The Structure of Mesoxylon Lomaxii and M. poroxyloides.

BY

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With Plates LXXXVII-XC.

THE genus *Mesoxylon* was established by Mr. Maslen and myself in 1910 for certain Palaeozoic stems, intermediate in structure between the genera *Poroxylon* and *Cordaites*. *Mesoxylon Sutcliffii*, one of the five species briefly characterized in our original Note, was very fully described by Mr. Maslen last year (Maslen, '11). His admirable account of this typical form, of which very ample material was available, enables me to deal somewhat more briefly with the two species now to be described, which are not so richly represented. The question of the specific value of the anatomical characters by which we distinguish the fragmentary remains of petrified Palaeozoic plants is a difficult one; we have thought it advisable to give distinct names to well-characterized forms, even though we cannot in all cases be certain that the distinction may not be bridged, as more numerous specimens come under observation.

It will be well to begin by recalling the characters assigned to the genus *Mesoxylon*:

Pith relatively large, discoid. Wood dense, with narrow, usually uniseriate medullary rays, and relatively narrow tracheides. Leaf-traces double where they leave the pith, the two strands uniting at a lower level, but undergoing further subdivision in the pericycle and cortex, before entering the leaf.

Centripetal xylem present in the stem, where it forms part of the leaf-traces at the margin of the pith and throughout their course outwards into the leaves.

Outer cortex strengthened by a system of sclerenchymatous bands of the *Dictyoxylon* or *Sparganum* type. Wood of the kind usual in Cordaitales, the bulk of the secondary tracheides having multiseriate bordered pits on the radial walls. Tracheides of the leaf-traces, spiral or scalariform.[1]

[1] The generic character is very slightly abridged from that given in our Note (Scott and Maslen, '10, p. 237).

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Mr. Maslen has pointed out that '*M. Sutcliffii* (as well as the other species of *Mesoxylon*) exhibits structural characters intermediate between those of *Cordaites* and *Poroxylon*, but on the whole stands much nearer to the former genus' (Maslen, '11, p. 409).

I think this opinion is justified; the chief character in which *Poroxylon* is approached is the very definite one of the presence of centripetal wood in the stem. It was on this ground that I at first put *M. Sutcliffii* provisionally in the genus *Poroxylon* (Scott, '09, p. 511). As regards most, if not all, of the species referred to *Mesoxylon*, the characters common to *Cordaites* are more numerous, if less important. The relation of our genus to certain other genera, recently established, will be briefly considered at the close of the paper.

Mesoxylon Lomaxii, Scott and Maslen.

The specimens of *M. Lomaxii* are larger than most of the others. The three fragments known at present, which may possibly have come originally from a single stem, measure respectively:

5·5 × 2·3 cm. (Slide 2325)
6·0 × 3·5 cm. (Slide 2326)
and 5·0 × 4·0 cm. (Slides 2327 and 2328).

These rough measurements are probably rather under the mark, owing to the difficulty of allowing accurately for the partial destruction of the cortex.[1]

All the specimens are from roof-nodules at Shore, and the preservation is of the usual roof-nodule type: much tissue has been lost altogether, but the remaining portions are often well preserved, though not remarkably so in this case. Fortunately the inner margin of the wood is one of the best preserved regions (Pl. LXXXVII, Figs. 1 and 2).

The pith is large: in the least distorted of the specimens (see Fig. 1) it measures 22 × 17 mm. in diameter. There is a continuous and persistent outer zone of pith, while the central region is in the usual discoid condition (Pl. LXXXIX, Fig. 17).

The other striking features of the species are the dense zone of wood, with numerous prominences, corresponding no doubt to the position of the leaf-traces, on the side towards the pith (Figs. 1 and 2); the evident groups of centripetal xylem in the primary strands of the wood (Pl. LXXXVII,

[1] The longitudinal sections, from the same specimen as the transverse section 2326, are numbered 2375–2383. There are five more sections in the Collection at University College, London, lent me by Prof. F. W. Oliver, F.R.S. Q 6 m is a transverse section cut immediately above my 2328, while Q 6 n, also transverse, belongs to the same fragment as 2326, and was probably cut below that section. Q 6 o–Q 6 q are three longitudinal sections cut from the same specimen as my transverse section 2325. All the University College sections are good, and of quite equal importance to those in my own collection.

Fig. 5; Pl. LXXXIX, Fig. 18): the phloem-zone with its large and conspicuous secretory sacs (Figs. 6 and 7), the broad cortex, mostly of secondary origin, and the rather narrow external, Dictyoxylon zone (Figs. 1, 2, and 6), which, however, is seldom preserved.

The Pith.

The persistent zone of the pith shows little differentiation; the outer portion has somewhat thicker walls than the inner layers, which consist of a delicate tissue; the cells of both portions are short.

The diaphragms constituting the central, discoid part of the pith are made up of thin-walled cells, similar to those of the inner portion of the persistent zone; they have the form usual in Cordaiteae; the diaphragms are thickest at the outer end, where they abut on the persistent zone, and thin out towards the centre of the pith, where they are usually broken and distorted (see the radial section, Pl. LXXXIX, Fig. 17).

The Leaf-traces.

As regards the course of the leaf-trace strands our data are incomplete, for no serial sections are available; the characteristic points, however, are clear. Traced inwards through the secondary wood the twin bundles of a leaf-trace converge (Pl. LXXXVII, Fig. 4), and fuse as soon as they reach the margin of the pith (Fig. 5). This rapid convergence and fusion of the twin strands may be taken, provisionally, as a specific character. As a result, the numerous circum-medullary primary strands are, in the case of *M. Lomaxii*, single bundles (Pl. LXXXIX, Fig. 18), with perhaps some slight indication of recent fusion. The tangential section shown in Fig. 3 passes through a pair of bundles (at *l.t.*), where they have not yet fused. If we now follow the trace outwards, we find that its course approaches the horizontal in passing through the wood, as is necessarily the case, where much secondary growth has taken place. In the phloem the two bundles reappear in approximately transverse section (Fig. 6). In passing through the cortex further subdivision goes on. Thus the four bundles of a single trace are seen in Fig. 7. Later stages of subdivision are not clearly shown, but it is evident that the bundles of the trace increased in number, for at least five are seen in a tangential section through the secondary cortex (slide 2376). Probably the ultimate number was eight, as in the other species.

The outgoing leaf-traces observed are not numerous. Though the loss of tissue, both in the wood and cortex, has no doubt often led to their being missed, it is probable that the leaves to which they ran were really more scattered than in the three species, *M. Sutcliffii*, *M. poroxyloides*, and *M. multirame*. At the most not more than four traces have been observed outside the wood, nor more than three in the wood itself, in

any one transverse section. It must, however, be remembered that the great development of periderm in the cortex must give the bundles a more horizontal course in this region, so that the conditions, even apart from the state of preservation, are not so favourable for observing them in transverse section as in specimens where there is less secondary growth.

On the other hand, the single primary xylem-strands, formed by the fused pairs, are present in large numbers around the pith; in each transverse section there are about twenty which show evident centripetal xylem, while other prominences, which are without this tissue, no doubt represent the lower ends of similar leaf-trace strands or the products of their anastomosis. Thus the whole inner margin of the wood is strongly undulated (Fig. 1), the intermediate secondary xylem only reaching the pith in the bays between the prominences. From the great number of primary xylem-strands it is evident that the phyllotaxis was complex.

In the structure of the leaf-traces, the first point to be noticed is the centripetal xylem. This is well developed, both in the bundles passing through the cortex (Pl. LXXXVII, Figs. 6 and 7), and in those which are approaching or have reached the edge of the pith (Pl. LXXXVII, Fig. 5; Pl. LXXXIX, Fig. 18). It forms, as seen in transverse section, an arc or crescent of considerable thickness; its irregularly grouped elements are sharply distinguished from the radial rows of the centrifugal wood (Fig. 18). The tracheides of the centripetal xylem are spiral or finely scalariform. It appears that the tissue persisted with little diminution for some distance downwards after the bundle reached the pith, for many of the circum-medullary strands have a well-developed centripetal portion. In others, however, it is extremely reduced, while it is altogether absent from many of the prominent xylem-strands. There can thus be no doubt that the centripetal wood eventually died out in a downward direction, as in other species of *Mesoxylon* and in *Poroxylon*, *Calamopitys Beinertiana*, &c.

The position of the protoxylem appears to have been, as is usually the case in this group, in contact with the centripetal wood (Pl. LXXXIX, Fig. 18, *px*). Here, as in other species, it is accompanied by some thin-walled parenchyma, which partially separates the centripetal from the centrifugal xylem.

A characteristic feature of the circum-medullary strands is the presence, in many cases, of a definite bundle-sheath separating the xylem from the pith. The sheath is limited to those strands which are seen in the upper part of their course; it dies out lower down. In a transverse section the sheath is found in about two-thirds of the strands which still have definite centripetal xylem. The simplest form of sheath occurs low down in the course of the strand. Here it consists of an arc, not more than two or three cells in thickness, of more or less radially elongated cells, with walls a little thicker than those of the adjacent pith-cells (Pl. LXXXIX, Fig. 18, *sh*).

The sheath encloses the whole prominent part, both centripetal and centrifugal, of the xylem-strand. Following the strand upwards in its course to the point where it is about to leave the pith, the sheath is here a much more important structure, consisting of numerous layers of radially arranged thick-walled cells, which have evidently increased in number by secondary divisions (Pl. LXXXVII, Fig. 5, *sh*). The double bundle shown in the photograph is in the act of fusion, or rather of separation, for we are tracing it in the upward direction. Still higher up, where the twin bundles are beginning to pass out into the wood, the sheath forms a double arc, corresponding to the two strands (Pl. LXXXVII, Fig. 4). In this region the cells of the sheath have reticulate, tracheoidal markings, which may be seen in Fig. 4 on using a lens. As we follow the trace on its outward course, we find that the sheath becomes merged in the secondary wood which here closes in behind the outgoing strands ; in the transitional region the short cells of the sheath are interspersed with the long, sinuous tracheides.

The Wood.

The structure of the wood, apart from the centripetal xylem of the leaf-traces, is of the usual Cordaitean type. In the parts corresponding to the primary strands a considerable amount of the inner centrifugal wood consists of scalariform tracheides, or in some cases elements with crossed spirals ; in the case of an entering bundle, fifteen layers of such elements were counted, and in one of the blunter prominences, representing a bundle lower down in its course, there were ten such layers.

In places, however, where the strictly secondary wood abuts on the pith, as in the depressions between the bundles, the pitted tracheides may extend right up to the inner margin. The scalariform elements are, as a rule, sculptured on all sides, while in the pitted tracheides the pits are limited to the radial walls. Transitional elements sometimes occur.

The tracheides of the secondary wood are rather small, ranging from 30 to 60 μ, the usual dimensions being 40 to 50 μ. The medullary rays are very narrow, 12 to 18 μ in width. As the tangential sections show, they may reach a considerable height, up to about twenty-five cells. They range from this down to a height of two cells or even one. Only in quite rare cases do we find a radial division, making the ray locally biseriate ; otherwise the rays are uniseriate throughout (Pl. LXXXIX, Fig. 19). In certain places the pits are well preserved. They form two or three series on the radial wall of the tracheide, and have the somewhat angular outline usual in Cordaitales. In a few cases the border of the pit is sufficiently perfect to show the inclined, elliptical slit, but usually the pore appears round (Pl. LXXXIX, Fig. 21). On the walls of medullary ray-cells in contact with tracheides the pits are arranged in two or three horizontal rows on the

ray-cell; they are less regular in form than elsewhere, and seem to be unbordered, though the preservation leaves this uncertain.

In the outer secondary wood the position of a double leaf-trace is marked, in tangential section, by the presence of two knots of irregularly interwoven tracheides, enclosing in their meshes the tracheides of the outgoing strand.

The Phloem and Pericycle.

The phloem-zone is traversed by long, sac-like elements, possibly of a secretory nature. In one of the specimens especially (slide 2325), they are very conspicuous; they are from 100 to 200 μ in diameter; their thick walls appear black and their contents brown (Pl. LXXXVII, Figs. 1 and 6). These elements extend into the pericycle, which may be distinguished from the phloem in longitudinal section by the fact that only short cells are present between the sacs.

In the phloem proper, which is imperfectly preserved, there are long tubes, about 40 μ in diameter, which in tangential section are seen to form a kind of mesh-work, enclosing the phloem-rays (LXXXIX, Fig. 20). Transverse or oblique walls appear to occur at long intervals. These tubular elements may probably be the sieve-tubes.

The Cortex.

The inner cortex is remarkable for the great development of secondary tissue, resembling periderm (Pl. LXXXVII, Figs. 2 and 6). The whole of the thin-walled zone has its cells radially arranged; the radial cell-rows, however, are not continuous throughout; the tangential divisions appear to have gone on in more than one layer, and not to have been limited to a definite phellogen. The zone in question, which reaches a thickness of at least 5 mm., may perhaps be more properly called secondary cortex rather than periderm.

In the hypodermal zone the radial sclerotic bands are usually narrow, and vary much in depth. There is no extensive tangential section of this zone, but some cases of anastomosis between the bands have been observed. Hence we may speak of the mechanical hypoderm as of the Dictyoxylon type. Towards the exterior the sclerotic bands unite in a continuous zone of moderately thick-walled tissue. The outer tissues are very imperfectly preserved, but the contour, as far as shown, appears to prove that the leaf-bases were scattered, and not crowded as in *M. Sutcliffii*.

Diagnosis.

An amended diagnosis of the species may now be given:

Mesoxylon Lomaxii, Scott and Maslen, 1910.

Leaf-bases scattered.

Pith large and discoid, with a persistent outer zone.

Twin-bundles of the leaf-trace converging rapidly in the wood, and fusing immediately on reaching the edge of the pith.

Centripetal xylem well developed, persisting for a long distance below the fusion of the twin-bundles.

Xylem-strands at the margin of the pith with a distinct and wide sheath in the upper part of their course.

Spiral and scalariform tracheides constituting the whole of the leaf-trace xylem and the inner part of the corresponding secondary wood, but almost absent from the intermediate secondary wood.

Bordered pits in two or three rows.

Medullary rays (with rare exceptions) uniseriate, 1–25 cells in height.

Secondary inner cortex or periderm of great thickness.[1]

Dictyoxylon zone relatively narrow.

Roof-nodules; Shore, Littleborough. Lower Coal Measures.

This species is named after Mr. James Lomax, to whom its discovery and that of the other species of *Mesoxylon* is due.

Mesoxylon poroxyloides, Scott and Maslen.

This species, like the last, was first named and shortly described in 1910, in the joint Note by Mr. Maslen and myself. It had, however, already been referred to, together with *M. multirame*, in the second edition of my 'Studies in Fossil Botany' (Scott, '09, p. 526), where I mentioned the occurrence of stems from Shore, in which the centripetal wood of a *Poroxylon* co-existed with the discoid pith and other characters of a *Cordaites*. *Mesoxylon poroxyloides* is a fossil from the ordinary coal-balls or seam-nodules of Shore; in this respect it is like *M. multirame*, and differs from *M. Sutcliffii*, *M. Lomaxii*, and *M. platypodium*, which are all roof-nodule specimens. The preservation of *M. poroxyloides* is consequently more complete than that of the species last mentioned, for it is free from the patchiness which is the peculiar defect of specimens from the roof-nodules. The detailed investigation has been carried out on one specimen, represented in my collection by seven sections (slides 2352–2358), of which four are transverse and three longitudinal. This may be called the type specimen.[2]

[1] This character must, of course, vary with the age of the specimen.

[2] There are six more sections of this specimen in the University College collection, for the loan of which I am indebted to my friend Prof. F. W. Oliver, F.R.S. Two of the sections, Q 6 a and Q 6 b, are transverse, and four, Q 6 c–Q 6 f, longitudinal. I have been able to determine the order of four of the transverse sections, which, from below upwards, run thus:

S. Coll. 2352
" 2353
Univ. Coll. Coll. Q 6 a
" Q 6 b

The other two transverse sections are not in series with the above, but 2355 comes below 2354.

Another stem, incompletely shown in slide 2397, may probably belong to this species, and is interesting from its close association with numerous leaves of the so-called 'Cordaitean' type (see p. 1022). A third stem (slide 2609) closely resembles the type, though not so well preserved. These are rather small stems from 2 to 3 cm. in diameter. A much larger specimen (slide 2608), of which the *radius*, measured only to the outer edge of the wood, exceeds 4 cm., has some points in common with *M. poroxyloides*, but in such large and incompletely preserved stems specific identification becomes very uncertain.

In the type specimen (Pl. LXXXVIII, Fig. 8), the pith measures about 12 × 4 mm. (8 mm. mean diameter), that of the whole stem being about 2·5 cm. In slide 2397 (the second specimen) the stem is too incomplete to measure accurately: the diameter may have been about 2 cm.; the stem is young and the pith therefore proportionately larger than in the type. The stem in slide 2609 approaches 3 cm. in diameter, that of the pith being little more than 6 mm. It thus appears that a comparatively small pith may be regarded as characteristic.

The pith, as in other species, has a persistent outer zone and a discoid middle (Pl. LXXXVIII, Fig. 13; Pl. XC, Fig. 22). In the convergence and early fusion of the twin-bundles of the leaf-trace as they reach the pith (Pl. LXXXVIII, Figs. 9 and 10) *M. poroxyloides* comes nearest to *M. Lomaxii*, from which it differs in the absence of a definite sheath round the primary xylem.

The centripetal xylem is well developed and is retained for some distance below the point of fusion of the strands (Pl. XC, Fig. 23). The secondary wood has the small tracheides and narrow medullary rays usual in the genus.

The phloem, chiefly secondary, forms a broad zone, well preserved in the type-specimen. The pericycle contains numerous large elements with dark contents, which may have been secretory sacs.

The Dictyoxylon zone of the cortex is wider than in other species. The leaf-traces subdivide in passing through the cortex, and on entering the leaf-base the full number of eight bundles is attained (Pl. XC, Fig. 24).

No axillary shoots or steles have yet been observed.

The Pith.

The pith is decidedly well preserved in places; the most favourable section for showing it as a whole is slide Q 6 c in the University College collection. The section illustrated in Pl. LXXXVIII, Fig. 13, and Pl. XC, Fig. 22, is not quite radial and the pith is somewhat broken and displaced, but the discoid structure is sufficiently evident. It is of rather a peculiar kind and may be described as compound, for the thick horizontal plates stretching inwards from the persistent zone subdivide towards the

middle into a number of thin discs (Pl. XC, Fig. 22; Pl. LXXXVIII, Fig. 13). Thus the rupture of the pith appears to have taken place in two stages. It is possible that this may have only happened locally.

The external, persistent zone of pith is about 0·8 mm. thick, and consists for the most part of thin-walled, fairly isodiametric cells. In the inner layers, the cells appear empty or have light-brown contents; those next the central cavity are sometimes flattened (Pl. LXXXVIII, Fig. 10). In the outer half of the zone the cells are a trifle smaller, and many of them have almost black contents. In contact with the wood a few narrow, vertically elongated, delicate-looking cells may be distinguished (Pl. LXXXVIII, Figs. 10, 11, and 14).

The diaphragms are composed of larger cells than those of the persistent zone; they appear round or somewhat hexagonal in transverse section, and when seen in longitudinal section are found to be much flattened (Fig. 13). The tissue of the thin central diaphragms has collapsed; connecting shreds of membrane show that the diaphragms have been torn apart by the growth of the stem (Fig. 13). The excellent preservation of the persistent zone is a clear proof that the partial destruction of the central tissue was a natural process occurring during life. It will be seen that the structure of the pith in *M. poroxyloides* agrees very closely with that of *M. Sutcliffii*, described by Mr. Maslen (Maslen, '11, p. 391).

The Leaf-traces.

In the zone of wood, as shown in a complete section, Pl. LXXXVIII, Fig. 8, three pairs of bundles are seen passing in, and seven more leaf-traces can be recognized at the margin of the pith, either in course of fusion or already fused. In all these strands the centripetal xylem is well developed.

As the twin xylem-strands come in through the secondary wood they converge (Pl. LXXXVIII, Fig. 9), and almost immediately on reaching the border of the pith they prepare to fuse. At this level the two centripetal xylem groups open out towards each other (see the right-hand bundle in Fig. 9), the xylem-parenchyma of the two strands becoming continuous across the medullary ray between them. At a slightly lower level the two centripetal arcs of xylem unite, so that the joint strand now has a single primary xylem-mass. The photograph in Pl. LXXXVIII, Fig. 10, shows a double strand in the act of fusion; the two centripetal groups of xylem have just become continuous. The drawing (Pl. XC, Fig. 23) shows a similar strand lower down in its course, where union is complete. That this is the actual course of the changes, as traced from above downwards, is shown on comparing the same strands in successive sections. Other strands around the pith have reduced remains of centripetal xylem, or the smallest elements are quite on the inner edge, showing that the structure has become endarch.

As regards the outward course of the leaf-traces, there is no essential difference from *M. Sutcliffii*. The bundles, however, run very obliquely through the secondary wood, the phloem zone, and the inner cortex; they are seldom seen well in transverse sections of these regions. We know, however, that the original pair divided up into eight, for all the eight bundles of a trace are seen in the section shown in Pl. XC, Fig. 24, where they are entering a leaf-base. Some sections show the strands passing almost horizontally through the wood, and subdividing as they enter the cortex.

The structure of the primary strand is essentially the same as in *M. Sutcliffii* and other species. The centripetal xylem is perhaps rather specially well developed; here also the protoxylem, where it can be clearly seen, is in contact with the centripetal part of the xylem, abutting on the internal parenchyma of the strand (Pl. XC, Fig. 23). Longitudinal sections show that the centripetal wood is composed, apart from the protoxylem, of close-wound spiral elements. The somewhat oblique tangential section from which the photograph (Pl. LXXXVIII, Figs. 11 and 12) is taken shows a pair of bundles approaching the pith. In the right-hand bundle the plane of section passes obliquely through the island of parenchyma and protoxylem (Fig. 12, *px.*).

No actual sheath is developed round the xylem-strands as they reach the pith. There is, however, a very near approach to this structure, for, where the double strand is entering through the wood and getting near the pith, the adjacent cells on the inner side have divided tangentially, and some of them show tracheal markings, just as in *M. Lomaxii* (Fig. 9, *sh*). The differences between the two species as regards the bundle-sheath is thus only one of degree.

The Wood.

The inner part of the centrifugal wood is composed of spiral, reticulate, or scalariform elements. The reticulate markings are often evidently formed by crossed spiral bands, such as are shown at one or two places in Mr. Maslen's figure from a leaf-trace bundle of *M. Sutcliffii* (Maslen, '11, Pl. XXXV, Fig. 14). The reticulate condition often forms the transition to the regular pitted sculpturing of the main mass of secondary tracheides. The zone of spiral and transitional elements is of considerable width, twelve to fourteen layers in the leaf-trace, and about six layers even where the wood appears to be purely secondary. This seems to be a specific difference from *M. Lomaxii*.

The typical, pitted, secondary tracheides have only two rows of pits on the radial wall, and sometimes only a single row (Pl. LXXXVIII, Figs. 14 and 16). Where a medullary ray is crossed, the pits are more numerous, narrower, and markedly oblique. The tracheides are about 20 to 40 μ in

diameter, most of them over 30 μ. The rays are almost invariably uniseriate, ranging in height from one to about ten cells; the diameter of a ray is commonly from 20 to 25 μ, the cells being about 36 μ in height. At the end towards the pith the rays become broader, and radial divisions of their cells are frequent. The wood of *M. poroxyloides* thus differs from that of *M. Lomaxii* in the somewhat smaller size of the tracheides, with a corresponding diminution in the number of rows of pits, and, so far as observed, in the absence of very high medullary rays. There is pretty close agreement with the wood of *M. Sutcliffii*, as described by Mr. Maslen. The greater development of the inner spiral and scalariform zone of tracheides in the secondary wood is characteristic of *M. poroxyloides*.

The Phloem and Pericycle.

The phloem in the type specimen forms a zone 0·8 mm. to 1 mm. in breadth (Pl. LXXXVIII, Fig. 15). Nearly the whole thickness is made up of radially seriated, secondary elements. The phloem is very fairly preserved, and is closely similar in structure to that of *M. Sutcliffii*, of which Mr. Maslen has given a full description (Maslen, '11, p. 400). The elongated elements with dense contents are very conspicuous; in some the contents are black, in others light brown, but the two appear to pass over into one another, and I cannot find any sharp distinction between the two forms. It may be mentioned that cells with dark contents also occur in the phloem rays, which are often dilated towards the exterior. It is probable, as suggested by Mr. Maslen in the case of his species, that the long elements with no obvious contents are the sieve-tubes. I postpone, however, any detailed account of the phloem to a later paper, as I have recently received from Mr. Lomax a series of sections from a remarkably well preserved stem, closely similar to *M. poroxyloides* as regards the phloem, though differing in some other details. Beyond the phloem comes another fairly broad zone, which may best be regarded as the pericycle. This contains a number of large sacs with dark contents (Fig. 15, *s.s.*). In longitudinal section the sacs often appear to be divided up into cells, but this may only be due to a breaking up of the contents.

The Cortex.

On the outer border of the pericycle is a layer of internal periderm, very unequally developed, and in some places reaching a thickness of about a dozen cells. Many of the periderm cells are flattened and rather thick-walled, suggesting a true cork. There is, however, no sign of any general desiccation of the outer tissues, so it is evident that they had not yet been completely cut off by cork from communication with the water supply of the stem. At many places the periderm is double, an outer layer or arc having formed in the adjacent cortical tissue. On general grounds one would

expect the outer periderm to have been formed before the inner; the latter, however, is sometimes the more developed of the two, and as the whole cortex appears to have been living up to the time when the plant itself met its fate, we cannot be certain as to the order in which the peridermal layers appeared.

The inner cortex, like the pericycle, contains large sacs with dark contents, though they are not so numerous here. Except where a leaf-trace is passing out, the inner cortex is little developed; we almost immediately reach the Dictyoxylon zone, which attains a considerable thickness—quite 2 mm. in places. The radial bands of fibres do not, however, extend quite to the outside of the stem; the fibres are little thickened, and the differentiation of the mechanical tissues, as seen in transverse section, not very marked.

The outer surface of the stem is incompletely preserved, and hence the arrangement of the leaf-bases is obscured. At first sight they appear to be scattered, but further examination shows that they must have been fairly close together. Thus, in one section (slide 2353) two leaf-traces are seen in the outer cortex; both consist of a number of bundles—probably eight in each case—though all are not preserved. The adjacent bundles of the two traces are only about 4 mm. apart.[1] The corresponding leaf-bases are not complete, but there can have been no great extent of stem-surface between them. The leaf-bases, however, were probably somewhat less closely set than in *M. Sutcliffii*.

As in other species, where a leaf-trace passes out through the cortex into the leaf-base it is surrounded by a large mass of parenchyma, which encroaches upon the Dictyoxylon zone. This is consequently considerably thinner opposite the outgoing leaf-traces than elsewhere.

It may be mentioned that the 'Cordaitean' leaves associated in slide 2397 with a stem, probably referable to *M. poroxyloides*, are of the type recently described by Prof. Margaret Benson under the name *Cordaites Felicis* (Benson, '12). This is shown by the well-developed sheath, the presence of complete longitudinal fibrous partitions between the bundles and of thickened masses of hypoderm between the bundles and the partitions, the partial 'inner sheath', and the arrangement of the centripetal and centrifugal xylem, which is often identical with that shown in Prof. Benson's text-figure (l. c., p. 204). Some of the leaves associated with the stem in question are, however, thicker (i.e. cut, no doubt, nearer the base) than any of Prof. Benson's specimens; one fragment reaches a thickness of 1·8 mm. In these thickest parts some of the partitions are missing; their absence may be correlated with a recent division of the bundles.

[1] The distance between the centre lines of the two traces would be about 8 mm.

It thus appears very probable that *Cordaites Felicis* was the leaf of a *Mesoxylon* of the *poroxyloides* type. Direct evidence from continuity may perhaps be hoped for. At any rate this probability may serve to call closer attention to the British specimens of 'Cordaitean' leaves, which had been much neglected until the appearance of Prof. Benson's paper. Many excellent specimens are now available.

Diagnosis.

The following is an amended diagnosis of the species :

Mesoxylon poroxyloides, Scott and Maslen, 1910.

Leaf-bases moderately crowded, not quite covering the surface of the stem.

Pith not very large, discoid, with a persistent outer zone.

Diaphragms sometimes splitting into finer plates towards the middle of the pith.

Twin-bundles of the leaf-trace converging and uniting soon after reaching the pith, subdividing in the cortex to form eight bundles.

Centripetal xylem very distinct, persisting below the fusion of the twin strands.

Xylem-strands without a sheath, or with only a rudimentary one, limited to the region where they first reach the pith.

Tracheides of the inner part of the intermediate secondary wood, as well as those of the leaf-traces, spiral, reticulate, or scalariform.

Bordered pits in one or two rows.

Medullary rays (with rare exceptions) uniseriate, 1–10 cells in height.

Dictyoxylon zone of cortex very broad, fibres not much thickened.

Seam-nodules; Shore, Littleborough. Lower Coal Measures.

Comparative Considerations.

Important forms of *Mesoxylon* still remain to be described, but the three species which have now been dealt with by Mr. Maslen and myself are sufficient to make the position of the genus clear. The existing classical accounts of the structure of the stem in *Cordaites* (Renault, '79 and '96) are not so full as we could wish, and a reinvestigation is desirable; so far as the stem is concerned we are now better acquainted, in some respects, with the anatomy of *Mesoxylon* than with that of the type-genus of the family. On the available data, however, it is evident that the affinity between *Mesoxylon* and *Cordaites* is a close one, and I agree with Mr. Maslen that our genus may best be included in the family Cordaiteae (Maslen, '11, p. 411). This is, of course, a departure from the position which I took up in the second edition of my 'Studies in Fossil Botany' (Scott, '09, p. 511), when I provisionally included what is now *Mesoxylon Sutcliffii* in the genus *Poroxylon*, though at the same time I referred to other forms, since added

to *Mesoxylon*, under Cordaiteae (l. c., p. 526). The centripetal wood of the stem, no doubt, died out gradually; in *Mesoxylon* it is still sufficiently well developed to justify generic separation from *Cordaites*, but not, I think, a position in a distinct family. The point, however, is of little importance; what really matters is, that the two families Cordaiteae and Poroxylae are now closely linked together.

The points of resemblance and difference between *Mesoxylon*, *Cordaites*, and *Poroxylon* have been well summarized by Mr. Maslen (l. c., p. 410). They hold good essentially for all the species investigated. It will be noticed that no definite distinction between *Mesoxylon* and *Cordaites* is given, beyond the presence of centripetal xylem in the stele of the former. In other respects there appears to be agreement, but we do not know enough about the exact course of the leaf-traces or the detailed structure of the phloem in *Cordaites*, to be certain how close the agreement really was. At any rate, we have the large, discoid pith, the dense wood with narrow rays,[1] and the histology of the xylem-elements, especially the great development of spiral and scalariform tracheides in the leaf-trace region, as definite characters common to the two genera. The species of *Mesoxylon* would have been left in *Cordaites* if it were not for the presence of centripetal wood in the stele. I feel no doubt that most of the British specimens of 'Cordaitean' leaves really belong to *Mesoxylon*, which is a much commoner type of stem in the Coal-Measure petrifactions than that of *Cordaites* itself. If this belief is confirmed, we shall have the close agreement in foliar characters as another proof of the near affinity of the two genera.

I thus regard *Mesoxylon* as the last term in the series of forms leading up from the Seed-Ferns to the typical *Cordaites* described by Grand'Eury and Renault.

Some additions have lately been made to the Cordaitales and their allies by Dr. Zalessky, who has founded no less than five new genera, partly for new forms, partly for plants already described under other names (Zalessky, '09, '11[1], and '11[2]).

The new forms are: *Callixylon Trifilievi*, Zal. (Zalessky, '09 and '11[1]), and *Caenoxylon Scotti*, Zal. (Zalessky, '11[2]). The other new genera are: *Eristophyton* (Zalessky, 11[1]), based on *Calamopitys Beinertiana* (Göpp.), and *C. fascicularis*, Scott; *Mesopitys* (Zalessky, '11[1]), based on *Dadoxylon Tchihatcheffi* (Göpp.); and *Parapitys* (Zalessky, '11[1]), based on *Dadoxylon Spenceri*, Scott.

Callixylon Trifilievi (Zalessky, '09) from the Upper Devonian of the Donetz basin in Russia is a very interesting fossil, evidently allied to the Lower Carboniferous genus *Pitys* (Scott, '02). Numerous (26) small, mesarch

[1] As a matter of fact somewhat wider rays occur in *Cordaites* than have yet been observed in *Mesoxylon* (Renault, '96, p. 334).

strands of primary xylem surround the pith, most of them in contact with the secondary wood, though some are separated from it by 1 to 3 rows of cells. These strands anastomose freely. At a distance from the pith the rays are usually uniseriate. The pith is horizontally ruptured (imperfectly discoid), and the pith-cells surrounding a primary xylem-strand are elongated radially with respect to it. Tangential pits occur in the secondary wood, as in *Pitys antiqua*. The agreement with *Pitys* seems to be decidedly nearer than with the other genera (*Parapitys* and *Eristophyton*) with which the author compares it. He separates the plant generically on the ground of its narrow medullary rays, the wedge-like segments of secondary wood, and the arrangement of the pits, on the radial walls of the secondary tracheides, in groups (Zalessky, '11[1], p. 28). At any rate this new form, of which a fuller description is promised by the discoverer, finds its place in the family Pityeae, and has no near affinity with *Mesoxylon*.

The fragment named *Caenoxylon Scotti* by Dr. Zalessky is of uncertain origin; it is of Upper Palaeozoic age, and possibly comes from the Permian of the Ural (Zalessky, '11[2]). The pith is 2 cm. in diameter, and the zone of wood, so far as preserved, about 13 mm. thick. The presence of distinct annual rings in the wood is an interesting feature, indicating a relatively late age. The pith is not stated to be discoid, but is described as consisting of distinct outer and inner regions, with a meristematic layer between them.

The primary xylem is divided into a number of bundles of various sizes and shapes, separated by medullary tissue with occasional signs of meristematic division. Some of the strands may be a considerable distance apart from the main mass of primary xylem, of which they are ramifications; in all, the structure is endarch. The leaf-traces are double, and the medullary rays uniseriate. The author regards *Caenoxylon* as undoubtedly allied to *Eristophyton*, *Pitys*, *Parapitys*, and *Mesopitys*, and more remotely to *Cordaites*, *Poroxylon*, and *Mesoxylon*. He suggests, on the ground of the arrangement of the primary xylem and the character of the double leaf-trace, that the fossil may possibly be on the line of descent of *Ginkgo*.

At present we have only a preliminary communication from Dr. Zalessky on this form. Except that I cannot recognize any but the most remote affinity to his *Eristophyton*, I have nothing to add to the author's remarks.

In connexion with *Caenoxylon* we may shortly refer to Dr. Zalessky's new genus *Mesopitys*, founded on the *Araucarites Tchihatcheffi* of Göppert. This, again, is a Permian plant, and was the first stem of that age in which the presence of annual rings in the wood was observed. The pith is small (3 mm. in diameter in one case), the stems (without cortex) ranging from 5 × 3 to 13 × 8 cm. No mesarch xylem-strands were observed; the primary wood, as in *Caenoxylon*, is all centrifugal, forming groups of irregularly

arranged tracheides with the smallest elements always on the inner side. The whole of the primary wood is composed of spiral or rayed tracheides which abut immediately on the pitted elements of the secondary wood. Unlike *Caenoxylon*, *Mesopitys Tchihatcheffi* has a single bundle constituting the leaf-trace, where it passes out through the wood. The medullary rays are uniseriate. The genus *Mesopitys* is established for stems with secondary wood of the *Dadoxylon* type, characterized by the arrangement of the feebly developed primary wood in bundles of endarch or even mesarch structure, and by the single bundles traversing the secondary wood (Zalessky, '11[1], p. 28). The author regards his new genus as forming the final term of the group of stems of the *Dadoxylon* type described by me in 1902, and considers it to be closely allied to his *Eristophyton Beinertianum* (*Calamopitys Beinertiana* (Scott)).

It is interesting to note that Dr. Zalessky is prepared to include stems with mesarch as well as those with purely endarch primary xylem in the same genus. I have no objection to this in principle, for the one structure, no doubt, passed over gradually into the other, nor do I dispute a certain degree of affinity between my *Calamopitys Beinertiana* and *Mesopitys Tchihatcheffi*. At the same time, the presence of very highly developed mesarch strands in the former plant (though they become endarch lower down in their course) appears to me a more important difference than Dr. Zalessky recognizes. I quite agree with the author that his *Mesopitys Tchihatcheffi* requires a new genus.

Another of Dr. Zalessky's new genera is *Parapitys*, founded for the reception of *Dadoxylon Spenceri* (Scott, '02). It was inevitable that sooner or later this form should acquire generic rank. It is characterized by the double leaf-traces, the small mesarch strands of primary xylem, and the relatively small pentagonal pith, the wood being of the ordinary Cordaitean type. Of all the forms discussed by Dr. Zalessky, *Parapitys* seems to me the nearest to *Mesoxylon*, from which it only differs (so far as we know at present) in the characters of the pith. It seems to be widely separated from the species of *Calamopitys* placed by Dr. Zalessky in *Eristophyton* by the double leaf-traces and the great reduction of the primary mesarch strands.

Dr. Zalessky devotes a good deal of space to an argument against my inclusion of *Calamopitys fascicularis* and *C. Beinertiana* in the genus *Calamopitys* of Unger, founding the new genus *Eristophyton* for their reception (Zalessky, '11[1]). I do not propose to enter fully into the question in this paper, because, from my point of view, these plants have very little to do with *Mesoxylon*. It is possible that the various, not very important characters, on which Dr. Zalessky lays stress, may in the aggregate justify generic separation. The author, however, has not quite realized what the characters are which I regard as essential to *Calamopitys*. As I stated (Scott, '02, p. 360): 'The *Calamopitys* group is characterized by the

relatively large dimensions and distinct mesarch structure of those primary xylem-strands which are about to pass out from the pith, while the same strands, lower down in their course, are reduced in size, and in some cases assume endarch structure, owing to the dying out of the centripetal xylem. A single strand passed out from the pith to form the leaf-trace.'

The really characteristic point in *Calamopitys* is the presence of the quite peculiar large, round mesarch xylem-strands, which are unlike those of any other plant I have seen. Their structure in *C. Saturni* and *C. fascicularis* (to take an example from each group) is identical, as I hope to show more in detail on another occasion. The only differential character of any weight between *Calamopitys* and the new *Eristophyton* is the width of the medullary rays, which are generally wide in the former and narrow in the latter. This, however, appears to be inconstant, for, in a section of *C. annularis*, very kindly lent me, among many other preparations, by Count Solms-Laubach, the rays are only one or at most two cells in width, thus differing from the pluriseriate rays usual in *C. Saturni* and even in other specimens of *C. annularis*. There is no reasonable doubt that the species of *Calamopitys* described by Count Solms-Laubach were Pteridosperms, as indicated by their *Kalymma* petioles. The important question at issue between Dr. Zalessky and myself is whether the species *C. fascicularis* and *C. Beinertiana* were likewise Pteridosperms, or belonged to a higher group. This goes much beyond the mere question of generic separation, which is of secondary importance.

At present I must adhere to my view that the agreement in the primary characters of the wood, between the species placed by Dr. Zalessky in *Eristophyton* and the type species of *Calamopitys*, is so close as to prove a very near affinity. The question will not, however, be finally decided until the cortex and leaf-bases of the former species are known.

One argument used by Dr. Zalessky must be shortly dealt with, as it appears to me somewhat misleading (Zalessky, '11[1], p. 27). He says that, if my view is just, we must suppose that the species *fascicularis* and *Beinertiana* had fern-like foliage. He regards his *Callixylon Trifilievi* as certainly allied to these species. He finds reason to believe that the latter plant may have had a stem reaching about a metre in diameter, and thinks it improbable that such trunks could have borne the foliage of a Fern.

Now, to begin with, *Callixylon Trifilievi* shows no close affinity to *Calamopitys fascicularis* and *Beinertiana*. It is practically a *Pitys*, and no one has attributed filicoid foliage to *Pitys*, which was more probably of Cordaitean habit. Secondly, there is no reason to doubt that in Palaeozoic days stems of great girth bore fern-like foliage. A specimen of *Medullosa stellata* discovered by Weber (Weber und Sterzel, '96, p. 25), though decorticated, measured nearly $\frac{1}{2}$ a metre (48 × 45 cm.) in diameter. It is well known that the foliage of *Medullosa* was fern-like (e. g. *Neuropteris*,

Alethopteris). Whether *Calamopitys fascicularis* and *Beinertiana* attained a very large diameter or not we cannot say; if they did so, the fact would certainly be no argument against their Pteridospermous affinities.

Summary.

The characters of *Mesoxylon Lomaxii* and *M. poroxyloides* have already been summarized in their specific diagnoses (pp. 1016 and 1023). The genus comes very near *Cordaites*, as shown by the characters of the pith and wood, and further indicated by those of the associated leaves. The affinity with *Poroxylon* is somewhat more remote, and the genus is best placed in the family Cordaiteae; it is at present definitely distinguished from *Cordaites* only by the presence of centripetal wood in the stele of the stem. *Mesoxylon* thus forms the last link in the chain of fossil types connecting the Pteridosperms with the typical *Cordaites* of the Upper Palaeozoic.

Of the new genera recently established by Dr. Zalessky, *Callixylon* is very near *Pitys* and should be placed in the same family. *Caenoxylon* and *Mesopitys* are advanced forms, and had reached an anatomical level corresponding to that of *Cordaites* itself, but on somewhat different lines.

Parapitys is best regarded as a near ally of *Mesoxylon*. *Eristophyton*, even if generically separable from *Calamopitys*, is closely allied to it, and both may provisionally be regarded as probably belonging to the Pteridosperms rather than to the Cordaitales. It is possible, however, that further discoveries may show that the Calamopityeae were an important transitional group.

The results already attained by Dr. Zalessky and others are very satisfactory, as demonstrating a considerable variety among the stems of Palaeozoic age, referable or allied to the Cordaitales.

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DESCRIPTION OF PLATES LXXXVII–XC.

Illustrating Dr. Scott's paper on *Mesoxylon*.

The photographic figures require to be examined with a lens.

PLATE LXXXVII.

Mesoxylon Lomaxii.

Photographs by Mr. W. Tams.

Fig. 1. General transverse section of the stem, showing the patchy preservation characteristic of roof-nodule specimens. × nearly 2. Slide 2328.

Fig. 2. Half of another transverse section, better preserved. *d*, Dictyoxylon zone; *pd*, periderm. × about 3. Slide 2325.

Fig. 3. Tangential section from inner part of wood, showing the twin-bundles of a leaf-trace (*l.t.*) and their junction below. × 10. Slide 2380.

Fig. 4. Somewhat oblique section, showing the converging twin-bundles of a leaf-trace (*l.t.*). *sh*, bundle-sheath; *p.*, pith. × about 30. Slide 2325.

Fig. 5. Leaf-trace in the act of fusion. *x*, centripetal xylem; *sh*, bundle-sheath; *p*, pith. × about 40. Slide 2328.

Fig. 6. Double leaf-trace in the phloem: bundles slightly displaced. *x*, centripetal xylem of a bundle; x^2, secondary wood of stele; *pd*, periderm; the dark bodies are the 'secretory sacs'. × about 45. Slide 2325.

Fig. 7. Quadruple leaf-trace in the inner cortex. *x*, centripetal xylem of a bundle. × about 45. Slide 2325.

PLATE LXXXVIII.

Mesoxylon poroxyloides.

Photographs by Mr. W. Tams.

Fig. 8. General transverse section. *d.s.*, displaced segment of stem, which has slipped from a different level; *d*, Dictyoxylon cortex. × 3·2. Slide 2352.

Fig. 9. Twin-bundles of a leaf-trace converging on approaching pith. *x*, centripetal xylem of bundles; *sh*, imperfectly developed sheath; *p*, outer zone of pith, here alone preserved. × about 40. Slide 2352.

Fig. 10. Double leaf-trace, just fused, at margin of pith. *x*, centripetal xylem; *p'*, inner, *p''*, outer zone of pith. × about 40. Slide 2352.

Fig. 11. Approximately tangential section through the twin-bundles of a leaf-trace reaching the pith. The plane of section passes gradually inwards towards the bottom. *l.t.*, leaf-trace; *p*, outer zone of pith. × about 30. Slide 2358.

Fig. 12. Lower end of right-hand bundle from Fig. 11 in slightly oblique tangential section. x^2, centrifugal xylem of bundle; *x.p.*, island of xylem-parenchyma; *px*, protoxylem; *x*, centripetal xylem. × 100. Slide 2358.

Fig. 13. Longitudinal section through the middle region of the pith, showing the finer diaphragms. × 32. Slide 2356. Cf. Pl. XC, Fig. 22.

Fig. 14. Radial section through peripheral pith and wood, passing in places through a primary xylem-strand. *p'*, inner, *p''*, outer layer of pith; *x*, primary xylem; between *p''* and *x* a few elongated cells can be detected; x^2, secondary wood with medullary rays. × 38. Slide 2356.

Fig. 15. Transverse section of wood, phloem, and pericycle. x^2, secondary wood; *ph*, broad zone of phloem, mostly secondary; *s.s.*, 'secretory sacs' of pericycle. × 42. Slide 2352.

Fig. 16. Tracheides of secondary wood, in radial section, showing pits. × about 160. Slide 2356.

PLATE LXXXIX.

Mesoxylon Lomaxii.

From Drawings: Fig. 17 by Mr. G. T. Gwilliam, Figs. 18–21 by Miss G. C. Harrison.

Fig. 17. General radial section of fragment of stem. *pd*, periderm or secondary cortex; *x*, wood; *p*, persistent zone of pith; *d.p.*, discoid pith, much broken. × $2\frac{1}{2}$. Slide 2383.

Fig. 18. Transverse section of a xylem-strand, after fusion, at the border of the pith. *sh*, bundle-sheath; *x*, centripetal wood, some of the elements badly preserved; *px*, probable protoxylem; x^2, centrifugal wood; *m.r.*, medullary ray. × about 150. Slide 2325.

Fig. 19. Tangential section of secondary wood. *m.r.*, medullary rays, of very varying length. × about 120. Slide 2377.

Fig. 20. Tangential section of phloem. *s.t.*, probable sieve-tubes; *m.r.*, medullary rays. × about 120. Slide 2377.

Fig. 21. Tracheide from a radial section, showing three rows of bordered pits. × about 300. Slide 2383.

PLATE XC.

Mesoxylon poroxyloides.

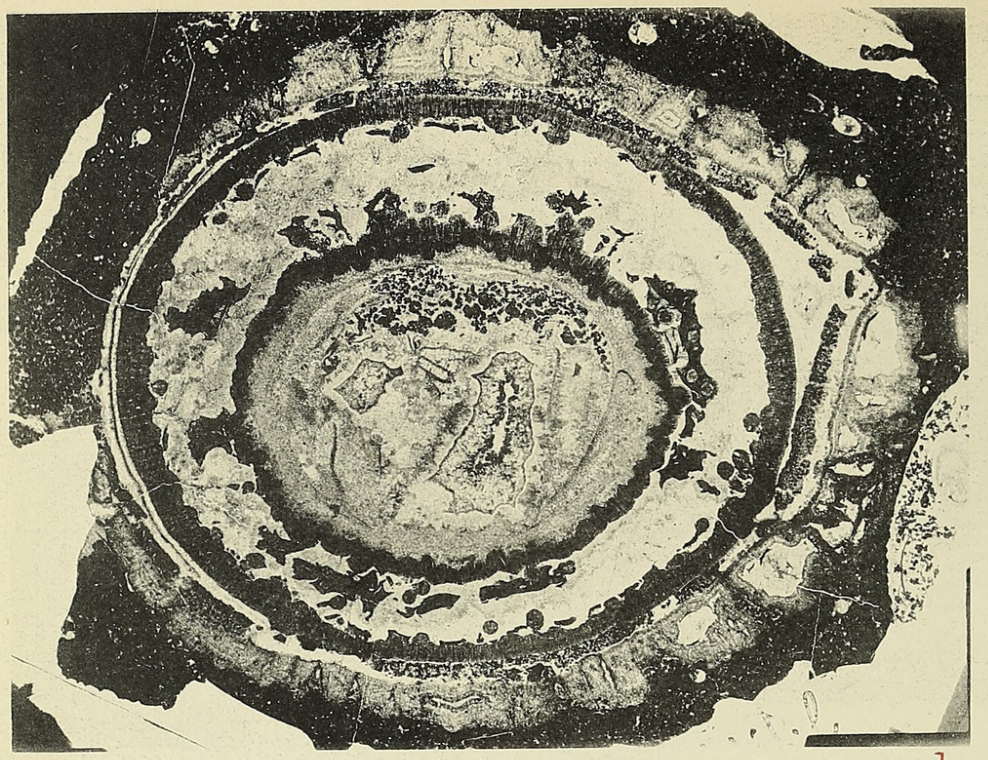
From Drawings: Fig. 22 by Mr. G. T. Gwilliam, Figs. 23 and 24 by Miss G. C. Harrison.

Fig. 22. General approximately radial section. *c*, cortex; *ph*, phloem; *x*, wood; *p*, pith, showing the persistent outer zone and the coarser and finer diaphragms of the middle discoid portion. × about 3. Slide 2356.

Fig. 23. Transverse section of a fused xylem-strand at the border of the pith. *x*, centripetal xylem; *px*, protoxylem; x^2, centrifugal xylem; *m.r.*, medullary rays. × about 200. Slide 2354.

Fig. 24. Row of eight bundles (*v.b.*) constituting a leaf-trace entering the base of a leaf. In the better-preserved bundles centripetal and centrifugal xylem can be distinguished. × 33. Slide 2352.

The slide-numbers all refer to the Scott collection.



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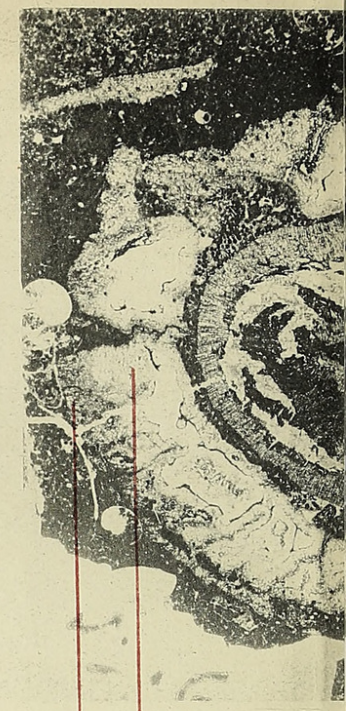

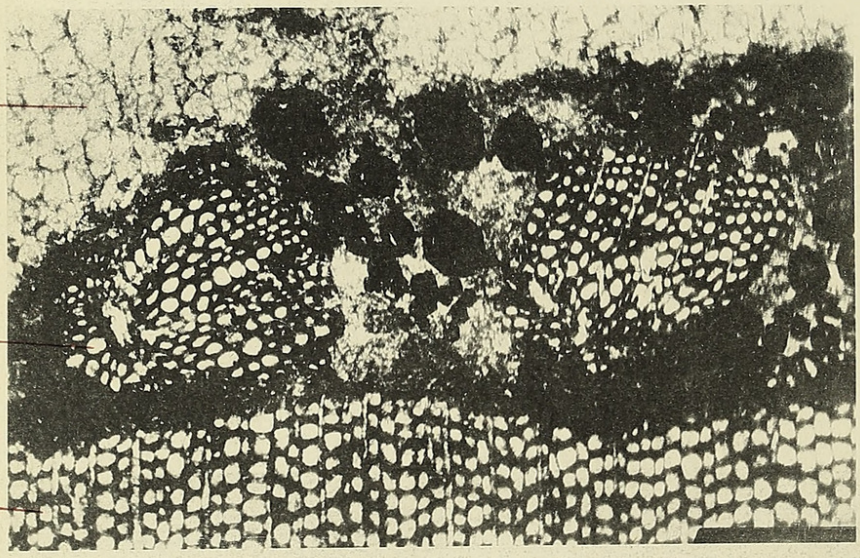

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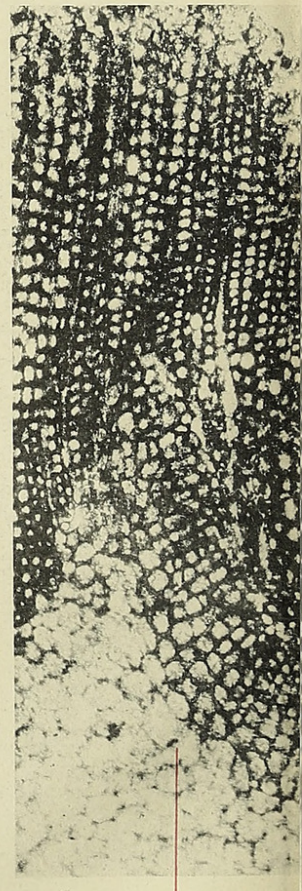

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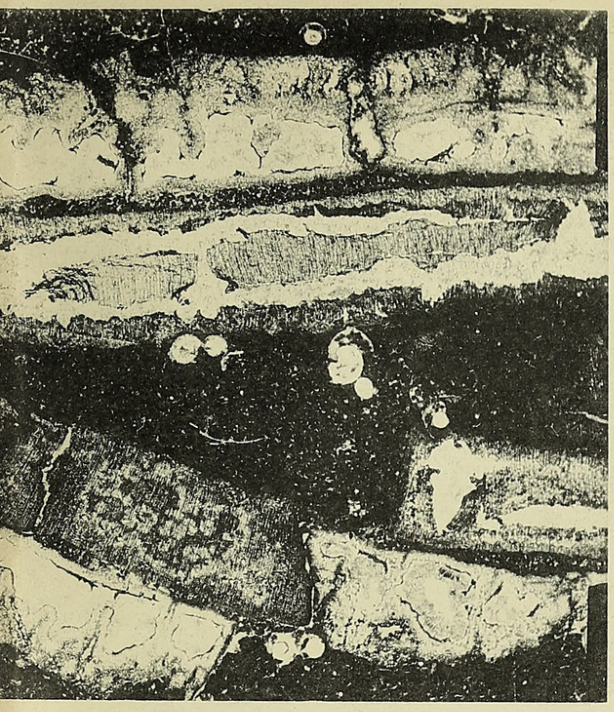
W. Tams, photo.

SCOTT —— MESOXYLON LOMAXII.



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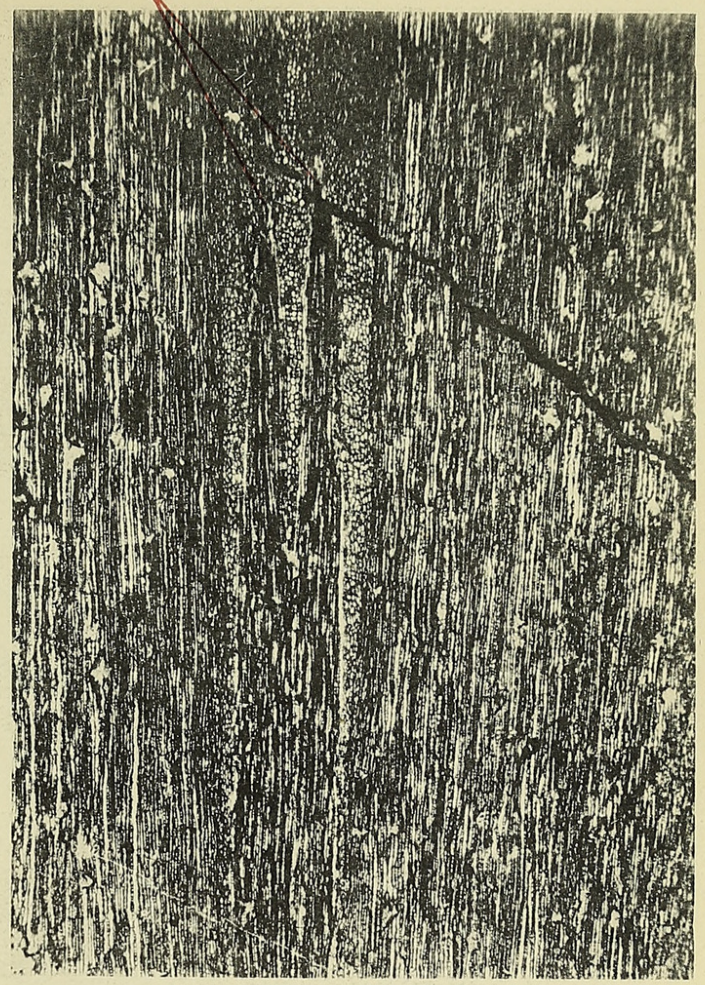

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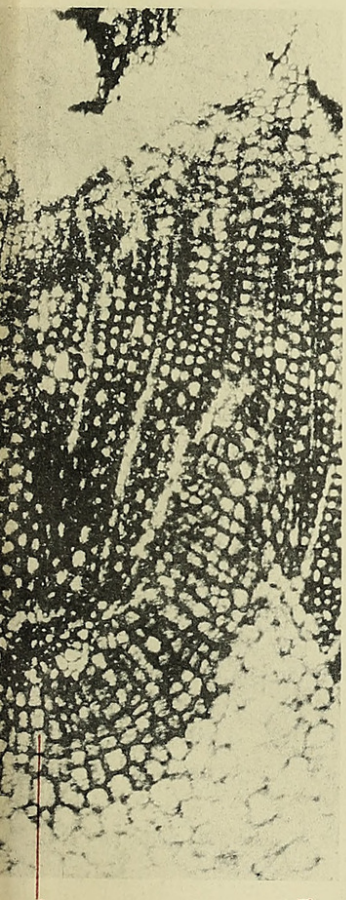

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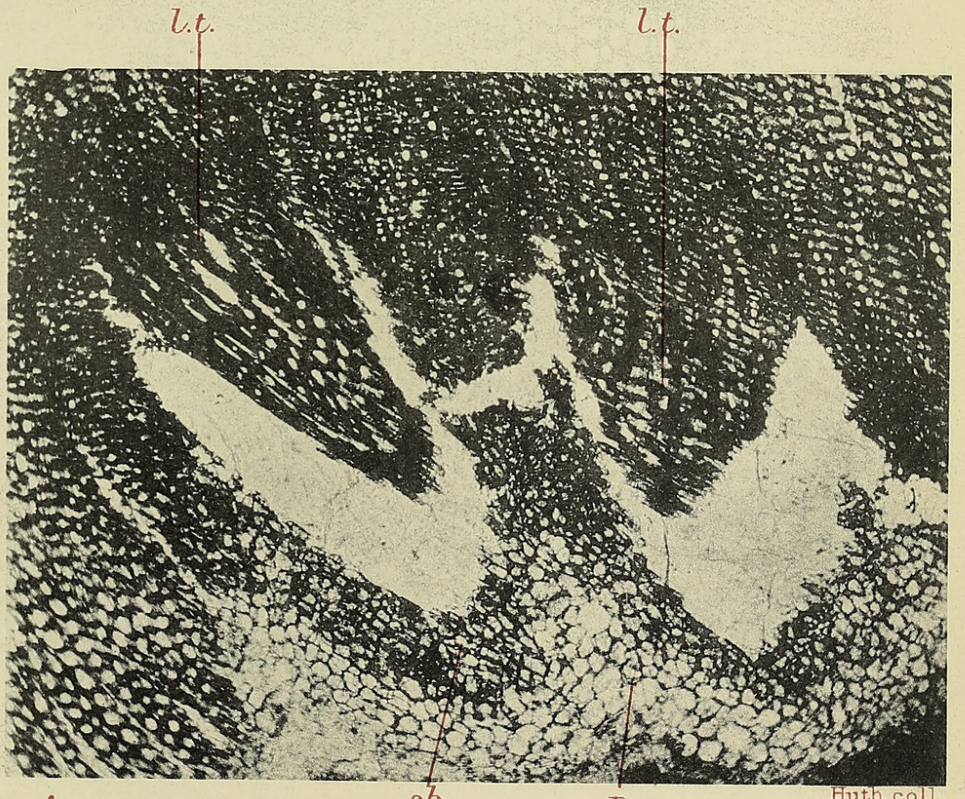

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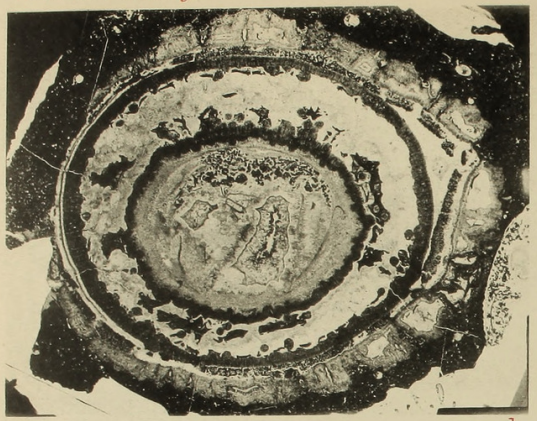

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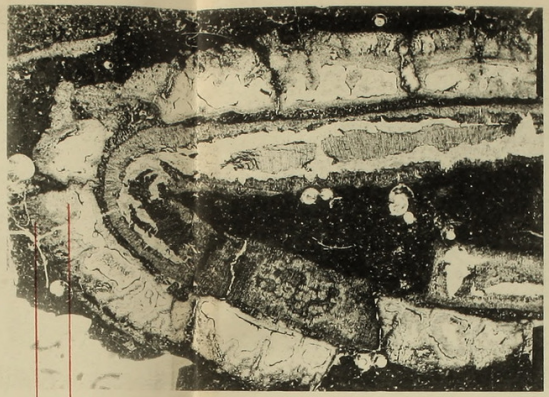

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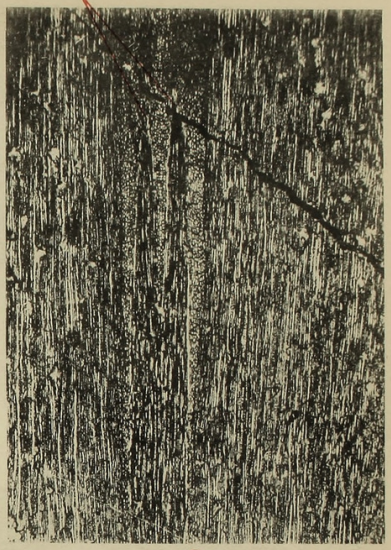

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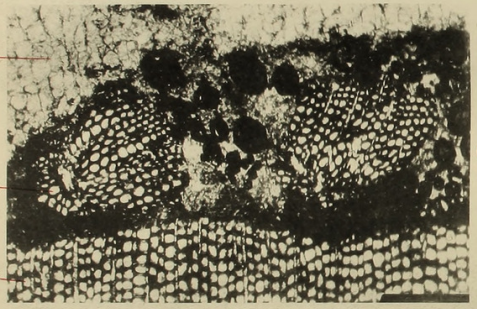

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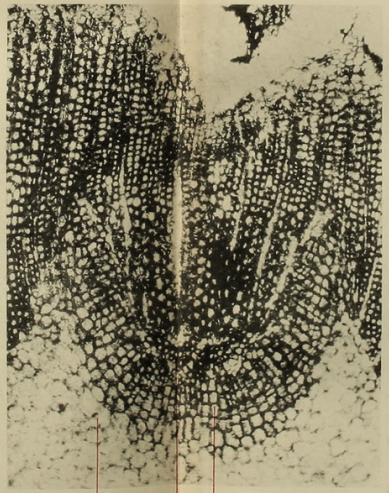

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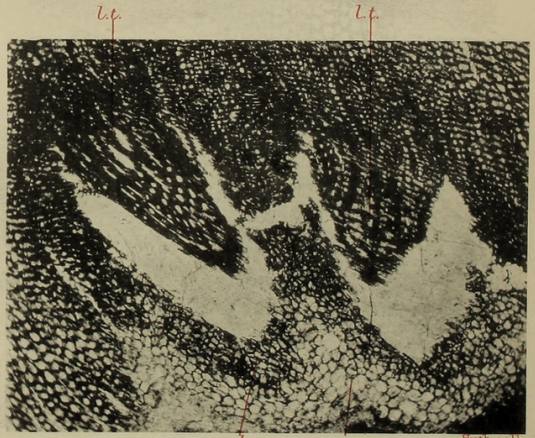
W. Tams, photo.



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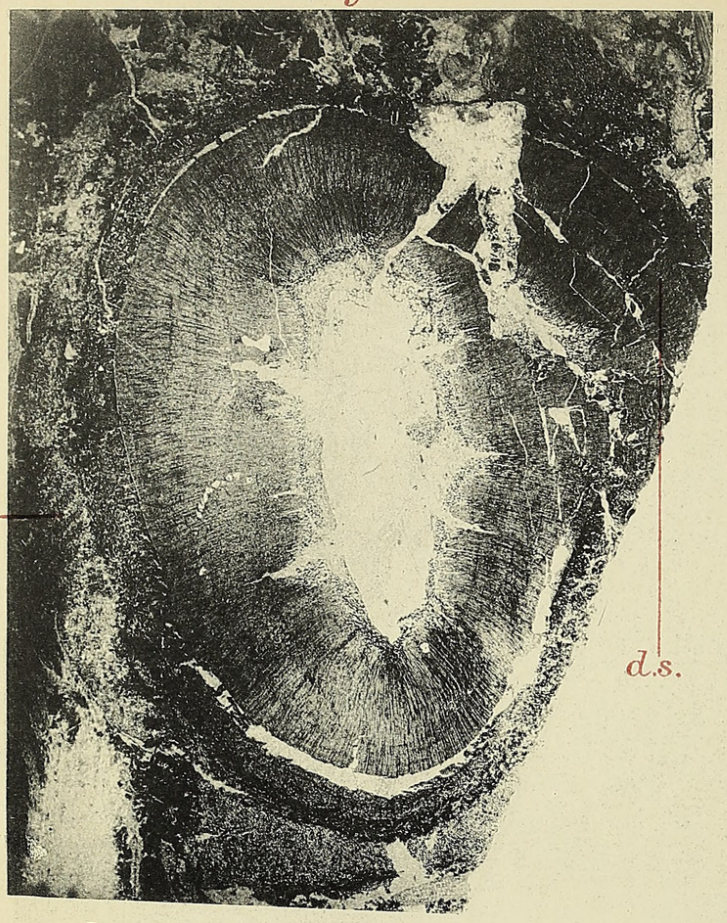
Huth, coll.

SCOTT—MESOXYLON LOMAXII.



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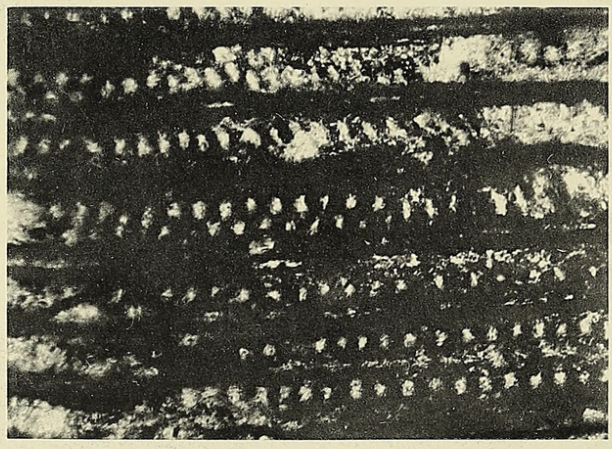

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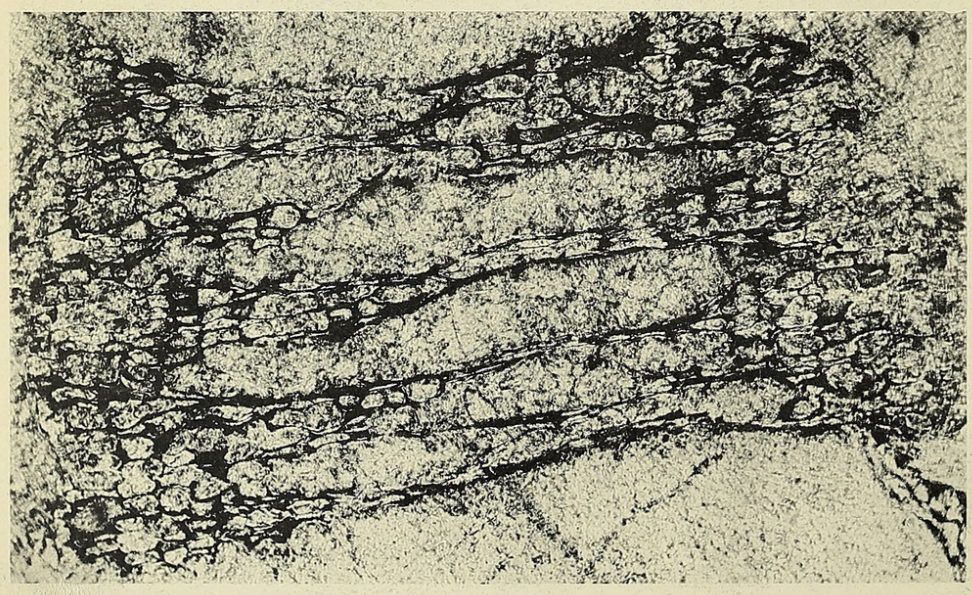

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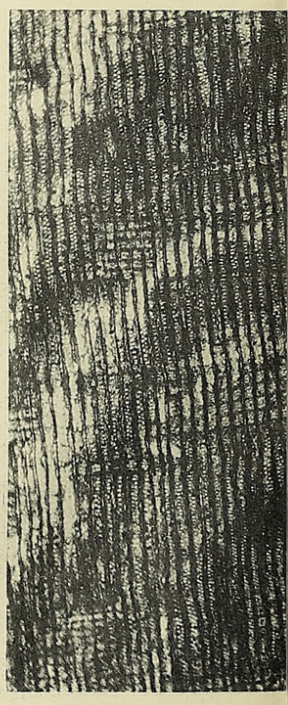
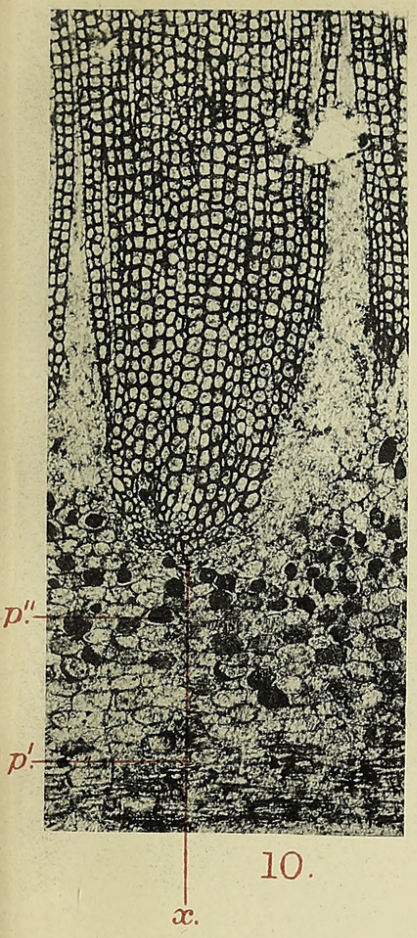


W. Tams, photo.

SCOTT—MESOXYLON POROXYLOIDES.



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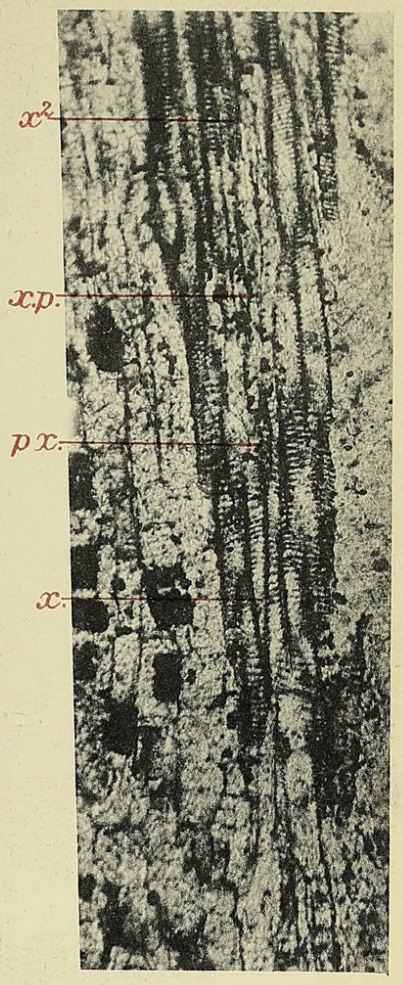

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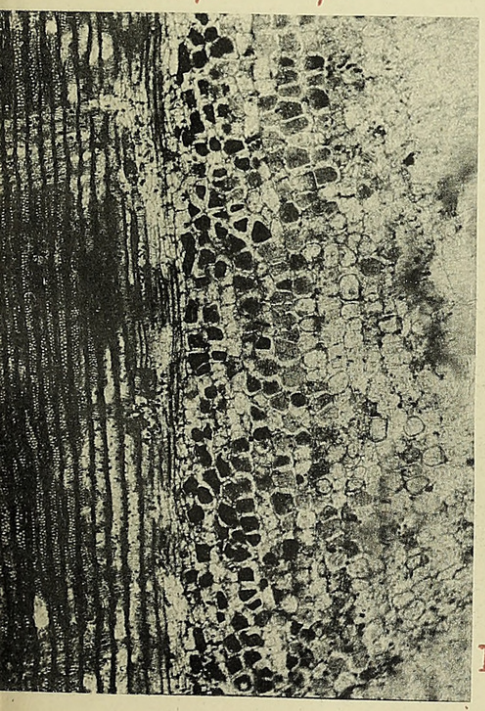

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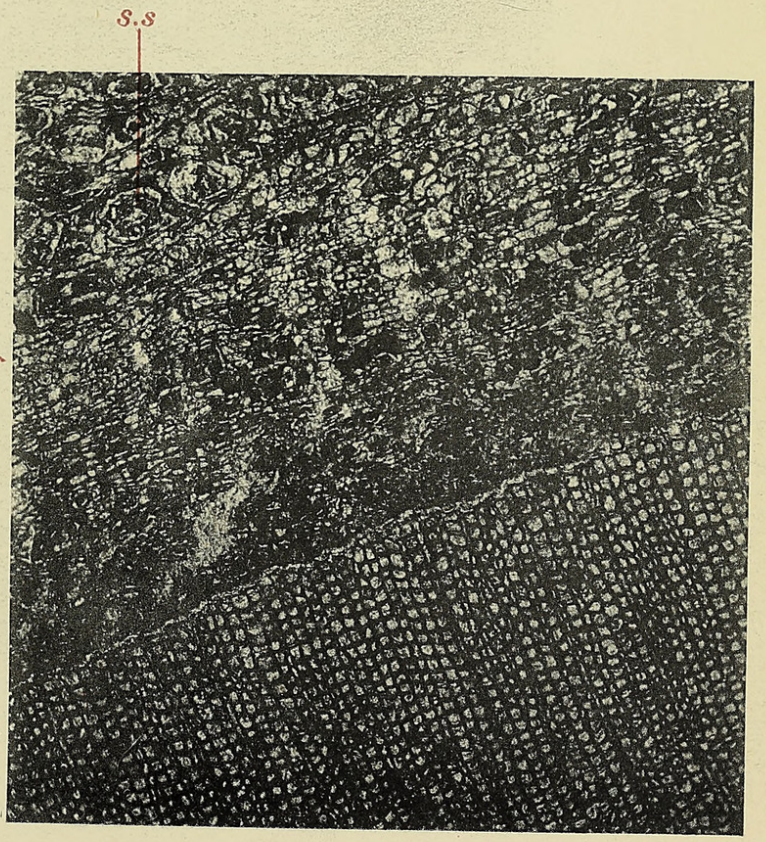

15.

Huth, coll

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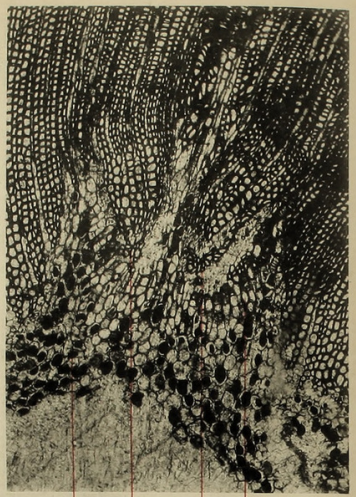

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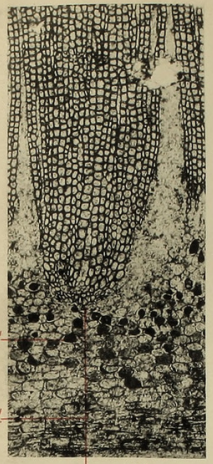

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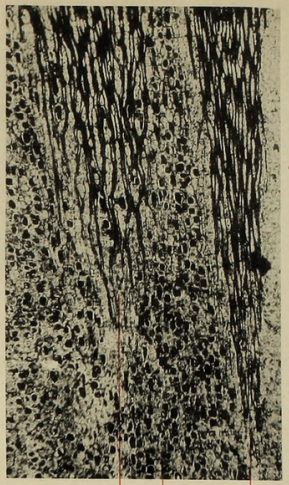

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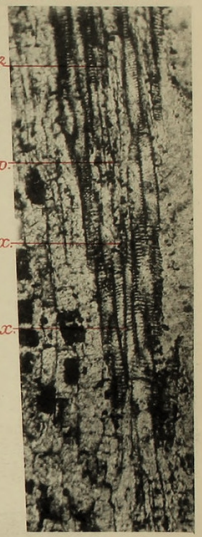

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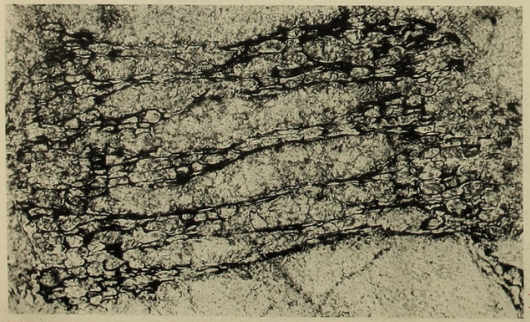

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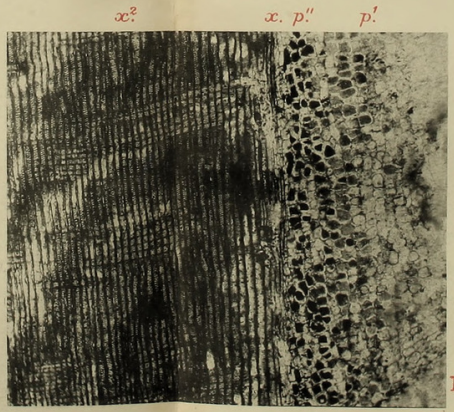

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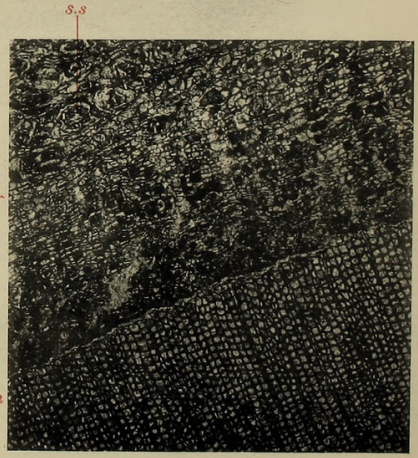
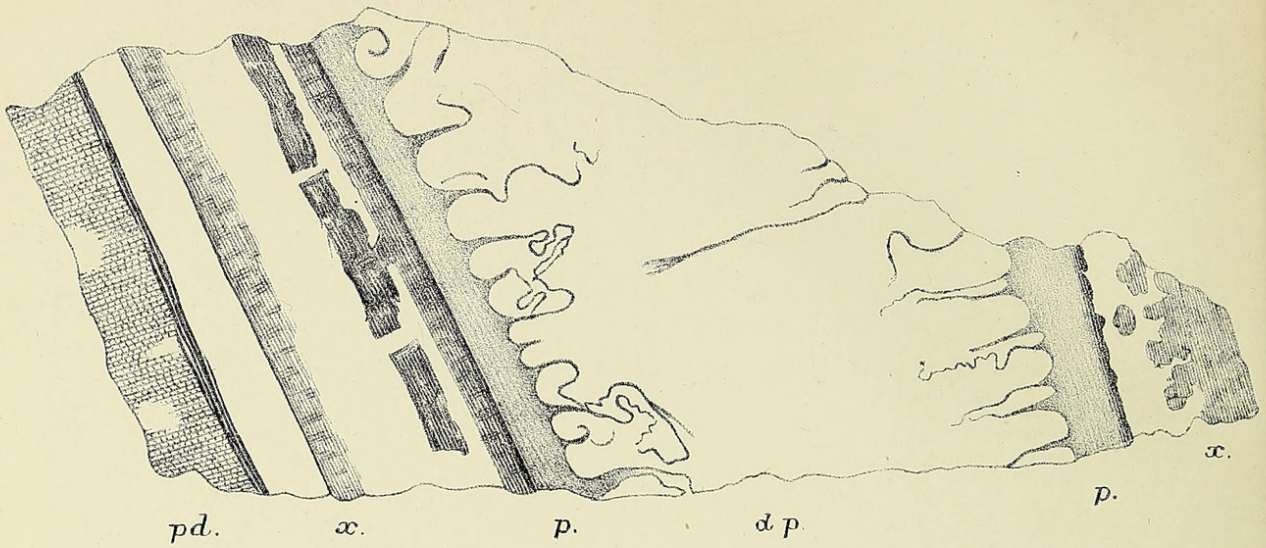


15.

Huth, coll

SCOTT—MESOXYLON POROXYLOIDES.



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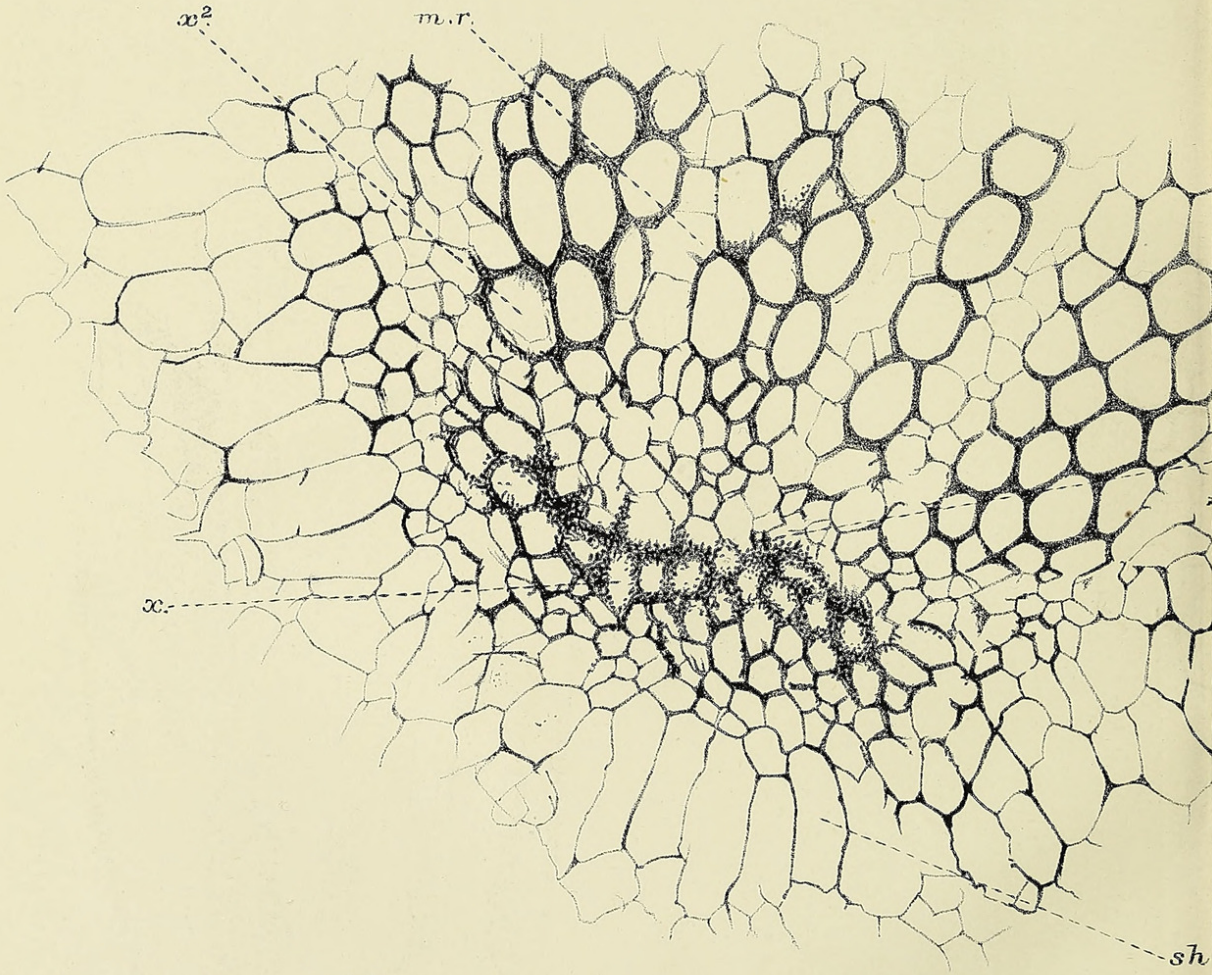
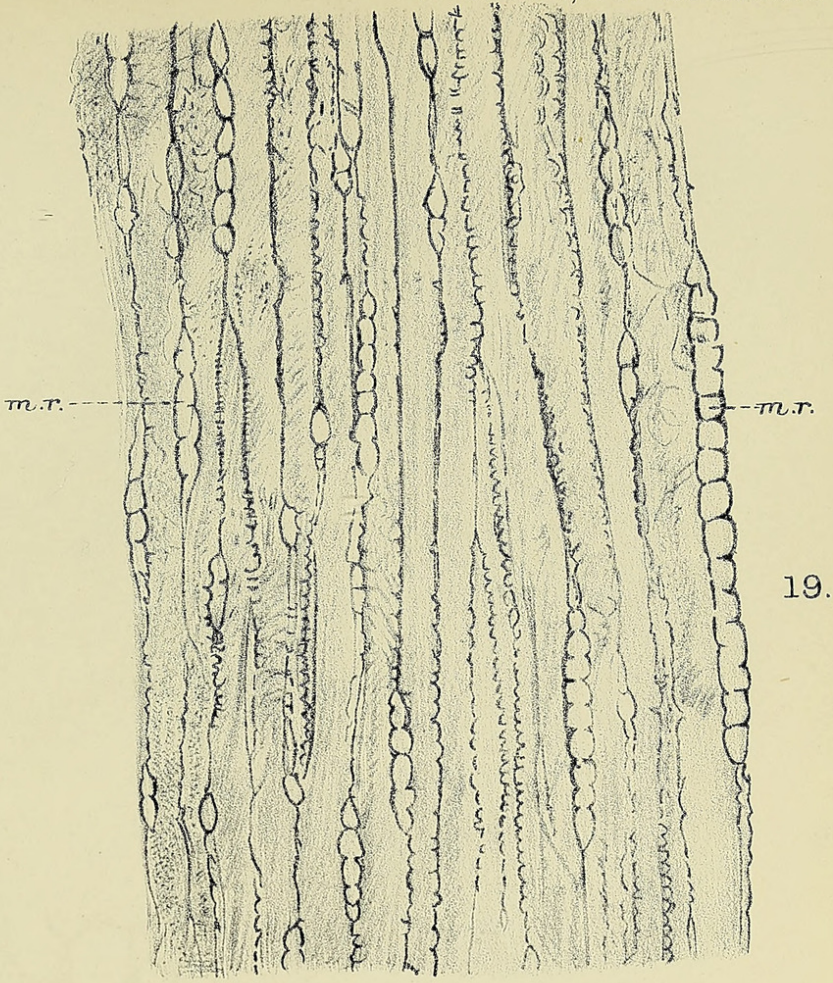


18.

G.C. Harrison & G.T. Gwilliam del.

SCOTT — MESOXYLON LOMAXII.



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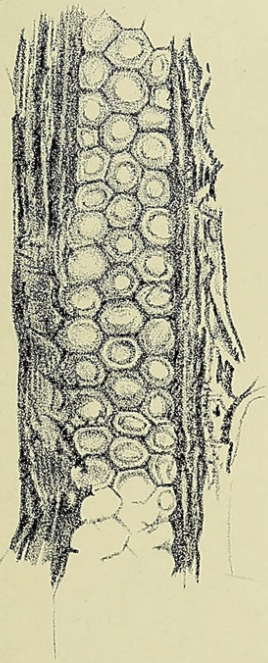

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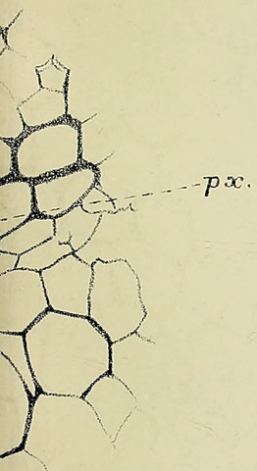
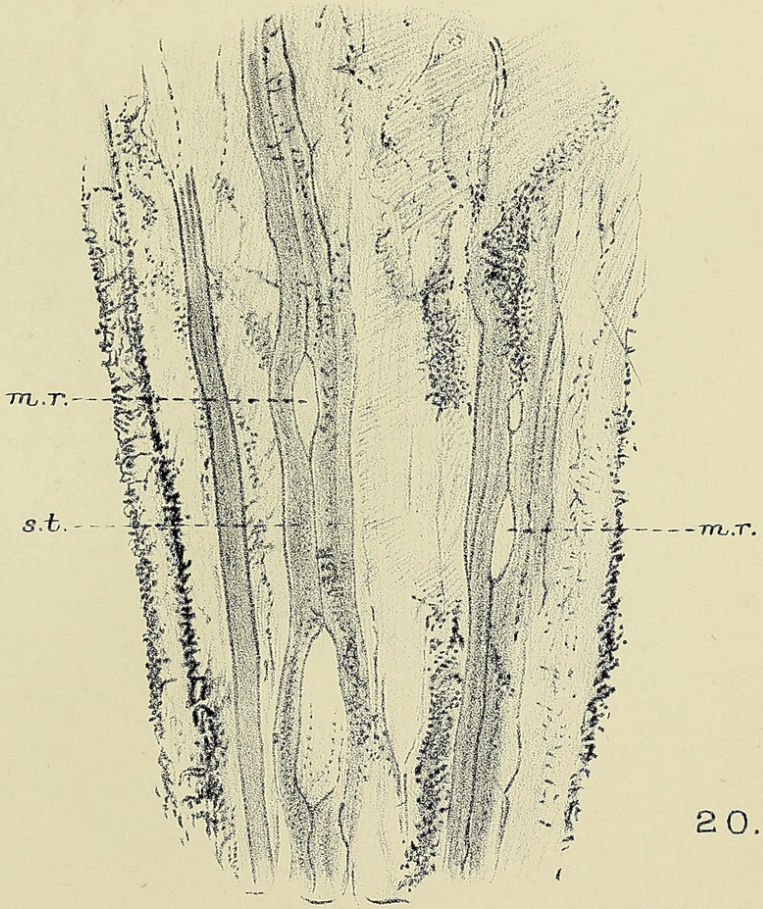
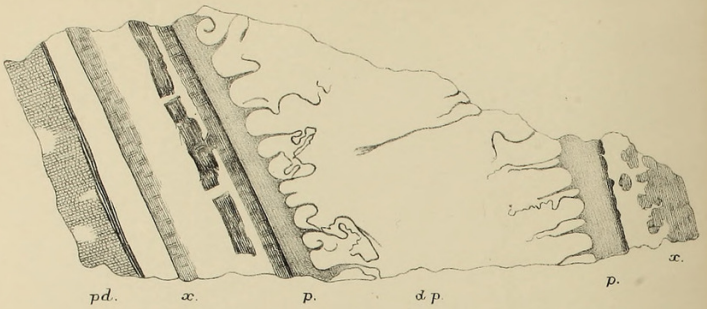




20.

Huth, lith. et imp.



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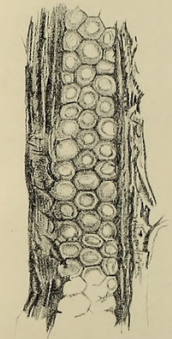

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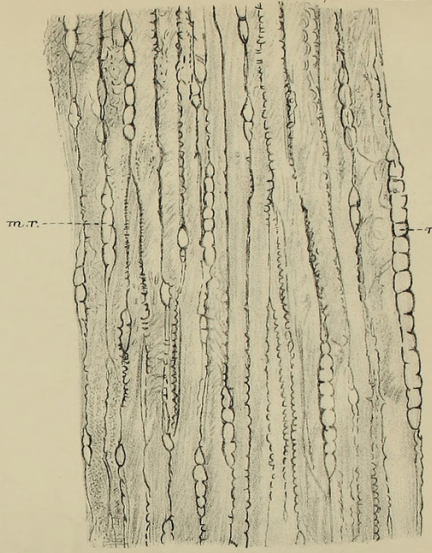

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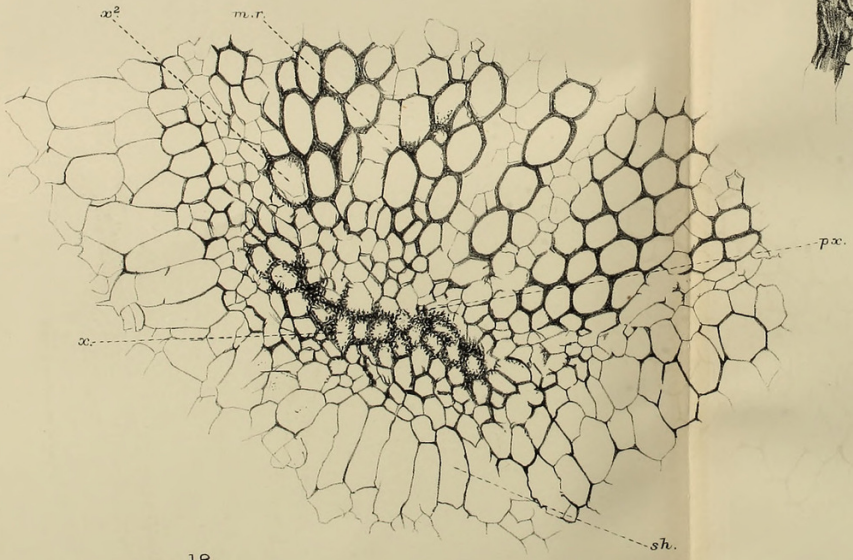

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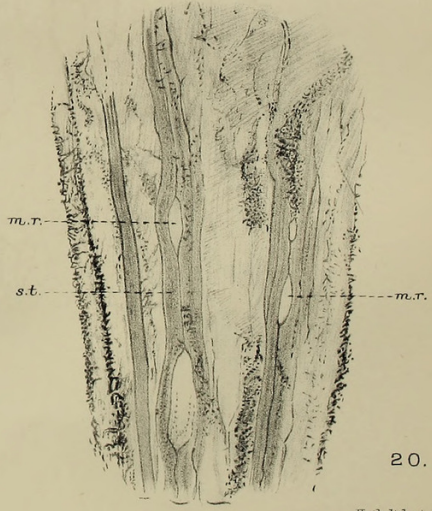
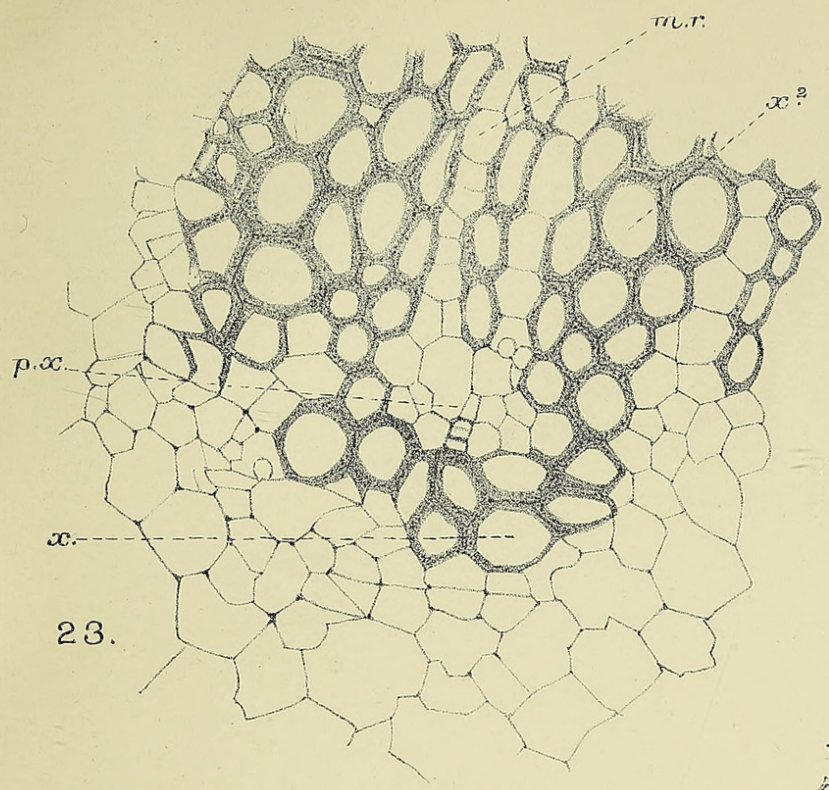


20.

G.C. Harrison & G.T. Gwilliam del.

Huth, lith. et imp.

SCOTT — MESOXYLON LOMAXII.



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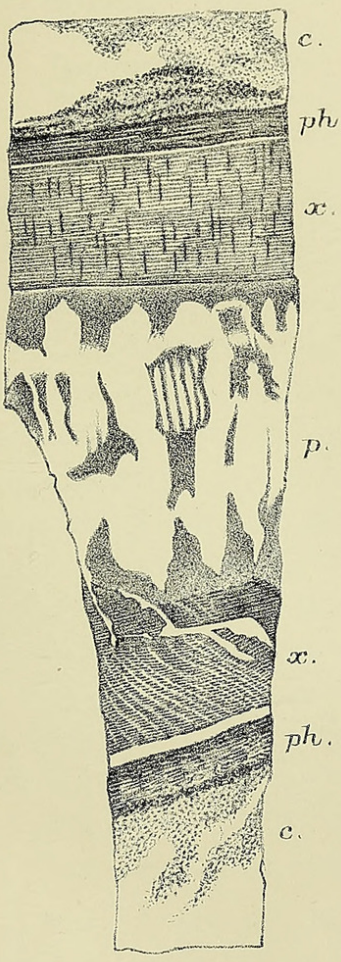

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24.

G.C.Harrison & G.T.Gwilliam del. Huth, lith. et imp.

SCOTT — MESOXYLON POROXYLOIDES.

Scott, Dukinfield Henry. 1912. "The structure of Mesoxylon lomaxii and M. poroxyloides." *Annals of botany* 26, 1011–1030. https://doi.org/10.1093/oxfordjournals.aob.a089429.

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