INTRODUCTION TO VOLUME II

As some years have necessarily elapsed since the publication of the First Volume of this Work, and since the volumes will be on sale separately, it seems desirable to offer a brief summary of the contents of the First Volume which shall serve as an introduction to the Second, and so to link the whole Work together into a coherent whole. It has been shown in Chapter III of Vol. I that those arrangements of the constituent Families of the Filicales which have their place in current Botanical Literature appear to be marked by chance rather than by considered method, and are often wanting in suggestion of phyletic, that is evolutionary, sequence. This is believed to have been a natural consequence of the insufficiency of the foundations upon which such systems have hitherto been based. Accordingly, a definite attempt has been made to extend those foundations by using wider comparisons, and by seeking new criteria for that purpose. The result has been that twelve leading characteristics of Ferns have been selected to serve as a broad basis for their comparison with a view to the phyletic seriation of the Class—this being the end aimed at in any Natural Classification. The number of such criteria used by different authors may vary, and will probably be added to by later writers. Those to be used here are these:

(1) The external morphology of the shoot.
(2) The initial constitution of the plant-body as indicated by segmentation.
(3) The architecture and venation of the leaf.
(4) The vascular system of the shoot.
(5) The dermal appendages.
(6) The position and structure of the sorus.
(7) The indusial protections.
(8) The characters of the sporangium, and of the spores.
(9) The spore-output.
(10) The morphology of the prothallus.
(11) The position and structure of the sexual organs.
(12) The embryology of the sporophyte.

Each of these criteria has been examined critically in Ferns at large, and the scope of variation noted in respect of each. The extreme variants have been checked according to the fossil record, so that it should become possible with some degree of confidence to assert for each criterion which of its variants are to be held as relatively primitive, and which as relatively derivative. The consequences of this procedure in respect of the several criteria have been found to work out as follows:

(1) The simple shoot, composed of an axis and an acropetal succession of leaves, is the unit of construction of the sporophyte. In primitive types it is commonly unbranched, upright, and radial. The prone position with dorsiventral symmetry is probably derivative. The branching of the shoot gives distinctive features. All the distal branchings (exclusive of adventitious buds) may be referred to dichotomy. Shoots which dichotomise equally may be held as primitive in that feature, and any departure from equality, so as to produce some form of dichopodium, may be held as derivative (Chapter IV, Vol. I).

(2) Comparison as regards cellular constitution of the apices of stem, leaf, or root, or of the wings of the leaf, or of the sporangia, shows variation from types having regular segmentation of a single initial cell, as in Leptosporangiate Ferns, to those where the segmentation is not referable to a single initial, but to several, as in the Eusporangiate Ferns. Comparison with related fossils shows clearly that the latter type is relatively primitive. Hence the provisional hypothesis is entertained that the more robust Eusporangiate Ferns appeared first in descent, and that the less robust Leptosporangiate Ferns are derivative and specialised forms, and appeared later in descent. In fact that there has been a progression from a more robust and less exact to a less robust and more exact type of organisation in Ferns (Chapter VI).

(3) The leaf is traceable in origin to an elongated rachis with a dichotomous distal region; and in primitive forms it may have basal stipular growths. In various ways sympodial development of the distal dichotomy may give dichopodia, the pinnae being essentially branches of the distal region. But in advanced types where a phyllopodium is strongly established the lower pinnae may arise monopodially, the later only arising by dichotomous branching. In primitive types the segments may be all separate, each with a single vein. All webbed expansions are held to be derivative. The primitive venation is always open with free endings: looping of the veins in various ways to form a reticulum is held to be derivative (Chapter V).

(4) The primitive vascular structure of the axis was the protostele. Those Ferns which in the adult state are structurally nearest to being protostelic are held to be relatively primitive in respect of that feature: those which have departed from it, showing solenostely, dictyostely, polycycly and perforation, are held to be relatively advanced. Similarly the primitive leaf-trace is an integral strand: the undivided horse-shoe curve of the Osmundaceous type which follows is probably the prototype of later Fern-petioles, while in yet more advanced types the meristele breaks up into parts still disposed in the original curve. The marginal pinna-trace is relatively primitive, and the extra-marginal derivative (Chapters VII to X).

(5) The dermal appendages may take the form of simple hairs or scales.

As a result of simple induction from the observed facts it may be stated generally that simple hairs are a primitive feature, and that branched hairs and in particular flattened scales are an indication of advance from that simple state. Evidence of this advance parallel with other indications of advance in other characters may be found in various phyletic sequences, and this fully substantiates the general correctness of the conclusion thus stated (Chapter XI).

(6) Comparison shows that the sorus is not a constant entity for Ferns at large. It is liable to vary in position, individuality, and constitution, and the differences afford material for phyletic comparison. The marginal position, more frequent in early than in late Fern-types, is shown to have passed in several distinct phyletic series into the superficial as the area of the leaf-blade increased. This makes it seem probable that the latter is a derivative state wherever it occurs. The individuality of the sorus is lost in many sequences, whether by fissions or by fusions: or the sori may be obliterated by spreading the sporangia generally over the leaf-surface. These states appear to be all derivative. The most important variations are, however, those of constitution of the sorus. Three types have been distinguished, viz. the Simple, Gradate, and Mixed types. The first is characteristic of Palaeozoic Ferns, though it survives to the present day. The last is the type which prevails at the present day but does not appear in Palaeozoic Ferns. The Gradate is an intermediate type in many but not in all phyletic lines. Thus the soral characters provide ample material for phyletic comparison (Chapter XII).

(7) Palaeozoic Ferns have no indusial protection, nor have those characteristic of modern conditions which are included in the old comprehensive genera *Polypodium* and *Acrostichum*. But between such extremes protection by various means has been achieved, notably by different types of indusium. An indusiate sorus is then a later and derivative type: on the other hand there is evidence that the modern non-indusiate state has often resulted from the abortion of an indusium previously present. Such facts afford ample material useful for phyletic seriation (Chapter XII).

(8) The characters of the sporangium are more important than those of the sorus. The sporangium shows consistent reduction in size, with increasing specialisation of the mechanism of dispersal, as we progress from the Palaeozoic to modern types. Moreover the form, length of stalk, and the position of the annulus and stomium vary in close relation to the constitution of the sorus. The ends of the series, viz. the Eusporangiate and the advanced Leptosporangiate types, are strongly dissimilar, but they grade one into the other by most gentle steps, which give plentiful phyletic material (Chapter XIII).

(9) At the back of this gently graded series are the facts of spore-output from each sporangium. The gradual diminution of the spore-number from

many thousands to a single one gives a numerical index of the progressive simplification that cannot fail to be impressive (Chapter XIII).

(10) The vegetative features of the prothallus are chiefly negative, and for phyletic purposes stand far behind those of the sporophyte. The structure is uniformly parenchymatous, and the form is plastic under varied conditions of lighting and moisture. The persistence of the cordate type is noteworthy, but it may under certain conditions take a filamentous form, while the latter is characteristic in certain genera. The massive mycorhizic type may very well be a special modification following on fungal nutrition. The Eusporangiate types have relatively massive prothalli as a rule, but it is difficult to found any consecutive phyletic argument on the vegetative characters of the prothallus (Chapter XIV).

(11) The sexual organs of Eusporangiate Ferns are apt to be more deeply sunk than those of Leptosporangiate Ferns, which habitually project from the prothallus. In this they compare with the sporangia. The archegonia appear highly standardised for the Class, presenting little of comparative value in Ferns. But it is not so with their antheridia. These are not only deeply sunk in the Eusporangiate Ferns, but are also massive: while in Leptosporangiate Ferns they project and are relatively delicate. The sperm-numbers in each antheridium run roughly parallel with the spore-numbers in the corresponding sporangia, the primitive Ferns having relatively large numbers in each of these distinct organs. This parallel cannot be pursued into strict numerical detail, but along the lines thus indicated the sexual organs provide useful confirmatory material (Chapter XIV).

(12) The embryology of Ferns took a new value for comparison when a suspensor was discovered in certain Ophioglossaceae and Marattiaceae. It seems probable that this is an archaic feature stamping a primitive character of the plants in which it occurs. In all others it is absent, and they may be held as derivative in this feature. Its existence in these and other plants suggests that the embryo was originally a spindle-like structure, one pole of which is the suspensor, the other the apex of the shoot: while the root is an accessory organ of lateral origin. From a phyletic point of view the presence or absence of a suspensor appears to be the most important comparative feature relating to the embryo (Chapters XV, XVII).

The strength of the field of comparison thus widened by new criteria, and supplemented by those already in use, does not lie simply in the number of the lines upon which the comparisons are based, but upon the degree in which those lines run parallel. In so far as they do so they mutually support one another. This may even be held as a test of the validity of the criteria themselves. As the application of the method proceeds in the present volume it will appear that the parallelism is impressively uniform. But it cannot be assumed that progressions in respect of all the criteria will necessarily march together. Not uncommonly a Fern may be advanced in respect of certain features, and still retain one or more primitive characters: or Ferns essentially primitive may show some single feature of advance. An example of the latter is seen in *Christensenia*, in which the anatomical and soral features are clearly Marattiaceous but the venation is reticulate. The like appears in *Anemia* § *Anemidictyon*, and in *Lygodium* § *Hydroglossum*: here, while the primitive characters of the Schizaeaceae are retained, the venation is reticulate, though in the rest of those genera it is open. It may be presumed that in such examples there has been an advance in the type of venation while other features retained their primitive state. Many species of *Eu-Gleichenia* bear dermal scales, though the rhizome is protostelic, and the sorus primitive in its structure and in its sporangia. A very notable example of discrepancy is that of *Cheiropleuria*, in which a protostelic axis, a singularly primitive leaf-trace, and unbranched dermal hairs are associated with a reticulate venation and a mixed and Acrostichoid sorus. The fact that such examples are exceptional makes them stand out prominently from the rest as witnesses to the fact that the progressions in respect of the several characters march as a rule parallel.

The criteria thus recognised and evaluated were at the close of Volume I abstracted, and the most primitive aspects of them combined into a verbal specification of an ideal plant which should embody them all. The archetype which was thus presented before the mind came out as a plant not unlike the type of vegetation characteristic of the Devonian Rhynie Flora. This need not in itself be held as evidence of actual ancestry. But at least the fact that plants, comparable to this archetype extracted by analysis of Ferns at large, did exist at a very early period, is in itself evidence that the method pursued in Volume I has led to conclusions not in any way improbable.

But a much more severe test will be the application of this method of analysis to the Ferns at large with a view to their seriation in time. If it appears that the phyletic grouping thus arrived at for modern Ferns harmonises with the appearance of the various families in successive geological ages, then it may be confidently felt that we possess a morphological weapon that has real value. This is the test that will be made in the succeeding Volumes. The order of presentment will be roughly in accordance with probable evolutionary sequence. But it is of course impossible in such arrangements to do more than avoid the more gross misrepresentations: for actual affinities are from the very first doubtful, and probably complex. As we progress to the more modern types the sequences of probable affinity become clearer, and the arrangement of the material will be such as to lead readily to their recognition. But the most modern present a fresh difficulty, for owing to parallel development in them the latest types become so standardised that it becomes difficult to assign them severally to their phyletic source.

The positive facts of Palaeontology relating especially to the Ferns have been summarised critically by Seward (*Fossil Plants*, ii). They indicate the following sequence of appearance for those Classes of Ferns which a general comparison has indicated as being relatively primitive. The first Ferns of which any record exists were the **Coenopteridaceae**[1], including the Botryopterideae, and Zygopterideae, with which the Anachoropterideae may also be associated. They are known as fossils only, and are represented from the Culm and Lower Carboniferous, extending onwards to the Permian (Seward, p. 432). They appear then to have died out, and to have left no direct representatives. Perhaps we are right in looking upon the Ophioglossaceae as the most nearly related of living Filicales to them (Seward, p. 427).

The **Marattiaceae**, as represented by the Psaronieae, have been recognised from the Upper Carboniferous and Lower Permian, while *Ptychocarpus unitus* with its Marattiaceous sorus (Fig. 407, p. 115) occurs in the Middle Coal Measures of France (Seward, p. 412). Some other Carboniferous fossils may well have been really of Marattiaceous affinity, but this family appears to have attained its maximum development in Mesozoic times. Its modern representatives are the living Marattiaceae.

Next in the palaeontological succession come the **Osmundaceae**, the reliable record of which opens with the Upper Permian of Russia. The type has persisted through the Mesozoic Age, and it is represented by the Osmundaceae of the present day (Seward, p. 325). Numerous sporangia exist in Carboniferous Rocks which in section are almost indistinguishable from sections of the sporangia of living Osmundaceae (Bower, *Ann. of Bot.* Vol. v, 1891, p. 109). It has been pointed out, however, that favourable sections of a sporangium of *Botryopteris* might yield a similar appearance. On the other hand, Kidston has summed up his own wide experience of Fern sporangia, as seen from without, thus: "In the great majority of cases where Carboniferous plants have borne annulate sporangia, these have most frequently been described as formed of a single row of cells: but in some cases at least the annulus is composed of two rows of cells[2]." This is seen in his genus *Boweria* (Fig. 310). The fact seems to be that in Carboniferous times the annulus as an opening mechanism was in its experimental stage: and the Botryopterid or the early Osmundaceous types of sporangium gave a favourable field for experiment.

The Ferns above mentioned were undoubtedly of Palaeozoic origin. In the Mesozoic Period a great evolutionary outburst of Ferns took place. Several of the families which were well represented then have been traced, though with doubtful credentials, to the Palaeozoic Period. This remark

[1] I prefer this title introduced by Seward, as expressing a generalised Filical type, to that of "Primofilices" suggested by Arber, which appears to convey more than is desirable. But I have ventured to change the form from Coenopterideae to the more comprehensive title Coenopteridaceae.

[2] *Fossil Plants of the Carboniferous Rocks*, Vol. ii, Part IV, 1923, p. 278

applies to the **Gleicheniaceae**: but the reference of *Oligocarpia* to this family may be held as doubtful. Seward sums up the case thus (*l.c.* p. 352): "Despite an agreement between *Oligocarpia* and *Gleichenia* as regards the form of the sori and the number of sporangia, it is not certain that the existence of a typical Gleicheniaceous annulus has been proved to occur in any Palaeozoic sporangia." But in Triassic and Jurassic times their presence is proved, and they survive in the modern Gleicheniaceae.

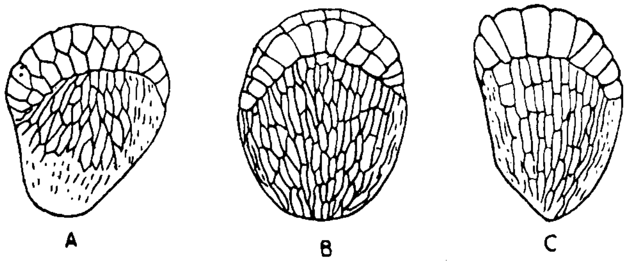

Fig. 310. *Boweria schlatzlarensis* Kidston. Sporangia enlarged about 50 times. *A*, from Clifton, Lancashire; *B*, *C*, from Monckton Main Colliery, near Barnsley. (After Kidston.)

The **Schizaeaceae** are also early Ferns in geological time. But according to Seward (*l.c.* p. 347), the first confident recognition of the Family is in the older Jurassic Rocks. It is true that earlier records have been quoted: in particular *Senftenbergia elegans* described by Corda from the Carboniferous of Bohemia was referred to this Family. But it seems now more probable that this and other early fossils, while bearing a resemblance to Schizaeaceae, are really generalised types foreshadowing lines of evolution rather than already representing the actually differentiated Family.

The **Matonineae** were undoubtedly represented in Mesozoic times by *Laccopteris* and *Matonidium*: and the type survives to the present day in *Matonia*.

The **Dipteridinae** also appear represented by numerous fossil types in the Mesozoic Age, while the family still exists in the living genus *Dipteris*, and it is probably represented also in a large number of those Polypodiaceae which may be looked upon as Dipterid-derivatives.

With regard to the **Cyatheaceae** (incl. **Dicksonieae**) Seward remarks that "we have as yet no satisfactory evidence of the existence of the Cyatheaceae in Palaeozoic Floras. It is not until we reach the Jurassic Period that trustworthy data are obtained" (*l.c.* p. 366). But then they appear to have been fairly well represented, and the type has survived in a large number of living species.

Certain early fossils have been referred to the **Hymenophyllaceae**, in particular *Hymenophyllum weissii* from the Coal Measures of Saarbrücken, and *Hymenophyllites quadridactylites* Gutbier from the French Coal Measures.

But after considering these carefully Seward concludes (*l.c.* p. 365) that "there is no evidence which can be adduced in favour of regarding the Hymenophyllaceae as Ferns of great antiquity which played a prominent part in the Floras of the past."

With regard to the **Polypodiaceae** Seward remarks (*l.c.* p. 375) that "we have as yet no satisfactory evidence of the existence of true Polypodiaceae in the Palaeozoic Era." As regards their Mesozoic existence, however, he quotes a probable example in *Onychiopsis mantelli* (Brongn.) from the Wealden. Various Ferns referred to the Polypodiaceae have been derived from the British Tertiary strata, and these lead on naturally to those Ferns which constitute the large majority of the living species. "It is noteworthy that apart from the absence of Ferns which can reasonably be included in this family, the anatomical features of the Botryopterideae (Coenopterideae) and of the Cycadofilices or Pteridosperms do not foreshadow those of Polypodiaceous Ferns. On the other hand, as we have already noticed, anatomical characters of such families as the Gleicheniaceae, Hymenophyllaceae, and Schizaeaceae are met with in certain generalised Palaeozoic types. These facts are perhaps of some importance as supplying collateral evidence in favour of the relatively more recent origin of the dominant family of ferns in modern floras" (Seward, *l.c.* p. 376).

From this brief summary, drawn from a reliable source, it will be gathered that the general trend of the results of Palaeontological enquiry runs parallel with that of Comparative Morphology. Together the two methods justify the recognition of certain Families as the most ancient. They are the **Coenopteridaceae** and **Osmundaceae**, which have had undoubted Palaeozoic existence, and with them may perhaps be associated the **Marattiaceae.** With the first of these the **Ophioglossaceae** may be ranked on comparative grounds, though they have not yet been definitely recognised as early fossils. These four Families include all the Eusporangiate Ferns now living.

The remainder of the Ferns, though prefigured in some measure by fossils of the Palaeozoic Period, first began to assume their ordinal characters in the Mesozoic Period, or later. They will be found to show more or less clear relationship to two relatively primitive Families, viz. the **Schizaeaceae** and the **Gleicheniaceae**, both of which became firmly established in early Jurassic times: one, the Schizaeaceae, is characterised by bearing its sori on the margins of the leaves; the other, the Gleicheniaceae, bears them superficially. The two series thus consistently defined have been designated respectively the **Marginales**, and the **Superficiales**. Both are regarded as having not improbably originated from some common earlier source. The order of treatment of the several Families will follow the lines thus indicated, the most ancient fossil types being taken first. But since the Class of the Filicales shows many indications of polyphylesis, the descriptions cannot possibly follow naturally in any simple linear sequence. The succession in which they are taken up must therefore be somewhat artificial. Short series may be suggested, and built up. But the actual evolutionary relation of those series to one another will still remain highly problematical. The time has not yet come for any confident reconstruction of an "evolutionary tree," which shall represent the phylesis of the Filicales as a series of connected branches springing from a common trunk, even if there ever was one. Nevertheless the relative position of those branches is a legitimate subject for discussion, and definite views may even be entertained regarding it.

In any Family of related organisms, excepting the very simplest, difficulties must be expected in grouping them phyletically. The more complex the organisms are, and the more numerous the criteria of their comparison, the greater those difficulties may be expected to be: for there is no reason to anticipate that evolution will have expressed itself equally in respect of all the features. And so it comes about that it appears to be sometimes impossible to sum up the results of comparison in respect of all the features into a conclusion, that genus or species (A) is more primitive than genus or species (B). Such difficulties naturally present themselves when any attempt is made to seriate any group of organisms phyletically: and any one who fully grasps the problem will place his own value upon the phyletic seriation of any group submitted for his judgment. Some may say, "If that is true, why attempt phyletic seriation at all?" The proper reply to that question is, "Why study Evolution at all?" Phyletic seriation is merely a form of recording tentative evolutionary conclusions: it has, however, the advantage of raising questions which otherwise might very likely remain dormant.

CHAPTER XVIII

COENOPTERIDACEAE

THE plants included under this heading are all fossils, and include the Botryopterideae, the Zygopterideae, and the Anachoropterideae: but it is possible that others may be added as knowledge of the fossils increases. They are all Palaeozoic types, and are distinct from any living Ferns. Still there is no reason to doubt their Fern-nature, though they appear as generalised rather than specialised types. Their recognition as Ferns is based upon the external characters of the shoot with pronounced megaphyllous character, while the usual circinate vernation of the large alternate leaves has been seen in some of them. But more particularly it rests upon the anatomical details of axis and leaf, and upon the fact that in some of them sporangia containing numerous homosporous spores have been found, borne upon the distal region of their relatively large branched sporophylls. Finally, Scott has shown in *Stauropteris oldhamia* that the spores possessed the capacity for germination within the sporangium, a feature seen in some modern Ferns (*Todea*) (*New Phyt.* v, 1906). As the three orders are somewhat divergent in their characters it will be well to describe them separately.

A. BOTRYOPTERIDEAE

To this family the genera *Grammatopteris*, *Tubicaulis*, and *Botryopteris* are referred. They were mostly plants of relatively small size with stems probably upright or straggling, which in some cases were short, bearing crowded leaves (*Grammatopteris*, *Tubicaulis*, *Botryopteris ramosa* and *hirsuta*, Fig. 311): in others the stem was slender with dichotomous branching, and it appears to have borne leaves at distant intervals (*Botryopteris cylindrica*, Fig. 312). The leaves are imperfectly known: they have never been seen to bear a well-developed lamina. They were repeatedly branched, with narrow fleshy pinnules upon which the sporangia were inserted (*B. forensis*). In the young state the circinate vernation has been seen. Stiff conical hairs are found upon the leaves having peculiar structure (*B. forensis*, Vol. I, Fig. 187). In some instances the plants bore numerous adventitious roots with diarch structure (*Tubicaulis*, *B. ramosa*, Fig. 311). Though the habit of these plants is still imperfectly known, their Fern-nature seems clearly established, while their anatomy, which is better understood, confirms that conclusion.

The vascular system of the stem is protostelic, giving off monodesmic leaf-traces to the several leaves. The roots which are often numerous also