author at the Royal Horticultural Society's Conference on Ferns, in July, 1890, and a statement of his views then put forward is printed in the Journal of the Society, N. S, vol. XII. pp. 496–505.

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comes more complex, the identity of the single initial is lost, and the regular sequence of segmentations gives place to a less definite arrangement. On these characters therefore, as well as on those of the mature parts to which the meristems give rise, the Ferns may be arranged as a series: at the one end are the typically more delicate Leptosporangiate Ferns, while at the other would be the typically more robust Eusporangiate forms. It was further remarked in the paper above quoted that this parallelism as regards complexity of structure does not appear only in the parts of the sporophyte, but also that it may be traced in the sexual generation: that in the Hymenophyllaceae, which have a peculiarly delicate structure of the sporophyte, the prothallus is frequently filamentous, and the sexual organs freely exposed, while in the more robust Eusporangiate Ferns, such as *Marattia* or *Ophioglossum*, the prothallus is massive, and the sexual organs deeply sunk in its tissue. Accordingly, whether the general character of the sporophyte, or of the gametophyte be considered, the divisions of the Filicineae might be arranged as a series, extending from the typically Leptosporangiate forms on the one hand to the typically Eusporangiate on the other; the Osmundaceae, and in some respects the Schizaeaceae, also taking an intermediate position, and serving as connecting links between the two extremes. The question whether or not this series is to be regarded as a simple linear sequence, will be discussed later on.

The series thus roughly blocked out appears to be a natural one, from the facts that the Filicineae themselves are obviously a natural group, and that the steps from one extreme to the other are gradual and consistent in all the parts. The next question will naturally be, which is the lower and which the upper end of the series; which is the more primitive, and which the more recent, and derivative type? It is to the reconsideration of this very important question that I propose to devote the following pages. The opinion currently held by botanists is that the simpler, Leptosporangiate Ferns are the more primitive, and that the Eusporangiate Ferns occupy

a higher position in the developmental tree: this view I shared when writing, two years ago, the paper above quoted: I there definitely stated, however, that the converse view was capable of defence (p. 374); in fact, that the simpler Ferns might be regarded as forms which had degenerated, and owe their more delicate structure to adaptation to life in moist shade: but this view I did not then accept. Subsequently the question has been taken up by D. H. Campbell[1], who has argued in favour of the Eusporangiate forms as being primitive rather than derivative: yet, though he has brought forward various points of interest and importance, the whole matter has not been by any means exhausted, and I therefore propose to look into the evidence which may be adduced in support of the two views, and to consider first what basis of evidence there actually is in favour of the view now currently held.

Seeing that the broadest lines of progress of evolution have commonly led from the smaller and simpler to the larger and more complex, there has been a general disposition to assume that the simpler terms of any series are the more primitive. This assumption has doubtless affected the views of botanists with regard to the Ferns, and has led to the established opinion that the Hymenophyllaceae, being structurally the simplest, approach the primitive Filicineous type more nearly than other living forms. But a simplification of structure has been recognised in so many cases as following on exposure to certain conditions of life, that the idea of degeneration has become a familiar one. We are therefore no longer justified in making the above assumption unless it be supported by a knowledge of the environment past and present, as well as by comparative evidence. For such evidence recourse must be had in the present case to lower rather than to higher forms, and the comparison has been commonly drawn between the Filmy Ferns and the Mosses: notwithstanding the wide differences between them, it has been generally held that of all Vascular plants the Hymenophyllaceae approach most nearly to the Bryophyta.

[1] Botanical Gazette, Jan. 1890.

It is not my object here to give a complete history of the origin and growth of this opinion: it is however one of long standing. Both Linnæus and Sprengel placed the Hymenophyllaceae at the end of the series of Ferns, while the Mosses immediately followed them: notwithstanding that R. Brown and Sir W. Hooker[1] preferred to make them 'part of the Polypodiaceae, ranking near *Davallia* and *Loxsoma*,' Presl[2] and Bernhardi separated them as a special family of Ferns, and the former writer concludes that the Hymenophyllaceae are rather far removed from the Filicineae, and must be regarded as a connecting link with the Mosses and Liverworts[3]. Van den Bosch[4] went so far as to erect them into an order, which he styled the Bryopterideae, and placed them between Mosses and Ferns. These views were however based chiefly on the external characters of the Sporophyte; when the internal structure of the Sporophyte as well as the characters of the prothallus had been investigated by Mettenius, he concluded[5] that the views of Van den Bosch were untenable, and that though the Hymenophyllaceae occupy the lowest position among the Ferns, being furthest removed from the Ophioglossaceae, still they are true Ferns. The affinity to the Bryophyta which he also recognised[6], was accepted by Prantl[7], but it remained for Goebel[8] to bring together evidence from the comparative examination of the sexual generation, in support of the Bryophytic affinity. Goebel remarks at the close of his memoir that we are able even now to follow, at least in part, the phylogenetic development of the sexual generation from the Bryophyta to the Pteridophyta, though the neutral generation fails to supply us with any

[1] Genera Filicum, description of Plate XXXI.

[2] K. B. Presl, Hymenophyllaceae, 1842, pp. 96, 97.

[3] l. c., p. 98.

[4] Versl. en Mededeel. d. k. Akad. Amsterdam, XI, 1861, and Journ. d. Bot Nederland., I, 1861.

[5] Ueber die Hymenophyllaceae, Abh. Sächs. Ges. d. Wiss. 1864, p. 500.

[6] He points out especially the affinity with the Sphagnaceae.

[7] Hymenophyllaceae, p. 62, 1875.

[8] Zur Keimungsgeschichte einiger Farne, Ann. d. Jardin Bot. de Buitenzorg, vol. VII.

suggestion as to the origin of the Fern from the Moss-sporogonium. The above brief statement will serve to show how long and how consistently the opinion has been held by special writers upon the Hymenophyllaceae, that they are the most primitive types of living Ferns. We will now consider wherein the points of similarity between them and the Mosses really lie, and try to estimate them at their true value in support of the primitive character of the Filmy Ferns.

Over and above the corresponding facts of alternation in the Mosses and Filmy Ferns, and the homosporous character which they both share, the chief points of similarity are these :—

(i) The filmy character of the leaf;
(ii) The filamentous prothallus ;
(iii) The projecting sexual organs ;
(iv) The presence of a single, well-defined apical cell ;
(v) The reputed absence of roots in some Filmy Ferns.

Each of these will be successively discussed and criticised.

(i) It was perhaps the filmy texture in the leaf more than any other character, which suggested the affinity of the Filmy Ferns to the Bryophyta: long before the phenomena of antithetic alternation [1] were properly apprehended, it was pointed out that a similarity of structure exists between the fronds of the Hymenophyllaceae and the leaves of the Mosses, since in both cases the filmy leaf may consist of only a single layer of cells. But while such a comparison was not unnatural some fifty years ago, it is to be borne in mind that the facts of antithetic alternation are now clearly before us [1]: that we are comparing the filmy leaf of these Ferns, which is part of the sporophyte, with the so-called leaf of the Moss, which is part of the gametophyte: the two are not strictly homologous parts, and accordingly their comparison cannot be accepted as convincing: at best we have here only an *analogy*, the leaf of the Fern not being the lineal descendant of the leaf of the

[1] In case this term be unfamiliar, reference may be made to an article 'On antithetic as distinct from homologous alternation of generations in Plants,' Annals of Botany, vol. IV, p. 347.

Moss. But there are still further reasons for thinking this comparison unsatisfactory. I have attempted elsewhere to show that the 'filmy' texture of the leaf is not a safe indication of close affinity even among the Ferns[1], by pointing out that within the Filicineous series it occurs at three distinct points, viz. among the Hymenophyllaceae, the Aspleniums, and the Todeas: if within the very natural group of the Ferns themselves it is not a certain index of affinity, but is rather to be viewed as a result of direct adaptation, how can the filmy texture of the leaf be held to strengthen the comparison between the Hymenophyllaceae and the systematically far distant series of the Mosses? If the affinity be a true one, the evidence of it must be based on firmer ground than that of the filmy leaf[2].

(ii) The existence of a filamentous, protonema-like prothallus in the Hymenophyllaceae, affords what is apparently a better ground for comparison. Various writers have recognised its counterpart in the protonema of the Moss, but none has treated the matter so fully as Goebel, who has made a comparative study of the sexual generation of certain Ferns, and based upon it views as to the phylogeny of Mosses and Ferns, and the relationship between them: he sums up in the following words[3]: 'We may accordingly regard as the starting-point of the Bryophyta and Pteridophyta, Alga-like forms, consisting of branched filaments, of which the female sexual organs produced on fertilisation the asexual generation. Even now we can partially trace . . . . . the phylogenetic development of the sexual generation, or at least form for ourselves a connected idea of it. Still it is not to be forgotten that besides the onward progress from the simple condition of

[1] Annals of Botany, vol. III, p. 379.

[2] Giesenhagen (Flora, Oct. 1890, p. 460) has cited the case of *Selaginella cuspidata* as having at the margins of the leaf a texture similar to that of the Hymenophyllaceae, also *Lycopodium linifolium*, which is a shade-loving species. He concludes (p. 462) that the simplest Hymenophyllaceae were derived from forms of more complex construction, and are the result of progressive simplification of morphological structure: also that the Hymenophyllaceae are as near to the Polypodiaceae as any other family of homosporous Leptosporangiates.

[3] l. c., p. 115.

a branched filament, there may have been also a degeneration of the sexual generation, as seems to me probable in the case of the Fern-prothalli even at the present day.' It is further added in a note that 'the degeneration is in many cases brought about by the transfer of the formation of sexual organs to earlier periods of development of the prothallus.'

That there is a similarity between the protonema of the Moss and the prothallus of the Hymenophyllaceae no one can doubt; but before it could be finally accepted that the filamentous form is in both families really a primitive character, and not a result of more direct adaptation to similar external circumstances, which took place independently in the two families, we should require more evidence as to the details of descent than is as yet forthcoming, and the conclusion will need to harmonise with other facts relating to form and development of these and other organisms. I am not prepared at present to concede this point without considering carefully the grounds on which the opinion is founded. To this end we may first take up the question whether the filamentous form was the original one for the sexual generation of the Bryophyta: and secondly, we may inquire whether the similarity of form between the protonema of the Mosses and the filamentous prothallus of the Filmy Ferns is an indication of real affinity.

Having shown that among the Mosses there are forms in which the leafy plant is of very small size, and simple structure as compared with most Mosses, so that the protonema constitutes the greater part of the sexual generation, Goebel states that 'the appearance of a protonema on the germination of spores of the Mosses cannot be regarded as a "phenomenon of adaptation," but as a peculiarity inherited from their ancestors[1].' This conclusion follows from the recapitulation-theory[2], which, however, is a much less safe guide in the embryology of plants than in that of animals. I have elsewhere expressed at length my doubts of the propriety of basing broad phylogenetic conclusions upon details of external

[1] l. c., p. 112. [2] Goebel, Muscineen: Schenks Handbuch, II, p. 387.

conformation of the sexual generation, in view of the extent of the direct impress of external circumstances upon it in certain known examples[1]: at the same time I am free to admit that a reasonable case (though not a demonstration) can be made out for the relatively primitive character of the Moss-protonema, notwithstanding that the formation of a protonema is not a constant phenomenon in all Mosses[2].

Passing to the second question, viz., whether the similarity of form between the protonema of the Moss and the filamentous prothallus of the Hymenophyllaceae is an indication of real affinity, we enter on different ground. Between the Mosses and the Ferns there is a very wide gap. Though the general facts of alternation are similar, still as regards the form and structure of the sporophyte the two families have virtually nothing in common; but in the general conformation of the prothallus, and in its propagation by gemmae, they are alike: can this be accepted as an index of affinity in face of so fundamental a difference in the neutral generation? Among the higher plants it is notorious how little attention is paid to similarities of external conformation of the vegetative organs if the other characters indicate strong divergence, and there is no reason why this principle should be neglected in dealing with the Cryptogams. Moreover in the protonematoid growths of the Hymenophyllaceae we see an excessively inconstant character: even within the genus *Trichomanes*, while the prothallus of *T. pyxidiferum* is throughout filamentous, with exception of the archegoniophores, that of *T. alatum* is most diverse in its form[3]: in *Hymenophyllum* on the other hand the flattened form is prevalent: thus within the Hymenophyllaceae there is great want of constancy in that very character to which, in accordance with current views, so much importance is attached as evidence of relationship to the Mosses. This is in itself sufficient to cast doubt upon it,

[1] Annals of Botany, vol. I, p. 292.

[2] *Andreaea* is an exception. See Berggren, Studien ofver Mossornas bygnad och Utveckling (Lunds Univ. Arsskrift. T. VII).

[3] See Annals of Botany, vol. I, Plates XIV, XV.

a doubt which is strengthened by the absence of other evidence. It is by no means an improbable view that the filamentous form of the Hymenophyllaceous prothallus is the result of adaptation to the very moist situations in which they commonly grow: an extreme case in fact of that lengthening of the germinal filament which may be produced by certain external conditions[1], and that we have here to deal with a phenomenon of analogy with the Mosses rather than with an index of true affinity; to this I shall return later.

(iii) It will doubtless be remarked, however, that in the freely exposed, projecting sexual organs of the Hymenophyllaceae, and especially of *Trichomanes*, there is an obvious character which is shared with the Mosses: that is so, but the correspondence applies rather to the position of the organs, than to details of their structure. The archegonium is a typical Fern-archegonium: it developes as a Fern-archegonium, and has the single neck-cell, common to Leptosporangiate Ferns[2]. The antheridia are borne, it is true, on a narrow pedicel, but their development and mature structure conform approximately to that in other Ferns. It is then their *position* which would provide ground for comparison rather than their structure; but this protruding position is a necessary result of the simple structure of the prothallus, and if that be a result of relatively direct adaptation, as above suggested, so also would be the exposed position of the sexual organs.

(iv) The presence of a single initial cell with definite segmentation at the apex of the young Moss-sporogonium, and also at the apex of the stem, leaf, and root of the Leptosporangiate Ferns, while such are absent or less definite in their segmentation in the Eusporangiate Ferns, is certainly a fact worthy of note. The common presence of a single initial in the lower forms, and the absence of it from most Phanerogams, may be regarded as pointing towards the conclusion that those organisms which show the single initial are lower in the scale. Examples are however known of the

[1] See Goebel, l. c., p. 115: also Dodel-Port, Kosmos, 1880, p. 11.

[2] Annals of Botany, vol. I, p. 210.

existence of a single initial cell in Phanerogams[1], while in certain Thallophytes and Bryophytes no single initial is present: this point cannot therefore be accepted as having much weight. The presence of a single initial seems frequently to follow a less robust habit and a sharp curvature of surface of the growing-point. Plants of aquatic position are commonly of delicate texture; most of the lower forms are more or less distinctively aquatic; accordingly the presence of a single initial, though common in the lower forms, is not necessarily to be viewed as an indication of a lower affinity.

(v) Again, some may see in the rootless condition of certain of the Hymenophyllaceae, evidence that these are primitive forms, which share this character with the sporophyte of the Mosses. This condition is reputed to occur in certain species of *Trichomanes*, but, as Giesenhagen has observed[2], we are not yet in a position to state that these Ferns are really rootless in every stage, and in those species in which the seedlings have been seen, a root is present. But even if they were proved to be actually rootless at all stages of their life, the absence of roots might be a result of degeneration, as it undoubtedly is in *Wolffia*, or in the Utricularias described by Goebel[3]: it is not necessarily to be accepted as a primitive character.

We have now reviewed those characters upon which the Bryophytic affinity of the Filmy Ferns may be based, and the most satisfactory character for purposes of comparison is the protonema. Against this, which as above pointed out, may be viewed as a more directly adaptive rather than as an ancestral character, is to be set the fact that the simpler Ferns are the only Leptosporangiate Vascular Cryptogams, and that living forms afford no clue as to any direct mode of origin of such simple sporangia[4]. Thus the comparison above dis-

[1] The most prominent example is the root of *Heleocharis palustris*.

[2] Flora, Oct. 1890, p. 460.

[3] Ann. d. Jard. Bot. de Buitenzorg, vol. IX, p. 98.

[4] It is not necessary to dwell upon Prantl's suggestion as to the origin of the Hymenophyllaceous sorus from some form like *Anthoceros*. A view which depends upon the conversion of the internal sporogenous layer into a number of superficial sporangia, without any evidence how such a conversion did or

cussed appears to rest on very slender grounds, and it may well be asked whether some alternative opinion may not be more probable. May we not find a more true affinity to the lower forms in the Eusporangiate Ferns? In discussing this question I propose to take a general survey of the supposed affinity. In view of the wide differences between the Bryophyta and the Pteridophyta, and of the great antiquity of the Ferns, it will not be desirable to compare directly any one living Filicineous type with any one living type of Bryophyte, but rather I would consider the more general question of probability of the Eusporangiate character being primitive and ancestral as compared with the Leptosporangiate. It may be noted, however, that on general comparative grounds the affinity of the Eusporangiate ferns would be to the Liverworts rather than to the Mosses, and the question may therefore resolve itself into this: whether the affinity of the Leptosporangiate Ferns to the Mosses, or of the Eusporangiate Ferns to the Liverworts, be the more true and natural one.

Looking at the question then in its broader aspect, it will be noted that of the three great phyla of Vascular Cryptogams, two are exclusively Eusporangiate. There is no evidence, either from present or fossil forms, that the Lycopodinae or Equisetineae have had any Leptosporangiate ancestry, and they therefore serve to show that a stock may be Eusporangiate from the first, and make it also the less probable that the Ferns should have originated otherwise. The absence of any intermediate steps leading to the Leptosporangiate type, except from the Eusporangiate Ferns themselves, adds weight to this argument.

In the second place, the more bulky type of sporangium is already foreshadowed by the capsule of the Liverworts; it would be going too far to say that the capsule of a *Jungermannia* or of a *Marchantia* is one Eusporangiate sporangium, for it is probable that in the evolution of the Ferns a sub-

could come about, will hardly commend itself to the reason as in any way probable. Moreover, it is not apparent on other grounds that there is any near affinity between the Anthoceroteae, and the Filmy Ferns. See Prantl, Hymenophyllaceae, p. 62.

division of the archesporium took place, not its mere repetition; but the resemblance is undeniable: there is thus in the sporogonium itself an indication of how the Eusporangiate sporangium may have been derived, however vague and uncertain that indication may be thought to be; whereas there is as yet no rational suggestion as to the mode of origin from the Bryophyta of the sporangium as it is seen in the Leptosporangiate Ferns.

Passing on to the apical meristems, the characters of these have been used by me as a basis for disposing the Filicineae in series, as above stated. It is to be remembered that such evidence cannot be expected to apply with equal force in all cases, and that it is of greater weight within narrow circles of affinity, than in the comparison of more remotely related organisms. It is, however, worthy of note that while a single initial is present in the young sporogonium of the Moss, in the Liverworts a single initial is not found, though in certain of the Jungermannieae four cells, which hold a central position at the apex of the sporogonium, suggest in some measure that structure which is characteristic of the meristems of the Marattiaceae: it would however be unwise to rest strongly on such a point as this.

In comparing the Hymenophyllaceae with the Mosses the mere vegetative characters of the gametophyte have been brought forward as weighty evidence: if we are to depart so far from the methods of classification applied to the higher plants, and consider vegetative characters in plants widely diverse in other respects, as much might I think be said for the similarity between, for instance, the prothallus of the Marattiaceae or Osmundaceae and the sexual plant of the Anthoceroteae: the flattened but massive green thallus, which may in either be branched, is not dissimilar in the two cases. The point of distribution of the sexual organs may appear to be an obstacle, they being on the upper surface in the Anthoceroteae, while in the Marattiaceous prothallus they are commonly on the lower; but Jonkman[1] specially states and

[1] La génération sexuée des Marattiacées, pp. 13–17. Figs. 53–57.

figures the fact that in these plants, both antheridia and archegonia are found on both surfaces, though they are more numerous on the lower.

As regards the sexual organs themselves there is a nearer correspondence between the Eusporangiate Ferns and the Liverworts than is to be found between the Leptosporangiate Ferns and the Mosses. I have elsewhere pointed out[1] that in the Eusporangiate Ferns the sexual organs are deeply sunk in the tissue of the massive prothallus, a position sufficiently distinct from that of the freely exposed and projecting organs of the Hymenophyllaceae. The same is the case with certain of the Thalloid Liverworts, and especially in the Anthoceroteae. D. Campbell[2] has drawn attention to the fact, demonstrated by Jonkman, that more than a single canal-cell is present in the archegonium of the Marattiaceae, a character in which, according to our present knowledge, they alone among the Vascular Cryptogams compare with the Bryophyta: it may also be noted that the embryo of *Marattia* assumes a vertical position of the axis from the first, according to Luerssen[3]; but this is a point to which too much importance should not be attached. Do what we will by drawing comparisons based on such points as these, the difference between any living Fern and any living Bryophyte is an uncommonly wide one, and it is almost useless to attempt to place any view of relationship upon a sound basis by comparison of mere details in organisms so widely different.

There is however a line of evidence which, though in itself not conclusive, will serve to give greater stability to the suggestion that the Eusporangiate Ferns are the more primitive type: I mean the evidence from Palaeophytology: in approaching the discussion of such a question as the present, too little attention has been paid to this branch. It is hardly necessary to premise that as negative evidence it is not strong: the fact that certain types of plants have not been

[1] Annals of Botany, vol. III, p. 370. [2] Botanical Gazette, 1890, p. 4.
[3] Handbuch d. Syst. Bot., I. p. 582, and Fig. 154.

found in the earlier rocks does not necessarily prove their absence at the periods when those rocks were formed, though the fact is worthy of note: for our purpose the *prevalence* of certain forms over others in the earlier formations will command greater attention, and we may at once proceed to consider how, in this respect, the facts of palaeophytology bear upon the present question.

Recent writers have repeatedly remarked the preponderance of Ferns of the Eusporangiate type in the primary rocks: though very many Fern-remains are represented only by barren fronds, where the sporangia have been found they are in the overwhelming majority of cases of a character allied to the Marattiaceae: it may further be stated that no drawing from a microscopic section showing internal details of an undoubted leptosporangiate sporangium from the primary rocks has yet been published[1], and it is from these, rather than from mere surface observations of prints, that the most trustworthy evidence is to be gathered. Perhaps the best authenticated example of a print of a Leptosporangiate Fern from the primary rocks is that of *Hymenophyllites delicatulus*, described and figured by Zeille[2], and referred by him to the Hymenophyllaceae: here the details of the impression were so well preserved that Zeiller was able to recognise and draw the oblique annulus, which corresponds very closely with that of a modern Filmy Fern. The original specimens of this fossil were examined by Graf zu Solms-Laubach, and from them he concluded 'that the fact is correctly stated, and that no other interpretation of the figures is possible[3].' The sporangia figured and described by Mr. Carruthers as being found in a section of a nodule from the coal must also be considered[4]. I have had the opportunity, through the kindness

[1] Renault states that he has specimens of sporangia of Gleicheniaceae and of *Trichomanes* in silicified sections from Grand-Croix, but did not publish them because he did not know to what fronds they belonged: Cours de Bot. foss. III. p. 218. The case of sporangia from a coal nodule figured and described by Mr. Carruthers, Geol. Mag., vol. IX, No. 2, 1872 (Plate II, Fig. 5), will be referred to below. [2] Ann. d. Sci. Nat., 6 Série Botanique, vol. XVI, 1883.

[3] Palaeophytologie, p. 157.

[4] Geol. Mag. vol. IX, No. 2, Pl. II, Fig. 5.

of Mr. Carruthers, of seeing the original specimen, and there certainly appears to be an oblique annulus, similar to that of the Hymenophyllaceae: it is however to be noted, as indeed Mr. Carruthers himself remarks, that these sporangia are larger than those of present Filmy Ferns, while the stalk appears to be a relatively short and massive one: these points make the further elucidation of the nature of such sporangia very desirable, while in my opinion they raise a doubt as to the near correspondence of this Carboniferous Fern with our present Hymenophyllaceae. The case of *Hymenophyllites Weissii*, Sch., figured by Schimper, from the coal of Saarbrücken is much less satisfactory[1], the reference of this to the Hymenophyllaceae depending chiefly upon the character of the sorus as a whole (if indeed that which is so described be really a sorus), while the sporangia themselves have not been distinguished or described in detail. The large and typical Devonian Fern, *Palaeopteris hibernica*, Schimper, (Archaeopteris hibernica, *Forbes*) has also been referred to the Hymenophyllaceae[2]: here again it is the character of the sorus as a whole, not of the sporangium, which has led to the conclusion: the sporangia themselves seem not to have yet been seen, and therefore the reference to the Hymenophyllaceae cannot be taken as more than a provisional suggestion[3]. Mr. Kidston, after a careful re-examination of the specimens of this species in the British Museum, and in Dublin, comes to the very divergent conclusion that 'the true position of *Archaeopteris hibernica* is in the Marattiaceae.' I have also examined specimens in the British Museum, and failed to recognise any distinct evidence of the Hymenophyllaceous affinity.

Stur in speaking of those Carboniferous Ferns which he refers to the Polypodiaceae, regards their position in that

[1] Compare Schimper, Traité d. Paléophytologie, Pl. XXVIII.

[2] Schimper, Traité, Pl. XXXVI; Carruthers, Geol. Mag., IX, 1872, p. 3 and Plate II.

[3] See also Kidston, on the fructification and affinities of *Archaeopteris hibernica*; Forbes, Ann. and Mag. of Nat. Hist. 1888.

family as no more than a provisional suggestion: he is careful to state[1] that in none of these has the sporangium itself been seen, but at most the indusium of the sorus, or the receptacle without sporangia.

Passing on to specimens of the carboniferous period, where the microscopic details can be seen in sections, evidence is found of the structure of the sporangia being more complex than that of the Leptosporangiate Ferns. This is the case in the sporangia figured by Williamson[2], for in these, traces of a second series of cells are found within the external layer of the wall, a character which is absent in the mature Leptosporangiate sporangium. Prof. Williamson has, with great liberality, shown me those of his sections of coal nodules which exhibit Fern sporangia, and the comparatively small number of these shows how rarely they are preserved. I was struck in looking over these specimens by their great uniformity of type, and have selected a few for detailed drawing (Figs. 1–4). In examining these it is to be borne in mind that the sections pass in irregular directions through the sporangia, but still the similarity is unmistakeable: in each case the superficial layer of cells has thickened and firm cell-walls, but the individual cells are of very irregular size and shape; no definite ring-like annulus can be traced. Within the outer layer are to be found in each case more or less distinct traces of internal cells (*i*, *i*), which do not constitute a regular and continuous layer, but only a partial internal sheath; at some points a simple line may be seen (as in Fig. 4. *x*), without any distinct layer of cells; this will be referred to subsequently. The number of spores in the single sporangium is relatively large, as may be judged from the sporangium shown in Fig. 4, where more than seventy are seen in the single section, and the total number in the sporangium must have been much larger. None of the sections show clearly the mode of insertion, and the sporangia

[1] Stur, Die Carbonflora, 1885, p. 235.

[2] Phil. Trans., vol. 167, Part I, on the organization of the Fossil Plants of the Coal Measures, Part VIII, Pl. 7, Figs. 25–30.

are commonly found quite isolated. I think it probable that these sporangia are similar to those represented by Mr. Kidston, and described by him as 'annulate sporangia [1];' though possibly not specifically identical with sporangia represented in my figures, and though the internal cells are not represented in Mr. Kidston's figures, still the correspondence of his sporangia to those examined by myself is certainly closer than to sporangia of Leptosporangiate Ferns. In searching among modern Ferns for sporangia structurally similar to these from the coal, I have found in *Todea barbara* a very remarkable resemblance: the main structural points of the Osmundaceous sporangium are already well known: their large size, and short stalk, the absence of a definite ring-like annulus, and dehiscence by a longitudinal slit. In longitudinal section the structure in *Todea barbara* is as in Fig. 6: the most noteworthy characters for our present purpose are the irregularity of the external layer of cells, which is composed of relatively large, thick-walled cells at (*a*), while elsewhere the cells may be relatively small and thin-walled. Within this, and especially towards the base of the sporangium, will be seen small and compressed cells, limited by oblique walls, which remain till the sporangium is mature, constituting a partial and irregular inner layer (*i*, Figs. 6–8), while, in sporangia not quite mature, a granular film may be traced lining the cavity in which the spores are produced. The stalk of this large sporangium is relatively thin, and appears in the longitudinal section as composed of about four rows of cells. The whole construction of the sporangium is of a more bulky type than that of the typical Leptosporangiatae, and I have elsewhere shown that this is its character from the very first stages of its development. In comparing this with the fossil sporangia, it is to be remembered that the

[1] Trans. Geol. Soc. of Glasgow, vol. IX, Part I, Figs. 11–13. In connection with Mr. Kidston's use of the words 'annulate' and 'ex-annulate,' it should be remarked that these terms are not to be taken as substitutes for 'Leptosporangiate' and 'Eusporangiate.' The fact that an annulus is absent from the Hydropterideae, though these are typically Leptosporangiate forms, shows that precision is necessary on this point.

latter are cut through in most irregular directions, and accordingly the comparison should be with irregular and oblique sections from the modern Fern: two such are represented in Figs. 7 and 8, and the similarity, even in details, between these and the sporangia from the coal is very notable: the comparison should specially be made with Fig. 3, and it will be seen that the position and appearance of the 'annulus' (*a*), the line of dehiscence (*d*), and the internal cells (*i*), as well as the relative size and appearance of the rest of the tissues shown, correspond to an extraordinary degree. Perhaps the most striking point is that the granular film (*x*), already noted in the modern sporangium, may be traced in the sporangium from the coal, for the delicate irregular line (*x*) in Fig. 4 is believed to represent that similarly marked in Figs. 6–8. It is thus seen that the correspondence between the structure of these sporangia from the coal nodules, and of the modern *Todea barbara*, is an unusually close one.

In interpreting this extraordinary resemblance it is to be remembered that these sporangia from the coal nodules are isolated from the fronds; there is thus no proof from what type of Fern they were derived, other than that yielded by their form and internal structure: it is not even suggested that they all belong to the same species or genus, and I would be far from urging on the above grounds that *Todea barbara* itself is a plant of very early date: it seems, however, that their Osmundaceous character is probable, and it is to be noted that the Osmundaceae have hitherto been believed to be of post-carboniferous origin. For the purposes of the present argument, these sporangia have an interest: they are clearly not Leptosporangiate, as the word is ordinarily understood, but occupy an intermediate position, connecting these with the Eusporangiatae; their size, their more complex structure, and the number of spores which they produce, all show this; and as this, though itself rare, is the prominent type of Fern sporangium from the coal nodules, of which the microscopic structure is known, we may see in

that fact a measure of farther evidence of the prevalence of Ferns with a more bulky sporangium in the earlier rocks over those of the true Leptosporangiate type.

From the above data the conclusion may be drawn that though it is not possible absolutely to deny the presence of Leptosporangiate Ferns in the primary rocks, still the evidences of their occurrence are at least exceedingly rare, and the question whether they existed at all in those early times is not even yet placed beyond the possibility of doubt by observation of microscopic sections [1]. But, as above remarked, it is not the present object to prove their absence, but to fully appreciate their rarity in the primary rocks, as compared with the Eusporangiate forms. On this point Stur [2] has put forward figures relating to the Carboniferous Ferns; in considering which it is to be remembered that many of the Ferns quoted are classified by their vegetative organs alone, and not by observation of their sporangia: his results may be tabulated as follows :—

		Present Flora.	Carboniferous.
Ophioglossaceae	genera	3	2
	species	17	19
Marattiaceae	genera	4	15
	species	23	98
Polypodiaceae (?)	genera	108	4 or 5
	species	2700	58

In estimating the value of these figures it must be remarked that our knowledge of the present Flora is

[1] Schenk, in his Handbuch (vol. IV, p. 37), writes of the Hymenophyllaceae, 'one observation due to Zeiller is the only evidence of the existence of this family in the older formations;' and again, speaking of other Leptosporangiate Ferns, 'they seem to be entirely absent from the older formations, and to appear first in the Mesozoic strata.'

[2] Die Carbonflora, Abh. d. k. k. Geol. Reichsanstalt zu Wien, 1885, p. 411.

infinitely more perfect than of the carboniferous plants, and that of the fossil Ferns here entered among the Polypodiaceae, the details of the sporangia are not known in any one case. Bearing these points in mind, it appears that the Ophioglossaceae stand roughly in the present as in the past, that the Marattiaceae of the coal preponderated greatly over those of the present era, both in genera and species, while the Polypodiaceae, which are the most typical Ferns of the present time, are represented in the coal by relatively few forms which are only doubtfully referred to this family. Stur further states that the Gleicheniaceae, Osmundaceae, and Schizaeaceae were entirely absent from the coal, and suggests for them a post-carboniferous origin; though I do not consider that, in the absence of all knowledge of their vegetative organs, the sporangia above described demonstrate beyond doubt the presence of Osmundaceous Ferns in the coal, I should not be prepared to maintain their absence in view of those facts. Speaking generally, the present Eusporangiate Ferns may be said to be the reduced remnants of a more prevalent race of former times, while the Leptosporangiates were in the main a race of later origin, and are now greatly more prevalent than in earlier periods. In the previous pages I have attempted to show that the comparison of the facts of structure and development of present living forms is not incompatible with the view that the Eusporangiates represent the more primitive type for the Filicineae: the palaeophytological evidence is clearly in favour of this, though it is not, and cannot be expected to be, absolutely conclusive.

In the memoir already referred to at the opening of this paper [1] I have dwelt at some length upon the adaptive nature of the differences of bulk of the various parts of the sporophyte and gametophyte in the Ferns: having demonstrated that, as regards bulk of the young parts, the Ferns form a series, it was recognised that the more robust Eusporangiate forms are better suited in all their parts to

[1] Annals of Botany, vol. III, pp. 366–374.

an exposed habitat, while the more delicate Leptosporangiate Ferns are less fitted to withstand exposure in dry air[1]. On grounds of comparison, which I now am disposed to think were insufficient, I then concluded that the series from the Hymenophyllaceae to the Marattiaceae represents an ascending series, illustrating the emergence of one phylum of the Vascular Cryptogams from the semi-aquatic to the aerial habit[2]. But, it may well be asked, have we not in the Leptosporangiate Ferns a peculiarly specialised type? They are found at the present day chiefly, and the Hymenophyllaceae, upon which the comparison with the mosses is specially based, almost exclusively, under the shade of larger growths[3]. Where in the earlier period would such shade be found? If, as I have elsewhere suggested[4], the origin and differentiation of the spore-bearing generation may be correlated with the migration from water to the land, it would be contrary to all reason to suppose that the primeval forms were such as we now see specialised to life under dense shade. Moreover, the plants which constituted the chief terrestrial growths of the primary rocks were not distinctively shade-giving plants, such as the more modern Angiosperms, under the shadow of which such plants now grow: there is thus a presumption against specialised, shade-loving forms such as the Hymenophyllaceae being really primitive. I am now disposed, on considering all the evidence, to hold that the Leptosporangiate Ferns are derivative and specialised forms, while the Eusporangiatae represent the more primitive type: that the similarities of the vegetative organs, such as they are, between the Mosses and the Hymenophyllaceae are the result of specialisation along two distinct, but parallel, developmental lines, in accordance with similar external con-

[1] On the extreme susceptibility of the Hymenophyllaceae to exposure, and their special adaptation to life in wet, densely shady forests, see Giesenhagen, Flora, 1890, p. 417.

[2] l. c., p. 374.

[3] Those more exclusively acquainted with the British Flora must bear in mind that Hymenophyllum tunbridgense, and Wilsoni, are exceptional among Filmy Ferns as regards their exposed habit.

[4] Annals of Botany, vol. IV, p. 347.

ditions: as the Cactaceae and Euphorbiaceae have independently adapted themselves to life in regions of prolonged drought, by reduction of leaf-surface, and succulent development of the axis, so may these two distinct stocks have adjusted their details of construction to a damp and often shaded habitat. The thin texture of the leaf is clearly an adaptive character, since it recurs in three distinct families of Ferns, in species of *Selaginella* and *Lycopodium*, and also in a minor degree in certain of the higher plants, in all cases a concomitant of shady and damp habitat. The same is probably the case with the filamentous prothallus; this seeming especially probable in face of the modifications of which prothalli are susceptible when grown in water: when the gametophyte is thus simplified in structure, the sexual organs must needs project, as they do in the Hymenophyllaceae. Thus the characters which are commonly cited as demonstrating an affinity between Mosses and Hymenophyllaceae may be recognised rather as being of a more directly adaptive nature, such as might be produced in the vegetative system of distinct groups of plants exposed to similar external conditions. Add to this the absence of any support for the affinity in the characters of the sporophyte, and the fact that the Mosses are entirely unrepresented in the earlier rocks, and do not appear until the Tertiaries, and the improbability of a true affinity between the Mosses and Hymenophyllaceae becomes in my opinion very strong indeed.

If this affinity be once given up, then the search for a point of attachment of the Filicineous series is necessarily transferred to the Liverworts, with the further result that the closest similarity to be traced is then with the Eusporangiate Ferns: in the anatomical characters of the sorus and sporangium a measure of support may be found for the suggested affinity, which, however, I would put forward only with that reservation which is necessary where the facts are but scanty. The sporophyte of the Fern corresponds to the sporogonium of the Liverwort, and the isolated archesporial cells of the former to the united archesporium

of the latter. It is probable that in the course of evolution of the Filicineae, the originally united archesporium became partitioned by bands of sterile tissue, each portion, thus isolated, developing together with its superficial covering of cells into a sporangium: if this were so, it follows that we may recognise in the synangia or so-called 'coalescent sporangia' of the Marattiaceae, and also in the 'sporangiophore' of *Ophioglossum*, instances of the incomplete separation of the individual sporangia, though the archespore in each is separate from that of its neighbours[1]. From a comparative point of view I am disposed to regard these synangia, which are found in more than one series of the Vascular Cryptogams, as primitive in character, and as indicating not a coalescence of sporangia which were distinct in more ancestral forms, but rather an incomplete separation of sporangia, whose distinct archesporial cells were derived by isolation from some such united ancestral archesporium as is seen in the Bryophyta of the present day. If such Eusporangiate forms with synangial sori were the more primitive, it is not difficult to conceive how in plants growing in moist and shaded positions, where the danger of exposure to drought is minimised, the sporangia might have become not only completely separate, but also reduced in bulk, as we see in the progression through the Osmundaceae to the truly Leptosporangiate Ferns: and parallel with this reduction of the sporangium, as I have shown elsewhere, would have proceeded the reduction in mass of all the other members of the sporophyte.

Again, this view that the Eusporangiate Ferns were the more primitive, and the Leptosporangiate derivative and specialised, may throw light upon what I have hitherto regarded as a perplexing phenomenon, I mean apospory: it was difficult to understand why this obliteration of a marked phase in the alternation should make its appearance in forms which we were accustomed to accept as primitive, seeing that on other grounds it is regarded as a terato-

[1] Compare D. Campbell, l. c.

logical phenomenon, and not as a reversion. If, however, the views as to the origin of the antithetic alternation, which I have elsewhere put forward, be accepted, and also that the Eusporangiate Ferns be really primitive, apospory appears in a new light: as at present recorded it is found to occur in Leptosporangiate Ferns and Mosses; in forms which, under the present hypothesis, are specialised in accordance with a moist and often shaded habitat; in these the circumstances of life on exposed land surfaces, which in my view conduced in the first instance to the antithetic alternation, are mitigated: living, as at least many of the aposporous plants do, in an almost uniformly moist habitat, it is to be expected, rather than wondered at, that the limits of the alternate generations should be obliterated: that the typically terrestrial sporophyte should, on exposure to surroundings more specially favourable to the growth of the gametophyte, grow out directly into the prothallus: and that the spore-formation, which is the distinctively sub-aerial mode of propagation, should be in abeyance: more especially is this to be anticipated in the Hymenophyllaceae when grown in closed cases; and what more pronounced example of apospory, of actual obliteration of the limits of the two generations, could be afforded than that of *Trichomanes alatum*[1]? The very existence of apospory in Leptosporangiate Ferns seems to me to support the view that they are derivative and specialised forms rather than primitive, and these remarks will apply equally to the Mosses, in which aposporous development is induced only under conditions of specially damp culture.

In the above pages it will, I think, have been sufficiently shown that the view of the Eusporangiate Ferns as relatively primitive is capable of defence: a comparison of form and development, the palaeontological evidence, and even the facts of apospory, all fall in with this theory, and give it more or less uniform support; but it is impossible at present to do more than put it forward as an hypothesis, and the question must still be held to be an open one. If the new view be

[1] Annals of Botany, vol. I, p. 278.

finally accepted, much of the theoretical writing at the close of my former paper[1] will need to be read in converse. I would, however, remark that whichever opinion be adopted, the *facts* of my former paper remain, and the serial arrangement of the Ferns there based upon the broad area of facts relating to the meristems stands as surely as before. A somewhat modified opinion may, however, be held as regards the families of Leptosporangiate Ferns, and instead of attempting to arrange them all in a linear sequence, it would probably be more in accordance with their characters, as well as with their position as derivative forms, to see in them a number of relatively distinct lines of individual development, which might have radiated, so to speak, from the Eusporangiate centre.

The effect of these opinions upon current views as to the main lines of descent would be as follows: In the first place, the thalloid Liverworts would take a more important place as primitive terrestrial plants, which probably approximate to those forms which gave rise to the Filicineous series: from the latter, as well as from the early Bryophyta, derivative forms sprang, which became specialised to a moist and shaded habitat, as an undergrowth below larger organisms: these parallel lines of development culminated in the Leptosporangiate Ferns and the Mosses of the present day, both of which may be regarded as blind branches. From some forms allied to our modern Marattiaceae and Ophioglossaceae, the Cycads probably sprang, and from some forms of Lycopodineous affinity, the Coniferae. Obviously, if this were so, the effect of recognising the Eusporangiate Ferns as relatively primitive is to carry down to a lower point in the whole scale of plants the insertion of the Gymnospermic type: this would coincide well with palaeophytological facts, for it appears that the Gymnosperms date back to as early formations as the three phyla of the Vascular Cryptogams themselves. That questionable organism *Isoetes* would now find a natural, but independent, place between the bases of the Filicineous and

[1] Annals of Botany, vol. III, p. 372, etc.

Lycopodineous series, for, while not distinctly referable to either of them, it shows affinities to both of them as well as to the Cycads. Thus, whatever other strength the view of the Eusporangiate, as the more primitive type for Ferns, may possess, it appears to me to have the effect of making the phylogeny of vascular plants more intelligible, and of harmonising it better with palaeophytology than the converse opinion, which most botanists have hitherto been accustomed to hold.

DESCRIPTION OF FIGURES IN PLATE VII.

Illustrating Professor Bower's paper on Ferns.

Figs. 1–5 represent sporangia found in sections of nodules from the coal of Halifax and Oldham; 1–4. are from slides belonging to Prof. Williamson; 5. from a slide belonging to Mr. Carruthers. The cabinet numbers are those of Prof. Williamson's Catalogue.

a = annulus. d = point of dehiscence. i = internal cells. x = granular film.

Fig. 1. A young sporangium, showing the internal layer very distinctly, and filled with the remains of immature spores. (Cabinet number, 1875.)

Fig. 2. An older sporangium which has probably ruptured at d and lost its spores. (Cabinet number, 1020.)

Fig. 3. A mature sporangium showing point of dehiscence (d) and internal cells. (Cabinet number, 1292.)

Fig. 4. A mature sporangium with spores still contained in it, the granular film (x) may be traced for a considerable distance lining the wall: the number of spores in the section is over 70. (Cabinet number, 1875.)

Fig. 5. Portion of a sporangium from Oldham showing internal cells (i): (× 150.)

Fig. 6. Sporangium of *Todea barbara* in longitudinal section: (× 150.)

Figs. 7, 8. Sections of the same in oblique directions, chosen so as to match Fig. 3 as nearly as possible: the position of the figures on the plate, as well as the lettering, correspond to those of Fig. 3: (× 150.)

Fig. 1.

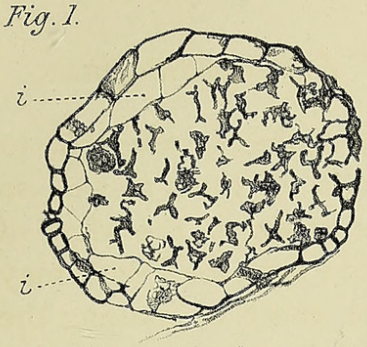


Fig. 2.

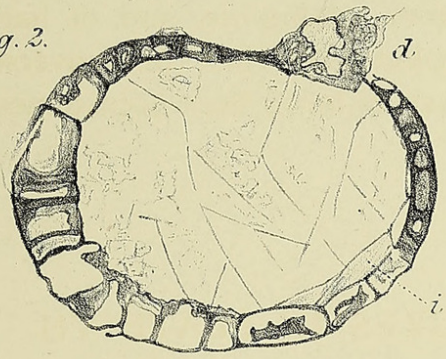


Fig. 3.

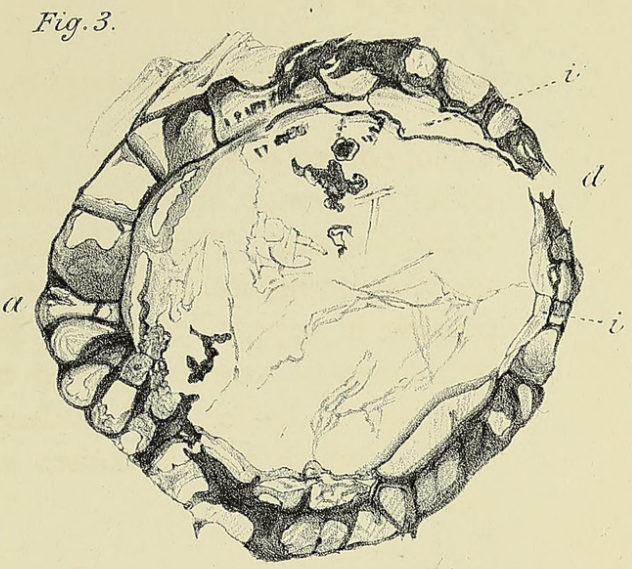


Fig. 4.

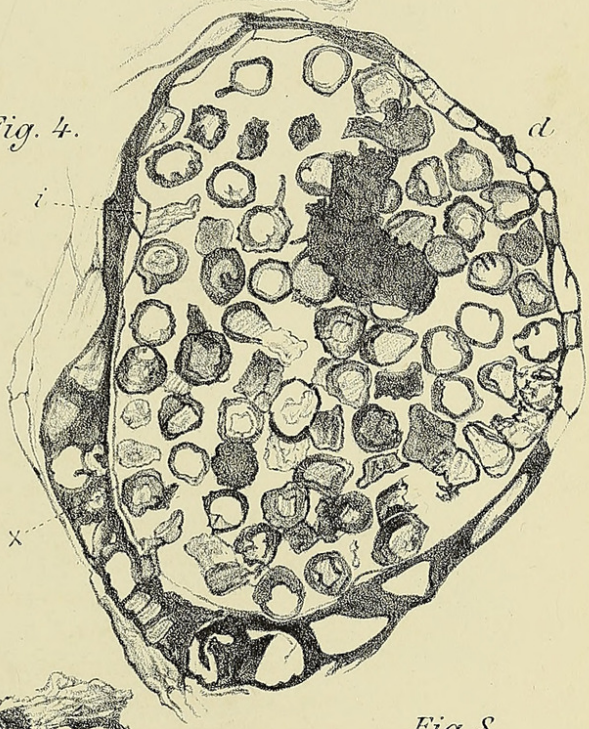


Fig. 6.

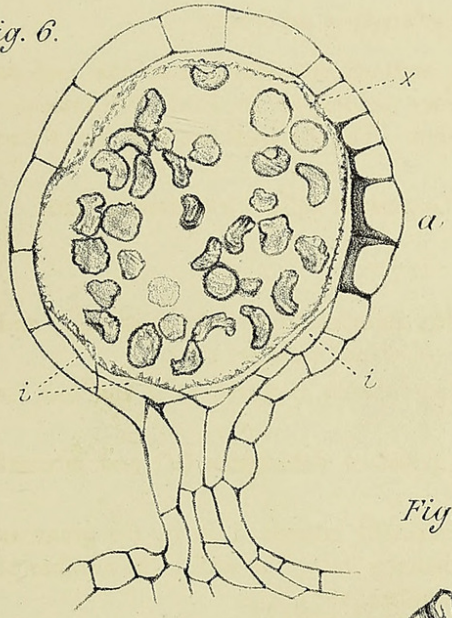


Fig. 5.

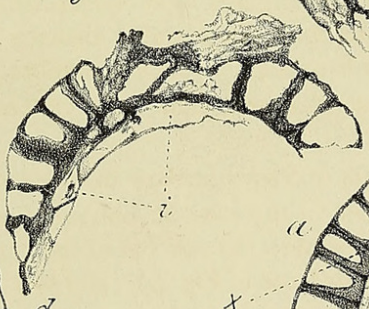


Fig. 7.

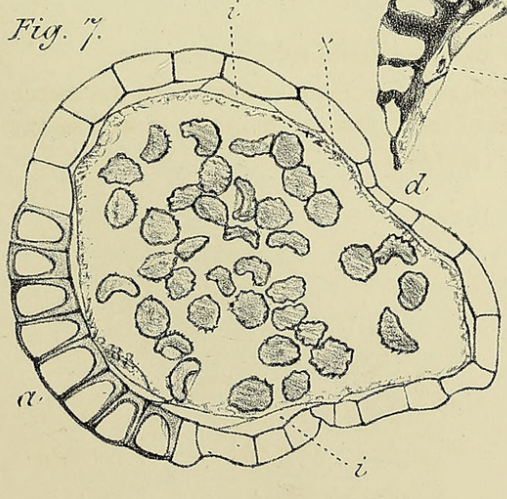
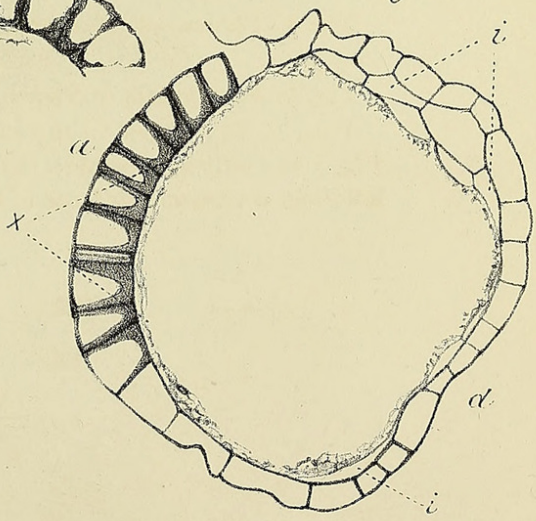


Fig. 8.



Bower del.

University Press, Oxford.

BOWER.—ON PHYLOGENY OF FERNS.