III. "Studies in the Morphology of Spore-producing Members. Preliminary Statement on the Equisetaceæ and Psilotaceæ." By F. O. Bower, D.Sc., F.R.S., Regius Professor of Botany in the University of Glasgow. Received January 30, 1893.

Still maintaining the same general views as were put forward in my preliminary statement on the Lycopodinæ and Ophioglossaceæ ('Roy. Soc. Proc.,' vol. 50, p. 265), I have now investigated other types from among the Vascular Cryptogams as regards the development of their spore-producing members. As some considerable time must still elapse before these and other results can be laid in full before the Society, a further preliminary statement will now be made of the more important facts recently obtained. It is assumed that readers will bear in mind the views put forward in the paper above quoted, as regards sterilisation of potential spore-producing tissue, the possible partitioning of an originally continuous sporogenous mass by bands of sterile tissue, and as regards the elaboration of external form which may follow on such partitioning. This will be specially necessary for the appreciation of the facts relating to the Psilotaceæ.

Taking first the Equisetaceæ, the development of the sporangia has been closely followed by Goebel ('Bot. Zeit.,' 1880–81); I find it, however, difficult to accept his conclusions as to the hypodermal origin of the archesporium.

On following the early phases of development in *Eq. arvense*, the sporangium is found to be eusporangiate, but the essential parts of the sporangium may be traced in origin to a single superficial cell, the cells adjoining this laterally contributing only to form the lateral portions of the wall. The first division of this cell is periclinal: *the inner resulting cell forms only a part of the sporogenous tissue;* the outer cell undergoes further segmentation, first by anticlinal, then by periclinal, walls, and *the inner cells thus produced are added to the sporogenous tissue, and take part in spore-formation.* The archesporium of *Eq. arvense* is thus shown to be not of hypodermal origin in the strict sense; the same appears to be the case in *Eq. limosum.* Similar additions to the sporogenous tissue by early periclinal division of superficial cells is commonly to be seen in *Isoetes*, and occasional cases, which are difficult to explain in any other way, have been observed in some species of *Lycopodium.* It would thus appear that Goebel's generalisation, that in all the Vascular Cryptogams which he investigated a hypodermal archesporium exists ('Bot. Zeit.,' 1880, p. 569), cannot be retained in the strict sense.

The tapetum is derived from the series of cells immediately sur-

rounding the sporogenous mass; it is, however, to be carefully distinguished from certain cells of the sporogenous mass, which also undergo an early disorganisation; for about one-third of the cells of the sporogenous mass do not form spores, but serve physiologically as a diffused tapetum, yielding up their substance to nourish the other young developing spores. This is another form in which sterilisation of sporogenous tissue may appear. A similar arrest of some of the sporogenous cells is found also in the Psilotaceæ.

I have already suggested a theory (*loc. cit.*, p. 273) of the mode of origin of the whole strobilus of *Equisetum* from a sporogonial head, and have no reason to alter my opinion on this point.

The synangia of the Psilotaceæ have given rise to voluminous discussions; one view, which is now very widely adopted, as to the morphology of the parts which bear the synangia of these plants is, that the synangium is terminal on an abbreviated axis, which bears in addition two foliage leaves. It will be seen that the investigation of the internal details of development will support a simpler and more probable explanation of the nature of these peculiar parts, that which was indeed generally held by the older botanists, viz., that the whole of each lateral appendage (*sporangiophore*) which bears the synangium is a single leaf. This conclusion had already been arrived at by Graf Solms, after examination of the external form of the developing organs in *Psilotum*, for he found the synangium to arise below the apex of the whole lateral appendage. No sufficient examination has, however, yet been made of the internal details of the development of these parts in the Psilotaceæ, excepting a few observations by Goebel on *Psilotum* ('Bot. Zeit.,' 1881, p. 688), which were, however, incomplete, through insufficiency of material.

Tmesipteris being the genus with the simpler structure, it may be described first. In their earliest stages of development, as lateral outgrowths from the axis, the sporangiophores are not readily distinguishable from the foliage leaves in form or structure, while they occupy a similar position upon the axis. In either case, a prismatic or wedge-shaped cell occupies the apex, as seen in radial section, but the tissues of the whole leaf are not readily referable to the segmentation of a single initial. The first appearance of a synangium is as an upgrowth of superficial cells of the adaxial face of the sporangiophore, immediately below its apex; meanwhile the cells of the abaxial side also grow strongly, while the apex itself does not grow so rapidly; so that the organic apex is soon sunk in a groove between these stronger growths. The superficial cells which are to form the synangium undergo periclinal and anticlinal divisions, to form about four layers of cells; all the cells of this tissue are at first very similar to one another, but, later, two sporogenous masses become differentiated; they are not, however, clearly defined while young

from the sterile tissue which forms the partition of the synangium, or from the wall, while the cells which form the partition are similar in their origin to the sporogenous cells. From the arrangement of the cells of these sporogenous masses it seems not improbable that each mass may be referable in origin to a single cell, but this has not been proved to be constantly the case. All the cells of the sporogenous tissue do not arrive at maturity, but here, as in *Equisetum*, a considerable number, serving as a diffused tapetum, become disorganised without forming spores. There is no clearly-defined tapetum in *Tmesipteris*. The leaf lobes begin to be formed almost simultaneously with the synangium, and appear as lateral growths immediately below the apex of the sporangiophore; their further development presents no characters of special note.

The synangium of *Psilotum* originates in essentially a similar manner, being formed from the upper surface of the sporangiophore, immediately below its apex. The details are different in accordance with the trilocular character of the synangium: but, as regards the structure of the wall and septa, the absence of any strict external limit of the sporogenous masses, and of any definite tapetum, as well as in the fact that a considerable proportion of cells of the sporogenous masses become disorganised without forming spores, *Psilotum* corresponds to *Tmesipteris*. Each sporogenous mass appears to be referable in origin to a single archesporial cell.

On the ground of the observations of internal development, of which the above are the essential features, I agree with the conclusion of Solms that the whole sporangiophore is of foliar nature, and that the synangium is a growth from its upper surface. The presence of the two lateral leaf-lobes need be no obstacle to this conclusion, while they serve an obvious purpose in protecting the synangium when young, more completely than a leaf of the form of the sterile leaves of these plants could possibly do.

For purposes of comparison with allied forms, *Tmesipteris* should be taken first: and the correspondence is most close with *Lepidodendron*, a fact which has a special interest since this genus and the Psilotaceæ are both very ancient types. In *Lepidodendron* the sporangium is very large; it is narrow and elongated in a radial direction, extending a considerable distance along the upper surface of the leaf. I have already communicated to the Society the fact that trabeculæ extend in *Lepidodendron* from the base of the sporangium far up into the mass of spores (*loc. cit.*, p. 272), and have compared these with the trabeculæ in the sporangium of *Isoetes*. Neither of these sporangia are, however, completely partitioned. I now suggest that comparatively slight modification of the condition in *Lepidodendron* would produce the state of things seen in *Tmesipteris*: if the sterile trabeculæ of *Lepidodendron* were consolidated into a

transverse septum, and the apical growth of the sporophyll arrested and taken up by two lateral lobes, the result would be such as is seen in *Tmesipteris*. This is not a mere imaginative suggestion: it proceeds from the observed fact that the septum in *Tmesipteris* is undistinguishable at first from the sporogenous masses: here, as in other cases, it seems to me probable that a partial sterilisation of a potential archesporium has resulted in a partitioned sporangium. *Psilotum* itself illustrates, in its abnormal forms, the possible progression from two to four or five loculi. It may further be noted, in connexion with the above comparison between *Lepidodendron* and *Tmesipteris*, that the vascular tissues of some of the former appear to correspond more closely to those of *Tmesipteris* than to any other living plant.

Looking at the whole plants of the Psilotaceæ from the point of view above indicated, they are to be regarded as lax strobili, bearing sporangiophores (sporophylls) of rather complex structure. Branching, which is rare in *Tmesipteris*, is common in *Psilotum*, and is to be compared with the branching of the strobilus in many species of *Lycopodium*. In both there are irregularly alternating sterile and fertile zones, not unlike those of some species of *Lycopodium* (*loc. cit.*, p. 270); at the limits of these, arrested sporangia are frequently found. It is not difficult to imagine how such plants as the Psilotaceæ may have originated from some strobiloid type, not unlike that of the genus *Lycopodium*.

Those who accept the above suggestion will be prepared further to admit the comparison of the synangium of the Psilotaceæ with the "fertile frond" of the Ophioglossaceæ, which has been made by various other writers—Mettenius, Prantl, Strasburger, Celakovsky. This I believe to be a true homology; I should, however, add to this the hypothesis that, in either case, we see the result of elaboration in size and form, together with partitioning, of a sporangium of an originally simple Lycopodinous type. In the Psilotaceæ the result may be 2—5 loculi; in the Ophioglossaceæ the number may be in the simplest cases as low as six, or may rise to many hundreds in the larger species of *Ophioglossum* or *Botrychium*. It may further be remarked that every fresh case such as the above, where the development supports the hypothesis of partial sterilisation of a potential archesporium, and resulting partition, as exemplified among these lowest vascular plants, is of importance. A large body of evidence, to which I am now adding by the investigation of the Marattiaceæ, leads me to conclude that such partitioning of originally simpler sporangia has played a very important part in the evolution of vascular plants.