

IV. *A Biseriate Halonial Branch of Lepidophloios fuliginosus.* By F. E. WEISS, D.Sc.,
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(Plates 23-26.)

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IN the autumn of 1898 I purchased from Mr. James Lomax an *Halonial*, together with an excellent series of transverse and longitudinal sections prepared by him from the same specimen and which showed the tissues to be very well preserved. From an examination of the latter Mr. Lomax had rightly identified the plant with that described by Williamson originally (1873) as *Lepidodendron Harcourtii*, but afterwards renamed *Lepidodendron fuliginosum* (1887).

I was unaware at the time that Dr. Scott had exhibited a photograph of the specimen at the Bristol Meeting of the British Association in that year and had commented on certain peculiarities of its structure. On expressing my willingness to leave the further examination and fuller description of this specimen to him, Dr. Scott most generously withdrew his prior claims upon it and also allowed me to make use of some preparations he possessed of this plant, from one of which one of the accompanying figures is taken. I desire here to express my indebtedness to him, both for his generosity and also for his helpful criticism of several points in connection with the structure of this halonial branch.

I. MORPHOLOGICAL CONSIDERATIONS.

The *Halonial* under consideration was contained in a large nodule weighing nearly 2 cwt., found by Mr. George Wilde at Hough Hill, near Stalybridge. Mr. James Lomax was able to extract from this nodule a large piece of the halonial branch measuring about 7 inches in height and $3\frac{1}{2}$ to $3\frac{3}{4}$ inches in its greatest diameter by about $2\frac{1}{2}$ inches in the shorter diameter (Pl. 23. fig. 1). There were eight tubercles arranged in two rows of four each, alternating with each other at the two sides which form the ends of the greater diameter of the stem. The internal structure shows so little sign of compression, that I think in all probability this difference in thickness in the two directions actually existed in the living plant, though it may have become slightly increased by pressure during mineralization.

There are no leaf-bases present, part of the specimen being clothed by the periderm formed beneath the leaf-bases and showing a slight indication of "dictyoxylon" markings. At other points of the surface the periderm has been removed, and the

outer cortex forms the boundary, with small elevations of tissue in connection with the leaf-trace bundles. The relative position of these is such that on connecting the two nearest lateral ones the distance between them is almost equal to that between two standing vertically one above the other.

The internal structure will be described in detail in a later portion of this paper; so that it will be sufficient to say here that it agrees very closely with that described by Williamson for *Lepidodendron fuliginosum* (*Lepidophloios fuliginosus*)—a fact already stated by Dr. Scott (1898) and Mr. Lomax (1899).

In his communication to Section K at the Bristol Meeting of the British Association, Dr. Scott mentioned this agreement in structure, and regarded this halonial specimen as probably belonging to *Lepidodendron fuliginosum*.

At the meeting of the British Association at Leeds, however, in 1890, Messrs. W. Cash and James Lomax (1890) had shown that a fossil revealing undoubtedly similar internal structure to that of *Lepidodendron fuliginosum* of Williamson had the typical transversely elongated leaf-scars of *Lepidophloios*. Hence they suggested the name of *Lepidophloios fuliginosus* for the stem previously described by Williamson. Williamson, however, in Part XIX. of his Memoirs on the Organization of the Fossil Plants of the Coal-Measures, which appeared three years later, 1893, still retained the name of *Lepidodendron fuliginosum* for the fossil described by himself, and probably did not sufficiently appreciate the separation of the two genera, for in a note to a "Correction of an Error of Observation in Part XIX. &c." in 1894, he states: "It appears to me that much uncertainty exists among palæobotanists respecting the structures that distinguish *Lepidodendron* from *Lepidophloios*" *.

It is probably due to the retention of the name *Lepidodendron fuliginosum* by Williamson after the publication of Messrs. Cash and Lomax's note, that their observation did not receive its full recognition for some time and that the name *Lepidodendron fuliginosum* was retained for so long.

Mr. Kidston (1893), however, in his memoir on *Lepidophloios* and on the British species of the genus, had duly recorded the observation of Messrs. Cash and Lomax, and after an examination of their specimen was inclined to identify it with *Lepidophloios acerosus*.

An examination of the transverse sections of the specimen described by Cash and Lomax (1890) in the Cash Collection, now in the Manchester Museum, has convinced me of the identity in structure of this *Lepidophloios* with that of Williamson's *Lepidodendron fuliginosum*, and also with the internal structure of the halonial branch forming the subject-matter of the present investigation.

Having identified the halonial branch now under consideration with *Lepidophloios fuliginosus* on the strength of its internal structure, the next and probably the greatest point of interest attaches to the fact that, if the identification is correct, we have in this instance an halonial branch of *Lepidophloios* with two vertical rows of tubercles, instead of the spiral arrangement of tubercles usually considered typical of the fruiting-branches of *Lepidophloios*. Indeed, according to some definitions of *Halonia*, our

* Proceedings of the Royal Society, vol. lv. (1894) p. 423, note.

specimen would not be an halonial but a ulodendroid branch, and therefore not referable to the genus *Lepidophloios*.

Thus Kidston (1893), in his memoir on *Lepidophloios*, states: "If it is necessary to define a difference between the *Ulodendron*-condition and the halonial condition even in the absence of the bark they can be separated, the former having two rows of alternate (usually) cup-shaped scars, the latter having more than two rows of (usually) conical tubercles spirally arranged."

On the other hand, Williamson in the same year (1893), after discussing at some length the various specimens of *Halonia* and *Ulodendron* known to him, comes to the conclusion "that the only distinction between halonial and ulodendroid conditions lies, not in the number or arrangement of the fruit-scars, but in the presence or absence of a pressure-disk surrounding each fruit-scar."

It will be seen from these two definitions that the halonial condition is according to Williamson a very different thing from the halonial condition defined by Kidston, the latter basing his definition on the number of rows of scars or tubercles, while Williamson disregards their number but distinguishes the elevated tubercles of *Halonia* from the cup-shaped pressure-disks of *Ulodendron*.

In calling the specimen under consideration an halonial rather than a ulodendroid branch, it will be seen that I incline to Williamson's view that the elevation of the tubercles is a more distinctive feature than their number or arrangement.

I cannot believe that absence or presence of an elevation is due merely to presence or absence of pressure during mineralization or to absence or presence of a well-preserved covering of leaf-bases. A number of fruiting-branches of *Lepidophloios* are known with the leaf-bases well preserved still showing fairly prominent tubercles, though of course in "decorticated" specimens the tubercles are more prominent*. Similarly, in an *Halonia* which has evidently been much compressed the tubercles are clearly distinguished, even on the surfaces which have been most exposed to pressure. Pl. 23. figs. 2 & 3 of the present memoir show the two sides of the same halonial branch, which exhibits distinct tubercles on one side (fig. 2), while on the other (fig. 3) the branches have the character of flattened or cup-shaped areolæ. This difference depends on differences of position or condition during mineralization.

I would therefore describe the "halonial condition" as the fruiting-branch of *Lepidophloios* bearing a number of more or less elevated tubercles either in quincuncial or in biserial arrangement.

This description of the halonial branch would agree in general with that given by Williamson (1893), and would also agree in this particular with the views expressed by Kidston (1886 and 1893) and by Potonié (1893 and 1899), that, so far as is at present known, the halonial condition is restricted to the genus *Lepidophloios*. On the other hand, the view I have adopted differs from that held by Kidston and Potonié in not

* The term "decorticated," so much in use in the description of halonial branches, is misleading, for it has not been employed to describe stems in which the cortex is absent but in which the leaf-bases or cushions are worn away and in which consequently the leaf-scars are not distinguishable. Thus the specimen under examination would be termed "decorticated," whereas even the outer cortex is completely preserved.

restricting the term "halonial" to branches with the quincuncial arrangement of tubercles. That *Lepidophloios* is, however, not restricted to multiseriate fruiting-branches is borne out from an examination of the halonial branch under consideration, which, on the strength of its internal structure, must be identified with *Lepidophloios fuliginosus*. As, however, an identification based solely on the internal structure might be disputed by some, I would seek to strengthen my conclusion by evidence from specimens showing external markings which can be identified with *Lepidophloios* and which at the same time possess only two rows of tubercles.

There is in the Manchester Museum a specimen, reproduced in figs. 2 and 3, which was found in the roof of the Four Foot Mine at Tonge, near Bolton. It was presented to the Museum by Mr. Dawes. It is a branch about 14 inches in length, and shows the commencement of a bifurcation at one end, an occurrence not infrequently met with in halonial branches. It is considerably compressed, so that its diameter in one direction is $3\frac{3}{4}$ inches, while in the other it measures only $1\frac{1}{2}$ inch. It possesses two rows of tubercles, two tubercles being visible on each side of the specimen about 4 to 5 inches apart. The pressure has been exerted on the sides bearing the two rows of tubercles; yet these are still distinctly recognizable as elevations, especially on the side shown in fig. 2. That this would be the case even if the leaf-cushions were present is evident from the thinness of the leaf-cushions where preserved. This outer layer of the leaf-cushions is the only carbonized portion of the plant, the central portion of the branch being entirely replaced by limestone. The width of the leaf-cushions and their imbrication, overlapping from above downwards (see Pl. 23. fig. 4), leave no doubt in my mind that this is a specimen of *Lepidophloios*, though it is true that no actual leaf-scar is distinguishable, as the specimen is not in the best state of preservation. But it agrees very closely with an halonial specimen described by Carruthers (1870) as *Ulodendron tumidum*, which has since been identified by Kidston (1886) as *Lepidophloios laricinus* (Sternberg). In this latter specimen some actual leaf-scars are preserved, but in parts these are not distinguishable, and there we have the closest agreement in its arrangement with the leaf-bases of the biserial *Halonial* of the Manchester Museum. In both cases the remains of the leaf-bases are drawn out in breadth and are ragged and torn.

I think, therefore, we are justified in assuming that this biseriate halonial branch is also referable to the genus *Lepidophloios*. In Mr. Carruthers's specimen the tubercles are rather irregularly arranged. From the name *Ulodendron* which he gave to this specimen, it is obvious that the biseriate arrangement is that which strikes the observer at first; but Kidston has shown that we have really more than two rows in this specimen.

Another specimen of *Lepidophloios* bearing two rows of tubercles I discovered in the Williamson Collection at the British Museum (Pl. 24. fig. 5). This halonial branch (cabinet-number 1946 B) is not described in Williamson's detailed and useful catalogue, but is merely entered as *Lepidophloios*. It is a small piece of a fruiting-branch, 3 to 4 inches long and 3 inches by 2 in thickness, thus showing very little compression. The leaf-bases are perfectly distinct over the whole surface, and their broad and fimbriating nature mark them out as belonging to *Lepidophloios*, as indeed was

recognized by Williamson. Their state of preservation is unfortunately not perfect, the actual leaf-scar not being distinguishable. In this specimen the tubercles are arranged in two distinct rows at the end of the greater diameter of the branch, and two tubercles are borne on each side. We have therefore here another case of an halonial branch of *Lepidophloios* with two rows of tubercles.

Unfortunately in this case, too, the interior of the branch is not well preserved, but has become impregnated with pyrites, so that we cannot say whether the tissues of this specimen agreed with those of *Lepidophloios fuliginosus* or not.

Evidence of *Lepidophloios* possessing fruiting-branches with only two rows of tubercles, based upon specimens not showing the external marking of the leaf-bases, but exhibiting well-preserved internal structure, will be found in Williamson's 'Memoirs.'

Thus in Part II. (p. 209) he describes a small specimen of *Ulodendron* received from Mr. Neild of Oldham, and states that the structure of its central axis is identical with that of the *Lepidodendron* of the *fuliginosum* type (then called by him *Harcourtii*). Although the figures of this specimen are not very good, the identification of its structure with that of *Lepidodendron fuliginosum* is correct, and we have therefore a specimen with the internal structure of *Lepidodendron fuliginosum* (now *Lepidophloios*) and bearing the two rows of "circular areolæ of *Ulodendron*." That the specimen is a *Lepidophloios* is ascertainable not only from the central axis of the *fuliginosum* type, but also from the leaf-bases seen in transverse section in fig. 28 of Williamson's memoir, and in longitudinal section fig. 27. Solms (1892), who is rightly rather sceptical about this specimen being referred to *Ulodendron* and considers that it is probably *Lepidophloios*, regrets that Williamson did not figure the surface-view so as to show the "circular areolæ of *Ulodendron* arranged in two vertical rows" (p. 232). Though this was no doubt a pity, yet in the light of the specimens referred to above, and on the strength of others to be mentioned below, we cannot now doubt that two such rows of scars were present, and the importance of this specimen becomes apparent.

In Part XIX. Williamson (1893) figures another halonial branch with its tubercles in two rows (fig. 22); but as this specimen shows no external markings of leaf-bases, and as Williamson does not figure its internal structure, it yields no evidence in support of the views I seek to maintain.

In the same memoir (Part XIX.) is described and figured (fig. 30) a transverse section of a branch of *Lepidophloios* which bears large "bilateral fructigerous tubercles." This specimen was collected by Mr. George Wilde from the Hough Hill Colliery of Stalybridge, the same locality from which the specimen now under consideration was obtained. In his description of this earlier specimen, Williamson says (p. 20): "The specimen was one in which the large halonial protuberances had been in two lateral series, three of these protuberances being preserved. Its leaves show that it belonged to the lepidophloiid group, and present every appearance of identity with the plant which is described and figured in my Memoir, Part II. (figs. 24-28)."

This statement is fully borne out by Williamson's figures as well as by an examination of some transverse and longitudinal sections of this specimen in the Wilde Collection in the Manchester Museum. What remains of the original specimen after the sections

were cut from it was carefully preserved by Williamson and is described in his Catalogue, under No. 1919 A, as "part of the original specimen preserved to show one of the large halonial tubercles." This piece, so judiciously preserved by Williamson, shows this remaining tubercle very clearly. Another piece of this branch was preserved by Mr. Wilde, and is now in the Wilde Collection at the Manchester Museum. This piece, from which the central portion of the axis has disappeared, consists of the outer portion of the nodule with the leaf-bases and part of the cortex preserved. It shows three large scars in vertical series, which were no doubt three of the "ulodendroid" scars.

The importance of this specimen lies in the preservation of the leaves, from which there is no doubt that the plant was referable to the genus *Lepidophloios*; and hence we have in this case, too, a fruiting-branch of *Lepidophloios fuliginosus* in which the cones were attached in two vertical rows. We see therefore that Williamson has in this case described a *Lepidophloios* with biseriate halonial tubercles.

In the case of the specimen (cabinet-number 379) figured by Williamson (1881) in his XIth Memoir (fig. 9), and for which he at first retained the name of *Lepidodendron Harcourtii* (see Proc. Royal Soc. vol. xlii. 1887), but which he subsequently transferred to *L. fuliginosum* (see his General and Morph. Index, Part II. p. 13, 1893), we have undoubtedly an halonial stem giving off a branch from the central vascular cylinder to an halonial tubercle, as Williamson himself thought was the case (p. 290). The elliptical shape of the stele and its general similarity in the mode of branching with that in Lomax's specimen would seem to point out that here also we have two rows of tubercles. If this should be the case, we shall have another instance of a biseriate halonial branch belonging to the genus *Lepidophloios*.

The consideration of the above-mentioned specimens of biseriate halonial branches shows that such branches may be referred to the genus *Lepidophloios* in some cases by their external markings, in other cases on the strength of their internal structure. These instances therefore support the view put forward with regard to the Hough Hill halonial branch now under consideration, that it is the fruiting-branch of *Lepidophloios fuliginosus*. This view is of course opposed to Kidston's definition of *Halonia*; for he considers halonial branches to be characterized by multiseriate tubercles, and these only to be referable to the genus *Lepidophloios*, and he does not recognize the "biserial Halonias" of D'Arcy Thompson (1880). The biseriate arrangement Kidston considers to be the ulodendroid fruiting-branch of *Bothrodendron*, *Sigillaria*, or *Lepidodendron*. He would therefore refer the specimen forming the subject of this paper, as he has done the *Halonia disticha* described and figured by Morris (1840) in Prestwich's account of the geology of Coalbrookdale, to *Sigillaria discophora*. In Morris's *Halonia*, however, neither the leaf-bases nor the internal structure is preserved, whereas in the present specimen the internal structure is undeniably that of *Lepidophloios*, as will be readily seen from the detailed account of its anatomical structure which follows.

II. ANATOMICAL STRUCTURE.

The identification by Dr. Scott (1898) of the halonial branch under consideration as belonging to *Lepidophloios fuliginosus* will be confirmed by the details of the structure which will now be given.

The general view of the transverse section (Pl. 24. fig. 6) will be seen to resemble in its chief features the *Lepidodendron fuliginosum* (previously called *Harcourtii*), figured by Williamson (1881) in Part XI. of his "Organization of the Fossil Plants of the Coal-Measures" (see pl. 52. fig. 9). Our specimen differs from Williamson's in the better preservation of the mid-cortex, which is practically perfect. This difference in preservation is doubtlessly due to a difference in the minute structure of this tissue. Though with small magnification there appears to be a considerable "uniformity in the composition of the entire cortex," as Williamson states (p. 7), yet there is, as we shall see on closer examination, a very considerable difference between the inner, the middle, and the outer cortex.

Another feature which distinguishes at a glance the specimen under consideration from *Lepidodendron Harcourtii* is the course of the leaf-trace bundles through the mid-cortex. It will be seen that these run very obliquely through this tissue, at times indeed nearly horizontally, as is especially the case in the bundles running in the direction of the longer diameter of the elliptical section. This character is more frequently found in *Lepidophloios fuliginosus* than in other *Lepidodendra*, and is certainly characteristic of that specimen to which Williamson first gave the specific name of *fuliginosus*; for it is to the specimen figured in plate 51 (fig. 10) of Part XI. that he referred in his note of 1887, when he introduced this new specific name, and in that specimen the leaf-trace bundles run very nearly horizontally through the middle cortex.

Other specimens of *Lepidophloios fuliginosus* in the collections of the Manchester Museum also show this very horizontal course of the vascular bundles; and I would like more particularly to mention one in the Wilde Collection (No. 158) which is labelled an halonial stem, and which, from its more circular outline and smaller dimensions, I think must have belonged to a multiseriate *Halonia*. That it is an halonial stem is indicated by the branch which is given off from the central vascular cylinder. The uniformity, both in respect to the course of the leaf-trace bundles and to the detailed structure of the cortex and other tissues, convinces me that no distinction can be made anatomically between this specimen and that under consideration.

Another feature which is characteristic of *Lepidophloios fuliginosus* is the peculiar formation of the secondary tissues formed around the primary xylem cylinder. This, as is seen in Pl. 24. fig. 7, Pl. 25. fig. 11, and Pl. 24. fig. 12, is of almost precisely the same nature as that figured by Williamson (Part XI. pl. 49. fig. 11) as the "rudimentary exogenous zone."

After these general observations, we will pass to a detailed consideration of the tissues.

The Stele.

The centre of the stele is occupied, as is seen from Pl. 24. figs. 6 & 7, by medullary tissues, the cells of which are for the most part considerably compressed. Only the three or four outermost rows of cells show a definite lumen, and from these the nature of the pith-cells can be established. In transverse section they are more or less polygonal in shape. In longitudinal section it will be seen (Pl. 25. fig. 10) that the primary cells have grown considerably in length and fit very closely together with pointed ends. These cells have divided up repeatedly by transverse and oblique walls. Sometimes two rows of these small polygonal cells are found within the elongated primary cells. A pith of this kind has been described and figured by Williamson (1873) (Pl. 24. fig. 14) for *Lepidophloios fuliginosus*, and occurs in other lepidodendroid stems. It is not an unusual condition for the medulla and cortex of recent plants. The cells seem all to be of a parenchymatous character; and I was not able to detect any elements with reticulated walls such as occur in *Lepidodendron vasculare* (Binney) *, and as have been described by Seward (1899) in a stem of *Lepidophloios fuliginosus*.

The primary wood which encloses the pith consists of eight or ten layers of tracheids decreasing in diameter towards the periphery, where the wood ends in sharp cusps composed of the smallest elements (protoxylem). From these the vascular supply of the leaf-trace bundles is given off, and in the depression between two consecutive cusps there will be seen to the outside of the primary xylem the vascular elements which have been given off at a lower level.

The inner portion of the primary wood is seen to consist of large tracheids with scalariform marking. The smaller elements near the periphery seem to be narrow tracheids. In transverse section the tracheids are more or less polygonal in outline, and often show a splitting apart of the wall between two contiguous cells. Most of the cells are devoid of contents, but in some cases the cell-space is filled with a dark brown mass.

The groups of elements which are given off to form the leaf-traces consist of both smaller and larger cells, the former generally enclosed by the latter, thus forming a mesarch group (Pl. 25. fig. 13). This mesarch arrangement is not always visible immediately on leaving the primary xylem. At first the course of the leaf-traces is nearly vertical, and it is not until they enter the mid-cortex that they become oblique or nearly horizontal.

The tissue immediately outside the primary wood consists of very small isodiametrical cells with dense contents, thus rendering them opaque and preventing their structure from being clearly seen. In this tissue lie the leaf-trace bundles just after they are given off from the primary wood. At a little distance from the primary wood the cells of the surrounding layer become larger and clearer and are more regularly arranged. Their contents are less dense than those of the cells nearer the wood, and they are consequently of a lighter colour. These are the layers that are considered from their regular arrangement to be of secondary origin.

* *Lepidodendron selaginoides* (Will.).

The transverse section shows that this secondary growth does not take place uniformly round the axis, but, as is very generally the case in the *Lepidodendraceæ*, it is more extensive on one side of the stem. In Pl. 24. figs. 6 & 7 it will be found largely, if not exclusively, on the lower side of the stele.

The specimen under consideration, though more than twice the size of that described by Williamson, has only a very little more secondary growth, confirming the belief that in this species the development of secondary wood did not take place to so great an extent as in other *Lepidodendraceæ*. At some parts of the circumference, indeed, there seems to be no secondary growth at all, and then there is a gradually increasing amount as one passes round the stem, decreasing again as one nears the starting-point. This condition allows us to see not only the actual secondary growth, but to follow out more or less the consecutive stages of its development.

Even where there is no actual secondary tissue formed, one notices, on the outside of the dense parenchymatous tissue in which the leaf-traces are at first embedded, a ring of more lightly coloured and thin-walled cells somewhat radially elongated. Within these, a little further on, will be found one or two rows of smaller squarish cells, and further on still they will be found to be more numerous and more regularly arranged. Seen in a transverse section, they are for the most part square in shape except the outermost layer just within the phloem, which, as stated above, is often considerably elongated in a radial direction (see Pl. 25. fig. 13) and very light in colour. This ring of radially elongated cells is probably not of a meristematic nature, as it occurs, as will be seen later on, in the lateral organs in which no secondary thickening takes place. Probably one or more of the rows of cells within the radially elongated cells were of a meristematic nature, differing somewhat from the flattened cambium-cells of recent plants.

In those parts of the circumference where a considerable amount of secondary tissue has been formed, it will be noticed that certain rows of the secondary cells become more enlarged and appear to have somewhat thicker walls. These cells are generally empty, and are in transverse section not unlike the secondary tracheids of other *Lepidodendraceæ*. They are somewhat irregularly arranged, as in the secondary wood of *Lepidodendron Wüschianum*, and form slightly spindle-shaped groups of cells.

A similar condition for the same species is figured by Williamson (1881), pl. 49. fig. 11, and in his description of this section (p. 290) he calls the larger empty elements "barred vessels." An examination of a longitudinal section of our specimen (Pl. 25. fig. 11), however, shows that these larger cells are short and square, and do not possess any scalariform marking.

It is of course possible that we have in this specimen a fairly young condition of the stem before the lignification of the secondary tissue. If this is the case, then it is conceivable that tracheids may yet be formed from the secondary tissue. But neither the transverse nor longitudinal sections are suggestive of the formation of tracheids, the whole of the secondary tissue having the appearance of parenchyma.

The very late development of secondary tracheids seems to be a characteristic feature of *Lepidophloios fuliginosus*, as far as can be gathered from the published accounts

of this species and as I have also observed in the various specimens in the collections of the Manchester Museum.

In some specimens of *Lepidophloios fuliginosus* in the Cash Collection, though only about half the diameter of the specimen now before us, lignified elements are more strongly pronounced and show, where they are obliquely cut, scalariform marking. But the proportion of such thickened tracheids is very small in comparison with the parenchymatous cells of the secondary zone.

Outside the secondary tissues we come to the phloem region. As in other specimens of *Lepidophloios fuliginosus*, the phloem area is occupied in this specimen by large cells or spaces embedded in a small-celled tissue, which is, however, but indifferently preserved, so that the individual cells are not always recognizable (Pl. 24. figs. 7 & 12). These large round spaces are characteristic of most stems of *Lepidophloios*, and have been described by Bertrand (1891) in *Lepidophloios Harcourtii* as phloem elements. Seward (1899), however, after very careful examination, has come to the conclusion that this tissue is not a true phloem, but a secretory tissue, the large spaces being probably formed for the most part "during the life of the plant by the separation and partial disorganization of thin-walled cells."

I have given my reasons in a previous paper (Weiss, 1901) for dissenting from Seward's views, and for believing that this tissue is true phloem comparable with that of existing *Lycopodiaceæ*.

This conclusion is based upon the examination of some very perfectly preserved specimens of *Lepidophloios* from the Cash Collection in the Manchester Museum, in which the large sacs or spaces mentioned above are not present and in which the phloem shows a distinct resemblance to that of existing *Lycopodia*. The spaces appearing in the phloem of the present specimen and in most other specimens of *Lepidophloios* I consider due to partial disorganization, previous to mineralization it is true, but not during the life of the plant. That this disorganization is not generally apparent in other tissues I think must probably be connected with the fact that the cell-walls of the phloem in *Lycopodiaceæ* are often composed of amyloid, a carbohydrate less resistant than cellulose, of which the cell-walls of the other tissues are composed.

In his criticism of my views Seward (1902), while maintaining his interpretation of the tissue under question as of a secretory nature, agrees with me "as regards the probable phloem-function of this tissue." As its position and its connection with the leaf-traces render this function most probable, I should prefer to retain for it the name of phloem, even were it not identical in structure with that of recent Lycopodiales. But even in the living representatives of this group we have a very considerable range in the structure of the phloem if we include *Isoetes*, for which Scott and Hill (1900) have definitely established the phloem nature of the secondary tissue of tabular cells. The difference between Seward and myself is, I think, largely one of terminology—Seward identifying the word phloem with a tissue possessing a definite anatomical character, whilst I use the term to describe a tissue having a certain physiological function.

The examination of the phloem in our specimen, where it has undergone some

degeneration, would not be of much value. In one portion of the section the large spaces are absent, and one can see, though somewhat indistinctly, that their place is taken by a small-celled tissue, which is, however, not well preserved (Pl. 26. fig. 9, *ph.*), and with a high power it can be seen that most of the cell-walls are broken. It is interesting, however, to note that the small-celled groups corresponding to the spaces in other parts of the section are lighter in appearance than the intervening tissue, which is not generally the condition of secreting tissues.

In longitudinal section it will be seen from Pl. 23. fig. 8 that even where the large spaces have made their appearance by absorption of some of the cellular tissue, the transverse walls are still in part preserved, and show that the groups of cells were arranged in vertical series separated by transverse walls following each other at no very considerable distance.

The phloem does not form a continuous cylinder around the stem, but is broken up into numerous pieces by the leaf-trace bundles which pass out through the phloem into the cortex. This is shown in fig. 7, Pl. 24, and is also represented in the drawing, Pl. 25. fig. 13. Here it will be seen that, in passing out through the phloem, the vascular leaf-trace becomes associated with a group of phloem elements which accompany it to the outside of the stem. This phloem-tissue gets rather darker, being composed of smaller and more closely-set cells.

As will be seen in Pl. 24. figs. 7 & 12, the tissue immediately outside the phloem has been split during mineralization almost along its whole extent. This is no doubt due to the very delicate character of its cells, which are thin-walled and rectangular, and from the regular sequence of their walls appear to be of a meristematic nature. As will be seen from Pl. 25. fig. 13, which shows an enlarged view of this region, there are never many of these thin-walled cells, but generally only two or three. Such a meristem I have observed in other specimens of *Lepidophloios fuliginosus*.

A tissue of very similar appearance, but belonging to the middle cortex, is found in the stems of *Lepidodendron vasculare* (Binney), and is well figured by Scott (1900)*. In my specimen, however, this meristematic zone lies within the inner cortex, and would be morphologically identical with the pericycle, in which the appearance of meristematic cells would not be surprising. This outer meristematic layer I would compare with the meristematic zone in the pericycle of certain monocotyledons, and it could also be compared with the meristem retained in *Isoëtes*, for, according to Scott and Hill (1900), the first normal cambium on the inner side of the phloem disappears at an early period in *Isoëtes Hystrix*, and is followed by a second cambium which soon arises further to the exterior. It is of interest, with regard to the systematic position of *Isoëtes*, to find in the *Lepidodendraceæ* so distinct a secondary meristem outside the phloem.

Whether any addition to the phloem region is made from the pericyclic meristem, it was not possible to definitely ascertain in these sections, but in one or two places the arrangement of the outer phloem elements suggested such an origin.

* Scott, D. H. (1900), fig. 54, p. 134.

Cortical Tissues.

In many parts of the transverse section we find, outside this apparently meristematic layer, a few layers of cells more or less longitudinally drawn out with black contents, and these, though not always clearly marked, have much resemblance to an endodermis. The dark cells go over into the inner cortex, of which they probably represent the inner layers, possibly specialized for storage of carbohydrate material, as is the case in those plants which possess a well-marked starch-sheath. The inner cortex as a whole is formed of a close and compact tissue, the cells of which are more or less elongated in a tangential direction and show few intercellular spaces, and seem to form a protective sheath to the stele. In longitudinal sections the cells are seen to be short and rounded.

The next portion of the cortex, the middle cortex, which is more or less clearly marked off from the inner cortex, consists of a very different tissue. Its cells are not at all closely set together, and thus leave very considerable intercellular spaces. The cells, moreover, are not all arranged with their long axis in a vertical position, but run obliquely and even horizontally, and have the appearance of a spongy parenchyma, or, when the cells are considerably drawn out, even of a felted mass of hyphæ. This trabecular cortex forms the bulk of the tissue of the stem, being 25 mm. thick in the direction of the broader diameter of the stem and 15.8 mm. in the narrower direction. Its extent is well shown in Pl. 24. fig. 5 (*m.c.*), and the structure in Pl. 26. fig. 15 (*m.c.*), in which it is seen in longitudinal section. Owing to the irregularity of its cells, it presents much the same appearance both in transverse and in longitudinal sections. It will be noticed that the cells are not all of the same diameter, there being larger lighter cells and smaller cells with dark contents. These latter are met with in various parts of the stem, but they are found to be very numerous and running horizontally close to the passage of the leaf-trace bundles from the middle to the outer cortex (see Pl. 26. fig. 15). The narrower and darker cells have often an appearance not unlike a laticiferous tissue, though it is impossible in the case of a fossil plant to make this identification complete. This loose middle cortex, generally defective or absent in other *Lepidodendraceæ*, is usually well preserved in *Lepidophloios fuliginosus*, so that it is a tissue of some importance in the identification of the specimen. The demarcation between the middle cortex and the outer cortex is marked in longitudinal section (Pl. 26. fig. 15) by the very small cells of the latter, which are drawn out tangentially and which are therefore very short in longitudinal view. An interesting feature of the longitudinal sections is the passage, in connection with each leaf-trace bundle, of a group of cells from the middle cortex through the outer cortex to the leaves, where they form the so-called parichnos. Bertrand (1891) and Hovelacque (1892) had traced the parichnos strand in *Lepidodendron* to the middle cortex, but by means of transverse sections. Unfortunately this delicate tissue is often defective in the *Lepidodendra*. But where, as in *Lep. fuliginosus*, the middle cortex is generally well preserved, the delicate parenchymatous nature of the parichnos tissue can readily be seen. It is well figured in transverse section by Binney (1872)*, and on a more enlarged scale by Seward (1900), in whose figure the hypha-like tissue can be seen. But the best

* Binney, E. W. (1872), pl. 15. fig. 4.

longitudinal view showing the continuity between the parichnos and the middle cortex is seen on a slide (No. 796) from the specimen now under consideration, kindly lent me by Dr. Scott. Pl. 26. fig. 15 is taken from this slide. In this figure the continuity is very well seen, as also the fact that the outer cortex runs for some distance down the leaf-trace on the upper side.

Potonié's (1893) researches on the nature of the parichnos have led him to the conclusion that the parichnos running out into the leaf-base was an organ to promote active transpiration, but, from the structure of the tissue, it is quite as possible to argue that it was a respiratory organ allowing a passage of air from the leaves into the inner portion of the stem and down to the roots. Considering the structure of the roots and the supposed habitat of the plants, this would seem to me a more natural explanation. The trabecular tissue of various species of *Selaginella*, which also accompanies the leaf-traces, probably has the same function as the middle cortex and the parichnos. But the persistence of the parichnos on the leaf-scars of the old stems of *Lepidodendra* enabled them also to supply the place of the lenticels of the recent dicotyledonous trees; for stems with secondary thickening, like the recent Dicotyledons and extinct Vascular Cryptogams, would require some such organs to supply the actively growing cells of the interior with the necessary oxygen.

The cells of the outer cortex are short and closely set together, and this tissue, which is about a third of the thickness of the middle cortex (Pl. 24. fig. 6), was no doubt largely of a protective nature and would have prevented any air from reaching the inner tissues, except where penetrated by the parichnos strands. Near the outside of the outer cortex, just on the periderm, there may be seen irregular patches of a darker colour running more or less tangentially. On closer examination it will be seen that they have the appearance of groups of secretory cells with thin walls and dark cell-contents. These are described and figured by Seward (1899) for *Lepidophloios fuliginosus* (fig. 6, p. 4 & p. 148) and also for *Lepidophloios Harcourtii* (Seward, 1900, pl. 1. fig. 3). In Pl. 24. fig. 14 will be seen the early stages of development of this tissue, and the perfection of the preservation of these delicate tissues can be gathered from this drawing. These patches tend to become continuous in a tangential direction. An examination of this tissue is not only convincing as to their secretory nature, but also shows it to be of a very different nature from the phloem-tissue to which Seward attributes a secretory character.

Close to these secretory patches we have the secondary tissue produced from the outer cortex. As will be seen from the section shown in Pl. 24. fig. 6, this tissue is only preserved in a portion of the section. It commences with fairly large square cells, and then near the outside the cells get smaller and more compressed. As the outer portion of the tissue is much disorganized it is impossible to distinguish an actual phellogen. In all probability this tissue will be morphologically a phelloderm with a phellogen on the outside; but the appearance of its cells, both in transverse and longitudinal section, suggests a function agreeing more with that of true cork. In longitudinal view the cells are seen to be much more elongate than the cortical cells and arranged in fairly close alternating series.

Leaf-traces.

The giving off of the leaf-traces from the primary wood was described in connection with that tissue. The mesarch bundles thus given off pass nearly vertically at first through the ground-tissue and the secondary elements lying between the xylem and phloem. This portion of their course is seen in Pl. 25. fig. 11. As they pass out through the phloem (Pl. 25. fig. 13) they carry outwards a portion of the phloem, which always remains separated from the xylem elements by a few rows of undifferentiated cells. In passing through the inner cortex the leaf-traces still retain their steeply inclined position, but when they reach the middle cortex (see Pl. 24. fig. 6) they become much more horizontal in position. This is more particularly the case with the leaf-traces passing in the direction of the longer diameter of the stem. These very oblique or horizontal leaf-traces in this region are very characteristic of most specimens of *Lepidophloios fuliginosus* in the Manchester Museum, and are not generally so found in other *Lepidodendraceæ*. An examination of the bundles whilst running through this middle cortex will show that they are surrounded by a firm sheath of cells, similar to those of the inner cortex through which the bundle has previously passed.

The course of the leaf-traces through the outer cortex is much the same as that in the middle cortex, and here too it is quite horizontal.

As the leaf-cushions are absent, we cannot follow the leaf-traces beyond this layer.

Branching of the Stele.

The branching of the stele to supply the halonial tubercle agrees in all respects with the cases described by Williamson (1873), (1881), (1893). The stele does not divide equally as in the case of ordinary branching, but displays a somewhat horseshoe-shaped segment in the case of halonial branches with two rows of tubercles at the two ends of the longer axis of the elliptical stele. This is well figured by Williamson (1881) for *Lepidophloios fuliginosus* (pl. 52. fig. 9), and is also seen in our figure of the transverse section of *Lepidophloios fuliginosus* (Pl. 24. figs. 6 & 7). In this specimen of *Lepidophloios*, however, the branch of the stele takes, like the leaf-trace bundles, a more horizontal course soon after separating from the central stele, so as to be seen more horizontally in subsequent sections where it is nearer the outside. This very oblique course gives us a less clear picture in the transverse sections, while longitudinal sections, such as that figured by Williamson (1893) (pl. 2. fig. 25), give us a better idea both of the course and of the structure of this stelar branch.

The commencement of the branching of the stele is characterized by the breaking up of the cylinder of primary xylem by intruding bands of medullary tissue. At the same time a corresponding piece of phloem is separated off by strands of cortical cells, which ultimately meet the projections from the pith.

The horseshoe-shaped piece of primary wood which is thus detached gives off numerous leaf-traces on the outside, as can be seen in Pl. 24. fig. 7. The gap in the stele becomes bridged over by a tissue the cells of which have dark contents, and which appears continuous with what I have described above as a possible endodermis. A similar dark

sheath forms around the stelar branch, which at a little distance from the main stele becomes clothed on the inside, too, with a layer of phloem-cells. At first the branch is destitute of pith, but a little way from the main stele a more or less definite medullary tissue of parenchymatous nature can be observed both in the radial longitudinal sections through the tubercle and also in transverse sections of it (tangential to the main axis). In sections of this latter kind, the appearance of the stelar branch is very much like that figured by Williamson (1881) (fig. 12, pl. 51).

The arrangement of the xylem around the pith (Pl. 25. fig. 19) is more or less radial, but has not the definite character of the stele in the peduncle of *Cheirostrobos*, *Spencerites*, or *Lepidostrobos* as described by Scott (1897 & 1898), Bower (1893), and Maslen (1899).

Outside the xylem we find a dark layer of small parenchymatous cells in which numerous leaf-traces are embedded. Then comes a very definite band of more lightly-coloured cells, rectangular in shape, with their long axis in a radial direction. This layer of cells is exactly similar to that found within the phloem of the main axis, where it apparently separates the phloem from the cambium.

Beyond this very definite layer of cells lie groups of phloem interrupted by leaf-trace bundles showing a very clear mesarch arrangement of their xylems (Pl. 26. fig. 18). As these leaf-traces pass outwards through the phloem, they carry with them some of the phloem-tissue, which generally appears considerably compressed. The phloem groups, however, which alternate with the xylem often show their structure very clearly, though some groups are more or less disorganized. Those which are best preserved exhibit in transverse section a number of large and clear polygonal cells, between which are here and there smaller and darker cells. Their appearance is therefore not unlike that of the phloem of recent Lycopodiales. In longitudinal section, however, where they can be easily recognized by their position and their size, the phloem-cells will be found to be short and rectangular, their length being about the same as that of the cells of the cortical sheath immediately outside. The width of the phloem-cells, however, is greater than that of the cortical cells. In longitudinal section these phloem-cells differ considerably from the phloem of recent Lycopodiales, except possibly *Isoëtes*, and they differ also from the phloem-cells described by Maslen (1899) in *Lepidostrobos*. In none of the groups of phloem in the stelar branch could I find any of those divisions which are found in the phloem-cells of the main axis (see fig. 9, Pl. 26). But I have pointed out, in connection with the phloem of *Lepidophloios* (1901), that in the leaf-trace bundles, too, there is an absence of these longitudinal divisions of the phloem-cells.

The stelar branch, on its way to the tubercle, is always surrounded by a sheath of dense cells continuous with the inner cortex which surrounds the main stele, and from its very commencement it gives off leaf-traces which can be seen cut transversely in this inner cortical sheath. Even when these leaf-traces pass out into the mid-cortex, they remain much more parallel to the stelar branch than is the case with the leaf-traces given off from the main stele.

In passing into the outer cortex, the stelar branch retains a fairly thick sheath of tissue continuous with the middle cortex, which can be seen in the transverse section of the stem (Pl. 26. fig. 16) and also in a section passing transversely through the base of the

tubercle (Pl. 26, fig. 17). This middle cortex is of the same nature as that of the main axis, but is remarkable for the great distinctness of the two kinds of cells described above, the smaller denser ones accompanying the stelar branch very much in the same way as they do the leaf-traces (see Pl. 26, fig. 16). In one or two places I have observed at the demarcation between the middle and the outer cortex a group of cells of the former showing an arrangement which indicated a certain amount of meristematic activity of the outermost part of the middle cortex. A similar phenomenon I have described (1901) in a rootlet which I consider belonged probably to *Lepidophloios fuliginosus*.

Whether or not the stelar branch supplied a strobilus cannot be determined from the present specimen. I have, however, pointed out above one or two points in which it diverges from the structure described for the peduncles of various lepidodendroid strobili.

The anatomical characters of the main axis, however, as described above leave, I think, no room for doubt that this halonial branch belonged to the plant now known as *Lepidophloios fuliginosus*.

The most important points in the structure of the halonial branch which support this identification are:—

- (1) The parenchymatous pith and the general arrangement of the primary xylem.
- (2) The very characteristic mode of secondary growth resulting in the almost exclusive formation of parenchymatous cells.
- (3) The well-preserved middle cortex and its peculiar structure.
- (4) The secretory tissue of the outer cortex.

These special points in which the plant differs from one or other of the various *Lepidodendraceæ* are, I think, sufficiently characteristic to confirm the identification made by Dr. Scott (1898).

On anatomical grounds, then, we may describe the specimen under consideration as a branch of *Lepidophloios fuliginosus*. The halonial branches of this species are generally of the multiseriate type, *i. e.* with a quincuncial arrangement of the tubercles. I have, however, pointed out in the first part of this paper that this was by no means always the case. Williamson has described specimens of *Lepidophloios* which could be recognized both by their internal structure and by their leaves, and also possessed two rows of tubercles. Similarly, in the first part of this paper, I have described specimens, both from the British Museum and from the Manchester Museum, which, to my mind, must be classed as *Lepidophloios* and which possess only two rows of tubercles.

There seems, therefore, to be no reason why the specimen under consideration should not be correctly described as a biseriata halonial branch of *Lepidophloios fuliginosus*.

[POSTSCRIPT, November 20, 1902.—The specimen forming the subject of this Memoir, together with a number of sections cut from it, has been deposited in the Manchester Museum, Owens College.—F. E. W.]

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EXPLANATION OF PLATES 23-26.

- Pl. 23. fig. 1. Photograph (nat. size) of the halonial branch of *Lepidophloios fuliginosus*, showing the two rows of tubercles. Near the upper and lower ends the periderm is preserved; where the latter is absent, the leaf-traces are seen forming small elevations in the cortical tissues.
The photograph is by Messrs. Gunn & Stuart, of Richmond.
- Pl. 23. fig. 2. Photograph ($\frac{2}{3}$ nat. size) of an halonial branch in the Manchester Museum, from the Four Foot Mine at Tonge, near Bolton. One of the two rows of tubercles is here visible, but no remains of the leaf-bases.
- Pl. 23. fig. 3. Photograph of the other side of the halonial branch depicted in fig. 2, showing the other row of tubercles, and near the top right-hand side the traces of bifurcation. On this side are seen the carbonized remains of the leaf-bases, showing that these were of the *Lepidophloios*-type.
- Pl. 23. fig. 4. A portion of the leaf-bases of the halonial stem illustrated in figs. 2 & 3, somewhat enlarged to show the downward imbrication of the leaves.
- Pl. 24. fig. 5. Photograph of an halonial branch from the Williamson Collection (British Museum), cabinet-number 1946 B, showing imbricating leaf-bases and two rows of tubercles.
- Pl. 24. fig. 6. Transverse section (slightly enlarged) of the halonial branch of *Lepidophloios* described in this Memoir, showing the general arrangement of tissues. The stele is interrupted, having just given off a branch (*b*) to one of the tubercles.
i.c. = inner cortex.
m.c. = the middle cortex, with horizontal leaf-trace bundles.
o.c. = outer cortex.
per. = periderm.
- Pl. 24. fig. 7. Enlarged view of stele of halonial branch.
m. = medulla.
p.x. = primary xylem.
s.t. = secondary tissues.
ph. = phloem.
i.c. = inner cortex, with leaf-traces.
b. = vascular branch.
- Pl. 23. fig. 8. Portion of phloem in longitudinal section, showing transverse walls (*tr.w.*) across the lacunæ formed by a breaking down of the phloem-cells.
- Pl. 26. fig. 9. Portion of transverse section, showing phloem-area (*ph.*) occupied by small-celled tissue, before decay of latter.

- Pl. 25. fig. 10. Longitudinal section through outer portion of medullary tissue (*m.*), showing the division of its elongated cells by transverse and oblique walls. The inner pith-cells on the left-hand side are much compressed.

p.x. = scalariform tracheids of primary xylem.

- Pl. 25. fig. 11. Longitudinal section of a portion of the stele in which there has been a considerable amount of secondary tissue formed (*s.t.*), showing its short-celled character.

l.t. = leaf-trace.

ph. = phloem.

i.c. = inner cortex.

p.x. = primary xylem.

- Pl. 24. fig. 12. Transverse section through secondary tissues (*s.t.*), consisting of small square cells.

Lettering as in fig. 11. *sp.*, split in tissues in the region of the pericycle; this is also seen in fig. 7.

- Pl. 25. fig. 13. Drawing of portion of transverse section representing the outward passage of mesarch leaf-trace (*l.t.*) through the phloem region.

ph. = phloem partially disorganized.

ph' = phloem group which will accompany leaf-trace bundle.

c.t. = columnar tissue, possibly of meristematic nature or immediately outside the cambium and the secondary tissues.

per. = pericycle, in part meristematic, on left-hand side.

i.c. = inner cortex.

- Pl. 24. fig. 14. Longitudinal view of the secretory tissue found immediately on the inside of the periderm. In the lower part of the drawing its mode of origin from the outer cortex is recognizable.

o.c. = outer cortex.

sc. = secretory tissue.

- Pl. 26. fig. 15. Portion of a longitudinal section from Dr. Scott's cabinet (No. 796), showing the origin of parichnos (*par.*) as a continuation of the middle cortex (*m.c.*) accompanying the leaf-trace bundle (*l.t.*) in its course through the outer cortex (*o.c.*).

- Pl. 26. fig. 16. Portion of a transverse section of halonial branch a little above the one represented in fig. 7, showing stele closed again after having given off bundle and the vascular branch to the tubercle running nearly horizontally through middle cortex and outer cortex.

v.b. = vascular branch to tubercle.

m.c. = middle cortex.

o.c. = outer cortex.

- Pl. 26. fig. 17. Tangential section through halonial stem near tubercle, showing the vascular branch surrounded by sheath of middle cortex (*m.c.*) making its way through the outer cortex (*o.c.*).

per. = periderm.

- Pl. 26. fig. 18. Drawing of portion of stele of the halonial tubercle seen in transverse section, showing one of the mesarch leaf-traces (*l.tr.*) passing outwards to the phloem (*ph.*).

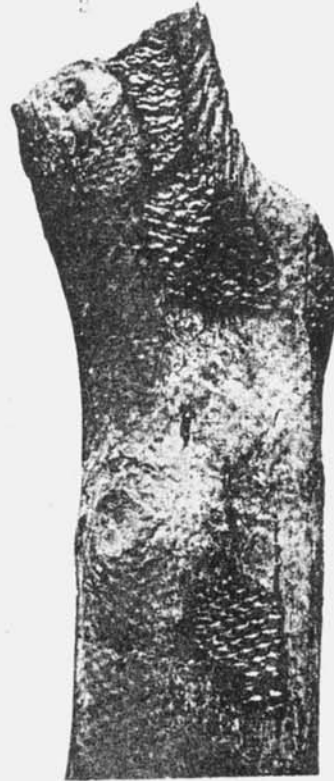
c.t. = columnar tissue lying between the xylem and phloem.

- Pl. 25. fig. 19. More enlarged view of the stele of the halonial tubercle, showing the somewhat irregularly arranged tracheids of the wood surrounding the parenchymatous pith.

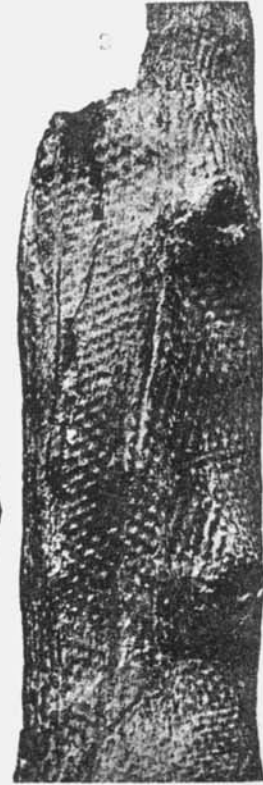
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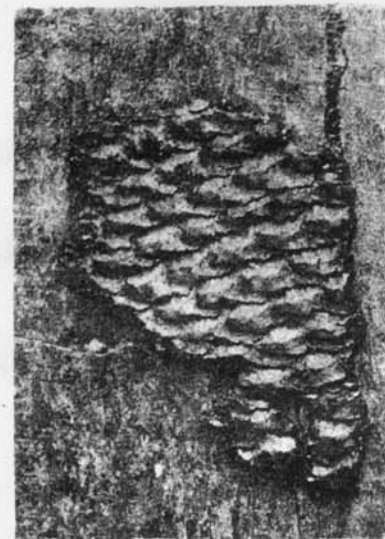
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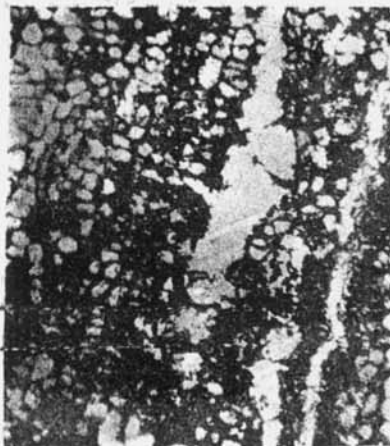
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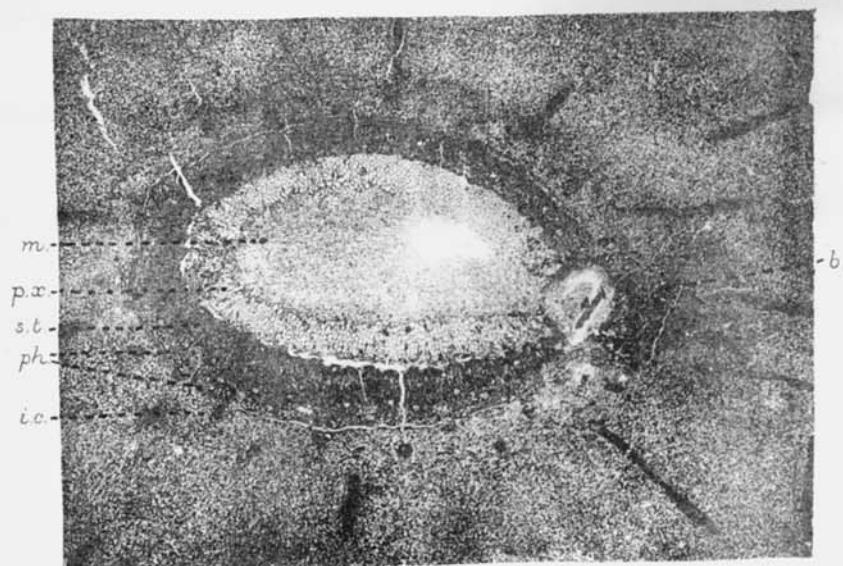
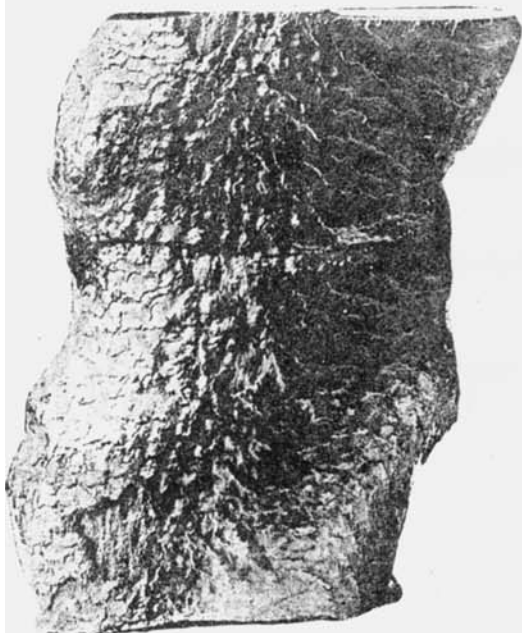
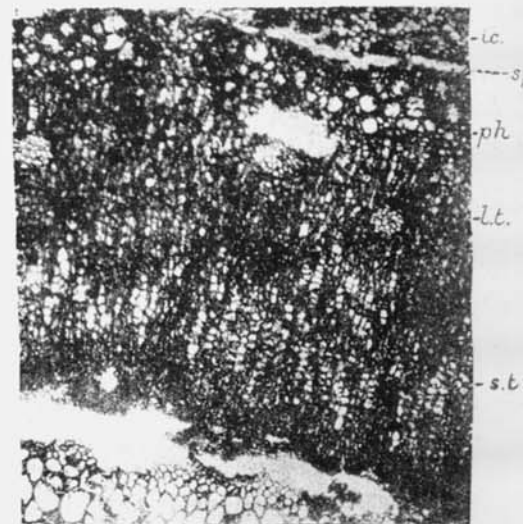
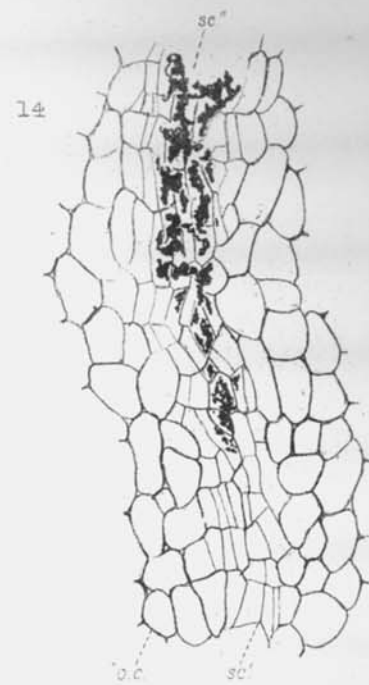
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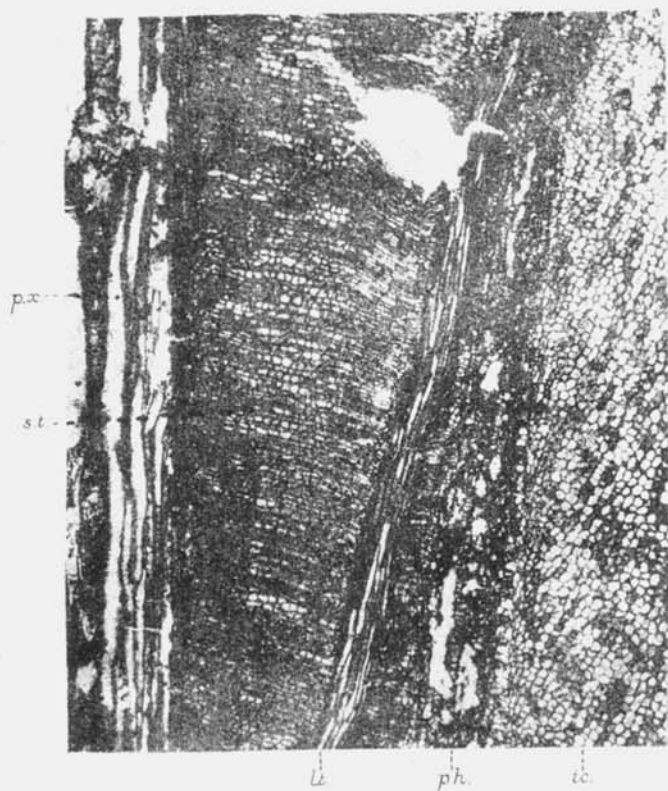
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tr. w. ---
tr. w. ---



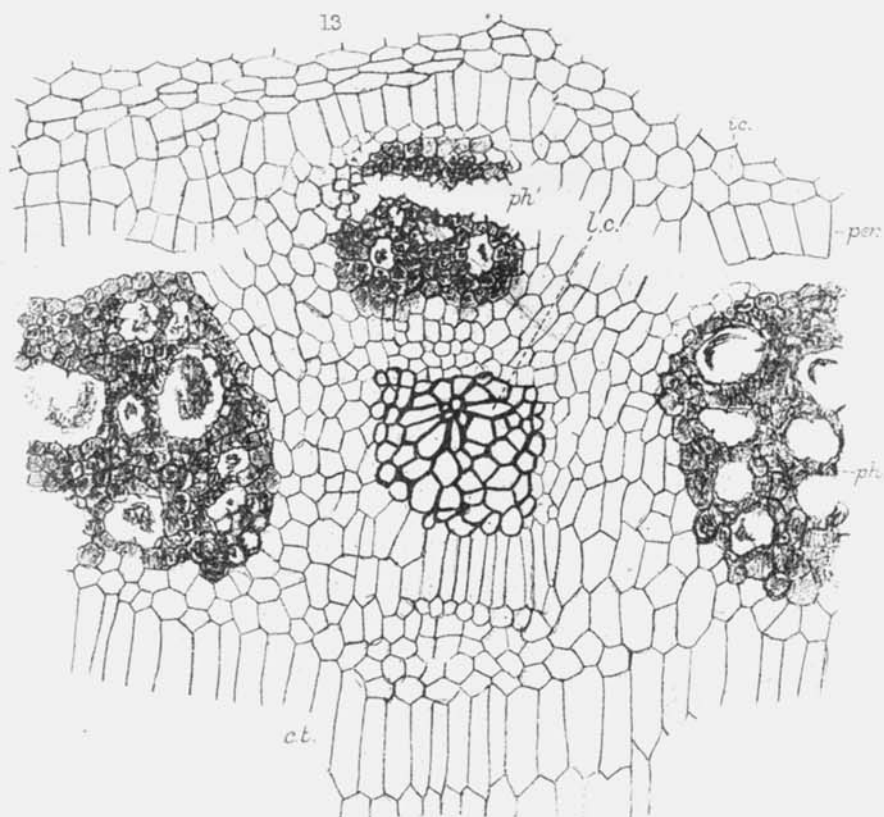
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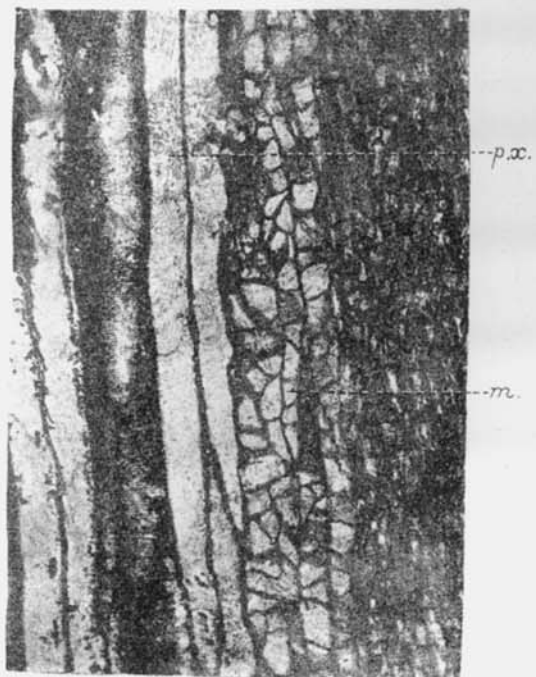
19



13



10

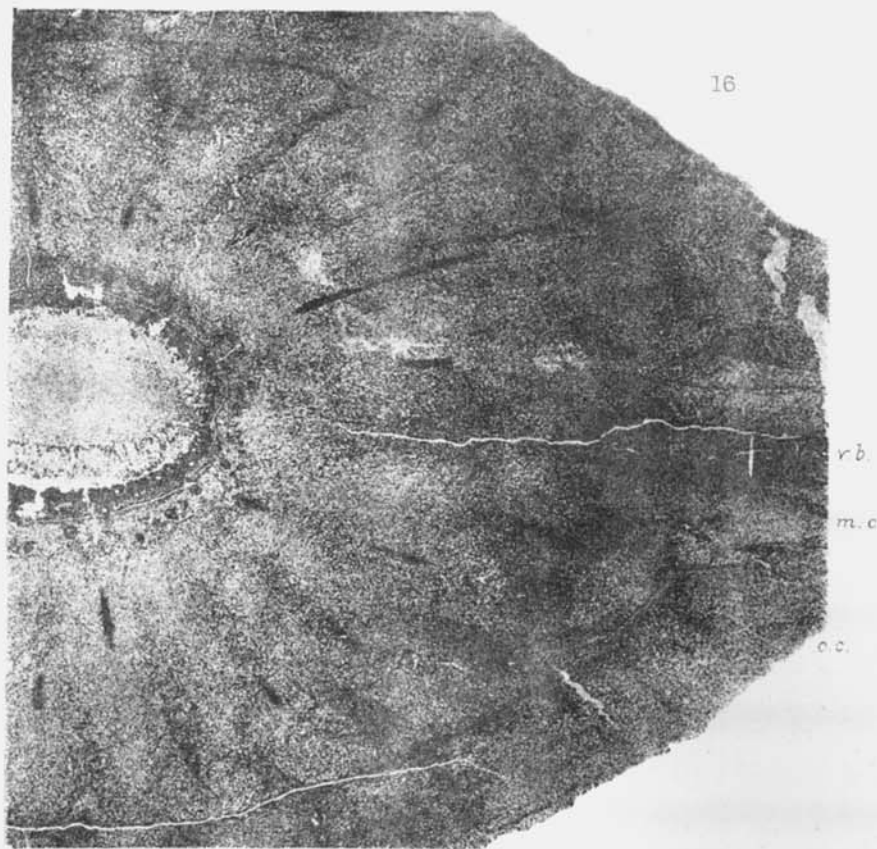


9



ph.

16



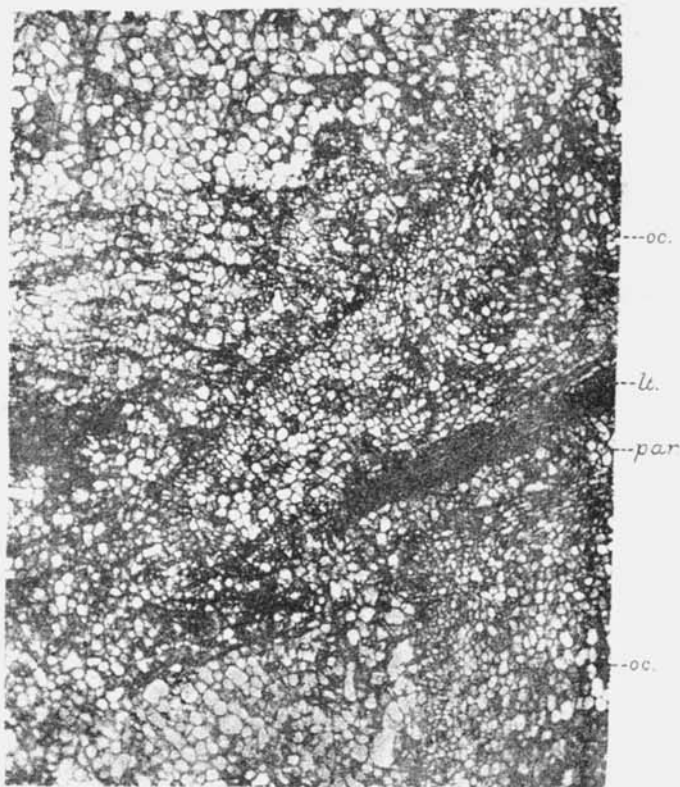
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m.c.

o.c.

o.c.

15



oc.

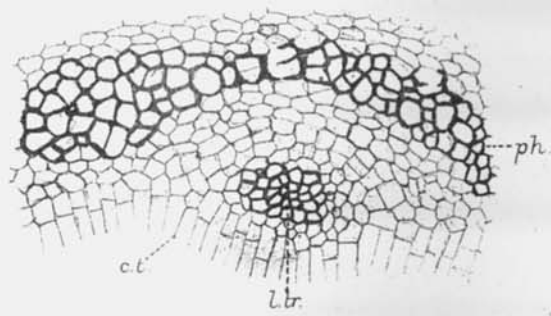
l.

par

oc.

mc

18



ph.

c.t.

l.b.

17



m.c.

o.c.

per

West Newman photo-lith