Studies in the Phylogeny of the Filicales.

II. Lophosoria, and its Relation to the Cyatheoideae and other Ferns.

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With Plates XXX-XXXVI.

I N my 'Studies in the Morphology of Spore-producing Members, No. IV. Leptosporangiate Ferns' ('Phil. Trans.', 1899, vol. cxcii, p. 122), the distinction was drawn according to the mode of development of their sori between the Ferns designated as the Simplices, the Gradatae, and the Mixtae. These were held to illustrate three steps in the evolution of the sorus. It was specifically stated that there was no intention to assert that the living Ferns of any one of these categories were the actual ancestors of those of any other. Nor was it suggested that the progression was by any single line of descent. Parallel development along a multiplicity of lines was distinctly contemplated, involving in any one of them progressions from the Simple to the Gradate, or from the Gradate to the Mixed state. It was even held as possible that a progression might have been effected directly from the Simple to the Mixed state (l. c., p. 124), a transition which has since been demonstrated to have occurred within the genus *Dipteris* (Miss Armour, 'New Phytologist,' 1907, p. 238), and it is highly probable that it has occurred also in the descent of *Plagiogyria* ('Annals of Botany', vol. xxiv, p. 438).

Perhaps the most obvious suggestion of transition from the Simple to the Gradate sorus that could be made is that from some *Gleicheniaceae* type to the *Cyatheaceae*. Already in 1899 it was pointed out (l. c., p. 123) that '*Gleichenia dichotoma* has a naked sorus' differing 'little in general construction from that of *Alsophila atrovirens*'. This case was not quoted then as indicating a true line of descent, but as an illustration how near one type may be to another in point of arrangement within the sorus. The widening of the basis of comparison, especially in respect of the vascular anatomy, led in 1908 to a more explicit statement ('Land Flora', p. 610), that 'there seems good reason to see in the *Cyatheaceae* a series having

probable genetic relations with the Gleicheniaceae, but advanced on the one hand to the basipetal succession of the sori, and on the other to a high complexity of the vascular system'.

The degree of closeness of those 'genetic relations' was left undefined, though certain species were indicated as outliers on either side of the gap separating the two families. On the one hand are *Gleichenia linearis*, Clarke (= *dichotoma*, Hk.), and *pectinata*, Pr., distinguished as relatively advanced species, both by their soral and their anatomical characters; on the other hand, *Alsophila quadripinnata*, C. Chr. (= *Lophosoria pruinata*, Pr.), and *A. (Metaxya) blechnoides*, Hk., were indicated as lying anatomically at the base of the Cyatheaceous series. It seems desirable, as material is at hand, and as some further advance has already been made in the anatomy of the more complex Gleichenias, to examine more closely the probable relations of the two families, and to widen as far as possible the basis of the comparisons. For it is only in this way that a dependable conclusion can be arrived at. In discussing such genetic relations in Ferns, soral characters are not sufficient, nor are anatomical data sufficient. Nor should we be satisfied even with a combination of them. To obtain a fully trustworthy result the characters of external form, of the superficial appendages, and of the gametophyte and sexual organs should be also used, together with the details of the ontogeny, while some attempt at seriation of the species within the genera will also assist in giving point to the comparisons. Many phyletic conclusions which are generally accepted fall short of this comprehensive foundation, and it will not be possible in the present case to carry out the programme fully. But it is well at the outset to visualize what is to be aimed at, even though a complete demonstration may not be actually attained at the moment. As the comparisons to be drawn will centralize themselves round the species above named, though with general references from time to time to these and to other genera as a whole, it will be well at the outset to become acquainted with the history, systematic position, and characteristics of them. Often it happens that plants which have a peculiar interest from a comparative point of view have in the past been given diverse systematic places by various authors. This will be seen to have been the case with one at least of the Ferns in question. Such a history at once suggests that the systematist has encountered a synthetic type. In fact the puzzles of the earlier systematists will often provide the opportunities of the phyletic morphologist.

GLEICHENIA.

The two species *Gleichenia linearis*, Clarke (= *Gleichenia (Mertensia) dichotoma*, Hk.), and *Gleichenia (Mertensia) pectinata*, Pr., have long been regarded as outstanding in the genus to which they belong, and recent anatomical observations have accentuated their aloofness from the

rest. But they share the general characteristics of *Gleichenia* so fully that there is no question of their real affinity with it. Both have the creeping rhizome, bearing upon it at intervals leaves which are endowed with the continued apical growth so characteristic of the genus. As in other species, the circinate apex of the leaf rests from active growth at intervals, appearing as a bud dormant between the last developed pinnules, and then resuming again its activity (Goebel, 'Organography,' ii, p. 318). In the disposition and development of the ultimate branchings of the leaf, these species have been recognized by systematists as forming each a separate section of the genus. Their segregation has also been based upon the fact that in the number of sporangia in the sorus they exceed the rest. Of *G. pectinata* Sir Wm. Hooker wrote that 'it is the only species of this section (§ 3), and not to be confounded with any other'; while he further remarked of his § 4, that 'as *G. pectinata* is a solitary species in its section, so is *G. dichotoma* of the present one' ('Syn. Fil.', p. 15).

Branching of the axis may be in *G. pectinata* either dichotomous in a horizontal plane, or monopodial in a vertical plane. Of the former branching Boodle and Hiley remark that 'it appears not to be known to occur in the rhizome of any other species of the genus' ('Ann. of Bot.', 1909, p. 426). It is true that collectors and systematic botanists have commonly neglected to provide evidence of, or to describe such features. But I have specimens of very perfect dichotomy of the axis in *Dicranopteris fulva*, Desv. Underw. (= *Gleichenia pubescens*, H. Bk.), and the same branching exists also in *G. flabellata*. Probably dichotomy of the axis is frequent within the genus. In the leaf, on the other hand, it is stated by Goebel ('Organography', ii, p. 319, footnote) that 'no species in *Gleichenia* has a dichotomous leaf', and these species appear to be no exceptions. Moreover, as Campbell has observed ('Ann. Jard. Bot. Buit.', 2^e série, vol. viii, p. 98), 'the cotyledon in *G. pectinata*, *G. dichotoma*, and *G. laevigata* shows a prolonged apical growth like that found in the adult leaves of the young sporophyte'. He notes (l. c., p. 94) that 'the cotyledon of *Gleichenia*, especially in the section *Mertensia*, differs from that of most Ferns. In the majority of Ferns the cotyledon is fan-shaped, the result of an early dichotomy. In *Gleichenia* the original apex seems to persist.' The complex leaf-forms of the genus are the result of repeated pinnation, modified, but not in any genetic sense altered, by unequal development of the parts, varied distribution of intercalary growth, and periodic arrest of apical activity. In *G. linearis* the unequal development of parts of the leaf makes itself apparent in the specialization of certain pinnules as a protection to the resting apex of the leaf. Goebel points out that these are neither 'adventitious structures' nor 'vestiges', but only pinnules which are developed for the protective function; and that they vary in different species according to the size of the resting apex, being absent where it is small, or

where scales or hairs form an efficient covering. In *G. linearis* (= *G. dichotoma*) they are highly specialized for the protective function (Goebel, 'Organography,' ii, p. 319, Fig. 206). In general form the leaves of these two species are very widely expanded, and are among the largest of the *Mertensia* division of the genus. They are thus in strong antithesis to the leaves of the *Eu-Gleichenia* division, which have the leaf-area reduced, probably in relation to a xerophytic habit.

The surface appendages have been too much neglected as a basis for comparison in Ferns. In many systematic treatises they are ignored. Even in the excellent work on the Filicales by Diels (Engler u. Prantl, 'Nat. Pflanzenfam.,' i. 4) their occurrence and peculiarities are often left unnoticed in cases where, as in *Gleichenia* and *Alsophila*, they have a comparative value. Long ago, however, the value of surface appendages for phyletic comparison was noted by Prantl ('Schizaeaceen', p. 37), who concluded that simple hairs were the primitive type, but that in many circles of affinity they developed in a flattened form. The ramentum or scale is thus derivative or secondary. This distinction of hair and scale was adopted by Max Kühn as the basis of a classification of the Polypodiaceae, which he divided into *Chaetopterides*, with hairs, and *Lepidopterides*, with flattened scales. Against the use of this as a leading criterion, which resulted in an unnatural juxtaposition of genera, Prantl protested ('System der Farne', 'Arb. K. Bot. Gart. z. Breslau,' p. 13). But, nevertheless, he adopted the existence of the scale as an expression of a progressive step of organization. This is the way in which the hair-scale criterion should be used as an indication of a relatively primitive or of a relatively advanced condition, which may be brought with other progressive features into a general argument; but with the full knowledge that the advance from hair to scale has probably been made in various phyletic lines, and that it does not necessarily progress coincidentally with other features of advance.

An examination of the dermal appendages of *Gleichenia* brings some interesting results. Of the section *Eu-Gleichenia* three species have been examined, viz. *G. polypodioides*, Sm., *G. dicarpa*, R. Br., and *G. circinnata*, Sw. In all of them broad scales were found protecting the dormant leaf-apices, as also on the leaf-bases and the rhizomes. But with them are associated hairs. In the first two species these were pale and soft, but in *G. circinnata* they were stiffer, and very beautiful transitions can be found between simple brown hairs and those which are branched and tufted, and finally to broadened scales, with stiff hairs projecting from their margins. It is as though the bases of the hairs had broadened to form the scales, and this is their probable origin. The hairs and scales fall off early from rhizome and leaf. It appears thus that both hairs and scales are present, probably with constancy, in *Eu-Gleichenia*, and this is biologically in accordance with their xerophytic habit.

In the *Mertensia* section observations were made on *G. Bancroftii*, Bl., *glauca*, Hk., *flabellata*, Br., *Cunninghamii*, Hew., *furcata*, L., *owhyhensis*, Hk., *flagellaris*, Spr., *vestita*, Bl., and *hirta*, Bl. In all of them both scales and hairs were present, the former especially upon the circinate leaf-apices. The scales vary, being large and broad in *G. Bancroftii*, but only narrow in *G. flagellaris* and *vestita*, while in the latter the hairs are soft and fluffy, of the type to be described in *G. linearis*. Thus, though *Mertensia* is, as a whole, of less xerophytic habit than *Eu-Gleichenia*, both hairs and scales are general, especially on the circinate leaf-apices.

But in § 3, *Gleichenia pectinata*, and § 4, *Gleichenia linearis*, no scales are found. They stand in this character apart apparently from the whole of the rest of the genus. Hairs are present in both, and they are of the tufted type, branching near to the base. In *G. linearis* these are of a softer texture, but in *G. pectinata* they are stiff and brown, with their peg-like branches often reflexed. These hairs, especially those near the insertion of the leaf on the axis, are long and curved, and coarse in texture. Each of them with its tuft of stiff branches is borne on the end of a rather massive emergence, which is a firm multicellular outgrowth. But the hair is readily broken away from its tip; the emergence then remains as shown in Pl. XXX, Fig. A, in the case of the two lower emergences. And as these are numerous and relatively large, they give to the rhizome and the base of the leaf that prickly character which is often seen about the base of the leaf in *Alsophila*, *Hemitelia*, and *Cyathea*, though here it is on a smaller scale. The prickles in these latter plants bear each a ramentum when young, and this may be seen with special clearness in the case of the large, more or less isolated scales borne on the young leaf of *Hemitelia horrida* (Pl. XXX, Fig. B). There can be little doubt that the structures in question in *Gleichenia pectinata* and in the Cyatheaceae are essentially comparable one with another; in that case, those of *Gleichenia* may be held as a prototype of the larger emergences of the Cyatheaceae. See Pl. XXXIII.

It appears from the above observations that the two species of *Gleichenia*, which are outstanding in other characters from the rest of the genus, are also exceptional in showing the more primitive type of dermal appendages only, viz. hairs and no scales. Their aloofness from the rest of the genus is further indicated by their anatomy. It will suffice here to quote briefly from the conclusions which have been arrived at on the basis of comparison of their vascular tissues.¹ Tansley sums up his discussion of the anatomy of *Gleichenia* thus (l. c., p. 46): 'We are therefore led to the conclusion that such a form as *G. flabellata*, on the whole, represents the most primitive type of the genus.' As regards *G. linearis* he remarks (p. 41) that it 'stands apart from the other *Mertensias*', being 'intermediate

¹ Tansley: *Lectures on the Evolution of the Filicinean Vascular System*, iv, p. 40, &c. Boodle: *Ann. of Bot.*, xv, p. 703, and xxiii, p. 419.

between the *Mertensia* and *Eu-Gleichenia* types'. The latter are generally accepted as being forms showing reduction from the typical *Mertensia* type, as represented by *G. flabellata*; they are in fact a side branch. Thus, as Boodle points out (l. c., p. 432), *Mertensia* includes not only the species of *Gleichenia* which is held to be the most primitive anatomically, viz. *G. flabellata*, but also the most advanced, viz. *G. pectinata*. The solenostelic structure which it shows is to be regarded as derived from a protostelic *Mertensia* type, like that of *G. flabellata*. And thus it appears that, putting *Eu-Gleichenia* aside as a line of xerophytic specialization, *Mertensia* illustrates a sequence in which *G. linearis* takes an intermediate place, leading from a protostelic to a fully solenostelic structure of the axial stele. It will be seen that this runs parallel with certain soral characters.

The structure of the sorus in certain species of *Gleichenia* has been described elsewhere (Studies, IV. Leptosporangiate Ferns; 'Land Flora', p. 555, &c.), and the conclusion is drawn that the sorus and sporangium of *G. flabellata* are probably the most primitive of the forms examined, a conclusion based partly upon the construction of the sorus, which is radiate and uniseriate with about 3-5 sporangia ('Land Flora', p. 554, Fig. 309), partly on the large output of spores from each sporangium. The species of the *Eu-Gleichenia* section show a diminution in number of the sporangia, and in their individual output of spores, as compared with *G. flabellata*, and they present no feature of special interest for our present comparison. But the two species which are outstanding from the rest of the genus in other respects, viz. *G. linearis* and *G. pectinata*, both show indications of advance beyond the condition normal for the *Mertensia* section. This is apparent in the larger number of sporangia in the sorus, in their arrangement, and in the diminished output of spores per sporangium. The facts have already been observed for *G. linearis*, where the number of sporangia in the sorus may be as large as ten, and the central area of the sorus, which is usually vacant in other species, is occupied by sporangia (Pl. XXX, Fig. C). Hooker ('Species Filicum', i, p. 13) mentions 'capsules 10-12'. The sorus being thus more crowded than in the usual *Mertensia* type, the question of dehiscence of the sporangia becomes a critical one. In *Gleichenia* the dehiscence is by a split in a median plane of the sporangium, and in order that the opening may be effective elbow-room is required right and left of each sporangium, and it is therefore only suitable for a laxly arranged sorus. The difficulty will be appreciated by examination of the sori in Fig. C, or better of the detailed drawing (Fig. D). From this it appears that even in a sorus with seven sporangia their close juxtaposition has led to an oblique opening of one of them. But the question is not here one of acute difficulty. As regards the spore-output the number of spores per sporangium counted in specific cases for *G. flabellata* were 794, 695, 838, 634, all these figures lying between the typical numbers 512-1024. For *G. linearis* the numbers

were in two specific cases only 251 and 319. This smaller number is in accord with the smaller size of the pear-shaped sporangia of the latter species, but it is nearly matched by the output in species of *Eu-Gleichenia*, where the relatively large sporangia produce large spores, but their numbers are in near proximity to the typical number 256.

A more special interest, however, attaches to the case of *G. pectinata*, which is sorally, as it is also anatomically, the most advanced species. It has long been known that the sori of this species contain the largest number of sporangia in the genus. Hooker ('Syn. Fil.', p. 15) mentions '8-10 capsules'. The drawing (Pl. XXX, Fig. E) shows that this is clearly under the mark, for the numbers vary from 10 to 15 in this specimen from Jamaica not specially selected. The sporangia, being long-stalked and all seated upon a central and slightly raised receptacle, are obviously crowded. They form two tiers, the upper tier fully occupying the central space, which in *Mertensia* is usually vacant. The enlarged drawing of a single sorus (Pl. XXXI, Fig. F) shows that the sporangia are even flattened against one another, a fact which is readily seen in their flattened sides when the sporangia lie separate and free. They are also far from uniform in size, and the orientation of the annulus is occasionally reversed. It is plain that shedding of the spores will here be a matter of difficulty if the median dehiscence is maintained. That the difficulty is a real one is shown by the fact that, though the sporangia arise and mature all simultaneously, many of them remain full long after other sporangia of the same sorus have been emptied. It appears then that in *G. pectinata* the Gleicheniaceous type of sorus has reached the point of ineffectiveness in its increase in number of the sporangia. There are four possible ways out of the difficulty, and they may be adopted singly or in combination: (1) by increasing the length of the sporangial stalk, (2) by adopting a lateral in place of a median dehiscence, (3) by extending the area of the sorus, and (4) by elongating the receptacle. But none of these has been adopted by the genus *Gleichenia* itself. Other Ferns have, however, adopted them, and have succeeded.

The development of the sorus of *G. pectinata* has been followed out for comparison with that of other species. The receptacle is present as a considerable upgrowth before the development of the sporangia begins (Pl. XXXIV, Figs. 1, 2). The sporangia themselves are almost simultaneous in their appearance, but not perfectly so. In Fig. 3 the middle sporangium is just dividing off its cap-cell, whereas those right and left have them complete. There is still more discrepancy in the state of development of the three sporangia in Fig. 4. But there does not appear to be any rule or method of succession. The sporangia themselves show a segmentation which, though variable in detail, conforms to that already described for other species of the genus.¹ In most cases it ranks most nearly with the type seen in the Schizaeaceae

¹ Compare Studies. IV. Phil. Trans., vol. xcii, pp. 32-8, and Plate II.

(‘Land Flora’, Fig. 349, *d*), but some show relations also with the types *c* and *e* of Fig. 349. In any case the segmentation is more massive than that of the Polypodiaceae. The result is a relatively bulky sporangium, with a stalk of several rows of cells (Pl. XXXIV, Fig. 5). When mature it closely resembles that of *G. linearis* both in shape and in average size. But there appears to be a smaller number of spore-mother-cells in each sporangium than in this species, and considerably less than in *G. flabellata*. Fig. 6 shows the definitive sporogenous group as seen in a section transverse to the axis of the sporangium, and the number of spore-mother-cells is fifteen, arranged roughly in four plates. Fig. 7 shows a section of a similar sporangium in a median longitudinal section, and the number of the spore-mother-cells traversed is twenty. Fig. 8 shows the condition where the spore-mother-cells have separated and rounded off. These drawings provide an interesting comparison with my drawings for *G. flabellata* and for *G. linearis* (Figs. 24–26, Pl. II of my Studies, V, and Figs. 27–30, Pl. III). From a comparison of such sections as those shown in Figs. 6 and 7 the total number of spore-mother-cells in *G. pectinata* may be estimated at some figure probably in excess of 64, which if all were matured would lead to an estimated output of spores something in excess of 256 per sporangium. Actual countings for sporangia of *G. pectinata* gave the result of 422 and 429 for large sporangia, and 228 and 236 for small sporangia. The larger are thus seen to approximate to the typical number 512, though falling a good deal short of it; the smaller approximate to, but fall short of the typical number 256.

A comparison of these facts with those for *G. linearis* and *G. flabellata* indicates clearly a sequence of reduction from the large sporangia of *G. flabellata*, which are few in a sorus, each with an individually large spore-output approximating to the typical number 1,024, through *G. linearis*, with its smaller sporangia, more numerous in each sorus, and with spore-output approximating to or exceeding 256, to *G. pectinata* with sporangia variable in size, but still more numerous in the sorus, and with a variable spore-output, approximating in large sporangia to 512, but in smaller falling to below 256. The variability in size of the individual sporangia makes precise statement precarious. An important point is that the variability exists in the species which is in various respects the most advanced in the whole genus.

Turning to the gametophyte of *Gleichenia*,¹ it presents characters of importance as indicating affinity with relatively primitive types. The massive form of the prothallus with a marked midrib is characteristic, and suggests comparison with *Osmunda*. It bears in some species ‘marginal

¹ Rauwenhoff : La Génération sexuée des Gleicheniacées. Arch. Néerland., 1890. Campbell : Mosses and Ferns, 2nd Ed., p. 336; also The Prothallium of *Kaulfussia* and *Gleichenia*. Ann. Jard. Bot. Buit., 2^e sér., vol. ix, p. 80.

leaf-like lobes', seen especially in *G. laevigata*. These are compared by Campbell with those of *Fossombronia*, or *Dendroceros*. But the most important characters for comparison are provided by the sexual organs. Campbell has shown that the neck-canal-cell of the archegonium (except in *G. polypodioides*) commonly divides into two cells. This is regarded as a primitive character. As regards the antheridium, Rauwenhoff examined various species of *Eu-Gleichenia*, but of the *Mertensia* section only *G. flabellata*, and found in all that he examined a general correspondence of the antheridium with that of the Polypodiaceae. But other species belonging to the *Mertensia* section examined by Campbell are characterized by the much larger size of the antheridium, this being especially marked in *G. laevigata* and *G. pectinata*.

The number of spermatocytes traversed in a median longitudinal section gives a numerical basis for comparison. From Campbell's published drawings the numbers appear as follows: *G. polypodioides* (§ *Eu-Gleichenia*)—19. *G. (Mertensia) laevigata*—95, 35, 76. *G. (Mertensia) linearis*—30, 42. *G. (Mertensia) pectinata*—46, 23, 60, 62. From this it appears that there is considerable variability not only within the genus, but also in specimens of the same species. It is a criterion which must be used with caution. The chief point is that the numbers are high compared not only with those of other Ferns, but also with Pteridophyta at large. From published figures (mostly taken from Campbell's 'Mosses and Ferns') it appears that typical numbers of spermatocytes seen in section are for *Ophioglossum* 87, *Kaulfussia* 61, *Marattia* 31, *Osmunda* 32, *Onoclea* 21, *Nephrodium* (Kny) 16, *Woodsia* (Schlumberger) 17, 18, 16, 14, 14, 13. In other Pteridophytes the numbers are for *Equisetum* 56, and *Lycopodium* 46.

From a comparison of these figures it follows that the antheridia of *G. laevigata* are exceptional in showing in specific cases a larger number of spermatocytes in median section than any of the Pteridophytes quoted. On the other hand, the figures for the *Mertensia* section of *Gleichenia* as a whole are in excess of those for the Leptosporangiate Ferns. *Nephrodium* with about 16, and *Woodsia* with an average almost the same, may be taken as typical for the Leptosporangiate types. And so it is seen that the *Mertensia* section of *Gleichenia*, together with the two outstanding species *G. linearis* and *G. pectinata*, occupy a position altogether exceptional among Ferns, while the latter species are extremes even among Pteridophytes at large, in respect of the number of their spermatocytes. This, going along with the large output of spores in the *Mertensia* section, and other relatively primitive characters, indicates in an unmistakable way that it is among the most primitive types of the living Filicales.

But the characters upon which this general conclusion is based do not always run parallel. Thus *G. flabellata*, which in its anatomy, its sorus, and its spore-output appears as the most primitive species, has not the

largest antheridia (cf. Rauwenhoff). Unfortunately, the extreme type in the latter respect (*G. laevigata*) has not been examined as regards its spore-output. *G. linearis*, which anatomically and sorally is more primitive than *G. pectinata*, is on the antheridial criterion more advanced. These discrepancies find some explanation in the irregularity of size of the individual antheridia of *G. pectinata*, which shows that this criterion must not be pressed too hard. It has long been a matter of note that the extent of projection and the bulk of sporangia and antheridia show some degree of parallelism, the more bulky and deeper sunk being held as the more primitive condition. It has also been pointed out at length elsewhere ('Land Flora', p. 641, &c.) that the numbers of spores produced in a sporangium give a rough numerical measure of the relative bulk of the sporangium for comparative purposes. It is also the fact that there is a parallel between these characters and the segmentation of the apices of axis, leaf, and root in the plants in question. To these criteria is now added that of the spermatocyte-production of the antheridium. But while we recognize these points, they must not be driven to the length of exact numerical comparison. It is becoming apparent that while such parallels are true in general, indicating conditions of relatively greater or less bulk of fundamental organization, still they are not invariably exact, and are open to exceptions.

From the details and comparisons advanced in the above pages the conclusion may be drawn with some degree of certainty that the Gleicheniaceae occupy a place among the most primitive of the Filicales; that *Mertensia* is more primitive than *Eu-Gleichenia*; and that in many characters, though not in all, *G. flabellata* is a central and an early type. Perhaps it may share this position with *G. laevigata*, which is as yet imperfectly investigated. From such forms as central, lines of specialization appear to have led, resulting on the one hand in *G. linearis*, which show various features of advance; on the other hand there is *G. pectinata*, which may be held as the most advanced species of the genus. This appears especially from its vascular anatomy, and from its sorus, the latter having arrived at the limit of development which can be practically effective in the Gleicheniacean type of soral construction. This species shows, however, in its hairs (scales being absent), in the relatively large spore-output of its larger sporangia, and in the large number of spermatocytes of its largest antheridia, traits that are primitive. But the variability of size of both its sporangia and of its antheridia indicates the readiness with which the type might advance progressively to characters shared by most Leptosporangiate Ferns. The question of genetic relations between the Gleicheniaceae and the Cyatheaceae is thus centred definitely upon *Gleichenia pectinata* above all other species of the genus. The next step will be to consider the question from the other side, and to see whether any outstanding species of the

Cyatheaceae show primitive characters, such as compare in any degree with those of *G. pectinata*.

LOPHOSORIA PRUINATA, PRESL.
(= *Alsophila quadripinnata*, Gmel.).

The Fern so named has passed under various designations, and has commonly been regarded as an outstanding species. It was called *Polypodium griseum* by Schkuhr. Swartz named it *Polypodium pruinatum*. In 1848 Presl isolated it as the only species of a distinct genus, under the name of *Lophosoria pruinata*, but Sir William Hooker reduced it to *Alsophila*, and it appears in the 'Species Filicum' (vol. i, p. 47) as *A. pruinata*, Kaulf. It is, however, there remarked that 'in habit and appearance this is extremely distinct from any other *Alsophila*, and the receptacles are very slightly elevated, so that it must be considered but a doubtful species of the genus'. It bears the same name in the 'Synopsis Filicum', where as species 34, not only is it not accorded the dignity of a special section of the genus, but it is ranked indiscriminately among the ordinary species. Diels ('Nat. Pflanzenfam.', i. 4, p. 135) treats it in somewhat the same way, but remarks that it is a peculiar species. Christ ('Farnkräuter', p. 236) passes it under the name *Alsophila pruinata*, Kaulf., but places it in the section *Lophosorus*, Presl. Grisebach ('Flora of the British West Indies', p. 703) names it *Lophosoria pruinata*, Pr., and goes so far as to place it as a substantive genus, with *Cyathea* intervening between it and *Alsophila*. Finally, in Christensen's Index it appears as *Alsophila quadripinnata*, (Gmel.) C. Chr.

The best description hitherto given is that by G. S. Jenman, in his 'Synoptical List of Jamaican Ferns'. Ranking the plant under *Alsophila*, as species 6, *A. pruinata*, Kaulf., his description is as follows:—

Stem short, rarely 3 ft. high, clothed densely with laniferous scales (*sic*); stipites 3–6 ft. long, or more, arching, faintly impressed, rather polished, naked, except at the base; fronds 4–6 ft. long, 3–5 ft. wide, subdeltoid, tripinnate, pale green above, frost-coloured beneath, coriaceous, costae and costulae pubescent above, the pinnulae lanate on the ribs beneath; pinnae large, apart, petioled, lowest pair deflexed and a little reduced, next above $1\frac{1}{4}$ – $2\frac{1}{2}$ ft. long, 6–10 in. wide; pinnulae lax, petiolate, 3–6 in. long, 1 – $1\frac{1}{2}$ in. wide, serrate-acuminate, the lowest segment situated on the superior side; tertiary segments $\frac{1}{2}$ – $\frac{3}{4}$ in. long, $1\frac{1}{2}$ –3 in. wide, acute, deeply cut into deltoid lobes in which the veins are pinnate; sori at the base of the lobes, at the apex of the lowest venule on the upper side near the crenulated sinus; sporangia few, rather large, roundish, mixed with copious lanate scales (*sic*). *Polypodium*, Swartz, *Lophosoria*, Presl, Plum-Fil. t. 33.

Very plentiful in forest shade from 3,000 ft. alt. to the highest ridges. The caudex, which is 3–4 inches in diameter, buds and throws up from the base a number of minor stems about half the size of the primary one. The petioles are sometimes as much as 10 ft. long, giving the fronds an immense

spread. In shape of frond, character of vestiture, and scant number of capsules, it differs materially from all the other species.

There has never been any question of the identity and distinctness of the plant, the uncertainty has been how it should be treated systematically; and this is an indication of its aloofness, which gives it an added interest in relation to the present inquiry.

As regards the details, beyond such facts as are used by descriptive botanists quoted above, little is known of this Fern, except what has been stated by H. Karsten ('Vegetationsorgane d. Palmen', p. 123). He described and figured transverse sections of the stem and leaf-bases, and of the adventitious buds. From his drawings and description it is clear that the axis is solenostelic, and that the leaf-trace is at its base a continuous horse-shoe (compare 'Land Flora', p. 605, where Karsten's figures are reproduced). This relatively primitive anatomical structure is so clearly divergent from that usual in the Cyatheaceae that the facts fix the attention still more forcibly upon this outstanding type.

Lophosoria is a widely spread Fern of the Western Tropics. It is found on the West Indian Islands as well as on the mainland, where it extends southwards as far as Patagonia. Its general characters, its habit, and large dimensions will be sufficiently gathered from Jenman's description, above quoted. Associated with each leaf is usually a bud, which may be only initiated in the case of the upper leaves, or it may be developed in the case of the leaves at the base of the plant; the bud takes then the form of a runner, which after growing horizontally, for a distance usually short, then turns upwards. The leaves on those parts that are underground may be arrested, but those at the distal end of a runner develop in the full form typical for the plant. The position which the buds hold is median at the base of the leaf that bears them, and on its abaxial side. There is in this way a very profuse provision for the vegetative expansion of the individual (Pl. XXXI, Fig. G).

As implied by the name '*quadripinnata*' which has been given to the species by some authors, the leaf is highly divided, and of the Cyatheaceous type, with a clean rachis without either basal pinnae or thorny emergences; except that in large leaves some low emergences may appear at the extreme base (Fig. G). The rachis, together with the axis, is covered by a dense felt of hairs—not 'scales' as Jenman described them. They persist till maturity on both axis and the base of the leaf-stalk, as shaggy rufous masses. They are present also on the under side of the pinnae and pinnules, giving a rusty appearance to the veins, while the rest of the under surface is glaucous. The upper surface of the mature pinnule is free from hairs. Numerous hairs are also associated with the sori. There are no scales on any part of the plant, though such appendages are

a marked feature of the Cyatheaceae. In this *Lophosoria* resembles *Gleichenia pectinata* and *linearis*.

The pinnules themselves are narrow, with crenate margin curved downwards, and their texture rather stiff. The venation is forked, without fusions (Fig. H), just as is the case in *Gleichenia*.¹ The sori are circular and compact, inserted with great regularity upon the lowest anadromic veinlet of the ultimate pinnule. It will be noticed that this corresponds to the position of the sorus in *Gleichenia linearis* (Pl. XXX, Fig. C), and also in *G. pectinata*. The number of sporangia in the sorus is small; they are seated upon a circular and slightly raised receptacle, and show a regularity of orientation of their sporangia, indicated by their oblique annulus, which resembles that in *Gleichenia* (Pl. XXXI, Fig. I). The actual numbers as shown in Fig. H range from 7 to 10, and their arrangement is more or less obviously in two tiers: a lower tier of about 6 or 7, which form a circular series, and are so orientated that the annulus is in a plane almost vertical to the surface of the leaf, or forming an angle with it by sloping outwards from the centre of the sorus. In fact, the orientation is as in *Gleichenia*. The upper tier of sporangia, consisting it may be of only one or of more sporangia, shows less regular orientation, much as is seen in *G. linearis* or *pectinata*. But in *Lophosoria* the crowded nature of the sorus presents no difficulty in dehiscence, for it will be seen later that the slit is not here in a median plane, but lateral.

It thus appears from the external characters that *Lophosoria* holds a peculiar position between the Gleicheniaceae and Cyatheaceae types. The internal structure and development will now be described, with a view to testing the validity of these indications.

Anatomy of Axis.

The axis and leaf-bases of *Lophosoria* are covered externally by a dense band of hard black sclerenchyma, without any of those lenticel-like perforations which are so marked a feature in the dendroid Cyatheaceae (Fig. G). There is also a sclerotic tissue within the solenostele, which in the young plant is a solid core as in *Gleichenia pectinata*, but in larger plants it expands into a hollow cylinder filled with softer pith, and lining the tubular stele internally. At the leaf-gaps it extends outwards in close relation to the leaf-trace, and a portion separates with it as a supply of mechanically effective tissue into the leaf-base. The gap in the sclerotic ring is then closed by a commissure, and the ring is thus completed again before the closing of the foliar gap. In fact, the sclerotic tissue accommodates itself to the conformation of the vascular system (Pl. XXXIV, Fig. 9).

¹ The figure of *G. pectinata* (Pl. XXX, Fig. D) appears to suggest fusions of the veins; but an examination of the pinnule from which the drawing was made, after removal of the sporangia, showed that no fusions were present.

Karsten's drawings and description of the structure, so far as they go, accurately represent the facts (see 'Land Flora', p. 605, and Fig. 336, where reference is made to the original paper). *Lophosoria* shows in certain sections a perfectly solenostelic state, the vascular ring opening in the usual way to give off a broad segment of the ring as a foliar strand. This is shown in Pl. XXXIV, Fig. 10, in which it is seen that the separation of the strand is not effected synchronously on both sides. One margin separates as a rule before the other, and this is in fact usual in Ferns with a creeping axis. After both are clear, a wide gap is left in the solenostele, which ultimately closes again. Sometimes the leaf-gaps almost overlap. A case is shown in Fig. 9 in which in a very large axis a foliar gap is seen still open, while on the obliquely opposite side the solenostele is already thinning out in preparation for the formation of the next succeeding leaf-trace. A clear idea of the behaviour can be obtained by comparison of a succession of sections, such as those shown in Fig. 11, which are similarly orientated, and are ranged in succession from below upwards. Fig. 11, i, shows the solenostele open on the side opposite to a leaf-trace which has just come off; the internal sclerotic ring has already closed, but not the stele. It may be noted that the leaf-trace shows the unusual state of having joined its margins, so as to form a complete ring; it may be remarked, however, that the leaf was a stunted one, the axis being a pushing adventitious shoot. Fig. 11, ii, shows a point higher up, where the foliar gap is closed, but the stele is still thinner there than the average. On the side almost opposite, the stele is thinning out for the formation of the next leaf-trace, but it is still a complete solenostele. In the next section, Fig. 11, iii, the leaf-trace thus prepared for is just separating at one margin, but connected by the other. In Fig. 11, iv, that leaf-trace is quite separate, and it shows again the closing in on the adaxial side, so as to form a complete ring. In the last section of the series, Fig. 11, v, the solenostele has closed completely, though two thinner points are seen, the one marking where the ring has closed after the departure of the last leaf-trace, the other showing where the next will come off, and this is already indicated also by the slight outgrowth of all the tissues on the side obliquely opposite to the preceding leaf. It is thus evident that the leaf-gaps do not actually overlap, though they may follow in rapid succession, and the structure is accordingly solenostelic, but with a rather compact arrangement of the leaves, which is specially marked where the plant has settled down to its normal vertical growth, with a terminal tuft of leaves.

The validity of these results is shown by Pl. XXXII, Fig. K. This does not represent any idealized conception of the vascular system, but it is an accurate delineation of an actual dissection of a large axis, from which the cortex has been removed, and the vascular system laid bare. The outer surface represented in the drawing is the solenostele itself, and it

is shown of the natural size. The leaves are at considerable distances apart, so that in transverse section the leaf-gaps do not overlap, and transverse sections of the parts lying between them would show the complete solenostele. It may be noted that in this case the adventitious buds are absent from the leaf-bases.

It has been pointed out that roots and adventitious buds are borne by the axis. The attachment of the roots is shown in Pl. XXXIV, Fig. 11. Their vascular supply comes away from the outer margin of the stele in the usual way. The adventitious buds are placed with regularity below the leaf-bases. Frequently there is one at the base of each, but their presence is not constant. In order to trace the vascular connexion of the bud and its related leaf, sections were cut transversely to the parent shoot, as in Fig. 12. Of these (i) is the lowest; it shows a foliar gap of a preceding leaf just closing, while almost opposite the thinning out and extension of the stele is beginning preparatory to the departure of the next trace. But already the related bud (b) is traversed, though the section was below the level of its vascular supply. In Fig. 12, ii, the bud is traversed in median section, and it is seen that not only does the vascular tissue extend directly out into it, but the sclerenchyma also; in fact, the vascular tissue of the bud arises as a diverticulum of that at the base of the related leaf. Closely above it, as shown in Fig. 12, iii, the leaf-trace itself comes off in the usual way. These results were checked by tangential sections, as shown in Fig. 13. Of the sections there shown (i) is a transverse section of the bud close to its base, showing its solenostelic structure, with numerous roots. A tangential section just below its insertion is seen in (ii), which shows the continuity of the sclerenchyma and pith of the main axis with that of the bud. It is also seen how the vascular supply of the bud arises from the leaf-trace strand itself. A section still lower is seen in (iii), where the ring has widened out, and merged into the curved strand of the trace.

It is thus seen that the adventitious buds may be solenostelic from the first. It is not improbable that small and weak runners may be protostelic at their base, but none have been observed. Unfortunately the youngest plants available from those collected in the open forest showed already the solenostelic structure; and as the cultures from spores did not come through to the formation of sporelings, the ontogenetic origin of the solenostelic structure in the plant must for the present remain in doubt.

Pl. XXXII, Fig. L, represents the vascular skeleton of a shoot of moderate size, showing the relation of the supply to the adventitious buds to that of the leaves. In this case most of the leaves bear an adventitious bud, but in some cases the bud was absent.

As regards the details of structure, the solenostele is of a very usual type. It is limited on either side by an endodermis with brown coloured walls, succeeded by a pericycle of two or three layers, and the broad band

of phloem on either side of the xylem presents no characters for remark. The xylem varies in its thickness, thinning off especially where a leaf-trace is about to depart. It consists of tracheides mixed with parenchyma. The tracheides are of uniform character, and, as is often the case in the Cyatheaceae, there appears to be no protoxylem. Not only is this absence of protoxylem seen structurally, but it is also shown in sections of young stems by the fact that the tracheides mature almost simultaneously over the whole transverse area.

Though the axis is often very bulky, no medullary vascular system has been seen.

Anatomy of the Leaf.

The leaf, which is slightly dilated at the base, is continued upwards with an almost cylindrical stipe, marked on either side by pale lines similar to those in the Bracken, and often accompanied by dark streaks of sclerenchyma. These are interrupted, just as in the Bracken, at the first pinnae, which are inserted in large leaves at two or three feet from the base.

The leaf trace has been seen to come off as a simple meristele, which soon assumes a complicated horseshoe outline, with lateral involutions. In small leaves it may remain throughout as a single continuous strand; but in large leaves it commonly divides close to the leaf-base into three distinct portions, which in very large leaves may be widely separated (Pl. XXXIV, Fig. 9). In leaves of smaller size the margins of these several portions may remain in close relation, or the strands may even fuse with one another from time to time. But sooner or later they finally join again to form a single band. This was found to be completed in a specific case within nine inches of the base of the leaf (Fig. 13 *bis*, *a*, *b*).

Very soon after leaving the axis protoxylem-groups make their appearance in the vascular strand, which had previously been without them. They are characterized in the usual way, but are very numerous, forty-seven being counted in a specific case. Each protoxylem acts as the centre of a 'divergent', and lies apparently nearer the periphery of the section than the metaxylem; but in actual fact the protoxylem elements, accompanied by cavity parenchyma, are really on the adaxial face of the xylem of the meristele. Since this arrangement impresses itself on the whole contour of the strand, a characteristically corrugated outline results (Pl. XXXIV, Fig. 13 *bis*; Pl. XXXV, Fig. 14). This condition is continued with little change in form of the trace, or even in number of the protoxylems, up to the level of the first pinna.

Opposite the involutions of the horseshoe-shaped strand a break in the continuity of the band of sclerenchyma which bounds the section may be seen on either side. The epidermis is there thin, with numerous stomata, while a lacunar ventilating tissue lies below it. This structure constitutes those lateral lines already observed from without (Fig. 13 *bis*).

The origin of the pinna-trace from the rachis has been followed. For purposes of description reference must again be made to the strand of the rachis. It is in outline like the Greek omega (Fig. 13 *bis, b*), thus corresponding to the chain of separate strands so characteristic of the leaf-trace in the Cyatheaceae. There are two internal bays on each side: these may be designated according to their position as the adaxial and abaxial bays. It is in relation to these that the pinna-trace arises. An example is seen in Pl. XXXV, Fig. 14, i-vii (left-hand side). The first sign is a deepening of the abaxial bay on the side where the pinna arises (Fig. 14, i). The xylems then come together a little short of the extreme curve and fuse, forming a loop of xylem, with conjunctive parenchyma enclosed (Fig. 14, ii). A constriction then takes place, so as to nip off the xylem-ring with its attendant tissues, while the phloem and sheaths close in so as to abstrict off an island of vascular tissue from the angle of the bay. Meanwhile the sheaths at the angle of the adaxial bay begin to widen out towards the island, and, joining with its sheaths, receive it as it separates from the abaxial bay (Fig. 14, ii, iii). After the junction has thus been made with the adaxial bay the xylem-ring connects with its xylem, and then opens out; the conjunctive tissue and the sheaths curve into the cavity, and the island thus takes its place as part of the adaxial bay of the trace (Fig. 14, iv, v). But meanwhile a constriction, and finally an interruption, appears further along the bay, on the adaxial side (Fig. 14, v); enlargements then appear facing one another upon the two sides of the adaxial bay: these meet and fuse (Fig. 14, vi), but shortly the bridge of fusion divides down its middle; when that is completed the pinna-trace becomes isolated, while the trace of the rachis resumes its original form (Fig. 14, vii). These successive steps are illustrated on the left-hand side of the sections seen in Fig. 14. It will be seen that similar steps are initiated on the right-hand side also; these are for the next pinna, which is seated almost opposite to the first, but slightly higher.

A comparison of these steps in the formation of a pinna-trace may be made with the description and drawings given by Tansley for the secondary pinna of *Cyathea excelsa* ('The Filicinean Vascular System', p. 118 and Fig. 97). There are differences of detail, partly in relation to the interrupted nature of the vascular tracts in *Cyathea*. But the essentials are the same, and the chief point is that in either case the pinna-trace is connected with both bays of the folded trace of the rachis. The median part of the pinna-trace is derived from the abaxial bay, and the lateral parts of it from the adaxial bay.

On the other hand, a comparison should be drawn with what is seen in *Gleichenia*, and a series of sections has been made from the rachis of *G. linearis*, at the level of insertion of a pair of pinnae. At first sight there does not appear to be much similarity. But in any such comparison

allowance has to be made for the habit. In *Gleichenia* there is a more restricted area of the transverse section, and consequently a greater compression of the vascular tract. This is evident in the absence of the lateral involution between the adaxial and abaxial bays, as well as in the stronger curving inwards of the hooks of the horseshoe, which actually meet and fuse (Fig. 15, i). Thus the changes which lead to the separation of the pinna-traces start from a simpler and more compact state than in *Lophosoria*.

The first changes are the separation of the hooks from one another, while the loops formed by them are completed (Fig. 15, ii). Each of the loops then becomes constricted in the middle, and a C-shaped vascular tract is separated off from its distal end (Fig. 15, iii-v). Meanwhile, two projections arise from the concave side of the main bundle, opposite to these C-shaped tracts (Fig. 15, iii-v), while the latter alter their form by producing processes opposite to these (Fig. 15, v). The pairs of processes then fuse, and subsequently each bridge of junction splits down its middle into equal halves (Fig. 15, vii). The result is the formation of three C-shaped tracts of vascular tissue lying in a row, which supply respectively the main rachis and the two pinnae. Putting aside the differences of detail, the points of similarity with *Lophosoria* are, (i) that the pinna-trace is intra-marginal in its origin, and (ii) that its separation is effected by the splitting down the middle of a bridge of junction between the internal faces of the curved trace. On the other hand, as points of difference may be noted, (i) the greater simplicity of the initial steps in *Gleichenia*, consequent on the absence of the lateral involution, (ii) the difference of behaviour of the margins of the trace, consequent on its constriction, and (iii) the equality of size of the traces of the rachis and the pinnae. Thus the comparison brings out fundamental similarities, while the differences which appear may be attributed to the peculiar habit of the Gleicheniaceae leaf, and the extreme contraction of its vascular supply.

It may not be out of place here to remark that notwithstanding the well-known contraction of the meristele at the base of the leaf in *Gleichenia*, which is correlated with its continued apical growth and straggling habit, the meristele may open out above into a widely curved horseshoe. Sections from the upper regions of the leaf of *G. flabellata*, and especially of *G. linearis*, show this clearly. In them the xylem widens out into a dilated curve of one to three layers in thickness, while the protoxylems, with their cavity parenchyma, lie on the adaxial face. The structure is in essentials like that of *Lophosoria*; the chief difference is in the much lower number and less prominent identity of the divergents.

Hairs.

The only dermal appendages found on the shoot of *Lophosoria* are simple hairs, composed of a single row of cells. They are thin at the base,

becoming thicker upwards, and narrowing suddenly near to the apex. They do not bear any glands, and are not branched (Fig. 16). Such hairs are of a very primitive type, and the absence of any broadening intoramenta or scales is in strong antithesis to what is seen in many related genera, and especially those of the Cyatheaceae. But the condition here seen compares in essentials with the condition of those species of *Gleichenia* (*G. linearis* and *pectinata*) with which comparisons have been drawn on other grounds.

The Sporangium.

It has been seen that the sorus of *Lophosoria* consists of about 7-10 sporangia, seated upon a slightly raised receptacle. Not only does observation of young stages show that the sporangia of a single sorus arise simultaneously, as in the relatively primitive *Simplices*, but there is an extraordinary simultaneity of development of the sporangia on the same pinnule, and even on the whole leaf. This condition, so different from what is usual in the more advanced Ferns, was entirely unexpected when the collection of material was made. The result was that only certain stages were at first secured, and those did not include the earliest. The difficulty as to material was, however, surmounted through the kindness of Mr. Harris, of the Hope Gardens, Jamaica, who made a second collection for me so as to secure the earliest stages of the sorus and sporangium. It is to be remembered that the condition thus shown by *Lophosoria* is characteristic rather of the lower than of the higher Filicales, and is conspicuously the case in the Gleicheniaceae.

The mature sporangium is of large size, and of almost spherical form. It is attached by a short stalk, which in transverse section shows six or more cells (Fig. 17). This corresponds to what is seen in *G. linearis* (Studies, IV, Fig. 9), and is distinctly more complex than is seen in *Alsophila excelsa* (l. c., Fig. 89). There are no internal cells such as are seen in the massive stalk of *Todea* (l. c., Figs. 48-50), or in *Lygodium* as clearly indicated by Binford's drawing ('Bot. Gaz.', vol. xlv, Fig. 18, p. 217), or in *Gleichenia circinnata* (l. c., Fig. 5), or in *Matonia* (l. c., Fig. 59), and occasionally seen in *Mohria* (Prantl, 'Schizaeaceae,' Fig. 143). In this detail, which is in itself an indication of the massive character of the sessile sporangium, *Lophosoria* takes a middle position between the larger sporangia of some *Simplices* and the smaller sporangia of the *Gradatae*.

The external form and structure of the sporangium is shown in Figs. 18-20, from three different points of view. The oblique annulus is well marked, and continuous past the stalk, thus marking off two areas of thin-walled cells, corresponding to those described as the 'peripheral' and 'central' faces in the case of *Gleichenia* (Studies, IV, p. 34). The peripheral face is shown in frontal view in Fig. 18, and is the face of the

sporangium which is directed obliquely outwards from the centre of the sorus in the normal orientation; this orientation we have seen to be habitual in those of the lower tier in *Lophosoria*. The central is the opposite face, which is directed obliquely inwards, to the centre of the sorus, just as in *Gleichenia*. It is shown for *Lophosoria* in Fig. 19. In Fig. 20, where the sporangium is seen from the side, showing clearly its turgid form, the two opposite faces are indicated by words. The annulus consists as a rule of a single row of cells of regular sequence; but in the neighbourhood of the stomium irregularities appear. In Figs. 19, 20, certain cells are divided, while in close proximity there appears a break in the regularity of the sequence. It is as though the distal part of the annulus were more nearly vertical than the proximal part. Such facts indicate an instability of exact position of the annulus such as might be anticipated in a case where that structure is in course of change from an inherited to a novel position; in fact, swinging from an oblique towards a vertical position.

The stomium is lateral in position—a marked difference from the case of *Gleichenia*, where the dehiscence is median. It is not exactly differentiated, and appears to be variable in the number as well as in the exact position of its cells. It serves, however, as a structural definition of the lateral dehiscence, though not with the constancy of structure seen in more advanced Ferns. Such a condition is what might have been expected in a type in which a recent change of the point of dehiscence from a distal to a lateral position had occurred.

The number of tabular cells covering the faces of the sporangium is relatively large, and it is markedly so when a comparison is made with the sporangia of the Cyatheaceae. Thus, over fifty cells are shown on the peripheral face of Fig. 18 of *Lophosoria*. In Studies, IV, Fig. 83 of *Cyathea* there are only six, in Fig. 86 of *Hemitelia* there are eight. The correspondence is, however, a closer one with the large sporangia of *Gleichenia*. Having noted thus the large size of the sporangium, and its complexity of structure, it was a matter of some surprise to find that the output of spores is low. Several countings gave figures closely approximating to, but not exceeding sixty-four, which appears to be the typical number in each sporangium.

The development of the sorus and sporangium has been studied in sufficient detail for bringing out the points that are essential for comparison. As in *Gleichenia* the receptacle makes its appearance on the lower surface of the pinnule, at some distance from the margin, as a multicellular upgrowth of rounded form (Figs. 21–2). Certain of its superficial cells begin to grow out as hairs (Figs. 24–6), while others become soon recognizable as the parent cells of sporangia (marked × in Fig. 23). These undergo divisions by walls inclined to one another, leaving a pyra-

midal cell at the apex of the upgrowing sporangium. From this by a periclinal wall the cap-cell is cut off. The number and relations of the cells which thus go to form the stalk of the sporangium do not appear to be precisely the same in all cases. The stalk which results is of a massive type (Figs. 25, 26). The whole segmentation of the sporangia, as well as their position on the receptacle, and the structure of the latter are strongly reminiscent of what has been demonstrated for *Gleichenia linearis* (= *G. dichotoma*) some years ago (Studies, IV, Pl. II, Figs. 15-17). In both cases the relatively thick stalk is indicative of a primitive sporangial type. On the other hand, a comparison may be instituted with the young sporangia of the Cyatheaceae, as shown for *Cyathea* (l. c., Figs. 78-80), for *Alsophila* (l. c., Fig. 87), and for *Onoclea* (l. c., Fig. 90). It is, however, to be remarked that in these the sporangium is of a rather more attenuated form, and projects more in its early stages of segmentation, which is an indication of its more advanced state.

A later state of the sorus and sporangia is shown in Figs. 28, 29, the former being cut so as to follow the course of the vein over which it is seated, while in the latter the vein is cut transversely. From the convex surface of the receptacle arise numerous hairs, which show a basal intercalary growth. The sporangia are few, and are always of uniform age in the sorus. There is no evidence of any succession in their appearance. Thus *Lophosoria* would be properly ranked, as *Gleichenia* is, among the Simplices. It may be noted that the sporangia in *Lophosoria* are raised further from the surface of the leaf than in *Gleichenia* (compare Figs. 28, 29 with Figs. 22, 24 of Studies, IV). This is owing to the greater height of the receptacle, a fact which accords with its relation to the Cyatheaceae, where the receptacle is higher still.

As regards the sporangia, their position when young naturally corresponds with that which they hold when mature. In Fig. 28 two are traversed in positions corresponding to those of *Gleichenia linearis*, as seen in Fig. 15 of Studies, IV. In Fig. 29 three are seen corresponding in their disposal to those of *G. linearis* shown in Studies, IV, Fig. 16. The sporangia themselves have their short massive stalk segmented in a way that would lead to a structure as seen in Fig. 17. It corresponds to that of *G. linearis*, rather than to the more massive structure seen in *G. circinnata*. The sporangial head has as usual the single peripheral layer of cells that will form the sporangial wall, lined with the tapetal layer, which surrounds the single sporogenous cell. The structure and proportions thus seen for *Lophosoria* are of a type common for the more primitive Ferns where the sporangium is large, such as *Gleichenia linearis*, *Matonia*, or *Loxsonia*, but not of the very largest size. As it grows older the annulus begins to be differentiated by enlargement of certain cells of the wall (Figs. 30-2), the tapetal layer divides in the usual way into two, and the sporogenous cell

divides into usually sixteen cells. These are as a rule arranged in two tiers of eight, so that in transverse sections that number is shown (Fig. 32). In one case, however, nine were found (Fig. 33). It would thus appear possible that a larger number than sixteen spore-mother-cells were present. But as this was an isolated example among many others, and as the countings of the spores showed consistently figures not exceeding sixty-four, stress should not be laid on this single divergent fact. Moreover, it is possible that a division may have been left out in the other tier of cells, so that the total of the spore-mother-cells would still be only sixteen. Then follows the tetrad division, and maturing of the spores in the usual way. The result is shown in a section from an almost mature sorus in Fig. 33. Here the position of the sorus relatively to the curved surface of the pinnule is seen, with the mass of tracheides which enters the receptacle. Of the four sporangia traversed, those right and left show the regularity of orientation characteristic of the *Gleicheniaceae* type. A comparison of these with the sporangia as seen from outside (Figs. 18–20) explains the relation of the large cells of the annulus to the body of the sporangium, and to its peripheral and central faces. But the two sporangia which occupy the centre of the sorus show irregular orientation, as would be anticipated from the drawing of the sorus as a whole (Pl. XXXI, Fig. I).

It has been seen that the stomium is lateral, and therefore the annulus on dehiscence behaves in the manner characteristic of the *Gradatae*, as seen in the *Cyatheaceae*. This makes no demand for 'elbow-room' as in the median dehiscence of the *Gleicheniaceae*. It is an arrangement which is practically effective in closely crowded sori, and it is evident from the relation of the sporangia, as seen in Fig. 33, that the mature sporangia of *Lophosoria* are in close contact.

It appears from the data thus given that the sorus of *Lophosoria* presents features of correspondence with, as well as of strong divergence from, that of the *Gleicheniaceae* type. The points of similarity are: (1) the superficial position, (2) the insertion on the anadromic branch of the forked veins, (3) the raised receptacle with vascular supply, (4) the simultaneous origin of the sporangia, (5) the disposition of the sporangia after the type of *G. linearis* and *pectinata*, (6) the segmentation of the sporangia, and (7) the oblique annulus. The points of difference are: (1) the lateral dehiscence, and (2) the smaller spore-output from the individual sporangium. As to the latter, the condition seen in *Lophosoria* is in some degree approached by the smaller sized and less prolific sporangia of *G. linearis* and *pectinata*, while in the last-named species a marked degree of variability of size of the individual sporangium is seen. There is, however, an obvious break in the series, leaving *Lophosoria* isolated. As to the dehiscence there is little evidence on either side of transition from the median to the lateral type. The want of strict definition of the stomium in *Lophosoria* may, however, be

held as some indication that shifting of its position had occurred. It is, on the other hand, quite possible that the Cyatheaceous type of dehiscence may have existed *ab initio*. This, however, seems to me to be the less probable reading of the facts.

Taking all the points of correspondence and of difference into account, it appears probable that *Gleichenia* and *Lophosoria* are genera which are descendants of a common stock which had a superficial sorus, of the type of the Simplicies; that in certain of the forms a departure was made from the originally radiate uniseriate type by formation of sporangia in the centre of the sorus, as in *G. linearis* and *pectinata*, the latter of which reached the limit of crowding of the sorus which could secure effectiveness of dehiscence by the median rupture; that this difficulty was avoided by another related stock, represented in its simplest form by *Lophosoria*, in which, either as an original character, or more probably as a result of later adaptation, the lateral dehiscence is now seen.

Spore and Prothallus.

The mature spore of *Lophosoria* is a very characteristic one. It is tetrahedral, and shaped like a kettle-drum. There are three flattened faces, separated by lines which converge to the central apex and marked by irregular spots. These represent the skin of the drum. The margin of the drum-head is expanded into a projecting circular band, while the rest of the rounded body of the spore is covered by a thick wall, marked by minute rounded bosses (Fig. 34).

On germination the rupture takes place along the three converging lines, and the three apical flaps of the outer wall come apart. The prothallus is at first filamentous, and in crowded cultures may continue so for some length. But sooner or later the apex widens out into a spatulate form, with its lobes ill-defined and unequal, as is usual in *Alsophila* (Fig. 35). My cultures have progressed to the stage of producing antheridia, which are of a usual type. They rupture by the extrusion of a single cell. Unfortunately, the first cultures at this stage damped off. But attempts are being made to raise fresh cultures from spores kindly supplied from Jamaica by Mr. Harris. A fuller statement on the gametophyte and observations on the young sporophyte will have to be deferred to a later communication.

Morphological Discussion.

A considerable number of characters have been mentioned in the above pages, according to which the Fern described as *Alsophila* (*Lophosoria*) *pruinata* occupies a peculiar position of aloofness; characters which were for the most part unknown to Sir William Hooker, or at least not regarded by him as important when he merged it as a species of *Alsophila*.

It will be shown that these characters indicate that *Lophosoria* is a more primitive type than the true species of *Alsophila*, and point with all the strength of parallel comparison to its position at the base of that series, where in point of fact it has been naturally placed by most systematists.

On the other hand, a somewhat similar aloofness has been indicated within their own genus for two species of *Gleichenia*, viz. *G. linearis* and *G. pectinata*. This has been commonly recognized by writers. It has been shown that their peculiarities mark them off as an advance upon the genus *Gleichenia* in general. By further comparisons between this advanced guard of the ancient genus *Gleichenia* and the *Lophosoria* type as the most primitive of the Cyatheoid Ferns, it appears that the two large groups approach one another. In fact, on the basis of the foregoing observations, together with other considerations now to be advanced, the conclusion may be drawn that the primitive and creeping Gleicheniaceae resembled the ancestry of the Cyatheoid series, and that of living types they most nearly represent the forerunners of that great body of dendroid Ferns.

The criteria which may be used for the purpose of this comparison are the following :—

- (i) The position and branching of the axis.
- (ii) The form and pinnation of the leaf.
- (iii) The dermal appendages.
- (iv) The characters of the vascular system.
- (v) The sorus, its position and constitution.
- (vi) The sporangia and spores.
- (vii) The prothallus and sexual organs.

Each of these will now be examined with a view to an opinion on the phyletic relation of the Ferns named.

1. In chapter xvi of the 'Land Flora' I have dealt broadly with the question of symmetry in the sporophyte, and drawn the conclusion that 'the radial mode of construction was primitive for the sporophyte at large, and that where dorsiventrality occurs it is a secondary condition'. If this were accepted in its baldest form, one might proceed to classify all radial types as relatively primitive, and all dorsiventral types as derivative. But that could only be done by making the quite gratuitous assumption that changes of symmetry could only occur once in any phyletic line. For this there is no warrant. It would seem probable rather that according to circumstances the change from radial to dorsiventral, and also from dorsiventral back to the radial condition of the shoot, may have occurred repeatedly in the course of descent. This subject has been already broached by Prantl in relation to the Hymenophyllaceae and the Schizaeaceae, and similar suggestions have been advanced by Boodle as explaining the anatomy of certain Hymenophyllaceae ('Annals of Bot.', xiv, p. 482). He contem-

plates it as probable for them that though the original ancestry may have been radial, all the living members of the order may have been evolved from creeping forms; some species retaining that character, and others having changed to the upright habit, and back again. It is necessary to keep an open mind on such questions, and to let opinion follow fact and comparison.

Applying this point of view to the present case, though we may contemplate the ultimate origin of the Gleicheniaceae from more primitive Ferns with radial upright axis, we see them to-day as characteristically a creeping family, with dorsiventral shoot. But if the facts indicate that any derivatives from them became in the further course of descent upright, and attained to a radial axis, there seems no reason to dissent from such a conclusion. On grounds especially of their sori reason has been found to contemplate the derivation of the Cyatheaceae from a source resembling the Gleicheniaceae. Our point now is, that if a careful examination of widespread character indicates that that was so, there is no inherent reason to doubt that the columnar upright axis, which is the most striking feature of the Cyatheoids, was itself a secondary character.¹

The question will largely turn upon the existence of intermediate types. There are no relatively advanced Gleichenias which have adopted a definitely upright, self-supporting habit. The two most advanced species, viz. *G. linearis* and *G. pectinata*, are both creepers. But on the other side, though the more advanced genera *Hemitelia* and *Cyathea* show no creeping species, such are seen in the more primitive *Alsophila*, in the species *A. (Metaxya) blechnoides*, and in less pronounced degree in *A. (Lophosoria) pruinata*. Moreover, both of these proclaim themselves as primitive by other characters. A detailed account of *Metaxya* will be held over to a later memoir of this series. It may suffice here to say that with its creeping habit go a solenostelic structure of the axis, an undivided leaf-trace, and hairs only as dermal appendages; all of these being relatively primitive features as compared with other Cyatheaceae. The same may be said for *Lophosoria*, which, however, as regards the mature plant has an upright, though short axis. But the buds which originate at the bases of many of the leaves give rise to runners, which at first take a horizontal course, with their leaves coming off at intervals right and left. The creeping habit with isolated leaves is thus actually shown in the early condition of these shoots. Thus, as regards position of the axis, *Metaxya* pronouncedly, and *Lophosoria* in a less degree, bridge over the gap between

¹ The question here considered, of the upright habit in the Cyatheoid Ferns being a secondary derivative from the creeping habit, has already been stated briefly (Ann. of Bot., xxv, pp. 567-8). The detailed evidence for the opinion is here stated, and it is essential that it should be, for the theory of medullation stated in the paper above quoted could not hold, if the vertical character were primitive. But the comparative evidence from external form, from dermal appendages, from anatomy, and from sorus and sporangium alike, as stated in the above and in the succeeding paragraphs, indicates that it was not.

the creeping habit of the Gleicheniaceae and the upright dendroid types of the Cyatheaceae.

In this connexion it may be noted that terminal branching occasionally is seen in the dendroid Cyatheaceae. An example of this is shown in Pl. XXXII, Fig. M, in a plant in the Glasgow Botanic Garden. Here there is an apparent dichotomy, the two resulting branches having continued their development equally. Anatomical examination would be necessary to prove that the branching was really dichotomous in this case, and naturally that cannot be undertaken. So it must suffice for the present to state that all the external indications are favourable to the branching having been a true dichotomy. If this were really the case, it would be a further point in common with the Gleicheniaceae, in which it has been shown that dichotomy is frequent.

2. As regards the form of the leaf the Gleicheniaceae and Cyatheaceae seem at first sight widely divergent, and *Lophosoria* does not appear to help any transition. But if a comparison be made between the ultimate pinnules of *Lophosoria* (Pl. XXXI, Fig. H) and those of some species of *Gleichenia* (Pl. XXX, Figs. C and E) a similarity of outline, of venation, and even of texture is apparent; the soral similarity is, however, the most important feature of all. The divergence is then in the general habit of the leaf rather than in the details. But even in general habit there are features which link the two families together. The most marked characteristic of the leaf of *Gleichenia* is its apical growth, which may be continued indefinitely though interrupted at seasonal intervals. Looked at broadly, however, the leaf is constructed upon the ordinary pinnate type, and its peculiarities depend upon irregularities in time and extent of the intercalary growth of the rachis, and of the branches of higher order. For the most part the intercalary growth between the pairs of pinnae is strong, so that they are far apart, and usually uniformly removed from one another. In the Cyatheaceae it is less strong, and the pinnae are more closely aggregated. But as a rule the pinnae stop short at some distance from the base of the mature leaf, intercalary growth having been strongest below the lowest pinnae. A special interest, however, for comparative purposes lies in those cases where this rule is not maintained, with the result that basal pinnae are left behind at the base of the leaf, the intercalation of the petiole having taken place above them. These basal pinnae have long been known as the so-called 'aphlebiae', and the example commonly quoted is that of *Hemitelia capensis*. But as a matter of fact it is a feature which exists sporadically in all the three genera of the Cyatheaceae. Pl. XXXIII, Fig. N shows a very pronounced example of *Hemitelia setosa*, Mett., from the Edinburgh Botanic Garden. Fig. O shows the case of an *Alsophila* from Jamaica, growing in the Glasgow Botanic Garden; and Christ has figured a very marked case of basal pinnae in a species of *Cyathea* ('Geographie der Farne', Fig. 24). It thus appears

that the existence of basal pinnae, left behind owing to the higher localization of intercalary growth having produced the petiole above them, is a feature in all the genera of the family of the Cyatheaceae. But in other Ferns it is virtually unknown. It seems to me that the existence of 'aphlebiae' thus exclusively in this family of upright Ferns is strongly reminiscent of an ancestry where the localization of intercalary growth between the pinnae and not exclusively below them was the rule. The unlimited growth and vigorous intercalation seen in the Gleicheniaceae would be impossible features in plants of dendroid habit. But, supposing these dendroid types to have sprung from an ancestry of Gleicheniacous habit, what more probable than that they should still retain some traces of that unusual distribution of intercalary growth? The absence of basal pinnae in other Ferns to which a near relation to the Gleicheniaceae is not ascribed gives strength to this interpretation of the 'aphlebiae' of the Cyatheaceae.

3. Comparisons based upon dermal appendages have mostly been neglected in the phyletic treatment of Ferns, or they have been put to too strenuous a use. The latter was the case when Kühn proposed to divide the Polypodiaceae into two groups on the basis of the simple hairs, as against flattened paleae ('Die Gruppe der Chaetopterideen unter den Polypodiaceen'). A middle course is, however, gradually coming into use, having been initiated by Prantl, who indicated very clearly in the Schizaeaceae how the hair is the more primitive, and the flattened scale, ramentum, or palea the derivative and later type. Other characters being in accord, the presence of hairs only may be held to indicate a relatively primitive condition; the existence of scales, with or without simple hairs as well, may be held to indicate a derivative or later condition.¹ There is reason to believe that a parallel transition from hair to scale was effected in several distinct phyletic lines.

Applying this criterion in the present case, the facts show that *G. linearis* and *G. pectinata* bear hairs only, whereas scales are widely present in other Gleichenias, and especially among the xerophytic types. Now *Lophosoria* and *Metaxya* also have hairs only, and no scales, whereas the genera *Alsophila*, *Hemitelia*, and *Cyathea* are characterized by scales, often of very large size. This superficial feature thus brings together in a very striking way those species upon which our comparison specially turns. But there is a further point to be noted in this connexion. The scales in many of the larger species of the Cyatheaceae are often borne each upon a massive conical emergence, which may persist after the scale itself dries and falls away, as one of those large spines which are specially developed about the bases of the leaves. A like condition has been found in *Gleichenia pectinata* (Pl. XXX, Fig. A), and the existence of such conical

¹ This line of comparison, based on dermal appendages, is being carried further into detail by C. Christensen (On a Natural Classification of the Species of *Dryopteris*, Biologiske Arbejder, Nov. 1911).

emergences about the leaf-bases justifies the comparison of the branched hairs which they bear with the broad scales of the Cyatheaceae. Similar emergences also exist in *Lophosoria* (Pl. XXXI, Fig. G). The progression of characters from the Gleicheniaceae to the Cyatheaceae through *Lophosoria* is in this case based upon a minor detail; but the existence of such a detailed progression supports all the more strongly the comparisons based upon more important characters.

4. By a general consensus of opinion the non-medullated stele is recognized as the primitive stelar type. The characteristic elaboration of this in Leptosporangiate Ferns was connected with the formation of foliar pockets, which intruded above the insertion of each leaf. This led to complete solenostely, with leaf-gaps. When the latter overlap one another the complete dictyostele is the result. No better illustration of these successive steps is to be found than in the Ferns under consideration. The sequence of stages of the elaboration is as follows: In *Gleichenia* in general the stele of the rhizome has a solid xylem-core; it is a protostele, from which the leaf-traces come off in some cases without any disturbance of the underlying tissues. The types of the genus described fall into a rough series, as regards their vascular characters, extending from the simple forms of *Eu-Gleichenia*, through *G. linearis*, to the typical Mertensias, and finally to *G. pectinata* (Tansley, 'Lectures,' p. 44). There is, however, reason to think that the first named owe their simplicity of structure to reduction in connexion with their xerophilous habit, and that *G. flabellata* may be regarded as a central and primitive example. It has a solid protostele, which gives off to each leaf a C-shaped trace, with a pocket of internal phloem, endodermis, and sclerenchyma, which is continued into the stele, but does not intrude far. *G. pectinata* is, however, a solenostelic form, which shows certain complications noted by Boodle and Hiley ('Ann. of Bot.', xxiii, p. 419). From the known facts it seems still uncertain what the exact steps were which led to the solenostelic structure there presented. This, however, is not the present question. What interests us is that, however produced, the solenostely exists in *G. pectinata* with a centrally placed sclerenchymatous pith, surrounded by endodermis and internal phloem. The internodes are long, so that the solenostelic structure is only interrupted by leaf-gaps at long intervals. Passing to *Lophosoria* the solenostelic structure is essentially the same as in *G. pectinata*, but the whole axis is on a more bulky scale. Though in the young plant of *Lophosoria* the sclerenchyma within the solenostele is at first solid, as in *G. pectinata*, in the older plant a parenchymatous core replaces the central region of that sclerenchyma, the remainder of which appears as a dark shell lining the solenostele internally, as is usual in the Cyatheaceae. The latter shows the usual amphiphloic structure, but there is no marked protoxylem: in this it differs from *G. pectinata*, but it shows a condition

which is common in the Cyatheaceae. The internodes are longest in the creeping lateral buds of *Lophosoria*, while in the upright shoots the leaf-gaps sometimes overlap, giving an elementary state of dictyostely. This is exactly what would result if a shoot of the type of *G. pectinata* were to adopt an erect habit. The leaves themselves, being of necessity mechanically self-supporting, must have relatively broad bases of insertion. The axis would necessarily be shortened, and become more bulky to accommodate the more crowded and relatively broad bases of the leaves. That condition is already seen in *Lophosoria*, but the leaf-gaps do not usually overlap. But they do overlap in the typical species of *Alsophila*, which are thus dictyostelic. *Lophosoria* forms accordingly, in the vascular characters of its axis, an intermediate step between the two types, as it does also in habit, and in other features.

The leaf-trace of *Lophosoria* comes off as a single broad strap, and often passes undivided up the leaf. But where the leaf is large it commonly divides up into three parts, though this separate course does not continue far, the three joining again into a single strand below the lowest pinnae. A very similar condition is seen in *Plagiogyria semicordata* ('Ann. of Bot.', xxiv, p. 431), and in some other Ferns. Such cases have their interesting bearing upon general views of the leaf and the relative primitiveness of its parts, a subject which will be held over for the present. From the comparative point of view *Lophosoria* in this detail again takes a middle place between *Gleichenia*, in which no such partition of the trace has been recorded, and the Cyatheaceae, where the dissolution of the trace into separate strands is present in much higher degree, and extends much further along the leaf than in *Lophosoria*. Further, in the horseshoe form of the trace, with its deep lateral depressions, as well as in the origin of the pinna-trace, *Lophosoria* also takes an intermediate place, but with a decided leaning to the Cyatheaceae. This comes out particularly in the large number of the 'divergents', and in the corrugation of the trace in accordance with their position. Thus the general conclusion from an anatomical comparison is that while the affinities of *Lophosoria* are distinctly with the Cyatheaceae, it shows in a number of anatomical features, which may themselves be held as primitive, a condition intermediate between that family and the Gleicheniaceae type. And among the latter it approaches most nearly to *G. pectinata*.

5. But it is upon the characters of the sorus, its position and its constitution, that the most frequent comparisons have been made. In the Gleicheniaceae, as in the Cyatheaceae, the venation of the fertile pinnule is without any fusions, except occasionally in *Hemitelia*. The veins fork, but not very profusely, and the branches run out free to the leaf-margin. In fact, in both the venation is of the primitive, Pecopterid type. In *Lophosoria*, as also in *G. linearis* and *pectinata*, the sorus is constantly seated upon the anadromic veinlet of the ultimate pinnule. This uniformity in position, com-

bined with the similarity of circular form, the absence of any indusium, the approximate uniformity in number of the sporangia, the simultaneity of their origin, and the likeness of their relation to the slightly raised receptacle, are characters that at once establish a sound basis of comparison between the plants named. Moreover, the two species of *Gleichenia* stand out from their genus in the arrangement of their sporangia in the sorus. There is little doubt that the 'radiate uniseriate' type of sorus, as it is seen in *G. flabellata*, is a primitive one—comparing as it does with what is seen in the Marattiaceae on the one hand, and in *Matonia* on the other. Here the centre of the sorus is unoccupied by sporangia. But *G. linearis* has the centre of the sorus occupied by one or more sporangia, while in *G. pectinata* it is habitually crowded with them, so that they are flattened against one another. The constitution of the sorus of *Lophosoria* is very like these, while in point of time of origin of the sporangia those of each sorus are in both cases simultaneous. Both belong technically to the Simplices, while *Lophosoria* is the only case hitherto recorded of this from the Cyatheaceae, which are typically Gradatae.

6. Turning to the sporangia themselves, both the Gleicheniaceae and Cyatheaceae have an oblique annulus, but they differ in that the dehiscence in the former is in the median plane and distal, while in the latter it is lateral. It has been pointed out above (p. 275) that *G. pectinata* with its median dehiscence, which requires lateral space to be effective, has in its crowded sorus reached fully to the limit of possible efficiency. A modification of its type of sorus or of its sporangium is necessary if any larger number of sporangia is to be accommodated, and each is still capable of dehiscence. One modification would be the adoption of a lateral dehiscence. Another would be an elongation of the receptacle. The best result would be by a combination of both. In *Lophosoria* the lateral dehiscence is adopted, but not the elongation of the receptacle. In the rest of the Cyatheaceae both modifications are carried into effect, together with a basipetal sequence of sporangia, which the elongation of the receptacle makes possible. A circumstance which is an indirect support of the view that the sorus of *Lophosoria* is a modification of the Gleicheniaceae type is that, though all the sporangia are simultaneous, the lower sporangia retain the orientation seen in *Gleichenia*. This orientation is of no practical importance where the sporangia are all simultaneous in origin, and the dehiscence is lateral. It may be held as one of those useless survivals which are on that account all the more cogent as phyletic evidence.

From the above considerations it would appear probable that, in the production of *Lophosoria* from some Gleicheniaceae source, a phyletic shifting of the point of dehiscence of the sporangium from the distal to a lateral position has taken place. This suggestion is supported by the fact that the stomium of *Lophosoria* is not highly differentiated, while there is inconstancy in the numbers and relations of the cells which compose it.

In this respect it shows a marked difference from other Cyatheaceae, in which the stomium shows a high degree of differentiation. In point of size also, and in the number of tabular cells forming its lateral walls, the sporangium of *Lophosoria* corresponds rather to the Gleicheniaceae than to the Cyatheaceae. But in the spore-output it is otherwise. The number per sporangium in the Gleicheniaceae is large. In *Lophosoria* it is only 64, a number which tallies with that of *Alsophila* and *Cyathea medullaris*, though that in *C. dealbata* is much lower. Taking all these soral characters together it seems clear that *Lophosoria* holds a very interesting middle position between the Gleicheniaceae and Cyatheaceae, and the characters are such as accord with the view that its sorus and sporangium were originally of the Gleicheniaceous type; but that while the plant has retained the sorus of the Simplicis, it has parted with the primitive mode of dehiscence, and the originally large spore output of the individual sporangium is here represented on a greatly reduced scale.

7. The details of the prothallus and sexual organs of *Lophosoria* being still deficient, comparison on these points must be deferred.

OTHER GENERA OF FERNS WITH SUPERFICIAL SORI AND BASAL INDUSIUM.

There are a number of genera of Ferns, containing each relatively few species, individually of moderate or small size, which share with the Cyatheaceae the possession of a superficial sorus with a basal indusium; some of these prove even to have also like them a basipetal sequence of origin of their sporangia upon the receptacle. They have been ranked by various systematists as related to the Cyatheaceae, and they are placed by Diels immediately after them (Engler u. Prantl, 'Nat. Pflanzenfam.' i. 4, p. 159). They are as follows: *Struthiopteris* and *Onoclea*, *Peranema* and *Diacalpe*, *Woodsia* and *Hypoderris*, *Cystopteris* and *Acrophorus*. Their characters show that these genera are naturally grouped together in pairs, as above, each of these being more nearly related to one another than the pairs themselves are *inter se*. In order to arrive at some conclusion as to the phyletic relations of these pairs of genera to the Cyatheaceae, and to one another, comparisons must be instituted so far as possible on the basis of those criteria which have been employed above. None of these Ferns, however, are essentially primitive types. This is indicated by the fact that they all show a more or less advanced state of dictyostely in the stock, in some cases with the peculiar basket-like structure owing to deep involutions of the superficial tissues. Their leaf-trace is divided, but not usually in an advanced degree. The venation is in most cases open, but in *Onoclea* and *Hypoderris* it is reticulate. Broad scales are common, in place of or in addition to the more primitive hairs. Some of them have a mixed sorus, while the sporangia usually have the annulus interrupted at

the insertion of the stalk. The sum of these characters indicates that we are dealing with Ferns of a middle position in the phyletic scale, a fact which makes the question of their suggested relation to the Cyatheaceous series all the more interesting. It will be convenient to take first the genera *Struthiopteris* and *Onoclea*, for they have for long been regarded as having some near relation to the Cyatheaceae.

Struthiopteris and Onoclea.

The genus *Struthiopteris* (= *Matteuccia*) includes two species, *S. germanica* and *S. orientalis*, which have obliquely ascending or upright stocks covered with the bases of the closely grouped leaves, and *Onoclea* with its single species, *O. sensibilis*, L., having a creeping rhizome bearing isolated leaves.¹ Of these three species *Struthiopteris orientalis* is the least familiar. It shares the leading characters of them all. It will be briefly described here, from observations made partly on plants obtained from India through the Calcutta garden, and my thanks are due to the Director for them; partly from plants living in the Glasgow Botanic Garden, originally obtained from Messrs. May of Edmonton. The points in which this Fern differs from the other two better known species will be noted as they arise.

S. orientalis is a rather coarse-growing Fern, which may attain about the same dimensions as *S. germanica*. It has an obliquely ascending, or upright stock, which is completely covered by the bases of the densely tufted leaves. There were no runners on any of the plants examined, such as are a conspicuous feature in *S. germanica*. The leaf-bases are enlarged as they are in the other species, and in *Plagiogyria*, while they bear rough brownish, rounded outgrowths, mostly along their margins, in appearance like the pneumatophores of that Fern. The leaf-bases and stalks are thickly covered by broad, brown, chaffy scales. The simply pinnate leaves are dimorphic, the broad pinnae of the sterile leaves being deeply pinnatifid, and showing the Pecopterid venation without any anastomoses (cf. Engler u. Prantl, i. 4, Fig. 90 B, of *S. germanica*, which it strongly resembles). But in *Onoclea* the venation is reticulate, a condition which is held to be one of phyletic advance. Frequent middle forms occur between the sterile and fertile leaves. The latter are also simply pinnate, but the segments are narrow, and their margins strongly turned downwards so as to protect the sori, just as in *Blechnum capense*, L., a plant which this species closely resembles.²

The massive stock is solid, and does not show that basket-like structure, due to deep pockets immediately above the insertion of the leaves, described by Gwynne-Vaughan for *S. germanica*, and in less degree for *Onoclea sensibilis* ('New Phyt.', vol. iv, p. 211). It is traversed by a dictyostele

¹ Dichotomy of the axis may be observed in *O. sensibilis*.

² It may be remarked that several species now placed in the genus *Blechnum* have from time to time been ranked in the genus *Struthiopteris*, a clear evidence of the similarity which the genera bear to one another. The significance of this will appear in a subsequent paper of this series.

with proportionately large meshes, from the lower margins of which are given off two large strap-shaped strands to the subtending leaf. There is a central pith which is very voluminous in proportion to the other tissues, so that the ring of meristeles lies very near to the periphery. It is to be noted that sclerenchyma is absent from it, in marked contrast to what is seen in the Cyatheaceae. In fact, the structure of the stock is strikingly similar to that of those species of *Nephrodium* which have a binary leaf-trace, such as *N. Oreopteris*.

The general character of the fertile leaf of *S. orientalis* resembles that of *S. germanica* and *Onoclea sensibilis*. The venation of the fertile pinna is on the same plan as that of the sterile pinna, but the branches of each vein from the midrib are only 5–6 as against 10–12 in the sterile. Anastomoses are again entirely absent in *S. orientalis*. The lowest branch of each vein is katadromic (Pl. XXXVI, Fig. 36). Each branch may bear a single sorus, as in *S. germanica*, but whereas there the sori of the lower branches are slightly nearer to the midrib than those of the upper, in *S. orientalis* they are all at an equal distance, so as to constitute a regular intra-marginal row. This will be found to be matched by *Blechnum capense* (see Mettenius, 'Filices Horti Lipsiensis,' Pl. IV, Fig. 21). Each vein is continued a short distance beyond the insertion of the sorus, but stops short where the margin of the pinna curves over as a continuous protective flap, which in this species is firm, and coloured brown. In addition to this protection each sorus is, as in *S. germanica* and *Onoclea*, covered by a shell-shaped indusium, attached at the side next the midrib. It is structurally of the nature of a ramentum or scale. A section through a sorus from one of Messrs. May's plants shows how the leaf-margin overlaps the scale indusium, the protection of the sorus being a very efficient one (Fig. 37). But in the specimens from India the indusium does not appear to be present.

The receptacle in *S. orientalis*, as seen in specimens from the Glasgow Garden, is a rather flat one, being hardly raised beyond the general level of the leaf-surface (Fig. 37). A tract of tracheides rising from the vascular strand which underlies it brings supplies to the sporangia. These are relatively few in number, as seen in the Glasgow specimens; but in the normally grown specimens from India the sori are larger, the receptacle more raised, and the sporangia more numerous. There is an evident basipetal succession of the sporangia, as has already been demonstrated for *Onoclea sensibilis* and *S. germanica* (Studies, IV, Pl. V, Fig. 90). This is apparent even from the drawings from garden plants, for the central sporangium at the apex of the convex receptacle is the most advanced, and the lateral sporangia younger.¹

¹ The absence of an indusium in the specimens from India, together with the much larger receptacle and more numerous sporangia, suggests further inquiry as to specific identity of the specimens. The Glasgow plants correspond most nearly to the specific descriptions for *Struthiopteris orientalis*.

The mature sporangium of *Struthiopteris orientalis* is long-stalked, and it is specially worthy of note that in the Indian specimens a glandular hair is, as a rule, attached to the stalk of each. This corresponds in character and position to the gland which accompanies the sporangium of *Nephrodium filix-mas*. These glands are absent in *S. germanica* and most of the other related Ferns. The annulus is nearly vertical, and it is interrupted at the stalk, being in this point similar to what has been shown for *S. germanica* (Studies, V, Fig. 91). It consists of about fifty cells, a larger number than is shown in *S. germanica*. It is to be noted that frequent cases occur where the series of cells of the ring is irregular, taking sometimes a zigzag or contorted course in place of the usual regular hoop-like series. Such irregularities may be expected in those forms where a transition between the oblique and the vertical annulus is in progress, according to our general hypothesis. It is in such Ferns that these irregularities have been observed.

The characters of *Struthiopteris orientalis* thus described correspond in essentials with those of *S. germanica* and *O. sensibilis*. The differences are in details, and there is no doubt of the naturalness of the group. But in *O. sensibilis* the venation is the most advanced, being reticulate, while in the rest it is an open, Pecopterid venation. The Onocleae appear to be nearly related on grounds of habit, of venation, of anatomy, and of sorus to the Cyatheaes, and probably *Struthiopteris*, with its upright habit and open venation, is the nearest. These Ferns have, however, adopted the dimorphic frond, though the existence of middle forms in both genera shows that the distinction has not been definitely impressed. The fertile leaf has rolled up its margin, as in *Plagiogyria* and the Pterideae, for the better protection of the sori. These, however, are all distinct, and have the *Hemitelia*-like indusium present in addition. This, with the gradate, superficial character of the sorus, stamps the relationship with the Cyatheoid Ferns. They may be held to be a series which has carried the Cyatheoid type into boreal and alpine climates, where additional protection is required. Further, *Onoclea* shows in its reversion to the creeping habit, and all of them in their deciduous foliage, evidence that they are the outstanding colonists of the family which have become modified in order to meet the conditions of the habitats to which they have spread.

Cystopteris, Bernh.

This genus was founded by Bernhardt in 1806, and includes thirteen species. Presl ('Tentamen', p. 93) recognized its affinity with *Aspidium* and *Asplenium*, and placed it in close juxtaposition with *Acrophorus* in his Aspleniaceae. Hooker ('Syn. Filic.', p. 103) places it between *Davallia* and *Lindsaya*, but remarks that it is 'allied to *Woodsia* and *Microlepia*'. Diels (Engler u. Prantl, i. 4, p. 163) places it in his 'Woodsiinae', in close

relation to *Acrophorus*. Christ ('Farnkräuter', p. 280) ranks it next to *Woodsia*. Influenced by the example of Sir W. Hooker, and after insufficient personal observations, I had in 1899 assented to the relation with *Davallia*, § *Leucostegia* (Studies, IV, p. 76, and 'Land Flora', p. 655). It will now be shown, on the basis of wider comparisons, that the relation is rather with *Struthiopteris* and other Ferns which have a superficial sorus, basal indusium, and a basipetal succession of sporangia.

The anatomy of the stock of *Cystopteris fragilis* has been examined by Gwynne-Vaughan, who found it to have, like *Struthiopteris*, a dictyostelic structure. The leaf-trace also consists of two vascular strands which arise separately from the dictyostele ('New Phytologist', vol. iv, p. 215). He remarks, with regard to the peculiar involutions above the insertion of the leaves, that its stem furnishes almost as good an example of the development of epidermal pockets as *Struthiopteris* (*Onoclea*) *germanica* itself, although the whole structure is on a smaller scale. Thus there is a substantial anatomical similarity with the stock of *Struthiopteris*. If the pockets be left out of account the structure corresponds also with that of *Woodsia*; though in *Cystopteris* the meristeles are smaller and further apart, the disposition of them is essentially the same.¹

Sections of the young sorus of *Cystopteris* show conditions resembling those of *Struthiopteris*, but on a reduced scale, and modified in relation to the flattening of the receptacle under an indusium which lies parallel to the leaf-surface. The formation of the sorus begins slightly back from the apex of the leaf-lobe, as an upgrowth subtended below by the scale-like indusium. The first sporangium, which Schlumberger (l. c., p. 408) describes as being prior to the indusium, appears with regularity on the middle of the convexity (Fig. 38, *a*), several large cells intervening between it and the insertion of the indusium. Transverse sections show that the first sporangium occupies also a median position in relation to the indusium (Fig. 38, *b*); in fact, it occupies the apex of the small flattened receptacle. A comparison may be made with what has been seen in *Struthiopteris* (Fig. 37). Later other sporangia appear right and left (Fig. 39), while the cells which intervene between them and the base of the indusium give rise also to a regular gradate succession in basipetal sequence (Fig. 40). A comparison of the latter drawing with Fig. 90 of my Studies, IV, shows how similar this condition of the sorus is to that of *Onoclea sensibilis*. A comparison with *S. orientalis* also shows correspondence, due allowance being made for the relatively small number of sporangia shown in the garden-grown specimens on which the observations were made. But whereas in these Ferns the

¹ This account does not accord with that of O. Schlumberger (Flora, 1911, p. 410), who states that only a single strand enters each leaf. His observations seem to have been made on a young plant ('Keimpflanze'), and it may be true for the first leaves; but the leaves of mature plants are supplied by two distinct strands, as in *Struthiopteris* and in *Woodsia*. This is already recorded by Luerssen (Rab. Krypt.-Fl., iii, p. 447.)

receptacle rises symmetrically from the leaf-surface, here it is compressed below the indusium, and develops its basipetal sequence as a rule only on the side away from the leaf-surface. None the less is it a gradate sorus, and, contrary to my statement of 1899 (l. c., p. 76) (which was made from old sori), irregularly intermixed stages of sporangia have not been observed in the young state. The segmentation of the sporangia is also a matter for note. It will be seen that the stalk is a relatively massive one with irregularly inclined walls (Fig. 38, *b*). This corresponds closely with what is seen in *Onoclea sensibilis*, and with the Cyatheoid series, and is in sharp contrast to the simple transverse segmentation of the stalk seen in *Davallia* (Studies, IV, Figs. 134, 135). In form the mature sporangia of *Cystopteris* correspond to those of *Struthiopteris* in having their annulus continued to the stalk, but there interrupted; while the stalk itself is relatively massive, and consists of three rows of cells. But the number of cells of the annulus is smaller than in *Struthiopteris*, being only about thirty. The conclusion is, then, that sorally *Cystopteris* is in near relation to *Onoclea* and *Struthiopteris*, and is essentially of the Gradate type; while the characters of anatomy and of habit support the alliance with the Cyatheoids, and especially with certain of their derivatives. Schlumberger, however, considers that the facts of development of the sorus indicate a relationship of *Cystopteris* to the Davallieae ('Flora', 1911, p. 408), rather than with the Cyatheoid series. This opinion I do not share, preferring to regard the peculiarities of the sorus as a consequence of a flattening of the receptacle between the indusium and the leaf-surface, together with an absence of the sporangia on the side of it next to the leaf-surface.

The characters of the prothallus of *Cystopteris*, as described by Schlumberger (l. c., p. 386), are of some importance in considering the relation of the genus to the other Ferns mentioned above. The hairs which it bears are only unicellular glandular hairs, as in the 'Polypodiaceae', not multicellular as in the Cyatheaceae. Further, the lid-cell of the antheridium is undivided, which is again a Polypodiaceous as against a Cyatheoid feature. These characters, together with the flattened type of the sorus above alluded to, accentuate the aloofness of the genus. But its gradate sorus and its anatomy and habit all indicate a relationship to the Ferns with a basal indusium. It may be held to occupy a middle position linking the Woodsieae, especially *Struthiopteris*, with the Aspidieae.

Acrophorus, Presl.

This genus was founded by Presl in 1836, to receive the single species now designated *A. stipellatus*, (Wall.) Moore. It was placed by him in close relation with *Cystopteris*: but the species had previously been styled *Aspidium nodosum* by Blume. Sir Wm. Hooker merged it in *Davallia*, but evidently with some doubt, as it stands in the 'Species Filicum', vol. i, p. 157, under

the name *D. (?) nodosa*, Hook. In the 'Synopsis Filicum', however, the query is dropped, and it appears (p. 92) as *Davallia (Leucostegia) nodosa*, Hk. Diels (Engler u. Prantl, i. 4, p. 164) upholds its generic distinctness, and names it *Acrophorus nodosus*, (Bl.) Presl, giving it a place in close relation to *Cystopteris*. Christ (Farnkräuter, p. 285) also upholds the genus, but places it in near relation to *Struthiopteris*.

It is clear from these diverse opinions that this isolated species shows characters apparently in common with two widely different affinities, both characterized by superficial sori, protected by an indusial structure attached on the side of it nearest the midrib. The *Davallia*-type is, however, a derivative of the Dicksonioid stock, with marginal sori, while the affinities of *Cystopteris* and *Struthiopteris*, as long recognized and as specially indicated on the widened basis of comparison in the above pages, are with the Cyatheoid stock with superficial sori. The former approaches the latter in appearance by a gradual phyletic shifting of the sorus from the margin to the surface of the leaf, a process clearly indicated by the comparative study of *Davallia*. Consequently the position of the sorus, supported merely by the comparison of habit, will not serve to determine the true affinity in any critical case. A careful examination of the anatomy, the superficial appendages, and especially of the structure and development of the sorus and sporangia will be required for a decision in any given example.

This seems specially necessary in the case of *Acrophorus*, and in the absence of material for detailed study I am not prepared to express an opinion whether its relation is truly with *Cystopteris* or with *Davallia*. There is, however, one feature which seems to make the former affinity doubtful. In all the Gleicheniaceae and Cyatheaceae, as well as in the other allied genera with basal indusium, the sorus is seated on a vascular strand, which is continued beyond its insertion. In *Acrophorus*, as its very name implies, the vascular strand stops at the sorus, which is described as being on its tip. This is the usual, though not invariable character of Ferns with marginal sori (Hymenophyllaceae, Dicksonieae, &c.), and is mostly retained, at least in cases with relatively simple venation, even where the sorus has become superficial. This fact appears to strengthen the Davallioid alliance of *Acrophorus*, but no definite expression of opinion on the point is here given.

This is an example of many like questions which must necessarily arise in the phyletic treatment of the more advanced Ferns; for they, perhaps as frequently as any well-represented group of plants, show converging lines of specialization. So that the most advanced representatives of stocks quite distinct in origin assimilate closely to one another, and can only be disentangled by minute comparative study, bringing all possible criteria which may serve to guide a final decision.

Peranema and *Diacalpe*.

I have left the detailed examination of these genera to Mr. Davie, whose paper on these Ferns precedes this (p. 245 above). I would merely remark here that the position which has been assigned to them at the base of the Aspidieae appears to be justified on the ground of their dictyostelic structure, divided leaf-trace, open venation, abundant chaffy scales, mixed sorus, with indusium of the nature of a highly modified scale covering the vascular receptacle. Lastly, the sporangia have an annulus, at least partially interrupted at the insertion of the stalk, but showing some indications of obliquity. These features, combined with the general habit of each, so like that of certain types of *Nephrodium*, indicate a relationship which has been already recognized on less extended grounds of observation by various writers, and specially by Christ (Farnkräuter, p. 286, and preface, p. vii).

On the other hand, the character of their sorus has from their first description been held to relate the Ferns to the Cyatheaceae, and this view is stereotyped in the name *Peranema cyatheoides*, D. Don. Though the detail of the correspondence now proves not to be so close as it was earlier thought to be, still there is sufficient indication that it is in the neighbourhood of the Cyatheaceae that their natural place is to be found. This follows from the position and general character of the sorus, and especially of the indusium; from the vascular receptacle, and from the indications of a basipetal sequence in *Peranema* in the appearance of the sporangia, as described by Mr. Davie. But perhaps the most convincing evidence of a Cyatheoid affinity lies in those characters of the gametophyte which have recently been described for *Diacalpe* by Schlumberger ('Flora', 1911, p. 385). In the first place, hairs of the Cyatheoid type are present upon its prothallus, while further, the lid-cell of the antheridium is divided as it is in the Cyatheaceae, but not in the 'Polypodiaceae'. These indications, in characters which are apparently isolated and not of any great biological importance, may on that account be held to be all the more important as evidence of the Cyatheoid affinity.

Woodsia, R. Br.

This genus was founded by Robert Brown in 1815, and now includes twenty-five species, which mostly inhabit cold or temperate zones of the Northern Hemisphere, and are of small size. The axis is short and ascending, the leaves show an open Pecopterid venation, and the shoot bears superficial scales, which are a specially prominent feature in *W. polystichoides*, var. *Veitchii*. Supplies of this Fern were given from the Edinburgh Botanic Garden. The superficial sori have a basal indusium, which is often reduced to mere hairs united at their base to form a Cyatheoid cup. The details of the indusium are, however, variable in different species.

The anatomy of the stock is on the same plan as in the preceding genera. It is traversed by a dictyostele. In *W. polystichoides* the foliar gaps are relatively narrow, and from the lower region of each two leaf-trace strands arise.¹ A distinct involution of the outer surface is found just above the insertion of each leaf, similar to those in *Struthiopteris*, *Onoclea*, and *Cystopteris*.

The leaves are densely covered with broad chaffy scales; these almost hide the sori, which form regular series near the margin. Vertical sections through them show that, as in other Ferns of this relationship, the vein does not terminate in the receptacle, but may pursue a further course towards the leaf-margin. This may be quite clearly seen in sections of *Woodsia obtusa*. It is a point of difference from *Acrophorus*. The receptacle itself is only slightly raised above the leaf-surface, and from its base springs the indusium; this consists of usually four overlapping scales, which may be separate down to their very base. They are similar in structure and origin to the protective scales of the leaf-surface. Upon the receptacle the sporangia are seated. They are not numerous. Such evidence as is available goes to show that the sorus is essentially a gradate one. This conclusion coincides with the observations of Schlumberger ('Flora', 1911, p. 407, Fig. 13) on *W. ilvensis* and *W. obtusa*; for though he makes no mention in his text of the order of succession of the sporangia, his drawings show the centrally lying sporangia as the earliest and the most advanced, while the peripheral are the lower and smaller. This is also indicated by Fig. 42, which represents a drawing of the sorus of *Woodsia ilvensis* in surface view, kindly sent me by Prof. Goebel.

In my Studies, IV, p. 59, the statements as to the condition of the sorus in the genus were rather indefinite. It was stated that '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 *W. obtusa*, Torrey, from the Edinburgh Garden'. And in a later passage the sorus of the genus was held to be a 'mixed' one. Examination of a large number of sections from *Woodsia obtusa*, of which additional material was obtained from the Edinburgh Botanic Garden, has convinced me that the sorus of that species is a gradate one. No interpolation of sporangia has been seen. But the receptacle is not raised far beyond the general leaf-surface, and the basipetal sequence of sporangia is very short (Fig. 41). It thus appears that my earlier statements with regard to this genus were incorrect, being based on insufficient observation. The sorus is probably a gradate one throughout the genus. The sporangia themselves show no special point of interest, and have the usual structure of stalk, with three rows of cells.

Observations have lately been made by Schlumberger on the prothalli

¹ See Schlumberger, *Flora*, 1911, p. 409, and Fig. 14, where the vascular skeletons of *W. ilvensis* and *obtusa* are described. Compare also Luerksen, *Rab. Krypt.-Fl.*, vol. iii, p. 498.

of *Woodsia*, which bring forward some welcome characters for comparison from the gametophyte generation. In particular he draws attention (l. c., p. 385) to the characteristic multicellular hairs on the under side of the cushion in the Cyatheaceae, and shows that similar hairs are present in *Diacalpe*, and also in *Woodsia*. A still more interesting point is that the antheridia both of *Woodsia* and of *Diacalpe* have a divided lid-cell, which is the condition shown by the Cyatheaceae, while the 'Polypodiaceae' have the lid-cell undivided. When these separate and apparently immaterial features of correspondence are put in relation to the characters of the sporophyte, which also indicate a Cyatheoid affinity for these Ferns, the evidence of such a relation appears to be very strong indeed. *Woodsia* may in fact be held to be a boreal and alpine type, derived from, but closely connected with, the Cyatheoid stock. In relation to its less favourable habitat we may note the small size of the plants themselves, and the small number of sporangia in the sorus. The latter fact carries with it the flattened receptacle. But still the basipetal sequence characteristic of the Cyatheaceae is retained.

Hypoderris, R. Br.

Hypoderris is a genus founded by Robert Brown in 1830. Mettenius included it in the genus *Woodsia* ('Fil. Hort. Lips.', 1856, p. 98), from which it is, however, properly separated by its habit, and by the copious anastomosis of the veins. It is represented by three species, of which the best known is *H. Brownii*, J. Sm., a Fern which grows upon damp and shaded rocks in the Antilles. The rhizome is creeping, and bears solitary leaves right and left, while leaves and axis are invested by soft brown scales. The leaf is broadly lanceolate, with two lateral lobes at its base, which are variable in their proportion to the central lobe. The venation is reticulate, and the numerous sori, with basal indusium, are 'inserted in lines or series parallel with the primary veins upon the confluent angles of the reticulate veinlets' (Hooker, 'Sp. Fil.' vol. i, p. 57). The general habit and appearance resembles that of *Aspidium trifoliatum*, while a comparison may also be drawn as regards habit with another shade-loving Fern, viz. *Kaulfussia aesculifolia*. As in the latter Fern, the sori of *Hypoderris* show frequent and various examples of fission (compare 'Land Flora', Fig. 281).

The vascular system of the rhizome of *Hypoderris* has been examined by Schlumberger ('Flora', 1911, p. 409, and Fig. 14, 5). He found that it is traversed by a dictyostele, with large leaf-gaps and additional 'perforations'. Four vascular strands pass from each leaf-base to the subtending foliar gap, while the upper and under strands between the laterally placed leaf-gaps show wide-meshed perforations. But Schlumberger's account leaves open the relation between the four-stranded leaf-trace of *Hypoderris* and the two-stranded trace of related Ferns. I have examined the vascular system

of *Hypoderris* in material kindly supplied to me by Professor Goebel. Tangential sections of the leaf-base make it clear that the two larger strands, which are inserted higher up upon the foliar gap, represent the margins of the trace as seen in *Woodsia* or *Struthiopteris*, for they show the hooked xylems characteristic of that position. The strands inserted lower down upon the foliar gap represent the more median portions of the trace. In fact, each pair of strands right and left is representative of one of the two strands of *Woodsia*, which has become divided, and its two parts have in *Hypoderris* widely diverged. This condition, which is an advanced one, harmonizes on the one hand with the stele of the axis, with its numerous 'perforations'; and on the other it occurs together with the profuse reticulation of the veining of the lamina. In all these respects *Hypoderris* shows evidence of phyletic advance on the related genera, an advance which is also matched by the condition of its sori.

An analysis of the sorus of *Hypoderris* was published by Sir W. Hooker in his 'Genera Filicum' in 1842, Tab. I. The drawings show its characters, with the cup-like basal indusium surrounding a dense mass of sporangia. Individually the sporangia are of small size, and long-stalked. A feature which is clearly brought out by the drawings 3 and 4 of his Plate is that the sporangia of different sizes are intermixed without order, a fact which has since been frequently ignored.

The sorus of *Hypoderris* is seated with a flat receptacle upon a vein of the reticulum which is so marked a feature of the leaf in this genus. The position of the sorus relative to the vein-endings is variable. Commonly it is seated upon an arch of the reticulum. At other times it may be seated upon a twig of the reticulum, which is not terminated at the receptacle. Occasionally, however, the vein appears to end below the receptacle. But the common rule appears to be that the vein does not terminate in the receptacle of the sorus. At first the receptacle is almost even with the general surface of the leaf, and it is never much raised above it. It is shielded by the cup-like indusium before the sporangia appear. These arise sporadically, and without any obvious order, upon the receptacular surface. But as fresh sporangia continue to arise, the sorus becomes crowded. The heads of those sporangia which mature first break away from the stalk just below the capsule, leaving the lower part of their stalks as a protection to the sporangia which follow. A section through an old sorus shows accordingly a crowded condition quite similar to that of certain *Mixtae* of quite different affinity from *Hypoderris*.

The sporangia themselves are relatively small and long-stalked. Vertical sections through the sorus show that the stalks are not of uniform structure, and when the sorus is cut transversely the sections of the stalks may show three cells, or only two, or one (Fig. 43). A comparison of young developmental stages of sporangia shows that this is connected with

the initial segmentation. Three different types of segmentation are illustrated in Fig. 44, *a, b, c*. In *c* there is a relatively massive stalk, such as might be found in any of the related genera above described. But in *b* the whole sporangium is more attenuated, while at the very base of the stalk it consists of a single cell-row with transverse segmentation. In *a* this condition is still more pronounced, and doubtless the three sporangia of Fig. 44 would correspond roughly in stalk-structure to the three sections shown in Fig. 43. But the condition does not appear to be uniform throughout the length of the stalk of any given sporangium; thus in Fig. 44, *b*, the stalk would consist at its base of a single cell-row, and in its upper parts of two or even three rows. Examination of sporangia dissected out separately from a sorus show that this is actually the case, one or two of the cell-rows stopping short before the base of the stalk is reached. In fact, the condition is closely similar to that shown by Müller's drawings of *Asplenium trichomanes*, quoted by Engler u. Prantl, i, 4, p. 81, Fig. 57.

The sporangium itself is of relatively small size. The annulus is indurated on one side of the sporangium right down to the insertion of the stalk, but there interrupted. On the other side is the stomium, composed of the usual group of four cells. Attached to the stalk of most sporangia is a hair, which often shows a glandular terminal head, similar to what is seen in *Nephrodium*. This fact acquires greater point when it is remembered how like *Hypoderris* is in habit to *Aspidium trifoliatum*.

The interest of the facts thus related for *Hypoderris* lies in the comparison of like conditions in other Ferns. No one has doubted that the natural place of *Hypoderris* is with *Woodsia*, and in less near relation with other Ferns with a basal indusium. But it stands apart from them in its relatively disintegrated vascular system of stock and petiole; its broad leaves with reticulate venation; in its mixed sorus, and reduced type of sporangium. The progression has been parallel along these distinct lines of character, and the changes from type thus shown here in an isolated genus of a well-defined affinity are matched very closely by similar progressions in other types of Ferns believed to be phyletically distinct. The more frequently such parallel progressions are traced the greater is the confidence in believing them to be indications of true phyletic advance. But the question why they should run so strictly parallel remains awaiting its full physiological explanation. As to *Hypoderris* itself, it may be held to be a member of the *Woodsia* affinity, modified as a tropical shade-form. The broad reticulate leaf follows on this habit; but not so clearly the disintegration of the stele, or the mixed character of the sorus. The reduction seen in the sporangium is, however, to be related with the continued production of sporangia in the mixed sorus.

Discussion of the Phyletic Relations of the Ferns described above.

Comparison has now been made between *Lophosoria* and those Ferns with which its relationship has habitually been recognized by earlier writers in respect of various leading characters, external and internal. The result has been in the first place to confirm on every count the recognition of its place at the base of the Cyatheaceous series, while the newly acquired facts have materially strengthened the relation of these Ferns with the Gleicheniaceae. It is not necessarily to be concluded that any present Cyatheaceae were directly derived from any Gleicheniaceae ancestors such as we now see them. What is concluded is that a stock of Ferns with the creeping habit, vascular structure, and soral characters essentially like those of the living Gleicheniaceae gave rise on the one hand to the Gleicheniaceae themselves, and on the other to the Cyatheaceae.

Among the living species of *Gleichenia*, we have concluded that *G. flabellata* represents a central type, with its protostelic creeping axis, its deeply pinnate *Mertensia*-type of leaf, and its superficial, uniseriate sorus, of few, laxly-grouped sporangia, each with a large spore-output. A line of xerophytic specialization resulted in the *Eu-Gleichenia* section of the genus, still with protostelic axis, and with sorus of the same type, but with the ultimate pinnules much smaller, like shells concave downwards, protecting the sori. There is, moreover, a profuse protection of the young stems and leaves by scales, shared in less degree by *G. flabellata*; this is probably a further sign of xerophytic adaptation.

But another line of specialization was without these xerophytic signs, while it retains the more extended pinnule, and shows only hairs and no scales as dermal coverings. It is represented by *G. linearis* and *G. pectinata*. The former is anatomically and sorally the nearer to the central *Mertensia*-type. But *G. pectinata* shows complete solenostely, while it has been pointed out that its sorus had reached the practicable limit of elaboration, so long as the receptacle remains short, and the sporangium retains the distal dehiscence in a median plane. This circumstance probably blocked further progress of an otherwise successful line; in fact, *G. pectinata* may be held to represent the ultimate realization of its own type. On this view, then, the Gleicheniaceae in their modern developments represent a blind evolutionary branch.

But either an extension of the receptacle or a lateral dehiscence of the sporangium, or better, a combination of both these factors, would make further advance possible.¹ The latter only is realized in *Lophosoria*, but both are combined in the typical Cyatheaceae. All these Ferns have, however, the same position and general type of sorus as the Gleicheniaceae,

¹ A third possible factor would be an enlargement of area of the receptacle. This was probably realized in *Metaxya*, a Fern to be specially investigated later, together with other phyletic consequences believed to have eventuated along this line of advance.

as well as many other characters of structure and conformation above noted, which clearly point to a relationship. The nature of this relationship has probably been that they sprang from a common stock. But while *Gleichenia* was conservative in its sorus, it specialized in its foliar development, so as to rival even *Lygodium*. On the other hand, the Cyatheaceae adopted an extension of the receptacle, and lateral dehiscence of the sporangium, combining these advantages with reduced spore-output per sporangium. In point of habit they became upright, and many of them definitely dendroid.

It is here that the phyletic interest of *Lophosoria* comes in. Its features mark it out as a synthetic type, both anatomically and sorally. Its solenostelic structure and creeping adventitious rhizomes link on with the similar structure seen in the most advanced *Gleichenias*. Its undivided leaf-trace comes off like theirs from the stele. But its internodes are short in the upright axis, though the leaf-gaps rarely if ever overlap, so that there is not actual dictyostely. Further, the meristele of its larger leaves may show a simple but temporary division into three parts, which anticipates the greater subdivision of the leaf-trace in *Alsophila* and *Cyathea*. The dermal appendages of *Lophosoria* are hairs only, like the most advanced *Gleichenias*. Scales are associated with the hairs in the definitely dendroid Cyatheaceae. There is thus a parallel progression in this apparently trivial character also. But it is most clearly in the sorus that *Lophosoria* shows its synthetic character. For while retaining the simple sorus of *Gleichenia* without extension of the receptacle in height or in area, it shows the lateral dehiscence of the sporangia. Thus anatomically and sorally it occupies an intermediate position.

It may accordingly be held that *Lophosoria* is a synthetic type, and represents a phyletically early condition of Cyatheoid development. In relation to it the three leading genera are readily seriated phyletically, *Alsophila* being the nearest to *Lophosoria*, *Hemitelia* taking a middle position, and *Cyathea* representing the most advanced type. This conclusion may be based partly on the sorus, partly on the anatomy, and the following brief statement will show that there is a parallelism in the progression in both of these respects.

The description given by Gwynne-Vaughan of the anatomy of the young plant of *Alsophila excelsa* shows that certain stages of structure believed to indicate a natural phyletic progression are passed through with varying rapidity by the young plant of that species ('Annals of Botany', xvii, pp. 709-111). It is at first protostelic; it then becomes solenostelic; this again merges into the dictyostelic structure by overlapping of the leaf-gaps; and finally the first indication of the internal vascular strands makes its appearance 'at about the tenth leaf'. Comparing this ontogeny with the vascular structure in the series we are contemplating, the first stage finds its correlative in *G. flabellata*; the second in *G. pectinata*, and also in

Lophosoria, with a nearer approach in the latter to dictyostely; the third stage, that of dictyostely, is not reached in this plant, though it is rapidly arrived at by *Alsophila* and both of the other genera of Cyatheaceae. These also show the fourth stage of complexity, viz. the addition of internal vascular strands, which are absent in the solenostelic *Lophosoria*. Gwynne-Vaughan remarks (l. c., p. 712) that 'it should be noted that in this plant (i. e. *A. excelsa*) the internal strands do not appear at all until the ordinary stelar cylinder has become more or less dictyostelic'. The fact that they are absent in *Lophosoria*, but present in the mature axes of *Alsophila*,¹ of *Hemitelia*,² and in *Cyathea*, appears to indicate that where the stem is massive and dictyostelic there accessory strands are liable to be present; where the leaf-gaps do not overlap, accessory strands are absent, even though the axis may be of large bulk as it is in *Lophosoria*. It thus appears that the phyletic progression we are contemplating is in direct accord with the progress in complexity of the vascular structure of the plants involved.

A similar phyletic progression, which shows parallel steps to those of anatomy, is to be traced in the sori, which are throughout superficial in position. And this will be specially evident in the details of their protection. In the protostelic *G. flabellata* the sorus is radiate-uniseriate, with 3-5 sporangia, and a spore-output of typically 512-1,024. In *G. linearis*, which is still protostelic, the sporangia are more numerous (10-12) and smaller, the centre of the sorus being usually occupied by one or more; the spore-output is 236 or more. In *G. pectinata*, which is solenostelic, the sorus is crowded with 10-15 sporangia, which are variable in size, and the output of the larger approximates to, but does not reach 512, while that of the smaller approximates to 256. In none of these are hairs a feature of the sorus. The reduction of the spore-output runs roughly, though not with numerical exactness, parallel to the increasing number of the sporangia in the sorus, and to the anatomical advance.

There is a marked break in passing to *Lophosoria*. Its axis is solenostelic as before, but much more massive, while after a short horizontal course the buds become upright and subdendroid. The sorus is constructed on the same plan as that of the more advanced *Gleichenias*, and all the sporangia are simultaneous in their appearance. But the sporangia have lateral dehiscence, and their spore-output is only 64, while numerous simple hairs are associated with the sporangia. *Alsophila* is the Cyatheaceous genus which is most nearly allied to *Lophosoria*. Its sorus has no protection, excepting numerous hairs which resemble those of *Lophosoria*. It has, however, a more or less pronounced basipetal succession of its more numerous sporangia, which are individually smaller, have lateral dehiscence, and

¹ This has been observed in *Alsophila crinita* in addition to cases already recorded.

² This has been observed in a large specimen of *H. (Amphicosmia) Walkerae* from Ceylon.

a spore-output of approximately 64. *Alsophila* has a definitely dendroid habit. The protostelic and solenostelic stages are quickly passed over in the young axis, and a dictyostelic structure is adopted, with internal accessory bundles. Superficially it bears broad scales as well as hairs, and the former at the leaf-bases are, as in *G. pectinata*, borne on peg-like emergences. These characters collectively indicate for *Alsophila* a state of advance upon what is seen in *Lophosoria*.

Hemitelia shares in the main the anatomical and soral characters of *Alsophila*, but its distinguishing feature is the 'indusium'. Christ ('Farnkräuter', p. 329) describes the genus appositely as a small one, 'which as regards the indusium is midway between *Cyathea* and *Alsophila*, since the sorus is in fact naked above, but is provided at the base with a scale-like rudimentary indusium'. This indusium is described as variable in size by various writers. In form and structure it is very similar to the scales found on the surface of stem and leaf, and the probable view which follows from this fact is that it simply represents one of these scales turned to a special protective use.

In *Cyathea* the most specialized type of the series is seen, with lofty dendroid habit, complex structure of the axis, profuse covering of the surface of axis and leaf with chaffy scales. The sori are gradate, and are protected and sometimes completely covered in by the basal, cup-like indusium. This is clearly comparable with that of *Hemitelia*, but it has lost its scale-like character, and is usually developed equally all round the sorus. The sporangia are of the same type as in the other genera, but in *C. dealbata* they are of specially small size, and show a spore-output reduced to the unusually low figures of 16, or even 8. These characters collectively indicate that *Cyathea* is the most specialized genus of the whole series.

When the parallelism of the external, the anatomical, and the soral facts for the sequence of Ferns thus laid out is fully taken into account, it seems impossible to doubt that in essentials it illustrates a true phyletic progression which has taken place. It is not asserted that any modern *Gleichenia* was the progenitor of *Lophosoria* or of any other Cyatheoid Fern. Probably the *Gleichenias* as we know them are a blind branch. What is concluded is that from an essentially *Gleichenioid* type long ago the Cyatheoid type of Ferns originated, and an essential link in the progression is supplied by *Lophosoria*. The progression involves a gradual change of habit from a creeping type with isolated leaves borne by an elongated rhizome, to an erect type which includes the largest of the Tree-Ferns. It necessarily follows that here at least the upright axis is a secondary result of evolution. A similar comparison applied among the members of the quite distinct sequence of the *Dicksonieae* leads to a like result; this will be taken up in detail on a subsequent occasion. From

both sources the result is arrived at that the dendroid character is secondary for the Gradate Ferns.¹

It also appears from the sequence in question that a natural progression is illustrated from the protostelic to the solenostelic, and finally to the dictyostelic type of vascular arrangement. Lastly, there is the further step to a dictyostelic state with accessory strands in pith and cortex. There is probably no series of nearly related Ferns which shows such progressions as these so clearly.

It is also indicated that while the hair is present in the lower members of the sequence, broad scales become a later feature, and that though these at their first appearance in *Alsophila* do not form an 'indusium', in the more advanced types they become specialized for that duty.

Finally, the sequence illustrates the progression from the simple to the gradate sorus, and from sporangia with large spore-output and median dehiscence to those with greatly restricted output and lateral dehiscence. It is the consistent parallelism of all these progressions, in characters physiologically quite distinct from one another, which gives them their special cogency as evidence, and forbids any of the progressions being read in converse.

Unfortunately the evidence from the fossils, which would be so valuable an adjunct to comparison, and especially in deciding whether or not the sequences contemplated were really progressive, is not of a distinctive character. As to the Cyatheaceae, Seward states ('Fossil Plants', vol. ii, p. 366) that 'it is not until we reach the Jurassic Period that trustworthy data are obtained'. The evidence as to the existence of the Gleicheniaceae, such as we at present know them, earlier than the Jurassic Period, where they are certainly represented, is not convincing. It turns upon the interpretation of specimens of *Oligocarpia*, which bear sori with a small number of sporangia, and have been referred by some authors to the Gleicheniaceae. But opinion as to their Gleicheniaceous character is divided. Zeiller and Scott (see Seward, l. c., p. 352) uphold the presence of an annulus such as would be indicative of a Gleicheniaceous affinity. But this is not admitted by Solms-Laubach, Stur, or Schenk. It cannot therefore be used as direct evidence here. Nevertheless the comparative considerations which have been advanced would make the occurrence of ancestral representatives of the family earlier than the Jurassic Period seem probable. And the character of the sorus of *Oligocarpia* suggests at least some such ancestral form, whether or not the sporangia have the exact type of annulus now recognized as characteristic of the Gleicheniaceae. There is no doubt that they had the median dehiscence; this is clear from specimens shown me by Dr. Kidston. There is, however, reason to think that the annulus in these early types may not have consisted of a single row of

¹ Compare footnote on p. 293, above; also Ann. of Bot., xxv, pp. 567-8.

cells, as is the case in the modern Gleicheniaceae, but of several rows. This has already been suggested by Dr. Kidston ('Les Végétaux houillers', Bruxelles, 1909, p. 35).

As regards the remaining genera with superficial sori and basal indusium, the details described above have only served to strengthen their relation to the Cyatheaceae, a relationship which has never been in doubt except in the case of *Acrophorus* and *Cystopteris*. The position of the former must remain uncertain until it has been properly re-examined. But of the Cyatheoid affinity of *Cystopteris* there can now be little doubt. Its sorus is superficial in origin, as it is in all of these Ferns. The demonstration of its basipetal sequence of sporangia upon the receptacle, which has itself become lop-sided in accordance with the lateral attachment of the indusium, combined with the superficial position, is distinctive; while the anatomy of the stock and petiole, so like that of *Struthiopteris*, gives independent and cogent support to the relationship suggested.

The importance of this conclusion lies, however, in the consequences which follow from it. The comparison of *Cystopteris* with the Aspidieae dates back to the time of Swartz and of Presl. The similarity of habit is unmistakable; in point of vascular structure *Struthiopteris* and *Cystopteris* compare very closely with such a type as *Nephrodium Oreopteris*. The sori of these Ferns are alike in position, and in their indusium, to those of the Aspidieae. Both have also a vascular receptacle. The similarity of the young sorus of *Nephrodium Filix-mas* when cut in median section to that of *Cystopteris* appears clearly from a comparison of Figs. 45, 46 of the former Fern with Fig. 38, *b*, of the latter. But while we thus compare its sorus with that of *Nephrodium*, it is to be borne in mind that the one is gradate in the sequence of its sporangia, the other mixed. The conclusion which naturally follows on such considerations is that there has been a further phyletic progression—the recognition of which is facilitated by the living genera *Struthiopteris* and *Cystopteris*—from Cyatheoid derivatives to certain Aspidieae, by the assumption of a mixed character of the sorus. Such a progression has already been recognized within this very sequence, in *Hypoderris*, while *Peranema* and *Diacalpe*, which are shown in Mr. Davie's paper (p. 245) to have mixed sori and a vascular system closely resembling *Nephrodium*, have in the form of the sorus and in the basal indusium clear Cyatheoid characters. As Mr. Davie justly points out, between them *Peranema* and *Diacalpe* seem to unite all the intermediate features between the Cyatheaceae and the Aspidieae. A similar transition from gradate to a mixed type of sorus is believed to have occurred in several other evolutionary lines. This change appears in the present case to have gone along with a flattening of the receptacle between the indusium and the leaf-surface. A further step was the lateral extension of the sporangium-bearing surface right and left, in the direction of the midrib of the pinnule,

so that it took a horseshoe form, the indusium following suit. And so the characteristic Nephroidoid sorus may be held to represent a flattened modification of the Cyatheoid type. A further step is seen in *Polystichum*, by the junction of the two lateral arms of the receptacle on the side next the midrib of the pinnule to form a complete ring. The indusium again following suit, it now appears in the well-known shuttlecock form. The last step is in the abortion of the indusium in certain derivative forms, giving again a 'Polypodioid' sorus of simple circular outline, almost like that of *Alsophila*. It would be out of place here to attempt to trace the various evolutionary lines within the Aspidieae.¹ It must suffice to have recognized the probability that they constitute a great group of Filicales, phyletically related with the Cyatheaceae, and ultimately with the Gleicheniaceae.

The biological advantages of the Nephroidoid type of sorus over the Cyatheoid are obvious. First there is the general advantage which a mixed sorus has over a gradate one, that while it spreads the physiological drain over a long period, it makes the best possible use of a limited length of receptacle. But a second advantage not hitherto recognized is the greater convenience in packing during the circinate condition of the young leaf. In the gradate sorus pressure of the next outer coil of the spiral on the apex of the sorus would tend to crush the first formed sporangia, and evidence of this is sometimes to be seen. This is avoided by the flattened form assumed by the sorus, as seen in *Cystopteris* or *Nephrodium*. But a sacrifice of sporangial space is made in *Cystopteris*. This is amply made up for by the ring-like extension of the receptacle in *Nephrodium* and *Polystichum*, as well as by the continued production of sporangia in their mixed sorus. Thus it appears that the modifications, which are believed to have been phyletic advances, show that physiological advantage is gained by them. This increases the probability that they are rightly so recognized.

The relation of *Hypoderris* to *Woodsia* has always been admitted, and the facts here given tend to strengthen the affinity. But *Woodsia* has a gradate sorus, though the sequence is not long continued, while *Hypoderris*, which is more advanced in vascular structure, in venation, and in foliar character, has a mixed sorus. There can be little doubt that a like soral progression from the gradate to the mixed state has occurred here to that in *Peranema* and *Diacalpe*, or in *Nephrodium*. There is, however, no reason to think that any of these genera had any place in the descent of *Hypoderris*. The conclusion must then be that *Hypoderris* illustrates another and a distinct progression from the gradate to the mixed sorus. It is, in fact, becoming plain that this transition has happened not once only, or twice, but by many parallel progressions.

There does not appear to be any sufficient reason for holding that any

¹ Compare C. Christensen, Biologiske Arbejder, Nov. 1911.

two of the pairs of genera discussed above, viz. *Struthiopteris* and *Onoclea*—*Peranema* and *Diacalpe*—*Woodsia* and *Hypoderris*—*Cystopteris* and *Acrophorus*—were related in the sense of being successive steps in a simple phyletic line. That is to say, no one of these groups can be held as the actual ancestors of another. It has been remarked above that none of these Ferns is really primitive. All show indications of a middle position in the general scale of the Filicales. The source from which they spread has without doubt been related to that of the Cyatheaceae, as shown by habit, by anatomy, by sorus, and in some cases by the details of the gametophyte. But in view of the anatomical and soral characters combined, it is difficult to relate any of them to any definite genus of the Cyatheaceae as we see them now. These Ferns with basal sori appear collectively to form a brush of separate minor lines of descent, related one to another by common origin, but separately specialized according to their habitat. The Cyatheaceae are essentially the intertropical forest representatives, showing increasing specialization in soral protection, in accordance with their dendroid habit. *Struthiopteris* and *Onoclea* are forms with still more special protection of the sori by incurving leaf-margins, in relation to their northern and mountain habitat. Similar circumstances have probably influenced *Peranema* and *Diacalpe*, and led to specialization of their sori along a distinct line of their own. *Woodsia* is a boreal dwarf type, and *Hypoderris* a type of tropical shade. *Cystopteris* is a world-wide type, but with its head-quarters in the temperate zones of both hemispheres. It is specially marked by its hardihood and resistance to alpine extremes. Most of the smaller genera are deciduous according to season, a character clearly indicating their specialization for life under marked seasonal change. This is in contrast to their larger and more successful correlatives, the intertropical Cyatheaceae, which maintain their constant tuft of leaves.

The Cyatheaceae are clearly the most successful, as measured by size, as well as by number of species. They were probably also the earliest type. The smaller genera show by their paucity of species, and in some cases by their limited spread, that they have met their external circumstances with only partial success. But indirectly in relation to two of them great phyletic developments have probably arisen. In near connexion with *Cystopteris* (and probably also in some relation with *Peranema* and *Diacalpe*), the great sequence of the Aspidieae has come into existence. Similarly, in relation to *Struthiopteris* has arisen the successful sequence of *Lomaria*, *Woodwardia*, and *Doodya*. Here it must suffice merely to suggest these lines of further progress, and the full discussion of them must be left over for a future occasion. The object here is to indicate that the Cyatheoid type, with gradate sorus and basal indusium, was not a blind or final evolutionary line, though very likely the genera of Cyatheaceae, as we see them to-day, were the ultimate exponents of it. Modifications, and espe-

cially the introduction of the mixed sorus, seem to have given a new phyletic impetus to some of the derivative forms, which has eventuated in the great Aspidioid sequence.

Returning lastly to the criteria above cited, we find the following progressions illustrated in our series :

(i) The dichotomous branching is frequent in the Gleicheniaceae, but becomes rarer in the higher types. The creeping axis of the earlier becomes in certain later types ascending or erect.

(ii) The peculiarities of the original Gleicheniaceae type of leaf are shown in reminiscent details in the Cyatheaceae, but lost elsewhere.

(iii) There is a progression from primitive hairs to scales, the former being characteristic of the lower, while all the higher terms of the series show the latter.

(iv) The vascular system, starting as a protostele in the *Mertensia* section of *Gleichenia*, becomes solenostelic in *G. pectinata* and *Lophosoria*, but is dictyostelic in all the rest. Special accessory strands occur in the Cyatheaceae. The foliar trace is correspondingly broken up into separate strands in the higher terms of the series.

(v) The sorus is superficial in all these Ferns, and is not distal on its supporting vein (the case of *Acrophorus* being left in doubt). It shows progression from a simple type in *Gleichenia* and *Lophosoria* to the gradate in Cyatheaceae, *Struthiopteris*, *Onoclea*, *Woodsia*, and *Cystopteris*. Finally, it becomes mixed in *Hypoderris*, *Peranema*, and *Diacalpe*, a condition leading probably to that of the Aspidieae.

(vi) The sporangia are large in the Gleicheniaceae, few in number, with large spore-output and median dehiscence. The size and spore-output fall in *G. pectinata*. In *Lophosoria* it is already of the number 64, and the dehiscence is lateral. In the Cyatheaceae the spore-number may fall to even lower figures, with oblique annulus and lateral dehiscence. But finally the annulus becomes almost vertical, and interrupted at the stalk in all the highest terms of the series.

(vii) The antheridium shows reduction in number of the spermatozoids which is roughly parallel with the reduction in the spore-number in the higher terms of the series. This goes with structural simplification, especially seen in the final absence of division in the cap-cell in the most advanced types.

It is believed that the Ferns here treated constitute a true phylum, though they probably include a brush of minor phyletic lines. This view is based primarily upon the constancy in the superficial position of the rounded sorus, borne not distally upon a vein, and the basal insertion of the indusium where present ; also upon the characters of the sporangia themselves. A substantial parallelism of progression has been traced within the phylum in respect of the characters of external form, of dermal

appendages, of anatomy, of soral construction, and of detail of the sporangia, together with certain gametophytic features. The constancy of the parallelism in features functionally so distinct is held to give just ground for drawing the phyletic conclusions sketched above. Further, it has been shown that they are in accord with physiological probability, and that the fossil record, so far as the known facts bear upon the question, supports the phyletic story thus reconstructed.

Accordingly it is held that in this phylum, which is believed to be quite distinct from that of the Ferns with originally marginal sori, a progression has been traced which extends from primitive forms showing the simple sorus, the protostelic axis, and undivided leaf-trace, to those with a mixed sorus, a dictyostelic axis, and highly divided leaf-trace; while in a middle position lie examples with a gradate sorus, and showing various conditions of solenostely in the axis, and of subdivision of the extended meristele of the petiole. Starting with the ancient *Gleichenia*-ceous type, we have arrived at the *Aspidieae* as relatively modern representatives of the phylum, while the *Cyatheaceae* and their smaller correlatives take a middle position. No attempt has, however, been made here to trace critically the ultimate phyletic derivatives of the *Aspidieae*. This must be left over for further investigation.

The relationships thus recognized have been more or less clearly indicated by various systematic writers. What has been attempted here has been to widen the scientific basis upon which such conclusions ought to be founded. There is accordingly no striking change in nomenclature, beyond the upholding of *Lophosoria* as a substantive genus, quite distinct from *Alsophila*, but related to it. The conclusions arrived at should, however, have the effect of recommending a grouping of the families involved in their probable phyletic sequence, thus: *Gleicheniaceae*—*Cyatheaceae* (with minor groups, e. g. *Woodsieae*, &c.)—*Aspidieae*.

DESCRIPTION OF FIGURES IN PLATES XXX-XXXVI.

Illustrating Professor Bower's paper on *Lophosoria* and its relation to other Ferns.

PLATE XXX.

Fig. A. Hairs of peculiar form, from the base of the leaf of *Gleichenia pectinata*. Each hair is seated on a massive emergence, from which it is easily detached, the emergence remaining as a hard peg-like projection. $\times 50$.

Fig. B. Part of petiole of *Hemitelia horrida*, bearing prickles, or peg-like emergences, and upon the tip of each is balanced a flattened scale, corresponding to the branched hairs in *G. pectinata*. Slightly enlarged.

Fig. C. Pinnule of *Gleichenia linearis*, showing venation and mature sori. Some of the sporangia are shown to have dehisced. Enlarged.

Fig. D. A single sorus of *Gleichenia linearis* on a larger scale, showing the disposition of the sporangia, several of which have opened by a median slit. Enlarged.

Fig. E. Pinnule of *Gleichenia pectinata*, showing the venation and mature sori. Some of the sporangia are shown to have dehisced. Enlarged.

PLATE XXXI.

Fig. F. A single sorus of *Gleichenia pectinata*, showing the sporangia so closely packed as to be flattened against one another. One has already dehisced. Note the inverted position of one of the outer sporangia on the right-hand side. Enlarged.

Fig. G. Upright stock of *Lophosoria*, after removal of the hairy covering. The erect appendages are all foliar, of which those inserted lower down are abortive, while those higher up are developed. From the base of several of them, but not all, arise the horizontal, solenostelic runners. Note the emergences on the bases of the fully developed leaves. From drawing by Mr. Thompson. Half natural size.

Fig. H. Pinnule of *Lophosoria pruinata*, showing venation and sori. Enlarged.

Fig. I. A single sorus of *Lophosoria*, showing the small number of sporangia, with their regular orientation. Each sporangium has its annulus apparently complete, the stomium being lateral, and therefore out of sight. Enlarged.

PLATE XXXII.

Fig. K. Dissection of a large stock of *Lophosoria pruinata*, showing the vascular solenostele exposed, by the removal of all superficial tissues. It is clear that the foliar gaps do not overlap, and transverse sections anywhere in the internode will show the complete solenostele. From drawing by Mr. Thompson. Natural size.

Fig. L. Dissection of a smaller shoot of *Lophosoria pruinata*, showing the vascular system exposed. The internodes are shorter than in Fig. K. Note the vascular supply to the runners arising horizontally from the bases of many of the leaf-traces. From a drawing by Mr. Thompson. Natural size.

Fig. M. Double-headed specimen of *Cyathea dealbata* in the Glasgow Botanic Garden. It is probably a dichotomy.

PLATE XXXIII.

Fig. N. Plant of *Hemitelia setosa* in Edinburgh Botanic Garden, showing numerous 'aphlebioid' pinnae. From a photograph prepared by the direction of Professor Balfour.

Fig. O. Plant of *Alsophila* sp. in Glasgow Botanic Garden, showing basal pinnae, comparable with the 'aphlebiae' of *Hemitelia*.

PLATE XXXIV.

Fig. 1. Very young sorus of *Gleichenia pectinata*, seen in vertical section, before the sporangia have been initiated. $\times 400$.

Fig. 2. A similar sorus, rather older. $\times 400$.

Fig. 3. A similar section of an older sorus, on which the sporangia have already been initiated. $\times 400$.

Fig. 4. A similar section, showing some difference of age of the sporangia borne upon the same sorus. $\times 400$.

Fig. 5. A young sporangium of *Gleichenia pectinata*, showing a typical segmentation of the relatively massive stalk. $\times 400$.

Fig. 6. Section cut through a sporangium so as to traverse the sporogenous tissue in a plane transverse to the axis of the sporangium. The number of the spore-mother-cells is fifteen. $\times 400$.

Fig. 7. A similar section cut in the median plane of the sporangium, and traversing twenty spore-mother-cells. $\times 400$.

Fig. 8. A similar section, showing the spore-mother-cells separated and rounded off. $\times 400$.

Fig. 9. A large stem of *Lophosoria* cut transversely, and represented natural size. A leaf-trace, subdivided into three strands, has recently been given off, leaving an open foliar gap, while preparation is being made for another opposite the mark $\times$.

Fig. 10. Transverse section of a runner of *Lophosoria*, showing a leaf-trace being given off from the solenostele. Note that the separation of the two margins is not simultaneous. Slightly enlarged.

Fig. 11. (i-v.) A series of transverse sections through a runner of *Lophosoria*. (i) is the lowest, and the series illustrates the successive stages of separation of a leaf-trace from the solenostele. In (v) the ring is again completely closed. Note that the leaf-traces in (i) and (iv) have their margins united to form a ring: this has only been observed in the traces of arrested leaves. Slightly enlarged.

Fig. 12. (i-iii.) Successive sections from below upwards transversely through an axis of *Lophosoria*, showing the relation of the vascular supply of a runner to that of the axis and leaf. *b* indicates the runner itself. $\times 4$.

Fig. 13. (i-iii.) Tangential sections through the base of insertion of a runner upon the leaf-base to which it is related. (i) shows the runner itself, with its solenostele; (ii) shows the solenostele now connected with the leaf-trace, which being cut tangentially appears as a broad sheet of vascular tissue. Slightly enlarged.

Fig. 13 *bis*. *a, b*. Transverse sections of the petiole of *Lophosoria*. *a* is from a point near the base, and shows the trace divided into three strands, while opposite the gap between them there is on either side an interruption of the superficial sclerenchyma for ventilation purposes. *b* was taken at a point higher up, and the trace is here a single continuous strand. $\times 4$.

PLATE XXXV.

Fig. 14. (i-vii.) Series of transverse sections of the rachis of *Lophosoria*, successively from below upwards, showing the origin of the pinna-trace. $\times 4$.

Fig. 15. (i-vii.) Series of transverse sections of the rachis of *Gleichenia linearis*, for comparison with Fig. 14, showing the origin of the pinna-trace. $\times 4$.

Fig. 16. Hairs from the sorus of *Lophosoria*, which are unbranched, and not obviously glandular. $\times 100$.

Fig. 17. Transverse section of the stalk of a sporangium, showing its relatively massive character. $\times 200$.

Fig. 18. Sporangium of *Lophosoria* presenting its 'peripheral' face, and showing that the annulus is uninterrupted and the dehiscence lateral, while the area surrounded by the annulus is very large. $\times 150$.

Fig. 19. A similar sporangium presenting its 'central' face. $\times 150$.

Fig. 20. A similar sporangium seen in lateral view, presenting the side which bears the stomium. The lower face, as seen in the drawing, would be opposite the surface of the leaf. $\times 150$.

Fig. 21. Section vertically through a very young sorus of *Lophosoria*, taken so as to include the margin of the pinnule. $\times 400$.

Fig. 22. Section of a similar sorus in a direction at right angles to that of Fig. 21. $\times 400$.

Fig. 23. Transverse section of a similar sorus. The cells marked $\times$ will produce sporangia. $\times 400$.

Fig. 24. Vertical section of a rather older sorus, in which the sporangia and hairs are becoming apparent. $\times 400$.

Figs. 25-7. Longitudinal sections of young sporangia of *Lophosoria*, showing details of their segmentation, and the hairs which accompany them. $\times 400$.

Fig. 28. Vertical section through a young sorus of *Lophosoria*, so as to follow the course of the vascular strand which supplies the receptacle. Two sporangia are traversed, and many of the simple hairs. $\times 200$.

Fig. 29. A similar sorus cut transversely to the course of the vascular strand, showing three sporangia and the hairs as before. $\times 200$.

Fig. 30. Vertical section through a sporangium of medium age. $\times 200$.

Fig. 31. Transverse section through a sporangium of like age, showing the usual number of spore-mother-cells. $\times 200$.

Fig. 32. A similar section, showing the unusual number of nine. $\times 200$.

Fig. 33. Vertical section through an almost mature sorus of *Lophosoria*. The vascular supply into the receptacle is shown, and four sporangia, together with numerous hairs. The spores are still in tetrads. Note that the orientation of the outer two sporangia, as shown by the position of the

large cells of the annulus, is according to the type for *Gleichenia*, but that the inner sporangia do not maintain that regularity. $\times 100$.

Fig. 34. The very characteristic spores of *Lophosoria*, and their germination. $\times 250$.

PLATE XXXVI.

Fig. 35. A young prothallus of *Lophosoria*, which has just begun to form antheridia. $\times 66$.

Fig. 36. The venation of the fertile pinna of *Struthiopteris orientalis*; the dots on the veins indicate the receptacles. Enlarged.

Fig. 37. Vertical section of a sorus of *Struthiopteris orientalis*, from a plant grown in the Glasgow Botanic Garden. It shows the indusium covering the basipetal sorus, and itself overlapped by the leaf-margin. Note that the vascular strand extends beyond the insertion of the receptacle. $\times 160$.

Fig. 37 *bis*. Another example, showing clearly the basipetal sequence of the sporangia. $\times 160$.

Fig. 38. *a, b*. Vertical sections of the sorus of *Cystopteris fragilis*. *a* cuts the leaf-lobe transversely; *b* cuts it longitudinally, so as to include the leaf-margin. The first sporangium appears in a median position, terminal on the convex receptacle. $\times 250$.

Fig. 39. Section of an older stage cut as in Fig. 38 *a*, or as indicated by the line crossing Fig. 40 vertically. The median sporangia, which are the oldest, have been cut through their stalks only; the lateral ones, being shorter, have been cut through their heads. The indusium forms an efficient covering. $\times 250$.

Fig. 40. Section of a sorus of *Cystopteris fragilis* corresponding to that of Fig. 38, but older. It shows clearly the basipetal succession of the sporangia, but only on one side of the receptacle. $\times 250$.

Fig. 41. Vertical section through a sorus of *Woodsia obtusa*, showing the vascular supply into the receptacle, the basal indusium, and the basipetal succession of the sporangia. $\times 160$.

Fig. 42. Very young sorus of *Woodsia hyperborea*, seen in surface view. *Sp.* indicates the sporangia. *i.i.* indicate the beginnings of the indusium. From a drawing kindly lent by Professor von Goebel.

Fig. 43. *a, b, c*. Transverse sections of the stalks of sporangia of *Hypoderris*, showing the differences which exist in complexity of the stalk, which shows sometimes three, sometimes two, or one cell in section. $\times 250$.

Fig. 44. *a, b, c*. Three types of sporangia, showing different segmentations, which tally with what is seen in Fig. 43. $\times 250$.

Figs. 45 and 46. Vertical sections of young sori of *Nephrodium Filix-mas*, cut in a direction corresponding to that of the figure (38, *b*) of *Cystopteris fragilis*. The similarity of structure is obvious. $\times 250$.

FIG. A

FIG. D

FIG. B

FIG. C

FIG. E

FIG. F

FIG. G

FIG. H

FIG. I

FIG. K

FIG. L

FIG. M

BOWER—LOPHOSORIA

FIG. N

FIG. O

BOWER—LOPHOSORIA

F.O.B. del.

F.O.B. del.

F. O. B. del.

Huth hth et imp.

F. O. B. del.

37. bis.

41.

40.

c

43.

b

a

42.

44.
b

c

45.

46.

F O B. del.

Huth lith et imp.

Bower, F. O. 1912. "Studies in the phylogeny of the Filicales.II Lophosoria, and its relation to the Cyatheoideae and other ferns." *Annals of botany* 26, 269–323. <https://doi.org/10.1093/oxfordjournals.aob.a089393>.

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