and associated parenchyma, surrounded by phloem composed of large sieve-tubes with numerous sieve-plates on the lateral walls, and phloem-parenchyma; an endodermis and pericycle surround each stele, and in the case of the annular steles these layers occur both internally and externally. At the nodes the outer annular stele bends up into the leaf-stalk, and a branch is also given off from the margin of a gap formed in the inner annular stele; the axial vascular strand may or may not be in continuity with the meristele of the leaf. The petiole is traversed by a single stele, similar in shape to that of certain Cyatheaceous Ferns; towards the top of the leaf-stalk the stele alters its form, and gradually gives off separate U-shaped branches to supply the pinnae.

The most interesting feature in the structure of the pinnules is the marked papillose form of the lower epidermal cells. The roots have a triarch stele enclosed by a few layers of thick brown sclerous cells.

In structure *Matonia pectinata* presents points of agreement with several families of Ferns, on the whole approximating more closely to Cyatheaceae than to any other family; but the peculiarities are such as to fully confirm the conclusion previously drawn from external characters that *Matonia* should be placed in a separate division of the Filices.

After comparing the structure of the Malayan species with that of other genera, the paper concludes with an attempt to give an account of the geological history of the Matonineae. The genera *Laccopteris* and *Matonidium* are dealt with at some length, and reference is made to other Mesozoic Ferns, which may probably be included in the same group.

The data furnished by an examination of palaeontological evidence lead to the conclusion that in *Matonia* we have a survival of a family of Ferns, now confined to a few localities in Borneo and the Malay peninsula, and represented by two living species, which in the Mesozoic epoch had a wide geographical range, being especially abundant in the European area.

STUDIES IN THE MORPHOLOGY OF SPORE-PRODUCING MEMBERS: IV. LEPTOSPORANGIATE FERNS.—By F. O. Bower, Sc.D., F.R.S., Regius Professor of Botany in the University of Glasgow¹. The characters used in current classifications

¹ Abstract of a paper read before the Royal Society, April 20, 1899.

of Ferns need strengthening. In recent years the more detailed knowledge of the prothallus has been used for this purpose; but while not denying its value in certain specific cases, the author holds that the vegetative development of the prothallus is an uncertain guide to a general classification. On the other hand the archegonium is so uniform in its character that it gives little help; the comparison of the antheridium is, however, a useful aid, though not sufficiently varied to serve in detail¹. Accordingly the sporophyte must be the main basis. Its vegetative organs have lately been largely used for systematic purposes by Christ²; but the same objection holds here as in Phanerogams to the use of these as characters of first rank for comparison. An attempt has therefore been made in this memoir to strengthen the characters derived from the sorus by a fresh examination of its details, and certain of its features will now be used for purposes of general comparison, which have hitherto received too little attention; they are—

1. The relative time of appearance of sporangia of the same sorus.
2. Certain details of structure of the sporangium, including its stalk.
3. The orientation of the sporangia relatively to the whole sorus.
4. The potential productiveness of the sporangium as estimated by its spore-mother-cells, and the actual spore-output.

Observations of these features extending over all the more important living genera, coupled with data of habit and the characters of the gametophyte as collateral evidence, have led the author to divide the Homosporous Ferns thus:—

¹ Heim, *Flora*, 1896, p. 355, &c.

² *Die Farrnkräuter der Erde*, Jena, 1897.

These divisions are primarily based on the order of appearance of the sporangia in the sorus, the Simplices having all the sporangia of the sorus formed simultaneously, the Gradatae having them disposed in basipetal succession, and the Mixtae having the sporangia of different ages intermixed. But it is found that other important characters run parallel with these: thus the Simplices and Gradatae have an oblique annulus (where definitely present), the Mixtae (with very few exceptions) have a vertical annulus. None of the Mixtae have been found to have a higher spore-output per sporangium than sixty-four, but this number is exceeded by some of the Gradatae, and large numbers are the rule in the Simplices. The Simplices and Gradatae have relatively short thick stalks, the Mixtae usually have long and thin stalks. The orientation of the sporangia in the Simplices and Gradatae is usually definite, in the Mixtae it is indefinite. The receptacle is often elongated in the Gradatae, but not in the Simplices or Mixtae. The sum of these characters, which for the most part run parallel to one another, appears to give a substantial basis to the classification.

Evidence as to the transition from type to type has been collected. In the case of the transition from a simultaneous to a successive sorus it does not amount to a demonstration: but it is specially pointed out how slight a step it is from such a sorus as that of *Gleichenia dichotoma* to that of an *Alsophila*: that given a basal indusium and marginal position, the similarity of sporangial structure and dehiscence between *Gleichenia* and *Loxsoma* is suggestive; as also the sporangial structure and high spore-output in *Hymenophyllum*. Though we may recognize these lines of similarity, they do not focus upon any one genus as the actual transitional link from the simultaneous to the basipetal. But the transition from the basipetal to the mixed sorus can be followed in detail; intermediate steps are seen in the Dennstaedtiinae, while the fully mixed type is seen in the closely allied *Davallia*. Probably this is only one of several such lines of transition from the basipetal to the mixed type.

It is shown that a biological advantage would be gained by the suggested transitions. In the Simplices the few sporangia are large, and, arising simultaneously, make a demand all at once on the nutritive resources of the part. In the Gradatae the smaller sporangia are produced in succession upon an elongating receptacle, and the drain on the part is spread over a longer period. But with the assumption of

the mixed character the drain may be spread over an equally long time, while, as the elongated receptacle disappears, the surface from which nourishment can be derived is enlarged, and the distance through which it has to be transferred is shortened. Thus it appears biologically reasonable that the succession should be as suggested.

It is shown how the various types of dehiscence and the action of the annulus stand in close relation to the orientation of the sporangia, and to their arrangement in the sorus. Thus the position of the annulus, which has played so important a part in classification, has been placed upon a footing of adaptation.

Estimates of numerical output of spores per sporangium have been made with a view to illustrating the relation of the Eusporangiate and Leptosporangiate Ferns in this respect. The estimated output in the Marattiaceae has been shown to be high¹; that of the Polypodiaceae is sixty-four or less. The result of numerous countings is to show that, of all Leptosporangiate Ferns, *Gleichenia* approaches most nearly to the Marattiaceae (*Gl. flabellata* may produce over 800 per sporangium); *Osmunda* may have over 500, and *Lygodium* 256. The most interesting results were derived from the Hymenophyllaceae, in which *Hym. tunbridgense* may have over 400, while species of *Trichomanes* may produce as few as thirty-two per sporangium. These results, when taken with those derived from the filmy *Todeas*, make it seem probable that the filmy habit is a condition leading to reduction of output per sporangium, and indicate that the Hymenophyllaceae are a derivative series of reduction.

A most important commentary upon the classification proposed is derived from comparison of the antheridia, which Heim² found to be the most dependable part of the gametophyte for comparative purposes. He recognizes two types according to their dehiscence: the one type includes, with the exception of two genera of Schizaeaceae, our Simplices and Gradatae, while the other includes the Mixtae. I can only regard this correspondence of parts, so aloof from one another as the antheridium and the sporangium, as establishing the relations of the Simplices and Gradatae upon a firmer footing; the facts also give substantial support to the distinction of the Gradatae and Mixtae.

The effect of the observations and comparisons in this memoir is rather confirmatory of the current classifications than disturbing. The divisions suggested would supersede those of Eusporangiateae and

¹ Studies, No. 3, p. 60.

² Flora, 1896, p. 355, &c.

Leptosporangiatæ, though these terms would still be retained in a descriptive sense. If the sub-orders Osmundaceæ, Schizæaceæ, and Marattiaceæ be transferred from the end of the 'Synopsis Filicum' to the beginning, and grouped with *Gleichenia* and *Matonia*, we have the Simplices before us. The Gradatæ include the Cyatheaceæ, Dicksoniæ (excl. *Dennstaedtia*), Hymenophyllaceæ, and Loxsomaceæ, sequences probably of distinct descent, and, in my view, derivative from some prior forms such as the Simplices; and in the arrangement of Sir William Hooker they hold a position following on the Gleicheniaceæ. The family of Dennstaedtiinæ, founded by Prantl to include *Dennstaedtia* and *Microlepia*, also has its place here, but it leads on by intermediate steps to undoubtedly mixed forms such as *Davallia*, *Cystopteris*, *Lindsaya*, and the Pterideæ. But this sequence is already laid out in this order in the Synopsis, and it illustrates one at least of the lines along which mixed forms are believed to have been derived from the Gradatæ. No attempt has been made to follow the natural grouping of the Mixtæ into detail, or to test the arrangement of them in the Synopsis. Sufficient has, however, been said to show that the systematic divisions of the Ferns now proposed fall in readily with the system of Sir William Hooker, notwithstanding that they are based upon details of which he cannot have been aware.

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