NOTES ON THE MORPHOLOGY OF THE SPORANGIUM-BEARING ORGANS OF THE LYCOPODIACEÆ.

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[WITH PLATES II. AND III.]

THE cones of several of the species described below were kindly sent by Mr. E. C. Jones, at the request of Professor Seward; others were obtained from material collected by Professor Yapp in the Malay Peninsula, by Mr. Stanley Gardiner in Fiji, and by Dr. Benson in Fiji, while Professor Weiss was so good as to supply me with specimens of *Phylloglossum*. Most of the plants examined were preserved in spirit, but, in a few cases, herbarium specimens alone were available; the double stain, iodine green and eosin, was chiefly employed.

My thanks are due to Professor Seward, both for obtaining material for me, and for his kind interest in my work.

I.—GENERAL DESCRIPTION OF A LYCOPODIAN SPOROPHYLL.

Each sporophyll is a leaf-like organ, more or less modified in accordance with its special functions, and bearing a single, stalked, tangentially placed sporangium, the position of which varies in the different species in its relations to the sporophyll and the main axis. The vascular bundle which supplies the sporophyll arises some distance below its base, from the stele; it pursues an obliquely upward course into the stalk, and traverses the whole length of the sporophyll, but does not give off a branch to the sporangium pedicel. In the latter, however, some cells with lignified walls are usually found, these cells often resembling in character those of the layer surrounding the stele in the axis of the cone.

The sporophyll encloses and protects the sporangium to a varying extent in the different species; its epidermis, especially on the abaxial surface, is usually composed of cells with strongly cuticularised walls; a mucilage cavity is often found in its basal portion; it may or may not be furnished with a flap which extends downwards from its dorsal surface¹ and protects the sporangium immediately below, giving to the sporophyll a peltate character.

¹ Goebel, *Organography* II., p. 503.

The sporangium dehisces by a longitudinal slit, along a line of cells which constitute a more or less definite annulus,¹ the position of which varies in the different species.² The wall of the sporangium is composed of two or more layers of cells, which generally increase in number towards the base of the sporangium, and a tapetum. The cells of the outer layer have their walls lignified in unequal strips. In a radial section of the cone the sporangium is a simple oval in shape, but in a section tangential to the axis, the sporangium is much elongated and is usually described as "saddle-shaped."

II.—GENUS I. PHYLLOGLOSSUM.

The cones of this genus have already been described by Bower.³ It is only necessary to remark here that the sporophylls differ slightly from the vegetative leaves, and that they are aggregated to form a definite cone. Each sporophyll is short and simple, rather thick, with incurved edges and a very short dorsal out-growth (Text-fig. 3) which partly protect the sporangium.⁴ It strongly

Text-fig. 3. Longitudinal section of sporophyll of *Phylloglossum*; shewing axillary sporangium. F., Small dorsal flap of sporophyll. B., Lignified cells in sporangium pedicel.

resembles that of *L. dalhousianum* (Pl. II., Fig. 4b), also, more remotely, that of *L. inundatum*, (Text-fig. 5). The sporangium arises in the axil of the sporophyll, but does not fit closely into the base of the sporophyll immediately above; a considerable portion of the sporangium is thus left exposed. Dehiscence of the sporangium takes place by an apical longitudinal slit.

A longitudinal section (Text-fig. 3) shews that the sporangium is borne on a short stalk in which a few cells with slightly lignified walls are often present.

¹ Goebel, Organography, II., p. 579, and cf. Smith, 1900

² Engler and Prantl, Teil I., Abt. 3, pp. 586 and 587.

³ Bower, 1885.

⁴ cf. Engler and Prantl, Teil I., Abt. 3, p. 576, Fig. 362 c.

III.—GENUS II. LYCOPodium.

I propose to follow Engler and Prantl's¹ classification of the genus *Lycopodium*, for, although this was chiefly based on external characters, it is interesting to find it generally firmly supported by the more minute study of the sporangium-bearing organs. Baker's arrangement², is found to be far less useful for the present purpose.

A. *Urostachya*, [*Selago* and *Phlegmaria* (Baker)].

(i) *a. Euselago*. It is characteristic of this group that any or all of the leaves may be fertile; the sporophylls are closely similar to the vegetative leaves and are not aggregated to form a definite cone. Fig. 1A, Pl. II. is drawn from the apical region of a plant of *L. selago*, showing the simple, crowded sporophylls, bearing sporangia which have no special protective apparatus but are exposed between the sporophylls. The drawings of separate sporophylls of *L. selago*, (Pl. II., Fig. 1. B, c) and *L. serratum*, (Pl. II., Fig. 1), show still more clearly the unprotected condition of the sporangium.

The position of the young sporangial rudiment was studied at the apex of a young plant of *L. selago*, (Pl. II., Fig. 1). It is seen that the young sporangium can here hardly be looked upon as foliar in origin, for it appears to arise from the meristematic tissue of the cone-axis in the axil of the sporophyll. Owing to the growth, later, of all the tissues except those between the sporangium and the leaf immediately below it, these two organs appear in the adult far more obviously associated than they were when young.³

The sporangia of the species belonging to this group are all large and are borne on stalks of varying length; these being shortest in *L. selago*, moderately long in *tetragonum*, *fontinalis*, and *lucidulum*, and much more elongated in *quadrangulum*, *dichotomum* and *serratum*. In every case the sporangium dehisces by means of an apical longitudinal slit. A mucilage cavity in the base of the sporophyll is present in several of the species (*selago*, *serratum*, *lucidulum*, *tetragonum*). In the sporangial stalks of *L. serratum* (Pl. III., Fig. 2), and *L. lucidulum*, the walls of some of the cells are found to be more or less lignified,⁴ thickened at the corners, and

¹ Engler and Prantl; *Pflanzenfamilien*. Teil I., Abt. 3 (Pritzel).

² Baker. *Fern-allies* p. 7.; cf. Hooker and Greville, *Botanical Miscellany*, Vol. II., p. 360, and Spring, *Mem. de l'acad. royale de Belgique*, XV. and XXIV.

³ cf. *Selaginella*; Bower, 1908, p. 316, Fig. 162.

⁴ cf. Cells of sporangial stalk in *Bothrodendron mundum* (D. M. S. Watson, Brit. Assoc. Leicester Meeting, 1907; similar cells are also indicated in Miss Berridge's preparations on the sporangium pedicel of *Spencerites*).

elongated longitudinally in the direction of the axis of the stalk; no connection can however be traced between these and the sporophyll bundle.

The cortex of the stem in *L. selago* is composed of loose spongy tissue, reminding one of the cortex of some *Lepidodendra*,¹ Pl. III, Fig. 3.)

(b). *Subselago*. In this group the upper leaves only are fertile; the sporophylls differ slightly from the vegetative leaves, forming an indistinct terminal spike.

L. squarrosus and *L. dalhousianus* were examined. The sporangia of both are large, and axillary in position. In the former species (Pl. II., Figs. 3A and B), the sporangium is borne on a very short stalk, and the sporophyll is not specially modified for protective purposes (Text-fig. 4, V.); in the latter species the sporangium has a

Text-fig. 4. II., III., IV. are drawn from sections of typical sporophylls of *Euselago*. II.—(*L. selago*) shews part of an elongated sporophyll, with a mucilage cavity in its base, bearing a very shortly-stalked sporangium. III.—(*L. fontinalis*), shows a very thick short sporophyll, with no mucilage cavity, bearing a sporangium with a slightly longer stalk. IV.—(*L. dichotomum*), is drawn from a very long, thin sporophyll, whose subtending sporangium is furnished with a long stalk. V., VI., drawn from sporophylls of *Subselago*. V.—is from a section of the short sporophyll of *L. squarrosus*, which has a mucilage cavity and bears a sporangium on a very short stalk. VI.—(*L. dalhousianus*), shews a longer-stalked sporangium. Diagonal shading=mucilage cavity.

¹ Bower, 1893, Figs. 8A, 11, etc.

much longer stalk, and, consequently, although the incurved edges of each sporophyll fold round its sporangium, so that the latter receives a certain amount of protection, it is still distinctly visible between the sporophylls; (Pl. II., Figs. 4A, B, and Text-fig. 4, VI.) Dehiscence of the sporangium takes place along an apical slit.

A mucilage cavity is present in the base of the sporophyll of *L. squarrosus*. No cells with lignified walls are found in the pedicels of the sporangia of either of these species.

(ii.) *Phlegmaria*. In this group the sporophylls are aggregated to form distinct terminal spikes or cones, and are more or less modified in shape. *L. nummularifolium* and *L. phlegmaria* were examined. The sporophylls of these species (Pl. II., Fig. 6), resemble those of *L. dalhousianum*, but their edges are more closely incurved round the sporangia. Cells with slightly lignified walls are found in the sporangium pedicels (cf. Pl. III., Fig. 2); no mucilage cavities are present in the sporophylls. The sporangium of *L. phlegmaria* has an exceptionally long stalk, and dehiscence by means of an apical slit.

B. *Rhopalostachya*.

(iii.) *Inundatum*. In the species *L. inundatum*, which by Baker is placed with *L. phlegmaria*, we find for the first time considerable modifications in the structure of the sporophyll, though the external difference between the sporophyll and the vegetative leaf is small.

Each sporophyll is of considerable thickness and has a prominent dorsal ridge (Pl. II., Figs. 5A, B). This ridge projects from the back of the sporophyll and overlaps the sporangium belonging to the sporophyll immediately below. The sporangium is thus far less exposed than it is in the *Urostachya*, but it is still visible on the exterior of the cone. A mucilage cavity is found in the ridge (Text-fig. 5, VII.) The sporangium is large and is borne on a very short, wide stalk, in the axil of the sporophyll; numerous elongated cells with strongly-lignified, pitted walls (Pl. III., Figs. 4, 5), are found in this stalk, but there is no connection between these and the vascular elements of the sporophyll trace. In the tracheides of the trace many interesting examples of a transition from scalariform to reticulate pitting were noticed¹ (Pl. III., Fig. 6).

Pritzel places *L. carolinianum* with *L. inundatum*, and a study of the sporophylls certainly confirms this arrangement². The

¹ cf. H. Gibson, 1894, Fig. 101, Pl. XII.

² See also Bower, 1908, p. 313.

position of the sporangium is nearly the same in both species, it is not quite in the axil in *L. carolinianum*, but is slightly pushed out on to the sporophyll axis (Text-fig. 6, VIII.); the cells of the very short sporangium-pedicel in *L. carolinianum* have their cell-walls lignified in patches like the similar cells in *L. inundatum*.

Text-fig. 5.

Text-fig. 6.

Text figs. 5 and 6 represent diagrammatic longitudinal sections of sporophylls of *L. inundatum* and *L. carolinianum*. (*m*=mucilage cavity, *b*=lignified cells in sporangium pedicel, *e*=cuticularised epidermis). Each sporophyll has a dorsal flap, and bears a shortly-stalked sporangium, which is axillary in *L. inundatum*, but not quite axillary in *L. carolinianum*.

The dehiscence of the sporangium in both these species is of some interest. It takes place in *L. inundatum* by means of a slit along a line of cells on the ventral surface of the sporangium, on the side furthest from the axis of the cone.¹ In *L. carolinianum* the slit is on the dorsal side, but is slightly displaced laterally. The two flaps of the dehiscent sporangium are thus of unequal size, and the spores are liberated in the most convenient position for dissemination, that is, nearest the opening between the sporophylls. This adaptation is still more strikingly illustrated in some of the more complicated cones.

The systematic position of *L. volubile* is a matter of some difficulty. It is placed by Baker in his sub-genus 4, which includes the other heterophyllous forms, *L. complanatum*, *L. carolinianum*, etc. Pritzel has split up this sub-genus, believing that the common possession of heterophylly is not a valuable systematic character, and while he places *L. carolinianum* with *L. inundatum*, and *L.*

¹ Goebel, Organography II., pp. 582, 583, Fig. 378.

complanatum with *L. alpinum*, he has connected *L. volubile* with *L. cernuum*. But an investigation of the sporangia and sporophylls by no means supports the last of these suggestions.

L. volubile has a large axillary sporangium, on a stalk of medium length. The sporophyll is perfectly simple, it has no mucilage cavity, and resembles in many respects a sporophyll of *L. dalhousianum* or *L. phlegmaria*. In the sporangium pedicel, cells are present whose walls are lignified and pitted like those of the cells in a similar position in *L. inundatum*. As in that species, no connection can be traced between these cells and the vascular elements of the sporophyll trace; in many cases, however, there is continuity between them and the elongated cells with lignified pitted walls which surround the trace and are continuous with similar cells surrounding the stele of the axis. Such continuity is also present in *L. inundatum*, but is not so striking. The line of dehiscence of the sporangium is in a position similar to that in *L. inundatum*, though not displaced quite so far onto the ventral surface.¹

It appears to me that this species occupies a position intermediate between the *phlegmaria* group of the *Urostachya* and the *inundatum* group of the *Rhopalostachya*, and it might be to well to place it in a new group (iii.) *Volubile*, at the end of the *Urostachya*, thus making the *inundata* into group (iv.).

Groups (iv.), *Cernua* and (v.), *Clavata*. The species belonging to these two last groups agree in one important point, in which also they differ from all other species. This point is concerned with the position of the sporangium, which here does not arise in the axil of the sporophyll but takes its origin from the sporophyll stalk. An intermediate stage has already been described in *L. carolinianum*. It is found that the sporangium is slightly nearer the axil of the sporophyll in the young cones of *L. clavatum* and *L. cernuum*, than in the adult; (Pl. III., Fig. 7).

In the species of both groups, the sporangium is very efficiently protected, by means of a flap² which grows down from the dorsal surface of the abaxial region of the sporophyll, and thus it is not visible on the exterior of the cone (Pl. II., Fig. 9A). The saddle-shaped appearance of the sporangium is very noticeable in all species. The sporophylls of *Clavata* appear to be less highly modified than those of *Cernua* and I will therefore describe them first.

¹ Engler and Prantl, Teil I., Abt. 3, Fig. 380, E F

² cf. *L. annotinum*, Goebel p 583

(v.) *Clavata*. The protective outgrowth is not well developed in *L. clavatum*, and the stalk of the sporangium of this species is simple in structure, being formed only of short parenchymatous cells which are slightly lignified at the corners (Pl. II., Fig. 7). The sporangium has a very large archesporial pad¹; there is no mucilage cavity in the sporophyll (Text-fig. 7, IX.)

In the sporophylls of *L. alpinum*, the protective flap is better developed (Pl. II., Figs. 8A, B), and the peltate form of the sporophyll is more pronounced. The cells of the sporangium pedicel are elongated and have more strongly lignified walls. The sporophylls of *L. complanatum* are extremely like those of *L. alpinum*. In neither species is there any connection between the lignified cells in the sporangium pedicel and those of the sporophyll bundle.² The sporangium dehisces by a slit which is nearly apical in *L. clavatum* but more displaced onto the abaxial side in the other two species.³

The sporophyll trace of *L. complanatum* differs from that of all the other species examined (Pl. II., Fig. 9). It arises in the usual manner from the axial stele and pursues an obliquely upward course, but this course is continued above the level of the sporophyll base and the trace then bends sharply downwards to enter the sporophyll. This curious behaviour is strikingly similar to that of the sporangium trace in *Calamostachys*⁴ and *Palæostachya*⁵, but it has no analogy among the Lycopods, except perhaps in the trace of *L. clavatum*, which makes a much rounded curve before it enters the sporophyll.

(iv.) *Cernua*. The sporophylls of *L. laterale* (Text-fig. 7, X.) closely resemble those of *L. alpinum*; the lignification in the sporangium stalk is even more strongly pronounced.

The most highly developed cones and sporophylls are those of *L. cernuum*. In this species a groove is present on the under surface of the stalk of each sporophyll, and into this groove (Pl. II., Fig. 9Bg.), fits the sporangium borne on the sporophyll immediately below. Obviously, this arrangement, combined with the dorsal flap (f), affords highly efficient protection to the sporangium (see Text-fig. 8, XI.) and

¹ Bower, 1894; p. 518. Note—A similar "pad" was found in an unnamed species which I could not identify but which apparently belonged to the Phlegmaria group.

² Bower noted that in *L. alpinum* there is a slight upward extension of the sporophyll trace towards the sporangium, 1894, p. 522.

³ cf. Engler and Prantl, Teil I., Abt. 3, Fig. 378D.

Renault, 1896, p. 130, Pl. LX., Figs. 3-8.

⁵ Hickling, 1907. Scott, 1907, pp. 159, 165.

a perfectly compact cone is formed, on the outside of which no signs of the sporangia are visible (Pl. II., Fig. 9A). The outer cell-walls of the sporophyll epidermis are provided with a cuticle which is everywhere thickened, but especially on the abaxial surface of the basal part of the dorsal flap¹. Here (c, Text-fig. 8, XI.), it seems to be of use in dragging apart the sporophylls, when they separate to let loose the spores.² The sporangium dehisces by means of a slit, which is placed laterally on the abaxial side, thus liberating the spores in the position most favourable for their dissemination.

There is a large mucilage cavity in the sporophyll stalk, running in a longitudinal direction beneath the vascular bundle.³ The pedicel of the sporangium is made up of short cells whose walls are strongly lignified in transverse bars⁴, (Pl. III., Fig. 7), and present a very striking appearance if stained with Iodine green and Eosin, when they are seen to be made up of alternate patches of pink and green. No connection can be traced between these cells and the vascular elements of the trace which supplies the sporophyll, but only one or at most two layers of cells separates the two tissues.

IV.—CLASSIFICATION.

It appears from the above description that the classification of the genus *Lycopodium* according to Pritzel is in the main supported by a study of the sporophylls of the various species. Throughout the *Urostachya* the sporangium is axillary in position, on a sessile sporophyll; in the higher groups of the *Rhopalostachya* the sporangium takes its origin from the stalk of a peltate sporophyll.

In the *Inundata*, the first group of the *Rhopalostachya*, an intermediate condition is maintained. The sporophylls are stalked and are furnished with a dorsal flap, but the sporangium is axillary in *L. inundatum* and almost axillary in *L. carolinianum*. It does not

¹ cf. Goebel, Organography II., p. 580.

² Experiments have been made on the cones of *L. cernuum*. Cones taken from spirit and herbarium material were soaked water and then were (1) dried in air, or, (2) placed in strong glycerine. In both series of experiments each sporophyll was gradually drawn backwards, at the same time folding its edges together over its dorsal surface, thus exposing the sporangia. Sections were also examined microscopically in strong glycerine. The lignified cells at the base of the sporophyll were seen to gradually contract and an air bubble finally appeared in each cell.

³ cf. T. G. Hill, 1906.

⁴ cf. Transfusion tracheides in Stigmarian rootlets, Weiss, F. E., 1904.

appear certain which of the two great divisions should contain this interesting group, whose half-way position is confirmed by a knowledge of embryology and the gametophyte, and in some ways it would seem more suitably placed in a division by itself. A striking link between it and the *Urostachya* is found in *L. volubile*, whose systematic position has been fully discussed.

In the *Rhopalostachya* it has seemed reasonable, in view of the obviously simpler nature of the *Clavata* to place them before the *Cernua*, but it is not therefore supposed that the two groups are necessarily connected, and indeed, other considerations appear to render it probable that the two groups may represent separate lines of development,¹ both connected with *L. inundatum*.

Text-fig. 7.

Text-fig. 8.

Text-figs. 7 and 8 represent longitudinal sections of species of *Cernua* and *Clavata*, in which groups the sporangium is not axillary but is borne on the stalk of the peltate sporophyll. IX. (*L. clavatum*), shews the large archesporial pad (x) of that species. X. is *L. laterale*. Fig. 8, XI. shews two sporophylls of *L. cernuum*. In each case oblique shading indicates mucilage cavity, and cross-hatching or dots=lignified cells in sporangium pedicel, d=line of dehiscence.

V.—THEORETICAL CONSIDERATIONS.

It has been shown that the sporophylls of the various species of *Lycopodium* can easily be arranged in a series of increasing complexity; considerable difficulty is felt, however, when an attempt is made to decide which end of the series is the more primitive. It

¹ Engler and Prantl, l.c.

has been usual to regard the simpler types as primitive, and this view, which is supported by Bower¹ and others, will be considered first.

Theory of Progression.

(a). *Anatomical and Developmental evidence.* Bower regards *L. selago*,² with its elongated, branched strobilus, as the most primitive form of Lycopod, and from such forms he thinks others, with a more restricted spore-producing area, were derived by means of "sterilisation of sporophylls." In *L. Selago*, the distribution of the sporophylls in fertile whorls,³ alternating with sterile ones, and also the presence of abortive sporangia in the axils² of some of the leaves of the sterile whorls, appears to support this theory. Strasburger, writing in 1873,⁴ looked upon the Lycopodian sporangium as a product of the main stem, axial in nature, which has become shifted on to the sporophyll by later growth, but is actually the morphological equivalent of an axillary bud. The relative positions of the sporangia in the young and old stages in *L. selago*,⁵ give support to this hypothesis. Examples of axillary buds in this genus are found in the bulbils of *L. selago* and its near allies, and have been regarded as evidence of the primitive nature of these species.

The position of *Phylloglossum* has been a question of some difficulty. Its simple structure, to which it owed its first name of a "permanently embryonic form of Lycopod,"⁶ is now no longer looked upon as primitive.⁷

Its protocorm and protophylls seem to connect it most closely with the Rhopalostachya, especially with the *Inandata* and *Cernua* from which it seems probable it may have been derived by reduction.⁸ Bower considers now that the protophylls may not be primitive, but are merely a vegetative adaption, and hence he regards them as abortive sporophylls,⁹ but it is extremely difficult to agree with him in this. In *Phylloglossum*, the last of the protophylls is sometimes smaller than the rest and is looked upon as an intermediate stage, while in *L. cernuum* and *L. inundatum* the protophylls are never sharply marked off from the sporophylls.

(b.) *Comparative evidence.* From the simpler Lycopods it is

¹ Bower, 1894 etc.

² Bower, 1901, pp. 246-249 and 1908, p. 711.

³ Bower, 1894.

⁴ Strasburger, 1873.

⁵ Pl. III., Fig. 1.

⁶ Bower, 1885; also 1894, p. 361.

⁷ Bower, 1901.

⁸ Engler and Prantl, Teil I., Abt. 3, p. 582.

⁹ Bower, 1901, p. 228.

fairly easy to derive such a form as *L. inundatum*, and then by increase in complexity to arrive at *L. cernuum*, but on this view it is hard to form an intelligible hypothesis as to the relations of *Lycopodium* with its fossil allies. For, although the external resemblances between *L. cernuum* and *Lepidodendron* suggest a relationship between these two plants, yet if we regard this as the most recent species of *Lycopod*, it can only be nearly related to *Lepidodendron* if that genus be still more recent in origin.

The simpler *Lycopods* are alone in having sessile sporophylls bearing axillary "foliar" sporangia. Bower regards this character as primitive, not only in the genus *Lycopodium*, but in the *Pteridophyta* as a class. But there is little comparative evidence for such a view; indeed recent work has made it almost inconceivable that the genus *Lycopodium* is to be regarded as more primitive than the larger strobiloid *Pteridophytes*.¹

It is almost as difficult to consider this position of the sporangium as primitive in the genus itself. For we must then suppose *Lycopodium* to be derived from some such form as *Spencerites*² by reduction of the sporophyll axis and a consequent simplification of the sporophyll. Then by a shifting of the sporangium and elaboration of the sporophyll the more complex species could be evolved. Here, once more we have a sporophyll which may be aptly compared with that of *Spencerites*, but the comparison is only an analogy, and the petiole of the sporophyll, —the structure found between the cone axis and the point at which the sporangium pedicel takes its origin—is not necessarily of the same morphological nature as the apparently homologous axial structure in the same position in *Spencerites*, *Lepidodendron*, etc. This conclusion may seem somewhat forced, but it appears to me to be the only logical outcome of a belief in the primitive nature of the simple *Lycopods*, if any attempt is made to compare them with fossil genera.

Theory of Reduction.

(a) *Anatomical and Developmental evidence.* A belief in the reduced nature of the simpler types of *Lycopodium* is gradually gaining ground,¹ and would no doubt find still more adherents were it not for the weighty evidence collected by Bower in favour of his "sterilisation theory."

¹ cf. Scott, 1907, p. 175, and Tansley, 1907.

² Berridge, E. M., 1905.

³ cf. Scott, 1907, p. 173.

L. cernuum is thought by Treub¹ to show a primitive type of embryology, and an examination of the prothalli of various species has also led both Treub and Lang² to look upon this species as primitive. They compare its prothallus first with *L. inundatum* and secondly with that of *Phylloglossum*. It has been shown above³ that an examination of the sporophylls of *L. cernuum* and *L. inundatum* led me to compare the two species, and it also appears to me that the sporophylls of *Phylloglossum*⁴ with their short dorsal outgrowths resemble those of *L. inundatum*. The presence of a protocorm and protophylls in all three forms is necessarily of great interest,⁵ and the absence of these in the simpler types is quite consistent with the theory of the reduced nature of the latter. Bower⁶ states that the embryo of *L. selago* very quickly forms short assimilating leaves, and thus its early nourishment is provided for without any necessity for the formation of an underground protocorm with protophylls. It would seem far more natural to regard the protophyll as an organ useful to the old types with underground prothallia, but lost in the later forms, than as an organ evolved for special purposes from a sterilised sporophyll.

Similarly, notwithstanding Bower's evidence for the origin of all the smaller leaves of a *Lycopodium* from sporophylls by sterilisation, it does not seem absolutely necessary to accept his interpretation of his facts. It is by no means certain that the presence of an arrested organ in any position indicates that a fully-developed organ was ancestrally present in that position.⁸ In other words, if *L. selago* is derived from the more complex types by an extension and simplification of the spore-producing area, we should reasonably expect more primordia to be formed than would become functional.

The study of the development of the sporangium does not throw much light on the question as to which position is the more primitive. The origin rather near the axil of the young sporangia of *L. cernuum*⁹ cannot be regarded as of any great importance since it is easy to see that the later position is brought about by the lengthening of the sporophyll axis. The development of the

¹ Treub; 1884 and 1888.

⁴ p. 42., also Bower, 1908, p. 315.

² Lang, 1899.

⁵ cf. p. 51.

³ p. 50 and p. 52.

⁶ Bower, 1901, p. 249.

⁸ cf. Goebel, I., p. 60. We must "guard against considering all arrested organs as being descended from organs which were developed in the ancestors of existing forms."

⁹ Pl. III., Fig. 7.

sporangium from the main axis in *L. selago* may be merely a contrivance to save time; perhaps the fact that even here it does not appear to be formed from leaf tissues may have some connection with the morphological question as to whether the sporangium is derived from tissues of axial or foliar nature

The series of species constituting the genus *Lycopodium* is far more easily interpreted as a reduction than as an elaboration series.

(I.) For, if the simpler species are primitive, it is difficult to understand the evolution of a stalked sporophyll with a dorsal flap, adapted for the protection of a distally-placed sporangium, whilst bearing its sporangium in an axillary position. Yet such is the state of affairs in *L. inundatum*, and it is easily explicable on the other hypothesis, by which the lax arrangement in *L. selago* arose from a compact cone like that of *L. cernuum* by a series of steps involving the gradual loss of specialised adaptations. For then, we have in *L. inundatum* an intermediate step, in which the dorsal protective flap is still present, but is no longer perfectly effectual, since the sporangium is now not in a distal position on the sporophyll.

(II.) Again the positions of the line of dehiscence in the various sporangia support the second view. A longitudinal section of *L. inundatum*, such as that drawn in Text-fig. 5, VII., shows that the spores are liberated opposite the space between the distal ends of two sporophylls. But the sporangia are not completely enclosed as in *L. cernuum*, and are exposed between the proximal ends of the sporophylls, so that the necessity for this mode of dehiscence is not clear here and is still less obvious in *L. volubile*, where there is not even a dorsal flap to the sporophyll. I think the displacement of the line of dehiscence is best explained in these two species as a reminiscence of the more complex cones in which it was really important, in order to ensure dissemination, to liberate the spores in a lateral position.

(III.) The appearance of the lignified cells at the base of the sporangium in *L. cernuum* so forcibly recalls vascular tissue that one cannot resist the temptation to regard them as primitively vascular in origin. Though of course it is true that the development of vascular tissue cannot be brought forward as evidence of undoubted phylogenetic value, yet these lignified elements are of especial interest in this species, coupled as they are with the existence of a well defined parichnos in the sporophyll. The lignified cells in *L. inundatum*, the walls of which are exactly

similar to those of the elongated elements surrounding the stele in that and other species, may possibly represent another step in the reduction of what may once have been a small vascular bundle while in *L. serratum*, etc., we find an almost complete absence of cells with lignified walls in the sporangium pedicel.

(b.) *Comparative evidence.* If the series of species of *Lycopodium* is a reduction series, a more intelligible hypothesis can be constructed concerning the relations of this genus with recent and fossil Pteridophytes. It is impossible to produce definite evidence as to the direct ancestry of *Lycopodium*. Of the *Lycopodites*,¹ their obvious relations, we know so little that in most cases we cannot ascertain whether any given form is a *Lycopodium* or a *Selaginella*; but there appear to have been no striking differences between this collection of species in the Palæozoic Era and the *Lycopodiums* of to-day.

It would not be difficult to derive such a plant as *L. cernuum* from *Lepidodendron* or one of its allies. For, even if *Lepidodendron* itself is more nearly allied to *Isoetes*,—as is suggested by the position of the sporangium, and the discovery of a ligule, a parichnos,² and sporangial trabeculæ in both genera—it is still possible to suppose a comparatively close relationship to *Lycopodium*, in the sporophylls of which genus a parichnos is also generally present.³ Perhaps the complex sporophyll present in the *Rhopalostachya* is sufficient for the protection of the young sporangia of such small cones,³ from too great evaporation, and the mucilage once secreted by the ligule⁴ is now no longer necessary. It is conceivable that some such theory may also explain the absence of the ligule in *Spencerites*, which may then be brought into connection with the above genera. It has been already stated that the sporangium in this plant is attached to the stalked sporophyll in a position which is recalled by the tangentially placed sporangium of *Lycopodium cernuum*, etc., while the small lump of tissue or "ventral lobe" found between the sporangium and the distal end of the sporophyll recalls the ligule of *Lepidodendron*⁵; it is possible to regard *Spencerites* as an ancient connecting link between the old *Lepidodendras* and the *Lycopodiums*,

¹ Goldenburg, 1855; Solms Laubach, 1891, p. 186; Engler and Prantl, Teil I., Abt. 3, p. 715.

² Hill, T. G., 1906; Potonie, '99, p. 239; Weiss, 1907.

³ c.f., Worsdell, 1902.

⁴ Halle, 1907; Gibson, 1896.

⁵ cf. also *Araucariæ*, Seward and Ford, 1906.

perhaps one of the first of a chain of genera which were to form a long reduction series.

Conclusion and Comparison with Conifers. If a series of relationships such as those sketched above could be proved to have existed, I should be inclined to regard the stalk of the "sporophyll" in *Lepidodendron*, *Spencerites* and *L. cernuum*, etc., as axial in nature,—comparable in all species with the similar structure in *Calamostachys*, *Palaeostachya*, *Psilotaceæ* and *Sphenophyllum*¹—and representing the axis of a branch, terminated by a single sporangium in the one series, by several sporangia in the other series, and bearing also a single leaf with which its association is probably secondary, not primitive.² In the simpler Lycopods this axis has become reduced and has then finally disappeared; but even here the young sporangium is not developed from the actual substance of the leaf rudiment, but from the cone axis, and hence arises in the position of an axillary bud. Rudiments, at first exactly similar in appearance to the sporangial rudiments, often give rise to axillary bulbils. These may be looked upon as due to the proliferation of the apex of the reduced axis, which is usually terminated by the sporangium.³ Such proliferation is not necessarily a primitive character, but may be traced to purely mechanical causes,—for instance, a bud developed from as small a mass of tissue as that found in the sporangium stalk of *L. cernuum*, etc., is necessarily itself small, and may well only produce a sporangium, but a bud arising from the axis of the cone has more material to draw upon, and can thus form stem and leaves.

It appears that the sum of evidence available is in favour of the hypothesis that the simpler Lycopods are reduced, not primitive, and that the whole genus *Lycopodium* contains a series of types which are reduced from the larger strobiloid Pteridophytes. The foliar position of the sporangium is looked upon as secondary, and the Lycopodian sporangium-bearing organ is here supposed to have been derived from a branch structure, which had the morphological value of an axillary bud.

Whilst our knowledge is still so uncertain, it is impossible to attempt any satisfactory comparison between the sporophylls of the Lycopodiales and those of Conifers. The female flower of *Taxus*, apparently terminal, but shown by Celakovsky (1879) to be

¹ cf. Sykes, M. G., 1908, pp. 80-83. Text-fig. A.

² Ibid, p. 82.

³ cf. Thomas, 1901, abnormalities in *Tmesipteris* sporophylls.

really axillary, is of course a proliferated axillary bud, and it is perhaps interesting to compare it with a bulbil of *L. selago*, though such analogies cannot have any morphological value.

VI.—SUMMARY OF RESULTS.

I. The sporophylls of the different species of *Lycopodium* can be arranged in a continuous series, increasing in complexity of structure. In the simplest forms, such as *L. selago*, the sporangium is almost completely exposed, whilst in *L. cernuum*, the most highly differentiated species, the sporophyll has a dorsal flap, and affords perfect protection to the sporangium.

II. In *L. cernuum*, and nearly allied species, the adult sporangium arises from the sporophyll stalk; but in all the simple forms it is found in the axil of the sessile sporophyll. In intermediate cases, such as *L. inundatum* and *L. carolinianum*, the sporophyll is stalked, but the sporangium is axillary. Even in *L. selago*, however, the young sporangium is not differentiated from leaf-tissue, but is formed from the axis of the cone itself.

III. No definite vascular bundle supplies the sporangium pedicel, but in it are often found elongated cells with more or less lignified walls. These are very simple in some species (*L. serratum*, *Phylloglossum*, etc.), very highly specialised in others (*L. volubile*, *L. inundatum*, *L. cernuum*, etc.), but they are never directly connected with the sporophyll trace, though in *L. volubile* they were found to be in continuity with the layer of cells with lignified walls which surrounds the trace.

IV. Our present knowledge of the relations of the Lycopods, both amongst themselves and with fossil genera, appears to be insufficient to determine certainly which way we shall read the above series, that is, whether we consider the simpler Lycopods to be primitive or reduced. Evidence, based on embryology and the structure of the gametophyte, tends to support the latter view; it is also easier to find connections between the more complex members of the series and fossil genera. The series itself is far more naturally regarded as a reduction series, and the intermediate forms are then far more easily explained. The sporophylls of *Phylloglossum* are found to be comparable with those of some of the intermediate species, and it seems probable that this genus represents a reduced form, as has been recently decided by Bower.

V. From anatomical, developmental, and comparative evidence, it is concluded that the genus *Lycopodium* is to be regarded as reduced from some of the larger strobiloid Pteridophytes, and that the genus itself is also composed of forms which can be arranged in a reduction series and the evolution of which is still traceable among the species alive to-day.

VI. If it be granted that the "sporophyll" of *L. cernuum* shows the more primitive arrangement, it would seem to me to be natural to regard it as an axial structure, morphologically equivalent to a reduced branch, which is terminated by a single sporangium, and bears also a single leaf, with which, however, its association need not necessarily be primitive. A similar interpretation has before been given to the sporophylls of some of the allied fossil and recent Pteridophytes.

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EXPLANATION OF PLATES II. AND III.

ILLUSTRATING MISS SYKES' PAPER ON LYCOPODIACEÆ.

PLATE II.

All the figures except 1A, 3A, and 4A, were drawn from preparations examined with the aid of a binocular microscope for the study of solid objects.

Fig. 1A. Apical region of a plant of *L. selago*, shewing numerous fertile leaves bearing sporangia; (natural size).

Fig. 1B., front, and Fig. 1C, side, views of sporophylls of *L. selago*.

Fig. 2. Sporophyll of *L. serratum*; (drawn in reversed position).

- Fig. 3A. Portion of fertile region of *L. squarrosus*; (natural size).
- Fig. 3B. Sporophyll of ditto.
- Fig. 4A. Apical portion of fertile region of *L. dalhousianum*; (natural size). The sporangia are to some extent hidden by the sporophylls.
- Fig. 4B. Sporophyll of ditto, showing incurved edges.
- Figs. 5A. & B. Side and back view of sporophyll of *L. inundatum*. r = dorsal ridge.
- Fig. 6. Sporophyll of *L. phlegmaria*, showing incurved edges.
- Fig. 7. Sporophyll of *L. clavatum* with small dorsal flap.
- Figs. 8A & B. Front and side views of peltate sporophyll of *L. alpinum*.
- Fig. 9A. Cone of *L. cernuum* (natural size). The sporangia are entirely hidden by the sporophylls.
- Figs. 9B & C. Sporophyll of *L. cernuum*.; f = downward flap; g = groove in stalk of sporophyll into which fits the sporangium borne by the sporophyll next below. The mucilage cavity present in the stalk gives it a transparent appearance.

PLATE III.

- Fig. 1. Longitudinal section of the apical region of the stem of *L. selago*, showing origin of (sp) sporangial, and (lf) sporophyll rudiments. $\times 78$.
- Fig. 2. Longitudinal section of the stalk of a sporangium of *L. serratum*, showing typical elongated cells with their walls lignified at the corners. $\times 116$.
- Fig. 3. Longitudinal section of axis of *L. selago*, comprising the area between two sporophyll traces. The inner and outer cortex are composed of more or less compact cells while the middle cortex is made up of very lacunar tissue. A few layers of compact cells surround the sporophyll trace and accompany it through the middle cortex. $\times 116$.
- Fig. 4. Longitudinal section of part of a sporophyll of *L. inundatum* showing cells with lignified walls in the sporangium pedicel; a = axis of cone; sp = stalk of sporophyll with trace; ep = epidermis of sporangium with strongly lignified bars; m.c. = mucilage cavity. $\times 78$.
- Fig. 5. Two cells from the pedicel in Fig 4. $\times 400$.
- Fig. 6. Part of a tracheide from the sporophyll trace in Fig. 4, showing a transition from a scalariform to a reticulate form of pitting. $\times 400$.
- Fig. 7. Longitudinal section of very young sporophyll of *L. cernuum* showing young sporangium, in a position nearer the axil than in the adult cone; letters as above. $\times 116$.
- Fig. 8. Longitudinal section of part of adult sporophyll of *L. cernuum*; st = sporangium pedicel, which is composed of cells whose walls are strongly lignified in bars. $\times 116$.
- Fig. 9. Longitudinal section of base of sporophyll of *L. complanatum*, showing the course of the sporophyll trace; (see text). $\times 78$.

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