

II. *Studies in the Morphology of Spore-producing Members.*—No. IV. *The Leptosporangiate Ferns.*

By F. O. BOWER, *Sc.D., F.R.S., Regius Professor of Botany in the University of Glasgow.*

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[PLATES 2–7.]

INTRODUCTION.

IN the three memoirs of this series already published,* all the genera of living Pteridophytes have been dealt with, excepting the Leptosporangiate Ferns. In many features the described species and genera of the Leptosporangiatae show such similarity to one another, that the classification of them presents difficulties to the systematist. It will be unnecessary here to sketch the earlier history of the classification of Ferns: it has been summarised in a compendious form by BOMMER.† Though at the date of this work systematists differed still as to the limitations and the grouping of genera, the classification of PRESL was widely accepted; it was, in fact, the representative classification of the middle decades of the century.

If we examine that system as adopted and modified by Sir WILLIAM HOOKER in his ‘Species Filicum,’ and embodied in the ‘Synopsis Filicum,’ it will be seen that it rests upon a narrow basis. The sexual generation is never referred to for purposes of diagnosis or comparison; the vegetative organs of the sporophyte are freely used, but chiefly in the arrangement of the species within the genus; the characters of the sorus which are used are restricted in their scope, being mainly those of its form and position, together with the presence or absence, and the nature, of the indusium. These remarks are not made in disparagement of the earlier systematic work, but only in order to show its limitations, which were a natural consequence of the then state of the science; for in the middle of the century strictly taxonomic, rather than developmental or evolutionary interests prevailed.

* “Studies in the Morphology of Spore-producing Members: I. Equisetineæ and Lycopodineæ,” ‘Phil. Trans.,’ B, 1894, p. 478; II. ‘Ophioglossaceæ,’ published by Dulau and Co., 1896; III. “Marattiaceæ,” ‘Phil. Trans.,’ B, 1897, p. 35.

† ‘Monographie de la Classe des Fougères,’ Bruxelles, 1867.

The research of later years has in a measure supplied the deficiency, not only as regards the sexual generation, but also in the anatomy and development of the sporophyte. So far as we yet have a comparative treatment of the prothallus of Ferns, it has been acquired since Sir WILLIAM HOOKER'S time; but while recognising the importance of the structure and position of the sexual organs for purposes of comparison, I have always entertained doubts how far it is desirable to follow out the comparison of the vegetative characters of the prothallus into detail.* Recently published observations sufficiently show how directly plastic the prothallus of Ferns really is,† and raise again the question how far such variable features are a fit subject for morphological comparison. The attempt will have to be made, as HEIM has already done,‡ to select such characters as are "typical for the groups in question, which recur even in altered conditions of culture"; these alone can be of real systematic value.

The vegetative organs of the sporophyte were accorded only a minor place in the method of Sir WM. HOOKER, but recently they have been brought into greater prominence. Dr. CHRIST,§ following the initiative of METTENIUS, attaches importance to the general structure of the plant for purposes of classification, as an offset against the too great importance attached to the sorus and indusium by HOOKER and his followers. He has in his Preface (p. 7) quoted cases where the affinities indicated by the sorus are opposed by those indicated by the vegetative organs. He gives precedence to the vegetative characters over those derived from the sporangium and sorus, and, accordingly, to take a specific example, he places *Loxosoma* with *Davallia*, at a point in his system far removed from *Trichomanes*, and also from the Gleicheniaceæ, notwithstanding important resemblances to these in the characters of the sorus.

Before adopting this method for Ferns, we shall do well to consider it from the point of view of systematic method as practised upon plants at large. In dealing with flowering plants systematists consistently give precedence to the floral structure, and use the external form and anatomical characters of the vegetative parts only as secondary evidence. In the same way, in Ferns, precedence should, I think, be given to the sorus over the vegetative characters of the Fern plant, and to the sexual organs over the mere vegetative conformation of the prothallus.

Accordingly, while duly appreciating the value of characters introduced, or freshly applied since the time of Sir WM. HOOKER, and with the definite intention of using these as aids to our comparison, it seems to me to be still as desirable as before to strengthen the taxonomic characters derived from the sorus, by fresh observation of the details of its structure and development. Elaborate observations of the origin

* See 'Annals of Botany,' vol. 1, p. 291.

† KLEBS, 'Biol. Centrbl.,' 1893, p. 649. GOEBEL, Sitz.-Ber. d. Akad. Wiss. zu München,' 1896.

‡ 'Flora,' 1896, p. 355.

§ 'Die Farnkräuter der Erde,' Jena, 1897.

and structure of the indusium have, it is true, been made by various investigators; but it has always appeared to me strange that so much attention should have been given to this inconstant organ, and so little to certain features of the sporangia, which are much more constant, and more directly important to the life of the plant. I propose now to return to these more essential parts, and I find it possible to bring into the sphere of a general comparison certain characters hitherto disregarded, or undervalued; they are these:—

- (a.) The relative time of appearance of the sporangia of the same sorus.
- (b.) The structure of the single sporangium, and of its stalk.
- (c.) The orientation of the sporangia relatively to the whole sorus.
- (d.) The potential productiveness as estimated by the number of spore-mother-cells, and the extent to which this is realised in the output of mature spores.

The first of these characters has frequently been noted for individual cases, but has not yet been made a subject of general comparison.* In certain Ferns, such as the Marattiaceæ, the sporangia of any one sorus are produced simultaneously, and pursue a synchronous course throughout development. This simple type is characteristic of many Palæozoic Ferns; its simplicity, together with its early occurrence, suggest that it may be a relatively primitive type. Among Leptosporangiate Ferns it is less common, but it is seen in *Platyzoma*, *Gleichenia*, and *Matonia*, and in the non-soral Osmundaceæ, while the Schizæaceæ also show a very simple condition as regards the relative time of origin of their sporangia. It will be shown, on the other hand, that the Cyatheaceæ, Loxsomaceæ, and most of the Dicksoniæ have a basipetal sequence of their sporangia in the single sorus, an arrangement seen in its greatest development in the elongated receptacles of the Hymenophyllaceæ. By this elongation of the receptacle, accommodation is given for a larger number of sporangia successively produced. But another method of increasing accommodation is that prevalent in the bulk of the Polypodiaceæ, where sporangia of various ages are intermixed. These three types are to be clearly distinguished, and the opinion is entertained that the first is probably a more primitive type, while the other two may be regarded as being probably derivative types.

The orientation of the sporangia relative to the whole sorus will be found to be constant, with few exceptions, in those sori where the sporangia are simultaneous, or arise in basipetal succession, and in these the annulus is oblique; but where the sporangia of various ages are intermixed, no constancy of orientation is maintained, and the annulus is usually vertical.

Finally, it will be shown that the potential output of spores, per sporangium, is commonly larger, and the whole sporangium more broadly seated, in the former than

* The only statements of a general nature on this point that I can recall are by PRANTL, in a footnote ('Die Hymenophyllaceen,' p. 38): "Diese basipetale Entwicklung ist nicht, wie METTENIUS glaubt, den Hymenophyllaceen eigen, sondern findet sich an allen erhabenen Receptaculis anderer Farne," and again in the text of 'Die Schizæaceen,' p. 39.

in the latter types. In fact, these characters run substantially parallel to one another, and form, collectively, a very convincing body of evidence upon which a natural system of classification may be based. The results acquired from this comparison of the sorus and sporangium will be further checked by reference to anatomy and the details of the gametophyte. It must not be anticipated that all the characters named will run parallel with strict exactness; all that is contended is that, allowing a reasonable margin for variation from type, there is a substantial parallelism of characters drawn from these varied sources.

We shall therefore be prepared to consider the following main divisions of the Ferns, based upon the characters of the sorus, but supported by collateral lines of evidence: (1) Those with simultaneous origin of the sporangia in the sorus, which may be designated *Simplices*; (2) those with a regular basipetal succession, which may be called *Gradatae*; and (3) those in which the various ages are irregularly intermixed, the *Mixtae*. It will be the object of this memoir to bring forward detailed facts in support of this division of the Ferns. As regards the arrangement of the description I shall, as far as is consistent with the clear statement of facts, follow the order of the 'Synopsis Filicum,' and it will be seen that in many respects the arrangement of that work coincides with the natural grouping which will be arrived at towards the close. The chief departure from HOOKER'S arrangement will be to bring the Schizæaceæ and Osmundaceæ into relation with the Gleicheniaceæ; this is done with the object of grouping together at once those Leptosporangiate Ferns which, together with the Marattiaceæ, constitute our first category of *Simplices*. *Matonia* will also be associated with these. I shall find it desirable to take *Loxsonia* next after the *Simplices*, as it differs from other Ferns with a basipetal sorus in the median dehiscence of the sporangia. Other rearrangements of genera will also be made; but without specifying these here, it may be said that the sequence of the 'Synopsis Filicum' will be adhered to as far as possible.

GLEICHENIACEÆ.

Platyzoma.

The genus *Platyzoma* is very nearly allied to *Gleichenia*; so much so that Sir WM. HOOKER remarked that it might perhaps, without violence to Nature, be united with the genus *Gleichenia*.* The sorus consists of few sporangia; these are essentially similar to those of the latter genus, and will therefore require no special description. The most interesting point for comparison is the form of the leaf, which is simply pinnate, in contrast to the often complicated branching in *Gleichenia*; but the leaf in *Platyzoma* is occasionally forked, as is seen in specimens of a "forma

* 'Species Filicum,' vol. 1, p. 2.

furcata” sent by the late Baron Sir F. v. MÜLLER to the Kew Herbarium. A further intermediate step is supplied by *Gl. spelunca*, BR. (*Gl. circinata*, SW.), in which also the leaves are either simple or forked, while in *Gl. simplex*, HK., we find a species characterised by its simply pinnate leaf.

Gleichenia.

On the highly branched leaves of *Gleichenia* the arrangement of the rosette-like sori, usually in a simple row on either side of the midrib of the pinna or pinnule, is well known. But though the mature sorus has been repeatedly figured, the drawings are often misleading. I am not aware that the development of the sorus and sporangium has ever been followed.

The naked sorus consists of a low circular receptacle, bearing a variable number of sporangia; in *Gl. rupestris*, BR., and *Gl. circinata*, SW., two of the species examined developmentally, the number of sporangia is usually three or four, but in *Gl. flabelata*, BR., it is commonly four to six; in other species (*Gl. pectinata*, BR., and *Gl. dichotoma*, WILLD.) the number may be ten or even more. But in most species it is two to five, and towards the apex of the pinnule it may even fall to one solitary sporangium. This is a feature of interest for comparison with the Schizæaceæ.

The sporangia are commonly quite separate from one another, though instances of synangia, which resemble a fusion of two sporangia, are not uncommon. The sporangia usually form a single row round the receptacle; their orientation is in this case constant, the longitudinal slit of dehiscence facing directly towards the centre of the rosette-like sorus. Where the number of sporangia in the sorus is more than five, single sporangia may be displaced, perhaps by lateral pressure, and point obliquely upwards. But in *Gl. dichotoma*, in which the number of sporangia in the sorus may be as high as ten, or even more, the central area of the sorus, which is usually vacant in other species, may also be occupied by sporangia. Fig. 1 (Plate 2), *a-e*, show cases of the insertion of sporangia on the apex of the receptacle; the number of these sporangia may vary from one upwards, and they form a second tier above the basal rosette. When one of these only is present it usually occupies a central position. The orientation of these central sporangia is not constant, nor can I ascertain that it follows any rule. By the presence of these supernumerary sporangia the gap is bridged over within a single genus, between two well-marked types of sorus; on the one hand are the Marattiaceæ, and most of the Gleicheniaceæ, representing the “radiate uniseriate” type, with a single linear series of sporangia, surrounding the periphery of the low receptacle; on the other hand are the Cyatheaceæ, Dicksoniæ, Loxsomaceæ, and Hymenophyllaceæ, with a more or less elongated receptacle covered to its apex with numerous sporangia.

As in other genera where the sorus is circumscribed, so also in *Gleichenia*, fissions of the sorus may be found, chiefly in conjunction with branching of the veins,

Examples of this are shown in fig. 2, *a*, *b*, *c*. It is to be noted that in *Gl. dichotoma* such examples lead towards a condition common in other Ferns, but characteristically absent in most *Gleichenias*, where the sori are restricted to a simple linear series on either side of the midrib. These peculiarities of *Gl. dichotoma* are conjoined with a smaller size of the individual sporangium, and mark the species off (possibly also with *Gl. pectinata*) from the rest of the genus, as approaching other Leptosporangiate Ferns. It is to be remarked that Sir WM. HOOKER places these two species last in his arrangement, that is, next to the Cyatheaceæ.

The sporangia have an annulus, which is complete round the head, with the exception of the region of dehiscence, which is on the side directed away from the lower leaf-surface. The position of the annulus is oblique, so that of the two thinner areas of the sporangial wall which lie on either side of it, the one faces obliquely towards the centre of the sorus, and away from the leaf-surface, the other obliquely away from the centre, and towards the leaf-surface. The former may be styled the acroscopic or central, the latter the basiscopic or peripheral face of the sporangium. In describing the obliquely annulated sporangia of the Hymenophyllaceæ, PRANTL used the term "Rückenseite" for the side which is here styled the "central," and "Bauchseite" for that which is here described as "peripheral."* But I think it is better not to continue these terms, which in themselves are so liable to misapprehension; the words "central" and "peripheral," which I shall adopt for such cases, keep the attention clearly on the apex of the receptacle, as the centre with reference to which the sporangia are placed.

There is considerable variation in size of the sporangia in the genus *Gleichenia*; this may be seen in some measure in sporangia borne by a single species or individual, but it is a more marked feature in different species. Those which have a small number of sporangia in the sorus, such as *Gl. rupestris* and *circinata*, have relatively large sporangia (figs. 3, 4, 5); those which have more numerous sporangia in the sorus have them of smaller size, e.g. *Gl. dichotoma* (figs. 6, 7, 8). Taking first the sporangia of the larger type, as seen in *Gl. circinata*, the form is almost that of a kettledrum (fig. 5); the "peripheral" face is almost flat, and lies in apposition to the leaf-surface, while the annulus runs round its margin; the "central" face is very convex. The stalk is short, and consists of a central group of cells, surrounded by a peripheral series; it is thus thicker than in ordinary Leptosporangiate Ferns.

The sporangium of *Gleichenia dichotoma* is of much more elongated form, the stalk is thinner, and has no central group of cells (fig. 9). The annulus rises more obliquely from the surface of the leaf; not only are the central and peripheral faces of the sporangium much smaller than in *Gl. circinata*, but the curvatures of them differ; the peripheral face, which in the latter is often almost flat, is in *Gl. dichotoma* strongly convex, while the central face, which is convex in *Gl. circinata*, is flatter in

* 'Die Hymenophyllaceen,' Leipzig, 1875, p. 40.

Gl. dichotoma. Thus, in actual size, in thickness of stalk, in position of the annulus, in convexity of the surface, in fact, in all the dimensions, there is considerable difference between these two types. *Gl. dichotoma* stands aloof from most species of *Gleichenia*; *Gl. flabellata*, which has been the subject of observations to be detailed below, holds a middle position as regards size and shape of the sporangium, though as regards numbers of spores produced, it will be found to be an extreme type.

With these facts before us we pass to the study of development. The sorus begins to make its appearance in the still tightly circinate pinnule; it arises as a smooth outgrowth opposite a nerve (fig. 10), a considerable number of cells being involved in its origin. Having grown to a height almost equal to the thickness of the pinnule, it becomes flattened at the apex; in those cases where the sorus is to be a simple rosette (figs. 11, 12), the convex margin begins to grow out as rounded processes, which develop into the sporangia. There is some variety of detail, according to the size of the future sporangium; in the larger type of *Gl. circinata* or *Gl. flabellata* each process undergoes segmentation, resulting in a conical sporangial cell (x); in this successive obliquely inclined divisions follow, the earlier of which contribute to form the relatively massive stalk (figs. 11, 12, 13). These divisions do not appear to be uniform, as will be seen on comparison of the four corners of fig. 12, and of vertical sections (fig. 14); the latter also show in the case of these more massive sporangia that the periclinal division, which cuts off the cap-cell, takes place at a time when the sporangial head projects but slightly from the surface of the receptacle. From this description, and from the figures it is apparent that the whole sporangium is from the first of more massive construction, and results from more numerous segmentations than that of ordinary Leptosporangiate Ferns, though the last segmentations which define the central cell follow the usual sequence.

In the more attenuated type of *Gl. dichotoma* the sporangium is from the first of more elongated form, and its stalk less massive (fig. 15); the formation of the cap-cell takes place at a time when the sporangial head is more clearly in advance of the adjoining tissue, and the central cell is thus never actually immersed in the tissue of the receptacle, as is the case in *Gl. circinata*. In this feature again, *Gl. dichotoma* approaches the ordinary Leptosporangiate type. The central sporangia, above noted as occurring in this species, arise, as far as can be seen, simultaneously with the rest, and actually occupy the central area of the sorus from the first (figs. 16, 17); this area is usually vacant in other species (compare fig. 11), and is sometimes vacant also in *Gl. dichotoma* (fig. 15). Since the sporangia originate in this central position, their presence there cannot be accounted for by displacement due to pressure; it is to be ascribed rather to extra development, or interpolation of one or more accessory sporangia, which arise in a position usually unoccupied in the genus.

The divisions in the sporangial head to form the lateral cells of the wall, the cap-cell, the tapetum and definitive archesporial cell, follow with slight deviations the type general for Leptosporangiate Ferns (figs. 14, 15, 18, 19, 20, 21): the arche-

sporophyll cell is of tetrahedral form, but from the first it is of relatively small size, while the tapetum, which soon divides periclinally into two layers, grows rapidly. The outer wall remains a single layer of cells (figs. 22, 23, 24, 25), but the cells divide freely by anticlinal walls, so that in the mature state the sporophyll wall consists of very numerous cells. The annulus soon becomes differentiated, and it appears that part of the annulus owes its origin to the cap-cell, but the larger part to the lateral segments. The outer layer of the tapetum, with occasional supernumerary cells near the attachment of the stalk, remains small, and forms a narrow inner investment of the wall; it is permanent for a considerable time, and traces of it may be found even in the mature sporophyll. The inner tapetal cells enlarge greatly, and often become polynucleate; their protoplasm becomes aggregated, with the nuclei in close proximity to the sporogenous mass (figs. 23, 24), while the cell-walls become absorbed.

The fate of the archesporophyll cell has been followed in *Gl. flabellata*. It undergoes successive divisions (figs. 22, 23, 24), but the divisions are continued beyond the limited number usual for Leptosporophyllate Ferns; the result is a very considerable cell-mass, so that a single vertical section through a sporogenous group of an average sporophyll may traverse as many as 46 spore-mother-cells (fig. 24); 45 was found to be the mean of countings in sections through eight different sporophylls. A section through a sporophyll parallel to the surface of the leaf may traverse even a larger number, as in the left-hand sporophyll of fig. 25, where 66 are shown in section. This difference may be in part due to the section traversing the curved sporogenous mass obliquely, but this explanation will not account completely for the variation in number. When we reflect, after comparison with fig. 25, which represents a section of a similar sporophyll at right angles to that in fig. 24, that any one section will only traverse about one-eighth of the whole number of sporogenous cells, we find that there will be about $45 \times 8 = 360$ spore-mother-cells in a single sporophyll, and the potential output of spores may be estimated at about $360 \times 4 = 1440$. Comparing this with the case of ordinary Leptosporophyllate Ferns, it is plain that the potential productiveness of an average sporophyll of *Gl. flabellata* is far in advance of the latter, a point which ought to be considered in connection with the smaller number, but larger size of the sporophylls in each sorus.

But the size of the sporogenous mass, and the number of spore-mother-cells is not uniform in *Gl. flabellata*; the estimate given above is for a sporophyll of average size. It may be remarked that fluctuations in size of the sporophyll and number of spore-mother-cells are not uncommon in the eusporophyllate pteridophytes.*

Comparing these results with those derived from *Gl. dichotoma*,† considerable

* Compare 'Phil. Trans.,' B, 1894, Plate 42, fig. 10, which shows variation of size of sporophylls of *Equisetum*; also 'Phil. Trans.,' B, 1897, Plate 10, fig. 58, which shows a similar inequality in *Marattia*.

† The material of this species was kindly sent from Buitenzorg by Dr. M. TREUB, and having been grown in the open, it may be assumed to be a normal sample.

fluctuations of size of the sporogenous mass were observed, but the number of cells traversed by any one section were usually lower than in *Gl. flabellata*; thus, in fig. 27 (Plate 3) the number is 25, in fig. 28 it is 26, in fig. 29 it is 32. Occasionally sporangia show as many as 40 (fig. 30), but these are rare, and no number like 66, as shown for *Gl. flabellata*, has ever been seen.

Subsequently, the spore-mother-cells separate, becoming rounded off (figs. 26, 29, 30), and undergo the usual tetrad division. Prior to this, the tapetal nuclei (*n*) make their way in among the developing spore-mother-cells, as has been described for other sporangia.

In order to test the results obtained from sections, and the estimates of potential spore-production based on them, countings of the actual spores produced from single sporangia have been made in various species of *Gleichenia*, with the following results:—

- Gl. flabellata*, 794, 695, 838, 634.
- Gl. circinata*, 241, 242.
- Gl. rupestris*, var. *glaucescens*, 220, 232, 244.
- Gl. hecistophylla*, 265, 272.
- Gl. dichotoma*, 251, 319.

From the figures it appears (1) that the output is considerably in excess of that in most Leptosporangiate Ferns; (2) that the estimated number in *Gl. flabellata* is not actually attained; and (3) that though in the four latter species the numbers approximate to 256, that figure is liable to be exceeded.

That the actual figure in *Gl. flabellata* falls below the estimate may be accounted for partly by the abortion of some spore-mother-cells, or young spores, of which there is evidence; partly by errors in counting such large numbers; but it may also be due to the number of spore-mother-cells being inconstant, or being actually not so large as the estimate, which is necessarily only a rough one; another reason for the deficiency is the frequently incomplete division of the spores of single tetrads.

There is no exact proportion between the size of the individual sporangium and its output of spores in this genus as a whole. *Gl. circinata*, with its large sporangium, has a smaller output than *Gl. flabellata*, of which the sporangium is a medium size. It is, however, to be noted that the spores in the latter species are smaller than in the former; this has already been remarked by RAUENHOFF,* who has given measurements for this and several other species. This whole question of size of the spores, as bearing on their number, will be taken up later (see p. 109).

Synangia occur not uncommonly, and specimens have been observed illustrating many intermediate steps between completely separate sporangia, through stages of incomplete septation, to sporangia, which are simply larger than the usual average. An example of a synangium is shown in fig. 31, and it may be seen that though the

* La gén. sex. des Gleicheniacées, 'Arch. Néer,' vol. 24, p. 175.

septum is complete, the annulus is continuous from one sporangium to the other. Such cases may be compared with similar bodies found in the Osmundaceæ, and in *Angiopteris*.

The dehiscence of the sporangium takes place by a slit in the median radial plane; the annulus, which is continuous all round, except along the line of rupture, becomes gradually straightened on drying, or even everted, the whole sporangium, thus widening laterally, so as to elbow aside the other sporangia in cases where these are numerous. Then a sudden jerk on both sides of the slit throws the spores out, right and left, as described by ATKINSON.* Plainly, this mode of dehiscence requires lateral space, to allow of the widening before the jerk, and it is thus ill-suited for a crowded sorus.

Summary for Gleichenia.

- (1) The type of sorus is that of the Marattiaceæ; the number of sporangia is variable.
- (2) Synangia are occasionally found.
- (3) The segmentation of the developing sporangial head is as in Leptosporangiate Ferns, but the stalk is short and thick.
- (4) The number of spores in each sporangium exceeds that of most Leptosporangiate Ferns, and approaches Marattiaceæ, such numbers as 838–220 have been actually counted from single sporangia.
- (5) But the number of spores produced is not directly proportional to the size of the sporangium in different species of the genus, and there may be considerable differences in the size of the spores also.
- (6) The mode of dehiscence by a median slit is suitable only for a sorus which is not crowded.
- (7) *Gleichenia dichotoma*, in the number and arrangement of the sporangia in the sorus, in their smaller size, and longer and thinner stalks, approaches nearest to other Leptosporangiate Ferns.

OSMUNDACEÆ.

Within the sub-order there is variety in the arrangement of the sporangia. In *Osmunda* the sporangia are disposed on branches of the pinnæ, and occupy both sides of them without being grouped in distinct sori. In *Todea* the sporangia are localised on the lower surface of the pinna or pinnule, and are seated along the course of all the nerves of the fertile region; but even here the sori are not more clearly defined than by this mode of insertion of the sporangia.

In both genera the sporangia in near proximity to one another originate simultaneously, and go through their development together. This is no interpolation of

* 'Biology of Ferns,' p. 73.

later formed sporangia between those already more advanced, nor is there any marked sequence of origin of the sporangia from the base of the leaf upwards, or the converse ; they all appear to originate at very nearly the same time.

As regards the orientation of the sporangia in these genera, there seems to be no regularity. In *Osmunda* sporangia in proximity to one another face in the most various directions ; and even in *Todea*, where their arrangement has some reference to the nerves of the leaf, the sporangia upon a single nerve show no common rule of orientation. This is in accordance with a developmental drawing published some years ago.*

The family has long been recognised as holding an intermediate position between Eusporangiate and Leptosporangiate Ferns, as regards the size, structure, and mode of origin of the sporangia. The observations on which this view has been based have been made chiefly on *Osmunda*.† Though I have already published a preliminary note on the development in *Todea barbara*,‡ as well as a brief description with figures,§ there are various facts of interest not there fully dealt with which will justify a fresh description for this species.

A point which comes out very plainly from comparison of a number of sporangia of *Todea barbara* is that there is a great variety of detail in the segmentation, size, and form of sporangia on the same leaf, notwithstanding that they represent actually similar stages of development. These differences start from the very first, as is seen from fig. 32, in which two sporangia are shown already projecting as convex outgrowths, but the segmentation is not uniform : it is further to be noted that the cells marked (*x*) do not compose the whole outgrowth, but that adjoining cells also contribute in a certain degree, so that strictly speaking the whole sporangium is not referable in origin to the single cell. The massive stalk is partly formed from surrounding cells, just as in *Gleichenia* the extra segmentations contribute to the same end ; these are features for comparison with Eusporangiate types. How various the subsequent segmentations may be will be seen from the figs. 33–36 ; these show that the large cell in the centre of the growing sporangium may be of prismatic or conical form, while they also prove that adjoining cells take part in the formation of the sporangial outgrowth ; a comparison of figs. 35, 36, also brings out clearly the very great difference of bulk occasionally seen in sporangia of the same age. The large cell in the centre divides usually by three anticlinal walls (figs. 34, 36, 37) corresponding to those seen in the usual Leptosporangiate type, though the cell which remains in the middle may still be either truncate or pointed at the base. But sometimes it appears that four lateral cells may be cut off by anticlinal walls, as in the

* 'Annals of Botany,' vol. 3, plate 24, fig. 84.

† PRANTL, 'Bot. Zeit.,' 1877, p. 64 ; GOEBEL, 'Vergl. Entw. ;' SCHENK'S 'Handbuch,' vol. 3, p. 387 ; BOWER, 'Annals of Botany,' vol. 3, p. 362.

‡ 'Quart. Journ. Micr. Sci.,' vol. 25, p. 100.

§ 'Annals of Botany,' vol. 3, p. 364, plate 24, figs. 83–87.

largest sporangium in fig. 38; thus the central cell after periclinal divisions in *Todea*, may sometimes have the form which is characteristic rather of the Eusporangiate sporangia, though this is exceptional. Then follows the periclinal division to separate the cap-cell from the Archesporium, as shown in fig. 39, which also demonstrates in two sporangia side by side the sort of variety in segmentation which may frequently be seen. The cell which thus undergoes periclinal division is believed to be truly comparable to the "central cell" of the Marattiaceous sporangium.

The archesporial cell thus surrounded by the tissue which will form the sporangial wall, and carried up by growth in the stalk accompanied by cell-divisions, undergoes segmentation to form the tapetum (figs. 38, 40); and the irregularity seen in other segmentations is fully maintained in this also. From a comparison of figs. 41-45 it will be seen that sometimes the segmentation of the tapetum is almost according to the ordinary Leptosporangiate type (fig. 41), or with comparatively slight variations (figs. 43, 44); the most interesting cases are, however, those in which the Archesporium is truncate at the base; in these it appears that the cell or cells below it contribute to the completion of the tapetum (fig. 45); this is a point of some special interest, for one of the hitherto constant differences between the Leptosporangiate and Eusporangiate Ferns has been in the origin of the tapetum. *Todea* occasionally shows an intermediate condition. The division of the tapetum into two or partially three layers follows (figs. 46, 47), together with the subdivision to form the sporogenous group; beyond this point it will, I think, be unnecessary to trace the development of *Todea barbara*. For illustrations of the more mature structure reference may be made to 'Annals of Botany,' vol. 5, plate 7, fig. 68; to ATKINSON ('Biology of Ferns,' p. 66), or to the classical drawings on Plate 46 of the 'Genera Filicum.' In conclusion, in order to demonstrate the variability of structure of these sporangia further, the figs. 48, 49, 50 are added, as showing differences of thickness and segmentation of the sporangial stalk; these are all from sporangia, of the age of fig. 47.

An abnormality, which has been observed occasionally in *Todea barbara*, has been found not unfrequently on certain fronds of *Osmunda regalis*, viz., the occurrence of synangia: one of these is represented in fig. 51, and each half shows, except on the side where it is coherent with the other, the ordinary sporangial structure. Such developments are no very surprising consequence of the origin of sporangia close side by side, with a deeply-seated central cell, as in fig. 34; normally, each develops separately as in fig. 39, but the obliteration of the groove in this case would give a structure like that in fig. 51, and clearly this is not a very great modification. But what interpretation is to be put upon such cases, whether they may be counted as retrogressions, or the reverse, must for the present be left open.

The more robust and massive origin and structure of the sporangia of the Osmundaceæ, than of ordinary Leptosporangiate Ferns, is to be connected with the greater number of spore-mother-cells produced, and consequently the greater potential

output of spores. This matter has already been alluded to elsewhere,* but further observations have now been made with a view to arriving at an approximate numerical estimate. In *Osmunda*, Russow† estimated the number of spores in the single sporangium at “over 500,” and assumes therefore the number of spore-mother-cells to be 128. Though it is difficult to enumerate large numbers of spore-mother-cells exactly from sections, we shall see that sections support this estimate. GOEBEL’S drawing of the sporangium of *O. regalis*‡ shows 30 spore-mother-cells in the single plane of section. I have ascertained by counting the spore-mother-cells in sections of a number of sporangia in which the rounding-off and tetrad division was just about to commence, that this was a fair average specimen, the mean of ten countings from median longitudinal sections coming out rather over 31. I have also counted them in transverse sections of similar sporangia, and find the average of twenty countings to come out also rather over 31 but under 32. It is to be noted that the sporogenous group is approximately spherical, and that it is composed of irregularly cubical cells. I am informed that supposing the sporogenous group to be actually spherical, the volume of the whole sphere would be equal to the volume of 113 cubes, of which the diameter was one-sixth that of the sphere itself. Now the diameter of the average spore-mother-cell in GOEBEL’S figure, as also in the numerous sections which I have examined, is about one-sixth that of the sporogenous mass; but as the cells are not of uniform size, some being distinctly smaller, and as their form is not exactly cubical, we may consider that the correct estimate would probably be larger than 113, and the true number of spore-mother-cells in *Osmunda* may thus probably approximate to 128 in each sporangium. Consequently the potential number of spores per sporangium would approximate to 512, so that sections distinctly support Russow’s estimate of “over 500.” The above result is based on well-developed sporangia; but it is not an uncommon thing to find sporangia of smaller size with fewer spore-mother-cells. For instance, I have a drawing of one with only six spore-mother-cells seen in section.

The estimates thus made on the grounds of number of spore-mother-cells seen in section have been put to the test of actual counting of the spores from single sporangia, with the following results:—

Osmunda regalis, 476, 462, 396, 373.

Todea barbara, 478, 445, 442, 255, 238.

Todea superba, 206, 306, 342.

Todea hymenophylloides, 112, 115, 120, 124, 204.

It will be noted that all these numbers fall short of the typical 512; in *Osmunda*, where all the figures fall about midway between 256 and 512, this may be accounted

* ‘Annals,’ III., p. 364.

† ‘Vergl. Unters.’ p. 87.

‡ ‘Vergl. Entw.’; SCHENK’S Handbuch, III., p. 388.

for by error in counting, abortion of spore-mother-cells, or incomplete tetrad division. But the case is probably different in *Todea*; it will be noted in *Todea barbara* the first three figures approximate to, though they fall short of 512; the remaining two figures nearly coincide with 256. It seems not improbable that in these the division of the cells of the sporogenous mass has not been carried to the full extent, and the 64 spore-mother-cells probably underwent the tetrad division without the last division, which would have been necessary to produce $4 \times 128 = 512$ spores. The case of *T. superba* and *T. hymenophylloides* has a further interest; these species are well known as "filmy" *Todeas*, with the assimilating apparatus reduced in accordance with a moist habitat; in these, though the sporangia are of the same type as in the robust *T. barbara*, the output per sporangium is lower; in *T. superba* it approximates to the lower countings in this species, but in *T. hymenophylloides* all the figures are lower than any in *T. barbara*. From this we may conclude that a lower output of spores accompanies a filmy habit; this will suggest an interesting comparison with the Hymenophyllaceæ.

It is thus seen that the output of spores in the Osmundaceæ is a variable one; certain species approximate to 512 (*Osmunda regalis* and *Todea barbara*), others approach 256 (*Todea barbara* in part, and *T. superba*); others again have a lower output, approximating to 128 (*T. hymenophylloides*).

The mode of dehiscence resembles that in *Gleichenia* (see ATKINSON, 'Biology of Ferns,' p. 78, and figs. 132-135), and requires elbow-room for its successful execution.

Summary for Osmundaceæ.

1. *Osmunda* is non-soral, while in *Todea* the sporangia are localised on the nerves of the fertile region; in neither genus is there regularity of orientation.
2. The sporangia are from the first more robust than those of typical Leptosporangiates.
3. Their form and segmentation are liable to vary within rather wide limits, and show points for comparison with Eusporangiate Ferns.
4. The number of spore-mother-cells in each sporangium may approximate to 128, and the typical number of spores to 512, though this exact number has not been counted. In *Todea barbara* the number may approximate in some sporangia to the type of 256; and in *T. hymenophylloides* to 128.
5. Synangia may occasionally be seen either in *Todea* or *Osmunda*.

SCHIZÆACEÆ.

This sub-order has been so fully dealt with by PRANTL* that only slight additions

* 'Die Schizæaceen,' Leipzig, 1881.

need be made to his description. The sporangia are characterised by their solitary position, large size, and peculiar beaked form, while the only plane of symmetry is a longitudinal one which includes the stalk and line of dehiscence. Their orientation is constant. The rosette-like annulus occupies the beaked tip. The sporangia are marginal in origin, and their succession is acropetal as regards the leaf or lacinia. In point of segmentation the young sporangium shows points comparable to the sporangia of *Gleicheniaceæ* and *Osmundaceæ* rather than the *Polypodiaceæ*; the whole of the annulus may be derived from the cap-cell.

The view of PRANTL that we have to do with a monangial sorus, and the comparison with those monangial sori, occurring frequently in *Gleichenia* towards the tips of the pinnules, suggests a nearer comparison of the sporangia themselves; it will be seen that they are essentially of the same type in these sub-orders. The annulus of the *Schizæaceæ* is close to the beaked tip; it is, however, a real ring, which surrounds an area, consisting, it may be, of only a single cell, but usually of a larger number, which was called the "platte" by PRANTL.* This "platte" I believe to represent the peripheral face of the sporangium of *Gleichenia*, however small it may actually be. We have already seen in that genus how the proportions of the sporangia may vary in different species; in *Gl. dichotoma* (fig. 6) both faces are almost equally convex, and of equal size; in *Gl. circinata* (figs. 3-5) the peripheral face is smaller and flat, while the central face is larger and very convex; if we imagine a type of sporangium where this inequality is further accentuated, while the same mode of dehiscence is maintained, the annulus becomes drawn into a close circle, and the result is a sporangium much like that of *Lygodium*. The two types are thus essentially similar, though differing in the proportion of the central and peripheral faces.

In this connection, the comparisons recently made by ZEILLER are interesting,† between the new fossil genus *Kidstonia*, *Senftenbergia*, the *Schizæaceæ*, and *Osmundaceæ*, as regards the structure of the annulus. These comparisons show more clearly, than it had before been recognised, that the relation of *Senftenbergia* to the *Schizæaceæ* is a very close one, while *Kidstonia* would appear to link these with the *Osmundaceæ*, again a family with large sporangia, and with a numerous output of spores from each.

Accordingly our interest will be again directed to the output of spores in the *Schizæaceæ*. PRANTL has already pointed out and figured‡ how, in *Aneimia*, the number of spore-mother-cells is 32, but he did not make any statement for the other genera, nor did he observe the actual number of spores produced from each sporangium. RUSSOW§ found that the number in *Aneimia* did not exceed 128. In

* *Loc. cit.*, p. 46, &c.

† 'Bull. de la Soc. Bot. de France,' vol. 44, p. 95.

‡ *Loc. cit.*, Plate 8, fig. 121.

§ RUSSOW, 'Vergl. Unters.,' p. 87.

the case of *Lygodium japonicum*, my countings of spores from single sporangia gave 237, 238, 245. Clearly these numbers point to 256 as the typical number of spores, and 64 as the number of spore-mother-cells. *L. dichotomum* gave 232 and 246 as the result of countings; on the other hand, *L. pinnatifidum* gave 127, 128. We shall therefore be justified in accepting the typical number of spores per sporangium, in this genus, as varying between the types 128 and 256. This variation of number from species to species of the same genus involves the occurrence or omission of one division of the sporogenous group; the interest of this point is similar to that already noted for the genus *Todea*, but there the difference may be between sporangia even on the same plant.

Similar observations were made on *Mohria caffrorum*, but the numbers were lower, viz., 101, 107, 107, while several shrunken bodies were also seen, which may have been abortive spores. These totals point towards 128 as the typical number, a conclusion supported by sections through sporangia with rounded-off spore-mother-cells, for these indicate such a number as 32 (fig. 52).

Observations were also made on *Aneimia phyllitidis*, the countings resulting in 114, 104, 111, numbers which tally with *Mohria*, and also with PRANTL'S (fig. 121). It may be added that numerous sections of developing sporangia bear out the conclusion that the typical number of spore-mother-cells in *Aneimia* is 32. The sporangia of *Trochopteris (Aneimia) elegans* also contain a larger number of spores than 64, but actual enumerations were not made on this rare Fern.

Thus all the observed genera of Schizæaceæ have a larger number of spores per sporangium than the ordinary Leptosporangiate Ferns. The largest sporangia are those of *Lygodium*, and they have the largest output. The fact that *Lygodium* exceeds the other genera is interesting, as it is the genus specially selected by ZEILLER, on other grounds, for comparison with *Senftenbergia*, one of the oldest known Fern types.

In its anatomy, also, *Lygodium* stands aloof from *Aneimia* and *Mohria*, and shows characters more nearly comparable with *Gleichenia*.

As regards dehiscence, the Schizæaceæ resemble the Gleicheniaceæ and Osmundaceæ; they require room laterally for successful dehiscence, a method suitable only for laxly grouped sporangia.

Summary for Schizæaceæ.

- (1) The sporangia correspond to the type of the Gleicheniaceæ, but with different proportions; their orientation is constant.
- (2) The output of spores is typically 256 or 128 from each sporangium of *Lygodium*, and 128 for *Aneimia* and *Mohria*.

MATONIA.

The genus *Matonia* was founded by R. BROWN; it was placed by Sir WILLIAM

HOOKEE in the *Cyatheæ*, and he remarks ('Species Filicum,' p. 206): "I am satisfied that the genus belongs to the *Cyatheaceous* group." But this was a curious inconsistency in a writer who appreciated so highly the character of the indusium, and this he seems to have felt, for he remarks in the Synopsis of Genera at the end of the 'Genera Filicum,' with reference to *Matonia*: "This assuredly does not harmonise with this tribe (*Cyatheaceæ*); it belongs rather to *Aspidiarieæ*." BAKER,* when describing the new species, *M. sarmentosa*, expresses the opinion: "*Matonia* ought clearly to form a tribe by itself, not to be united with the *Cyatheaceæ*." To this I should agree, noting beside that the affinity of *Matonia* seems to be with the *Gleicheniaceæ* rather than with the *Cyatheaceæ*.

The investigation of the anatomy and development of this rare Fern by Mr. SEWARD will shortly provide better grounds for a conclusion as to its affinity†; meanwhile he has generously handed over to me material for the study of the sorus, from that supplied to him by Mr. SHELFORD, of the Museum, Sarawak, Borneo. To both of these gentlemen I return my thanks.

The distribution of the sori is usually in two rows, one on either side of the pinnule, but, as in *Gleichenia dichotoma*, this arrangement is sometimes departed from. The general structure of the mature sorus is well known‡; the sporangia, commonly six to nine in number, form a simple ring-like series round the receptacle, and are covered till maturity by the thick and leathery, hemispherical indusium, which is ultimately deciduous. The orientation of the sporangia is not exactly uniform; that of the majority is as in *Gleichenia*, but many have the annulus inclined, a consequence probably of crowding; this is seen also in the fossil *Laccopteris*. The annulus is incomplete at one side, an ill-defined lateral stomium being present, while the rupture is by a ragged lateral slit, opened by the straightening annulus.

The sorus originates as a smooth upgrowth from the lower surface of the pinnule, opposite a nerve, a considerable number of cells being involved from the first (fig. 53); no definite mode of segmentation has been recognised. As development proceeds, the margin of the upgrowth extends all round, as the overarching indusium; this, undergoing a somewhat regular segmentation by anticlinal walls, curves so as to cover in the sporangia which arise below (s., fig. 54); the indusium precedes the appearance of the sporangia, as in other indusiate Ferns. The sporangia originate from single cells, which have commonly a square base (s., fig. 54), though it may be a question whether this is always so. The segmentation is by walls inclined to one another (fig. 55); the first wall is usually on the side next to the leaf-surface (basiscopic side, figs. 55, 56), and meets one of the lateral walls of the parent cell; then follow three

* 'Journ. Linn. Soc.,' 24, p. 256; also 'Ann. of Bot.,' vol. 5, 1891, pp. 11, 12.

† 'On the Structure and Affinities of *Matonia pectinata*,' R. BR., read before the Roy. Soc., March 9, 1899.

‡ Compare F. BAUER'S drawings, 'Genera Filicum,' plate 43.

other inclined walls, and the segments thus produced surround a central triangular wedge-shaped cell, from which finally the cap-cell is cut off in the usual way (fig. 56).

The further segmentation of the central cell follows the usual course for Leptosporangiate Ferns; a double tapetum is formed (fig. 57) of which the inner cells become greatly enlarged, and their nuclei, clustering round the sporogenous group of cells, and undergoing fragmentation, present an appearance very like that in *Gleichenia* (fig. 58); the archesporium divides into 16 spore-mother-cells, and the typical number of spores seems to be 64; countings of mature spores gave figures between 48 and 64 as the produce of single sporangia. Sections of sporangia, when cut so as to traverse the annulus throughout its course, show the wall as a single layer, but composed of more numerous cells than is the case in many of the Leptosporangiate Ferns (fig. 57); this is also brought out plainly in views of the mature sporangia from without (figs. 59-62). It may be noted further that the stalk, which remains very short, is rather massive, and consists of a peripheral series of 6 or 7 cells, surrounding a central cell (fig. 59), which corresponds to the structure of the stalk in the massive sporangia in *Gleichenia* and *Osmunda*.

The mature sporangium is a body of rather irregular and variable form, owing apparently to pressures in the developing sorus. The annulus is incomplete and variable in position; it consists of a series of large cells, 20 or more in number, which takes an oblique and sinuous course, corresponding in the main to that in *Gleichenia*. The sporangia are liable to be tilted right or left, as shown in fig. 60, which represents two sporangia *in situ*, as seen from the side facing the indusium. Sporangia in which the annulus is not tilted are shown in figs. 59, 61, 62; from these it will be seen that the annulus starts close to the stalk (fig. 59); it first curves downwards towards the basiscopic side of the sporangium, then circling round it, curves upwards, the highest point being reached at the distal end of the sporangium; passing this it again curves downwards towards the basiscopic side, and stops short at some distance from the stalk; it is at this point that the dehiscence takes place, but though the cells immediately beyond the end of the annulus may show some regularity of division, there is in *Matonia* no highly specialised stomium as is the case in most Leptosporangiate Ferns. Fig. 62 shows the rupture; it also shows a case of the annulus stopping short of the stalk on either side, and that there is not here any continuous series of non-indurated cells, such as that seen in *Loxsona*.

Here then in *Matonia* is a sporangium, with a short and massive stalk and a large head, in which the annulus is not of a highly specialised, nor even of a constant structure, though in the main features it corresponds to the Gleicheniaceous type. It differs, however, from *Gleichenia* in the lateral dehiscence, and in the comparatively small output of spores.

Summary for Matonia.

1. The indusium is formed from the summit of the receptacle before the sporangia appear.
2. The sporangia arise simultaneously and show in the main the Leptosporangiate segmentation ; they have short, thick stalks.
3. The annulus is oblique, and shows a variable orientation, fundamentally similar to that of *Gleichenia* ; it is incomplete, stopping short of the insertion of the stalk ; the stomium is not well differentiated.
4. The output of spores is typically 48-64.

The Ferns so far described, however different in detail, all correspond in producing those sporangia that are in near juxtaposition *simultaneously* ; the sporangia themselves are of large size with short, usually massive stalks ; the output of spores per sporangium is commonly in excess of that in other Leptosporangiate Ferns. *Matonia* is however an exception to this, having not more than 64 spores ; as also in its dehiscence, which is lateral, while in all the rest it is in a median plane. We shall now proceed to types in which the sporangia appear not simultaneously, but in *basipetal succession*. In these the position of the sorus may vary, as indeed it does in those with simultaneous sporangia ; while the Marattiaceæ, Gleicheniaceæ and Matonineæ have superficial sori, the sporangia in the Schizæaceæ may be marginal ; in the Osmundaceæ the sporangia may be on the lower surface only (*Todea*), or cover both surfaces and margins (*Osmunda*). So we shall find similar variations of position in the basipetal sori ; *Loxosoma*, the Hymenophyllaceæ, Dicksonieæ, Dennstædtiineæ, have marginal sori, while in the Cyatheaceæ they are superficial. Such difference of position may serve as a useful character separating the tribes, but I do not admit that it in any way vitiates our comparisons. In other words, I estimate the method of internal arrangement of the sorus as a more important character than the position which the sorus holds upon the leaf which bears it. We shall take first a type with marginal sori.

LOXSOMA.

This rare genus, endemic in New Zealand, is represented only by the single species, *L. Cunninghami*, BR. It unites in itself characters of several distinct tribes, and, as a consequence, its systematic position has been difficult to fix ; it has the habit of a coriaceous *Dicksonia*,* or of a *Davallia*,† and a sorus like a *Trichomanes* ; but it differs from all Leptosporangiate Ferns except the Gleicheniaceæ, Schizæaceæ, and Osmundaceæ, in having a dehiscence of the sporangia in a median plane. This combination of characters has led to its having been variously placed by systematists ;

* 'Synopsis Filicum,' p. 56.

† CHRIST, 'Farnkräuter,' p. 7.

it was first described as a *Davallia* (*D. dealbata*),* afterwards as a *Trichomanes* (*T. Cænopteroides*).† The genus *Loxsoma* was finally founded for it by ROBERT BROWN. The fern was figured and described by Sir WM. HOOKER,‡ with the remark, “The aspect of the plant is perfectly *sui generis*, allied, however, on the one hand to *Davallia*, and on the other to *Trichomanes*.” Later he wrote§: “We are satisfied to place it in the Dicksoniæ along with *Davallia* and *Hymenophyllum*.” It has frequently been classed with the Hymenophyllaceæ,|| or regarded as a connecting link between them and other Ferns.¶ PRESL, however, who entertained peculiar views as to the Hymenophyllaceæ, remarks** that “*Loxsoma* must without any doubt be placed with the Helicogyratæ, amongst which it will stand alone as a rudiment of a new division or tribe between the Gleicheniaceæ and the Cyatheaceæ.” Subsequently, BOMMER again suggested the formation of a separate family of Loxsomaceæ,†† and discussing the relations of the genus,‡‡ he concludes that it “forms the natural passage from the Hymenophyllaceæ to the Polypodiaceæ by the Davalliaceæ.” CHRIST§§ ranks it as a genus of Davalliaceæ, placing it between *Davallia* and *Microlepia*, in a position far removed on the one hand from the Hymenophyllaceæ, and on the other from the Gleicheniaceæ. In his Preface (p. 7) he remarks that it is a *Davallia* bearing a sorus like that of *Trichomanes*, and sees in it an example of “the tendency of ferns of all groups to revert or advance in single isolated forms to the conformation of other often widely-remote groups.” Following his method of giving systematic weight to the general vegetative conformation, he ranks *Loxsoma* with *Davallia*. Before expressing an opinion on these divergent views, the details should be re-examined.

Hitherto the sorus has only been investigated in the mature state, the best representations of it being those of F. BAUER.|||| The sorus is marginal, with a cup-like indusium surrounding the elongated receptacle; this bears numerous sporangia laxly arranged and intermixed with fluffy hairs. The sporangia are of large size and pear-like form, with a rather elongated stalk; they are described as having an oblique annulus and vertical dehiscence, but the various accounts differ as to the completeness or incompleteness of the ring.

* A. CUNNINGHAM, MSS.

† HARVEY, MSS.

‡ ‘Genera Filicum,’ Tab. XV.

§ ‘Garden Ferns,’ 1862, Plate 31.

|| ‘Synopsis Filicum,’ p. 55. PRANTL, ‘Die Hymenophyllaceen.’ METTENIUS, ‘Filices Hort. Bot. Lips.,’ p. 112.

¶ METTENIUS, “Ueber die Hymenophyllaceæ,” ‘Abh. K. Sächs. Ges.,’ vol. 7, p. 500.

** ‘Hymenophyllaceæ,’ p. 98.

†† BULL, ‘Soc. Bot. d. France,’ vol. 20, p. 35, 1873. See also LUERSSSEN, ‘Hand. Syst. Bot.,’ vol. 1, p. 555.

‡‡ ‘Monographie de la Classe des Fougères,’ 1867, p. 100.

§§ ‘Die Farnkräuter,’ pp. 10, 306.

|||| ‘Genera Filicum,’ Tab. XV.

As it is clearly a form of importance, an effort was made to secure material for fresh observation of the facts. Through the kindness of friends in New Zealand specimens have been supplied upon which the following description of the sorus is based. A vertical section through a sorus of medium age shows, as in fig. 63, the short receptacle, sporangia, and hairs are included within the cup-like indusium; there is an obvious basipetal sequence of the sporangia, and I have never observed any departure from this order. The orientation of the sporangia (well shown in the drawings of F. BAUER) is constant, on the Gleicheniaceus type. A comparison of the sorus of *Loxosoma* with that of *Dennstædtia apiifolia* (fig. 130) shows general similarity, though that of *Loxosoma* is the larger. The pear-shaped sporangia, which rise obliquely upwards, have a complete annulus, as is shown in fig. 66, which represents the "peripheral" face; but though the complete series of cells of the ring can usually be traced, the induration of the walls is very unequal; commonly the cells of the distal half are enlarged, and their walls thickened; these are mechanically functional, while the lower part may be composed of thinner-walled cells, sometimes slightly or irregularly thickened, but usually not differing from the rest of the cells of the wall, except in their form and arrangement. This is shown in side view in fig. 65. If we compare figs. 65 and 66 with figs. *x*, *x*, *y*, &c. of *Gleichenia*, it is plain that the sporangia are of the same type, as regards the position of the annulus, though differing in the details; or the comparison might be extended to the Schizæaceæ on the one hand, or the Hymenophyllaceæ on the other (figs. 95-98), as regards the position of the annulus or the size of the sporangium.

The longitudinal slit of dehiscence traverses the distal part of the annulus, following the median plane of the sporangium, and may extend some distance down the peripheral side of the sporangium, so that it faces outwards from the receptacle, as is shown in BAUER'S drawings (plate 15, figs. 6-9). The orientation of the sporangia being strictly upon the Gleicheniaceus type, it appears that the main difference is that, while maintaining the same position of the annulus, the slit gapes towards the peripheral face of the sporangium rather than on the central side of it. There is no differentiation of a stomium, but the rupture occurs regularly at the distal end (*x*, fig. 66). The portions of the annulus on either side of the slit straighten as they dry and curve outwards in the usual way; they even become reflexed, tearing away irregularly from the rest of the wall, or carrying fragments of it outwards; in this state the two flaps may appear like the covers of an open book; as the induration stops short about half-way down the side, the general form of the sporangium is not altered by the dehiscence, so as to press upon or displace neighbouring sporangia; in fact, no elbow-room is required, as in *Gleichenia*, and this is a distinct advantage in a sorus where sporangia are numerous; in this we may perhaps see the rationale of the incomplete annulus. No sudden jerks of the annulus have been observed, nor would such jerks be very efficient, since the majority of the spores lie below the flaps of the annulus; the shedding of the spores seems to be mainly on the principle of the pepper-box.

The receptacle performs an important part in connection with dispersal. At first it is short, so that the sporangia are all included within the indusium (fig. 63), and this is so till the oldest sporangia are mature; an intercalary growth then takes place at the base of the receptacle, the thin-walled cells above the terminal mass of tracheids (*tr.*) become greatly elongated (fig. 64), forming a sort of pseudopodium (*ps.*), upon which the sporangia are raised so as to project beyond the lip of the protective indusium, and are thus free to scatter their spores. The arrangement is similar to that seen in the Hymenophyllaceæ, but here, in *Loxsonia*, the pseudopodium is formed independently of the long continued formation of a series of sporangia.

The spores themselves are of very large size, and the number in each sporangium is typically 64. The stalk of the sporangium, though elongated, is thick, and shows usually six cells in transverse section (fig. 67).

Material was not at hand for tracing the first stages of the sorus, but the order or succession of the sporangia upon the convex receptacle is strictly basipetal. The sporangium makes its first appearance as a massive deeply sunk cell, near the base of the groove between the receptacle (*r*) and the indusium (*ind.*) (figs. 68, 69); the first segmentations in it (*x.x.*) pass down to the base of the cell (figs. 69, 70), the later ones cut the wall (*x.x.*) obliquely, and thus a three-angled conical cell is in the usual way surrounded by three lateral segments; one edge has been seen to be directed towards the apex of the receptacle, but it is doubtful whether the position of the segments is constant. The cap-division, and segmentations forming the tapetum take place in the usual way (figs. 71, 72, 73); the inner series of tapetal cells enlarge considerably, and become polynucleate, thus resembling other large sporangial types. The sporogenous group is composed of 16 spore-mother-cells, which undergo a tetrad division in the usual way to give typically 64 large spores.

From a comparative point of view, *Loxsonia* is one of the most interesting Ferns; it appears to be a "generalised" type, while its rare and local occurrence countenances this view. In habit it shows similarity to such genera as *Dennstædtia*, *Microlepia*, and *Davallia*, a comparison which finds support in the anatomy of the vascular system.* I have little doubt of its real affinity with these closely-related genera, for not only does the habit and anatomy support it, but also the form of indusium and receptacle, and the basipetal succession and orientatation of the sporangia link it with *Dennstædtia* and *Microlepia*. The affinity with the Hymenophyllaceæ is also unmistakable, though probably not so close as has often been assumed: against it are the texture of the leaf, the mode of dehiscence, the structure of the sporangium, and the low output of very large spores; and in any case the affinity is with the less specialised types (*e.g.* *Hym. dilatatum*) rather than the specialised (*e.g.*

* I do not enter into anatomical details here, but merely state that this side of the comparison has already been pursued by Mr. GWYNNE-VAUGHAN in the Glasgow Laboratory and at Kew. The results will appear as a separate publication.

Trichomanes, sp.). The sporangium, and its annulus and dehiscence, point clearly towards the Gleicheniaceæ and Schizæaceæ; and though the habit is different from these Ferns, the structure of the creeping rhizome shows some degree of resemblance. The similarity of position of the annulus, and constancy of orientation are important, especially when taken with the very peculiar facts of induration. For as we have seen, the distal side of the annulus is indurated, while the proximal can still be followed, though it is commonly thin-walled; but occasionally single cells, or groups of cells, of the proximal side are also indurated: these cannot be functionally active, since they do not form a connected series. In them I think we can only see a decadent vestige of a completely indurated annulus, and conclude that *Loxsoma* was derived from ancestors with a complete oblique annulus, probably with a median dehiscence. Such ancestry might be found in the neighbourhood of *Gleichenia*. In *Gl. dichotoma* we have a type in which the sporangium and the sorus are similar in their main character. If we imagine these sori to be marginal (as they are in *Lygodium*), surrounded by a cup-like annulus which is already suggested in some *Gleichenias*, with the annulus modified as explained above to suit the more crowded sorus, and with a smaller number of spores, balanced by a larger number of sporangia produced in basipetal order, the sorus of *Loxsoma* would be before us. I do not suggest that any living *Gleichenia* was a progenitor of *Loxsoma*, but *Loxsoma* appears to me to be a link connecting the *Gleichenia-Schizæa* affinity with the type of *Dennstädtia* and *Microlepia*. On the other hand, putting aside the low output of spores, it is from just such a type as *Loxsoma* that the Hymenophyllaceous series may have arisen. In all these cases the anatomy of the sporophyte will present points of interest, and especially the arrangement of the vascular system in their creeping rhizomes. But this I leave over for discussion by others who are already at work on this special aspect of the question.

From the facts before us, I conclude that the suggestion of PRESL and of BOMMER is a sound one, viz., that the Loxsomaceæ should be regarded as a distinct tribe, having affinities with the Gleicheniaceæ and Schizæaceæ on the one hand, and on the other with the Hymenophyllaceæ and Dennstædtiineæ; the attempt should not be made to force it into any other tribe of living Ferns.

Summary for Loxsoma.

1. The marginal sorus consists of a basal indusium surrounding a conical receptacle, upon which the sporangia arise in basipetal succession.
2. The sporangia are pear-shaped, with complete, but only partially indurated oblique annulus, and rather long stalks of medium thickness.
3. The segmentation is of the ordinary Leptosporangiate type, starting from a deeply sunk mother-cell.
4. The dehiscence is in a median plane, without any well-defined stomium.

5. The output of spores is typically 64.
6. The receptacle elongates by intercalary growth, so as to lift the ripe sporangia above the edge of the indusium.

CYATHEÆ.

The sorus of these Ferns is borne on the under surface of the leaf, with an inferior cup-like indusium, which arises as a more or less complete ring from the base of the central receptacle. The succession of sporangia in such a typical genus as *Cyathea* is found to be strictly basipetal; but in certain genera, which have been commonly grouped in this tribe, the sorus will be found to be mixed. It is not improbable that there has been a progression, even within this series, from the one type to the other.

Though the sori appear to be so strictly circumscribed, they are not always separate and distinct; this is clearly illustrated by *Cyathea Brunonis*, WALL.; fig. 74 (*a*) shows a normal sorus, in which the indusium and receptacle are persistent, while the sporangia have fallen away; fig. 74 (*b*) shows an elongated form, while (*c*) is constricted in the middle; (*d*) and (*e*) are still more complex examples, associated with branching of a vein, or near proximity of two veins. Fig. 75 illustrates a similar condition in *Hemitelia grandifolia*, SPR.; here again the branching of nerves appears to be associated with partial fissions of sori. Such examples, which are not uncommon, will serve to show that the individuality even of these circumscribed and apparently definite sori is not always strictly maintained, and similar irregularities may be observed in other species than those named.

Cyathea.

The development of the sorus has been studied in *Cyathea dealbata*, Sw. It appears first as a swelling on the under surface of the pinnule, and it quickly becomes conical in form (fig. 76). I do not find any exact regularity in the segmentations of this upgrowth, but commonly a single cell, which undergoes successive divisions, occupies the extreme tip. The cup-like indusium makes its appearance early, and very soon overreaches the conical receptacle.

The sporangia appear upon this receptacle in basipetal order, but the succession is not long continued. I have repeatedly observed that the extreme apex develops directly into a sporangium (figs. 77 and 78), which is slightly in advance of those in a lateral position; that there is a basipetal succession is demonstrated by figs. 76, 77, 78, but as the total length of the receptacle is small, and the sporangia produced not very numerous, the succession is not here so prominent a feature as it is in the Hymenophyllaceæ. Gaps often occur between the young sporangia (figs. 77, 78) and those superficial cells which have not at first taken part in the development of

sporangia may be seen subsequently to project as papillæ; but these only grow into thin hairs (fig. 76). I have not observed any case of younger sporangia being intercalated among those more advanced.

The sporangium is derived from a single parent cell, which projects, undergoes oblique segmentation, and finally the cap-cell is cut off in the manner usual for Leptosporangiate Ferns (fig. 80); the tapetum is also formed in the usual way (fig. 81). The annulus now begins to be differentiated, and, as is well known, it occupies an oblique position, similar to that of the Gleicheniaceæ on the one hand, and of the Hymenophyllaceæ on the other; accordingly the terms "central" and "peripheral" may be applied here in the same sense as in *Gleichenia* to the two faces of the sporangia. But whereas in the simpler *Gleichenias* there is a constant orientation of the sporangium, so that the "central" face of the sporangium is towards the centre of the sorus, in *Cyathea dealbata* there is not the same constancy of orientation of the sporangium relatively to the sorus as a whole; this will be concluded from the median section (fig. 82, Plate 5), in which the sporangia (S''') and (S'') face in exactly opposite directions. The orientation, however, shows some degree of regularity in the basal part of the sorus. It will be remembered that in *Gleichenia dichotoma* the sporangia occupying the middle of the sorus show no regularity of orientation, while in those nearer its base it is constant, as we now see it in *Cyathea*.

The cells which form the oblique annulus become enlarged early, and are partly derived from the cap-cell, partly from the lower lateral segments; in fact, the origin of the annulus appears to be as in the Hymenophyllaceæ (see PRANTL, 'Hymenophyllaceæ,' p. 40).

The appearance of a peripheral face in a young sporangium, as seen from without, is shown in fig. 83; the complete ring surrounds an area of the wall ("Platte"), smaller than that in *Gleichenia*, but comparable in position (see fig. 7 of *Gleichenia*). In fig. 83 the attachment of the stalk is on the side away from the observer; the stomium (*st.*) is already defined at this early stage by cells of narrow form and smaller size; it is lateral, whereas in *Gleichenia* the rupture takes place in the median plane (*x*, fig. 7). Fig. 84 represents a rather younger sporangium of *Cyathea*, as seen from the "central" face (compare fig. 8 of *Gleichenia dichotoma*). The sporangia of *Cyathea* are so well known in their mature state that it seems unnecessary to pursue the details of their structure further.

The archesporial cell undergoes divisions in the usual way; but the number of spore-mother-cells produced is small in specimens of *Cyathea dealbata* from the Glasgow Garden; examination of numerous sections shows their number to be four to eight, but four seems to be the most common (fig. 82); countings of the spores of mature sporangia bear this out, but the number of spores matured is even lower than might be expected. Sporangia from the Glasgow plants gave 16, 8, 8, 16, as the numbers of spores matured. From this it will appear that though four spore-mother-cells frequently undergo tetrad division, it may happen that only *two* do so. It may

remain a question whether such a result is really normal, though I see no reason to doubt that it is.

Observations have also been made on *Cyathea medullaris* from the Glasgow Garden, with the result that numbers of spores counted from a single sporangium (such as 57, 61) point to 64 as the typical number for this species.

Summary for Cyathea.

1. The sorus is not always strictly circumscribed ; fissions may be found.
2. The sporangia appear upon the receptacle in strictly basipetal succession.
3. The annulus is oblique, corresponding in position to that of *Gleichenia*, but the dehiscence is lateral instead of median.
4. The orientation of the sporangia is not uniform towards the apex of the receptacle, but towards the base it is similar to that in *Gleichenia*.
5. The output of spores per sporangium in *Cyathea medullaris* is typically 64 ; but in *Cyathea dealbata* the number may be as low as 16, or even 8.

Hemitelia.

Observations have been made on the sori of *Hemitelia capensis*, BR., from Kew, and from the Edinburgh Garden. They correspond in all essential points to those of *Cyathea*, but show more regular orientation of the sporangia in the sorus, the annulus running obliquely, and following the Gleicheniaceous type of orientation. The succession of appearance of the sporangia is strictly basipetal, but the difference of age of those in the same sorus is not great, though sufficient to make their sequence clear. The structure of the mature sporangium is shown in figs. 85, 86 ; the former present the lateral view, the latter the view of the peripheral face. The number of spores observed on counting has been 48-64 from each sporangium.

Alsophila.

Excepting in the absence of the indusium, a character which this genus shares with *Gleichenia*, the sorus of *Alsophila* is closely similar to that of *Cyathea* ; the similarity extending to the basipetal succession of the sporangia, the position of the annulus, and in the main to the orientation of the sporangia.

The development of the sorus has been followed in *A. atrovirens*, and though, in this species, the number of the sporangia is but small, a basipetal succession is still to be recognised. This is shown in fig. 87, in which the sporangia near the apex of the receptacle have the cap-cell already formed, while in the lower sporangia on either side it is not yet cut off. The sporangia are from the first rather more robust than those of *Cyathea*, but follow essentially the same segmentation. Drawings have

been made of the sporangia of *A. excelsa* (figs. 88, 89), and these are interesting for comparison with *Gleichenia dichotoma*. The bulky sporangium presents an oblique annulus corresponding in position to that of *Gleichenia*; in point of its convex form and actual size it does not differ widely from that of *Gl. dichotoma* (compare figs. 6, 7, and 8); but the stomium is lateral, as against the median dehiscence in *Gleichenia*; it is obvious in fig. 88 that the cells of the stomium form part of the very regular series of the annulus.

The regularity of the orientation has already been delineated by F. BAUER for *A. excelsa**; though this is according to the type of *Gleichenia* in the basal part of the sorus, it is not strictly maintained by the sporangia at the apex of the receptacle; in this *Alsophila* corresponds to *Cyathea*, and to *Gl. dichotoma*.

The output of spores per sporangium has been noted in *A. atrovirens* (57, 62) and *A. excelsa* (64, 60), and the typical number appears to be 64.

The genus *Alsophila* shows certain points of interest for comparison with *Gleichenia*, notwithstanding the difference of habit, it corresponds in the position of the sorus, and the absence of the indusium, while the number of sporangia in the sorus (in *A. atrovirens*) is not far in excess of *Gleichenia dichotoma*. There is also some similarity in the form of the sporangium, its oblique annulus, and the orientation of the sporangia, at least at the lower part of the sorus, though in both there is irregularity of orientation of those at the apex of the receptacle. But there are important differences in the position of the dehiscence, and in the number of the spores produced from each sporangium.

Onoclea.

This genus was placed, along with *Hypoderris* and *Woodsia* in the Dicksoniæ, in the Synopsis Filicum, more perhaps on the ground of the basal indusium than anything else. Other writers have moved it elsewhere; thus PRANTL† includes it in his Aspidiïnæ, placing it next to *Nephrodium*. CHRIST includes it in the Aspidiaceæ, Mett., together with *Hypoderris* and *Woodsia*. Now it is in cases such as this that the additional characters of the sorus will be of use; we shall find that while *Onoclea* has a basipetal succession of the sporangia on the receptacle, *Nephrodium*, *Hypoderris*, and *Woodsia* have the various ages intermixed. While we may entertain the opinion that in certain lines of descent the one type may have passed over into the other, still to the existence of such a difference as this due systematic value should be accorded.

The well-known sporophylls of *Onoclea* have been sufficiently described elsewhere.‡

* 'Genera Filicum,' plate 9, fig. 4.

† 'Arb. Königl. Bot. Gart. zu Breslau,' 1892.

‡ HOOKER, 'Genera Filicum,' plate 82. CAMPBELL, Mem. of Bost. Soc. of Nat. Hist., 1887, &c., &c.

The early development of the sorus has been observed by GLÜCK* in *Onoclea struthiopteris*; the receptacle is superficial in origin, not marginal, though it may originate very close to the margin. The protection of the receptacle is carried out partly by the margin of the pinnule which curves over the sorus, forming what is sometimes called the "false indusium"; partly by the true indusium, which arises by upgrowth of superficial cells within the margin, at the base of the young receptacle; it precedes the sporangia. As no statement of the order of succession of the latter has been made to my knowledge, I have looked into the matter. CAMPBELL describes† "the development of sporangia beginning very early, and new ones forming up to the time that the leaf is full grown," but he does not give the facts we require.

Observations were made on *O. sensibilis*, with the result that the basipetal order of succession was demonstrated. The receptacle is elongated as in *Cyathea*, and the sporangia appear first at the apex of it, followed in quick succession by those below. The number of the sporangia produced is not very large in *O. sensibilis*, but there was sufficient evidence of a basipetal sequence, as shown in fig. 90. It will be noted that a number of cells remain at the base of the receptacle, which have not begun to develop into sporangia; these commonly do not progress further. They are interesting for comparison with *O. struthiopteris* in which the order of succession is also basipetal, while the number of sporangia may be larger. In the latter Fern, numerous immature sporangia may be seen clustering round the base of the receptacle, at a time when the majority of those seated higher are mature. There is no evidence of intercalation of young sporangia between the older ones, in fact, the mode of development of the sorus is like that of the Cyatheæ, and especially *Hemitelia*.

But when the sporangium itself is examined the correspondence with *Cyathea* is not borne out in detail; a definite regularity of orientation of the sporangia is certainly suggested by the section shown in fig. 90, but it is not maintained in the mature sorus, and the sporangia do not show that "testudo-like" overlapping which is seen in some *Cyatheæ*, and in perfection in the Hymenophyllaceæ. This is to be put in relation with the structure of the sporangium itself. The head is still unequally convex on its two sides, but the annulus is nearly vertical, and runs directly downwards to the stalk; there it stops short on either side of the insertion of the head upon the stalk (figs. 91, *a*, *b*, *c*). I do not find even that near relation of the two ends of the annulus to one another, across the stalk which is seen, for instance, in *Dennstaedtia*; in fact, the annulus is of the type characteristic of the Polypodiaceæ, while the sorus is characteristic of the Cyatheæ.

The spores are large, and the number produced from each normal sporangium is, in *O. struthiopteris*, between 48 and 64.

* 'Flora,' 1895, p. 341.

† *Loc. cit.*, p. 37.

Sphaeropteris.

This Fern has only been available in herbarium material. The stipitate sori are well shown by F. BAUER,* and they would no doubt repay developmental study. The insertion of the sori is superficial, as in the Cyatheæ.

BAUER'S drawings show the sporangia all of similar age, but I have found some of younger condition about the periphery of the sorus, and have no reason to doubt that their development is in basipetal sequence, even though those occupying the central region of the sorus appear to be all of the same age. BAUER'S drawings suggest a regularity of orientation, which is not, however, to be recognised as constant in herbarium specimens.

The sporangia are not adequately represented in BAUER'S drawings. In obliquity of the annulus they compare with those of *Dennstædtia*. The annulus itself is almost longitudinal (fig. 92), but with a slightly oblique course it passes behind the attachment of the stalk; it is, however, variable in its induration towards the base; the thickening sometimes stops short of the stalk, though it oftener is continuous behind it. The stalk itself consists of three rows of cells, and it is attached as in *Dennstædtia*. It is interesting to note that the very slight obliquity of the annulus goes along with an irregularity of orientation of the sporangia in the sorus, and it will be subsequently shown (p. 104) how these two facts are related to one another.

Diacalpe.

In the 'Synopsis Filicum,' p. 45, HOOKER remarks that "this genus seems more appropriately placed with the Cyatheæ than with the Dicksoniæ," and in the 'Genera Filicum' (pl. xcix.) *Diacalpe* is described as "a genus very closely allied to *Sphaeropteris* or *Peranema*, and differing only in the absence of the stipes to the sorus."

The sori were examined in herbarium material only. I am therefore unable to make precise statements as to development; but the succession of sporangia is probably basipetal, and there is no evidence to hand of a mixed condition of the sorus. I have not been able to detect any regularity of orientation of the sporangia.

The sporangia are of an elongated form, as in *Cyathea* (fig. 93), the annulus is very slightly oblique, and rather variable in its details; it is continuous to the base, but stops short at the insertion of the stalk, and does not pass continuously behind it, as in *Cyathea*; nevertheless the sporangium is not symmetrical, the annulus being usually slightly curved out of the plane, at the distal end.

A comparison based on these facts leads to the conclusion that *Diacalpe* has a near relation to *Sphaeropteris*, and that it is further removed than this genus from the *Cyathea* type.

* 'Genera Filicum,' tab. 22.

Comparison of Onoclea, Sphæropteris, and Diacalpe.

These three genera show an interesting relation as regards the sorus to the Cyatheæ and Dennstædtiinæ, with which they are usually classed. They have the superficial sori of the former, but show the almost vertical annulus which is characteristic of the latter. The series of indurated cells of the annulus may, as in *Sphæropteris*, be still recognised, sometimes as continuous past the insertion of the stalk of the sporangium, or the induration may sometimes be absent; or, as in *Diacalpe* and *Onoclea*, the annulus may actually be longitudinal, and stop short at the insertion of the stalk. It is not to be expected that the two characters shall go exactly parallel in specific cases, but these genera appear to me to illustrate how, when the basipetal succession is not long continued, and the orientation of the sporangia not strictly maintained, the annulus is no longer markedly oblique, but passes into the vertical position, and may be even interrupted at the insertion of the stalk. This will be noted also in the *Dicksonia-Davallia* series, and the mechanical rationale of the matter will be suggested later.

Hypoderris.

The genera *Hypoderris* and *Woodsia* have, on account of the basal indusium, and rounded superficial sorus, been placed by Sir WILLIAM HOOKER in the Dicksoniæ, sharing that position on the one hand with *Onoclea*, and on the other with *Sphæropteris*. We shall see that in an important character they differ from all the true Cyatheæ, and from Eu-dicksonia.

CHRIST has placed *Hypoderris* and *Woodsia* together with *Onoclea* and *Diacalpe* in the Aspidiaceæ. This appears to be done chiefly on grounds of external habit, quite irrespective of the internal arrangements of the sorus, and notwithstanding the fact that the indusium is basal in the former, while it arises from the tip of the receptacle in the latter.

Observations were made on the sorus of *Hypoderris Brownii*, J. SM., and first it may be noted that the outline of the sorus shows some variety, numerous cases of fission being found. There is a thin basal indusium, and sporangia of various ages are mixed together with no apparent order of succession, though the majority of the young sporangia originate towards the centre. There is no regularity of orientation of the sporangia; they have long stalks, and after dehiscence the heads fall away, while the stalks remain, forming a protection for those younger sporangia which appear later. The receptacle is only very slightly convex, and does not become elongated as in most Ferns with basipetal sori. The sporangia are slightly unequal on the two sides, but the annulus is vertical, and stops short at the stalk, as in most Polypodiaceæ.

Woodsia.

The genus *Woodsia*, which was founded by ROBERT BROWN,* was placed in the Dicksoniæ by Sir WM. HOOKER. F. BAUER'S drawing † shows the superficial sorus with few sporangia, which have no regularity of orientation, while the receptacle is not enlarged, but almost flat. FITCH'S drawing also, of *W. polystichoides*,‡ shows an absence of regularity of orientation.

Some species (*W. mollis*, J. SM.) suggest that the central sporangia mature first, and the peripheral ones later, but this is not borne out by *Woodsia obtusa*, TORREY, from the Edinburgh Garden. In this Fern the number of sporangia in the sorus is small, but nevertheless they are not simultaneous in origin, though the series of succession is not long continued. The very globular sporangia have a projecting vertical annulus, which stops short of the stalk.

The basal indusium of *W. obtusa* is a continuous disc below, and though it has a fimbriated margin, it shows points of similarity to that of *Hypoderris*, with which the genus seems to be naturally related.

These two genera appear to be out of place in the Dicksoniæ, and no less in the Aspidiaceæ of CHRIST; they show as regards the basal, flat, cup-like indusium, and superficial position of the sori, more similarity to the Cyatheæ. But from both Cyatheæ and Dicksoniæ they appear to me to be removed by the mixed character of the sorus, while the vertical annulus, stopping short at the stalk, is another feature pointing in the same direction. My own opinion is that while they show a *Dicksonia-Cyathea* affinity, they represent an intermediate type between these families and certain of the Polypodiaceous Ferns with mixed sorus. In MOORE'S 'Index Filicum' (1857) they were included together with *Sphæropteris* and *Diacalpe*, &c., in the group *Peranema* (DON, 1825); this arrangement was amended by BOMMER (*loc. cit.*, p. 89), who included them under his Tribe III, Sphærochlamideæ. Some such position, intermediate between those with oblique annulus and basipetal succession on the one hand, and those on the other with mixed sorus and vertical annulus seems to be their natural place, and this opinion is susceptible of support from the anatomical side.

The preceding genera share with *Gleichenia* a superficial position of the sorus; where an indusium is present it is basal and cup-like, or it may be one-sided. The genera illustrate a probable progression from a type with basipetal succession of sporangia with oblique ring to a mixed sorus without definite orientation of sporangia, and with a vertical ring.

We shall now turn to the type with marginal sori, in which the indusium, which is still basal, may be two-lipped. A similar progression will be noted in these also, and

* 'Misc. Bot. Works,' vol. 2, p. 251.

† 'Genera Filicum,' plate 119.

‡ HOOKER'S 'Second Century of Ferns,' vol. 2.

it may be left for the present an open question, whether these two series which resemble one another in so many features, should really be separated on so slight a point as the marginal or superficial position of the sorus, a character which is itself variable in *Deparia*.

HYMENOPHYLLACEÆ.

This family of Ferns has undergone vicissitudes of classification : they fell into the *Helicogyratæ* of BERNHARDI* ; they were placed in the *Gyratæ* (*Polypodiaceæ*) by R. BROWN, in his 'Podromus,'† and were included among the *Polypodiaceæ* by various other writers. BRONGNIART‡ first separated them as a special family, though the name of ENDLICHER§ is usually associated with the establishment of the *Hymenophyllaceæ*. The family were thus recognised as ranking on an equal footing with the *Cyatheaceæ*, *Polypodiaceæ*, &c.

But their peculiarities so impressed PRESL that after prolonged investigation he concluded|| that the *Hymenophyllaceæ* are somewhat far removed from the *Filicineæ*, and must be regarded as a connecting link with the Mosses and Liverworts ; it was further suggested by VAN DEN BOSCH that the term *Bryopterideæ* should be given them. The actual separation of them from the *Filicineæ* was opposed by METTENIUS,¶ but the comparison of their vegetative structure with that of certain Bryophytes was maintained, and strengthened by fresh observations ; it was pursued subsequently by PRANTL** with regard to the sporophyte, and by GOEBEL†† as regards the gametophyte. Dr. GIESENHAGEN has stated the case as follows‡‡ : "The most important result which the investigations on *Hymenophyllaceous* prothalli have hitherto had is expressed obviously in the results of GOEBEL's work, which brings clearly and succinctly before the eyes the phylogenetic connection between the Mosses and Vascular Cryptogams, and thereby bridges over the gap which formerly existed between these circles of affinity in the sequence of development of the *Archegoniataæ*." As the result of a comparison of the sporophyte of these Ferns, GIESENHAGEN states later (p. 463) as follows : "But the latter (*i.e.*, morphology and development), the regular structure of the shoots, the sort of development of the sorus, the development and form of the sporangia, the spore-formation, and, further, the presence of a root in the embryo in all observed cases, indicate with definiteness that the *Hymenophyllaceæ* are at least as near to the *Polypodiaceæ* as to any other family of the homosporous Lepto-

* 'Dritter Versuch einer Anordnung der Farnkräuter' (1806).

† 'Podromus Floræ Novæ Hollandiæ' (1810).

‡ 'Histoire des végétaux Fossiles' (1828).

§ 'Genera Plantarum' (1836-1840).

|| 'Hymenophyllaceæ,' pp. 97-98 (1842).

¶ "Ueber die Hymenophyllaceæ," 'Abh. d. K. Sächs. Ges. d. Wiss.,' 1864, p. 403.

** "Unters. d. Morph. d. Gefässkryptogamen," 'Die Hymenophyllaceen' (1875).

†† 'Buitenzorg Annals,' vol. 7, p. 17 ; also, "Archegoniatenstudien," 'Flora,' 1892, p. 93, &c.

‡‡ "Die Hymenophyllaceen," 'Flora,' 1890, p. 423.

sporangiatæ.” In accordance with such views as these, we find the Hymenophyllaceæ placed first in the system of CHRIST,* and removed far from those other Ferns with oblique annulus (*Loxsonia*, *Cyatheaceæ*, *Gleicheniaceæ*) with which they are associated in the ‘Synopsis Filicum.’

I have elsewhere expressed my dissent from the view that the Hymenophyllaceæ are the most primitive type of Ferns.† GIESENHAGEN‡ remarks at the close of his comparative study of the vegetative organs of these Ferns: “We have thus before us organs which have begun to be reduced, and they tell us that the simplest Hymenophyllaceæ, springing from forms of more complex structure, have advanced to a simplification of the morphological structure, which is expressed in the suppression of the root-formation, in the simplification of the leaf-form, and the reduction of the vascular bundles.” I conclude from these quotations from GIESENHAGEN that his view is that, while the Hymenophyllaceæ show in their sporophyte evidences of reduction from some more complex type, the simplicity of their gametophyte is to be accepted as truly primitive; that the very critical line which lies between reduced and rudimentary characters is to be drawn between the sporophyte and gametophyte of these Ferns. It is possible that this is the correct view, but I do not think it probable, since both generations are commonly exposed to those very conditions which he recognises as conducive to reduction in the sporophyte, and which are known to affect the prothallus of Ferns and the gametophyte of the Bryophyta, in the direction of filamentous form. I shall offer an alternative opinion as to the relationship of this interesting family, which involves a probability of reduction in both of the generations.

The comparative study of their sorus leads to the conclusion that while the Hymenophyllaceæ show the highest complexity of the receptacle, the sporangia themselves are related in character to more massive types, and that this will justify a systematic position near to the *Loxsoniaceæ* and *Gleicheniaceæ*, such as that assigned to the family in the ‘Synopsis Filicum.’ The general construction of the Hymenophyllaceous sorus is well known. Many satisfactory drawings are given by PRESL,§ and other descriptive writers, which show how the sporangia with their oblique annulus are disposed with regularity of orientation upon the elongated receptacle, so that they overlap one another like the shields of a Roman *testudo*. The orientation for each single sporangium corresponds essentially with that seen in *Gleichenia*, *Cyathea*, *Thyrsopteris*, *Dennstaedtia*, and *Loxsonia*. This is well shown both for *Hymenophyllum* and *Trichomanes* in the drawings of PRESL, and in the Genera Filicum (Plates 31 and 32). The sporangia are, like those of *Cyathea*, produced in basipetal succession upon the more or less elongated receptacle. This fact was noted

* ‘Die Farnkräuter der Erde,’ 1897, p. 1.

† ‘Annals of Botany,’ vol. 5, p. 109.

‡ ‘Flora,’ 1890, p. 462.

§ ‘Die Hymenophyllaceen,’ plates 2, 8, 11, and 12.

by METTENIUS,* and demonstrated developmentally for *Trichomanes* by PRANTL.† The development in *Hymenophyllum* was also described by him in the text of his paper, and I now add a drawing of the young sorus of *Hymenophyllum Wilsoni* (fig. 94), which shows the young sporangia near the apex of the receptacle, while below there are clear indications of the active intercalary growth; this drawing may be compared with fig. 11 of *Gleichenia*. The extent of the intercalary growth of the receptacle is greater in *Trichomanes* than in *Hymenophyllum*, and the genera were by early writers distinguished on this ground, those with the receptacle exerted being ranked with the former, while those with it included fell into *Hymenophyllum*. Though this generic distinction will not hold accurately, still the general statement is correct that intercalary growth of the receptacle, and basipetal succession of the sporangia are longer continued in *Trichomanes*; it is the extreme example of this mode of development of the sorus, but none the less is it similar in kind to that described for the Cyatheaceæ and *Loxsonia*. It will be a matter for consideration whether this extreme elongation is more probably a primitive or a derivative condition.

The sporangia in the Hymenophyllaceæ differ greatly in size, between a large, almost spherical type, such as that of *Hymenophyllum dilatatum* (figs. 95, 96, 97, 98), and small compressed bodies such as are formed in many species of *Trichomanes* (figs. 99, 100, 101, 102); it will be shown that with this goes a very wide difference in the output of spores. The large sporangia of *Hym. dilatatum* are produced in relatively small numbers upon the short, but rather broad, receptacle; in size and form they are comparable to those of *Gleichenia circinata* (compare fig. 95 with fig. 3 of *Gl. circinata*), while the annulus shows a similar degree of obliqueness. Externally there is close similarity, excepting in the dehiscence, which is lateral in *Hymenophyllum* (fig. 96), a position which we shall see later may be correlated with the close packing of the sporangia in the sorus. The view of the sporangium from the side on which dehiscence takes place shows that the annulus is not continued throughout as a distinct series of cells (fig. 96); there is no definite group of cells of the stomium, such as is seen in the Cyatheaceæ; this feature is again comparable to that in *Gl. circinata*; the drawings of the central (fig. 97) and peripheral faces (fig. 98) will complete the knowledge of the external form of the sporangium in this species. The stalk is short and rather thick, and the insertion by a rosette of cells, some six in number; this harmonises with the segmentation of the parent cell, demonstrated by PRANTL for *Trichomanes*,‡ and verified in *Hymenophyllum*, in which the first oblique segmentation wall is inserted on the basal wall of the parent cell; this is a common type for Ferns with large sporangia and short stalks, as against those with smaller sporangia and long stalks.

* 'Die Hymenophyllaceen,' p. 474.

† *Loc. cit.*, p. 35, and plate 5.

‡ *Loc. cit.*, p. 35, &c.

The sporangia of *Trichomanes speciosum** have been exhaustively treated by PRANTL. I have made observations on several species of the genus which substantially support his facts; but as PRANTL did not give drawings of the mature sporangia, and as numerous drawings of them have been published by various authors which do not represent their exact form, and frequently take no account of the orientation, I have represented the sporangia of *Tr. radicans* in figs. 99–102, from four different points of view. Fig. 101 shows the sporangium presenting its central face; the close analogy with fig. 97 of *Hym. dilatatum* is obvious, though it is smaller in size, and with fewer cells in the annulus; but fluctuations less in extent though similar in nature are found in *Tr. radicans* itself, the cells of the annulus varying between 20 and 25. There is also a greater simplicity in the region of the stomium, which in *Trichomanes* is represented by two cells only. Fig. 102 represents the “peripheral” face, the thin-walled region (“Platte”) being surrounded by the annulus, which takes the form of a twisted loop. This twisted form is clearly shown in fig. 99, which demonstrates also the relation of the sporangium to the receptacle, and that the distal part of the annulus is directed obliquely towards its apex. This being the case for all the sporangia, the free action of the annulus on dehiscence is assured for each individual sporangium; this may be compared with fig. 95 of *Hym. dilatatum*. The stomium in *Tr. radicans* is of very simple construction: it consists of two cells (seen in figs. 100, 101, 102), and in the last of the drawings it is shown in surface view, with the slit of dehiscence gaping between the two cells. Comparing this with fig. 96 of *Hym. dilatatum*, we see again that *Trichomanes* is constructed on the same general plan, of which it appears as a simplified edition.

These observations on the sorus and sporangium of the Hymenophyllaceæ lead us to regard *Hymenophyllum* as nearer than *Trichomanes* to certain other Fern types, and especially to those with large sporangia; this is borne out by the enumeration of the spores per sporangium, which brings results of peculiar interest for comparison with other Ferns. The Hymenophyllaceæ show among their species a wider range of number of spores produced from the single sporangium than has been noted for any other family of Ferns. While certain of their species approach or equal the high numbers of the Gleicheniaceæ, Schizæaceæ, and Osmundaceæ, in others the number is distinctly low. It will be seen that species of *Hymenophyllum* give for the most part a higher output of spores than *Trichomanes*. The results may be stated thus in a tabular form:—

* ‘Die Hymenophyllaceen,’ p. 35, &c.

Name.	Results of actual counting.	Typical number.
<i>Hym. Tunbridgense</i>	413, 416, 421	258-512
<i>Trich. reniforme</i>	247, 243	256
<i>Hym. sericeum</i>	216, 239	256
" <i>dilatatum</i>	127, 127, 127, 127	128
" <i>Wilsoni</i>	119, 121	128
<i>Trich. radicans</i>	46, 58, 62	48-64
" <i>crispum</i>	51, 52, 59	48-64
" <i>rigidum</i>	32, 48, 56	32-64
" <i>spicatum</i>	48	48
" <i>javanicum</i>	38, 42, 42	32-48
" <i>pinnatum</i>	32, 48, 32	32-48

It may be remarked that in almost every case the results from fresh material from Kew and other gardens were checked by countings from Herbarium material, so that the results may be taken as representing the normal condition of the species named.

Seeing that in *Trichomanes* the usual output per sporangium is lower than in *Hymenophyllum*, while on the other hand the receptacle is usually longer, and has more continued intercalary growth, the question arises whether the larger number of sporangia will approximately compensate for the lower individual spore-output. It is admitted that the enumeration of sporangia per sorus can hardly be exact, where the basipetal growth is long continued; but estimates have been made with such accuracy as possible with the results which are given in the subjoined table:—

Name.	Sporangia per sorus.	Spores per sporangium.	Output per sorus.
<i>Hym. Tunbridgense</i>	20	420	8,400
<i>Trichomanes reniforme</i>	40	256	10,240
<i>Hym. dilatatum</i>	90	128	11,500
<i>Trich. radicans</i>	140	64	8,960

It thus appears that, notwithstanding the great variations in spores per sporangium, the resulting output per sorus is approximately uniform for the cases quoted. Doubtless exceptions may occur; all I desire to do is to show that the increased length of receptacle, and higher number of sporangia, tends to counterbalance the smaller output per sporangium, which is seen in its extreme form in some species of *Trichomanes*.

The facts before us, of external form, of anatomy, and of the gametophyte, may bear either of two interpretations from the comparative point of view: the Hymenophyllaceæ may be regarded as a relatively primitive series leading on to more complex derivative forms, or they may be a series of reduction, derived from a more complex ancestry. The new facts relating to the sorus are important in this connection; such large sporangia as those of *H. dilatatum* compare with those of *Gleichenia*; their

annulus and orientation are similar, though the dehiscence is lateral, and though they arise in basipetal sequence instead of simultaneously. The output of spores per sporangium in *H. Tunbridgense* compares favourably with that in Ferns which have a simultaneous sorus, and even the single sporangium of *H. dilatatum* produces as many as those of most of the Schizæaceæ. These facts are of the more importance since the Hymenophyllaceæ are the only other Leptosporangiate Ferns whose sporangia have been found to produce numbers of spores comparable to those which rule in the Gleicheniaceæ, Osmundaceæ, and Schizæaceæ.

With the exception of *Trichomanes reniforme*, which is certainly an unusual type of the genus in having a more massive structure of the lamina,* all the species of *Trichomanes* which have been examined show low numbers; and this I take to be a result of reduction from a larger type, similar in nature to that seen in *Todea*, though carried further. We have noted above (p. 41) that the "filmy" *Todeas* have a smaller output per sporangium than *T. barbara*; this suggests that reduction of output accompanies the "filmy" habit, and if this be so, then we may look upon the simple sporangia of most species of *Trichomanes* as simple by reduction, not by primitive character.

Trichomanes is the simpler type of the Hymenophyllaceæ in its prothallus; while the prothallus of *Hymenophyllum* consists of a broad, ribbon-like expansion; that of *Trichomanes* is usually filamentous; the archegonia in Ferns do not show distinctive features, but HEIM,† who has drawn attention to the value of their antheridia for comparative purposes, specially notes the similarity of those of the Hymenophyllaceæ and of the Gleicheniaceæ. This is a fact of importance when taken along with the data of spore-output now disclosed, since features of the reproductive organs of both generations indicate a similar affinity. The result of a general comparison of the Hymenophyllaceæ with other Ferns is summed up by CAMPBELL in the following sentences‡:—"The Hymenophyllaceæ, on the whole, approach most nearly the Gleicheniaceæ, with which they agree in many points, both in the sporophyte and the gametophyte, but they also recall the Osmundaceæ, and possibly may form a branch somewhere between the two, but nearer the former. The peculiarities of the gametophyte are probably in large measure the result of environment, and the filamentous prothallium of some species of *Trichomanes* is beyond question a secondary and not a primary condition." This expresses the view which I entertain,

* See 'Annals of Botany,' vol. 3, Plate 22, fig. 51. In *Trichomanes reniforme* the lamina is more robust than in other species of the genus, it consists of four to six layers of cells. This more massive assimilating system is seen in the very species which has the largest output of spores per sporangium in the genus. This appears to me to be a very significant fact, and a definite support of the view that there is a close casual relation between the filmy character and a lower spore-output in certain Osmundaceæ and in the Hymenophyllaceæ.

† 'Flora,' 1896, p. 363.

‡ 'Mosses and Ferns,' p. 420.

while the facts of output of spores per sporangium, and of structure of the sporangia above stated, appear to me to add considerable weight to the evidence. I look upon the Hymenophyllaceæ as a blind line of descent characterised by specialisation of both generations, which has taken the form of simplification; and in both generations *Trichomanes* shows the greater simplicity. Comparison of their sporangia, however, and especially their spore-output, suggest that they were derived from some ancestry with simultaneous sporangia. There seems to me no evidence that they lead on directly to any other type of Homosporous Ferns; as regards the sorus, they supply the extreme types of elongation of the receptacle and long-continued basipetal succession of the sporangia.

Summary for Hymenophyllaceæ.

- (1) The Hymenophyllaceæ form a sequence, of which species of *Hymenophyllum* are less extreme types than species of *Trichomanes*.
- (2) The former show a shorter receptacle, larger sporangia, and larger output of spores from each.
- (3) The output of spores per sporangium in some species of *Hymenophyllum* and in the robust *Trichomanes reniforme* compares favourably with that of Gleicheniaceæ and Osmundaceæ; in most species of *Trichomanes* it is low.
- (4) The typical numbers in the family vary between wider limits than is found in any other family, viz., from over 256 to 32.
- (5) The output per sorus is approximately equalised by the longer receptacle and more numerous sporangia where the individual sporangia are small.
- (6) The orientation of the sporangia and basipetal succession on the receptacle is constant.
- (7) There is a correspondence between the Gleicheniaceæ and Osmundaceæ on the one hand and the Hymenophyllaceæ on the other, not only in the sporangia and spore-output, but also in the antheridia: that is, in the reproductive organs of both generations, notwithstanding their diversity of vegetative character.

DICKSONIÆ.

Another apparent sequence, which leads on by gradual steps towards other types of Leptosporangiate Ferns, such as *Lindsaya* and *Cystopteris*, is composed of the genera *Thyrsopteris*, *Dicksonia*, *Dennstædtia*, *Microlepia*, and *Davallia*. The sori are marginal, or at most only slightly intra-marginal, while the forms which they lead to have an intra-marginal sorus. The order of succession of the sporangia is typically basipetal in the first four genera, but it may be mixed in some species of *Dennstædtia* and *Microlepia*, and this is the typical condition for the true *Davallias*, which lead further to other genera with mixed sori, such as *Lindsaya*, *Cystopteris* and the Pterideæ.

Those with a basipetal succession have an oblique annulus, while in *Davallia* the annulus becomes almost vertical, as it is also in *Lindsaya* and *Cystopteris*. In the first named genera the receptacle is marginal, but certain *Davallias* seem to lead on naturally towards *Cystopteris*, in which the sorus is plainly superficial. Thus a number of characters of the sorus vary in a parallel direction as we pass along the series indicated; and this variation of characters is to be compared with that already explained for the Cyatheaceous affinity. The two sequences are separated chiefly on the marginal as against the superficial position of the sorus.

Thyrsopteris.

This rare monotypic genus, which is endemic in the island of Juan Fernandez, was first placed by Sir WILLIAM HOOKER with *Dicksonia*, but in the Synopsis it is included by him in the Cyatheæ. It appears to have a relation to both. The sori, which are terminal on the branchlets of the "much compound or thyrsoidal" fertile pinnæ, have a cup-like basal indusium, surrounding a receptacle which bears numerous sporangia. Since the young sori of this Fern have never been examined, and as suitable material has been supplied by the Director of the Royal Gardens, Kew, their development will now be described.

As in *Dicksonia*, the receptacle is the actual apex or margin of the pinnule; it appears at first, while the pinna is still tightly coiled, as a smooth cone, slightly flattened on the adaxial and abaxial faces. Below this, before the sporangia make their appearance, the indusium begins to be formed, as a massive outgrowth; a transverse section at this stage often shows that the indusium is slightly two-lipped (fig. 103), and here we may trace an indication of correspondence with *Dicksonia* (*Cibotium*); but this two-lipped character is only slight, and is not obvious at later stages. In fig. 103 the receptacle is almost circular in section, but it is commonly flattened as in *Cibotium*, parallel to the surfaces of the leaf (fig. 104). The formation of sporangia soon follows, and their succession is basipetal; the first appear at the extreme margin, of which one is shown in fig. 105, the section being perpendicular to the surfaces of the leaf; others then appear in lower positions. The marginal sporangium thus seen is only one of a series which arise along the edge of the flattened receptacle (fig. 106, Plate 6); thus the receptacle is a flattened lobe developed from the margin of the pinnule, as in *Dicksonia*, while the indusium, as in this genus, originates as a growth within the margin, on either side of the pinnule.

The form of the parent cells of the sporangia is not constant; commonly the cell has a square base, and the first segment-wall passes obliquely to the basal wall (fig. 107), the next segment-wall being inserted obliquely on the first; the result is from the outset a sporangium with a short massive stalk, as shown in fig. 108. Transverse sections through the stalk of older sporangia show that it consists sometimes of a simple rosette of cells (fig. 109); sometimes periclinal walls occur (fig. 110),

and the result may be such as is shown in longitudinal section in fig. 108. The further segmentation of the sporangial head follows the type usual for Leptosporangiate Ferns (figs. 111, 108, 112). Very soon, however, the sporangium takes an unsymmetrical form, the more strongly growing side being that directed towards the apex of the receptacle (fig. 108); the oblique annulus, which in this genus presents peculiar characters, makes its appearance early, and occupies a position comparable to that in *Gleichenia*; the orientation of the sporangia is thus on the Gleicheniaceous type.

The sporangia are of large size, and rather peculiar form; fig. 113 shows one in longitudinal section, at the stage when the spore-mother-cells are rounded off; the annulus (*a.*) projects at the distal end of the central or acroscopic face; the peripheral or basiscopic side is more convex, and the annulus is again encountered at a point close to the short, thick stalk, where it projects in the mature sporangium as a basal flange. Seen from without the sporangium presents some curious features; fig. 114 shows one presenting its central face; the annulus, starting from the base, runs round two sides, but at the point (*) it appears to stop, but it does not do so actually; it merely curves round upon the peripheral face, and disappears behind the body of the sporangium. That the annulus is really a continuous one is seen from fig. 115, which represents the peripheral face; it is very irregular, especially at the base of the sporangium, and consists of a large, but not definite number of rather narrow cells; together they form a twisted hoop, so disposed that the distal end of the hoop is curved in the direction of the apex of the receptacle, and this curvature makes the sporangium a peculiarly difficult object to represent in a drawing. The thickening of the walls is greater at the distal part of the annulus than at the proximal, while at one side or the other is a part not strictly defined, where rupture will take place. There is no definite stomium, and though rupture usually takes place about the region marked (*r*) in fig. 115, the actual point of dehiscence may vary.

The features thus noted mark off the annulus of *Thyrsopteris* as one of the least specialised among Leptosporangiate Ferns; the inequality of its thickening suggests a comparison with *Loxsoma*. It seems to me probable, that while showing clear points for comparison with *Dicksonia*, it has been derived from a type with a completely indurated annulus, and median rupture; that this became modified in consequence of the close packing of the sporangia in the sorus, which would interfere with a median dehiscence; that a lateral rupture had been adopted, but the sporangium not definitely specialised for it; this whole question of dehiscence will be discussed below (see p. 118).

The central cell undergoes the usual segmentation to form a tapetum of the usual type, and 12 to 16 spore-mother-cells. From countings of the spores it has been concluded that the typical number for each sporangium is from 48 to 64.

Summary for Thyrsopteris.

- (1) The receptacle is the true margin of the pinnule.

- (2) The indusium arises from the upper and lower surfaces of the leaf, and is sometimes obscurely two-lipped.
- (3) The succession of the sporangia is basipetal on the receptacle, and their orientation typically as in *Gleichenia*.
- (4) The sporangium is massive and short stalked, with an unequally thickened annulus, which is oblique as in *Gleichenia*, but lateral dehiscence takes place by a non-specialised stomium.
- (5) The number of spores in each sporangium is 48 to 64.

Dicksonia.

The old comprehensive genus *Dicksonia* was ranged under three sections in the 'Synopsis Filicum,' *Cibotium*, *Eudicksonia*, and *Patania* (= *Dennstædtia*). While *Cibotium* and *Eudicksonia* have obvious relations to *Thyrsopteris*, *Patania* (*Dennstædtia*) clearly approaches the genus *Davallia*, and especially to that section of the old genus which has been separated as the independent genus *Microlepia*; these relationships will now receive the support of developmental evidence. I shall follow PRANTL* in separating *Dennstædtia* and *Microlepia* from the position given them in the 'Synopsis Filicum,' and recognise them as constituting (with certain other genera?) a natural sub-tribe under the name of the *Dennstædtiinae*, PRANTL, having a position between *Dicksonia* and *Davallia*, and constituting with them a natural sequence. It will be shown that following this series from *Thyrsopteris* to *Davallia* we shall pass from a type with basipetal sequence of the large, short-stalked sporangia, with oblique annulus, to forms with a mixed sorus, smaller, long-stalked sporangia, and a vertical annulus. The receptacle, which is a prominent feature in the former, is reduced, or represented only by a flat surface in the latter types. The gradual nature of these parallel steps seems to indicate that the whole series is one of natural affinity, as indeed has always been recognised by systematic writers.

Dicksonia (excl. *Patania*).

The sorus in this genus has been investigated by BURCK † and by GLÜCK, ‡ but in both cases attention was devoted rather to the indusium than to the more important parts of the sorus, viz., the receptacle and sporangia. GLÜCK, however, points out that the receptacle arises from the original leaf-margin, while the two lips of the indusium spring from the upper and lower leaf-surfaces.

The structure of the young receptacle as seen in *Dicksonia* (*Cibotium*) *Schiedei*,

* 'Arb. Königl. Bot. Gart. zu Breslau,' 1892, p. 18.

† 'Indusium der Varens,' Haarlem, 1874.

‡ 'Flora,' 1895, Heft 2.

BAKER, is like that of a leaf-margin, with a marginal series of actively dividing cells. In sections perpendicular to the leaf-surface the young sorus appears as in fig. 116, the cell marked (*m*) being one of the marginal series. A section of a similar sorus in a plane (*x, x*) appears as shown in fig. 117, while at the lower level (*y, y*) it is as in fig. 118. It is thus seen that the receptacle is structurally like a normal leaf-margin, a conclusion again supported by fig. 119, which shows a similar sorus traversed in a plane (*z, z*) indicated in fig. 116. The formation of the sporangia has begun in the marginal cells, and it is seen that their appearance is almost simultaneous, a point better shown in fig. 120, which represents a slightly more advanced stage; as GLÜCK has intimated for *Dicksonia* (*Cibotium*) *spectabile*,* these marginal sporangia are succeeded by others produced in a basipetal sequence, but the succession is not long continued, and in *D. Culcita* L'HERIT it is not clearly marked; there is, however, no evidence of intercalation of younger sporangia between those already present.

As seen from figs. 119, 120 the sporangial mother-cells are deeply sunk, and the first segment-walls may insert themselves upon the basal wall, as is shown in sporangium (3), fig. 120; in other cases the segment walls may cut the lateral walls of the mother-cell (*e.g.*, sporangium 4). But, however this may be, the first segmentations are those characteristic of bulky sporangia.

The sporangia themselves are of large size, and vary somewhat in form, being in *D. Culcita* of an almost pear-like shape with very oblique ring, while in *D. Menziesii* the ring is more longitudinal. The stalks are relatively thick though elongated, and show in transverse section a rosette of six or seven cells (fig. 121). As the published drawings of *Dicksonia* sporangia are not altogether satisfactory, I have represented those of *D. Menziesii*, HOOK. and BAKER, from four different points of view. Fig. 122 shows how, on the peripheral face, the continuous ring of the annulus surrounds the relatively large thin-walled area; the indurated part of the annulus is shaded, and of the rest, four smaller cells (connective cells) are seen on either side of the group of five cells which form the stomium. The central face is shown in fig. 123; but in this case the stomium is composed of only four cells, while five connective cells are seen on either side of it. Fig. 124 shows a lateral view of the side on which the annulus is completely indurated, and fig. 125 shows the stomium as again a group of five cells, while two pairs of "connective" cells are seen on either side of it. From these drawings the form and large size of the sporangium, and the position of the annulus are clearly seen, while we also conclude from them that the number of cells of the stomium and connective is not constant.

The orientation of the sporangia has been examined in *D. Schiedeii*, *Chamissoi* and *Menziesii*; at the margin of the flattened receptacle it is not uniform, but the sporangia seated on the sides nearer its base show in the majority of cases, though with no strict uniformity, an orientation on the Gleicheniaceous plan.

* *Loc. cit.*, p. 22, GLÜCK names his plant *Cibotium spectabile*, without author's name. I assume that this stands for *Dicksonia Wendlandi* BAKER, since *C. spectabile* HORT (?) has been included in that species.

Notwithstanding the large size of the sporangia, the output of spores in *Dicksonia* is not a high one. Enumerations were made for *D. Menziesii* with 62, 63 as the result, and in *D. antarctica*, 64. Clearly 64 is the typical number for these Ferns.

Summary for Dicksonia.

- (1) The receptacle arises from the leaf-margin and is distinctly flattened; the two lips of the indusium arise from the upper and lower surfaces of the leaf.
- (2) The sporangia arise in basipetal sequence.
- (3) They have an oblique annulus and lateral dehiscence. The stalks are long, but of relatively massive structure.
- (4) The orientation is somewhat irregular at the apex of the receptacle, but below it follows the Gleicheniaceus type.
- (5) The output of spores is typically 64 per sporangium.

DENNSTÆDTIINÆ.

This sub-tribe was founded by PRANTL,* and placed under the tribe Aspidiæ, to include the genera *Dennstædtia*, *Microlepia*, *Leptolepia*, *Saccoloma*, and *Hypolepis*. The most important of these genera are the two first, which were placed apart in the 'Synopsis Filicum': *Dennstædtia* (as the § *Patania*) was included in *Dicksonia*, while *Microlepia* was included as a section of *Davallia*. But evidently systematists had reason to know how closely allied these two were, since the synonyms have been numerous. The fact is that *Dennstædtia* is not very nearly related to *Dicksonia*; the form of sorus is different, and the details of the sporangium; these characters should weigh more strongly than any similarity of habit. On the other hand *Microlepia* while it resembles *Dennstædtia* in its sorus, differs in certain essential points from *Davallia*. My own observations confirm by new facts the soundness of PRANTL'S systematic method in founding the sub-tribe; and I shall show that the sub-tribe occupies a peculiarly interesting position, as a connecting link between the basipetal type of sorus seen in the *Dicksoniæ*, and that of the *Davallias*.

Microlepia (= *Davallia*, § *Microlepia*).

The sorus has been examined in *Microlepia speluncea* (L.), MOORE, *hirta* (KAULF), PRESL., *strigosa* (THUNB.), PRESL., and *platyphylla* (DON), J. LM. In all these it shows in the main a basipetal succession. This is seen in *M. speluncea*, in fig. 126, in which the two lips of the indusium appear with the characteristic inequality, the

* 'Arbeiten Königl. Bot. Garten zu Breslau,' vol. 1, p. 18.

superior lobe (*s.*) having the aspect of a continuation of the leaf, while the inferior lobe (*i.*) is smaller, and has some similarity in position to the indusium of *Cystopteris*. The receptacle is conical, but the sporangia are not very numerous, and it is not greatly elongated; it is traversed by a band of tracheides (*tr.*). The order of appearance of the sporangia is in a strict basipetal succession, but this is not long maintained. The sporangia themselves are on short, rather thick, three-rowed stalks, and the head shows a slightly oblique form (sporangia two and three), the peripheral face being the more convex. The annulus is almost longitudinal, but still it shows a slight degree of obliquity, such as will be described below in *Dennstædtia apiifolia*; the orientation of the sporangia shows a considerable regularity on the Gleicheniaceous type.

In *Microlepia hirta* there is general correspondence to *M. speluncæ* as regards structure of the sorus and sporangium, though the succession of sporangia is longer, and the receptacle accordingly more elongated; but cases occur occasionally in which the strict basipetal succession is not maintained. One of these is represented in fig. 127, in which there is a larger sporangium at the tetrad stage, below a small one in which the spore-mother-cells have not yet expanded; fig. 128, Plate 7, shows another example of departure from the strict basipetal succession; still the receptacle is seen to be elongated and traversed for a considerable distance upwards by a strand of tracheides. Such exceptions occur in about one in every five sori cut, and are therefore not excessively rare. These irregularities are of interest for comparison with those to be described for *Dennstædtia*.

In *Micr. platyphylla* and *M. strigosa* the sorus was found to be basipetal, the receptacle conical, and the sporangia of the same type as in the other species. Thus it may be concluded for *Microlepia* that the sorus is typically one showing basipetal succession of rather short-stalked, slightly oblique sporangia, with reasonable regularity of orientation, inserted upon a conical receptacle, and protected by two unequal indusial flaps. But that in some species occasional departures from the strictly basipetal succession occur, younger sporangia being found inserted between those which are more advanced.

Dennstædtia (= *Dicksonia*, § *Patania*).

This genus includes numerous species of more delicate habit than *Dicksonia*, and having creeping rhizomes, traversed by a closed cylindrical stele which gives off a single bundle to each leaf. The small sori are marginal, and PRANTL had already noted (*loc. cit.*, p. 19) that the receptacle is derived from the leaf-margin, while the cup-like indusium originates on two flap-like outgrowths of the lower and upper surfaces; excepting that the indusium is not two-lipped, and that the receptacle is cylindrical instead of flattened, it resembles in its main features the sorus of *Dicksonia* (fig. 129). The relations of the sporangia within the sorus have been

examined in *Dennstadtia apiifolia*, Hook., with the result that the basipetal succession has been found to be much more marked than in *Dicksonia*. The receptacle is cylindrical and elongated, and traversed by tracheides for a considerable distance (fig. 130); upon it the sporangia arise, as a rule, in strictly basipetal order. The sporangia themselves undergo the usual segmentation; when mature they have long stalks composed of three rows of cells; the head is not bilaterally symmetrical, but one side is more strongly convex than the other; and it will be seen from fig. 130 that the more convex side is the peripheral one. The annulus is not exactly vertical, but, running round the margin of the sporangium to the attachment of the stalk, it is there slightly diverted to one side (fig. 131); usually the sequence of cells of the annulus is not wholly interrupted by the insertion of the stalk, but its cells are more or less in contact with one another, and the annulus is in such cases actually continuous at the base, as it is in those sporangia where it is more conspicuously oblique. In fact the sporangium of *D. apiifolia* shows, though in a less obvious degree than in *Dicksonia*, the oblique annulus. The nearer side of the sporangium shown in fig. 131 is the less convex one; it is the "central" face, and corresponds structurally to that shown in fig. 89 of *Alsophila*, or to that shown by KNY for *Nephrodium*,* the middle part of the wall being derived from segment II., which takes no part in the formation of the annulus. The more convex side is the peripheral face (fig. 130), and it is on this side that the annulus may be seen to show the last traces of continuity at the base. Thus *D. apiifolia* has this interest: that with a typically basipetal sorus the long-stalked sporangia show an almost vertical annulus, but it is still sufficiently oblique to serve for comparison with those basipetal types in which the obliqueness is much more obvious.

The orientation of the sporangia as described, is not always maintained in the mature state; transverse sections of the mature sorus show some latitude in this respect; but this may be due merely to a twisting of the long thin stalk. This seems the probable explanation, since the young sporangia show a fairly accurate orientation.

Sections of sporangia show that the number of spore-mother-cells in each sporangium is variable: eight, twelve, and sixteen have been observed. Countings of mature spores have shown that in certain cases the full number of 64 may be produced.

The basipetal succession is not always maintained in this genus with exactness; deviations from it have been observed in *D. davallioides* (BR.), MOORE, and in *D. rubiginosa* (KAULF.), MOORE. Even in *D. apiifolia* (fig. 129) isolated cases have been seen of a sporangium seated near the apex of the receptacle, apparently arrested in its development, and representing a less advanced state than those surrounding it. In *D. davallioides*, cases of this sort are of fairly common occurrence towards the apex of the rather elongated conical receptacle. These may be held to be transitional

* Wandtafeln 95, fig. 4, b.

forms to what is seen in the allied species *D. rubiginosa*, the sorus of which is represented in longitudinal section in fig. 132. Here, upon a relatively short receptacle, and between indusial flaps which are also short, the sporangia are disposed with no definite succession; the persistent stalks of two old sporangia are near the apex of the receptacle in fig. 132, and the younger sporangia below, with spores and tetrads, give a slight indication of a basipetal succession, but still younger sporangia are disposed irregularly among them. The sorus, though showing some slight signs of a basipetal succession at first, is clearly of that type which we shall designate "mixed," that is, with the sporangia produced in no definite succession, but the younger interspersed irregularly among those which are more advanced; correlated with this we find the receptacle short, but wide. The sporangium also shows a difference from *D. apiifolia*, the annulus being definitely interrupted at the insertion of the stalk, as is shown in fig. 133, which represents a dehiscent sporangium seen from below (*st.*), indicating the insertion of the round stalk. We shall subsequently see that, by these gradations in *Dennstædtia*, a transition is indicated between two fundamental types of soral arrangement, the *basipetal succession* of sporangia, and the *mixed*, where the various ages are irregularly interspersed. *Dennstædtia* is thus found to correspond to *Microlepidia* in the occasional departure from the typical basipetal succession of the sporangia in the sorus. This condition leads on to that seen in the genus *Davallia*.

The other genera included in the Dennstædtiinae by PRANTL* are *Leptolepidia*, *Saccoloma*, and *Hypolepidis*. The first two of these are closely related to *Microlepidia*, as their numerous synonyms show: many of their species have indeed been included in that genus. I regret not having had opportunity of examining their sori from the developmental point of view. *Hypolepidis* is mentioned by PRANTL himself as an uncertain member of this sub-tribe. An examination of its sorus shows the sporangia of various ages intermixed, and without definite orientation. On these grounds the affinity of this genus would appear to be elsewhere than in the Dennstædtiinae (see p. 77.)

Summary for the Dennstædtiinae.

- (1) The sorus, with two unequal indusial lips, bears sporangia in typically basipetal succession, upon a shortly conical receptacle.
- (2) But the basipetal succession is not always maintained; both in *Microlepidia* and in *Dennstædtia* sporangia are formed out of order, younger ones being occasionally found near the apex of the receptacle than older ones.
- (3) The sporangia have the peripheral side slightly the more convex, and the annulus very slightly oblique; the orientation is typically on the Gleicheniaceous type, but is not always strictly maintained.

* 'Arb. Königl. Bot. Gart. zu Breslau,' p. 18, &c.

DAVALLIA.

The genus *Davallia*, as it stands in the 'Synopsis Filicum,' is a comprehensive one. Sir WILLIAM HOOKER remarks ('Species Filicum,' 1, p. 150) of the Davalliæ: "No two authors are agreed as to the limits of this group, nor of the genera which compose it; and no wonder, seeing how gradually the genera seem to run one into another. To me the genera seem to have been needlessly multiplied, upon very insufficient grounds, so that in many cases I cannot even adopt them as sub-genera." The result of Sir WILLIAM HOOKER'S view, as thus expressed, has been that he grouped several genera of other authors under the comprehensive genus *Davallia*. But the tendency has since been to reinstate some of his sub-genera as substantive genera, the most prominent case being that of *Microlepia*. Clearly this whole *Dicksonia-Davallia* affinity, bristling as it does with synonyms, is one of those very groups where fresh comparative observation has an opportunity of establishing new characters, which shall help the systematic arrangement upon natural lines; such characters derived from the sorus have been described above, and justify the removal of *Microlepia* from the genus *Davallia*.

Taking first the § *Eu-Davallia* of the 'Synopsis Filicum,' observations have been made on *D. griffithiana*, HOOK, *pyxidata*, CAR., *canariensis*, SMITH, *solida*, SWARTZ, and *divaricata*, BLUME. In all of these the sorus shows various ages of sporangia intermixed, while they are inserted upon a wide, flat receptacle. The sporangia themselves have long stalks when mature, so that the ripe sporangial head is raised far above those of the younger sporangia, and thus scattering of the spores is ensured without an elongated receptacle.

The development has been specially studied in *D. griffithiana*. Fig. 134 shows a young sorus with the first sporangia appearing. It may be noted that on the flat receptacle the first sporangium is in a median position, and this may be taken as a slight trace of basipetal succession; but even this is not constant, and as the development proceeds, any superficial cell of the receptacle may grow up into a sporangium, developing as such in any order whatever, and without any regularity of orientation. The confused mass which results is shown in fig. 135, and this also illustrates how, as the sporangia grow older, their stalks, composed in the lower part of but a single row of cells, become elongated. The vascular strand runs upward to a point immediately below the surface of the sorus, and there widens out into a considerable mass of tracheides, surrounded by a thin band of parenchyma, and limited by a brown layer, which is doubtless of the nature of an endodermis.

This condition is typical also for other sections of the genus *Davallia*; of the § *Humata*, I have examined *D. heterophylla*, SMITH, and *D. angustata*, WALLICH; both have a mixed sorus, and flat receptacle. In § *Leucostegia*, which approaches *Cystopteris* in its characters, *D. immersa*, WALLICH, showed, in material which was rather young, sufficient evidence of a mixed sorus and flat receptacle. In § *Odonto-*

loma, which shows affinities with *Lindsaya*, the species *Dav. repens*, Desv. showed a mixed sorus and flat receptacle, and no regularity of orientation of the sporangia. In § *Loxoscaphe*, *Dav. thecifera*, H.B.K. (= *D. concinna*, SCHRAD.), the sorus was found to be mixed, but the receptacle, at least when old, rather conical. The orientation of the sporangia seems to be largely determined by the narrow space between the lips of the indusium. Lastly, in § *Stenoloma*, I have examined *Dav. tenuifolia*, SWARTZ, and found the sorus to be mixed, the receptacle flat, and the orientation of the sporangia various. Observations were also made on *Dav. aculeata*, SWARTZ; the sori bear very few sporangia, and the succession is thus not easily seen, but there appeared to be no reason to look upon this species as differing from the rest in type; the orientation is various.

It is thus seen that, with the exception of *Microlepidia*, which had already been removed on other grounds by PRANTL (*loc. cit.*), and accorded a separate place by CHRIST ('Farnkräuter,' p. 10), the genus *Davallia* shows uniformity of structure of the sorus on the mixed plan, with flat receptacle, and no definite rule of orientation of the long stalked sporangia.

Summary for Davallia (excl. Microlepidia).

- (1) The unequal lips of the indusium surround a receptacle which is usually flat.
- (2) On this sporangia arise in no definite order, various ages being intermixed.
- (3) There is no regularity of orientation of the sporangia.

CYSTOPTERIS.

This genus has been generally recognised as being closely related to *Davallia*, and especially to the section *Leucostegia*, which, it will be remembered, has a sorus of the mixed type. *C. fragilis*, BERNH., bears its sori not on the margin, but on the lower surface of the leaves, and they are covered by an indusium with a single flap; this is an advance on the inequality of the indusial lips seen in *Microlepidia* and *Davallia*, with the result that the superior lip takes its place as a continuation of the leaf-lobe. There is no regular succession of the sporangia, but the various ages are intermixed, and there is no regularity of orientation. Each sporangium contains as a rule 64 spores.

LINDSAYA.

This genus is closely related to *Davallia*, § *Odontoloma*. *L. retusa*, METT., and *L. reniformis*, DRY, have been examined; both have sori of the mixed type, with no regularity of their orientation, but the annulus is slightly oblique according to the *Dennstaedtia* type.

DICTYOXIPHUM.

Herbarium material of *D. panamense*, Hk., shows that the sorus is mixed, and there is no regularity of orientation of the sporangia.

DEPARIA, HOOK. and GREV.

This genus of Ferns has been recognised as having a near relation to *Dennstædtia*, from which they differ "mainly by their extramarginal sori";* indeed, *D. concinna* was placed in *Dennstædtia* by MOORE, and is described as closely resembling *Dicksonia* (*Dennstædtia*) *adiantoides* in habit. In this connection *D. Moorei*, Hk., is of special interest, since it bears not only the marginal stipitate sori characteristic of the genus, but also superficial sori. This important fact, which was noted by MOORE,† has been verified on herbarium specimens at Kew and at Glasgow.

The sorus of *D. Moorei* shows sporangia of various ages intermixed and with no definite orientation. The sporangia are of small size, and have long stalks, and a head which is almost bilaterally symmetrical, the inequality of the two sides being very slight (fig. 136).

HYPOLEPIS.

It will be remembered that this genus was included by KUHN and by PRANTL‡ in the Dennstædtinæ, though by other writers it has been placed in the Pterideæ. It is in cases such as this that new characters of the sorus may be used with effect in deciding the true position of a genus. The marginal sori, covered by the reflexed margin of the leaf, consist of a slightly convex receptacle, upon which the sporangia of various ages are inserted in no definite order; it is a mixed sorus, with no definite orientation of the sporangia, while the annulus is definitely interrupted at the insertion of the stalk.

I would not assert that there is *no* affinity with the Dennstædtiinæ; the position and character of the sori, the habit, and certain anatomical features point to a relationship. I should rather regard the genus as holding an intermediate position between the Dennstædtiinæ and *Polypodium*; the relationship to the latter has been the subject of remark; for instance, in the 'Synopsis Filicum,' p. 130, Dr. GRISEBACH§ is quoted as writing of *H. Purdieana*, Hk.: "Not to be distinguished from *P. rugulosum* but by the specially transformed involucreal appendages, and probably passing into that widely-ranging species." Again ('Syn. Filic.,' p. 312), under *Polypodium* (PHEG.) *punctatum*, THUNB. (which HOOKER regarded as including

* 'Synopsis Filicum,' p. 55.

† 'Journ. Linn. Soc.,' vol. 2 (1858), p. 129. Note on some suprasoriferous Ferns.

‡ 'Arb. k. Bot. Gart. Breslau,' 1892, p. 18, &c.

§ 'Flora Brit. West Indies,' p. 67.

P. rugulosum, LABILL.) he remarks: "Very closely related to *Euhypolepis*." All this seems to me to indicate a probable sequence which would consist of (a) some Dennstædtiinous Ferns with basipetal sori, (b) some type with mixed sorus and receptacle within the margin, which is curved over as an indusium as in *Hypolepis*, (c) such a type as *Polypodium punctatum*, THUNB., with its definitely-superficial, unprotected sorus, with ages intermixed, and no regularity of orientation.

Before proceeding to review the great mass of the remaining Leptosporangiate Ferns, we may here pause, and consider the position at which we have arrived. Two series have been traced, which show many points of close analogy, but are usually separated systematically on the ground of the position of their sori. The Cyathææ have superficial sori, the *Dicksonia-Davallia* series have marginal sori. But as the latter series is pursued onwards to *Cystopteris* or *Lindsaya*, or to *Hypolepis* and *Polypodium*, the marginal position, already in *Davallia* showing a bias to the lower surface, is definitely abandoned. The validity of the distinction, by position of the sori, is still further discredited by what is seen in *Deparia Moorei*. Whether or not these two series represent truly distinct evolutionary sequences, we may note that in both of them the same progression in another feature is now demonstrated; in the *Dicksonia-Davallia* series the steps from the basipetal to the mixed type of sorus are so gradual as to leave no doubt that the one type has merged into the other. In the series with superficial sori, the intermediate steps are less clearly made out, but comparison leaves little room for doubt that a transition has taken place here also.

It would thus appear probable that in Ferns, which may represent two distinct lines of descent, this transition from the basipetal to the mixed sorus has taken place; these may be only two of many such lines of descent. I do not attempt exhaustively to treat so difficult a subject as this: it will have to be approached with a fuller knowledge of anatomy, and of the characters of the gametophyte. At present I shall be content to show that (with the possible exception of *Platynerium*) all the remaining *Polypodiaceæ* have sori of the mixed type, and leave others to work out in detail their probable lines of relationship.

The remaining genera of Leptosporangiate Ferns are included in the Tribes VI.-XIII. of the *Polypodiaceæ* according to the arrangement in the 'Synopsis Filicum.' I propose to take them in order as they stand in that work; but they will be dealt with only in brief notes, which will refer chiefly to the mixed or other character of the sorus, and the position of the annulus, number of spores, and some few other points which may be of interest for purposes of comparison on the lines above indicated. It is only after an examination of the bulk of the Leptosporangiate Ferns with reference to these details of the sorus that we can arrive at their true comparative value in the genera which have been taken up first.

TRIBE VI. PTERIDEÆ.

21. ADIANTUM.
A. reniforme, L.—Sorus mixed.
A. acuminatum, HK. and ARN.—Sori mixed, with the sporangia produced in a succession not long continued; orientation not uniform; annulus vertical.
A. polyphyllum, WILLD.—Ditto.
22. OCHROPTERIS.
O. pallens, J. SMITH.—Herbarium material shows the sorus to be mixed; many hairs surround the sporangia. Orientation various.
23. LONCHITIS.
L. pubescens, WILLD.—Sorus mixed. Orientation various.
24. HYPOLEPIS, see above, p. 77.
25. CHEILANTHES.
Ch. (§ *Eucheilanthus*) *vestita*, SWARTZ.—Sporangia not simultaneous in origin; but there is no marked succession or order of them. Orientation various.
Ch. (§ *Physapteris*) *Fendleri*, HK.—Sporangia isolated, without constant orientation; no clear indication of a succession of them.
Ch. (§ *Aleuritopteris*) *farinosa*, KAULF.—Sporangia either solitary or so few that no statement can be made as to their succession in appearance. Orientation not constant.
26. CASSEBEERA.
C. triphylla, KAULF.—Sorus mixed; no regularity of orientation.
27. ONYCHIUM.
O. auratum, KAULF.—Sorus mixed; no regularity of orientation.
28. LLAVEA.
L. cordifolia, LAGASCA.—Sorus mixed; no regularity of orientation.
29. CRYPTOGRAMME.
C. crispa, BR.—Sorus mixed; apparently no long succession; orientation various; great variation in size of the sporangia.
30. PELLAEA.
P. columbina, HK. (= *P. lomariacea*, B. HK.).—Sorus mixed; no regular orientation; spores in sporangium typically 64.
31. PTERIS.
P. aquilina, L.—Sorus mixed; no regularity of orientation. The spore-mother-cells are usually twelve in number, but some of them may be abortive (figs. 137 and 138), and the output of spores be thus reduced to a lower figure.
P. cretica, L.—Closely similar, but differing in the absence of the lower indusium.

32. CERATOPTERIS.

C. thalictroides, BRONG.—KNY, writes as follows on the origin of the sporangia* :—

“Their sequence of appearance is mainly acropetal. Below the leaf-margin which elongates at the apex, one can reckon upon finding quite young rudiments; still new sporangia arise also later between those which are more advanced.” From this description, and from KNY’s drawing, it appears that while there is an acropetal succession as regards the whole leaf or pinna, there is a mixed sequence of sporangia as regards the widely-spread sorus, comparable to that seen in so many other Ferns.

The sporangia themselves are large; they show no uniformity of orientation, and are seated on short thick stalks. The number of spores in each is estimated by KNY to be 16. I have counted the spores in material from Kew and from Glasgow, and have found the number to be uniformly 32. It is possible that under certain circumstances the last divisions of the sporogenous group may be omitted, and that KNY’s estimate was based upon such specimens. A similar variation of number has been noted for *Cyathea dealbata* (8 to 16), and for *Todea barbara* (256 to 512).

33. LOMARIA. § *Eulomaria*.

L. Patersoni, SPRENG., and *L. media* (?), both from the Edinburgh Botanic Gardens, have been examined. The sorus is mixed; the sporangia have no definite orientation; the annulus is definitely interrupted at the stalk, though it may show some slight signs of being oblique. The number of spores is 48 to 64. In fact, there is in these species no feature calling for special remark, as distinct from allied genera. This result is not in accord with the observations of METTENIUS,† who described and figured for *Lomaria Patersoni* a sporangium with an oblique annulus, and a thick stalk. I have not found this in the specimens from the Edinburgh Garden; the annulus is definitely interrupted at the stalk, though it may be slightly oblique. This has been verified also on material from the Glasgow Herbarium.

Lomaria, § *Plagiogyria*.

This section of the genus was distinguished first by KUNZE,‡ and afterwards by METTENIUS||, on the ground of the oblique annulus; the occurrence

* ‘Die Parkeriaceen,’ p. 49. Compare Taf. 4, fig. 11.

† ‘Filices Horti Lipsiensis,’ p. 61, Taf. 4, fig. 6.

‡ ‘Bot. Zeit.,’ vol. 7, 1849, p. 867.

|| ‘Ueber einige FarnGattungen, II., *Plagiogyria*,’ Frankfurt, 1858. ‘Abh. d. Senckb. Nat. Ges.,’ vol. 2, 265.

of this character did not appear to KUNZE to be a sufficient reason for separating the species which showed it from *Lomaria*, with which their other characters showed a natural affinity. METTENIUS held, on the other hand, that *Plagiogyria* should be ranked with the Cyatheaceæ. Sir WM. HOOKER, however, still retained the Ferns in question as a section of the genus *Lomaria*. CHRIST again takes a middle position; he has retained *Plagiogyria* as a substantive genus,* separated from *Lomaria* "by the sori not being inserted upon a nerve-arch, but terminal, and by the absence of a special lateral indusium." He ranks the genus with the Pterideæ.

I have verified CHRIST'S points on specimens of *L. (Pheg) pycnophylla*, and have seen that the sorus is not really a continuous one, but that the sporangia are in numerous groups, inserted over the nerve-endings, though covered by a common indusial flap. The sporangia appear to be almost simultaneous in origin, and no evidence was found of the sori being mixed as in *Eu-Lomaria* and *Blechnum*; this is a feature which strengthens the comparison with *Dicksonia*, but it will require verification upon more suitable material.

I have examined, in herbarium material, *Lomaria (Plagiogyria) pycnophylla*, KUNZE; *euphlebia*, KUNZE; *semicordata*, BAKER; and *glauca*, BLUME, and find in them all the complete oblique annulus as described. Drawings have been made for *L. euphlebia* (figs. 139-142) for purposes of comparison with *Dicksonia*, and the correspondence of these with the details of *D. Menziesii* (figs. 122-125) is certainly remarkable. The same elongated and rather massive stalk bears the sporangial head of almost the same size, with the annulus oblique, and traced as a continuous ring; it is, however, subject to irregularities; on the side opposite to the stomium (fig. 141) it is usually seen as a continuous and regular ring; it may, however, be interrupted at times even on this side (*L. semicordata*). The induration extends commonly along this side, but stops short opposite the insertion of the stalk (fig. 139), while it also stops at some distance back from the apex, leaving about one-third of the annulus between these points thin-walled. This is the region of the stomium, and the cells here often show irregularity of shape and sequence, as also in number. It was seen in *Dicksonia* that the number of cells in the region of the stomium was not uniform; this and the main structural points indicate an uncommonly close similarity between this genus and *Plagiogyria*, and the question arises whether the sorus in the latter be basipetal or mixed. This I have been unable to decide from the herbarium material at my disposal,

* 'Farnkräuter,' pp. 6 and 175.

though the general arrangement of the sorus has points of similarity to *Dicksonia*, notwithstanding the striking difference in extent. As regards the general habit, it is to be noted that the *Plagiogyrias* have an erect axis, but it must remain for future investigation to show how far there is resemblance with *Dicksonia* in the internal structure.

I find it necessary, therefore, while indicating the close resemblance of the sporangia to those of *Dicksonia*, to leave the final decision of affinity for the present open.

TRIBE VII. BLECHNEÆ.

34. BLECHNUM.

B. occidentale, LINN.—Sorus mixed; the stalks of sporangia are long and thin; the annulus vertical, and definitely interrupted at insertion of the stalk.

B. brasiliense, DESV.—Sorus mixed, no regularity of orientation; the annulus vertical, interrupted at the stalk.

35. SADLERIA.

S. cyatheoides, KAUFM.—Sorus mixed, orientation of sporangia various. Only 16 spores observed in sporangia.

36. WOODWARDIA.

W. orientalis, SWARTZ.—Sporangia in the sorus of slightly different ages intermixed, but the succession not long continued; orientation various. The annulus is interrupted at the stalk.

37. DOODYA.

D. caudata, R. BR.—Sorus mixed. Orientation of sporangia various; annulus interrupted at stalk.

TRIBE VIII. ASPLENIEÆ.

38. ASPLENIUM.

A. Ceterach, L.—See 'Rab. Krypt. Flora,' vol. 3, fig. 129, which shows a mixed sorus, with various orientation.

A. macrophyllum (?) 'Edin Bot. Gard.' Sorus mixed, orientation various; annulus interrupted at the stalk, but its position may be somewhat oblique at the distal end.

39. ALLANTODIA.

A. Brunoniana, WALL.—Sorus mixed; orientation various; annulus interrupted at stalk.

40. ACTINOPTERIS.

A. radiata, LINK.—Sorus mixed; orientation various; annulus interrupted at stalk.

TRIBE IX. SCOLOPENDRIEÆ.

41. SCOLOPENDRIUM VULGARE, SM.—Sorus mixed, orientation of sporangia various; annulus interrupted at the stalk. (See 'STRASBURGER'S

Practicum,' fig. 156, p. 455; also 'Rab. Krypt. Flora,' III., fig. 26, p. 21.

TRIBE X. ASPIDIEÆ.

42. DIDYMOCHLAENA.

D. lunulata, DESV.—Sorus mixed, no regular orientation of the sporangia.

43. ASPIDIUM.

A. Lonchitis, SWZ.—Sorus mixed, but the succession apparently not long continued; no regular orientation of the sporangia.

A. aculeatum, SW.—Sorus mixed, but succession of sporangia not long continued. Orientation various.

44. NEPHRODIUM.

N. Filix-mas, RICH.—Sorus mixed, no regularity of orientation of sporangia; annulus definitely interrupted at the stalk. There is no apparent order of appearance of the sporangia in the first instance in the sorus.

N. molle, DESV.—Similar to the above.

45. NEPHROLEPIS.

N. cordifolia, PRESL.—Sorus mixed, orientation of sporangia not uniform; annulus definitely interrupted at stalk.

46. OLEANDRA.

O. articulata, CAV.—Sorus mixed, orientation of sporangia not regular, though in many cases they lie with the plane of the annulus flat in the narrow space between the indusium and leaf.

47. FADYENIA.

F. prolifera, HOOK.—Sorus mixed; orientation of sporangia not regular; annulus interrupted at stalk.

TRIBE XI. POLYPODIEÆ.

48. POLYPODIUM.

P. aureum, L.—Sorus mixed; no regularity of orientation of sporangia; annulus interrupted at stalk.

P. Meyenianum, SCHOTT.—Sorus mixed; no regular orientation of sporangia; annulus interrupted at stalk.

P. vulgare, L.—Sorus mixed; orientation various. (See ATKINSON, 'Biology of Ferns,' p. 51, fig. 57.)

N.B.—Included by some writers in the genus *Polypodium*,* but excluded by others as the type of a substantive genus,† are the Ferns known under the name of *Lecanopteris*. In the 'Synopsis Filicum' (p. 365), *Lecanopteris carnosa*, BLUME, is referred to *Polypodium lomarioides*, KUNZE, of which it "appears to be an abnormal form." The plant was described by BURCK† as being identical with *Poly-*

* CHRIST, 'Farnkräuter,' p. 115.

† BAKER, 'Annals of Botany,' 1892, p. 19. See also BURCK, 'Ann. Jard. Bot. Buitenzorg,' vol. 4, p. 96.

podium (*Phymatodes*) *patelliferum*, NOB., and distinct from *P. lomarioides*, but undoubtedly allied to that species, and must be placed near that species in the genus *Polypodium*. But BAKER subsequently upheld *Lecanopteris* as a separate genus, and suggested that its location should be near to *Dicksonia*. CHRIST, however, still includes it in *Polypodium*. This will be a good test case in the use of the characters introduced in this paper. If the annulus be interrupted at the stalk, the sorus mixed, and orientation of sporangia be various, the affinity of the Fern should be with *Polypodium* rather than with *Dicksonia*.

Only herbarium material has been available, but from it I have verified the fact already observed by CHRIST (*loc. cit.*, fig. 330, p. 115) that the annulus is interrupted at the stalk, and longitudinal. The sorus is mixed, and the orientation of the sporangia various. This being so, the inclusion of these Ferns in the comprehensive genus *Polypodium* would appear to give them their right position, rather than placing them, as BAKER suggests, "as a distinct genus in the neighbourhood of *Dicksonia*."

TRIBE XII. GRAMMITIDEÆ.

49. JAMESONIA.

J. glutinosa (?).—Sorus mixed; orientation various; annulus interrupted at the stalk.

50. NOTHOCHLÆNA.

N. sinuata, KAULF.—Sporangia not formed simultaneously, but apparently there is no long succession; orientation of sporangia various. Number of spores, 24–32 in each sporangium, with evidence of abortion of some spore-mother-cells.

51. MONOGRAMME.

M. seminuda, BAKER.—As regards the whole leaf, there is an acropetal progression of development of the sorus, but at any given point in the sorus the sporangia of different ages are intermixed; there is no definite orientation, though the majority have the annulus in the plane cutting the leaf transversely. That the ages are intermixed is already shown by the drawings of SCHOTT, 'Gen. Filic.' plate 17, figs. 5, 9, 10.

52. GYMNOGRAMME.

G. schizophylla, BAKER.—Various ages intermixed; no definite orientation of sporangia.

G. trifoliata, DESV.—Ditto.

G. calomelanos, KAULF.—Ditto.

53. BRAINEA.

B. insignis, HK.—Various ages of sporangia intermixed; no regular orientation of sporangia.

54. MENISCIUM.

M. serratum, CAV.—Various ages intermixed. Orientation of sporangia various.

55. ANTROPHYUM.

A. semicostatum, BL.—Only herbarium material was available, and the results were not conclusive. All the sporangia are not of the same age, but it is impossible to say how far there is a successive development of them; apparently the succession is not long continued. Orientation of sporangia not constant, but that of the majority is as seen in *Platyserium*.

56. VITTARIA.

V. stipitata, KUNZE.—Sporangia of various ages intermixed, and showing no regular orientation.

V. lineata, SW.—Sorus mixed; no regular orientation.

57. TÆNITIS.

T. lanceolata, R. BR.—Sorus mixed; no regular orientation.

58. DRYMOGLOSSUM.

D. carnosum, HK.—Sporangia of various ages intermixed; no regular orientation.

D. piloselloides, PRESL.—Sporangia of various ages intermixed; no regular orientation.

59. HEMIONITIS.

H. cordata, ROXB.—No regular orientation of sporangia; various ages intermixed.

H. palmata, L.—The sporangia are sparsely scattered over the reticulum of nerves. The dry herbarium material used gives no evidence of a succession of sporangia.

TRIBE XIII. ACROSTICHEÆ.

60. ACROSTICHUM.

A. cervinum, SW.—The sporangia, which cover the surface of the fertile region, are not all of exactly the same age, but such succession as there is, is not long continued, for where the first sporangia are beginning to be coloured brown, the youngest stages to be found in near proximity have the spore-mother-cells already rounded off. Clearly this slight succession is only a step removed from the simultaneous development seen in *Platyserium*. The orientation of the sporangia shows no strict rule; the annulus is interrupted at the stalk. The number of spores in the sporangium is 64.

A. drynarioides, HK.—There is here also a slight succession, and different ages intermixed, but where some sporangia are quite mature either no young ones are found, or only few.

A. acuminatum, Hk.—A slight succession has been observed similar to the above.

61. PLATYCERIUM.

P. alcicorne, Desv., *P. aethiopicum*, Hk., and *P. Wallichii*, Hk., have been examined.—In all of these it may be seen in the young state that the soral patch is not continuous, but that the sporangia are disposed along lines which form a reticulum. Two or more rows of sporangia follow each of these lines, and are inserted upon them. Transverse sections show that a small vascular bundle runs closely below each of these lines, and that it is far removed from the much larger bundles of the main system of the leaf; the latter occupies a central position between the two surfaces of the fleshy leaf. There are thus two series of bundles in different planes; in specimens made transparent by clearing agents it may be seen that the two series ramify independently of one another. In all the three species examined the double system is restricted to the fertile area.

A somewhat similar condition has been described by HOFMEISTER, for the humus leaves of *P. alcicorne* ('Higher Cryptogamia,' p. 252). He remarks: "Their vascular bundles lie, not in one, but in two planes parallel to the surfaces of the frond. These bundles form two many-meshed nets, one close under the upper side, the other immediately above the lower side of the frond; the two networks are united in many places by frequent ramifications which pass through the mass of the frond in a transverse direction." An examination of the margin of the fertile patch in *P. alcicorne* shows that bundles of the central system there branch in an antero-posterior plane, those branches next the lower surface passing towards the epidermis, and there forming the subsoral system. It is certainly a peculiar thing that the condition of the humus-leaves should be thus repeated, but in the fertile regions of the sporophylls only.

The sporangia show considerable regularity of orientation, being so placed that the plane of the ring cuts the direction of the underlying nerve at right angles, so that one limb of the annulus is directed towards the centre of the sorus; it will be noted that this is not the case in the Gleicheniaceæ. The sporangia originate for the most part simultaneously; no new sporangia have been seen to be inserted between those already advanced; but where more than two rows are inserted on one nerve, those which are peripheral arise later than those centrally above it. No sporangia have been seen inserted on the free leaf-surface, apart from an underlying nerve; in this genus, contrary

to Sir WM. HOOKER'S description,* the sporangia appear to be confined to the nerves. The annulus is longitudinal, and interrupted at the stalk.

A very peculiar abnormality has been observed in the sporangia of *P. Willinkii*, which may be comparable to that described for a presumed hybrid, *Aneimia hirsuta* and *Phyllitidis* by PRANTL.† The spore-mother-cells appear normal up to the time of their rounding off, but then they enlarge unequally; some remaining relatively small, as in the case with those which undergo the tetrad division; others increase greatly in size (figs. 143–145), assuming sometimes irregular forms, while they contain sometimes one large granular nucleus, sometimes more. Whether this is simply a pathological condition must remain uncertain, but I have not observed a tetrad division to take place in them. The first impression such bodies give is that of a heterosporous condition; but this the later stages of development do not countenance.

The above notes, referring as they do to all the chief remaining genera of Leptosporangiate Ferns, will afford a basis for a general view. They show that the mixed condition of the sorus, with no definite orientation of the sporangia, and with the annulus not complete, but interrupted at the insertion of the stalk, is the type for the bulk of the Leptosporangiate Ferns. This being so, a correspondingly greater importance must be attached to the fact that in certain tribes the sequence is regularly basipetal, the orientation definite, and the annulus complete, and oblique in position. The occurrence of exceptions, such as that in *Plagiogyria*, cannot in my opinion be admitted as discounting the weight of these facts. If, as I shall suggest, the Ferns which have an oblique annulus, and a definite orientation of the sporangia, produced in basipetal succession, gave rise to those with vertical annulus, indefinite orientation, and mixed sori, what could be more natural than that the transition from the one type to the other should in some cases have been incompletely carried out? In such exceptions as these I see rather a support of my view, than a reason for discounting such characters for purposes of comparison with a view to tracing probable lines of descent.

MORPHOLOGY OF THE SORUS.

To those who have made Ferns a special study, the sorus is apt to become a definite conception; seeing it frequently appearing as a circumscribed body, leads to the ready admission that this is one of its essential characters. But such is by no means the

* 'Synopsis Filicum,' p. 399. The character of the Acrosticheæ is given thus, "Sori spread in a stratum over the under surface or rarely over both surfaces of the frond, not confined to the veins only."

† 'Schizæaceæ,' p. 56, Taf. VIII., figs. 126, 127.

case; not only are there numerous Ferns in which no definite sori exist, such as the Osmundaceæ, and the Acrosticheæ, but even in those in which the sorus appears to be most strictly circumscribed, such as *Cyathea* and *Hymenophyllum*, the identity of the individual sorus is not always maintained. A few illustrations of this from the most varied sources may be adduced. In *Kaulfussia* I have shown* the various intermediate forms which may be seen between the single circular sorus, and two such lying in near proximity to one another. In *Danaea* also similar cases are to be seen, especially in leaves which are only partially fertile,† and the same is found, though less obviously, in *Marattia* and *Angiopteris*. In the Gleicheniaceæ such partial fissions are found (fig. 2), and have been described above; they have been seen also in *Matonia*, and in the Cyatheaceæ they are common. They are found even in Hymenophyllaceæ, and a series of drawings from *H. dilatatum* are shown in fig. 146a-d. In less strictly circumscribed sori, such as *Polypodium* or *Scolopendrium*, they are of very common occurrence. By such observations as these the soral types of Ferns are to be linked with the non-soral, while they will prevent too stiff and definite a view being taken of the sorus, as a morphological conception.

I do not think that it is desirable to start the study of sori with a preconceived idea of its having any one position on the leaf rather than any other. PRANTL, though he gave up his earlier comparison of the Hymenophyllaceous sorus with the Moss-sporogonium, adhered to the last to the conception of the primitive sorus having been marginal; he saw in the sorus "not merely an aggregation of sporangia, but a fertile leaf-ray" (Blattstrahl).‡ This then pre-supposes a shifting ("Verschiebung") of this primitive marginal sorus from the margin to the lower surface, and he suggests (p. 12) that this happened repeatedly, so as to result in the arrangement seen in the Cyatheaceæ, the Gleicheniaceæ, Osmundaceæ, and Polypodiaceæ. It seems highly probable that such a shifting of position has taken place in certain circles of affinity, as, for instance, the *Davallia*, *Lindsaya*, *Cystopteris* sequence; it may have happened more than once. But I demur entirely from the necessity of explaining every superficial sorus as a lacinia (Blattstrahl), which has been moved from the margin to the surface. This view was, perhaps, a natural consequence of the assumption that the Hymenophyllaceæ are a primitive parent type; those who do not share this belief will be free from the demands which it has made on the morphological faith of a generation of botanists.

As against this view of PRANTL, that the sorus is a lacinia (Blattstrahl) I prefer the alternative, which he rejects, viz., that it is merely a group of sporangia, and we shall presently see how the existence of certain definite types of sorus with elongated receptacle and protective indusium may be looked upon as results of specialisation of other simpler types. The fact that a vascular supply runs to the base of the sorus,

* "Studies, III.," 'Phil. Trans.,' B, 1897, Plate 8, fig. 31.

† *Loc. cit.*, Plate 7, fig. 1, a, b, c.

‡ *Loc. cit.*, p. 12.

or is even continuous into the receptacle, carries for me no morphological weight whatever, as determining the nature of the sorus. In it I merely see the response to a nutritive demand. The morphological character of a leaf is not defined by the presence or absence of vascular strands; why, then, should it be assumed that a lacinia should be so defined? Moreover, in many Ferns which are undeniably of very early type, such as *Angiopteris* and *Marattia*, the vascular strand which is below the sorus does not terminate in the receptacle, but is continued beyond it towards the margin of the leaf.*

Accordingly we shall proceed to the comparison of the sorus without any such morphological preconception of its nature as that put forward by PRANTL, and I shall now discuss the different parts of the sorus in succession, and then proceed to consider it from the biological aspect, as a spore-producing body.

The Indusium.

The term "indusium" has been applied to bodies of the most various form, position, and structure, borne in relation to the Fern-sorus, and serving for the protection of the sporangia. It is hardly necessary to point out that these, however similar in their function, cannot be regarded as homogeneous throughout; they are often only examples of homoplasy. We call the basal indusium of *Cyathea* by the same name as the umbrella-like indusium of *Matonia*, or *Polystichum*, or the marginal flap of an *Adiantum*. It may be possible, by regarding the indusium as having had a high degree of plasticity, to accept some of its different forms as being modifications of one another, and a reasonable case can be made out sometimes, such as that in the transition from the Dennstædtiineæ to the Pterideæ, which will be considered presently. But such cases as *Cyathea* and *Matonia* seem incompatible with any opinion of homogeneity of the two structures, especially when it is remembered that in *Alsophila* and *Gleichenia*, genera which are respectively allied to the above, an indusium may be entirely absent. We shall then hold the indusium to be an inconstant body, varying in occurrence, and in position, and the term "indusium" will be used to designate outgrowths protective of the sorus, whatever their position and whatever their evolutionary history may have been.

In many of the Ferns with massive sporangia an indusium is entirely absent, for instance, *Kaulfussia*, some *Danaeas*, *Osmundaceæ*, and most *Gleichenias*. Slight protective arrangements are, however, seen in their allies. In the 'Species Filicum,' in the generic description of *Gleichenia*, the sori are described as "superficial or immersed." The most prominent case of this "immersion" which I have seen is in a specimen in the Kew Herbarium, named *G. spelunca* (?) in pencil, by Sir J. HOOKER, but in ink in Sir W. HOOKER'S writing: "*Gleichenia microphylla*, BR. Fissures of

* This is conspicuously the case in *Archangiopteris*, the new genus of Marattiaceæ, described by CHRIST and GIESENHAGEN, 'Flora,' 1899.

rocks on the Upper Victoria, N.W. Australia, Dr. MÜLLER, 1857." In this plant, not only are the sori sunk in depressions of the leaf-surface, but they are partly over-arched by a lip-like growth on the lower leaf-surface, which suggests a comparison with the basal cup-like indusium of *Cyathea*, though in this case much less elaborate. If two sori, thus protected, were in close apposition, as they are in *Danaea*, the appearance in section would be almost precisely that seen in *D. elliptica*.*

It is interesting to find in place of such basal growths as those of *Danaea* or *Cyathea* dimly prefigured in *Gl. spelunca* (?), that in *Matonia* an apical, umbrella-like indusium of large size occurs. I find it impossible to avoid the conclusion that this, though serving a similar protective purpose, and called by the same term, "indusium," is really of quite distinct origin. It is possible that a similar absence of true homogeneity by descent holds for other basal and apical indusia, such as those of the *Cyatheaceæ* and *Hymenophyllaceæ* on the one hand, and such genera as *Nephrodium* and *Polystichum* on the other. But I do not propose here to go over the beaten ground of description of the various types of indusium of Leptosporangiate Ferns; I shall merely offer remarks on a few points of special interest.

It is demonstrated in many cases that the indusium is formed before the earliest sporangia appear †; this is probably a case where physiological opportunism, rather than any recapitulatory habit, determines the order of succession. It is impossible to believe that those constant bodies, the sporangia, are of later evolutionary origin than the less constant body, the indusium. It is important to recognise such cases as this, for they go far to break down that dogma, which I believe to be still one of the great obstacles to morphological insight in regard to plants, that the prior existent parts in the development of the individual were necessarily prior existent in the evolution of the race.

There is reason to believe that a reduction of the indusium has taken place along more than one line of descent; one such probable series of reduction may be traced from the *Cyatheaceæ*. It may be a question whether in *Alsophila* the sorus is primitive in its absence of an indusium, or the result of a reduction; but very interesting conditions are seen in *Hemitelia*, with its one-sided indusium, and in *Woodsia* and *Hypoderris*, in which, with superficial sori and sporangia of different ages intermixed, there is an exiguous, fimbriated indusium. It is but a slight step from these to some forms of the comprehensive genus *Polypodium*, in which, with a similarly superficial and mixed sorus, the indusium is absent. Another line of possible reduction may be traced from the *Dennstædtiinae*, through *Hypolepis*, to certain types of *Polypodium*. In support of such a sequence, it must be remembered that PRANTL placed *Hypolepis* in his sub-tribe of *Dennstædtiinae*, but I find it to have a mixed sorus, and conclude that its proper position is in the *Pterideæ*.

* "Studies, III.," Plate 7, fig. 2.

† BÜRCK, 'Indusium der Varens. Inaug. Diss.,' 1874. GLÜCK, 'Flora,' 1895. Heft 2.

H. Purdieana, HK., is specially quoted by Dr. GRISEBACH* as "not to be distinguished from *Polypodium angulosum*, but by the specially transformed involucral appendages, and probably passing into that wide-ranging species." The probability is that there is here again a progression, as in the former case, from a type with basipetal succession protected with a basal indusium, to a mixed type in which the indusial protection is less essential, and the indusium is accordingly abortive. The final decision on these relationships must stand over till they can be tested on anatomical grounds; meanwhile we may contemplate a probable reduction of the indusium as having taken place along more than one line of descent.

The views of PRANTL have already been quoted, which involve a comprehensive shifting (*Verschiebung*) of sori from the margin, which he held to be their primitive position, to the surface. While rejecting this general explanation as necessary for all superficial sori, we do not deny that such a change of position ever occurred; and there is reason to think that such a shifting did take place in the probable progression from the *Dennstædtiinæ* to some forms of the *Davallieæ*, *Lindsayeæ*, and *Pterideæ*.

Starting with a strictly basipetal sorus, with cup-like indusium, slightly two-lipped it may be, such as is seen in *Loxsonia* (fig. 63), we have seen that the type in *Dennstædtia apiifolia* (fig. 129) is similar in position and structure, though there may be occasional lapses from the strict basipetal sequence. The indusial lips, which are equal in the above plants, become unequal in *Microlepia spelunca* (figs. 126, 128), the superior lip (*s*) being both longer and thicker than the inferior (*i*), and taking on itself the structural characters and appearance of a continuation of the leaf; this is repeated in *Davallia Griffithiana* (figs. 134 and 135), in which, however, the transition to a mixed sorus is shown in a complete form. The transition from *Microlepia* and *Davallia* to *Cystopteris* and *Lindsaya* is by the most gradual steps, and systematists have always recognised the close relations of these genera. Within this very natural affinity the transition in two concomitant features is thus shown, viz., from the basipetal to the mixed sorus and from the marginal sorus with almost equal indusial lips, to the superficial sorus with the smaller indusial lip still present, but rising apparently from the surface of the leaf. It seems clear that there has been a shifting of the sorus in this series from a marginal to a superficial position, and it is possible that a similar change of position may have taken place also elsewhere.

The Receptacle.

The form of the body on which the sporangia of a sorus are inserted has been made use of by systematists as a diagnostic character. In many cases where there is no obvious projecting body of tissue, there is no mention of it in the diagnoses of the

* 'Flora Brit. West Indies,' p. 67. See 'Synopsis Filicum,' p. 130.

older writers; but where there is a prominent basis of the sorus, we find it included in the generic description. Thus, in the 'Species Filicum' the receptacle is mentioned in the diagnosis of *Dicksonia*, *Loxsona*, *Hymenophyllum*, and *Trichomanes*, in all of which it is a prominent feature.

But the body thus recognised at first in a merely descriptive sense, was made later the basis for a theoretical treatment by PRANTL,* who saw in it, as it exists in the Hymenophyllaceæ, the correlative of the Columella of the Moss-sporangium; he thus attributed to the primitive Fern-sorus the presence of an elongated receptacle, which in derivative forms was liable to reduction.

PRANTL subsequently† gave up his comparison of the receptacle with the Columella of a Moss; but he seems still to have retained his view that the sori with an elongated receptacle are primitive, at least for his series of "Pteridales," which included the Hymenophyllaceæ, Cyatheaceæ, and Polypodiaceæ, together with the Salviniaceæ, and Marsileaceæ. The remaining Ferns, including the Schizæaceæ, Gleicheniaceæ, Osmundaceæ, Marattiaceæ, and Ophioglossaceæ, he grouped under the name "Osmundales," and notes (*loc. cit.*, p. 5) that in them no receptacle is present. He remarks further on (*loc. cit.*, p. 14), "I cannot simply recognise in this organ the expression of a perfect arrangement to meet physiological ends; if this were the case, one would expect a certain relation to the number or size of the sporangia in a single sorus; one could not then see why the large sori of the Marattiaceæ are without this organ, while the small sori of many species of *Microlepia* or of *Nephrodium* have this organ. These facts indicate conclusively that this receptacle is a peculiarity of the Pteridales. I must assume that its absence in a large number of Polypodiaceæ is due to its being abortive in them; I am impelled to this view by the circumstance that those Polypodiaceæ which have a receptacle are in all points directly allied with the Cyatheaceæ." After limiting his use of the term receptacle to those cases where there is a special development of tracheides, he continues that such a receptacle occurs in the genera *Dennstædtia*, *Microlepia*, *Leptolepia*, and *Hypolepis*, which were grouped as Microlepieæ by KUHN, and also in *Saccoloma*, *Aspidium*, *Oleandra*, *Nephrolepis*, *Nephrodium*, *Onoclea*, *Woodsia*, *Acrophorus*, *Cystopteris*, and *Athyrium*. All these genera he groups with the Microlepieæ under his tribe Aspidieæ, "which is characterised by having a receptacle which contains tracheides. In all the remaining genera the sporangia arise from the apex or the back of the nerves, without a special tracheid-bearing continuation, or branching being present."

From these quotations it appears that PRANTL assigned a considerable morphological, as well as systematic importance to the receptacle; and this was a consequence of his conclusion that the Hymenophyllaceæ were the starting-point for his whole series of the Pteridales. He recognised, it is true, that, as the sequence

* 'Die Hymenophyllaceen,' p. 62.

† 'Arbeiten a. d. K. Bot. Gart. zu Breslau,' p. 14.

progressed, a reduction of the receptacle took place, and he follows this with care in his treatment of the Microlepiæ; but he did not associate the greater or less development of it in any way with the succession of development of the sporangia in the sorus.

If we for the moment accept PRANTL'S definition of the receptacle as a body containing tracheides, his statement that it is absent in his Osmundales breaks down at once. It is true that in many genera (*e.g.*, *Danaea*, *Angiopteris*, *Aneimia*, *Mohria*, *Todea*) no extension of vascular tissue below the insertion of the sporangia is seen; but in others a considerable extension is found; I have shown this in *Kaulfussia* ("Studies," III., Plate 8, fig. 42); and similar developments, though smaller, are found in *Marattia Kaulfussii*, and *frazinea*. In *Gleichenia dichotoma* also, quite a considerable mass of tracheides extends into the projecting receptacle, so that if it be cut in transverse section, the whole receptacle appears circular in outline, with a central circular mass of tracheides. These facts prevent my accepting the position of PRANTL in recognising the receptacle (in his peculiar sense) as a peculiarity of his Pteridales. On other grounds, his division of the Ferns into Osmundales and Pteridales itself does not seem to me to be an expression of a natural difference; this opinion is greatly strengthened by the breakdown of one of his chief distinguishing characters.

To me the "receptacle" is merely the basis upon which the sporangia are inserted; in order to meet certain mechanical and physiological requirements it is liable to certain elaborations of form and structure, which may result in its becoming in extreme cases large and prominent. But I cannot find any reason for seeing in it any more recondite morphological meaning; it need not be regarded as a modification of any other part of the plant, such as a pinnule, or the termination of a nerve. That a sorus may be seated on the tip of a nerve, while the vascular tissue is continued directly out into it, is common, and physiologically very practical; but against these cases there are so many among the ancient types of Ferns (Marattiaceæ, Osmundaceæ, Gleicheniaceæ) where the sorus is seated above a nerve at some distance from its tip, that I think it an error to associate the idea of the receptacle in any general way with nerve-endings.

The requirements to be met by the receptacle are:—

- (1) Transfer of nourishment to the sporangia.
- (2) Mechanical support in such a position that the spores can be scattered when mature.

These will have to be considered in the three cases, (*a*) where the sporangia are simultaneous in origin, (*b*) where they are successive, and (*c*) where the various ages are intermixed.

(*a*) Where the sporangia are simultaneous in origin, they are produced in such moderate numbers that there is room for them all on the leaf-surface which bears them; there appears to be no need in these cases for a raised receptacle to carry the sporangia, while such a development would at once increase the difficulty of nutrition,

It is true in some few cases, such as *Marattia kaulfussii*, an elongated "podium" is formed, but it is provided with an extension of tracheides which doubtless aids nutrition. In most cases the receptacle is hardly developed as such, but the large sporangia receive their supplies directly from the leaf through their short thick stalks. The Schizæaceæ, with their isolated sporangia, have naturally no enlarged receptacle, but the Gleicheniaceæ show certain points of interest. Those species which have few sporangia in the sorus have only a comparatively small receptacle; but in *Gl. dichotoma*, where the sporangia are more numerous, and room has to be made for them all, the receptacle is slightly elongated, while it is well provided with vascular tissue within.

(b) This elongation and structural adaptation of the receptacle becomes much more pronounced where there is a continued succession of sporangia. The basipetal sequence seen in the Cyatheaceæ, Dicksoniæ, Hymenophyllaceæ, and Dennstædtiæ would hardly be possible without an elongating receptacle; the continual moving upwards of the more mature sporangia, so that they can freely shed their spores, leaves space for the initiation of younger ones below, while the latter are in their early stages close to the source of supply, and protected by the basal indusium. This seems to me to be the *raison d'être* of the elongated receptacle in such cases, and I apprehend that, given a basipetal succession, it has been a response to the need of space, by upgrowth from the base, not the result of "metamorphosis" of any pre-existing vegetative part. An indirect support for this opinion is found in the fact that the receptacle disappears in those Ferns where the mixed sorus is acquired.

(c) In cases of "mixed" sori the receptacle is commonly flat, though some exceptions do occur. A peculiar interest attaches to those closely allied Ferns of the *Dicksonia-Davallia* affinity, in which a transition from the basipetal sequence to the mixed sorus is believed to have taken place. In *Dennstædtia* and *Microlepia* the receptacle is clearly conical, though it does not show an elongation at all comparable to that of the Hymenophyllaceæ; for the number of the sporangia is but small, though the succession of them is for the most part strictly basipetal. Occasionally in *Denn. davallioides* and in *Dav. hirta*, but more commonly in *Denn. rubiginosa*, the strict basipetal succession which is seen in the first stages of the sorus is departed from, though the receptacle still maintains in some degree its conical form. But in *Eudavallia*, which is without doubt closely allied to the above, the sorus is a mixed one, and the receptacle is almost flat, though still provided below with a considerable mass of tracheides. Here, since the basipetal succession is not maintained, an elongated receptacle is not required, and since this difference occurs between Ferns which are certainly of a common stock, it is probable that a reduction has taken place. PRANTL is probably right in his opinion that in many of the Polypodiaceæ, where there is no obvious receptacle, it has become abortive in the manner above recognised in the *Dennstædtia-Davallia* affinity; that seems to be the most probable view in explanation of the sorus with flat receptacle and sporangia of various ages

intermixed. For us then an elongated receptacle is not in itself an important morphological feature; it is to be correlated with a continued basipetal succession of sporangia, and it is this last which is the essential morphological feature in such cases.

There remain, however, cases where there is an enlarged receptacle on which the sporangia are borne not in basipetal succession, but in mixed order; these (excluding *Onoclea*, which is basipetal) constitute the remainder of PRANTL'S Aspidiæ (*loc. cit.*, p. 16); as an example, the familiar sorus of *Nephrodium* may be quoted, with its large receptacle and internal mass of tracheides; it may be urged that these are inconsistent with the view expressed in the last paragraph. But there may be other causes than the one noted, which may have led to, or maintained, an enlargement of the receptacle. It may be a survival in these cases of an ancestral receptacle of large size, which, though the sorus has become a mixed one, may still be a convenience, as it certainly is in *Nephrodium*, where its size allows space for the sporangia between the indusium and the leaf-surface. I do not see in these cases any sufficient obstacle to the view above put forward, which may be formulated into these general propositions:—Those Ferns which show a basipetal succession of the sporangia in the sorus have a more or less elongated receptacle, and it may attain very considerable dimensions where the succession is long continued, as it is in *Trichomanes*. Those Ferns which have the sporangia of different ages intermixed have commonly (though not always) a flat receptacle, as in *Hypoderris*, or *Polypodium*. One line of transition from the one type of receptacle to the other has been demonstrated in the genera *Dennstaedtia* and *Microlepidia*, and it is possible that other transitions have also taken place elsewhere.

The Sporangium.

The equivalence of the sporangia in Ferns from the morphological point of view will be generally admitted throughout the family, whatever their modifications of detail may be. It is customary to distinguish Leptosporangiate from Ensporangiate types, on the basis of the origin from one or from several parent cells. The tendency of the observations above detailed, and especially those on the Osmundaceæ and Gleicheniaceæ, has been to show that this distinction is not founded on a difference in kind, but only in degree. The Osmundaceæ are especially marked out as intermediate in their mode of segmentation, while the Gleicheniaceæ show in addition a similarity in the type of the sorus. From these Ferns with large sporangia, oblique annulus, and short stalks, through equally short stalked forms with relatively bulky sporangia, such as the Dicksoniæ, Cytheaceæ, and *Loxsonia*, all with basipetal succession, we proceed towards the types with mixed sori, smaller sporangia, with vertical annulus, and usually long stalks, included under the comprehensive name of the Polypodiaceæ. The several variable parts of the sporangium will now be taken in order, and submitted to a comparative examination.

The Stalk of the Sporangium.

A part of the sporangium which deserves more attention than it has yet received is the stalk. It is well known that some sporangia are sessile, others borne on long stalks; that some stalks are thick and others thin; but it remains to submit them to a general comparison, and to place the facts observed in their relation to such features as the mass of the sporangium, its output of spores, and the mechanism of dehiscence as it may be influenced by neighbouring sporangia.

Omitting for the purpose of this comparison all synangial sori, the short thick stalk of the single sporangium as seen in *Angiopteris* will form one extreme of the series; at the other extreme, as showing the greatest simplicity of structure, lie those of the Leptosporangiate Ferns in which the whole sporangium is derived from a single papillar cell; if this undergo at first transverse segmentation, the stalk will consist, in part at least, of only a single-rowed filament of cells; this is actually the case in many Ferns, for instance in *Scolopendrium vulgare*.* Between these extremes lie many Ferns which bridge over the difference by almost imperceptible steps.

As we pass on from the Marattiaceæ, we find in certain Leptosporangiate Ferns short massive stalks, which at least approach them in structure. Taking first those in which the stalk consists of a central cell or group of cells, surrounded by a peripheral series of cells, we find this in such plants as *Gleichenia circinata* (fig. 5), in which there is a central group of three; in *Todea barbara* (figs. 48, 49, 50), in which the structure seems variable, examples having been seen with four, two, or one of these, surrounded by a peripheral series. *Matonia* (fig. 59) shows a single central cell. *Thyrsopteris*, with its massive sporangium, has a thick stalk, which may have two central cells (fig. 110), or it may consist of only a large rosette of some eight cells (fig. 109); *Lygodium* also seems to fall into this category, for though PRANTL does not actually give drawings of the stalk in transverse section, still his figs. 92, 95† leave no room for doubt that a central group exists. This is shown by him to be the case in some of the sporangia of *Mohria*‡; in each of the uppermost attachments a single central cell is seen, but the same fluctuation is shown here as in *Thyrsopteris*, for some of the stalks appear merely as a rosette of seven cells.

In the simpler type the stalk appears in transverse section merely as a rosette of cells. This is seen in some cases of *Thyrsopteris* and *Mohria*, but it appears to be constant in *Schizæa*.§ In the Hymenophyllaceæ the short thick stalk appears in transverse section as a rosette of six cells,|| though it may in some species consist of five or four (*Tr. radicans*); *Loxsonia* also has a six-celled rosette (fig. 67). KNY has

* STRASBURGER, 'Præticum,' p. 455.

† 'Schizæaceæ,' Plate 6.

‡ *Loc. cit.*, Plate 8, fig. 143.

§ PRANTL, *loc. cit.*, Plate 5, fig. 62.

|| PRANTL, 'Hymenophyllaceæ,' Plate 6, fig. 110.

figured a similar condition for *Ceratopteris*,* while the younger state (fig. 8a), with three cells clearly shows how this condition is derived from the three lateral segments formed on division of the sporangium-mother-cell. In the Dicksoniæ, *Dicksonia* (*Eudicksonia*) *culcita*, with its long stalk, shows in transverse section six or seven cells; but the number is smaller in other cases; thus *Alsophila* and *Cyathea* have sporangia with four-rowed stalks; in *Dicksonia* (*Patania*) *apiifolia* three or two-rowed stalks may be found; three is a common number for many Polypodiaceæ (*Nephrodium Filix mas*), while in extreme cases of elongation of the stalk, such as *Scolopendrium*, and even in *Davallia spelunca* and other *Eu-Davallias*, &c., the stalk may consist, through part of its length at least, of only a single row of cells.

Examining this series thus laid out according to the complexity of structure of the stalk, two main points are to be noted: first, that all those Ferns which show a larger output of spores (Gleicheniaceæ, Osmundaceæ, Schizæaceæ, and in a less degree Hymenophyllaceæ) have relatively thick stalks; it is not suggested that there is any exact numerical relation of the spore-output to the cell-rows in the stalk, but plainly a rough relation does exist, though open to exception. Secondly, the thinner stalks are more frequently elongated, while extremes of elongation, as in *Scolopendrium*, may be accompanied by the greatest tenuity of stalk. It is to be noted, nevertheless, that certain Dicksoniæ (*D. culcita* and *Menziesii*), and also certain Blechnums and Lomarias, show considerable elongation of a stalk which is still massive. The biological importance of the elongation of the stalk will be discussed in connection with the Biology of the whole sorus.

It will hardly be necessary to point out how close a relation there is between the thickness of the sporangial stalk and the mode of segmentation in the early stages of development of the sporangium. All those with a massive stalk show a deeply-seated sporangial mother-cell, in which the first segmentations may run down so as to meet its basal wall, or at least are inserted on its lateral walls. The consequence of this is that the stalk is massive from the first, being composed of the lower segments, or of the lower lying parts of the later formed segments, and they may undergo further divisions, either anticlinal, increasing the number of cell-rows to more than three, or periclinal, cells being thus cut off which will constitute the central group. To these must further be added in some cases the results of upgrowth of surrounding cells, which growth is shown already initiated in figs. 18, 19, 20 of *Gleichenia*, and in figs. 32, 36 of *Todea*. Such upgrowth round the products of the sporangial mother-cell point out these as approaching more than any other Ferns to the condition of the Eusporangiatae.

The Annulus.

The annulus has been used as a character for the classification of Ferns from the time of J. J. BERNHARDI, who first introduced it. He separated Ferns into two

* 'Parkeriaceæ,' Plate 25, fig. 18.

divisions, Filices Gyrateæ, and Filices Agyrateæ, according to the presence or absence of an annulus. The character thus introduced was used in various ways by subsequent writers, the position and form of the annulus being noted, as well as the mode of dehiscence. It is not necessary here to follow through the detailed history of the matter, as this has been efficiently done by BOMMER* ; it suffices to say that the use of the annulus culminated in the classification of PRESL.† His Ordo. I. Filices, which excluded Hymenophyllaceæ, Parkeriaceæ, Schizæaceæ, Osmundaceæ, Marattiaceæ, Ophioglossaceæ, was divided into two sub-orders, *Helicogyrateæ*, BERNH., and *Cathetogyrateæ*, BERNH. ; according as the annulus was oblique or vertical. This character has been used with greater or less prominence by all subsequent writers on the subject, but exceptions were found by G. KUNZE,‡ in the case of certain Japanese Ferns referred to the genus *Lomaria*. These sporangia showed an oblique annulus, with lateral dehiscence, and a short massive stalk ; in fact, characters which resemble those of the Cyatheaceæ ; he styles them “sporangia Plagiogyrateæ” (see above, figs. 139–143). The question was thus raised of how such Ferns are to be classified. KUNZE did not hold the oblique annulus to be a sufficient reason for removing them from the genus *Lomaria*, with which their affinity had been recognised on grounds of habit, but founded for them the section *Plagiogyria*, which was adopted by Sir WM. HOOKER, and remains in the ‘Synopsis Filicum.’ METTENIUS,§ on the other hand, concluded that, recognising the oblique direction of the complete ring as the character of the Cyatheaceæ, and the vertical direction of the incomplete ring as that of the Polypodiaceæ, with the same right as *Alsophila* is separated from *Phegopteris*, *Hemitelia* from *Cystopteris*, *Cyathea* from *Woodsia*, *Cibotium* from *Dicksonia*, so ought *Plagiogyria* to be ranked with the Cyatheaceæ.

The opinions thus far considered all assumed the essential constancy of the annulus in any given type of Fern. But M. J. E. BOMMER,|| in discussing the classification of the Cyatheaceæ, mentions that the position of the annulus is not exact and invariable, “for in a single species of *Cyathea* or *Alsophila* one may meet with sporangia furnished with either vertical or oblique annulus ; this variation in the position of the annulus is due to a very simple cause ; it is the result of a greater or less degree of pressure which the sporangia undergo in their association in the sorus, and which thus brings about the deviation of the annulus, which appears to present so stable a character, and upon which BERNHARDI has founded his *Helicogyrateæ*.” BOMMER remarks that in most Polypodiaceæ the sporangium is free and bilaterally symmetrical ; but in *Cyathea*, where the sporangia arise on a columnar receptacle, they are not symmetrical. “It follows that the annulus, in place of being vertical, which it should

* ‘Monographie de la Classe des Fougères,’ 1807.

† ‘Tentamen Pteridographiæ,’ Prag., 1837.

‡ ‘Bot. Zeit.,’ 1849, p. 865 ; also KUNZE, ‘Farrnkräuter,’ vol. 2, pp. 61, 91.

§ “Ueber einige Farngattungen.—II. *Plagiogyria*.” ‘Abh. d. Senckb. Nat. Ges.,’ vol. 2, p. 265, &c.

|| ‘Bull de la Soc. Bot. d. France,’ 1873, p. 16.

be (qu'il devrait être), becomes more or less oblique, according to the part of the sporangia where the pressure is produced. The sporangia which are not exposed to this deviating action (action déviatrice), those situated at the tip of the receptacle, have an annulus occupying the position which a normal development assigns to them in the greater part of the Polypodiaceæ." This was verified by BOMMER especially in *Alsophila*, and it is in species of this genus that a greater frequency of sporangia with a vertical annulus (connecticules droits) has been noted by him. He further states that the forms of the sporangia are sometimes very variable; and he mentions *Alsophila australis* as having sporangia with an annulus sometimes vertical, sometimes oblique; the same is stated to be the case in various species of *Alsophila* and *Cyathea*. BOMMER finally concludes that the position of the annulus is not a good character for the Cyatheaceæ.

I have examined mature sporangia of *Alsophila australis*, *excelsa*, *plagiopteris*, and *radens*; also of *Hemitelia capensis* and of *Cyathea sinuata*, and *Brunonis*, species for the most part mentioned by BOMMER as showing this inconstancy of position of the annulus. In all cases the annulus is continuous across the stalk; it is thus a complete ring, and is therefore essentially oblique; but though this *structure* of the sporangium is constant, the *form* may vary considerably, and the position of the annulus be apparently altered, though its structural relations may still be really constant; the sporangia are subject to changes of form owing to pressure, just as figs when pressed into a box, but the structure of the sporangium does not appear to be fundamentally altered, any more than that of the fig. I do not, therefore, admit BOMMER'S conclusion from this series of facts, that the position of the annulus in the Cyatheaceæ is determined by pressure.

Nor do I think that pressure upon the developing sporangium can be held to be the determining cause in other cases. The following facts bear on the question:—In the Osmundaceæ, and especially in *Todea barbara*, the young sporangia are pressed together in the still circinate leaf, so that they assume most irregular shapes; the apex may be flattened, and the sides may be squeezed and thrown into three, four or five angles; but when mature, the sporangia show in their structure no trace of these irregular early pressures. The same is the case also in *Thyrsopteris*. Conversely, in *Gleichenia* the sporangia stand quite aloof and free in their young state, and are uniformly oval in form; there is no sign of external or mutual pressure when young, yet they develop a uniformly oblique annulus. This shows that in *Gleichenia* the oblique position is not simply due to pressure. Further, in *Matonia*, though the sporangia are not subjected to pressure while young, they show obvious signs of mutual pressure in their flattened sides when mature; but this pressure late in their development does not appear to determine the position of the annulus, as may be concluded from such a case as the pair of sporangia shown in fig. 60.

From such considerations as these I conclude *that the oblique position of the annulus cannot be directly attributed to pressure during development of the individual.* It

seems to be a character inherent in the race, like any other inherited structural character.

Further, I do not admit the propriety of such an expression as "should be" ("devrait être"), used in the passage quoted above from M. BOMMER. There is no need to assume that Ferns with an oblique annulus were descended from those with a vertical annulus; I shall presently show that there is a reasonable probability that the converse was the case, and that there may still be seen, in many Ferns with a reputed vertical annulus, structural traces of an oblique type.

In discussing the annulus, an important question is that of its real homology, or speaking more exactly, its *homogeny*, in the various types of Ferns. The constancy of the presence of such a mechanism in homosporous Ferns, serving the same purpose, though with varieties of detail, points towards its having been a constant feature in the course of descent at least of the ordinary land-growing Leptosporangiate Ferns. To those who accept the view that the sporangia of the whole series of Ferns are really comparable to one another as regards descent, it may be a question whether the mechanism which has been described for *Angiopteris*, differing as it does in detail from that in Leptosporangiate Ferns, is really their true correlative; we may even hold the case of *Osmunda* to be doubtful. Still, a comparison of the indurated tissues in the sporangia of *Angiopteris*, *Osmunda*, and *Gleichenia* shows certain points of essential similarity, though the details do not correspond. The firm resistant arch of indurated tissue described in *Angiopteris*,* consists of cells of a similar nature to those which form the annulus of *Gleichenia*; its position is in the main the same, though it does not stretch as a continuous hoop round the back of the stalk, but stops short on either side of its base. When we consider the similarity of the sorus in these two genera, the sporangia with the same orientation and dehiscence, the comparison of these two bands seems inevitable, notwithstanding that the one is usually (though not always) a single row, and the other a broad and ill-defined band.

The mechanism of dehiscence in the Osmundaceæ may also be compared; it is adequately figured by CAMPBELL† as regards outward appearance, while I have represented its structure as seen in section in *Todea*.‡ Here the indurated tissue is more limited, forming a roundish patch, which does not extend far downwards. The main position of this relatively to the dehiscence may be compared with that in *Angiopteris*, but it is so different in detail from this Fern, and also from *Gleichenia*, that any near comparison of detail is undesirable. Such Ferns illustrate, among types which are certainly archaic, that some variability did exist. This may illustrate the sort of origin from which, by specialisation in smaller sporangia, the annulus as we see it in the true Leptosporangiates was derived; but of this we have no direct proof. In the remaining Leptosporangiate Ferns the homogeny of the annulus seems

* 'Studies, III.,' p. 55, Plate 11.

† 'Mosses and Ferns,' p. 356, fig. 184.

‡ 'Annals of Botany,' vol. 5, pl. 7, figs. 6, 7, 8.

the only view which is in accord with the constancy of its occurrence in plants which are so clearly related to one another. In addition, we see from the particular case of *Loxsonia* that the identity of the annulus may be maintained even when it is partially non-functional* ; the complete ring can still be traced occupying the same general position as that in *Gleichenia*, though through a considerable distance the cells are not indurated ; such persistency in an individual example makes it appear probable that the annulus has been a persistent feature also in cases where its modification has been of a less pronounced order.

Maintaining then that the annulus is homogeneous at least in the clearly annulate Leptosporangiates, we may now discuss the various forms and positions which it may assume. As a central though not necessarily the most primitive type, from which to start our comparison, *Gleichenia* may be taken ; here the annulus is an almost complete oblique ring, consisting for the most part of a single series of indurated cells, with a not highly specialised line of rupture which follows the median plane ; the remainder of the sporangial wall is divided by the annulus into two thinner walled areas, the "central" and "peripheral" faces. Within the genus *Gleichenia* these faces may vary in size and in convexity (comp. figs. 6 and 3), and as a consequence the annulus in different species may take slightly different angles from the leaf-surface, and vary in position relatively to the bulk of the sporangial body. We thus see indicated within a single genus a variation which might readily serve as a basis for selection.

The variation which is thus seen in *Gleichenia* gives the clue for comparison of the Schizæaceous sporangium ; if we imagine the "peripheral" face reduced in area to a small group of cells as in *Aneimia*,† or even a single one as in *Schizæa*,‡ while the annulus contracts accordingly, the result is a closely grouped ring of indurated cells, such as is seen in *Schizæa* and *Lygodium* ; and the latter genus has been shown to approach in the details of structure of the annulus to that in the ancient fossil *Senftenbergia*.§ At the same time, if the central face be enlarged, so as to become convex and protuberant, the whole sporangium would assume the well-known form seen in *Lygodium*. I do not assert that these modifications actually took place in the course of evolution : the actual progression may have been in the opposite direction, or both may have originated from some unknown stock ; all I purpose at present is to show that the two forms of sporangium are fundamentally of the same type, with the same mode of dehiscence, and that the differences are of the same nature as,

* In the Hydropterideæ the annulus is not represented, though it is not improbable that they originated from an annulate ancestry. I have not thought it necessary to take up their case in the present memoir, partly because they have been the subject of many careful investigations by others, partly because their affinities are so very uncertain.

† PRANTL, 'Schizæaceæ,' pl. 7, fig. 104.

‡ PRANTL, 'Schizæaceæ,' taf. 5, fig. 81.

§ ZEILLER, "Obs. sur quelques Fougères," 'Bull. Soc. Bot. de France,' tome 44, p. 195.

though greater in extent than, those which a comparison of species of *Gleichenia* brings to light.

On the other hand, we may link with the Gleicheniaceous type other modifications of sporangial structure, which lead from those with oblique annulus and median dehiscence towards those with vertical annulus and lateral dehiscence by a transverse slit. Of the Leptosporangiate Ferns, exclusive of the *Gleicheniaceæ*, *Osmundaceæ*, and *Schizæaceæ*, the only genus which has a median dehiscence is *Loxsoma*, and in it the annulus has the same relative position as in *Gleichenia*, though it is not completely indurated; beyond this there is no great difference of the annulus from the Gleicheniaceous type. But in all others the slit of dehiscence is in a lateral position, while the annulus has in many of them a more or less exactly vertical direction; as we proceed to these types the two faces become gradually equalised, and the sporangium itself becomes symmetrical relatively to its median plane, while it may also be symmetrical relatively to its antero-posterior plane. It will be shown later how these changes answer the biological requirements of the closely-packed sorus. There are thus two points for consideration: the position of the slit of dehiscence and the position of the annulus.

If we contemplate a derivation by descent of Ferns with a lateral dehiscence from those with median dehiscence (and grounds for such a view will be advanced below), we shall have to inquire whether on comparative grounds there is any probability that such a change did take place; are there any evidences of shifting of the point of dehiscence? The specialised "stomium" of the Polypodiaceous sporangium is well known; its position is constant, and it determines with constancy the point of dehiscence laterally. Again, in the Gleicheniaceæ, the line of dehiscence is laid down structurally, though there is no highly specialised stomium, the cells near the line of rupture being somewhat irregular (compare fig. 4 of *Gl. circinata*). Now, in the sporangium of *Hymenophyllum dilatatum*, the similarity of which as regards form and orientation of the sporangium and output of spores to *Gl. circinata* has already been remarked, the structure leads to a lateral rupture. It appears a reasonable suggestion that there has been a shifting of the position of the thin-walled region which determined dehiscence; that while the annulus itself maintained its oblique position, certain of the cells of the wall in a lateral position were not indurated, and the lateral dehiscence followed. The case of *Loxsoma* strengthens this suggestion, for in it we see that cells which are typically indurated may remain thin-walled, or even isolated cells of the part usually thin may be thick-walled. This shows a want of constancy of the induration in an individual case. Again, in *Thyrsopteris*, the large sporangium has an irregular annulus, oblique in position, of which the induration is incomplete on one side, and it is an interesting fact in this connection that the actual point of dehiscence is not uniform in this case. *Matonia*, again, though it maintains characters of the sorus and sporangium which suggest comparison with *Gleichenia*, has a lateral dehiscence determined in position by the incomplete annulus.

It is to be noted that in these cases there is no highly specialised stomium, such as is found in many Leptosporangiate Ferns. They appear to illustrate just such non-specialised dehiscence as might be expected in cases where there has been a shifting of the line of dehiscence from the median to a lateral position. Though the facts noted do not in any way demonstrate that such a shifting has taken place along any sequence of descent, they at least countenance the suggestion that there probably has been a change from the median to the lateral dehiscence.

Taking now the position of the annulus as a whole, we see that it is oblique in the Schizæaceæ, Gleicheniaceæ, Hymenophyllaceæ, &c., while it is usually described as vertical in most of the Polypodiaceæ. The facts I have described above show that the one type graduates by almost imperceptible steps into the other, while even in those which are described as having a vertical annulus, details may often be traced which compare with those where it is oblique; we shall not, therefore, look upon the two types as essentially distinct.

If the development be compared, it will be seen that the annulus is not specially localised in any one of those segments which appear with such constancy in the early stages of the Leptosporangiate sporangium. PRANTL* showed that in *Schizæa* the whole annulus is derived from the cap-segment, and this is probably the case for the rest of the Schizæaceæ. He also showed how the oblique annulus of *Trichomanes* is derived only in part from the cap-segment, while the segments I. and III. contribute the basal portion of it, but that segment II., which lies constantly on the side next to the apex of the receptacle, contributes only to the stalk, and to the thin-walled region of the wall which we have styled the "central" face.† KNY‡ and MÜLLER§ have given a detailed description of the development of the sporangium in *Nephrodium Filix-mas*, from which it appears that here again segment II. takes no part in the formation of the annulus, but contributes only to the stalk, and to the "central" face of the sporangium; the annulus is entirely derived from the products of the cap-cell, and of the segments I. and III. This statement is not in accord with the results of J. KUNDIG,|| who finds that segments II. and III. give rise to the ring in the Polypodiaceæ; but the very exact account given by KNY and MÜLLER hardly leaves room for doubt that their description is the correct one.

Though the segments here involved are the same as in *Trichomanes* the details of their sub-division are different, as plainly must be the case, for in the latter the annulus is a continuous ring at the insertion of the stalk; and there are other differences of detail besides.

From these well-known examples it is plain that *the formation of the annulus in*

* 'Schizæaceæ,' p. 50, plate 5, figs. 73-80.

† Compare 'Hymenophyllaceæ,' p. 39-40, plate 6.

‡ 'Wandtafeln.' Text, IX. Abth., p. 418.

§ 'Ber. d. D. Bot. Ges.,' vol. 11, p. 54.

|| "Beitr. z. Entw. d. Polypodiaceen sporangium," 'Hedwigia,' 1888, pages 1-11, plate 1.

Ferns at large, does not stand in any constant relation to the segmentation of the sporangium-mother-cell, though that segmentation itself shows so singular a constancy. This fact leaves the question of a shifting of the annulus more open than it would otherwise appear.

My own opinion is that the annulus of the Leptosporangiate Ferns is homogeneous throughout; that it has in the course of evolution undergone a shifting, not only of its position as a whole, but also of the point of dehiscence. That the more primitive type of complete annulus is that seen in the Gleicheniaceæ and Schizæaceæ, with oblique position and median dehiscence; that while *Loxsonia* maintained the oblique position and median dehiscence, part of its annulus is incompletely indurated. In others, while the complete oblique ring was maintained the point of dehiscence was shifted laterally, the result being as in the Cyatheaceæ, Hymenophyllaceæ, and others with a basipetal sorus. With the transition from the basipetal sorus to the mixed, came also a change of the annulus; maintaining the lateral dehiscence, the annulus became vertical, stopping short on either side of the stalk, which interrupts it. But in many cases a slight obliquity was retained, as seen in *Dennstædtia apiifolia* (fig. 131) and *Diacalpe* (fig. 93), the two sides being so far dissimilar that it is possible still to distinguish the "central" from the "peripheral" face; this is also the case in *Davallia*, *Lindsaya*, *Nephrodium*, and many others. But there are other outstanding cases of an oblique annulus among Polypodiaceæ which have been the subject of discussion, and have even been considered a sufficient reason for rejecting the oblique or vertical positions of the annulus as characters which are not dependable; I refer to the genus *Lomaria*, in which the § *Plagiogyria* has a well-marked continuously oblique ring of the annulus, somewhat similar to that seen in the Dicksoniæ. So far from looking upon such cases as these as being subversive of views based on the character of the annulus, I see in them exactly what might have been anticipated if, as I suggest, the types with a vertical annulus were derived from forms in which the annulus was oblique; it is hardly to be expected that the transition would be carried out completely in all cases; we shall regard these exceptions as being occasional survivals of the earlier type, and be prepared to find others, with greater or less degree of obliquity of the annulus, scattered through the numerous genera of the Polypodiaceous Ferns. These exceptions may even serve as an actual support of my general view of the descent of Ferns.

Spore-Enumerations.

At first sight a method of comparison based on the enumeration of the spores produced from a given part of a plant, such as a leaf, a pinna, a sorus, or a single sporangium, may appear to have no serious morphological value. It will probably be remarked in criticism of it that the physiological condition of the plant at the time will determine the output of spores. While this is admitted to be true within certain

limits, the morphological interest in enumerations of spores begins as soon as we can recognise what the limitations are for any given species, genus, or group.

It is not to be anticipated that this method of comparison will be of general use, and I do not propose to make estimates at present of the very large and fluctuating numbers of spores produced from the whole plant, the leaf, or the pinna of Ferns; such estimates, though leading to most surprising figures, would not, I think, serve any good morphological purpose. The comparisons offered will relate only to the sorus and the sporangium. But even in the case of sporangia, where they are very large, the numbers of spores are so great, and the variations range between such wide limits, that no useful result can be anticipated from their computation and comparison. For instance, in *Lycopodium* the size of the typical sporangium of different species varies greatly, and I do not see how comparisons of numbers so large and at the same time so fluctuating as they are, would be of real value. Even in the individual strobilus great variation of size is found; for instance, in *L. clavatum*, while the normal sporangium is large, and the normal output amounts to many thousands from each, at the upper and lower limits of the fertile region smaller sporangia are produced, from which the output of spores is comparatively low. This wide fluctuation is probably due to local differences of nutrition, and in such examples it is clear that, though there may be a maximum limit of size, the single sporangium is not a sufficiently definite spore-producing unit to allow of its output of spores being used in a strict morphological discussion.

But the case is different where the sporangia are smaller, as they are in the Ferns, and especially in the Leptosporangiatae. These stand absolutely alone among homosporous plants, not only in the small size of their sporangia, but also in the accuracy of their segmentations during development, and often in the very definite number of the spores produced from each. Here the physiological resources of the plant determine rather the number of sporangia produced than the number of the spores in the sporangia; the latter, with its smaller size, appears, in the species or in the genus, as a more definite and constant unit than is the case where the individual sporangium is large; and in proportion as the sporangium becomes thus a definite unit, the value of its details for morphological comparison is enhanced. It is, therefore, with some degree of confidence that I shall use spore-enumerations for purposes of comparison among the Ferns, and especially the Leptosporangiatae.

Such enumeration has received little systematic attention hitherto, though most of those who have described the development of Fern-sporangia have alluded to the number of spore-mother-cells, and deduced from them the number of the spores. Thus it has become familiar that the usual number of spores in Leptosporangiate Ferns is 48 to 64, corresponding to 12 to 16 spore-mother-cells.* A smaller output

* REES, 'Pringsh. Jahrb.,' vol. 5, 1866. RUSLOW, 'Vergl. Unters.,' 1872, p. 86, &c. SACHS, 'Lehrbuch,' 1874, p. 430; also p. 435. KNY, 'Parkeriaceen,' p. 54; also 'Botan. Wandtaf.,' Lief. 9, and text MÜLLER, 'Ber. d. D. Bot. Ges.,' 1893, p. 54.

has been recorded by KNY for *Ceratopteris*, in which, on the basis of 4 spore-mother-cells, he estimated the number to be 16; and by RUSROW for *Pteris cretica*,* where it is 32, presumably the product of 8 spore-mother-cells. On the other hand, larger numbers have been noted in certain other cases; RUSROW* and PRANTL† have shown that the spore-mother-cells in *Aneimia* number 32, and the presumable number of spores will thus be not more than 128 from each sporangium; for *Osmunda*, RUSROW concludes that the numbers are four times as great, viz. :—128 spore-mother-cells, while he counted “in most cases over 500 spores.” There the matter stands at present, and I am not aware that any systematic attempt has been made to trace a correlation between the number of spores in the sporangium and the structure of the sporangium, or of the sorus.

There are two ways of arriving at an estimate of the output of spores from a single sporangium: (1) by examining preparations of sporangia with spore-mother-cells, (2) by actual counting of the spores produced. Where the output is small, a reasonable degree of precision is to be expected by either method; but where the numbers are large, there are various sources of error, and the results must be taken as mere approximations. The first method has been used in the Marattiaceæ,‡ and from sections longitudinal and transverse through the sporogenous group, the number of its cells can be computed; but this is only a rough method, and liable to error where the group is large and approaches a spherical form. There is a second source of error in the incomplete maturing of some of the spore-mother-cells; they have been repeatedly observed in various stages of arrest, and examples of it are given in figs. 137, 138. The second method, by actually counting the spores, is the more certain, though it also is open to error where the numbers are large; single sporangia are opened on the slide in a drop of fluid, and, after scattering the spores through the drop, they are pricked off under a low power, by help of the *Camera lucida*, upon a sheet of paper and counted; in the process it is always possible that single spores may be lost, and the numbers thus frequently fall short of the typical number.

Since all the spore-mother-cells in Leptosporangiate Ferns are derived by division from a single archesporial cell, and since the successive divisions go on nearly simultaneously in the whole mass, the numbers attained are commonly some power of 2, and it will be seen that the results approximate to such figures as 4, 8, 16, (24), 32, (48), 64, 128, 256, 512, 1024; these will be styled the “typical” numbers. I shall now give, in tabular form, the result of *actual countings* of spores in various Ferns; these figures have been in many cases verified by sections through the sporangia and by estimates of the number of the spore-mother-cells, as the result of examination of those sections.

* ‘Vergl. Unters.,’ pp. 86–89.

† ‘Die Schizæaceen,’ p. 52, and Plate 8, figs. 120, 121.

‡ ‘Phil. Trans.,’ B, vol. 189, p. 146, &c., and p. 60.

Name.	Result of countings.	Typical number.
<i>Gleichenia flabellata</i>	838, 794, 695, 684	512-1024
„ <i>dichotoma</i>	319, 251	256 or more
„ <i>hecostophylla</i>	265, 272	256 „
„ <i>circinata</i>	241, 242	256
„ <i>rupestris</i> , var. <i>glaucescens</i>	244, 232, 220	256
<i>Osmunda regalis</i>	476, 462, 396, 373	256-512
<i>Todea barbara</i>	478, 445, 442 ; 225, 238	256-512
„ <i>superba</i>	206, 306, 342	256 or more
„ <i>hymenophylloides</i>	112, 115, 120, 124, 204	128 „
<i>Lygodium dichotomum</i>	232, 246	256
„ <i>javanicum</i>	237, 238, 245	256
„ <i>pinnatifidum</i>	128, 127	128
<i>Aneimia phyllitidis</i>	114, 111, 104	128
<i>Mohria caffrorum</i>	107, 107, 101	128
<i>Hymenophyllum Tunbridgense</i>	413, 416, 421	256-512
<i>Trichomanes reviviforme</i>	247, 243	256
<i>Hymenophyllum sericeum</i>	216, 239	256
„ <i>dilatatum</i>	121, 127, 127, 127	128
„ <i>Wilsoni</i>	119, 121	128
<i>Trichomanes crispum</i>	51, 52, 59	64
„ <i>rigidum</i>	32, 48, 56	32-64
„ <i>radicans</i>	46, 58, 62	48-64
„ <i>javanicum</i>	38, 42, 48	32-48
„ <i>spicatum</i>	48	48
„ <i>pinnatum</i>	32, 48, 32	32-48
<i>Loxsona Cunninghamii</i>	64, 62, 63	64
<i>Alsophila excelsa</i>	64, 60	64
„ <i>atrovirens</i>	57, 62	64
<i>Cyathea medullaris</i>	57, 61	64
„ <i>dealbata</i>	16, 8, 8, 16	8-16
<i>Dicksonia antarctica</i>	64	64
„ <i>Menziesii</i>	62, 63	64
<i>Dennstaedtia apiifolia</i>	61, 62	64
<i>Thyrsopteris elegans</i>	48-64
<i>Davallia spelunceæ</i>	64, 64	64

In addition to the above, numerous countings have been made from various Polypodiaceous Ferns, with the result *that among them no case has been found of a number exceeding 64*. The numbers are very frequently below that figure, 48 and 32 being typical numbers, while in *Notochlena sinuata* the countings resulted in 24, 32, 32, an interesting parallel to the typical numbers of 48 and 64; in *Sadleria cyatheoides* the number is 16. I may remark here that actual countings from material of *Ceratopteris thalictroides*, from Kew and from the Glasgow Garden, gave consistently

the number 32, not 16, as stated by KNY*; it is possible that this discrepancy of result may be due to a fluctuation between the typical numbers 16 and 32, similar to that which we have noted between 256 and 512 in *Todea barbara*, or between 8 and 16 in *Cyathea dealbata*; such differences plainly imply the completion or the omission of one of those divisions which take place almost simultaneously in all the cells of a sporogenous group. With these remarks we may leave the bulk of the Polypodiaceous Ferns on one side, though it is probable that a careful and critical examination of their output of spores in various types and under various circumstances would yield facts of interest.

On estimating the value of the results of these computations, it is first to be remembered that the figures previously arrived at for the Marattiaceæ† are high, viz., for *Kaulfussia*, 7850 per sporangium; for *Marattia*, 2500; for *Danaea*, 1750, and *Angiopteris*, 1450. The largest numbers are associated with more complete syngangial fusion, the smaller number in *Angiopteris* with separate sporangia, though the stalk is short and thick. The potential number estimated for *Gleichenia flabellata* is nearly equivalent to that of *Angiopteris*, though the actual countings run considerably below; still they are in excess of those for any other Leptosporangiate Fern observed, and as this is seen in a Fern in which the type of sorus is the same as in *Angiopteris*, it strengthens the affinity between these two genera, notwithstanding that the one is, as regards the mode of segmentation of the young sporangium, a typical Eusporangiate, while the other shows the segmentation of the Leptosporangiates.

From *Gleichenia*, as we pass through the table, successively lower numbers are seen, and the question arises whether there is in these facts any indication of an evolutionary sequence. It will be necessary to examine the results critically before such an interpretation is allowed to our enumerations.

With a view to a better knowledge of the circumstances affecting the question, measurements have been made of the size of spores, stated as the mean of their diameters, and of the size of the sporangial cavities stated as the mean of their internal diameters; these are given, together with the typical output of spores, in the subjoined table:—

* 'Die Parkeriaceen,' p. 57.

† 'Studies, III., Marattiaceæ,' p. 60.

Name.	Typical number of spores.	Mean diameter of spore.	Mean internal diameter of sporangium.
<i>Gleichenia flabellata</i>	512-1024	millims. 0.026	millims. .265
„ <i>dichotoma</i>	256 or more	0.026	.17
„ <i>circinata</i>	256	0.037	.27
<i>Osmunda regalis</i>	256-512	0.042	.465
<i>Todea barbara</i>	256-512	0.037	.315
<i>Todea superba</i>	256 or more	0.033	.24
<i>Todea hymenophylloides</i>	128 or more	0.04	.24
<i>Lygodium dichotomum</i>	256	0.063	.515
„ <i>javanicum</i>	256	0.075	.382
„ <i>pinnatifidum</i>	128	0.080	.50
<i>Mohria caffrorum</i>	128	0.077	.386
<i>Aneimia phyllitidis</i>	128	0.049	.30
<i>Loxsonia Cunninghami</i>	64	0.06	.327
<i>Hymenophyllum Tunbridgense</i>	256-512	0.030	.20
„ <i>dilatatum</i>	128	0.060	.30
„ <i>Wilsoni</i>	128	0.033	.20
<i>Trichomanes reniforme</i>	256	0.054	.27
„ <i>radicans</i>	48-64	0.030	.10
„ <i>spicatum</i>	48	0.033	.13
„ <i>pinnatum</i>	32-48	0.026	.093
<i>Alsophila excelsa</i>	64	0.035	.17
„ <i>atrovirens</i>	64	0.037	.17
<i>Cyathea medullaris</i>	64	0.051	.165
„ <i>dealbata</i>	8-16	0.040	.115

In comparing these figures it is obvious that, in the case either of the spore, or of the sporangial cavity, the most satisfactory comparisons are those where the parts in question are of approximately spherical form; allowances will have to be made where the spores are of the elongated type, as in *Gleichenia flabellata*, or where the sporangial cavity is of a long oval form, as it is in *Lygodium*, *Aneimia*, or *Loxsonia*; whereas in *Mohria* the cavity is almost spherical. In the case of *Trichomanes* also, where in the smaller types the sporangial cavity is actually in form of a flattened disc, it is clear that measurements of the mean of the diameters of the disc will not give a true proportional value of the volume of the cavity. It is thus seen that the figures can only be rough approximations, though where the form of the spore or sporangial cavity is approximately spherical, they will be reliable for purposes of comparison.

In the first place it appears that, in a general sense, the number of the spores is not always inversely proportional to their size. It may at first sight be assumed, without reference to sequences of descent, that there is a constant inverse proportion between the size of the spore and the number produced; as evidence it may be

quoted how RAUWENHOFF* states that the spores of *Gl. flabellata* are the smallest which he has measured, while we now see that this same species has the largest numerical output observed hitherto among Leptosporangiate Ferns. But the following facts show that an inverse proportion of size and number is not constant.

The smallest spores measured were those of *Trichomanes pinnatum* (0·026), which has only 32–48 per sporangium; while conversely the largest, e.g., those of *Lygodium pinnatifidum* (0·08), and *Javanicum* (0·075), *Mohria caffrorum* (0·077), of *Hymenophyllum dilatatum* (0·06), and *Trichomanes reniforme* (0·054) are produced in numbers which equal, or even exceed considerably the output in other allied cases where the spores are of smaller size, such as *Lygodium dichotomum* (0·063), *Anemia phyllitidis* (0·049), *Hymenophyllum Wilsoni* (0·033), *Trichomanes radicans* (0·03), and *spicatum* (0·033). But though from these cases it is sufficiently proved that this inverse proportion will not apply in a general sense, still in specific cases, and within circles of near affinity, such an inverse proportion may at times be clearly traced, and there can be little doubt that it is a factor in the problem; it is, however, closely connected with the further factor of the size of the sporangial cavity, as the following examples will show. In *Gleichenia flabellata* (spores 0·026—sporangia ·265) the number of spores is 512–1024; in *Gl. dichotoma* (spores 0·026—sporangia ·17) the number is typically 256, or it may be more; here the size of the spores is the same, but the larger sporangial cavity in *Gl. flabellata* allow of the larger output of spores. In *Gl. circinata* however (spores 0·037—sporangia ·27) with virtually the same size of sporangium as in *Gl. flabellata*, the larger spores are produced only in the smaller typical number of 256; here is a specific case of the number of spores being inversely as their size. Again in *Hymenophyllum Tunbridgense* (spores 0·03—sporangia ·20) the output is 256–512; in *Hym. Wilsoni* (spores 0·033—sporangia ·20) the slightly larger spores are produced only to the number of 128. On the other hand comparing *Hym. Tunbridgense* (spores 0·03—sporangia ·20) with *Trichomanes radicans* (spores 0·03—sporangia ·10) the spores in the larger sporangium of the former species number 256–512, while the spores of equal size are produced in the smaller sporangium of the latter only to the number of 64. A very beautiful case of parallel variation of both factors is seen in the Osmundaceæ; in *Osmunda regalis* (spores 0·042—sporangia ·465) the output is 256–512; in *Todea barbara* (spores 0·037—sporangia ·315) approximately the same output may be attained, though the individual spore and the individual sporangium are both smaller than in *Osmunda regalis*.

And so two factors may be recognised as affecting the number of spores produced, viz., the size of the individual spore and the size of the sporangial cavity, though it may be a question how far these are causes, and how far mere effects. Clearly, the question as to what determines the numerical output of spores is not exhausted by

* RAUWENHOFF, 'Archives Néerlandaises,' 1890, vol. 24, p. 175.

their recognition, however interesting their relation to one another may be. In ignorance of more specific factors determining the number, it can only at present be stated as an empirical fact that, while there may be variation in specific cases to smaller numbers, the larger numbers are only hitherto found in certain groups of Ferns. In the Polypodiaceæ, with their vertical annulus and mixed sorus, the number 64 has never been found to be exceeded; the larger numbers, though liable to reduction, as in the Hymenophyllaceæ, are only found among the types with oblique annulus, and basipetal or simultaneous sorus. There is, then, what in absence of better knowledge I must style an inherent higher productiveness, which commonly goes along with the simultaneous or basipetal sorus, and the oblique annulus of the short-stalked, usually massive, sporangium; these parallel features appear to link the types which show them on to the similarly highly-productive Marattiaceæ, which share some, though not all, of the concomitant characters.

Another point which comes out clearly from the results of enumeration of spores, is that variations of number occur within near circles of affinity. This is seen within moderate limits in the Gleicheniaceæ, Osmundaceæ, and Schizæaceæ, in which the numbers approximate for the most part to the typical numbers 512, 256, 128. In some cases it is difficult to see any circumstances which serve as an explanation; thus the variation between *Gleichenia flabellata* (512–1024) and *Gl. dichotoma* (256 or more), where the size of the spore remains constant, though the latter sporangium is smaller, is not susceptible of ready explanation. Nor is that within the genus *Lygodium*. In other cases, however, the conditions of life and the structure of the assimilating apparatus throw some light on the matter; thus *Todea barbara*, with its thick assimilating leaves, gives higher numbers per sporangium than *T. superba* and *hymenophylloides*, with their thinner pellucid leaves. But the most interesting series in this connection are the Hymenophyllaceæ, for the limits of variation in number are here very wide, ranging between such numbers as 421 and 32. Here the variation in number of spores per sporangium runs fairly parallel with the size of the sporangia, the smaller number of spores being contained in smaller sporangia (compare *Tr. reniforme* and *Tr. pinnatum*). Further, there is a correlative elongation of the receptacle, on which there is thus space for a larger number of the smaller sporangia to be inserted and produced in succession. On these characters the Hymenophyllaceæ may be laid out as a series, extending from types chiefly of the less specialised genus *Hymenophyllum* with short receptacle, large sporangia, and large output of spores from each, to types of the more specialised genus *Trichomanes*, with longer receptacle, smaller sporangia, and smaller output of spores from each. The former link on naturally to the Gleicheniaceæ in the characters named as well as in the general appearance of the sporangia (compare fig. 3 with fig. 95), and it seems not improbable that in the Hymenophyllaceæ we may see a series of specialisation in which the “filmy” character is the most salient vegetative feature, and that this carries with it, as in the genus *Todea*, a decrease in size of the

sporangia, and in the number of spores produced from each. Meanwhile, the length of receptacle and number of sporangia increases, so that, as we shall see later, the total output of spores is approximately maintained, but their maturing may be spread over a longer time in accordance with the powers of the less efficient assimilating apparatus.

Taking the facts thus acquired from Ferns with simultaneous or basipetal sori, and mostly with oblique annulus, they show that within circles of near affinity there may be a wide margin of variation in the number of sporangia in the sorus, and succession of their production, in the size of the sporangia, thickness of stalk, and in output of spores per sporangium.

But these are among the very characters by which the Marattiaceæ are distinguished from Leptosporangiate Ferns. Though naturally it is not possible to establish an exact numerical proportion of spore-output to other morphological characters, still the figures above given so far follow parallel to other structural details, such as size and thickness of stalk, that the spore-enumerations may be taken as a fair indication of them. The several families may be laid out on these grounds as probable sequences, and we may see in those with larger spore-output a suggestion for a nearer affinity to the more massive types, while those with smaller output from smaller sporangia will be recognised as more remote. An extreme case is that of *Gleichenia flabellata*, which shows a higher numerical output per sporangium than any other Leptosporangiate Fern, and approaches in this respect most nearly to the Marattiaceæ. The fact that its sorus is of the very same type—with a radiate uniseriate arrangement of sporangia, simultaneously produced, and with median dehiscence—is in itself a strong justification of the method of comparison on the basis of spore-enumerations.

BIOLOGY OF THE SORUS.

In contemplating the sorus from the biological point of view, its modifications may be traced as fitting it to attain three ends :—

- (1) The production and nutrition of numerous effective spores.
- (2) Their adequate protection till maturity.
- (3) The proper mechanical facilities for their dissemination when mature.

It is to be noted at the outset that (2) and (3) are conflicting factors, for the more completely the young sporangia are enveloped for purposes of protection, the more elaborate will need to be the mechanical arrangements for the successful shedding of the mature spores. We shall be disposed, unless there are grave comparative reasons against it, to look upon those sori which are simplest in construction and in protective arrangement as being probably the most primitive, and the complex as being probably derivative types. But there are cases where a simplicity of arrangement may have resulted from reduction; thus certain types of the compre-

hensive genus *Polypodium* appear to have attained the unprotected, non-indusiate condition of the sorus by suppression of the indusium.

(1.) *Production and Nutrition of the Spores.*

The size of the individual spore is a matter of importance. The larger the spore the better its chance on germination, since it can contain a larger store of nutriment than a small spore. But, on the other hand, small spores can be produced in larger numbers with a given amount of nourishment, and are more easily thrown out of the sporangium, and conveyed to a distance. These two conflicting factors will operate in the case of spores in the same way as in seeds. Commonly the size of the spores in a single sporangium is almost uniform, but there are cases where there is variation; a good example is seen in *Dennstaedtia* (*Dicksonia*) *davallioides*.

A tabular statement has been given above of the numerical output of spores per sporangium for a number of Ferns. I shall now give a similar tabular statement of the output per sorus:—

Name.	Spores per sporangium.	Average number of sporangia per sorus.	Output per sorus.
<i>Cyathea dealbata</i>	8-16	100	800-1600
<i>Alsophila excelsa</i>	64	50	3,200
<i>Gleichenia flabellata</i>	750	4	3,000
" <i>dichotoma</i>	300	8	2,400
<i>Athyrium Filix—foemina</i>	48	48	2,304
<i>Nephrodium Filix—mas.</i>	48	200	9,600
<i>Hymenophyllum Tunbridgense</i>	420	20	8,400
<i>Trichomanes reniforme</i>	256	40	10,240
<i>Hymenophyllum dilatatum</i>	128	90	11,500
<i>Trichomanes radicans</i>	64	140	8,960
<i>Angiopteris evecta</i>	1450	10	14,500
<i>Marattia fraxinea</i>	2500	18	45,000
<i>Polypodium aureum</i>	48	1200	57,600
<i>Dancea alata</i>	1750	20	35,000
<i>Kaulfussia esculifolia</i>	7850	12	94,200

This table shows that the output of spores per sorus in Ferns at large is very variable; in the cases quoted the numbers vary one hundredfold. I do not see that any general importance can be attached to the actual numbers as regards Ferns at large. It is noteworthy how often the output per sorus is similar in Ferns which are systematically remote from one another; for instance, *Marattia fraxinea* (45,000) and *Polypodium aureum* (57,600); *Angiopteris evecta* (14,500) and *Hymenophyllum dilatatum* (11,500); *Alsophila excelsa* (3,200) and *Gleichenia flabellata* (3,000). These examples show how a similar result may be obtained by various means, a large number of small sporangia balancing a smaller number of large ones. The similarity of output in such cases may be merely a consequence of similarity in the powers of

the underlying nutritive mechanism. The real interest, however, arises when in nearer circles of affinity, with varying size of sporangia, and of output per sporangium, the result per sorus is kept approximately constant by converse variation of the number of sporangia. This is illustrated in the above table in the genus *Gleichenia*, and in a less precise way in *Alsophila excelsa* and *Cyathea dealbata*. But the best demonstration of it is seen in the Hymenophyllaceæ (see p. 64), undoubtedly a very natural series, in which the sorus has a uniform type of construction, though the size and number of the sporangia, and the length of the receptacle are variable. The Table shows that the number of sporangia and the number of spores per sporangium vary inversely in the species named, producing an approximately constant tale of spores.

The production of numerous spores is a drain upon the resources of the plant. There is evidence that in many homosporous plants provision is made for producing a larger number than the nutritive resources can bring to maturity, and the study of the methods of self-adjustment of the number to the resources presents many points of interest. It has been seen how in the Equisetineæ,* Psilotaceæ,† and Ophioglossaceæ,‡ all the sporogenous cells do not come to maturity, but that many are disorganised, and their materials absorbed to help in the nourishment of the remainder. The existence of smaller, or even of abortive sporangia, at the limits of the Lycopod strobilus suggest that here also the plant is prepared to produce sporangia up to, and even beyond the limit of, nutritive convenience. In such cases there is a self-adjustment of output to resources. Cognate arrangements are also seen in Ferns, and they may be ranged under two heads: (a) abortion of spore-mother-cells, and (b) various methods of succession of sporangia, continued up to the limit of nutritive supply.

(a) The countings of spores actually matured per sporangium have given results which, while they approach certain typical numbers, often fall short of them (see table p. 107). It has been suggested that one of the sources of discrepancy is the abortion of some of the spore-mother-cells, and examples of such abortive cells are shown in figs. 137, 138. But it does not appear that this method of adjustment is so prevalent in Ferns as it is in certain other Pteridophytes. In Ferns with a small number of spores in each sporangium the frequent recurrence of exact typical numbers, such as 8, 16 (*Cyathea dealbata*), 32 (*Ceratopteris*), 32, 48 (*Trichomanes pinnatum*), 64 (*Davallia spelunca*), &c., show that the full number of the type is actually matured. The adjustment of output to resources in Leptosporangiate Ferns may sometimes be aided by abortion; but the small sporangium is here a more definite unit than in the sporangium of larger size, and the adjustment is rather by variation of the number of the sporangia than by variation of their individual output.

* "Studies, No. 1," 'Phil. Trans.,' B, 1894, p. 500, Pl. 43, fig. 21.

† *Ibid.*, Pl. 51, figs. 138, 143, 144.

‡ ROSTOWZEW, 'Beiträge z. Kennt. d. Ophioglosseen,' 1892, pl. 3.

(b) The drain of spore-development may be relieved within the sorus by the development of a succession of sporangia, the demand being thus spread over an extended period, and being carried on up to the limit of nutritive supply. Sori may in this respect be distinguished as of three different types.

- (1) Those in which the sporangia are produced simultaneously (*Simplices*).
- (2) Those in which there is a definite succession in time and space (*Gradatæ*).
- (3) Those in which there is a succession in time, but no regular succession in space (*Mixtæ*).

These will now be considered from their biological aspect, and first compared as regards nutrition.

(1) Among living Ferns the simultaneous appearance of sporangia is found in the Marattiaceæ, Osmundaceæ, Schizæaceæ, Gleicheniaceæ, and in *Matonia*. These are all Ferns having relatively large, short-stalked sporangia, and, excepting *Matonia*, a large output of spores per sporangium. It is true that as regards the whole leaf or pinna an acropetal succession of the sporangia is to be seen, but the difference of their age is not great, and whether sori are formed, as in the Marattiaceæ and Gleicheniaceæ, or where the sporangia are less regularly grouped, as in *Osmunda*, those near together are of the same age. The physiological drain by the developing sporangia upon the part which bears them thus comes at one time, and is not spread over a long period. This method is well represented among early fossil Ferns, and is, physiologically speaking, a simple and probably primitive, rather than a highly adaptive arrangement. It is to be noted that a simultaneous condition is seen also in *Platycerium*, and an approach to it occurs also in *Woodsia*, and in some other Polypodiaceous Ferns, where but few sporangia are produced.

(2) A definite succession in time and space is found among the Hymenophyllaceæ, *Loxsona*, Cyatheaceæ, Dicksoniæ, Microlepiæ, and Dennstædtiinæ, many of which are Ferns with relatively large, short-stalked sporangia. Two cases are possible, an acropetal or a basipetal succession. The former has never been found, and it can hardly be expected that it should; for an acropetal succession upon a receptacle elongating at its apex would present difficulties both of protection and of nutrition, while the shedding of the spores would not be carried out so readily as we see it in the basipetal sori. In these the base of the receptacle is covered by the successively younger sporangia, which are carried gradually upwards by its intercalary growth. The basal position of the young sporangia gives them the advantage of being near to the source of nutritive supply, at a time when they are most in need of it, while those which are approaching maturity are successively removed from it. In such cases numerous advantages are gained over the simultaneous sorus; the greatest probably is that the physiological drain is not sudden and severe, but is spread over a long time; in *Trichomanes* it may be a period of years.

(3) The majority of living Ferns show a succession of sporangia in the sorus in

time, but no regular succession in space; in point of living species this type far exceeds the other two categories. The main feature is that, in place of the regular basipetal sequence, there is here no definite order of succession of the sporangia in the sorus, but the new sporangia appear scattered without regularity or order between those already present. The physiological drain is as before spread over a long period, so that in this respect the mixed and basipetal sori appear equally practical. In mixed sori the receptacle is found to be usually wide and flat; this has the double advantage of enlarging the surface from which nutriment can be derived, and of shortening the distance through which it must be transferred.

The types (2) and (3) are connected by intermediate steps, along at least one natural sequence of living species, and it is not improbable that others may also exist. Within the genera *Dennstædtia* and *Microlepia* not only are species found with basipetal sequence (*Microlepia spelunca*, fig. 126), and conical receptacle according to type (2), but others also where the sporangia are occasionally (*Microlepia hirta*, figs. 127, 128), or frequently (*Dennstædtia rubiginosa*, fig. 132) out of strict order; these lead on to the nearly allied genus *Davallia* (fig. 135), in which the mixed sorus, according to type (3) is the rule. Such cases show a probability of an evolutionary transition from the one type to the other, which on the grounds above noted, as well as those of protection, would appear to be physiologically reasonable.

(2.) *Protection till Maturity.*

In aerial plants the parts are commonly protected while young from too free exposure to light and air. The sporangia of Ferns are well provided for in this respect, and the means are varied in detail and complexity. It is not intended here to give an exhaustive account of this matter, but merely to note briefly the various ways in which protection is effected in Ferns.

(a) The most general mode of protection is by the circinate vernation; before the young leaf is uncurled the sori have in most cases already passed their initial stages. Frequently a very adequate covering to the young sorus is thus given, though it is usually helped out by other methods, and this is especially to be seen in the *Leptosporangiatæ*, where the sporangial wall is thin.

(b) The usual position of the sori on the lower surface of the leaf secures both protection from the sun's rays and ready scattering of the spores on dehiscence; in this we may see justification of its prevalence in Ferns. Special cases of departure from this position have been noted in *Deparia Moorei** and *Polystichum anomalum*, and their rarity would seem to indicate that they are unpractical innovations. But though distinctly prevalent, the position on the lower surface is not general; *Osmunda* and *Acrostichum* are peculiar cases, where the sporangia are exposed with virtually no protective arrangements. There are also the large series of Ferns with

* 'Journ. Linn. Soc.,' vol. 2, p. 129.

marginal sori to be considered; but in these efficient protective arrangements are commonly present, for instance the indusial flaps in the Schizæaceæ, and the very efficient basal indusium in the Hymenophyllaceæ, Dicksoniæ, *Loxsona*, &c.

(c) This leads to the subject of the indusium, which is the most efficient, as it is also the most prevalent of the special organs of protection. This has already been discussed at some length above (p. 89) from the general morphological aspect; it only remains to point out its biological fitness for its protective duties. A continuous film of tissue is obviously a better protection than detached filaments; not only will the surfaces reflect light, and help to screen the young sporangia, but in many cases the overlapping of the indusial flaps is so close that the young sporangia live through their early stages in a completely closed space. I do not propose to discuss in detail the different forms which indusia may take to attain this end; they have been sufficiently described elsewhere.* I would merely remark upon the appositeness of certain types of them. Perhaps the most striking is the prevalent basal, cup-shaped, or two-lipped indusium in sori with basipetal succession; given a slow intercalary growth of the receptacle, and consequent formation of fresh space below, this is as regularly occupied by successive young sporangia, which are most perfectly protected, partly by the indusium, which is usually several layers of cells in thickness, partly by the older sporangia above. And this protection is specially necessary where, as in so many cases of these basipetal types, the sorus is marginal; for this position brings advantages for the shedding of spores, but also the disadvantage of exposure, a difficulty which is met by the development of a thick, almost fleshy indusium in many Ferns (*Dennstædtia*, *Microlepia*, *Davallia*); but in the filmy Ferns the indusium of these marginal sori may be filmy also.

The two-lipped indusium is commonly found in sori with a short receptacle (*Dicksonia*, *Hymenophyllum*); in sori with a longer receptacle (*Trichomanes*, *Loxsona*, &c.) the cup-like form is seen. The latter is certainly the more efficient protection, but the former, allowing as it does for opening of the two valves, offers less obstacle to dehiscence, and this is important where the receptacle is short, though where the receptacle is long it is immaterial, for the sporangia are lifted up by it beyond the barrier. In mixed sori the indusium commonly takes the form of lateral or over-arching flaps, and these conform less to settled types than where the sorus is basipetal.

(d) The protection is often assisted by paraphysis-like hairs, which arise from the receptacle and form a packing round the sporangia, as in *Cyathea* (fig. 76), *Alsophila* (fig. 87), and *Loxsona* (fig. 63), &c. Or hairs may be borne on the stalk (*Nephrodium Filix mas*), or head† of the sporangium. In many cases, such as *Loxsona* or *Cyathea*, though the paraphyses arise from the receptacle together with the sporangia, they are from the first structurally distinct, and there is no reason to see in them

* BURCK, 'Indusium der Varens,' Inaug. Diss. Haarlem, 1874; GLÜCK, 'Flora,' 1895, Plate 2.

† 'Genera Filicum,' Plates 29, 38; GLÜCK, *loc. cit.*, p. 13.

any evolutionary connection. But in other cases, especially among the Grammitideæ, various intermediate forms are to be seen between normal sporangia and paraphysis-like hairs. Thus in *Brainea insignis* the capitate hairs show segmentation after the manner of sporangia, and their similarity to the hairs in *Antrophyum*, *Vittaria*, and *Hemionitis* make it appear probable that in this affinity the paraphyses are really metamorphosed sporangia. But this cannot be asserted generally for hairs occurring within the sorus, even when they take capitate or discoid forms.* The importance of such bodies for purposes of protection needs no further remark, and their efficiency as regards protection from light is often increased by a dark colouring.

(e) Another rather similar form of protection is found in mixed sori, by means of the persistent stalks of older sporangia. In these cases a brittle region, sometimes constricted, is found below the head; the latter, when ripe, ruptures and breaks away from the stalk at the brittle neck, the stalk remaining as a paraphysis, protective of the later formed sporangia. This is seen in *Hypoderris*, and various other Ferns.

(f) Protective arrangements found on the plant at large must frequently be of importance to the sori as well. In such cases as that of *Asplenium Ceterach*,† or of *Hymenophyllum sericeum*, the sori are so covered in by scales and hairs as to be almost or quite invisible from without.

In the above paragraphs the chief modes of protection of the young sporangia have been briefly mentioned. I have not thought it necessary to quote extensively from such observations as have been previously made; anyone acquainted with the literature will be able to supply himself with numerous further examples. We see that in the matter of protection Ferns vary greatly; those with the largest sporangia commonly show the least specialisation to this end (Marattiaceæ, Osmundaceæ), while in the typical Leptosporangiates many devices are seen, and protection secured in various ways. Speaking generally, we should be disposed to regard those which have the most elaborate and varied protective arrangements as the more specialised, derivative types, while those with less adaptation in this respect may be looked upon as probably more primitive, and our conclusion from the point of view of this comparison would be that the Eusporangiate types fall into the latter category.

(3.) *Dispersion of Spores.*

The facilities for shedding the spores when mature will be considered from a mechanical point of view, but without entering upon the vexed question of the physical working of the annulus. It will be seen that the grouping of the sporangia, the position of the annulus, and of the point of dehiscence are closely interdependent. So far from attaching but small importance to the position and details of the annulus,

* "*Polypodium lineare*, THUNB. (*Pleopeltis nuda*, HOOK.)," 'Genera Filicum,' Table 18; see also GLÜCK, *loc. cit.*, p. 14.

† RABENHORST, 'Krypt. Flora,' vol. 3, fig. 128, p. 283.

as has been the view of PRANTL* and other writers,† we shall see in these an adaptability in position, and in extent of induration, which depends closely upon the whole arrangement of the sorus. To the sum of these cognate characters due systematic weight will have to be accorded; but at present we shall examine them merely as arrangements leading up to the satisfactory shedding of the spores.

In Leptosporangiate Ferns there are three main types of dehiscence of the sporangium:—

- (1) By a slit in the *median* plane, as in Gleicheniaceæ, Schizæaceæ, Osmundaceæ, and *Loxsona*.
- (2) By a slit in an *oblique lateral* plane, as in the Cyatheaceæ, Hymenophyllaceæ, Dicksoniaceæ, *Matonia*, &c.
- (3) By a slit laterally, in a *transverse* plane, as in the Polypodiaceæ.

All these depend, for the successful opening of the fissure and ejection of the spores, upon the straightening of the curved mechanical tissue, or annulus; this requires free space in one direction or another, and the dehiscence can only be properly carried out when free movement of the mechanical tissue is allowed, without meeting external resistance. Accordingly the grouping of the sporangia in the sorus is a determining factor in the position of the mechanical ring; we shall see that, subject to some exceptions, the median dehiscence is characteristic of simultaneous sori; the oblique dehiscence of basipetal sori, and the transverse dehiscence of mixed sori. These three cases will be severally considered, and the mechanical fitness of each recognised.

The *median dehiscence* (which is characteristic also of the Marattiaceæ)‡ is seen in the definite sori of *Gleichenia*, in the Osmundaceæ, where the sporangia are not arranged in definite sori, and in the Schizæaceæ, where the sporangia are usually solitary. It is also seen in *Loxsona*. Where, as in the Leptosporangiates, there is a definite annulus and a free sporangium, the whole body alters its form on dehiscence. ATKINSON§ has shown for *Osmunda* and *Gleichenia* how the sporangium widens laterally, requiring free elbow-room on either side before the sudden springing of the annulus throws the spores out right and left. I have verified this in *Gleichenia*, and the case is similar for *Osmunda*. It thus appears that the median dehiscence of an annulate sporangium is a practical working arrangement where the sporangia are not in close lateral juxtaposition, and this is the case in those Ferns where it is found.

* 'Arb. Breslau Gart.,' vol. 1, p. 4.

† The following quotation illustrates the position taken by many botanists at the middle of the century: "Whether the band is vertical or horizontal, complete or incomplete, or otherwise, seems unconnected with any physiological peculiarities that can be pointed out, and to be of no greater importance than for subordinate purposes of classification." LINDLEY, 'Veg. Kingdom,' 3rd Ed., 1853, p. 78.

‡ In *Danaea*, *Kaulfussia*, and *Marattia* the opening of the median slit is a consequence of the drying-up of the tissue adjoining it, while the sporangia conjoined into a firm framework do not materially alter in form.

§ 'Biology of Ferns,' p. 73, figs. 132-135.

The Gleicheniaceæ have only sporangia laxly disposed round the central receptacle; in the Schizæaceæ the sporangia are solitary; in the Osmundaceæ their arrangement leaves ample room for this mechanical opening. Finally, in *Loxsonia*, the sporangium is so constructed with its incomplete ring that though the dehiscence is median, still the sporangium as a whole does not widen on dehiscence. It is, in fact, a compromise; with its basipetal sorus it retains the median dehiscence, but the annulus is so modified as to be still compatible with that type of sorus; the half of the annulus is mechanically ineffective, and the median rupture is maintained at the sacrifice of much of the propulsive power. Thus it appears that in all known cases of median dehiscence, excepting *Loxsonia*, the lax grouping of the sporangia is such as to allow of successful mechanical ejection.

The *dehiscence by an oblique lateral slit*, worked by an oblique annulus, is found in *Matonia*, Cyatheaceæ, Dicksoniæ, and Hymenophyllaceæ; also in a modified degree in the Dennstædtiinae, and some others, and in the *Plagiogyria* section of *Lomaria*. With the exception of the last-named genus and *Matonia*, all the Ferns showing the oblique dehiscence have basipetal sori, and a constant orientation of the sporangia on the plan typified by *Gleichenia*. A moment's consideration will show how suitable the oblique dehiscence is for dissemination of the spores in cases where the succession of the short, thick-stalked sporangia is basipetal, and the orientation constant. The sporangia overlap one another like the shields of the Roman *testudo*, while all are so closely packed together that no space is given, as in the former case, for lateral expansion before the springing of the annulus. But some space is necessary for the straightening of the annulus before the sudden jerk; the free space available for these overlapping sporangia is that obliquely upwards, towards the apex of the receptacle; in that direction the annulus is free to straighten itself out, dehiscence taking place at one side, near to the attachment of the stalk; it can then execute without obstacle that sudden jerk by which the spores are scattered. It is thus seen that while the relative position of the annulus is the same as in the sporangia with median dehiscence, the comparatively slight difference in the position of the slit at the side, instead of being in the median plane, makes all the difference of success in shedding the spores, where the sorus is crowded with a sequence of closely appressed sporangia.

It has been noted that all the Ferns with oblique dehiscence, except *Matonia* and *Plagiogyria*, have basipetal sori; it remains to consider these exceptions. The simultaneous sorus of *Matonia* resembles that of *Gleichenia* in general arrangement, but differs from it in the presence of a firm indusium; not only does this protect the sporangia, but it also cramps them for space, so that they commonly show a compressed form, with mutual flattening of their sides (fig. 60). So long as the indusium is persistent, dehiscence will be mechanically impossible, and by the time the indusium falls away, the tissues of the sporangium are fully developed, and no longer capable of change. An alteration of the dehiscence has followed this cramping effect of the

annulus; the close lateral packing prevents dehiscence in the median plane, with lateral widening as in *Gleichenia*; accordingly, a lateral dehiscence is the rule in *Matonia*, the annulus obtaining free play outwards, as soon as the indusium falls away; but as already explained there is no exact specialisation of a stomium. The sorus of *Matonia* may then be regarded as a modification of the *Gleichenia* type, in which the dehiscence has been controlled by the advent of an indusium, and the consequent lateral contact of the sporangia.

The other exceptional case is *Plagiogyria*, which shows so peculiarly detailed a resemblance of its sporangium to that of *Dicksonia* (compare figs. 122–125 with figs. 139–142). There appears to be no mechanical necessity for the oblique annulus in this case; but if, as I suggest, the vertical annulus be a modification of the oblique, then, as in *Plagiogyria*, the oblique position can do no harm in the rather lax sorus, it may well have been retained as an ancestral feature.*

The Dennstædtiinae are a peculiarly interesting transitional series; they have typically a basipetal sorus, though this order may be departed from in *D. apiifolia* and *rubiginosa*. The annulus is but very slightly oblique, and though the orientation is strictly maintained while the sorus is young, the great elongation of the stalk lifts the sporangial head up aloft, so that the oblique position of the annulus has no mechanical importance; here the annulus is found to be almost exactly vertical, though it still retains slight traces of obliquity (fig. 131). This is matched also by *Sphaeropteris* (fig. 92). Such traces of slight obliqueness of the annulus, occurring as they do in Ferns, where we see also the transition from the basipetal to the mixed sorus, appear to me to give strong evidence of the correctness of the mechanical explanations here brought forward, and of the general view as to descent, which will be advanced later.

The dehiscence by a *lateral transverse slit*, worked by a *vertical annulus*, is the prevalent type in the rest of the Leptosporangiate Ferns. They have commonly a flat receptacle, on which the various ages of the sporangia are intermixed. The ripe sporangia usually have long stalks, and show no regularity of orientation. The vertical annulus with transverse dehiscence is a mechanical arrangement which makes use of the free space immediately above the surface of the sorus for the straightening of the annulus prior to the jerk of ejection; a bias to either side is quite unnecessary, and might be a positive disadvantage. As the young sporangium grows in a mixed sorus, for instance of a *Polypodium*, its stalk elongates, carrying the head vertically upwards from the receptacle; it is thus lifted above the crowd of younger sporangia, and the space directly above it is free for the movement of ejection. The vertical annulus thus satisfies the conditions of the mixed sorus.

It was above pointed out that adequate protection of the young sporangia, and

* The question of real affinity of *Plagiogyria* and *Dicksonia*, so strongly suggested by the sporangia, must remain uncertain till the development and anatomy have been examined. Meanwhile it may be remarked that the erect habit would support such a relationship.

facilities for dissemination of the spores are conflicting factors. In non-indusiate Ferns the difficulty does not arise; interest is thus centred in the indusiate Ferns. In many cases the indusium is firm and persistent, and in these the receptacle is frequently of importance in the shedding of the spores. Elongated receptacles are commonly absent in mixed sori, though they are a feature in basipetal sori. The elongation is not only important for the accommodation of numerous sporangia, but also in raising those which are mature above the protective indusium, which in these sori is at the base. This is seen conspicuously in the Hymenophyllaceæ, the sporangia being successively exposed beyond the lip of the indusium, where they can dehisce as circumstances dictate. *Loxsonia* is a particularly interesting case of this, for in it the receptacle elongates by intercalary growth below the lowest sporangia, forming a sort of pseudopodium, on which all the sporangia are carried up, so as to be exposed above the indusium (fig. 64). This shows that the elongated receptacle is not merely a basis for sporangia, but also a part which places them suitably for dehiscence.

But on the other hand the indusium itself may change at maturity. It may be deciduous as a whole; this rare condition is shown in the hard, almost woody indusium of *Matonia*. Or it may shrivel as it grows old, and expose the ripening sporangia which it had protected; this is seen frequently, *e.g.*, in *Nephrodium* and *Polystichum*, or it may roll back, the inner concave side becoming convex. These are merely specimens of the way in which the indusium is removed from acting as an obstacle to the shedding of the ripe spores.

COMPARISON.

Three main types of Ferns have now been distinguished, on the ground of many parallel characters of the spore-producing parts. The importance of these above the characters drawn from the vegetative organs, as a basis for systematic arrangement, has been insisted upon above. The distinctive characters may be briefly formulated as follows:—

Simplices.—Sporangia of simultaneous origin, upon a receptacle which may be slightly sunken, flat, or slightly projecting; they are of relatively large size, sessile, and usually produce a large output of spores (only *Matonia* has less than 128 as typical number). The annulus, where present, is oblique; dehiscence in a median plane (except *Matonia*); protective arrangements usually absent or inefficient (except Schizaceæ and *Matonia*). These include the Marattiaceæ, Osmundaceæ, Schizæaceæ, Gleicheniaceæ, and Matonineæ.

Gradata.—Sporangia borne in basipetal succession, with regular orientation, upon a more or less elongated receptacle; they are usually of smaller size, sessile, or with short stalks; output of spores smaller, typically 64,

or lower (except some Hymenophyllaceæ); dehiscence lateral and oblique (except *Loxsonia*), and annulus oblique; indusium present (except *Alsophila*) as a basal cup, or basal flaps. These include the Loxsomaceæ, Hymenophyllaceæ, Cyatheaceæ, Dicksonieæ, and Dennstædtiineæ.

Mixta.—Sporangia of various ages intermixed, without regular orientation (except *Platyserium*), upon a sunken, flat, or slightly projecting receptacle; they are relatively small, with more or less elongated, thin stalks; output of spores 64 or under. Annulus vertical (except *Plagiogyria*), dehiscence transverse. Protective arrangements various, and often elaborate. These include all the remaining genera of Leptosporangiate Ferns.

The Ferns which fall under these three divisions appear to me to illustrate three steps in the evolution of the sporophyte in the order. I do not by any means intend to assert that the living Ferns of any one of these divisions were the actual ancestors of those in any other; nor do I wish to suggest that the progression was by any single line of descent; the probability is rather that a similar adaptation may have made its appearance in more than one evolutionary sequence. The idea of parallel development is now a familiar one; no one would now assert, for instance, that all seed-bearing plants sprang from one stock; the "seed" has probably made its appearance in several distinct series; and yet we class seed-bearing plants (Spermatophyta) together. Similarly with our three types of sorus, the members of each category are not all to be taken as necessarily of common descent, but are grouped according to common adaptation, affecting parts which carry out the first office of the sporophyte, viz., spore-production.

The "Simplices" with their simultaneous sorus show, it is true, a massive type of sporangium, which might seem inconsistent with their name; but they have at the same time the simplest type of construction of the sorus as a whole, this body being formed once for all, and having no definite form of intercalary increase of the receptacle, or succession of sporangia; they are also the simplest in the methods of protection of the sorus, and in dehiscence. They include Ferns of the Eusporangiate type, as well as some Leptosporangiates which approach them in the size and structure of their sporangia. In all of these the sporangia show a greater similarity to those of other Pteridophytes in size, development, and spore-output than do those of the rest of the Ferns, and their simultaneous appearance also resembles the common rule for Equisetineæ and Lycopodineæ. On these comparative grounds I look upon the "Simplices" as being relatively primitive and less specialised types of Ferns, though more direct evidence on this point comes from the palæophytological side.

From certain sori of the "Simplices" to some of the "Gradatæ" is but a slight step; *Gleichenia dichotoma* has a naked sorus, differing little in general construction from that of *Alsophila atrovirens*. I do not suggest this as a true line of descent, but merely quote it as an illustration how near the one type may be to the other in

point of arrangement within the sorus. Again, a comparison may be drawn between the sorus of *Gleichenia* and of *Loxsonia*; with the striking similarity of sporangium and dehiscence, the chief differences are in the intercalary growth of the receptacle, and basipetal sequence of the sporangia, together with the cup-like indusium of *Loxsonia*. But there are traces of an intercalary growth of the receptacle even in *Gleichenia* (fig. 90); the strictly uniseriate sorus is departed from in *Gl. dichotoma*, and as explained above (p. 89) in *Gl. spelunca*, there is a slight overlapping basal flap. It is not suggested that any species of *Gleichenia* represents the ancestry of *Loxsonia*, but I do point out that the salient differences in the sori are differences of degree rather than differences in kind, while the basipetal sorus being an advance, physiologically, on the simultaneous, there is thus a reasonable probability that such a transition should take place.

One of the most interesting, and from a comparative point of view most important and continuous series among the Gradatæ is that of the Hymenophyllaceæ. It appears to me clear that it is a line of specialisation of a nature similar to that indicated in the "filmy" *Todeas*, but carried much further, and represented by many more species in our present Flora. In *Todea* the "filmy" habit is accompanied by a smaller number of spores per sporangium. The fact that some species of Hymenophyllaceæ have a larger output per sporangium than any others of the Gradatæ or Mixtæ, gives the series a special significance, if as the genus *Todea* suggests, the "filmy" habit leads to reduction of the output per sporangium.

The transition from the Gradatæ to the Mixtæ has probably taken place through various lines of descent, and, as we may believe it to have been a more modern change, so we find the steps of the transition quite clearly indicated in living species. That such a passage from the basipetal to the mixed sorus did take place, seems to me to be the only explanation of the facts stated at length above for the genera *Dennstædtia*, *Microlepia*, and *Davallia*, while these lead on naturally to the bulk of the Pterideæ. A reasonable probability of a similar transition has also been made out for the *Cyatheaceæ*, *Woodsia*, *Hypoderris*, &c. The biological considerations brought forward above confirm the probability of this view.

It is possible that a mixed condition of the sorus may have arisen also by interpolation of successive sporangia without order in a typical simultaneous sorus, such as that of *Angiopteris* or *Gleichenia*; but evidence of this has not yet come to hand.

The above paragraphs contain an expression of my own opinion on this matter, based upon a study of the sori in all the important genera of homosporous Ferns. But conclusions of this nature ought not to rest upon the study of one part only. It remains for us to see how far they will be supported by comparison of external form and anatomy of the Sporophyte, and by the form of the Gametophyte, and the sexual organs. While considering these lines of comparison, I maintain still the position stated broadly in the first Memoir of this series,* that priority of morphological

* "Studies, I.," 'Phil. Trans.,' B, 1894, p. 475.

importance is to be given to the comparative and developmental study of the spore-producing members over the vegetative, and similarly of the sexual organs over the vegetative conformation of the prothallus.

The form of the stem is clearly an uncertain basis for comparison; it varies quite independently of the sorus, so that differences of axis may be found within near limits of affinity. For instance, in such closely allied species as *Onoclea sensibilis*, L., and *Onoclea struthiopteris*, Sw., the one has a creeping, the other an upright stock. But though many instances might be quoted as showing the instability of the characters of the axis, even within the limits of the genus, still in certain tribes there is a constancy which cannot be ignored. The creeping axis is characteristic of the Gleicheniaceæ, *Lygodium*, *Matonia*, *Loxsonia*, most Hymenophyllaceæ, *Dennstaedtia*, *Microlepia*, and *Davallia*; in fact, it is the prevalent form in those Ferns which illustrate the probable transition from Simplices to Gradatæ and Mixtæ. It has been suggested to me that, under circumstances of stress, the creeping stem would be more likely to survive than the upright, or arborescent. The Lycopodiaceæ are a good example of this; the aborescent forms are extinct, and the creeping or epiphytic species of *Lycopodium* and *Selaginella* survive. Similarly with *Equisetum* as compared with the fossil Calamariaceæ. Thus we may see in the creeping habit of such important connecting links as *Matonia* and *Loxsonia*, and other Ferns above quoted, one of the factors which may have led to their survival.

Again, it may be shown that the form and texture of the leaf vary independently of the characters of the sorus. It suffices to mention that simple-leaved species exist in such genera as *Danaea*, *Cyathea*, *Trichomanes*, *Adiantum*, and *Asplenium*, &c., and it is plain that the outline of the leaf does not closely follow the characters of the sorus, upon which the generic distinctions are chiefly based. The texture of the leaf is also an uncertain guide: it is true that the Hymenophyllaceæ are "filmy," but the same character appears in greater or less perfection in *Danaea*, *Todea*, and *Asplenium*, a sufficiently widely spread series of genera to show that the filmy character does not follow any one soral type.* Accordingly, the main features of external form can only be of minor use in a system which is based upon comparison of the sorus. But as an example where such facts may be of value *Plagiogyria* may be quoted, in which the peculiar similarity of the sporangia to those of *Dicksonia* is accompanied by the erect, more or less, aborescent trunk.

Similarly with anatomy, which in a measure follows variations of external form, though at such a distance behind as to give it an additional title to respect, anatomical characters do not exactly follow those of the sorus, and cannot, therefore, be used as a general basis for diagnosis, though anatomical facts have an interesting bearing in special cases. For example, the sorus of *Angiopteris* is similar in many features to that of *Gleichenia*, but the former has in its trunk one of the most complex vascular

* POIRAULT, 'Ann. Sci. Nat.,' Botan., 1893, p. 196. GIESENHAGEN, "Hygrophile Farne," 'Flora,' 1892.

systems known, while *Gleichenia* has a simple cylindrical stele. On the other hand, the genera *Gleichenia*, *Matonia*, *Loxsonia*, *Hymenophyllum*, *Trichomanes*, *Dennstaedtia*, *Microlepia*, and *Hypolepis* all have either a single solid stele, or a cylindrical one, with or without internal accessory steles. This may be a mere concomitant of the creeping habit and solitary insertion of the leaves. But whatever the reason, it provides material for interesting comparisons.* The vascular supply to the leaf, and its mode of insertion on that of the axis also provides useful facts. A single stele enters the petiole in *Osmunda*, *Matonia*, *Loxsonia*, *Schizaceae*, *Gleicheniaceae*, *Hymenophyllaceae*, &c. The uniformity of this simple condition becomes the more important when it is remembered how frequently in Ferns with a mixed sorus the leaf-trace is composed of numerous smaller steles.

It appears that the general arrangement of the vascular system will fairly countenance a relationship between the tribes of Ferns above named, and especially of the *Gradatae* with such genera as *Gleichenia* and *Matonia*. It will remain for more detailed work to show how far these comparisons may be pressed; meanwhile, I see in the anatomical data no obstacle to the grouping proposed, but rather a measure of support for it.

It would be unsatisfactory to accept conclusions on questions of classification or descent of Ferns simply on the comparison of the sorus, or even of the sporophyte at large†: the gametophyte must also be considered. We shall not anticipate that any strict parallelism between the two generations must necessarily exist; the degree of development of the gametophyte and sporophyte does not correspond in the *Hepaticae*, and this makes it difficult in that group to decide which forms are the most primitive. The same holds for certain Mosses, for instance *Buxbaumia*, where, with a very simple gametophyte, we find a relatively large and complex sporogonium. The genus *Lycopodium*, again, with its remarkable uniformity of the sporophyte, shows great variety of form and habit of the prothallus.‡ It is true that we may see in these only modifications of one common plan, but still the genus serves well to teach how plastic and adaptive the prothallus may be in plants whose sporophyte retains a uniform character. LANG has rightly pointed out the biological importance of this variation. He remarks§: "Since the struggle for existence tells largely upon plants in their attempts to seize upon fresh situations, it becomes all important in the case of a vascular cryptogam that favourable modifications should take place in the prothallus. It is thus, on *à priori* grounds, quite comprehensible that a genus of this group, which is known to have had a long geological history, might retain the spore-

* This comparative work is being carried on at Kew, and in Glasgow. I am indebted to Mr. GWYNNE-VAUGHAN for some of the facts on which these remarks are founded.

† Compare GOEBEL, "Archeogoniatenstudien," 8, 'Flora,' 1896, p. 67.

‡ TREUB, 'Buitenzorg Annals.' BRUCHMAN, "Ueber die Prothallien und die Keimpflanzen mehrerer Europäischer Lycopodien," Gotha, 1898. LANG, 'Annals of Botany,' vol. 13, p. 311.

§ *Loc. cit.*

bearing generation, but slightly modified, and owe its survival almost entirely to the adaptations of the gametophyte to new conditions."

The truth is that, as regards the vegetative development, the prothallus of Ferns is highly plastic under varied external conditions, and directly influenced by them.

When writing on the prothallus of *Trichomanes** some years ago, I expressed the opinion that the vegetative characters of the prothallus are not a secure guide in the comparative treatment of Ferns. Subsequent observations from various quarters have strengthened that opinion,† while they have shown more clearly than before what conditions they are which influence the form of the prothallus. HEIM,‡ in attempting a comparison of Leptosporangiate Ferns on the basis of the prothallus, rightly aims at the selection of those organs which are typical for the groups in question, and recur under altered cultural conditions. He puts the form of the thallus into the background, and uses for his comparison the structure of the antheridia, the occurrence of certain characteristic hairs, the position of the sexual organs and rhizoids, and the presence or absence of an active apical region.

He lays the greatest weight upon the structure and mode of dehiscence of the antheridium, of which he recognises two types:—

Type A, in which at maturity the cap-cell breaks away; this includes the Hymenophyllaceæ, Osmundaceæ, Cyatheaceæ, Dicksoniæ, Gleicheniaceæ, and *Lygodium*.

Type B, in which the antheridium has a star-like dehiscence; this includes *Aneimia* and *Mohria*, and the whole body of Polypodiaceæ.

Within the limits of these broad divisions distinct series are recognisable by other characters, which are detailed in the original work (pp. 355–369). It is noted incidentally that the antheridia of the Hymenophyllaceæ come nearest in their structure to those of the Osmundaceæ (p. 357); that the Cyatheaceæ show similarity in the structure of the prothallus to the Polypodiaceæ, but their antheridia rupture with the lid-like cap-cell which distinguishes them from the Polypodiaceæ. The Dicksoniæ correspond to the Cyatheaceæ, but they have another quite peculiar hair-formation, which one may regard as a transition to the Polypodiaceæ (p. 362). He compares the Gleicheniaceous antheridium with that of the Hymenophyllaceæ (p. 363), though the archegonia correspond to those of other Ferns. Of the Schizæaceæ he shows that *Lygodium* has antheridia of the Cyatheaceous type, with lid-like cap-cell, while those of *Mohria* and *Aneimia* correspond to the Polypodiaceous type. In this detail *Lygodium* is nearer to other Ferns with an oblique annulus than are *Mohria* and *Aneimia*; but these genera not only have smaller spore-output than *Lygodium*, but also differ more in their anatomy from such a genus as *Gleichenia* than does *Lygodium*.

* 'Annals of Botany,' vol. 1, p. 291.

† KLEBS, 'Biol. Centralblatt,' 1893, p. 649; GOEBEL, 'Sitz. Ber. d. Akad. Wiss. zu München,' 1896, p. 447.

‡ 'Flora,' 1896, p. 329, &c.

Thus, in giving to *Mohria* and *Aneimia* a more independent position, spore-numbers, anatomy, and antheridial characters run parallel.

The outcome of HEIM'S comparison of Antheridia, together with other details of the prothallus, is to show that, with the exception of *Mohria* and *Aneimia*,* all Ferns with oblique annulus fall into his type A, all those with vertical or approximately vertical annulus conform to his type B. This is a most important fact as regards systematic arrangement, whatever our views may be as to the origin of a correspondence in characters so little related to one another as the position of the annulus and the structure and dehiscence of the antheridium. We see that a comparison of features selected by an independent author as the most constant of the Gametophyte leads to a grouping substantially similar to that at which we have arrived by comparison of the sorus and sporangia, for the Simplicēs and Gradatæ fall into type A, and the Mixtæ into type B.

Our division of the Ferns on the basis of sporangium and sorus will thus stand the test of collateral comparisons on other grounds, these even lead to a measure of direct support. I therefore definitely propose that the order Filices should be divided into three sub-orders :—

SIMPLICES.

GRADATÆ.

MIXTÆ.

The relation of these to the Leptosporangiatæ and Eusporangiatæ will be made clear by the following table, which places the main families of Ferns in linear sequence; it is hardly necessary to remark that this is merely a concession to convenience.

* I am not aware that observations have yet been made on the prothalli of *Plagiogyria*; it would be a matter of interest to see how the case stands with them, as also with *Dennstedtia*, *Microlepia*, and *Davallia*; also with *Woodsia* and *Hypoderris*, which, as we have seen, stand on the border line of the series with oblique annulus and basipetal sequence.

FILICES.

ISOSPOREÆ.

SIMPLICES . . .	{	Marattiaceæ Osmundaceæ Schizæaceæ Gleicheniaceæ Matonineæ	}	EUSPORANGIATE
GRADATÆ . . .	{	Loxsomaceæ Hymenophyllaceæ Cyatheaceæ Dicksoniæ (excl. <i>Patania</i> , <i>Woodsia</i> , <i>Hypoderris</i> , and <i>Deparia</i>) Dennstædtiæ	}	LEPTOSPORANGIATE
MIXTÆ . . .	{	Davalliæ (excl. <i>Microlepia</i>) Lindsayæ Pterideæ and other Polypodiaceæ, together with <i>Woodsia</i> , <i>Hypoderris</i> , and <i>Deparia</i>	}	

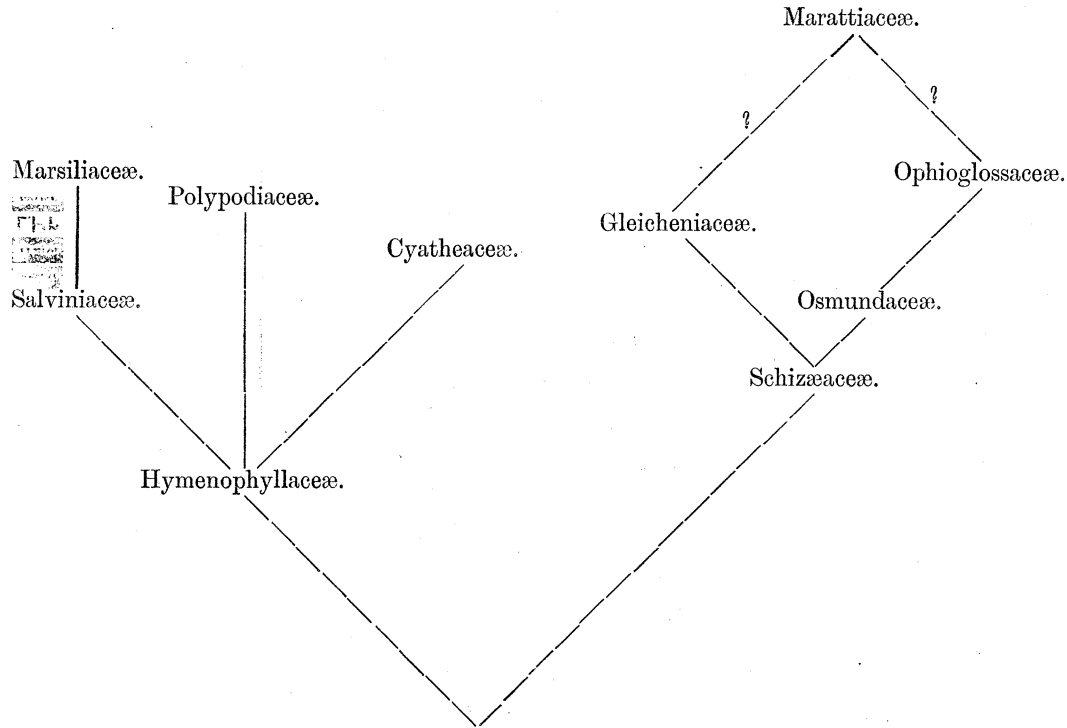
There is no need to drop the terms Eusporangiate and Leptosporangiate, but I think they should be kept as descriptive words rather than as designating systematic divisions. The difference of mode of origin implied by them marks no important biological feature, whereas the distinction between Simplicēs, Gradatæ, and Mixtæ rests on facts of far-reaching biological significance in the production of spores, and at the same time commends itself as conveying definite morphological conceptions; it is true intermediate steps may be found, especially between Gradatæ and Mixtæ, but such transitions are inevitable in classifications where numerous allied genera and species are involved.

PRANTL'S divisions of Leptosporangiatæ into Polyangia, Oligangia, and Monangia do not commend themselves as either definite or useful. They touch the central idea of number of sporangia, but that idea seems to me to be more fully embodied in the divisions which I propose.

Probably no one would now uphold the exact converse of the views put forward above, and contend that the Mixtæ were the source from which the Gradatæ and ultimately the Simplicēs sprang; the Palæophytological record,* as well as compara-

* I hope that Mr. SEWARD will shortly write a statement showing how far the view here set forth will accord with the facts of Palæontology; and with the prospect of this being done by one having more

tive considerations, would prevent this. But a middle position has been definitely stated by PRANTL,* and illustrated by a graphic figure, thus :—



PRANTL (*loc. cit.*, p. 9) regarded the Hymenophyllaceæ as the starting-point of his Pteridales, while the Schizæaceæ were recognised as representing the progenitors of his Osmundales. He admitted that we know nothing of the hypothetical common stock from which the Hymenophyllaceæ and Schizæaceæ sprang, but he suggested that perhaps Palæophytology may supply the blank. Those who have followed me through the above pages will see that the line of separation between the two arms of the Filices thus distinguished by PRANTL coincides with the limit between our Simplices and Gradatæ, for his Osmundales include all our Simplices, together with the Ophioglossaceæ. Across the barrier between the Pteridales and Osmundales PRANTL recognised no direct transition, but merely traced them from a common hypothetical ancestry.

It is true that we have not demonstrated that there has been a transition from any of our Simplices to any type with a basipetal sorus. Though wide-spread similarities

special knowledge of that branch of the science than myself, I have not attempted to take up this side of the evidence. I shall only quote one opinion, that of RACIBORSKI ('ENGLER'S Jahrb.,' 1891, p. 1), as bearing on our question. He writes: "While at present the Polypodiaceæ form the majority of Fern species, in the Jurassic formation the Osmundaceæ and Cyatheaceæ with allied families (Matonieæ, Protopolypodiaceæ) are almost as much in the foreground as the Marattiaceæ in the Carboniferous Period."

* 'Arb. Königl. Bot. Garten zu Breslau,' 1892.

do exist in the characters of the sporophyte between Ferns on opposite sides of the barrier, they do not focus definitely upon any two genera sufficiently to demonstrate a community by descent. But to these similarities, widespread though they are, must be added the comparisons of the Gametophyte advanced by HEIM, and the facts of Palæophytology; the former establish with increased strength the affinity of the Gradatæ to the Gleicheniaceæ and Osmundaceæ, while the fossil evidence will hardly allow the Marattiaceæ to be regarded in any other light than as relatively primitive Ferns. And when, in addition to these considerations, we contemplate the physiological probability of an advance from the simultaneous to the successive sorus, as a mode of spreading the physiological drain over a longer period, a strong case appears to me to be made out in favour of a transition having taken place in the course of descent from some types of Simplices to the Gradatæ, as against the suggestion of PRANTL that they represent two distinct evolutionary branches.

In conclusion, I may point out that the views put forward in this memoir will harmonise in many features with the arrangement in the 'Synopsis Filicum.' Doubtless the system of Sir WM. HOOKER is in many ways open to amendment, not only in details, but even in some of its general features. GEBEL has recently established a case for detailed amendment in *Hecistopteris*,* a nearer examination of both generations showing that it is not a *Gymnogramme*, but that it belongs to the Vittarieæ. The chief amendment in general arrangement of that of the 'Synopsis Filicum' (if this is intended to show natural affinities by descent) will be to change the grouping of some of the sub-orders. The Schizæaceæ, Osmundaceæ, and Marattiaceæ, which are at the end of the book, would in any natural system have to be placed at the beginning, in close relation to the Gleicheniaceæ. But however clearly we may now see the need for amendments such as these, still we shall do well to recognise the naturalness of many of the features of the classification, rather than to denounce the whole system as thoroughly artificial.† Examples may be quoted showing how the arrangement of the 'Synopsis' will stand the test of more extended observation; in grouping the species of *Gleichenia*, the species *Gl. dichotoma*, which has the smallest sporangia, and a low spore-output, but the most numerous sporangia, arranged almost like an *Alsophila*, is placed last of the genus, and nearest to the Ferns which constitute our Gradatæ. The three sequences of Cyatheaceæ, Dicksonieæ, and Hymenophyllaceæ follow; and (though some of their genera will have to be re-arranged, e.g. *Woodsia* and *Hypoderris*) these sequences with their basipetal sori, and oblique annulus, all have in our present view a position as derivative series from the Simplices; it appears immaterial in what order they follow

* *Hecistopteris pumila*, J. SM. = *Gymnogramme pumila*, SPREUG, 'Flora,' 1896, p. 67.

† GEBEL ('Flora,' 1896, p. 75), in his paper on *Hecistopteris*, writes as follows: "Es ist dies ein weiteres Beispiel dafür, dass die systematische Gruppierung der Leptosporangiaten Farne, wie sie derzeit z. B. in der 'Synopsis Filicum' vorliegt, eine durchaus künstliche ist, die zwar gestattet Farne zu bestimmen, aber über die Stammesverwandtschaft der einzelnen Formen keinen zuverlässigen Aufschluss giebt."

after *Gleichenia*, though probably the Hymenophyllaceæ are really the nearest. Taking now the special case of the Hymenophyllaceæ (which in the 'Synopsis' includes *Loxsoma*), our results indicate that in certain features *Loxsoma* is isolated, and nearer to the Simplices than *Hymenophyllum*, and that *Trichomanes* is a more specialised genus than the latter; accordingly, in our view, the natural order of these as following from the Simplices, would be precisely that given in the 'Synopsis.' Then follows in the 'Synopsis' the old comprehensive genus *Davallia*, which thus occupies an intermediate position between the Ferns with basipetal sori and the Pterideæ in which the sori are mixed; that is the position which our comparison also assigns to it. We assent to the separation of *Dennstædtia* from *Dicksonia*, and of *Microlepia* from *Davallia*, and the construction from them of PRANTL'S family of the Dennstædtiinae, which takes its place with the Gradatæ. From these onwards to *Davallia*, and then to *Cystopteris* and *Lindsaya*, and finally to the Pterideæ seems to be a natural sequence, involving a transition from the Gradatæ to the Mixtæ, together with changes in the position of the sorus, and of the indusium; but this again is the order of their arrangement in the 'Synopsis.'

These examples will suffice to show that the arrangement in the 'Synopsis Filicum' is not simply an artificial system. It coincides in important features with the results of later detailed investigations, carried out with a view to tracing relationship by descent rather than systematic convenience. Thus while engaging in the discussion of the problems of evolution of Ferns, I have at the same time had cause to recognise the results of that perspicacity which belongs to the great systematists. For I have been able by observation of details which Sir WM. HOOKER cannot have foreseen, to support at certain points, though not throughout, the classification which he adopted; and this has given me all the more pleasure, since this great Pteridologist once occupied the Chair of Botany in the University of Glasgow, and much of his work on the Ferns was done while he held that office.

It is a pleasant duty to acknowledge the kindness of many friends in the supply of material, often rare, without which this work would have been impossible. My thanks are specially due to the Director of the Royal Gardens, Kew, for liberal supplies from that historic collection; also to the Keeper of the Botanical Collections of the British Museum; Professor BAYLEY BALFOUR; Dr. M. TREUB; Mr. SEWARD; and many others, at home and abroad.

DESCRIPTION OF FIGURES.

PLATE 2.

Gleichenia. Figs. 1-31.

- Fig. 1, *a-e*. Sori of *Gl. dichotoma*, WILLD, showing arrangement of the sporangia of the upper tier, varying in number from one to four. ($\times 20$.)
- Fig. 2, *a-c*. Fissions of sori in *Gl. dichotoma*. ($\times 20$.)
- Fig. 3. Sporangium of *Gl. circinata*, SW., viewed from the side. ($\times 75$.)
- Fig. 4. Sporangium of *Gl. circinata*, viewed from the distal end; (*x*) shows the line of the dehiscence. ($\times 75$.)
- Fig. 5. Sporangium of the *Gl. circinata*, viewed from the proximal end, showing insertion of the stalk. ($\times 75$.)
- Fig. 6. Sporangium of *Gl. dichotoma*, viewed from the side. ($\times 75$.)
- Fig. 7. Ditto, presenting its peripheral face. ($\times 75$.)
- Fig. 8. Ditto, presenting its central face. ($\times 75$.)
- Fig. 9. Transverse sections of stalks of two sporangia of *Gl. dichotoma*. ($\times 75$.)
- Fig. 10. Transverse section of pinnule of *Gl. flabellata*, BR., showing origin of sorus as a smooth swelling. ($\times 300$.)
- Fig. 11. Similar section of an older sorus of *Gl. flabellata*; showing two young sporangia (*x, x*). ($\times 300$.)
- Fig. 12. View of a similar sorus from above, showing four sporangia. ($\times 300$.)
- Fig. 13. View of a similar sorus with three sporangia. ($\times 300$.)
- Fig. 14. Vertical section of a sorus slightly older, showing cap-cells, and irregular segmentation of deeply sunk sporangia. ($\times 300$.)
- Fig. 15. Vertical section of sorus in *Gl. dichotoma*, showing the less deeply sunk sporangia, with regular segmentation of the stalk. ($\times 300$.)
- Fig. 16. Sorus of *Gl. dichotoma* in vertical section, showing two lateral and one median sporangium. (Compare fig. 1*b*.) ($\times 300$.)
- Fig. 17. Ditto, with sporangia less regularly disposed. ($\times 300$.)
- Figs. 18, 19. Older states of sporangia of the type of *Gl. circinata*. ($\times 300$.)
- Fig. 20. Older state of the same, with tapetum and archesporial cell, longitudinal section. ($\times 300$.)
- Fig. 21. Ditto, transverse. ($\times 300$.)
- Fig. 22. Vertical section of sorus, showing receptacle with tracheides (*tr.*), and a single sporangium with tapetum divided. ($\times 300$.)
- Fig. 23. Sporangium of *Gl. flabellata*, cut parallel to the leaf-surface; the whole sporangium has enlarged greatly, and especially the inner tapetum, which surrounds the sporogenous group. *a, a*, cells of the annulus. ($\times 150$.)

- Fig. 24. Vertical section of sporangium of *Gl. flabellata*, showing further enlargement, with sporogenous group divided up so as to show 46 spore-mother-cells in the single section. ($\times 150$.)
- Fig. 25. Horizontal sections of two similar sporangia of *Gl. flabellata*, showing respectively 66 and 42 spore-mother-cells cut through. (x, x) show the position of dehiscence. ($\times 150$.)
- Fig. 26. Spore-mother-cells of *Gl. flabellata* separated and rounded off, showing nuclei (n) of the tapetum making their way inwards. ($\times 300$.)

PLATE 3.

- Figs. 27, 28. Sporogenous groups from sporangia of *Gl. dichotoma* before rounding off, with respectively 25 and 26 spore-mother-cells. ($\times 300$.)
- Figs. 29, 30. Similar groups after rounding off, with respectively 32 and 40 spore-mother-cells in section, though some lie out of the exact plane. ($\times 300$.)
- Fig. 31. Syngangium of *Gl. flabellata* in section. ($\times 150$.)

Osmundaceæ. Figs. 32-51.

- Fig. 32. *Todea barbara*, MOORE, section of pinnule showing two young sporangia (x). ($\times 300$.)
- Figs. 33-36 and 39. Ditto, showing variety of segmentation. ($\times 300$.)
- Figs. 37, 38, 40. Ditto, cut transversely. ($\times 300$.)
- Figs. 41-45. Ditto, cut longitudinally, showing further variations. ($\times 300$.)
- Figs. 46-47. Ditto, showing typical sporangia of medium age, cut transversely and longitudinally. ($\times 300$.)
- Figs. 48-50. Transverse sections of sporangial stalks, showing variation of type. ($\times 300$.)
- Fig. 51. *Osmunda regalis*, L. A syngangium cut longitudinally. ($\times 300$.)
- Fig. 52. *Mohria caffrorum*, DESV., section showing 16 rounded spore-mother-cells in a single plane. ($\times 150$.)

Matonia pectinata, BR. Figs. 53-62.

- Fig. 53. Transverse section through pinnule, showing a young sorus. ($\times 300$.)
- Fig. 54. Sorus older, showing indusium (i), and young sporangium (s). ($\times 300$.)
- Fig. 55. Ditto, more advanced. ($\times 300$.)
- Fig. 56. Sporangium with cap-cell. a = acroscopic, b = basiscopie side. ($\times 300$.)
- Fig. 57. Sporangium with tapetum doubled. ($\times 300$.)

PLATE 4.

- Fig. 58. Section of sporangium parallel to the leaf-surface, showing double tapetum. ($\times 300$.) The arrow points to the centre of the sorus.
- Fig. 59. Mature sporangium of *Matonia*, view of proximal end, showing the attachment of the stalk and the incomplete annulus. *c* = central; *p* = peripheral side. ($\times 75$.)
- Fig. 60. Two mature sporangia in natural juxtaposition, seen from the indusial side, showing irregular position of the annulus; the arrow points to the centre of the sorus. ($\times 75$.)
- Fig. 61. Lateral view of a mature sporangium, showing the position of the incomplete annulus. *s* = stalk. ($\times 75$.)
- Fig. 62. View of a mature sporangium from the basisopic side, showing the incomplete annulus and dehiscence (*x*). ($\times 75$.)

Loxsona Cunninghamsi, BR. Figs. 63-73.

- Fig. 63. Sorus of *Loxsona*, of medium age, in longitudinal section *i.* = indusium; *tr.* = tracheides at the end of the vascular bundle. ($\times 35$.)
- Fig. 64. Ditto, older, showing the sporangia (*s.*) borne up on the elongated pseudopodium (*ps.*). ($\times 35$.)
- Fig. 65. Mature sporangium of *Loxsona*, seen in lateral view, showing the incompletely indurated annulus. ($\times 75$.)
- Fig. 66. Ditto, seen from the peripheral side, showing the continuous but incompletely indurated annulus and the distal point of dehiscence (*x*). ($\times 35$.)
- Fig. 67. Attachment of stalk to the base of the sporangium. ($\times 150$.)
- Fig. 68. Vertical section through the base of the receptacle (*r.*), showing the indusium (*i.*) and one young sporangium (*s.*). ($\times 300$.)
- Fig. 69. Ditto, showing two sporangia, one merely a deeply-sunk mother-cell with square base, the other with the cap-cell already cut off. ($\times 300$.)
- Fig. 70. Ditto, showing a sporangium before the cap-cell is cut off. ($\times 300$.)
- Fig. 71. Sporangium, with tapetum as a single layer, in longitudinal section. ($\times 300$.)
- Fig. 72. Ditto, cut transversely. ($\times 300$.)
- Fig. 73. Sporangium, with double tapetum, before rounding off spore-mother-cells. ($\times 300$.)

Cyathea. Figs. 74-84.

- Fig. 74. Old sori of *Cyathea Brunonis*, WALL, after the sporangia are shed, with indusium and receptacle persistent, showing various stages of fission of the sorus; enlarged.

- Fig. 75. Similar conditions in *Hemitelia grandifolia*, SPR.
 Fig. 76. Young sorus of *Cyathea dealbata*, SW., before the sporangia make their appearance. ($\times 300$.)
 Fig. 77. Ditto, older, with the first sporangia (*s.*). ($\times 300$.)
 Fig. 78. Ditto, showing basipetal sequence. ($\times 300$.)
 Fig. 79. Ditto, apical part of the receptacle with sporangia (*sp.*) and hairs (*h.*). ($\times 300$.)
 Fig. 80. A single sporangium with cap-cell already divided. ($\times 300$.)
 Fig. 81. Ditto, older, with double tapetum, and annulus (*a*) already distinguishable. ($\times 300$.)

PLATE 5.

- Fig. 82. Sorus of *Cyathea dealbata*, more advanced, showing basipetal succession, the somewhat irregular orientation, and the small number of the spore-mother-cells. ($\times 150$.)
 Figs. 83, 84. Young sporangia of *Cyathea dealbata*. Fig. 83 presenting the peripheral, fig. 84 the central face. ($\times 300$.)
 Figs. 85, 86. Mature sporangia of *Hemitelia capensis*, BR. Fig. 85 seen laterally, fig. 86 presenting the peripheral face. ($\times 75$.)
 Fig. 87. Vertical section through the sorus of *Alsophila atrovirens*, PRESL., showing slight trace of basipetal succession. ($\times 300$.)
 Figs. 88, 89. Sporangia of *Alsophila excelsa*, BR., seen laterally (fig. 88), and presenting the central face (fig. 89). ($\times 75$.) Fig. 89, *b*, shows a transverse section of the sporangial stalk. ($\times 75$.)
 Fig. 90. *Onoclea sensibilis*, L. Sorus in vertical section, showing basipetal succession. ($\times 300$.)
 Fig. 91. Preparation of sporangia of *Onoclea germanica*, W., showing that the annulus is completely interrupted at the insertion of the stalk. (*a*) is a vertical section through insertion of the stalk, (*b*) is a vertical section at right angles to (*a*), and (*c*) is the view of the three-rowed stalk from below. ($\times 150$.)
 Fig. 92. Mature sporangium of *Sphaeropteris barbata*, WALL. ($\times 75$.)
 Fig. 93. Mature sporangium of *Diacalpe aspidioides*, BL. ($\times 75$.)

Hymenophyllaceæ. Figs. 94-102.

- Fig. 94. *Hymenophyllum Wilsoni*, HK. Sorus in vertical section, showing the receptacle with divisions indicating intercalary growth, and the first sporangia (*s.*) originating near the apex. ($\times 150$.)
 Figs. 95, 96, 97, 98. Sporangia of *Hymenophyllum dilatatum*, SWARTZ, seen respec-

tively from the two sides (figs. 95, 96) and from the central (fig. 97) and peripheral (fig. 98) faces. ($\times 75$.)

Figs. 99, 100, 101, 102. Similar figures, to the same scale, of *Trichomanes radicans*, SWARTZ. Figs. 99 and 100 are the lateral views, fig. 101 shows the central, and fig. 102 the peripheral faces. ($\times 75$.)

Thyrsopteris elegans, KZE. Figs. 103-115.

Fig. 103. Transverse section through the young sorus, showing the two-lipped indusium (*i.*, *i.*) and receptacle (*r.*). ($\times 300$.)

Fig. 104. Transverse section through the receptacle, showing its usual elliptical form. ($\times 300$.)

Fig. 105. Longitudinal section of a sorus of *Thyrsopteris*, showing the indusium (*i.*, *i.*) and first formation of sporangia on the apex of the receptacle, in basipetal succession. ($\times 300$.)

PLATE 6.

Fig. 106. Section of sorus of *Thyrsopteris* parallel to the surface of the leaf. ($\times 300$.)

Fig. 107. Two young sporangia. ($\times 300$.)

Figs. 108, 111, 113. Sporangia cut longitudinally. ($\times 300$.)

Figs. 109, 110. Transverse sections of sporangial stalks. ($\times 300$.)

Fig. 112. Transverse section through the wall of a young sporangium. ($\times 300$.)

Figs. 114, 115. Drawings of sporangia, showing respectively the central and peripheral faces. ($\times 75$.)

Dicksonia. Figs. 116-125.

Fig. 116. Vertical section through a young sorus of *Dicksonia schiedei*, BAKER. ($\times 300$.)

Fig. 117. Transverse section through the margin of a very young receptacle. ($\times 300$.) Compare line *x*, *x* in fig. 116.

Fig. 118. A similar section lower down, with the two-lipped indusium (*ind.*). ($\times 300$.) Compare line *y*, *y* in fig. 116.

Fig. 119. A section along a line indicated as *z*, *z* in fig. 116. ($\times 300$.)

Fig. 120. Part of a similar section, but rather more advanced. ($\times 300$.)

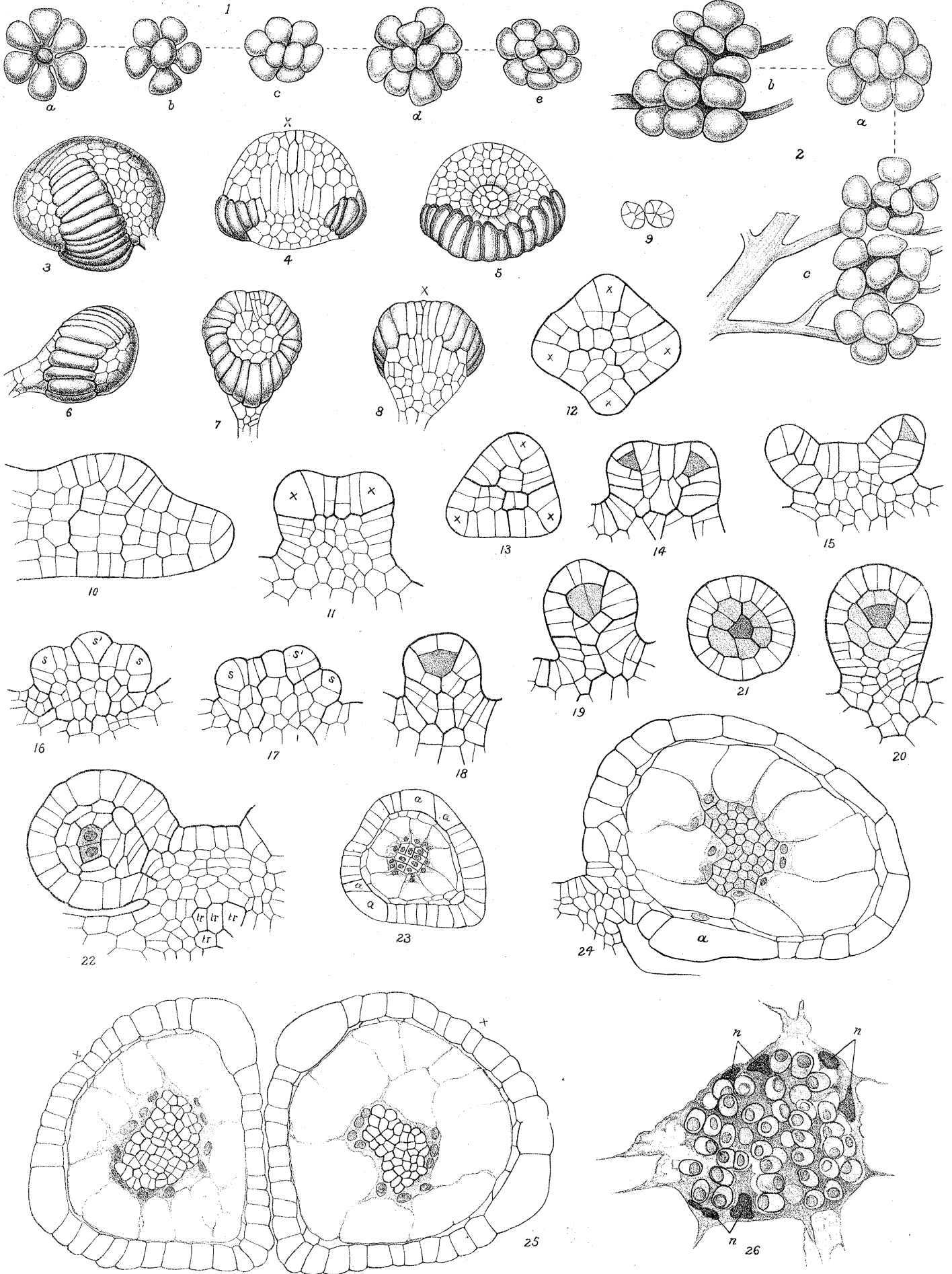
Fig. 121. Transverse sections through sporangial stalks of *Dick. culcita*. ($\times 150$.)

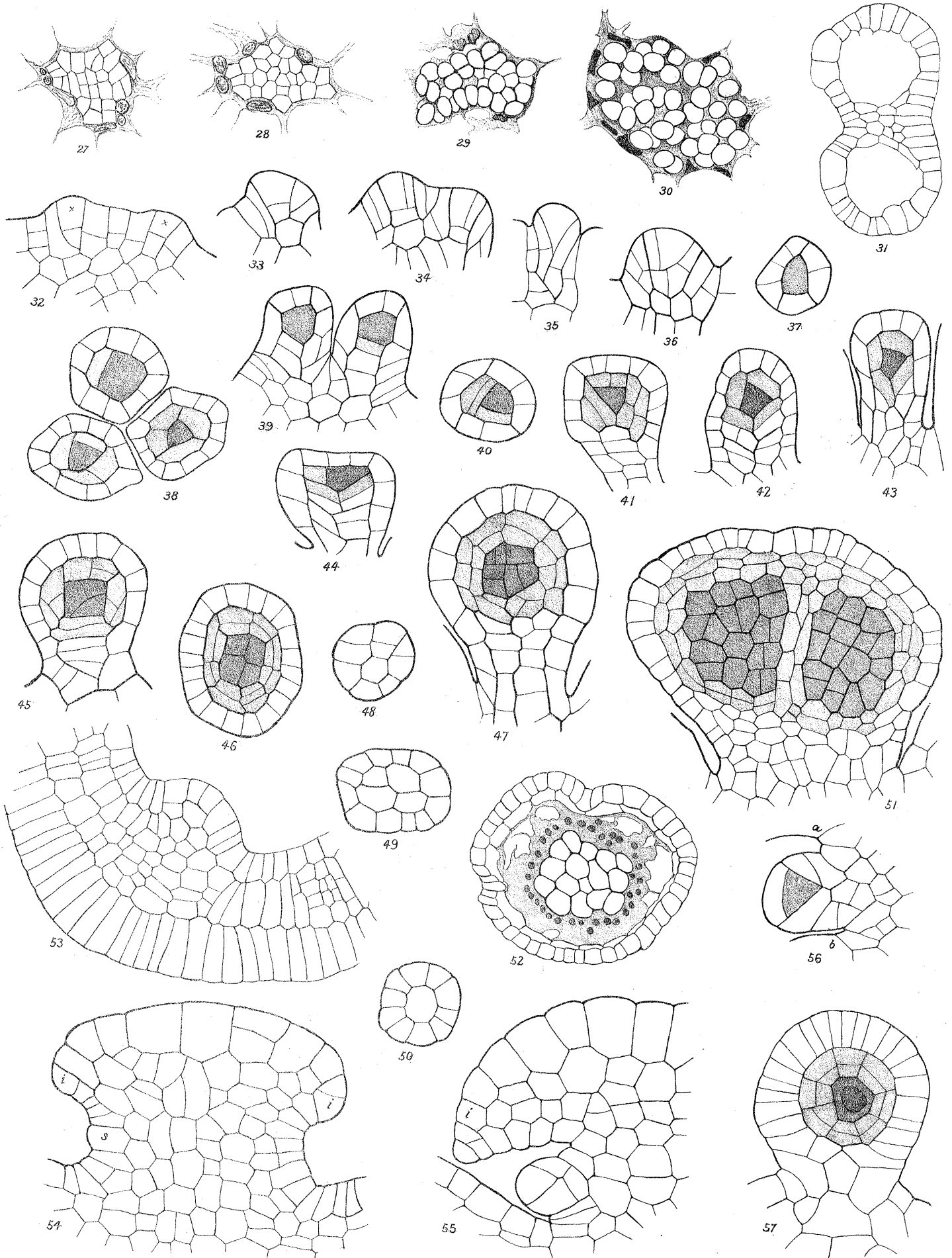
Figs. 122, 123, 124, 125. Drawings of sporangia of *Dicksonia Menziesii*, HOOK and BAKER, showing respectively the peripheral face (fig. 122), the central face (fig. 123), and two lateral views (figs. 124, 125). ($\times 75$.)

- Fig. 126. *Microlepidia spelunca*, BAKER. Sorus cut longitudinally, showing unequal lips of the indusium, and basipetal succession of sporangia. ($\times 150$.)
- Fig. 127. *Microlepidia hirta*, KAULF. Part of a similar section, showing a departure from the strict basipetal succession. ($\times 150$.)

PLATE 7.

- Fig. 128. *Microlepidia hirta*, KAULF. Longitudinal section of sorus, showing in the diameter basipetal succession, but with one sporangium out of proper order. ($\times 150$.)
- Fig. 129. Sorus of *Dennstaedtia apiifolia*, Hook., showing basipetal succession, but with one central sporangium of small size. ($\times 35$.)
- Fig. 130. Sorus of *Denn. apiifolia*, showing regular basipetal succession throughout ($\times 150$.)
- Fig. 131. *Denn. apiifolia*. Sporangium mature, showing very slightly oblique annulus. ($\times 150$.)
- Fig. 132. *Denn. rubiginosa*, KAULF. Sorus in vertical section, showing that it has been at first basipetal, but with a mixed character supervening. ($\times 150$.)
- Fig. 133. *Denn. rubiginosa*. View of dehiscent sporangium from its base, showing that the annulus stops short on either side of the insertion of the stalk (*st.*). ($\times 150$.)
- Fig. 134. *Dav. Griffithiana*, Hk. Young sorus in vertical section, showing first formation of sporangia. ($\times 150$.)
- Fig. 135. *Dav. Griffithiana*. Old sorus, showing the mixed condition. ($\times 150$.)
- Fig. 136. *Deparia Morei*, Hk. Mature sporangium. ($\times 75$.)
- Fig. 137. *Pteris aquilina*, L. ($\times 300$.) Contents of sporangium, showing five spore-mother-cells rounded off, and developing normally, but one at the centre undergoing disorganisation.
- Fig. 138. Ditto, showing two of the spore-mother-cells undergoing disorganisation. ($\times 300$.)
- Figs. 139, 140, 141, 142. Drawings of mature sporangia of *Plagiogyria (Lomaria) euphlebia*, KUNZE. ($\times 75$.) Fig. 139 represents the "peripheral," fig. 140 the "central" face, figs. 141 and 142 show the lateral views.
- Figs. 143, 144, 145 show contents of sporangia of *Platyserium Willinkii*, with spore-mother-cells developing in various abnormal ways. ($\times 300$.)
- Fig. 146, *a-d*. Various examples of fission of the sorus in *Hymenophyllum dilatatum*. The sporangium and one flap of the indusium have been removed, leaving the receptacle exposed. (\times about 5.)

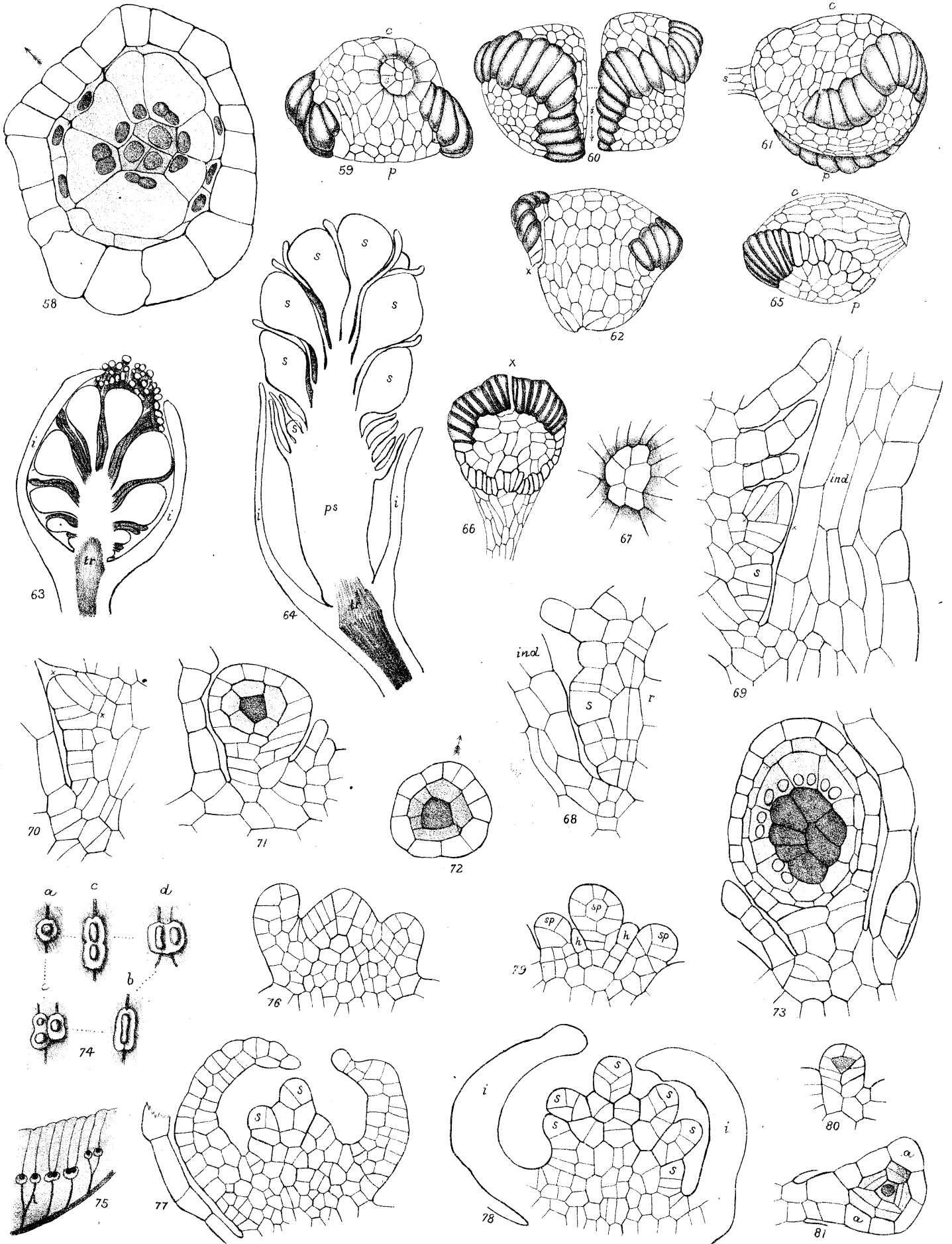




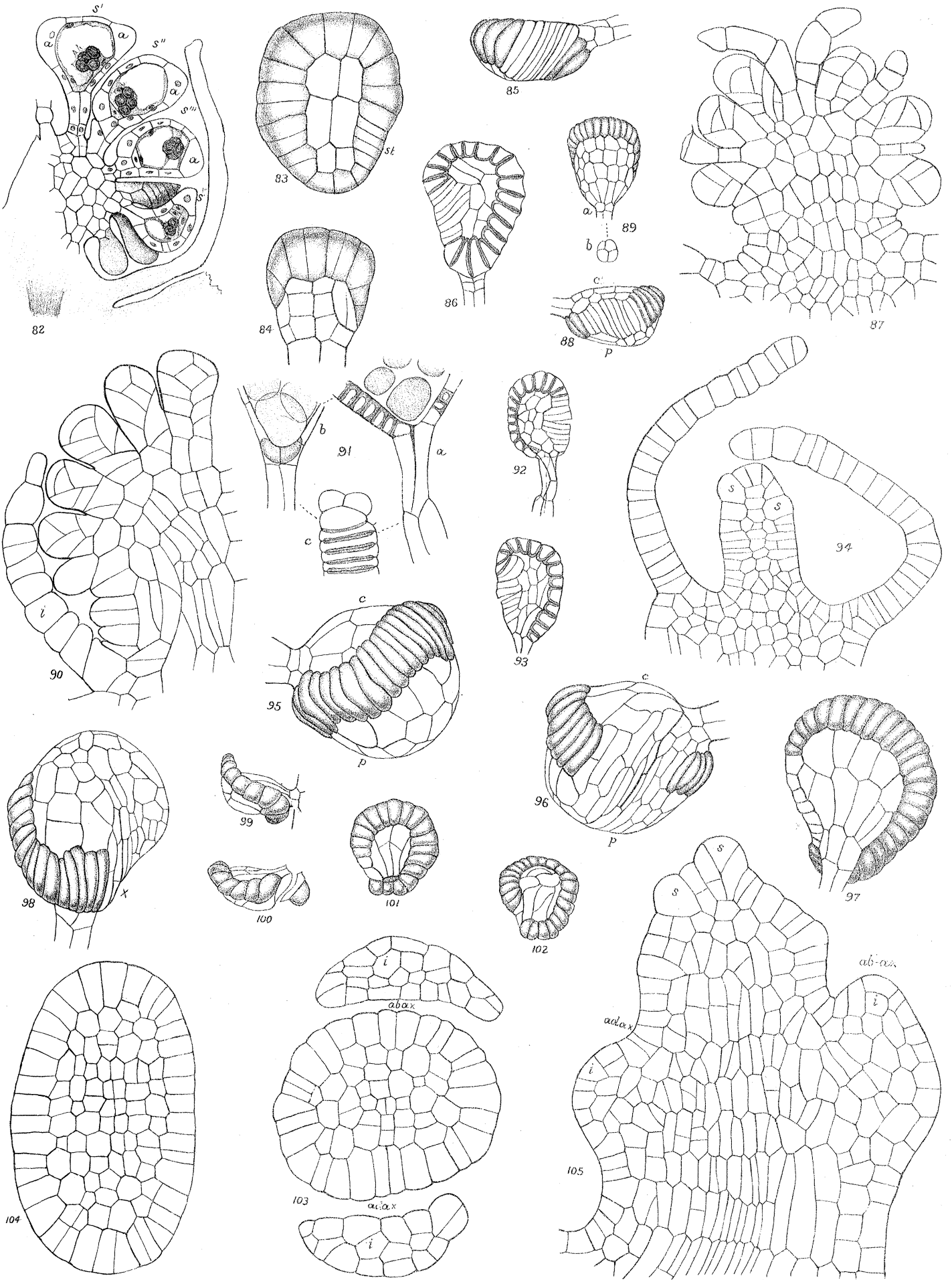
F.O.Bower del.

P.Highley del.

Figs 27-31. GLEICHENIA. Figs 32-50. TODEA.
 » 51. OSMUNDA. » 52. MOHRIA.
 Figs 53-57. MATONIA.



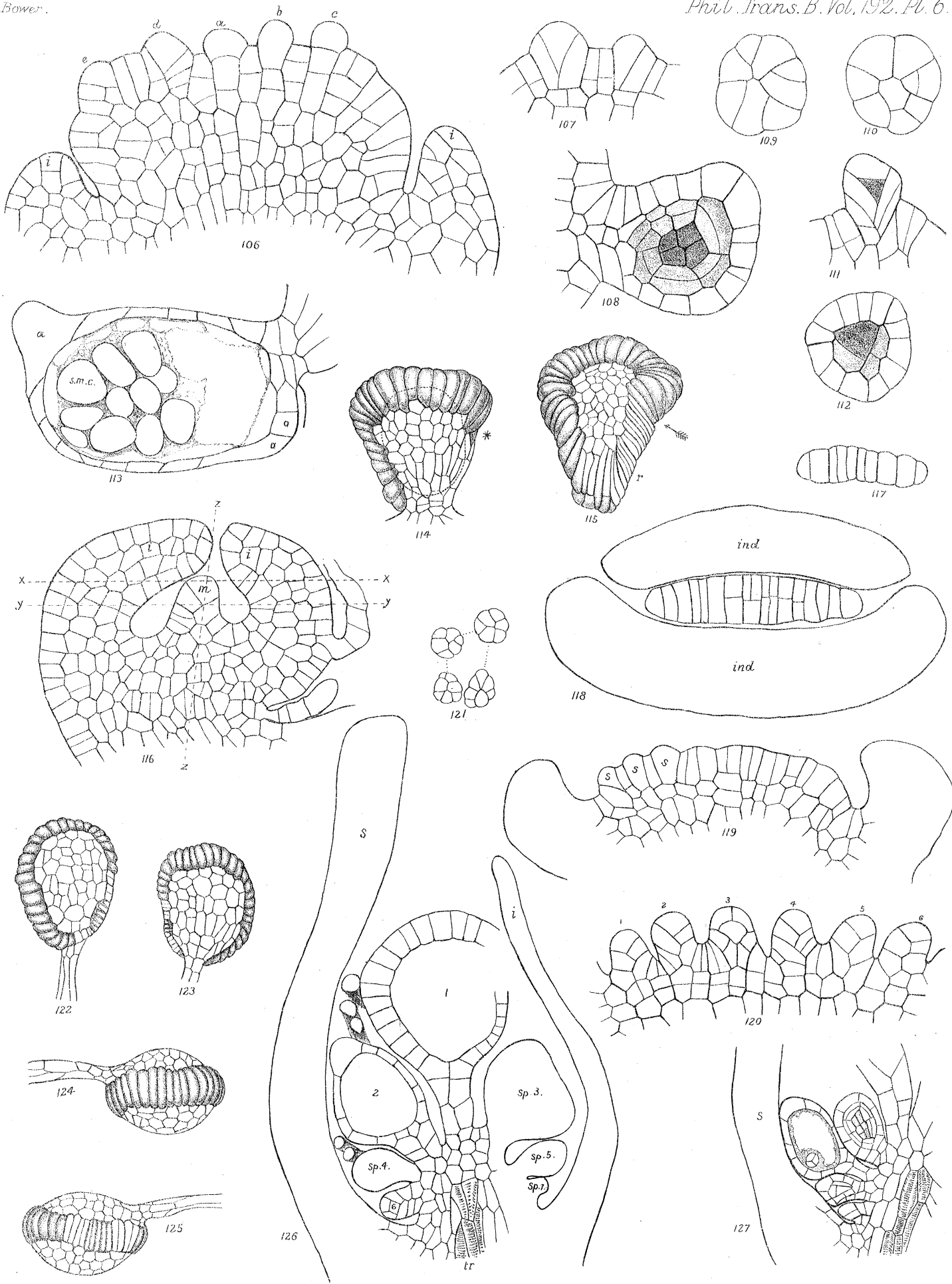
Figs. 58-62. MATONIA . Figs. 63-73. LOXSOMA .
Figs 74-81. CYATHEA .



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P. Highley lith.

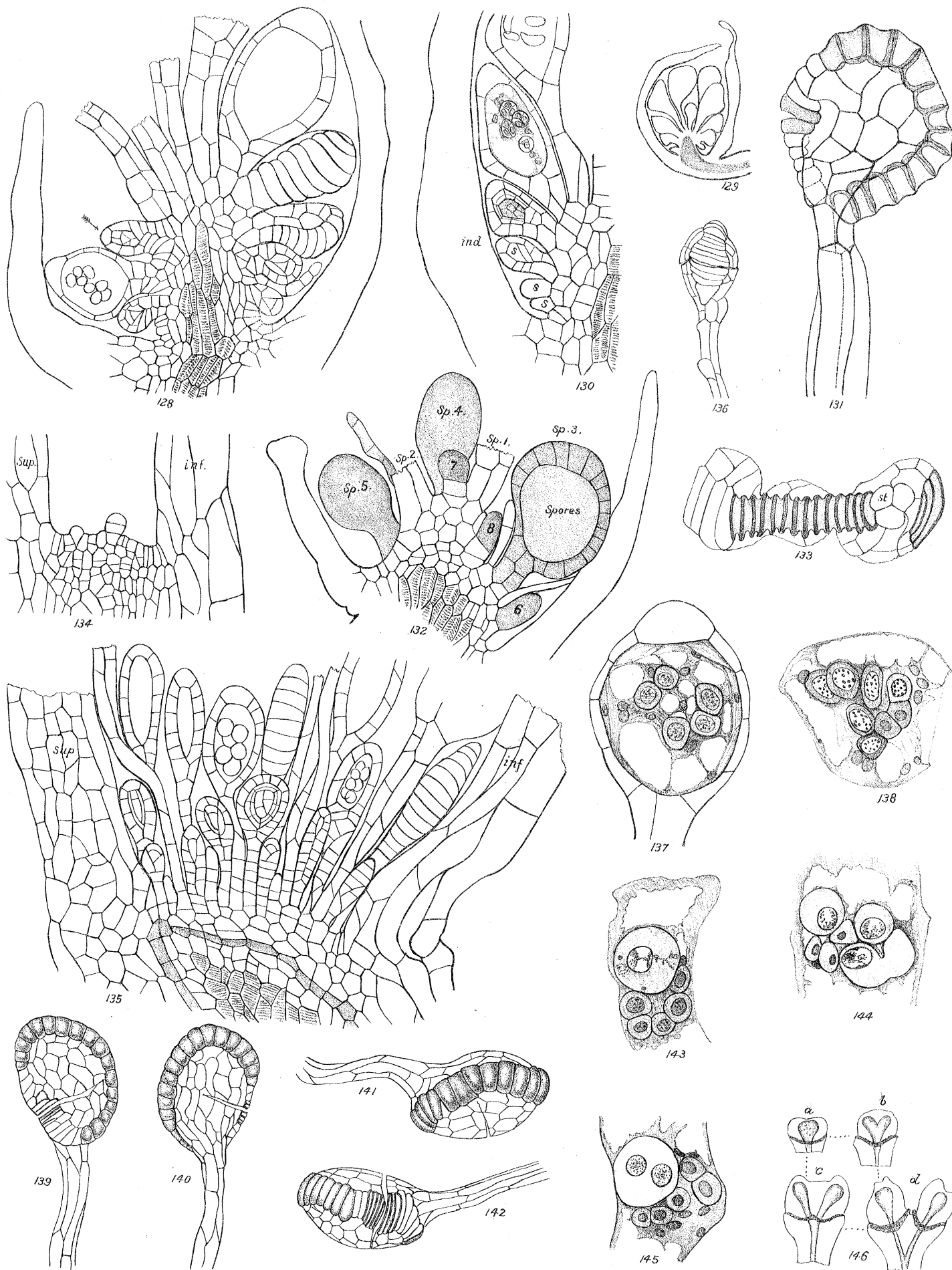
Figs 82-84. CYATHEA. Figs 90-91, ONOCLEA. Figs 94-98. HYMENOPHYLLUM. .
 » 85-86. HEMITELIA. » 92. SPHÆROPTERIS. » 99-102. TRICHOMANES.
 » 87-89. ALSOPHILA. » 93. DIACALPE. » 103-105. THYRSOPTERIS.



Bower del.

Figs. 106-115. THYRSOPTERIS. Figs. 116-125. DICKSONIA. Figs. 126-127. MICROLEPIA.

P. Highley lith.



Bower del.

Figs. 128. MICROLEPIA .

» 129-133. DENNSTAEDTIA .

» 134-135. DAVALLIA .

Figs. 136. DEPARIA .

» 137-138. PTERIS .

» 139-142. PLAGIOGYRIA .

Figs. 143-145. PLATYCIERIUM .

» 146. HYMENOPHYLLUM .

P. Highley lith.