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XIX. *Further Observations on the Organization of the Fossil Plants of the Coal-Measures.*—Part I. *Calamites, Calamostachys, and Sphenophyllum.*

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[PLATES 72-86.]

PRELIMINARY NOTE BY W. C. WILLIAMSON.

A FEW words in explanation of the origin of this new enquiry may be desirable. During the investigations into the organization of the fossil carboniferous plants upon which I have been engaged for more than forty years, I have brought to light a number of structural features different from any discoverable amongst allied plants living at the present day. Though morphological truth was the main object of my researches, it was impossible wholly to exclude thoughts respecting the modes of growth by which these structural combinations have been produced. Many such suggestions are scattered through my numerous memoirs; some of them I believe to be true; others are fairly open to such doubts as have been expressed by my friend, Graf zu SOLMS, and others.

My morphological enquiries seem to have reached a stage that makes a more minutely careful examination of these questions of development and growth desirable; but before specially undertaking this, I saw clearly the extreme importance of doing so in combination with some younger colleague whose familiarity with the details of the physiology of living plants was greater than my own. Under these circumstances I have secured the co-operation of Dr. D. H. SCOTT, and the present paper embodies the results of our united investigations. The work has been carried out in the Jodrell Laboratory of the Royal Gardens, Kew.

W. C. W.

I. CALAMITES.*

INTRODUCTION.

The fossil stems which we are about to consider, and which we include, in conformity

* References to the extensive previous literature of our subject will be found scattered through the series of memoirs, by W. C. WILLIAMSON, in the 'Philosophical Transactions of the Royal Society' (1871-1893). A full summary of our knowledge, up to 1887, is given by Count SOLMS-LAUBACH in his

with the usage of most English and German palæobotanists, under the generic name of *Calamites*, are characterized anatomically by the following features :

1. The axis is traversed by a well defined central cylinder, consisting of a large pith (which became fistular in all but the smallest specimens), and of a ring of distinct, collateral vascular bundles, separated from one another by broad radial bands of interfascicular tissue, or primary medullary rays (see Plate 72, photographs 1, 2, and 3 ; Plate 77, figs. 1, 2, and 3). Each vascular bundle has an intercellular space, or canal, on its inner side, and from the outer margin of this canal the radial series of xylem-elements extend.

The bundles run parallel to one another, without anastomosis, through the internode. At each node they turn outward, taking an almost horizontal course. The out-going bundles are all situated at the same level, forming a whorl. There can be no doubt from their position and course that they were leaf-trace bundles, supplying a whorl of leaves (see Plate 72, photographs 5 and 6 ; Plates 77 and 78, figs. 6, 7, 8, 11). As all the bundles of a whorl are alike, and they are equidistant one from another, there is a strong presumption that each leaf received a single bundle only. This presumption is fully confirmed by all that we know, from other sources, of the foliage of *Calamites*.*

The course of the vascular bundles in some cases follows the well-known simple type characteristic of *Equisetum*, those of successive internodes alternating regularly with each other. Considerable deviations, however, from this type are met with, and will be considered below.

2. The central cylinder is surrounded by a cortex, only preserved in comparatively few specimens (see Plate 72, photographs 1, 2, 3 ; Plate 77, figs. 1, 2, 3 ; Plate 78, fig. 12 ; Plate 79, fig. 18). In some cases the cortex is but little differentiated, showing only a few thick-walled elements among the parenchyma, while in others it consists of two distinct zones, of which the outer is more sclerotic than the inner.

3. The *branches* are placed immediately above the node, each branch being so situated, in almost all cases, that its centre-line lies midway between two of the leaf-traces which pass out at that node (see Plate 72, photographs 5 and 6, and Plate 80, fig. 21). The number of branches developed is very variable, but seems to be always much less than that of the leaf-traces. Although placed above the node, the wood of the branch is directly continuous with that of the bundles below it.

4. Neither leaves nor roots have been found, so far, in connection with the specimens investigated by us, in which the internal structure is preserved. As regards the roots, however, we have now some important information from other sources, which we shall consider at a later stage.

"Introduction to Fossil Botany" (English Translation, 1891, chapters 13 and 14), where the literature is very completely cited. Only the most necessary references are given in the present paper.

* See, for example, WEISS, "Steinkohlen-Calamarien," vol. 2, p. 26, plate 1 ; RENAULT, "Cours de Botanique fossile," vol. 2, plate 17.

5. The above general characters are common to all the stems observed. The specimens, however, present great differences among themselves, which are due (1) to the *order* of the branch in question, or to the *part* of the branch from which the specimen is derived; (2) to age; and (3) to specific distinctions. The differences under the first two heads can be readily distinguished from one another with proper care. It is, however, we believe, as a rule, impossible to distinguish between branches of different orders belonging to the same species and those of different species, though in special cases, as in the form originally described as *Calamopituis*, the specific distinction is evident.* The same difficulty would exist in the case of *Equisetum* if we had to depend on isolated fragments of branches for our anatomical knowledge.

6. Variations in structure, due to the *part* of the branch from which the section is cut, are as follows:—

a. In the size of the pith and consequently of the primary central cylinder (see Plate 73, photographs 7, 8, and 9);

b. In the number of the vascular bundles;

c. In the presence or absence of the canals accompanying the bundles.

a. The size of the pith, in most if not in all cases, is at a minimum at the base of the branch, and increases rapidly upwards, until its approximate maximum is attained, after which it remains nearly constant.

b. In like manner the number of vascular bundles is at a minimum at the base of the branch, and increases in the ascending direction in successive internodes, until a maximum is reached, when it remains approximately constant.

c. The canals accompanying the bundles are absent from the base of the branch, but are otherwise almost always present in the internodes.

The evidence on which these conclusions are founded will be fully given below.

7. Variations known to be due to the *order* of the branch are: (*a*) in the size of the pith† and primary cylinder, and (*b*) in the number of the vascular bundles. It is probable that the solid or fistular character of the pith may also vary with the order of the branch, as well as with age, as is the case in many species of *Equisetum*.

8. Differences in the relative width of the bundles and primary medullary rays, in the structure of the rays, in the size of the canals, and in many other points, may either be of specific value, or be due to the order of the branch, or to mere individual variations.

9. Differences due to *age* consist (*a*) in the degree of preservation of the pith. The presence of a broad zone of persistent pith within the ring of bundles (see Plate 72,

* WILLIAMSON, "Organization of the Fossil Plants of the Coal-Measures," Part I., 'Phil. Trans.,' 1871, p. 488; 'Memoirs of the Literary and Philosophical Society of Manchester,' ser. 3, vol. 4, 1869.

† These variations are enormous in degree. The diameter of the pith in the specimen figured in Plate 77, fig. 1, is at most 0.3 millim. BRONGNIART describes his *Calamites gigas*, a medullary cast, as "*diametro pedem subæquante*." The ratio is about as 1 : 1000.

photograph 2; Plate 77, fig. 3, &c.) may, however, characterize certain branches, or even, perhaps, certain species.

(b) In the secondary growth of the vascular cylinder. In every stem of the types examined by us secondary thickening took place; only the very smallest twigs are destitute of it. So far as the evidence before us shows, there is not the slightest reason to believe in the existence of any *Calamite* which did not form a secondary zone of wood. Its formation has been observed at every stage. The radial arrangement of the elements is exceptionally clear as compared with most recent plants which have secondary growth. The phloëm and cambium are rarely preserved, but, as we shall see, they can be demonstrated in favourable cases.

(c) In the secondary growth of the cortex. It attained, in some old stems, a thickness even greater than that of the wood, and its increase was accompanied by an extensive development of periderm. To this subject we shall return.

There can be no doubt as to the specimens in question forming a perfectly natural group. With the exception of the *Calamopituis* type, and of *Calamodendron*, which latter we have not dealt with in this paper, all the forms examined might even have belonged to a single species, though it is much more probable that several allied species are included.

There is, further, no doubt that the specimens showing structure, with which we are more particularly concerned at present, belong to the same plants as the macroscopic specimens long known under the name of *Calamites*. The proof that the common form of preservation of these fossils represents merely the cast of the hollow pith, has been sufficiently enforced in previous memoirs.* Specimens, such as one in the WILLIAMSON collection, in which a cast of the pith is still partly enclosed by the well-preserved cylinder of wood, show quite clearly that the furrows on the surface of the cast correspond to the inner edges of the vascular bundles, while the ridges of the cast fit into the spaces left by the softer tissue of the broad medullary rays. Medullary casts from the base of branches, of which several are figured, agree perfectly with the form of the pith, as shown in specimens of the same parts, with structure perfectly preserved (see Plate 79, fig. 20; Plate 80, fig. 22; Plate 73, photographs 7, 8, and 9). In cases of doubt the medullary casts can be identified by their having a constriction at each node, while the opposite condition is conspicuous where the wood and cortex are present. (Compare the figures of casts in Plate 86 with the photograph 4, Plate 72; and with "Organization," Part XIV., figs. 5 and 6, 'Phil. Trans.,' 1888, vol. 179, B). The cortex presents no superficial ridges and furrows.

We may assume, then, that we are dealing with the histological structure of the same plants which have so long been known under the name of *Calamites*, of which the medullary casts are the most familiar form of preservation. The commonest type

* See "Organization," Part I., 'Phil. Trans.,' 1871, and Part IX., 'Phil. Trans.,' 1878, Plate 2. See also STUR, "Zur Morphologie der Calamarien," 'Sitzber. d. k. Akad. der Wiss. z. Wien., Math.-naturwiss. Classe,' Bd. 83, Abth. 1, Heft. V., 1881. SOLMS, 'Fossil Botany,' p. 301.

of these fossils in the English Coal-Measures is that of the so-called *Arthropitys*, GÖPP. As this genus was only separated from *Calamites* on account of its secondary zone of wood, which we now know to have been common to the whole group,* we shall retain the older generic name. The question, so keenly discussed since the time of BRONGNIART, as to the Cryptogamic or Phanerogamic nature of these remains, seems now to be definitely decided in favour of the former alternative.† As regards the vegetative organs, the presumption, derived from the occurrence and character of the secondary formations, seemed at first entirely in favour of Phanerogamic affinities, and we cannot wonder at the view so long held by BRONGNIART and many botanists of his school. Only a consideration of the whole body of evidence, both from recent and fossil plants, has decisively turned the scale the other way.

Among the Cryptogams the affinities of *Calamites* have always been sought in the neighbourhood of the Equisetaceæ. In considering the vegetative organs, then, the most interesting question is whether the *primary structure* shows a sufficiently close agreement with that of *Equisetum* to establish any presumption of relationship. The most obvious resemblances, which attracted the attention of the earlier palæobotanists, have turned out to be fallacious. Thus we now know that the supposed *Equisetum*-like ribbed stem is no ribbed stem at all, but merely a cast of the pith-cavity. The external surface of the larger specimens could not possibly have shown ribs like those of *Equisetum*, for in the latter genus these ribs represent the course of the vascular bundles, and these are overlaid in the older *Calamites* by an immense zone of secondary wood and cortex.‡

The points of vegetative structure on which stress may fairly be laid, for purposes of comparison with *Equisetum*, are the following :—

1. The arrangement, and relative position of leaves, branches, and adventitious roots.
2. The course of the vascular bundles.
3. Their orientation, and the order of development of their elements.
4. The details of histological structure.

The points under the first category are of manifest morphological importance; the others are each, by themselves, of secondary value, and only a strong resemblance in the *sum* of such characters could weigh for much in estimating affinities.

* Cf. GRAND'EURY, "Calamariées—Arthropitus et Calamodendron," 'Comptes Rendus,' 1889, vol. 108, p. 1086; also 'Flore Carbonifère du Gard,' 1890.

† We believe that M. RENAULT is now the only author who still attributes Phanerogamic fructifications to some of the Calamariæ. See his "Étude sur le Terrain Houillier de Commeny," livre 2, 'Flore Fossile,' Part II.

‡ The shorter-lived branches no doubt had a comparatively thin secondary zone, and these, in the fossil state, may appear to show superficial markings. It has already been shown that these markings are simply due to the ribs of the medullary cast, which have become impressed on the thin carbonaceous layer to which the external tissues are reduced (see WILLIAMSON, "Organization," Part I., 'Phil. Trans.,' 1871, p. 495).

Now as regards the general morphology, the simple leaves, arranged in whorls of many members, form an obvious point of resemblance to *Equisetum*. In the specimens of *Calamites* showing structure, we can, indeed, only infer the position of the leaves from that of the outgoing vascular bundles; the macroscopic specimens however, leave no doubt as to the facts.*

On the other hand, it is quite certain that the leaves were separate, not cohering to form a sheath, as in *Equisetum*. Further, the alternation of the leaves of successive whorls was less constant in *Calamites* than in the recent genus.

The *branches* of the stem in *Equisetum* are alternate with the leaves of the whorl, in the axil of which they arise. This agrees substantially with the position of the branches in *Calamites* (see Plate 72, photographs 5 and 6, Plate 80, fig. 21). The relation of the vascular bundles to those of the main stem seems also to agree in the two genera, but this will be considered below. The insertion of the branches *below* the node in *Equisetum* is, of course, only apparent. The branches arise in the axil of the whorl, and therefore above it. Subsequently they become overgrown by the leaf-sheath, and ultimately break through it at its base. If the leaves of *Equisetum* were distinct like those of *Calamites*, the insertion of the branches above the node would be equally evident in both genera.†

As regards the insertion of the adventitious *roots*, we know that in *Equisetum* they arise from the base of the lateral branches, one to six on each branch. From the specimens of *Calamites* showing structure, we have at present no evidence as to the insertion of the roots. There is, however, no doubt, from the evidence of impressions and casts, that the roots arose at the node or immediately above it, from the base of the internode. Sometimes they were placed in a regular circle, sometimes they are grouped in tufts, and these tufts may arise at the base of a branch.‡ It does not seem probable, however, that they had any constant relation to the branches, such as we find in *Equisetum*.

So far as our knowledge of the external morphology of the vegetative organs of *Calamites* extends, we thus find a general agreement with *Equisetum*, sufficient to be quite consistent with a relationship between the genera, but not by itself conclusive.

(1.) It has already been mentioned that in the course of the vascular bundles the resemblance to *Equisetum*, though evident, is incomplete; the differences consist in the facts that a bundle may traverse more than one internode, and that the bundles of successive internodes do not constantly alternate with one another (see Plate 72, photograph 5, and Plate 78, fig. 11).

* See especially WEISS, "Steinkohlen-Calamarien," II., 1884, cap. 3, "Beblätterung der Calamarien."

† Cf. JANCZEWSKI, "Recherches sur le Développement des Bourgeons dans les Prêles." 'Mém. de la Soc. des Sci. Nat. de Cherbourg.' XX., 1876. His principal figures are reproduced in the modern textbooks, such as those of GÖBEL or VAN TIEGHEM.

‡ WEISS, "Steinkohlen-Calamarien," II., 1884, cap. 4, "Wurzeln der Calamiten"; LINDLEY and HUTTON, 'Fossil Flora of Great Britain,' vol. I, plates 78 and 79.

(2.) The arrangement of the vascular bundles in a single regular ring, enclosing a large pith-area, agrees well with *Equisetum*, but equally well with any normal Gymnosperm in Dicotyledon. We shall show in detail below that the canal at the inner edge of each bundle represents the disorganized protoxylem, so that in this respect the agreement with *Equisetum* is exact. We shall further show that in favourable cases there are distinct remains of the phloëm to the outside of the wood, so that there is no doubt as to the bundles being normally collateral, with centrifugal xylem, just as in the recent genus.

(3.) For the comparison of the minute histological structure, we are practically limited to the wood, and as only the primary region can be compared, the material is somewhat meagre. The primary xylem-elements of *Calamites*, the spiral, reticulated and scalariform tracheæ, are on the whole such as we find in *Equisetum*, and certainly agree less closely with those which we find in the corresponding position in other groups of vascular plants. The distinctive structure of the nodal, as compared with the internodal xylem, also shows a close agreement in the two genera.

In a few cases the structure of the cortex shows the distinct peripheral strands of sclerenchyma, which are frequent in the sub-aërial stems of *Equiseta*.*

To sum up our preliminary anatomical comparison. Although there is no secondary thickening, so far as we know, in any recent *Equisetum* (if we except the slight indications investigated by Mr. CORMACK)†, yet the primary structure, on which in the *Calamites* the secondary zone is superposed, is almost identical in the two genera.

PRIMARY STRUCTURE OF THE STEM.

a. *The Internodes.*

The first subject to be considered in detail is the primary structure of the stem. It is comparatively rare to find specimens in which this primary structure is unaltered. Where this is the case the specimens in question are usually, though not always, small twigs, with few vascular bundles. It must not be supposed that these twigs represent the earliest stages of the principal branches. They are probably ramuli of a high order, which in many cases seem never to have undergone any great degree of secondary thickening. In such small branches the pith is often solid,‡ just as is the case in the ultimate ramuli of some *Equiseta*, as, for example, *E. pratense*. In other

* See WILLIAMSON, "Organization," Part XII., 'Phil. Trans.,' 1883, II., Plate 33, fig. 19 (C.N. 62).
NOTE.—Reference numbers preceded by the letters C.N. (= *Cabinet Number*) always indicate the number of the slide or specimen in the WILLIAMSON collection.

† "On a Cambial Development in *Equisetum*," 'Annals of Botany,' vol. 7, 1893.

‡ See WILLIAMSON, "Organization," Part IX., Plate 19, figs. 8 and 9 (C.N. 1 and 2). See also our own fig. 1, in Plate 77, though here the pith is not quite complete.

cases, however, the pith of these minute twigs is hollow.* It is impossible to doubt that in most cases, and apparently in all the larger branches, it soon became fistular in the living plant. This is shown both by the frequency and regularity of the casts of the medullary cavity, and by the very sharp limit of the outer persistent zone of the pith (see Plate 72, photographs 2 and 3, and Plate 77, fig. 3).

In a few cases specimens are preserved which evidently represent the young condition of branches of considerable size. The most striking of these is the *Calamopituis* described and figured in 1871.† Here there were about eighty vascular bundles, and though there had been some secondary formation of wood, its amount—about a dozen layers—is little in comparison with the dimensions of the stem. Other sections show from fifteen to twenty-one vascular bundles, with little or no secondary tissue. Early stages of development of the more considerable branches, are, however, much rarer than mere twigs, as we should expect.

In the arrangement of the vascular bundles, as seen in transverse section, we find the same variations as among species of *Equisetum* at the present day. While the most common type is one with the bundles rather near together, the primary medullary ray having a width scarcely greater than that of the bundle itself, we sometimes find the bundles much more scattered, and separated from one another by rays more than twice their own width.‡

Similar differences are found, if, for example, we compare *Equisetum pratense* with *E. limosum*.

In the earliest stages observed, the vascular bundles, so far as their primary structure is concerned, appear to be already fully formed. In all cases the fascicular canal is open and well defined,§ and in all cases, too, there is a strand of thick-walled elements bordering on the outer side of the canal (see Plate 72, photograph 1, Plate 77, figs. 1 and 2). It is not always easy, in a strictly transverse section of a very young stem, to see which elements represent the xylem. When, however, the section is rather oblique, so that the markings on the lateral walls of the elements can be distinguished, it becomes evident that the thick-walled cells on the outer side of each canal are tracheæ, and constitute the xylem-groups (see Plate 77, fig. 4).

The most important question relating to the vascular bundle in its primary condition concerns the nature of the canal which is always present on its inner margin. The presence of these canals, the *internodal* canals of previous memoirs, gives to the transverse sections an extraordinary resemblance in habit to corresponding sections of an

* Plate 72, photograph 1, and Plate 77, fig. 2; also WILLIAMSON, *loc cit.*, fig. 10.

† WILLIAMSON, "Organization," Part I., p. 488, Plate 25, figs. 19, 20, &c.

‡ See WILLIAMSON, "Organization," Part I., figs. 9, 14, 15, 20, 26. Our own figures are all of the former type.

§ We leave out of consideration some exceptional cases in which the canal is filled with a parenchymatous tissue. These will be discussed subsequently; here it need only be said that in such instances the filling of the canal seems to have taken place long after its formation.

Equisetum. Is this resemblance accidental, or are the two structures really homologous? If the latter alternative be true, then the canal, in *Calamites* as in *Equisetum*, must represent a disorganized strand of protoxylem—the first-formed part of the wood of the collateral bundle. It is impossible to follow the development in the fossil; as already stated, the youngest stages preserved have their canals fully developed. All that we can expect is to find recognizable remains of the elements which originally filled the cavity; if these elements have the character of primitive tracheæ, then the homology with the carinal canals of *Equisetum* may be taken as established.

Happily, there is a long series of sections in the Williamson collection which serve to set this question completely at rest.

In every well-preserved transverse section it is common, or in fact the rule, to find isolated rings of about the diameter of a small trachea, within the canal. The resemblance of these annular fragments to the remains of tracheæ always seen in the carinal canals of *Equisetum* has long attracted our attention. The same point has been observed and figured by Mr. CORMACK,* who, we believe, was the first to publish the true interpretation. Occasionally, where the canal is small, these rings may collectively occupy the greater part of its area.† In some cases, also, we can trace a transition from the isolated rings in the canal itself, to the loosely arranged and partly disorganized tracheæ which abut on its outer margin.‡ Even in transverse sections the elements in the canal sometimes lie obliquely; in these cases we can see that the rings are placed one above another, as in an annular trachea, while sometimes we find portions of a spiral or a reticulated cell-wall. That we have really to do with the remains of tracheæ is evident. The tracheal remnants are most frequent towards the outer edge, or at the sides of the canal. For reasons which will appear immediately, they are less commonly met with at its *inner* edge. Transverse sections, however, can rarely afford by themselves conclusive evidence as to the nature of the elements contained in the canal. It is only when we examine a decidedly oblique section of a well-preserved specimen that all doubt is removed. Such a preparation is represented in Plate 77, fig. 4. The specimen is a corticated one, but the cortex has not been shown in the figure. Here the section is sufficiently transverse to show clearly the position of the canals, and at the same time sufficiently oblique to leave no doubt as to the character of the elements within them. Annular, spiral, or laxly reticulated tracheæ are evident in every canal, and sometimes extend to its inner margin. The gradual transition from these primitive tracheæ to the more scalariform elements towards the exterior can be clearly traced. Such a section is convincing by itself, but

* 'Annals of Botany,' vol. 7, *loc. cit.*, 1893.

† As in C.N. 19. We have thought it convenient, for the benefit of future investigators, occasionally to refer to the cabinet number of specimens in the Williamson collection other than those figured.

‡ As in C.N. 10, 1007, &c.

the study of accurately longitudinal sections is necessary in order to complete the argument.

Tangential sections passing through the primary wood of the bundles are of special value, as in them the position of the canals is clearly shown, and there can be no doubt that we are really examining the fascicular passages, and not any chance lacunæ. Such a section is represented in Plate 80, fig. 21. The part figured touches on two canals, and shows the partly disorganized protoxylem and primary xylem of two bundles.* In all such preparations, when sufficiently well preserved, remains of the primitive tracheæ are found in the canals and can be recognized at once, though more or less broken up, by their annular, spiral, or reticulated thickenings. By careful comparison of sections in somewhat different planes it is easy to prove that the innermost tracheæ of the solid xylem-strand are themselves somewhat disorganized, the disruption becoming much greater towards the interior, where the canal itself is reached.

Having become familiar with the appearances presented in oblique and tangential sections, the canals can easily be recognized with certainty in radial view.† (See Plate 77, fig. 5; Plate 78, fig. 10.) Where remains of tracheæ are found quite at the inner margin of the canal, they are usually of the annular type, with remote rings. Many of the elements are broken up in such a way that a series of several consecutive rings is left in position; then there is a gap, then another short series of rings, and so on. The nearer the tracheæ are to the inner side of the canal, the longer are the gaps, and the shorter the series of persistent rings. (See Plate 77, fig. 5.) Evidently here, as in *Equisetum*, the development of the primary xylem is centrifugal; the innermost elements have been differentiated earliest, and have consequently undergone the greatest amount of disruption during the extension of the internode. In many of the tracheæ the rings are connected here and there to form short spirals or reticulations.

In some cases, a radial section passes through a canal so as to show its termination at a node. Here it is clear that the protoxylem in the internodal canal is continuous with the innermost elements of the nodal xylem. This point is illustrated in Plate 78, fig. 10.

In no case, except where the preservation is bad, has a canal been examined in longitudinal section, without traces, at least, of the protoxylem being discovered.

From these observations we conclude: that the internodal canals of *Calamites* represent the earliest-formed xylem of the primary vascular bundles; that this primitive wood became disorganized and ruptured, owing to the longitudinal and transverse extension of the growing internode; and that the formation of the canal was due to a tearing of the tissue caused by the presence of a strand of inextensible lignified elements among the actively-growing parenchymatous cells.

* Other tangential sections showing the same facts are C.N. 24, 37, 38, 49, 91, 130*, and 1937.

† Especially good radial sections for this purpose will be found in C.N. 20, 20A, 21, 22, 48, and 1937.

In fact, all the evidence goes to show that the internodal canals of *Calamites* are identical in nature and origin, as well as in position, with the carinal passages of *Equisetum*. The demonstration of this homology is a considerable step towards establishing the essential agreement between the stem of a Calamite and that of an *Equisetum*.*

We will now go on to consider the structure of the remainder of the primary wood, *i.e.*, of those xylem-elements which lie on the outer side of the canal. Here we often find a difficulty in distinguishing between primary and secondary xylem. In transverse sections the regular radial series can often be traced inwards, as far as the canal, while, in other cases, the elements nearest to the latter are irregularly placed. Where all the tissue in question is radially arranged, such sections do not enable us to draw the line between primary and secondary wood. The same difficulty exists in many recent plants with an early development of secondary tissue.

Longitudinal sections, however, especially those in the radial plane, show us the elements which are characteristic of the primary xylem. The tracheæ just outside the canal are either densely spiral, or reticulated. Spirals capable of unrolling seem only to occur in the protoxylem of the canal itself. Scalariform tracheæ come next, or may themselves adjoin the canal. (See Plate 77, fig. 5; Plate 78, figs. 7 and 10.) Their pits are bordered, as in similar elements of recent plants. This is shown in fig. 9A, on Plate 78, which is taken from a tangential section passing so near the pith that we regard it as showing the structure of the primary wood. Where one of the tracheæ is in contact with a parenchymatous cell, the pits are only bordered towards the tracheæ, just as in so many recent plants. Short parenchymatous cells are embedded here and there among the tracheæ. The latter seem to be tracheides, but further histological details will be more conveniently considered when we come to the secondary wood.

The sections of the very young stems afford little information as to the phloëm, which is in no case preserved in such specimens. There is, however, no doubt that the bundles were collateral. In all the corticated specimens there is a gap between xylem and cortex, which is only obliterated where the latter has evidently been crushed in upon the former. (See the various transverse sections shown on Plates 72, 77, and 78.) In this gap, disorganized carbonaceous matter, sometimes showing signs of cellular structure, is present. In very early stages (see Plate 77, fig. 2) the interfascicular tissue is sometimes continuous from pith to cortex, but more usually it is interrupted by a disorganized layer, which presumably represents the delicate pericyclic tissue from which the interfascicular cambium would have arisen.

The preparation which shows the most satisfactory remains of the phloëm, is one from which photograph 3, on Plate 72, and figs. 12, 13, and 14, on Plate 78 are taken. In the group shown in fig. 13 the whole tissue, though much crushed, is preserved

* After the above was written, Count SOLMS-LAUBACH very kindly lent us some beautiful sections of a Calamite from Halifax, which afforded additional evidence of the facts just stated.

from cambium to cortex. Similar groups can be seen at several points of the section, and the preservation is sufficiently good to show that the phloëm was formed in greater abundance opposite the primary bundles than in the interfascicular regions. The regular brick-shaped cells seen in fig. 14, are either cambium, or at least derivatives of the cambium, which have retained their original form. This specimen is one which already has a broad zone of secondary wood, about twenty-five cells in radial thickness.

The external limit of the vascular cylinder is always quite sharp. This is due, however, to the almost constant presence of disorganized tissue on the boundary-line, not to the differentiation of any evident limiting pericycle. As to the presence of such a layer we have very little direct evidence. In the rare cases where the phloëm is preserved, we sometimes find one or more layers of larger, thin-walled cells at its periphery (see fig. 13); these may have belonged to the pericycle.

As regards the structure of the primary *cortex*, we find considerable variations among the comparatively few corticated specimens which are preserved. In the smaller twigs there is but little differentiation. The whole thickness of the cortex is made up of parenchyma, in which a few elements with thicker walls are scattered. (See Plate 72, photograph 1; Plate 77, figs. 1 and 2). Some of the cells have especially abundant carbonaceous contents, and may possibly represent secretory sacs.

In other branches, of somewhat greater diameter, a more differentiated cortex is present, consisting of an inner and an outer zone, of distinct structure. (See Plate 72, photographs 2 and 3; Plate 77, fig. 3; Plate 78, fig. 12.) In all these cases the inner zone is characterized by larger cells, with thinner walls, than those of the outer region. In the specimen illustrated in photograph 3, and fig. 12, in which the cortex is remarkably well preserved, the outer zone is itself differentiated, its cells becoming smaller and more sclerotic towards the periphery. The supposed secretory sacs may occur in any parenchymatous part of the cortex. We find, however, no indication of intercellular secretory *canals*.

In a third type, already referred to, the outer cortex has sharply defined, wedge-shaped bands of sclerenchyma, alternating with thin-walled tissue. (See WILLIAMSON, "Organization," Part XII., Plate 33, fig. 19, from C.N. 62.)

The more complex cortex seems to be characteristic of the somewhat larger branches; the number of corticated specimens is, however, too small to admit of any safe generalization.

A definite endodermis at the inner margin of the cortex has not been detected with certainty. In several preparations however, the innermost cortical layer, where preserved, consists of regular, thin-walled cells, fairly distinct from the rest of the tissue.

The above description sums up what we know of the primary structure of the internode. We have next to consider the modifications of structure presented by the

nodes, and in connection with this subject to examine, more fully than we have yet done, the longitudinal course of the vascular bundles.

b. *The Course of the Vascular Bundles and the Structure of the Nodes.*

In considering the question of the longitudinal course of the vascular bundles, it is obviously necessary to start from specimens in which we know for certain which is the upper and which the lower end. A specimen for which the cabinet is indebted to Mr. WILD affords this evidence in a very convincing manner. The branch in question has a pith which tapers rapidly at one end; a series of eight transverse sections were cut from this part, three of which are shown in the photographs 7, 8, and 9, on Plate 73. We shall return to these sections later; here we need only point out that the *base* of the branch is the end at which the pith has its *minimum* diameter. That this is so has long been proved: it is sufficient to refer to our figures, Plate 79, fig. 20, and Plate 80, fig. 22; to the figures 27 and 30 in Part IX. of WILLIAMSON'S series of Memoirs in the 'Philosophical Transactions,' 1878, Part II.; and to Plates 2, 3, 4, &c., in WEISS'S 'Steinkohlen-Calamarien,' Part II. From the upper part of Mr. WILD'S specimen a longitudinal section has been cut (C.N. 1937), on which the upper and lower ends are marked. A part of the section is approximately tangential, and shows the course of the bundles with perfect clearness, so that here we have the desired evidence in an unmistakeable form. The same section shows further that the lateral branches were inserted immediately *above* the node. We can, therefore, use this fact as a means of orientation in other cases; in all sections which show branches we know that the adjoining node is *below* the branch, and thus the top and bottom of the specimen are determined. Another useful clue is afforded by the fact that the outgoing foliar bundle is generally situated in the median line of the bundle running up to it from *below*, while this is seldom the case with the bundles above the node.* Another indication which can sometimes be made use of is the fact that the xylem of the stem-bundles is directly continuous with that of the outgoing leaf-trace, from *below* only. On the upper side the tracheæ overarch the leaf-trace bundle, but are generally separated from its xylem-elements by some parenchymatous tissue. (See Plate 78, fig. 8.) These latter indications (to which others might be added) are of service where there are no branches to afford a more certain guide. When we have once become familiar with the structure of specimens in which the direction is known, there is seldom any difficulty in determining the position of apex and base in any case where we have a tangential section through the wood.

In Mr. WILD'S specimen, and in some others, the course of the bundles is essentially that of *Equisetum*. If we trace any bundle from below upwards, we find that at the

* This indication, however, can only be trusted where the tangential section passes very near to the pith. The width of each woody wedge increases towards the exterior, and this increase is not always symmetrical with reference to the leaf-trace bundles.

node it bends out in a horizontal direction, forming the foliar bundle, which is therefore cut transversely in a tangential section. At this point branch-bundles are given off to the right and left, which unite with the corresponding branches of the neighbouring strands, and thus constitute the bundles of the next internode above. Here, therefore, we have a regular alternation in successive internodes, and each leaf-trace extends through one internode only. This simple arrangement is, however, by no means constant. Thus, we often find the bundles of adjacent internodes lying nearly in the same straight line; the forks of a bundle at the node curve round the outgoing leaf-trace, and unite on its opposite side (see one of the bundles in photograph 5, on Plate 72). This may occur in the same specimen which in other parts shows regular alternation.*

In other cases, the bundles at the node are about twice as numerous as the outgoing foliar bundles—or, in other words, only about every alternate bundle passes out at a given node. (See Plate 78, fig. 11.) Here each bundle must pass through two internodes, instead of one, before joining on to the trace of another leaf. In all the tangential sections, including those of *Calamopituis*, similar variations occur.†

We may sum up the facts considered as follows:—The bundle-system of *Calamites* bears a general resemblance to that of *Equisetum*. A single leaf-trace enters the stem from each leaf, and passes vertically downwards to the next node. In the simplest cases the bundle here forks, its two branches attaching themselves to the alternating bundles which enter the stem at this node. In other cases both the forks attach themselves to the same bundle, so that, in this case, there is no regular alternation. In other cases, again, the bundle runs past one node without forking, and ultimately forms a junction with the traces of the *second* node below its starting-point. These variations may all occur in the same specimen. The xylem at the node usually forms a continuous ring, for, where the regular dichotomous forks of the bundles are absent, their place is usually taken by anastomoses. Occasionally, however, the ring is interrupted. (See photograph 5, on Plate 72.)

The nodal xylem, *i.e.*, the commissural ring of primary wood, composed of the forks and anastomosing branches of the bundles, differs considerably from the primary xylem of the internode. In the first place, the former is much greater in amount than the latter. The nodal wood projects conspicuously into the pith, forming the well-known constriction, so familiar in the medullary casts. It is also somewhat prominent on the outer side, so that the secondary tracheæ deposited upon it are arched outward at the node, as has often been described in former memoirs.‡ (See Plate 72, photograph 4; Plate 78, figs. 7 and 10.) It may, indeed, be questioned whether this mass of wood at the node is properly to be regarded as altogether

* As in C.N. 20, A and B, 24, &c.

† See WILLIAMSON, "Organization," Part I., Plate 26, fig. 25, &c. In these figures *m* indicates the foliar bundle.

‡ See WILLIAMSON, "Organization," Part I., p. 483.

primary or as mainly secondary. No sharp line can be drawn between the short and somewhat irregularly arranged tracheæ of the nodal wood, and the longer elements with definite radial seriation, which the cambium has added on their outer side. We prefer, however, to regard the short-celled wood of the node as primary, and that for two reasons: (1) in very favourable preparations (see, for example, Plate 78, fig. 10) we see that the nodal wood is continuous with the primary wood of the adjoining internode; (2) in recent *Equiseta* an exactly similar mass of wood is developed at the nodes, as we have seen especially well in preparations of *E. pratense*.* Additional evidence in favour of the primary nature of the nodal xylem is afforded by the anatomy of the axis of the strobilus in the Calamitean fructification described in the previous memoir.† Here the tissue in question is fully formed in an organ which is without secondary thickening. At the node the tracheæ are relatively short, and have a more or less oblique position with reference to both the radial and tangential planes. They may even be nearly horizontal, especially in the neighbourhood of the outgoing foliar bundle.

The cell-walls of the nodal tracheæ are often reticulated or pitted, while those of the adjacent elongated tracheæ of the internode are scalariform. Sometimes this difference is very conspicuous. Some of the pith-cells bordering on the wood of the node are also conspicuously pitted.

As regards the mode of exit of the foliar bundles we already know that they bend out almost at a right angle with the axis (see Plate 72, photographs 5 and 6; Plate 77, fig. 6; Plate 78, figs. 7 and 8). Our knowledge of their structure is limited to their xylem, for we have no specimens to show the leaf-trace bundles passing through the cortex, where alone their phloëm could be shown. Their tracheæ often have a typical spiral thickening; sometimes their walls are reticulated or scalariform (figs. 6 and 7). They are accompanied on their outward course by some parenchymatous elements. As already mentioned, the xylem of the foliar-bundle is continuous with the protoxylem of the stem-bundle which forms its downward prolongation.

It is evident that during the formation of secondary wood the elements of the foliar-bundle must have been subject to tension and consequent rupture. In spite of this they can be traced for a long distance through the wood of old stems, especially in tangential sections, though they become very hard to find in the outer layers. It is possible that elements may have been added to them for some time, by the cambium.‡

Apart from the irregularities of distribution already sufficiently dwelt upon, we may say that the structure and arrangement of the primary vascular bundles in *Calamites* present an agreement with those of *Equisetum*, which could scarcely be closer than it is.

We have for the present left the lateral branches out of account, although they

* Mr. CORMACK regards the nodal wood of *Equisetum* as being itself partly secondary. See his paper above cited. We do not think this view will hold good for the whole genus.

† WILLIAMSON, "Organization," Part XIV., 'Phil. Trans.,' vol. 179, B., 1888, Plate 10, fig. 5.

‡ Cf. STRASBURGER, 'Histologische Beiträge,' vol. 3, p. 121.

obviously formed part of the primary structure. All the preparations which we have, showing the insertion of branches, are sections of comparatively advanced stems, in which the secondary growth in thickness has already made considerable progress. Hence the structure of the branch-bases is much complicated, owing to changes connected with the formation of secondary wood, and until the latter has been studied in detail, the phenomena presented by the branches cannot be understood.

THE SECONDARY TISSUES.

So far as the first origin of the secondary tissues is concerned, the type of development in *Calamites* always corresponds to the simplest of the various modifications with which we are acquainted in recent Dicotyledons and Gymnosperms.* We have only to distinguish between *fascicular* and *interfascicular* tissue, the former including all the tissue developed within the limits of each primary bundle, while the latter arises by the division of cells belonging to the primary medullary rays. In no case is there any preliminary formation of intermediate cauline strands, as so frequently happens among Dicotyledons. The secondary thickening of *Calamites*, in fact, so far as concerns its earlier stages, is of diagrammatic simplicity (see Plate 72, photographs 1, 2, and 3; Plate 77, figs. 1, 2, and 3).

As soon, however, as the zone of secondary tissue begins to attain any considerable thickness, variations make their appearance, depending chiefly on the degree in which the fascicular and interfascicular strands remain distinct in the secondary region, or in other words, on the part played by the principal medullary rays† during secondary growth.

Among the specimens examined by us we find four distinct types as regards this point. These distinctions are, of course, purely anatomical, and may have little or no systematic value. We may group the various forms as follows:—

- A. Principal rays remain parenchymatous throughout the whole thickness of the secondary wood.

As sub-divisions of this type we have :

- A 1. The ray maintains about the same thickness throughout.

- A 2. It becomes narrowed towards the exterior by the greater tangential growth of the fascicular wood.

- B. The principal rays disappear, as such, towards the exterior, owing to the formation of interfascicular wood.

* See DE BARY, 'Comparative Anatomy of Phanerogams and Ferns,' English Translation, p. 455, &c.

† We propose to limit the term *primary* ray to the truly primary interfascicular tissue. When this is prolonged into the secondary tissues by the cambium, we speak of it as a *principal* ray; the term *secondary* ray is applied, as usual, to those intermediate rays, which are entirely of cambial origin.

As sub-types we have :

- B 1. The change takes place suddenly, the interfascicular wood at once extending across the whole width of the ray.
- B 2. It takes place gradually, the ray becoming narrowed and subdivided by the formation of new strands of tracheæ, both at the sides, and in the middle of the ray.

The sub-type A 1 is exceptional among our specimens. We have examined stems* with wood about eighteen elements in radial section, in which the rays are certainly parenchymatous throughout and do not diminish in thickness. Tangential sections of this type of stem† leave no doubt of the purely parenchymatous structure of the principal rays. In no case, however, is the stem of any considerable age, so we cannot be certain that the condition is anything more than a transitory one, and it is quite possible that at a later stage interfascicular wood might have been formed.

The peculiar form described in former memoirs under the name of *Calamopitus*,‡ may either come under this head or under B 1. Here the interfascicular tissue does not appear to contain true tracheides, but the elements are very prosenchymatous, so that the character of the tissue is totally different from that of ordinary parenchymatous rays. The prosenchymatous ray-cells of *Calamopitus* have no visible pits on their walls; and cannot well be classed as tracheides; they differ from the tracheides in the wood of the same plant in shape and size, for the ray-cells are somewhat shorter and decidedly broader. In tangential sections, small parenchymatous secondary rays, sometimes only two cells in height, are seen between the prosenchymatous elements of the interfascicular tissue, like those between the tracheides of the fascicular wood.§ The whole structure shows a decided approach to that of *Calamodendron* BRONGR., of which we have examined some beautiful sections cut from a specimen found in the Permian of Chemnitz, and kindly presented to the collection by Count SOLMS-LAUBACH. *Calamodendron*, however, is not known to occur in the English coal-measures, and we have not included it in the present paper.

We think the genus *Calamopitus* should be retained. Besides the peculiar structure of its principal medullary rays it is characterized by the predominance of reticulated elements in its wood, by the characteristic arch-like form of the commissural bundles at the node (as seen in tangential section), and by the very large and definite "infranodal canals." Further information from additional specimens is however much needed.

The sub-type A 2 is a very unimportant one, and has only been observed in two very small Calamitean stems, with wood not exceeding seventeen elements in radial

* *E.g.*, C.N. 13 and C.N. 18.

† *E.g.*, C.N. 33.

‡ WILLIAMSON, 'Mem Lit.' and 'Phil. Soc.,' Manchester, ser. 3, vol. 4, 1869. "Organization," Part I., 1871.

§ As in C.N. 54.

thickness.* Here the principal rays narrow out rapidly towards the exterior, the marginal series of the ray dying out altogether, while the more median rows become attenuated. These changes appear to be due to the vigorous tangential growth of the elements of secondary fascicular xylem; there is no formation of interfascicular tracheides, the ray being wholly parenchymatous throughout.

The great majority of the specimens investigated belong to the type B, with interfascicular wood. In some cases (sub-type B 1) the principal rays come almost at once to a sudden end; little or no secondary interfascicular parenchyma is formed, and the interfascicular wood immediately assumes, so far as the transverse section shows, the same structure as the fascicular wood, appearing to consist of radial strands of tracheides, with narrow secondary rays, usually only one cell in breadth, between them.†

This case, however, though frequent, is exceptional. In the great majority of our English specimens the principal rays narrow gradually towards the exterior, the interpolation of interfascicular series of tracheides taking place step by step. This, the prevalent case (sub-type B 2, in the arrangement adopted), is the one which we have been able to study most in detail. It will therefore be best to base our description on stems of this variety (see Plate 72, photographs 2 and 3, Plate 77, fig. 3‡).

With the exception of *Calamopituis*, all our English specimens would probably fall under GÖPPERT'S genus *Arthropitys*, which is simply a synonym of *Calamites*, as we propose to limit that genus. The forms which we are about to consider may be taken as the type of *Calamites* in the above sense. Count SOLMS-LAUBACH has pointed out the urgent need for further investigation of the structure of the wood in Calamariæ.§ So far as the typically Calamitean structure is concerned we are now in a position to supply fairly complete information, the preservation of many of the specimens from the English coal-fields being so perfect that the structure can be studied nearly as well as in a recent wood.

The earliest stages of secondary growth scarcely need any further description. In fig. 1, on Plate 77, we have a transverse section of a stem, in which the very first tangential divisions have taken place in the interfascicular tissue, while the very definite radial seriation of the xylem of the bundles indicates that here also cambial activity has begun. This is in a twig about .7 millim. in diameter—the smallest yet observed. Another specimen, two sections of which are shown in photograph 1, on Plate 72, and in fig. 2, on Plate 77, though of larger size, shows scarcely a trace of any addition to the primary structure. In the bundles themselves there was pro-

* Shown in some new sections not yet incorporated in the collection.

† See WILLIAMSON, "Organization," Part I., Plate 24, fig. 15. WEISS, 'Steinkohlen-Calamarien,' Part II., p. 10, fig. 3. Shown in C.N. 15, 16, 17, one section in 118*, &c. Good longitudinal sections of this form are still required.

‡ See also WILLIAMSON, "Organization," Part I., figs. 9, 14, 16, 17, 26.

§ 'Fossil Botany,' English translation, p. 298.

bably no definite interval between the primary and secondary tissue-formation, hence it is convenient to take the interfascicular divisions as marking the commencement of secondary growth. In fig. 2 then, we have a stage immediately before, and in fig. 1, a stage immediately after the beginning of cambial increase. We can scarcely expect to fix the starting-point more exactly than this.

In describing the secondary tissues we will begin with the fascicular wood. The elements are arranged with remarkable regularity in radial series. Passing from within outwards, the number of the series gradually increases, by the occasional duplication of a row, but the regularity of the tissue is always maintained.

In good transverse sections we can easily see that the wood consists of two kinds of elements; the majority of the radial series are composed of relatively large elements, with rather thick walls, while other rows, between the former, consist of narrower cells, with thinner walls (see Plate 72, photograph 3; Plate 77, fig. 3; Plate 78, fig. 12, &c.). The comparison of tangential and radial sections show that the former elements are tracheæ, the latter constitute small secondary medullary rays (see Plate 72, photograph 6, also WILLIAMSON, "Organization," Part I., Plate 23, fig. 5; Part IX., Plate 20, fig. 16). As we advance from within, outwards, we find that the number of these secondary rays increases, new ones making their appearance successively, just as happens in the secondary wood of a Gymnosperm or a Dicotyledon. Most often the secondary rays are one cell only in breadth, frequently they are two cells broad, sometimes more. The radial diameter of their cells is equal to, or somewhat greater than that of the tracheæ; their tangential diameter is much less. The height of the ray-cells is generally their greatest dimension, so that they belong to the "upright" type of DE BARY.* In other cases, however, the ray-cells are approximately square, as seen in radial section, and the two kinds of elements may occur in the same ray. Uniseriate rays (only one cell in height) are very common; their form, as appearing in a tangential section, is lenticular.

The proportion of tracheæ to secondary rays varies in different specimens; the tracheal series, however, are always the more numerous.

As regards the nature of the tracheæ, the most important question which we have to decide, is whether they are true vessels or tracheides. These elements are of very considerable length, and have very oblique terminal walls, inclined to the radial plane at an acute angle (see figs. 16 and 17, on Plate 79). It is not an easy matter to measure their length, as the whole trachea is not often included in the plane of section, and it is only in the best-preserved specimens that it is even possible to determine whether this is the case or not. We have, however, succeeded in making some measurements. In a tangential preparation (C.N. 20 B, from part of which fig. 8 on Plate 78 was drawn), five tracheæ were measured; their length varied from 1.7 to 2.4 millims., the average being about 2 millims. This, however, is much exceeded in other cases. In another tangential section, perhaps the most perfect in the collection

* *Loc. cit.*, p. 486.

(C.N. 1554, from which photograph 6, on Plate 72 was taken), we measured two tracheæ, the lengths of which were almost the same, namely 4.1 and 4.2 millims. This is just equal to the maximum length of the tracheides in *Pinus*.* In the fascicular wood the tracheæ run approximately vertically, with only trifling curvatures.

We have found it a very general rule that the pits in the secondary tracheæ are limited to their radial walls. This statement is based on the evidence of all the tangential sections which are sufficiently well-preserved to show the structure in detail. The absence of pits on the tangential walls cannot be merely apparent, or due to imperfect preservation, for the same tangential sections, which show no pits in surface view, present quite obvious pits, seen in section, on the radial walls of the tracheæ (see Plate 78, figs. 8 and 9), while radial sections of the same specimens, show the pits in surface view with perfect clearness (see Plate 78, figs. 7 and 10).† We regard the establishment of this fact as of considerable interest, for it indicates that the mechanism for the passage of sap through the wood of *Calamites* was of the same kind as that existing in recent Coniferæ. Such a character is, of course, of no *systematic* value, as is shown by the well-known case of *Drimys* among the Dicotyledons.‡

It is only in the most internal part of the fascicular wood, immediately outside the canal, that we find tangential pits on the tracheæ. They were either limited to the primary xylem, or at most extended to a few of the first-formed secondary layers (see Plate 80, fig. 21). As already mentioned, the peculiar short-celled wood at the nodes has pits on all surfaces of its elements, but we have already given reasons for regarding this wood as primary.

The pits on the radial walls are sometimes of the scalariform type, that is, they are transversely elongated, so as to extend across the whole width of the wall; in other cases they are shorter, having an elliptical outline. More than one row of pits may be present on the same radial wall. In some radial sections it appears that the scalariform pitting is limited to the more internal tracheæ, sometimes even to those which may be regarded as primary, while all the pits seen on the more external tracheæ are of the shorter form. This, however, is not a constant rule. For example, in the largest specimen of which we have examined sections,§ the scalariform type of thickening prevails in all parts of the wood, which is 2 inches thick, though tracheæ with shorter pits are seen here and there. As the nature of the pitting may vary in different parts of the same trachea, we attach little importance to these differences. They probably depend in part on the relative positions of the tracheæ. Where the elements in two adjacent radial rows correspond, so as to be in contact with each other by their entire radial surfaces, we generally find scalariform pitting. Where, however, the elements

* See DE BARY, *loc. cit.*, p. 506.

† The preparations on which these statements are chiefly based are, C.N. 20, 20A and B, 21, 22, 65-68, 83-87, 88-91, 130* and 131*, and 137*, 138*, 1554, and 1937.

‡ See STRASBURGER, 'Histologische Beiträge,' vol. 3, p. 161.

§ The radial section is C.N. 80. See WILLIAMSON, "Organization," Part IX., Plate 20.

overlap, so that each trachea abuts on portions of two others in the next row, we find the shorter pits.

Where tangential pits are present, *i.e.*, on the walls of the more internal tracheæ, they are usually scalariform. Sometimes a few oval pits are seen on the tangential walls in the transitional region, before they disappear altogether.

The very oblique terminal walls of the tracheæ have similar pits to those of the radial walls, from which indeed they are in no way marked off.

In tangential sections we frequently find the pits well shown in sectional view.* In all cases they are evidently bordered, the thickened ridges distinctly over-arching the delicate closing membrane, which is, of course, only preserved in the most favourable cases. Between two tracheæ the pits are bordered on both sides; between a trachea and a cell belonging to a medullary ray, whether principal or secondary, we find one-sided bordered pits, the border being on the side towards the trachea. (See Plate 78, fig. 9, A and B.)

From the general form of the tracheal elements, and especially from their tapering ends, the impression is strongly conveyed that they are tracheides and not vessels. Their oblique terminal walls have the same pitted structure as the lateral walls, and there is no evidence that the pits were perforated in either case, though, of course, it is impossible to prove that this never happened. Direct evidence of the development cannot be expected from a fossil, but when we come to consider the interfascicular wood we shall find some facts which speak strongly for the origin of each trachea from a single cell. There is no reason to doubt that the same mode of origin held good for the fascicular tracheæ.

In exceptional cases, however, we have found occasional traces of transverse walls in the tracheæ. Though such traces are sometimes doubtful, they are not always so. In a very few instances† the transverse wall is unmistakeable, and indeed seems to have formed a permanent septum. It must be understood, however, that such indications of septa are extremely rare, only occurring in certain preparations, and in a few tracheæ in each case. In those tracheæ which show the transverse walls, their position is quite irregular. We by no means believe that this casual appearance of an occasional septum points to the origin of the tracheæ by cell-fusion. It is doubtful whether the septa, when present, were ever absorbed at all. Two explanations are possible; either the young tracheide, while still a living cell, occasionally underwent septation, as is sometimes the case with sclerenchymatous fibres,‡ or else these transverse walls are not normal, but mark the limit between the cells of a thylosis.

There is no evidence for the existence of any xylem-parenchyma, apart from the medullary rays, in the secondary wood. Radial sections are decisive on this point, for all the parenchymatous cells manifestly form part of radial plates of muriform

* They are shown in great perfection in C.N. 20A and B, 137* and 138*, 1554 and 1937.

† Such an instance occurs in C.N. 138*.

‡ See DE BARY, *loc. cit.*, p. 134.

tissue, or at least (*i.e.*, in the case of uniseriate rays) form continuous radial series. The fascicular wood consists of tracheæ and medullary rays only.

The great differences in shape between the cells of the medullary rays suggest the possibility of a physiological differentiation, such as has been found by STRASBURGER in certain Dicotyledons, in which the upright and horizontal elements of the rays differ considerably in structure, and presumably in function also.* But we have no evidence of this in the fossil. Neither have we any reason to suppose that tracheides were present in the secondary rays, as is the case in the Abietineæ, although the general absence of tangential pits in the secondary wood might have led us to expect such an arrangement.† Only the nature of the pitting can guide us in such a question, and the evidence available is not conclusive, for such details can only be adequately studied in the best preserved specimens.

Pits on the walls separating the cells of the medullary rays from one another are seldom shown at all clearly. These cells usually have rather thin walls, and such pits as they may have had could have been of no great depth.

It now remains for us to consider the structure of the principal medullary rays, and more especially to investigate the process by which, in most of our specimens, they become bridged over by interfascicular wood.

The principal rays in the type (B 2) which we are now considering are of maximum breadth next the pith, and taper off rapidly (as seen in transverse section) towards the exterior (see Plate 72, photographs 2 and 3; Plate 77, fig. 3). The width of the inner end of the principal ray is much increased, in the older specimens, by the tangential dilatation of the more internal cells of the ray.‡ We find this phenomenon in many of the older stems,§ but its occurrence is inconstant; the dilatation may take place in some rays and not in others, within the same transverse section. The tangential width of a dilated ray-cell may amount to .25 millim. or more, which is from two to three times that of the neighbouring unaltered cells. It is the middle cells of the ray which become dilated; those adjoining the wood on either side remain unaffected. It is evident that so considerable an extension of the width of the medullary rays allowed of a perceptible enlargement of the pith-area during the earlier stages of secondary growth. It is probable that the circumference of the pith may have increased in this manner to $1\frac{1}{2}$ times its original extent, or even more.

It can be proved that the tangential extension of the inner ray-cells was an active process, and not simply due to the tensions set up by the growth of other tissues. This is shown by the fact that the dilatation of the rays sometimes led to the crushing of the wedges of fascicular wood between them, and thus to the obliteration of the

* STRASBURGER, 'Histologische Beiträge,' vol. 3, p. 209.

† See STRASBURGER, *loc. cit.*, p. 9.

‡ See the figure in WILLIAMSON, "Organization," Part I., Plate 27, fig. 26, which, however, only shows a small degree of dilatation compared with many larger stems.

§ As in C.N. 133,* &c.

protoxylem canals.* This is a familiar process in recent plants, where parenchymatous tissues show active dilatation; we may specially cite the case of the tuberous roots of *Thladiantha*, formerly described by one of us.†

The structure of a principal medullary ray, as seen in a tangential section cut near the pith, is fairly constant in the various specimens examined. The middle rows of cells of the ray, varying in number in different cases from 2 to 8 or more, are short, often isodiametric, and sometimes tangentially dilated. The cells at the margins of the ray, adjoining the fascicular wood, are much elongated, but generally have square ends, like the rest (see Plate 79, fig. 15). If another tangential section, a little further to the exterior, be examined, we find that the principal rays are narrower; the elongated marginal cells have pointed ends, or are replaced by tracheides. The middle short-celled part of the ray shows little change (see Plate 79, fig. 16). A third section, taken still further towards the outside of the wood, shows a more profound change of structure. The principal rays are here no longer continuous throughout the internode, but are partitioned up into a number of short, lenticular rays by tracheæ, or strands of tracheæ, which cut obliquely through the original ray (see Plate 79, fig. 17). The same process is carried still further as we advance yet more towards the exterior, until, in some cases, the principal rays can scarcely be recognized any more, but are completely broken up into short rays, one or two cells in thickness, which differ but little from the secondary rays of the fascicular wood.‡

The comparison of transverse sections confirms the above observations. Tracing the radial cell-series of the principal ray outwards, we find, not only that the marginal rows of parenchymatous elements are succeeded by rows of tracheæ, but also that new rows of tracheæ make their appearance at various places in the interior of the ray. The latter sometimes appear to form the direct outward continuation of parenchymatous series, while sometimes they are interpolated between them; in the second case some of the parenchymatous radial series die out altogether.§

Favourable radial sections, which exactly follow the course of a principal ray, may also show how the more elongated parenchymatous cells are succeeded, towards the exterior, by tracheæ.||

There are many variations in detail; sometimes, for example, all the cells of the ray become more elongated towards the exterior of the wood. A more important

* This is very conspicuous in C.N. 123*, where the inner part of each strand of wood is quite crushed. [This evidently took place during life, for the rest of the tissue, including the dilated ray-cells, is perfectly preserved.]

† SCOTT and BREBNER, "Internal Phloëm in Dicotyledons," 'Annals of Botany,' vol. 5, 1891.

‡ The above outline description is founded primarily on the series C.N. 65-68, from which the figures are taken, and has been confirmed by the study of several other series, as C.N. 20A and B, C.N. 83-87, C.N. 88-91, C.N. 130* and 131*, and C.N. 137* and 138*, as well as by that of single tangential sections, which are scarcely less instructive, when, as often happens, they are very slightly oblique, so as to pass gradually from an inner to a more external region of the wood, as in C.N. 1937, &c.

§ See especially WILLIAMSON, "Organization," Part I., Plate 25, figs. 17 and 18.

|| As in C.N. 132***.

fact is, that as we trace the ray outwards we often meet with elongated cells of prosenchymatous form, but apparently without pits (see fig. 16). Such cells are most often found at the margins of the ray, but also occur in its interior. We must regard these prosenchymatous elements as intermediate forms between ray-cells and tracheides.*

The study of transverse sections shows us that the intruding tracheides, whether appearing at the sides or in the middle of the ray, are not isolated, but form, almost from their first origin, continuous radial series.†

The question now arises how this interfascicular wood which we have described is developed. The principal medullary rays consist of relatively short cells, which, judging from the analogy of recent plants, must have arisen from cambial cells of like form. Now the difficulty is, that wherever interfascicular tracheæ appear, we find these short elements replaced by extremely long ones. A numerical estimate of this difference has little value, in view of the great variations in length of both ray-cells and tracheides, but in many cases we may safely assume that the interfascicular tracheides are twenty times as long as the parenchymatous cells of which they take the place. Yet the radial seriation of the elements is scarcely disturbed by this enormous change in their dimensions. "Sliding growth" to such an extent would inevitably bring with it a complete obliteration of the original radial arrangement of the secondary tissues.‡

The hypothesis that the interfascicular tracheæ arose by cell-fusion is at first tempting, but there is no sufficient evidence to support it. We have already discussed the rare cases in which there are traces of transverse walls; in the vast majority of tracheæ nothing of the kind is visible. There is no analogy among recent plants for the existence of xylem-vessels without any trace of the limits of the cells from which they are formed.§

The sculpturing of the cell-wall is so often perfectly preserved in the fossil *Calamites*, that remains of transverse walls can scarcely have escaped observation, considering how obvious they are wherever they exist in recent plants.

Besides this negative evidence, the existence of elements intermediate in form and length between the parenchymatous cells of the ray and the tracheæ is a strong argument for the origin of the latter by growth rather than by cell-fusion, especially as these transitional elements appear just where they are wanted, namely, where the interfascicular wood is beginning to form.

The solution which we suggest is that the interfascicular tracheæ arose by the

* They are well shown in C.N. 20B, 83, 90, and 130*.

† See WILLIAMSON'S figure above cited, Part I., Plate 25, fig. 17.

‡ Cf. DE BARY, *loc. cit.*, p. 470; KRABBE, 'Das Gleitende Wachsthum,' 1886.

§ Cf. DE BARY, *loc. cit.*, p. 165. The case of *Dracena* and its allies which might once have been supposed to afford such an analogy, is now known to be one of sliding growth (see SCOTT and BREBNER, "Secondary Tissues in Monocotyledons," 'Annals of Botany,' vol. 7, 1893).

elongation of single cells, but that this elongation took place in the cambium-cells before the tracheæ were cut off from them. We may suppose that an ordinary short cambial-cell, belonging to a principal ray, before beginning to produce tracheæ instead of ray-cells, itself became elongated by sliding growth. The existence of intermediate forms renders it probable that this elongation did not take place all at once. It is probable that a cambial-cell, after growing to some extent in length, divided, and cut off a short tracheide or transitional element; before the next division the cambial-cell may have grown to a greater length, and then have cut off a longer tracheide, and we may suppose this process continued until the interfascicular cambial-cells attained a nearly constant length, after which the development would go on uniformly, as in the fascicular wood.

This account of the process is, of course, only a hypothesis, for the direct observation of the successive stages of histological development is impossible, even in the best-preserved fossil. We think, however, that our hypothesis is one which explains the facts, and we do not see how the great elongation of the tracheides can be reconciled with the preservation of radial seriation in any other way.

A certain small additional amount of sliding growth may also have taken place in the young tracheides themselves, after their separation from the cambium, just as is known to happen in *Pinus*.^{*} The existence of occasional intruding ends of elements, presumably tracheides, seen in transverse section among the cells of the ray, renders this probable.

We have not had an opportunity of making a similar study of the type (our sub-type B1) in which the interfascicular wood at once bridges over the entire width of the principal rays. Probably a like explanation would apply here also; we need only suppose that a larger proportion of the cambial cells forming the ray undergo simultaneous elongation. It is evident that in both cases the process must involve the interruption of a considerable number of the parenchymatous cell-series of the ray, and we have already seen that this actually occurs.

Before leaving the subject of the principal medullary rays, something must be said of their modified structure in the infranodal region. Such a ray almost always broadens out just below the node, forming, as seen in tangential section, the "lenticular organ" of previous memoirs.[†] In this region the cells of the ray are very numerous, and generally isodiametric throughout, often contrasting sharply with the more elongated elements in the rest of the ray (see Plate 72, photographs 5 and 6). The cells toward the middle of the infranodal tissue of the ray are generally smaller, and frequently have thicker walls than their neighbours. The most careful investigation, however, has failed to reveal any traces of vascular tissue in this position. The preservation of the specimens is often so perfect, that such tissue, if it had been

^{*} See KNY, "Zur Kenntniss der Tracheiden," 'Ber. d. Deutsch. Bot. Gesellschaft,' vol. 4, 1886.

[†] WILLIAMSON, "Organization," Part IX., p. 326.

present, could not have been overlooked.* The infranodal portion of the ray is persistently parenchymatous throughout the whole thickness of the secondary wood, and scarcely ever contains any interpolated tracheides. Hence, in tangential sections through the outer wood, where the principal rays generally are obliterated by interfascicular wood, the lenticular masses of parenchyma below each node form a most conspicuous feature (see photograph 6, also WILLIAMSON, "Organization," Part IX., Plate 20, fig. 24). Somewhat similar persistent tracts of parenchyma are sometimes found immediately *above* the node, but they are on a much smaller scale.

It very frequently happens that the infranodal tissue of the principal rays undergoes disorganization of its inner cells, leading to the formation of the radial *infranodal canals*, so fully discussed in previous memoirs.† It is well known that these infranodal canals afford the explanation of those protrusions on the medullary casts, which are placed immediately below the nodes, and between the furrows corresponding to the bundles (see the photographs in Plate 86). This explanation has been accepted by Count SOLMS-LAUBACH,‡ and indeed admits of no doubt, if, for example, we compare the wonderfully preserved cast figured in a former paper,§ with such a tangential section as that shown in our photograph 6. The agreement between the radiating, spoke-like rods of the cast, and the infranodal rays, as shown in the sections, is exact, not only as regards position, but also in size and sectional form.

The extent to which the disorganization of the infranodal parenchyma took place *during life* may well have varied in different specimens. In any case it would have perished during fossilization much sooner than the woody tissue surrounding it, and this is quite enough to account for the marks on the casts.

THE SECONDARY CORTICAL TISSUES.

It is extremely rare to find the cortex of the older specimens in any degree preserved. Except in the comparatively young stems already discussed, all the tissue from the cambium outwards has usually disappeared. The only instance of a really large corticated stem, with which we are acquainted, is that described in a former memoir,|| and already referred to above.

Here the zone of cortex preserved is even broader than the wood, and measures $2\frac{1}{4}$ inches in thickness. The preservation is very imperfect, but in the radial section (C.N. 80) it is possible to distinguish at least two zones of elongated, square-ended cells, with a regular radial arrangement. We cannot doubt that this tissue was of

* As in C.N. 20B, 138*, and others, besides those photographed.

† WILLIAMSON, "Organization," Parts I. and IX. As regards the true Calamitean stem (as distinguished from that of *Calamopituis*), these canals are especially well shown in C.N. 24, 91, 138*, and 1943.

‡ *Loc. cit.*, p. 312.

§ WILLIAMSON, "Organization," Part IX., Plate 21, fig. 31.

|| WILLIAMSON, "Organization," Part IX., Plate 20, figs. 14-21. The sections are C.N. 79-87.

the nature of internal periderm. In other parts the cortex consists of prosenchymatous cells.

A specimen of a comparatively small stem, which we have recently examined, throws great light on the origin of the periderm from the primary cortical tissues (see Plate 79, fig. 18). The transverse section shows that the cortex is well-preserved throughout, though in most places somewhat separated from the wood by the intrusion of rootlets of *Stigmaria*. Many of the large parenchymatous cells of the cortex are divided up by tangential septa into short radial series. The divisions are not limited strictly to any one zone of the cortical tissue, but occur chiefly in its inner portion, through which a fairly regular band of dividing cells can be traced. We think that there can be no doubt that we have here to do with an early stage of the formation of periderm. It is certain that a secondary tissue of some kind is being formed by the division of cortical cells. We know, from the older specimen, that internal periderm was formed abundantly in the cortex; we can scarcely be wrong in correlating the two facts.

It may be worth while to state expressly that the specimen from which fig. 18 is drawn has the whole thickness of the wood perfectly preserved, and is a typical *Calamites*, such as that shown in Plate 72, photograph 3.

THE DIAPHRAGMS.

Before leaving the subject of secondary changes in the stem of *Calamites*, we wish to call attention to the formation of periderm on the diaphragms. These persistent plates of parenchyma, which separate the internodal cavities of *Calamites* from one another, have often been described.* When well preserved it is always evident that they are several cells in thickness. The inner layers of cells of the diaphragm often have thicker walls than those towards the upper and lower surfaces. We have often observed that the thin-walled superficial cells are divided up by cell walls parallel to the surface. In some specimens these divisions have taken place so freely that a layer of regular periderm-like tissue coats the diaphragm on either side (see Plate 79, fig. 19). It is most probable that this secondary tissue really represents a layer of internal cork, which isolated the persistent diaphragm from the disorganizing tissue, by the destruction of which the medulla became fistular.

Analogies are not wanting, among recent plants, for the formation of periderm in the pith. It occurs, for example, in certain anomalous Campanulaceæ and Gentianeæ, and in *Aconitum*.† In *Calamites*, however, so far as we have observed, the medullary periderm seems to be limited to the surface of the diaphragms, and not to extend to the peripheral layer of persistent pith which surrounds the medullary cavity.

* See WILLIAMSON, "Organization," Parts I. and IX.

† See JOST, 'Bot. Zeitung,' 1890, pp. 443 and 491; HÉRAULT, "Recherches sur l'Anatomie comparée de la tige des Dicotylédones," 'Ann. Sci. Nat., Bot.,' series 7, vol. 2, 1885.

THE BRANCHING OF CALAMITES.

Many of the specimens investigated show the insertion of lateral branches upon a relatively main axis.* In the great majority of these instances the branches are of small diameter compared with the stem which bears them. In judging of the relative dimensions, however, caution is necessary, for we know that in many cases the pith of the branch tapered almost to a point towards its insertion, giving rise to the well-known conical terminations of many of the medullary casts (see the figures in Plate 86). But, making due allowance for this fact, there can still be no doubt of the relatively small size of the lateral branches in very many cases, especially in those where several were given off at the same node. As already stated, the branches are always inserted immediately above a node, and are nearly always placed between two of the outgoing foliar bundles (see Plate 72, photographs 5 and 6 ; Plate 80, fig. 21 ; also WILLIAMSON, "Organization," Part IX., Plate 21, fig. 28, where *m* indicates the foliar bundles).† An exception is presented in a section of *Calamopituis*, in which a branch appears to be inserted immediately above one of the bundles,‡ and in one case, so far as we have observed, in the typical *Calamites*.§

The branches often have a verticillate arrangement, but do not seem to have been disposed in the whorl with any great regularity. Thus the transverse sections of one of the largest stems showing structure,|| pass through four lateral branches at the same node, which are placed at irregular intervals. Sometimes a single branch only was developed at a node, as is very clearly shown in the specimen¶ from which fig. 20, on Plate 79, is drawn. On the other hand a tangential section of a large stem shows four branches, regularly arranged at the same node, and suggests that here the whorl (of which such a section can only show a small part) may have been complete. Two of the four branches are shown in photograph 5, on Plate 72.

The structure of the branch at or near its insertion is very clearly shown in a number of preparations (see Plate 72, photographs 5 and 6 ; Plate 79, fig. 20 ; Plate 80, figs. 21 and 22). Tangential sections through the inner part of the wood of the main stem show the basal portion of the branch in transverse section. In such preparations** we see that the branch has a parenchymatous pith, often completely preserved, sometimes partly fistular. Surrounding the pith we find a ring of xylem, arranged in more or less distinct bundles, which, though less obvious than those of an ordinary free stem, are still quite indubitable in good sections. That in these bundles

* See the descriptions and figures in former Memoirs ; WILLIAMSON, "Organization," Parts I. and IX.

† Also well shown in C.N. 20B, 90, 138*, &c.

‡ See WILLIAMSON, "Organization," Part I., Plate 28, fig. 38.

§ C.N. 1937.

|| C.N. 133*, 134*, &c. From 134* the fig. 22 on Plate 80 is taken.

¶ C.N. 132**.

** As in C.N. 20B, 90, 138*, besides those figured ; see also WILLIAMSON, "Organization," Part IX., Plate 21, fig. 28.

we really have the primary wood of the branch, is conclusively proved by sections which are transverse to the main stem, and pass tangentially through the base of the branch (see Plate 79, fig. 20).^{*} Here we see the bundles of the branch in longitudinal section, with their annular and spiral tracheæ, and the bands of interfascicular parenchyma between them. In the tangential sections of the main stem (transverse to the branch) it is also easy to demonstrate the elements of the primary xylem of the branch, when they are cut at all obliquely. Our best example of this is the section shown in Plate 80, fig. 21, which passes close to the pith of the parent stem, and therefore shows the branch at its actual base. Here the groups of primary xylem around the pith of the branch are perfectly obvious, and we can distinguish their spiral tracheæ. On the lower side of the branch we can directly trace the continuity of its primary xylem with the nodal wood of the main axis.

The characteristic internodal canals of the Calamitean stem are not present at the actual base of the branch (see photograph 9 on Plate 73, and fig. 21 on Plate 80). Neither are they found, in their typical form, in any part of the branch, so far as it is embedded in the wood of the main axis. In sections which pass transversely through the branch, at any point beyond its actual inner extremity, we frequently find a ring of gaps in its tissue (not to be confused with accidental lesions), situated immediately within the xylem-bundles (see Plate 72, photograph 5, and more especially photograph 6). These gaps are less regular in form than the normal canals, and also differ from them in a more important point, for, as a rule, they are not empty, but are occupied by a lax tissue, consisting of rather large and thin-walled cells. Within the gap, among the thin-walled cells, we can often detect the protoxylem elements of the primary bundle.[†] Hence we regard these gaps as corresponding to the typical canals of an ordinary stem, in so far as they mark the position of the disorganized protoxylem-groups. As to the lax tissue which usually fills these spaces, two views are possible. It may have been primary, consisting of parenchymatous cells which were present among the primitive tracheæ from their first origin; or it may have been a new formation, analogous to a thylosis, such as has been observed in the carinal canals of *Equisetum*.[‡] We regard the latter view as the more probable. All our specimens showing branching are comparatively advanced stems, with a considerable thickness of secondary wood. Hence it is almost certain that the primary tissue at the base of the branch would have already become functionless, especially since many of these branches were evidently abortive, as will be shown below. The formation of thyloses under such conditions is quite probable. We are the more inclined to this hypothesis from the fact that the tissue filling the gaps is conspicuously different from the sur-

^{*} The same point is shown in a similar section of another specimen, C.N. 132*. In one of the preparations kindly lent to us by Count SOLMS-LAUBACH, this structure is, if possible, even more beautifully preserved than in the section figured.

[†] As in C.N. 20B, and 1554.

[‡] See STRASBURGER, 'Histologische Beiträge,' 3, p. 437.

rounding parenchyma. A similar filling of the canals with parenchyma has once or twice been observed in the ordinary free stems.

The primary xylem-bundles of the branch are usually surrounded on the outside by a zone of radially-arranged secondary wood, no doubt the product of the cambium of the branch. In fig. 21 we see that secondary wood has only been formed towards the upper side of the branch. On the lower side the primary wood was continuous with that of the stem, and so no cambium could be formed. Further towards the exterior this hindrance no longer exists, and the zone of secondary wood becomes complete (see photographs 5 and 6, Plate 72).

The secondary wood of the branch is connected in the most complete manner with that of the main stem on which it is inserted. The direct connection is mainly from below. Here the secondary tracheides of the parent axis abut immediately on those of the branch. Other tracheides pass up from below, at the sides of the branch, and bend over to join its lateral strands of xylem, while others again curve round over the top, and bend down to form a union with the wood on the upper side of the branch. The whole structure bears a most striking resemblance to the insertion of a lateral shoot of *Pinus*, as figured, in tangential section, by Professor STRASBURGER.* Occasionally, a few tracheides appear to be continuous in the upward direction, from the branch into the wood.

A radial section through the insertion of a branch, figured in a previous memoir,† shows with great clearness how the pith of the branch terminates inwards in a narrow neck, by which it is continuous with the pith of the parent stem. The same fact is shown in various transverse sections (see Plate 79, fig. 20, which, however, is not *median* through the branch; and Plate 80, fig. 22). The series of transverse sections cut from the base of the specimen discovered by Mr. WILD, and already referred to, also illustrates the point (see Plate 73, photographs 7, 8, and 9). At a distance from its base the branch has a large fistular pith, surrounded by a ring of about 24 bundles, of the normal structure (photograph 7). Lower down the pith is much smaller; the bundles are still normal, but are much reduced in number (photograph 8, which shows 14 bundles). At the base itself the pith is reduced to a minute body, and is no longer fistular. The vascular bundles are not more than 10 in number, are crowded closely together, and their canals can no longer be recognized (photograph 9). In fact, we have here almost reached the inner termination of the branch, such as is shown, in connection with the main axis, in Plate 80, fig. 21. All these facts agree exactly with the appearances presented by the medullary casts (see Plate 86).

So far as we have gone, the structure of the branches in their basal regions has been sufficiently intelligible. Certain difficulties, however, remain. If we examine tangential sections through the outer layers of the secondary wood, and passing

* 'Histologische Beiträge,' vol. 3, plate 2, fig. 40.

† WILLIAMSON, "Organization," Part IX., Plate 21, fig. 27 (C.N. 97).

transversely across a branch at some little distance from its actual base, we often find a highly peculiar structure, already described and figured in former memoirs.* The transverse section of the branch shows no well-defined pith and no clear traces of the primary groups of xylem. It consists of a parenchymatous mass, into which tracheides penetrate in all directions from the surrounding secondary wood. These intruding tracheides describe strange curves, and extend as far as the middle of the branch, cutting up the parenchyma into isolated groups.† In fact, in these cases, as we trace the branch outwards, its structure, instead of approaching more nearly to that of the normal Calamitean stem, becomes more and more anomalous. Such a structure is in fact totally different from that of a *Calamites* or any other known stem. From the sections of Mr. WILD's specimen we know that no such peculiarities are found in a normal branch, at any point, from its base upwards. We believe that the true explanation is to be sought in the fact that the remarkable structure in question is not a normal one, but is due to the abortion of the branch, and the consequent enclosure of its base by the secondary wood of the parent stem.

We have direct evidence proving that branches became abortive and were enclosed by the wood. A good illustration of this is afforded by the radial section already mentioned.‡ Here the normal pith of the branch can be traced outwards, up to a certain point, at which it is suddenly cut off by a layer of secondary wood seen in radial section. The section is obviously median, so there can be no doubt that the wood really shuts off the end of the truncated branch. Precisely the same phenomenon is shown in some of the transverse sections (see Plate 80, fig. 22), which pass through the median plane of a branch. Here also the parenchymatous pith of the branch extends for a certain distance from the base, and is then suddenly cut off by a mass of secondary wood, which, in this case, is seen in transverse section. The line between the pith of the branch and this callus-wood, if we may call it so, is nearly straight, or if anything convex towards the interior, so the appearances cannot possibly be explained by obliquity of section. We have, in fact, two other sections of the same branch, passing one above, the other below, its median plane, and the three together prove conclusively that the truncated end is completely shut in by secondary wood.§

In these, and other similar cases, it is evident that a meristem was formed across the pith of the branch, at a certain stage, by which secondary wood was formed, completely cutting off the basal portion of the branch from all direct communication with the exterior. We can hardly doubt that the free end of the branch was previously or simultaneously cast off. It is impossible to say at what stage of

* See WILLIAMSON, "Organization," Part IX., Plate 21, fig. 26.

† As shown in C.N. 88, 131*, and other preparations.

‡ C.N. 97, WILLIAMSON, "Organization," Part IX., Plate 21, fig. 27.

§ The sections in question are C.N. 133*, 134*, and 135*. From the middle one our figure is drawn. Other branches in the same preparations show the same structure.

development of the branch abortion took place. Possibly it never advanced much beyond the condition of a bud, more probably it formed a shoot of limited duration, comparable to the short leaf-bearing shoots of *Pinus*.

This then we believe to be the explanation of the apparent intrusion of tracheides into the middle of the branch. The tracheides which appear to penetrate into the branch, represent, in our opinion, the commencement of that formation of callus-like wood, by which the base of the lateral shoot soon became completely enclosed.

We have gained, then, this additional fact respecting the branches of *Calamites*: in many cases they were abortive, or of short duration, and their bases then became shut in, like "knots," by the wood of the parent stem.

One specimen, previously figured,* shows a branch somewhat different from those already described. The stem and branch are enclosed within a common zone of secondary wood, and the sections show that the dimensions of the two are approximately equal, as is also the number of their vascular bundles. Evidently we have here to do with a different order of branching from that which we have just considered. In this specimen the branch repeats the characters of the main stem, and was presumably of equal morphological importance; in the previous cases the branches were relatively small lateral appendages, and probably of limited duration.

As regards the mode of origin of the branches, we are necessarily without any direct evidence. Now, however, that the continuity between the primary tissues of the branch and those of the main stem has been demonstrated, there can be no doubt that the ramification took place while the axis was still young. In fact we have every reason to suppose that the branching was normal, not adventitious, and that the lateral shoots arose, like the normal branches of *Equisetum* or any other vascular plant, in the immediate neighbourhood of the growing point. The secondary wood in which the base of the branch is imbedded, was evidently deposited after the branch had been formed; the stem and branch together became invested simultaneously by a common woody zone. In fact the conditions in *Calamites* are the same as in the branching of any stem with secondary growth in thickness, and present no special difficulties, now that the facts are known.

The successive changes in structure which we find in a branch, as we trace it from its base upwards, have already been described. The changes consist essentially in a rapid increase in the diameter of the pith, and in the number of vascular bundles surrounding it.

These facts, which have been already demonstrated by the study of specimens showing structure, are exactly reproduced in those medullary casts which represent the pith-cavity of lateral branches. After the fundamental truth had been established, that the sandstone and other allied specimens, which were long believed to be the actual stems of *Calamites*, were merely inorganic casts of a central cavity from which

* WILLIAMSON, "Organization," Part IX., Plate 21, fig. 31, A and B (C.N. 102).

the medullary tissue had disappeared,* the study of these plants underwent a radical change. The idea that the base of a large lateral branch adhered to the stem solely by a minute constricted neck, having been shown to be an impossible thing,† search had to be made for the true sustaining structures, and these were found in the strong zone of secondary xylem.

The following series of photographs, taken from seven specimens of medullary casts, preserved in the Natural History Department of the British Museum, illustrate the structure of the branch, from its base upwards. Such casts, when perfect, invariably terminate at their lower extremity in a very narrow conical point, on which no traces of the vertical grooves and ribs, indicating the number and position of the vascular bundles, and the primary rays, are present. This point corresponds to what, in the following tables, is designated the *proto-medulla* of the branch, *i.e.*, the basal portion of its pith by which it was connected with that of the parent stem.

These tables give the length and circumference of each internode, as well as the number of its woody wedges (vascular bundles); in all these respects an increase takes place in each successively higher internode, for a limited distance, as we ascend. Beyond the point where this increase is checked, which is usually within a few inches from the conical base of the pith of the branch, the latter is prolonged to a more or less considerable height, with very little further change in the features referred to. This fact was remarkably illustrated by the medullary cast of a stem, discovered by Mr. GEORGE WILD in the roof of a colliery under his superintendence near Ashton-under-Lyne. This specimen, which was a portion of the middle part of a Calamite, was 30 feet in length, but while the diameter of the pith at its lower end was 11·5 centims., at its upper extremity it had only increased to 15·2 centims., a very small increase in a stem of such a length.

The photographs represent (with the exception of F) the basal portions of the specimens, and the accompanying tables give the measurements and number of vascular bundles in each internode, as above explained.

* WILLIAMSON, "Organization," Part I., 1871.

† WILLIAMSON, "Organization," Part IX.; see Plate 21, fig. 30.

TABLES and Photographs from Medullary Casts.

Specimen A.

Column I. Number of internode.	Column II. Vertical length of internode.	Column III. Circumference of inter- node.	Column IV. Number of vascular bundles in circumference of internode.
7	Imperfect		43
6	4.1 centims.		39
5	1.8 "		31
4	1.3 "		22
3	1.0 centim.		16
2	0.4 "		11
1	0.35 "		Not distinct
	Proto-medulla	almost destroyed.	

See Photograph A, Plate 86.

Specimen B.

Column I. Number of internode.	Column II. Vertical length of internode.	Column III. Circumference of inter- node.	Column IV. Number of vascular bundles in circumference of internode.
7	3.0 centims.	8.0 centims.	61
6	2.0 "	8.0 "	55
5	1.5 "	8.5 "	49
4	1.1 "	8.6 "	45
3	1.4 "	8.1 "	46
2	1.0 centim.	6.2 "	35
1	0.65 "	5.0 "	27
Basal portion*	0.70 "		

See Photograph B, Plate 86.

* Upper half with ill-defined traces of bundles ; lower half proto-medulla of branch,

Specimen C.

Column I. Number of internode.	Column II. Vertical length of internode.	Column III. Circumference of inter- node.	Column IV. Number of vascular bundles in circumference of internode.
10	6.0 centims.	8.5 centims.	36
9	4.5 "	Imperfect	Imperfect
8	4.5 "	8.5 centims.	31
7	2.5 "	8.3 "	29
6	1.5 "	8.0 "	24
5	1.0 centim.	7.6 "	20
4	1.0 "	6.5 "	15
3	0.4 "	5.5 "	12
2	0.3 "	4.8 "	6 or 7
1	0.3 "	3.2 "	5 or 6
Proto-medulla . . .	..	1.1 " at its upper portion	

See Photograph C, Plate 86.

Specimen D.

Column I. Number of internode.	Column II. Vertical length of internode.	Column III. Circumference of inter- node.	Column IV. Number of vascular bundles in circumference of internode.
9	3.8 centims.	9.0 centims.	50
8	3.1 "	8.3 "	49
7	2.5 "	7.7 "	40
6	2.2 "	7.7 "	41
5	1.5 "	7.5 "	35
4	1.1 "	5.1 "	32
3	0.7 centim.	3.7 "	23
2	0.5 "	3.1 "	14
1	Imperfect	Imperfect	Imperfect

See Photograph D, Plate 86.

Specimen E.

Column I. Number of internode.	Column II. Vertical length of internode.	Column III. Circumference of inter- node.	Column IV. Number of vascular bundles in circumference of internode.
11	1.9 centim.	23.5 centims.	38
10	1.4 "	All lower internodes more or less com- pressed	32
9	1.3 "		30
8	1.3 "		26 or 27
7	1.1 "		25
6	1.0 centim.		23
5	0.8 "		19
4	1.0 "		20
3	0.8 "		About 18
2	0.8 "		13
1	Partly disorganized		Some well-formed, but partly disorganized and broken away

See Photograph E, Plate 86.

Specimen F.

Column I. Number of internode.	Column II. Maximum vertical length of internode.	Column III. Semi-circumference of internode.	Column IV Number of vascular bundles in semi-circum- ference of internode.
5	6.0 centims.	15.2 centims.	about 50
4	5.5 "	15.3 "	53
3	5.5 "	15.5 "	53
2	5.5 "	15.5 "	54
1	4.0 "	15.5 "	54

This specimen is from a part of a branch some distance above its base, and consequently the dimensions are fairly uniform throughout.

See Photograph F, Plate 86.

Specimen G.

Column I. Number of internode.	Column II. Vertical length of internode.	Column III. Circumference of internode.	Column IV. Number of vascular bundles in circumference of internode.
10	4.0 centims.	9.2 centims.	33
9	3.4 "	9.5 "	34
8	3.0 "	9.0 "	28
7	2.1 "	9.0 "	23
6	1.6 "	8.6 "	19
5	1.3 "	8.1 "	18
4	0.85 centim.	8.0 "	18
3	0.65 "	7.3 "	about 14
2	0.60 "	6.5 "	" 12
1	0.50 "	4.8 "	" 10,
Basal portion without distinct bundles, but probably too large for protomedulla			but indistinct

See Photograph G, Plate 86.

THE ROOTS OF CALAMITES.

When we began writing the present paper we did not expect to be able to throw any light on the structure of the root of *Calamites*. Specimens showing the roots in connection with the stems, and having at the same time the internal structure preserved, were not yet known to us. Consequently it was impossible to determine which, if any, of the petrified remains were to be assigned, as roots, to the Calamitean stems.

One of us, however (D. H. SCOTT) has recently had the opportunity, through the kindness of M. RENAULT, of examining certain specimens in his collection, which place the question in quite a different light. Two of these specimens show an axis, with the structure of *Astromyelon*, in actual continuity with the stem of an Arthropitoid Calamite, identical with such as we have described in this paper. Hence the opinion which M. RENAULT first expressed in 1885,* is confirmed in a most striking manner. There can be no doubt, from the evidence of these specimens, that the *Astromyelon* in question is an appendage of the stem of *Calamites* (Arthropitys of the French authors). Whether this appendage is to be regarded as morphologically a *root*, is another question, but the anatomy renders it highly probable that this is its true nature.

Yet another question remained; are the English specimens on which the genus

* "Nouvelles Recherches sur le genre *Astromyelon*," 'Mém. de la Soc. des Sci. Nat. de Saône et Loire,' 1885.

Astromyelon was founded identical with the Calamitean appendages of M. RENAULT'S collection?

We propose to reserve the detailed consideration of *Astromyelon* for another occasion, but a preliminary examination of the slides in the WILLIAMSON Collection shows that the larger specimens, at any rate, namely those with a distinct pith,* have the same structure as M. RENAULT'S specimens, which are directly borne on a Calamitean stem. The question as to the identity of *all* the forms grouped under *Astromyelon* in a former memoir,† will have to be reconsidered in the new light which has now been thrown on these fossils. It is, however, highly probable that we possess, in the various forms of *Astromyelon*, not merely the principal roots, but also the finer rootlets of *Calamites*.

It is interesting to recall the fact that the first specimens of *Astromyelon* were originally described under the name of *Calamites*,‡ but subsequently separated, on the ground of certain structural differences which find a sufficient explanation, if the organs in question are to be regarded as roots and not stems.§

We still require much further information respecting the earliest stages of the development of *Calamites*, in order to fill up the gap between two states, as to which we already possess considerable knowledge. We now know the spores of *Calamites pedunculatus*|| which we may regard as a typical fructification of the Arthropitoid *Calamites*, and which appears to have been homosporous. We also know that at a later stage the true *Calamites* sprang from rhizomes, with normal nodes and internodes, which were very slender, as compared with the typical stems. We are indebted especially to M. GRAND'EURY for this information.¶ He figures, among many other specimens, one of these rhizomes, which gives off from several points stems of the normal Calamitean type. These stems, though merely preserved as sandstone medullary casts, devoid of all traces of xylem or cortex, are many times larger than the rhizome from which they spring. We unfortunately know nothing of the organization of these rhizomes. If their structure should turn out to be simpler than that of the normal stem of *Calamites*, we may find in them an early stage of development of the plant.

We cannot doubt that *Calamites*, like the *Equiseta*, and all recent Vascular Cryptogams, possessed a sexual prothallus, though its discovery is doubtless impossible. We may conjecture that the first product of the prothallus after fertilization may have

* Such as that figured in WILLIAMSON, "Organization," Part XII., Plate 27, fig. 3.

† *Loc. cit.*, Part XII.

‡ WILLIAMSON, "Organization," Part I., Plate 25, fig. 16.

§ WILLIAMSON, *loc. cit.*, Part IX., p. 319.

|| The name which we propose to give to the strobilus described by WILLIAMSON, in "Organization," Part XIV. See below, p. 916.

¶ 'Flore Carbonifère du Département de la Loire, &c.,' 1877.

been of the nature of a rhizome. If so, the latter forms an important link in the life-history leading from the spore to the typical plant.

II. CALAMOSTACHYS.

The following observations relate to three forms belonging to this genus :

1. *Calamostachys Binneyana*, SCHPR. (homosporous).
2. *C. Casheana*, WILLIAMSON (heterosporous).
3. A doubtful form, which may, however, *possibly* be referable to *C. Casheana*.

Calamostachys Binneyana, which we will first consider, is one of the best-known of the fructifications found in the Coal-Measures,* and we are now in a position to describe almost every detail of its structure. Unfortunately, however, the specimens before us afford no direct evidence whatever as to the nature of the stem on which the fructification was borne. In no case has *C. Binneyana* been found in connection with vegetative organs of any kind. In endeavouring to determine to what kind of plant the strobilus belonged, we can, therefore, only be guided (1) by the morphology and anatomy of the strobilus itself, and (2) by the specimens in which similar, though not identical fructifications have been found in actual connection with the stems which bore them. Many such specimens have been described and figured by WEISS and other authors,† and they leave no doubt that fructifications of the *Calamostachys* type belonged to plants of the family Calamariæ. The whole question, however, can only be profitably discussed after the structure of *Calamostachys* has been described in detail.

CALAMOSTACHYS BINNEYANA.

1. General Morphology.

The specimens available for examination consist solely of strobili or portions of strobili ; not even a peduncle is found in connection with the fructifications, and its constant absence leads us to suppose that the fruit was a sessile one.

The largest strobilus known to us measures $1\frac{3}{8}$ inches (3·4 centims.) in length, and is probably not an absolutely complete specimen. The photographs 10 and 11 on Plate 73,

* See, for example, BINNEY, "Observations on the structure of Fossil Plants found in the Carboniferous strata (*Calamodendron commune*)," 'Palæontographical Society,' 1867; CARRUTHERS, "On the structure of the fruit of *Calamites*," 'SEEMANN'S Journal of Botany,' vol. 5, 1867; WILLIAMSON, "Organization," Part V., 1873; Part X., 1880; Part XV., 1889; WEISS, "Steinkohlen-Calamarien," I., 1876, and II., 1884. STUR, 'Calamarien der Schatzlarer Schichten.'

† WEISS, *loc. cit.*, Parts I. and II. See especially the closely allied *C. Ludwigi*, Part II., 'Atlas,' Plate 18, fig. 2. WILLIAMSON, "Organization," Part V., Plate 5, fig. 32. RENAULT, 'Cours de Botanique Fossile,' vol. 2, &c.

represent portions of this strobilus. The maximum diameter is about 7·5 millims. Most of the specimens are considerably smaller.

The fructification consists of a rather slender axis, bearing numerous whorls of appendages, which are of two kinds, fertile and sterile. The former will be spoken of as *sporangiphores*, the latter as *bracts*. The sterile and fertile verticils succeed one another in regular alternation. Above each whorl of bracts is one of sporangiphores, then another of bracts, and so on (see Plate 73, photographs 10 and 11).

The whorls are equidistant from one another, each fertile whorl being placed exactly in the middle of the internode between two verticils of sterile bracts. This character at once sharply distinguishes the *Calamostachys* type of fruit from the Calamitean strobilus described in previous papers,* and from the forms described by WEISS,† under the name of *Palæostachya*, in both of which the sporangiphores arise from the angle between the sterile whorl and the internode above. In the large cone already mentioned (see photographs 10 and 11) eighteen whorls of bracts were present, with the corresponding whorls of sporangiphores between them. The total number in the strobilus, when complete, was probably somewhat greater.

Each sterile whorl consisted of about twelve‡ coherent bracts, forming a horizontal disc, at the margin of which the bracts became separate from one another, and bent sharply upwards, extending at least as far as the second sterile whorl above (see photograph 10). Consequently any transverse section of the strobilus passes through at least two alternating series of these overlapping extremities of the bracts. It follows that each fertile verticil is enclosed by a ring of free bracts belonging to the two sterile whorls below (see Plate 73, photographs 12 and 13 ; Plate 74, photograph 14).

The bracts of successive sterile whorls, as already indicated, alternate with one another, so that the free extremities of the bracts of any verticil pass between those of the verticil next above. This is easily seen in tranverse sections of the strobilus, such as those shown in the photographs just referred to. The fact is also evident from the tangential sections, in which the distribution of the vascular bundles in the coherent disc affords a useful clue, if the free tips of the bracts cannot be seen (see Plate 73, photograph 11).

The cohesion of the bracts serves to distinguish *C. Binneyana* from the very similar *C. Ludwigi*, CARR., in which they are free throughout almost their whole extent.§

The fertile whorls consist of the sporangiphores, a name which we prefer to

* WILLIAMSON, "On a new form of Calamitean strobilus, &c.," 'Mem. Lit. and Phil. Soc. of Manchester,' Series 3, vol. 4, 1870; "Organization," Part XIV.

† 'Steinkohlen-Calamarien,' Part I., 1876, Plate 15, and Part II., 1884, Plate 16, fig. 2; Plate 21, fig. 4; Plate 22, fig. 15. See also RENAULT'S *Volkmannia gracilis*, 'Ann. des. Sci. Nat., Bot.' Sér. 6, vol. 3, Plate 2, 1876.

‡ There were thirteen in C. N. 997, from which the Photograph 12, on Plate 73, was taken.

§ See WEISS, *loc. cit.*, Part 2, 'Atlas,' Plate 22, fig. 8.

sporophylls, as the morphological nature of these organs is somewhat doubtful, in view of their remarkable variations in position, in various Calamarian fructifications.

The sporangiophores in each verticil are usually about half as numerous as the bracts of a sterile whorl (see Plate 73, photograph 13). We have found 6, 7, and 8 in different whorls, and the number seems to have varied even in the same specimen. Six seems to be the most frequent number. It is evident that the sporangiophores cannot always have been exactly half as numerous as the bracts, for the number of the latter may be uneven (see photograph 12 on Plate 73), nor have we seen any sterile whorl with as many as 16 bracts.

The sporangiophores, unlike the bracts, do not alternate with one another in successive whorls, but are placed one above the other, in vertical rows (see Plate 73, photograph 11). Hence, it is evident that their position can bear no constant relation to that of the bracts.

Each sporangiophore consists of a stalk or pedicel, having a peltate expansion at its free end. The pedicel is broadest at its base (see Plate 73, photograph 13, and Plate 81, fig. 29).

The peltate expansion of the sporangiophore bears four sporangia, which are attached to its underside, at the extreme edge. A tangential section of the strobilus constantly shows the four diagonally placed sporangia grouped around the pedicel of each sporangiophore (see Plate 73, photograph 11, Plate 81, fig. 30).

The whorl of sporangiophores, with their sporangia, appears to have almost filled up the space between two successive verticils of bracts.

The short sketch which we have given of the general morphology of the strobilus is sufficient to show that, so far as the sporangiophores are concerned, *Calamostachys* shows a general resemblance to *Equisetum*, as has often been pointed out before. The smaller number of sporangia on each "peltate scale" is not a difference of much importance.

The alternating verticils of sterile bracts are, however, without an analogue in *Equisetum*, unless indeed we regard the "annulus" in the latter genus as representing a single whorl of bracts at the base of the strobilus. It is evident that *Calamostachys*, and indeed all the allied fructifications, were more highly differentiated than those of existing *Equiseta*.

We will now proceed to consider the structure of *C. Binneyana* in detail, beginning with that of the axis.

2.—Structure of the Axis.

The axis of the strobilus is in all cases traversed by a central cylinder, or *stele*,* which consists of a pith, surrounded by a ring of vascular bundles. Two distinct

* We adopt the convenient term, introduced by M. VAN TIEGHEM, for the whole central cylinder, whether of a root or stem, including pith (if present), vascular bundles, interfascicular tissue, and

types of stele are present in different specimens. The one, as seen in transverse section, has a bluntly triangular form, with the vascular bundles situated at the prominent corners (see Plate 80, figs. 23 and 24). In the other type, the stele is approximately quadrangular, with a bundle at each angle (see Plate 74, photograph 14; and Plate 80, fig. 25). In the specimen photographed the angles are especially prominent, and the sides concave, so that the whole section of the stele is somewhat cruciform. The triangular and quadrangular types are quite distinct. The difference between them does not depend on the level at which the transverse section is taken; for we find the two structures indiscriminately in sections passing through the sterile node, the fertile node, or an intermediate internode. On the whole the triangular form is the more frequent of the two. We found the quadrangular form of stele only in cases where the number of sporangiophores in a verticil is 8; the converse, however, does not hold good, for in one preparation showing eight sporangiophores, the stele is distinctly of the bluntly triangular type.*

We will describe this type first. The whole middle portion of the cylinder, forming much the greater part of its mass, so far as primary structure is concerned, consists of the pith. The whole of the pith appears to have been persistent; sometimes a few cells near the centre have disappeared (Plate 80, fig. 23), but this is obviously due to imperfect preservation. In many cases the outer zone of medullary cells has thickened walls, while those nearer the middle are more delicate (Plate 80, figs. 23 and 24). In other specimens the entire pith is thick-walled throughout.†

It is often difficult or even impossible to distinguish the thick-walled medullary cells from tracheides, in a transverse section. From this difficulty the mistake arose of regarding the stele of *Calamostachys* as a solid vascular axis, a mistake which was corrected in a previous memoir published in 1889.‡

Longitudinal sections show that the cells of the pith are elongated and often prosenchymatous, especially those towards the periphery (see Plate 81, fig. 27).

The vascular bundles are placed at the projecting angles of the triquetrous stele. It is often difficult to say whether one bundle or two are present at each corner. In some of the clearest sections it is evident that there are two, so that the total number of bundles in the cylinder is, in these cases, six (see Plate 80, figs. 23 and 24).§

At the inner margin of each bundle is an empty space, less definite and regular than an internodal canal in *Calamites*, but constantly present, except at the sterile nodes. These spaces or canals always contain the disorganized remains of spiral or annular tracheides, and evidently mark the position of the protoxylem-group of the

pericycle (see VAN TIEGHEM, "Sur la Polystélie," 'Ann. des Sci. Nat., Bot.,' sér. 7, vol. 3, 1886; and 'Traité de Botanique,' 2nd édition, p. 765.)

* C.N., 1898.

† See WILLIAMSON, "Organization," Part V., Plate 6, fig. 38. (C.N. 989.)

‡ WILLIAMSON, "Organization," Part XV., p. 160; Plate 2, fig. 7.

§ See also the figure in WILLIAMSON, "Organization," Part X., Plate 15, fig. 15.

vascular bundle (see Plate 80, figs. 23 and 24; Plate 81, figs. 27 and 28). Where two distinct spaces are present at each corner of the stele, we are therefore justified in assuming that two distinct vascular bundles existed, as is especially clear in fig. 23. Often however these spaces are not distinct from one another, and it may be impossible to say, in such cases, whether one or two protoxylem-groups were present. We have noticed that the bundles at each corner are most evidently separate at the level of the sporangiophores, as for example in fig. 23. They seem to have diverged a little from one another at the points where the traces of the sporangiophores were given off.

We find then that each prominent angle of the triquetrous stele contains either one vascular bundle, or a pair of bundles in close proximity, the total number of bundles thus being either three or six.*

The amount of primary xylem must have been very small. Some of the preparations show only a single layer of tracheides, to the outside of the protoxylem-gap. In the less perfectly preserved specimens the wood has often broken away altogether, and only the pith is left in position.

The later-formed tracheides were reticulated or scalariform.

Before going further, it will be well to describe shortly the quadrangular type of stele, for much of what remains to be said applies equally to both forms.

In the four-cornered stele the pith shows precisely the same structure as in the type already described (see Plate 80, fig. 25, and Plate 74, photograph 14). At each angle there is a vascular bundle, with a well-marked intercellular space at its inner margin. In this space the remains of the protoxylem-elements can be detected, just as in the previous type. There is no reason to suppose, in this case, that more than one bundle was present at each corner. The somewhat peculiar form of the stele in the beautiful specimen from which Photograph 14 was taken has already been noticed.

The structure of the xylem is identical with that in the triquetrous form.† In the figure referred to in the footnote it will be noticed that the two bundles on the left show no spaces at their internal edge, but are solid strands of tracheides. In the text of the memoir cited,‡ it is pointed out that this part of the section approached a node. As a matter of fact, we have always found, in both types of cylinder, that the intercellular spaces come to an end at the *sterile* nodes, but are continued without interruption through the nodes at which the sporangiophores are borne. This is one of the points in which the sterile, or bract-nodes, of *Calamostachys* resemble the ordinary nodes of *Calamites* (see Plate 81, fig. 28, which shows the structure at a sterile node).

* The structure and arrangement of the vascular bundles are well described, from independent specimens, by Mr. T. HICK, 'Proceedings of the Yorkshire Geological and Polytechnic Society,' vol. 12, 1893.

† See WILLIAMSON, "Organization," Part XV., Plate 2, fig. 7.

‡ *Loc. cit.*, p. 160.

At the bractigerous nodes we also find a girdle of short reticulated tracheides, reproducing, on a small scale, the structure of a typical Calamitean node (see Plate 81, fig. 28, also photograph 10, on Plate 73).

The bundles which pass out to the whorl of bracts leave the cylinder with an obliquely upward course, but soon become perfectly horizontal. These bundles can very seldom be traced through the cortex, for they are usually broken away, in the region where the inner cortical tissue has perished. In one or two cases, however, the continuity is perfect.

The fertile nodes, at which the sporangiophores were inserted, show scarcely any modification of structure, as compared with the internodes. Here the bundles passed out at a right angle, but are very seldom preserved throughout their whole course. The node through which the section shown in Plate 80, fig. 23, was taken, bore seven sporangiophores. It will be noticed that while the stele, as a whole, has an obtusely triangular section, the xylem shows seven small projecting points (*sp.* in the figure). To these were attached the bundles of the seven sporangiophores; the bundle at *sp*⁺ is partly preserved.

It is not possible to give any regular scheme for the longitudinal course of the leaf-trace bundles in *Calamostachys*, for, as we have seen, the number of bundles in the axis bears no *constant* relation to the number of lateral appendages in a whorl. We may, however, point out that the bundles appear to have passed up the axis in a straight line, and not to have alternated in successive internodes (see Plate 81, fig. 28).

From what has been already said there can be little doubt that the structure of the bundles was collateral. For a long time, however, direct evidence of this was wanting, for in nearly all cases the whole tissue between the wood and the sclerotic outer cortex has perished. In one instance, however, we have found these tissues completely preserved at one side of the axis (see Plate 80, fig. 26). It is highly probable that here the group of small delicate cells, *ph.*, represents the phloëm, while the larger thin-walled cells further to the exterior belong to the inner cortex, or rather perhaps to the pericycle.

In some specimens the primary tissues already described are alone present. Often, however, a well-marked zone of secondary wood is added, as has been fully explained in previous memoirs* (see Plate 80, fig. 24). The secondary xylem is both fascicular and interfascicular; it consists mainly of scalariform tracheæ, with a few parenchymatous rays between them. The radial arrangement of the elements is sufficiently regular to leave no doubt of their origin from a cambium; the secondary wood may attain a thickness of eight or more cells.

In some specimens the growth in thickness had evidently stopped short at a very early stage, when only a few tangential divisions had taken place in the interfascicular

* WILLIAMSON, "Organization," Part V., Plate 10, &c.

tissue (see Plate 74, photograph 14, Plate 80, figs. 23 and 25). Manifestly, the amount of secondary growth in thickness in the axis of the strobilus was relatively small and inconstant, just as we know to be the case in the peduncles of Dicotyledons at the present day. The formation of secondary wood in many cases, however, is amply sufficient to prove that the mode of growth was essentially similar to that of *Calamites*.

The *cortex* of the axis of the strobilus needs no detailed description. Its outer layers, which in most cases are alone preserved, consist of thick-walled elongated cells, often prosenchymatous in form. When portions of the inner cortex are preserved, its cells are similar to those of the more external layers in form, but have thin walls. It is possible that this inner layer should be referred to the pericycle, but we cannot undertake to determine the limits of these tissues with accuracy (see Plate 73, photographs 10–13, Plate 74, photograph 14; Plate 81, fig. 27, where only the inner layers are shown).

The epidermis consists of small cells, often with rather thick walls; we were not able to prove the presence of stomata, but it is quite possible that they existed. The specimens rarely have their epidermis so well preserved as the more internal tissues.

3. *Appendages of the Axis.*

A. *The Bracts.*

The general arrangement of the whorled bracts has been already described. The coherent part of the whorl, or disc, is traversed by vascular bundles equal in number to the free limbs of the bracts, into each of which one of the bundles runs out (see Plate 73, photographs 11 and 12; also Plate 81, figs. 30 and 32). As a rule, only the small xylem-strand of the foliar bundle is preserved; this lies within an empty space, from which the soft tissue has perished. Sometimes a part of this soft tissue is preserved, and then we find it on the *lower* side of the xylem. It thus appears that the bundles were normally collateral, as we should expect.

The mesophyll of the coherent disc usually shows a marked differentiation. Towards the upper surface it consists chiefly of thick-walled sclerenchymatous fibres. Its lower portion is composed of more parenchymatous cells, with wider lumina, and usually thinner walls. Next the lower epidermis we find a small-celled hypodermal layer. The epidermis on both surfaces has small cells, and is seldom very well preserved, so that here also the question of stomata must be left open.

There are many variations in detail in different specimens; sometimes the whole tissue of the coherent region is comparatively thin-walled (see Plate 81, fig. 30); sometimes, on the other hand, the parenchyma, as well as the fibrous tissue, is considerably thickened (see Plate 73, photographs 10 and 11). In some cases a strand of specially thick-walled sclerenchyma follows the course of each vascular bundle on its upper side (photograph 11). Certain large parenchymatous cells towards the

lower surface often contain dense masses of carbonaceous matter, which may represent some secretion formed during life.

As the outer edge of the coherent disc is approached, we find that its upper surface becomes undulated, as seen in tangential section. Each elevation of its surface corresponds to the position of one of the free bracts, which here begin to separate from each other. The free portions of the bracts, as already stated, are of great length. They gradually taper off towards their tips, and their structure undergoes a corresponding simplification.

In its lower region the free part of a bract is composed of the same tissues as are found in the coherent disc, arranged in the same manner. The secretory sacs (if that is their real nature) are especially conspicuous in this part. The upper extremity of the bract consists of sclerenchyma only, through which the fine vascular bundle can be traced for some distance.

The free bracts are shown in longitudinal section in Plate 73, photograph 10, and in transverse section in photographs 12 and 13. In Plate 74, photograph 14, some of them are also shown in oblique superficial view.

It need scarcely be pointed out again that the whole of the highly differentiated bract-system, so characteristic of fossil Calamarian fructifications, has nothing clearly corresponding to it among existing *Equiseta*. In this fact we have a striking illustration of the general rule, that the Palæozoic Cryptogams known to us, were far more highly organized plants than their allies which are living in the present age.

B. *The Sporangiphores.*

The general form of the peltate sporangiphores, and their relation to the axis, have been described above. The pedicel consists of a zone of somewhat sclerotic cortical tissue, enclosing a single vascular bundle (see Plate 73, photographs 11 and 13; Plate 81, figs. 29 and 30). Immediately below the peltate expansion, or head, which terminates the sporangiphore, the pedicel becomes broader, and here the vascular bundle forks into two branches, which lie in the same horizontal plane. Each of the branch-bundles forks again, and the four ultimate ramifications run out to the bases of the four sporangia, which are placed diagonally at the margin of the peltate head (see Plate 81, figs. 29 and 32). The parenchyma of the peltate portion is thin-walled; the free external surface and edges are covered by a very characteristic layer of elongated, palisade-like, epidermal cells. This palisade-layer is very delicate, and is rarely perfectly preserved; it is best shown in a specimen figured in a former memoir* (see also Plate 73, photograph 13; in Plate 81, fig. 29, only fragments of this layer are shown; in the tangential section, Plate 81, fig. 32, the layer is evident).

The general outline of the peltate expansion of the sporangiphore, as seen in

* WILLIAMSON, "Organization," Part XV., Plate 2, fig. 8 (C.N. 1000).

a tangential section of the strobilus, was square, probably somewhat lobed, with depressions between the insertions of the sporangia (Plate 81, fig. 32).

The sporangia were attached to the edge of the peltate head, at its four corners, and on its lower side. Each sporangium is connected with the sporangiophore by a narrow neck of tissue only, through which the vascular bundle passes, to end at the base of the sporangium itself (see Plate 81, fig. 29).^{*} The palisade-layer extends over the short stalk of the sporangium on its outer side, its cells becoming shorter here, and appears to have been continuous with the sporangium-wall.

C. *The Sporangia.*

Each sporangium has the form of a somewhat elongated sac; its long axis is parallel to the pedicel of the sporangiophore, and is therefore radial to the axis of the strobilus. As seen in tangential section the sporangia are approximately square.

In most instances, the sporangium, as preserved in our specimens, has a wall which is one-cell only in thickness. Remains of tissue lining the inside of this persistent layer are frequent, but only show structure in exceptional cases, to be considered presently.

The cells of the sporangial wall are lozenge-shaped, as seen in surface view, their long axes being parallel to the major axis of the sporangium (Plate 81, fig. 31, A). Their lateral walls are thin, but are stiffened by vertical plates, which project, like buttresses, from the cell-wall, and correspond to one another in adjacent cells. These buttresses are broadest at the base, *i.e.*, where they abut on the inner cell-wall, next the cavity of the sporangium (fig. 31, A and B). In a tangential section of the whole strobilus, which gives a transverse section of the sporangium, the cells of the wall are cut across, so that we see the buttresses on either side of each vertical septum (fig. 31, B). In transverse or radial sections of the strobilus, however, which give longitudinal sections of the sporangia, the cells of the wall are cut lengthwise. In this case the narrow edges of the buttresses are seen, so that the vertical septa appear to be much more numerous than they really are (fig. 31, C). The actual cell-walls are seldom seen well in this view, no doubt because they are usually cut obliquely. The mode of thickening of the cell-membranes of the sporangial wall bears a considerable resemblance to that of the "fibrous layer" of some anthers, and may very probably have discharged the same function, that of effecting dehiscence.

In certain cases a layer of thin-walled tissue, two or three cells in thickness, is found lining the whole or part of the sporangial wall (Plate 82, fig. 35). One is tempted at first to regard this layer as a persistent *tapetum*, but the inconstancy of its occurrence, even in the most perfectly preserved specimens, and its very variable thickness when present, are scarcely consistent with such a view. In other instances the entire

^{*} See also WILLIAMSON, "Organization," Part XI., Plate 54, fig. 23 (C.N. 1017).

sporangium appears to be filled with parenchymatous tissue.* These apparently parenchymatous sporangia are sometimes associated in the same strobilus with others which show the lining tissue only.†

It is a question whether such sporangia are ever really filled with tissue, or whether the sections may not in these cases be tangential to the sporangium, so as to pass through the lining layer, without reaching the spores within. This is a possible view, but we do not think that all these instances can be thus explained. The sporangia with parenchymatous contents cannot represent a normal early stage of development, for they occur side by side with others in which the spores are fully formed, and in which there is often no trace even of the lining tissue. On the whole we are disposed to regard all the structures in question as representing more or less completely abortive sporangia in which either the whole, or the outer portion only, of the sporogenous tissue has remained sterile. This view is supported by the relatively small size of those sporangia which appear to be completely filled with parenchymatous tissue.

D. The Spores.

It has long been known that the spores of *Calamostachys* are often found associated together in tetrads, each tetrad being enclosed within a common membrane, which is doubtless the wall of the mother-cell. Cases of this kind have been figured in previous memoirs,‡ and have also been observed and figured by M. RENAULT in allied fructifications.§ The latter author lays great stress on the arrangement of these cells in tetrads, regarding this fact as an argument for the bodies in question being of the nature of pollen-grains, rather than spores.||

In *Calamostachys Binneyana*, at any rate, there is no ground for such a view, for the spores certainly did not remain associated in tetrads when mature. Isolated spores are just as common as tetrads, and sometimes occur together with them in the same sporangium (see Plate 81, fig. 33), while in other cases the whole sporangium is occupied by isolated spores.¶ The separation of the sister-spores from one another must have taken place relatively late, but it certainly happened before maturity.

We have paid special attention to the spore-tetrads, which are shown on various scales, in Plate 81, fig. 33, and Plate 82, fig. 34. In some cases the group of four spores is perfectly normal, all four being of approximately equal size (fig. 34, A). Very often, however, the spores of the same tetrad are of extremely unequal dimen-

* An example of this has been previously figured; see WILLIAMSON, "Organization," Part X., Plate 16, fig. 18.

† As is the case, for example, in C.N. 1008, and 1898 A.

‡ WILLIAMSON, "Organization," Part V., Plate 7, fig. 43, Part X., Plate 15, fig. 17.

§ E.g. in his *Bruckmannia Grand'Euryi*, 'Ann. Sci. Nat., Bot.,' Sér. 6, vol. 3, Plate 3, Fig. 7.

|| 'Comptes Rendus,' vol. 102, March 15, 1886.

¶ See WILLIAMSON, "Organization," Part V., Plate 6, fig. 7 (C.N. 989).

sions, the diameter of the smallest sister-cell being often scarcely a quarter that of the largest. Sometimes three out of the four remain quite small, and occasionally an entire tetrad seems to have been abortive (see the figures cited ; in fig. 34, B and C, one spore in each tetrad is of relatively minute size).

Such very minute spores are also frequently found, among the normal ones, in sporangia in which the spores are already isolated from one another. If these latter cases stood alone, we might have doubted whether the small spores were not foreign bodies ; their presence, however, as members of the tetrads, within the mother-cell-wall, proves conclusively that they are really sister-cells which have remained behind the others in their development. The phenomenon is extremely frequent, as is sufficiently indicated by the figures.

We do not think there is any reason to doubt that four spores were regularly formed within each mother-cell, as is constantly the case in all recent vascular Cryptogams. It seems, however, to have been the exception for all four to be equally developed.

This frequent abortion of many of the spores in a sporangium, so frequent that we cannot but regard it as a normal process, seems to us to be a fact of extreme interest.

We cannot doubt that *Calamostachys Binneyana* was a homosporous form. The large number of specimens available for investigation, many of them including all parts of the strobilus, establishes the strongest presumption that macrospores must have been found, if they existed.

We know, however, that the closely similar species, *C. Casheana*, was heterosporous, its microspores not being very different in size from the normal spores of *C. Binneyana*. When we come to describe the heterosporous species, we shall find strong reason to believe that in its macrosporangia a constant abortion of some of the spores went on.

We would suggest the hypothesis that the abortion of certain of the spores, and the consequent increased nutrition of their surviving fellows, may have been the physiological condition which ultimately rendered possible the development of specialized macrospores.

We know that among existing heterosporous vascular Cryptogams the abortion, either of the majority of the mother-cells (Ligulatæ), or, in addition, that of the sister-cells of the macrospore (Rhizocarpeæ), is a constant accompaniment of the favoured development of the surviving spore or spores.

We know also that in *Equisetum*, which is homosporous, but in which the prothalli are regularly diœcious, it depends upon the nutrition whether a spore develops into a male or female prothallus. The better fed prothalli become female, the worse fed, male.*

In *Calamostachys* we have the intermediate conditions. In *C. Binneyana* we find the beginning of spore-abortion, involving improved nutrition of the surviving spores.

* BUCHTIEN, "Entwicklung des Prothalliums von *Equisetum*," 'Bibliotheca Botanica,' 1887.

In *C. Casheana*, the same process, carried further in certain sporangia, has led to the formation of specially favoured macrospores, to which, as we may presume, the production of a female prothallus was entrusted. Even in *C. Casheana*, however, the heterospory is not so extreme as in some other Cryptogams, for numerous macrospores are still developed in each sporangium, and their diameter is only about three times that of the microspores.

We suggest then, that in *Calamostachys* we have a genus in which the first rise of the phenomenon of heterospory can be traced. That the same phenomenon arose independently in various groups of vascular Cryptogams, has long been recognized.

We have found no evidence in *C. Binneyana* for the existence of a cellular body within the spore, such as M. RENAULT believes to be present in the spores of this and other species. One of us (D. H. SCOTT) has had the advantage, through the kindness of M. RENAULT, of seeing some of the preparations in question, but was not convinced that the structure within the spore was really cellular.

Compared, for example, with the cellular mass in the pollen-grain of *Cordaitea*, as shown in M. RENAULT's classical preparations, the appearances in the *Calamostachys* spores appeared very doubtful. In our own specimens, the endosporium has usually contracted away from the exosporium. When the endosporium and its contents are much shrivelled, an appearance resembling a cellular structure is sometimes produced, but such appearances are quite inconstant, and are, we believe, illusory.

In the mature spores of *Calamostachys Binneyana* we often observe three radiating cracks at one pole, such as are so frequently seen in the spore-membranes of recent Cryptogams. Between these cracks three well-defined brown masses can usually be detected. In sectional views of the spore we find that these bodies are attached to the inner surface of the spore-membrane (see Plate 81, fig. 33a; Plate 82, fig. 34, D). Other specimens proved that the attachment is to the exosporium. We regard these masses as local thickenings of the cell-wall, not by any means as distinct cells.

Before discussing further the affinities of *Calamostachys Binneyana*, it will be necessary to take into consideration the structure of the other forms which we have examined.

CALAMOSTACHYS CASHEANA. WILL.

The heterosporous form of *Calamostachys* was originally described in 1880* from a specimen found at Halifax. In this specimen three whorls of sporangia are shown in the obliquely tangential section. The uppermost whorl shows microsporangia only; in the lowest, only macrosporangia are found, while the intermediate whorl contains both kinds intermixed.

The general habit of the specimen is very similar to that of *C. Binneyana*, with

* WILLIAMSON, "Organization," Part II., p. 298; Plate 54, fig. 24 (C.N. 1024 and 1025). M. RENAULT has also established the existence of heterospory in *Annularia longifolia*, BRONGN. 'Ann. Sci. Nat., Bot.,' sér. 5, vol. 18, 1873. (Also in 'Cours de Botanique Fossile,' vol. 2, 1882, p. 126.)

which it was at first regarded as identical. Subsequently the species *C. Casheana* was established for the heterosporous form.*

Apart from the heterospory, there are some slight differences between the species. While in *C. Binneyana* both bracts and sporangiophores stand out exactly at a right angle with the axis, in *C. Casheana* they seem to have been placed rather obliquely, sloping slightly upwards. Further, in a tangential section of *C. Casheana*, passing through the sporangia, the bracts are beginning to separate from one another; whereas in similar sections of *C. Binneyana*, they form a perfectly coherent disc. It appears then, that the coherent portion of the bracts did not extend so far in the heterosporous as in homosporous species (see Plate 74, photograph 15). These differences, however, are very slight, and it is certainly a most striking fact that species so nearly alike in general characters should exhibit so important a physiological distinction as that between homospority and heterospory.

A second specimen of *C. Casheana*, obtained from the Strinesdale Pit, Saddleworth, has more recently been discovered. Two sections have been cut of the strobilus, the one tangential (Plate 74, photograph 15), the other transverse (photograph 16). The former shows parts of three verticils of sporangiophores; the highest and lowest verticils show macrosporangia only; the intermediate whorl also contains a single microsporangium, which is borne on the same sporangiophore with three macrosporangia (photograph 15, also Plate 82, fig. 38). The relative size of the microspores and macrospores agrees exactly with that in the former specimen, *i.e.*, the diameter of the macrospores is, on the average, just three times that of the microspores. The absolute dimensions of both are perhaps a trifle smaller than in the original specimen, but the difference is insignificant.

The transverse section of this strobilus (C.N. 1588, Plate 74, photograph 16; Plate 82, fig. 36) is very interesting. The section passes through macrosporangia only; the pedicels of the sporangiophores are cut obliquely, which agrees with their ascending direction, as shown in the other specimen.†

The structure of the axis is extremely well shown, and agrees exactly with that of *C. Binneyana*. The axial cylinder, or stele, is of the obtusely triquetrous form, and has a somewhat sclerotic pith. The arrangement of the vascular bundles agrees with that of the homosporous species. Traces of the protoxylem-groups are found in the usual position, namely within irregular gaps on the inner side of the vascular bundles, of which there seem to have been six altogether.

The most interesting point, however, is that the axis has a well-marked zone of secondary wood (see fig. 36); the radial arrangement of its elements is such as to leave no doubt as to their origin. We thus find in this specimen the direct proof that secondary growth in thickness co-existed with heterospory; in other words the

* WILLIAMSON, in 'Report of the British Association for 1886.'

† C.N. 1024. See WILLIAMSON, *loc. cit.*, Part XI., Plate 54, fig. 24.

specimen is, by itself, sufficient to prove the occurrence of secondary formation of wood in an undoubted Cryptogam.

It is probable that no botanists any longer dispute the conclusion that secondary growth by means of cambium may take place in Cryptogams as well as in flowering plants, or that in the Carboniferous epoch, most families of vascular Cryptogams exhibited this phenomenon. The "*petitio principii* of BRONGNIART's school,"* which for so long a time was accepted by many leaders of botanical opinion, is no longer maintained. Evidence so direct and convincing as that afforded by this specimen of the heterosporous *Calamostachys* is, however, sufficiently rare to be of quite special interest.

Some remains of the thin-walled tissue which surrounded the wood are preserved, but, as is usually the case, very imperfectly. The outer cortex, on the other hand, is perfect, and has the same structure as in *C. Binneyana*, the cells becoming smaller and more sclerotic towards the periphery.

The details of structure of the bracts, the sporangiophores, and the sporangium-wall agree so closely with the corresponding features in the homosporous species, that no special description is called for.

The Spores.

We have already (p. 911) referred to the small, presumably abortive spores, found in the macrosporangia, among the macrospores. Their dimensions are very variable, but they are always much smaller even than the microspores of the same strobilus. (See figs. 37 and 39, which are from different specimens.) They are very similar to the abortive spores described above, in the case of *Calamostachys Binneyana*. As we never found the tetrad stage in *C. Casheana*, there was no possibility of tracing the origin of these minute spores. They occur, without exception, in every macrosporangium of both specimens, and are often found in large numbers. (See fig. 37, B and C; fig. 39.) We have never found them in the microsporangia. For these reasons we think it out of the question that the minute spores can be foreign bodies. We regard them as being, in all probability, undeveloped sister-cells of the macrospores, the latter having attained their large dimensions at the expense of their ill-nourished companions.

We desire especially to call attention to the fact that we find no signs of spore-abortion in the microsporangia. Here all the spores appear to develop equally, and a uniform small size is attained (about .075 millim. in diameter). In the homosporous species, *C. Binneyana*, where some of the spores are abortive, the survivors attain somewhat greater dimensions, about .09 millim. in diameter.

As regards the structure of the spores, we have little to add to the previous description above cited. Apart from the difference in size, there is a close similarity

* SOLMS, 'Fossil Botany,' p. 330 and 341.

between macrospores and microspores. In both we find a thick exosporium, within which, and somewhat separated from it, is a much more delicate membrane, which we will term the endosporium. In the case of the macrospores, the exosporium is often somewhat flattened at the surfaces of contact of the rather closely packed spores. Within the endosporium, in both microspores and macrospores, is usually a relatively small, dark-coloured mass, probably representing the carbonized remains of the cell-contents.

The more recently discovered specimen is, in one respect, better preserved than the one originally described. In the latter, the endosporium is almost always somewhat shrivelled, in the case of both micro- and macrospores. In the former, the endosporium has usually retained a perfectly spherical form; the exosporium, however, has often, to some extent, split away from the inner layer.

It may be mentioned that in one or two cases the exosporium appeared to be double, so that, very probably, an episporial membrane was present, but cannot usually be distinguished.

In the case of the small abortive spores, associated with the macrospores, it was not possible to distinguish the separate layers of the cell-wall.

CALAMOSTACHYS, *sp.* ?

A specimen of *Calamostachys* from the Oldham Coal-Measures, shows a somewhat different habit from *C. Binneyana* (see Plate 74, photographs 17 and 18). Both bracts and sporangiospheres have the same obliquely upward direction which we observed in *C. Casheana*. Five whorls of sporangiophores, with their sporangia, are present in the specimen. The latter are filled with small spores (not associated in tetrads), which agree precisely in dimensions with the microspores of *C. Casheana*. It is possible that the specimen may belong to that species, the macrosporangia not being preserved. No certain conclusion, however, can be drawn, except that the specimen is at any rate not identical with *C. Binneyana*.

AFFINITIES OF *Calamostachys*.

The description given of the structure of the strobilus in the homosporous and the heterosporous species, leaves no doubt that both must have been the fructifications of Calamariæ. In view of the close agreement in structure which we have been able to demonstrate, the suggestion of M. RENAULT that while the heterosporous forms are obviously cryptogamic, the others may represent the male flowers of seed-bearing plants, appears to us to be quite untenable.

The whorled appendages, the constant presence of a medulla, and of primary medullary rays, and the collateral bundles with centrifugal xylem, form a combination of characters peculiar to the Calamariæ among the known Cryptogams of the

Carboniferous epoch. The arrangement and structure of the peltate sporangiophores, so closely resembling those of *Equisetum*, are typical of *Calamariæ*, and indeed constitute the most essential characters on which that family has been founded.

The question remains, however, to which, if any, of the known Calamarian stems, did the *Calamostachys* fructifications belong? At present the question must remain open, for the only way of answering it with certainty, would be to find stem and strobilus in connection, and this has not yet been done in the case of the species in question.

So far as the anatomical evidence is concerned, there is no reason why a strobilus of the *Calamostachys* type should not have been borne on the stem of a Calamite, such as we have described in the first part of this paper. The differences in structure are no greater than we should be prepared to find between the axis of a fructification and a vegetative stem, and no greater than we actually do find between branches of different order in one and the same species of *Equisetum*. In some points, indeed, such as the presence of an intercellular space at the protoxylem of each bundle, and the structure of the nodal wood, the agreement is even surprisingly close.

We have, however, to take account of the fact that a fructification of a different type has been proved, in previous memoirs, to have been that of a *Calamites*. The first specimen of this fructification was described in 1869.* Long subsequently other and more complete specimens were discovered, and a full account of the whole structure was laid before the Royal Society in 1887.† We have re-examined the specimens for the purposes of the present paper, but, except in one point, have nothing to add to the previous descriptions.

A summary, however, of the facts relating to this fructification must be given here, for the sake of comparison with the structure of *Calamostachys*.

The strobilus of the "Calamitean" fructification was pedunculate, and consisted of an axis bearing numerous whorls of bracts, which were coherent for some distance from their insertion, the coherent part forming the "disk" of previous descriptions. The bracts after leaving the axis at a right angle, or with a slightly downward curvature, turned sharply upwards, their superior portions becoming approximately parallel to the axis.

The sporangiophores were borne at the base of the coherent bracts, on their upper surface, and were thus very nearly axillary. They numbered sixteen, eighteen, or twenty in a whorl; their direction was obliquely upward. The number of the bracts seems to have been double that of the sporangiophores.

Each sporangiophore bore four sporangia, though it is not quite certain that this number was absolutely constant. They surround the pedicel of the sporangiophore, as

* WILLIAMSON, 'Mem. Lit. and Phil. Soc. of Manchester,' Series 3, vol. 4.

† WILLIAMSON, "True Fructification of *Calamites*" ("Organization," Part XIV.); 'Phil. Trans.,' vol. 179, B.

in *Calamostachys*. As no peltate expansion is preserved in the specimens, there is no evidence as to the mode of attachment of the sporangia.

In tangential sections the sporangia have an elongate, oblong form, thus differing from those of *Calamostachys*, which appear square in the corresponding view. This difference, however, seems to depend only on the oblique position of the sporangia in the "Calamitean" fructification.

The sporangial wall resembled that of *Calamostachys* in structure. The spores are all of approximately equal size, and average .075 millim. in diameter. As sections were cut from all parts of several strobili, including their bases, it is not probable that macrosporangia, if they had existed, could have been missed.

The anatomy of the peduncle is exactly that of a young stem of *Calamites*, as above described. The pith is fistular, only the peripheral zone being persistent. The wedge-shaped bundles, sixteen to twenty in number, form a ring. Each bundle has a canal at its inner margin. We have been able to prove that here, as in the vegetative stems of *Calamites*, the canal contains the remnants of the protoxylem of the bundle. In longitudinal sections the spiral thickenings of the primitive tracheides in the canal can be easily seen.*

Secondary wood, distinguished by the radial seriation of its elements, was formed in the peduncle just as in the vegetative stem. In fact the peduncle agrees in every respect with the typical vegetative axis of a young specimen of *Calamites*.

The axis of the strobilus has essentially the same structure as that of the peduncle, of which it is the prolongation. The number of the bundles, which is equal to that of the sporangiophores, remains constant. Their structure is unaltered, except that, as we ascend the axis, we leave the secondary wood behind. At the nodes the arrangement of the tracheides is identical with that in *Calamites*. The bundles however show a slight difference in their arrangement. In the peduncle they are equidistant from one another; in the axis of the strobilus they become approximated in pairs. The cortex contains a ring of large cavities, half as numerous as the bundles, and alternating in position with the bundle-pairs. These cavities, which recall the "vallecular canals" of *Equisetum*, are best seen at the nodes, where the cortical tissues are best preserved.

Now there can be no doubt that this remarkable fructification, specimens of which are unfortunately extremely rare, is that of a *Calamites*. If the peduncle were found alone it could not be distinguished from the stem, of corresponding age, of a typical Arthropitoid Calamite.

We wish to call attention to the very close resemblance between this strobilus of *Calamites*, and that described by M. RENAULT under the name of *Volkmannia gracilis*, but placed by Count SOLMS-LAUBACH in WEISS's genus *Palæostachya*.† In the

* C. N. 1569 and 1573.

† RENAULT, 'Ann. Sci. Nat., Bot.,' Sér. 6, vol. 3, Plate 2; also 'Cours de Bot. Fossile,' vol. 2; SOLMS, 'Fossil Botany,' p. 332.

latter specimen the relative position of the bracts and sporangiophores is all but identical with that in the English fossil. The chief differences are that the bracts in *Palæostachya gracilis* are less extensively coherent, and that the insertion of the sporangiophores is more exactly axillary, and less adherent to the bracts themselves. In both plants the number of the bracts is double that of the sporangiophores.

The anatomy of the stem in *Palæostachya gracilis*, as shown in M. RENAULT'S figures, has quite a Calamitean character. The medulla is fistular, and the vascular bundles are accompanied by their usual canals. The number of the bundles here also, is equal to that of the sporangiophores.

In M. RENAULT'S plant the peltate scales are perfectly preserved; their structure and the mode of attachment of the sporangia are manifestly the same as in *Calamostachys*.

The character of the genus *Palæostachya*, as defined by WEISS, is as follows:

"Sporangiophores arising from the axil of the bract, or its immediate neighbourhood, ascending obliquely."*

As this definition applies both to the Calamitean fructification of WILLIAMSON, and to the *Volkmannia gracilis* of RENAULT, we may speak of this type as the *Palæostachya* form of fructification. As however the English specimens are so obviously strobili of *Calamites*, we do not propose to give them a distinct generic name, but to distinguish them as *Calamites pedunculatus*, which is thus the equivalent of the "true fructification of *Calamites*," described in previous memoirs.

We have now to discuss this question: Are the differences between the *Calamostachys* and the *Palæostachya* types of strobilus so great that they cannot have belonged to closely allied plants?

The essential differences are two: (1) in the position of the sporangiophores, which are approximately axillary in the *Palæostachya* type, but are inserted midway between the whorls of bracts in *Calamostachys*; (2) in the anatomy of the axis, which is completely Calamitean in the *Palæostachya* strobilus, while *Calamostachys* differs in the small number of vascular bundles, and in its relatively small persistent pith.

A form described by M. RENAULT under the name of *Bruckmannia Grand'Euryi* (the *Calamostachys Grand'Euryi* of WEISS'S nomenclature) seems to bridge over the gap in a very satisfactory manner.† In this species the arrangement of the sporangiophores is exactly that of a typical *Calamostachys*; they form independent whorls, inserted midway between the verticils of bracts. Their structure, also, is identical with that of the sporangiophores of *C. Binneyana*. The anatomy of the axis, however, is that of a Calamite. The medulla is large and fistular; the numerous bundles surrounding it have well-defined canals. It appears, then, that in this species the external morphology of *Calamostachys* co-existed with an anatomical structure identical with that of *Calamites* or *Palæostachya*.

* 'Steinkohlen-Calamarien,' vol. 2, 1884, p. 161.

† RENAULT, 'Ann. Sci. Nat., Bot.,' Sér. 6, vol. 3. Plates 3 and 4.

In view then of the fact that a renewed examination of *Calamostachys Binneyana* has tended to show that its anatomy is much more similar to that of *Calamites* than was formerly supposed, while another species of the genus has an exactly Calamitean structure, we think that the relation of our British species of *Calamostachys* to *Calamites* may well have been a close one. It is even possible that some of the stems which have been described under the general name of *Calamites*, may have been those on which *Calamostachys* fructifications were borne.* Beyond this we cannot go, until evidence of continuity has been produced. We know for certain that the *Palæostachya* type of strobilus was that of a Calamite, as is proved by the case of *Calamites pedunculatus*; it is possible that fructifications of the *Calamostachys* type may have belonged to other Calamitean stems.

The solution of the problem must await further evidence.

III. SPHENOPHYLLUM.

The genus *Sphenophyllum*, BRONGNIART, is characterized externally by its comparatively slender, articulated stems, bearing verticillate leaves, the number of which in each whorl is always some multiple of 3, as 6, 9, 12, 18, or even more. The leaves of successive verticils are superposed, not alternate. In the species on which the genus was founded (such as *Sphenophyllum Schlotheimii*, BRONGN., and *S. emarginatum*, BRONGN.), the sessile leaves are cuneate, widening rapidly from a narrow base, and having an entire or toothed anterior margin. From the form of such leaves as these the genus derived its name. In other species, however, the leaf is repeatedly divided in a dichotomous manner, into narrow segments, as in *S. trichomatosum*, STUR. In others, again, as in *S. plurifoliatum*, WILL., one of the species which we are about to describe, the leaves are linear.

The forms with deeply divided, or with linear leaves, cannot always be distinguished, by their external characters alone, from *Asterophyllites*, to which genus the species about to be described were originally referred.† Happily the anatomy of several undoubted species of *Sphenophyllum* is now well known,‡ and agrees in all essentials with that of our own specimens, which have already been transferred to that genus.§

It is said that the finely divided foliage may occur on the lower portions of the same stems which bear cuneate leaves above.|| This has been compared with the

* Mr. T. HICK, in his paper above cited (see p. 905) arrives at substantially the same conclusion; *loc. cit.*, p. 291.

† WILLIAMSON, "Organization," Parts V. and IX.

‡ Chiefly through the researches of M. RENAULT, 'Ann. Sci. Nat., Bot.,' Sér. 5, vol. 18, 1873, and Sér. 6, vol. 4, 1877; also 'Cours de Bot. Fossile,' vols. 2 and 4.

§ WILLIAMSON, 'General, Morphological, and Histological Index,' Part 2, p. 3, 1893.

|| COEMANS et KICKX, "Monographie des Sphénophyllum d'Europe," 'Bull. de l'Acad. Roy. de Belgique,' Sér. 2, vol. 18, 1864.

arrangement of the leaves in the heterophyllous species of *Ranunculus*, of the subgenus *Batrachium*. Several authors have inferred that *Sphenophyllum* was of aquatic or at least semi-aquatic habit. The anatomy, however, as other authors have already pointed out,* lends no support to such a view, for in all cases the xylem is extremely well developed, whereas its reduction is one of the most constant characteristics of aquatic plants.

The species which we are about to consider are three in number :

(1.) *Sphenophyllum plurifoliatum*, identical with the *Asterophyllites sphenophylloides* of WILLIAMSON (Parts 5 and 9). This includes the Oldham specimens.

(2.) *Sphenophyllum insigne*, the *Asterophyllites insignis* of the memoirs above cited. To this the Burntisland specimens belong. In these two we know only the vegetative organs.

(3.) *Sphenophyllum Dawsoni*. This is the *Bowmanites Dawsoni* of previous memoirs,† and the *Volkmannia Dawsoni* of BINNEY. The specimens of this form are, with one exception, limited to the fructifications.

We will begin with the Oldham species, *S. plurifoliatum*, which, in its internal structure, agrees most nearly with the species described by other authors.

1. SPHENOPHYLLUM PLURIFOLIATUM, NOBIS.

Although this form has not been identified with any of the species known as impressions, yet the fragments showing structure are sufficient to give also a general idea of the external morphology.

The stems are conspicuously jointed with somewhat tumid nodes.‡ The internodes are of considerable length, amounting to about 1 centim. in one of our specimens,§ which shows two nodes, but no doubt much more in others.

In no case is a complete whorl of leaves preserved; judging, however, from specimens such as C.N. 874,|| in which the bases of 6 leaves are shown, the total number in the verticil could not have been less than 18, and may even have reached 24. The leaves are sometimes preserved for a considerable part of their length, exceeding that of the internode. They remain linear in form throughout, so far as can be seen, and there is no distinct evidence for their dichotomizing, though they may have done so at some considerable distance from the base.¶

The cortex of the young stems, as shown in transverse sections, has a very charac-

* See SOLMS, 'Fossil Botany,' p. 344.

† WILLIAMSON, "Organization," Parts XVII. and XVIII.

‡ See WILLIAMSON, "Organization," Part V., Plate 3, fig. 15, and Plate 1, fig. 5.

§ C.N. 904.

|| Figured in WILLIAMSON, *loc. cit.*, Part V., Plate 3, fig. 16.

¶ M. ZEILLER has shown that truly linear leaves also occur in *S. cuneifolium*, STERNB. See his paper in 'Mém. de la Soc. Géol. de France; Paléontologie,' Mém. 11, p. 13, 1893.

teristic outline.* There are three sharp depressions, or furrows, which bear a definite relation to the internal structure, each depression lying midway between two of the prominent angles of the triquetrous strand of primary wood. The cortical surfaces between the furrows are nearly flat. This is the form in the internode; close to the nodes, however, a secondary elevation is found in the middle of each furrow.†

The characteristic outline of the cortex agrees with that in several other species of *Sphenophyllum*.‡ It is only to be observed in the younger stems, for, as we shall see, the whole primary cortex soon becomes replaced by periderm, and cast off.

We will now describe the anatomical structure. Many points can be passed over rapidly, as they have already been sufficiently dealt with in the previous memoirs above cited.

Primary Structure.

The stem is traversed by a vascular cylinder or stele, the primary structure of which is simple, though, for a stem, highly peculiar.

The wood, as seen in transverse section, is triangular; the sides of the triangle are somewhat concave, the angles are slightly truncated. The xylem is a solid mass of tracheides; there is no trace either of a medulla or of xylem-parenchyma. The tracheides near the middle of the stele are pitted, and of large size; as we approach the three prominent angles we find that the size of the tracheides rapidly diminishes, and their walls have here scalariform thickening. At the actual angles we find reticulated and spiral elements of very small diameter (see Plate 83, figs. 40 and 41). There can be no doubt that the tracheides at the angles are the primitive elements, or protoxylem, and that the primary wood constitutes a centripetal triarch strand—a structure which is very unusual in stems, though so familiar in the case of roots.

The angles of the triquetrous xylem are often blunt, though this is not always the case. We could not convince ourselves that more than a single group of protoxylem is present at each angle, though, in other species, there are undoubtedly two such groups, and the stele is then hexarch (see Plate 76, photograph 24, from the Autun *Sphenophyllum*; also many figures in M. RENAULT's works above cited).

The wood is surrounded by a thin-walled tissue of considerable width, but in the youngest specimens, such as we are now describing, this zone is seldom well preserved. The cells near the wood are smaller than those more towards the exterior. We can hardly be wrong in regarding the tissue immediately surrounding the wood, as phloëm; the outer thin-walled region is, perhaps, best interpreted as a pericycle, in which case we should take the commencement of the more peripheral thick-walled zone as the inner limit of the cortex. It must, however, be remembered that, in the

* See WILLIAMSON, *loc. cit.*, Part V., Plate 1, fig. 1, &c.

† WILLIAMSON, *loc. cit.*, Part V., Plate 1, fig. 4.

‡ See RENAULT, *loc. cit.*

absence of developmental data, such delimitation of the tissues is necessarily arbitrary.

The thin-walled zone is very sharply marked off from the rather sclerotic cortex. The latter consists of somewhat elongated cells, which become narrower and more sclerenchymatous as the exterior is approached. The structure of the epidermis is not clear in any of our specimens.*

The vascular system is strictly *cauline*; it passes through the nodes without any appreciable change of structure. A single bundle entered each leaf; from the analogy of other species of *Sphenophyllum*, it may be presumed that the foliar bundles were given off from the angles of the central strand. The number of foliar bundles given off at each node cannot have been less than eighteen.† It is possible that these may have arisen from the subdivision, within the cortex, of a smaller number, but as regards this species, such a conclusion is merely conjectural.

For the mode of *branching* of the stem, we have only the evidence of one preparation.‡ In this case a single branch evidently arose at the node; its vascular cylinder was to all appearance given off from one of the angles of the stele of the main stem.

Secondary Changes.

In *S. plurifoliatum*, as in other species of the genus, a large amount of secondary tissue, both wood and bast, was formed in the stem as growth proceeded. We have specimens with the secondary wood of every thickness, from a single layer of elements up to thirty-seven such layers. Some of the stages have already been figured.§ Others are illustrated in the photographs and figures accompanying the present paper. There is no break in the series, and, except for the changes involved in the secondary growth itself, the structure is the same in all. Hence there is no doubt that we are dealing with successive stages in the development of one and the same plant. The great extent of the secondary cortical tissues is a characteristic feature of the genus.

We will begin our description with the secondary wood.

The radial seriation of the elements is in most cases remarkably regular (see the photographs on Plate 75; also Plate 83, figs. 40–43). In one large specimen, for example, the rows are quite continuous throughout the secondary wood, which here attains a thickness of twenty-four elements (photograph 21). The same is the case in the specimen, a portion of which is shown, in transverse section, in photograph 22. Here the maximum thickness of the wood is thirty-seven elements.

* For the details of primary structure, just described, reference must be made to the Memoirs of WILLIAMSON above cited.

† See WILLIAMSON, *loc. cit.*, Part IX., Plate 21, fig. 28 (C.N. 908).

‡ C.N. 908, see figure just cited.

§ See WILLIAMSON, *loc. cit.*, especially Part V.

In some other cases the regular seriation is disturbed by the presence of a more or less complete zone of smaller xylem-elements, at first suggesting the idea of an annual ring. No such explanation however is admissible, for these small-celled regions are of very inconstant occurrence, and, when present, they by no means always extend round the entire circumference. Evidently the young wood-cells underwent some additional subdivisions in these zones. Beyond them, the regular radial series of large elements are resumed.

Occasionally these slight irregularities co-existed with a very unequal growth of the opposite sides of the stem. Extreme cases of this kind have been previously figured.* These excessive irregularities are quite exceptional, and were no doubt due to some accidental interference with the normal growth.

The structure of the secondary wood is highly characteristic. The large elements, which in transverse section appear nearly square, often with truncated corners, are tracheæ. Their radial walls are marked by numerous small pits (see Plate 83, figs. 40, 42, 44, and 44A) of somewhat oval outline. When the wall is seen in section it appears that these pits were bordered.

Pits are also sometimes found on the tangential walls, but less constantly. As regards the structure of their walls, the secondary tracheæ are quite similar to those of the middle portion of the primary xylem, except that the latter are pitted equally on all surfaces (see Plate 83, figs. 40 and 41).

A more important difference is the fact that the primary elements have pointed ends, and are no doubt to be regarded as tracheides, while the secondary tracheæ appear to form continuous tubes. It is possible that the latter were really vessels, but the evidence is insufficient to prove this. We shall see that the supposed remains of transverse walls are really of quite a different nature.

Between the corners of the tracheæ we find parenchymatous cells, occupying the space left free by their truncated angles. (See Plate 75, photographs 20 and 22; also Plate 83, figs. 43 and 44A.) Occasionally one such cell appears in the transverse section, in each space; more often there is a little group of them, sometimes six or more in number.

Every here and there the transverse section shows a radially placed cell, or a strand of two or three such cells, side by side, passing between the tracheæ, and uniting the parenchymatous groups with one another.

In a radial section we see that the thin-walled parenchymatous cells at the corners of the tracheæ, form longitudinal strands of considerable length, which are connected at intervals by the radially elongated cells. (See Plate 83, figs. 44 and 44A.)

In a tangential section of the wood, only the lenticular cross-sections of the horizontal parenchymatous cells are seen, for none of them lie in a tangential plane.†

It was these radial parenchymatous cells which M. RENAULT at one time regarded

* WILLIAMSON, *loc. cit.*, Part V., Plate 2, figs. 11 and 12.

† See WILLIAMSON, *loc. cit.*, Part V., Plate 2, fig. 13.

as the remains of transverse walls in the tracheæ,* a view which he has elsewhere abandoned in favour of the true explanation.†

The arrangement of the cells, two or three of which are often placed immediately above one another (see fig. 44) is quite inconsistent with the former view, which is also negatived by the fact that no such transverse markings are seen in a tangential section.

It is important to notice that the radial cells in question do not, as a rule, form *continuous* radial series, and thus differ from the true medullary rays, such as are present in *Sphenophyllum insigne*. (Compare Plate 83, fig. 44, with Plate 84, fig. 49.) It must, however, be pointed out that the absence of continuous medullary rays is not constant even in *S. plurifoliatum*. In the outer layers of the secondary wood, continuous radial tracts of parenchyma, sometimes several cells in breadth, make their appearance. (See Plate 75, photograph 22.)

The description given so far applies more especially to that part of the secondary wood which is formed *between* the angles of the primary xylem; we may term this part of the wood *interfascicular*, using this term for the tissue formed between the protoxylem-groups, in contradistinction to that which is formed opposite them; for the latter the term *fascicular* wood will be used.

The fascicular wood is sharply distinguished from the interfascicular, as seen in transverse sections. (See Plate 75, photographs 19, 20, and 21; Plate 83, fig. 43.) This is due in the first place to the much smaller dimensions of the fascicular tracheæ. The secondary wood is necessarily thinnest opposite the prominent angles of the primary xylem, for the general outline of the wood becomes circular as soon as secondary growth is established. The number, both of tangential and radial series is, however, usually greater in the fascicular region, so the reduced size of the elements here is easily explained. There is a general continuity of the concentric series of xylem-elements all round the stem; the fascicular cells have simply undergone some additional subdivisions. The structure of the tracheæ is the same in both regions. The most important distinction consists in the presence of continuous medullary rays, from the first in the fascicular wood, while in the interfascicular region, they only appear, if at all, in the outer layers. The boundary between fascicular and interfascicular wood is fairly sharp in the inner secondary zones; the distinction, however tends to disappear in the outer part of the wood of very old stems (see photograph 21).

That the whole zone of wood, outside the triquetrous strand, is really secondary, has been sufficiently shown by M. VAN TIEGHEM.‡ In *Sphenophyllum plurifoliatum*, we are able to give the final proof, for in several of our specimens the cambium itself,

* 'Cours de Botanique Fossile,' vol. 2, p. 99, 1882.

† 'Ann. des. Sci. Nat., Bot.,' Série 6, vol. 4, p. 297, Plate 8, figs. 2 and 4, 1877 (*sic*). 'Cours de Botanique Fossile,' vol. 4, p. 8, Plate C, fig. 4, 1885.

‡ "Sur quelques points de l'Anatomie des Cryptogames Vasculaires." 'Bull. de la Soc. Bot. de France,' vol. 30 (1883), p. 169.

by which the secondary tissues were formed, is well preserved. It is especially evident in the section from which fig. 42 on Plate 83 was drawn, in which the correspondence of the thin-walled tabular cambial-cells, with the radial series of secondary tracheæ, is perfectly clear. Other specimens in which the cambium is preserved, are illustrated in the photographs 19 and 20 on Plate 76.

A relatively enormous amount of secondary cortical tissue was developed on the outer side of the cambium (Plate 75; Plate 83, figs. 40 and 43). It is often difficult to distinguish, in transverse sections, between the true phloëm, formed directly from the cambium, and the internal periderms, which arose in abundance from deeply-seated layers of phellogen. The transverse section, shown in photograph 19 and in fig. 43, is especially instructive. Here the actual cambium is only partially preserved; immediately outside it the wide secondary cortex* begins. At the place shown in fig. 43, its maximum thickness was about 16 cells.† The radial series are continuous throughout, and a general continuity with those of the wood can also be traced. The inner zones of the secondary cortex consist of thin-walled cells; each cell is occupied by a carbonaceous mass (omitted in the figure for the sake of clearness, but recognizable in the photograph). This carbonaceous matter may perhaps indicate the original presence of abundant cell-contents. The outer cortical layers are formed of cells with much thicker walls, and without any considerable carbonaceous contents. Between the two zones is a layer of somewhat flattened cells, with specially thin walls, which have sometimes broken down.

The explanation which we propose for this structure is, that the inner zone is true phloëm, formed directly by the cambium on its exterior surface, while the outer layers, with thicker cell-walls, constitute an internal periderm. The intermediate flattened layer would, in this case, be the phellogen, which must have arisen by the division of cells themselves belonging to the secondary phloëm-parenchyma. This explanation also applies well to the other preparations in which the secondary cortical tissues are shown, though the carbonaceous contents of the inner layers are not always present.

Longitudinal sections show that the periderm consisted of short cells, in very regular series, while the inner tissue, presumably phloëm, was composed of much longer elements, possibly the sieve-tubes.‡ In some specimens (see photograph 22) the phloëm-elements are less regularly arranged than those of the periderm.

The development of periderm seems never to have been external, but to have started, from the first, in deeply-seated tissues. A good example of its first forma-

* It is convenient to use the general term "secondary cortex" for all secondary tissues external to the wood. (July 15, 1894.)

† The thickness of the secondary cortical tissues is very unequal at different parts of the circumference of the stem. It often, but not always, shows a maximum opposite each of the three protoxylem groups.

‡ See WILLIAMSON, "Organization," Part V., Plate 1, fig. 7.

tion is shown in a specimen previously figured,* in which a zone of radially arranged tissue, thin-walled at its inner edge, intervenes between the wood and the primary cortex. It is probable that this peridermal tissue arose from the division of cells belonging to the pericycle. At any rate, the whole of the primary cortex, lying outside this first-formed periderm, soon perished. Its remains, in various stages of disorganization, are found surrounding many of the more advanced stems (see, for example, Plate 83, fig. 40, where only a part of the primary cortex is represented).

Soon, however, the original periderm was itself replaced by more internal layers, arising, as we have seen, from the secondary phloëm-parenchyma. The oldest specimens had a regular scale-bark, formed by successive incomplete layers of periderm, cutting more and more deeply into the secondary cortical tissues (see photographs 22, and more especially 23, on Plate 75). At some places as many as five distinct peridermal masses can be traced, one outside the other. Each of these masses consists of thick-walled cells towards its external side, and of very regularly arranged thin-walled tissue, towards its inner margin.

Before leaving *Sphenophyllum plurifoliatum* we will return for a moment to the subject of the cambium, in order to consider the question of its first origin. We very constantly find an irregular layer of comparatively thin-walled tissue, between the concave sides of the primary xylem-strand, and the first layer of interfascicular secondary wood (see especially Plate 75, photograph 20, and Plate 83, fig. 40). At the angles of the primary xylem on the other hand, the first secondary tracheæ appear to abut directly on those of the protoxylem (see also photograph 19 and fig. 43). We may infer then that the *fascicular* cambium (in the sense above explained) arose from the first parenchymatous layer immediately adjoining the protoxylem, while the *interfascicular* cambium at its first origin was separated from the central wood by at least one layer of permanently parenchymatous cells.

It is probable that the formation of secondary wood always began in the interfascicular region.† Sometimes it extended at once round the protoxylem-angles; in other cases the completion of the ring was delayed, so that we may even find three layers of interfascicular wood, while no trace of secondary tissue has as yet appeared opposite the groups of protoxylem.

2. SPHENOPHYLLUM INSIGNE, NOBIS.

This is the species originally described under the name of *Asterophyllites insignis*,‡ and includes all the specimens of *Sphenophyllum*, showing structure, received from Burntisland. At the time when the fossil was first described, nothing was known of

* C.N. 874, WILLIAMSON, *loc. cit.*, Part V., Plate 3, fig. 16.

† See WILLIAMSON, *loc. cit.*, Part V., Plate 1, fig. 2. (C.N. 872.)

‡ WILLIAMSON, "Organization," Part V., 1873.

its foliage. Now we are in a somewhat better position, though our information on this subject is still imperfect.

One of the most important of the additional specimens is that of which a part is represented, in longitudinal section, in Plate 84, fig. 47. This section passes through a node, which is very clearly shown, and corresponds well with the nodes of other species of *Sphenophyllum*. On both sides the bases of the leaves are evident. Below these the cortex is dilated for some distance. The vascular bundles appear to have passed out obliquely; on one side the outgoing tracheæ could be seen. The identity of this specimen with the other Burntisland examples of *Sphenophyllum* is sufficiently proved by the structure of the secondary wood. If fig. 47B, which is taken from the specimen with the node, be compared with fig. 50, which is taken from one of the largest specimens, the agreement in structure is manifest, the peculiar medullary rays being especially characteristic.

We have another preparation which shows something of the leaves. This is an approximately transverse section of a very young stem (see Plate 83, fig. 46). A part of the whorl of leaves is shown, with two vascular bundles passing out through it. Judging from this specimen, the leaves in each verticil could not have been very numerous; probably not more than six. They were evidently coherent for some distance from their base.

Primary Structure.

The primary structure of the stem of *S. insigne* is on the whole similar to that of *S. plurifoliatum*. The cortex of the young stem has the same characteristic form as seen in transverse section. There is a marked depression opposite each of the concave sides of the triarch strand of wood (see Plate 76, photograph 23; Plate 83, fig. 45).

The primary xylem agrees in general anatomical features with that of the former species. Here also the triquetrous strand of tracheæ is quite solid, and destitute of parenchymatous elements of any kind. The tracheæ are of smaller size than those of *S. plurifoliatum*. Towards the middle of the strand they are pitted; their pits are very variable in form; sometimes they are oval, and not unlike those of the former species; often, however, they are more transversely elongated, and approach the scalariform type. Towards the angles of the strand the elements become rapidly smaller; at each corner there is constantly an intercellular space or canal, which affords a good distinctive character from *S. plurifoliatum*, in which such canals are never found (Plate 76, photograph 23; Plate 83, fig. 45). Surrounding the canal are spiral tracheæ, which are much more frequent here than in the last species. Fragments of spirals are also often found in the canal itself (see Plate 85, fig. 53).

It would be rash to assume that the canals existed, as such, during life. It is possible that they may represent the position of thin-walled tissue which accompanied the spiral elements. It is, however, equally likely that they were actual lacunæ,

formed by the rupture of the tissues, as so often happens in similar positions. The numerous, often uncoiled spiral tracheæ, at the angles of the primary xylem, are an indication that growth was still in active progress when the differentiation of the tissues began. Spirals are comparatively rare in *S. plurifoliatum*, a fact which harmonizes well with the absence of canals in that species.

There can be no doubt that in *S. insigne*, as in other species, the primary xylem was triarch and centripetal, the three peripheral groups of spiral tracheæ marking the three points at which differentiation started. We cannot see any proof that there were two groups of protoxylem at each angle. It might indeed be possible to consider the canal as separating the two arms of a crescentic group of primitive tracheæ, as is so conspicuously the case in the Autun species (see Plate 76, photograph 24). But the fact that we have repeatedly found spiral tracheæ immediately to the *outside* of the canal (see Plate 85, fig. 53) appears to us to negative such a view, and to prove that the protoxylem at each angle was a single group.

As regards the other primary tissues there is little to detain us. The inner cortical layers, which cannot be distinguished from the pericycle and phloëm, were thin-walled, and are very imperfectly preserved in the less advanced specimens. We can therefore give no information as to the *primary* phloëm, though we shall find that the *secondary* phloëm was well preserved in some of the older stems.

The outer cortex consisted of somewhat thick-walled tissue, but less sclerotic than that of *S. plurifoliatum*. The cells which, in the internodes, are of considerable length, were generally parenchymatous in form (Plate 84, fig. 47).

As regards the course of the leaf-trace bundles, it appears probable from the preparation shown in Plate 83, fig. 46, that two foliar bundles were given off from each angle of the triarch stele.

For the mode of *branching*, we have only the evidence of one specimen,* the interpretation of which is doubtful. We shall return to the consideration of this specimen, after describing the secondary tissues.

Secondary Changes.

The development of secondary wood and phloëm and of periderm proceeded in *Sphenophyllum insigne* in the same general manner as in *S. plurifoliatum* and other species of the genus. The structure of the secondary tissues, especially of the wood, differs in some respects from that in any other species at present investigated.

As regards the largest specimens of *S. insigne*, certain authors have expressed doubt or disbelief as to their belonging to *Sphenophyllum* at all, and have supposed them to be roots, either of a Cycad, or of some unknown plant.†

* C.N. 926; see WILLIAMSON, "Organization," Part V., Plate 5, fig. 27.

† *E.g.*, RENAULT, 'Cours de Botanique Fossile,' vol. 4., p. 12 (1885); SCHENK, "Die Fossilen Pflanzenreste," in 'Handbuch der Botanik,' Bd. 4, p. 103; SOLMS, 'Fossil Botany,' p. 349.

These doubts, as we shall proceed to show, are groundless. We have a series of specimens with secondary wood of all thicknesses up to 36 elements in each radial series. The smaller of these specimens (such as that shown in the photograph 23, on Plate 76) still retain the characteristic primary cortex, and no doubts have been, or can be, entertained as to their nature. Their structure, however, already presents the same peculiarities which have given rise to suspicions in the case of the larger specimens. The latter only differ from the former in the greater bulk of their secondary tissues and in the loss of their primary cortex, which is cast off in *S. insigne* exactly as in other species of the genus.

If we first consider one of the moderately thickened specimens (such as that shown in photograph 23), we find that the primary triarch wood has the structure already described (*cf.* fig. 45 on Plate 83). Upon this primary strand several layers (7–10 in the specimen photographed) of secondary xylem have been deposited. This tissue is thickest opposite the middle of each of the three concave sides of the primary wood, and thins out considerably towards its angles. The xylem elements are arranged with characteristic regularity in radial series. The distinction between fascicular and inter-fascicular wood is already well marked.

There are, however, two distinctive characters presented by this wood as compared with that of the other species.

(1.) The tracheæ have scalariform markings, at least on their radial walls. This is shown very plainly, both in oblique sections* and in the longitudinal section already referred to (C.N. 1420, see Plate 84, fig. 47). The tangential walls do not generally show any pits; when present on these walls the pits are small and rounded.

(2.) The more striking difference consists in the presence, in all parts of the wood, of regular medullary rays, one or two cells in breadth, extending through the whole thickness of the secondary zone. Occasionally isolated cells occur at the corners of the tracheæ, but, as a rule, the parenchyma of the wood takes the form of continuous rays. Comparison with a longitudinal section (see Plate 83, fig. 47B) shows that these rays may be one cell in height or more. Their elements have a lenticular form, as seen in tangential sections of the stem.

The primary cortex is well preserved in these younger specimens (see photograph 23). A zone of secondary tissue, no doubt including both phloëm and periderm, surrounds the wood; its structure is more evident in the more advanced specimens.

Other examples, with secondary wood from 11 to 22 elements in radial thickness, show precisely the same structure.†

Here, however, the secondary cortical tissues have reached a considerable thickness, and their cells are in regular radial series. Outside this zone the remains of the primary cortex can still be traced.‡

* As in C.N. 910.

† For the details of the wood, see Plate 84, figs. 49–52, and compare with the structure of the younger stem shown in fig. 47.

‡ C.N. 922 and 926.

Lastly, we have the largest specimen, figured in transverse section by WILLIAMSON,* the identity of which has been disputed.

The primary xylem in this specimen has exactly the same structure as in the smaller stems; the canals at the angles, containing fragments of spiral tracheides, are perfectly evident. The secondary wood, which reaches a maximum thickness of 36 elements, agrees in every respect with that of the less advanced specimens; the medullary rays are alike, and so are the tracheæ, with their scalariform radial walls.† In fact, if the more central portion of the largest specimen were seen alone, it could not be distinguished from the corresponding region of one of the younger stems, which still retain the typical cortex of a *Sphenophyllum*.

In the most advanced specimens the primary cortex has, as we should expect, entirely disappeared; it is replaced by an enormously thick bark, formed by successive layers of internal periderm (see Plate 84, figs. 48, 51, and 52).

We maintain, then, that there is no longer the slightest reason to doubt that the largest, as well as the smallest, specimens under consideration belong to one and the same species, namely, to that species of the genus *Sphenophyllum* to which we give the name of *S. insigne*.

The sections in which no primary cortex is shown would, *by themselves*, suggest to any botanist the idea of a root. The root-like anatomy, however, is common to all specimens of the genus *Sphenophyllum*, and is no more remarkable in a large stem than in a small one. The comparison of specimens of various dimensions shows that the only change consists in the formation of additional secondary layers, and in the casting off of the primary cortex, owing to the development of internal periderm.

The presence of true medullary rays in all parts of the wood is certainly exceptional in *Sphenophyllum*, so far as our present knowledge extends. This peculiarity, however, is not confined to the larger specimens of *S. insigne*, but is already present in stems which still retain the unmistakeable cortex and node of a *Sphenophyllum*.

Of the details of structure of the secondary wood little remains to be said. The medullary rays vary much in height. Many consist of a single series of cells, others of two series; in extreme cases even as many as 15 rows may be superposed to form a single ray. The larger rays are usually two or more cells in breadth in some parts. The uniseriate rays, as seen in radial section, are perfectly similar to the radially-elongated cells of *S. plurifoliatum*, except that in *S. insigne* these cells lie in one and the same straight line (compare Plate 83, fig. 44, and Plate 84, fig. 49). The importance of this difference is not to be underrated. It probably indicates a different mode of development from the cambium. We must, however, remember that even in

* *Loc. cit.*, Part V., Plate 4, fig. 21.

† Our figures 48, 49, 51, and 52 (all on Plate 84), are from this largest specimen. The figures in WILLIAMSON, *loc. cit.*, Part V., Plate 4, should also be compared. Our figures 47, 50, and Plate 85, fig. 53, are from smaller stems.

S. plurifoliatum continuous rays do occur, more especially in the fascicular part of the wood,* so the distinction is by no means an absolute one.

The pitting of the tracheæ is often beautifully preserved; in tangential sections it is evident that the scalariform pits were bordered (Plate 84, fig. 50). On the surface of junction of tracheæ and ray-cells the border is unilateral.

Whether the tracheæ were true vessels or tracheides can hardly be determined. If they were tracheides they must have been of great length, for they can often be traced all through a section without finding any terminal wall. In some cases, however, we have observed, in tangential sections, what appear to be the very tapering ends of tracheæ. We do not regard this observation as decisive, for such appearances might possibly be due to slight obliquity of the section. The question must therefore be left open. Now that the transverse lines seen in radial sections have been proved to represent the walls of cells external to the tracheæ, there is no longer any evidence for the existence of transverse septa in the latter.

The cambium appears to have originated in exactly the same position in this species as in *S. plurifoliatum*.

Appearances suggestive of annual rings are sometimes met with in *S. insigne*, but the same remarks apply here as in the case of the former species.

In a longitudinal section of the largest stem† a protoxylem-canal is shown, which is partly blocked up by polygonal cells. As the canals are empty in the younger specimens, it is probable that these cells were of the nature of *thyloses*.

It remains to consider the secondary tissues external to the wood. In the more advanced specimens (see Plate 84, fig. 48) the thick cortical zone‡ is composed of radially arranged cells. Their radial series correspond with, but are usually more numerous than, those of the wood. The walls of the cortical cells become thicker towards the exterior. The limit between phloëm and internal periderm is not always obvious. In favourable cases, however, where the delicate phloëm happens to be particularly well preserved, or where, perhaps, it was developed in unusual amount, the whole structure is clear. This is the case, for example, in the largest specimen, of which corresponding transverse and radial sections are shown in Plate 84, figs. 51 and 52. Adjoining the wood we see evident remains of the tabular cambial cells. Outside these we find a group of thin-walled tissue, in which the arrangement of the cells, though somewhat irregular, shows traces of a radial seriation. Some of the cells in this group are of large size, in fact not much smaller than the tracheæ of the wood. Beyond these, again, are flat, thin-walled cells, passing over on the outside into thicker-walled periderm, only a small part of which is represented in fig. 51. If we compare the radial section with this the corresponding parts are evident. The

* This seems to be also the case in the Autun *Sphenophyllum*. See RENAULT, 'Cours de Bot. Fossile,' vol. 4, plate A, fig. 4, r.

† C.N. 924.

‡ Cf. foot-note above, on p. 925.

outer limit of the wood is sharply defined ; next comes a layer of excessively delicate, elongated cells, doubtless the cambium. Further to the exterior we find a zone of long, thin-walled elements, some of which are of considerable diameter, and are somewhat dilated at the transverse septa. These evidently correspond to the large, thin-walled cells of the transverse section. The resemblance of these elements to the sieve-tubes of the higher plants is very striking, nor are sieve-tubes of similar form unknown among the vascular Cryptogams. In *Marattia*, for example, they are sometimes quite of this type. We think it quite possible that these elements in *Sphenophyllum insigne* may really have been of the nature of sieve-tubes.

Still further towards the outside we find the very regular, short-celled periderm ; its inner cells have thin walls, and no doubt represent the phellogen. The gap in the figure, separating the periderm from the phloëm, is merely a local lesion, for, in other parts of the same section, all the tissues are continuous.

From the study of the transverse section, as a whole, it appears that the phloëm was not equally developed all round the stem, but was specially localized at certain points.

The periderm attained a great thickness ; in the largest specimen four distinct zones can be recognized, so that here, as in *S. plurifoliatum*, there was evidently a repeated formation of phellogen in successively deeper-seated layers. This great development of internal periderm, and consequent throwing-off of the whole primary cortex, seems to have been a striking characteristic of the genus.

Before concluding our account of this species we will return to a specimen, already referred to, which shows the base of a lateral appendage. The section in question* is an incomplete transverse one, showing only one angle of the primary wood. About ten layers of secondary wood are present, and both primary and secondary cortex are fairly preserved. Opposite the protoxylem-group a large bundle of scalariform or reticulated tracheæ, accompanied by parenchyma, runs out in an horizontal direction. The outgoing strand is too large for a leaf-trace ; it must have belonged either to a branch or an adventitious root. The cortex appears to be ruptured at the exit of the strand. On the whole, we are inclined to regard the appendage as a root, for its origin seems to have been endogenous. No certain conclusions, however, can be drawn from this isolated specimen.

To sum up, we find that the chief anatomical characteristics of *Sphenophyllum insigne*, are the following :

1. The presence of a canal at each angle of the primary triarch xylem.
2. The scalariform thickening of the secondary tracheæ, at least as regards their radial walls.
3. The presence, throughout the secondary wood, of continuous medullary rays.

* C.N. 926 (see WILLIAMSON, *loc. cit.*, Part V., Plate 5, fig. 27).

4. The occurrence of very large elements, resembling sieve-tubes, in the phloëm-region.

These characters are sufficient to differentiate the species. In the arrangement of the leaves, the outline and structure of the primary cortex, the centripetal triarch xylem, and the mode of growth in thickness, the plant is a typical *Sphenophyllum*, in which genus it finds its natural resting-place.

THE FRUCTIFICATION OF SPHENOPHYLLUM.

SPHENOPHYLLUM DAWSONI, NOBIS.

The fructification which we are about to consider was first described in 1871, under the name of *Volkmannia Dawsoni*, unless, indeed, as M. ZEILLER suspects, the plant described by BINNEY, in the previous year, as *Bowmanites cambrensis*, be the same species.*

Further accounts of the same fossil were published in 1873 and 1890, and, in 1891, a very complete description was given of its structure, on the basis of a number of newly-discovered specimens.†

In 1884 the species was placed by WEISS in BINNEY'S genus *Bowmanites*,‡ a view which was accepted in the later memoirs of WILLIAMSON.

In 1892, M. ZEILLER§ communicated to the French Academy the results of his examination of some extremely fine fructifying specimens of *Sphenophyllum cuneifolium*, STERNB., from the French and Belgian Coal-Measures. He expressed himself as convinced of the complete identity of WILLIAMSON'S specimens of *Bowmanites Dawsoni*, with the fructifications of his *Sphenophyllum*.||

This year (1893) M. ZEILLER has published his work in full.¶ His detailed descriptions, and especially his beautiful photographic illustrations, leave no doubt as to the essential agreement between the undoubted strobili of *Sphenophyllum*, which he investigated, and the English specimens described as *Bowmanites Dawsoni*. The question of *specific* identity of the latter with *Sphenophyllum cuneifolium*, is one which we prefer to leave open for the present. One of us (D. H. SCOTT) has had the

* WILLIAMSON, "On the Organization of *Volkmannia Dawsoni*," 'Mem. Lit. and Phil. Soc. of Manchester,' Ser. 3, vol. 5; BINNEY, "Observations on the Structure of Fossil Plants," Part 2, 'Palæontographical Society,' volume for 1870.

† WILLIAMSON, "Organization of Fossil Plants of the Coal-Measures," Part V. (1873); Part 17 (1890); and Part 18 (1891); 'Phil. Trans.'

‡ WEISS, 'Steinkohlen-Calamarien,' vol. 2, p. 200.

§ 'Comptes Rendus,' vol. 115, July 11, 1892.

|| This conclusion has already been provisionally accepted by WILLIAMSON, 'Nature,' vol. 47, Nov. 3, 1892.

¶ "Étude sur la constitution de l'appareil fructificateur des *Sphénophyllum*," 'Mém. de la Soc. Géol. de France; Paléontologie,' Mém. 11, 1893.

opportunity, through the kindness of M. ZEILLER, of thoroughly examining his original specimens, and was able completely to confirm his conclusions.

We propose first to give a general account of the organization of the strobilus, as shown in the English specimens, in which alone the internal structure is preserved. The facts already known will be briefly recapitulated, while some additional points of interest, which have been revealed by our renewed examination of the specimens, will be described more fully. Finally, we shall state the reasons which have induced us to accept M. ZEILLER's conclusion that this strobilus is the fructification of a *Sphenophyllum*.

For the present we propose to retain the specific name originally given to the English specimens, which we shall therefore describe as *Sphenophyllum Dawsoni*.

General Morphology.

The strobilus consists of a somewhat slender axis (attaining 2.5 millims. in diameter) bearing a number of successive verticils of coherent bracts. The largest number of whorls preserved in any of our specimens is 8 (in C.N. 1898 K, part of which is represented in Plate 85, fig. 54); the total number was no doubt much greater.

The coherent portion of the bracts, forming the *disc* of previous memoirs, extended for a distance about equal to the diameter of the axis. It then divided up into the free bracts, or "disc-rays." The latter had a somewhat lanceolate form, broadening out for some distance from the base, and then tapering again towards the apex. On leaving the axis the bracts take an obliquely upward course, curving rapidly towards the apex of the strobilus, until their direction is nearly vertical (Plate 85, fig. 54). The free limbs of the bracts were of great length, as is shown by the fact that in transverse sections we may find as many as six overlapping whorls, proving that the extreme vertical length of the bracts must sometimes have been equal to about six internodes, giving an extreme absolute length of perhaps 12 millims.*

The number of bracts in a verticil could not be determined with certainty; apparently it was about fourteen in some of the smaller specimens, and not less than twenty in the larger.

From the position of the overlapping tips it appears that the bracts of successive whorls alternated with one another. This is somewhat surprising, for the leaves in the vegetative verticils of *Sphenophyllum* were superposed. This is, however, no argument against the identification of our specimens with *Sphenophyllum*, for in M. ZEILLER's strobili, borne on the stems of typical *Sphenophyllum crucifolium*, the alternation of the bracts is still more evident.

The sporangia are not borne directly on the bracts, but each is seated on the end of a long pedicel or sporangiophore. The pedicels are twice as numerous as the bracts;

* M. ZEILLER's estimate, based on the figures of Memoir XVIII., is 8 millims. Some of his specimens of *S. cuneifolium* have bracts 10-13 millims. in length. See his Memoir above cited, p. 21.

they arise from the upper surface of the coherent disc near the axil. The extent to which they adhere to the surface of the disc varies greatly; in some cases they become free at once; in others they do not become wholly free until the point is reached where the bracts themselves begin to separate from one another.* It does not appear, however, that there was ever more than a single verticil of sporangiophores belonging to each verticil of bracts; appearances to the contrary seem to be due to the varying degree of adhesion between the two organs (Plate 85, fig. 54).

A transverse section of the strobilus may show one or two circles of sporangia between two whorls of bracts; sometimes even a part of a third circle is present. The same variations are observable in tangential sections. These differences can only be explained by the fact that the sporangiophores overlap each other, so as to bring their sporangia to different levels. Where additional sporangia appear within the same internode, their position is both *exterior* and *superior* to those of the first circle (see Plate 76, photographs 25 and 26, and compare with the figures in WILLIAMSON, Part XVIII.). Hence the longer pedicels must have passed to the outside of the sporangia borne on the shorter ones, as is often well shown both in transverse and tangential sections.†

The longer sporangiophores considerably exceed an internode in length, for we find sporangia belonging to two successive verticils of bracts appearing in the same transverse section.‡

The sporangiophores follow the upward curvature of the bracts, keeping at a little distance from their superior surface. Each bears at its end a single sporangium, which is attached in a very characteristic manner. The pedicel bends inwards at its extreme end, and the sporangium is suspended from it, so as to hang almost parallel to the pedicel, occupying a position rather like that of an anatropous ovule in relation to its funicle (Plate 76, photograph 25; Plate 85, figs. 57 and 58).

This short account of the general morphology of the strobilus may suffice as an introduction, considering the full descriptions which have already been published. We will now proceed to consider its internal structure.

The Axis.

The axis of the strobilus is traversed by a solid vascular cylinder, of which only the wood retains its structure. In the larger specimens the wood forms a very bluntly triquetrous strand.§

Each of the obtuse corners is prolonged into two projecting points, with a marked bay between them. The smallest tracheæ are at the points, so that we may

* See WILLIAMSON, "Organization," Part V., Plate 5, fig. 28; Part XVIII., Plate 26, fig. 7.

† WILLIAMSON, *loc. cit.*, Part XVIII., Plate 26, fig. 2; and Plate 25, fig. 8.

‡ WILLIAMSON, *loc. cit.*, Part V., Plate 5, fig. 28.

§ See WILLIAMSON, *loc. cit.*, Part V., Plate 5, fig. 29; and Part XVIII., Plate 25, fig. 1.

reasonably assume that in this case there were six distinct groups of protoxylem, as in some of the species of *Sphenophyllum* investigated by M. RENAULT (see Plate 76, photograph 24, from the Autun form). It is noticeable that the whole periphery of the woody mass is occupied by elements decidedly smaller than those of the interior. There is not the slightest indication of a pith, or of any parenchymatous cells among the thick-walled tracheæ. Longitudinal sections show tracheæ only, the larger of which appear to have pitted walls. One section (see Plate 85, fig. 54) which probably passed through the xylem near one of its angles, also shows scalariform and spiral tracheæ; the latter are small and no doubt represent the protoxylem.

The soft tissues surrounding the wood have entirely perished, except for a mere structureless film, which, in one specimen, extends between the angles of the wood.

In one of the smaller specimens (see Plate 86, photograph 26) the xylem-strand is excessively slender, and its angles acute, though here also there are some indications of a double group of protoxylem at each. It is doubtful whether these small specimens are identical with the larger ones, which have a massive strand of xylem. It is possible that they may belong to a second species, but we have not sufficient evidence to justify their separation. The spores of the larger and smaller strobili show no constant difference in size.

The specimen from which fig. 54 is drawn, evidently belongs to the smaller form; the diameter of the whole strobilus is only about 6 millims., while those of the larger type are on the average at least 12 millims. in diameter.

The outer cortex of the axis is well preserved. Its inner cells are thin-walled and parenchymatous, but towards the exterior they have thicker walls and are more prosenchymatous in form.

As regards the course of the leaf-trace bundles running out into the bracts, our data are incomplete. None of our sections show the out-going bundles at the point where they diverge from the central cylinder. On the other hand we have some excellent preparations showing the bundles in the outer part of their course. In several sections we see them just at the inner edge of the cortex, or rather of that outer zone of cortex which is alone preserved.* The bundles in this position are of considerable size, and may contain as many as twenty tracheæ. Their smaller elements are towards the exterior, and are spirally thickened, while the inner and larger tracheæ are scalariform, or at least their spiral band is more closely coiled. These facts can be made out where the section is oblique. We may infer then, that the xylem of the leaf-trace bundle was *centripetal*.

The bundles which we meet with in the cortex are often larger than those which pass out into the whorl of bracts, and no doubt sometimes subdivided on their way through the outer cortical layers.

* See WILLIAMSON, *loc. cit.*, Part XVIII., Plate 27, fig. 3. They are also well shown, on a small scale, in our photograph 25, on Plate 76.

The Bracts.

In transverse sections passing through the base of the disc, or coherent whorl of bracts, we find the out-going bundles again, just where they leave the cortex, and pass out obliquely into the verticil (see Plate 85, fig. 55, which is from the same section as the more general figure in WILLIAMSON, Part XVIII., Plate 27, fig. 9).

At this point each bundle undergoes a division into three. One branch, the most external of the trio, continues its course through the disc; the two others are given off on the inner side, towards the axis, and supply two sporangiophores (compare figs. 55 and 56, on Plate 85). The external branch in each case runs straight out through the disc into one of the free bracts, each of which always contains a slender vascular bundle, a fact which has been previously overlooked.

The bundle-system of the appendages then, is clear; each bract receives a single bundle from the axis; immediately on entering the verticil the bundle gives off two branches in an upward and inward direction. These branches constitute the bundles of the two sporangiophores corresponding to the bract in question. The determination of this fact supplies the answer to a question raised by M. ZEILLER in his memoir above cited,* as to the relation between bracts and sporangiophores. The anatomy, as well as the external morphology, indicates plainly that the sporangiophores are appendages of the bracts, and not independent outgrowths of the axis.

As regards the structure of the bracts, a few words will suffice. In the coherent portion of the whorl the parenchyma is, on the whole, very uniform, except that we find a palisade-like layer near the insertion of the whorl and towards the lower surface (Plate 85, fig. 54). The xylem of each vascular bundle is surrounded by an empty space, which no doubt marks the position of the phloëm and thin-walled tissue. It is not possible to determine whether the bundle was collateral or concentric.

The free bracts have a well preserved epidermis, in which smaller cells are seen here and there, but no definite stomata can be detected. Usually only the middle part of the mesophyll is preserved; towards the edges of the bract the space within the epidermis is empty. Through the middle of the persistent central tissue runs the slender vascular bundle, which can only be well seen in the most favourable sections. In other respects, a previous figure gives a sufficient idea of the structure.†

The Sporangiophores and Sporangia.

The insertion of the sporangiophores, as determined by the point at which their vascular bundles are given off from those of the bracts, appears to be constant, while the amount of adhesion, beyond this point, between the sporangiophores and the coherent disc, is very variable, as has already been explained.

* *Loc. cit.* p. 21.

† WILLIAMSON, *loc. cit.*, Part XVIII., Plate 27, fig. 12.

The sporangiophore, in its lower part, is a small cylindrical pedicel, of simple structure. Its diameter near the base is only about .15 millim. It has a well-marked epidermis, beneath which there is sometimes a rather sclerotic hypodermal layer.* The delicate inner tissue is more or less disorganized. The xylem of the vascular bundle, which here consists of two or three tracheæ only, is placed towards the adaxial surface.

As we follow the sporangiophore upwards, we find a gradual change in its structure. Certain of the epidermal cells become enlarged. Sometimes one cell on each side projects beyond its neighbours, giving a winged appearance to the transverse section. As we approach the sporangium, the sporangiophore grows thicker, attaining a diameter of about .4 millim. In this part all the epidermal cells of its outer or dorsal surface are enlarged. The transverse section is here approximately semi-circular (see Plate 85, fig. 57). The vascular bundle contains many more tracheæ than in its lower part; we can now see clearly that while the xylem, as a whole, is situated towards the inner surface (an indication that the bundle was collateral), its smallest tracheæ are directed outwards. This is constantly the case wherever the preservation permits the structure to be clearly seen. It appears then that in the sporangiophore, as in the leaf, the xylem was *centripetal*. All the tracheæ are spiral.

The sporangiophore bends over at its extremity, towards the axis of the strobilus. Here the sporangium is attached to it with a fairly broad base. The xylem preserves its full thickness to the last, and comes to a sudden end, being obliquely truncated where the cavity of the sporangium begins. The thin-walled tissue surrounding the xylem extends further into the sporangium, and gradually thins out along its walls (see Plate 85, fig. 58; Plate 76, photograph 25, and more especially WILLIAMSON, Part XVIII, Plate 27, fig. 16).

The sporangium, as already mentioned, lies back nearly parallel with the pedicel, with the flat side of which it is in contact (figs. 57 and 58).

In our specimens the wall of the sporangium is but one cell in thickness, except near the base. The wall is similar in structure to the epidermis of the adjoining portion of the sporangiophore. M. ZEILLER has suggested several questions as to the sporangial wall, which we have endeavoured to solve.† He enquires whether there is a regular diminution in the size of the cells of the wall, as the distance from the pedicel increases. There is certainly a diminution, but it is not quite regular. We often find a constriction near the base of the sporangium, which we may take as marking the limit between the sporangial wall and the epidermis of the pedicel (see photograph 25, and figures above cited). Beyond this constriction, large cells, just like those of the epidermis, recommence. They gradually diminish in size, as we trace the sporangial wall towards the free end, but soon their diameter becomes uniform.

* WILLIAMSON, *loc. cit.*, Part XVIII., Plate 28, fig. 15.

† *Loc. cit.* p. 22.

Quite at the end of the sporangium, however, we often find a group of specially narrow cells, suggesting that here dehiscence took place. Measurements give the following average results :—

Large epidermal cells of pedicel . . .	·12 millim. radial diameter.
Largest cells of sporangial wall . . .	·12 " " "
Ordinary cells of wall	·073 " " "
Narrowest cells of wall	·036 " " "

What has just been said answers another of M. ZEILLER's enquires (*loc. cit.* p. 23), namely, whether the largest cells belong exclusively to the pedicel, or whether some also belong to the sporangium itself. Undoubtedly the latter is the case.

A third point suggested by M. ZEILLER for investigation relates to the thickening of the membranes of the large cells in question. He compares them to the annulus in Ferns, and enquires whether, like the cells of that organ, they are more thickened on their inner than on their outer surface. We have carefully examined the cells both of the pedicel, and of the sporangial wall, from this point of view. They are quite similar to each other, and their membranes show a distinct thickening in the form of bars, running along their lateral walls in the radial direction. In some cases the thickened ridges extend also over the inner and outer cell-walls, but we could detect no difference between them as to thickness.

The Spores.

The spores of *Sphenophyllum Dawsoni* are already well known; their cell-wall possesses a highly characteristic ornamentation, consisting of prominent spines, which are connected together on the external surface of the exosporium, by a reticulum of elevated ridges.* This structure is quite constant; in one strobilus only did we find any deviation from it. In this specimen only two of the sporangia shown in the section† contain typical spores, which are here about ·1 millim. in diameter. The other sporangia contain thin-walled spores, without spines, and of somewhat smaller size, though not smaller than the typical spores of some other specimens. It is probable that the thin-walled spores in this strobilus were immature.

There is nothing whatever, in any of our specimens, to suggest that the fructification was heterosporous. As about a dozen distinct specimens have now been examined, it is highly probable that if two kinds of spores were present, both must have been observed. The variations in the size of the spores are inconsiderable, ·076 millim. to ·104 millim. being the extreme range; these extremes are connected by spores of intermediate dimensions.

* See WILLIAMSON, *loc. cit.*, Part XVIII., Plate 25, figs. 17 and 18. See also our own figures 57 and 58, on Plate 85.

† C.N. 1049 C, figured by WILLIAMSON, *loc. cit.*, Part XVIII., Plate 28, fig. 6.

The Vegetative Stem.

A specimen which appears to throw light on the structure of the stem of this plant in its vegetative region, has been described and figured in a previous memoir.* This specimen is a mere fragment, of which we know only the transverse section. It was obtained from the same source, the Foot-mine at Oldham, which has yielded some of the specimens of the strobilus itself.

The primary wood is bluntly triquetrous, and appears to consist of a perfectly solid mass of tracheæ. The details of its structure, so far as the transverse section can show, are absolutely identical with those of the xylem-strand in the axis of the strobilus.†

In the vegetative specimen, however, the primary xylem is surrounded by a zone of secondary wood, 12–15 elements in thickness. The structure of this secondary wood agrees exactly with that of *Sphenophyllum plurifoliatum*, except that the distinction between fascicular and interfascicular wood is somewhat less marked than in that species.

Portions of the secondary cortex are also preserved; the cortical cells are arranged in radial series, which generally correspond to those of the wood. At one place we could distinguish three zones of cortical tissue.‡ It is probable that we have in this stem, as in the species of *Sphenophyllum* above described, a succession of deep-seated peridermal layers.

So far as the evidence extends, there is every reason to suppose that this specimen is a stem of the same plant as that to which the strobilus belonged. It differs from the axis of the latter just in those points (secondary thickening, and loss of primary cortex) in which we should expect a persistent vegetative stem to differ from the short-lived axis of a fructification. The primary structure of the two, so far as it can be compared, is identical.

Now the anatomy of the vegetative specimen is that of a *Sphenophyllum*, though somewhat different from that of any of the species of which the structure has been previously described. This specimen thus established a presumption that "*Bowmanites Dawsoni*" was the fructification of a *Sphenophyllum*, or of some closely allied plant. This presumption has now been raised to a certainty by M. ZEILLER's observations.

AFFINITIES.

M. ZEILLER's investigation of his fine specimens of the fructification of *Sphenophyllum cuneifolium* has established the following facts: the bracts of each verticil

* WILLIAMSON, "Organization," Part XVII., Plate 15, fig. 19.

† Compare WILLIAMSON, *loc. cit.*, Part XVII., Plate 15, fig. 19, with Part V., Plate 5, fig. 29, or with Part XVIII., Plate 25, fig. 1.

‡ Not clearly shown in the figure cited.

are coherent at the base, forming a funnel-shaped disc; they then become free from one another, and their free portions extend to a height equal to two or three internodes; the outline of each bract is linear-lanceolate. The sporangia are pluriseriate in each internode, being ranged in two, three, or perhaps, sometimes four circles, of increasing radius, and placed one above another. The sporangia are not attached directly to the bracts, but are borne singly at the end of filiform pedicels of varying length, which are thickened at their summit; these pedicels start from the coherent portion of the bracts, and run parallel to the latter, keeping a little above their superior surface; the pedicels become erect near their summit, and curve back towards the axis, following the external outline of the sporangium, which is attached by its superior extremity. Near the point of attachment, large cells, with more or less thickened lateral walls, can be distinguished on the dorsal surface of the pedicel, and, as it seems, on the sporangium itself.* In all these points the fructification of *Sphenophyllum cuneifolium* agrees exactly with the English specimens of *S. Dawsoni*. The only exception is that, in the latter, the bracts are sometimes of greater length relatively to the internodes.

M. ZEILLER adds a detailed comparison of the actual dimensions of his own specimens (derived from three distinct sources) with those of the English fossil; in all parts there is a most striking agreement.†

The appearance and form of the sporangium and pedicel in *S. cuneifolium* correspond exactly with our observations on the English specimens, and the same remark applies equally to the whorl of bracts.‡

The agreement in all respects is so close as to leave no doubt that the strobilus described by us is that of a *Sphenophyllum*, nearly related to, and perhaps identical with the species *S. cuneifolium*. We prefer, however, not to assume the identity of the species until we have some further information as to the vegetative organs of the English specimens.

Four other species of *Sphenophyllum* were examined by M. ZEILLER: *S. emarginatum*, BRONGN.; *S. gracile*, CRÉPIN.; *S. oblongifolium*, GERM. et KAULF.; and an unnamed species from M. RENAULT's collection. They all show an essential agreement with *S. cuneifolium*, especially as regards the main point, that the sporangia are borne singly on pedicels which arise from the upper surface of the bracts. In *S. oblongifolium*, M. ZEILLER was able to isolate some of the spores. Though much smaller than those of *S. Dawsoni*, they are similar in form (*loc. cit.*, p. 28).

Finally, M. ZEILLER reviews all the previous cases in which the fructification of *Sphenophyllum* has been described, and shows that all the previous observations are consistent with the presence of pedicellate sporangia rather than of sporangia borne directly on the bracts. We need not follow the details of this critical survey, but

* The above account is taken from M. ZEILLER's summary on p. 20 of his Memoir above cited.

† See his comparative table, *loc. cit.*, p. 21.

‡ See M. ZEILLER's figures, *loc. cit.*, Plate 1, figs. 1B and 4A; Plate 2, figs. 1A, 1B, 3A, &c.

will only call attention to one case, that of the fructification of *Sphenophyllum trichomatosum*, STUR, recently described by Mr. KIDSTON.*

The author states (p. 60) that "the oval sporangia (which have thick walls, as indicated by the amount of carbon they possess) stand upright on the bracts a short distance from their point of attachment to the cone." This statement is quite exact as regards the two sporangia to which Mr. KIDSTON is specially referring (see his fig. 1A), but from his other figures it appears that the relation of the sporangia to the bracts, and to the axis, was very inconstant. Sometimes they appear exactly in the axil, sometimes at a distance from it; in certain cases they are shown in close contact with the upper surface of the bracts, while in others they are quite separate from them. These variations would find an adequate explanation if the sporangia were borne on pedicels, which would allow of a considerable degree of displacement.

It must be remembered that the specimens of *Sphenophyllum Dawsoni* are, with two exceptions to be mentioned immediately, the only ones known in which the internal structure of the strobilus is preserved, while among the specimens in the form of impressions, those described by M. ZEILLER would appear to be by far the most perfect. The morphology of the strobilus must necessarily be interpreted in the light of those specimens in which alone it is clearly exhibited.

Two silicified fragments of fructifications, referred to *Sphenophyllum*, have been discovered by M. RENAULT. One of them has been mentioned above, and is described in M. ZEILLER's Memoir (*loc. cit.*, p. 28). Its organization agrees well with that of *S. cuneifolium* and *S. Dawsoni*. The other fragment has been interpreted by M. RENAULT as demonstrating the heterospory of *Sphenophyllum*.† M. ZEILLER has pointed out that in this specimen the sporangia were certainly borne on pedicels (*loc. cit.*, p. 34). His interpretation of the supposed macrosporangium is different from that of M. RENAULT. M. ZEILLER regards the "macrospore" as being in reality a part of the sporangial wall, while the supposed wall of the macrosporangium belongs, in his opinion, to the pedicel. One of us (D. H. SCOTT) was enabled through M. RENAULT's kindness, to examine the specimen in question, and was disposed to accept M. ZEILLER's interpretation.

Although we cannot regard the evidence derived from this specimen (which is imperfectly preserved) as by any means sufficient to establish the fact of heterospory, yet we fully allow the *possibility* that heterosporous species of *Sphenophyllum* may have existed. That both heterosporous and homosporous species may occur, within the limits of a single genus, is sufficiently proved by the case of *Calamostachys*.

The morphology of the strobilus of *Sphenophyllum* cannot be fully interpreted until the true homologies of the sporangiophores are established. Four views appear possible:—

* 'Proc. Royal Phys. Soc. of Edinburgh,' vol. 11, 1891, p. 56.

† 'Ann. des Sci. Nat., Bot.,' Sér. 6, vol. 4, 1877, p. 303, Plate 9, figs. 9–11; 'Cours de Bot. Fossile,' vol. 2, p. 102, Plate 15, figs. 7 and 8, Plate 16, fig. 3.

- (1.) The sporangiophore may be a branch borne in the axil of the bracts.
- (2.) It may be a leaf, which has become adherent to the whorl below.
- (3.) It may be a ventral lobe of a leaf, of which the bract is the dorsal lobe.
- (4.) It may simply be a sporangium-pedicel, which, unlike those of any other Cryptogam, possesses a vascular bundle of its own.

In the last case we might compare the sporangiophore with the funiculus of an ovule, but such a comparison would not advance the question much, for the true nature of the funiculus itself is still disputed.

That the sporangiophore is an axial structure, *i.e.*, a branch, does not seem to us probable. We have seen that the vascular tissue of each pair of sporangiophores is given off from the bundle of a bract, and has no direct relation to the vascular system of the axis. Further, the bundle of the sporangiophore is to all appearance a single, collateral one, a fact which would ill accord with a stem-structure.

That each sporangiophore represents an independent leaf, is a forced, though not perhaps an impossible view. We should, on this hypothesis, have to imagine a succession of alternating sterile and fertile whorls, the latter having twice as many members as the former; and we must further suppose every alternate internode to have been shortened until each fertile verticil came to be adherent to the sterile verticil next below. In the absence of any developmental data such speculations are baseless, though analogies might no doubt be found in the floral structures of certain Angiosperms. Another analogy might be traced with the Calamarian strobili. If the sporangiophores in *Equisetum* and *Calamostachys* are really leaves, as most botanists assume, then in the *Palæostachya* type, there must have been just such a shortening of the alternate internodes as is required by the hypothesis, in *Sphenophyllum*. The morphology of the Calamariæ is, however, itself too doubtful for us to employ it in order to explain that of a remote genus.

The view that each sporangiophore is a ventral lobe of the corresponding bract is that held by M. ZEILLER,* and is perhaps the most natural of the hypotheses so far considered. In this case we must suppose each leaf to have had one dorsal lobe (the bract) and two ventral lobes (the sporangiophores). M. ZEILLER lays great stress on the analogy with *Marsilia*, and also with *Ophioglossum*. Even if we accepted these comparisons the question would be far from settled, for the morphology of *Ophioglossum*, at any rate, is itself a subject of controversy. Professor BOWER† maintains that the whole fertile spike of *Ophioglossum* is homologous with a single sporangium of *Lycopodium*. If we were to apply this view to the case of *Sphenophyllum*, we should be led back to the idea that here the sporangiophore is nothing but the stalk of a sporangium. We do not ourselves think, however, that the comparison with the complex conditions in *Ophioglossum* throws any light on the much simpler case of *Sphenophyllum*.

* *Loc. cit.*, p. 37.

† ‘Proceedings of the Royal Society,’ vol. 50, p. 265, 1891.

The chief objection to the simple view that the whole sporangiophore is nothing else than the pedicel of a sporangium, is the absence of any analogy among Cryptogams for such a great elongation and high differentiation of that organ. We have thought it best to state briefly the views which appear to us to be possible. We make no attempt to decide between them, and indeed regard the question as insoluble, in the absence alike of developmental facts and of satisfactory material for comparative study. We prefer to leave the whole question open, and, provisionally, to speak of the sporangiophore as a pedicel simply, without prejudging its possible homologies.

Our knowledge of the organization of *Sphenophyllum* is now fairly complete. We have not, it is true, been able ourselves to say anything as to the structure of the roots, nor to give any detailed account of the leaves. Considerable information on these points, as regards other species of the genus, will however be found in the works of M. RENAULT, cited above. But though *Sphenophyllum* is now, for a fossil plant, very thoroughly known, it still seems to us impossible to determine its affinities. That it is a vascular Cryptogam there can be no doubt, nor has this been questioned by any modern writer. Among the vascular Cryptogams, *Sphenophyllum* must rank as one of the most highly organized genera, on account both of the great histological complexity of its vegetative organs, and of the peculiar morphology of its fructification. However we may interpret the latter, it certainly has a highly specialized character. In fact *Sphenophyllum* affords yet another example of a Carboniferous Cryptogam, which, so far from representing a primitive type, is in many ways more elaborately modified than any recent forms.

It is not surprising that the most various systematic positions have been assigned to the genus by different authors. For example, SCHENK, VAN TIEGHEM, and others, have placed it near Lycopodiaceæ; STUR refers it to Calamariæ, RENAULT to Salviniaceæ, while ZEILLER has recently traced a relationship, on the one hand, to Marsiliaceæ, and on the other to Ophioglosseæ. Mr. KIDSTON thinks that "the *Sphenophylla* form a peculiar group of plants, which, though standing close to the Lycopods, cannot be included with them, but must be placed in a class by themselves—the Sphenophylleæ."* Count SOLMS-LAUBACH also places these plants in a class of their own, thinking it best "to renounce for the present all forced attempts at classification, and to regard the group as *sui generis*, as standing by itself, and independent."† To this cautious view of the matter we give our adhesion, until additional forms shall be discovered, which may link on the genus to other families.

The chief characters which have to be taken into account, seem to us to be these: (1) the jointed axis, with superposed verticils of leaves; (2) the centripetal triarch or hexarch xylem, without a pith; (3) the structure of the strobilus, especially the mode in which the sporangia are borne, and the relation of their pedicels to the bracts.

* *Loc. cit.*, p. 61.

† 'Fossil Botany,' p. 354.

The phenomena of secondary growth, remarkable as they are, have appeared in so many diverse groups of Cryptogams and Phanerogams, that we cannot attach much systematic importance to them.

The special peculiarities of the secondary tissues in *Sphenophyllum* appear to us to have been somewhat exaggerated by previous authors. For example the absence of medullary rays, on which so much stress has been laid, does not seem to have been constant in any species, while in *S. insigne*, which we have proved to be a true *Sphenophyllum*, such rays are present in all parts of the wood. The structure of the secondary tracheæ does not seem to us to differ essentially from that in other Cryptogams with indefinite growth in thickness. Their structure has been misunderstood in the past, and represented as much more peculiar than it really is. The question whether these elements are vessels or tracheides must, indeed, be left open. Even if they are true vessels they are not without analogy among recent Cryptogams. Prof. HARVEY GIBSON has been good enough to inform us that in *Selaginella rupestris* and *oregana*, he finds perfectly typical vessels, with transverse septa which become completely perforated, only leaving an annulus to mark their position.*

The cambium of *Sphenophyllum* is perfectly normal, we might almost say typical. The most remarkable point is the repeated formation of internal layers of periderm. This has no exact parallel in other Cryptogams, though familiar enough among higher plants.

The root-like anatomy of the stem is highly characteristic, and indeed peculiar to the genus. The nearest approach to it is to be found in the centripetal xylem-strands of such Lycopods as *Psilotum* or *Tmesipteris*, with which, however, our plant has otherwise nothing in common.†

In conclusion, we must return for a moment to the fructification, in order to explain more clearly M. ZEILLER'S views of its relation to that of *Marsilia* and of *Ophioglossum*. This author (*loc. cit.*, p. 37) points out the similarity between the pedicel of the sporangium in *Sphenophyllum*, and the stalk of the sporocarp in *Marsilia*. In both, the position is that of a ventral lobe of the leaf, while the mode of attachment of the sporangium in the former is similar to that of the sporocarp in the latter. We cannot, for our part, see more than a superficial resemblance here, for it seems to us impossible to compare morphologically the single sporangium of a

* Prof. GIBSON will give details in his forthcoming paper on the "Comparative Anatomy of *Selaginella*." [This has since appeared in the 'Annals of Botany,' vol. 8, number for June, 1894. July 15, 1894.]

† We cannot follow Count SOLMS-LAUBACH in his remarks on this subject. He says (*loc. cit.*, p. 354): "Assuming that the primary central bundle [in *Sphenophyllum*] belongs to the concentric type, then it may no doubt be compared with the axile strand of Lycopodiæ. But this is as yet only an assumption; the bundle might just as well be a triarch radial strand, and then there would be no resemblance to the structure of the stalk in any known living plant." We have little doubt that the central strand in *Sphenophyllum* is radial, in DE BARY'S sense, and that it is either triarch or hexarch. But surely the central strands of existing Lycopods are radial also, as DE BARY long ago showed, and as the development clearly proves.

Sphenophyllum with the elaborate sporocarp of a *Marsilia*, which is obviously a highly specialized foliar structure, containing two series of sori, with numerous sporangia in each sorus. Whatever view be taken of the *pedicel*, we see no reason to doubt that the *sporangium* of *Sphenophyllum* is simply a single sporangium and nothing more.

The comparison suggested with the Ophioglosseæ is based partly on the ventral position of the pedicel, partly on the apparently eusporangiate character of the sporangium, which could scarcely have arisen from a single cell. In order to carry out the comparison we should have to imagine the fertile spike of an *Ophioglossum* bearing a single sporangium. Here again the resemblance seems to us too remote to be suggestive of affinity.

We must be content for the present to leave this remarkable genus in its isolated position, in the hope that the extensive knowledge of its organization, which we now possess, may in the future afford an adequate basis for comparison, when additional forms of palæozoic Cryptogams shall have been brought to light.

In concluding this paper, we desire to acknowledge the essential help of those gentlemen who have contributed the illustrations.

All the drawings reproduced in Plates 77 to 85 are the work of Mr. GEORGE BREBNER, formerly Marshall Scholar in Biology at the Royal College of Science, London.

Of the micro-photographs, occupying Plates 72 to 76, the first two were taken by Professor J. B. FARMER, of the Royal College of Science, while all the rest, 24 in number, are the work of Mr. A. E. TUTTON, Demonstrator in Chemistry at the same College.

The seven photographs in Plate 86, representing medullary casts of *Calamites*, were kindly taken for us by Mr. A. GEPP, of the British Museum, Natural History Department. For the loan of these specimens for photographic purposes, we have been indebted partly to Dr. WOODWARD and partly to Mr. CARRUTHERS.

EXPLANATION OF PLATES 72-86.

PLATES 72-76.—Photographs from the actual sections. Many of the photographs need to be examined with a lens.

PLATE 72.

Calamites.

- Photograph 1. Transverse section of a very young twig, corticated. Seven vascular bundles are shown, each with a large canal on its inner side. Primary structure still unchanged. C.N. 1020. $\times$ about 60. See also Plate 77, fig. 2.
- Photograph 2. Transverse section of a larger branch, with 19 vascular bundles ;

cortex well preserved. Several layers of secondary wood have already been formed. Outer part of the pith persistent. C.N. 1553. $\times$ about 15. See also Plate 77, fig. 3.

Photograph 3. Part of a transverse section of a larger branch, at a more advanced stage; seven of the vascular bundles (21 in all) are shown. Numerous layers of secondary wood have been formed. The cortex is differentiated into two layers. C.N. 118*. $\times$ about 25. See also Plate 78, figs. 12, 13, and 14.

Photograph 4. Radial section of part of a decorticated branch, showing two nodes, with their diaphragms. There is a considerable zone of secondary wood. Above the upper node, on the right hand, part of the base of a branch is shown. C.N. 1937. $\times$ about 9. From Mr. WILD's specimen.

Photograph 5. Tangential section through the wood of an advanced stem. The section passed through the inner part of the secondary wood. Five outgoing foliar bundles are seen in transverse section, as well as two branches out of the four which the complete section shows at this node. Observe that there is no regular alternation of the vascular bundles above and below the node. Observe the small-celled tissue of the medullary rays below the node. C.N. 130*. $\times$ about 12.

Photograph 6. Similar section of another specimen. This section has passed somewhat further towards the exterior. Several foliar bundles are shown, and one branch. Observe that its connection with the tracheæ of the main stem is chiefly from below. C.N. 1554. $\times$ about 12.

PLATE 73.

Photographs 7, 8, and 9. *Calamites*.

Photograph 7. Transverse section of Mr. WILD's specimen, at some distance from the base of the branch, showing typical Calamitean structure, with a large pith-cavity, and 24 bundles, each with its canal. C.N. 1941. $\times$ about 10.

Photograph 8. Another section of the same, nearer the base. Pith-cavity much smaller, bundles normal, but only 14 in number. C.N. 1934. $\times$ about 10.

Photograph 9. Third section of the same, taken close to the base. Pith of minute size, with small irregular cavity, probably of *post-mortem* origin. Only 10 bundles, very crowded together, and with no distinct canals. C.N. 1933A. $\times$ about 10.

Photographs 10-13. *Calamostachys Binneyana*.

Photograph 10. Part of a radial section through a large strobilus. There are 18 whorls of bracts in the specimen, of which 4 are shown. Between them are

the whorls of sporangiophores, of which 5 are shown, with their sporangia. Note the well-preserved central cylinder of the axis. C.N. 1022. $\times$ about 8.

Photograph 11. Part of a tangential section of the same specimen, showing the alternate whorls of coherent bracts, and of sporangiophores. In the former note the vascular bundles. The sporangiophores are seen in transverse section, each surrounded by its 4 sporangia. C.N. 1022A. $\times$ about 8. See also Plate 81, figs. 27 and 28.

Photograph 12. Transverse section passing through a whorl of coherent bracts, of which there are 13. Their vascular bundles can be seen. The small transverse sections, seen immediately outside the whorl, are those of bract-tips rising up from below. They alternate with the bracts of the next whorl. The still smaller transverse sections, seen in some places between the larger, are those of extreme tips of bracts from the second whorl below. C.N. 997. $\times$ about 20.

Photograph 13. Transverse section passing through a whorl of 6 peltate sporangiophores, some of which are shown completely, with the sporangium attached to the lower surface of the peltate expansion, at its edge. Here, again, the tips of the two whorls of bracts below are shown in transverse section surrounding the strobilus. C.N. 1020. $\times$ about 16.

PLATE 74.

Photograph 14. *C. Binneyana*. Transverse section of strobilus, passing through an internode. In the axis the stele has four prominent corners, with a bundle and its canal at each corner. A ring of sporangia surrounds the axis, and beyond these again are seen the extremities of bracts, some in section, others in surface-view. C.N. 1037A. $\times$ about 16.

Photograph 15. *Calamostachys Casheana*. Tangential section. Parts of three whorls are shown. All the sporangia are macrosporangia except one. The single microsporangium belongs to the middle whorl, and to a sporangiophore which also bears three macrosporangia. C.N. 1587. $\times$ about 18. See also Plate 82, fig. 38.

Photograph 16. Transverse section of the same specimen. Only macrosporangia are shown. The central cylinder has formed some secondary wood. C.N. 1588. $\times$ about 25. See also Plate 82, figs. 36 and 37.

Photograph 17. *Calamostachys* sp. Part of a radial section of the strobilus. The bracts and sporangiophores are obliquely ascending, not horizontal as in *C. Binneyana*. C.N. 1896. $\times$ about 8.

Photograph 18. Tangential section of the same specimen. C.N. 1897. $\times$ about 8.

PLATE 75.

Sphenophyllum plurifoliatum.

- Photograph 19. Transverse section of a stem of moderate age, which has already cast off its primary cortex. The triarch primary xylem is shown; also the radially arranged fascicular and interfascicular secondary wood and, beyond that, the layers of phloëm and periderm. C.N. 894. $\times$ about 18. See also Plate 83, fig. 43.
- Photograph 20. Transverse section of another stem at a similar stage. The details of the wood and of the periderm are especially clear. C.N. 899. $\times$ about 18.
- Photograph 21. Transverse section of a very advanced stem. Structure of wood identical with that of previous specimens. To the exterior, successive scales of bark are shown. C.N. 1893. $\times$ about 8.
- Photograph 22. Part of a transverse section of a still older stem, with secondary wood reaching 37 elements in thickness. Details of wood, especially xylem-parenchyma, very clear. Phloëm only partially preserved, but 4 successive layers of periderm are present. C.N. 901. $\times$ about 30.

PLATE 76.

- Photograph 23. *Sphenophyllum insigne*. Transverse section of a stem, which still retains its primary cortex. Triarch primary wood has a canal at each angle. 5-8 layers of secondary wood, with narrow medullary rays, have been formed. There are traces of periderm within the primary cortex. C.N. 919. $\times$ about 30.
- Photograph 24. *Sphenophyllum* from Autun. Transverse section of a specimen presented by M. RENÀULT. Observe the *hexarch* primary xylem, which is imperfectly differentiated towards the centre. Secondary wood as in *S. plurifoliatum*. C.N. 929. $\times$ about 12.
- Photograph 25. Part of an approximately transverse section through the strobilus of *S. Dawsoni*. The central cylinder is absent, but leaf-trace bundles, within the cortex, are well shown. Several sporangia show attachment to sporangiophore, with its vascular bundle. C.N. 1898, H. $\times$ about 14.
- Photograph 26. Approximately transverse section of a small strobilus of the same. The triangular xylem is shown in the axis. Part of the whorl of bracts seen is surface view, and sections of other bracts more to the exterior. One sporangium is shown attached to sporangiophore. C.N. 1898, I. $\times$ about 12.

PLATES 77-85.—Figures from camera-lucida drawings executed by
Mr. GEORGE BREBNER.

PLATE 77.

Calamites.

- Fig. 1. Transverse section of a very young twig. The pith is nearly solid, but slightly disorganized near the centre. There are seven vascular bundles, each with its canal. In most of the canals rings can be seen (as at *px*), which are the remains of the primitive tracheæ. Secondary wood, both fascicular and interfascicular, has just begun to be formed. The simple cortex is well preserved. C.N. 116*. $\times 100$.
- Fig. 2. Transverse section of a larger twig, but at a still earlier stage of development. The pith is hollow. There are twelve bundles, each with a canal, on the outer edge of which is the primary xylem. No secondary tissue has yet appeared. The cortex shows little differentiation. This is another section of the same specimen which is shown in Plate 72, photograph 1. C.N. 1561. $\times 50$.
- Fig. 3. Part of a transverse section of a larger and more advanced stem, the same as that of which another section is shown in Plate 72, photograph 2. A broad outer zone of pith is preserved. Two vascular bundles are shown. About twelve layers of secondary wood have been formed. The narrower elements belong to the secondary medullary rays. Interfascicular wood is already formed across the principal rays. The phloëm and cambium are disorganized, but their position is evident (*ph*). The well-preserved cortex is differentiated into two distinct layers. C.N. 14. $\times 50$.
- Fig. 4. Oblique section of a young branch; its cortex was preserved, but is not shown. The pith is hollow. There are twelve vascular bundles. In the canal of each bundle the fragmentary rings and spirals of the primitive tracheæ, or protoxylem, are seen, as at *px*. They sometimes extend to the inner margin of the canal (see especially the bundle marked *a*). Only the primary xylem of the bundles exists at this stage. C.N. 1002. $\times 100$.
- Fig. 5. Part of a radial section passing through the primary wood of a bundle. On the left are pith-cells. In the middle is the canal, which is still partly filled by the disorganized remains of the protoxylem (*px*). The tracheæ are partly annular, partly spiral. Towards the right they become more continuous. Still further to the right we see the persistent scalariform tracheæ (*sc*) of the primary wood external to the canal. C.N. 20A. $\times 200$.
- Fig. 6. Part of a transverse section, showing a leaf-trace bundle passing out horizontally through the secondary wood. On the left are pith-cells; *px*, protoxylem of a bundle passing into the next internode. The reticulated tracheæ

belong to the nodal wood. The tracheæ of the foliar bundle, *f*, are spiral and scalariform. C.N. 118*. $\times 150$.

PLATE 78.

Calamites.

Fig. 7. Part of a radial section, showing a leaf-trace bundle passing out through the nodal and secondary wood; disorganized pith (*p*) is on the left. The nodal wood can be distinguished by its short tracheæ. The leaf-trace consists of tracheæ (on some of which the spiral thickening is seen) and surrounding parenchyma. The section not being quite in the plane of the outgoing bundle, the latter appears to die out towards the right. *px*, protoxylem of bundle below the node. C.N. 22 $\times 100$.

Fig. 8. Part of a tangential section, showing a leaf-trace bundle cut transversely. The section passes through the inner part of the secondary wood. The pitting is almost entirely confined to the radial walls of the tracheæ. The shaded parts of the latter represent the unpitted tangential walls; the parts left white are in section; several secondary rays are shown (as at *r*). Some of the tracheæ show traces of transverse septa, but most of these appearances are due to oblique section of their tangential walls. The leaf-trace has a gap, where some of its primitive tracheæ are disorganized. It is surrounded by parenchyma. C.N. 20B. $\times 100$.

Fig. 9. *A*. Short tracheide and neighbouring cells, in tangential section, to show bordered pits. Towards the parenchyma the border is unilateral (as at *a*). C.N. 20A (same specimen as 20B, but from a section nearer the pith). $\times 200$.

B. Wall between two tracheæ, to show bordered pits, in tangential section. C.N. 1554 (shown in Plate 72, photograph 6). $\times 500$.

Fig. 10. Part of radial section, passing through a node. The pith is to the left. Above the node part of a primary ray (*r*) is shown. The canal of a bundle, containing remains of the protoxylem (*px*) passes up to the node from below. The protoxylem is continuous with the innermost elements of the nodal wood. The rest of the nodal wood is continuous with the persistent primary xylem (*x*) immediately outside the canal. C.N. 21. $\times 50$.

Fig. 11. Tangential section, to show course of vascular bundles. Three outgoing leaf-trace bundles are shown, in transverse section, at the node. Only the alternate bundles pass out at this node; the intermediate bundles do not pass out, but fork and attach themselves to the neighbouring strands. The relatively broad, small-celled rays (as at *r*) show that the section passes near the pith. C.N. 26. $\times 13$.

Fig. 12. Part of transverse section, showing cortex and outer layers of wood (*x*).

Remains of the phloëm (*ph.*) are seen. The cortex consists of two distinct layers (*c* and *c'*); the outer layer becomes more sclerenchymatous towards the periphery. C.N. 118*. $\times 50$.

Fig. 13. Another part of the same section showing a phloëm-group (*ph*). The cambium (*cb*) between wood and phloëm is also preserved, and the phloëm itself is complete, though crushed. The large cells above belong to the cortex (*c*) C.N. 118*. $\times 150$.

Fig. 14. From the same section, showing a small portion of wood (*x*), cambial cells (*cb*) and their derivatives, and cortex (*c*). C.N. 118*. $\times 150$.

The figs. 12, 13, and 14 are from the section, a part of which is shown in Plate 72, Photograph 3.

PLATE 79.

Calamites.

Fig. 15. Tangential section passing through a principal medullary ray near the pith. On either side are seen tracheides and one or two secondary rays (as at *r*). The principal ray is entirely parenchymatous; the elements towards the middle are quite short; those near the edges are narrower and more elongated (*m*). C.N. 65. $\times 50$.

Fig. 16. From another section of the same stem, showing a principal ray further towards the exterior. The whole ray is narrower; the marginal cells (*m*) are more elongated, and are already partly replaced by tracheides. The ray to the left (*r*) may probably have been cut off from the principal ray by interpolated tracheides. C.N. 66. $\times 50$.

Fig. 17. A third section of the same stem, still further towards the exterior. The principal ray is no longer continuous, but is completely broken up by interpolated tracheides. Some of its isolated parts (*r*) are quite similar to secondary rays. C.N. 67. $\times 50$.

Fig. 18. Part of a transverse section showing cortex, and a small part of the secondary wood (*x*); the gap between them was caused by the growth of a Stigmarian rootlet, which is not figured. Remains of the phloëm (*ph*) are shown. Many of the cortical cells, especially those at a short distance from the interior, show recent tangential divisions, indicating the formation of periderm (*pd*). From a slide (No. 6) prepared by Mr. LOMAX, in the possession of D. H. SCOTT. $\times 70$.

Fig. 19. Part of a median section, passing through a diaphragm. The cells towards both surfaces of the diaphragm have undergone regular tangential divisions (best shown on the upper surface), forming a layer of periderm. C.N. 132***. $\times 30$.

Fig. 20. Part of a transverse section passing tangentially through the base of a branch,

which is inserted between two bundles (*v.b.*) of the main stem. The primary vascular bundles (*v.b'*), and interfascicular tissue of the branch are shown, and the connections with the wood of the main stem. C.N. 132** (from same stem as the last). $\times 30$.

PLATE 80.

Figs. 21 and 22. *Calamites*.

Fig. 21. Part of a tangential section, passing through the primary wood, and showing the base of a branch. Near the bottom of the figure the section has touched on the canals of two bundles, and shows their disorganized protoxylem (*px.*). All the tracheæ have tangential pits—characteristic of the inner wood. In the direction of the arrow (*f*), a foliar bundle is shown. In the same straight line, further to the right, is another group of cells, which represents a similar bundle at the point when it begins to curve outwards. The branch has a minute pith, surrounded by groups of primary xylem. The connection of the latter with the nodal wood of the stem can be clearly seen at the lower side of the branch. Secondary wood has only been formed towards the upper side of the branch. The connection with the wood of the stem is entirely from below. From a slide (No. 53) prepared by Mr. LOMAX, in the possession of D. H. SCOTT. $\times 30$.

Fig. 22. *A.* Part of a transverse section of a very large stem, showing in median section, the base of an occluded branch. The pith of the main stem is below the figure. In the branch the pith tapers towards the base. The connection of the wood of branch and stem is shown. Midway between the inner and outer limits of the wood of the stem, at the level indicated by the arrows, the pith of the branch comes to a sudden end, and is replaced by secondary wood seen in transverse section. $\times 6$.

B. Portion of same enlarged, showing transition from pith of branch (*p*) to anomalous wood (*x*) in region indicated by the arrows in *A.* $\times 70$. C.N. 134*.

Figs. 23–26. *Calamostachys Binneyana*.

Fig. 23. From a transverse section of a strobilus, showing the central cylinder or stele of the axis. The section passed through a fertile node, bearing 7 sporangiophores. The stele is obtusely triquetrous, with the vascular bundles at its prominent corners. There appear to have been 7 bundles in all; the projecting points of the xylem (*sp*) mark the places where the bundles passing out to the sporangiophores were given off. One such bundle is partly preserved (*sp*⁺). On the inner side of the bundles in the cylinder are

irregular canals, in which remains of the protoxylem (*px*) can be traced. All the tissue within the ring of bundles is pith. A few tangential interfascicular cell-divisions have taken place. C.N. 991. $\times 70$.

Fig. 24. From a transverse section of another strobilus, showing the stele and part of the cortex. Here there are probably 6 bundles, in groups of 2 (as at *px*, where their protoxylem is shown). Secondary thickening has made considerable progress. In other respects the structure is similar to that in the last figure. C.N. 1016. $\times 70$.

Fig. 25. From a transverse section of a strobilus, showing the quadrangular stele and part of the cortex. There are 4 vascular bundles, one at each corner. Tangential divisions have begun in the cells of the interfascicular tissue. *px*, the 4 groups of protoxylem. C.N. 1013A. $\times 70$. Compare Plate 74, photograph 14.

Fig. 26. Part of a somewhat oblique transverse section, showing a vascular bundle in connection with the cortical tissues. *p,p*, pith; *x,x*, xylem; *px*, protoxylem; *ph*, phloëm-group; *pc, pc*, probable pericycle; *c,c*, cortex. C.N. 1013. $\times 200$.

PLATE 81.

Calamostachys Binneyana.

Fig. 27. Part of an approximately median longitudinal section of the axis of a large strobilus. *p,p*, the wide pith of the cylinder; on either side is the xylem of a vascular bundle. Two canals are shown with remains of the protoxylem (*px*), (*px*). *c,c*, the cortex, of which only the inner layers are shown. The section passes through a whorl of sporangiophores. C.N. 1022A. $\times 70$.

Fig. 28. Tangential section through a vascular bundle of the same strobilus. The section passes through a node bearing a whorl of bracts (the second sterile node from below, shown in photograph 10, on Plate 73). The canal of the bundle, with the protoxylem (*px*), is shown both above and below the node. The nodal wood has short reticulated tracheides. In the internode the tracheæ are generally scalariform. The parenchyma on either side belongs to the stele. C.N. 1022. $\times 70$.

Figs. 27 and 28 are from the same preparations as photographs 10 and 11, on Plate 73. Fig. 27 is from a part not shown in the photographs.

Fig. 29. Peltate sporangiophore, with a sporangium attached, from an approximately transverse section of a strobilus. The vascular bundle is shown in the axis of the sporangiophore, and a branch-bundle is seen passing through the peltate expansion, to the base of the sporangium. The sporangium is attached to the edge of the peltate scale, at *a*. Within the sporangium are numerous spore-tetrads, enclosed in their mother-cell membranes. C.N. 996. $\times 70$.

Fig. 30. Part of a tangential section of a strobilus, showing a sporangiophore-pedicel (*sp*) in transverse section, surrounded by its 4 sporangia. The vascular bundle of the sporangiophore is seen. Parts of the adjacent whorls of coherent bracts, *br*, *br*, are shown. Three vascular bundles are shown in the lower, and two in the upper whorl. C.N. 1023. $\times 50$.

Fig. 31. Details of sporangium-wall,

A. In surface view; "buttresses" seen (as at *bu*) projecting from cell-walls into interior of cells;

B. In transverse section of sporangium (tangential of strobilus). Here the "buttresses" (*bu*) are seen from the side, with the thin cell-wall between them. Such a section cuts *across* the cells shown in *A*.

C. In longitudinal section of sporangium (transverse or radial of strobilus). Here the narrow edges of the "buttresses" (*bu*) are shown. Such a section cuts the cells shown in *A* *lengthwise*. The difference in the thickness of the wall in *B* and *C* is accidental. C.N. 1003. $\times 200$.

Fig. 32. Part of a tangential section, passing through the peltate expansions of the sporangiophores (*sp*), 4 of which are shown, and also part of the whorl of bracts (*br*) between them. In *sp*. 1 the right-hand dichotomy of the vascular bundle (*vb*) is well shown. In *sp*. 2 the section shows one bundle in transverse section, and a branch-bundle cut longitudinally. In *sp*. 3 parts of the vascular bundles are shown. At two points the section passes through the concavities of the under surface of the scale, and shows part of the wall of 2 sporangia, *w.*, *w.*; *br'*., *br'*., outline of adjacent bracts. C.N. 1898A. $\times 30$.

Fig. 33. Part of a sporangium containing spore-tetrads. The extremely unequal size of the different spores of the same tetrad is the point specially illustrated. In many cases (as at *b*) certain spores appear to be quite abortive. At *a*, a mature spore is shown, with the 3 radiating fissures in its membrane. C.N. 1007. $\times 100$.

PLATE 82.

Figs. 34 and 35. *Calamostachys Binneyana*.

Fig. 34. Part of a sporangium containing spore-tetrads, to show abortive spores with normal sister-cells. In a tetrad towards the left-hand, 3 out of the 4 spores are abortive (*b*). C.N. 1011. $\times 100$.

A, *B*, *C*, and *D*. Tetrads and spores more highly magnified.

A. A normal tetrad. All 4 spores are about equally developed. C.N. 1005. $\times 200$.

B. A tetrad in which one spore is abortive. C.N. 1013A. $\times 200$.

C. A tetrad with one abortive spore, and one of intermediate size. C.N. 1011. $\times 200$.

D. Two mature spores to show fissures and thickening of the spore-membrane. C.N. 1007. $\times 200$.

Fig. 35. Part of a sporangium, to show layer of parenchyma lining the sporangial wall. Within this are mature spores. C.N. 1008. $\times 150$.

Figs. 36-39. *Calamostachys Casheana*.

Fig. 36. Transverse section of the axis of the strobilus. In the middle is the central cylinder, with a large pith, surrounded by 6 vascular bundles. The structure is the same as in fig. 24 (Plate 80), from *C. Binneyana* (*px.*, two of the protoxylem-groups). There is a well-marked zone of radially arranged secondary xylem. Outside this are remains of thin-walled cells, and surrounding the whole is the well-preserved outer cortex. The outlines to the exterior mark the position of the sporangia. This is from the same preparation as photograph 16, on Plate 74. C.N. 1588. $\times 70$.

Fig. 37. Section of a macrosporangium (that marked $\times$ in fig. 36), containing several macrospores (as at *ma*), and a large number of abortive spores (as at *b*). There are slight remains of tissue lining the sporangial wall. C.N. 1588.

A. Microspores from the tangential section of the same specimen. C.N. 1587.

B. Macrospores and abortive spores. C.N. 1587.

C. " " " C.N. 1588.

All the above $\times 100$.

Fig. 38. Group of four sporangia from a tangential section, with the pedicel of their sporangiophore (*sp.*) between them. One is a microsporangium; the other three are macrosporangia. Among the macrospores abortive spores are seen. Also shown in Plate 74, photograph 15. C.N. 1587. $\times 30$.

Fig. 39. Parts of two adjacent sporangia from a tangential section of the other specimen of this species. To the right is a microsporangium, containing microspores (*mi*) only. To the left is a macrosporangium, in which one of the macrospores (*ma*) and several abortive spores (*b*) are shown. C.N. 1025. $\times 100$.

PLATE 83.

Figs. 40-44A. *Sphenophyllum plurifoliatum*.

Fig. 40. Obliquely transverse section of a moderately young stem. In the middle is the triarch primary xylem. The three protoxylem groups at the angles (*px.*), with their small, spiral or reticulated tracheæ, are clearly seen. The more central primary tracheæ are pitted. About four layers of secondary wood

have been formed. The parenchymatous cells at the corners of the tracheæ are shown. The wood is surrounded by secondary cortical tissues, probably including both phloëm and periderm. At *c, c*, remains of the primary cortex are present, but only a part of this has been drawn. C.N. 897. $\times 30$.

Fig. 41. Part of an oblique section, showing a portion of the primary xylem. In the direction of the arrow (*px*) is a group of protoxylem, with spiral tracheæ, partly uncoiled. Adjoining these below are scalariform tracheæ, and below these again are pitted elements. Above the protoxylem a small portion of the secondary wood is indicated. C.N. 893. $\times 200$.

Fig. 42. Part of an approximately transverse section, to show secondary wood, *x*²; cambium, *cb*; and phloëm, *ph*. C.N. 882. $\times 70$.

Fig. 43. Part of a transverse section (the same as that shown in photograph 19 on Plate 75); *x*, part of primary xylem; *x*², secondary xylem; *cb*, cambium; *ph*, phloëm; *pd*, internal periderm. C.N. 894. $\times 50$.

Fig. 44. Part of a radial section through the secondary wood, showing the *radially-elongated* parenchymatous cells (as at *r*), passing between the tracheæ. C.N. 884. $\times 50$.

Fig. 44A. Part of another, approximately radial section, showing the longitudinal strands of xylem-parenchyma, *x.p.*, *x.p.*, and portions of the radial cells connecting them. C.N. 903. $\times 50$.

Figs. 45 and 46. *Sphenophyllum insigne*.

Fig. 45. Approximately transverse section of a young stem, without any secondary thickening. In the middle is the triarch primary xylem, with protoxylem at the three angles. Surrounding this are the primary cortical tissues. C.N. 911. $\times 50$.

Fig. 46. Transverse section of a very young stem, showing part of a whorl of coherent leaves, in which two foliar vascular bundles are seen (*v.b.*). The fragments of tissue seen to the exterior are probably portions of leaves. *st* = stele of stem. C.N. 917. $\times 50$.

PLATE 84.

Sphenophyllum insigne.

Fig. 47. *A*. Longitudinal median section, passing through a node. *l, l*, bases of leaves. $\times 13$.

B. Portion of wood from the same preparation, seen in tangential, but somewhat oblique section. The scalariform markings of the tracheæ, and the medullary rays (*r*) are seen. *Cf.* fig. 50. C.N. 1420. $\times 100$.

- Fig. 48. Part of the transverse section of the largest stem, showing secondary wood, x^2 ; cambium, cb ; phloëm, ph ; and internal periderm, pd . C.N. 914. $\times 50$.
- Fig. 49. Part of the secondary wood of the same specimen, in radial section; r , medullary rays. C.N. 924. $\times 100$.
- Fig. 50. Part of the secondary wood of a large stem, in tangential section, showing the medullary rays (r), of various heights, and the scalariform pits of the tracheæ; compare with fig. 47B. C.N. 921. $\times 100$.
- Fig. 51. Part of a transverse section of the largest stem. x^2 , secondary wood; cb , cambium; ph , phloëm; pd , inner layers of periderm. C.N. 913. $\times 100$.
- Fig. 52. Corresponding radial section from the same specimen; lettering as before. Note the elements in the phloëm resembling sieve-tubes.

The separation between periderm and phloëm is accidental; in other parts of the section they are continuous. The delicate layer which is severed is probably phellogen. C.N. 924. $\times 100$.

PLATE 85.

- Fig. 53. *Sphenophyllum insigne*. Part of a longitudinal section of the wood, passing through the canal, and showing the spiral tracheæ of the protoxylem, px . To the left of the canal is primary xylem, x ; to the right the secondary wood, x^2 , begins. The section is somewhat oblique.

From a stem of moderate size, with secondary wood 7–9 cells thick. C.N. 922. $\times 100$.

Figs. 54–58. *Sphenophyllum Dawsoni*.

- Fig. 54. Part of a longitudinal section of a small strobilus, showing 4 whorls of bracts. The section is partly radial, partly tangential. x , part of xylem of axis; sp , various sporangiophores, showing attachment to bracts. Fragments of sporangia, and numerous spores, are shown. C.N. 1898K. $\times 15$.
- Fig. 55. Part of a transverse section, through the whorl of bracts close to its insertion on the axis. From the section figured by WILLIAMSON, "Organization," Part XVIII., Plate 27, fig. 9. Three bundles are shown just separating from one another. b , bundle going to a bract; sp , sp , bundles going to two sporangiophores. C.N. 1049A. $\times 200$.
- Fig. 56. Corresponding section from the same specimen, taken through the whorl of bracts, a little higher up than the last. From the section figured by WILLIAMSON, *loc. cit.*, Part XVIII., Plate 26, fig. 2. The three bundles have now quite separated, and the projecting bases of the sporangiophores are seen. b , bundle going to bract; sp , sp , bases of sporangiophores. C.N. 1049B. $\times 100$.

Fig. 57. Transverse section through a sporangium, *sm*, and its sporangiophore, *sp*. In the former, delicate tissue lining the wall is shown, and within this the spores. In the sporangiophore, the xylem of the vascular bundle is evident. C.N. 1898H. $\times 60$.

Fig. 58. Corresponding longitudinal section of a sporangium and part of its sporangiophore, showing the attachment. The vascular bundle of the sporangiophore is shown. The section is somewhat oblique. C.N. 1898E. $\times 60$.

PLATE 86.

This contains figures, from photographs, of medullary casts of *Calamites*. For description, see text, pp. 896–899.

All the figures are much reduced. F is rather more than a quarter of natural size ; all the rest are rather more than half natural size.

Fig. 1.

Fig. 2.

Fig. 6.

Fig. 3.

Fig. 5.

Fig. 4.

Fig. 7.

Fig. 8.

Fig. 9.

Fig. 10.

Fig. 11.

Fig. 12.

Fig. 13.

Figs. 7-9. *Calamites*.

Figs. 10-13. *Calamostachys Binneyana*.

Fig. 14.

Fig. 17

Fig. 18

Fig. 15

Fig. 16

Fig. 14 *Calamostachys Binneyana*.
Figs. 15-16, *C. Casheana*. Figs. 17-18, *Calamostachys* sp.

Fig. 19

Fig. 21

Fig. 22

Fig. 20

Fig 23

Fig 24

Fig. 26

Fig 25.

Fig. 23, *Sphenophyllum insigne*. Fig 24, *Sphenophyllum* sp.
Figs. 25-26 *Sphenophyllum Dawsoni*.

Fig. 1.

Fig. 2.

Fig. 3.

Fig. 4.

Fig. 5.

Fig. 6.

Fig. 7.

Fig. 8.

Fig. 9.

Fig. 10.

Fig. 12.

Fig. 14.

Fig. 13.

Fig. 11.

Fig 15

Fig. 16

Fig. 17

Fig. 19.

Fig 20.

Fig 18

Fig. 27.

Fig. 28.

Fig. 29.

Fig. 30.

Fig. 31.

Fig. 32.

Fig. 33.

Fig. 34

Fig. 38.

Fig. 35.

Fig. 36.

A

Fig. 39.

Fig. 37.

Fig. 40

Fig. 41.

Fig. 42.

Fig. 43

Fig. 44

Fig. 44A.

Fig 46

Fig 45.

Fig 47.

Fig 48

Fig 51.

Fig 49.

Fig 50

Fig 52

Fig. 53.

Fig. 54.

Fig. 55.

Fig. 57.

Fig. 56.

Fig. 58.

A—G, Calamites.

XVI. *Further Observations on the Organization of the Fossil Plants of the Coal-Measures.*—Part II. *The Roots of Calamites.*

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[PLATES 15–17.]

Introduction.

UNTIL quite recently our knowledge of the roots of the *Calamites* has been very scanty and limited to such characters as can be seen with the naked eye, in specimens preserved as casts and impressions. LINDLEY and HUTTON,* in 1833, figured a *Calamite* with two branching roots, inserted immediately above the nodes of the stem in which they were borne, besides other more doubtful specimens of the same kind.†

Many similar casts have been observed by more recent investigators. GRAND'EURY, for example, has figured numerous specimens of *Calamites*, bearing roots, both on their rhizomes and their upright stems. So far as his figures show, the roots are always inserted exactly at the nodes.‡

C. E. WEISS has given an excellent account of the external appearance and arrangement of *Calamitean* roots, with extremely clear figures.§ In some of the specimens which he has illustrated the insertion of the verticillate roots on the nodes of the stem is quite evident. The central cylinder of the roots can be easily traced and is seen to be continuous with the vascular bundles at the node.|| In other cases the

* 'Fossil Flora of Great Britain,' vol. 1, Plates 78 and 79.

† See also WILLIAMSON, "Organization of the Fossil Plants of the Coal-Measures," Part I., 1871, 'Phil. Trans.,' Plate 28, fig. 35.

‡ GRAND'EURY, 'Flore carbonifère du dépt. de la Loire,' 1877, Plates 1, 2, and 3.

§ C. E. WEISS, "Steinkohlen-Calamarien," Part I., 1876, and Part II., 1884; published in 'Abhandlungen zur geologischen Specialkarte von Preussen.'

|| See especially Part II., Plate 2, fig. 2.

roots are grouped in tufts, which arise at, or immediately above, the nodes, and close to the insertion of lateral branches.*

STUR, in his account of the roots of *Calamites*, mentions one point of considerable interest.† He finds that the woody cylinder of the root is not always median, but is often laterally displaced, showing that it was *freely movable* within the outer cortical envelope. This fact finds its explanation now that we know that the middle cortex of Calamitean roots was traversed by large lacunæ, and would thus offer little resistance to the displacement of the central cylinder.

STUR mentions that some of the roots observed by him bear rootlets, while others do not. He is disposed to regard the latter as floating roots, the former as having grown in the soil.

A fine specimen of a Calamitean stem, showing clearly the insertion of the roots exactly on the nodes, has been figured by RENAULT.‡

From the sources mentioned, as well as from others, we thus have a general idea of the external characters of the adventitious roots of *Calamites*, and of their arrangement on the stem. It is only quite recently, however, that we have acquired any exact knowledge of their structure. As mentioned in our former paper,§ RENAULT has now found decisive proof that certain fossils formerly described under the name of *Astromyelon*|| are identical with the roots of *Calamites*, thus confirming the conclusion at which he had already arrived in the year 1885.¶

Relation of Root and Stem.

The evidence for the fact that roots with the structure of *Astromyelon* were borne on Calamitean stems, depends at present on the discoveries of RENAULT, who in his latest work repeatedly figures such roots in direct connection with the stem of his *Arthropitys* (our *Calamites*) as well as of *Calamodendron* and *Bornia*.**

* See Part II., Plate 8, fig. 1, and Plate 9, fig. 1.

† D. STUR, "Die Calamarien der Carbon-Flora der Schatzlarer Schichten," 1887, p. 1; published in 'Abhandlungen der Kaiserlich-Königlichen Geologischen Reichsanstalt.' Vienna.

‡ RENAULT et ZEILLER, 'Flore houillère de Commentry,' Part II., Plate 57, fig. 1.

§ WILLIAMSON and SCOTT, "Further Observations on the Organization of the Fossil Plants of the Coal-Measures," Part I., p. 899, 'Phil. Trans.,' B., 1894.

|| WILLIAMSON, "Organization," Part IX., 1878, p. 319; Part XII., 1883, p. 459. HICK and CASH, "Flora of the Lower Coal-Measures of Halifax," Part III., 1881, and Part IV., 1884; published in 'Proc. Yorkshire Geological and Polytechnic Society,' vols. 7 and 8. Their specimens are named by them *Myriophylloides*; the question of the identification of the latter with *Astromyelon* will be considered below. See also RENAULT, "Végétaux fossiles du genre *Astromyelon*," 'Ann. des Sci. Géol.,' vol. 17, 1885.

¶ "Nouvelles Recherches sur le genre *Astromyelon*," 'Mém. de la Soc. des Sci. Nat. de Saône et Loire,' 1885.

** RENAULT, "Flore fossile du bassin houillier et permien d'Autun et d'Épinac," Part II., 1894; published in 'Études des Gîtes Minéraux de la France.' See especially Plates 42, 43, 44, 53, 54, 55, 59. The text of this memoir has not yet appeared.

Among our own specimens, which RENAULT regards as specifically distinct from his own, such evidence is scanty. In one case, however, we believe that the connection between root and stem is distinctly shown. The sections numbered C.N. 1351—C.N. 1355 (see Plate 15, photographs 1 and 2), in the WILLIAMSON Collection, were all cut from the same specimen. They are all approximately tangential sections of the wood of a main axis, on which lateral roots* are borne. Three of these roots are cut through transversely on their way out through the wood. Two of them are placed side by side, and appear in the same section (C.N. 1355). All three exhibit the typical structure of the larger specimens of *Astromyelon*—a considerable pith (which has been bored by Stigmarian rootlets, but was probably solid in life), a ring of centripetal xylem-groups (10 to 12 in number), and a zone of secondary wood, which is connected with that of the parent axis (see photograph 1).

There can be no doubt that the specimen shows the attachment of the roots to a main axis of some kind. The question to be solved is, whether this main axis was itself a root or a stem. This question appears to be decided by one of the sections (C.N. 1353; see Photograph 2), which distinctly shows three of those "lenticular organs," or enlarged medullary rays, which are so characteristic of the stem of *Calamites*, in its infranodal regions, but which, so far as we know, are entirely absent from the roots themselves.† At two points, also, the transverse sections of outgoing leaf-trace bundles can be distinguished. Photograph 2 shows one of the "lenticular organs," and one of the leaf-traces, which is especially clear. These facts demonstrate that the section passes through a node, and therefore that the axis is a stem. This conclusion is further strengthened by the fact that immediately above the node we find the base of a branch (probably abortive) which is thus in the normal position for branches of the stem of *Calamites*.‡

This specimen may therefore safely be regarded as affording additional evidence that organs with "*Astromyelon*" structure, were borne on Calamitean stems.

The nature of the organs hitherto known under the name of *Astromyelon*, is now so far established that we know them to have been appendages of the stem of *Calamites* (*Arthropitys* of the French authors). RENAULT has shown that very similar appendages, also showing the *Astromyelon* type of structure, were produced on the stems of *Bornia* and *Calamodendron*.§ So far as our English specimens of "*Astromyelon*" are concerned, we have no reason to doubt that they all belonged to the genus *Calamites*, though it is very probable that various species may be represented among them. The direct evidence of continuity applies only to the larger specimens, such as those originally described, in which there is a conspicuous pith.||

* The proof that these organs are, morphologically, *roots*, will be fully given below.

† See our previous memoir, "Further Observations," &c., Part I., p. 887; also WILLIAMSON, "Organization," Part IX., p. 325.

‡ See our "Further Observations," Part I., pp. 890 and 893.

§ *Loc. cit.*, "Flore fossile d'Autun," Part II., Plates 42 and 43, 59 and 60.

|| See WILLIAMSON, "Organization," Part IX, Plate 19, figs. 1-7.

The smaller specimens, such as those which were first described by HICK and CASH under the name *Myriophylloides*,* but have since been united with *Astromyelon*,† were no doubt branches of the larger organs, as will be shown below.

Structure of the Roots.

We have now to consider in detail the structure of these appendages, with special reference to those points by which their morphological nature has been established. That they were quite different from the ordinary branches of a Calamitean stem became obvious as soon as their organization was understood.‡ Their characteristic lacunar cortex, the entire absence of nodes, the usually solid pith, and the absence of canals accompanying the vascular bundles, all serve to distinguish them. That these organs were of the nature of *roots* could, however, only be established by a minute investigation of their structure and mode of development, so far as the latter could be ascertained. We hope that, by our observations, we have been able to add something to the evidence already brought forward by RENAULT, who recognizes most of these organs as true roots, though in certain cases he prefers to regard them as "stolons."§

The characters (likely to be traceable in petrified specimens) on which we have to depend in distinguishing a root from a stem, are the following :—

1. Centripetal development of the primary xylem.
2. Alternate arrangement of the primary groups of xylem and phloëm.
3. Endogenous mode of origin of the organ itself, and of its branches.
4. Absence of nodes.

Though no one of these characters is necessarily conclusive by itself, the sum of them is sufficient to determine with certainty the root-nature of the organ.

In describing the structure it will be best to begin with the typical specimens, possessing a well-marked medulla, such as those which have been found in direct connection with Calamitean stems. We will afterwards pass on to the more minute specimens, many of them destitute of any evident pith, which we regard as the rootlets, or finer branches, of the same organs.

The largest specimen in the collection is one figured in a ¹prévious memoir.|| This is somewhat compressed, and measures, in its decorticated condition, about 25 millims. in greatest and 11 millims. in least diameter. The pith is hollow, and this is the only specimen in which, from the definite inner limit of the persistent peripheral portion of the medulla, it appears probable that the latter was really fistular during life. In

* *Loc. cit.*, 'Proc. Yorkshire Geol. and Polytechnic Soc.,' vol. 7, 1881.

† By WILLIAMSON, "Organization," Part XII., 1883.

‡ WILLIAMSON, *loc. cit.*, Parts IX. and XII.

§ *Loc. cit.*, "Flore fossile d'Autun," &c., Part II., Plates 55, 56, 57, 59, 60.

|| WILLIAMSON, "Organization," Part IX., Plate 19, fig. 5; C.N. 1334.

all other specimens the pith is either solid, or, if hollow, there is every appearance of the cavity being due to decay or to the intrusion of Stigmarian rootlets.*

The pith varies enormously in size in the different specimens, and may only consist of three or four cells, as seen in transverse sections, while in the smallest rootlets it disappears altogether. Except in these extreme cases the structure is fairly uniform in all. The pith consists of rather large-celled parenchyma, and presents no peculiarities (see Plate 16, figs. 1, 2, and 3). It is surrounded by a ring of primary xylem-groups, varying in number from 25 downwards. When the pith is large the xylem-bundles are usually separated from one another by broad primary rays (see Plate 15, photographs 1 and 3); when it is small the bundles may be nearly in contact with one another, and in the latter case their limits may be somewhat difficult to trace. The presence, however, of these primary groups of xylem is absolutely constant, and their structure is always essentially the same. Each group, as seen in transverse section, has an approximately triangular form, with one angle directed outwards (see Plate 16, figs. 1 and 2).† It consists of a varying number of tracheides, of which there are often about 20. The elements become smaller towards the peripheral angle, and it is constantly at the angle itself that the most minute tracheide is situated (figs. 1 and 2, *px.*).

In accurately transverse sections, if the cells of the pith have rather thick walls, it may not be easy to distinguish them from the primary tracheæ. With care, however, this can always be done, in good preparations. Wherever the section is at all oblique, the primary tracheæ can be recognized with ease by the pits on their walls.

The arrangement of the tracheæ at once suggests, even from the inspection of transverse sections alone, that the development of each group of primary xylem was *centripetal*, the small tracheæ at the external angle representing the protoxylem, or first-formed elements. This conclusion is rendered certain by the examination of oblique and longitudinal sections, in which we find that the smallest and most external elements of the primary xylem are spirally thickened. This, for example, is beautifully shown in the radial section (C.N. 1317) a part of which is represented in fig. 3. The spiral protoxylem-tracheæ are quite unmistakable, both at the place figured, and at several other points in the section. Similar observations have been made by RENAULT, who has shown clearly that the development of the primary wood was centripetal in his specimens, which he refers to different species from ours.‡ We find that the spiral tracheides are few, and their spirals densely coiled, a peculiarity characteristic of the root in recent plants, and due to the shortness of its growing region. (See DE BARY, "Comp. Anat.," p. 352.)

* See WILLIAMSON, "Organization," Part IX., Plate 19, figs. 1-7; Part XII., Plates 27 and 28, figs. 2, 3, and 6; also Photographs 1, 3, 4, 6, and 7 in the present paper.

† See also WILLIAMSON, "Organization," Part I., Plate 25, fig. 16; Part XII., Plate 27, fig. 3.

‡ RENAULT, "Recherches sur les Végétaux fossiles du Genre *Astromyelon*," 'Annales des Sciences Géologiques,' vol. 17, 1885; see p. 12, Plate 8, fig. 8, &c.; 'Flore fossile d'Autun,' Part II., Plate 57, fig. 7, &c.

The elements which adjoin the actual protoxylem on the inner side are often reticulated. Further towards the interior the primary tracheæ become considerably larger, and have pitted walls, the pits being often transversely elongated, so as to give a scalariform character to the thickening (fig. 3). Some of the pits show a slight border. The primary tracheæ have very oblique terminal walls, which are pitted like the lateral walls; there is no reason to doubt that these elements were closed tracheides, and not open vessels.

The primary xylem-groups, then, were evidently developed centripetally, and so far agree with those of recent roots.

The primary strands of *phloëm* can of course only be recognized in the most favourable preparations. A good example is represented in fig. 1, which is drawn from a section previously figured as a whole.* The specimen is the original one of "*Myriophylloides Williamsoni*," described by HICK and CASH in 1881, and another transverse section of it is figured in the memoir by those authors.† Neither of the former figures, however, show either the phloëm or the primary xylem. The details are remarkably clear in this specimen. The root has nine groups of primary wood, and shows the commencement of secondary growth; the secondary wood is as yet only three or four cells in thickness. Immediately outside the wood is a zone of very delicate tissue; opposite the protoxylem-groups this zone is excessively narrow—only two cells in thickness—and evidently represents the dividing cambium only. *Between* the groups of primary wood, however, the delicate tissue attains a thickness of about five cells; evidently phloëm is present at those places, to the outside of the cambial layer (fig. 1, *ph*, *ph*, on either side of the protoxylem, *px*). The alternation of the primary strands of xylem and phloëm is quite regular. Here, then, is another point, in which these organs conform to the typical structure of recent roots.‡

Secondary tissues, as is already well known, were formed in great abundance, and the various preparations show them at all stages of development—the wood, in the larger specimens, sometimes attaining a radial thickness of at least 60 elements.

* WILLIAMSON, "Organization," Part XII., Plate 28, fig. 2.

† HICK and CASH, *loc. cit.*, 'Proc. Yorkshire Geol. and Polytechnic Soc.', 1881.

‡ HICK and CASH describe the whole of this thin-walled zone as cambium, *loc. cit.*, p. 402. These authors have expressed doubts as to the identification of their *Myriophylloides* with *Astromylon* (*loc. cit.*, 'Proc. Yorkshire Geol. and Polytechnic Soc.', vol. 8, 1884, p. 375). They point out, quite justly, that the similarity in cortical structure is not by itself sufficient to prove identity. They go on, however, to state that the *axial* structure of *Astromylon* bears "by no means a close resemblance to that of *Myriophylloides*." This is a mistake, arising from the fact that, at that time, the primary wood of *Myriophylloides* had not been recognised. The structure of the original specimen of *Myriophylloides* is in fact identical with that of *Astromylon*. For example, there is no real difference, except in age, between the root shown in "Organization," Part XII., Plate 28, fig. 2 (*Myriophylloides*), and that shown in Plate 27, fig. 3 (typical *Astromylon*). On comparing our own fig. 1 (*Myriophylloides*) with fig. 2, which is from a typical *Astromylon*, the essential identity of structure becomes obvious. The question of the identification of the smallest pithless specimens presents greater difficulties, and will be discussed in the text.

The general structure of the secondary wood is identical with that of the stem of *Calamites*. The fascicular wood abuts directly on the external elements of the primary xylem (see fig. 2). The interfascicular wood is soon formed across the whole width of the primary rays, which, consequently, cannot be traced far outwards (see Plate 15, photographs 3, 6, and 7). In some cases the cells of the primary ray show tangential dilatation, exactly as we described in the case of the stem in our last paper.*

In these, as in other roots, the primary interfascicular rays are necessarily limited to the wood, for each of them corresponds in position to a strand of primary phloëm.

A characteristic feature of the secondary wood is the regular presence of a ray one or two cells in thickness, exactly opposite each protoxylem-angle (see Plate 16, fig. 2, *f.r.*). These rays, which often consist of cells rather broader than the tracheæ, can sometimes be traced for a long distance through the wood. In some cases they become subdivided by intercalated series of tracheæ. We may call them *fascicular* rays, to distinguish them from the broader *interfascicular* rays which lie between the bundles of primary xylem. The fascicular rays can be recognized in radial sections also, wherever the plane of section exactly passes through the protoxylem (see fig. 3, *f.r.*). They can also be distinguished in tangential sections which pass through the inner part of the wood. These rays were observed by RENAULT, in his *Astro-myelon augustodunense*, in 1885.†

The formation of a ray opposite each protoxylem-group is a well-known phenomenon in recent roots.‡

The wood also contains numerous secondary rays of the ordinary type.§

The tracheæ agree in all respects with those of the stem. Their pits are usually limited to the radial walls, and are distinctly bordered, as can best be seen in good tangential sections.

Remains of the cambium and phloëm have been observed in several of the more advanced specimens, as well as in the younger roots already mentioned. Perhaps the best specimen in this respect is that illustrated in Plate 15, photograph 3, and in Plate 17, figs. 10 and 11. This root shows a distinct layer of phloëm (fig. 10, *ph.*), which has split away from the wood, and remains attached to the cortical zone. Here and there a tabular cambial cell is seen at the outer edge of the wood (*cb.*). We cannot be certain that the whole thickness of the phloëm remains; the part preserved is six or more cells in width, and its elements show traces of a radial arrangement. Most of this tissue, no doubt, belonged to the secondary phloëm; some more irregular groups in the outer part of the zone probably represent the primary phloëm.

The structure of the *cortex* has been fully described in former memoirs.|| Only a

* "Further Observations," Part I., p. 884.

† *Loc. cit.*, "Nouvelles Recherches," p. 98.

‡ DE BARY, 'Comparative Anatomy of Phanerogams and Ferns,' Engl. ed., p. 474.

§ See WILLIAMSON, "Organization," Part IX., Plate 19, fig. 6, c.

|| See especially "Organization," Part XII.

brief recapitulation, with the addition of one or two details, is needed here. The question of the presence of a distinct pericycle and endodermis will be postponed until the smaller rootlets have also been taken into consideration.

In all cases where the cortex is preserved, it consists of three well-marked zones: (1) an inner cortex, of continuous parenchyma, immediately surrounding the central cylinder; (2) a middle cortex, which is *lacunar*, consisting of radial plates of tissue, separated from one another by wide intercellular spaces; (3) an outer cortex, consisting, like the inner zone, of continuous parenchyma.* The relative thickness of the three zones varies considerably in different specimens, as is sufficiently shown in the figures cited. The lacunæ, however, are always arranged in a single circle only. The large root shown in photograph 3 has a somewhat peculiar cortex, which, at the first glance, appears to consist entirely of solid parenchyma. More careful examination, however, reveals the existence of a rather narrow lacunar zone (see Plate 17, fig. 11, *l.z.*) in the usual intermediate position. The trabeculæ have been crushed in upon the inner cortex, so as almost to obliterate the lacunæ between them.

The specimen shown, in transverse section, in photograph 4, has a cortex of the "*Astromylon*" type, but differing considerably from the more usual form. It is, in all probability, specifically distinct from the more ordinary examples. The trabeculæ are much more numerous than usual, and the lacunæ between them are narrower in a corresponding degree. At some places the lacunæ are not empty, but contain large, irregular, rounded cells. Similar intralacunar cells have been found occasionally in other specimens; their nature will be discussed below (p. 693).

The structure of the trabeculæ is well shown in longitudinal or oblique sections, from which it is evident that they formed continuous vertical partitions, each of which was only one cell in thickness (see fig. 8; also "Organization," Part XII., Plate 31, fig. 4). The cells of which they are composed are cylindrical in shape, so that the partitions, as seen in tangential section, have a moniliform appearance. The inner cells of each trabecula are usually short, while those further to the exterior are often much elongated in the radial direction. Some further details as to the cortex will be given when the rootlets are considered.

The Rootlets.

Under the name "rootlets" we group those smaller specimens, which, while agreeing in other respects with the forms already described, differ from them in having little or no pith, and no primary rays, so that the groups of primary xylem either meet at the centre of the stele, or are, at least, laterally confluent. Specimens of this kind were included by HICK and CASH in their genus *Myriophylloides*,† the type-specimen of which, as we have seen, had a considerable pith and typical *Astromylon*

* See the figures in "Organization," Part XII.

† *Loc. cit.*, 'Proc. Yorkshire Geol. and Polytechnic Soc.,' vol. 8, p. 377, 1884. See also RENAULT, "Nouvelles Recherches," p. 101, 1885.

structure. The pithless specimens, however, really differ conspicuously from the ordinary type of *Astromylon*. Now that we know that *Astromylon*, in its typical medullate form, is nothing but the root of *Calamites*, it becomes desirable to reconsider the evidence for the identification with it, of the minute pithless specimens. We believe we are able to prove that here also the identification is correct, and that the smallest specimens, without medulla, are, in fact, the finer branches, or rootlets, which were borne on the larger medullate organs. We shall, therefore, employ the word "rootlet" throughout the description, though, as we shall find, there is no sharp distinction between these finer branches and the larger medullate specimens which we term simply "roots."

The structure of the rootlets will first be described, after which we will discuss the evidence as to their nature.*

In some of them the middle of the central cylinder is entirely occupied by the primary xylem, and there is no pith whatever. Neither does there seem to be parenchyma of any kind among the primary tracheæ (see figs. 5, 7, and 8; also fig. 1 in "Organization," Part XII.). In other cases, a very few elements, with somewhat thinner walls, can be distinguished at the centre (see, for example, fig. 4). In such cases it is often impossible to make out for certain whether these elements are really parenchymatous cells or merely thin-walled tracheæ. In other specimens, however, there is no doubt of the existence of a very small pith.† In the remarkable branched specimen, figured in a previous memoir,‡ the rootlets seen in longitudinal section show no pith, while the branch, which is cut transversely, has a little thin-walled tissue within the primary wood.§

In all these rootlets the primary wood, whether actually reaching the centre of the stele or not, is perfectly continuous, so that the number of strands of which it is composed is indicated by the protoxylem-angles alone. The latter are often quite distinct, as, for example, in Plate 16, fig. 4, where the rootlet was evidently tetrarch. So also, no doubt, was the rootlet shown in Plate 15, photograph 5.||

In the typical rootlets, with little or no pith, we have never found more than four

* The rootlets are illustrated in "Organization," Part XII., figs. 1, 5, and 7; and in photograph 5 and figs. 4, 5, 7, and 8 in the present paper.

† See, for example, the rootlet figured in "Organization," Part XV., Plate 3, fig. 23, which is almost certainly of the same nature. This rootlet occurs inside the stem of a *Lepidodendron selaginoides*, in the hollow zone left by the decay of the middle cortex. It is very probable that the rootlet had made its way, by its own growth, into the decaying stem, as so constantly happened in the case of the rootlets of *Stigmaria*.

‡ "Organization," Part XII., Plate 29, fig. 7.

§ Another very clear case of a minute pith (not figured) is C.N. 1348. Here the tetrarch rootlet has a perfectly distinct thin-walled medulla, consisting of three or four cells only, as seen in transverse section.

|| See also WILLIAMSON, "Organization," Part XII., Plate 30, fig. 5, which shows another tetrarch rootlet.

groups of protoxylem; triarch and diarch specimens also occur. Thus our fig. 7 shows a triarch rootlet, and one of those figured in a previous memoir was probably also triarch.* We have figured a very characteristic *diarch* rootlet in fig. 5. Another rootlet (see fig. 8), itself probably tetrarch, bears a diarch branch. Minute diarch rootlets are excessively common in the preparations, but, as a rule, their structure is not sufficiently definite for us to be certain to what they belong. We have, however, figured one of these doubtful rootlets in fig. 9. It occurs in the same preparation as that shown in fig. 8, so it is very probable that it may be of the same nature as the diarch branch shown in the latter figure, borne upon a rootlet of the usual structure. Fig. 9 is in itself of considerable anatomical interest. The rootlet, which is very young, is seen in oblique section. The diarch xylem-plate is not yet completely lignified in the middle; the minute tracheæ of the protoxylem are clearly shown at either end of the plate. A branch, which is obviously of endogenous origin, is seen in median section. Its xylem is directly continuous with one of the protoxylem-strands of the parent rootlet. A more typical example of root-structure would be difficult to find; we have therefore thought the specimen worth figuring, though we cannot be quite certain that it is of the same kind as the other rootlets.

Returning to the typical specimens, we find that the rootlets, in some cases, possess the primary tissues only, while others have undergone a greater or less degree of secondary growth in thickness. Such differences are no doubt dependent simply upon age. Thus the rootlet shown in fig. 7 is destitute of any secondary tissues, while fig. 4 shows the first commencement of their formation. The diarch rootlet, represented in fig. 5, already has about five layers of secondary wood. A tetrarch rootlet, previously figured,† has a broad secondary zone, the wood of which is about ten layers thick. Other rootlets, with much thicker secondary wood, in one case amounting to sixty layers of tracheæ (C.N. 1309), are included in the collection. The structure of the wood of these rootlets is in all respects identical with that of the larger roots, except, of course, that in the former, owing to the absence of primary rays, the wood is not broken up into wedges.

Fascicular rays, corresponding to the protoxylem-groups, can often be distinguished in the rootlets, as well as in the larger roots.

Remains of the phloëm are frequent in the better-preserved rootlets (see figs. 4 and 5). The secondary phloëm does not seem to have attained any great thickness. The tetrarch rootlet, shown in transverse section in fig. 4, is very instructive. The position of the four protoxylem-groups (*px.*) is quite clear; at these four points no secondary growth had as yet taken place. In two cases the cell lying immediately outside the protoxylem has undergone a single tangential division; at the other two points there seems to have been no division, though it is possible that the delicate septa may have perished. Opposite the protoxylem-groups there is evidently an

* WILLIAMSON, "Organization," Part XII., Plate 27, fig. 1.

† "Organization," Part XII., Plate 30, fig. 5.

entire absence of phloëm, while between them four distinct bands of phloëm (*ph*) are shown. Thus the usual alternation, characteristic of roots, is maintained. Within each of the four bands of phloëm growth in thickness has commenced, and from three to four layers of secondary wood have already been formed in this position.

The rootlet shown in Plate 15, photograph 5, is essentially similar, but here the wood has already attained a somewhat greater thickness.*

We now come to the subject of pericycle and endodermis. The rootlet shown in Plate 16, fig. 4, has four rows of cells between the phloëm and the beginning of the lacunar zone. The two outer of these layers have intercellular spaces, and evidently form part of the inner cortex. The next layer, towards the interior (*en*, in fig. 4), consists of closely-fitting cells, and a slight thickening of their radial walls can be made out. This was almost certainly the functional endodermis. The innermost layer, abutting on the phloëm and protoxylem, consists of thin-walled cells. Now it is remarkable that these four layers of cells are arranged, on the whole, in radial series. The same is the case in the rootlet shown in Plate 15, photograph 5. The important point is that the layers which occupy the respective positions of pericycle and endodermis fit on to each other as if they had had a common origin. Traces of the same arrangement are found in other specimens, both rootlets and larger roots.† In some of the latter the thin-walled layer is two cells thick. Outside this comes the functional endodermis, and sometimes all three layers are in radial seriation. Too much stress must not be laid on these facts, which are not absolutely constant. At the same time they are not without interest, for we know that in the roots of *Equisetum* there is no pericycle, but a double endodermis, in which the outer layer alone has the typical endodermal structure, while the inner layer is thin-walled, and gives rise to the rootlets.‡ If the indications above mentioned are to be trusted it would appear that the same may have held good for the roots of *Calamites*, in which case we should have to speak of the thin-walled layer immediately surrounding the stele, not as pericycle, but as inner endodermis.

The cortex of the rootlets does not differ from that of the larger roots. We find the same three zones, of which the middle one is lacunar (see photograph 5, and figs. 4, 5, 7, and 8). Occasionally we find cells in the cortex which have rather thicker walls than their neighbours, and dark carbonised contents (see fig. 4). These may very probably have been secretory sacs of some kind. Similar cells also occur in the cortex of the largest roots (see fig. 11).

Attention has already been called to the occasional presence of irregular rounded cells within the lacunæ. This peculiarity appears both in the medullate roots and in

* Cf. "Organization," Part XII., Plate 30, fig. 5, which represents a similar rootlet at a more advanced stage of development.

† As for example in C.N. 1308.

‡ See, for example, VAN TIEGHEM et DOULIOT, "Origine des membres endogènes," 1889, p. 394, Plate 27, figs. 413-416.

the rootlets (see photographs 4 and 5, figs. 7 and 8). The specimens shown in photograph 5 and in fig. 8 throw great light on the origin of these intralacunar cells. It is evident that they arose as hernia-like outgrowths from the cells of the trabeculæ. An early stage of this process is shown in fig. 8; in photograph 5 the outgrowths have become larger and more numerous, while in the specimens represented in photograph 4 and in fig. 7 they have increased to such an extent as to block up some of the lacunæ. The process is evidently of the nature of *thylosis*, which is known to occur in the intercellular spaces of *Equisetum*.*

Wherever the outermost tissues of the cortex are preserved, whether in a rootlet, or in one of the larger roots, we find the surface protected by a special thick-walled layer of cells. The outer wall of this layer in some cases attains a great thickness, which may exceed the diameter of the cell-cavity. The thickened membrane often shows a distinctly laminated structure (see photograph 5, and figs. 5, 7 and 8).†

We propose to call this outer, protective layer of cells, the *epidermoidal* layer; it has the structure of a thick-walled epidermis, and appears to correspond in all respects with the epidermoidal layer‡ described by OLIVIER in many recent roots. It is probable that the epidermoidal layer in the roots of *Calamites* was not superficial in origin, for in some cases the remains of a layer of cells exterior to it can be traced. Most probably the actual absorptive epidermis of the young root was cast off, and the protective function was assumed by the cortical layer next below (the *exodermis*§), just as is the case in so many roots of recent plants.

In one of the larger roots the epidermoidal layer is evidently more than one cell thick (see fig. 11). It is possible that we here have the commencement of periderm-formation, such as was observed by RENAULT in one of his specimens.||

From the description already given, it is evident that the rootlets and the larger roots show a complete agreement in structure, except for the absence of pith and of primary rays in the former. In order, however, to prove decisively that the rootlets were really the minor branches of those roots which, as we know, belonged to *Calamites*, further evidence of two kinds is necessary. (1.) The most conclusive proof would be given, if we could find the small pithless rootlets borne as branches upon the typical medullate roots of *Calamites*. (2.) The point could also be proved by showing that an unbroken series of intermediate forms exists, connecting the smallest rootlets with the undoubted Calamitean roots.

The evidence available is chiefly of the latter kind, but we have some specimens which appear to show direct continuity between rootlet and root. It will therefore

* STRASBURGER, "Histologische Beiträge," vol. 3, p. 437.

† In "Organization," Part XII., fig. 5 (Plate 30), shows the layer in question at *e*, and it is also conspicuous in the rootlet figured in Part XV., Plate 3, fig. 23.

‡ OLIVIER, "Appareil tégumentaire des Racines," 'Ann. des Sci. Nat., Bot.,' sér. 6, vol. 11, 1881.

§ Cf. STRASBURGER, 'Das botanische Practicum,' 2nd ed., 1887, p. 181.

|| RENAULT, "Genre *Astromyelon*," 'Ann. des Sci. Géologiques,' vol. 17, 1885, Plate 7, fig. 2.

be well shortly to pass in review the principal specimens in which branching is shown, with special reference to the light which they throw upon this question.

Branching of the Roots.

Some examples of branched roots have been figured in previous memoirs,* while others are illustrated in the present paper (see photographs 6 and 7, figs. 6 and 8). Most of these specimens have no direct bearing on the question, for in some the branches, as well as the main root, have a distinct medulla,† while in others both the main axis and the branches are rootlets, with little or no pith (fig. 8).‡

The specimen shown in photograph 6 is of considerable interest. Here the principal root is probably hexarch, and has a perfectly well-defined, though small pith, 8 to 10 cells in diameter. Opposite two of the protoxylem-groups branches are given off, both of which are cut sufficiently near their median plane to show the continuity of their primary xylem with that of the main axis. In one branch there is no sign of any pith; in the other, one or two rows of parenchymatous cells can be distinguished. Such evidence is not conclusive, but the specimen certainly appears to show the bases of two rootlets, with little or no medulla, inserted upon a root, which, though small, has the typical internal structure of "*Astromyelon*," i.e., of the Calamitean root.

Another specimen§ shows no less than four rootlets, in a tangential section of the main root, which, from its having distinct primary rays, was in all probability of the medullate type.

Plate 16, fig. 6, shows a tangential section (from another specimen) through the wood of a relatively main root, with a branch seen in approximately transverse section. Here the branch has a small pith.

The specimen represented in Plate 17, fig. 8, is interesting, for it proves very clearly that the branch rootlet is an *endogenous* appendage of the parent axis. In this case neither has any pith.

In Plate 15, photograph 7, we have illustrated a specimen which appears to deviate from the normal mode of branching. The main root, in its decorticated condition, is about 8 millims. in maximum diameter. It has a large pith, and no less than sixteen groups of primary xylem. The secondary wood is from fifteen to thirty elements in radial thickness. A branch, which is shown in nearly median section, lies exactly opposite one of the protoxylem-strands, but is separated from it by about fifteen layers of secondary wood. The inner extremity of the branch, in which both medulla and primary xylem are evident, ends quite sharply, and there is no

* WILLIAMSON, "Organization," Part IX., Plate 19, figs. 2 and 4; Part XII., Plate 29, fig. 7.

† As in "Organization," Part IX., Plate 19, figs. 2 and 4.

‡ So also in "Organization," Part XII., Plate 29, fig. 7. It seems that in this curious specimen the relatively main axis is that marked *a'*, which is seen in longitudinal section.

§ C.N. 1321 (not figured).

appearance of obliquity. The base of the branch is embedded in a sheath of secondary xylem, which is not perfectly continuous with the normal wood upon which it is superposed. The peculiarity of this case lies in the want of connection between the base of the branch and the primary xylem of the parent root. As we have no other sections of the specimen, we cannot be absolutely certain that the actual base of the branch may not have passed obliquely inwards, and attached itself to the protoxylem of the main axis in another plane. The structure, however, shows no sign of such obliquity, and there is every appearance that the abrupt inner termination of the branch is its real base. If so, the branch must either have been an adventitious one, formed after secondary growth had already made some progress, or else it may have been a normal branch to begin with, which became separated from its place of origin by the intercalation of secondary wood. An analogous process is well known to happen in the case of "sleeping buds" in some recent trees, such as the beech.

We have examined a longitudinal section, from a different specimen, which shows essentially the same peculiarities.

The following conclusions may be drawn from the study of branched specimens.

1. The roots of *Calamites*, like those of the recent *Equiseta* and of vascular plants generally, branched endogenously.
2. The minute, pithless rootlets were, in some cases, borne on parent roots of the ordinary "*Astromylon*" type, with a distinct pith.
3. In exceptional cases it appears that the base of the branch-root was separated from the primary xylem of the main axis by a zone of secondary wood.

Conclusion.

A general survey of the numerous specimens which we have investigated, shows conclusively that there is no sharp distinction between the small pithless rootlets and the large medullate roots. The extreme types are connected by an unbroken series of intermediate forms. As regards the number of primary xylem-strands, every number, from 2 up to 14, is represented; while we also find larger roots with 16 and 25 strands. As regards the size of the pith we find it of all dimensions, from a microscopic group of two or three cells, up to a diameter of nearly 2 centims.; nor is there any break in the series. We will only call attention here to two of the intermediate forms. In a previous memoir* a root is figured which at first sight one might take for a pithless rootlet. We have re-examined the specimen, and find that it has a perfectly distinct pith, about seven cells in diameter, surrounded by seven groups of primary xylem, which form an almost continuous ring. The root shown in photograph 6 has a slightly larger pith, eight to ten cells in diameter; its structure is probably hexarch, but as the primary xylem-strands are well separated from one another,

* "Organization," Part XII., Plate 28, fig. 6 (C.N. 1809).

there is a nearer approach to the original type of "*Astromyelon*" than in the specimen last considered. We might have added indefinitely to the list of intermediate forms, but it is unnecessary to do so. The secondary wood has precisely the same structure throughout, and so also has the cortex, wherever it is preserved.

There is thus no longer any doubt that the forms such as were first grouped together in Part XII. of the previous series of memoirs, under the name of "*Astromyelon Williamsonis*," really belong to the same plant, and that they consist of the roots and rootlets of various orders of branching of *Calamites*. The only form which seems to us strongly to suggest even a specific distinction from the rest, is that shown in photograph 4, in which, as already mentioned, the cortex has a somewhat peculiar character.

RENAULT speaks of some of his larger specimens as *stolons*, not roots. The organs to which he applies this name belong, some to *Calamites* (his *Arthropitys*), others to *Calamodendron*. The specimens in question are beautifully illustrated in his latest work,* and agree perfectly in structure with the larger roots such as we have described. We fail to see any reason for applying the name *stolon* to any of these organs. A stolon is a modified stem, and should show the structure characteristic of stems. In the organs, however, which RENAULT figures, the structure is distinctly that of a root, as is especially shown by the centripetal primary wood. In the *stem* of *Calamites*, as we showed in our former paper, the primary wood is centrifugal.†

Our general results may be summed up as follows :—

1. The fossils hitherto described under the name of *Astromyelon Williamsonis* are the adventitious roots of *Calamites*.
2. Their structure is in all respects that characteristic of roots, as is proved by the centripetal primary wood, the alternating strands of xylem and phloëm, the endogenous mode of branching, and the absence of nodes.
3. The smallest specimens, with little or no medulla, represent the finest branches of the same roots, of which the large medullate forms are the relatively main axes.

EXPLANATION OF THE PLATES.

PLATE 15.

Photographs from the actual sections, taken by the late Mr. W. KIRMAN, F.C.S.

Photograph 1. Part of a tangential section through the wood of a stem, showing the base of a root, with "*Astromyelon*" structure, in transverse section. The

* *Loc. cit.*, "Flore d'Autun," &c., Part II., Plates 55, 56, 57, 59, and 60. The text of this work not having yet been published, we depend entirely on the figures and descriptions.

† "Further Observations," Part I., p. 872.

- pith (*P*) of the root has been perforated by a Stigmarian rootlet. Eight strands of primary xylem are shown (as at *X*), around the pith; some are missing. The secondary wood (*X*²) of the root is continuous with that of the stem on which it is borne. C.N. 1352. $\times$ about 10. (See p. 685.)
- Photograph 2. Part of another tangential section from the same stem. One of the large infranodal rays or "lenticular organs" is shown (*M.R.*). Above this, and to the right, is the transverse section of an outgoing foliar bundle (*L.T.*). C.N. 1353. $\times$ about 16. (See p. 685.)
- Photograph 3. Transverse section of a large corticated root. (For cortex and phloëm, see Plate 17, figs. 10 and 11.) Pith (*P*) perforated by a Stigmarian rootlet. Fourteen primary xylem-strands are shown (as at *X*); some are missing. The secondary wood (*X*²) has a maximum thickness of about 50 cells. C.N. 1891. $\times$ about 10. (See p. 687.)
- Photograph 4. Transverse section of a corticated root. Pith (*P*) solid, surrounded by about twelve strands of primary xylem. Secondary wood (*X*²) only about three cells thick. Cortex (*C—C*) lacunar, with very numerous trabeculæ. Intralacunar cells (? thylosis) are seen. Possibly a different species from the other specimens. C.N. 1891A. $\times$ about 12. (See p. 690.)
- Photograph 5. Transverse section of a tetrarch rootlet, without pith; *CY*, centre of cylinder. Formation of secondary wood has begun. The double endodermis (the inner layer of which is thin-walled) can be recognized (*EN*). The trabeculæ of the lacunar cortical zone show thylosis. The cortex (*C*) is limited externally by a thick-walled, epidermoidal layer (*EP*). C.N. 1890A. $\times$ about 25. (See p. 691.)
- Photograph 6. Transverse section of a pentarch or hexarch root (decorticated), showing the bases of two branches. There is a small solid pith (*P*). Five primary xylem-strands (*X*) are plain. Opposite two of them are the branches (*BR*), which show little or no pith. Secondary wood of branches continuous with that of principal root. C.N. 1892A. $\times$ 22. (See p. 695.)
- Photograph 7. Part of transverse section of a root, showing the base of a branch (*BR*). The root had sixteen strands of primary xylem (*X*), of which four are shown, with part of the pith (*P*). The base of the branch-root is separated from the primary xylem, opposite which it arises, by about fifteen layers of secondary wood; *X*², limit between the two layers of secondary wood. C.N. 1323. $\times$ 22. (See p. 695.)

*Plates 16 and 17 ; figures from camera-lucida drawings, made by
Mr. GEORGE BREBNER.*

PLATE 16.

Fig. 1. Part of a transverse section of a young 9-arch root, at the commencement of secondary thickening. C.N. 1308. $\times 100$. (See p. 687.)

p, p, Cells of pith.

x, x, Primary xylem.

px, Protoxylem at the exterior of primary xylem.

x², x², Secondary wood, bordered externally by cambium.

ph, ph, Two groups of primary phloëm.

en, en, Probably the functional endodermis. The thin-walled layers within this may be either pericycle or inner endodermis.

c, c, Cells of the inner cortex.

This figure represents part of the section figured by WILLIAMSON in "Organization," Part XII., Plate 28, fig. 2 (near *d''*), and is from the original specimen of "*Myriophylloides*," HICK and CASH.

Fig. 2. Part of a transverse section of a more advanced 9-arch root. C.N. 1314. $\times 100$. (See p. 689.)

p, p, Cells of pith.

x, x, Strand of primary xylem.

px, Protoxylem.

x², Secondary wood.

f.r., Fascicular ray.

Fig. 3. Part of a radial section of a similar root. C.N. 1317. $\times 100$. (See p. 687.)

p, p, Pith.

x, x, Primary xylem.

px, Protoxylem at the outer border of *x*, consisting of spiral tracheæ.

x², Secondary wood.

The parenchymatous tissue, *f.r.*, belongs to the fascicular ray.

Fig. 4. Transverse section of a tetrarch rootlet. The outer cortex (similar to that shown in photograph 5) was partly preserved, but is not represented. C.N. 1888. $\times 100$. (See p. 691.)

px, The four protoxylem-groups of the primary wood, which probably reached the centre, though the central thin-walled cells perhaps represent a minute pith.

x², Secondary xylem, which is beginning to form between the protoxylem-groups. (Reference-line omitted.)

ph, Phloëm, of which there are four groups, alternating with the protoxylem.

en, Endodermis, which is evidently double.

c, c, Cells of inner cortex.

l.z. Part of lacunar zone. The dark cells may have been secretory sacs.

Fig. 5. Transverse section of a diarch rootlet. C.N. 1318. $\times 70$. (See p. 692.)

px, px, The two protoxylem-groups of the primary xylem-plate.

About five layers of secondary wood have been formed.

ph, Remains of phloëm.

The endodermis has divided tangentially ; lacunar zone (*l.z.*) and epidermoidal layer are shown.

Fig. 6. Part of a tangential section of the wood of a root, showing the base of a lateral root. C.N. 1358. $\times 100$. (See p. 695.)

x², Secondary wood of main root.

r, Secondary rays.

p, Pith of lateral root.

x, Primary, *x''*, secondary xylem of lateral root.

From the course of the tracheæ, we infer that the bottom of the figure is directed towards the organic base of the main root. Cf. STRASBURGER, 'Histologische Beiträge,' III., p. 136.

PLATE 17.

Fig. 7. Transverse section of a rootlet, probably triarch, without secondary wood. C.N. 1890. $\times 50$. (See p. 692.)

l.z. Lacunar zone of cortex.

ep, Epidermoidal layer, which is especially clear.

One side of the cortex is omitted.

Fig. 8. Oblique section of a branching rootlet, probably tetrarch, with little or no secondary wood. C.N. 1892c. $\times 30$. (See p. 692.)

l.z. Lacunar zone of cortex ; the trabeculæ show the commencement of thylosis.

ep, Epidermoidal layer.

br, Branch-rootlet, probably diarch, passing out through the cortex of the main rootlet.

Fig. 9. Oblique section of a branching diarch rootlet, from the same preparation as fig. 8. The xylem-plate is not yet lignified in the middle. C.N. 1892c, $\times 100$. (See p. 692.)

px, px, The two protoxylem-groups, to one of which the xylem of the branch-rootlet, *br*, is attached.

en, Endodermis.

The endogenous origin of the branch is evident.

Fig. 10. Part of transverse section of the root shown in photograph 3. C.N. 1891. $\times 100$. (See p. 689.)

*x*², Outer part of secondary wood.

cb, Cells of the cambium, adhering to the outer surface of the wood.

ph, Phloëm, separated from the wood by a gap, due to the tearing of the cambium.

en, Endodermis, probably double, including also the thin-walled cells adjacent to the phloëm.

Beyond *en*, a portion of the inner cortex is shown.

Fig. 11. A part of the cortex, from the same root, in transverse section. The whole thickness is shown. The inner cortex is thin-walled. C.N. 1891. $\times 40$. (See p. 690.)

l.z. Lacunar zone of middle cortex; the lacunæ are obliterated by the crushing in of the trabeculæ.

ep, Epidermoidal layer, here multiseriate, probably owing to commencement of periderm-formation.

PHOT. 1.

PHOT. 2.

PHOT. 5.

PHOT. 3.

PHOT. 4.

PHOT. 6.

PHOT. 7.

Fig. 1.

Fig. 2.

Fig. 3.

Fig. 4.

Fig. 5.

Fig. 6.

Fig. 7.

Fig. 8.

Fig. 9.

Fig. 10.

Fig. 11.

INDEX SLIP.

WILLIAMSON, W. C., and SCOTT, D. H.—Further Observations on the Organisation of the Fossil Plants of the Coal-Measures.—Part III. Lyginodendron and Heterangium. Phil. Trans. B 1895, p. 703.

SCOTT, D. H., and WILLIAMSON, W. C.—Further Observations on the Organisation of the Fossil Plants of the Coal-Measures.—Part III. Lyginodendron and Heterangium. Phil. Trans. B 1895, p. 703.

Anatomy of Fossil Plants—Lyginodendron and Heterangium. Williamson and Scott, Phil. Trans. B 1895, p. 703.

Lyginodendron Oldhamium (a fossil Coal-measure plant). Williamson and Scott, Phil. Trans. B 1895, p. 705.

Heterangium Grievii, a fossil Coal-measure plant. Williamson and Scott, Phil. Trans. B 1895, p. 745.

Heterangium tiliaoides, a fossil Coal-measure plant. Williamson and Scott, Phil. Trans. B 1895, p. 760.

Lyginodendron, Leaf of = Rachiopteris aspera, Will. Williamson and Scott, Phil. Trans. B 1895, p. 724.

Lyginodendron, Root of = Kaloxylon Hookeri, Will. Williamson and Scott, Phil. Trans. B 1895, p. 733.

Rachiopteris aspera, Will. = leaf of Lyginodendron. Williamson and Scott, Phil. Trans. B 1895, p. 724.

Kaloxylon Hookeri, Will. = root of Lyginodendron. Williamson and Scott, Phil. Trans. B 1895, p. 733.

Lyginodendron, affinities to Ferns and Cycadææ. Williamson and Scott, Phil. Trans. B 1895, p. 765.

Heterangium, affinities to Ferns and Cycadææ. Williamson and Scott, Phil. Trans. B 1895, p. 765.

Ferns, affinities with Cycadææ through Lyginodendron and Heterangium. Williamson and Scott, Phil. Trans. B 1895, p. 765.

Cycadææ, affinities with Ferns through Lyginodendron and Heterangium. Williamson and Scott, Phil. Trans. B 1895, p. 765.

Lycopodium, supposed Carboniferous species of, really Heterangium. Williamson and Scott, Phil. Trans. B 1895, p. 771.

Coal-measures, organisation of fossil plants of the ; Part III. Williamson and Scott, Phil. Trans. B 1895, p. 703.

*Fossil Plants of the Coal-
erangium.*

*of Botany in the Owens
F.R.S., Honorary
Gardens, Kew.*

	Page
.	704
.	705
.	705
.	705
.	707
.	711
.	714
.	717
.	718
.	720
.	722
.	725
.	725
.	726
.	728
.	730
.	732
.	733
.	733
.	736
.	739
.	740
.	741
.	744
.	744
.	745
.	745
.	745

XVII. *Further Observations on the Organization of the Fossil Plants of the Coal-Measures.*—Part III. *Lyginodendron and Heterangium.*

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[PLATES 18–29.]

CONTENTS.

	Page
Introduction	704
I. <i>Lyginodendron</i>	705
A. The Stem	705
1. General Structure	705
2. Course of the Vascular Bundles	707
3. Structure of the Vascular Bundles	711
4. The Secondary Tissues	714
5. The Pith and Pericycle	717
6. The Cortex	718
7. On certain small Stems of the <i>Lyginodendron</i> type	720
8. Structural anomalies	722
B. The Leaf.	725
1. Connection between Leaf and Stem	725
2. Form of the Leaf	726
3. Structure of the Petiole and Rachis	728
4. Structure of the Lamina	730
5. On a peculiar Bud-like Structure	732
C. The Root.	733
1. Connection between Root and Stem	733
2. Primary Structure of the Root.	736
3. Secondary Tissues of the Root	739
4. Branching of the Root	740
D. Habit and Dimensions of the Plant	741
II. <i>Heterangium</i>	744
Introduction	744
i. <i>Heterangium Grievii</i>	745
A. The Stem	745
1. General Structure	745
	9.4.96

	Page.
2. Course of the Vascular Bundles	747
3. Primary Structure of the Stele and Leaf-trace Bundles	748
4. The Secondary Tissues	751
5. The Cortex	753
6. Branching of the Stem	753
B. The Leaf	754
1. Connection between Leaf and Stem	754
2. Form and Structure of the Leaf	755
C. The Root	756
1. Connection between Root and Stem	756
2. Structure of the Root	758
D. Habit and Dimensions of the Plant	759
ii. <i>Heterangium tilixoides</i>	760
iii. On a <i>Heterangium</i> of uncertain species	764
III. Affinities of <i>Lyginodendron</i> and <i>Heterangium</i>	765
Explanation of the Plates.	771

INTRODUCTION.

The two genera, *Lyginodendron* and *Heterangium*, are among the most interesting, and at the same time the most puzzling, representatives of the Carboniferous Flora. Although, unfortunately, we are still without any satisfactory evidence as to the nature of the reproductive organs in either genus, yet the structure of all their vegetative parts is preserved with such completeness and perfection as to enable us to show, that these fossils present a combination of characters such as exists in no group of plants now living. So long as the mode of reproduction is unknown, it will remain impossible to assign these genera definitively to their systematic position; in the mean time, we can only weigh with due care such evidence as is afforded by their vegetative structure. This evidence, as we shall show, clearly indicates, so far as it goes, a position intermediate between Ferns and Cycads.

At least two other fossil genera, *Poroxydon*, which was investigated by MM. BERTRAND and RENAULT, and *Protopitys*, our present knowledge of which is chiefly due to Count SOLMS-LAUBACH, appear to share this intermediate position.* Curiously enough, in these genera, also, the vegetative characters alone are known.

The further consideration of affinities will be postponed to the end of the paper, and we will now go on at once to consider the organization of *Lyginodendron*, which, of our two genera, appears to stand the nearer to Cycadeæ, though many of its characters are obviously Fern-like.

* BERTRAND et RENAULT, "Recherches sur les Poroxytons," 'Archives botaniques du Nord de la France,' 1886.

SOLMS-LAUBACH, "Ueber die in den Kalksteinen des Kulm von Glätzisch-Falkenberg in Schlesien enthaltenen Structur-bietenden Pflanzenreste—II.," 'Botanische Zeitung,' 1893.

I.—LYGINODENDRON.

The history of this genus has been given in a previous memoir.* The fossil in question was first described by BINNEY, in 1866, under the name of *Dadoxylon Oldhamium*, was next transferred by WILLIAMSON, in 1871, to his genus *Dictyoxylon*, and was subsequently placed by him in GOURLIE'S genus *Lyginodendron*, previously known from cortical impressions only. *Lyginodendron* is now characterized by its structural features, which are quite distinct from those of any other genus. Its relation to the cortical impressions is a question of some difficulty, to which we shall return below (p. 741).

All the forms with which we are concerned may be provisionally referred to the same species, or rather type, namely, *Lyginodendron Oldhamium*. Its stems are among the commonest fossils preserved in the calcareous nodules of the coal-measures of Lancashire and Yorkshire, and they have also been found in those of Langendreer and Orlau, in Germany, but not, it seems, in any of the French coal-fields. The Sphenopteroid foliage of the plant is often found in association, and sometimes in connection, with the stem. The petiole is identical with the fossil formerly described as *Rachiopteris aspera*, as was shown in Memoir XVII., above cited. We have already recorded our discovery† that *Kaloxylon Hookeri* represents the adventitious roots of *Lyginodendron*. The evidence for these conclusions will be given in later paragraphs (see pp. 725 and 733).

The abundance of the material and its remarkably perfect preservation have placed us in a very favourable position for working out the structure, and have enabled us to distinguish characters which are constant and essential from mere individual peculiarities. Variations of the latter kind are rather frequent and include some interesting anomalies.

A.—THE STEM.

1. General Structure.

The stems, which we are about to describe, are of very variable dimensions. The smallest specimens do not exceed 3 millims. in diameter; the largest *undoubted* stem of *Lyginodendron* which we possess attained a diameter of about 4 centims. We leave out of consideration for the present both Mr. NEILD'S specimen‡ and the cortical

* WILLIAMSON, "Organization of the Fossil Plants of the Coal Measures," Part IV., 'Phil. Trans.,' 1873, p. 377.

The other memoirs of the series relating to *Lyginodendron* are: Part VI., 1874, vol. 164, Part II., p. 675 (*Rachiopteris aspera*, now known to be the petiole of *Lyginodendron*); Part VII., 1876, vol. 166, Part I., p. 1 (*Kaloxylon Hookeri*, now known to be the root of *Lyginodendron*); Part XIII., 1887, vol. 178, B., p. 289 (*Kaloxylon*); Part XVII., 1890, vol. 181, B., p. 89.

See also SOLMS-LAUBACH, "Fossil Botany," English translation, 1891, p. 358.

† WILLIAMSON and SCOTT, "The root of *Lyginodendron Oldhamium*," 'Roy. Soc. Proc.,' vol. 56, 1894.

‡ See "Organization," Part IV., p. 386.

impressions. These must have belonged to stems of enormously greater size, but we cannot absolutely prove their identity with *Lyginodendron* (see below, p. 741).

Full descriptions of the characteristic structure of the stem have been given in previous memoirs.* It will, however, be necessary to recapitulate what is already known, for our re-examination of the material, with the aid of additional specimens, has thrown new light on various points. Photograph 1, Plate 18, represents the transverse section of a stem of medium size which we may take as a typical example. This specimen, however (of which we have three sections), though unrivalled for the preservation of the most important details, is not so perfect, as a whole, as are some of the others. In fig. 1, Plate 21, a transverse section of another stem from an entirely new specimen is shown, the preservation of which is remarkably complete.

The middle of the central cylinder is occupied by a solid parenchymatous pith, imbedded in which are groups of dark sclerotic cells. At the periphery of the pith there are several distinct strands of primary xylem. Two of these, from the same specimen as photograph 1, are shown on a larger scale in Plate 21, figs. 2 and 3. Beyond the primary strands of xylem, we come to a broad zone of secondary wood, the elements of which are arranged with great regularity in radial rows. This secondary wood is divided up by numerous medullary rays, both primary and secondary.

If any doubt could be entertained as to the mode of development of the woody zone, it is removed by the fact that at its outer limit the cambium itself is often preserved in great perfection (see Plate 22, fig. 7).

On its outer side the cambium is continuous with a zone of thin-walled tissue, which is made up of phloëm-groups, separated from one another by the phloëm-rays. The greater part of this layer is secondary, as is shown by the radial seriation of its elements. On its external border, however, the primary phloëm-groups can still sometimes be recognized (see Plate 21, fig. 1, and Plate 22, fig. 7, *ph.*). The phloëm-zone is again surrounded by a ring of thin-walled tissue, which is best regarded as a pericycle (see Plate 22, figs. 5, 6, and 7). Imbedded in this we find groups of the same somewhat sclerotic cells, which are so conspicuous in the pith. At the exterior of the pericycle there is usually a layer of periderm.

Beyond the periderm we come to the cortex proper. Its inner zone is usually the worst preserved part of the specimen. Only fragments of it are present in the specimen shown in Plate 18, photograph 1; in the stem represented in the drawing, Plate 21, fig. 1, it is better preserved. The inner cortex consists of large-celled parenchyma, among which numerous sacs (probably secretory) are scattered.

The outer cortex is made up of the well-known alternate radial bands of sclerenchymatous fibres and parenchyma, forming what is termed by Count SOLMS-LAUBACH the *Dictyoxylon* cortex.† As has often been described, the sclerenchymatous strands anastomose in the tangential direction, forming long meshes, which are occupied by

* WILLIAMSON, "Organization," Parts IV. and XVII.

† "Fossil Botany," p. 7.

the parenchyma. Beyond the sclerenchymatous zone, there are a few more layers of parenchyma more or less imperfectly preserved. The epidermis itself is never perfect and has generally been destroyed.

One of the most important features remains to be mentioned, namely, the so-called cortical vascular bundles. These are in reality the leaf-traces on their way out to the petioles; their true nature was pointed out in a previous memoir,* and additional evidence is brought forward in the present paper (see Plate 18, photographs 3 and 4, and Plate 23, fig. 10). In most specimens, including those shown in photograph 1 and fig. 1, five of these leaf-traces are present in the transverse section; the majority of these traces are double, forming the "twin-bundles" so characteristic of the plant. All these bundles are imbedded in the pericycle, a position which they maintain until they turn out into the leaf-bases. The innermost bundles constantly possess a fan-shaped mass of secondary xylem and phloëm on their outer side.

The above may suffice for a summary of the more obvious points of structure in a typical stem of *Lyginodendron*. In order to gain a more complete conception of the anatomy, the first thing necessary is to obtain a clear knowledge of the course and structure of the primary vascular bundles. To this subject we have devoted special attention, and we will take it first in our more detailed survey.

2. *Course of the Vascular Bundles.*

In considering the distribution of the primary vascular tissues of the stem we have to determine the course of the cortical bundles,† and of those which lie at the periphery of the pith, and to trace the relation between the two systems. The former are complete bundles with both xylem and phloëm (see Plate 22, figs. 5 and 6); the latter are xylem-strands only, for their phloëm has been removed towards the outside by the intercalation of the secondary tissues. That the cortical strands are leaf-traces has already been proved; we shall endeavour to demonstrate below, that the perimedullary strands are simply the lower internal portions of the same leaf-trace system, thus confirming a conjecture of Count SOLMS-LAUBACH'S.‡ First of all, however, it is necessary to determine with greater exactness the course of the bundles in the cortical region, and their relation to the leaves. These points are best studied by the comparison of transverse sections. Longitudinal sections are obviously necessary as auxiliaries, but the leaf-traces pass out so very gradually, that it is never possible to follow their whole course in any one preparation.

In any good transverse section through an internode, we see that the external bundles lie at somewhat different distances from the centre of the stem. Thus in

* WILLIAMSON, "Organization," Part XVII., p. 90, 1890.

† The external bundles are conveniently spoken of as *cortical*, though we more usually find them within the limits of the pericycle.

‡ "Fossil Botany," English edition, p. 360.

Plate 21, fig. 1 the relative position of these bundles is evident and is indicated by numbers, *l.t.*¹ being the most internal, and *l.t.*⁵ the most external of the five leaf-traces.

The innermost leaf-trace, *l.t.*¹, is still within the general contour-line of the secondary wood, while *l.t.*² has only just passed beyond it. Both these traces are solitary bundles, and each has a secondary arc, which is more developed in *l.t.*¹ than in *l.t.*². The next outer trace, *l.t.*³, is already double, and has no secondary tissues; *l.t.*⁴ is similar, but lies a little further out, while *l.t.*⁵ is still nearer the periphery. This last trace, like the rest, is within the pericycle, which, however, here shows a marked outward protrusion. It will be noticed that, behind each of the four inner strands, there is a gap in the secondary wood occupied by parenchyma, while, behind the outermost leaf-trace, *l.t.*⁵, this gap has already been filled up by intercalated secondary tissues. We will speak of this gap as the *trace-gap*.

The order of the outgoing bundles can be traced in a similar manner in the stem shown in Plate 18, photograph 1. The same general rules hold good for all transverse sections, where the preservation is sufficiently perfect.

We now have a number of specimens showing the leaf-trace bundles actually passing out into the base of the leaf. Previous figures (Part IV., Plate 16, fig. 25; and Part XVII.,* Plate 12, fig. 1) show the twin bundles in transverse section as they traverse the cortex and enter the leaf-base. Plate 18, photograph 3 and Plate 23, fig. 10 in the present paper represent two transverse sections from the same specimen showing a petiole in connection with the stem. The vascular bundles have here passed out so far as to belong definitively to the petiole. In Plate 18, photograph 4, a corresponding radial section from another specimen is shown. Here the foliar vascular bundle can be traced from the pericycle of the stem, through the cortex, and can be followed for a long distance in the petiole itself.

There is in the WILLIAMSON collection a series of eight successive transverse sections from the same stem.† Considerations of space have prevented us from figuring the series, which throws great light on the course of the vascular bundles. The lowest section shows the base of a petiole attached to the stem, and a second petiole makes its appearance towards the upper end of the series, which thus extends through one internode. The divergence between these two successive leaves is $\frac{2}{5}$, and this seems to have been the most usual phyllotaxis in *Lyginodendron*. The trace, which passes out into the upper of the two leaves, can be followed throughout the series; it is a double bundle all through this part of its course. In the sixth section from below it begins to bend out into the leaf-base, and, as it does so, its two bundles unite somewhat, forming a V with the angle outwards; this very frequently happens at the base of the petiole, though sometimes the bundles remain quite distinct (see

* These references are to the WILLIAMSON Memoirs fully cited above (p. 705, footnote).

† C.N. 1191-1198. The proper order of these sections *from below upwards* is as follows: C.N. 1198, 1192, 1193, 1194, 1195, 1197, 1196, 1191.

Plate 18, photographs 3 and 5, and Plate 23, fig. 10 ; *cf.* Part VI., Plate 52, fig. 6 ; Part XVII., Plate 13, fig. 2).

Another point of great interest is shown by the same series ; the *innermost* of the leaf-traces shown is, at the bottom of the series, deeply imbedded in the secondary wood. In the next section it has passed a little way out, and its position and structure are almost exactly similar to those of the bundle (from another stem) shown in Plate 22, fig. 5. As we trace it further up, we find that its secondary wood gradually disappears. At the top of the series the strand, which now consists of primary tissues only, has become a double bundle, similar to that shown in fig. 6. Hence we may infer that, roughly speaking, the change of structure shown by the comparison of figs. 5 and 6 is gone through in about one internode. This is confirmed by the fact that the bundles shown in those two figures, both of which belong to the same transverse section,* are separated by a divergence of $\frac{2}{5}$.

In the series C.N. 1198-1191 only four cortical traces are present in each transverse section of the internode, because one trace has passed out at the bottom of the series and is not replaced until the next node is reached. More usually five such traces are seen in any transverse section of an internode, as shown in photograph 1 and in fig. 1.

The following conclusions may be drawn from the facts brought forward, which are supported by confirmatory evidence from numerous specimens :

1. The phyllotaxis is spiral, and the divergence (except in very small stems) $\frac{2}{5}$.
2. As a rule each trace passes through five internodes between entering the pericycle and bending out into a leaf.
3. In its course through the lowest of the five internodes the trace usually loses its secondary arc of tissue, and begins to divide into two bundles.
4. The now double trace continues its course with but little change through the remaining four internodes, but passes very gradually outwards, the pericycle bulging somewhat to make room for it.
5. Ultimately it becomes free from the pericycle, and passes out through the cortex into a petiole, where its two bundles often become partially reunited.

As each internode must have been, as our specimens show, at least an inch long, it is evident that the outward passage of the leaf-traces must have been exceedingly gradual. The trace turned out rather sharply, however, where it entered the leaf, as shown in Plate 18, photograph 4.

The nature of the "cortical bundles" and their relation to the leaves is thus made clear ; we have now to consider their relation to the internal xylem-strands.

The number of these strands, as seen in transverse section, is more variable than that of the external bundles. We usually find five of the latter, never more. The internal bundles also often number five (see Plate 18, photograph 1), but are sometimes

* As a matter of fact they were drawn from two *adjacent* sections, between which there is no appreciable change of structure.

more numerous, the maximum number observed being eight, as shown in Plate 21, fig. 1. Where their number is equal to that of the cortical bundles, they alternate quite regularly with the latter, as shown in photograph 1.* Where they are more numerous, we find the reason is, that certain of the single medullary bundles are replaced by a pair (see Plate 21, fig. 1). The alternation, however, is always preserved.

That the medullary bundles are continuous with the cortical leaf-traces is proved by the fact that we often find bundles in the intermediate position, in the act of passing out from pith to pericycle. If, as is almost always the case, the stem possesses secondary tissues, the bundle is here enclosed by the secondary wood, which has formed on its outer side only, while behind it is a parenchymatous gap (see Plate 23, fig. 9). We find examples of these transitional bundles in all positions between pith and pericycle. In the case figured the bundle is scarcely half-way out. On one side its own cambium is continuous with that of the rest of the cylinder. On the other side the main cambium bends inward. In Plate 21, fig. 1 a corresponding bundle, *l.t.*¹, is shown a little further out. Here the general cambium has already formed behind it. In the series C.N. 1198–1191 already referred to, a bundle can be traced all the way from near the pith into the pericycle. At the top of the series another bundle is just beginning to pass out from the pith.†

The identity of the medullary and cortical bundles is further proved by the study of very young stems (which are rare), such as that of which a transverse section is shown in Plate 18, photograph 2. Here only three or four layers of secondary wood have been formed. Consequently, there is comparatively little separation between the medullary and cortical bundles. Four cortical traces are shown, the fifth appears to have passed out into a petiole. The innermost cortical trace, namely, that which has not yet split into two bundles, is only just free from the ring of wood. There are six medullary bundles, which alternate (either singly or in pairs) with those of the cortex. The study of this section at once shows that cortical and medullary strands are identical bundles cut through at different parts of their course, and thus confirms the evidence obtained from more advanced stems.

We may, therefore, draw this further conclusion, as to the course of the vascular bundles in the stem: the medullary bundles form the downward continuation of the xylem-strands of the same leaf-traces which pass out through the cortex into the leaves. The question now arises, How do the bundles behave on entering the pith, and how is the alternation of the medullary and cortical strands to be accounted for? The evidence on this point is imperfect, but certain indications are afforded by the comparison of transverse sections. In the series so often referred to (C.N. 1198–1191) a bundle is shown in the uppermost section just entering the pith. As we trace it downwards, it appears to attach itself to one of the adjacent medullary

* This fact was already recorded in "Organization," Part IV., p. 383.

† C.N. 1191. See also C.N. 1140 and C.N. 1190, 1138, and 1885 E.; the three last form a series from below upwards.

strands, namely that on the kathodic side. Unfortunately the preservation of this part is not good enough for the course of this bundle to be followed with absolute certainty.

One point, however, throws considerable light on this question. If we determine the outermost leaf-trace in any transverse section, we know that its place will be taken a little higher up the stem by a bundle passing out from the pith. Consequently it is from the medullary bundles adjacent to the gap corresponding to this leaf-trace, that the next cortical strand will be supplied. Now, we often find that this gap has a double bundle on its kathodic and a single one on its anodic side (see Plate 18, photograph 1, *l.t.*⁵; the kathodic medullary bundle is shown in Plate 21, fig. 3, the anodic in fig. 2; see also fig. 1, *l.t.*⁵).

If, however, we examine a bundle, which is already passing out through the wood, we find that the medullary strands on either side of it are both single bundles. All this points to the conclusion that a leaf-trace, when followed downwards into the pith, turns aside and joins the next medullary strand on its kathodic side.

If this were all, it would involve the fact that each medullary strand is a sympodial bundle, built up of the lower parts of all the leaf-traces of one orthostichy. It is, however, more probable that connections also take place in the opposite direction, for it is not likely that the bundle system of each orthostichy was quite isolated from the rest. The frequent occurrence of double medullary bundles in other positions than that already determined (see Plate 21, fig. 1) perhaps points to the existence of these additional fusions.

In any case, we may safely draw the following general conclusion as to the course of the vascular bundles: the bundle-system in the stem of *Lyginodendron* is entirely a leaf-trace system. The longitudinal course of each leaf-trace extends through at least ten internodes, about five of which are passed through in the cortex and pericycle, and the same number at the outside of the pith.

The medullary strands are thus sympodial bundles formed of the united lower portions of the adjacent leaf-traces.

The general similarity to the bundle-system of *Osmundaceæ* is evident.*

3. *Structure of the Vascular Bundles.*

There can be no question that the vascular bundles in the stem were of *collateral* structure. This is most certainly shown by the medullary strands, which consist solely of xylem elements, abutting directly on the cells of the pith. There is no trace of phloëm on their inner side, and the preservation is often so perfect as to make it certain that no elements have been lost (see Plate 21, figs. 2 and 3, transverse, and Plate 22, fig. 4, longitudinal). The phloëm of these bundles has been entirely displaced towards the exterior owing to the interposition of secondary wood by the

* See DE BARY, "Comparative Anatomy of Phanerogams and Ferns," English translation, p. 280. The similarity is not diminished by the more recent observations of ZENETTI, 'Bot. Zeitung,' 1895, p. 53.

cambium. In good preparations the group of primary phloëm belonging to each medullary xylem strand can be clearly recognized at the corresponding point of the phloëm-zone (see Plate 21, fig. 1 and Plate 22, fig. 7, *ph.*).

The leaf-traces in the external part of their course demonstrate the same fact. Although there is small-celled tissue on the internal side of the bundle, yet the more delicate phloëm (Plate 22, fig. 6, *ph.*') is perfectly distinct and is evidently limited to the outer side of the xylem. The collateral structure is equally evident in bundles in the intermediate position, which have a cambial arc of their own. Here there is secondary as well as primary phloëm, both of which are found on the external side of the bundle only (see Plate 22, fig. 5, *ph.*'', also Plate 23, fig. 9). Longitudinal sections of the outgoing bundles afford confirmatory evidence.*

In the petiole, as we shall see more fully below, the structure of the bundles becomes *concentric*. It is a question of considerable interest, at what point this important change of structure takes place. It is not easy to answer the question with absolute accuracy, for it is only in the best preserved sections that the position of the phloëm, as distinguished from mere small-celled parenchyma, can be determined with certainty. This much, however, is clear: so long as the outgoing bundles remain in the pericycle of the stem they maintain a collateral structure; on the other hand, when they have definitely entered the leaf-base they are certainly concentric. Thus, in our Plate 21, fig. 1, the four traces, marked *l.t.*¹–*l.t.*⁴, consist of purely collateral bundles; the outermost trace, *l.t.*⁵, which is already bulging the pericycle, shows some signs of an encroachment of the phloëm on the inner edge of the xylem-groups.

The double bundle in the base of the leaf, shown in Plate 18, photograph 3 and Plate 23, fig. 10, is distinctly concentric. The change then takes place in the region, where the bundle passes out through the cortex to enter a leaf-base.†

We have next to consider in detail the structure of the xylem of the primary bundles. We will begin with the medullary strands, which, as we have seen, simply represent the leaf-traces in the lower part of their course. The inspection, even of transverse sections alone, at once reveals a characteristic feature; the smallest elements of the xylem lie neither at the outer nor inner edge, but are placed in an intermediate position, nearer the outer than the inner surface. This statement holds good without exception for all the very numerous transverse sections investigated. A few typical instances are shown in the illustrations (see Plate 18, photographs 1 and 2, and more especially Plate 21, figs. 2 and 3, and Plate 23, fig. 8). The smallest xylem-elements are accompanied by a few parenchymatous cells; the surrounding xylem is entirely composed of tracheæ. The similarity to the xylem of a bundle in

* *E.g.*, C.N. 1982, from which photograph 4 is taken.

† These statements are based on the comparison of many sections, among which the following may especially be mentioned, in addition to those figured for this purpose: C.N. 1144 D., 1190, 1191–1198, 1640, 1885 G.

the leaf of a Cycad at once suggests itself. Longitudinal sections justify the comparison, for they prove that the small xylem-elements are spiral tracheæ, which thus constitute the *protoxylem* or first-formed elements of the primary wood (see Plate 22, fig. 4, which represents a radial section, passing through a primary xylem-strand, bordering on the pith). It will be seen that the tracheides to the exterior of the protoxylem are scalariform, while those on its inner side are pitted. There is a sharp distinction between the primary xylem and the tracheides of the secondary wood. The structure described remains constant throughout the stem. The position of the protoxylem is maintained, as the bundle passes out from the pith (see Plate 23, fig. 9) and remains the same after it has reached the pericycle (see Plate 22, figs. 5 and 6). It cannot be too strongly emphasized, that the protoxylem does not lie on the limit of the primary and secondary wood, but is placed in the interior of the primary strand itself, so that the development of the primary wood must have been partly centripetal and partly centrifugal. This fact is well illustrated by fig. 6. The leaf-trace shown in that figure has reached a point on its outward course where secondary wood is no longer formed, yet the position of the protoxylem in the interior of the ligneous strand is quite obvious. That the centrifugal wood to the outside of the protoxylem is not secondary but primary, is proved, both by the irregularity of its arrangement, as shown in transverse section (see figs. 2, 3, 5, 6, and 8), and also by the character of the markings on its walls (see fig. 4). The limit between the centrifugal primary wood and the true secondary wood with radially arranged elements is perfectly sharp (see figs. 2, 3, 4, 5, and 8). In many cases the two are actually separated by parenchymatous cells.

We are convinced that the same interpretation holds good for the foliar bundles of Cycadeæ, and that here also the centrifugal part of the wood must be regarded as a primary structure, though in certain cases it may receive subsequent additions from a cambial layer.

We regard then the structure of the vascular bundles in the stem of *Lyginodendron* as identical with that of the foliar bundles of Cycadeæ.

This type of structure has been called *diploxylic*, but this term is so used by MM. BERTRAND and RENAULT* as to imply that the centrifugal part of the wood is secondary. We may either coin a new term, and call bundles in which the protoxylem lies in the interior of the primary strand of wood *mesoxylic*, or adopt the word *mesarch*, suggested by Count SOLMS-LAUBACH.† The stem-bundles then of *Lyginodendron*, like the leaf-bundles of Cycadeæ, are *mesarch* or *mesoxylic*‡ in structure.

* "Faisceaux foliaires des Cycadées actuelles," 'Archives Bot. du Nord de la France,' 1886.

† "Fossil Botany," p. 257. The term *mesarch*, which has the advantage of being the shorter, implies that the development *begins* in the *middle* of the strand of wood.

‡ This new term corresponds to the terms *perixylic* and *centroxyllic* used by M. VAN TIEGHEM, the former term implying that the protoxylem is peripheral, the latter, that it is directed towards the centre of the stem. In *mesoxylic* bundles the development of the primary wood is partly centripetal, partly centrifugal.

As regards the number of protoxylem-groups in each bundle, we usually find one such group in each strand in the medullary part of its course (see Plate 21, fig. 2), except at places where there has been a fusion of strands.

As a bundle leaves the pith on its outward course, its protoxylem soon becomes doubled (see Plate 22, fig. 5 and Plate 23, fig. 9). Where the leaf-trace first divides into two bundles, each has a single protoxylem-group (see fig. 6). Further out towards the leaf these again double (see Plate 21, fig. 1, *l.t.*³, *l.t.*⁴, and *l.t.*⁵).

In the medullary part of its course the xylem of the bundle contains little or no parenchyma, except that adjoining the protoxylem-elements (see figs. 2, 3, and 8). Further out, the amount of parenchyma in the xylem becomes greater and it is not always limited to its original position. The only other change which need be mentioned is that in the outer part of the course of a bundle, scalariform or densely spiral tracheæ become more numerous in comparison with the pitted elements (see Plate 23, fig. 13, which is from a petiole). This change begins within the stem.

As regards the primary phloëm of the vascular bundles there is, as might be expected, little detail to be given. The large groups, lying in the pericycle immediately opposite the medullary strands of woods (see Plate 21, fig. 1 and Plate 22, fig. 7, *ph.*) are in some cases surprisingly well preserved, and must have contained elements more resistant than those of the secondary phloëm, though the thickness of the cell-walls is not sufficient to justify one in speaking of them as hard bast. Secretory sacs occur in the primary phloëm, as well as in the other soft tissues of the plant. Longitudinal sections passing through the phloëm of leaf-trace bundles, sometimes show the structure tolerably well. We find a combination of elongated elements, with oblong parenchymatous cells, and may conjecture that the former were the sieve-tubes (see fig. 13, *ph.*, from a petiole).

The conclusions at which we have arrived respecting the structure of the primary bundles of *Lyginodendron* may be stated as follows: 1. The vascular bundles in the stem are normally collateral. As they pass out into the leaves, however, their structure becomes concentric. 2. The xylem of the bundles in the stem developed like that of the foliar bundles in Cycadeæ. The protoxylem-elements lie in the interior of the primary wood, but nearer its outer surface. Thus, the greater part of the primary xylem was centripetally developed, while a smaller portion was centrifugal. 3. The primary xylem consisted of spiral, scalariform, and pitted tracheides, together with a little parenchyma. 4. The primary phloëm consisted of sieve-tubes and parenchyma, together with secretory sacs.

4. *The Secondary Tissues.*

With the rarest exceptions all known stems of *Lyginodendron* already possess secondary tissues. The young stem, represented in transverse section in Plate 18,

photograph 2, shows the structure at a very early stage. Similar specimens have been observed with little or no secondary wood, but these are always in a somewhat fragmentary condition.

That the zone of wood and bast, superadded to the primary bundle system, was really of a secondary character, is conclusively proved by well-preserved specimens in which the actual cambium is often quite evident (see Plate 18, photograph 1, Plates 21 and 22, figs. 1, 5, and 7). It is also manifest that the cambium was a normal one, forming wood on its inner and bast on its outer surface. We leave out of consideration for the moment certain individual anomalies, which we shall describe below (p. 722).

The cambial cells, which form the xylem and phloëm elements, were of the usual tabular form, as seen in transverse section (see fig. 7). In the development of the medullary rays the tangential divisions were no doubt less frequent, for the cambial cells in this region have a greater radial diameter. The general character of the secondary growth resembles that of the stem in the Cycads.

In the very young stem, shown in photograph 2, it will be noticed that the thin zone of secondary wood, whether fascicular or interfascicular, is of about the same thickness all round the stem. It evidently formed, from the first, a continuous ring, only interrupted at the point of exit of a leaf-trace bundle. Hence we must infer that the interfascicular cambium began its activity almost simultaneously with that in the bundles themselves (see also photograph 1 and fig. 1).

It is clear that the cambium followed the course of the outgoing bundles for some little distance, for these bundles have their own arcs of secondary wood and bast up to a certain point in their outward course. The secondary arc dies out as we trace the bundle upwards (see Plates 21–23, fig. 1, *l.t.*¹ and *l.t.*², figs. 5 and 9). Below this point, however, the cambium has already closed in behind the outgoing bundle, so that for a certain distance there is a double layer of cambium. There is the special arc of cambium belonging to the leaf-trace bundle itself (fig. 5, *cb.*"), and, besides this, there is the general cambium, which is continuous behind it. The parenchyma, occupying the gap behind the leaf-trace bundle, where the cambium had not yet closed in (see figs. 1 and 9), followed the secondary growth by dilatation, accompanied, no doubt, by irregular cell-divisions. Some curious anomalies which appear in this region are described below (p. 723).

The whole secondary zone is made up of radiating laminæ of xylem and phloëm, with medullary rays between. We see no reason for departing here from the usual terminology, which would be applied without hesitation to the stems of Cycadeæ, the plants which most nearly resemble *Lyginodendron*, so far as the secondary tissues are concerned.

The primary medullary rays usually became divided up at once by the formation of interfascicular laminæ of wood and bast (see photographs 1 and 2, fig. 1, &c.).

Conversely the wood and bast, which are formed opposite the primary bundles, are from their first origin subdivided by secondary rays (see figs. 2 and 3). Additional

secondary rays appear *de novo* in the later-formed layers, as secondary growth proceeds (see fig. 1, &c.). The proportion of rays to wood and bast varies much in different specimens, and in different parts of the same specimen. On the whole, the interfascicular wood is richer in ray-tissue than the fascicular, but this is not a constant rule. All the medullary rays are continuous through the cambium into the phloëm, so that we can speak of xylem-rays and phloëm-rays just as in the case of recent trees (see Plate 22, fig. 7).

The structure of the secondary wood is excessively simple; it consists of tracheides and ray-parenchyma only. The tapering ends of the tracheides can often be clearly seen, and sometimes it is evident that the pits are closed throughout, so that we have direct evidence that the xylem elements were really tracheides, and not vessels (see Plate 22, fig. 4B). The tracheides are of great length, but we have not attempted measurements, as we could not make sure of following the same element throughout its whole length.

The tracheides have very numerous pits, which usually, if not always, are limited to their radial walls. The pits are crowded together, and as many as seven longitudinal rows may exist on the same wall. They show signs of an arrangement in inclined series, as if they formed part of a spiral system. The pits are distinctly bordered, as can be seen both in tangential and radial sections. The opening of the border is a wide inclined slit; the pits between tracheides and ray cells are, as usual, unbordered on the side towards the latter (see figs. 4A and 4B).

The rays are of very variable height and width; their cells are decidedly thin-walled, and consequently are only well-preserved in good specimens. They are radially elongated, and thus show in radial sections the muriform appearance characteristic of most medullary rays in recent plants.*

The cells with dark carbonaceous contents, which we interpret as secretory sacs, and which are so general in all parenchymatous tissues of *Lyginodendron*, frequently occur in the medullary rays.

The secondary phloëm has a very characteristic structure; it is divided up into small groups corresponding to the tracheal groups in the wood, and separated from one another by the parenchymatous phloëm-rays (see Plate 22, fig. 7 and 7A). In each radial series of phloëm elements, there is a regular alternation of larger and smaller cells (see fig. 7). The tangential section appears to show that the smaller elements of the phloëm were rather elongated, with occasional transverse walls, while the larger elements had oblique terminations. Great caution, however, is necessary in interpreting the structure, on account of the presence of articulated fungal hyphæ in the partially disorganized phloëm (see fig. 7A).

The preservation does not allow us to say for certain which are the sieve-tubes. We think it most likely that the larger elements were of this nature, while the

* See WILLIAMSON, "Organization," Part IV., Plate 23, fig. 9; also our fig. 4.

narrower cells were parenchymatous. The analogy of *Heterangium tiliæoides*, in which the phloëm is perfectly preserved, supports this view. MM. BERTRAND and RENAULT however, have come to the opposite conclusion in the case of *Poroxylon*, the phloëm of which much resembles that of *Lyginodendron*.*

The medullary rays broaden out somewhat in passing through the phloëm zone. The secretory sacs are more frequent here than in the xylem portion of the rays (see figs. 1, 5, and 7). Occasionally the medullary rays of the wood show signs of tangential dilatation, owing perhaps to the long-continued growth of the pith, but this is exceptional.

We may sum up our results as to the secondary tissues in the stem as follows :
 1. The stem of *Lyginodendron* constantly formed a large amount of secondary wood and bast by means of a normal cambial layer. 2. The secondary wood consisted of tracheides and xylem-rays; the former possessed numerous bordered pits on their radial walls. 3. The secondary bast-zone consisted of groups of phloëm separated by the phloëm-rays. In the phloëm larger and smaller elements alternated regularly. It is probable, though not certain, that the larger elements were the sieve-tubes. 4. The secondary tissues bear a general resemblance to those in the stem of *Cycadææ*.

5. *Pith and Pericycle.*

The pith of *Lyginodendron* consists of moderately thin-walled parenchyma, in which large groups or nests of dark-coloured tissue are imbedded. These almost black masses, which also occur in the pericycle, and sometimes in the cortex, give a most characteristic appearance to the sections (see photographs 1 and 4, fig. 1, &c.). It is not easy to determine the nature of the tissue of which they are composed. The cells in question do not differ greatly in form from those of the thin-walled medullary parenchyma. Their walls, however, are decidedly thicker and their arrangement is more regular, showing a fairly definite longitudinal seriation. Their cavities are more or less completely filled with carbonaceous contents. It is a question whether these carbonaceous bodies represent the actual contents of the cells or whether they are due to the degradation of the inner layers of the much thickened cell-walls. We incline to the latter view: (1) because the apparent contents often show a distinctly laminated structure and (2) because the fibres of the outer cortex, which were certainly sclerenchymatous, are often filled with similar material. We will, therefore, provisionally speak of the dark-coloured groups as the *sclerotic nests*.

The pith further contained numerous thin-walled sacs, with more uniform carbonaceous contents, which we regard as probably of a secretory nature. They are sometimes isolated, sometimes arranged in vertical rows (see Plate 21, figs. 2 and 3,

* 'Recherches sur les *Poroxylons*,' *loc. cit.*, p. 289.

also Plate 25, fig. 19, in which the same organs are shown in the cortex of a root). These organs are of universal occurrence, throughout the soft tissues of *Lyginodendron*, and may even be found within the limits of the vascular bundles. In a previous memoir* these structures have been described and figured as *gum-canals*; on careful examination, however, we have failed to find any good evidence of an epithelium, while in satisfactory longitudinal sections, transverse or oblique walls, separating the constituent cells, can generally be detected (see fig. 19). We therefore prefer to describe all these organs as secretory sacs. It is useless to speculate on the question what they secreted.

Certain regions of the pith evidently retained the power of meristematic activity for some time, as is proved by the anomalous tissues to which they occasionally gave rise (see p. 722). Through the trace-gaps the pith is perfectly continuous with the pericycle. Where a bundle leaves the pith on its outward course, it is constantly accompanied by some of the sclerotic nests (see figs. 1 and 9); similar nests, however, are also frequent in the pericycle without special relation to the bundles.

The pericyclic tissue consists, like the pith, of rather delicate, short-celled parenchyma, together with sclerotic nests and numerous secretory sacs (see photograph 1 and figs. 1, 5, 6, 7, and 9). The pericycle is often of great thickness, especially at the point where a leaf-trace is approaching its place of exit into a leaf (see photograph 4 and fig. 1).

In all except the youngest stems the pericycle is bounded externally by a zone of radially arranged cells which we interpret as *periderm* (see photograph 1, and figs. 1, 5, 6, 7, and 9, *pd.*). This layer, which was evidently formed from a phellogen, appears not to have originated until secondary growth had made some progress. In a stem with secondary wood about twelve elements thick the first tangential divisions had taken place in the outer layer of the pericycle.† The outer elements of the radially arranged zone have somewhat thick walls, while its inner cells are quite delicate, and no doubt constituted the cork-cambium or phellogen (see figs. 5, 6, and 7). It is natural to suppose that this periderm must have ultimately caused the throwing off of the whole cortex, but we have no direct proof that this took place. The periderm curves outwards opposite the leaf traces, following their outer surface. In the specimen shown in photograph 4, the periderm extends along the external surface of the outgoing trace as far as the base of the petiole. The length of the peridermal cells, as shown in longitudinal sections, is about equal to their tangential diameter.

6. *The Cortex.*

The cortex, as distinguished from the pericycle, may be divided into two layers. The inner layer is parenchymatous, while the outer consists of alternating radial

* WILLIAMSON, "Organization," Part XVII., p. 90, Plate 12, fig. 4.

† C.N. 1915 H.

bands of sclerenchyma and parenchyma, constituting the characteristic *Dictyoxylon* cortex, as it is called by Count SOLMS-LAUBACH. The cortex may be passed over in few words, as its structure has been sufficiently described in former memoirs. It must, however, be pointed out that "the inner parenchyma of the bark," described in Memoir IV., p. 382, includes both phloëm and pericycle, in addition to the inner cortex of our present description. The specimens discovered up to 1872 were not sufficiently well preserved for all the zones to be distinguished.

The inner cortex presents little of interest; it is generally the worst preserved part of the stem, although its cells had somewhat thicker walls than those of the pericycle. Its frequent disorganization in specimens otherwise perfectly preserved (see Plate 18, photograph 1) may be an indication that it had begun to die off in consequence of the formation of internal periderm while the plant was still living. For the structure of this layer, see Plate 21, fig. 1, and Plate 18, photograph 4. In some of the specimens many of the cells seem to have collapsed, giving the appearance of a tissue with larger elements than actually existed.*

The secretory sacs are specially abundant in the inner cortex. We rarely find sclerotic nests in this region except at the bases of leaves, where they are very numerous (see Plate 18, photographs 3 and 4, and Plate 23, fig. 10), and whence they extend into the cortical tissue of the petiole. As regards the outer cortex the only point which need be mentioned is the great tangential dilatation of the parenchymatous bands, owing to the secondary growth in the interior of the stem (see photograph 1 and fig. 1). This dilatation, which reaches its maximum in the outer cortex, applies to all regions external to the cambium. In some cases it is very conspicuous in the pericycle, where it sometimes leads to a wide separation between the two bundles of a leaf-trace. Secretory sacs occur in the parenchymatous portions of the outer cortex. As already mentioned, a few layers of tissue are sometimes preserved to the exterior of the "*Dictyoxylon*" zone. The remarkable outgrowths or emergences which arise on the outer surface of the cortex have been fully described and figured in Part XVII., Plate 12, figs. 1 and 6. They each consist of a sclerotic envelope enclosing a parenchymatous core, these two tissues being continuous with the corresponding parts of the external cortex. The apex of the outgrowth is blunt. The emergences (for they are certainly too deep-seated to be called hairs) are by no means equally frequent in all the specimens; in many cases they probably became detached, together with the superficial cortical layers. Very similar appendages are found on some recent tree-ferns, as *Alsophila armata*, and more especially *Alsophila australis*, in which the blunt spines are much like those of *Lyginodendron*. In these ferns the spines are surmounted by paleæ, which soon become detached, but whether this was the case in *Lyginodendron* also cannot be determined.

The emergences have played an important part in the scientific history of the plant,

* See WILLIAMSON, "Organization," Part XVII. Plate 13, fig. 3.

for it was the identity of these structures on the stem of *Lyginodendron* and on the petiole known as "*Rachiopteris aspera*" which first suggested that these organs might be different parts of one and the same plant—a suggestion which has been amply confirmed since by their discovery in direct continuity.*

7. On certain Small Stems of the *Lyginodendron* type.

In a previous memoir attention has been called to the peculiarities of certain very small stems which, from their general structure, appear to belong to *Lyginodendron*.† At that time the roots of *Lyginodendron* were not yet understood; it now turns out that the smallest of the supposed stems, including all those with the "central axis solid," were really roots. This applies to the following specimens, enumerated on p. 94 of the memoir cited: C.N. 1885 C., 1885 A., 1883 and 1885.

There remain, however, a certain number of very small true stems, the nature of which is proved beyond doubt by the presence of leaf-trace bundles in their cortex. Examples of such stems are shown in figs. 11 and 12 of Part XVII., and in fig. 2 of Part IV.

A clear distinction must be drawn between those *small* stems which differ in their primary structure from the typical forms, and merely *young* stems, which are characterized simply by the absence or small development of the secondary tissues. One of these young stems is shown in transverse section in photograph 2, and has been already mentioned (pp. 710 and 714). Here there is a well-marked pith, and the bundles surrounding it are distinctly separated from one another. Other examples at about the same stage of growth are known, some of which are of considerable size. They present no special difficulties, being evidently stems of the normal type at an early stage of development. In these young specimens the outer cortex is mainly sclerenchymatous, with only narrow radial bands of parenchyma. The great development of the latter in older stems was, no doubt, largely due to dilatation induced by the secondary growth.

Returning to the stems in which the primary structure is on a small scale and is peculiar in type, we may distinguish two categories. The one is represented by fig. 2 in Memoir IV. and fig. 11 in Memoir XVII., the other by fig. 12 in Memoir XVII. In the former type the primary xylem forms an almost complete ring, or, at least, is not differentiated into distinct bundles; in the second type, the bundles surrounding the pith are quite distinct and normal, but the whole is on an extremely small scale. In fact, the smallest stems we have, one of which is only 3 millims. in diameter, belong to this type. These smallest stems have secondary wood of considerable thickness (about 14 cells thick). Cambium and phloëm are well preserved, and the leaf-traces are evident in the cortex. The phyllotaxis appears to have been $\frac{1}{3}$. In one

* WILLIAMSON on "Organization," Part IV., p. 405; Part VI., p. 682; Part XVII., p. 91.

† WILLIAMSON, "Organization," Part XVII., p. 92.

of the specimens the outer cortex is of the normal "*Dictyoxylon*" type, with the parenchymatous bands already dilated. On the whole, we may say that these tiny stems have all the characteristic structure of *Lyginodendron*, except that the sclerotic nests are absent.*

The small stems of the type with an almost continuous ring of primary wood (see Memoir XVII., fig. 11) are never quite so minute as those just described, the smallest found having a mean diameter of barely 4 millims. (C.N. 1137). The structure only differs from that of the typical *Lyginodendron* stem in having a continuous xylem-ring and a very small pith. Specimens of this kind are connected by an unbroken series of intermediate forms with the typical stems, which have a large pith with separate bundles at its periphery. These differences are quite irrespective of the amount of secondary thickening, and therefore cannot depend on the age of the branch. It might be easy to explain them as dependent on the order of the branch, but we have at present no evidence, that the stem of *Lyginodendron* branched at all. It may have done so, but not a single branching specimen has yet been detected. The supposed branches mentioned in earlier memoirs have all turned out to be either roots or petioles. We are, therefore, not justified in assuming the presence of a highly developed system of ramification such as would be necessary to account for the existence of branches of various orders.

The explanation we would suggest is, that the small specimens, with a continuous ring of primary wood, may represent the *basal, first developed* portions of normal stems.

Osmunda, as is well known, resembles *Lyginodendron* in the fact that the normal stem possesses a ring of collateral bundles, which are distinct, so far as their xylem is concerned. M. LECLERC DU SABLON in his interesting memoir on the development of the stem in Ferns, has shown that the lower internodes of the stem of *Osmunda* have a continuous ring of wood enclosing the small pith, this ring being only interrupted at the nodes. It is only in the later-developed part of the stem that the pith enlarges and the bundles become permanently distinct.†

A similar stage is passed through by the stems of many other ferns. Until we have been able to trace the transition in one and the same stem of *Lyginodendron* from the small pith and continuous xylem of the basal portion to the large pith and separate bundles of the upper stem, our suggestion must remain an hypothesis. In the mean time, however, it may serve as a provisional explanation, which is in harmony of what we know of the development of those recent Ferns which in their anatomy most nearly resemble our fossil. The fact that *Lyginodendron* had secondary growth in thickness, while the Ferns with which we have compared it have not, does not invalidate the comparison. We have good reason to believe that the secondary thickening in *Lyginodendron* and its allies was relatively a recently-

* See C.N. 1139 and 1141 (same specimen), 1199, and especially 1885 D.

† LECLERC DU SABLON, "Recherches sur la formation de la tige des Fougères," p. 9, figs. 25 and 26, 'Ann. des Sci. Nat. (Bot.),' sér. 7, vol. 11, 1890.

acquired character. It is highly probable that they still retained the mode of growth characteristic of plants which are destitute of secondary thickening. In like manner *Dracana* or *Aristea* resembles any other Monocotyledon in the earlier stages of its development though it ultimately forms secondary tissues.*

The very small stems with a normal pith and separate bundle (see "Organization," Part XVII., Plate 14, fig. 12) remain unexplained. They are not connected by any clear intermediate forms with the typical specimens, yet it is impossible to doubt that they belong to *Lyginodendron*. Their xylem elements are decidedly smaller than those of the ordinary stems, but the latter vary so much among themselves in this respect, that we cannot attach much importance to such differences. Stems of this kind must apparently represent some kind of lateral axis, which has not yet been found in connection with the main stem. The somewhat deficient formation of sclerenchyma suggests that they may have been weak runners or subterranean shoots.

8. *Structural Anomalies.*

So far we have concerned ourselves with the normal structure of the *Lyginodendron* stem, such as is common to a majority of the numerous specimens investigated. Some interesting departures from this typical anatomy occur in individual specimens. The most remarkable and perhaps the most frequent of these anomalies depended on the appearance of a secondary meristem at the outer border of the pith. In some stems this medullary meristem gave rise merely to secondary parenchyma, with somewhat thickened walls; in other cases, however, it acted as a regular cambium, producing medullary wood and bast with inverted orientation. In the latter case, we have precisely the same anomaly as in *Tecoma*, *Iodes*, or *Acantholimon* among recent plants. It is a most remarkable fact, that this peculiarity should have already appeared as an *occasional variation* in a carboniferous plant, so absolutely remote from the Dicotyledons as is *Lyginodendron*. A more striking warning against the *indiscriminate* use of, even conspicuous anatomical characters cannot be imagined. Such a warning, it is true, is not needed by those who have experience in anatomy. The anomaly in question is known to be of very inconstant occurrence at the present day. Both in the genera, *Tecoma* and *Iodes*, some species show it and others do not, though analogous peculiarities (internal phloëm for example) are often characteristic of entire natural orders. Anatomical characters, in fact, like any other characters, are sometimes of great constancy, sometimes highly variable, while the same character, which is relatively constant in one family may be most inconstant in other groups.

In the present paper, we have been compelled, in the absence of organs of fructification, to make great use of anatomical characters. We have, however, endeavoured to rely

* The following slides show a more or less continuous xylem-ring:—C.N. 1137, 1150 ("Organization," Part IV., Plate 22, fig. 2); 1161, 1885 H ("Organization," Part XVII., Plate 13, fig. 11); 1915 N, 1915 R.

on those which are known to be of great persistency in families which presumably belong to the same cycle of affinities as the plants with which we are dealing.

Characters dependent on the activity of the cambium are perhaps peculiarly liable to variation. Whenever a plant has acquired the power of secondary tissue-formation, all the anomalies, even of the most abnormal Dicotyledons become possible; in *Lyginodendron* some of these possibilities are actually realized.

We do not find the slightest reason to believe that the anomalous medullary cambium of *Lyginodendron* was a character even of specific value; among stems, which are perfectly similar in other respects, some show it and some do not, while in those that possess this anomaly, the degree in which it is developed is most variable.

A characteristic example of the formation of anomalous medullary wood and bast has been previously figured.*

Our fig. 8 (Plate 23), from another section of the same stem, shows plainly that there is a true cambium on the medullary side of the primary bundles, giving rise to secondary xylem on its outer side, and to secondary phloëm towards the interior. The figure cited from Memoir XVII. demonstrates an interesting point, confirmed by other specimens, namely, that the anomalous medullary tissues extend through the leaf-trace gap along the sides of the normal secondary wood. In the section from which this figure was drawn, the zone of secondary wood is sub-divided by parenchymatous trace-gaps into four masses, each of which is completely surrounded by cambium. We have, in fact, in this case precisely the anomaly described by DANGEARD in *Acanthophyllum*.† It is probable that the new cambial divisions spread from the normal cambium through the parenchyma of the leaf-gaps into the pith, just as ROBINSON found to be the case in *Iodes tomentella*.‡ Thus in another stem, from which fig. 9 was drawn, there is a small amount of anomalous wood (x^3) behind the outgoing trace figured. The anomalous tracheæ found at the edges of the leaf-trace gaps sometimes have a horizontal course ("Organization," Part XVII., Plate 13, fig. 3).

In one or two instances, where the anomalous tissue is mainly parenchymatous, the internal cambium appears to have arisen partly from the parenchyma of the primary xylem, so that some of the tracheæ belonging to the latter have been carried inwards into the pith.§ We omit one or two specially complicated forms of anomalous medullary tissues, which are of isolated occurrence.||

* "Organization," Part 17, Plate 13, fig. 3. The cabinet contains four sections of this specimen, C.N. 1138, 1142, 1190, and 1885E.

† DANGEARD, "Monographie Anatomique des *Acanthophyllum*;" "Le Botaniste," 1889.

‡ ROBINSON, "On the Stem-structure of *Iodes tomentella*, &c.," "Annales du Jardin Botanique de Buitenzorg," vol. 8, 1890.

§ C.N. 1114 and 1118. One of us found a similar mode of development in *Acantholimon* (see SCOTT and BREBNER "On Internal Phloëm in the Root and Stem of Dicotyledons," "Annals of Botany," vol. 5, 1891, p. 296.)

|| The following specimens in the WILLIAMSON collection show anomalous tissues in the pith: C.N. 1114, 1118, 1138 and other sections of the same stem; 1153.

Other individual anomalies are connected with the leaf-trace bundles in the outer part of their course. In most cases the secondary tissues only accompany the outgoing trace so long as it remains undivided; sometimes, however, both the twin bundles of a divided trace possess an external layer of secondary wood and bast.* In another case we found one bundle of a pair unthickened, while its twin developed an enormous fan of secondary tissue with wood about 40 cells thick (C.N. 1114). A more remarkable anomaly of rather rare occurrence consists in the formation of cambium all round the leaf-trace bundle instead of on the peripheral side only. An instance of this is shown in the first figure of *Lyginodendron* published.† In another stem both the twin bundles of a divided leaf-trace showed the same peculiarity on a still larger scale, while another pair approached the same structure. In these cases the thickened bundle acquires a concentric structure, and may easily be mistaken for the stele of a branch, as actually happened in the first instance referred to. These pericyclic anomalies sometimes coexist with abnormal formations in the pith. In one case, a little nest of sclerotic cells in the pericycle had served as a centre for a concentric development of anomalous xylem and phloëm, similar to that around the leaf-trace bundles. These varied eccentricities of development are only of interest, as showing the same plasticity of structure in these ancient stems as we find in so many modern plants, which resemble them in nothing except their mode of secondary growth. The anomalous developments in certain Cycadeæ, among which we should most naturally look for parallel cases, bear only a remote resemblance to those which we find in *Lyginodendron*.‡ The concentric cortical strands which are formed in *Cycas* appear to be of purely secondary origin.

Frequent peculiarities, scarcely amounting to an anomaly, consist in the differentiation of the normal secondary wood into distinct zones, chiefly differing in the dimensions of their tracheides. When a narrow zone of small tracheides is formed with large elements on both sides of it, an appearance suggestive of annual rings may result. These phenomena, however, are far too inconstant for us to draw any inference as to a regular periodicity of growth. It is much more probable, that the differences between successive zones of wood, which only appear in certain individual stems, were due to some accidental interference with the normal course of development. Examples of these peculiarities have been previously figured.§

* See Plate 2, photograph 8, also WILLIAMSON, Part IV., Plate 22, fig. 1; Plate 25, figs. 19 and 20.

† WILLIAMSON, Part IV., Plate 22, fig. 1.

‡ See DE BARY, 'Comparative Anatomy,' Eng. edition, pp. 608-613.

§ See WILLIAMSON, Part IV., Plate 22, fig. 4; Plate 23, fig. 6.

B.—THE LEAF.

1. *Connection between Leaf and Stem.*

The history of our knowledge of the leaves of *Lyginodendron Oldhamium* is briefly as follows: In Memoir IV. (1872) the opinion was already expressed that the "small stems or petioles" to which the provisional name of *Edraxylon* had been given, might probably prove to belong to *Lyginodendron* (*loc. cit.*, p. 403). In Memoir VI., the specimens first named *Edraxylon* are fully described, and are incorporated in the provisional genus *Rachiopteris* (founded for the reception of fossil fern-petioles) under the name of *R. aspera*. The structure is fully described, and the discovery of leaflets in connection with the branched petiole, led to the conclusion that the leaf belonged to BRONGNIART'S genus, *Sphenopteris*. The species *S. Hæninghausi*, which agrees with *R. aspera* in possessing a tuberculated rachis, was specially suggested for comparison.

At a later period * the conclusion "that *Rachiopteris aspera* is merely the petiole of *Lyginodendron Oldhamium*"† was definitely stated, and proved by specimens in which the base of the petiole was found in actual connection with the stem, as well as by the presence of identical cortical outgrowths on both organs.

It only remains for us to call attention to some additional specimens, in which the connection between leaf and stem is still more manifest. Two of these new specimens have been figured.

Photographs 3 and 8A and fig. 10 (Plates 18, 19, and 23) are from the same specimen, of which we have four transverse sections.‡ The order of the sections illustrated, from below upwards, is photograph 3, fig. 10, photograph 8A. In all the sections figured the petiole is in manifest continuity with the stem, and, at the same time, it already presents the characteristic structure of *Rachiopteris aspera*. Other sections show the same petiole after it has become free; thus, fig. 11 represents the upper part of the same petiole in longitudinal section, at a point where it is beginning to branch. This figure shows several of the characteristic cortical emergences, thus affording the direct proof that *Rachiopteris aspera*, the only known *Rachiopteris* that possesses these outgrowths, was the petiole of *Lyginodendron*.

Photograph 4, from another specimen, shows a radial section through a stem bearing a petiole. Both are in admirable preservation, so that all the details of the leaf-base can be made out. We also have series of sections from two other specimens, showing the connection between stem and petiole, and also the structure of the

* See WILLIAMSON, Part XVII., 1890.

† *Loc. cit.*, p. 91.

‡ C.N. 1980 and 1981, and two sections in the possession of D. H. SCOTT. All these were cut by Mr. LOMAX, as well as those mentioned in the next foot-note. Other slides belonging to these series are in the Botanical Collections of the Royal College of Science, London.

petiole after it has become free, where it presents all the characteristics of *Rachiopteris aspera*. *

The leaf is attached to the stem by a massive base, which, however, is not at all sheathing (see photographs 3 and 4, fig. 10). The leaf-trace bundles, which had traversed the pericycle almost vertically through about five internodes, bend out somewhat sharply into the base of the leaf (see photograph 4). It has already been mentioned that the bundles, which are collateral in the stem, become concentric as they enter the leaf. The extent to which the two bundles of the trace fuse on entering the petiole varies in different specimens; in that represented in fig. 10 they partially fuse; in other cases (*e.g.*, C.N. 1984) they remain distinct. All the primary tissues, vascular bundles, pericycle, inner and outer cortex are, as we should expect, perfectly continuous between stem and leaf. The limit between cortex and pericycle is, however, difficult to trace at the point of junction. The sclerotic nests, which in the stem are almost always limited to the pericycle, become distinctly cortical in the petiole, forming a conspicuous feature which helps to characterize the species.†

There is always a great development of these sclerotic masses in the axillary region, a fact which is worth noticing because these conspicuous groups of cells might be mistaken for rudimentary axillary buds. We find no evidence that such buds existed.

Exactly below the axil a characteristic transverse hypodermal band of black sclerotic tissue is found (see photograph 4 and fig. 10). This helps us to fix very exactly the position of the transverse as compared with the longitudinal sections of the node. The outer cortex of the stem closes in again almost immediately above the level of the sclerotic band.

The subject of phyllotaxis has already been dealt with. The arrangement is evidently $\frac{2}{5}$ in all the larger stems, in which the relative position of the leaf-trace bundles is clear. In the smallest stems the divergence seems to have been $\frac{1}{3}$.

2. Form of the Leaf.

This subject was discussed in Memoir VI., at a time when the relation of *Rachiopteris aspera* to *Lyginodendron* had not yet been determined.

The stems of *Lyginodendron* are almost invariably found to be surrounded by a multitude of fragments of foliage, among which petioles of all sizes, often in the act of branching, are to be recognized, as well as portions of leaflets. Wherever the structure is sufficiently well preserved, the characters of *Rachiopteris aspera* are

* C.N. 1983 and 1984; also three sections from this series in the possession of D. H. SCOTT.

Numerous single sections in the WILLIAMSON collection also show the connection between petiole and stem, as C.N. 1140, 1144 B, 1144 D, 1190, 1191 and 1198 (two nodes of the same stem), 1885 G, 1915 C.

† See WILLIAMSON, Part VI., p. 682.

evident in the petioles, as indicated by the V- or W-shaped bundle as seen in transverse section, the Dictyoxylon cortex and the peculiar emergences. Sometimes, of course, there is an accidental admixture of other fern petioles.

In all cases where the petioles can be determined as belonging to *Rachiopteris aspera* we now know that we have to do with the foliage of *Lyginodendron*. The finer branches of these petioles, as was already shown in Memoir VI., are sometimes found in connection with portions of the compound lamina. Where the latter are seen in surface view, some idea of the form of the leaf may be obtained. Since Memoir VI. was published, additional evidence has been accumulated, and the conclusion then reached is confirmed, namely, that the leaf would fall under the form-genus *Sphenopteris* of BRONGNIART, as shown by the finely cut foliage and the acute angles between the veins.* It is impossible to reconstruct the leaf from the fragmentary remains, which are alone available: but we may take it as certain that it was a highly compound leaf of the *Sphenopteris* type. The leaflets appear to have been decurrent on the finer branches of the rachis. We cannot venture to refer the leaf to any known species of *Sphenopteris*, but a certain resemblance to various forms can be traced. (See, for example, the figures of *S. Hæninghausi*, *S. tridactylites*, *S. linearis*, &c., in BRONGNIART'S "Histoire des végétaux fossiles.")

The mere fact, that the foliage of *Lyginodendron* resembled that of certain Ferns is in itself no proof of affinity with *Filices*. The classical case of *Stangeria* is a sufficient warning against any such hasty inference. It must, however, be remembered that in the foliage of *Lyginodendron* we have not only fern-like *form* and venation, but also fern-like *structure*, whereas in the case of *Stangeria* a single transverse section of the petiole would be sufficient to prove that the plant is no Fern but a Cycad.

Where a number of sections have been cut from the same specimen, it is possible to trace the repeated branching of the rachis and to observe the insertion of the leaflets upon its branches. The leaflets shown in section in Plate 19, photograph 7, and Plate 24, fig. 16 are from the series C.N. 1191-1198, and belong to leaves, the petioles of which, seen in other sections of the same series, present the characteristic structure of *Rachiopteris aspera*. A section of one of the petioles from this series, no doubt a secondary branch, has been figured in Memoir XVII., Plate 13, fig. 7. Though not actually one of those which have been traced up to the leaflets, it is identical with them in structure, and most probably formed part of the same compound leaf. These leaflets and branch petioles accompany the stem, which, as already mentioned, runs through the entire series. They, no doubt, belong to a lower leaf than the two which are seen in connection with the stem.

The section shown in Plate 18, photograph 6, evidently passed through a portion of the lamina, just where the segments are beginning to separate from one another. Appearances of this kind are not uncommon in the preparations, and become readily intelligible on comparison with the surface view of the foliage (*cf.* Memoir VI., Plate 52, fig. 15).

* See Memoir VI., Plate 52, fig. 13; also Memoir XVII., p. 91.

The following conclusions as to the form of the leaf may be drawn from our observations :—

1. The leaf of *Lyginodendron* was a highly compound one, the branches of the rachis being given off alternately.

2. The form and venation of the leaflets were those of a *Sphenopteris*.*

3. *Structure of the Petiole and Rachis.*

This again is a subject which has been so fully dealt with in previous Memoirs, that only a few points need be discussed here.

None of the preparations hitherto figured afford conclusive evidence as to the structure of the vascular bundle. We will, therefore, first call attention to Plate 18, photograph 5, which shows a petiole in transverse section; from its small size—2 millims. in maximum diameter—it no doubt represents one of the ramifications of the main petiole. The preservation is remarkably perfect, in fact, scarcely a cell is lost. The concentric structure of the bundle comes out with astonishing clearness, which could not be exceeded in a preparation from a recent Fern. The small celled, thin-walled tissue constituting the phloëm is absolutely perfect and completely surrounds the V-shaped xylem. The maximum thickness of the phloëm-zone is found on the convex or morphologically lower side of the bundle; it thins out somewhat at the lateral angles, and again attains a considerable thickness on the concave upper face. The larger thin-walled cells bordering on the cortex are best regarded as pericycle. Neither here nor in any other specimen, do we find any differentiated bundle-sheath or epidermis; considering the perfection of the preservation we are probably justified in concluding that in *Lyginodendron*, as in the Marattiaceæ of the present day, a specialized endodermis was not developed. Secretory sacs are scattered among the phloëm-elements.

Every well-preserved transverse section of a petiole shows the same fact, that the bundle was concentric. Where two bundles are present, as usually happens in main petioles, and sometimes in their secondary branches, each bundle is surrounded by its own zone of phloëm, except where the two are on the point of fusing (*cf.* Memoir XVII., Plate 13, fig. 2). Longitudinal sections confirm these conclusions.†

The position of the spiral tracheides or protoxylem in the petiolar bundle is not always easy to determine in the transverse sections, but with the help of the longitudinal sections this can be done. There were always several such groups. Thus, in the specimen shown in photograph 5, there were certainly three, one near the

* The following are the most important specimens which throw light on the form of the leaf :—C.N. 134, 135, 137, and 139; these four form a series; 143, 147; 1191–1198, a series; 1855, 1856, 1885b, 1979.

† See especially C.N. 1978 and 1985; from the latter, fig. 13 was drawn. Both these sections are from petioles found in actual continuity with the stems of *Lyginodendron*. For additional good transverse sections of petioles, *cf.* C.N. 139, 146, 1194, 1854, 1857, 1984.

bend at the middle of the xylem and one near each end; in larger bundles they were more numerous. The smallest elements were not situated at the periphery of the xylem, but were imbedded in its mass, nearer the lower than the upper surface. That the elements in question are really the spiral tracheides or protoxylem is proved by the longitudinal sections (see Plate 23; fig. 13, *px.*, *cf.* also C.N. 1982).

We thus see, that the position of the initial strand is essentially the same as in the bundles of the stem. We desire to call special attention to the fact that there is not the slightest reason for regarding the *centrifugal* or lower portion of the xylem in the leaf* as secondary, which is the view of MM. BERTRAND and RENAULT in the case of *Poroxylon*. In *Lyginodendron* this tissue shows no sign of radial seriation and consists mainly of spiral or reticulate elements, while pitted tracheides chiefly occur in the centripetal portion of the xylem. In *Poroxylon*, true secondary wood was no doubt formed in the leaf, but we do not feel certain from the figures that there may not have been some *primary* centrifugal wood here also.†

The wood of the petiole resembles the primary wood of the stem except that it has a larger proportion of spiral and reticulated as compared with pitted elements. A certain amount of thin-walled parenchyma was present among the tracheides. It is probable that a layer of parenchyma also separated the tracheides from the phloëm.

The phloëm, as seen in longitudinal section, consists of very elongated elements, probably the sieve-tubes, and of shorter parenchymatous cells (see fig. 13, *ph.*).

The great point to be emphasized as regards the bundles in the petioles of *Lyginodendron* is, that they are the typical concentric bundles of a Fern, whereas those in the stem have a distinctly Cycadean character.

We have preferred to use the old term *concentric bundle* rather than *stele* in this case, because the vascular tissue of the petiole forms the direct continuation of the collateral strands of the stem, which no one could regard as anything else than vascular bundles of the usual type.

The inner cortex of the petiole presents one or two points of interest. It is traversed longitudinally by great numbers of those elongated tubes with carbonaceous contents which we regard as being of the nature of secretory sacs. The individual sacs must have been of great length in the petiole, for their terminal walls are rarely met with. They sometimes anastomose with one another, but we cannot say whether an actual fusion ever took place. The cortical parenchyma is crossed in a horizontal direction by transverse bands of short sclerotic cells. These often form, together with the longitudinal secretory organs, a most conspicuous network.‡ It

* In every petiole of *Lyginodendron* the upper and lower side can easily be determined in any transverse section. The upper side is flat or concave, the lower side is convex. The form of the bundle or bundle-pair follows the same rule (see Memoir VI., figs. 1, 6, 7, Memoir XVII., Plate 13, fig. 7, also our photographs 3 and 5 and fig. 10).

† See BERTRAND and RENAULT, 'Sur les *Poroxylons*,' figs. 219, 220.

‡ Something is shown of this on a small scale in fig. 11. This and many other anatomical details could not be adequately figured without increasing the number of illustrations beyond all bounds.

is doubtful, however, whether the two kinds of elements really had any special relation to one another, though, on the other hand, it is possible that some of the cells at the edges of the sclerotic bands may themselves have been of a secretory nature.*

The outer cortex has the familiar "*Dictyoxylon*" structure, consisting of alternate radial strands of sclerenchyma and parenchyma. On its outer surface are seated the curious emergences to which the specific name of "*Rachiopteris aspera*" owed its origin. As a rule, they are quite similar to those borne on the stem, but sometimes the outer sclerenchymatous layer is less developed and may appear merely as a thick-walled epidermis (see Memoir XVII., in which fig. 6 should be compared with fig. 7). The form of these protuberances is somewhat variable; usually they are bottle-shaped. Count SOLMS-LAUBACH† speaks of them as *winged ribs*, an expression which might convey the idea that they are longitudinal ridges, of which the figures cited show the cross sections. This, however, is not the case. The petioles, it is true, are often somewhat winged on their upper edges, but such wings are quite distinct from the emergences, which may arise from any part of the surface. That they are not wings is shown by the fact that in a series of sections of the same petiole, their position never remains constant. Further evidence as to their real form is afforded by the fact that in longitudinal sections their appearance is essentially the same as in transverse section (see Memoir XVII., fig. 8), and also by the fact that the cross section of the emergence itself is circular (*loc. cit.*).

We have figured a peculiar form of these emergences, which is not unfrequently met with (see Plate 23, fig. 12). The emergence has the usual thick-walled superficial layer; its internal parenchyma is generally thin-walled, but near the free extremity, there is a sharply defined group of well-preserved cells, with strongly marked walls and brown contents. This group appears to be limited externally by a somewhat flattened layer of cells. The structure certainly suggests a *gland* of some kind. In several cases, even when there was no such well-defined mass of specialized cells, the appearance of the parenchyma in the emergence is that of a tissue, which had been rich in cell contents. It is quite possible that a glandular function may have been discharged in certain cases by these emergences.

4. *Structure of the Lamina.*

Hitherto nothing has been known as to the histological structure of the leaflets of *Lyginodendron*. Now, however, we have several sections which show the tissues in great perfection. Two such sections are represented in Plate 19, photograph 7, and Plate 24, fig. 16. Both are from the series C.N. 1191–1198 so often referred to, and form part of leaves, the petioles of which show the characteristic structure of

* For the sclerotic bands, see "Organization," Part VI., Plate 52, figs. 11 and 12.

† "Fossil Botany," p. 361.

"*Rachiopteris aspera*." We therefore know that these leaflets really belonged to our plant. Specimens in which such details of the leaf-structure are well preserved, are necessarily rare.

A vertical section such as those represented, shows first of all, that the structure of the lamina was distinctly bifacial or dorsiventral. Towards the upper convex surface of the leaflet, the mesophyll consists of closely packed cells, elongated at right angles to the surface. Towards the lower concave surface, the cells, though still somewhat elongated, become more irregular, are sometimes branched, and leave considerable intercellular spaces between them.

Where the section passes through a vascular bundle, we see that the latter is enclosed within a very definite parenchymatous sheath, consisting of large cells elongated parallel to the bundle. We have endeavoured to find out whether the fine bundles of the lamina are concentric or collateral, a question of considerable difficulty. In one or two cases we have seen that the spiral tracheides, of which the xylem is exclusively composed, are in direct contact with the bundle sheath on the side towards the upper surface of the leaf, while on the lower side some intermediate thin-walled elements could be recognized (see fig. 16; C.N. 1856 shows this point well). Most probably the bundles of the lamina were collateral, as in recent Ferns, though throughout the rachis they were certainly concentric. The tracheæ became dilated in some cases towards the ends of the veins. This dilatation may have been connected with the presence of a water-gland.*

We were unable to determine the position of the protoxylem in the vascular bundles of the lamina.

The leaf possessed a distinct hypodermal layer beneath the epidermis of the upper surface (see photograph 7 and fig. 16). The epidermis itself is not so well-preserved as the mesophyll, but in one or two places the stomata can be recognized. The clearest is seen in sectional view in fig. 16A. Here there seems to be no doubt, that we have the two guard cells (*g.c.*), lying at the base of a depression formed by the prominent subsidiary cells. We have so far found no trace of stomata on the upper surface of the leaf.

The lamina of the leaf occasionally has outgrowths on its lower surface, similar to those on the petiole and stem (see photograph 7 and fig. 16). It is a curious fact, that in the best sections of the leaf, almost every cell contains a round mass of carbonaceous matter, very suggestive of a nucleus. We do not desire to lay any stress on this appearance, but its constancy in the best preserved preparations is certainly remarkable. (See photograph 7 and fig. 16.)

The following conclusions result from our observations :—

1. The lamina of the leaf in *Lyginodendron* had a distinctly bi-facial structure with well differentiated palisade and spongy parenchyma.

* C.N. 1856. See POIRAUT, "Recherches sur l'anatomie des Cryptogames vasculaires," 'Ann. des Sci. Nat., Bot., Sér. 7, t. 18, 1894.

2. The finer vascular bundles were probably collateral.
3. There was a hypoderma towards the upper surface *

5. *On a Peculiar Bud-like Structure.*

Before leaving the subject of the foliage, we wish to call attention to a very peculiar and indeed unique structure, which is represented in Plate 24, figs. 14 and 15. The organ at first sight strongly suggests the idea of a cone, and therefore attracted our special attention in the hope that we were at last on the track of the long-sought fructification of *Lyginodendron*. Subsequently, however, we found reason to give up this idea. The organ consists of an axis, imperfectly preserved in our specimen, which is densely clothed with prominent appendages, bearing a close resemblance to the well-known cortical emergences of the stem and leaf of *Lyginodendron*. The appendages are elongated and somewhat tapering; each has an envelope of sclerenchyma which becomes solid at the top. The central tissue is parenchymatous and has often perished, leaving a hollow. In no case is there any trace of a vascular bundle in an appendage. The transverse sections of the appendages are more or less semicircular near the base, becoming circular in their free part.

The axis of the whole structure, where it is cut radially, is found to be hollow (see fig. 14). In one of the sections the surface of the axis is shown in tangential view, and is seen to be marked with a number of patches of lighter coloured parenchyma, which no doubt represent the bases of as many appendages (see fig. 15). Between the parenchymatous areas the superficial tissues of the axis appear to have been fibrous, but the preservation is very imperfect.

We have two sections of this curious object. The extreme length of the whole structure is 14 millims., but it is doubtful whether the whole of this belongs to one specimen. The continuous portion represented in figs. 14 and 15 is only 4 millims. long.

We have rejected the idea of this specimen being a cone for two reasons:—

1. The appendages show no trace of vascular tissue, and therefore could hardly have been either sporophylls or sporangiophores of any kind, while on the other hand they agree exactly with the cortical emergences of *Lyginodendron*.
2. There is no trace of sporangia in connection with the organ.

The evidence for the specimen belonging to *Lyginodendron* at all depends solely on the structure of the appendages, the identity of which, with the cortical outgrowths of that plant, can scarcely be doubted, if, for example, our figures 14 and 15 be compared with Memoir XVII., Plate 12, fig. 6.

The explanation we would suggest is, that the structure represents either a bud or more probably a very young leaf covered with protective appendages of the nature

* The best preparations for showing the structure of the leaflets are: C.N. 1196, and others of the same series, 1856, 1885 D, and 1979.

of paleæ. The paleæ, or at least their bases, have remained, while most of the delicate young tissue of the organ which they protected has perished, leaving a hollow in the axis of the whole structure. The specimen is so remarkable, that we considered it worth figuring and describing, though its nature must at present remain problematical.

C.—THE ROOT.

1. *Connection between Root and Stem.*

We have already briefly recorded our discovery that *Kaloxylon Hookeri* was the root of *Lyginodendron Oldhamium*.* We will now bring forward the evidence on which this conclusion is based.

It has long been known that the stem of *Lyginodendron* bore appendages quite distinct from the petioles. Several examples of these are described and figured in Memoir IV., p. 387, figs. 11, 12, 14, 16, 22, and 24. The appendages in question are shown passing out more or less horizontally from the wood, and traversing the cortex. They were at that time regarded as branches, though another specimen—which was really, no doubt, of the same nature—was already recognized as being probably a root (*loc. cit.*, fig. 7).

A number of better preserved specimens also showing these organs in connection with the stem have since been obtained. These afford evidence—

1. That the appendages in question were of endogenous origin, and presented in all respects the characteristic structure of roots.
2. That these roots are identical with the fossil previously described as *Kaloxylon Hookeri*.

We will first state the facts which prove that the appendages are morphologically roots.

Adventitious roots, with the rarest exceptions, are of endogenous origin; they arise from deep-seated tissues (pericycle or endodermis), and have to grow out through the cortex of the parent stem. Hence they are readily distinguished from stem-branches, which are almost always of exogenous origin, arising from superficial tissues. A section of the cortex of the parent stem, passing through the base of an adventitious root, will show the latter as a complete organ, possessing a cortex and epidermis of its own; a corresponding section at the base of a branch would show only the vascular tissues, which connect the bundles of the branch with those of the stem.

We have the clearest evidence that the appendages of the *Lyginodendron* stem were of the former kind. Plate 19, photograph 8, represents part of a transverse section of a large stem. An appendage, which evidently made a sharp bend close to its base, is

* 'Proc. Roy. Soc.,' vol. 56, 1894. [Mr. T. Hick arrived independently, and almost simultaneously, at the same conclusion, but solely on the evidence of comparative anatomy. See 'Mem. and Proc. Manchester Lit. and Phil. Soc.,' ser. 4, vol. 9, Session 1894-5. (D. H. S., Dec. 14, 1895.)]

shown in approximately transverse section in the inner cortex of a stem. Its vascular cylinder, which had undergone considerable secondary thickening, is surrounded, except on the inner side, by its own cortical zone, which is sharply marked off from that of the stem itself. At the same time, owing to the curvature of the organ, the connection of its xylem with that of the parent axis is clearly shown. Some of the tracheæ, which are here seen in longitudinal section, are continuous with those of the secondary wood, while others extend inwards as far as the primary xylem of the stem; the latter, however, is somewhat crushed.

Photograph 9 is from a tangential section of another stem, and here the appendage is shown passing through the outer or "*Dictyoxylon*" cortex. On the right a leaf-trace bundle on its way to a leaf is shown. Here again the transverse section of the appendage is evidently that of a root. The solid vascular cylinder, with its well-developed secondary wood, is enclosed within a cortex of its own. It will be noticed that, in this instance, the appendage is passing out horizontally, which is the more usual case. The appendage is slightly compressed laterally, owing to the limitation of its growth by the sclerenchymatous strands of cortex through which it had to pass. The same phenomenon is observed in the adventitious roots of the Marattiaceæ—in which, however, the growth is, of course, primary only.

In photograph 10 another of these organs is shown from the same preparation. It is just becoming free from the cortex of the stem, a portion of which is shown to the right; the appendage still retains its compressed form, due to cortical pressure. The interesting point is, that it is itself beginning to branch. The two branches shown in the section have all the appearance of rootlets. The central cylinder has a primary mass of xylem without pith, and possesses abundant secondary wood; the cortex is well preserved, its large-celled outer layers are especially evident. In Plate 19, photograph 8A, another of these appendages is shown in longitudinal section (the stem being cut transversely), passing out from the wood, through the whole thickness of the cortex. We do not think that any botanist will hesitate, from the evidence already brought forward, in regarding these appendicular organs as *adventitious roots*, the name by which we shall henceforth call them.

Another specimen affords in some points still more conclusive proof of the nature of these organs. In this case we have three successive sections of the same specimen. Two of these sections are figured (Plate 25, fig. 18 and fig. 18A). They pass obliquely through a stem of *Lyginodendron*, and at the same time show several of the roots. In fig. 18 two of the roots shown (*rt.* 1 and *rt.* 2) are quite free, and remain so throughout the series. Two other roots (*rt.* 3 and *rt.* 4) are shown in transverse section, so far as their central cylinders are concerned. These roots, however, are curved, so that the section passes tangentially through a portion of the cortex of each, and shows that it is continuous with the *Lyginodendron* stem. The cortex of root 3 can be traced right through the outer cortex of the stem. Towards the interior, a portion of the vascular tissue of the root is also shown in longitudinal section. A fifth root is seen

exactly at its junction with the wood of the stem. It may be mentioned that root 4 is giving off a rootlet. Fig. 18A from the next section shows the roots 3 and 4 in obliquely longitudinal section, the plane of which passes through their central cylinders. The vascular tissue of root 4 can here be traced through the cortex of the stem. The great interest of this series lies in the fact that it shows at one and the same time the characteristic root-structure of these organs and their continuity as endogenous appendages with the stem of *Lyginodendron*.

In order to bring out the point in question more clearly, we have figured one of the roots on a larger scale (Plate 24, fig. 17). This is root 3 of figs. 18 and 18A. The more magnified figure is taken from the third section of the series, in which this root has become free from the stem, and is seen in complete transverse section. The root-like anatomy is here perfectly evident. The primary wood of the central cylinder has seven angles, at which the smallest tracheæ are situated, and is thus of *heptarch* structure. A certain amount of conjunctive parenchyma is present among the primary tracheæ. There is a zone of secondary wood, which is so distributed that a principal ray corresponds in position to each of the protoxylem angles of the primary wood. The inner cortex is somewhat lacunar, and contains a great number of the dark-coloured elements, which we regard as secretory sacs. The cortex is limited on the exterior by a well-marked zone of large, clear elements.

This brings us to our second point. Not only do these appendages of the stem of *Lyginodendron* present all the characters of roots, they are further identical with *Kaloxylon Hookeri*. This becomes evident at once on comparing our fig. 17 with Memoir VII., Plate 5, fig. 23, or with other transverse sections represented in Memoirs VII. and XIII., or again with our own, Plate 20, photograph 13, all of which represent transverse sections of typical *Kaloxylon*. In every respect the identity is perfect: in the structure of the primary wood, the character and arrangement of the secondary tissues, the details of the cortex, and especially in the characteristic external zone, termed the "epidermal layer" in previous memoirs.* In all the points, in fact, by which *Kaloxylon Hookeri* was characterized, the roots of *Lyginodendron* show an exact agreement with that fossil.

If, after the consideration of this specially clear case, we refer back to photographs 8, 9, and 10, we shall see that the roots there figured are of the same nature, though their *Kaloxylon* structure is less obvious, owing to slight modifications in that part of the root, which passes through the cortex of the stem.

As regards the distribution of the adventitious roots on the stem, we have little to add to what has already been said. The bases of roots are very commonly found, especially on the larger stems. On the other hand, they were not present on all parts of the stem. Thus the series 1191-1198, which extends through the whole length of an internode, with the adjacent nodes, nowhere shows any sign of an adventitious root.

* WILLIAMSON, "Organization," Part VII., 1875, p. 16; Part XIII., 1887, p. 295.

The roots occur on all sides of the stem, a point of some importance with reference to the habit of the plant. Longitudinal sections show that they were scattered quite irregularly, occurring both on nodes and internodes; their position shows no relation to that of the leaves.* We arrive, then, at the following conclusions:—

1. The stem of *Lyginodendron* bore numerous adventitious roots of endogenous origin, which occurred both at the nodes, and on the internodes.
2. These adventitious roots are identical with the fossils previously described under the name of *Kaloxylon Hookeri*.

2. Primary Structure of the Root.

The organization of *Kaloxylon Hookeri* has been fully described and illustrated in former memoirs.† Now, however, that its true nature is known, it becomes necessary to reconsider its structure in the light of our present knowledge.

When once the right clue has been obtained, there is no difficulty in recognizing all the specimens of *Kaloxylon* as roots. This is evident on inspecting the various figures in Memoirs VII. and XIII., or our own photographs 11–15. Following our usual course, we will first consider the primary structure of the root, and then the changes due to cambial activity.

The central cylinder of the root, before the commencement of secondary thickening has a perfectly typical radial structure, the number of xylem-groups varying from 8 down to 3, or possibly even 2 in the finest rootlets. The smallest primary tracheides are invariably at the peripheral ends of the radiating xylem-strands (see Plate 20, photograph 11 and Plate 25, fig. 20). That these peripheral elements really represent the protoxylem is proved by radial longitudinal sections, such as that shown in fig. 19. This section passes exactly through one of the primary strands of wood, and shows a narrow spiral tracheide, *px*, at its outer limit. Towards the interior the tracheides become rapidly wider, and here their walls are pitted. The border of the pits is sometimes well preserved. The absolute dimensions of the more central tracheides vary greatly, the diameter ranging from .036 to .09 millim. in different specimens.

Among the tracheides there is a considerable amount of conjunctive parenchyma, which is relatively most abundant in the largest steles. Sometimes this tissue separates the xylem-groups from one another (see photograph 11), sometimes it is irregularly scattered among the tracheides (see photograph 12). The conjunctive parenchyma consists of square-ended prismatic cells (see fig. 19). This combination of tracheides and parenchyma gives a highly characteristic appearance to the transverse sections of the larger steles. The parenchymatous bands sometimes extend to the

* The most important preparations for the connection between root and stem are the following:—C.N. 1144, A.; 1144, B.; 1147; 1148; 1883; 1885; 1885, A., B., and C. (same specimen); 1885, I., K., and L. (same specimen); and 1981.

† WILLIAMSON, "Organization," Parts VII. and XIII.

centre of the cylinder, but we never find a definite pith. Secretory sacs sometimes occur in the conjunctive tissue.

The best transverse sections of young roots show the primary phloëm-groups quite clearly (see photograph 11 and fig. 20, *ph.*). They are distinguished at once from the conjunctive parenchyma by their smaller cells, with thinner walls, and by a peculiar brownish tint, which may be due to the presence of carbonaceous matter derived from the abundant cell-contents. These groups alternate in a perfectly regular way with the xylem groups (photograph 11, fig. 20). They are always separated from the adjacent xylem by one or more layers of conjunctive parenchyma. In longitudinal sections, the elongated phloëm elements are even more sharply distinguished from the short-celled parenchymatous tissue (C.N. 1633).

The limits of the central cylinder are not very well defined. It appears, however, that the pericycle was one cell only in thickness, at least, opposite the xylem-groups, though sometimes thicker opposite the phloëm, and that the layer next beyond this, which has rather stouter walls, represents the endodermis (figs. 19 and 20). It is only in the rarest cases that any trace of the radial marks* characteristic of endodermal cells can be distinguished.

The broad inner zone of the cortex, constituting the greater part of its bulk, consisted of lax somewhat lacunar parenchyma, traversed by an enormous number of secretory sacs, the dark contents of which give a characteristic appearance to the sections (see photographs 11–14, figs. 17, 19, and 20). The transverse septa in these sacs are very evident in longitudinal sections, proving that these organs were formed from cells and not from intercellular canals.

In this cortical zone branched and septate fungal hyphæ are often met with—a proof, if any were needed, that true Fungi (“Mycomycetes” of BREFELD) already existed in the Carboniferous epoch.

The outer zone of the root is formed by the very well-marked “epidermal layer,” consisting of two or more series of rather large thin-walled cells, which are often much better preserved than the rest of the cortex, so as to stand out conspicuously, when the more internal tissue has become disorganized (see the various figures in Memoirs VII. and XIII., also Plate 24, fig. 17 of the present paper). The general appearance of this layer is often suggestive of a velamen, but there are no special markings on the cell-walls. We find no signs, even in the youngest rootlets, of any cells exterior to this zone, which we may therefore assume to have been really superficial. No root-hairs have been observed, but the external cells are often somewhat papillate. We may speak of this zone as the *outer cortex* or *epidermal layer* indifferently, for we have no means of determining its strict morphological nature.

The typical roots of *Lyginodendron* usually attain, before secondary thickening, a

* They are visible in a small tetrarch root (C.N. 1234), previously figured on a small scale, WILLIAMSON, “Organization,” Part XIII., Plate 24, fig. 22.

diameter of from 2 to $2\frac{1}{2}$ millims. The largest root has a diameter of 7 millims. This possesses a considerable zone of secondary tissue, but even without this the diameter would have been about 5 millims. We also find, however, many rootlets of quite small dimensions, several examples of which were figured in Memoir XIII. It requires a good deal of care, in the case of these very minute specimens, to determine with certainty to what plant they belong. We believe, however, that the structure of the cortex may be safely relied on. Where the inner cortex consists of lax tissue, with very numerous secretory sacs, while, at the same time, the well-marked "epidermal layer" is present, we feel justified in referring the rootlet to *Lyginodendron*. The organs with which confusion is possible are :

1. The finest rootlets of *Calamites*, formerly known as *Astromyelon* ;* and
2. Those of *Rhizonium*, a root of unknown affinity.

From the Calamitean rootlets, those of *Lyginodendron* can usually be distinguished by the absence of the thick-walled superficial layer, which is so characteristic of the former. The inner cortex of the rootlets of *Lyginodendron* has also less definite lacunæ than that of the rootlets of *Calamites*, a distinction which, however, becomes of doubtful value in the case of the very finest rootlets.

The rootlets of *Rhizonium* differ from those of *Lyginodendron* in the entire structure of the cortex, which is formed throughout of uniform closely-fitting cells, with few secretory sacs. *Rhizonium* † is also characterized by its extraordinarily abundant branching, much exceeding that even of the roots of *Lyginodendron*. In some even of the small rootlets, the identification is quite satisfactory. Thus *triarch* rootlets, with the characteristic structure of the *Lyginodendron* root, are found, as to the true nature of which there can be no doubt.‡

When Memoir XIII. was published, the fact that these finer branches were rootlets was already recognized as probable, though *Kaloxylon* was at that time regarded as an independent plant. The doubt suggested in that memoir as to the centripetal development of the xylem disappears as soon as we realize that the rootlets of different sizes are not developmental stages of the same organ, but represent branches of different orders or simply of different dimensions.

The typical roots of *Lyginodendron*, before the commencement of secondary growth, often bear a striking resemblance to the smaller roots of recent Marattiaceæ. On the other hand, they have little in common with those of any Cycadeæ at present investigated.

* See "Further Observations," &c., Part II. The Roots of *Calamites*.

† See WILLIAMSON, "Organization," Part XV., Plates 3 and 4, figs. 16-21.

‡ As in C.N. 1907, where *triarch* rootlets of *Lyginodendron* and of *Rhizonium* lie side by side. The former measures about 6 millim. in diameter. The still smaller rootlets, some of which are *diarch*, are more doubtful, but some of them, such as those figured in Memoir XIII., most probably belong to our plant.

3. *Secondary Tissues of the Root.*

Among the numerous specimens of roots of *Lyginodendron* which we have examined, we find the secondary tissues in every stage of development, from their first appearance (see Plate 20, photograph 12 and Plate 25, fig. 20) up to a stage when the secondary wood has attained a radial thickness of about 20 cells (see photograph 14). The process takes place exactly in the manner typical for roots of Dicotyledons, so that this fossil might very well be used for purposes of demonstration as illustrating the secondary growth of a root with diagrammatic clearness.

The cambium first appeared immediately within the groups of phloëm, arising from the division of the conjunctive cells lying in that position. It thus formed at first a series of isolated arcs separated from one another by the protoxylem-groups. This is well seen in fig. 20 which shows the first layer of wood formed from the cambium, *cb.** It is probable, that in the meantime a few additional tracheæ, the "metaxylem" of VAN TIEGHEM (*loc. cit.*, p. 684), had been differentiated from the conjunctive tissue between the primary groups of xylem (*cf.* photograph 11 with photograph 12).

The cambial divisions soon spread to the pericycle outside the protoxylem-elements (see photograph 12) so as now to form a complete though not a circular ring. The whole ring, however, did not behave alike. Opposite the primary phloëm, secondary xylem consisting of tracheæ with narrow secondary rays was formed, while outside the primary xylem, parenchyma, constituting the large principal rays, was at first chiefly developed.†

We thus find the secondary tissues broken up into distinct bundles corresponding in number and position to the primary groups of phloëm and separated from one another by the principal rays, which correspond to the protoxylem-strands. In fact, the mode of secondary growth is exactly that which is characteristic of a large number of roots among recent Dicotyledons.‡ Among Gymnosperms, curiously enough, we find a less close analogy, though in some of the finer roots of Cycads, as, for example, in rootlets of *Stangeria*, the process is essentially similar.

Sooner or later the principal rays often become sub-divided by the intercalation of additional strands of xylem and phloëm (see especially photograph 14).

The details of the secondary wood require no special description. It is composed of tracheides and rays exactly as in the stem. The pits of the tracheides are usually limited to the radial walls.§

* See also WILLIAMSON, "Organization," Part XIII., Plate 24, fig. 27; *cf.* VAN TIEGHEM's figure of the root of *Pisum*, "Traité de Botanique," second edition, p. 722, fig. 481.

† See photographs 13 and 14, also WILLIAMSON, "Organization," Part VII., Plate 5, figs. 23 and 26; Part XIII., Plate 23, fig. 26.

‡ See DE BARY, "Comparative Anatomy," English edition, p. 474; VAN TIEGHEM, 'Ann. des Sci. Nat., Bot.,' Series V., vol. 13, 1871, p. 274.

§ WILLIAMSON, "Organization," Part VII., Plate 4, fig. 29; Plate 5, fig. 27; Plate VI., fig. 30.

Both cambium and secondary phloëm are often preserved in great perfection (see photographs 13 and 14, also WILLIAMSON, Part VII., Plate 6, fig. 31). The phloëm is essentially similar to that in the stem. The position of the primary phloëm groups can still be clearly recognized even in advanced roots (see photographs 13 and 14, also WILLIAMSON, Part XIII., Plate 23, fig. 21).

We find no distinct formation of periderm in the older roots, though sometimes a few tangential divisions took place in the pericycle (see photograph 14). The primary cortex became a good deal compressed by the secondary growth within it, but, so far as our specimens show, it was not thrown off.

Small rootlets, as well as the larger roots, were evidently capable of considerable secondary growth. Thus, the most advanced specimen figured (photograph 14) can have had only a small tetrarch cylinder to start with, and must in its primary condition have been considerably smaller than the other roots figured.

4. *Branching of the Root.*

Specimens showing branches in connection with the principal axis have been previously figured.* Additional specimens are represented in our photographs 10, 12, and 15. The ramification was evidently abundant. Thus, the specimen shown in photograph 12 was giving off four branches, almost at the same level, two of which are shown in approximately median section. The branches were always of considerably smaller size than the main axis. They were evidently rootlets, borne on a relatively main root. Two points of interest arise in connection with these rootlets:—

1. Each rootlet is invariably placed exactly opposite one of the protoxylem-groups of the main root which bears it (see photograph 12, fig. 20, and the figures above cited). This fact is shown with special beauty in the longitudinal section represented in photograph 15. Here one of the rootlets is cut exactly in the median plane, and its connection with the smallest peripheral xylem-elements of the main root is clear. The tracheides of the rootlet bend at a right angle on joining those of the main root. The bend was no doubt directed towards the organic base of the latter.

2. The rootlets are evidently of endogenous origin. Although we cannot observe their development, this is sufficiently proved by the fact that the rootlet always has a cortex of its own, which can be traced through that of the parent root (see photographs 12 and 15, also WILLIAMSON, Part XIII., Plate 24, fig. 27).

In every respect, then, the branching of these organs is that characteristic of roots.

The knowledge which we have now obtained of the roots of *Lyginodendron* forms a striking addition to the characteristics of this extraordinary fossil. We have already

* WILLIAMSON, "Organization," Part VII., Plate 6, fig. 33; Plate 7, fig. 34; Part XIII., Plate 24, fig. 27.

pointed out the remarkable combination of fern-like and Cycadean characters presented by the stem and foliage of the plant. We now see that its roots show still more striking peculiarities. With a primary structure like that of the roots of Marattiaceæ they combine a mode of secondary growth which recalls that of a typical *Dicotyledon*, a resemblance which, we need hardly say, is not indicative of affinity.

D.—HABIT AND DIMENSIONS OF THE PLANT.

The specimens of *Lyginodendron*, on which the preceding description has been based, are all of comparatively small size, the maximum diameter of the stem not exceeding about 4 centims.

It has been supposed that the plant attained arborescent dimensions. The evidence from this belief is derived partly from certain cortical impressions of large size, partly from a single large specimen, with the structure of the secondary wood preserved, the real nature of which, however, is not certain.

Four examples of the cortical impressions in question were figured in Memoir IV., Plate 27. They obviously represent the casts of a "*Dictyoxyton*" cortex of a very large stem. The furrows, no doubt, correspond to the print of the sclerenchymatous network, the elevations to the soft parenchyma by which the meshes were filled.

A general resemblance to the outer cortex of *Lyginodendron* is obvious; but this seems to be the only reason for connecting these impressions with our plant. The meshes of the cast are of very large size, reaching a length of as much as 8 centims. We have received, through the kindness of Mr. A. C. SEWARD, F.G.S., a photograph of a still finer specimen of this kind from the "Third Grits" in the neighbourhood of Harrogate. This impression is almost a metre (38 inches) long and 28 centims. (11¼ inches) in maximum width. The meshes of the cast are long and pointed in form and very variable in size, reaching a length of at least 14 centims. Some of the larger meshes are sub-divided by oblique furrows, which no doubt represent the prints of subsidiary connecting strands of sclerenchyma. The specimen seems to be nearly flat, so that it is impossible to form any definite idea of the size of the stem to which it belonged, but it must certainly have been a good-sized tree.

We do not think, at present, that there is any sufficient proof that these large cortical impressions belong to *Lyginodendron*. We have no undoubted *Lyginodendron* in which the meshes of the outer cortex at all approach the dimensions of those in the casts. The length of the meshes in *Lyginodendron* rarely exceeds 6 millims.

It seems quite possible that the large casts may represent the outer bark of some species of *Sigillaria*, in which case their dimensions would present no difficulty. We know that the outer secondary cortex of *Sigillaria* possessed "*Dictyoxyton*" structure,* as is well shown in sections of *Sigillaria spinulosa* from M. RENAULT'S

* See SOLMS-LAUBACH, "Fossil Botany," p. 247, &c.

collection.* The meshes in this specimen are sometimes sub-divided by fine sclerenchymatous strands exactly as we find in the casts. The only "Dictyoxylon" cortex, with which we are acquainted in *Lyginodendron*, was primary. We have good evidence that periderm was formed to the interior of this zone, and therefore it seems certain that, if the stem attained any large size, the characteristic cortical layer must have been cast off, and so could not have left the impressions which we see on the casts. We think, therefore, that no convincing evidence for the arborescent dimensions of *Lyginodendron Oldhamium* can be derived from the cortical impressions.

There remains the large specimen showing structure, received from Mr. NEILD, and referred to in Memoir IV., p. 386. The specimen includes the pith and a portion of the wide zone of secondary wood. Sections in the three directions have been cut and clearly exhibit the structure so far as it is preserved.† The diameter of the pith is 3.3×2.3 centims. The maximum radial thickness of the secondary wood is 5.8 centims., but we cannot be certain that its whole thickness is preserved. Assuming, however, that we have the whole thickness of the wood, the radius of the stem up to the cambium would have been over 7 centims., and its diameter over 14 centims. We cannot tell what was the diameter of the whole stem, for we know nothing of the cortex. No authentic specimen of *Lyginodendron* which we have seen, however, has secondary wood of a greater thickness than about 6 millims.; so, if we judge by this dimension, the stem in question must have been nearly ten times as large as that of any undoubted *Lyginodendron* in the WILLIAMSON collection.

Unfortunately, the only structure preserved is that of the secondary wood. Its general anatomy is identical with that of certain specimens of *Lyginodendron*.‡ The tracheides are smaller than is usual in *Lyginodendron*, but not smaller than in some undoubted stems of that plant. The radial section shows the muriform rays and the pits on the walls of the tracheides, which, in so far as their preservation allows of comparison, agree very well with those of our plant. The pith is completely disorganized and no trace of the primary wood can be recognized. There is, however, a narrow incomplete zone of internal secondary wood, distinct from the rest, at the margin of the pith—which recalls the anomalous medullary tissue sometimes found in *Lyginodendron*. Although the parenchyma of the pith has perished, the cavity contains clusters of dark brown cells, which are much like the sclerotic nests characteristic of the pith in *Lyginodendron*.

On the whole, until some other fossil has been found which agrees better with this doubtful stem, we think there is a presumption that it really belonged to a *Lyginodendron*, or to some plant of the same type of structure.

* C.N. 665 and 668 (presented by M. RENAULT). See also C.N. 703, figured in WILLIAMSON, "Organization," Part IX., Plate 25, figs. 93-95.

† The sections are C.N. 1131, 1132, and 1133.

‡ Cf. especially C.N. 1124, 1176, and 1183.

Mr. NEILD's specimen thus affords a certain amount of evidence that *Lyginodendron Oldhamium*, or some allied species, may have attained the dimensions of a small tree.

As regards the habit of the ordinary small specimens, with which we are familiar, the radial symmetry of the stem and the fact that adventitious roots, when present, are given off on all sides, render it probable that the plant grew in an upright position. The longest piece of stem which we have is barely three inches (7·6 centims.) in length (C.N. 1207 A). The position of the nodes in this specimen is not very evident; two, however, can be distinguished and they are about one inch (2·5 centims.) apart.

From the course of the vascular bundles we know that the total length of the stem must have included many internodes, for, if our interpretation of the facts be correct, it follows that each transverse section of the stem usually shows the traces of the next ten leaves above. We must, therefore, picture *Lyginodendron* to ourselves as having a tall, upright stem rising to a height of several feet and bearing somewhat remote, spirally arranged, highly compound, fern-like leaves. The base of the stem, where the adventitious roots were given off, must have been buried for some depth in the earth or mud. Probably the bases of stems would be the parts most often preserved, which would explain the frequency with which adventitious roots are met with in connection with the stem. It is not probable that the roots were aërial; the fact that they branched freely immediately on leaving the stem militates against such an idea (see photograph 10, fig. 18). The velamen-like outer layer, which might suggest an aërial root, is common to the finest rootlets, and these must almost certainly have been subterranean. The well-developed xylem of the roots renders it probable that they vegetated in a fairly firm soil.

The stem is mechanically well-constructed and thus fitted to maintain an upright position while bearing abundant foliage. We have no distinct evidence for any rhizome-like organs, but it is possible that some of the small shoots which are rather deficient in sclerenchyma may have been creeping or subterranean. The small specimens, which constitute almost the whole of our material, could not have been branches borne on main stems, for in that case they would not have borne adventitious roots. If the plant really attained a relatively large size, then we must assume that our material is made up of *young* specimens.

This brings us to the most important of all questions, that as to the fructification. It is a remarkable fact, that though *Lyginodendron Oldhamium* is one of the commonest of our English coal-fossils, and though all its vegetative organs are preserved with astonishing perfection, no certain traces of reproductive organs have ever been discovered.

If the plants constituting our material had borne anything at all of the nature of a cone, it is difficult to understand why its remains should never have been found. The only cone-like body discovered had, as we have shown above, nothing to do with the fructification.

On the other hand, Fern sporangia are occasionally found among the fragments of *Lyginodendron* foliage, though never in actual continuity with it.*

Two possibilities suggest themselves :

1. It may be, that *Lyginodendron* was, as to its fructification, a true Fern (in spite of its anatomical peculiarities) and bore sporangia on its leaves ; they might very easily have become detached, and the want of any evidence of continuity between sporangia and leaf would not be surprising.

2. It is possible that our material consists entirely of young plants, in which case the absence of fructification is easily accounted for.

On the whole, we incline to the latter view ; if our specimens had often been fructifying ones, it is probable that sporangia, even though detached, would be much more commonly found than is actually the case. The few examples observed are easily explained by accidental admixture of foreign material.

We think, therefore, that the whole question of fructification must be left open for the present.

We shall not enter further into the consideration of affinities, until the genus *Heterangium* has been dealt with, for the two genera throw much light on each other and must be discussed together.

II.—HETERANGIUM, *Corda*.

INTRODUCTION.

The genus *Heterangium* was founded by CORDA in 1845, on a fragmentary specimen from the Bohemian coal-measures. The first British specimens were discovered in 1871 among Mr. GRIEVE'S Burntisland fossils. This form was originally named *Dictyoxyylon Grievii*, but in 1872 was placed in CORDA'S genus, and now bears the name of *Heterangium Grievii*, WILL.†

In addition to the Burntisland specimens, fossils which appear to be referable to the same species were discovered at a later date by Mr. LOMAX, at Dulesgate, in Lancashire.‡

In the mean time, a second species, in a marvellous state of preservation, had been discovered in the Halifax coal-measures. To this form the name of *Heterangium tiliæoides*, WILL., was given.§

A French species, *Heterangium Duchartrei*, B.R., originally referred to the genus *Poroxylon*, was discovered by M. RENAULT, and shows a considerable resemblance to

* See, for example, C.N. 1630, 1979, 1980.

† WILLIAMSON, 'British Association Reports,' 1871 ; "Organization," Part IV., 1872, pp. 394 and 404.

‡ WILLIAMSON, "Organization," Part XVII., 1890, p. 96.

§ WILLIAMSON, "Organization," Part XIII., 1887.

our *H. tiliæoides*. A second species, *H. Bibractense*, B.R., has since been described by M. RENAULT.*

Our present detailed knowledge of the structure of *Heterangium* has been derived almost entirely from the study of the English and Scotch specimens.

As is well known, the genus *Heterangium*, while closely resembling *Lyginodendron* in habit and many points of structure, is sharply distinguished from it by the primary structure of the central cylinder in the stem. In *Heterangium* there is no pith; the whole interior of the stele is occupied by the primary wood, consisting of a mass of tracheæ, arranged in groups and interspersed with irregular bands of conjunctive parenchyma.†

Important as this difference is, we find that the agreement in details of structure with *Lyginodendron* is in many points so exact, as to leave no doubt of the close affinity of the two genera. The foliage, of which we have some knowledge in the case of *H. Grievii*, bore a general resemblance to that of *Lyginodendron*. We have good reason to believe that the roots were also of the same type of structure as in that genus.

We will begin our description with *H. Grievii*, the species of which we have the most complete knowledge, though its detailed preservation is seldom equal to that of *H. tiliæoides*.

i. HETERANGIUM GRIEVII, Will.

A. THE STEM.

1. General Structure.

The stems of *Heterangium Grievii*, so far as our specimens show, rarely exceeded a diameter of 1·5 centim. The smallest stems observed attained about half this diameter (see branch in Plate 26, fig. 21); so the range of dimensions is inconsiderable, contrasted with that among the authentic specimens of *Lyginodendron*. The general structure is uniform throughout, the differences depending almost entirely on the extent to which secondary growth has taken place.

There are some slight differences between the Burntisland and the Dulesgate specimens, though we have not regarded them as sufficient to necessitate a specific separation between these forms.

The typical structure has been so fully described in former memoirs, that only a brief recapitulation is necessary here.‡

* RENAULT, "Structure comparée de quelques tiges de la Flore carbonifère," 1879, pp. 276-278, Plate 14, figs. 4-8. BERTRAND and RENAULT, "Recherches sur les *Poroxylons*," 'Archives bot. du Nord de la France,' 1886, p. 245. RENAULT, "Flore fossile d'Autun, &c.," Part II., Atlas, Plate 65, 1894.

† See WILLIAMSON, "Organization," Part IV., Plate 28, fig. 30; Part XIII., Plate 21, fig. 1; Plate 22, fig. 2; also our Plate 28, fig. 30.

‡ WILLIAMSON, "Organization," Parts IV. and XVII.

The central cylinder, with its large axial mass of primary wood, traversed in all directions by anastomosing bands of parenchyma, by which the tracheæ are separated into irregular groups, presents a most characteristic appearance. We recognize at once that the smaller elements of the primary wood lie near the periphery, where we can distinguish definite groups of tracheæ, recalling the perimedullary xylem-strands of *Lyginodendron* (see Plate 26, figs. 21 and 24; also WILLIAMSON, Part IV., Plate 28, fig. 30; Part XVII., Plate 14, fig. 14). The whole structure at first suggests a Lycopodiaceous stem a suggestion which, as we shall see, is altogether fallacious. A better parallel will be found in certain stems of Ferns.

In many stems the primary structure has remained unaltered (fig. 21; WILLIAMSON, "Organization," Part XVII., Plate 14, fig. 14); in others a certain amount of secondary wood has been added. At the exterior of the secondary wood the cambium and phloëm are found in favourable cases (see fig. 24), though not so well preserved as in *Lyginodendron* or in the next species of *Heterangium*.

The cylinder is surrounded by a zone of rather large clear cells, very well marked in many cases, which we regard as constituting a pericycle (see Plates 26 and 27, figs. 21, 26, 28, *pc.*; WILLIAMSON, "Organization," Part IV., Plate 28, fig. 30, *g.*). The inner cortex is of great width, and consists of parenchyma, in which are imbedded large and conspicuous nests of sclerotic tissue (fig. 21, *sc.*). In longitudinal section we see that these nests form horizontal bands—a most characteristic feature of both stem and petiole (figs. 22, 23, 28; WILLIAMSON, "Organization," Part IV., Plate 29, fig. 32; Plate 31, figs. 45 and 47; Part XVII., Plate 15, figs. 17 and 18).

The outer cortex is of the "*Dictyoxylon*" type, but with narrower parenchymatous meshes than in *Lyginodendron* (WILLIAMSON, Part IV., Plate 28, fig. 30; Plate 29, fig. 35). In young specimens the parenchymatous bands are very inconspicuous (fig. 21). Leaf-trace bundles are scattered throughout the inner cortex, and can readily be traced from the pericycle out into the bases of the leaves (see WILLIAMSON, "Organization," Part IV., Plate 30).

The outer surface of the stem was distinctly ribbed, the ribs, no doubt, corresponding to the decurrent bases of petioles. The "restoration" of a portion of the stem, represented in WILLIAMSON, "Organization," Part IV., Plate 31, fig. 49, still appears to us, after our renewed investigations, to be accurate in all essential points.

Apart from the structure of the stele, the chief differences from *Lyginodendron* which strike us in a general survey of the organization of the stem are in the distribution of the sclerotic nests and in the course of the vascular bundles.

In *Heterangium*, the former distinctly belong to the cortex, while in *Lyginodendron* they are usually limited to the pericycle. The vascular bundles in *Heterangium* leave the pericycle early in their outward course and pass gradually outwards through the cortex, while in *Lyginodendron* they keep within the pericycle until they approach their exit from the stem.

2. *Course of the Vascular Bundles.*

The main facts as to the course of the vascular bundles in *Heterangium Grievii* have always been understood, since the first description of the plant was published in 1872. A series of eight transverse sections from a piece of stem nearly two inches long, figured in Part IV., Plate 30, affords conclusive proof that the vascular bundles, which are found in the cortex, pass gradually outwards and enter the bases of the leaves, each of which receives a single bundle. At the same time the lower ends of these bundles were traced downwards to their point of union with the central cylinder.*

It has only been necessary for us to consider two points:—

1. What light does the course of the bundles throw on the phyllotaxis of the plant?

2. To what extent can the leaf-trace bundles be recognized, as distinct strands, at the periphery of the primary wood?

Some of the specimens are sufficiently complete and well-preserved to enable us to determine the succession of the leaf-trace bundles in the same way as was done for *Lyginodendron* (p. 708).

In some of the larger stems as many as nine or even ten leaf-traces are seen in the transverse section, counting all those which have once begun to separate from the central cylinder. Their arrangement points distinctly to a $\frac{2}{5}$ divergence.† In one case, for example, the 9th bundle (counting from within outwards) lies directly outside the 1st, while the 10th corresponds in like manner to the 2nd. Here the phyllotaxis must evidently have been $\frac{2}{5}$. It is possible that a higher divergence may have sometimes occurred. In the smaller stems a $\frac{2}{5}$ arrangement has been observed (C.N. 1293).

As regards the second question, the careful observation of good transverse sections shows clearly that the arrangement of the tracheæ in the primary wood is not an irregular one, but that a number of definite bundles can be distinguished at the periphery of the stele. These peripheral strands have essentially the same structure as the xylem of the leaf-trace bundles, with which they are in continuity.‡

We have now determined that each of the peripheral groups corresponds very exactly in structure with one of the perimedullary strands of xylem of *Lyginodendron*. In *Heterangium* the number of these strands at the periphery of the cylinder is very large—(from 16 to 20)—greatly in excess of the number of orthostichies which appear to have existed. This is a point of difference from *Lyginodendron*, in which,

* WILLIAMSON, "Organization," Part IV., p. 401; Plate 28, fig. 30, *m'''*, &c.

† The position of the two leaves of which the bases are shown in the series figured in WILLIAMSON, "Organization," Part IV., Plate 30, also indicates a $\frac{2}{5}$ phyllotaxis.

‡ See figs. 21, 24, and 26; also the transverse sections figured in "Organization," Part IV.

as we have seen, the number of perimedullary strands is either equal to that of the cortical leaf-traces or not greatly in excess of it.

This we can explain in three ways :

1. The leaf-traces on joining the cylinder may have branched, or
2. They may have extended down through a very large number of internodes turning aside sufficiently to make room for each other, or
3. It may be that some of the peripheral strands of the cylinder are cauline and not directly continuous with the leaf-trace bundles. It is not possible to decide between these suppositions ; the strands in question are not isolated like those of *Lyginodendron*, but form part of a continuous mass of wood. Hence their course could only be determined with certainty by tracing the actual protoxylem-elements through a series of sections, and that is more than we can expect to do, though in individual cases the protoxylem is clear enough.

We must, therefore, be content to sum up our knowledge of the course of the bundles in *Heterangium Grievii*, as follows :—

1. The leaves were spirally arranged, the phyllotaxis being $\frac{3}{8}$ in some of the larger, and $\frac{2}{5}$ in some of the smaller stems.
2. Each leaf received a single trace. The traces passed very gradually through the cortex, and joined the central cylinder at a distance below the node equal to from 6 to 10 internodes.
3. The traces can be followed for some distance downwards at the periphery of the central cylinder.

3. *The Primary Structure of the Stele and Leaf-trace Bundles.*

In most specimens the tracheæ occupy the larger part of the whole area of the transverse section of the primary wood.* In some cases the stele is more parenchymatous and the scattered tracheæ form a relatively small part of the whole tissue.† In no case, however, is there any sign of a definite central medulla. The parenchymatous bands extend to the periphery of the primary wood, where they separate the more external xylem-strands from one another, and are continuous with the principal rays of the secondary wood (see fig. 24, *c.p.*).

The conjunctive parenchyma is made up of short, thin-walled, square-ended cells (see fig. 25, *c.p.*).

In the specimens of *H. Grievii* from Burntisland we found no other elements in this tissue ; in the stems from Dulesgate, Lancashire,‡ however, the conjunctive parenchyma is traversed by rows of elongated cells with dense carbonaceous contents, similar to the structures which we have termed “secretory sacs” in *Lyginodendron*.

* WILLIAMSON, Part IV., Plate 28, fig. 30.

† C.N. 1254.

‡ WILLIAMSON, “Organization,” Part XVII., p. 96.

There is every reason to believe that the tracheal elements of the primary wood were all *tracheides* and not true vessels. No signs of transverse walls are ever observed, while sometimes we find the very tapering ends of the elements. Their length must have been great, as terminations are by no means frequently seen.

The tracheæ of the interior of the wood are always pitted. Where they are in contact with one another the pits, which are very numerous and hexagonal in outline, are most distinctly bordered, as shown in fig. 25. The borders of the pits, which have not been described before, can only be seen in well-preserved specimens; in many cases the borders have perished, leaving behind an apparently reticulate sculpturing. On the other hand really simple pits occurred on the surface of contact between tracheæ and parenchyma.

The most important point, however, connected with the primary wood is the structure of its peripheral region, for it is here that a clear analogy with *Lyginodendron* shows itself.

The "coalesced clusters of small vessels which occupy the peripheral portion of the vasculo-cellular medullary axis" were described in the first memoir on *Heterangium*, and their continuity with the leaf-trace bundles was also observed.*

We have paid special attention to the structure of these peripheral "clusters" of tracheæ, which in many of the specimens are very distinct. A good typical example is shown, in transverse section, in Plate 26, fig. 24. The close resemblance to a perimedullary xylem-strand of *Lyginodendron* becomes evident if the figure cited be compared with Plate 21, fig. 2. In *Heterangium*, as in the former genus, the smallest elements of the xylem-strand are situated in its interior, though at no great distance from its peripheral surface. In both genera these elements are accompanied by parenchymatous cells. Indications of the spiral thickening of the smallest tracheides can sometimes be observed even in the transverse sections (see fig. 24, *px.*). To determine their true nature, however, recourse must be had to the corresponding radial sections, such as the section represented in fig. 25, which should be compared with Plate 22, fig. 4, from *Lyginodendron*. Here we see that the smallest tracheides have a loosely spiral thickening and evidently constitute the *protoxylem* of the strand.

The elements to the exterior of the protoxylem (*x'*), which form the centrifugal part of the primary wood, are more densely spiral. In other cases they are somewhat reticulate. They are quite distinct from the secondary xylem, which in the part figured is represented by a ray (*x^{2r}.*). On the interior of the protoxylem we find some parenchyma and then the large pitted tracheides (*x.*) of the centripetal wood.

The same structure has been found in all the well-preserved specimens, so that there can be no doubt that the peripheral strands of xylem are "mesarch" in the sense defined above (p. 713), and so far resemble the xylem of the foliar bundles

* WILLIAMSON, "Organization," Part IV., p. 401.

in Cycadeæ. It is quite evident that the protoxylem is not peripheral, and that the centrifugal elements exterior to it still belong to the primary wood.*

These definite xylem-bundles, each with its own protoxylem, do not always occupy the whole periphery of the primary wood. They are often separated from one another by portions of the same irregular tracheal groups which extend throughout the whole interior of the cylinder. For convenience of distinction, we propose to apply VAN TIEGHEM's term "metaxylem" to these latter groups, reserving the term "primary xylem-strands" for those peripheral bundles which are continuous with the leaf-traces. Usually, however, no sharp limit can be drawn between the two, for, as a rule, the xylem-strand passes over gradually on its inner side into the general metaxylem of the cylinder (see Plate 26, fig. 24, *x.* and *m.x.*).

It may be mentioned, that in the specimens of *H. Grievii* from Lancashire, the protoxylem-elements lie somewhat nearer the external surface of the xylem than in those from Burntisland.

We have no information to give as to the structure of the primary phloëm. Remains of soft tissue in a more or less disorganized condition can always be found between the wood and the pericycle, but the structure of this zone is never preserved in stems without secondary thickening.

The pericycle is sharply marked off from the disorganized phloëm-zone; the latter has a characteristic brown tint, while the pericyclic cells are clear (see Plate 27, fig. 26, *p.c.*). The short-celled pericyclic tissue is often well preserved, though its cell-walls are thin. In the Dulesgate specimens the pericycle is traversed by secretory sacs, which are less evident in the original Burntisland form.

It remains to consider the structure of the leaf-trace bundles on their outward course.

Fig. 26 shows the transverse section of one of these bundles, which is just separating from the stele, but is still enclosed within the pericycle. The position of the protoxylem is not certain, but we believe, from the comparison of many sections, that there are two such groups at the points indicated, *px.* Some of the longitudinal sections pass through out-going leaf-trace bundles, and show clearly the position of the laxly spiral elements in the interior of the xylem strand.†

The collateral structure of the bundle figured in fig. 26 is fairly evident; the thin-walled phloëm is tolerably well preserved and undoubtedly seems to be limited to the outer side of the strand. Unfortunately the preservation in *H. Grievii* is seldom

* The best slides for showing the protoxylem and primary xylem-strands are:—

Transverse, C.N. 1291, 1293, 1294 (Burntisland).

1915 C. (Dulesgate).

Longitudinal, C.N. 1266, 1268 A, 1276, 1286, 1288 (Burntisland).

1915 G. (Dulesgate).

† The following preparations show leaf-trace bundles in longitudinal section: C.N. 1265, 1282, 1284, and 1915 G.

sufficiently good to enable us to decide, with certainty, whether the bundles in the outer part of their course are collateral or concentric. In the original Burntisland specimens a certain amount of tissue has usually perished all round the xylem of the bundles in the cortex, and there is no means of telling whether the whole of this delicate tissue consisted of phloëm. The Dulesgate specimens are somewhat better preserved in this part, so that in some cases it is possible to see that the phloëm of the cortical leaf-traces is limited to the external side of the xylem.*

We may, therefore, regard it as probable that the collateral structure shown in fig. 26 was maintained throughout the course of the bundle in traversing the stem. Although the leaf-trace bundles sometimes became somewhat lobed (as seen in transverse section) in passing through the cortex, yet we have no clear evidence that they ever divided into twin bundles as in *Lyginodendron*.

Our knowledge of the primary structure of the stele and vascular bundles of *H. Grievii* may be summed up as follows :

1. The stele consisted of a central mass of primary xylem (made up of tracheides and conjunctive parenchyma) surrounded by a zone of phloëm. The whole was enclosed by a well-marked pericycle.
2. The primary wood may be divided into the peripheral xylem-strands, which are continuous with the leaf-trace bundles, and the metaxylem. Each of the peripheral strands had the same mesarch structure as the perimedullary strands of *Lyginodendron*, or as the xylem of the foliar bundles in *Cycadeæ*.
3. The leaf-trace bundles were collateral in structure on leaving the central cylinder and probably remained so in passing through the cortex.
4. The primary tracheides, with the exception of the protoxylem and adjoining elements, possessed numerous bordered pits.

4. *The Secondary Tissues.*

It is not uncommon to find stems of *H. Grievii* which retain the primary structure unaltered, such as the stem represented in Plate 26, fig. 21, where the main axis is quite without any secondary tissues, though, curiously enough, they are present to a small extent in the branch. The majority of the stems, however, have a secondary zone, which is often of very unequal thickness on different sides of the same stem, and is on the whole less developed than in *Lyginodendron*. The secondary wood is very sharply marked off from the primary; this is owing partly to the regular radial arrangement of the secondary elements and partly to their smaller size (see Plate 26, fig. 24; also WILLIAMSON, "Organization," Part IV., Plate 28, fig. 30). In cases where the secondary wood attained any considerable thickness, the size of its elements increased towards the exterior.

* See especially the four transverse sections C.N. 1915-1915 C.

A local increase in the thickness of the secondary wood is sometimes found near the bases of adventitious roots (see Plate 10, fig. 28, x^2).

The wood has the same structure as in *Lyginodendron*, consisting of radial rows of tracheides, with rays between them (see Plate 26, figs. 24 and 25). The tracheides have numerous bordered pits on their radial walls similar to those of the primary wood. It is probable that a few pits also occurred on the tangential walls, as was certainly the case in *H. tiliæoides*, in which the preservation is more perfect.

The rays consist of thin-walled cells often showing in radial section a characteristic muriform arrangement.*

Fig. 25 shows in radial section the inner part of a ray at a place where the secondary wood is still very thin. The ray is as yet scarcely differentiated from the pericyclic cells by the division of which it arose. Some of the rays are continuous with the conjunctive parenchyma of the primary stele (see fig. 24). We may call these the primary or principal rays, but they do not differ essentially from those which abut on the tracheides of the primary wood. Secondary rays were occasionally intercalated, where the wood attained a sufficient thickness.†

Secretory sacs, which often run in a radial direction, are especially frequent in the rays of the Dulesgate specimens. A figure in a previous memoir gives a sufficient idea of the appearance of the secondary wood as seen in tangential section.‡ The rays, however, are often of greater breadth than those shown in that figure.

Cambium and secondary phloëm are never very perfectly preserved in our specimens of *H. Grievii*, though, as we shall find, their preservation in *H. tiliæoides* is perhaps more perfect than in any other known fossil. In some of the best specimens of *H. Grievii* the tabular form of the cambial cells can be made out in transverse section (see especially Plate 26, fig. 24, *cb.*; also Plate 27, figs. 26 and 29). As regards the phloëm, the transverse sections, as shown in the figures just cited, prove that it consisted of thin-walled elements of smaller diameter than the adjacent cells of the pericycle. Some of the longitudinal sections show that the phloëm-elements were much elongated.§

There is no doubt whatever, that here, as in *Lyginodendron* and in *Heterangium tiliæoides* the cambium was a perfectly normal one, forming wood on its inner and bast on its outer surface.

Where the leaf-trace bundle passes out from the stele a parenchymatous gap is left in the secondary wood, corresponding to the "trace-gap" in *Lyginodendron*.||

Although we sometimes find traces of tissue-formation by tangential cell-division

* See WILLIAMSON, "Organization," Part IV., Plate 29, fig. 33.

† As in C.N. 1915 C.

‡ WILLIAMSON, "Organization," Part IV., Plate 29, fig. 33a.

§ See especially C.N. 1268 A. and 1915 G. and R.

|| See WILLIAMSON, "Organization," Part IV., Plate 28, fig. 30, *m'''*.

in the outer layers of the pericycle,* yet the formation of a regular periderm does not seem to have been general in this species.

5. *The Cortex.*

The wide inner cortex consisted of short-celled parenchyma, interrupted by very regular horizontal plates of sclerotic tissue (see Plate 26, figs. 21 and 22†). These sclerotic plates give a most characteristic appearance to the sections both of stems and petioles. They appear to have been of the same nature as the "sclerotic nests," which are so general in *Lyginodendron*, but their distribution is different. In *Lyginodendron* they occurred mainly in the pith and pericycle of the stem and in the cortex of the petioles. In *H. Grievii* they are always cortical in both organs. Their sclerotic character is more easily recognized in the latter plant, where their walls are often perfectly preserved. In some cases, even the numerous fine pits running through the whole thickness of the cell-wall can be distinguished.‡ These elements bear a considerable resemblance to the *stone-cells*, which are so often found in the cortical tissues or petioles of recent plants, as, for example, in *Hoya*.

The sclerotic plates were evidently placed one above the other in vertical series, for a radial section either shows a whole row of them or else misses them altogether.§ The arrangement of their constituent cells is very regular and indicates that they were formed by a special meristem.||

The outer cortex consisted of the well-known alternating strands of sclerenchymatous fibres and parenchyma. The parenchymatous portions are often very narrow, especially in the Dulesgate specimens, in which the sclerenchyma appears nearly continuous and is only interrupted here and there by small patches of parenchyma¶ (see fig. 21).

The epidermis is sometimes preserved and consisted of rather thick-walled cells. In one case we noticed an appearance suggestive of a depressed stoma, lying over one of the parenchymatous groups of the outer cortex.**

6. *Branching of the Stem.*

We have only a single specimen in which the branching of the stem is shown. This is one of those from Dulesgate. A transverse section of this specimen is shown

* C.N. 1276.

† Also WILLIAMSON, "Organization," Part IV., Plate 29, fig. 32, *h'*, and Part XVII., Plate 15, figs. 17 and 18.

‡ See C.N. 1915 F.

§ C.N. 1276.

|| WILLIAMSON, "Organization," Part XVII., Plate 15, figs. 17 and 18.

¶ WILLIAMSON, "Organization," Part XVII., Plate 14, fig. 14.

** C.N. 1915 M.

in Plate 26, fig. 21. The continuity of the cortical tissues of the branch with those of the main axis is evident. Although the branch shows no leaf-traces, it is certainly a stem-structure. It is not a root, for its origin is clearly exogenous. It is not a leaf, for the stele has the same structure as that of the stem, and has even formed some secondary wood. The structure of the cortex of the branch is identical with that of the main stem. We have other sections of the same specimen, one of which shows the branch at a point where it has just become free from the parent axis.*

B. THE LEAF.

1. *Connection between Leaf and Stem.*

Several specimens show the bases of petioles in connection with the stem. Thus, in the series of sections previously figured the bases of two petioles are shown.† The same series contains a transverse section of another petiole, which has become free from the stem.‡

We have figured in Plate 26, fig. 22, a longitudinal section of a stem, passing through the insertions of two petioles (*pt.*). These examples show that the leaves were inserted alternately on the stem. The length of the internodes shown in fig. 22 appears to have been only about 5 millims. In the series first mentioned the length of the internodes must have been much greater, for the bases of two leaves only were met with in a piece of stem nearly two inches long. Fig. 22 shows that the cortex of the petiole contained the same horizontal sclerotic bands as that of the stem. In most specimens it is evident that only a single bundle entered the leaf from the stem, and not a double bundle, as in *Lyginodendron*. The only exception is one of the Dulesgate specimens, in which two quite distinct bundles are seen in transverse section in the cortex, which appear from their position to be destined for the same petiole.§

In most respects the leaf-traces agree closely with those of *Lyginodendron*.

The specimens showing petioles in connection with the stem enable us to identify other petioles, which have become free. Their cortical structure is quite characteristic, owing to the horizontal sclerotic plates of the inner cortex and the "*Dictyoxyton*" structure of the outer zone. The only difficulty is the possibility of confusion with the petioles of *Lyginodendron*. Two distinctions, however, exist.

1. The characteristic emergences, to which the petioles of *Lyginodendron* owed their former name of *Rachiopteris aspera*, are absent from the petioles of *Heterangium Grievii*.

* C.N. 1885 H.

† WILLIAMSON, "Organization," Part IV., Plate 30, figs. 42 and 44.

‡ C.N. 1244.

§ C.N. 1915 M.

2. The secretory sacs, which are so conspicuous in petioles of *Lyginodendron*, are either absent, or, at least, much less noticeable in those of *Heterangium*.*

2. *Form and Structure of the Leaf.*

We are only able to obtain a very general idea of the form of the leaf in *H. Grievii*. Several of the preparations show a confused mass of petioles of various orders, intermixed with fragments of leaflets. The petioles vary in diameter from 4 millims. to 0.4 millim., or even less. All alike show the characteristic structure of the cortex, which distinguishes these petioles from that of any other known plant, with the exception of *Lyginodendron*, from which they can be separated by the characters mentioned in the last paragraph. In some of the specimens the branching of the petioles is shown. Plate 26, fig. 23, represents a small portion of one of the preparations in question, but gives only an imperfect idea of the complexity of the mass of foliage which it contains. Sections of leaflets are found among the petioles, and are sometimes in connection with their finer branches. The structure of the leaflets is never well preserved, but the form of the sections indicates a decided resemblance to the leaflets of *Lyginodendron*.

Although the evidence available does not admit of our attempting any detailed reconstruction of the form of the *Heterangium* leaf, yet one conclusion of great importance follows with certainty from the facts observed. The leaf of *H. Grievii* must have been a highly compound one, with a much branched rachis, bearing numerous small leaflets. In other words, the foliage of our plant was certainly of a Fern-like character, and was totally different from any leaves known among the Lycopodiaceæ.

Our knowledge of the structure of the leaf is practically limited to that of the petiole and its branches. It is true that in some of the preparations from the Dulesgate specimens beautiful sections of leaflets are shown.† Unfortunately, however, these preparations contain specimens of *Lyginodendron*, as well as of *Heterangium*, so it is impossible to decide for certain to which plant the leaflets belong.

The sections of the petiole are not equal to those of *Lyginodendron*, but the chief points in the structure can be determined. The vascular bundle was no doubt concentric. The central mass of wood is always surrounded by a zone of thin-walled tissue, which, though imperfectly preserved, can hardly be interpreted otherwise than as phloëm.‡

* For specimens showing leaf-bases in connection with the stem, see the series C.N. 1240–1247; also C.N. 1281, 1286, 1294, 1915 A, and 1915 M.

† See C.N. 1915–1915 C.

‡ Transverse sections of the petiole are contained in the following preparations: C.N. 1244, 1283, 1289, 1300. The last-named is figured in WILLIAMSON, "Organization," Part IV., Plate 28, fig. 46. It was then termed "a young twig." For longitudinal sections see especially C.N. 1286, 1287, and 1292.

The structure of the xylem is essentially similar to that of the petiolar bundle of *Lyginodendron*. The majority of the tracheides are spiral or reticulate, but some are pitted. The lax spiral elements (protoxylem) lie in the interior of the strand.

The structure of the cortex of the petioles has been sufficiently described above.

One point remains to be discussed; in two, at least, of the preparations, sporangia, like those of certain Ferns,* are found in association with *Heterangium* foliage.† A portion of one of these preparations is represented in fig. 23. The sporangium, *sm.*, is in close contact with a fragment of leaf, which appears to be continuous with a small petiole of *Heterangium*. If the continuity between the sporangium and the leaf could be established, the fact would be of the greatest importance. Careful examination of the preparation, however, leads us to doubt much whether this was the case. The fragment is in bad condition, and we found it impossible to prove that the shred of tissue on which the sporangium is seated, really belonged to the *Heterangium* foliage.

The other preparation in question (C.N. 1292) contains numerous sporangia, none of which, however, are connected with the foliage. This slide contains petioles of *Rachiopteris Oldhamia*, WILL., as well as of the *Heterangium*, so that here it is plain that no definite conclusion can be drawn. In other cases seeds have been found in association with specimens of *Heterangium*,‡ but there is not the slightest reason for supposing that they have anything to do with our plant. Here, again, the question of fructification must for the present remain undecided.

Our conclusions as to the foliage of *Heterangium Grievii* are the following:—

1. The leaves were arranged spirally on the stem, the phyllotaxis being usually either $\frac{3}{8}$ or $\frac{2}{5}$.
2. The leaves were repeatedly compound, with long and much-branched petioles, bearing small leaflets.
3. The petiole contained a single vascular bundle of concentric structure.
4. The cortex was characterized by the horizontal sclerotic plates in its inner zone and by the "*Dictyoxyton*" structure of its external portion.
5. Both in form and structure, so far as they can be determined, the leaves of *Heterangium* closely resembled those of *Lyginodendron* and were of a Fern-like character.

C. THE ROOT.

1. Connection between Root and Stem.

Several specimens of *Heterangium Grievii* show adventitious roots in connection with the stem. Two such specimens have been previously figured, both of which are

* Cf. WILLIAMSON, "Organization," Part VIII., Plate 7, fig. 29.

† C.N. 1287 and 1292.

‡ C.N. 1915 D, G, H, and O.

seen in transverse section of the stem, the root passing out through the cortex in an approximately horizontal direction.*

There can be no question that these appendages were really roots. In both cases the organ possesses a cortex of its own, distinct from that of the stem on which it grows. The organs in question must, therefore, have been *endogenous* in origin.

We have figured part of a remarkably fine longitudinal section from one of the Dulesgate specimens, showing the bases of three adventitious roots, placed one above the other in a vertical row (Plate 27, fig. 28). This specimen has the central cylinder, including the pericycle, preserved in great perfection; the cortex, however, is almost destroyed, so that at first there seemed to be some doubt whether the main axis was a root or a stem. That the latter is the case is proved by the persistent cortical sclerotic masses (*sc.*), which are quite characteristic of the stem, and also by the fact that another part of the section shows a leaf-trace bundle, passing through the pericycle.

One of the three adventitious roots is seen in exactly median section. The connection of its tracheæ with those of the primary wood of the stem is quite clear; the root lies exactly opposite one of the protoxylem strands of the stem. The base of the root has formed some secondary wood, which is continuous with that of the parent stem. The phloëm is not shown in this root, but can be recognized in the next, which, as well as the third one, is cut somewhat tangentially. In all the roots the limits of their cortex can be traced. The stem has formed a much larger amount of secondary wood near the bases of the roots than elsewhere. This wood is chiefly developed *above* the insertion of the roots, *i.e.*, in the direction towards the apex of the stem, as determined by the course of the leaf-trace bundles. The pericycle has also undergone an enormous thickening, with tangential cell-divisions, around the bases of the roots. Between their bases secondary tissue, partly consisting of wood, has been formed in the pericycle in a very anomalous manner; much of this tissue is seen in transverse section, so the direction of the tracheides must have been tangential with reference to the stem. There seems, in fact, to have been a special "réseau radicifère," as it is called by VAN TIEGHEM,† in connection with the bases of these roots.

In fig. 29 we have shown a curious structure which we think may probably represent a very young root enclosed within the cortex of the stem. The section is a nearly complete transverse one of a good-sized stem with a considerable amount of secondary wood. The root-like organ is embedded in the cortex, immediately beneath the outer sclerenchymatous layer, and is seen in approximately transverse section.

A central cylinder can be distinguished, but we could detect no lignified elements.

* WILLIAMSON, "Organization," Part IV., Plate 30, fig. 36; Part XVII., Plate 14, fig. 14.

† "Traité de Botanique," p. 787. The same structure is beautifully shown in transverse section in C.N. 1915 A.

The more central cells of the cylinder are relatively large and may well represent undeveloped tracheæ. Immediately outside the latter we find groups of small cells, possibly young phloëm. The outer layers of the wide cortex are large-celled, as in roots of the "*Kaloxylon*" type. Numerous "secretory sacs" are present throughout the tissues of the organ. We see no other explanation for this structure than that it represents a young adventitious root, and, if so, it is of some interest, for organs at such an early stage of development are necessarily rare in the fossil state. The presence of such a rudimentary root in a mature stem is not very surprising, for we know that adventitious roots may arise at all ages of the stem, and also that such roots may remain for a long time undeveloped.*

2. *Structure of the Root.*

Our knowledge of the structure of the root in *H. Grievii* is at present a matter of inference rather than of absolute proof, for we have no clear transverse sections of those roots which are in actual connection with the stem. The longitudinal sections of the root-bases show that the xylem extended to the centre of the cylinder, and mainly consisted of tracheides like those of the stem.

In the Burntisland preparations transverse sections of roots are rare and unsatisfactory. The Dulesgate specimens, however, contain many beautifully preserved roots, which in some of the preparations are seen in transverse section in close contact with the same stems on which the bases of adventitious roots are found. All these roots are of the "*Kaloxylon*" type, and, as the same material contains stems of *Lyginodendron*, it is quite probable that some of them belong to the latter plant. Yet we feel sure that among these roots those of *Heterangium* are included, for we know that the stems of *Heterangium* in this material produced roots freely, and there are no other root-like organs present which could possibly be referred to them. We believe the explanation to be that the roots of *Heterangium Grievii* were themselves of the "*Kaloxylon*" type, and not always readily distinguishable from those of *Lyginodendron*.

There is one special form of root, however, which we feel pretty strongly convinced belonged to *Heterangium Grievii*. We refer to certain tetrarch roots, such as that shown in transverse section in Plate 27, fig. 27. Roots of exactly this kind are excessively common in the preparations from Dulesgate material containing *Heterangium Grievii*, while we have never found them associated with *Lyginodendron* when *Heterangium* is absent. The characteristics of these roots (which, as the figure shows, are often perfectly preserved) consist in the large tetrarch primary wood, with very prominent angles, and in the almost geometrical regularity with which the tissues are arranged. Roots of *Lyginodendron* with a tetrarch cylinder are, it is true, well

* The best preparations illustrating the connection between root and stem in *H. Grievii* are C.N. 1260, 1294, 1915, 1915 A, 1915 G, and 1915 H.

known, but in these the primary wood is of small extent and has much less prominent protoxylem angles (*cf.* Plate 20, photograph 14). Another distinction consists in the fact that the primary wood in the roots of *Lyginodendron*, when of comparable extent to that of the roots in question, contains a larger amount of conjunctive parenchyma. The difference in anatomical "habit" between the roots which we are describing and those of *Lyginodendron* is well marked, though easier to see than to describe (*cf.* photographs and figures of *Lyginodendron* roots with fig. 27).

The cambium and phloëm are exquisitely preserved in this and other specimens. The secondary thickening took place with remarkable regularity, the bands of secondary wood being strictly limited to the regions opposite the phloëm. The pericycle appears to be several cells thick opposite the protoxylem. The inner cortex, which is a good deal crushed in most of the specimens, contained a large number of "secretory sacs." The large-celled outer cortex or "epidermal layer" is extremely conspicuous.

Longitudinal sections of this form of root show little difference from the root of *Lyginodendron*, except the smaller amount of conjunctive tissue.

From the evidence brought forward we feel no doubt, though the point is not yet strictly demonstrated, that the adventitious roots of *Heterangium Grievii*, like those of *Lyginodendron*, were of the *Kaloxylon* type of structure, but that the special form of root, characterized by a large tetrarch primary stele, with prominent protoxylem angles and little conjunctive tissue, was peculiar to *Heterangium*.*

D. HABIT AND DIMENSIONS OF THE PLANT.

As regards the dimensions of *H. Grievii* we have no evidence that the stem attained any larger size than is shown in our specimens, which reach a diameter of about 1.5 centim., though, of course, it is quite probable that it may have done so. The habit of the plant must have been like that of a small *Lyginodendron*. The stem was probably upright, as is indicated by its radial symmetry and strong mechanical construction. It bore spirally arranged, highly compound, Fern-like leaves, while in its lower part it gave off adventitious roots. The stem occasionally branched, though apparently this was rare. The general appearance of the plant would probably have been that of a Fern.

As regards the fructification, we have no evidence which we regard as of any weight. We must, however, point out that the entire absence of any cone-like structure is remarkable, especially as in this case there is no reason to suppose that we have to do exclusively with young plants. This negative evidence, if we allow ourselves to be influenced by it at all, rather tends to favour the idea that the plant may have had a Fern-like form of fructification.

* The best preparations showing this form of root are: C.N. 1885 H, 1915 B, D, M, O, P and R. The "quadrate *Kaloxylon*" shown in C.N. 1635 is probably of the same nature.

ii. *HETERANGIUM TILLÆOIDES*, Will.

This species of *Heterangium* (from the coal-measures of Halifax) was first described in 1887, when a full account of its general structure was given.* The specimens are few, but are remarkable for the astonishing perfection with which the anatomical details are preserved. We are enabled to add some information on the minute structure to the facts previously brought forward.

The stem in its general organization and dimensions resembles that of *H. Grievii*. We do not propose in this case to give a detailed description of the whole structure, which is unnecessary in view of what has already been done, but merely to state in order the fresh points which our renewed examination of the specimens has brought to light.

The first point to which we desire to call attention is the great distinctness of the primary xylem-strands at the periphery of the central mass of wood. They at once strike the observer as definite bundles† (see Plate 28, fig. 32) and can easily be counted. Thus in one of the larger stems‡ they number 20, and in a smaller specimen§ they number 16. The structure of each of these strands is perfectly clear, as shown in transverse section (see figs. 32 and 33), and exactly agrees with that of the corresponding strands in *H. Grievii* or with that of the perimedullary strands of *Lyginodendron* (cf. Plate 21, figs. 2, 3, and Plate 26, fig. 24). The spiral or annular protoxylem-elements are placed in the interior of the xylem-strand, but near its outer margin, and are usually accompanied by parenchyma (see the radial section shown in Plate 29, fig. 34). To the outside of the protoxylem we find more densely spiral elements, which evidently still belong to the primary wood, while on the inside tracheides with bordered pits at once appear. It would be quite legitimate to compare the central cylinder of this *Heterangium* to that of a *Lyginodendron*, supposing the primary bundles of the latter to be connected together throughout the pith by a network of metaxylem. The analogy with *Lyginodendron* is more evident in *H. tillæoides* than in *H. Grievii*, though the structure is essentially similar in these two species. The great majority of the peripheral xylem-strands show the structure described; a few, however, appear to be destitute of spiral elements.

The secondary growth bore a definite relation to the peripheral strands of the primary wood. Opposite each of the latter a fan-shaped mass of secondary tissue was developed (see fig. 32).||

* WILLIAMSON, "Organization," Part XIII.

† WILLIAMSON, "Organization," Part XIII., Plate 21, fig. 1, and Plate 22, fig. 2.

‡ C.N. 1619.

§ C.N. 1320.

|| Also WILLIAMSON, *loc. cit.*

These masses were separated from one another by the broad principal rays, which were continuous towards the interior with the bands of conjunctive tissue lying between the primary xylem-strands. There was no *inter-fascicular* formation of either wood or bast, and consequently the definite distribution of the secondary tissues gives a very characteristic appearance to the transverse sections.

Both primary and secondary tracheides are nearly though not exactly similar to those of *H. Grievii*; the spirally-arranged bordered pits have narrow inclined slit-like openings.*

The secondary tracheides, in addition to the crowded bordered pits on their radial walls, had more scattered, sometimes simple, pits on their tangential faces.

Many of the secondary rays by which the wood is divided up extend inwards as far as the primary xylem.

In many places the cambium is extremely well-preserved (see Plate 29, figs. 35, 36, and 37). The fascicular cambium is of the usual character, but here, as in *Lyginodendron*, the cambium by which the principal rays were formed shows less frequent tangential divisions.

In the radial section represented in fig. 37, a tracheide (*tr.*) adjoining the cambium is shown, the wall of which is areolated, though not yet pitted in the usual manner. This is evidently a tracheide in course of development; the primordial pits are already marked out, but the deposition of the borders has not yet begun. This is not an isolated case. We have observed in the same material a tracheide, with a still finer areolation, representing a still earlier stage, and another somewhat more advanced, with the borders of the pits beginning to appear. Such stages of histological development are certainly rarities among fossil specimens.

The enormous masses of phloëm constitute the most interesting feature of the fossil. The phloëm attains a thickness little less than that of the secondary wood, and is preserved in marvellous perfection.

The primary rays in passing through the phloëm become greatly dilated, widening out into large wedges, as seen in transverse section, and thus exactly resembling the well-known phloëm-rays of the lime tree, a resemblance to which the fossil owes its specific name.†

At the exterior of each phloëm-strand the irregularly arranged, somewhat thick-walled elements of the *primary* phloëm can be easily recognized (fig. 35, *ph.*). The greater part of the bast, however, is secondary, as shown both by its radial seriation corresponding with that of the cambium and wood, and by the proportion which its thickness always bears to that of the secondary wood.

The secondary rays of the phloëm are often dilated in the same way as the primary rays, but to a less extent. The phloëm groups lying between the rays show no very obvious differentiation of their elements as seen in transverse section (figs. 35 and 36).

* See WILLIAMSON, Part XIII., Plate 21, fig. 16.

† See WILLIAMSON, Part XIII., Plate 21, figs. 1, 4, and 10; Plate 22, fig. 2; Plate 23, fig. 9.

Longitudinal sections, however, show that the secondary phloëm contained long parenchymatous cells in addition to the sieve-tubes. In the latter transverse walls are not found, and their ends appear to have been tapering (figs. 37 and 38). Generally, the larger elements appear to have been sieve-tubes, but the difference in size is not very marked.

The preservation of the sieve-tubes is astonishingly perfect, so as to leave no doubt as to their nature, a point which was spoken of with some reserve in Memoir XIII. (p. 291), at a time when the detailed structure had not yet been observed. In several cases the sieve-plates on the radial walls of these elements can be recognized with certainty. This is the case, for example, at the place marked *svp.*, in fig. 37, where the markings on the wall clearly indicate a compound sieve-plate. A much better example, however, is shown in the oblique section, from which fig. 38 was drawn. The sieve-tube in question is shown on a larger scale in fig. 38A. The sieve-plates are marked on the wall in brown carbonaceous matter and exactly resemble those of some recent Gymnosperms and vascular Cryptogams. The smallest areas into which the plates are sub-divided no doubt represent the minute sieve-fields within which the actual pores were grouped.

We may well wonder how structures so delicate, which are often difficult to demonstrate in recent plants, can have been preserved in the fossil state. That the markings in question really represent sieve-plates will not be doubted by any botanist who examines the sections for himself and sees how often these appearances occur, and how invariably they are limited to those elements which, from their position and form, must be regarded as sieve-tubes. Sieve-plates in fossil plants have occasionally been figured by previous writers; among the most satisfactory are those shown by Messrs. BERTRAND and RENAULT, in *Poroxydon Edwardsii*, which much resemble those of our plant.*

It is not at all likely that minute differences in the thickness of a cellulose wall, or even minute perforations, would be recognizable so distinctly in the fossil condition. It is much more probable that what we see represents the carbonized remains of that portion of the contents of the tube, which adhered to the plate, so that the sculpturing of the latter has remained in the form of a carbonaceous print.

Beyond the phloëm there is a zone of tissue which we interpret as pericycle; it attained a great thickness, much exceeding that of the corresponding region either in *Heterangium Grievii* or in *Lyginodendron*.† It consisted, like the pericycle of those plants, of short-celled parenchyma, but contained in addition numerous short sclerotic cells either isolated or in groups (see WILLIAMSON, "Organization," Part XIII., Plate 21, fig. 19), a feature in which this species differs from *H. Grievii*, where

* "Recherches sur les *Poroxydons*," figs. 192 and 193.

† This layer was termed "inner cortex" in Memoir XIII., *loc. cit.*, Plate 21, fig. 1; Plate 22, figs. 2 and 5, *p.*

the sclerotic masses are limited to the cortex, while it agrees with *Lyginodendron*.*

The outer layers of the pericycle have generally undergone somewhat irregular tangential cell-divisions. Beyond these layers we often find a zone of flattened cells, which may represent an incipient periderm.†

Elements of the kind which we regard as secretory sacs are excessively abundant throughout the soft tissues of *H. tiliæoides*, especially in the medullary rays and pericycle.

The cortex, the outer layers of which are usually much shattered, bears a general resemblance to that of *H. Grievii*, especially to the specimens of that type from Dulesgate.‡

The leaf-trace bundles are seen in all the transverse sections at various points of their outward course. Sometimes they are met with in the pericycle, sometimes in the cortex. Their close agreement in structure with those of *H. Grievii* or of *Lyginodendron* leaves no doubt as to their nature, though in the present species we have no specimens actually showing their passage into a leaf. One specimen (C.N. 1301) shows a petiole in connection with the stem; the stem is seen in transverse section, the petiole is cut obliquely, but in a nearly longitudinal direction. The continuity of the cortical tissues between petiole and stem is evident. The vascular bundle is well shown in the petiole, but the plane of section does not allow us to trace it into the stem. The structure of the petiole is essentially the same as in *H. Grievii*. It is remarkable that it appears to contain a single vascular bundle only, for the leaf-traces in the stem of this species are nearly always in pairs, as in *Lyginodendron*.§ The twin bundles may have completely fused on entering the leaf. We think there is no doubt that the pair of bundles imbedded in the pericycle, figured in Memoir XIII., Plate 22, fig. 5, are leaf-trace bundles, which are just separating from the stele, and each of which still retains its own external arc of secondary tissue. Exactly parallel cases are well known in *Lyginodendron* and have been fully described above.

Beyond the fact that the stem bore adventitious roots, we have no information as to these organs. We regard the body represented in Memoir XIII., Plate 23, fig. 12, as the base of an adventitious root at its junction with the wood of the stem. It is very probable that the structure represented in Plate 22, fig. 13, is also connected with the base of a root.

* Some doubt was expressed in Memoir XIII., p. 293, as to these elements being really thick-walled cells. It was suggested that their appearance might be due to the conditions of mineralization producing inorganic deposits on the cell-walls. We now find that the structure of these cells is the same as that of the undoubtedly sclerotic elements which constituted the horizontal plates of the cortex. Like the latter they persist when the surrounding soft tissue has perished. Similar cells occur in the dilated phloëm-rays.

† C.N. 1302, 1619, 1627.

‡ See WILLIAMSON, "Organization," Part XIII., Plate 21, figs. 1 and 6, *r*, *t*; Plate 22, figs. 2 and 11, *r*, *t*.

§ See WILLIAMSON, "Organization," Part XIII., Plate 22, figs. 7 and 8.

H. tiliæoides appears to us to agree in all essential points of structure with *H. Grievii* and certainly to be rightly placed in the same genus. It differs from that species in the exceptional development of its secondary phloëm and phloëm-rays, in the greater distinctness of the primary bundles at the periphery of the stele, in the consequent separation of the secondary tissues into distinct strands, in the presence of sclerotic elements in the pericycle, and in the double leaf-trace bundles. In several of these points the present species approaches *Lyginodendron* somewhat more nearly than *H. Grievii* does. On the whole, we must regard *H. tiliæoides* as the more highly differentiated of the two *Heterangiums*. Its great interest to the botanist depends chiefly on the extraordinary perfection with which the details of its structure are preserved, affording the clearest proof, that in the carboniferous flora, the histological elements were identical with those of existing plants, however much the arrangement of these elements may have differed.

iii. ON A *Heterangium* OF UNCERTAIN SPECIES.

We have a single specimen of the stem of a *Heterangium*, probably from Halifax, which we are not able to refer with certainty to either of the preceding species. A transverse section of this specimen is shown in fig. 30, and a part of the longitudinal section in fig. 31. The general structure of the stele agrees with that of the other two species. The appearance of the transverse section rather suggests *H. tiliæoides* than *H. Grievii*. The presence of sclerotic groups in the pericycle is a definite character in which it resembles the former species. The longitudinal section, however, shows that the primary tracheides exactly resemble those of *H. Grievii*, while they are somewhat different from those of *H. tiliæoides*. In the latter many of the primary tracheides show curious spiral lines of thickening between the series of pits. Nothing of the kind is visible in *H. Grievii* or in the undetermined specimen. Only a very slight formation of secondary wood has taken place in this specimen. The cortex is of moderate thickness and has a smooth outer surface, so that the stem, as a whole, has a cylindrical form, and is thus very different from the conspicuously ribbed stem of *H. Grievii*. The comparison with the form of the stem in *H. tiliæoides* is difficult, as the cortex is never complete in the specimens of the latter species.

The inner cortex contains masses of dark sclerotic tissue, arranged in vertical series (see fig. 31), while the outer zone consists chiefly of sclerenchymatous fibres. There is thus nothing peculiar in the structure of the cortex; its appearance is somewhat unusual and suggestive of charring. The transverse section shows a fairly-preserved pair of leaf-trace bundles (fig. 30, *lt.*). The fact of their forming a pair suggests a comparison with *H. tiliæoides*, though this arrangement is not absolutely unknown in the other species.

A tetrarch root of the type which we have referred to *Heterangium*, lies close to the stem opposite an interruption in the cortex. It is not unlikely that it may have

belonged to the plant (fig. 30, *Rt.*). Other roots of the same kind occur in the preparations.

We think it certain that this specimen does not belong to *H. Grievii*, or at least that it does not represent the ordinary form of stem in that species. We should have suggested that it might be a young specimen of *H. tiliæoides*, were it not for the want of exact agreement in the details of the primary wood. It is possible that it may represent some peculiar form of stem, such as a rhizome, belonging to one or other of the known species. If it is desirable to give the specimen a provisional name, we may speak of it as *H. cylindricum*, but without desiring to imply that its claims to specific distinctness are likely to hold good permanently.

III. AFFINITIES OF *Lyginodendron* AND *Heterangium*.

So long as we are without information as to the reproductive organs of these genera, it is evident that any discussion of their affinities must be conducted with the greatest caution. Considering, however, the very thorough knowledge of their vegetative parts which we now possess, we may reasonably hope to throw considerable light on the question, although we cannot yet solve it finally. Some encouragement in the attempt may be derived from the experience of palæobotanists in other families. In the case of the *Lepidodendreæ*, for example, there can, we think, be no doubt that an unprejudiced consideration of their vegetative structure alone is sufficient to lead to a true estimate of their relationships, which is only confirmed by our knowledge of their fructifications. So also with the *Calamariæ*; as we showed in a former paper,* a minute examination of the anatomical characters, especially those of the primary tissues, affords by itself the strongest presumption of *Equisetaceous* affinities, and so helps us to the right interpretation of the evidence from the fructifications.

A really accurate knowledge of vegetative characters, especially of those derived from the internal structure, may, we believe, be trusted to put us on to the right track in cases where the larger systematic groups are alone in question.

The fact that in various respects both *Lyginodendron* and *Heterangium* strongly resemble Ferns has been noticed since the first discovery of these plants, and has been demonstrated in the preceding pages. As regards the former genus, we have now proved beyond doubt that the highly compound leaves were those of a *Sphenopteris*, and in *Heterangium* the general character of the foliage was evidently similar. The external form and even the venation of the leaf, however, would by themselves carry no decisive weight, though hundreds of fossil species have been referred to the Ferns on no better grounds. But beyond this, the internal structure of the leaf is now well known in *Lyginodendron*, and to a less degree in *Heterangium*, and proves to be in all respects that of a Fern, as is shown most clearly by the concentric structure of

* WILLIAMSON and SCOTT, "Further Observations on the Organization," &c., Part I.

the vascular bundles in the petiole and rachis. This fact holds good for both genera. Both in structure and form, then, the leaves of *Lyginodendron* and *Heterangium* are Fern-leaves, their one point of difference being the occurrence of pitted as distinguished from scalariform tracheides in their xylem.

Now, as regards *Lyginodendron*, the distinctively Fern-like character is limited to the foliage; this, however, is not the case with the other genus. Apart from the secondary growth, the stem of *Heterangium* is essentially that of a monostelic Fern of the *Gleichenia* type. The resemblance of the stele of *Heterangium* to that of a *Gleichenia* is, in fact, very marked, as regards the distribution of the tracheides and conjunctive parenchyma, the position of the protoxylem-groups, and the presence of a wide pericycle. We think the comparison with *Gleichenia* may prove to be a fertile one, and hope to pursue it further on another occasion. It is not at all unlikely that the *Gleichenia* type of structure may be of great antiquity. We see, then, that if we left the secondary thickening out of account, there would be no serious reason against regarding *Heterangium* as a fairly typical monostelic Fern. We notice, however, certain peculiarities:

1. The presence of pitted tracheides.
2. The collateral structure of the bundles passing from the stele to the leaves.
3. The differentiation of the peripheral part of the stele into more or less distinct bundles continuous with the leaf-traces. The last named character is more marked in *H. tiliæoides* than in *H. Grievii*.

The occurrence of secondary thickening in a Fern-like plant is not in itself very surprising. We know that it takes place in a perfectly typical way, though not to any great extent, in the stems of *Botrychium* and *Helminthostachys* at the present day.

The question now arises, What is the relation between *Lyginodendron* and *Heterangium*? The latter, as we have seen, shows a great preponderance of Fern-like characters. This does not seem to be the case in *Lyginodendron*, in which the stem, apart from the leaves, suggests anything rather than a Fern. Yet the essential differences between the two genera are limited to their steles. In typical specimens of *Lyginodendron* the whole interior of the stele is occupied by pith, around which we find a ring of scattered bundles. The most remarkable point, however, is the exact agreement in structure between the bundles of *Lyginodendron* and the peripheral strands, which form part of the stele in *Heterangium*. We said, above, that a *Heterangium* might be regarded as a *Lyginodendron*, with the bundles connected together by medullary xylem. Conversely we might look on *Lyginodendron* as a *Heterangium* in which all the primary xylem except the peripheral strands has disappeared. It seems as if in *Lyginodendron*, which is probably the more advanced type, as it appears to be the later in geological origin, only that part of the primary vascular tissue is developed which is in direct connection with the leaves. All the

rest has disappeared, having, perhaps, been sufficiently replaced by the newly acquired secondary tissues.

Platyzoma, one of the Gleicheniaceæ, resembles *Lyginodendron* in possessing a pith,* but the nearest analogy to *Lyginodendron* among recent Ferns is probably to be found in *Osmunda*, which has recently been investigated afresh by ZENETTI.† *Osmunda* is a monostelic Fern with a large pith, collateral bundles in the stem, and a concentric bundle in the petiole. The leaf-trace bundles, however, unlike those of *Lyginodendron*, become concentric immediately on leaving the stele. Another difference from the fossil genus is that in *Osmunda* the phloëm forms a continuous ring, which does not seem to have been the case with the primary phloëm of *Lyginodendron*. The position of the protoxylem is also different: in *Lyginodendron*, as we have seen, all bundles are mesarch, with the protoxylem-strands embedded in the primary wood nearer its outer than its inner surface. In *Osmunda* the bundles only have protoxylem at all in the upper part of their course.‡ In the bundles, where they first enter the stele, the protoxylem lies on the inner concave side of the xylem horse-shoe. Lower down, where the horse-shoe becomes a closed curve, the protoxylem comes to be surrounded by wood, so that here we have a certain resemblance to the *Lyginodendron* bundle, though perhaps only an accidental one.§

The example of *Osmunda* is, at any rate, sufficient to show that the general primary structure of *Lyginodendron* is consistent with Fern affinities.

So far we have considered only the points in which our two genera approach the Ferns. We have now to call attention to the remarkable relation which their structure shows to that of Cycadeæ.

The secondary tissues strongly recall those of Cycads; the resemblance shows itself especially in the simple structure of the secondary wood, the great number of the medullary rays, and the tracheides with multiseriate bordered pits on their radial walls. The structure of the phloëm also agrees well with that of Cycadeæ, and in the case of *Heterangium tiliæoides* the agreement extends to the details of the sieve-plates. The rarity of the tangential divisions in the medullary rays, causing an apparent interruption of the cambium at these points, is another peculiarity which both our fossil genera share with Cycadeæ.||

So far as the secondary tissues are concerned, the Cycadean characters apply to both *Heterangium* and *Lyginodendron*, though, on the whole, more marked in the latter. The primary structure of the stele in *Heterangium* bears no resemblance to

* Some account of the anatomy of Gleicheniaceæ will be found in POIRAUT, "Recherches anatomiques sur les Cryptogames vasculaires," 'Ann. des Sci. Nat., Bot.,' Ser. 7, T. 18, p. 171, 1894.

† 'Botanische Zeitung,' 1895, Abth. 1, p. 53.

‡ An interesting analogy for this is found in the fossil *Poroxydon*; see BERTRAND et RENAULT, "Recherches sur les *Poroxydons*," p. 283.

§ See ZENETTI, *loc. cit.*, woodcut 2, p. 57, Plate 2, figs. 2 and 3.

|| See DE BARY, "Comparative Anatomy," &c., p. 611.

that of a Cycad, while in *Lyginodendron* the presence of a pith and distinct bundles create a certain similarity.

The most interesting and remarkable point, however, which our investigations have brought to light, is the fact that the vascular bundles in the *stem* of *Lyginodendron* have exactly the same structure as those in the *leaf* of existing Cycads. This applies also to the leaf-traces and the bundles which form the outer part of the stele in *Heterangium*. Both in our fossil genera and in Cycadeæ the bundles in question are *collateral* and *mesarch*, the primary xylem being chiefly centripetal, while a smaller part is centrifugal. The essentially Cycadean structure of the bundles illustrated in Plates 21 and 22, figs. 2, 3, 4, 5, and 6 is evident to any botanist.

This type of bundles among existing plants is limited to Cycadeæ, and until now has only been observed in their leaves, in which it is of universal occurrence.*

Among fossil plants the same structure occurs most clearly in the leaves of Cordaitæ,† and also in Cycadoxyæ and *Sigillaria*, though, in the last case, the true interpretation of the structure is doubtful.‡ In the petiole of *Myeloxylon*, according to SEWARD, the xylem of the bundles appears to have been wholly centripetal, so that the agreement with Cycadeæ is here imperfect.§

Poroxylon, according to the investigations of MM. BERTRAND and RENAULT, appears to have had the Cycadean type of bundle in both stem and leaf.

We regard it as an essential characteristic of this type of bundles that the centrifugal, as well as the centripetal, portion of the xylem belongs to the *primary* tissue. This was certainly the case in the stem-bundles of both *Lyginodendron* and *Heterangium*, and the observations of one of us leave no doubt that the same holds good for the foliar bundles of recent Cycadeæ.

The occurrence of mesarch bundles in the stem of *Lyginodendron* and *Heterangium* at once suggests the view that this structure in Cycads is not a mere peculiarity of the leaf, but may rather be an ancestral character which once existed in the stem also, but has disappeared from that organ (in relation, perhaps, to the progress of secondary growth), while it has survived in the leaf.

These considerations suggested to one of us (D. H. SCOTT) the question whether some traces of this structure may not still exist in the stems of recent Cycadeæ. A preliminary investigation of this point has yielded the interesting result that, in the peduncles of both male and female flowers of *Stangeria*, the bundles are often mesarch. There is in these cases a well-marked centripetal xylem, in addition to the normal centrifugal portion of the wood. A full account of these observations will be published on another occasion.

* The foliar bundle of *Isoetes* is somewhat similar, but not identical.

† RENAULT, "Structure comparée de quelques tiges de la Flore Carbonifère," Clichy, 1879, Plate 16, figs. 2-8.

‡ RENAULT, *loc. cit.*, Plate 12, figs. 1, 2, and 6. See, however, SOLMS-LAUBACH, "Fossil Botany," chap. xi.

§ SEWARD, "On the Genus *Myeloxylon*," 'Annals of Botany,' vol. 7, 1893.

MM. BERTRAND and RENAULT have expressed on purely theoretical grounds a somewhat similar view of the origin of the Cycadean type of bundle, and they also have cited *Lyginodendron* for comparison, relying not on any original investigations but on the figures published in WILLIAMSON'S Memoir IV. They have, however, misunderstood the structure, owing to their assumption that the whole of the centrifugal wood is secondary and the whole of the primary wood centripetal. This, as we have shown, is not in accordance with the facts. It is, to a great extent, in consequence of this error that they are led to derive *Lyginodendron* and *Heterangium*, as well as their own genus *Poroxydon*, from Lycopodiaceæ, a conclusion which, as regards the genera investigated by us, is completely negatived by the whole organization of the leaf, while it is quite unnecessary as an explanation of the stem-structure.*

In *Lyginodendron* then, we have this remarkable combination of anatomical characters, namely, collateral, mesarch Cycadean bundles in the stem, passing over into concentric Fern-bundles in the petiole. In *Heterangium* we have the further complication, that the mesarch bundles in the lower part of their course occupy the periphery of a pithless stele, the whole interior of which consists of wood.

We wish to add one word as to the roots; we have called attention above to their great similarity, when young, to Marattiaceous roots, and to their regular mode of secondary growth recalling that of a typical Dicotyledon. They are less similar to roots of Cycads than we might have expected, but then we must remember that Cycadean roots are generally fleshy, and consequently much modified in structure. We may reasonably regard the roots of *Lyginodendron* and *Heterangium* as those of Fern-like plants, which have already thoroughly adapted themselves to secondary growth by means of a cambium. Certainly they bear no resemblance whatever to any known roots of Lycopodiaceæ.

We have seen how extraordinary a combination of characters belonging to various groups these genera present. In different parts of their structure they have been found to present points in common with Gleicheniaceæ, Osmundaceæ, Marattiaceæ, Ophioglosseæ, and Cycadeæ.

The view of the affinities of *Lyginodendron* and *Heterangium*, which we desire to suggest, is, that they are derivatives of an ancient and "generalized" (or rather non-specialized) Fern-stock, which already show a marked divergence in the Cycadean direction. Of the two genera *Heterangium* appears to be the more ancient, and certainly stands nearer to the Filicinean ancestry. *Lyginodendron*, while still retaining conspicuous Fern-like characters, has advanced much further on Cycadean lines.

We do not intend to suggest that in these plants we have the actual ancestors of

* BERTRAND et RENAULT, "Remarques sur les faisceaux foliaires des Cycadées actuelles," &c., 'Arch. Bot. du Nord de la France,' 3rd année, No. 35, 1886, p. 237. "Recherches sur les *Poroxydons*," *loc. cit.*, p. 382, &c.

existing Cycadeæ. The search for "missing links" has met with little encouragement of late years, and we now realize how much the chances are against our lighting on the direct ancestors of living forms. We believe, however, that in *Lyginodendron* and *Heterangium* we have examples of Fern-like plants of a primitive type, which have undergone modifications of the same kind as those to which the Cycadeæ owed their origin.

How far, in the case of these genera, such modification had proceeded cannot be determined until their reproductive organs have been found. Possibly these plants had only varied in their vegetative characters and still retained an essentially Fern-like fructification; possibly, on the other hand, they had already acquired some Gymnospermous type of reproductive organs. As to all this we know nothing. All we can say is, that such divergence from a Fern-type, as is actually shown by the known characters, is distinctly in a Cycadean direction.

Our view as to *Lyginodendron* and *Heterangium* is in essential agreement with that of Count SOLMS-LAUBACH, who has described in *Protopitys Bucheana* another of these types, intermediate between Filicineæ and Gymnosperms.*

We think it very probable that *Poroxydon*, so beautifully investigated by MM. BERTRAND and RENAULT, will find its place in a similar intermediate position. In many respects the similarity of structure between this genus and *Lyginodendron* is quite unmistakable, extending even to minute anatomical details, and we think it not unlikely that the agreement may turn out to be even closer than appears from the statements of the authors. *Poroxydon* certainly approaches Cycads more closely than *Lyginodendron* does. SEWARD'S *Rachiopteris Williamsoni*,† as well as *Myeloxylon*, must probably be added to the list. As to *Sigillariopsis*, we prefer not to express any opinion.

We think the existence of a fossil group on the borderland of Ferns and Cycadeæ is now well established. The relation of these forms to those very ancient Gymnosperms, the Cordaiteæ, is a difficult and most interesting question, which cannot, however, be discussed here.‡

The photographic illustrations to the present paper (Plates 18–20) are the work of the late Mr. W. KIRMAN, formerly of the Royal College of Science, London. The camera-lucida drawings, reproduced in Plates 21–29, like those in our former joint papers, were made by Mr. GEORGE BREBNER.

* 'Bot. Zeitung,' 1894, Abth. 1, p. 206.

† 'Ann. of Bot.,' vol. 8, 1894.

‡ NOTE.—In Memoir IX. (p. 352, Plate 25, figs. 90–92) a remarkable piece of stem from the volcanic ash of Arran was described under the provisional name of *Lyginodendron* (?) *anomalum*. We have nothing to add, except that we do not now think the fragment has anything in common with the genus *Lyginodendron*, and would rather suggest a comparison with a *Cycadeoxylon*, figured by M. RENAULT ("Structure comparée de quelques tiges," &c., Plate 14).

NOTE, ADDED DECEMBER 19, 1895.

In 1869 M. RENAULT described two specimens from the upper coal-measures of Autun, under the names of *Lycopodium punctatum*, B. Ren., and *Lycopodium Renaultii*, Ad. Br. ('Ann. des Sci. Nat.' (Bot.), Sér. 5, T. 12, pp. 178-185, Plates 12-14). M. RENAULT now kindly informs me that in the text of his 'Flore fossile du bassin houiller et permien d'Autun et d'Épinac,' Part 2, which I have not yet had an opportunity of seeing, he has transferred these fossils to the genus *Heterangium*. I had already convinced myself, by comparison of his figures with our specimens, that this was their proper position. The plants in question have nothing in common with *Lycopodium*, for the structures described as leaf-traces in the memoir of 1869 are not really of that nature. Those shown in the inner part of their supposed course probably represent medullary rays, while those in the cortex are certainly identical with the sclerotic bands so often figured and described from the English specimens. (See our figs. 22, 28, and 31; WILLIAMSON, Part IV., figs. 32, 45, &c.)

The agreement in structure with our own species of *Heterangium* is remarkably close. M. RENAULT's *H. punctatum* is much like our *H. tiliaoides*, while *H. Renaultii* recalls the specimen which we provisionally term *H. cylindricum*. The genus *Heterangium* evidently had a great vertical range in the carboniferous formation.—D. H. SCOTT.

EXPLANATION OF PLATES.

Plates 18-20. *Lyginodendron Oldhamium*. Photographs by the late Mr. W. KIRMAN, from the actual sections. Many require to be examined with a lens.

PLATE 18.

Photograph 1. Transverse section of a medium-sized stem passing through an internode. The outer, or *Dictyoxyylon* cortex is perfect; the inner cortex only remains here and there, especially on the left. *l.t.*¹-*l.t.*⁵, the five leaf-traces in the pericycle, numbered in order from within outwards. Note that *l.t.*¹ is a single bundle, the rest more or less double (*l.t.*⁵ accidentally displaced); *w.*¹-*w.*⁵, the perimedullary xylem-strands alternating with the external bundles; they are numbered according to the leaf-traces on their anodic side. Between *w.* and *l.t.* are the secondary wood and the phloëm. Compare Plate 21, fig. 1, and for details see Plates 21 and 22, figs. 2, 3, 5, 6 and 7. $\times 6\frac{1}{2}$. C.N. 1640 (see p. 706).

Photograph 2. Transverse section of a young stem at the commencement of secondary growth. *d.c.*, *Dictyoxyylon* cortex; *l.t.*¹, the innermost of the four leaf-traces;

the remaining three are double; *w.*, one of the six perimedullary strands of xylem. Between *w.* and *l.t.* a thin zone of secondary wood is seen. The external layer of cortex to the right is not evidently connected with this stem. $\times 11$. C.N. 1144b (see pp. 710 and 714).

Photograph 3. Part of transverse section of a stem, showing the base of a petiole in connection with it. *st.*, stem; *pt.*, petiole. The petiole contains a double bundle, which is concentric. Plate 19, photograph 8A, and Plate 23, fig. 10 show other sections of the same specimen. $\times 3$. C.N. 1980 (see p. 725).

Photograph 4. Radial section of stem and petiole, showing the connection between them. *d.c.*, *Dictyoxylon* cortex of stem; *pc.*, pericycle; *x.*², secondary wood; *p.*, pith; *pt.*, petiole, cut off at this point; *sc.*, axillary sclerotic band; *c.*, outer limit of cortex of petiole; *lt.*, leaf-trace bundle, entering petiole from stem. $\times 3\frac{1}{2}$. C.N. 1982 (see p. 725).

Photograph 5. Transverse section of a small secondary branch of a petiole. The outer cortex has the usual *Dictyoxylon* structure; *s.s.*, secretory sacs of the inner cortex; *v.b.*, the concentric vascular bundle with V-shaped xylem completely surrounded by phloëm. $\times$ about 35. C.N. 145 (see p. 728).

Photograph 6. Transverse section of part of the lamina, cut through a number of leaflets just separating from one another. A part of one of the leaflets is displaced and seen in obliquely superficial view. $\times$ about 35. C.N. 1885D (see p. 727).

PLATE 19.

Photograph 7. Vertical section of a leaflet. *p.p.*, palisade parenchyma; above this is the hypoderma, and then the epidermis; *s.p.*, spongy parenchyma; *v.b.*, vascular bundle, in obliquely longitudinal section. On the under side of the leaf is an outgrowth, perhaps of the same nature as the cortical emergences. $\times$ about 70. C.N. 1196 (see p. 730).

Photograph 8. Part of a transverse section of a large stem, passing through the base of an adventitious root. *rt.*, outer limit of cortex of root; *cy.*, central cylinder of root, which has formed secondary wood; *tr.*, tracheides connecting the base of the root with the wood of the stem; *x.*, remains of primary wood of stem; *x.*², its secondary wood; *pd.*, periderm; *d.c.*, *Dictyoxylon* cortex; *l.t.*, large leaf-trace bundle. $\times$ about 12. C.N. 1144B (see p. 733).

Photograph 8A. Another section of the same specimen as photograph 3, taken higher up. *st.*, stem; *pt.*, petiole. Note the dark axillary band at the junction of the two. At *rt.* a root is seen in longitudinal section, passing out from the wood through the cortex. $\times 3$. C.N. 1981 (see pp. 725 and 734).

Photograph 9. Part of tangential section of the cortex of a large stem, showing base of adventitious root; *l.t.*, leaf-trace bundle of stem; *d.c.*, part of the *Dicty-*

oxylon cortex; *rt.*, outer limit of cortex of root; *cy.*, its central cylinder, with abundant secondary wood. $\times$ about 15. C.N. 1883 (see p. 734).

Photograph 10. Another root from the same preparation; it has just become free from the stem, part of the cortex of which is seen at *d.c.* *c.*, *c.*, cortex of root; *cy.*, middle of its central cylinder; *br.*, *br.*, two rootlets arising from the root. $\times$ 28. C.N. 1885 (see p. 734).

PLATE 20.

Photograph 11. Transverse section of a young root, before secondary growth has begun. *c.*, cortex of root; *e.c.*, external cortical layer; *cy.*, the pentarch stele, in which the alternating xylem and phloëm-strands are seen. The cortex is full of secretory sacs. $\times$ about 30. C.N. 1634 (see p. 736).

Photograph 12. Transverse section of a root branching. *br.*, *br.*, two rootlets, arising opposite two of the protoxylem-groups, of which there are six in all, two being lettered *px.*; *x.²*, secondary wood, beginning to form between the protoxylem-groups. $\times$ about 30. C.N. 1899 (see pp. 738 and 740).

Photograph 13. Transverse section of a pentarch root, with secondary thickening. *px.*, the five protoxylem-groups, to each of which a ray corresponds; *ph.*, a phloëm-group; *x.²*, secondary wood; *cb.*, cambium; *c.*, outer limit of cortex. $\times$ about 30. C.N. 1631 (see p. 739).

Photograph 14. Transverse section of a very advanced tetrarch root. *px.*, the four protoxylem-groups; *ph.*, a phloëm-group, in which the primary phloëm is very distinct; *x.²*, secondary wood; *cb.*, cambium; *c.*, outer limits of cortex. $\times$ about 20. C.N. 1632 (see p. 739).

Photograph 15. Longitudinal median section of a root, giving off two rootlets. *br.*, *br.*, the two rootlets; *c.*, cortex of main root; *x.*, xylem of its stele. $\times$ about 12. C.N. 1899A (see p. 740).

Plates 21–29.—Figures from camera-lucida drawings by Mr. GEORGE BREBNER.

Plates 21–25.—Lyginodendron Oldhamium.

PLATE 21.

Fig. 1. Transverse section of a very well-preserved stem. The *Dictyoxyylon* cortex shows dilatation conspicuously. Next comes the inner cortex. *pd.*, periderm, at outer limit of pericycle; *lt.¹–lt.⁵*, five leaf-traces passing through the pericycle, numbered in order from within outwards; their arrangement corresponds to a $\frac{2}{5}$ phyllotaxis; *ph.*, one of the primary phloëm-groups; secondary phloëm and cambium shown; within these is the wide secondary wood; *x.*, one of the eight perimedullary xylem-strands; pith and

pericycle contain numerous sclerotic groups. $\times 6$. From a new specimen (in the possession of D. H. SCOTT), obtained through Professor BOWER, F.R.S., from Oldham (see pp. 706 and 708).

Fig. 2. Part of transverse section from the same specimen as Plate 18, photograph 1, showing the xylem-strand marked $w.^2$ in that photograph. The mesarch structure is evident. $px.$, protoxylem; $x.$, centripetal portion of primary wood; $x.^1$, centrifugal portion of the same; $x.^2$, part of secondary wood; $r.$, $r.$, rays; $p.$, $p.$, pith; $s.s.$, secretory sac. $\times 100$. C.N. 1884 (see pp. 709 and 712).

Fig. 3. Another section from the same specimen, showing the large double xylem-strand, marked $w.^5$ in photograph 1. Lettering as in fig. 2. $\times 100$. C.N. 1640 (see pp. 709, 711, and 712). (C.N. 1640 and 1884 are adjacent and practically identical sections from the same stem.)

PLATE 22.

Fig. 4. Part of a radial section, passing through one of the primary xylem-strands, and showing mesarch structure. Lettering as in figs. 2 and 3. $\times 100$. C.N. 1982 (see p. 712).

Fig. 4A. Parts of secondary tracheides from same section, to show bordered pits. $\times 150$.

Fig. 4B. Ditto in tangential section. $r.$, secondary rays. $\times 150$. C.N. 1985 (see p. 716).

Fig. 5. Part of transverse section showing the leaf-trace bundle, marked $l.t.^1$ in photograph 1, illustrating the collateral mesarch structure. $px.$, $px.$, the two protoxylem-groups of the bundle; $x.$, centripetal part, $x.'$, centrifugal part, of its primary wood; x'' , secondary wood of bundle; cb'' , its cambium; ph'' , its phloëm; $x.^2$, secondary wood of the stem; $cb.$, cambium; $ph.^2$, phloëm; $s.s.$, secretory sacs; $pd.$, periderm, at outside of pericycle. $\times 70$. C.N. 1640 (see pp. 709 and 712).

Fig. 6. Transverse section through the leaf-trace bundle, $l.t.^2$, of photograph 1. At this level the bundle has become double, and is without secondary tissues. The structure is exactly that of foliar bundles in Cycadeæ, e.g., *Stangeria*. Lettering as in fig. 5. $\times 70$. C.N. 1884 (see pp. 709 and 713).

Fig. 7. Part of transverse section from the same specimen, to show cambium and phloëm. $x.^2$, secondary wood; $r.$, $r.$, rays; $cb.$, cambium; $ph.^2$, secondary phloëm; $ph.$, primary phloëm; $s.s.$, secretory sacs in pericycle; $pd.$, periderm. $\times 70$. C.N. 1640 (see p. 715).

Fig. 7A. Part of a tangential section through the secondary phloëm. $ph.^2$, strands of sieve-tubes and elongated parenchyma; $r.$, $r.$, phloëm-rays; $hy.$, branched fungal hypha. $\times 70$. From one of the new Oldham specimens (D. H. S.) (see p. 716).

PLATE 23.

- Fig. 8. Part of a transverse section to show anomalous secondary tissues in the pith, x^2 , normal secondary wood; $r., r.$, rays; $px.$, protoxylem of normal primary xylem; $x.$, centripetal, x' , centrifugal, part of primary xylem; x^3 , anomalous medullary wood; cb^3 , anomalous cambium; ph^3 , anomalous phloëm; $p., p.$, pith. $\times 70$. C.N. 1190 (see p. 722).
- Fig. 9. Part of a transverse section, to show a leaf-trace bundle in the intermediate position between pith and pericycle. $lt.$, leaf-trace, with a large fan of secondary tissue; $ph.$, phloëm of the leaf-trace, continuous on the left with the phloëm-zone (ph^2) of the stem; x^2 , secondary wood of stem; x^3, x^3 , patches of anomalous wood in trace-gap; $p., p.$, pith; $pd.$, periderm. $\times 14$. From one of the new Oldham specimens (D. H. S.). (see p. 710).
- Fig. 10. Part of a transverse section, to show petiole in connection with the stem. From the same series as photographs 3 and 8A, and intermediate between them. $pt.$, petiole; $f.b.$, its double bundle; $sc.b.$, sclerotic axillary band (*cf.* photograph 4); $d.c.$, Dictyoxylon cortex of stem; $lt.$, part of a leaf-trace bundle; x^2 , secondary wood. $\times 7$. Slide 56 (D. H. S.) (see p. 725).
- Fig. 11. Obliquely longitudinal section of the *same* petiole, when it has become free from the stem. pt^2 , branch of the petiole; $f.b., f.b.$, vascular bundles of main and branch petioles; $c.$, outer cortex; $i.c.$, inner cortex; $e., e.$, cortical emergences. $\times 6\frac{1}{3}$. C.N. 1979 (see p. 725).
- Fig. 12. Part of outer cortex of a petiole, to show an apparently glandular emergence. $sc.$, sclerenchyma of cortex; $e.$, emergence; $g.$, supposed glandular tissue. $\times 100$. C.N. 139 (see p. 730).
- Fig. 13. Part of a longitudinal section of a petiole, passing through the bundle, of which about half is shown. $px.$, protoxylem; $x.$, centripetal, x' , centrifugal, part of xylem; $ph.$, phloëm; $c.$, cortical tissue. $\times 70$. C.N. 1985 (see p. 728).

PLATE 24.

- Fig. 14. Radial section through a bud-like structure. $ax.$, hollow axis of the whole structure; $e., e.$, outgrowths, resembling the cortical emergences of *Lyginodendron*. $\times 20$. C.N. 1859 (see p. 732).
- Fig. 15. Tangential section of the same. e' , bases of the outgrowths. $\times 20$. C.N. 1858.
- Fig. 16. Leaflet in vertical section. $ep.$, epidermis; $h.$, hypoderma; $p.t.$, palisade tissue; $s.t.$, spongy tissue; $v.b.$, vascular bundles, the one in transverse, the other in longitudinal, section. $\times 100$. C.N. 1197 (see p. 730).

- Fig. 16A. From a section of another leaflet, to show a stoma on the lower surface. *s.t.*, part of the spongy tissue; *ep.*, epidermis; *s.c.*, prominent subsidiary cells; *g.c.*, depressed guard-cells of the stoma. $\times 500$. C.N. 1197 (see p. 731).
- Fig. 17. Transverse section of *the same root*, *rt.*³, which in figs. 18 and 18A is seen in connection with a stem of *Lyginodendron*. This is from a third section of the specimen, where this root has become free. Note its typical *Kaloxylon* structure. *px.*, *px.*, two of the seven protoxylem-groups; *x.*, primary wood; *x.*², secondary wood; *ph.*, phloëm; *c.*', inner cortex; *c.*, outer cortex, or epidermal layer. $\times 30$. C.N. 1885B (see p. 734).

PLATE 25.

- Fig. 18. Oblique section of a stem of *Lyginodendron*, showing roots (= *Kaloxylon Hookeri*) in connection with it. *rt.*¹ and *rt.*², two free roots; *rt.*³ and *rt.*⁴, two roots in connection with the stem; *r.x.*, part of xylem of *rt.*³, traversing cortex of stem; *br.*, rootlet given off by *rt.*⁴; *rt.*⁵, base of a fifth root, at its junction with wood of stem; *d.c.*, *Dictyoxylon* cortex of stem; *x.*², its secondary wood; *p.b.*, primary xylem-strands. Cf. fig. 17. $\times 6$. C.N. 1885A (see p. 734).
- Fig. 18A. Another section of the same specimen. All the four roots, *rt.*¹–*rt.*⁴, are shown; *rt.*¹ and *rt.*² remain free, *rt.*³ and *rt.*⁴ are here seen in obliquely longitudinal section; *r.x.*, xylem of roots; that of *rt.*⁴ can be traced through cortex of stem. Lettering as before. $\times 6$. C.N. 1885c (see p. 734).
- Fig. 19. Part of a radial section of a root, to show position of protoxylem. *px.*, protoxylem; *x.*, primary xylem; *c.p.*, conjunctive parenchyma; *pc.*, *en.*, probable pericycle and endodermis; *s.s.*, secretory sacs in cortex. $\times 100$. C.N. 1633 (see p. 736).
- Fig. 20. Part of a transverse section of a hexarch root, at the commencement of secondary growth; *px.*, three of the protoxylem-groups. That to the left is connected with the base of a rootlet. *x.*, *x.*, primary xylem; *c.p.*, conjunctive parenchyma; *ph.*, three phloëm-groups, alternating with the protoxylem; *cb.*, cambium, just beginning its activity opposite the phloëm-groups; *en.*, endodermis. $\times 100$. C.N. 1631 (see pp. 736 and 739).

Plates 26 and 27.—*Heterangium Grievii*.

PLATE 26.

- Fig. 21. Transverse section through a young stem giving off a branch, *br.* *pc.*, pericycle of main stem, enclosing the stele; *l.t.*, *l.t.*, leaf-trace bundles; *i.c.*,

- inner cortex; *sc.*, sclerotic masses seen in both stem and branch; *d.c.*, outer cortex of stem and branch; *cy.*, stele of branch, with commencement of secondary wood. $\times 8$. C.N. 1915N (Dulesgate) (see pp. 745 and 753).
- Fig. 22. Somewhat oblique, longitudinal section of a stem, showing the bases of two petioles, *pt.*; the left-hand petiole is seen in nearly radial section. *cy.*, stele of stem; *i.c.*, inner cortex, which in both petiole and stem is marked by the transverse sclerotic bands; *d.c.*, outer, or *Dictyoxyylon* cortex. $\times 2\frac{1}{4}$. C.N. 1286 (Burntisland) (see p. 754).
- Fig. 23. Fragments of foliage from another section of the same block. Portions of petioles, *pt.*, of all sizes, are shown, characterized by the cortical structure. At *l.* are fragments of leaflets; *sm.*, a fern-sporangium. $\times 14$. C.N. 1287 (Burntisland) (see p. 755).
- Fig. 24. Part of a transverse section of a stem, showing one of the primary xylem-strands at the periphery of the stele. *px.*, protoxylem; *x.*, centripetal, *x.¹*, centrifugal, part of xylem; *mx.*, metaxylem, which extends through the whole interior of the stele; *c.p.*, conjunctive parenchyma; *x.²*, secondary wood; *cb.*, cambium; *ph.²*, secondary phloëm. $\times 200$. C.N. 1293 (Burntisland) (see pp. 748 and 751).
- Fig. 25. Radial section through the corresponding region of another stem, to show the mesarch structure of the xylem-strand. *x.²r.*, ray belonging to the secondary wood. Other lettering as in previous figure. Note the well-preserved bordered pits of the centripetal xylem. $\times 200$. C.N. 1266 (Burntisland) (see pp. 748 and 751).

PLATE 27.

- Fig. 26. Part of a transverse section of a stem, showing a collateral leaf-trace bundle, just separating from the stele. *px.*, *px.*, probable position of the protoxylem-groups; *x.*, centripetal, *x.¹*, centrifugal, part of xylem of bundle; *ph.¹*, its phloëm; *x.²*, secondary wood of stem; *ph.²*, phloëm; *pc.*, pericycle; *c.*, inner cortex. $\times 70$. C.N. 1253 (Burntisland) (see p. 750).
- Fig. 27. Transverse section of a tetrarch root, probably belonging to *H. Grievii*. *px.*, *px.*, two of the four protoxylem-groups, at the corners of the massive primary wood; *x.²*, secondary wood; *cb.*, cambium; *ph.*, phloëm; *c.¹*, inner cortex; *c.*, outer cortex, or epidermal layer. $\times 40$. C.N. 1915R (Dulesgate) (see p. 758).
- Fig. 28. Radial section of a stem, bearing three adventitious roots, *Rt.* *rx.*, xylem of root, connected with that of stem; *x.²*, secondary wood of stem, chiefly developed near bases of roots, and partly seen in transverse section; *x.*, primary wood of stem; *pc.*, pericycle; *sc.*, sclerotic masses, the only remains of the cortex. $\times 15$. C.N. 1915G (Dulesgate) (see p. 756).

- Fig. 29. Part of transverse section of a stem, showing what is probably a young adventitious root (*Rt.*) enclosed in the cortex. The supposed root has a definite stele. *c.*, its outer cortex, or epidermal layer; *d.c.*, part of the *Dictyoxyton* cortex of stem; *ph.*, phloëm; *x.*², secondary wood. $\times 50$. C.N. 1915 (Dulesgate) (see p. 757.)

PLATE 28.

Figs. 30 and 31. *Heterangium* sp.

- Fig. 30. Transverse section of stem. *cy.*, stele; *x.*, tracheides of the xylem which occupies the whole interior; *x.*², secondary wood, not much developed; *ph.*, remains of phloëm; *sc.*', sclerotic nests in pericycle; *c.*, cortex; *sc.*, sclerotic cortical mass; *lt.*, pair of leaf-trace bundles; in the left hand one, xylem, *x.*, and phloëm, *ph.*', can be distinguished; *Rt.*, a tetrarch root, perhaps connected with the stem; *br.*, rootlet. $\times 18$. C.N. 1304A (see p. 764).

- Fig. 31. Part of the longitudinal section of the same specimen. Lettering as before. The scale is too small to show the details of the tracheides, which have crowded bordered pits. $\times 18$. C.N. 1304B (see p. 764).

Figs. 32 and 33. *Heterangium tiliæoides*.

- Fig. 32. Part of a transverse section of a stem, showing portions of the primary and secondary wood. *px.*, protoxylem of one of the peripheral xylem-strands of the stele; *x.*, its centripetal, *x.*', its centrifugal, primary xylem; *mx.*, meta-xylem, which extends all through the interior of the stele; *c.p.*, conjunctive parenchyma; *x.*², secondary wood; *r.*', *r.*', the two principal rays, limiting the bundle; *r.*, *r.*, secondary rays. $\times 70$. C.N. 1619 (see p. 760).

- Fig. 33. Part of transverse section of another stem, showing mesarch xylem-strand more in detail. Lettering as before. Note the pitting on the walls of the primary tracheides. $\times 150$. C.N. 1301 (see p. 760).

PLATE 29. *Heterangium tiliæoides*.

- Fig. 34. Part of radial section of another stem passing through the corresponding region and showing the position of the protoxylem, *px.* (here much disorganized) in the xylem-strand. Lettering as in last two figures. $\times 150$. C.N. 1628 (see p. 760).

- Fig. 35. Another part of the same transverse section as fig. 32, to show cambium and phloëm. *x.*², secondary wood; *r.*', principal ray; *r.*, *r.*, secondary rays; *cb.*, cambium; *ph.*², secondary phloëm; *ph.*, primary phloëm; *pc.*, pericycle. $\times 70$. C.N. 1619 (see p. 761).

- Fig. 36. Small part of transverse section of another stem, specially good for cambium. *x.*², strand of secondary wood; *r.*, *r.*, secondary rays; *cb.*, cambium; *ph.*², secondary phloëm. $\times 150$. C.N. 1302 (see p. 761).

- Fig. 37. Part of the same radial section as fig. 34, to show developing wood, cambium, and phloëm. *x*.², secondary wood; *tr*.', fully developed tracheides with bordered pits; *tr*., developing tracheide with primordial pits only; *cb*., cambium; *ph*.², secondary phloëm; *s.v*., sieve-tube; *s.v.p*., compound sieve-plate (also visible at other places); *r*., secondary phloëm-ray. × 150. C.N. 1628 (see p. 761).
- Fig. 38. Oblique longitudinal section through phloëm of another stem. *r*., *r*., phloëm-rays; *s.v*., sieve-tubes; on several of the walls the sieve-plates are evident. × 150. C.N. 1304 (see p. 762).
- Fig. 38A. Part of a sieve-tube enlarged from the previous section, at *a*, showing the sieve-plates, *s.v.p*. × 500. C.N. 1304 (see p. 762).

PHOT. 1

PHOT. 2

PHOT. 4

PHOT. 3

PHOT. 5

PHOT. 6

[Hor.]

PHOT. 3.

PHOT. 4.

PHOT. 5.

PHOT. 6.

PHOT. 7.

PHOT. 8.

PHOT. 8. A

PHOT. 9.

PHOT. 10.

PHOT. 11.

PHOT. 12.

PHOT. 13.

PHOT. 14.

PHOT. 15.

Fig. 1.

Fig. 2.

Fig. 3.

Figs. 1-3. Lyginodendron Oldhamium.

Fig. 4.

Fig. 4^A

Fig 7^A

Fig. 4^B

Fig. 5.

Fig. 6.

Fig. 7.

Figs. 4-7^A Lyginodendron Oldhamium.

Fig. 13.

Fig. 8.

Fig. 12.

Fig. 10.

Fig. 9.

Fig. 11.

Figs. 8-13, *Lyginodendron Oldhamium*.

Fig. 14

Fig 15.

Fig. 16

Fig. 17.

Fig. 16^A

Figs. 14-17, *Lyginodendron Oldhamium*.

Fig. 18 *dc.*

Fig. 19.

Fig 18^a

Fig 20

Figs. 18.—20, *Lyginodendron Oldhamium*.

Fig. 21.

Fig. 25.

Fig. 22.

Fig. 23.

Fig. 24.

Figs. 21-25. *Heterangium Grievii*.

Fig. 26.

Fig. 27.

Fig. 29.

Fig. 28.

Fig 30

Fig 31

Fig 32.

Fig 33.

Figs.30 and 31, *Heterangium* sp
Figs.32 and 33, *Heterangium tilæoides*.

Fig. 34.

Fig. 35.

Fig. 36.

Fig. 37.

Fig. 38^a.

Fig. 38.