THE SPORANGIOPHORE—A UNIT OF STRUCTURE IN THE PTERIDOPHYTA.

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[Text-Figs. 25, 26.]

ONE of the many contributions to our knowledge of the phylogeny of the Vegetable Kingdom that are due to Palæobotany is the conception of the structure known as a sporangiophore.

As far back as 1900 Dr. Scott brought together in the first edition of his "Studies in Fossil Botany" a series of facts pointing to the wide occurrence of such a body and the great range of form which it might assume.

The number of types known to us has now greatly increased. The range of form in the Sphenophyllales may be from a tetrasporangic to a monosporangic condition; from a sessile to a pedicillate; it may be inserted on a bract or on an elongating axis.

In the Equisetales it may be tetrasporangic or polysporangic. It is generally radially symmetrical, but in the forms known as *Stachannularia* and *Cingularia* it is dorsiventral. It may appear associated with sterile bracts or without them, but is always inserted directly upon the elongating axis.

In the Psilotales the sporangiophore may be bi-sporangic or tri-sporangic. In this recent group variations have also been recorded by Professor Thomas[1] and Miss Sykes[2], which further accentuate the plasticity of the sporangiophore. Miss Sykes records cases in both *Tmesipteris* and *Psilotum* in which the sporangiophore is terminal on an axis, and in which the structure is monosporangic.

The three sub-phyla thus far referred to are sometimes grouped together under the name "Sporangiophoric Pteridophyta," as, for instance, by Professor Bower in Chapter XXIX. of his "Origin of a Land Flora." In the succeeding chapter, however, he uses the term "sporangiophore" for the fertile part of the leaf of the Ophioglossaceæ. I will discuss the application of the term in this sense in a later paragraph. Yet a second problem arises in connection with the use of this term. It has been again and again suggested that we have in the Lycopodineous "sporange" a reduced structure which is homologous with the sporangiophore of the

[1] Thomas. Proc. R. S., Vol. LXIX.

[2] Sykes. Annals of Botany, 1908, January and July.

Sphenophyllales. The evidence in favour of this "reduction hypothesis" is still very inadequate, although Miss Sykes's work on the "Sporangium-bearing Organs of *Lycopodium*[1]" has shown the wide range of form and structure that the "sporange" exhibits.

For the sake of comparison with her results it may be interesting to refer to two Palæozoic types of Lycopodinean "sporange" which unfortunately still await description. I append diagrammatic figures.

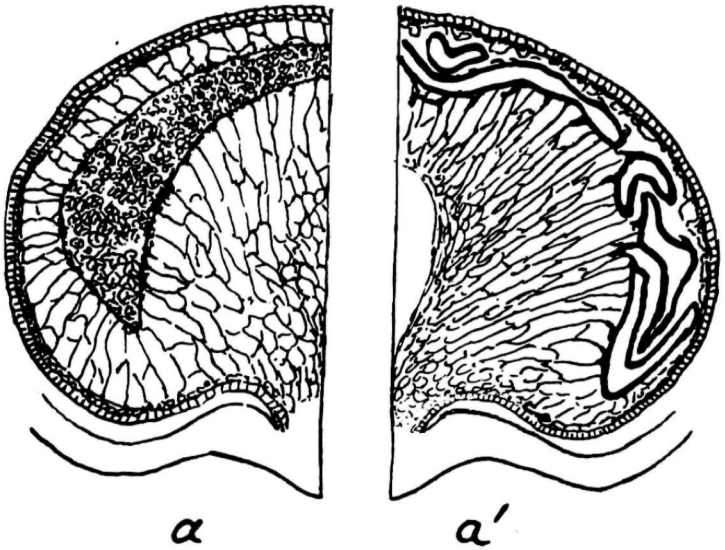

Fig. 25. Diagrams of halves of tangential sections of a micro- and megasporophyll respectively. x 30. Royal Holloway College Collection, C.N., 266·4 and 192n. Both specimens are referred to as *Lepidostrobus Mazocarpon*.

Fig. 25 is from two specimens met with in the Burntisland rock. a and a[1] represent halves of tangential sections of a micro- and a megasporophyll of what I assume to be a species of *Lepidostrobus*. They are associated with the branching stems of *Lepidodendron Pettycurense*, which has recently been shortly described by Mr. Kidston[2] as showing a solid protostele. Owing to the resemblance in some respects which these sporophylls show to *Mazocarpon* I will refer to them here as *Lepidostrobus Mazocarpon*. They are interesting not only because of the large amount of sterile tissue, but because of its character. A wide layer abutting on the sporogenous regions consists of elongated tapetal cells. The divergence of these cells leads to a split which may be seen in the median plane of the megasporophyll. This is somewhat suggestive of a multiple origin of the sporogenous region.

[1] Sykes, NEW PHYT., 1908, Vol. VII., p. 41.

[2] Kidston, Proc. R. S. Edin., Vol. XXVII.

If these two figures be compared with Fig. 26, which is a diagrammatic representation of a tangential section of *Mazocarpon*[1] from the Upper Carboniferous Rocks, one sees again a relatively enormous development of sterile tissue which has given rise to the name proposed for this form (μαζη=a loaf). This extends into ridges on the sporange wall which have been compared with an incipient indusium, but which may be a vestigial structure. The tetrads are here ranged along the two sides, and the space around them was filled with tapetal cells which have perished. One seems

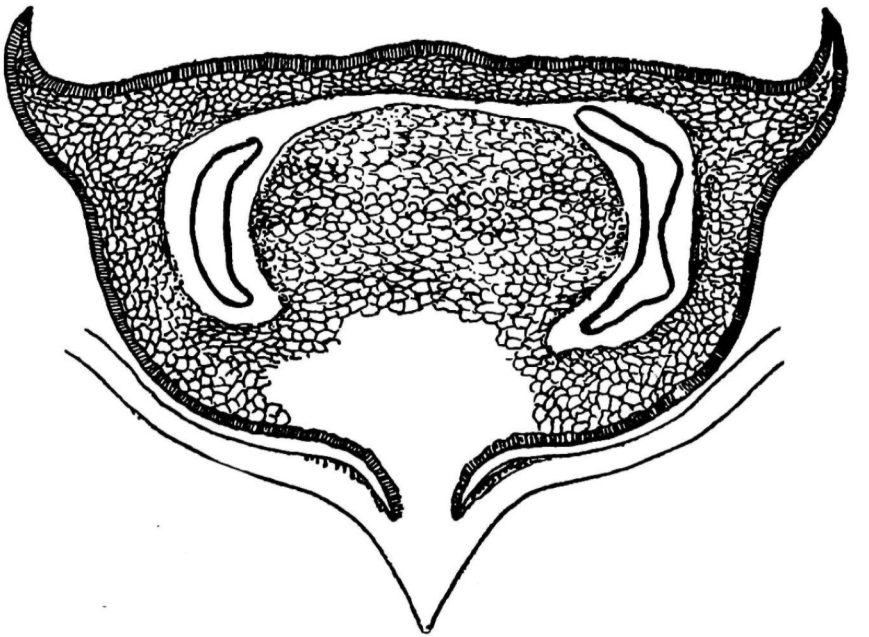

Fig. 26. Diagram from tangential section of a megasporophyll of *Mazocarpon*. ×30. Royal Holloway College Collection of Dulesgate Plants, C.N. 30.

to see in this sporange an explanation of the saddle form of many of the "sporangia" of recent Lycopods, accompanied as such a form is by a well developed "archesporial pad," *e.g.*, in *Lycopodium clavatum*. It would be a very natural sequence that the sporogenous regions of a single sporangiophore should become confluent, and the gradual reduction of the sterile tissue to a mere "archesporial pad" and pedicel would next follow. The inclusion of the Lycopodiales among the "Sporangiophoric Pteridophyta" would make this term as extensive in application as Jeffrey's term Lycopsida.

But have we even then really reached the full extent of the legitimate application of the expression? Have we no representative

[1] Scott. "Studies," second edition, 1908.

of the sporangiophore in Pteropsida? Is it possible that a body so characteristic of one half of the Pteridophyta should not have its homologue in the other? I wish to lay stress on the resemblances between the synangium or sorus of the Pteropsida and the sporangiophore or synangium of the Lycopsida.

In the vast majority of both Fossil and Recent Ferns the sporangia are aggregated together in tufts or groups, or even in more compact bodies called synangia. Examples of such aggregations are found in the Palæozoic ferns *Diplolabis*, *Botryopteris*, *Zygopteris*, where the constituent members have relatively little cohesion, and in the Marattiaceæ where the cohesion may be complete.

The range in the form and number of parts of the Fern sporangiophore is greater than in that of the Lycopsida, this being probably partly due to the prevalence of the strobiloid habit in the latter.

In the Fern the sporangiophore (sorus) occurs on the margin or lower surface of the frond. In the latter case a peltate form would be a disadvantage, and we see a great contrast in the method of dehiscence of the sorus of *Kaulfussia* and that of *Equisetum*. When the pedicel is continued into a peltate shield as in *Matonia* we find it is caducous. The sporangiophores of Ferns are more comparable in structure with those of non-strobiloid types, such as *Psilotum*. The exceptional cases among the Ferns in which there is no aggregation of sporangia at first appear to present considerable difficulty, and I will refer to them in detail.

I will select *Senftenbergia* and *Archæopteris* for discussion as they are both Palæozoic forms and hence *a priori* might be considered primitive. *Senftenbergia* is essentially of the Schizæaceous type and bears single sporangia at the ends of veins on the under surface of dorsiventral pinnæ, while *Archæopteris* may bear its sporangia peripherally on a pinna.

We do not know what were the antecedents of these Ferns, but I would suggest that the scattered condition of the sporangia may be due either to the great expansion and dorsiventral development of the sporangiophore, or to the reduction of a number of sporangiophores each respectively to one sporange. Both of these evolutionary processes are known to occur. In *Acrostichum* most morphologists would accept the view that the loss of the soral identity is due to expansion. In *Dipteris bifurcata*[1] the sorus is still

[1] Armour. NEW PHYT., 1907, Vol. VI., p. 238.

intact and the sporangia are simultaneous in origin, but in *Dipteris conjugata* all stages of the disintegrating process can be seen side by side on the same frond.

Again in *Osmunda* we see an early phase of the loss of soral identity in that the sporangia of a single tuft face in different directions. A later stage is seen in the scattered sporangia of *Todea*.

Such an explanation might conceivably be applicable to Schizæaceæ, but Prantl's view that the sorus has become monosporangic is far more probable. That reduction of this sort takes place is shown in various degrees among the species of *Gleichenia*, and can be traced ontogenetically in the megasporangial sorus of *Azolla*.

In the case of the Ophioglossaceæ the "sporange" appears on the other hand to represent a reduced sporangiophore comparable with the monosporangic form found in *Psilotum*. It is not uncommon to find sporangia on the so-called sterile segment of *Botrychium lunaria*. I have also a specimen of *B. lanuginosum* showing the same phenomenon.

In a specimen of *B. lunaria* gathered this season in Yorkshire, and sent me by Miss Beard, B.Sc., the sporangia are rather on the abaxial surface of the margin of the pinnæ. Some of them are stalked and curve over on to the upper surface, and thus bear a curious resemblance to the sporangiophores of *Sphenophyllum Dawsoni*. The dehiscence of each sporange is effected along a stomium resembling that of the Psilotaceæ. In *Ophioglossum* the fertile spike appears to be a condensed structure with the sporangia sunk in an unbranched lobe of the frond. The existence of such forms as *Marsilia* with fairly typical Fern sori and dorsiventral segmentation of the frond seems to justify us in looking upon dorsiventral segmentation of the frond in Ophioglossaceæ as a character of no great taxonomic value, and as affording no justification for the view that the whole fertile lobe is homologous with the sporangiophore of the Sphenophyllales. I would also strongly deprecate the use of this term in a non-morphological or non-committal sense, a use which is sometimes adopted by Professor Bower in his recent work.

Evidence has gradually been accumulating during the last few years of the convergence of the various groups of Pteridophyta in past epochs. *Pseudobornia ursina*, a most interesting Devonian plant of probably Calamitean affinity, seems to be a type in which the microphyllous habit of the Lycopsida had not yet been evolved.

Protocalamites Pettycurensis, of which much new material has recently come to hand, is a Calamite of Lower Carbiniferous age which exhibits a stelar anatomy comparable with that of many Ferns. Such facts as these point to a monophyletic origin of the Pteridophyta. If the Pteridophyta are monophyletic it would appear that their ancestors possessed a generalized type of sporangiophore. Such a structure must have equally given rise to the "synangium" of *Marattia* and the "sorus" of *Matonia*, to the "sporange" of *Lepidostrobus*, the "sporangiophore" of *Equisetum* and the "synangium" of *Tmesipteris*. Hence I would suggest the following definition of a sporangiophore. A sporangiophore is a structure characteristic of the sporophyte of Pteridophyta, and consists of a central, generally pedicillate, mass of sterile tissue with sporogenous regions occupying either one or more sporangia which may be terminal, lateral or basal. Eventually in some Ferns the sporangia may become completely separated from one another, in which case the common pedicel is obsolete.

Morphological Value of the Sporangiophore.

The hypothesis that leaf and stem are but specialized parts of a common dichotomizing Propteridophytic thallus—an hypothesis which was favourably discussed by Mr. Tansley in the first of his valuable series of Lectures on the Evolution of the Filicinean Vascular System[1], is becoming increasingly important as our knowledge of the earlier Pteridophyta increases. We not only find sporangiophores inserted indiscriminately upon axis or upon leaf, but a more exact knowledge of several of the Palæozoic Ferns has revealed the fact of the existence of adventitious sterile structures which may be inserted either on axis or on rachis.[2] Hence in both sections of Pteridophyta comparable anomalous structures occur. With the new hypothesis in view such organs may be explained as units of the Propteridophytic thallus which still exist as relics of the condition in which the limits of axis and leaf were not fixed.

The sporangiophore in all known Ferns and in many of the Lycopsida has been obviously taken up on to the leaf, and it is possible that that was universally the ancestral condition. The appearance of the sporangiophore on the axis in Equisetales, &c., would then be due to a secondary change, which resulted from

[1] Tansley, New Phyt., 1907, p. 15.

[2] Scott, "Studies," Second Edition, 1908, p. 313.

the reduction and chorisis of the leaf during the evolution of microphylly. A leaf wholly composed of sporangiophores, as I interpret the case in *Sphenophyllum fertile*, assists one to realize this conception.

It is, of course, yet possible that Palæozoic ferns may be found with sporangiophores inserted directly upon the axis. I refer to this possibility because in the same way it is conceivable that such ancient seed-plants as *Cordaites* may have derived their spore-bearing organs directly from sporangiophores *inserted on lateral axes*. Such a hypothesis is of course unnecessary, as the commonly accepted leaf-reduction hypothesis could meet the case, but I think there is nothing incredible in the suggestion that throughout the Cordaitales and Taxoideæ we are dealing with plants which have never had their sporangiophores taken up upon leaves, and that, in fact, they are constructed in this respect upon the Equisetal plan, where the sporangiophores are merely associated with bracts.

The "stamens" of *Cordaites* and *Taxus* are radially constructed consisting of a pedicel bearing sporangia. We have in *Torreya* evidence of the evolution of the dorsiventral stamen from such a structure[1]. If the dorsiventral stamen of *Torreya* is derived from a radially symmetrical sporangiophore it is probable that that of other Coniferæ has a similar origin.

In these groups of Gymnosperms, and in the Pteridosperms and their descendants (where the sporangiophore is obviously taken up upon the leaf) it seems a reasonable corollary to look upon *the evolution of the seed* as a further elaboration of the mega-sporangiophore. Space does not allow of a discussion of this problem here.

Conclusion.

On the whole, a review of the great central phylum, Pteridophyta, as a group of plants derived from a common ancestor whose sporophyte generation bore a special type of asexual spore-producing organ called a Sporangiophore, seems illuminating and possibly useful as tending to concentrate attention on the probable origin of the structure in question.

[1] Coulter and Land. *Torreya taxifolia*, Bot. Gazette, 1905, p. 159.