external influences on the biophors and determinants' (p. 415). '*These very minute fluctuations [i.e. continual changes of composition in the elements of the germ-plasm] which are imperceptible to us, are the primary cause of the greater deviations in the determinants which we finally observe in the form of individual variation*' (p. 417).

Finally, I must express my regret that so careful a technique and such powers of observation as the author's should have been overweighted with *a priori* and obsolete views. It is not good to follow too literally the adage '*Eher eine schlechte Hypothese als gar keine.*'

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Feb. 14, 1896.

STUDIES IN THE MORPHOLOGY OF SPORE-PRODUCING MEMBERS. PART II: OPHIOGLOSSACEAE¹.—

In a paper published in the Philosophical Transactions (Series B, 1894), the comparative study of the spore-bearing members of the Lycopodineae, including the Psilotaceae, has led to the conclusion that there is reasonable probability that septation of sporangia originally simple, to form synangia, has taken place; that a septate body (synangium) may be homologous with a non-septate body (simple sporangium); and that there is no essential difference between tissue which will form septa or trabeculae, and that which will form spores, since the tissues can mutually undergo conversion one into the other.

But the considerations there brought forward do not amount to an actual demonstration that septation has occurred. For the purpose of our discussion, it is important to ascertain whether such demonstration can be given in the case of parts which are undoubtedly homologous; it is afforded by the study of septate anthers, which occur in several distinct families of Angiosperms, e.g. Mimoseae, Onagraceae, Loranthaceae, Myrsineae, Rhizophoreae, Orchidaceae, Rafflesiaceae. Taking the case of the Onagraceae, the common type of the anther is the ordinary quadrilocular type, but in certain genera transverse septa are formed in each of the four pollen-sacs by conver-

¹ Read before the Royal Society, Dec. 5, 1895: reprinted by permission from Proc. Roy. Soc., No. 354, Vol. lix.

sion of certain cells of the potential archesporium into sterile tissue; the unavoidable conclusion already drawn by other writers for this and other cases, is that these septate anthers are derived from those of the ordinary quadrilocular type, and the process of septation thus illustrated is essentially similar to that described for the Lycopodineae in my previous paper. *We thus see that septation of sporangia has actually occurred, and that it is a rather wide-spread phenomenon in Angiosperms.* It will therefore be merely a question of probability whether, and how far, it has also occurred in lower forms, and whether it is by septation that those synangia were produced, which are so marked a feature in certain Pteridophyta.

The argument from developmental evidence is comparatively simple where, as in the Angiosperms, the meristems are distinctly stratified, and the archesporium is a definite layer, ultimately hypodermal in origin; but in applying a similar argument to the Pteridophyta, in which the meristems are not clearly stratified, it is less easy to arrive at a conclusion. The principle is to be laid down that *the study of the sporangia or synangia of a plant is to be carried out in the light of a knowledge of the segmentation of its apical meristems.* The sporangia are parts of the plant-body, and their segmentations do not differ essentially from those of the meristems of the other parts of the plants on which they occur. Where the meristems are stratified, as in Angiosperms, a clearly stratified structure of the sporangia is commonly found; where, as in the Pteridophyta, the meristems are not stratified, it would be plainly unreasonable to expect a stratified structure of the sporangia, and such structure is not found. Accordingly, in using developmental evidence in solving the question whether synangia in Pteridophytes resulted from septation, the existence of a continuous hypodermal archesporium cannot reasonably be demanded as evidence of septation, though of course it may occur, as indeed it does in *Isoetes*; it is, however, to be remembered that in this plant the meristems are more clearly stratified than in most Pteridophyta.

The considerations thus briefly epitomized are a necessary prelude to the comparative study of the Ophioglossaceae. In my preliminary statement (Roy. Soc. Proc., Vol. 1, p. 265) I have described, chiefly from examination of *Ophioglossum pendulum*, a continuous hypodermal band as the potential archesporium, which subsequently was differentiated into sporogenous groups and septa; such a band appears

with some degree of regularity in this species, but it is not constant, and is not found with any clearly defined outer limit in *O. vulgatum* or *reticulatum*; thus far I admit the validity of Rostowzew's criticism of my preliminary statement (Beitr. z. Kenntniss der Ophioglosseae. 1. *Oph. vulgatum*, L., Moscow, 1892). On looking more carefully into this question, however, I have found that a band of superficial cells, differing in origin and segmentation from the surrounding cells, may be recognized as the *sporangiogenic band*; this gives rise to the sterile septa, the sporogenous groups, and the external wall of the sporangia; the band usually consists of two longitudinal rows of cells, possibly referable in origin to a single row, but there is some variety of detail. The observations have been made on three species, viz. *O. vulgatum*, L., *O. reticulatum*, L., and *O. pendulum*, L.

The band, at first undifferentiated, subsequently forms (i) archesporia at intervals, (ii) sterile septa which intervene between them, and (iii) the outer sporangial walls. The cell-groups which give rise to septa and to archesporia are sister cell-groups, having a common origin, and no difference can be seen between them in early stages; the distinction only becomes apparent as the archesporia attain their characteristic denser contents, and the difference is thus functional, not genetic. The archesporium of the single sporangium has not been found to be referable in origin to a single cell, and it is not defined by the first periclinal wall of the cells of the sporangiogenic band. These facts are all compatible with a theory of the origin of the spike of *Ophioglossum* by septation from a simple sporangium of the Lycopodinous type, and the sporangiogenic band may be compared with the band of cells, sometimes a single row, or two or three, which, after periclinal division, give rise to the archesporium of *Lycopodium*.

The development of the sporangia of *Botrychium* and *Helminthostachys* has also been traced, but these facts do not bear so directly upon the question of the nature and origin of the Ophioglossaceous spike as those derived from the study of *Ophioglossum*.

Abnormalities have played a large part in former discussions upon the morphology of the spike in the Ophioglossaceae. While recognizing the obvious correlation which exists between vegetative development and spore-production, it has been concluded that the abnormalities in this family do not form a sufficient basis for argument, certainly not when the conclusions drawn from them are in opposition to the

results of comparison of normal specimens. Such comparison led Mettenius, Strasburger, Celakovsky, and others to recognize a relationship of the Ophioglossaceae to the Lycopods. This comparison has been developed at considerable length, on grounds not only of the similarity of the development and position of their spore-bearing members, but also by comparison of the synangia of the Psilotaceae; the Gametophyte, also, and sexual organs and embryology, as far as known, have been taken into account, and a detailed comparison made of certain features in the anatomy of the Lycopods and Ophioglossaceae. From these various sources a general support of the relationship has been traced, the nearest point of comparison appearing to be between *O. Bergianum* and *Phylloglossum Drummondii*; it is contended that this is not a case of mere mimicry, but of real relationship, though such relationship probably dates from a remote and unknown ancestry.

Such a relationship would involve the idea of septation of the simpler type of Lycopodinous sporangium, to form the spike of *Ophioglossum*, but it has been shown that septation of a very similar nature has occurred in the anthers of certain Angiosperms, and that the developmental details of *Ophioglossum* are compatible with such a view. The conclusion of Celakovsky is, therefore, regarded as probably true, viz. 'that both the Lycopodiaceae and Ophioglossaceae sprang from a common stock, which had the simple sporophylls of the Lycopodiaceae. The Lycopods are probably, of living plants, the nearest prototypes of the Ophioglossaceae.' Thus, the view put forward is not new nor original, but, being now based on a wider area of fact, may take rank as a reasonably probable theory.

A comparison of the Ophioglossaceae among themselves shows that probably the genus *Ophioglossum* forms a series of increasing complexity, extending from such types as *O. Bergianum* or *lusitanicum* to such forms as *O. pendulum* and *palmatum*. Comparison of a large number of specimens of the latter species shows that the many-spiked condition is led up to by specimens with one, two, or three spikes, which are matched by abnormal specimens of *O. vulgatum*. The view is put forward that the many-spiked condition occasionally met with in other species has become the typical state in *O. palmatum*, and that it has been brought about by a chorisis or interpolation similar to that of the stamens of certain Angiosperms. It is further to be added that the insertion of the spikes is commonly on the

adaxial surface of the frond, rarely upon the margin; the facts accordingly do not support the hypothesis that the many spikes are of the nature of pinnae: thus, in *Ophioglossum* the progression appears to be towards multiplication of sporangia and formation of a plurality of spikes.

In *Botrychium* the progression appears to be from types such as *B. simplex*, in which there is close similarity to a simple *Ophioglossum*, by branching of the spike which is closely connected with enlargement and septation of the sporangia, to the condition seen in such species as *B. virginianum*, the branching of the spike running parallel with that of the subtending frond. The formation of sporangia abnormally on the latter, a condition commonly seen in *B. Lunaria*, but rare in most other species, is believed to be an example of reversion of a part typically vegetative to the sporogenous condition, and not indicative of a common character of the spike and the vegetative frond. Finally, *Helminthostachys* occupies an interesting intermediate position; the replacement of the sunken sporangia of *Ophioglossum* by projecting sporangiophores in *Helminthostachys* suggests, as already indicated in the preliminary statement (Roy. Soc. Proc., Vol. I, p. 265), an interesting analogy with the hypothetical origin of the strobilus of *Equisetum* from a body of the nature of a sporogonial head.

The chief object in view in these investigations has not been the mere tracing of homologies of parts among living forms; but, by developmental study and comparison, the following out of the probable methods of progression in the evolution of the more complex from the simpler types. It is believed that all the three methods of increase in number of separate sporangia, suggested in the former memoir (Phil. Trans., 1894, Vol. B, p. 473), have been employed, viz. (i) septation, (ii) branching or chorisis, (iii) a reversion of vegetative parts to the sporogenous condition. In addition to these, however, there has probably occurred also an eruption of appendicular organs from a previously smooth surface. This has already been suggested elsewhere (Annals of Botany, Vol. viii, p. 343); the sporangiophores of *Helminthostachys* may be taken as an interesting example of such eruption. It will be thus seen that the memoir, of which this is a very brief abstract, touches some of the most fundamental conceptions of the morphology of vascular plants, approaching them, not from the point of view derived from comparison of higher forms,

but from the study and comparison of organisms which are believed to be nearer to the border line between Bryophyta and Vascular plants, viz. the *Homosporous Pteridophyta*.

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PRELIMINARY STATEMENT ON THE SORUS OF DANAEA¹. The sorus of *Danaea*, though its structure in the mature state has been repeatedly described, has not yet been studied as regards its development.

The oblong, cake-like sori lie parallel to one another on the lower surface of the leaf, their longer axes following the course of the vascular bundles. Each sorus consists of two rows of loculi, of approximately equal size, completely sunk in the rather massive tissue of the wall. Dehiscence is described as being by a pore at the apex of each loculus.

The sporogenous tissue of each loculus is usually referable to the segmentation of a single superficial cell, which gives rise to it, and to the portion of the sporangial wall above it. There is, however, great variety of bulk, number of cells, and mode of segmentation in adjoining sporangia; though the sporangia of the same sorus develop simultaneously, such extreme differences of number as between four and sixteen cells may be seen in the same section. Moreover, the whole sporogenous group is not always referable to a single parent cell. These facts stand in marked contrast to the uniformity of size and segmentation so characteristic of the Leptosporangiate Ferns.

The dehiscence is by slits, which appear in the sporangial wall above the loculus. By the drying and contraction of the adjoining cells the slit gapes widely, and appears as a pore; but the details are very like those of other Marattiaceae, excepting that there is no 'annulus' of indurated cells. This, which is absent in *Danaea*, where the loculi are deeply sunk, is present in those Marattiaceae in which the sporangia project as separate papillae. In the latter case the annulus is mechanically effective in widening the slit; in the former, the sporangia being closely united, such mechanical effect would be impossible.

Though the loculi of a sorus are frequently of nearly uniform size,

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