and near the poles were changed. From the capillary there was but a feeble glimmer, not of an orange tint, while the orange tint was now observed near the poles, the poles themselves being obscured by a coating on the glass of brilliant metallic lustre.

After attempting in vain for some time to determine the cause of the inversion of D_3 and 447 in various photographs I had obtained of the spectra of the products of distillation of many minerals, it struck me that these results might be associated with the phenomena exhibited by the tube, and that one explanation would be rendered more probable if it could be shown that the change in the illumination of the tube was due to the formation of platinum compounds, platinum poles being used. On May 21st I accordingly passed the current and heated one of the poles, rapidly changing its direction to assure the action of the negative pole, when the capillary shortly gave a very strong spectrum of hydrogen, both lines and structure. A gentle heat was continued for some time and apparently the pressure in the tube varied very considerably, for as it cooled the hydrogen disappeared and the D_3 line shone out with its pristine brilliancy. The experiment was repeated on May 24th and similar phenomena were observed.

III. "Further Observations on the Organisation of the Fossil Plants of the Coal-measures. Part III. *Lyginodendron* and *Heterangium*." By W. C. Williamson, LL.D., F.R.S., Emeritus Professor of Botany in the Owens College, Manchester, and D. H. Scott, M.A., Ph.D., F.R.S., Honorary Keeper of the Jodrell Laboratory, Royal Gardens, Kew. Received May 14, 1895.

(Abstract.)

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 we are still without any satisfactory evidence as to the reproductive organs in either genus, yet the organisation of their vegetative members is preserved with such completeness and perfection as to show that these fossils present a combination of characters such as exists in no living group of plants.

The evidence afforded by the vegetative characters clearly points to a position intermediate between ferns and Cycadeæ.

I. Lyginodendron.

Lyginodendron oldhamium, Will.,* is one of the commonest fossils preserved in the calcareous nodules of the Lancashire and Yorkshire coal-measures, and has also been found in those of Germany and Austria. A renewed investigation, with the aid of numerous additional specimens, has enabled us to clear up many doubtful points in the structure of the plant, and to give for the first time a complete account of all its vegetative organs.

A. *The Stem.*

1. *General Structure.*—The middle of the central cylinder or stele is occupied by a parenchymatous pith. Surrounding this is the primary wood, which usually forms a ring of from five to eight distinct strands. Beyond this we find, in all but the youngest specimens, a broad zone of secondary wood, then the cambium, and next the phloëm. The whole stele is bounded by a well-marked pericycle. The inner cortex is mainly parenchymatous, while the outer zone consists of alternating strands of fibres and parenchyma, constituting the well-known "dictyoxylon cortex" of Count Solms-Laubach.

The pericycle and cortex are traversed by the leaf-trace bundles, which alternate with the perimedullary xylem-strands.

2. *Course of the Vascular Bundles.*—We have obtained direct proof that the perimedullary strands of xylem form the downward continuation of the bundles which pass out into the leaves. Thus the entire bundle-system of the stem is built up of the leaf-traces. Each leaf-trace extends through at least ten internodes; five internodes are traversed while it is passing through cortex and pericycle, and five more after it has reached the periphery of the pith. On entering the pith the trace turns aside in the kathodic direction, and unites with the adjacent perimedullary strand on that side. We thus see that these strands are sympodial bundles, made up of the united lower portions of adjacent leaf-traces.

In the upper part of its course, each leaf-trace consists of two bundles, which unite into one in passing through the pericycle.

The phyllotaxis was usually two-fifths, but in the smallest stems was probably one-third.

3. *Structure of the Vascular Bundles.*—The preservation is so good that we have been able to determine with certainty that the bundles in the stem were normally *collateral*, having xylem on their inner, and phloëm on their outer side. As they passed out into the leaves

* See Williamson, "Organisation of the Fossil Plants of the Coal-measures, Part IV," 'Phil. Trans.,' 1873; Part VI, 'Phil. Trans.,' 1874; Part VII, 'Phil. Trans.,' 1876; Part XIII, 'Phil. Trans.,' 1887; Part XVII, 'Phil. Trans.,' 1890.

their structure became *concentric*, the phloëm here extending all round the xylem.

The xylem of the bundles in the *stem* of *Lyginodendron* exactly resembles that in the *leaves* of existing Cycadeæ. The protoxylem lies in the interior of the primary wood, but near its outer side, so that the greater part of the primary wood was centripetally developed, while a smaller portion was centrifugal. We propose to term such bundles *mesoxylic* or *mesarch*.* All statements as to the position of the protoxylem are based on longitudinal as well as on transverse sections.

4. *The Secondary Tissues.*—A few young stems have been observed with little or no secondary thickening; in most specimens it has made considerable progress. A large amount of secondary wood and bast, both fascicular and interfascicular, was formed, by means of a normal cambial layer, which is often well preserved.

The tracheides of the wood have numerous bordered pits on their radial surfaces. Similar elements occur in the primary wood also. The rows of tracheides are separated by numerous medullary rays.

The phloëm is often well preserved, so that primary and secondary phloëm can be distinguished.

The secondary tissues bear a general resemblance to those in the stems of Cycadeæ.

5. *Pith and Pericycle.*—Both these tissues contained nests of dark coloured elements, probably of a sclerotic nature. They are also traversed by numerous rows of cells with carbonaceous contents, which may have been secretory *sacs*, but not intercellular *canals*. At the outer border of the pericycle a characteristic internal *periderm* was developed.

6. *The Cortex.*—The parenchymatous portions of the outer cortex became much dilated in the older stems, in consequence of the secondary growth.

7. *On Small Stems of the* Lyginodendron *Type.*—Certain very small stems have been described, differing in structure from the usual form. In some of these the primary xylem forms a continuous ring, instead of being divided into distinct bundles. We now suggest that these specimens may represent the *basal*, first-developed region, of normal stems. In *Osmunda*, which in many respects resembles *Lyginodendron*, it has been shown by M. Leclerc du Sablon, that the embryonic stem has the same peculiarity.

8. *Structural Anomalies.*—Some of the specimens show remarkable individual anomalies, the most frequent and conspicuous of which consists in the appearance of a cambium at the periphery of the pith,

* One of the authors has recently found that this peculiarity sometimes extends to stem-structures in Cycadeæ; in the peduncles of both male and female flowers of *Stangeria* the bundles are often mesoxylic.

forming medullary wood and bast, with inverted orientation. This is precisely the anomaly shown by certain species of *Tecoma*, and other dicotyledons. The anomalous medullary cambium is continuous with the normal cambium through the leaf-trace gaps. This case is a striking instance of the independent appearance of the same structural peculiarity in families as remote as possible from each other.

B. *The Leaf.*

1. *Connexion between Leaf and Stem.*—New and conclusive evidence has been found, confirming the conclusion previously arrived at (in Mem. XVII), that "*Rachiopteris aspera*" is the petiole of *Lyginodendron*. In several specimens petioles with the characteristic structure of that fossil, are found inserted on the stems of *Lyginodendron*. The vascular bundles on leaving the pericycle of the stem bend out rapidly into the base of the leaf, becoming concentric at the same time. Petioles, continuous with the *Lyginodendron* stem, have been traced up to the point where they begin to ramify.

2. *Form of the Leaf.*—The petioles, which we now know to belong to our plant, branch repeatedly, and ultimately give rise to small palmately-segmented leaflets. The leaf was thus a highly compound one, and we can confirm the statement previously made, that the character of the foliage was that of Brongniart's form-genus *Sphenopteris*.

3. *Structure of the Petiole.*—The most important point here is that throughout the petiole and rachis, the vascular bundles, of which either one or two are present, are of typical concentric structure, as in a fern.

The cortex of the petiole has essentially the same structure as that of the stem.

4. *Structure of the Lamina.*—We have examined sections of leaflets (found in connexion with petioles of *Lyginodendron*), in which the structure is perfectly preserved. The lamina had a distinctly bifacial structure, with well-differentiated palisade, and spongy parenchyma. Stomata have only been observed on the lower surface. The vascular bundles in the lamina appear to have been collateral, as is also the case in recent ferns.

5. *On a Peculiar Bud-like Structure.*—This is a unique specimen, consisting of an axis, of obscure structure, bearing numerous appendages which exactly resemble the well-known cortical outgrowths of the stem and petiole of *Lyginodendron*. At first sight, the specimen bears some resemblance to a cone, but it was more probably a bud or young leaf, from which the inner delicate tissues have perished, leaving the protective outer coat, bearing the appendages, which may represent the bases of paleæ.

C. *The Root.*

1. *Connexion between Root and Stem.*—We have already briefly recorded our discovery that "*Kaloxylon Hookeri*" is the root of *Lyginodendron.** We have found that certain appendages of the stem of *Lyginodendron*, most of which were formerly described as "branches," are in reality of endogenous origin, as is shown by the fact that the appendage, in passing through the cortex of the parent stem, is surrounded by a well-defined cortex of its own. These appendages are further shown to be roots, by the structure of their central cylinder and their mode of branching. Sections of the free part of the same organs, which are in connexion with stems of *Lyginodendron*, show that they agree in all respects with "*Kaloxylon Hookeri*," namely, in the structure and arrangement of both primary and secondary wood, and in the details of the cortex, which is well characterised hy its double or treble external or epidermal layer.

We find then that the stem of *Lyginodendron* bore numerous adventitious roots, of endogenous origin, and that these roots are identical with the fossils previously described under the name of "*Kaloxylon Hookeri.*"

2. *Primary Structure of the Root.*—All the specimens of "*Kaloxylon Hookeri*" have been re-examined, and are found to present a perfectly typical root-structure. The stele varies from triarch to octarch structure in different specimens. The protoxylem is external, showing centripetal development of the primary wood. In favourable specimens the regular alternation of the phloëm-groups with those of xylem is quite clear. The stele has no pith, but there is a considerable amount of conjunctive parenchyma. Both pericycle and endodermis are present. The inner cortex contains abundant "secretory sacs."

The young roots much resemble the smaller adventitious roots of Marattiaceæ.

3. *Secondary Tissues of the Root.*—These are beautifully preserved, and are found at all stages of development. The cambium is often specially clear. Secondary growth began opposite the phloëm-groups, and the secondary wood is generally interrupted by large rays opposite the protoxylem-strands. The secondary tissues resemble those of the stem. The whole process of secondary growth was perfectly normal, as in dicotyledons at the present day.

4. *Branching of the Root.*—The numerous specimens showing branching prove that the rootlets were endogenous, and that they arose opposite the protoxylem-groups of the main root.

* 'Roy. Soc. Proc.,' vol. 56, 1894.

D. *Habit and Dimensions of the Plant.*

In none of our authentic specimens is the stem more than 4 cm. in thickness. Certain cortical impressions, belonging to much larger stems, have been referred to *Lyginodendron*, but on inconclusive grounds.

There is one large specimen showing structure, in which only the secondary wood and portions of the pith are preserved. So much of the structure as remains agrees closely with that of *Lyginodendron*. This specimen may have reached a diameter of 30 cm. or 40 cm., and establishes a certain probability that *L. Oldhamium*, or some allied species, may have attained the dimensions of a small tree.

The ordinary specimens must have had upright stems of considerable height, bearing spirally-arranged, compound, fern-like leaves, separated by internodes about an inch long. The lower parts of the stem gave off on all sides numerous adventitious roots.

The entire absence of fructification is remarkable, considering the great frequency and admirable preservation of our fossil. It may be explained, either on the hypothesis that the leaves bore very caducous, fern-like sporangia, or by supposing that our material consists entirely of immature specimens.

II. Heterangium.

Introduction.

The genus *Heterangium* differs conspicuously from *Lyginodendron*, in the structure of the stele of the stem, which in *Heterangium* contains no pith, but has a solid axis of primary wood. In most other respects the two genera much resemble each other.

i. *Heterangium Grievii*, Will.*

The original specimens of this species were derived from the Burntisland deposits. At a later date, specimens were found in the coal-measures of Dulesgate, Lancashire, which have been referred to the same species, though they show some slight differences from the original form.

A. *The Stem.*

1. *General Structure.*—The whole interior of the stele is occupied by the primary wood, consisting of tracheides intermixed with conjunctive parenchyma. In most specimens a certain amount of secondary wood has been formed around the central mass. Outside

* Williamson, 'British Association Reports,' 1871; "Organisation," Part IV, 1872; Part XVII, 1890.

the wood a zone of phloëm can be traced, and this again is surrounded by a parenchymatous belt, which we regard as pericycle. The inner cortex is characterised by the presence of horizontal plates of sclerotic tissue. The outer cortical zone has a structure similar to that of *Lyginodendron*. In the pericycle and cortex numerous leaf-trace bundles are met with.

2. *Course of the Vascular Bundles.*—The bundles can be traced from the stele into the bases of the leaves. Their arrangement indicates that the phyllotaxis was three-eighths in the larger and two-fifths in the smaller stems. Each leaf received a single bundle. The leaf-trace bundles can be followed downwards for some distance at the periphery of the stele, where they form distinct strands, though united with the axial wood.

3. *Primary Structure of the Stele and Leaf-trace Bundles.*—The strands at the periphery of the stele, as well as the leaf-trace bundles with which they are continuous, have the same collateral and mesoxylic structure as the bundles in the stem of *Lyginodendron*, or the foliar bundles of Cycadeæ. The essential difference from *Lyginodendron* consists in the fact that in *Heterangium* these bundles are united by the axial xylem, which extends throughout the whole interior of the stele. The primary tracheides, with the exception of those adjoining the protoxylem, have numerous bordered pits.

4. *The Secondary Tissues.*—The secondary wood, when present, has essentially the same structure as in *Lyginodendron*. Cambium and phloëm, in the normal position, are fairly preserved in some of the specimens.

5. *The Cortex.*—The most characteristic feature here consists in the horizontal plates of sclerotic cells in the inner cortex. Their structure is precisely that of the "stone-cells," found in the cortical tissues of many recent plants. Their presence in the cortex of the stem is a point of difference from *Lyginodendron*, where the sclerotic masses are usually limited to the pith and pericycle.

6. *Branching of the Stem.*—In one specimen a young stem bears a branch much smaller than itself. This is the only distinct case of branching observed in either genus. All other supposed branches have turned out to be either petioles or adventitious roots.

B. *The Leaf.*

1. *Connexion between Leaf and Stem.*—The bases of petioles, in connexion with the stem, have been observed both in transverse and longitudinal section. These specimens show that the cortical tissues of the petiole have the same characteristic structure as those of the stem; we are thus enabled to recognise the petioles of *Heterangium Grievii* when detached from the stem. Unlike *Lyginodendron*, the

petiole of *H. Grievii* usually receives from the stem a single bundle only.

2. *Form and Structure of the Leaf.*—We find innumerable portions of petioles, varying from 4 mm. to 0·4 mm. in diameter, sometimes branching, and intermixed with fragments of leaflets. We can only infer that the leaf of *H. Grievii* was a highly compound one, probably not very different from that of *Lyginodendron*.

The petiole is traversed by a single bundle of *concentric* structure. Thus the bundles underwent the same change on entering the leaf as in *Lyginodendron*.

The petioles bear a considerable resemblance to those of the latter plant, from which they chiefly differ in the absence of cortical outgrowths.

C. *The Root.*

1. *Connexion between Root and Stem.*—In several cases endogenous appendages, evidently adventitious roots, have been found arising from the stems of *H. Grievii*. In one specimen the bases of three such roots are seen in a vertical row, and the connexion of their tissues with those of the stem can be exactly traced.

2. *Structure of the Root.*—We have good evidence, though not so direct as in the case of *Lyginodendron*, that the roots of *H. Grievii* also belonged to the "*Kaloxylon*" type. A special form of root, with a large tetrarch stele of characteristic shape, seems to be peculiar to *Heterangium*.

D. *Habit and Dimensions of the Plant.*

In habit, *Heterangium Grievii* must have been similar to *Lyginodendron*, but its dimensions were considerably smaller. Sporangia, like those of ferns, have occasionally been found in close association with the foliage, but not in connexion with it.

ii. *Heterangium tiliœoides*, Will.

This species differs from *H. Grievii* in several points, but evidently belongs to the same genus. The specimens are from the coal-measures of Halifax,* and are remarkable for the astonishing perfection with which the histological structure is preserved. The general anatomy was fully described in 1887. In primary structure the stele agrees with that of *H. Grievii*, but the peripheral bundles are more distinct. The secondary tissues are subdivided by broad primary rays (enormously dilated in the phloëm), which correspond to the conjunctive tissue separating the primary bundles. Cambium

* Williamson, "Organisation," Part XIII, 1887.

and phloëm are perfectly preserved; the latter is of great thickness, almost equal to that of the secondary wood. So perfect is the preservation, that stages in the development of the tracheides from the cambium have been observed, while the compound sieve-plates on the radial walls of the sieve-tubes are quite clear. Sclerotic groups occur in the pericycle, as well as in the cortex, and the leaf-trace bundles are in pairs—two points in which this species resembles *Lyginodendron* and differs from *H. Grievii*. Thus the close relationship of the two genera, in spite of the different arrangement of the primary wood, comes out even more clearly in this species than in *H. Grievii*.

We have a single specimen of a *Heterangium*, which differs in some respects from the two species above described, and may turn out to represent a third type.

III. *Affinities of* Lyginodendron *and* Heterangium.

The vegetative organs of these genera show a remarkable combination of fern-like and cycadean characters. The leaves of *Lyginodendron*, which are now well known, are so like fern-leaves, not only in form and venation but in minute structure, that if they stood alone they would, without hesitation, be referred to Filices. Although many leaves simulate those of ferns in external characters (*Stangeria*, *Thalictrum*, &c.), none are known which at the same time show the characteristic anatomy of fern-leaves. Hence we are led to attach great weight to the characters of the *Lyginodendron* foliage. That of *Heterangium*, though less well preserved, was evidently of the same type.

In *Heterangium* the primary structure of the stem is much like that of a monostelic fern such as *Gleichenia*, but the leaf-trace bundles closely resemble the foliar bundles of a Cycad.

In *Lyginodendron* the whole structure of the *stem* suggests a Cycad, but with the remarkable peculiarity that the bundles here have the structure which in Cycadeæ is usually (though not always) limited to those of the leaf. The cycadean characters are too marked to be accidental, though the general anatomy of *Lyginodendron* is not inconsistent with a close relationship to ferns, for in *Osmunda* we have a monostelic fern, with a large pith, collateral bundles in the stem, and concentric ones in the leaf.* The mere occurrence of secondary growth in a fern-like plant is not surprising, considering that it takes place in *Botrychium* and *Helminthostachys* at the present day.

In various respects *Lyginodendron* and *Heterangium* have points in common with Gleicheniaceæ, Osmundaceæ, Marattiaceæ, Ophioglosseæ,

* See Zenetti, 'Botanische Zeitung,' 1895.

and Cycadeæ. The view of their affinities, which we suggest, is that they are derivatives of an ancient generalised race of ferns, from which they have already diverged considerably in the cycadean direction. Of the two genera, *Heterangium* appears to be geologically the more ancient, and certainly stands nearer to the filicinean stock. *Lyginodendron*, while retaining conspicuous fern-like characters, has advanced much further on cycadean lines. This view by no means involves the improbable assumption that these plants were the actual ancestors of existing Cycadeæ. How far their divergence from the fern stock had proceeded cannot be determined until we are acquainted with their organs of reproduction.

The existence of a fossil group on the border-land of ferns and Cycads seems now to be well established. Count Solms-Laubach places his *Protopitys* in this position, which is probably shared by *Myeloxylon* and *Poroxylon*. Messrs. Bertrand and Renault have indeed endeavoured to derive the last-named genus from Lycopodiaceæ, and have extended the same view to *Lyginodendron* and *Heterangium*. In the latter cases their theory is completely negatived by the organisation of the leaves, and by many structural details.

The relation of the genera which we have described to those ancient gymnosperms, the *Cordaiteæ*, will form one of the most interesting palæobotanical problems of the future.

The paper is illustrated by micro-photographs and by camera-lucida drawings.

IV. "On the Origin of the Triradiate Spicules of *Leucosolenia*." By E. A. Minchin. Communicated by Professor Lankester, F.R.S. Received April 30, 1895.

(Abstract.)

In *Leucosolenia coriacea* the youngest spicules are found to be surrounded by six cells, which are similar in all their characters to the cells of the external flat epithelium of the sponge, and undoubtedly derived from this layer. It appears that three cells of the external epithelium wander inwards, and give rise to six by division of each cell into two, the six cells being arranged in such a way, that three are placed more internally, *i.e.*, towards the gastral surface of the body wall, and three more externally, towards the dermal surface. Each of these sets of three cells has a form which might be compared to a trefoil, and the whole mass may be described as two such trefoils superposed, the cells of one trefoil exactly corresponding to those of the other.

The spicule is formed by the three inner cells, a ray being formed