NOTES ON PALAEOZOIC BOTANY 1907—1927

by

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Twenty years ago I contributed to Progressus Rei Botanicae, an article of some length on the position of Palaeozoic Botany at that time (Scott, 1907). The present occasion seems appropriate for taking a brief survey of the chief changes and advances in the subject since 1907. The space available demands that such a survey should be as concise as possible. It will be limited to the land vegetation of the period, and to work of outstanding morphological and evolutionary interest.

We may group the Palaeozoic plants to be considered as follows:

Bryophyta	Lycopodiales
Psilophytales	Ferns
Articulatae	Spermophyta.

1. Bryophyta.

Up to 1925 our direct evidence for the existence of Palaeozoic Bryophytes was so slight as to be almost negligible. In that year Mr. John Walton published his discovery of Carboniferous Hepaticae (Walton, 1925) chiefly from the Middle Coal-measures of Shropshire. Of the four species so far described, one, *Hepaticites Kidstoni,* is clearly a foliose Liverwort with a thick stem, well differentiated lateral leaves, and two rows of small leaves or amphigastria. The resemblance to a modern Liverwort of the *Jungermannia* type is most striking. The author compares the fossil with such living genera as *Fossombronia* and *Blasia*. *H. lobatus* is more thalloid, but still with leaf-like lobes, while the other two species *H. Willsi*[1]) and *H. Langi* are wholly thalloid.

Mr. Walton is justified in stating that these fossils remove all doubt as to the presence of Liverworts of a comparatively high degree of specialization in the Palaeozoic. This demonstration of the high antiquity of the Hepaticae was unexpected and is an important addition to our knowledge. As we shall see in the next section, some of the early Devonian fossils may throw some further light on the history of the Bryophyta.

2. Psilophytales.

The discovery, or rather recognition of the Psilophytales is undoubtedly the most important event in the progress of Palaeozoic Botany during the last 20 years. The genus *Psilophyton* is an old one, founded by Sir William Dawson as long ago as 1859. But botanists were very doubtful about it, and its existence as a definite genus of plants was questioned by good authorities. The recent work has rendered it probable that Dawson's reconstruction of his original species was substantially correct. Difficulties, as we shall see, still remain, but at least we may say that the presence in the older Devonian Flora of a group of plants of the Psilophyton type is now well established.

The class Psilophytales is based essentially on plants from the chert bed at Rhynie in Aberdeenshire. The plant-containing deposit was discovered by Dr. Mackie in 1913; the flora of the bed has been fully and admirably

[1]) Originally discovered by Miss L. Wills in 1914.

described by the late Dr. Kidston and Professor W. H. Lang. Seldom indeed has a newly discovered group of fossil plants been so thoroughly elucidated (Kidston and Lang, 1917—1921).

Confining ourselves to the vascular plants, the Rhynie species are four in numer: *Rhynia major, R. Gwynne-Vaughani, Hornea Lignieri* and *Asteroxylon Mackiei.* The first three are placed in a family Rhyniaceae, containing by far the simplest Vasculares known. Rhynia major, for example, was an absolutely leafless and rootless plant, consisting of a forking, cylindrical stem or thallus, springing from a horizontal rhizome, bearing rhizoids, but otherwise similar to the aerial shoots. The anatomy is that of a land plant. The stem and its branches are traversed by a slender concentric strand of wood and bast; as there are no appendages there are of course no leaf-traces. The epidermis containing scattered stomata of a normal, if somewhat simple type (W. Zimmermann, 1926).

The sporangia are long sacs, reaching 12 mm. in length, borne terminally on the ends of branches of the stem. The sporangial wall is of rather complex structure, including a columnar layer; the cavity is filled with spores, which are often grouped in tetrads and have a firm, resistant cell-wall; in fact they resemble in all respects the spores of Pteridophytes, and were evidently adapted for dispersal in air.

Rhynia Gwynne-Vaughani was a smaller plant, but somewhat more complex in its organisation. The aerial stem bears hemi-spherical outgrowths, which cannot be interpreted as rudimentary leaves, for there is evidence that they were formed late in the life of the plant, as new formations, usually localised beneath the stomata. Often these outgrowths became the seat of adventitious branching, additional to the dichotomy constant in both species. The adventitious shoots were commonly without any vascular connection with the axis, and readily became detached, no doubt serving as a means of vegetative propagation.

Hornea, of which only the one species, H. Lignieri, is known, was as simple a plant as Rhynia major, but had the peculiarity that the rhizome was tuberous, recalling the „protocorm" found as an embryonic stage in some recent Lycopods. Otherwise the interest of the fossil centres in the sporangia. They are terminal organs; the end of the branch which assumed reproductive functions is but little modified; for example, a sporangium is sometimes forked, like a vegetative branch. The most remarkable feature of the sporangium is that it possesses a columella, a central column of sterile tissue. The spore-bearing zone is dome-shaped, over-arching the columella, an arrangement much like that in the Bog-mosses (*Sphagnum*) and a few other Bryophytes.

A similar columellate structure had previously been detected by Professor Halle in a fossil fructification which he named *Sporogonites,* from the Lower Devonian of Norway (Halle, 1916). In general form Sporogonites suggests the capsule and seta of a large moss, but we do not know how it was borne. At any rate the characters of Hornea and Sporogonites indicate a possible affinity with the Bryophytes, which, if accepted, must be extended to the Rhyniaceae generally. Professor Bower has said on this point: „Comparison of the Bryophytes will leave little doubt that the sporangium of the Psilophytales and the sporogonium are kindred structures". „The new facts are thus seen to link the Bryophytes and the Pteridophytes more closely together than ever before". (Bower, 1920). So far we may safely go, though it would be well to restrict the comparison to the Rhyniaceae, for Asteroxylon, as we shall see, is another story.

Dr. A. H. Church has gone further; he says: „Rhynia and Hornea between them present all the characters deduced as significant for early Bryophyta, so far as the sporophyte stage is concerned": and further on he adds: „Hornea is in fact, little more than a slightly ramified and free-growing Anthoceros". He considers that the only objection to such an interpretation is the presence in the main axis of the Rhyniaceae of tracheidal cells with ring-thickenings. He points out that there is no evidence of lignification and calls attention to the occurrence of similar cells in the capsule of Pellia, and elsewhere in Hepaticae. Thus Dr. Church endeavours to explain away the Pteridophytic characters, and lays all the stress on the points in common with Bryophytes (Church, 1926, p. 177).

We see then that the Rhyniaceae may be and have been assigned to three different main divisions of the Plant Kingdom. Dr. Church, as we have said, would place them in Bryophyta; the late Dr. Arber regarded Psilophyton (which he identified with Rhynia) and some other Devonian genera as belonging to „a now obsolete race of Thallophyta" (Arber, 1921); the discoverers and most other writers, including myself, class them with Pteridophyta. That this view is justified is clear, for the spore-bearing generation is a vascular plant, and neither Thallophytes nor Bryophytes fulfil this condition. On the other hand it must be granted that the vegetative body is to all intents and purposes a thallus, no more differentiated externally than that of many Algae; and further, as already pointed out, the sporangial structure, at least in two genera, is strongly suggestive of the sporogonium of a Bryophyte.

In connection with the Rhyniaceae we may briefly consider one or two early fossils recently described which may throw some further light on the position of the group.

Hicklingia Edwardi, from the Middle Old Red Sandstone (Devonian) of Caithness forms a tuft 7 inches in diameter, consisting of slender stems, radiating from a common base, and branching by equal or unequal dichotomy. A slight longitudinal line, observed on some of the stems, may indicate the presence of a vascular strand. The internal structure is not preserved. Round bodies (presumably sporangia) are borne on the tips of the branches. *Hicklingia* is compared with the Rhyniaceae, but a possible relationship to the Algae is recognised (Kidston & Lang, 1923).

A fossil from the Upper Devonian of Ohio, orginally described by Dawson under the name *Sporocarpon furcatum,* has been re-investigated by Kidston and Lang, and has been re-named *Foerstia furcata.* Only the tips of branches are known; they are usually forked. They form hollow sacs with the wall several cells thick. The inner side of the fork is grooved, and in these grooves spores are present. They are large bodies (200 μ diam.) grouped in tetrads, and have a tough cell-wall, showing the usual tri-radiate marking. They are thus quite like Pteridophyte spores. A cuticle is present on the stem. These features suggest a land plant, though the structure is otherwise that of an Alga. The plant, we are told, almost serves to „break down any sharp distinction between the Algae and the simplest Pteridophyta" (Kidston & Lang, 1924).

Without going into more doubtful cases we may adopt Kidston and Lang's remark (made before the investigation of Hicklingia and Foerstia) that the Rhyniaceae and Sporogonites suggest „the convergence of Pteridophyta and Bryophyta backwards towards an Algal stock" (Kidston & Lang, 1920, p. 625).

We have now to consider the remaining genus of Rhynie vascular plants, Asteroxylon. Here we have the great advantage that a second species has since been described by Drs. Kräusel and Weyland, from the Middle Devonian of Germany.

The Rhynie species, A. Mackiei, had a totally different habit from that of the Rhyniaceae, for it was a leafy plant, something like a large Club-moss in appearance. The stem attained a diameter of over a centimeter; it was freely branched both by dichotomy and by lateral shoots. The aerial stems sprang from a prostrate rhizome, bearing neither roots nor rhizoids, and anatomically of a simple structure like that of Rhynia. The aerial stems, clothed with small leaves, had a far more complex organisation. The wood was stellate in transverse section, and surrounded by phloem. From the arms of the xylem leaf traces were given off. They entered the bases of the leaves, one to each, but never reached the lamina, which was thus left without any vascular system of its own. This deficiency may be regarded as a primitive feature; the absence of any true roots, and the want of differentiation among the tracheides of the wood (all being spiral) point in the same direction; for these reasons Asteroxylon was included in the Psilophytales. Habit and anatomical details suggest a comparison with Lycopods, and some botanists have detected an affinity with the Psilotaceae, an isolated recent family of epiphytes.

No reproductive organs were found in connection with the Rhynie Asteroxylon, but closely associated with some of the specimens there were peculiar naked branches, and associated again with these, sporangia were found. It was suggested that the leafless branches were the sporangiophores of the plant, to which the sporangia found had been attached. This interpretation seemed probable, but there was no decisive evidence. The sporangia themselves are unlike those of the Rhyniaceae, and rather resemble those of some Carboniferous Ferns, such as *Stauropteris*.

The plant discovered by Kräusel and Weyland and named *Asteroxylon Elberfeldense*, comes from the „Honseler Schichten", near Elberfeld, belonging to the lower beds of the Upper Middle Devonian, perhaps somewhat later than the Rhynie chert-bed. (Kräusel & Weyland, 1926).

It was a large plant, probably reaching a metre in height. The lower part of the stem is clothed with leaves, like the

Rhynie species. Further up, the leaves are replaced by spines as in Dawson's Psilophyton, while the uppermost branches are slender and naked, such as have been referred to Hostimella. Thus the Elberfeld plant combines in itself three so-called genera; the leafy stems corresponding to Thursophyton, the middle spiny region to Psilophyton and the bare branches at the top to Hostimella. Kidston and Lang had already recognised in their species the close agreement with Thursophyton, and had placed the plant in the same family with Psilophyton, but we were not prepared to find the three types actually united in the same individual. Of course it must not be supposed that every Hostimella, Psilophyton or Thursophyton belonged to Asteroxylon; each name has no doubt been used for various heterogeneous objects. All we can say is that Asteroxylon passed through all three forms in the course of its development.

The Hostimella branches, which in two cases have been found to terminate in sporangia, are regarded as corresponding to Kidston and Lang's sporangiophores. Thus the German species affords strong evidence that these organs and the associated sporangia were rightly attributed to the Rhynie Asteroxylon.

Anatomically A. Elberfeldense shows a general agreement with A. Mackiei, but present well-marked specific differences, notably in the presence of a pith in the stele of the stem; also the structure of the terminal „Hostimella" branches is more like that of the main stem than is the case with the sporangiophores of the Rhynie plant. The species are very distinct, but one throws light on the other.

The affinities of the genus are difficult if not impossible to determine. In habit and anatomical structure there is, as we have seen, a decided resemblance to Lycopods. The anatomy agrees fairly with that of the Psilotaceae also and the absence of true roots has been noted as another character in common.

On the other hand, the fructification, sporangia borne on the ends of a special branch-system, is totally unlike anything in either group. The arrangement recalls what we find in some Palaeozoic Ferns of the Zygopterid family, especially Stauropteris. The dehiscent sporangia are rather strikingly similar. But the branched stalks on which they are borne are in the Zygopterids part of the leaf, while in Asteroxylon they belong to the stem. The distinction may not be so absolute as it sounds. The leaf, according to Lignier's well known theory, originated in two ways: by the outgrowth of emergences (phylloids) and by the specialization of thallus-branches (fronds and true leaves generally). Asteroxylon undoubtedly had leaves of the former kind; possibly the „Hostimella" branches were beginning to assume foliar characters as nascent fronds. These branches had circinate tips, a frond-like feature which has also been observed in terminal branches of Dawson's *Psilophyton princeps* and other plants of the period. It is therefore not an untenable hypothesis that the Hostimella-like sporangiophores of Asteroxylon might have been the forerunners of the fertile fronds of Zygopterid Ferns.

On this view Asteroxylon might be considered, as Kidston and Lang suggested, a highly synthetic genus, combining certain characters of Lycopods, Psilotaceae and Ferns. Even before the discovery of Asteroxylon, Professor Halle, on the basis of fossils then referred to Psilophyton, had pointed out that „from this point of view the whole pteridophytic stock would be monophyletic, Lycopsida and Pteropsida being derived from a common form already vascular" (Halle, 1916, p. 39). All such theorecal conclusions can only be tentative; polyphyletic theories are also in the field, and judgment mus be suspended until we have many more facts to go by[1]).

[1]) For a fuller discussion of the position of Psilophytales see Scott, 1924, pp. 197—207.

3. Articulatae.

We will take the Articulatae next, not because they show any connection with the Psilophytales, but because some early Devonian representatives have recently been recorded. Previously we did not know of any Articulatae older than the Upper Devonian, from which species of *Sphenophyllum* with filiform foliage, and Nathorst's remarkable isolated genus *Pseudobornia* had been recorded. No authentic case of a Devonian Calamarian was known.

About 1914 Nathorst described a plant from West Norway, probably of Upper Middle Devonian age, which he named *Hyenia sphenophylloides*. The stems, which appear to radiate from a common base, bear whorls of slender, forked leaves, probably superposed, the number in each verticil being at least four, possibly six. The resemblance to a Sphenophyllum is manifest, but the nodes are not sharply marked, as in that genus. The discoverer regarded the plant as a precursor of Sphenophyllum, possibly with Calamarian affinities also (Nathorst, 1914—15).

In their important work on the Middle Devonian Flora of Elberfeld, Kräusel and Weyland describe a second species of *Hyenia, H. elegans*. In habit the German species bears a general resemblance to Nathorst's plant; the point of interest is the presence of the fructification. This consists of loose spikes; the axis bears numerous forked sporangiophores but bracts are absent. Two or three sporangia hang down from each arm of the bifurcate sporangiophore. Thus the strobilus was of a simpler type than in Sphenophyllum or most of the Calamariaceae.

The other Elberfeld representative of the Articulatae was a very different plant, nemed *Calamophyton primaevum*. Here the stem was thick and woody and freely branched by dichotomy, an unusual feature in the class. The younger branches show distinct articulations with small forked leaves in whorls. The fructification agrees nearly but not quite with that of Hyenia. Here too the cones bear loosely arranged sporangiophores; they are forked, as in the former genus, but only one sporangium was observed on each arm of the fork. Bracts are absent as before. In the case of Calamophyton something is known of the anatomy of the stem. The wood was found to be triangular in transverse section as in Sphenophyllum, while it resembled that of the Calamarians in possessing a pith.

These two genera, Hyenia and Calamophyton, are the oldest plants known of the Articulate type. Kräusel and Weyland find that they cannot be included in any of the recognized groups of Articulatae, and place them in a new class, Proto-articulatae, in which they represent two distinct families and series. Hyenia was a small plant and Calamophyton a relatively large one; the former suggesta a relation to Sphenophylls, the latter to Calamarians. But the fructification is nearly the same in both, and, as Lady Isabel Browne points out, agrees much better with a Calamarian than a Sphenophyllaceous type. A cone bearing sporangiophores but no bracts is familiar in the Horsetail series, both in ancient fossils (as *Archaeocalamites*) and in the living genus. It is not known in Sphenophylls, except in the very special case of *Sphenophyllum fertile.* The bractless cones of these earliest known Articulatae support Lady Isabel Browne's contention that the bracts of the Carboniferous Calamarians were a later intercalation (Browne, 1927).

As regards the Sphenophyllales themselves there is not much to record. One or two new cones of Sphenophyllum have been described from impressions but no fresh type has been revealed. It is now evident that while in some species (e.g. *S. Dawsoni, S. fertile*) cones were sharply differentiated, in others (e.g. *S. majus, S. tenuissimum*) the „Selago'. condition occurred, the ordinary leaves of the plant serving as bracts, so that no distinct cone was formed.

The roots of British species of Sphenophyllum, both from the Lower and Upper Carboniferous, have now been recognised. They are easily distinguished from the stems by their simpler cortical structure and by the small size of the primary xylem, which is usually diarch. The roots, like the stem, developed much secondary tissue. There is evidence that they were borne on the nodes of the stem. A general agreement is shown with the roots, long known, of French species (Scott, 1920, p. 86).

The remarkable and complex cone *Cheirostrobus,* of Lower Carboniferous age, was originally placed in Sphenophyllales, with which there are several points in common. The obvious differences from Sphenophyllum were recognised by making Cheirostrobus the type of a distinct family. More recent writers have separated Cheirostrobus in a class of its own, Cheirostrobales. Dr. Gothan advocates this separation on the ground that the Burntisland plant differs from Sphenophyllum in the polyarch stele and the presence of parenchyma in the wood, and further argues that in our ignorance of the vegetative organs we cannot be certain that the leaves (as distinguished from the sporophylls) were in superposed whorls, or in whorls at all. It does not much matter which view we take. Cheirostrobus agrees with the Sphenophylls in certain definite features (superposed verticils; dorsiventral relation of sporangiophores and bracts; branching of trace-bundles in cortex; palmatifid segmentation of appendages). These characters are best recognised by inclusion of the genus in the Sphenophyllales. On the other hand if we place Cheirostrobus in a class by itself we can the better nealise its affinities in other directions, namely with the Equisetales. The sporangiophores and sporangia agree almost in every detail with those of Calamariaceae. As for *Pseudobornia,* the compound leaves present some analogy with the compound sporophylls of Cheirostrobus, but there has never been any question of near affinity[1]). (Gothan, 1921).

We are not directly concerned with the recent Psilotales in this survey, but it may be mentioned that the theory of a relationship between that group and the Sphenophyllales, once held, has now been abandoned. The Psilotales are not Articulatae, and the resemblance between their sporangial apparatus and that of the fossil group now appears to be merely superficial (Scott, 1923, p. 396).

Passing to the Calamariaceae (Carboniferous Equisetales) progress has been made in several directions, notably in our knowledge of the leaves. Dr. Hamshaw Thomas has described the anatomical structure of five types of leaf, all of the section *Calamocladus*. The usually broader leaves of the *Annularia* section were not found petrified. All the leaves were small with a single median bundle. The types differ in the extent and distribution of the sclerenchyma, palisade layer and melasmatic tissue. The last-named tissue is regarded as a highly developed bundle-sheath, which may have originally contained starch in its cells. Dr. Thomas was able to refer three of his types to species of *Calamites* known as impressions (*C. charaeformis, C. grandis* and probably *C. equisetiformis*). The author made the interesting observation that the stomata of the Calamites exhibit the characteristic structure seen in modern Equisetums. (Thomas, 1911).

Fructifications, at least those with structure preserved, are commonly found isolated. In some cases, however, such Calamarian cones have now been referred to the plants which bore them. For example the well-known species *Calamostachys Ludwigi*, of which the original specimens show beautifully preserved structure, has also often been identified in the form of impressions and Dr. Renier

[1]) Dr. Gothan (l.c. p. 158) takes what I have said on this point somewhat too seriously!

has shown that these cones were borne on the shoots of *Asterophyllites* (*Calamocladus*) *longifolius* (Renier, 1911). Further, a cone of the familiar species *C. Binneyana* has been found by Dr. Hamshaw Thomas attached to a shoot identified by the leaves as Asterophyllites (Calamocladus) grandis. (Thomas, 1909, where other cases are given).

As regards the Calamarian cones themselves, while there have been no striking new discoveries, there have been various attempts to elucidate the morphology. Thomas, in his paper of 1909, just cited, rightly pointed out that the bracts are evident leaves, and cannot be interpreted as sterile sporophylls or lobes of sporophylls. Hickling made a careful investigation of the structure of Calamostachys Binneyana, and endeavoured to show that the vascular supply of the sporangiophores arises from the same node as that of the bracts below; this had been previously stated by Renault in the case if his *Calamodendrostachys Zeilleri.* This interpretation would make the sporangiophores appendages of the bracts next beneath them, a view which has found favour from its harmonizing the Calamarian cone-structure with that of the Sphenophylls (Hickling, 1910).

This interpretation is rejected by Lady Isabel Browne in her recent paper, cited above (Browne, 1927). The author maintains the view that the Calamarian cones originally bore whorls of sporangiophores only, perhaps with a few leaves at long intervals, as indicated in *Pothocites,* between which whorls of protective leaves (bracts) became intercalated in certain cases, as in the Carboniferous genera *Calamostachys* and *Palaeostachya.* This theory undoubtedly explains the facts very well, so far as the Equisetales are concerned. The complete independence of bracts and sporangiophores which the theory involves, does not admit of any ready comparison with the Sphenophylls, in which sporangiophores and bracts are lobes of the same organ, at least in the cases most fully investigated. Thus difficulties still remain, for, as we have seen, one can hardly doubt that there is a certain affinity between the cone of Cheirostrobus and that of a Calamarian. The same author has also undertaken a very desirable re-investigation of the classical specimens of Calamarian cones in the French collections (Browne, 1925).

A paper by Dr. Max Hirmer on Calamostachys breaks new ground. It has long been known that in cones of this type, the bracts are commonly about twice as numerous in a whorl as the sporangiophores, and further that while the bracts in successive whorls are alternate with each other the sporangiophores are superposed throughout. It thus appeared that there could be no constant relation of position between the two organs. Dr. Hirmer has restored order and shown that a certain definite symmetry is maintained. In the successive pairs of whorls, two alternative arrangements prevail. In the one case half the bracts stand exactly opposite the sporangiophores next above, while the other half are situated exactly between them. In the alternative case two bracts are placed laterally opposite the edges of each sporangiophore. Of course the arrangement is liable to be disturbed, where an odd number of bracts occurs, but it is well to have a regular system established, even if subject to occasional exceptions. Dr. Hirmer found his formula to apply to Calamostachys Binneyana, with 6—8 sporangiophores and 12—16 bracts, and to C. Ludwigi (numbers 6 and 12) and probably also to Renault's *Calamodendrostachys Grand'Euryi* with no less than 18 sporangiophores and 36 bracts in a whorl (Hirmer, 1925).

It will be understood that here as elsewhere our scheme does not admit of reference to purely taxonomic works descriptive of species, valuable as they are to the systematist.

4. Lycopodiales.

Our knowledge of Palaeozoic Lycopods stands where it did; there have been no fundamental changes, though much detalied work has been done.

The first question one may ask is whether the Lycopods can be traced back to the earlier Devonian Floras, about which we have learnt so much of late. There is no certain evidence at present. As we have seen, Asteroxylon, both in habit (*Thursophyton* region) and anatomy, recalls a Club-moss but the fructification, now referred definitely to the genus, negatives any near affinity. Other *Thursophytons* have been described with a supposed Lycopodiaceous type of fructification, but this is now discredited.

The genus *Protolepidodendron*, originally founded on specimens from the Middle Devonian of Bohemia, was recognised by Kidston and described by Lang in a fossil from the Middle Old Red Sandstone of Caithness. The stem shows a characteristic pattern of Lepidodendroid leaf-bases, to which, in the Scottish specimen, small simple leaves are sometimes attached. The external characters strongly suggest a Lycopod, but nothing further is known (Lang, 1926).

A somewhat similar genus, *Archaeosigillaria*, with the leaf-scars mostly in vertical rows, is represented by a Middle Devonian species occurring in the State of New-York; where a magnificent specimen, at least 3.25 metres in height, was discovered (White, 1907). It appears impossible to doubt that Archaeosigillaria was related to the *Lepidodendrons* and *Sigillarias* of later times, but here also we have to depend on external characters.

Among the numerous and varied spores, discovered by Dr. Lang in the Fish-Beds of Cromarty (Middle Old Red Sandstone), it is possible that some may have belonged to early Lycopods, but of this we have no evidence. Some are of almost megaspore dimensions (Lang, 1925).

In the Upper Devonian the Lycopods were already very highly developed. The genus *Cyclostigma* of Haughton has now been revived for Upper Devonian Lycopods once included under *Bothrodendron*. The absence of a ligule in the older species is the chief character on which the genera have been separated. The Stigmarian root-stock of *Cyclostigma Kiltorkense* has been identified by Professor T. Johnson. The large, stout cones were heterosporous in a high degree, the megaspores measuring 1 millimetre in diameter. We do not yet know anything of the anatomy, but there is no reason to doubt that the Devonian Cyclostigmas were already as far advanced as most of their successors among the Carboniferous Lepidodendreae (Johnson, 1913 and 1914). Other Upper Devonian Lycopods are refered to *Lepidodendron*. In one of these, *L. caracubense*, from the Donetz Basin of Russia, Dr. Zalessky was able to investigate the anatomy. The stem possessed a solid stele, without a pith, the wood extending to the centre, a condition also found in some of the oldest Carboniferous species.

As regards the reproductive organs of Palaeozoic Lycopods, new species of cone have been described, old species examined in greater detail, and valuable monographs published, (A. Arber, 1914) but only one or two points are so novel as to require notice here.

The most striking is the very curious genus *Mazocarpon* founded and investigated by Dr. Margaret Benson. The cone was of the *Lepidostrobus* type, but the sporangia were quite peculiar. Externally each megasporangium possessed a lateral flange; internally it contained a large mass of sterile tissue in which the great sausage-shaped megaspores were embedded — they were quite 2 mm. long. The sporangium was readily detached from the cone and underwent fragmentation. We commonly find single megaspores, each clothed in a mantle of sporangial tissue. Before dehiscence, the concave side of the curved megaspores fitted on to the central, sub-archesporial pad. It was on this inner side that the open beak of the megaspore was placed. The prothallus is sometimes preserved, and there are remains of the archegonia below the beak. Hence they were in an inaccessible position, and we can only suppose that fertilization took place after the megaspores were set free by the breaking up of the sporangium. The single-spored units were termed „seed-like bodies" by the discoverer. The microsporangium likewise shows a great development of sterile tissue, interspersed with nests of microspores.

Dr. Benson regards Mazocarpon as a Sigillarian cone, with structure preserved, a view for which there is some good evidence. But we must not suppose that all Sigillarian cones were of such a peculiar nature (Benson, 1918).

The small heterosporous cone of a Bothrodendron (*B. mundum*) has been identified by Dr. Watson (Watson, 1908). It is as different as possible from the bulky cones of Cyclostigma above mentioned.

Further observations of prothalli and archegonia go to show that the heterosporous Lycopods of Palaeozoic times were reproduced by the same methods as their living successors. The „seed-bearing" plants of that affinity are still limited to the two, very diverse genera *Lepidocarpon* and *Miadesmia*. A specimen, believed to be referable to the former genus, from the Westphalian of Staffordshire, was described by Dr. Kidston under the name *Lepidocarpon Westphalicum*. Its relation to the petrified specimens has yet to be proved. (Kidston, 1914).

The question of the nature of the Ulodendroid scars found on various stems of Lepidodendreae has been to a great extent settled. For a long time it was generally supposed that these large biseriate prints were the marks of sessile cones. This view has proved to be untenable; the scars are often too large to fit any cones, and we know that the cones were borne on twigs. It is now generally admitted that the Ulodendroid scars indicate the bases of caducus lateral branches, as has been shown by Dr. Renier and Dr. Watson, though these investigators differ as to the exact mode of attachment of the branch. (Watson, 1908 and 1914; Renier, 1910). The idea that the organs in question were roots or rhizophores has also been revived, but on inadequate grounds (Lashevsky; see Scott, 1925). It is further probable that the tubercle-bearing branches of *Lepidophloios*, known as *Halonia*, had no direct relation to the cones.

As regards anatomical structure, though there is nothing very recent to record, it may be pointed out that the anatomy of the stem of *Sigillaria* is now well known in several species. The near relation between this once much-discussed genus and Lepidodendron is now fully established.

An elaborate investigation of the periderm of Lepidodendreae by Miss Kisch led to the conclusion that this important tissue was of the nature of secondary cortex, serving as the main supporting tissue of the stem, and probably also as a storage for reserve food-substances. It is not to be compared with the corky periderm of other trees (Kisch, 1913).

Stigmaria, constituting the rhizophores or roots of various Palaeozoic Lycopods, continues to present difficulties. It is seldom that a given *Stigmaria* can be correlated with the stem to which it belongs. As regards the origin of the rootlets it still remains uncertain whether it was exogenous or endogenous.

Dr. Suzanne Leclercq, in her important investigation of Belgian coal-balls, has discovered a new and remarkable Stigmaria with perfectly solid primary xylem, pith being completely absent. This is a new type, *S. Lohesti* (Leclercq, 1925).

5. Ferns.

The question whether Ferns, as such, already existed in the older Devonian Flora is still an open one. It has already been mentioned that some of the thalloid branches of plants of that period have circinate vernation and this has suggested a possible relationship to Ferns. But of actual indubitable Ferns there seems to be no evidence at present.

Professor Lang has founded a new genus, *Milleria,* on a plant from the Middle Old Red Sandstone of Scotland, hitherto known as *Ptilophyton Thomsoni* (Lang, 1926: Arber, 1921). He defines the genus thus: „Dorsiventral, alternately branched, frond-like branch-systems, sometimes with sub-pinnate, ultimate, vegetative divisions, and bearing elongated, linear sporangia, in relation to other ultimate ramifications." The tips are circinate. Professor Lang adds: „The types that have been associated in the genus Milleria appear to approach, without reaching, the more definitely fern-like forms that come into evidence in the Upper Devonian". The elongated sporangia demonstrated by Lang appear quite unlike anything known in true Ferns.

There are some striking plants of more or less Fern-like habit from similar horizons (*Aneurophyton, Eospermatopteris, Cladoxylon*) but these will be considered in the next section.

When we come to the Upper Devonian there is no doubt about the presence of highly developed, completely Fern-like plants. The magnificent „Ferns" refered to *Archaeopteris* are familiar to all palaeobotanists. I am not aware of any reasons which compel us to remove these fine plants from the Ferns to the Pteridosperms. Dr. Kidston, it is true, said in 1906 „The structure of the sporangia of Archaeopteris seems to point almost conclusively to their belonging to the group of *Cycadofilices*" (Kidston, 1906, p. 440). But in the absence of petrified specimens, so little is known of the sporangial structure that any conclusion must be hazardous. Professor Johnson found indications that the sporangia (elongated, pointed bodies, seated on more or less modified pinnules) are transversely septate; he suggested a comparison with the sporangiferous spike of Ophioglossum. There is at present no evidence for the occurrence of seeds, in association with specimens of Archaeopteris. Professor Johnson was wise in giving no answer to his question: „Is Archaeopteris a Pteridosperm?" (Johnson, 1911). Though many palaeobotanists would no doubt venture on an affirmative answer, there is really no evidence to go on.

But apart from the somewhat dubious evidence of impressions, there is proof from the structural side of the presence of true Ferns in the Upper Devonian. *Asteropteris noveboracensis*, discovered in 1881 by Dawson, and re-investigated by Dr. Paul Bertrand, is clearly a member of the family Zygopterideae, as shown by the stellate xylem, with peripheral loops at the ends of the slender arms, and by the structure of the leaf-traces (P. Bertrand, 1911², p. 255). The plant came from the Portage beds of the Upper Devonian of New York. Another typical Zygopterid, *Clepsydropsis australis*, is from rocks in New South Wales, assigned to the Upper Devonian (Mrs. Osborn, 1915) (Sahni, 1919). It is remarkable that these oldest known members of the family are not by any means specially simple in structure. The race must be very ancient.

Passing on to the Ferns of the Carboniferous, there is much new work falling within our period, especially on the Primofilices, to adopt Dr. Arber's name. Under this head he included Ferns characteristic of the Primary Rocks. The best known Primofilices are the Botryopteridaceae, embracing the three families Zygopterideae, Botryopterideae and Anachoropterideae.

It is impossible to go into details here; that must be left to the text-books. As regards the Zygopterids, which have received the largest share of attention, the most characteristic point is the organisation of the leaf-stalk, which has been worked out with the utmost accuracy by Dr. Paul Bertrand (P. Bertrand, 1909, 1911, 1911[2]). The main foliar bundle, often of a peculiar H, or double anchor form, is so organised that the pinna-traces which arise from it are oriented at right angles to the plane of the frond, and not parallel to this, as in other compound leaves. Thus the Zygopterid frond was of an unusual anatomical type; in several genera, as *Dineuron, Metaclepsydropsis, Diplolabis* and *Etapteris,* the peculiarity goes much further, for two rows of pinna-traces were given off on each side of the main rachis. It would seem that these exceptional structural feactures must have involved a peculiar habit of the frond. I am not aware that any fronds are known as impressions which show any such unusual orientation or duplication of the pinnae. The relation of structure to habit in these plants seems to require elucidation. (Sahni, 1918).

The most extreme case is that of *Stauropteris.* Here the quadriseriate pinnation, instead of being limited to the first branching, is repeated again and again in the successive ramifications of the frond, so that the form of the whole has been compared to a bush. The fronds of Stauropteris were altogether remarkable, for there was no lamina, the whole leaf being nothing but a much-branched naked rachis. There are, however, other Zygopterids in which a lamina may also have been absent.

The stem, known in several genera, varied much both in form and structure. In some it was erect, like a little tree-fern, and clothed with crowded leaf-bases (e.g. *Clepsydropsis, Asteropteris*), in others it was a slender, creeping rhizome, with nodes at long intervals (e.g. *Metaclepsydropsis, Diplolabis*). In the genera just mentioned, the stem was discovered by Dr. W. T. Gordon, who was able to work out the whole organisation of the plants (Gordon, 1911, 1911[2]).

The vascular structure of the stem, always monostelic, ranges from a simple concentric cylinder, with solid wood, to an elaborate stellate axis with a „mixed pith" extending into the arms (see especially *Asterochlaena*, P. Bertrand, 1911[3]). But even in the simplest case (Diplolabis) there is some differentiation, the central tracheides being smaller and shorter than those of the outer zone of xylem.

Mrs. Osborn's discovery that the simplest form of petiole, Clepsydropsis, was borne on a complex stem like that of an *Ankyropteris*, is a useful warning against too facile phylogenetic speculations.

As regards the branching, it was definitely axillary in some species of Ankyropteris, but dichotomous in the other cases observed, including *Ankyropteris corrugata*. In *Botrychioxylon* secondary wood was formed to a considerable extent. It is indicated in a smaller degree in some other instances (Scott, 1912).

There appears to be no new information as to the reproductive organs of the Zygopterids. The sporangia, as is well known, show considerable variety; in *Etapteris Lacattei* they are large sacs, with a broad multiseriate annulus, and occur in terminal tufts on branches of the rachis; in *Stauropteris oldhamia* they are round, exannulate and, borne singly on the extremities of the branched rachis. In a fructification attributed with much probability to Diplolabis, the sporangia are exannulate and occur in definite groups, on a common pedicel.

The Zygopterideae were a highly specialised group of Palaeozoic Ferns, and it seems doubtful if they had any direct connection with the subsequent evolution of the class. Points of analogy with the Ophioglossaceae on the one hand and the Osmundaceae on the other have been insisted on; whether or not they are indicative of affinity remains an open question.

The family Botryopterideae is much simpler than the preceding. The stele of the stem is a simple concentric cylinder with an undifferentiated xylem; the petiolar bundle has adaxial protoxylem-points and according to Dr. Bertrand the pinna-traces were in the same plane as the main bundle of the leaf — not at right angles to it. Thus the structure was altogether of a more ordinary kind than that of Zygopterideae, and the simple Botryopterids may perhaps have been nearer the main current of Filicinean evolution.

The simplest species of *Botryopteris* is also the oldest — *B. antiqua*, discovered by Dr. Kidston in the Lower Carboniferous Burntisland deposit (Kidston, 1908; Benson, 1911). The Coal-measure species differ but slightly, while Renault's Permo-carboniferous plant, *B. forensis*, remains the most complex of the family, at least so far as the petiolar structure is concerned. The sporangia associated with the older species, have a multiseriate annulus, and may be compared with the well-known fructification of Renault's species, though on a much smaller scale.

The genera *Tubicaulis* and *Grammatopteris* occupy a somewhat doubtful position as between the Zygopterid and Botryopterid families.

The genus *Anachoropteris*, of Upper Carboniferous age, appears to demand a family of its own, on account of the peculiar and advanced character of the fructification. The stem is unknown; the petiole has a characteristic structure owing to the curiously curved, revolute form of the vascular strand. The reproductive organs, long ago described by Corda under another name, have now been identified by Dr. Kubart. The sporangia are grouped in fours into definite synangia, similar in structure to the most highly organised spore-fruits of the supposed Marattiaceae of the period (e.g. *Ptychocarpus*). The synangia were borne on the incurved margins of the small leaflets of a compound frond. Thus to judge by the fructification Anachoropteris must be ranked as the most advanced genus referred to the Primofilices. (Kubart, 1916).

As soon as we get beyond the Primofilices we are faced by the question whether the Fern-like plants we meet with so abundantly were really Ferns or Pteridosperms. First we may mention some Lower Carboniferous fossils, recently described by Mr. Walton. In the genus *Rhacopteris*, with the fronds usually simply pinnate, this author has discovered the stem for the first time, in a species named *R. inaequilatera*, and has found a specimen of the fructification, only once before described for the genus. The piece of stem looks like a rhizome; of course no structure is preserved. The fertile frond is forked, dividing into two panicles on which the sporangia are borne in dense clusters; they are ovoid and exannulate. Mr. Walton compares both sterile and fertile fronds with those of *Botrychium*; he thinks that the evidence is perhaps in favour of a Fern rather than a Pteridosperm connection (Walton, 1926).

In connection with Lower Carboniferous Ferns two somewhat doubtful fossils may be mentioned, from the Waverley Shale of Kentucky, i.e. low down in the Lower Carboniferous. Both are petrified and appear to be petioles. The one, *Stereopteris annularis*, contains a single large vascular strand, recalling that of some of the Zygopterids, but not agreeing with any of them. The plant presumably belongs to the Primofilices, and perhaps stands nearest to the family just cited.

The other petiole, *Periastron perforatum*, is still more problematic. Another species of the genus was described long ago by Unger. There are about ten concentric vascular bundles, ranged in a straight median line across the petiole. The structure is quite unique. The affinity appears to be with Ferns, but no more can be said (Scott & Jeffrey, 1914).

The best known Ferns of the Upper Carboniferous are undoubtedly the so-called Marattiaceae, magnificent plants of tree-fern habit, with the fronds often exquisitely preserved. The stems are well known in a petrified condition (*Psaronius*) and have been exhaustively studied from an anatomical point of view. They usually show a highly complex, polystelic structure; in the earliest known representatives, however, there may be only a single solenostele (*Ps. Renaultii*). The nature of the root-zone enveloping the stem has been cleared up by the late Court Solms-Laubach. The roots do not, as was once supposed, traverse the cortex, but the tissue in which they are embedded is formed of felted hairs or filaments, chiefly belonging to the roots themselves, but in part springing from the surface of the stem (Solms-Laubach, 1911).

The fructifications are of the type regarded as Marattiaceous, usually forming definite synangia (*Ptychocarpus, Asterotheca, Scolecopteris* & c.) In this group the anatomy of both stem and root, and the character of the fructification, all seem consistent with Marattiaceous affinities. There has been nothing in the later work to affect the position, so far as the facts are concerned. Dr. Hoskins has quite recently described a Scolecopteris with structure (*S. minor*) from the newly discovered coal-balls of the Pennsylvanian (Upper Carboniferous) in the State of Illinois (Hoskins, 1926). The synangia are borne as usual on *Pecopteris* foliage; the sporangia are attached by a common central pedicel to the lower surface of the pinnule; they are slightly connected at their bases. Thus Dr. Hoskins's plant appears to be a true Scolecopteris, like *S. elegans*, in which the synangium is borne on a pedicel. Dr. Kidston has revived Schimper's genus *Acitheca* for the type represented by *S. polymorpha*, in which the synangium is sessile, the sporangia being only united laterally to the central column, not borne upon it.

It has usually been assumed hitherto that the important group we are considering belonged to the true Ferns, with special affinity to the Marattiaceae. Doubts may have arisen in the minds of some palaeobotanists, but they had not been definitely expressed until the publication of the late Dr. Kidston's last and greatest work, „Fossil Plants of the Carboniferous Rocks of Great Britain".[1]) The Memoirs are primarily taxonomic describing and fully illustrating all the British species, but the more general parts contain observations of the utmost importance for the wider questions of Palaeobotany.

Ir is interesting to trace the growth of Dr. Kidston's scepticism in the matter of Carboniferous Marattiaceae. In Part 1 of the Memoirs he said: „it seems tolerably certain that the Cyatheites Pecopterideae, which have exannulate sporangia united into synangia, are ferns" (p. 17). In Part 4 he is more cautious: „if the Fern stems known as Caulopteris and Psaronius are those of Asterotheca (as there is good reason to believe) then Asterotheca may be Marattiaceous. Probably a few other Carboniferous plants that bear exannulate sporangia may be also referable to the Marattiaceae". Here he instances only „Asterotheca and perhaps Ptychocarpus which are possibly Marattiaceous" (p. 277).

In Part 5 he has lost all confidence, saying: „The evidence available for arriving at a decision as to the systematic position of Asterotheca perhaps favours its being regarded as containing Marattiaceous Ferns, but I do not think the evidence is conclusive. I prefer, therefore, to leave the systematic position of Asterotheca an open question". „The generic differences which separate Scolecopteris from

[1]) Kidston, 1923—1925. Four of these magnificent memoirs appeared in Dr. Kidston's lifetime, and two more have been issued since his death. It is hoped that the work may eventually be completed with the help of material he left. All the six Parts published deal with „Ferns and Fern-like Plants".

Asterotheca are those of degree rather than of structure. The former genus I believe to be more probably a Pteridosperm than „a Fern." (p. 483). Thus Dr. Kidston had already given up Scolecopteris and the companion genus threatened to follow!

Lastly, in the final Part published, we reach the full measure of his scepticism. „If then this opinion as to the systematic position of Acitheca be correct, I do not see on what grounds Asterotheca and Scolecopteris can be excluded from the Pteridosperms. It would therefore appear that the evidence in support of the occurrence of Marattiaceous Ferns in Carboniferous times rests on supposition rather than on satisfactory proof." (p. 538).

Thus, in the end, Dr. Kidston not only doubted the Fern-nature of the so-called Carboniferous Marattiaceae but was inclined to transfer them bodily to the Pteridosperms. At the time he wrote Dr. Kidston was no doubt the greatest authority on Palaeozoic plants; we have therefore to face the question: Did true Ferns (other than the modest Primofilices) exist in Carboniferous times?

The arguments on the Pteridosperm side are briefly as follows: The synangia of Acitheca, Scolecopteris and in a less degree Asterotheca are remarkably similar to those of *Telangium,* a genus generally accepted as representing the male organs of Pteridosperms. It was this comparison which appears to have chiefly influenced Dr. Kidston.

Crossotheca, a species of which was identified by Dr. Kidston as the male fructification of the Pteridosperm *Lyginopteris,* contains other species with the foliage of *Pecopteris.* Now Pecopteris is the form-genus to which the leaves of the supposed Marattiaceae generally belong. Crossotheca was regarded as a Marattiaceous fructification before Dr. Kidston's discovery.

Pecopteris (*Dicksonites*) *Pluckeneti,* once included among Marattiaceous Ferns, is now known to have been a Pteridosperm, Grand 'Eury having discovered specimens covered with small seeds.

A further point, important if confirmed, may be mentioned, as it has been referred to in a published paper. Dr. Hoskins, in his account of *Scolecopteris minor*, above cited, states that „unpublished researches by Halle, according to a letter from Dr. Scott, give excellent evidence that a new Pteridosperm bore seeds attached to the frond of a Pecopteris type of foliage similar to that on which has been found the Asterotheca type of sporangia". (Hoskins, 1926, p. 435). I cannot discuss Professor Halle's unpublished work, but must point out that Dr. Hoskins goes too far in assuming that the Pecopteris in question was a new Pteridosperm bearing seeds. Until the connection of the seeds with the frond is absolutely proved the nature of the specimen remains doubtful.

We have seen that there are grounds for the suspicion that the so-called Marattiaceae of the Carboniferous may after all have been Fern-like Spermophyta: but, except in the case of Pecopteris (Dicksonites) Pluckeneti, there is no proof. Whether this undoubted Pteridosperm is strictly comparable to such typical „Marattiaceae" as Asterotheca and Scolecopteris remains to be proved. We know nothing of the stem or of the anatomy in the Dicksonites[1]). In the absence of such evidence a careful comparison of the cuticular structure of the fronds in question would be of value.

Apart from the close agreement of the fructifications, borne both in the recent and the supposed Palaeozoic Marattiaceae on the ordinary fronds, the great argument in favour of the Fern-nature of the plants under discussion

[1]) Neither does it appear that the microsporangia have ever been adequately figured. They are described as forming „star-like groups of very carbonaceous anthers" (Grand'Eury, in Kidston, 1924, p. 404).

is drawn from the anatomy. There appears to be no room for doubt that Psaronius is Caulopteris with structure preserved, or that Caulopteris bore the fronds attributed to Marattiaceae. Now the structure of the Psaronius stem and petiole is quite clearly that of a Fern, and in most cases of a highly polystelic Fern. The agreement with Marattiaceous anatomy, as Dr. Paul Bertrand has pointed out, (P. Bertrand, 1911, p. 291) is not exact, but it is at least consistent with Marattiaceous affinities. At the same time the Psaronius structure is totally unlike that of any Pteridosperm or any Seed-plant whatever. An anatomist will find it difficult to believe that plants with the anatomical structure of Psaronius were anything else but true Ferns. For this reason, more than for any other, I still incline to the old-fashioned opinion that a considerable group of such Ferns, with an arborescent habit and certain Marattiaceous characters, actually flourished in Carboniferous times.[1])

6. Spermophyta.

The oldest Seed-plants of which we have any definite knowledge are those from the fossil forest of Gilboa in the State of New York. The trees have been known since 1869 and were described by Sir William Dawson as Tree-ferns, a name which appears to express their true habit. The stumps are of great size, reaching 3 feet or more in diameter; branches have been identified, bearing, at least in one case, the petioles of the large, compound fronds. „The seeds were borne in pairs at the end of forked branchlets and were probably borne near the tip of the frond". The small seeds are each enclosed in an outer husk or cupule. The discovery of the seeds is due to Miss Winifred Gold-

[1]) Professor F. O. Bower's great work on the Ferns contains excellent accounts of the Palaeozoic representatives in relation to recent forms. (Bower, 1923 and 1926).

ring, who named the genus *Eospermatopteris*. Two species are distinguished (Goldring, 1924). The horizon is Upper Devonian or late Middle Devonian (Goldring, 1926).

A plant or tree (*Aneurophyton elberfeldense*) of similar habit to Eospermatopteris has been discovered by Drs. Kräusel and Weyland in their investigation of the Upper Middle Devonian Flora of Elberfeld. Here the anatomy could also be observed; it is a curious point that the rachis of the frond had the same structure as the stem; only the ultimate pinnules are regarded as truly foliar in nature. The structure of the stem shows the presence of secondary wood with scalariform and pitted tracheides. So far as preserved, it agrees with the wood of *Palaeopitys Milleri*, Hugh Miller's famous „cone-bearing tree", from the Middle Old Red Sandstone of Scotland, recently investigated afresh by Kidston and Lang (1923).

Sporangia were found on special pinnules of the fertile fronds. There is at present no evidence of seeds in Aneurophyton, but the apparent relationship to Eospermatopteris and the anatomical structure suggest that it may have been a Pteridosperm.

From the same beds Kräusel and Weyland have described a plant of great interest, *Cladoxylon scoparium*, the first *Cladoxylon* in which the foliage and sporangia have been observed. It is also considerably older than any other known species. Hitherto Cladoxylon has been characterized only by its extraordinary anatomy, the stem having a most complex system of steles, each growing in thickness on its own account. In the Elberfeld plant the anatomy was sufficiently well preserved to identify the genus. The leaves are spirally arranged, small (not more than 18 mm. long), deeply cut and forked. The sporophylls are somewhat different — fan-shaped, with the edge deeply lobed; each lobe appears to have borne a small, round sporangium. Here too, no seeds have been found. Most authors have inclined to the view that the Cladoxylons were Pteridosperms, but their systematic position remains quite uncertain. (Kräusel & Weyland, 1926).

Professor Lang has described from the Middle Old Red Sandstone of Orkney a sporangium-bearing branch-system, to which he gives the provisional name *Hostimella racemosa*. It consists of a somewhat narrow axis bearing in its upper portion a number of shortly-stalked bodies, which may be interpreted either as sporangia or seeds. The lateral bodies themselves are oval and sharply defined. No spores were obtained from them. There is thus a possibility that the fossil represents an early seed-bearing plant, but there is no proof (Lang, 1925).

Thus our evidence for the presence of Seed-plants in the Devonian Floras is very scanty, and in fact limited, so far as direct proof is concerned, to the trees of Gilboa. The indirect evidence, however, is strong. The fossil stems known as *Callixylon*, found in the Upper Devonian of Russia and North America, have a purely Gymnospermous structure, the wood being as highly organised as that of a modern Conifer, though on somewhat different lines. One can hardly doubt that such a stem belonged to a seed-bearing tree. Even further back, Hugh Miller's „cone-bearing tree" has some title perhaps to its designation. The structure of the wood is not exactly that of a typical Gymnosperm but it is more like a Gymnosperm than anything else.

In the Lower Carboniferous, seeds are common and some of them are referred on good grounds to Pteridosperms, e.g. Nathorst's plumose seed, *Thysanotesta*, borne on the frond of a *Sphenopteridium*. A seed with the complex structure well preserved (*Sphaerostoma*) has been described by Dr. Margaret Benson, and is closely associated with the well known stems of *Heterangium Grievii* (Benson, 1914).

I do not propose to go at all fully into the subject of

Carboniferous Gymnosperms. The position of the Pteridosperms has long been well established. A few more cases of seeds in connection with fronds have been recorded; Dr. Gothan has found seeds like a small *Trigonocarpus* on the foliage of *Sphenopteris Dicksonioides,* and Kidston and Jongmans have discovered very large seeds on the rachis of *Neuropteris obliqua* (Gothan, 1923); (Kidston & Jongmans, 1911). Indirect evidence, from the association of seeds with fronds, has also accumulated.

We have further gained a little more knowledge of the male organs of Pteridosperms, though mostly by means of impressions lacking in detail. The genus *Telangium,* already mentioned, is regarded as constituting the pollen-bearing apparatus of various Pteridosperms with the foliage of *Sphenopteris.* We owe to the Abbé Carpentier and Professor P. Bertrand the discovery of the male fructification (*Potoniea*) of *Neuropteris gigantea* in the form of fleshy, adiantiform leaflets bearing numerous microsporangia. Similar organs, bearing microsporangia containing the microspores, were found by Dr. Kidston in a species which he named *N. Carpentieri.* The remarkable fructification known as *Whittleseya fertilis* Kidston, consisting of two scales fitting together, and enclosing the microspores, has been referred to *Alethopteris* and allied genera. Mr. Hemingway has pointed out to me that such male organs may bear a deceptive resemblance to seeds of the *Rhabdocarpus* type. (Carpentier, 1923).

When the Pteridosperms were first recognised, some of us were apt to regard them as the descendants of true Ferns, as „Ferns which had become Spermophytes" to use an old phrase of Professor Oliver's. Dr. Kidston, however ,was more cautious and never accepted this theory. Subsequently I convinced myself that the two lines, Ferns and Seed-Ferns were parallel and distinct, having at most had a possible common origin in very early times (Scott, 1922).

I now think that the question cannot be further discussed with advantage until the position of the supposed Carboniferous Marattiaceae is settled. An argument on which great stress was laid was the profound difference in anatomical structure between the recognised Pteridosperms and any true Ferns. Personally I think this argument still holds good, but if it should turn out that plants with so completely Fern-like a structure as that of *Psaronius*, were after all Seed-plants and not Ferns, it is obvious that the whole position would have once more to be reconsidered.

Space forbids any mention of the numerous seeds which have been attributed on good grounds to Pteridosperms, and often most accurately described, but without any evidence of connection with the plant. Neither can we discuss the purely anatomical work of which also much has been done, on stems provisionally referred to this group. Of the families founded on anatomical characters only two, the Lyginopterideae and the Medulloseae are actually known to have been seed-bearers, though, from analogy of structure it is highly probable that some others were of kindred nature.

As regards the important group of the Cordaiteae, it is unfortunate that after nearly 50 years we are still dependent on Renault's preparations for our knowledge of the floral organisation. The fertile shoots of a *Mesoxylon*, a close ally of *Cordaites*, have, it is true, been recorded, but neither ovules nor pollen-sacs were present. A re-investigation of Renault's old slides by the late Professor C. E. Bertrand has thrown doubt on the long-cherished idea that the ovule of Cordaites was borne on a short axillary shoot (C. E. Bertrand, 1911). Professor Schoute has since maintained that the ovule occupied the place of a leaf in the phyllotaxis of the catkin (Schoute, 1925).

There is no fresh light on the reproduction of the Poroxyleae, and none at all on that of the ancient family of the

Pityeae. In the genus *Pitys*, however, Professor Gordon, besides purely anatomical results, has been able to describe the needle-like foliage, singularly different from that either of Cordaiteae or Pteridosperms (Gordon, in Scott, 1923).

It has been necessary to out short our survey and much valuable work has inevitably been left unnoticed. At the present moment the chief centre of interest in Palaeozoic botany no doubt lies in the Devonian Floras. Next to that, the problem of the status of the true Cryptogamic Ferns in Carboniferous times is the most urgent question before us.

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