

III. *On the Structure and Affinities of Fossil Plants from the Palæozoic Rocks.*—III. *On Medullosa anglica, a New Representative of the Cycadofilices.*

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## [PLATES 5--13.]

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1. *Introduction.*

FOR some years past the existence of a group of fossil plants, combining in their organization certain characters of Ferns and Cycads, has been recognized by several Palæobotanists.\* POTONIÉ, in his new “Lehrbuch der Pflanzenpalæontologie,”† has proposed the convenient name Cycadofilices for this group, in which he includes the genera *Næggerathia*, *Medullosa*, *Cladoxylon*, *Lyginodendron*,‡ *Heterangium*, and

\* See, for example, WILLIAMSON, “Organization of the Fossil Plants of the Coal Measures,” Part XIII, ‘Phil. Trans.’ B, 178, p. 299, 1887; SOLMS-LAUBACH, ‘Fossil Botany,’ 1887, Engl. Ed., pp. 141 and 163, and in many subsequent papers; WILLIAMSON and SCOTT, “Further Observations on the Organization of the Fossil Plants of the Coal Measures,” Part III., ‘Phil. Trans.’ B, 186, p. 769, 1895; SCOTT, Address to Botanical Section of British Association, Liverpool, 1896; SEWARD, “A Contribution to our Knowledge of *Lyginodendron*,” ‘Annals of Botany,’ March, 1897.

† Leipzig, 1898, p. 160.

‡ Re-named *Lyginopteris* by POTONIÉ.

*Protopitys*. Among these the genus *Medullosa*, with its allies *Colpoxylon*, BRONGN., and *Steloxylon*, SOLMS, is by no means the least remarkable.

The large stems, reaching half a metre in diameter, have an extraordinarily complex structure, containing a system of numerous vascular rings, of the most various dimensions and shapes, each ring growing in thickness by a cambium of its own. The structure bears, at first sight, a striking resemblance to that of the anomalous Sapindaceæ, with which it was compared by GOEPPERT and STENZEL,\* but more recent writers† have found a better analogy in the organization of a polystelic Fern-stem, each stele, in the case of the Medulloseæ, having its own zone of secondary growth, a condition not known among recent plants. The general character of the secondary tissues, and the anomalies presented by certain of the older stems, are strongly suggestive of Cycadaceæ, though the ground plan of the structure is rather that of a Fern.

The investigations of SCHENK, SOLMS-LAUBACH, and WEBER and STERZEL, have left no doubt that these extraordinary stems bore, as their petioles, the fossils known under the generic name of *Myeloxylon*, BRONGN.‡ These leaf-stalks, which are often of huge dimensions, have, in essentials, the structure of those of Cycadaceæ, but RENAULT, in his turn, has shown that they bore the foliage of *Alethopteris* and *Neuropteris*, genera of which the external characters are entirely Fern-like.§

The above remarks are only intended to indicate, in the briefest way, the remarkable combination of characters which the Medulloseæ present. Any further consideration of the existing literature on the group, and all discussion of its affinities, will be postponed to the end of the paper.

Although fragments of *Myeloxylon* are common enough among the fossil remains, with structure preserved, found in the calcareous nodules of the English Coal-measures, no specimen of *Medullosa* itself, has, so far as I am aware, as yet been recorded from this country. This apparent absence of the stems, to which the leaf-stalks must have belonged, would be surprising, were we not familiar with the fragmentary character of such petrified specimens.

Recently, however, I have had the opportunity of investigating several fine specimens of the stems of a *Medullosa*, obtained by Mr. G. WILD and Mr. J. LOMAX,

\* 'Die Medulloseæ, eine neue Gruppe der fossilen Cycadeen,' *Palæontographica*, vol. 28, 1881.

† ZEILLER, 'Études des gîtes minéraux de la France, Bassin houiller et permien d'Autun et d'Épinac, Flore fossile,' Part I., p. 286, 1890; SOLMS-LAUBACH, 'über *Medullosa Leuckarti*,' *Bot. Zeitung*, 1897, p. 182.

‡ SCHENK, 'über *Medullosa elegans*,' ENGLER'S 'Botan. Jahrbücher,' vol. 3, 1882; 'über *Medullosa* und *Tubicaulis*,' *Abhandl. d. K. Sächs. Gesellsch. d. Wiss., Math. Phys. Cl.*, vol. 15, 1889. SOLMS-LAUBACH, über *Medullosa Leuckarti*, *loc. cit.* The original discovery appears to have been due to WEBER; See WEBER and STERZEL, 'Beiträge z. Kenntniss der Medulloseæ, XIII. Bericht der Naturwiss. Gesellsch. zu Chemnitz,' 1896. *Myeloxylon*, BRONGN., *Stenzelia*, GOEPP., and *Myelopteris*, REN., are synonyms. COTTA'S *Medullosa elegans* is, of course, a *Myeloxylon*. See p. 111.

§ RENAULT, 'Cours de Botanique Fossile,' vol. 3, p. 159, 1883. STUR, however, inclined to regard these leaves as Cycadaceous.

from the colliery at Hough Hill, Stalybridge, a locality already well known to the student of British Carboniferous plants.

The late Professor W. C. WILLIAMSON, F.R.S., received a transverse section of one of these stems (which we will call Specimen I.) from Mr. LOMAX, about the year 1892, but it was never incorporated in his collection. The slide, which is labelled, in Professor WILLIAMSON'S handwriting, "Very large *Heterangium*, crushed, and a crushed *Myelopteris*," came into my possession, with other rejected material, after his death, in 1895. The section was then a rough, unfinished one, and it is not surprising that WILLIAMSON had failed to recognise its importance. On having it thinned and covered the true nature of the fossil became evident.\* Subsequently (in September, 1897), Mr. LOMAX sent me another section, evidently cut from the same specimen, and I then learnt that the block was still in his possession. It appears that it had been originally discovered by Mr. WILD and himself, when collecting at Hough Hill. Mr. LOMAX sent me the principal piece of the block for macroscopic examination, and prepared from it a great number of admirable sections, in various directions. From first to last not less than 100 sections, transverse and longitudinal, from this one specimen have been examined.

The investigation of this specimen was already far advanced, when Mr. LOMAX, in June of this year (1898), was so fortunate as to discover two more stems in material obtained by Mr. WILD from the same colliery. One of these (Specimen II.) is the magnificent specimen, a portion of which is represented in its external aspect in Plate 9. The third specimen was peculiar in having entirely lost its external cortex. Still more recently (in September last) yet another stem was found by Messrs. LOMAX and WILD, once more in the Hough Hill material. This (Specimen IV.) again shows the external characters very well, and is otherwise of importance. Another fragment accompanying this was probably a detached piece of the same.

From all these specimens numerous preparations have been made for me by Mr. LOMAX. The skill and precision with which he has cut the necessary sections, often of large size and forming long consecutive series in definite directions, deserve the highest praise.

In addition to the four principal specimens just enumerated, I have to thank Mr. J. BUTTERWORTH, of Shaw, and Mr. G. WILD, for the loan of other specimens, which, though fragmentary, have had an important bearing on special points in the enquiry.

For the investigation of the roots, other material again has been brought into requisition.

The fossils in question are of very considerable interest, not only as being the first recorded British specimens of the genus, but also from their geological horizon, which is considerably more ancient than that of the continental *Medulloseæ*; the latter are essentially plants of the Permian and Upper Coal-measures; the British examples,

This section is now No. 226 in my collection. See Plate 5, photograph 2.

like the other calcareous vegetable remains of Lancashire and Yorkshire, are from the Ganister beds of the Lower Coal-measures, and are associated in the Hough Hill material, with such fossils as *Calamostachys Binneyana*, *Lyginodendron Oldhamium*, *Rachiopteris Oldhamia*, and *R. hirsuta*.

The structure of the specimens shows, as we shall see, that they represent a true *Medullosa*, differing however in certain important respects, and chiefly in the direction of greater simplicity, from any species previously described. The significance of these differences, and the question of the relation of our fossil to BRONGNIART's genus *Colpoxylon*, will be discussed at a later stage. As it is necessary to distinguish the British form by a specific name, I propose to call it *Medullosa anglica*.

## 2. General Structure.

The main features of the organization of *Medullosa anglica* are best shown in Specimen II., on which the following general description is primarily based, while the anatomical details have been more especially studied in Specimen I. The latter, indeed, had been worked out before the other specimens were discovered.

The block containing Specimen II. was originally about a foot long, and is traversed from end to end by the *Medullosa*. The specimen was cut, in approximately transverse planes, into three pieces.\* In the lowest of the three the stem is embedded in the matrix, but the whole of the upper two-thirds of the block has split in such a way as to expose the surface of the plant on one side. (See Plate 9, fig. 1, which represents, in natural size, the whole exposed surface of the stem.) Sections were cut from all the transverse planes, and a piece at the top of the specimen (not shown in the figure) was utilized for obtaining a series of longitudinal sections.

The transverse section shown in photograph 1,† was taken from the top of the lowest piece, and consequently immediately below the level at which the surface of the stem becomes exposed. The crack shown in the transverse section represents the line along which, in the upper portion of the block, the split took place, and so enables us to see exactly what part of the specimen is exposed by it.

The stem, where the section shown in photograph 1 passes through it, is somewhat flattened, having a diameter of  $10\cdot5 \times 3\cdot7$  centims. It has a roughly triangular sectional outline. In a position corresponding to the three angles are three large and prominent masses of cortical tissue, together occupying almost the whole periphery of the stem. These masses clearly represent the bases of leaves, still in continuity with the stem.

These leaf-bases have in all respects the typical *Myeloxylon* structure. The hypoderma, composed of several series of sclerenchymatous strands, with interspersed

\* A short piece was also removed from the top; see below.

† The explanatory diagram on p. 126 should be compared throughout with photograph 1, to which it serves as a key.



gum-canals, is characteristic of the type named by RENAULT *M. Landriotii*.<sup>\*</sup> The inner parenchyma is traversed by numerous gum-canals, and by collateral vascular bundles, agreeing exactly, as will be shown below, with those already so well known in *Myeloxylon*. Two of the leaf-bases (*a* and *b*, photograph 1) are only marked off from the interior of the stem by the internal periderm, which extends all round the stem. The third leaf-base, however (*c*), is delimited on its inner side by an interrupted sclerenchymatous band, similar to, though not so thick as the hypoderma. This leaf, then, should be the first of the three, as traced upwards, to become free from the stem. An examination of the exposed surface of the specimen shows that this is the case. Up to about the line *z* the surface *c* (Plate 9, fig. 1) is somewhat concave, and as is shown by the position of the crack in the transverse section (Plate 5, photograph 1), represents the inner surface of this leaf-base. At about *z* the striæ bend off to the left, and no doubt it was in this region that the petiole of *c* became free from the stem. It is lost, for the outer part of the block had here split away. Above *z* the surface becomes slightly *convex*, and, as shown by comparison with the transverse section at the level 3, here represents part of the *external* surface of a new leaf-base, appearing in the angle between *b* and *c*. At the level of the section shown in photograph 1, this leaf-base (*bc*) is only represented by a thickening of the hypoderma. It extends to the top of the specimen (see Plate 9, fig. 1). The leaf-base, *a*, remains in connection with the stem all through, though marked off from it in the upper sections by an internal band of sclerenchyma. In the upper third of the specimen this leaf-base is much flattened, and forms the greater part of the exposed outer surface.

The leaf-base *b* (which, of course, is not seen in surface view, as it lies on the embedded side of the specimen) is marked off by internal sclerenchyma at the level 3, and at the top of the specimen has become free, but is here only represented by some shreds of tissue. Although large free petioles of *Myeloxylon* occur in the surrounding matrix, they have not so far been followed to their connection with the stem in this specimen, but in the case of one free petiole of Specimen I. the connection has been traced. The petioles usually appear to have been torn from their bases; there is no sign of a regular abscission. At the level 3, in Specimen II., another new leaf-base (*ab*) makes its appearance between *a* and *b*. It will be seen from this specimen that the leaves were spirally arranged; the facts agree well with a 2/5 phyllotaxis (see diagram, p. 126). The leaf-bases were evidently adherent to the stem for a long distance. That marked *a* can be traced with certainty for more than five inches before it detaches itself from the stem. In this length only two leaves become free, namely, *c*, in the lower part, and *b* near the top. The vertical distance between successive leaves may be roughly estimated at about four inches.

Judging from this specimen, there was but little free surface of the stem between the prominent bases of the leaves. The other specimens are less favourable for

<sup>\*</sup> RENAULT, 'Étude du genre *Myelopteris*,' Mém. prés. par divers savants à l'Acad. de Paris, vol. 22, No. 10, 1875; also 'Cours de Botanique Fossile,' vol. 3, p. 159 (petiole of *Alethopteris*), 1883.

deciding this point. Specimen I. has lost a great part of its outer cortex and leaf-bases. The portion of hypoderma at *oc* (Plate 10, fig. 2, on the left) might be regarded as belonging to the stem, but may also be explained as part of a flattened leaf-base. Specimen III. has lost everything outside the periderm. Specimen IV. shows the outer surface well, but is very much flattened. It agrees, however, in general appearance and structure, with Specimen II., and the external surface, so far as can be seen, belongs almost entirely to the leaf-bases. The habit of the stem, clothed with the long, almost vertical, overlapping leaf-bases, may have been not unlike that of some of the Tree-ferns, such as *Alsophila procera*.

In the narrow furrows between the leaf-bases the hypoderma appears to have been interrupted, and it was no doubt from these furrows that the adventitious roots sprang, as will be shown below.

So much for the more external characters of our fossil. We have so far learnt that the stem was densely clothed by the spirally disposed, adherent bases of its *Myeloxylon* petioles.

The interior tissue is surrounded by a broad ring of periderm (see photograph 1), which is strongly developed in all the specimens except Specimen I., in which it only forms a thin layer. On other grounds also this stem seems to have been the youngest of the four. In Specimen III., all the outer tissues, including the bases of the leaves, have disappeared, leaving the periderm exposed. This may have been the result of a natural casting-off of the outer bark with advancing age, or may have been due merely to *post-mortem* maceration. This question we will consider later. The periderm cut off something more than the leaf-bases, for between the periderm and the internal sclerenchyma of the leaf-base a band of cortical tissue, containing vascular bundles, is present.

We now come to the most important feature in the stem—the structure of its vascular system. As a rule every transverse section of the stem shows three distinct masses of wood and bast, which, as we shall see, represent so many separate *steles*. This is the case throughout Specimens II. and IV., so far as observed. All the sections of Specimen III. are incomplete; two steles only are usually shown, but there are fragments of a third. In Specimen I. there are three, but one of these divides into two parts for a short distance (see Plate 5, photograph 4), reuniting above and below. The three steles are shown with great clearness in photograph 1, from Specimen II., and in photograph 5, from Specimen I. (see also Plate 10, fig. 2). Each stele always has an elongated sectional form, corresponding to that of the shorter “plate-rings” of GOEPPERT and STENZEL, but it often shows irregular curvatures and protrusions, thus approaching the “snake-ring” form. The shape of the steles, in spite of frequent fractures, does not seem to have been essentially altered by pressure, at least in the better-preserved specimens, I. and II. On the other hand, they have no doubt often suffered considerable displacement from their natural positions. The whole system of steles must have formed collectively a somewhat triangular figure in the normal condition, as is still clearly shown in Specimen II. (photograph 1 and diagram, p. 126).

There is an entire absence of the small "star-rings" (slender cylindrical steles) so characteristic of other species of *Medullosa*. In this respect *M. anglica* resembles the genus *Colpoxylon* of BRONGNIART.

A most satisfactory feature of our specimens is the very perfect preservation of the internal tissue of the steles, a part which in other *Medulloseæ* is so often damaged and obscure. The whole interior of each stele is occupied by a mass of tracheides, forming confluent groups, interspersed with thin-walled conjunctive parenchyma (see Plate 6, photographs 5-9); usually the tracheides are much more abundant than the parenchyma, and even where the latter is more largely developed it never forms a coherent medulla, so that the expression "partial pith," so often loosely applied to the interior of the "rings" in *Medulloseæ*, is wholly inappropriate here. The whole of the internal mass constitutes the primary wood; the spiral elements form scattered groups near its periphery.

Surrounding the primary xylem is a zone of secondary wood, of variable thickness, amounting in some places, as in parts of Specimen II., to more than forty elements in a radial series. Beyond the wood we come to the phloëm, which is best preserved in Specimen I., though even here only at certain places.

It is evident that in this fossil we have before us a *polystelic* stem, fully comparable to that of many Ferns, except that here each stele is surrounded by its own zone of secondary wood and bast. The structure of any one stele in *Medullosa anglica*, is almost identical with that of the single central cylinder in the stem of *Heterangium*.<sup>\*</sup> So far as the organization of the stem is concerned, it would be quite admissible to describe this form of *Medullosa* simply as a polystelic *Heterangium*. The comparison is not new,<sup>†</sup> but the relatively simple structure of the English species brings out the relation between the two genera far more clearly than has previously been possible.

From the steles, leaf-trace strands are given off, which at their base are of large size, and probably of concentric structure, but which, in passing through the cortex, break up into smaller collateral bundles of the *Myeloxylon* type (see Plate 6, photographs 6-9; Plate 7, photographs 14 and 15). These bundles pass out in great numbers into the massive bases of the leaves (Plate 5, photograph 3).

The stems bore, between the leaf-bases, numerous adventitious roots, usually triarch in structure (Plate 8, photograph 19; and Plate 13, fig. 20), and characterized by a great development of periderm. Young and old roots and rootlets have been investigated, both free and in connection with the stem, and will be fully described below (p. 102).

The preliminary survey which we have now taken leads to three main conclusions: (1) that our fossil was a polystelic stem, with secondary tissues developed around

<sup>\*</sup> Cf. WILLIAMSON, "Organization of the Fossil Plants of the Coal-Measures," Part IV., 'Phil. Trans.,' 1873, Pl. 28, fig. 30; Part XIII., 'Phil. Trans.,' B, 1887, Pl. 21, fig. 1.

<sup>†</sup> See ZEILLER, "Études des gîtes minéraux de la France; Bassin houiller et permien d'Autun et d'Épinac; Flore Fossile," Pt. 1, 1890, p. 286; SOLMS-LAUBACH, "über *Medullosa Leuckarti*;" 'Bot. Zeitung,' 1897, p. 182.

each stele, (2) that this stem bore leaves with petioles like those of *Myeloxylon Landriotii*, and (3) that it gave rise to triarch adventitious roots.

We will now proceed to examine the various structures more in detail, and then to consider the facts observed in their bearing on the affinities of our plant and of the Medulloseæ generally.

### 3. *The Steles.*

The individual steles, as seen in a transverse section of the stem, vary much in dimensions, reaching from 2 to 3 centims. in their greater, and from 6 to 10 millims. in their lesser diameter. Their form is sometimes fairly regular, as in one of the steles represented in Plate 6, photograph 5; while in others, as shown in the same preparation, the transverse section is irregularly lobed.

The whole interior of each stele, as already stated, is occupied by the primary wood, which consists of elements of two kinds—tracheides and parenchymatous cells. The arrangement and relative proportions of the two constituents vary much in different steles, and in different parts of the same. At some places, the tracheides form a continuous system over a considerable area, only interrupted by scattered strands of parenchyma (Plate 6, photograph 8). In other cases the tracheides are arranged in definite groups, separated from one another by a network of parenchyma (photograph 6), while sometimes the cellular tissue predominates, and is traversed by comparatively few tracheides, isolated, or in small groups.\* This is shown in Specimen I., in a bifurcating stele (photograph 4), and has also been observed elsewhere (Plate 10, fig. 4). In no case is there any differentiation of a true “partial pith,” or even any marked increase in the amount of parenchyma towards the middle of the stele.

The great majority of the primary ligneous elements are pitted tracheides of large size (averaging about .15 millim. in diameter) (Plate 7, photograph 12). That they are really tracheides and not vessels, is rendered probable by their pointed, tapering ends, and by the absence of any appearance of perforation in their terminal walls. This is a point, however, on which it is rarely possible to obtain conclusive evidence in dealing with fossil plants.

The pits on the tracheal walls are very numerous, and are arranged in transverse or inclined series (see Plate 10, fig. 5). They have borders like those of the secondary tracheides, to be described below, but the latter are usually better preserved and more favourable for the observation of details. Such pitted tracheides extend throughout the whole internal region of the primary wood, and at many points also reach its outer limit, bordering on the secondary zone. In the peripheral primary wood, however, other strands of tracheides occur, which have a different structure. These peripheral strands are not always easy to recognize in transverse

\* Precisely similar variations occur in *Heterangium Grievii*. See WILLIAMSON and SCOTT, “Further Observations on the Organization of the Fossil Plants of the Coal-measures,” Part III., ‘Phil. Trans.’ B, 186, 1895, p. 748.

section, but are conspicuous enough when met with in longitudinal sections (Plate 10, fig. 5). They consist of tracheides smaller than the pitted elements, with densely spiral, or finely scalariform, markings on their walls. The delicacy of the sculpturing on these elements contrasts sharply with the coarser structure of the pitted tracheides, though transitional forms are not wanting.

These peripheral strands pass out to form part of the xylem of the leaf-traces, but in doing so they are accompanied by a number of the pitted tracheides. The spiral and scalariform elements were no doubt among the first to be differentiated. In favourable cases the actual protoxylem can be detected, in the form of one or two narrow, laxly spiral tracheæ, lying near the outside of the xylem-strand, but not at its extreme margin (see Plate 10, fig. 5). Thus the whole arrangement of the primary tracheæ, as well as their minute structure, is almost identical in each stele of the *Medullosa*, with that in the single stele of *Heterangium*.\*

The conjunctive parenchyma consists of short thin-walled cells, as is best shown in Plate 10, fig. 4, which is drawn from a part of one of the steles of Specimen II., where the parenchyma is exceptionally abundant. In this case it will be noticed that the spiral tracheides are not limited to the periphery of the primary wood. The section, however, cuts through a narrow protrusion of the stele, and not through its central portion. Where the intertracheal bands of primary parenchyma are thin, they may offer a deceptive resemblance to medullary rays, as seen in tangential sections of the secondary wood. Sometimes large, thick-walled elements are found among the delicate cells, but such appearances may be due to pathological changes, for the tissues in question are often infested with fungal spores and fragments of mycelium.

Around every stele a broad zone of secondary wood and bast is constantly present; the former is at once distinguished from the primary wood by the radial seriation of its elements (see the photographs on Plate 6; also Plate 10, fig. 3). The thickness of the secondary wood is very variable; it often greatly exceeds the diameter of the primary mass. It might be expected, from the analogy of other species of *Medullosa*, that the secondary thickening would be greatest in each stele on the side towards the exterior of the stem, but no such rule holds good here, and indeed the reverse is often the case.

At the points where leaf-traces separate from the stele, the secondary zone is interrupted. Immediately below the gap thus formed, the secondary wood is both smaller in quantity, and composed of smaller elements than elsewhere (see photographs 6-9).

The radial series of tracheides are as a rule more numerous than the medullary rays; usually from two to four series of tracheides intervene between two rays. The latter are in most cases of great vertical height, and from one to three cells in thickness, but short rays, one cell thick, sometimes occur (Plate 10, fig. 3, and Plate 11, fig. 8). At some places the secondary, like the primary wood, is very parenchymatous, each ray occupying as much space as several rows of tracheides. The cells of the rays are

\* Cf. WILLIAMSON and SCOTT, *loc. cit.*, pp. 749 and 760, Plates 26-29, figs. 24, 25, 32, 33, and 34.

longest in the radial direction, and have the usual muriform arrangement (see Plate 10, fig. 4). The principal rays, which extend throughout the whole thickness of the secondary zone, are connected towards the interior with the primary conjunctive tissue of the stele. Secondary rays, starting far out in the wood, are found where the latter reaches a considerable thickness.

Where, as is usually the case, the medullary rays are narrow, the tracheides have a very regular and fairly vertical course (see Plate 11, fig. 8). Where, however, the rays are of great breadth, the tracheides follow a more devious path, curving round the ends of the broad rays, and even passing through them in an horizontal direction; in a radial section of the wood such tracheides may be cut more or less transversely (see Plate 7, photograph 12). The significance of these deviations from the normal arrangement is no doubt to be sought in the necessity for keeping up communication between the different water-conducting channels. Similar irregularities are frequent in the wood of recent Cycads.

The sculpturing of the secondary tracheides consists of multiseriate bordered pits, with narrow slits, which are often extremely well preserved (see Plate 7, photograph 13; and Plate 10, fig. 5). The pits are as a rule limited to the radial walls, and appear only to be present on the tangential surfaces when the regular arrangement of the secondary elements is disturbed, as happens near the exit of a leaf-trace, or where the medullary rays are of exceptional width. Where the pits communicate with the cells of a ray they are, as one would expect, unilateral, the thickening being developed only on the tracheal side of the wall.

It occasionally happens that the continuity of the secondary wood is interrupted, the radial series of elements starting afresh at a certain distance outwards, and no longer corresponding to those previously formed. The resemblance to an annual ring is merely superficial, and the peculiarity is evidently due to some local interference with the cambial activity.

The phloem is only preserved here and there, but in some parts of Specimen I. is well shown (see Plate 10, fig. 3; and Plate 11, fig. 9). The phloem-elements are arranged in radial rows, corresponding to the series of tracheides in the wood. They appear to have very thick cell-walls, so that the lumen, as seen in transverse section, is often reduced to a mere dot. Precisely the same peculiarity has been noticed by Count SOLMS-LAUBACH in the phloem of *Medullosa Leuckarti*.\*

It is remarkable that these elements should present the same appearance in the calcified English material as in the silicified specimens investigated by Count SOLMS. Probably this observer is right in regarding them as representing sieve-tubes and not bast-fibres, for their walls, which are very light in colour, present a totally different aspect from the undoubtedly sclerenchymatous fibres of the ypoderma (*cf.* Plate 12, fig. 14). And further, if the phloem-elements were of a fibrous nature, it is almost certain that they would be preserved much more generally than is actually the case.

\* 'Ueber *Medullosa Leuckarti*,' p. 179.

The argument used by Count SOLMS, that there are no other elements in the phloem which could be the sieve-tubes, if these are not they, applies with equal force to the English *Medullosa*. Probably the cell-walls of the elements in question were comparatively thin during life, but swelled up greatly under the influence of maceration and decay in the interval preceding petrification. It is also possible that the thick-walled appearance may be altogether delusive, depending rather on some change in the cell-contents. In this case the apparent "middle lamella," which is sharply defined, would really represent the whole thickness of the cell-wall.

Longitudinal sections show that the sieve-tubes, as we may provisionally call them, were of great length, with tapering ends. Their course and relation to the medullary rays are well shown in Plate 11, fig. 9, drawn from a tangential section of the phloem at one end of the same stele, which is shown in transverse section to the left of photograph 5 (*st.*<sup>1</sup>).

The phloem-rays, occupying the meshes between the strands of sieve-tubes, are somewhat broader than the corresponding xylem-rays, and consist of short-celled parenchyma.

Beyond the phloem is a zone of ill-preserved tissue, in which mucilage-canals are contained; this zone may have been of the nature of a pericycle, but no details can be made out.

The cambium between wood and bast is never well-preserved, though some traces of it can be seen in Plate 10, fig. 3. The regular radial seriation of the elements leaves no doubt as to their mode of development.

There is evidence that the steles in their course through the stem underwent both fusion and division, though probably only at long intervals. Thus, if we compare photograph 5 with photograph 2, from two approximately transverse sections about two inches apart, we find that the tissues have undergone a certain amount of rearrangement. Photograph 5\* is from the lower, and photograph 2 from the upper, of the two sections. One of the steles (*st.*<sup>1</sup>) goes through, not, indeed, unaltered, but without joining either of the others. Stele 2 of photograph 5 has, however, fused with the adjacent end of stele 3, to form a new mass which we may call stele 2'. The remaining portion of the original stele 3 has reorganised itself as a complete stele (*st.*<sup>3'</sup> in photograph 2). It is unfortunate that, owing to accidental ruptures of the tissues, no section shows the actual fusion clearly, but the course of the steles has been satisfactorily made out by carefully following them through six intermediate transverse sections cut between those shown in the photographs cited. The prevalence of the number three for the steles may indicate that at the same level three leaf-bases were usually receiving bundles from the stem, a suggestion which finds some support from Specimen II. in particular (photograph 1, and diagram, p. 126).

The stele marked *st.*<sup>1</sup> in photograph 5 and in the diagram (fig. 2) is peculiar, in that it undergoes division for a short distance into two parts, which have just re-united

\* See also diagram, Plate 10, fig. 2. In photographs 2 and 5 the right and left are reversed.

before reaching the level of photograph 2. Photograph 4 is from one of the intermediate sections, and shows the stele divided. Only one of the halves becomes completed by the closing in of the secondary zone. The other half never becomes converted into a complete stele, but its primary wood remains open on the side towards the twin-half, passing over, without any sharp break, into the intermediate parenchyma. Just above the division all the middle part of the stele is unusually rich in parenchyma, and this condition appears to have allowed of an extension of the cambium across the primary wood. The whole process is exceptional (though something similar has been observed in another specimen), and does not seem to be related to the normal bifurcation of the steles.

#### 4. *The Leaf-trace Bundles.*

The question of the relation between the foliar bundles and the vascular system of the stem in *Medullosa*, is quite cleared up by the specimens under consideration. The leaf-traces are met with, in the various transverse sections, in all parts of their course, from their first leaving the stele to their finally passing out into the petiole. The series of successive transverse sections which have been prepared from every specimen, render it possible to follow the same strand for long distances, while in many cases the leaf-traces shown in the corresponding transverse and longitudinal sections can be identified with one another.

The leaf-traces are always given off from the free faces of the steles, *i.e.*, from the sides or ends directed towards the cortex; they are never found in the central space between the steles. Where, however, a stele projects beyond its neighbours, leaf-traces may arise from both sides of the projecting part.

Where a leaf-trace first starts from one of the steles, it constitutes a large strand, more or less circular in transverse section, and surrounded, completely or partially, by a zone of secondary wood and bast (see Plate 6, photographs 6-9; Plate 11, fig. 10). Further out in the cortex the original leaf-trace divides repeatedly, to form several smaller bundles, at the same time losing its secondary tissues (see Plate 6, photograph 9; and Plate 11, fig. 12). In the outer cortical layers these branch-bundles have assumed collateral structure, and now precisely resemble the typical *Myeloxylon*-bundles of the petioles (see Plate 7, photographs 14 and 15).

The junction of the leaf-traces with the steles is shown at many places in all the specimens, and often with the greatest clearness (see photographs 6 and 8). A large strand, at the periphery of the primary wood, detaches itself from the main mass, and passes very gradually outwards, accompanied on its outer side by a crescent of secondary tissue. The tracheides of the outgoing strand diverge but slightly from the vertical direction, and the arrangement of the elements in the rest of the stele is not disturbed. I have seen nothing here of the horizontal or very oblique strands of tracheides, which Count SOLMS-LAUBACH observed in the case of *M. Leuckarti*, and



believed to be connected with outgoing bundles.\* Where such irregularities occur in the primary wood of our specimens, they have no relation to the leaf-traces, which pass out in the same orderly manner as in *Heterangium*.

The trace passes gradually out through the secondary wood, which then closes in behind it (see photographs 6–9). The secondary tracheides accompanying, or in the immediate neighbourhood of a leaf-trace, are usually smaller than in other parts of the stele. As soon as the bundle is free, its own secondary tissues extend all round it (photographs 7, 8, 9; fig. 10); they may be irregular, but are developed indiscriminately on all sides of the strand. It is probable that the leaf-traces, in this part of their course, were really concentric bundles, though this cannot be strictly proved, as it is impossible to determine with certainty whether the phloem was, from the first, continuous all round the xylem. We know that in *Lyginodendron Oldhamium*, where the leaf-traces while within the stem are certainly collateral, the secondary tissues, in certain exceptional cases, extended all round the bundle;† in *Medullosa anglica*, however, this condition is constant. The distribution of the secondary tissues around the leaf-trace, and its general appearance, certainly point to a primarily concentric structure.‡

The gradual exit of the leaf-trace from a stele can also be well followed in some of the longitudinal sections (see Plate 7, photograph 11). The intercalation of secondary wood behind the trace, in connection with the latter and with the stele, is well shown, where the direction of the section is favourable.

The structure of an undivided leaf-trace near its base, bears much resemblance, on a small scale, to that of the stele itself (Plate 11, fig. 10), and recalls the “stellate rings” described in other *Medulloseæ*. The primary xylem includes a certain amount of parenchyma. Most of the tracheides are large and pitted, like those which form the bulk of the primary wood in the steles (see Plate 11, fig. 11, which is from the same leaf-trace, *lt.*<sup>2</sup>, which appears in transverse section in Plate 6, photograph 8). One or more groups of smaller elements are present, and are shown by longitudinal sections to consist of spiral and scalariform tracheides (fig. 11). Where the bundle first leaves the stele, its protoxylem is directed outwards; irregularities in orientation, which one sometimes observes, may be due merely to displacement.

The secondary wood of the leaf-trace often contains, in addition to the ordinary elements, a number of extremely short tracheides with square ends (fig. 11); their longer axis may be tangential to the wood.

In two cases it was noticed that a leaf-trace after diverging from the stele was connected with it for a considerable distance, by radial bridges of short tracheides. There is reason to believe, as we shall see below, that this peculiarity was correlated with the insertion of an adventitious root.

\* “Ueber *Medullosa Leuckarti*,” ‘Bot. Zeit.’ 1897, p. 180, Plate 6, fig. 1.

† WILLIAMSON, ‘Organization, &c.’ Part IV., Plate 22, fig. 1, x; WILLIAMSON and SCOTT, ‘Further Observations, &c.’ Part III., p. 724.

‡ Cf. SOLMS-LAUBACH, ‘Ueber *Medullosa Leuckarti*,’ p. 194, Plate 6, fig. 4.

The phloem can usually be recognised round the whole circumference of the bundle, but its preservation is imperfect (Plate 11, fig. 10).

Several leaf-traces are often given off near together, as shown, for example, in photograph 9. Considering the great size of the leaf-bases borne on the stem, there can be no doubt that a number of the principal traces went to supply a single leaf. The stele marked *st.*<sup>1</sup> in photographs 2, 4 and 5 and in the diagram (fig. 2) can be traced through 18 transverse sections, representing a length of about  $3\frac{1}{2}$  inches (9 centims.). In this part of its course it gives off at least 10 leaf-traces. Considering the great vertical height of the leaf-base, which, as we know from Specimen II., exceeded 5 inches (13 centims.), there can be no doubt that many of these, perhaps even a larger number, were destined for the same leaf. There is evidence, as we shall see below, that each leaf-base continued to receive bundles from the stem up to the point where it was shut off by internal sclerenchyma.

It has not been possible to determine whether each leaf received bundles from a single stele only, or whether the adjacent parts of two steles contributed.

The number of bundles entering a leaf was largely increased, as we shall now see, by the subdivision of the original traces in passing through the cortex. The first stage of such a subdivision is shown on comparing photograph 8 with photograph 9. The vertical distance between the two sections represented was about a centimetre. In the lower section (photograph 8) the larger leaf-trace, *l.t.*<sup>2</sup>, is undivided, but in the upper (photograph 9) it is separating into two strands. The secondary arc is still complete on one side, but the primary xylem is severed into two halves by the intrusion of parenchyma. An intermediate section shows the first beginning of the fission, while in a section higher up in the series the division is complete. Various other cases have been observed. In Specimen III. a leaf-trace was followed, in 13 successive transverse sections, through a vertical distance of about  $2\frac{1}{2}$  inches (6 centims.). It gradually lost its secondary tissues in its upward course, and divided twice.

It appears that the leaf-traces underwent further subdivision in the upper part of their course. Thus Plate 11, fig. 12, shows two groups of bundles, each of which must have arisen by the division of a single strand, for in a section about a centimetre lower down, the bundles of each group are still connected with each other. These are strands which have lost all trace of secondary tissues, and which lie outside a band of internal sclerenchyma, so that they were evidently still undergoing division when already far advanced on their outward course.

The leaf-traces as they divide, lose their concentric structure and become collateral. At the stage of division shown in fig. 12, this change has already taken place. Probably the collateral structure was assumed lower down, for it is found in bundles which are still in the cortex of the stem, as distinguished from that of the leaf-bases. This is beautifully shown, for example, in the pair of bundles (probably arising from the division of a single one) represented in transverse section, Plate 7, photograph 14. These bundles, with many others like them, lie well within the internal sclerenchyma

(see Plate 6, photograph 5, *v.b.* The phloem is excellently preserved, and is evidently limited to the outer side of the xylem. The smallest xylem-elements are adjacent to the phloem, and in fact the structure is in all respects that of the well-known "exarch" vascular bundles of *Myeloxylon*.

Photograph 15, showing a similar pair, is taken from a more external part of the cortex, lying within the triangular space indicated in Plate 10, fig. 2, between the hypoderma, *o.c.* and the internal sclerenchyma *sc.* This space, as proved by the comparison of successive transverse sections, represents the base of a leaf, which at a higher level begins to become free from the stem (photograph 2, *Pet.*).

We see, then, that the structure characteristic of the vascular bundles of the petiole is already assumed, not only in the leaf-base, but within the cortex of the stem.

As shown by the longitudinal sections (Plate 12, fig. 15), the collateral strands, resulting from the division of the original leaf-traces, no longer possess any pitted elements in their xylem, which here consists entirely of spiral or finely scalariform tracheides accompanied by a few parenchymatous cells. The latter appear, in the collateral bundles, to lie only at the edge of the wood, and not in the midst of the tracheides. Where the spiral bands of two contiguous walls cross one another an appearance of reticulation is produced. A narrow laxly spiral tracheide of the actual protoxylem can be recognized in the radial section figured, separated only by one layer of cells from the delicate and elongated elements of the phloem (see fig. 15). In every detail we find the closest agreement with typical *Myeloxylon* bundles.\*

The conclusions arrived at respecting the leaf-trace system of *Medullosa anglica* may be summed up as follows :—

- (1) The leaf-trace strands are given off from the external side of the steles, a number of such strands contributing to supply a single leaf.
- (2) On first leaving the steles, the leaf-traces are large, probably concentric bundles, each surrounded by its own zone of secondary wood and bast.
- (3) In passing through the cortex the leaf-traces lose their secondary tissues, and divide up to form several smaller bundles, which assume the collateral, exarch structure characteristic of *Myeloxylon*.

##### 5. *The Ground-tissue and Periderm.*

The central ground-tissue, lying between, or immediately surrounding the steles, is generally much disorganized. Between the steles there was probably but little intermediate tissue during life, the pericycles of the vascular masses coming near together (see Plate 7, photograph 10). The tissue immediately outside the group of steles consisted of thin-walled parenchyma traversed by numerous leaf-trace bundles and

\* Cf. SEWARD, "On the Genus *Myeloxylon*," 'Annals of Botany,' vol. 7, Plates 1 and 2; especially figs. 16 and 17 (1893).

gum-canals. The latter occur in all parts of the extrastelar tissues as well as in the pericycles; those shown in Plate 12, fig. 14, from the hypoderma, will serve as examples.

In Specimen I. the more external part of the ground-tissue is very well preserved, especially on one side of the stem (Plates 5 and 6, photographs 2 and 5), where the infiltrating substance was different from that of the rest of the specimen, as shown by its less easy solubility in acetic acid. This tissue, however, probably belongs for the most part to the leaf-bases, for it agrees very closely with the tissues of the evident leaf-bases shown so well in Specimen II. (photographs 1 and 3). It is clearly impossible to draw a sharp distinction between leaf-base and cortex, for the one merges imperceptibly into the other, except in the upper part of the leaf-base, where the internal sclerenchyma serves to mark the limit. The cortical parenchyma shown in Plate 5, photograph 2 and neighbouring sections, is very poor in both vascular bundles and gum-canals, and therefore probably belongs to the region at the bottom of a leaf-base. Further description of the more external tissues will be postponed until the leaf-bases and petioles are dealt with.

In Specimen I. sclerenchymatous bands sometimes appear isolated in the ground-tissue (see Plate 10, fig. 2, diagram), and, so far as the transverse sections show, are not in connection with the hypoderma. They, no doubt, represent the downward continuation of the sclerenchyma which, at a higher level, passes out to form the inner surface of the petioles.\* The relation of the internal sclerenchyma to the leaf-bases is clearer in Specimen II. (see photograph 1, and diagram p. 126).

The development of an internal *periderm* is a striking feature in most of the specimens (see Plate 5, photographs 1 and 3; Plate 7, photograph 16; Plate 10, figs. 6 and 7). It forms a continuous though very irregular zone, running round the stem a little within the bases of the leaves. The regular radial arrangement of the cells at once characterizes this zone as a secondary formation; it attains in places a thickness of at least 25 elements. The cells, as seen in radial or transverse section, have a tabular form; their walls are of moderate thickness. Seen in tangential section (fig. 7), the arrangement of the peridermal cells is, as one would expect, quite irregular, but the zone is at once recognized by the uniformity and marvellous preservation of its elements.

Towards the interior the periderm passes over into the primary cortex, and, on the boundary, cells are found with very delicate tangential walls, which are evidently the result of the last divisions, and thus indicate the position of the phellogen (fig. 6). The great bulk of the periderm was evidently formed to the outside of its generative layer, thus corresponding morphologically to cork. It is extremely probable, from the very perfect preservation of its cell-walls, that the tissue was actually suberized. There was little, if any, phelloderm to the interior of the cork-cambium. In Specimen I., unlike the other three, the periderm is very little developed, and cannot

\* Cf. SOLMS-LAUBACH, 'Ueber *Medullosa Leuckarti*,' p. 191.

be traced as a continuous ring. Evidently it was only beginning to form in this specimen (see Plate 11, fig. 12, *pd.*). From the first, the formation of the periderm was very irregular; thus in Specimen I., where it is so little developed, it already appears here and there in the form of loops or rings enclosing leaf-trace bundles, or portions of sclerenchyma. The same thing is even more conspicuous in the more advanced stems, where prominent bulges or deep invaginations of the periderm are of constant occurrence, and sometimes a closed ring of periderm appears, quite isolated from the main zone, though probably connected with it at a different level (diagram, p. 126). It is in the excision of effete tissues that we must seek the significance of these anomalous developments. The most extreme case of the kind is found where the periderm cuts deeply into the interior of the steles themselves. This pathological process has gone on to a great extent in Specimen III., which was evidently in a senile condition. The periderm can be traced into the steles, from the cortical tissues, through the leaf-trace gaps; clearly the cell-division had spread from one cell to another, until it invaded the parenchyma of the primary wood, with the result that the latter has become cut up in various directions by bands of intrastelar periderm.

At one place in another specimen (No. II.) still more extraordinary phenomena have occurred, for here not only has periderm extended deeply into the interior of a stele, so as to obliterate most of its primary wood, but it has even replaced a great part of the secondary wood, completely changing the whole structure of the stele affected. The abnormality is quite local, and was probably due to some injury at an early stage of growth. It is of interest chiefly as a warning, for in less perfect material such pathological symptoms might easily be confused with normal processes of growth. Those who have worked at the anatomy of recent Cycads will readily recall parallel cases.

Certain very definite outgrowths of the periderm, which occur in connection with the bases of the adventitious roots, will be best considered below, together with the roots themselves.

The normal zone of periderm must obviously have cut across all the vascular bundles on their way out to the leaves; we consequently often find them imbedded in the thickness of the periderm. Possibly they may have kept up communication between the inner and outer tissues for some time, for Specimens II. and IV. show that the leaf-bases remained on the stem, without any apparent withering, after a thick zone of periderm had been formed. Specimen III., as mentioned above, is peculiar in having lost all its tissues exterior to the periderm. The specimen was old, compared with the others, as shown by the great thickness of its secondary wood, and by the wide-spread occurrence of pathological new-formations in its tissues. It is, therefore, very probable that it may have reached a stage at which the exfoliation of all the external tissues normally took place. It is difficult to see the object of the well-marked periderm-formation characteristic of the species, unless exfoliation eventually occurred, but at the same time we cannot absolutely prove that the loss

of the external tissues, in such a case as that of Specimen III., may not have been due merely to maceration and decay.

#### 6. *Accessory Vascular Strands.*

In addition to the regular constituents of the vascular system of the stem, namely the normal steles and leaf-traces, we sometimes find accessory strands of wood and bast, which do not fall under either of these categories. Their occurrence is very inconstant; where present at all, they are always found in the cortex, outside the regular group of steles. An anomalous structure of this kind is present in Specimen I., a little to the exterior of the subdivided stele described above (see Plate 5, photograph 4, *an*). Another example (from Specimen II.) is shown in Plate 12, fig. 18, on a larger scale. The structure is essentially similar in both. The strands are of considerable size; thus, in the case first mentioned (photograph 4), where there are two of these anomalous rings side by side, the larger of the two has a maximum diameter of 7 millims., its long axis lying tangentially. The general structure in these cases somewhat resembles that of a normal stele. The secondary tissues form a more or less irregular ring, enclosing a parenchymatous central region, in which tracheides are scattered. All the elements are small, compared with those of the regular steles; the internal tracheides are often quite short, with square ends, and reticulated walls. The secondary wood has broad rays; cambium and phloem are sometimes fairly preserved (Plate 12, fig. 18). The anomalous strands in Specimen I. (photograph 4) are more irregular than that figured in detail from Specimen II.; thus on one side of the ring in the former case the secondary wood is undeveloped for some distance, and is here replaced by an excessive growth of phloem or secondary parenchyma.

Longitudinal sections of Specimen I., cut immediately below the transverse section from which phot. 4 was taken, show that the anomalous strand fused, in the downward direction, with the adjacent normal stele. This fact may have some relation to the division of the latter about the same point.

In other cases also accessory vascular tissues have been found, which sometimes take the form of irregular bands, and not of closed rings.

These anomalous vascular strands are probably best regarded as extrafascicular new formations, comparable to the cortical bundles of *Cycas*, which they much resemble, or to the irregular strands which sometimes occur in the extrafascicular region of *Macrozamia*.\*

We know, from the investigations of WEBER and STERZEL, that some *Medullosa* (e.g., *M. stellata*, var. *gigantea*) formed successive extrafascicular zones of wood and bast outside their stelar system, just as we find in *Cycas*, *Macrozamia*, and *Encephala-*

\* See WORSDELL, "Comp. Anat. of certain Genera of the Cycadaceae," 'Linnean Society's Journal—Botany,' vol. 33, 1898, pp. 441–444, Plate 20, figs. 6–8; "Anatomy of the Stem of *Macrozamia*," 'Annals of Botany,' vol. 10, 1896, p. 610, figs. 2, 9, and 10.

*lartos* at the present day.\* It is therefore not surprising that in our species we should meet with other characteristic Cycadean anomalies.

The accessory strands in *M. anglica* are certainly quite different from the normal steles and leaf-traces; neither can they be identified with the strands supplying adventitious roots, which had a more horizontal course. There is no indication of their connection with any other form of lateral appendage.

### 7. *The Leaves.*

The structure of the leaf-bases in connection with the stem is best shown in Specimen II. (Plate 5, photographs 1 and 3), though also evident in parts of Specimens I. and IV. The outer cortex or hypoderma, as seen in transverse section, is represented in detail in Plate 12, fig. 14. The fibrous strands, which have a rounded transverse section, are ranged three or four deep, the smallest towards the outside, with dense, large-celled parenchyma filling the interstices between them. In some places a more delicate parenchyma, forming an external layer outside the fibrous zone, is preserved, and no doubt this was always present during life. When this external parenchyma is well preserved, it is found to consist of smaller and thin-walled cells, with abundant cell-contents. The outermost cortical layer, as well as the actual epidermis, had a well-marked palisade form. This external zone probably formed the assimilating tissue of the organ (see Plate 11, fig. 13).

Gum-canals are abundant in the hypodermal parenchyma, and often abut on the fibrous strands. As a rule the actual epithelium of the canal has perished; in a few cases some remains of it can be traced. A carbonaceous strand, representing no doubt the fossilised secretion, often traverses the canal.

Tangential sections of the external cortex show that the fibrous strands have a straight course, without anastomosis (see Plate 7, photograph 17). This is extremely evident, even to the naked eye, on the exposed surface of the specimen, as shown in Plate 9, fig. 1, where the prominent ribs, representing the fibrous strands, can be traced for several inches without finding any fusions. For this form of hypodermal tissue, which is characteristic of "*Myeloxylon*," among other fossils, Count SOLMS-LAUBACH has proposed the name "*Sparganum* cortex,"† taken from an obsolete genus established by UNGER for certain fern-petioles. The "*Dictyoxylon* cortex" (typically shown in *Lyginodendron Oldhamium*) differs from the *Sparganum* type in the reticulate arrangement of the fibrous strands.

The fibres are of great length, with thick walls, while the intermediate parenchyma consists of very short cells, often broader than long. The internal parenchyma of the leaf-bases, which is very well preserved in some cases (see Plate 5, photograph 3;

\* WEBER and STERZEL, 'Beiträge zur Kenntniss der Medulloseæ,' p. 27, Plate 8, fig. 2.

† "Pflanzenreste des Untereulm von Saalfeld," 'Abhandl. d. K. Preuss. Geol. Landesanstalt;' Neue Folge, Heft 23, p. 49, 1896.

Plate 7, photograph 17), consists uniformly of large but short cells, with rather thin walls. There are no fibres in this part of the tissue, except in connection with the vascular bundles. The parenchyma is traversed by numerous gum-canals, like those of the external cortex, but often larger. In some cases, however, the cavity of the canal is small, or even almost absent. When this is so, the surrounding cells had evidently undergone active cell-division, by cell-walls tangential to the cavity, as is shown both in transverse and longitudinal sections. Canals in this condition appear at first sight to be at an early stage of development. It is, however, improbable that new canals should have been in course of formation in the base of a leaf already separated from the inner tissues by a broad zone of periderm (photograph 3). A more probable interpretation is that the canals in question were undergoing obliteration, by dilatation and division of the surrounding cells.

The numerous vascular bundles in the leaf-bases have the collateral exarch structure already described. The phloem is only occasionally preserved, but its position on the outside of the bundle is quite clear. The xylem has its smallest elements next the phloem; it is separated from the surrounding parenchyma by a sheath of small thick-walled elements, which are shown by longitudinal sections to be fibres. The fibrous sheath does not extend round the phloem. Traced longitudinally, it begins to appear in the base of the leaf, but is best shown in sections of free petioles, which are abundant in the blocks containing *Medullosa anglica*. The bundles, in their course through the leaf-base and petiole, sometimes anastomose.

The number of bundles to be counted in the transverse section of a leaf-base varies according to the level at which the section is taken. Thus, in the leaf-base marked *c* in photograph 1, which, as we know, was near its point of separation from the stem, nearly 80 bundles were found, while in that shown in photograph 3 there are only about 30. The latter is not yet marked off from the stem by internal sclerenchyma, and we know that it did not begin to become free for more than 3 inches above the plane of section. Another leaf-base, cut still lower down, only showed about 15 bundles. It is evident then that new sheaves of bundles successively entered the leaf-base at different levels, probably up to the point at which the appearance of internal sclerenchyma formed a barrier between leaf and stem. In the leaf-base shown in photograph 3 the more external bundles are ranged in a very definite horse-shoe curve, just within the hypoderma; these probably represent the first sets which entered the leaf-base, while those grouped more to the interior have passed in at a higher level. This regularity of arrangement is gradually lost as the leaf-stalk receives its full complement of bundles. In some transverse sections, the hypoderma appears of exceptional thickness, and is evidently cut obliquely (see Plate 7, photograph 16). There is little doubt that in these cases the plane of section passes immediately above the axil of a leaf. The sclerenchymatous strands which, in the photograph referred to, are seen passing out from either side of the thickened hypoderma, must belong to the upper free surface of the petiole, the rest of which is lost,



The larger free petioles accompanying the stem are absolutely identical in structure with the leaf-bases still attached to it. The large leaf-base, part of which is shown in photograph 2 (from Specimen I.), is already almost free from the stem, and becomes quite free, as traced upwards in successive sections, without showing any change of structure. The petiole shown in transverse section in Plate 8, photograph 18, is from another part of the same block, and probably at some distance from its attachment to the stem. The mean diameter of this fragment is about 1·75 centims., whereas the leaf-bases at their insertion on the stem are about double that size, taking transverse measurements. Except for its smaller dimensions the petiole referred to shows in all respects the same structure as the leaf-base; the hypoderma is distinctly of the type of *Myeloxylon Landriotii*, REN. The parenchyma has here become crushed along certain lines, forming a coarse net-work, precisely as in some of M. RENAULT's sections. Among the larger petioles are smaller ones of various dimensions. Some of these, with a diameter of 4 or 5 millims., may represent the rachis of the main pinnae. These have the same structure as those already described, on a smaller scale. The hypoderma is, however, here comparatively thin, with a single row of wedge-shaped strands of sclerenchyma. Still smaller branches have the structure shown in Plate 12, fig. 16, drawn from a rachis only 1·25 millims. in diameter. It has distinct wings on one side, no doubt representing the upper surface. A continuous band of sclerotic tissue runs round the periphery; in the parenchyma many gum-canals are contained. In the middle is a group of five or more bundles, apparently surrounding a canal. As far as can be seen, they are of the usual type, with their phloem, which is crushed, directed outwards. This may well have been the rachis of a secondary pinna, bearing the ultimate pinnules.\*

Sections of leaflets, such as are usually found associated with *Myeloxylon*, are very common among the fragments of the petioles and rachis. One of the best is shown in transverse section in Plate 12, fig. 17. The midrib contains two bundles close together, which, so far as the imperfect preservation allows one to judge, appears to have been collateral, with the phloem directed outwards. The lamina, which is incurved at either margin, has a distinct palisade layer, and is manifestly of bifacial type. A vascular bundle of the lamina, which runs near the lower surface, is well shown in longitudinal section. I have not yet found absolute proof that these leaflets belong to the "*Myeloxylon*" rachis, but the constancy of association, and general agreement in the structure leaves no real doubt. The leaf must have been very large; in one slide a rachis (probably of a primary pinna) can be traced in longitudinal section for fully 5 inches, apparently without branching. In other cases branching is shown. The facts just detailed show that *Medullosa anglica* bore large, highly compound leaves, the petioles of which have the structure of the *Myeloxylon Landriotii* of RENAULT. The latter is not to be regarded as a *species* in the same sense as in

\* In another section a small rachis, like that shown in fig. 16, is seen arising as a branch from one of larger dimensions.

speaking of recent plants, but rather as a type of petiolar structure, common, no doubt, to a certain group of the *Medulloseæ*.

M. RENAULT found reason to believe that *Myeloxylon Landriotii* represents the petiole and rachis of leaves belonging to the form-genus *Alethopteris*. The organization of the leaves of our *Medullosa* renders it highly probable that they too would fall under the same category. The resemblance in structure to M. RENAULT's specimens is, in fact, a very close one.\* The identification of the leaf of *Medullosa anglica* cannot, however, be finally settled without further investigation, on which I am now engaged.

### 8. *The Roots.*

It appears that the structure of the root has not been described as yet in any species of *Medullosa*.

The material from Hough Hill contains a number of specimens of a very characteristic root, of triarch structure, with well-marked secondary wood and bast, and a conspicuous zone of periderm (see Plate 8, photograph 19, and Plate 13, fig. 20). The larger roots attain a mean diameter of about half an inch (12 millims. or more), and are accompanied by rootlets of various dimensions and similar structure.

Of the specimens examined, many were found in close association with the *Medullosa* stems, while others occurred in separate nodules from the same locality; of these Mr. LOMAX also prepared the sections. In all cases the roots are associated with fragments of the "*Myeloxylon*" petioles, which we now know to have belonged to the *Medullosa*.

The histological structure of the wood in these roots and in the stem of *Medullosa anglica* was found to agree so closely, as to suggest at once the probability that the organs belonged to one and the same plant, a conclusion which has now been confirmed by direct proof of continuity between root and stem.

The structure of the roots and rootlets will first be described, after which the evidence will be given which demonstrates their connection with the stem of *Medullosa anglica*.

If we examine a well-preserved specimen of one of the larger roots, such as those shown in transverse section in photograph 19 and fig. 20, we find the following structure.

The root is bounded externally by a broad zone of radially seriated parenchymatous tissue, having a thickness in different specimens of from eight to twenty-four or more cells. This tissue is evidently of the nature of periderm; the narrowest cells, with the thinnest tangential walls, lie towards the interior of the zone, so we may conclude that its development was mainly centripetal, the bulk of the tissue having been formed, like cork, on the outer side of the phellogen. The cell-walls of the large peridermal cells are sharply defined, though of no great thickness; it is highly probable that they were suberized. The periderm of the root bears a strong general resemblance to that of the stem of our *Medullosa*. Within the periderm but little

\* RENAULT, 'Cours de Botanique fossile,' vol. 3, Plate 27.

parenchyma is preserved; what there is occurs chiefly at the corners of the compressed root, where it has escaped crushing. This tissue was probably pericyclic, for, as we shall see presently, the periderm was of internal origin. The radial sections show the seriation of the peridermal cells with equal clearness (see Plate 8, photograph 20), and indicate that the vertical height of these elements was about equal to their tangential width.

Almost the whole interior of the root is occupied by the vascular cylinder, which is well preserved. In all the clear transverse sections the structure is evidently triarch; in one somewhat doubtful case only it appeared to be tetrarch. The three arms of the primary xylem are long, and run out to slender points, as seen in transverse section. Longitudinal sections confirm the obvious conclusion that the protoxylem (represented by very small densely spiral tracheides) lies at these points. In the primary wood the tracheides, which are accompanied by much conjunctive parenchyma, are largest about the middle of the strand, and diminish in size towards the angles. The larger tracheides have multiseriate bordered pits distributed equally on all their walls; as the protoxylem is approached the markings become more scalariform.

The secondary wood, which in all the larger roots much exceeds the primary in amount, forms three well-defined arcs, corresponding to the three sides of the triarch strand. Opposite the xylem-angles little or no secondary wood is developed. The radial rows of the secondary tracheides correspond in size to the primary elements on which they abut. Thus those series which start from the more central part of the primary wood consist of large elements, while the series abutting on the smaller tracheides of the arms gradually become narrower as the angles are approached, thus giving a very characteristic habit to the transverse sections.

The secondary tracheides, like the larger elements of the primary wood, are marked with multiseriate bordered pits, but here the pits are limited to the radial walls (see Plate 8, photograph 20). The medullary rays can, in favourable cases, be traced through the whole thickness of the secondary zone, from the conjunctive parenchyma to the outside of the phloem. The latter, when it is preserved, consists of narrow elongated elements.

On the outer border of the phloem are traces of secretory organs, which may have been either sacs or canals.

The sections occasionally show the roots in the act of branching (Plate 8, photograph 19, *rt.*). The branches are always rootlets of much smaller size than the parent root. In the example illustrated, the xylem-elements of the rootlet abut directly on one of the protoxylem-angles of the main root. Very short tracheides are often found ensheathing the wood of the rootlet at this point. The phloem and pericyclic parenchyma of the rootlet are well preserved, but its endogenous origin is by no means evident. This is no doubt due to the fact that the periderm which envelops both root and rootlet was an internal one, so that the primary cortex of both is lost.

Rootlets much smaller than the main roots hitherto considered, are often met with

in transverse section; in favourable cases their structure leaves no doubt as to their identity. An especially clear specimen,  $1.5 \times 1$  millim. in diameter, is shown in Plate 8, photograph 21. The periderm is here 10 to 12 cells thick, and agrees exactly with that of the main roots; the phellogen is beautifully preserved. The triarch stele has begun to form secondary wood, which has only reached a thickness of about three elements. The phloem, and even parts of the cambium, are in good preservation. The phloem-groups are evidently placed between the angles of the xylem, so that the structure is typically that of a root. The thin-walled, tabular cells of the phellogen lie so close to the phloem as to leave no doubt that the periderm arose in deep-seated tissue, and probably in the pericycle.

Direct proof of this fact is afforded by a still smaller rootlet (with a mean diameter of scarcely a millimetre), shown in transverse section in Plate 12, fig. 19. This rootlet retains its primary cortex, while the formation of periderm has already begun. The xylem, though slightly deformed, is evidently triarch, and agrees well with that of the other specimens, but in this case no secondary growth had yet taken place. Immediately beyond the phloem, which is partly preserved, is a zone of larger cells which were evidently undergoing active tangential division. This zone, in fact, represents the periderm at an early stage of its development. Adjoining it, on the outside, is a single layer of large cells, which do not fit on to those of the periderm. We can hardly interpret this layer otherwise than as an endodermis, though I could not satisfy myself as to the presence of the characteristic marks on the radial walls. Beyond the endodermis comes the primary cortex, which resembles that of the root of *Lyginodendron Oldhamium* in its lax, lacunar structure, the presence of "secretory sacs," and the definite double layer of cells at the periphery.

The rootlet might, in fact, be taken for a young triarch rootlet of *Lyginodendron*, if it were not for the very distinct formation of periderm, which I have never found so well marked, even in the oldest roots of the latter plant.\* The specimen, on the other hand, agrees so closely with the *Medullosa* roots now described, that there can be no doubt of its identity. It thus proves, in conjunction with other specimens, the pericyclic origin of the periderm in these organs.

It is unnecessary to take up more time with a description of the rootlets, which occur in great numbers, associated with the larger roots and with the stems of *Medullosa anglica*. In many cases their identity is certain, while others are more dubious. It is evident that the roots in question branched freely, and that their ultimate rootlets were extremely slender.

The root-nature of these organs does not seem open to question. The anatomy is in all respects that of a root. The example of *Sphenophyllum* warns us, indeed, that a very root-like anatomy may be found in a stem, but in the present case there are no indications whatever of cauline structure. Nothing like a node is to be found; the

\* WILLIAMSON and SCOTT, 'Further Observations, &c.,' Part III., p. 740. The root of *Lyginodendron Oldhamium* is shown in that paper to be identical with the old *Kaloxylon Hookeri* of WILLIAMSON.

appendages are all of one kind, and are manifestly rootlets; that they are not obviously endogenous is fully explained by the early appearance of periderm, which so soon removed the whole of the primary cortex.

The organs are not, so far as I have been able to ascertain, identical with any fossil roots previously described. They differ from those of *Lyginodendron* in the presence of periderm and in the prevalence of triarch structure, which is exceptional in that plant. In both the points mentioned our specimens resemble *Amyelon radicans*, but they differ from it in the whole character of the wood, which in *Amyelon* is much denser, with smaller tracheides and much less parenchyma. The pitting of the tracheæ is also quite different, nor does the periderm itself agree in detailed structure. *Amyelon* requires further investigation, but in the mean time there can be no doubt that it is quite distinct from the roots under consideration. It is not impossible that the finer rootlets above described may turn out to be identical with one or other species of *Rhizonium*, but at present I have found no proof of this.

The agreement in histological detail between these roots and the stem of *Medullosa anglica* (shown especially in the structure of the wood and periderm), together with the constant association of the stems and leaves of the *Medullosa* with the roots, strongly suggested that the one belonged to the other. We have now to examine the direct evidence for this connection. A specimen found by Mr. G. WILD, in the same material which yielded the stems of *Medullosa anglica*, throws important light on the subject. Plate 8, photograph 22, represents a section of this specimen, kindly lent me by the owner. Four large roots, evidently of the same nature with those already described, are shown in transverse section. Each root is surrounded by a broad zone of periderm, within which is a layer of parenchyma, containing secretory organs, and within this again the phloem can be traced. The secondary wood is divided up by broad medullary rays, and agrees in all respects, including the pitting of the tracheæ, which can be seen where the section is oblique, with that of the free roots. The primary wood is rather obscure, owing no doubt partly to pressure, and partly to natural irregularity; in two out of the four roots the general form of the primary strand, and the position of the principal rays, point to triarch structure.

The roots are crowded together, and their outline is more or less irregular. Between them are packed masses of tissue, some of which are of a different nature from the roots themselves. Both these intermediate masses and the tissue bounding the group of roots laterally, are continuous in places with the adjacent roots. This tissue (*M.c.* in photograph 22) shows, in longitudinal section, the structure of the *Medullosa* cortex, including sclerenchymatous strands, gum-canals, and vascular bundles with tracheides like those shown in Plate 12, fig. 15. The only possible interpretation of the facts is that the section is a tangential one of the cortex of a *Medullosa* stem, passing through the base of a group of adventitious roots.

By Mr. WILD's permission eight more sections of the specimen were cut for me by Mr. LOMAX, parallel to the first. These, as it proves, cut successively deeper

into the stem, and render it possible to trace the connection between the tissues of the roots and those of the parent axis. The peridermal zones of the various roots become confluent with each other and with the periderm of the stem itself, while the vascular cylinders of the roots open out, and join on to longitudinal strands of vascular tissue, which are themselves continuous with a stele, seen in longitudinal section, and showing in all details the structure of a stele of the *Medullosa* stem. Plate 8, photograph 23, is from the innermost section of the series, and shows the stele (at *st.*) with which the roots have united. The fragment was evidently a part of one of the stems of *Medullosa anglica* (and, in all probability, of Specimen I.). It is the only specimen I have seen which shows large and mature adventitious roots in connection with the stem, but in the case of younger roots the connection has been established repeatedly.

A good instance of this also is afforded by Mr. WILD's specimen, just described. The same section (photograph 23) which passes through one of the steles of the stem, also shows the cortical tissues, which are obliquely cut. Towards one side the inner cortex forms a vertical row of conspicuous outgrowths (*ped.*) in contact with one another, where the arrangement has not been disturbed by the intrusion of the ubiquitous Stigmarian rootlets. These outgrowths are each coated on three sides by periderm, which is also continuous between their bases. The cortical tissue of the outgrowths consists of thin-walled parenchyma, in which many of the elements have dense carbonaceous contents, and may be provisionally called secretory sacs. Within each outgrowth is a vascular cylinder, seen in oblique section, and extending inwards, towards the interior of the stem. In addition to the outgrowths, two free appendages are seen in transverse section, one of which is included in photograph 23; others appear in an adjacent section. These structures are clearly roots (see Plate 13, fig. 21); most of their cortex has been thrown off by the formation of internal periderm; the parenchyma (presumably pericyclic) lying within the periderm, is of considerable thickness, and resembles the tissue of the cortical excrescences. The vascular cylinder (which has little or no secondary thickening, showing that the roots were still young) is asymmetrically triarch, two of the arms forming a well-developed vertical band, with a shorter horizontal arm. Small rootlets accompany the larger roots. At one place (fig. 21) the base of a similar root is still in connection with a cortical outgrowth, of which it forms one lobe. As we shall see presently, it was often the case that two roots sprang from each cortical excrescence. Mr. WILD's specimen thus affords evidence that young roots may spring from the same part of the stem which bears mature roots, which have far outstripped the former in their development. The growth of the immature roots may very probably have been arrested.

Still clearer evidence, as regards the mode of connection between the young roots and the stem, is found in another specimen, namely, that which I distinguish as Specimen IV. This stem is much compressed, but otherwise well-preserved, and shows with perfect

clearness, on both sides, the external characters of the cortex,\* agreeing in all respects with those of Specimen II., as represented in fig. 1. The base of a petiole is also shown, and the internal anatomy is identical with that of the other stems of *M. anglica*. It is in longitudinal sections, taken from the lower end of the specimen, that the adventitious roots appear. One of these sections (Plate 8, photograph 24) passes almost radially through the undulating layer of periderm. To two of its protrusions adventitious roots (*r*) are attached, the continuity of the tissues being uninterrupted. Both these roots are cut in an obliquely tangential direction, the section passing at such a depth as to show the dense internal periderm of the root, outside which is the somewhat lax tissue of the primary cortex, containing numerous short secretory sacs. Opposite the third peridermic protrusion, but not in connection with it, is an appendage seen in oblique transverse section, which is no doubt another root. All these roots were evidently quite young, as shown by their intact primary cortex, though even at this stage periderm had begun to form. From the root-bases strands of tracheides extend inwards into the stem, and attach themselves by means of an irregular network (Réseau radicifère of VAN TIEGHEM) to a nearly vertical bundle, which, from its structure, is clearly a leaf-trace (*lt.*) passing out gradually from the stele (*st.*), which is seen further towards the interior. The leaf-trace, as it diverges from the stele, remains connected with it by means of a system of short tracheides. This radial connection between leaf-trace and stele (referred to above, p. 93) has been observed in another specimen (No. II.), where it was probably also connected with the presence of adventitious roots. Provision appears to have thus been made for abundant water-communication between the roots and the stem which they supplied. Another radial section of Specimen IV. shows two cortical outgrowths in approximately median section (Plate 8, photograph 25). One of these contains a bifurcating strand of vascular tissue; one fork is cut off obliquely, but the other runs out into an evident root, of small size, cut sufficiently near the median plane to show the xylem. In this case it is clear that the cortical outgrowth bore *two* roots, one above the other. These outgrowths may best be regarded as the *pedicels* of the adventitious roots.† The other pedicel also shows a forked bundle, but less clearly. Immediately outside this pedicel, and evidently belonging to it, a root is well shown in transverse section (Plate 13, fig. 22). The stele is asymmetrically triarch, just as in the young roots of Mr. WILD's specimen above described. In the present case, however, the broad zone of primary cortex is well preserved to the outside of the internal periderm.

\* These characters, so well marked in the fossil state, by no means represent the natural appearance of the plant during life. We know that the ribs of sclerenchyma, which form the main feature of the fossil surface, were covered in nature by a layer of cellular tissue, which must have hidden them from view, or at most have allowed but slight elevations to appear externally.

† Cf. VAN TIEGHEM, "Origine des Membres Endogènes," 'Ann. des. Sci. Nat. (Bot.),' Ser. 7, vol. 8, 1888; p. 540.

The specimens described prove conclusively that triarch adventitious roots were borne on the stem of *Medullosa anglica*, and it is unnecessary to dwell on other cases in which the evidence is less complete. It is interesting, however, to point out that these observations explain the nature of a very curious specimen, lent me some time ago by Mr. J. BUTTERWORTH, of Shaw, the significance of which long remained a problem. A section of this specimen is represented in Plate 13, fig. 23. It shows a four-lobed structure; the lobes are in a row, and though in close lateral contact are only confluent with each other at the base (towards the left of the figure). The lobes are coated with periderm, the cortex within this is rich in "secretory sacs"; three of the lobes contain each a stele, seen in obliquely transverse section, and in two this structure is very well preserved. The resemblance of the lobes to the cortical excrescences or root-pedicels, as shown in Plate 8, photographs 23 and 25, is obvious. The lobes of Mr. BUTTERWORTH'S specimens are rather larger than those compared with them, the vertical diameter of each lobe being about 6 millims. in the Butterworth specimen, and about 4 millims. in the others; but in Specimen II. of the *Medullosa* we find similar pedicels still larger than the former, so the differences in size go for nothing.

Of the two steles clearly shown, one (that in *b*) has a pith, or central parenchyma, in which, however, some tracheides are scattered. Around this is a well-preserved zone of secondary wood and bast. The other (*c*, in Plate 13, fig. 23, shown in detail in fig. 24) has a fairly distinct triarch primary xylem, with its tracheides much compressed, perhaps by dilatation of the adjoining parenchyma; beyond this is a broad zone of secondary wood, succeeded towards the outside by cambium and phloem.

Fragments of leaflets, such as are usually associated with *Myeloxylon*, occur in the matrix. Mr. BUTTERWORTH kindly prepared five additional sections of the specimen, cut successively in planes parallel to the first. The next section to that figured shows the stele of the lobe *c* losing its triarch character and acquiring a medulla containing scattered tracheæ. The succeeding section is still more important, for it shows two of the steles anastomosing in an oblique direction with a vertical vascular strand, in which the tracheæ are pitted like those of our *Medullosa*. Other sections, cutting still deeper into the parent organ, no longer show the pedicels as distinct organs, but pass through an irregular periderm, within which are fragments of secondary wood. The preservation of this part is imperfect, but comparison with the sections already described, showing the insertion of the roots in *Medullosa anglica*, leaves no doubt as to the nature of the specimen, which evidently consists of the bases or pedicels of a series of adventitious roots, in connection with a fragment of a *Medullosa* stem. There is a decided general resemblance to the arrangement of the adventitious roots in *Heterangium*, as figured in a previous memoir,\* but the agreement is much closer with our *Medullosa*. Whether the Butterworth specimen is *specifically* identical with *M. anglica* may remain an open question.†

\* WILLIAMSON and SCOTT, 'Further Observations, &c.,' Part 3, Plate 27, fig. 28.

† It is fair to my friend, Mr. SEWARD, to mention that he was the first to notice the resemblance of the



Before leaving the roots, a word may be said as to their place of insertion on the stem. There is nowhere any sign of their breaking through the strong armour of fibrous sclerenchyma by which the leaf-bases were protected. Considering how much of the external surface is exposed in Specimens II. and IV., besides what is shown in tangential sections, the passage of roots through the hypoderma, if it occurred, could scarcely have failed to come under observation. In some cases, on the other hand, there is a distinct interruption of the hypoderma between the bases of adjacent leaves, as shown in Specimen II. (Plate 9, fig. 1), and also in Specimen IV. I have no doubt that it was at these places that the vertical series of adventitious roots were inserted, though, as the specimens are usually somewhat crushed, it has not been easy to determine the exact relation of the roots to the leaf-bases. Some of the transverse sections of Specimen II., however, show a root embedded in the cortex, exactly between the bases of two leaves (see Plate 5, photograph 1, and diagram, p. 126, *r*), and all the other preparations showing roots are quite consistent with such a position.

We may sum up our knowledge of the roots of *Medullosa anglica* as follows:—

- (1.) The stem of *Medullosa anglica* bore numerous adventitious roots, ranged in vertical series, and escaping between the leaf-bases.
- (2.) The roots were borne on short pedicels, often two on each pedicel, and were connected with one of the steles of the stem, either directly or by means of a leaf-trace bundle.
- (3.) The roots developed at different periods, for young and mature roots may occur on the same stem at about the same level.
- (4.) The roots were almost invariably triarch; the stele formed a large amount of secondary wood and bast. The primary cortex was cast off early, owing to the formation of periderm in the pericycle. The periderm attained a great thickness in the older roots.
- (5.) The roots branched abundantly, the rootlets repeating in essentials the structure of the main root.

#### 9. *Summary and Diagnosis.*

The account of the general structure of our plant given in Section 2 (pp. 84–88) renders any detailed summary unnecessary. It will suffice to recapitulate very briefly the chief points established.

*Medullosa anglica* (like the other species of the genus) had a polystelic stem, with secondary wood and bast developed around each stele.

Butterworth specimen to the triarch roots of *Medullosa anglica*, when I showed him the sections at which I was working. Mr. BUTTERWORTH himself was inclined to refer his specimen to *Heterangium*—a very reasonable supposition before the English *Medullosa* was known. I may further mention that I was indebted to Mr. BUTTERWORTH for my first acquaintance with Mr. WILD'S specimen of the roots. These two observers recognized that their respective specimens were of a similar nature.

In this species the steles are few (3 or 4) and uniform, having a somewhat elongated and irregular sectional form. No "star-rings," in the sense of GOEPPERT and STENZEL (*i.e.*, small internal steles with circular transverse section) are present.

The interior of the steles is occupied entirely by their primary wood. The structure of each stele in *Medullosa anglica* resembles in all points that of the single vascular cylinder of a *Heterangium*.

The steles divide and anastomose at long intervals.

They give off large leaf-trace bundles, which, on first leaving the steles, are concentric strands, with secondary wood and bast. As they pass through the cortex, the leaf-traces divide repeatedly, lose their secondary tissues, and assume the collateral exarch structure of "*Myeloxylon*" bundles. Accessory vascular strands, somewhat similar to the normal steles, were occasionally developed in the cortex.

Externally the stem was clothed by large, spirally arranged, decurrent leaf-bases, having in all respects the structure of *Myeloxylon Landriotii*, REN.

The leaf-bases received numerous vascular bundles from the stem; the vascular supply of each leaf consisted of the groups of bundles resulting from the subdivision of a number of the primary leaf-traces.

The surface of the fossil is marked by a system of fine longitudinal ribs, representing the fibrous hypodermal strands of the leaf-bases.

An internal periderm was developed around the stem, and may perhaps have ultimately caused the exfoliation of the leaf-bases and outer cortex. The leaf, as shown by the ramification of the petiole and rachis, was a highly compound one. The structure of the fine branches of the rachis and of the pinnules shows a general agreement with the corresponding parts of *Alethopteris* leaves, as described by RENAULT.

Gum-canals are numerous in the hypoderma and parenchyma of the leaf-bases, in the cortex of the stem, and in the pericycle of the steles. They extended throughout the rachis of the leaf.

The stem bore numerous adventitious roots of triarch structure, with abundant secondary wood and bast, and an early development of internal periderm. The roots branched freely.

For purposes of diagnosis, a still more concise abridgement of the characters must be attempted. The specific value of the types of *Medullosa*, to which names have been previously assigned, is admitted to be doubtful. WEBER and STERZEL,\* to whom we owe the best account of the genus, prefer to speak of "form-cycles" (Formenkreise) rather than of species. In the case of our English form there is no reason to doubt that all the specimens hitherto investigated (with the possible exception of Mr. BUTTERWORTH's fragment) are specifically identical.

\* 'Beiträge zur Kenntniss der Medulloseæ,' p. 88.

*Medullosa anglica*, sp. nov.

Stem vertical, clothed by large spirally-arranged decurrent leaf-bases, perhaps cast off in old stems. External surface of leaf-bases longitudinally striate.

Vascular system of stem consisting of a few (usually three) uniform steles, somewhat elongated and lobed, as seen in transverse section. Star-rings absent. Interior of each stele wholly occupied by primary wood.

Secondary wood and bast of moderate thickness, developed on all sides of the steles. Tracheides usually with bordered pits.

Leaf-traces concentric on leaving the steles, branching and becoming collateral in traversing the cortex.

Leaf-bases and petioles with the structure of *Myeloxylon Landriotii*, REN.

Leaves highly compound.

Gum-canals abundant in the petioles and leaf-bases, and in the cortex, and around the steles of the stem.

Adventitious roots borne in vertical series, triarch, with secondary wood and bast, and periderm.

Stem, with leaf-bases, about 7–8 centims. in mean diameter.

Petioles, about 2·5–4 centims. in diameter at base, diminishing to about 1 millim. in the ultimate branches of the rachis.

Leaflets about 3 millims. wide.

Roots reaching 12 millims. in diameter.

*Locality*.—Hough Hill Colliery, Stalybridge, Lancashire.

*Horizon*.—Lower Coal-measures.

Found by Messrs. G. WILD and J. LOMAX, 1892–1898.

10. *General Conclusions.*

The specimens of *Medullosa anglica* just described appear to be the most complete examples of the genus hitherto investigated (though the crucial point, the fructification, is unfortunately still lacking), and are certainly the most ancient. They are, therefore, of considerable importance for the elucidation of the affinities of the group as a whole.

This is not the place to give a history of our knowledge of the Medulloseæ, but the chief steps in its progress may be indicated.

The first description of *Medullosa* is due to CORTA,\* and dates from 1832. He described two species of the stem (*M. stellata* and *M. porosa*), and, by an odd coincidence, included in his genus a third species, *M. elegans*, which, after having long been separated as type of the genus *Myeloxylon*, has eventually proved to be the petiole of a *Medullosa*. CORTA's inclusion of *M. elegans* in its right genus was

\* 'Die Dendrolithen in Bezug auf ihren inneren Bau,' Dresden, 1832.

no more than a lucky accident; petiole and stem are, as we know, totally distinct in structure, and it was only owing to a complete misinterpretation that CORTA placed them together, for he confused the hypodermal sclerenchyma of the petiole with the peripheral wood of the stem, an error which BRONGNIART set right.\*

It was almost half-a-century before the botanical study of the *Medullosa* stems made any essential advance, although additional specimens were, of course, described in the mean time. In 1881 GOEPPERT and STENZEL† showed that the whole vascular system of the stem, as seen in transverse section, consists of a number of closed rings, the peripheral wood being built up by a variable number of flattened "plate-rings," differing from the central "star-rings" in size and shape, but not in structure.

This discovery showed at once that the structure of *Medullosa* was essentially different from that of the stem of any recent Cycads.‡

The organization revealed by the researches of GOEPPERT and STENZEL needed interpretation, and an important step in this direction was made by SCHENK, who, in 1889, discovered the presence of primary wood in the interior of each ring.§ His account, correct as far as it goes, of the structure and course of the leaf-trace bundles in *M. stellata*, also marks a real advance.

The interpretation of the structure of the *Medullosa* stem as *polystelic*, thus at once bringing it into line with the stem of most Ferns, is probably the most important step yet made in the anatomy of these fossils, and is due to ZEILLER.||

The value of this conclusion lies in its giving a new clue to affinities, and is quite independent of the special importance we may attach to VAN TIEGHEM's anatomical terminology.

ZEILLER's interpretation received some support from the comparison between the structure of *Medullosa* and that of *Psaronius*, drawn by WEBER and STENZEL,¶ but its complete confirmation is due to Count SOLMS-LAUBACH. This observer showed in 1896 that in the *Cladoxylon* of UNGER, a genus of Fern-stems from the Culm, each of the many steles may have its own zone of secondary wood.\*\* The clear analogy with Medulloseæ is pointed out by the author, who in a more recent publication has shown that the primary wood of each stele in *Medullosa Leuckarti* may best be compared with that of the single stele of a *Heterangium*, *Medullosa* thus standing in the same relation to *Heterangium* as *Primula Auricula*, &c., to the normal species of *Primula*.†† His description of *M. Leuckarti* is altogether the most complete that we have hitherto

\* 'Tableau des Végétaux Fossiles,' Paris, 1849, p. 60.

† GOEPPERT u. STENZEL, 'Die Medulloseæ; eine neue Gruppe der fossilen Cycadeen,' 1881.

‡ Cf. SOLMS-LAUBACH, 'Fossil Botany,' 1887, p. 102 (English edition).

§ A. SCHENK, "Ueber *Medullosa* u. *Tubicaulis*," 'K. Sächs. Gesellsch. d. Wiss., Math. Phys. Cl.,' vol. 15, p. 535, 1889.

|| *Loc. cit.*, 'Flore Fossile d'Autun et d'Epinac,' Part 1, 1890, p. 286.

¶ *Loc. cit.*, 'Beitr. z. Kenntniss d. Medulloseæ,' 1896, p. 100.

\*\* SOLMS-LAUBACH, 'Pflanzenreste des Unterculm von Saalfeld,' p. 55, 1896.

†† SOLMS-LAUBACH, "Ueber *Medullosa Leuckarti*," 'Bot. Zeit.,' 1897, p. 182.

possessed of any species of the genus, though certain points, such as the origin of the leaf-traces from the steles, could not be made out in this form.

An interesting addition to our knowledge of the anatomy of the genus was made by WEBER and STERZEL, who showed that in one exceptionally large specimen (*M. stellata*, var. *gigantea*), and possibly in one other case (*M. Solmsii*, var. *lignosa*) successive extrafascicular zones of wood and bast were developed outside the whole system of steles, so that in these cases the anomaly characteristic of *Cycas*, *Macrozamia*, and *Encephalartos* coexists with the polystely proper to the genus *Medullosa*.

While the anatomy of the stem was thus being elucidated by the discoveries of successive observers, the nature of the leaf was also becoming known. The discovery that *Myeloxylon* is the leaf-stalk of *Medullosa*, originally made by WEBER, was referred to by SCHENK in 1882, but the stem bearing the *Myeloxylon* was by him simply described as that of a Cycad.\*

The connection with *Medullosa* was recognised as probable by Count SOLMS-LAUBACH in 1887,† and further confirmed by SCHENK in 1889.‡ ZEILLER, however, in 1890 still treated the question as an open one. The memoir of WEBER and STERZEL (1896) for the first time gave the evidence fully, and, as it seems to me, established, beyond reasonable doubt, the fact that the species *Medullosa Leuckarti* bore as its leaf-stalks a *Myeloxylon* of the type *M. Landriotii* of RENAULT.§ The latest investigations of Count SOLMS-LAUBACH have fully confirmed their conclusion, though that author reserves his judgment as to the *specific* identification of the *Myeloxylon* in question.||

The connection of *Myeloxylon* with *Medullosa* having been finally established, the previous discovery by RENAULT that the *Myeloxylon* petioles belonged to compound leaves with the characters of *Alethopteris* and *Neuropteris*,¶ became of the greatest importance, as determining the nature of the foliage of *Medullosa*. It now became clear, as STUR had previously suggested, that the fronds of these genera (to which others may probably have to be added) were not those of true Ferns, but of the peculiar semi-Cycadaceous family, Medulloseæ.

We have now to consider the fresh light thrown upon the question of the affinities of Medulloseæ by the new species *Medullosa anglica*, in which, for the first time, it has been possible to examine the entire vegetative structure of a plant of this genus in all its parts.

The first point of cardinal importance is the close agreement in stem-structure between our fossil and *Heterangium*. It is not a mere case of analogy, but of a

\* A. SCHENK, "Ueber *Medullosa elegans*," ENGLER'S 'Bot. Jahrbuecher,' vol. 3, 1882.

† 'Fossil Botany,' p. 161 (English edition).

‡ 'Ueber *Medullosa* u. *Tubicaulis*.'

§ WEBER and STERZEL, *loc. cit.*, p. 43 (84), Plates 4, 5, and 9; text-figs. 14-22.

|| 'Ueber *Medullosa Leuckarti*,' *loc. cit.*, p. 187.

¶ RENAULT, 'Cours de Botanique fossile, etc.,' 3, chaps. 12 and 13; STUR, 'Morph. u. Systematik der Culm und Carbonfarne,' p. 638, 1883.

detailed correspondence so exact as to be explicable only by a true affinity. In the structure of the stele, as regards both primary and secondary wood, every detail agrees, including the mode of pitting of the tracheides, their distribution relative to the conjunctive parenchyma, the position of the protoxylem-groups, and the relation between the leaf-traces and the stele. The *Medullosa* is polystelic and the *Heterangium* monostelic, but that difference, as we know from the case of *Selaginella* and other genera, is consistent with the closest affinity.

The structure of the hypoderma is another point, though one of secondary importance, in which our *Medullosa* and *Heterangium* agree, and the arrangement of the adventitious roots is also similar.\* It is, however, on the agreement in the stelar structure that stress is to be laid. This comes out much more clearly in *M. anglica*, even than in *M. Leuckarti*, partly because we know the details better in the former species, and partly because its structure is much simpler, and so allows of more direct comparison.

The affinity which, as it seems to me, is now demonstrated between *Medullosa* and *Heterangium*, is of much interest, for the genus *Heterangium* is one of the most Fern-like of the Cycadofilices. Apart from the secondary thickening, the structure of the stem in *Heterangium* is closely similar to that in the recent *Gleichenia*, while the foliage is altogether Fern-like, and in fact almost certainly identical, as STUR's description shows, with that of *Sphenopteris elegans*.† It would thus appear that *Medullosa*, though so complex and highly specialized in many of its representatives, may well have been derived, by fairly direct descent, from a simple Fern-stock. This does not, of course, imply that any known form of *Heterangium* was the ancestor of any *Medullosa*—a most improbable supposition—but that the Medulloseæ generally may have sprung from plants related to, and with the same type of stem-structure as *Heterangium*. Such a view agrees better with the facts than would an attempt to derive the Medulloseæ from the Cladoxyleæ. The latter, indeed, conspicuously resemble the former in having polystelic stems with secondary growth, but the structure of the individual steles is strikingly different, notably in the fact that the primary wood of *Cladoxylon* consists exclusively of scalariform tracheæ, without conjunctive parenchyma.‡ I should, therefore, incline to regard the Cladoxyleæ as representing a parallel line of development to that of the Medulloseæ, rather than as primitive members of the same series.

In the organisation of the leaves, and in the course and structure of the leaf-trace bundles, *Medullosa anglica* diverges widely from the *Heterangium* type, and stands on the same level with *M. Leuckarti*, assuming, as I think the evidence justifies, that the petioles of the latter really had the structure of *Myeloxylon Landriotii*. It

\* The arrangement of the adventitious roots in *Medullosa* is also closely similar to that in some of the recent Tree-ferns. See the figures of *Cyathea* in DE BARY'S 'Comp. Anat.,' figs. 140 and 141.

† STUR, "Die Culmflora," 'Abhandl. d. K. K. Geol. Reichsanstalt zu Wien.,' vol. 8, 1877. See also KIDSTON, "Fructification and Internal Structure of Carboniferous Ferns," 'Trans. Geol. Soc. Glasgow,' 1889, p. 49.

‡ SOLMS-LAUBACH, 'Pflanzenreste des Unterculm von Saalfeld,' p. 54.

is rather surprising that our plant appears to have been quite as highly differentiated with respect to its leaves, as any of the Permian *Medulloseæ*, while its stem-structure was so much simpler. This suggested at the outset a doubt whether the single specimen which had then been examined might not represent the first-formed, basal portion of a stem which had not yet attained its full complexity. This idea, however, appears to me no longer tenable. All the four specimens show just about the same degree of complexity, all alike having three (or locally four) similar steles. And further, it is significant that no appreciable difference in structure is apparent between the upper and lower ends of the individual specimens. In Specimen II. the part actually sectioned was about nine inches long, and in Specimen I. nearly the same. It must therefore, I think, be taken as proved that the structure of the stem in our species was really far simpler than in any other known *Medullosa*, as regards the small number of the steles, and the absence of differentiation among them. This fact agrees well with its greater antiquity. Possibly some botanists might regard this difference as sufficient to justify generic separation. I do not think so myself, bearing in mind the close agreement with other species of *Medullosa* in leaf-characters, and in the structure of the individual steles. In both points the agreement appears to be closest with *M. Leuckarti*.

This leads us to consider the possible relation of *Medullosa anglica* to the *Colpoxylon aeduense* of BRONGNIART, which is known to have much in common with *M. Leuckarti*, while showing a far simpler anatomical structure. *Colpoxylon*, to judge from the admirable figures and description in M. RENAULT's splendid contribution to the 'Fossil Flora of Autun,'\* was monostelic in parts of the stem, the large single vascular cylinder having a very irregular outline. In other parts there are two such cylinders, and their number may even reach six or seven at the summit of the stem. M. RENAULT correlates this multiplication of the cylinders with a repeated dichotomy of the stem, a view which is not accepted by Count SOLMS-LAUBACH, who has examined the specimens.† Scattered groups of tracheæ are present in the interior of the cylinder; "star-rings" are altogether absent, as is also the case in our species of *Medullosa*. In many details, such as pitting of tracheides, structure of the leaf-trace bundles, and of the cortex, and in external characters, there is a striking resemblance to *Medullosa anglica*, and I do not doubt that the resemblance indicates real affinity. Until, however, something more is known of the leaves of *Colpoxylon*, it would not be admissible to unite our species with that genus: of specific identity there can of course be no question. It may be doubted whether *Colpoxylon* will ultimately maintain its claims to generic rank, though the attempt of WEBER and STERZEL to identify it specifically with *Medullosa Leuckarti* seems quite inconsistent with its very distinct structure.

In so simple a form of *Medullosa* as *M. anglica*, the Fern-characters come out so

\* *Loc. cit.*, vol. 2, p. 299, Plate 68.

† 'Ueber *M. Leuckarti*,' p. 196.

distinctly that one might be inclined to doubt, with M. ZEILLER, whether these plants were after all anything more than peculiar and highly modified Ferns.\* Yet even in this species clear indications of Cycadean affinities are present. The whole structure of the petiole and leaf generally is strikingly like that of the Cycads; just as much so, in fact, as in any other "*Myeloxylon*."† The occasional formation of accessory bundles in the cortex of the stem is suggestive of Cycadean anomalies, comparable with those observed by WEBER and STERZEL in other species of *Medullosa*. The structure of the roots, never before observed in any member of the group, weighs appreciably on the Cycadean side, though, on the other hand, the abundant production of adventitious roots is in itself a decidedly Pteridophytic character. The course of the leaf-trace bundles—a number of the principal traces passing out into each leaf, and at the same time increasing their number by repeated sub-division—is quite peculiar, differing essentially both from the system in existing Cycadaceæ, and from that in the extinct Bennettiteæ.‡ A better analogy may be sought in those polystelic Ferns which have numerous leaf-trace bundles, markedly smaller than the steles of the stem.§

On the whole, however, it is evident that *Medullosa anglica*, like other Medulloseæ, combined Cycadean with Filicinean characters, though in this comparatively simple species the resemblance to Ferns is more prominent than in other members of the group.

The fact, now, as it seems to me, established, that the leaf-traces of *Medullosa* were concentric in structure on first leaving the steles, throws a welcome light on SEWARD'S *Rachiopteris Williamsoni*, a fossil petiole which that author separated from *Myeloxylon* on the ground, among others, that its vascular bundles are concentric and not collateral.|| The general resemblance to *Myeloxylon* is manifest, and there is no reason to doubt that it indicates near relationship, for it is perfectly conceivable that in some of the Medulloseæ the foliar bundles may have retained concentric structure in the petiole, instead of losing it in their passage through the cortex. Similar variations among recent Ferns will at once occur to any botanist. The wood of the bundles in *Rachiopteris Williamsoni* is quite comparable in structure to the primary part of the undivided leaf-traces in *Medullosa anglica*, and, as sections in my possession show, the pitting on the tracheæ is of the same kind. We may

\* ZEILLER, 'Flore Fossile d'Autun et d'Épinac,' vol. 1, p. 289; "Observations sur quelques Fougères des Dépôts Houillers d'Asie Mineure," 'Bull. Soc. Bot. de France,' vol. 44 (1897), p. 201.

† I have not found anything but *exarch* bundles (with centripetal wood only) in the leaf-stalks. In one or two cases *mesarch* (diploxylic) bundles have been described in other "*Myeloxylon*" petioles and in the cortex of *Colpoxylon*, but as a rule the structure is exactly as in our species.

‡ SOLMS-LAUBACH, "Die Sprossfolge der *Stangeria*," 'Bot. Zeitung,' 1890, p. 177.

§ Cf. DE BARY, 'Comp. Anat. of Phanerogams and Ferns,' English Edition, pp. 284–296.

|| SEWARD, "On *Rachiopteris Williamsoni*, a new Fern from the Coal-Measures," 'Annals of Botany,' vol. 8, 1894, p. 207.



reasonably suppose, then, that *Rachiopteris Williamsoni* was the petiole of some unknown Medullosean stem.

If we now compare the organization of our *Medullosa* with that of the species previously known, we find that the essential difference consists in the fact that in *M. anglica* the few steles are similar to one another, while in the other species they are differentiated into a central and a peripheral system.\* Polystely together with secondary thickening is a somewhat unpractical combination, which could never have reached any high development in the crude form in which it exists in *Medullosa anglica*. The steles, as they grew in thickness on all sides, must ultimately have got in one another's way. The structure, as shown in all the specimens investigated, is, in fact, not adapted to the attainment of arboreal habit. The difficulty is met in the four species, *M. stellata*, COTTA; *M. porosa*, COTTA; *M. Solmsii*, SCHENK; and *M. Leuckarti*, GÖPP. et STENZ., by the differentiation of a distinct system of peripheral steles forming a circle round the stem.† It was on the free outer side of these steles, where the space for new growth was unrestricted, that the chief formation of secondary wood and bast took place; on the inner side of the peripheral ring, and around the smaller internal steles, the growth in thickness was necessarily limited. Where, as in old specimens of *M. stellata* (var. *lignosa* of WEBER and STERZEL), the external secondary zone attained an enormous relative thickness,‡ and especially where the "pith" of the stem was small to begin with, the *Medullosa* characters sink into the background, and the structure might almost be taken for that of a somewhat anomalous stem of the ordinary Cycadean type. Can we regard such an organization as having really led on to the stem-structure of true Cycads? This hypothesis has been clearly stated by Mr. W. C. WORSDELL, with special reference to the relation between Medulloseæ and Cycadaceæ. He is led to the "provisional suggestion," "That the anomalous structures in Cycadean stems . . . . are remnants of some ancient structure once common to a large group of plants. That this structure consisted of rings or layers of concentric vascular strands. That, as time went on . . . . the cambium of the inner portion of each such concentric strand gradually became less and less functional, that of the outer portion, on the contrary, more and more active," and so on. "The result," he adds, "is finally the structure, as we at present know it, in the stem of *Cycas*, *Encephalartos*, and *Macrozamia*."§ Mr. WORSDELL is speaking especially of the anomalous zones of wood and bast in those genera, but would, I believe, extend his theory to the normal vascular ring. POTONIÉ arrived independently at a similar conclusion.|| Personally I regard these

\* Compare the illustrations of the various types in WEBER and STERZEL's monograph.

† The peripheral ring often becomes gamostelic in VAN TIEGHEM's sense, and in some cases appears to have constituted a single annular stele, like that in the *Dennstaedtia* section of *Dicksonia*, and many other Ferns.

‡ See, e.g., WEBER and STERZEL, *loc. cit.*, Plate 7, fig. 3. Here only one internal "star-ring" is present.

§ W. C. WORSDELL, "Anatomy of the Stem of *Macrozamia*," 'Annals of Botany,' vol. 10, 1896, p. 618.

|| 'Lehrbuch der Pflanzenpaläontologie,' 1897, p. 168.

views as fallacious, because the primary ground-plan of the stem-structure of a polystelic *Medullosa* was fundamentally different from that of the monostelic Cycadaceæ, though the ultimate result, in old stems, may have a certain similarity. If we are to suppose that the Cycadaceous type of stem came from that of the Medulloseæ at all (which is not my own view), I should prefer to derive it from some monostelic form, such as we find indicated in *Colpoxylon*. It is not impossible that such a stem, by gradual disappearance of the scattered internal tracheides, might have given rise to Cycadean structure. Extrafascicular zones occur in the same form in some Medulloseæ, as in certain recent Cycads, so it appears unnecessary to derive this part of the structure from a reduced system of rings.

The opinion is expressed by Count SOLMS-LAUBACH that the Medulloseæ may probably form a group different at once from the Ferns and from the Cycads, and may possibly represent the last derivative (becoming extinct in the post-carboniferous strata) of a series springing from the common parent-stock of those two classes.\* On present evidence I am disposed to accept this view of the Medulloseæ as a short divergent branch of the phylogenetic tree. That they have real affinity with Cycads (in the wide sense) is certain, but it does not seem probable that they lie on the direct line of descent of any of the later Cycadales at present known to us. As regards the "common parent-stock" referred to by Count SOLMS, I think it is probably to be sought among simple Ferns, or Fern-like plants, with a structure more like that of *Heterangium* than of any other known genus.

As regards the origin of the later groups of the Cycadales, I still think that *Lyginodendron* affords the best clue; that is to say, I regard plants with that type of stem as nearer the direct line of descent than the Medulloseæ. From *Heterangium* we may perhaps trace two divergent series, the one advancing in the direction of polystely through such a form as *Medullosa anglica* to the more complex Medulloseæ, the other advancing by elaboration and modification of the single stele, through *Lyginodendron* *Oldhamium* to *L. robustum*, *Cycadoxylon*, and *Ptychoxylon*.† The two last genera may well have been already true Cycadales, with foliage perhaps of the *Pterophyllum* or *Sphenozamites* type, and the fructification of Gymnosperms.

It is useless at present to speculate on what the fructification of the Medulloseæ themselves may have been like, but it is quite possible that they also had attained to the formation of some kind of seed.

I have not thought it necessary to discuss the views of M. RENAULT, who still appears inclined to derive the whole of his Cycadoxyleæ (including Medulloseæ) from Lycopods rather than from Ferns. Considering the clear points of agreement which *Heterangium*, *Lyginodendron*, and *Medullosa* all present with the Ferns, in the structure of the stem, the structure and form of the leaf, and in habit, while there are

\* 'Ueber *Medullosa Leuckarti*,' p. 198.

† See RENAULT'S account of the Cycadoxyleæ in vol. 2 of the 'Flore Fossile d'Autun et d'Epinaç.' Also, SEWARD, "A Contribution to our Knowledge of *Lyginodendron*," 'Annals of Botany,' vol. 11, 1897.

no clear points of agreement with Lycopods, I cannot regard this view as consonant with the present state of our knowledge.

It is very interesting to find how the evidence is gradually accumulating which connects the Cycads (and by a less direct line, probably the other Gymnosperms also)\* with the Ferns. The fossil evidence, very strong by itself, is supported by the morphology of the reproductive organs, and by the great discovery of the multiciliate spermatozoids which we owe to IKENO and HIRASE, and to WEBBER. We thus see that external resemblance is not always fallacious; the Fern-like foliage of *Stangeria*, or of the "Maidenhair Tree," pointed in the right direction long before botanists were able to follow the clue.

The illustrations to this paper are partly photographic, partly from drawings. Of the photographs, some were taken for me by Dr. E. C. BOUSFIELD, others by Mr. L. A. BOODLE, while the drawings are the work of Mr. BOODLE and of Mr. G. T. GWILLIAM. The exact share taken by these three gentlemen in the illustration of the memoir is stated in the explanation of the plates.

I should like especially to express my thanks to Mr. L. A. BOODLE for the help he has given me in various ways during the preparation of the paper.

#### EXPLANATION OF PLATES.

Plates 5-8, photographs from the actual sections; many of these need to be examined with the aid of a lens. Photographs 2, 5, 6, 7, 8, 9, 10, 12, 13, 14, 15, 19, 20, and 21 are by Dr. E. C. BOUSFIELD; the remainder by Mr. L. A. BOODLE.

#### PLATE 5.

Phot. 1. Complete transverse section of Specimen II., taken from the lower part of the specimen, immediately below the portion shown in Plate 9; *a*, *b*, *c*, the three leaf-bases. At a higher level a new leaf-base (*bc*), shown in surface-view in Plate 9, fig. 1, and in section in photograph 3, appears between *b* and *c*, and still higher another (*ab*) arises between *a* and *b*. The order of the leaves from below upwards is *c*, *b*, *a*, *bc*, *ab*, indicating a  $\frac{2}{5}$  phyllotaxis. *pd.*, internal zone of periderm; within this the three steles, each with primary and secondary wood, are evident.  $\times 1\frac{2}{5}$ . S. 737.† (See p. 84. Compare diagram on p. 126.)

Phot. 2. General transverse section of Specimen I. *Pet.*, part of a large petiole, just becoming free from the stem. *o.c.*, outer cortex or hypoderma of another leaf-base; *ct.*, cortical parenchyma; on this side the hypoderma is lost;

\* Cf. COULTER, "Origin of Gymnosperms," 'Bot. Gazette,' vol. 26, 1898.

† Figures preceded by the letter S indicate the number of the slide in the author's collection.

*st.*<sup>1</sup>, *st.*<sup>2'</sup>, *st.*<sup>3'</sup>, the three steles; *st.*<sup>1</sup> is almost perfect, the others more broken.  $\times 2$ . S. 226. (See p. 86.)

Phot. 3. Part of a transverse section of Specimen II., at the level 3 marked in Plate 9, showing the leaf-base *bc* (of which the external surface is seen in Plate 9, fig. 1), and part of *b* (*cf.* phot. 1). The leaf-base shows the characters of *Myeloxylon Landriotii*, REN. *v.b.*, one of the vascular bundles; *m.c.*, a gum-canal; *pd.*, part of the periderm of stem; *sc.*, internal sclerenchyma between the leaf-base *b*, and stem.  $\times 3$ . S. 740. (See p. 100.)

Phot. 4. Part of a transverse section of Specimen I., at a level below that of phot. 2, and above that of phot. 5. The stele *st.*<sup>1</sup> is here divided into two parts; *an.*, accessory vascular strand outside *st.*<sup>1</sup>; *st.*<sup>2'</sup>, part of the next stele. A number of leaf-trace bundles are also shown.  $\times 2\frac{1}{2}$ . S. 578. (See p. 91.)

#### PLATE 6.

Phot. 5. Transverse section of Specimen I., including all three steles. Right and left-hand reversed as compared with photos. 2 and 4. The level is about 2 centims. below that of phot. 4, and about 4 or 5 centims. below that of phot. 2. The two halves of *st.*<sup>1</sup> have reunited. At its right hand end the phloem is preserved. The other steles are also well shown, and their limits evident, in spite of fractures. *o.c.*, hypoderma of a leaf-base, identical with *Pet.* in phot. 2; *sc.*, its internal sclerenchyma; numerous leaf-trace bundles are shown; *v.b.*, the two bundles shown enlarged in phot. 14. For details, see photos. 7 and 9.  $\times$  nearly 3. S. 579. (See pp. 86 and 91).

Phot. 6 (Specimen I.). Part of stele 1 in transverse section. *x*, primary wood, consisting of tracheides and conjunctive parenchyma; *x*<sup>2</sup>, secondary wood; *l.t.*, leaf-trace bundle just separating from stele; it has a fan of secondary wood on its outer side.  $\times 18$ . S. 581. (See p. 92.)

Phot. 7 (Specimen I.). The same part, from a section about 1 centim. higher up the stem. *px.*, probable position of a protoxylem group; *l.t.*, the leaf-trace shown in phot. 6, which has here become free from the stele, and is surrounded by secondary wood.  $\times 18$ . S. 579. (See p. 92.)

Phot. 8 (Specimen I.). Parts of steles 1 and 2 in transverse section; primary and secondary wood evident, and phloem of stele 2 partly preserved. *l.t.*<sup>1</sup>, leaf-trace beginning to detach itself from stele 2; *l.t.*<sup>2</sup>, large leaf-trace already free. Other leaf-traces are shown.  $\times 10$ . S. 581. (See pp. 92 and 94).

Phot. 9 (Specimen I.). The same part, from a section about 1 centim. higher up the stem. The leaf-trace, *l.t.*<sup>1</sup>, is here just free from its stele; *l.t.*<sup>2</sup> is beginning to divide. Other leaf-traces shown.  $\times 10$ . S. 579. (See pp. 92 and 94).

## PLATE 7.

- Phot. 10 (Specimen I.). Radial section from a series cut a little below the transverse sections figured in Plate 6, crossing steles 1 and 2 at right angles. *st.*<sup>1</sup>, shown in tangential section through the secondary wood; *st.*<sup>2</sup>, shown in radial section. Leaf-traces are seen in the cortical tissue on either side.  $\times 3$ . S. 596. (See p. 95.)
- Phot. 11. From an adjacent section to the preceding, showing part of stele 2 in radial section, with a leaf-trace, *l.t.*, passing out from the stele.  $\times 4$ . S. 595. (See p. 93.)
- Phot. 12 (Specimen I.). Part of a longitudinal section, from a series cut between transverse sections 578 (phot. 4) and 226 (phot. 2), parallel to long axis of stele 1, a part of which is shown in radial section. *x.*, primary wood, showing the strands of tracheides and conjunctive tissue; *x.*<sup>2</sup>, secondary wood in radial section. The arrow marks the limit between the two.  $\times 10$ . S. 576. (See p. 88.)
- Phot. 13. Secondary tracheides from the same radial section, to show bordered pits.  $\times 90$ . (See p. 90.)
- Phot. 14 (Specimen I.). Part of the transverse section 579, to show the two collateral leaf-trace bundles marked *v.b.* in phot. 5. *x.*, xylem of one of the bundles, with its protoxylem towards the phloem, *ph.*; cortical tissue of stem and a fragment of internal sclerenchyma (*sc.*) also shown.  $\times 35$ . (See p. 94.)
- Phot. 15 (Specimen I.). Two similar bundles from the base of a leaf. *x.*, xylem; *ph.*, phloem of one of the bundles.  $\times 55$ . S. 581. (See p. 95.)
- Phot. 16. Part of a transverse section from a detached piece of stem, probably forming part of Specimen IV., showing the axil of a leaf. *st.*, part of a stele; *pd.*, periderm of stem; *o.c.*, hypoderma, in oblique section, continuous with the torn hypoderma of the petiole, *pet.*  $\times 1\frac{1}{10}$ . S. 792. (See p. 100.)
- Phot. 17 (Specimen II.). Tangential section, from a longitudinal series, cut immediately above the level 4 at top of fig. 1, Plate 9, and parallel to the free surface of specimen. The section passes chiefly through the hypoderma, showing "*Sparganum*" structure and gum-canals. To the right it cuts more deeply into the tissues, showing the parenchyma and vascular bundles (*v.b.*) of a leaf-base.  $\times 1\frac{3}{4}$ . S. 742. (See p. 99.)

## PLATE 8.

- Phot. 18. Partial transverse section of a free petiole from the same block as Specimen I. Structure as in *Myeloxylon Landriotii*, REN. *m.c.*, gum-canals, also conspicuous in hypoderma. *v.b.*, collateral vascular bundles.  $\times 4$ . S. 685. (See p. 101.)

- Phot. 19. Transverse section of a large triarch root. *px.*, the three prominent protoxylem-angles, two of which have broken away from the stele. In the middle is the primary wood, with secondary wood and bast between the protoxylem-groups. *rt.*, vascular strand of rootlet, connected with *px.*; *pd.*, periderm.  $\times 8$ . S. 567. (See p. 102.)
- Phot. 20. Longitudinal section of two roots, *r.*<sup>1</sup> and *r.*<sup>2</sup>, the former complete, but somewhat compressed. *pd.*, periderm; *x.*, wood of root. The secondary wood is partly in radial section, showing pits and medullary rays.  $\times 20$ . S. 569. (See p. 103.)
- Phot. 21. Transverse section of triarch rootlet, showing the stele, with primary and secondary xylem, phloem-groups, pericycle, phellogen, and broad zone of periderm. At *rt* a lateral rootlet branches off, opposite one of the protoxylem-angles.  $\times 50$ . S. 569. (See p. 104.)
- Phot. 22. Tangential section from a fragment of stem, showing the bases of four adventitious roots (*r.*<sup>1</sup>–*r.*<sup>4</sup>). *M.c.*, cortex, with *Medullosa* structure, connected with the roots on either side.  $\times 2$ . From outermost section of Mr. WILD's specimen, lent by him. (See p. 105.)
- Phot. 23. Part of another tangential section of Mr. WILD's specimen, cut further to the interior. *st.*, a stele of the stem, with which the roots *r.*<sup>1</sup>–*r.*<sup>4</sup> in phot. 22 have united; *ped.*, series of root-pedicels, in oblique section; *r.*, two young roots, one free, the other attached to a pedicel. These roots are shown on a larger scale in Plate 13, fig. 21.  $\times 3\frac{1}{4}$ . S. 720. (See p. 106.)
- Phot. 24. Part of a radial section from Specimen IV. of *Medullosa anglica*, to show insertion of adventitious roots. *st.*, a stele of the stem; *lt.*, leaf-trace bundle connected with stele by radial system of tracheides; *pd.*, periderm; *r.*, young roots in tangential section, connected with cortex; *r.*', free root.  $\times 4$ . S. 782. (See p. 107.)
- Phot. 25. From another radial section of Specimen IV. *st.*, part of a stele; *ped.*, root-pedicel in median section, showing bifurcating bundle; *r.*, young root borne on pedicel; *r.*<sup>1</sup>, larger root, in transverse section, shown on an increased scale in Plate 13, fig. 22; *o.c.*, sclerenchyma of a leaf-base.  $\times 4$ . S. 783. (See p. 107.)

Plates 9–13. Figures from drawings. Figs. 1, 2, 4, 8, 10, 12, 14, 18, and 20 are by Mr. G. T. GWILLIAM; the remainder by Mr. L. A. BOODLE.

## PLATE 9.

Fig. 1. External view of Specimen II., showing all that part of the block in which the surface of the *Medullosa* is exposed. 2, 3, 4, planes from which transverse sections have been prepared. Phot. 1 is from a section cut

at the top of the lowest piece (not shown), immediately below the plane 2. The longitudinal sections were cut just above 4, from a piece not shown.  $\alpha$ ., external surface of a leaf-base which extends the whole length of specimen (*cf.* phot. 1). In the upper part it is much flattened out by pressure.  $c$ ., *inner* concave surface of another leaf-base,  $c$ ., which had split away (see crack in phot. 1). Note the finer striation of the internal sclerenchyma. Between  $\alpha$ . and  $c$ ., at the bottom, the inner cortex is exposed.  $bc$ ., a new leaf-base, which appears about at the line Z; its external surface is *convex*. This leaf-base is shown in transverse section, at the plane 3, in phot. 3. The leaf-base,  $b$ , shown in photograph 1, is not seen here, as it lies at the back of the specimen. Natural size. (See p. 84.)

## PLATE 10.

- Fig. 2. Diagrammatic transverse section of Specimen I., at a level just below that of phot. 5.  $st.^1$ ,  $st.^2$ , and  $st.^3$ , the three steles, as shown in detail in phot. 5.  $lt.^1$ , large undivided leaf-trace bundles;  $lt.^2$ , smaller leaf-traces after sub-division; many of both kinds are shown.  $o.c.$ , hypoderma;  $sc$ ., internal sclerenchyma. The triangular space between  $o.c.$  and  $sc$ . (towards C) is part of a leaf-base, identical with the petiole shown, at a higher level, in phot. 2. On the side A the hypoderma is lost, but the ground-tissue better preserved. On the side B is a part of another leaf-base. The ground-tissue is shaded, where preserved.  $\times 2$ . S. 580. (See p. 86.)
- Fig. 3 (Specimen I.). Transverse section of secondary wood and bast of stele 3.  $x.^2$ , secondary wood;  $ph.^2$ , secondary phloem, the larger elements probably the sieve-tubes; slight remains of cambium are present between wood and phloem.  $\times$  about 50. S. 578. (See p. 89.)
- Fig. 4 (Specimen II.). Radial section through part of the primary and secondary wood of a stele.  $x$ ., primary wood, with tracheides and abundant parenchyma. One primary tracheide is pitted, the rest spiral or scalariform.  $x.^2$ , secondary wood, showing medullary rays.  $\times 35$ . S. 751. (See p. 89.)
- Fig. 5 (Specimen I.). Radial section through part of the primary and secondary wood of stele 1.  $px$ ., spiral elements of protoxylem;  $x$ ., inner part of primary wood; some tracheides pitted; parenchyma only partly preserved;  $x.^2$ , secondary wood; bordered pits of tracheides shown in places.  $\times$  about 110. S. 597. (See p. 89.)
- Fig. 6 (Specimen II.). Part of periderm of stem in radial section, with phellogen and cells of primary cortex to the left. The transverse section is quite similar.  $\times 43$ . S. 747. (See p. 96.)
- Fig. 7 (Specimen III.). Small portion of periderm of stem, in tangential section.  $\times 43$ . S. 770. (See p. 96.)

## PLATE 11.

- Fig. 8 (Specimen II.). Tangential section of secondary wood. *tr.*, tracheides; *m.r.*, medullary rays.  $\times 44$ . S. 750. (See p. 89.)
- Fig. 9 (Specimen I.). Tangential section of phloem from stele 1. *ph.*<sup>2</sup>, strands of sieve-tubes in secondary phloem; *r.*, phloem-rays; *m.c.*, gum-canal in pericycle (?); *hy.*, fragments of fungal hyphæ.  $\times 40$ . S. 595. (See p. 90.)
- Fig. 10 (Specimen I.). Transverse section of a large undivided leaf-trace bundle, given off from stele 1. *x.*, primary xylem, consisting of large tracheides, with a little conjunctive parenchyma; *px.*, protoxylem; *x.*<sup>2</sup>, secondary wood, extending all round, except for accidental ruptures. On the border of primary and secondary wood, the pitted walls of short tracheides are seen. *ph.*, phloem, imperfectly preserved.  $\times 50$ . S. 582. (See p. 92.)
- Fig. 11 (Specimen I.). Radial section of the large leaf-trace, *l.t.*<sup>2</sup>, shown in transverse section in photos. 8 and 9. *x.*, primary wood of leaf-trace, consisting chiefly of pitted tracheides, becoming scalariform and spiral towards the protoxylem, *px.*; *x.*<sup>2</sup>, secondary wood, of very unequal thickness on the two sides. Towards the left many short tracheides are shown.  $\times$  about 45. S. 601. (See p. 93.)
- Fig. 12 (Specimen I.). Transverse section, showing a number of small leaf-trace bundles, probably belonging to a leaf-base, as they lie outside the internal sclerenchyma, *sc.* The two groups *v.b.*<sup>1</sup> and *v.b.*<sup>2</sup> each arise from the subdivision of a single strand. *pd.*, double layer of periderm enclosing part of the sclerenchyma.  $\times 12$ . S. 580. (See p. 94.)
- Fig. 13 (Specimen I.). Small portion of the external tissue of a leaf-base, in transverse section. *cu.*, probably cuticle. The epidermis and next layer have palisade form. *sc.*, part of hypodermal sclerenchyma.  $\times 88$ . S. 735. (See p. 99.)

## PLATE 12.

- Fig. 14 (Specimen I.). Transverse section of the hypoderma of a leaf-base. The outer surface (from which the external tissues have perished) is directed upwards. The fibrous strands and intermediate parenchyma are obvious. *m.c.*, gum-canals.  $\times 23$ . S. 580. (See p. 99.)
- Fig. 15 (Specimen I.). Radial section of a collateral vascular bundle from a leaf-base. *x.*, xylem, containing scalariform and spiral tracheides only; *px.*, protoxylem; *ph.*, phloem.  $\times$  about 85. S. 588. (See p. 95.)
- Fig. 16. Transverse section of the rachis of a pinna, from same block as Specimen I.



Note the wings on upper surface; *v.b.*, vascular bundles, forming a ring, with phloem outwards, around a gum-canal; *m.c.*, other gum-canals. The hypoderma is almost continuous.  $\times$  about 50. S. 687. (See p. 101.)

Fig. 17. Transverse section of a leaflet (associated with rachis, petioles and stem of Specimen I.). *v.b.*, vascular bundles. The two in the midrib have their phloem directed laterally; those in the lamina are in longitudinal or oblique section. Note the palisade tissue towards upper surface.  $\times$  36. S. 691. (See p. 101.)

Fig. 18 (Specimen II.). Accessory vascular strand from a transverse section of the stem, cut at the level 2 (*cf.* Plate 9, fig. 1). *tr.*, tracheides in the central parenchyma. *x.<sup>2</sup>*, secondary wood; some of the tracheides are horizontal. *ph.*, remains of phloem and cambium; *i.c.*, inner cortex.  $\times$  28. S. 738. (See p. 98.)

Fig. 19. Transverse section of small rootlet. *px.*, the three protoxylem-groups. *pd.*, pericyclic periderm beginning to develop. Beyond this are the endodermis and primary cortex, as described in text.  $\times$  90. S. 696. (See p. 104.)

#### PLATE 13.

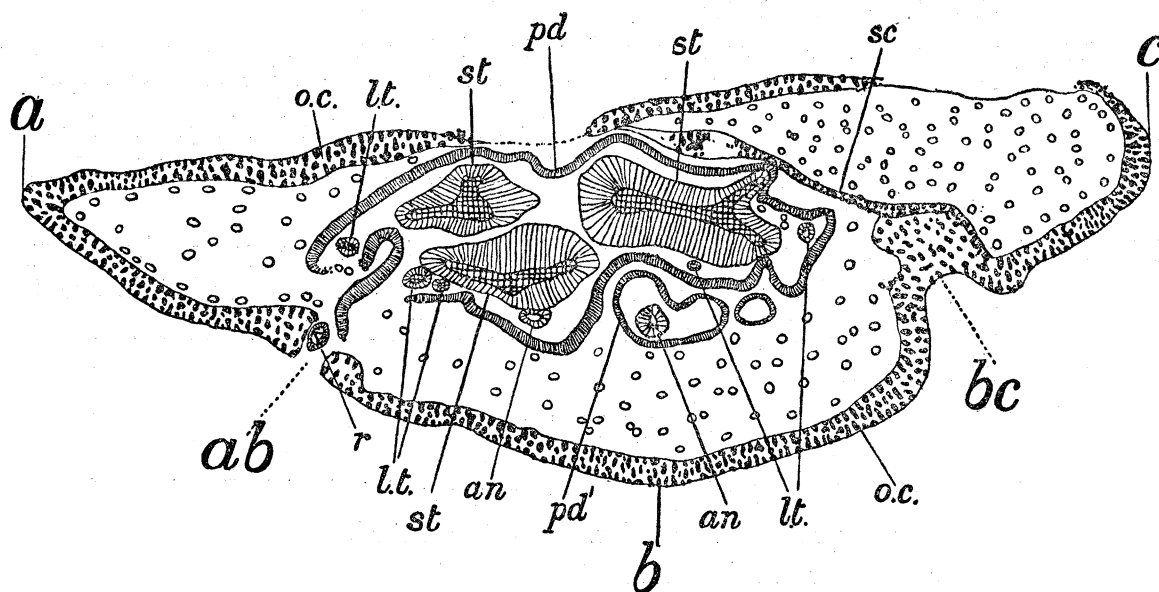
Fig. 20. Transverse section of a large triarch root, associated with Specimen I. *px.*, the three protoxylem-angles. To the interior is the primary wood. *x.<sup>2</sup>*, secondary wood, interrupted opposite the protoxylem-groups; *ph.*, phloem; *pd.*, periderm.  $\times$  25. S. 731. (See p. 102.)

Fig. 21. From Mr. WILD's specimen, showing the two roots marked *r.* in phot. 23. One root is free, the other is still seated on its pedicel, which forms part of the cortex of the stem. *px.*, the three protoxylem groups of the two triarch roots. (The long axis of the xylem is vertical in nature.) *pd.*, periderm; *c.*, primary cortex of the free root, partly cast off; *rt.*, rootlets. (In the free root the parenchymatous cells are shown rather too small and numerous.)  $\times$  19. S. 720. (See p. 106.)

Fig. 22 (Specimen IV.). Part of the root marked *r.<sup>1</sup>* in phot. 25, in transverse section. *px.*, the three protoxylem-groups of the asymmetric wood. In the natural position the long axis is vertical. *pd.*, internal periderm. Beyond this is primary cortex, with "secretory sacs."  $\times$  36. S. 783. (See p. 107.)

Fig. 23. Section of Mr. BUTTERWORTH's specimen, showing four root-pedicels, *a*, *b*, *c*, *d*. In *b*, the stele has an apparent pith; in *c* it is triarch. The pedicels are coated by periderm, and united at their bases. *My.*, associated *Myeloxylon* leaflets.  $\times$   $4\frac{2}{3}$ . (See p. 108.)

Fig. 24. Stele of pedicel *c* in the last figure, shown in obliquely transverse section. *px.*, one of the three protoxylem-angles of the triarch primary xylem; *x.<sup>2</sup>*, secondary wood; *ph.*, phloem.  $\times$  about 30. (See p. 108.)

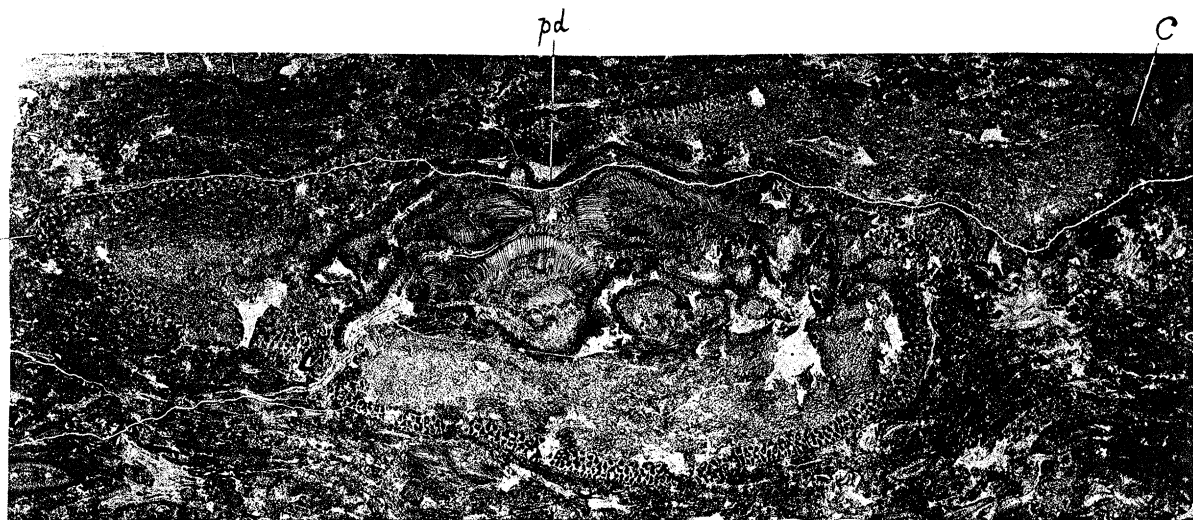


*Medullosa anglica*.—Diagrammatic transverse section of Specimen II., to serve as a key to photograph 1. *a, b, c*, the three leaf-bases; *bc, ab*, position of the next two leaf-bases above; *st*, the three steles, each with primary and secondary wood; *lt.*, leaf-traces given off from the steles; *an*, accessory vascular strands; *pd*, zone of periderm; *pd'*, isolated rings of periderm, one of which encloses an accessory strand; *o.c.*, outer cortex or hypoderma; *sc*, internal sclerenchyma delimiting the leaf-base *c*, on the inner side; *r*, root passing out between two leaf-bases.

Compare Plate 5, photograph 1, which is from the same section, and on the same scale. In the diagram the *relative*, but not the absolute, number of vascular bundles in the three leaf-bases is indicated.

The order of insertion of the leaf-bases, from below upwards, is *c, b, a, bc, ab*, which corresponds to a  $\frac{2}{5}$  phyllotaxis.

PHOT. 1



PHOT. 2



v.b.  
m.c.

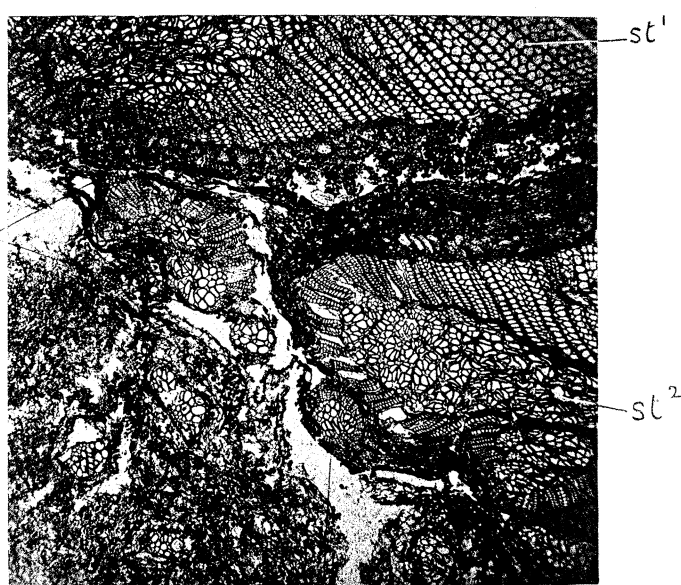
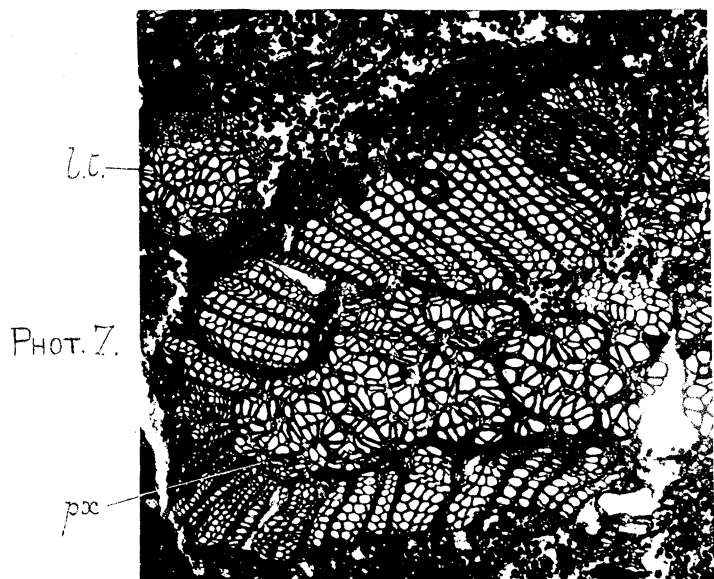
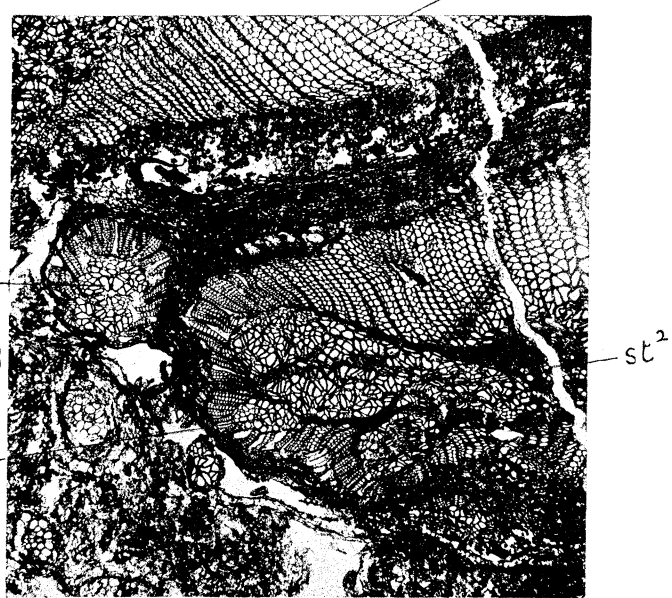
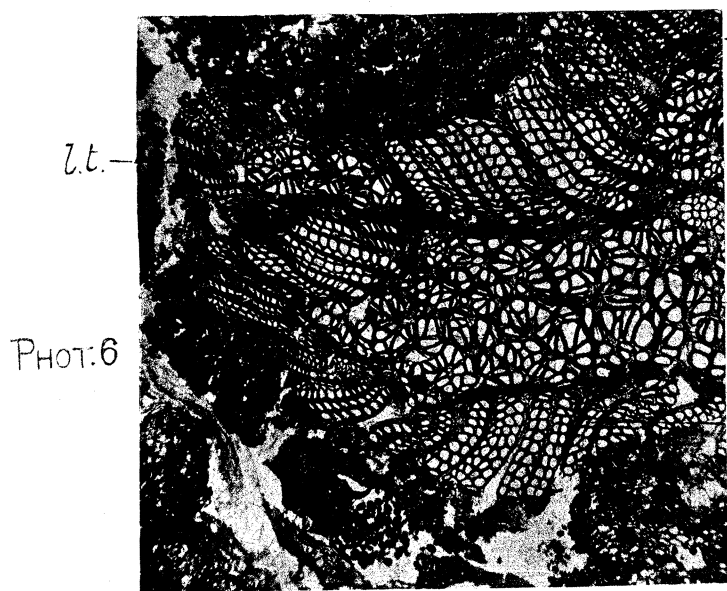
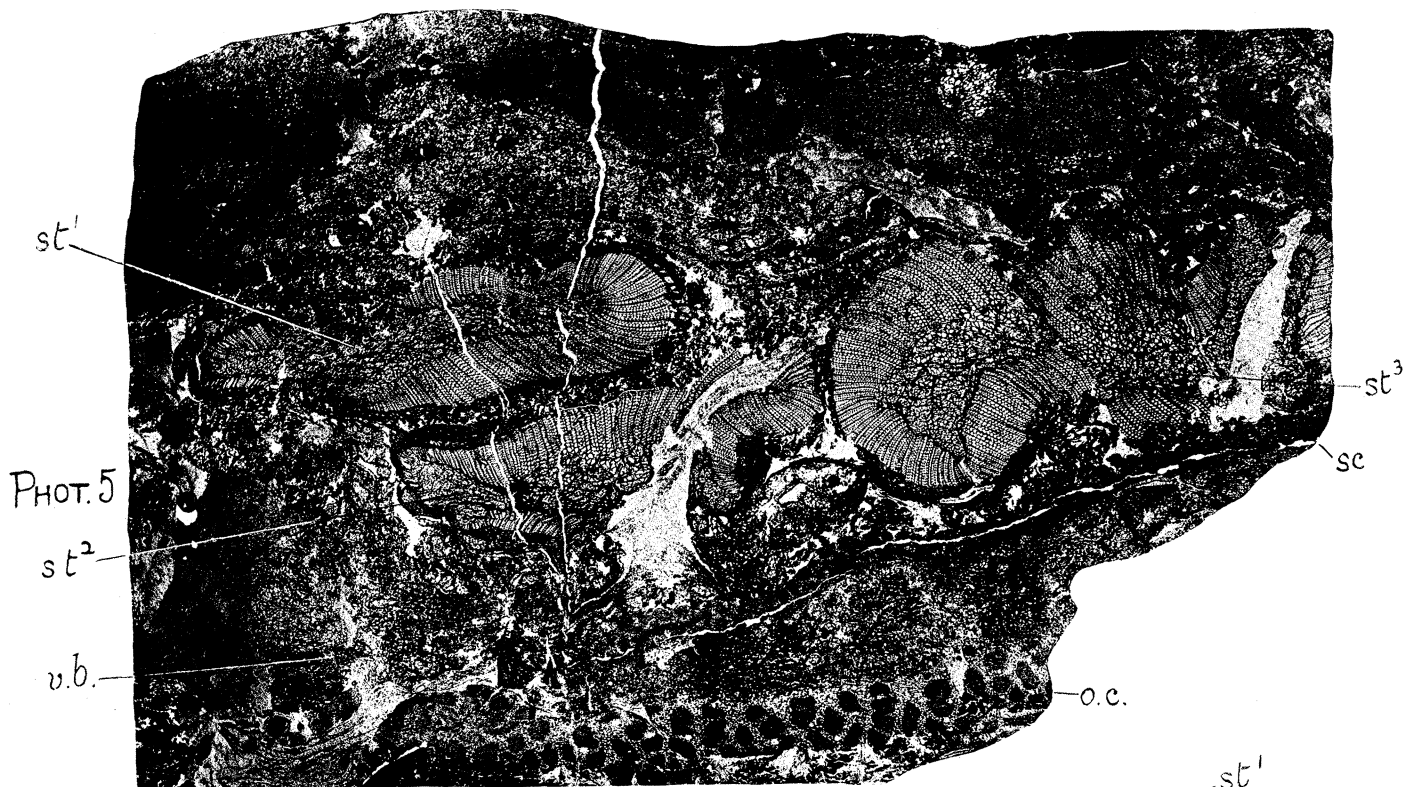


PHOT. 3.



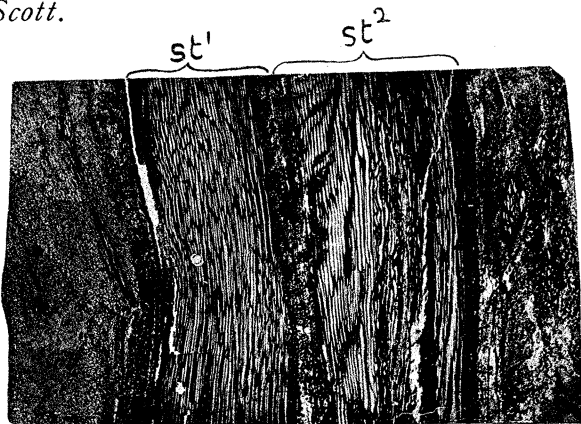
PHOT. 4.

Medullosa Anglica.





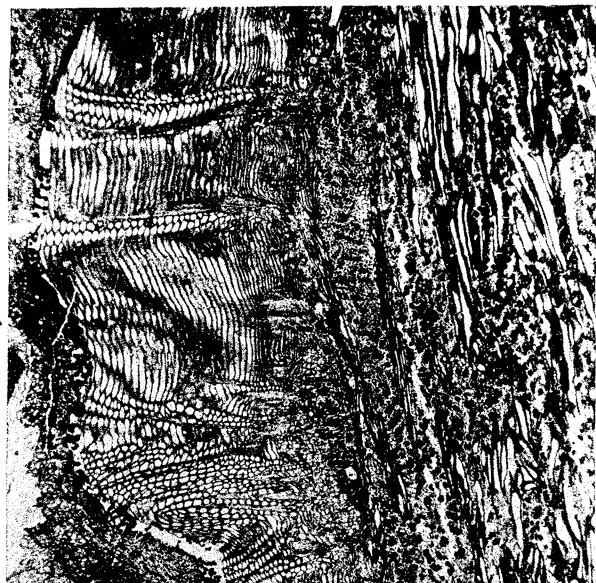
PHOT. 10.



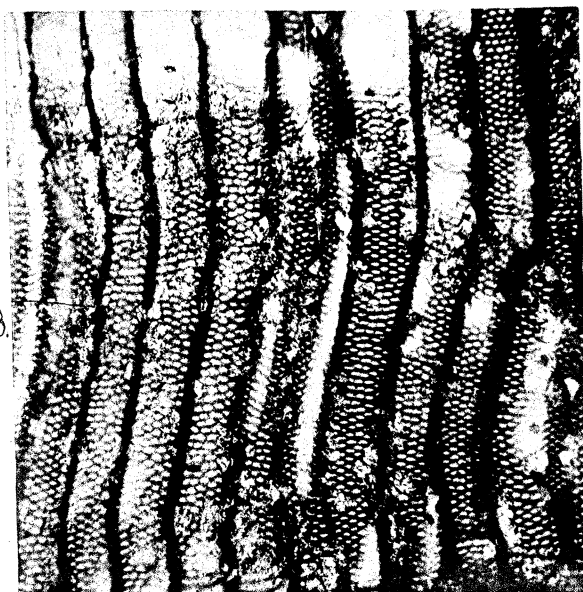
PHOT. 11



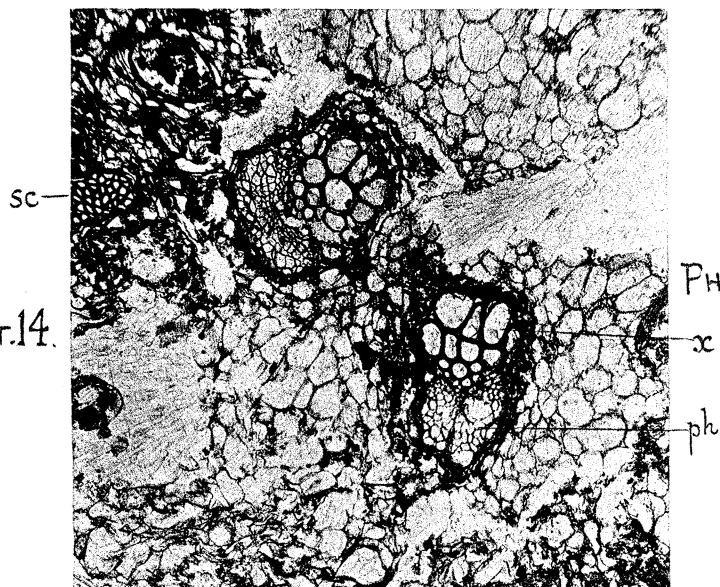
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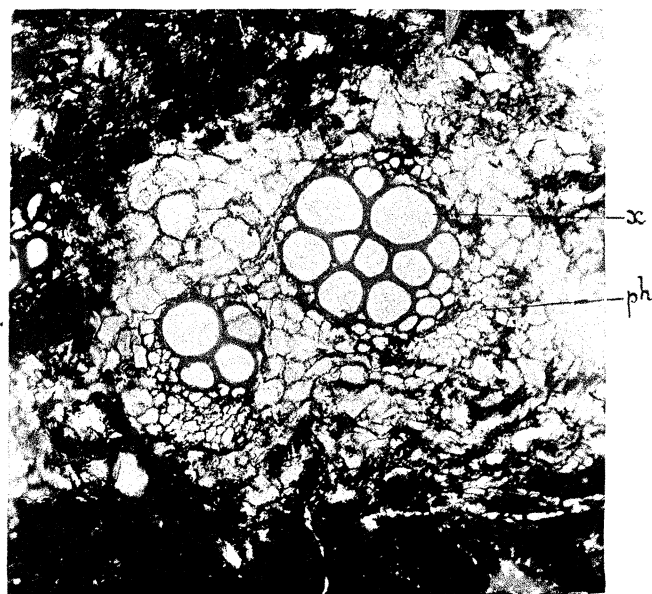
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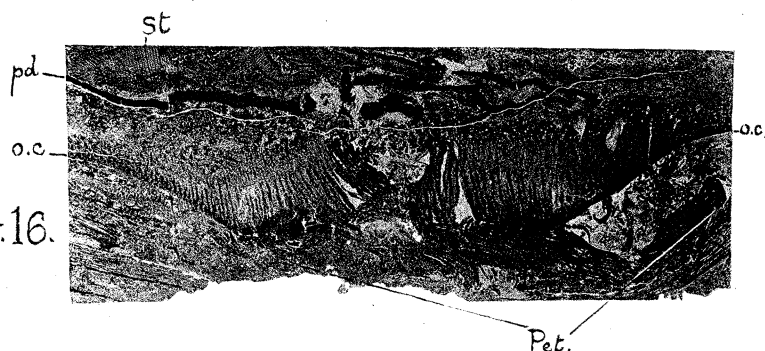
PHOT. 14.



PHOT. 15.

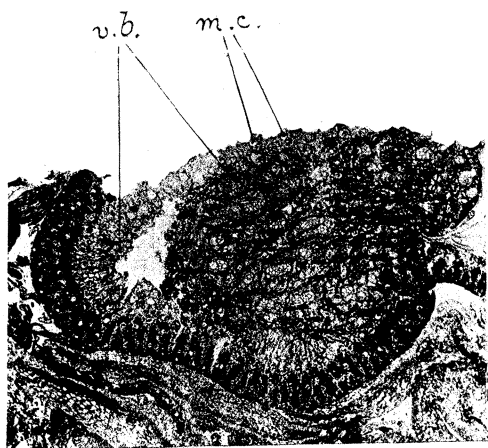


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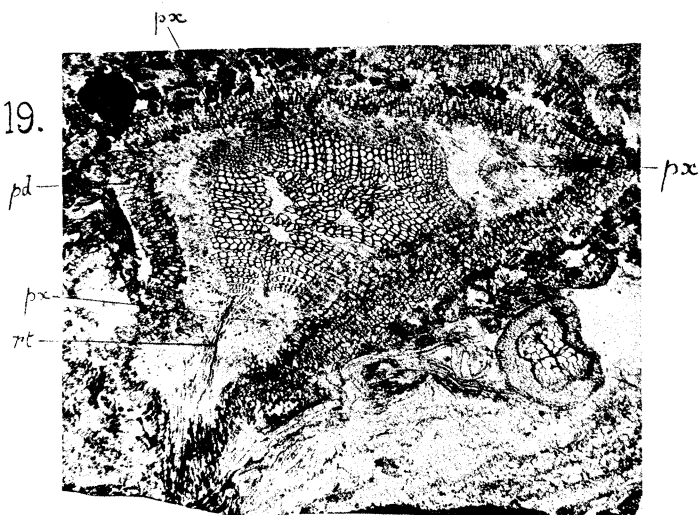


PHOT. 17.

PHOT. 18.



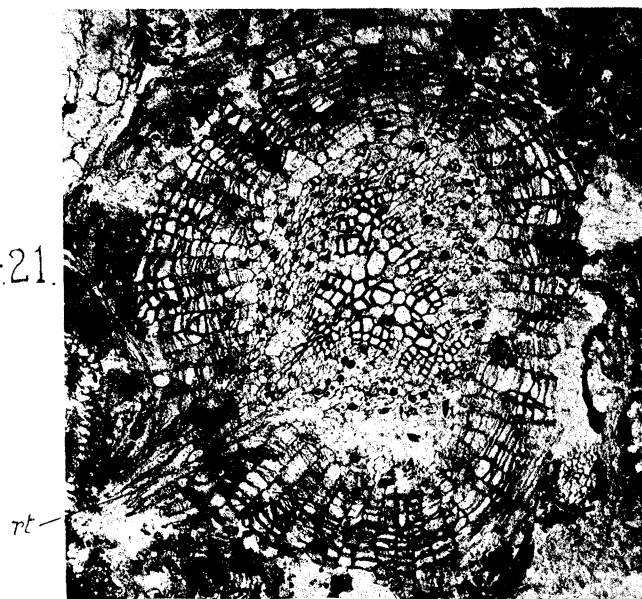
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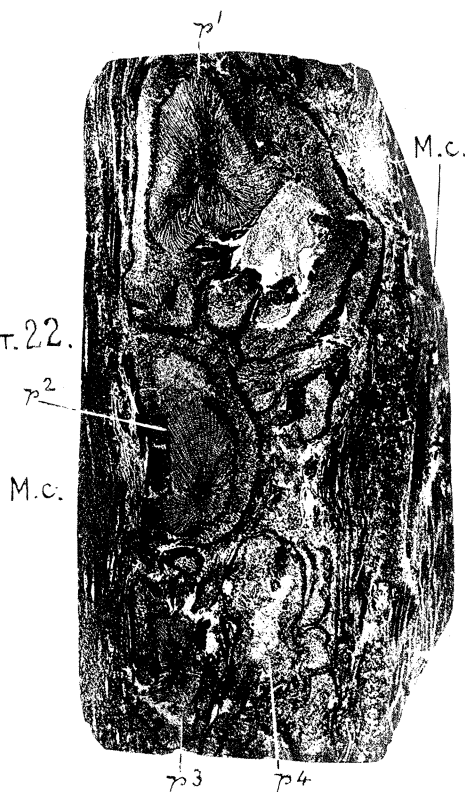
PHOT. 20.



PHOT. 21.



PHOT. 22.



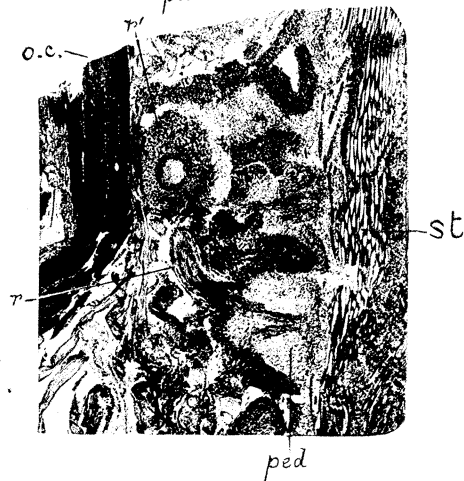
PHOT. 23.



PHOT. 24.



PHOT. 25.



Medullosa Anglica.

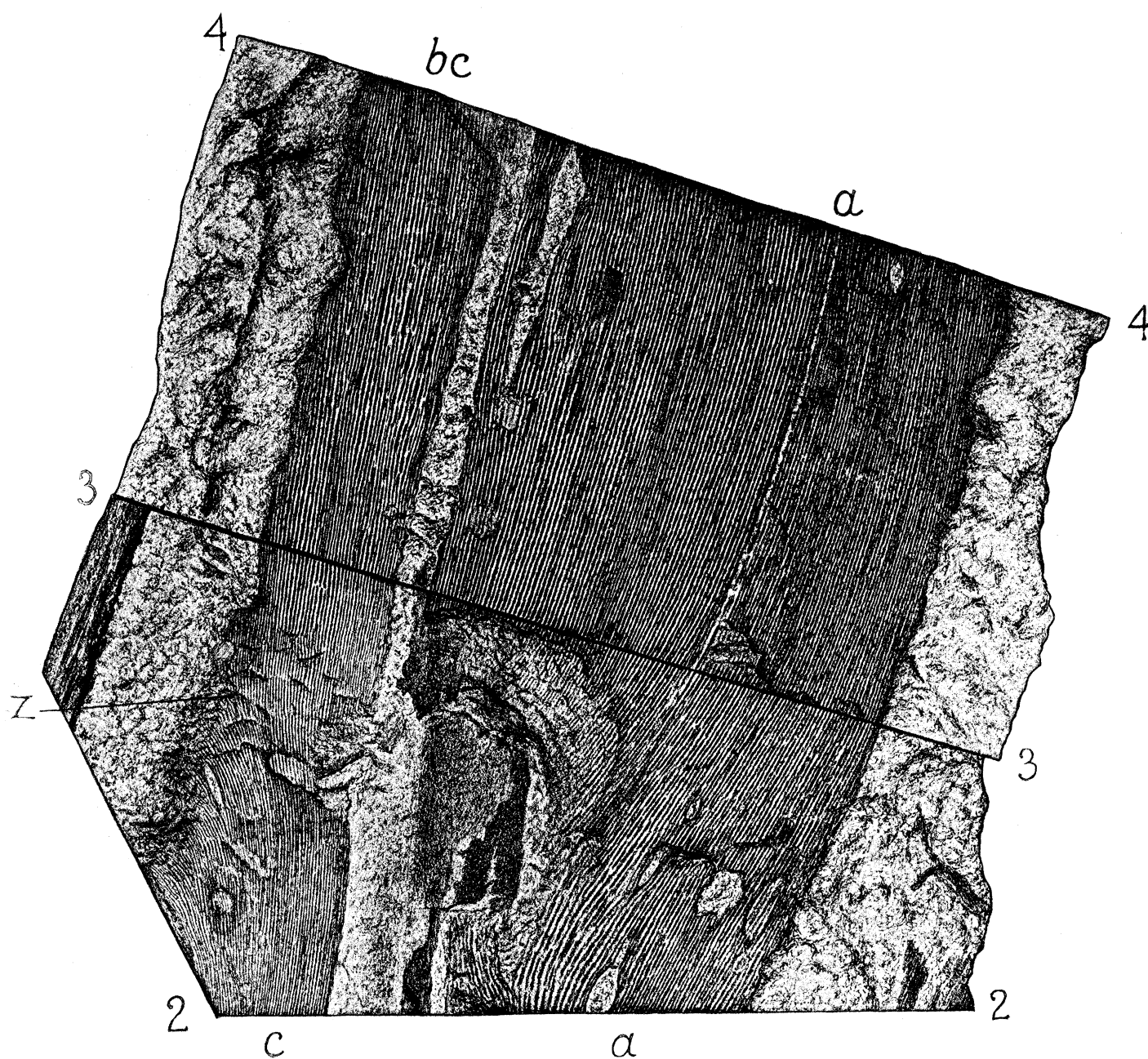
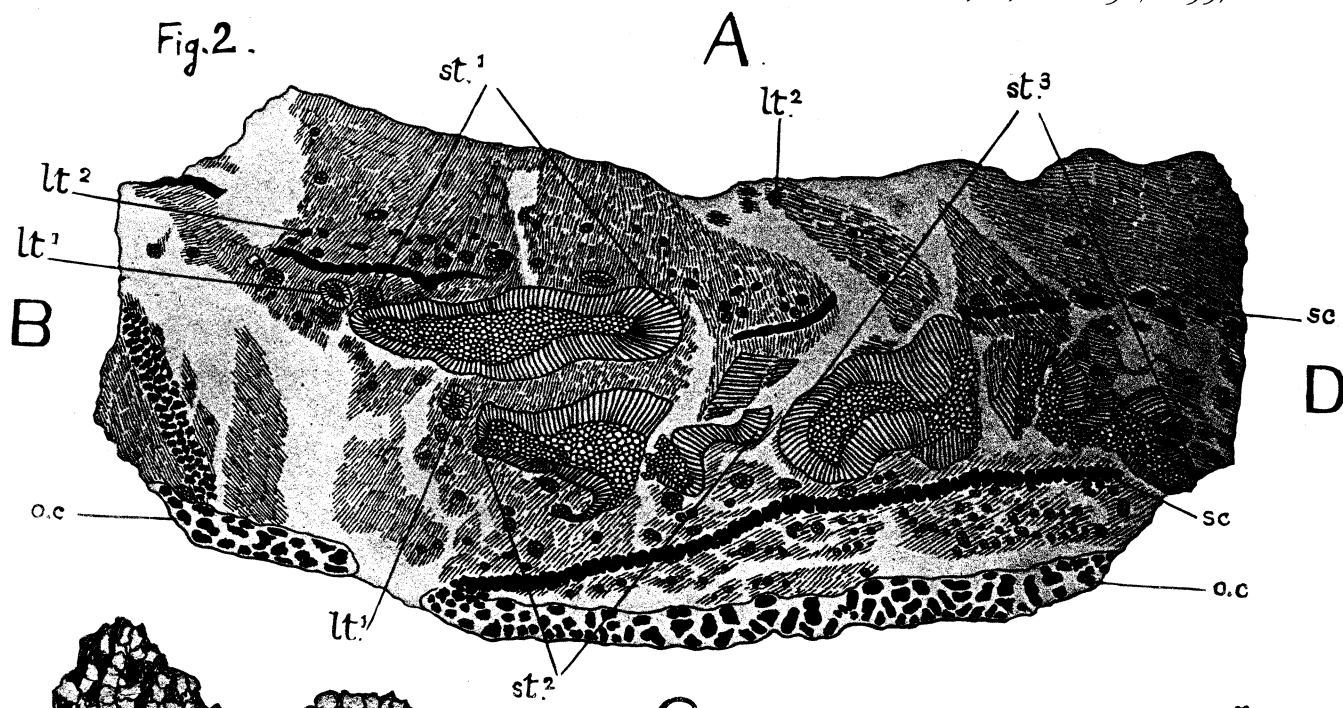


Fig. 1.

Medullosa Anglica.



Fig. 2.



C

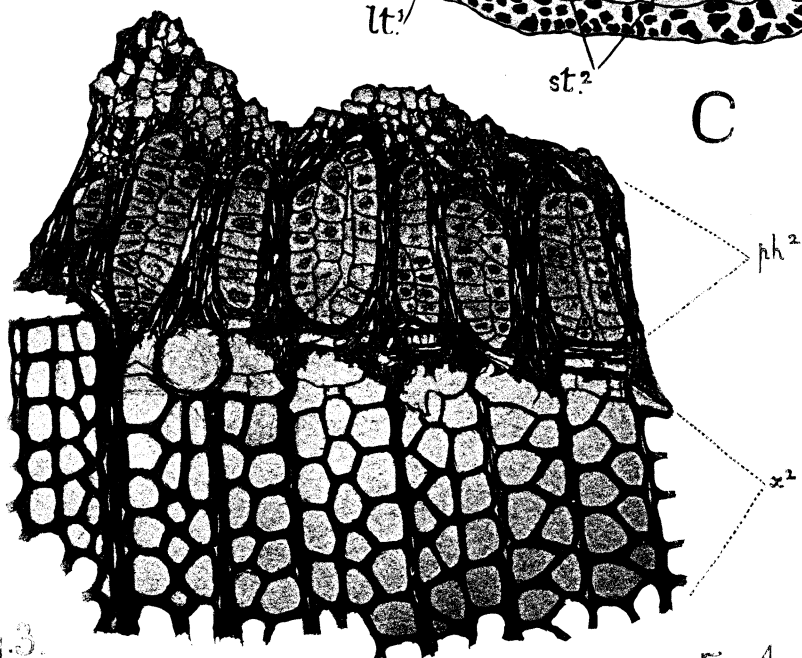


Fig. 4.

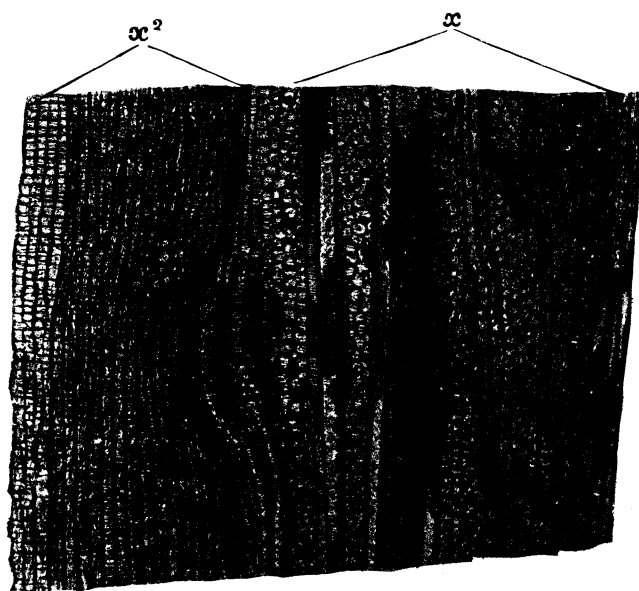


Fig. 3.

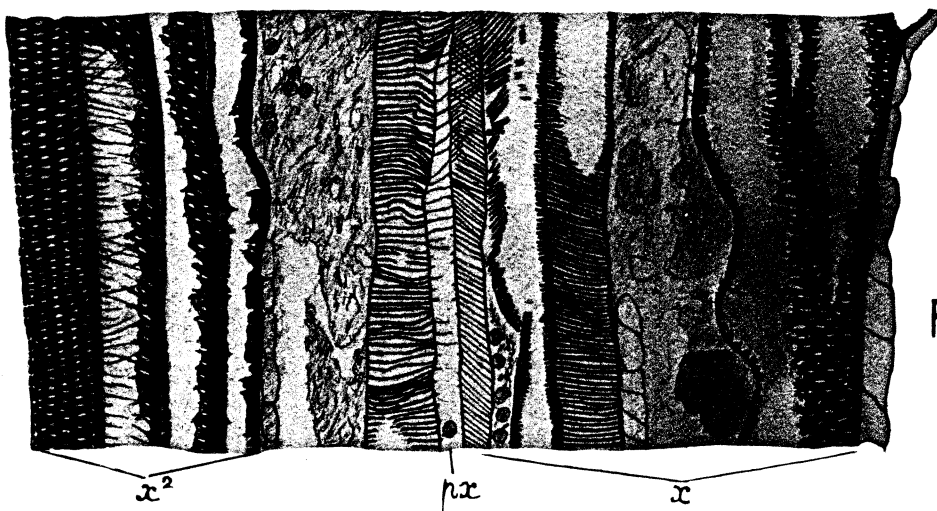


Fig. 5.

Fig. 6.

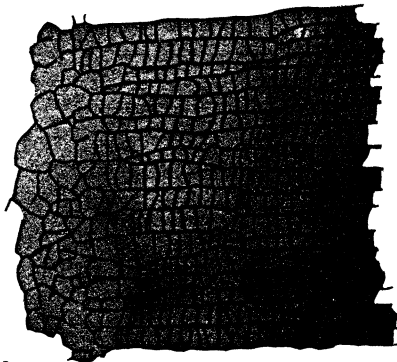
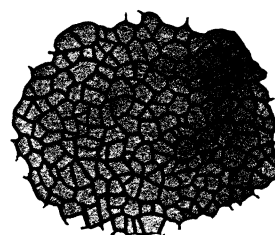


Fig. 7.



Medullosa Anglica.



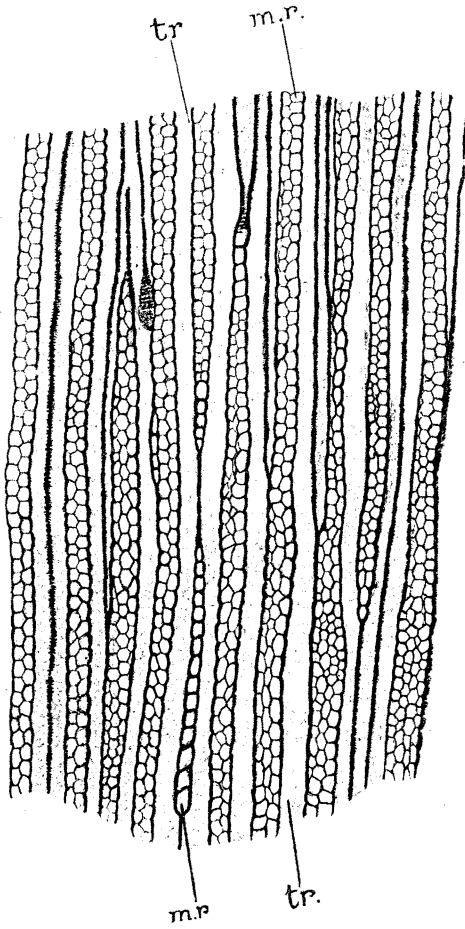


Fig. 8.

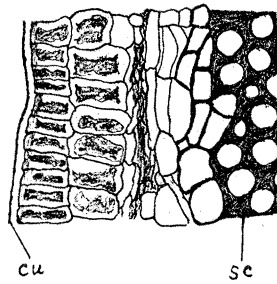


Fig. 13.

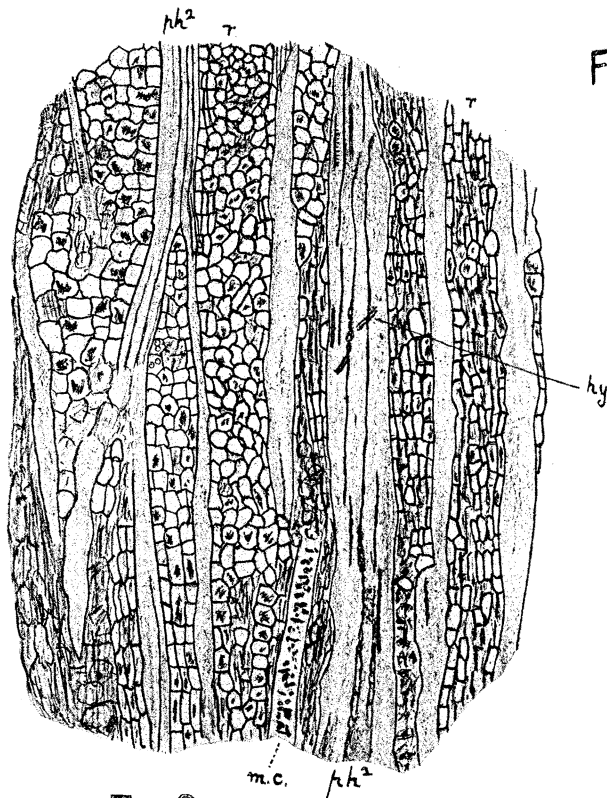


Fig. 9.

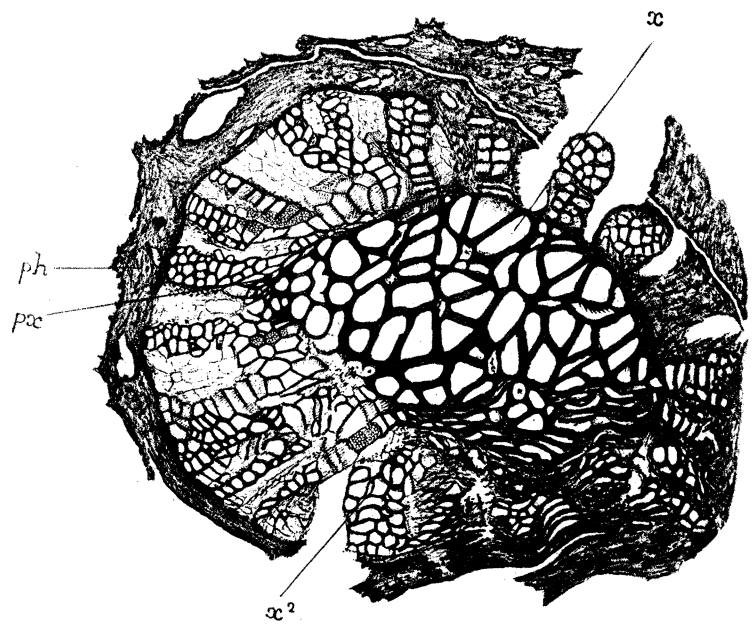


Fig. 10.

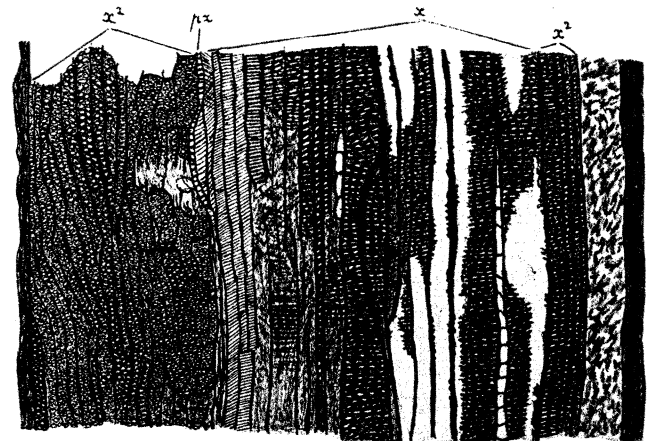


Fig. 11.

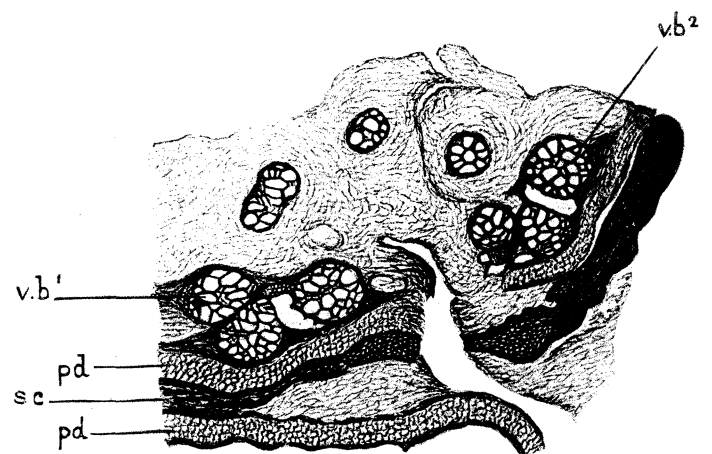


Fig. 12.

Medullosa Anglica.

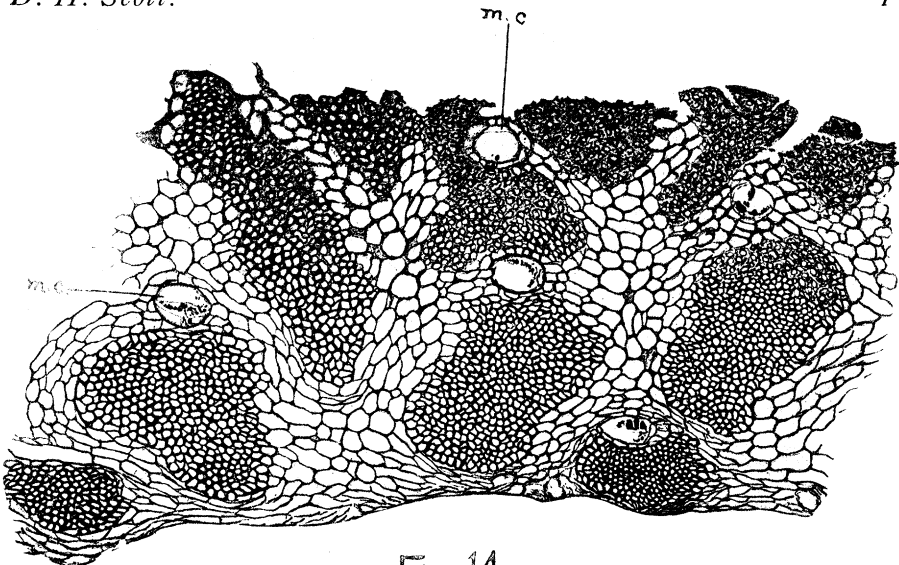


Fig.14

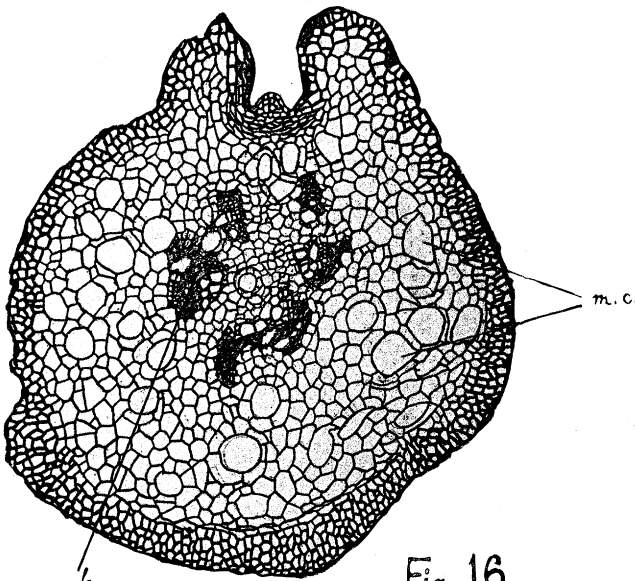


Fig.16.

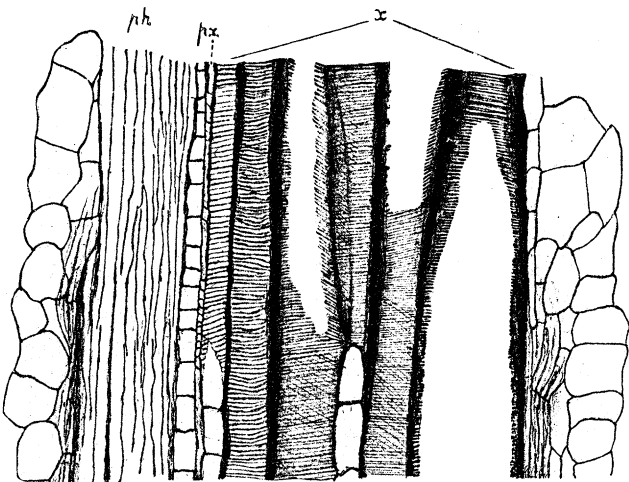


Fig.15.

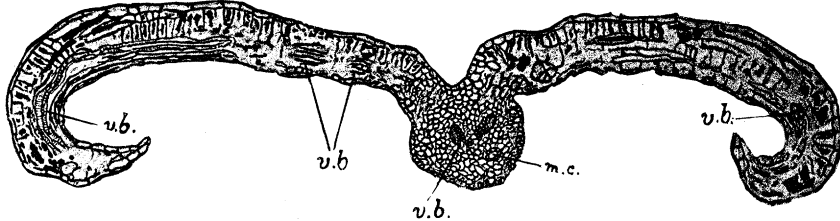


Fig.17.

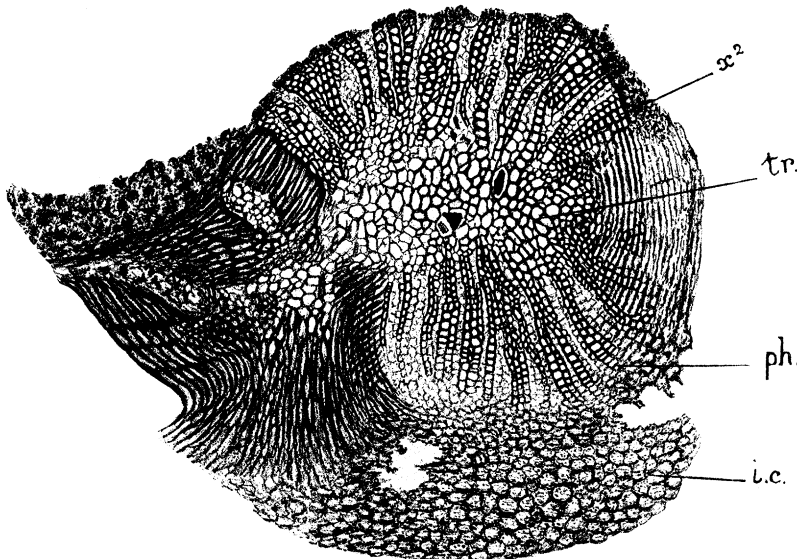


Fig.18

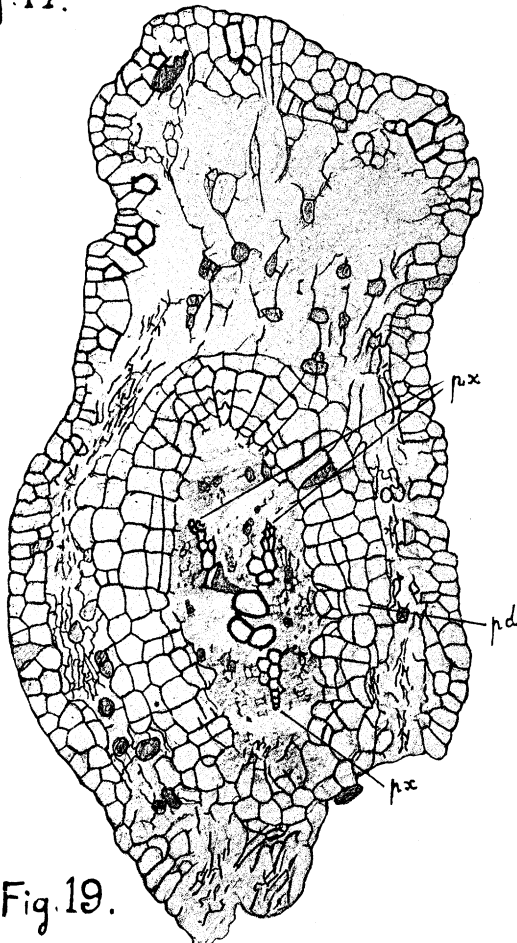
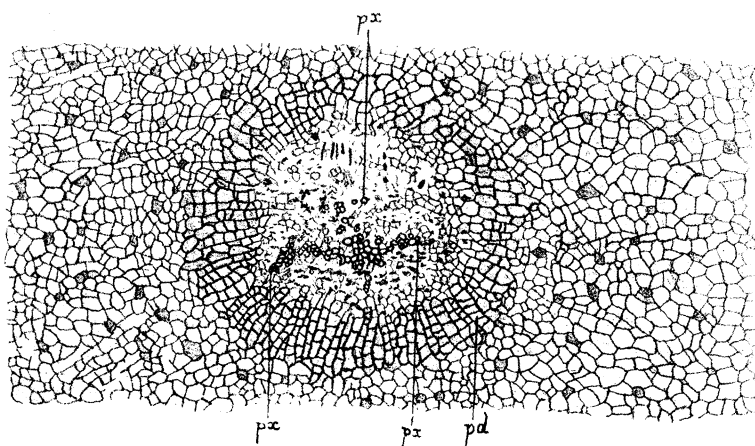
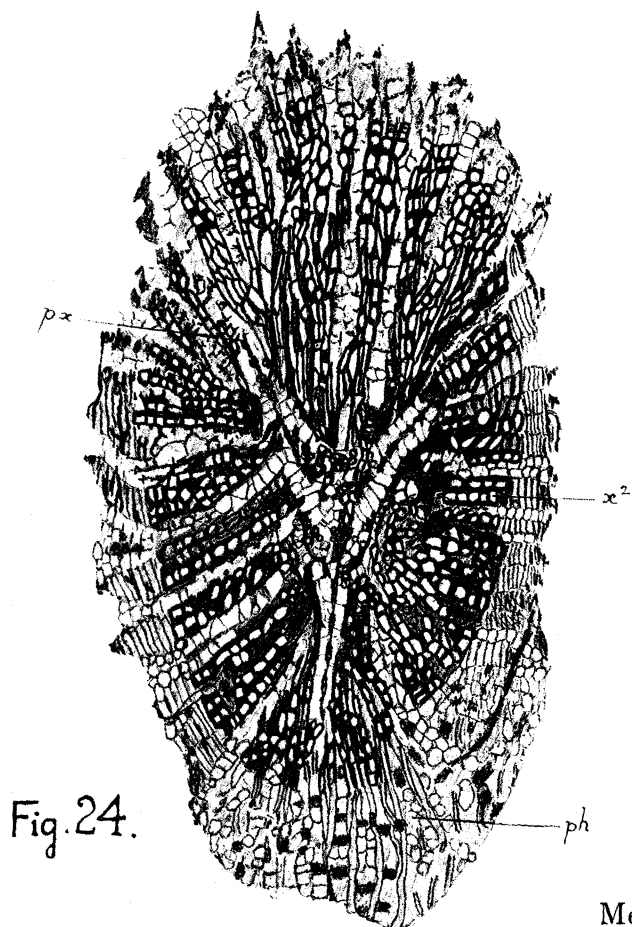
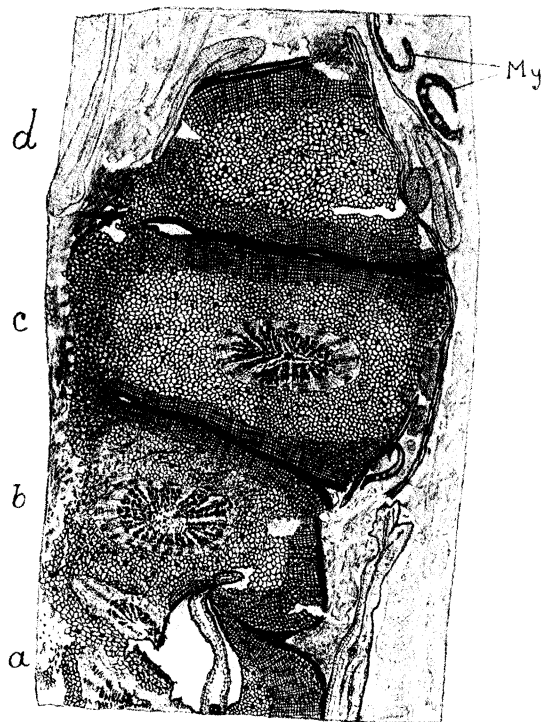
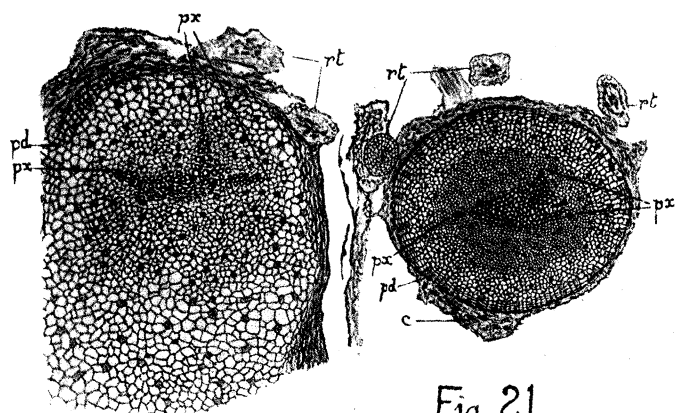
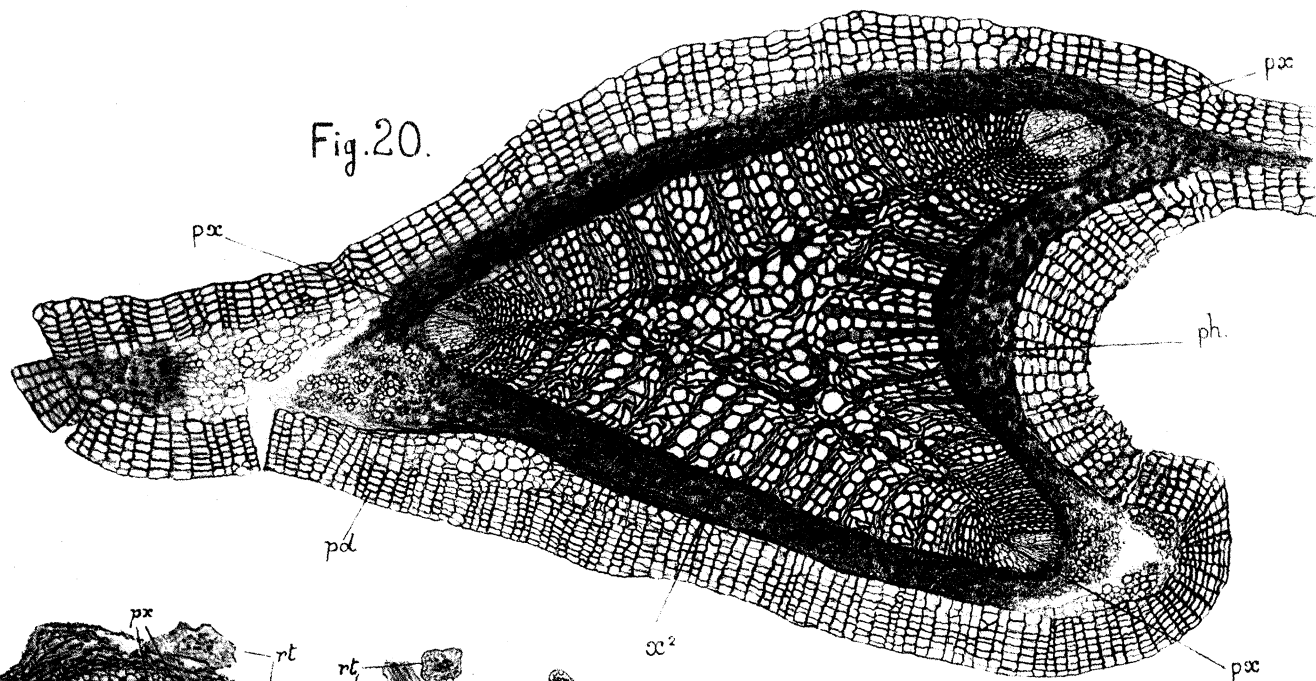


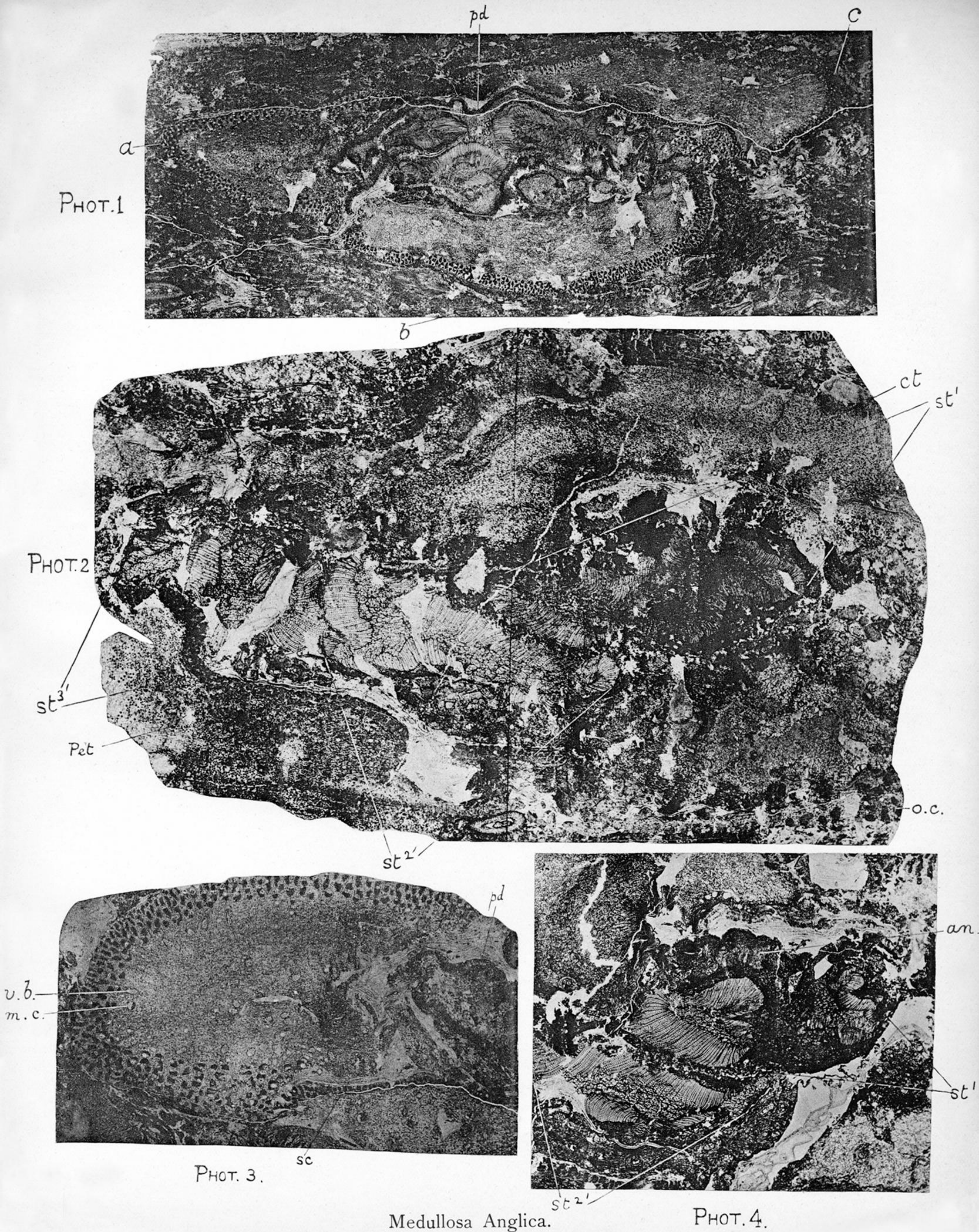
Fig.19.

Medullosa Anglica.



Medullosa Anglica.





Medullosa Anglica.

PLATE 5.

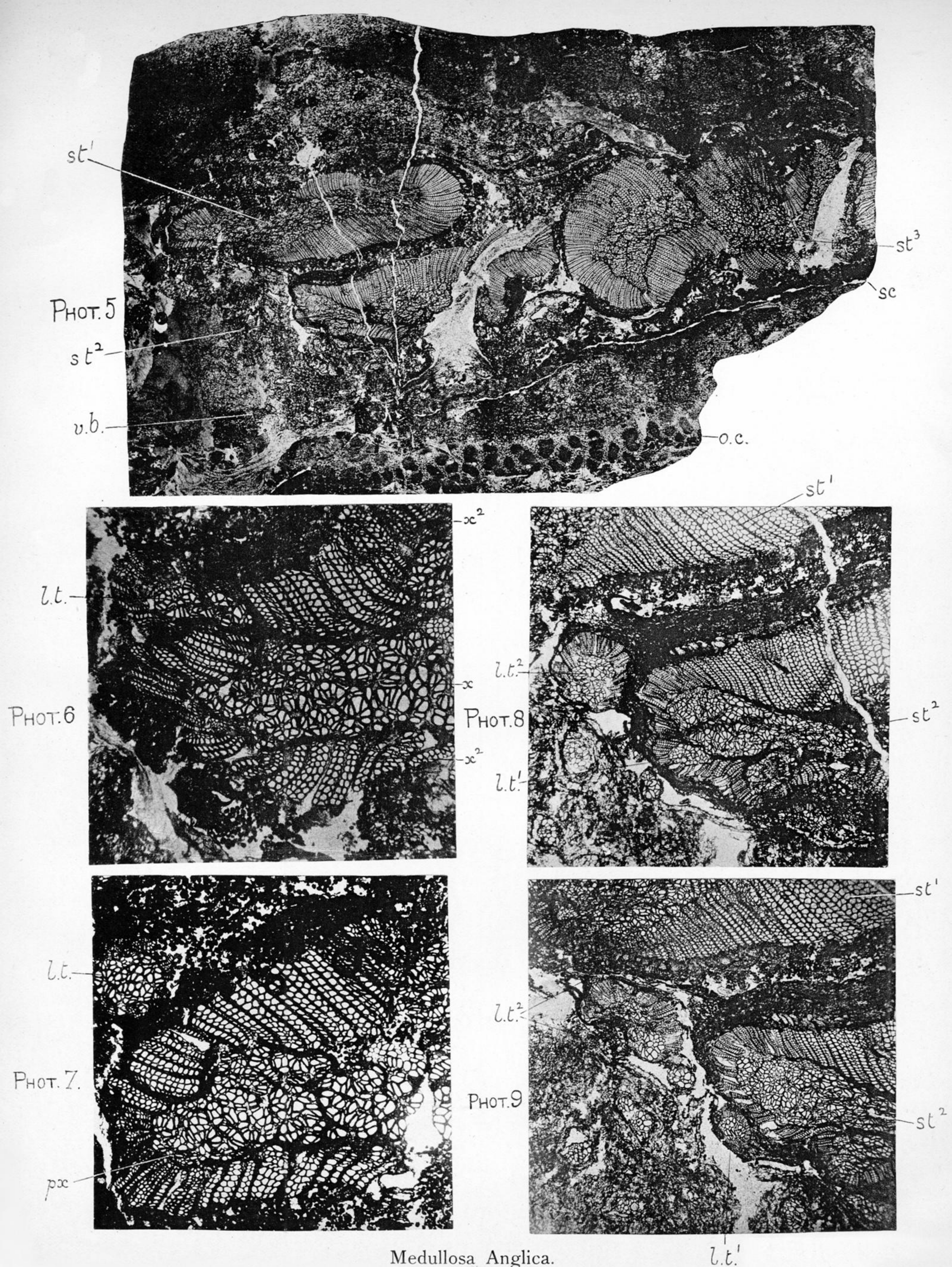
Phot. 1. Complete transverse section of Specimen II., taken from the lower part of the specimen, immediately below the portion shown in Plate 9; *a*, *b*, *c*, the three leaf-bases. At a higher level a new leaf-base (*bc*), shown in surface-view in Plate 9, fig. 1, and in section in photograph 3, appears between *b* and *c*, and still higher another (*ab*) arises between *a* and *b*. The order of the leaves from below upwards is *c*, *b*, *a*, *bc*, *ab*, indicating a  $\frac{2}{5}$  phyllotaxis. *pd.*, internal zone of periderm; within this the three steles, each with primary and secondary wood, are evident.  $\times 1\frac{2}{5}$ . S. 737.† (See p. 84. Compare diagram on p. 126.)

Phot. 2. General transverse section of Specimen I. *Pet.*, part of a large petiole, just becoming free from the stem. *o.c.*, outer cortex or hypoderma of another leaf-base; *ct.*, cortical parenchyma; on this side the hypoderma is lost; *st.*<sup>1</sup>, *st.*<sup>2</sup>, *st.*<sup>3</sup>, the three steles; *st.*<sup>1</sup> is almost perfect, the others more broken.  $\times 2$ . S. 226. (See p. 86.)

Phot. 3. Part of a transverse section of Specimen II., at the level 3 marked in Plate 9, showing the leaf-base *bc* (of which the external surface is seen in Plate 9, fig. 1), and part of *b* (cf. phot. 1). The leaf-base shows the characters of *Myeloxylon Landriotii*, REN. *v.b.*, one of the vascular bundles; *m.c.*, a gum-canal; *pd.*, part of the periderm of stem; *sc.*, internal sclerenchyma between the leaf-base *b*, and stem.  $\times 3$ . S. 740. (See p. 100.)

Phot. 4. Part of a transverse section of Specimen I., at a level below that of phot. 2, and above that of phot. 5. The stele *st.*<sup>1</sup> is here divided into two parts; *an.*, accessory vascular strand outside *st.*<sup>1</sup>; *st.*<sup>2</sup>, part of the next stele. A number of leaf-trace bundles are also shown.  $\times 2\frac{1}{2}$ . S. 578. (See p. 91.)





Medullosa Anglica.

PLATE 6.

Phot. 5. Transverse section of Specimen I., including all three steles. Right and left-hand reversed as compared with photos. 2 and 4. The level is about 2 centims. below that of phot. 4, and about 4 or 5 centims. below that of phot. 2. The two halves of  $st^1$  have reunited. At its right hand end the phloem is preserved. The other steles are also well shown, and their limits evident, in spite of fractures.  $o.c.$ , hypoderma of a leaf-base, identical with *Pet.* in phot. 2;  $sc$ , its internal sclerenchyma; numerous leaf-trace bundles are shown;  $v.b.$ , the two bundles shown enlarged in phot. 14. For details, see photos. 7 and 9.  $\times$  nearly 3. S. 579. (See pp. 86 and 91).

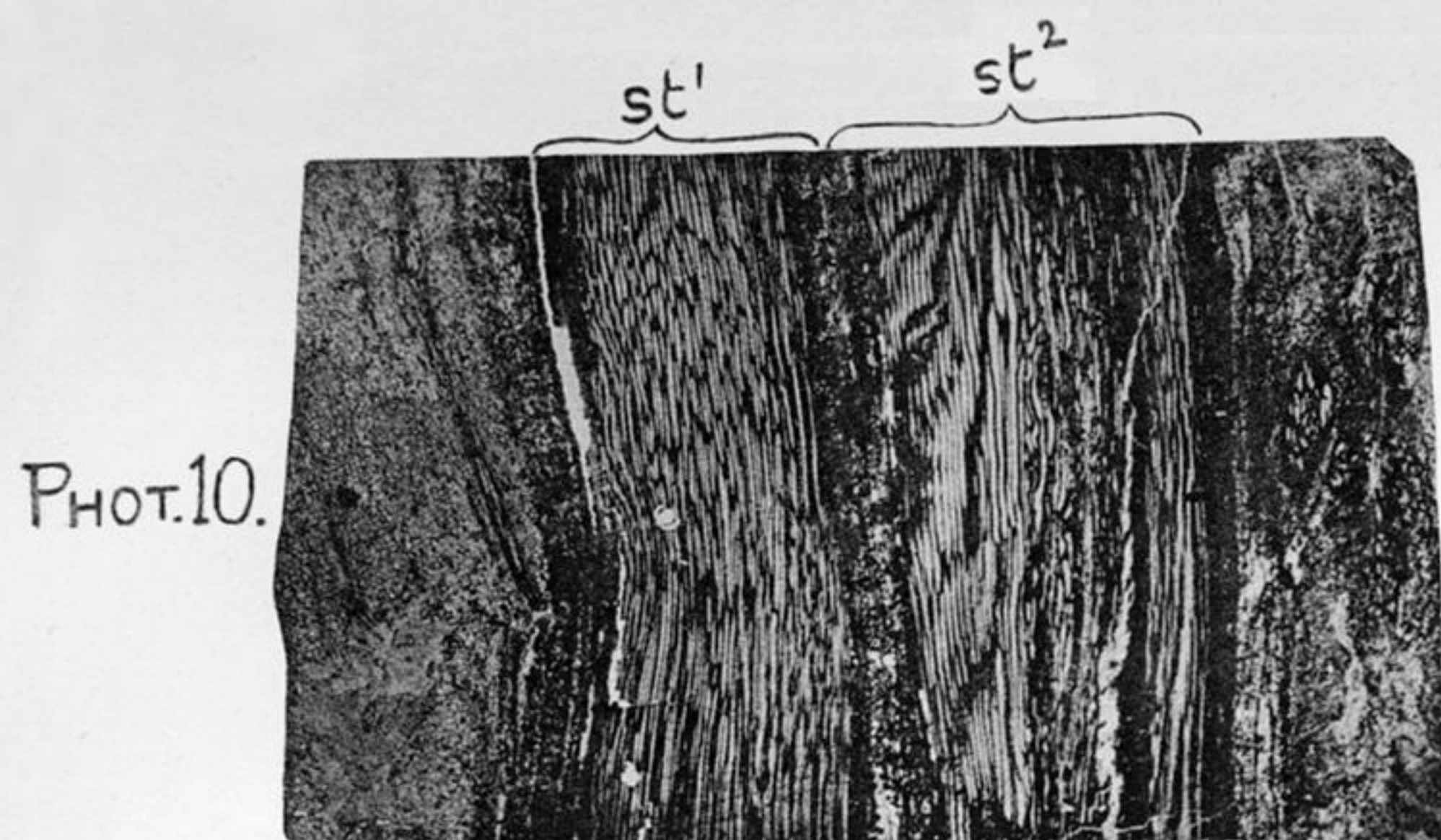
Phot. 6 (Specimen I.). Part of stele 1 in transverse section.  $x$ , primary wood, consisting of tracheides and conjunctive parenchyma;  $x^2$ , secondary wood;  $l.t.$ , leaf-trace bundle just separating from stele; it has a fan of secondary wood on its outer side.  $\times 18$ . S. 581. (See p. 92.)

Phot. 7 (Specimen I.). The same part, from a section about 1 centim. higher up the stem.  $p.x.$ , probable position of a protoxylem group;  $l.t.$ , the leaf-trace shown in phot. 6, which has here become free from the stele, and is surrounded by secondary wood.  $\times 18$ . S. 579. (See p. 92.)

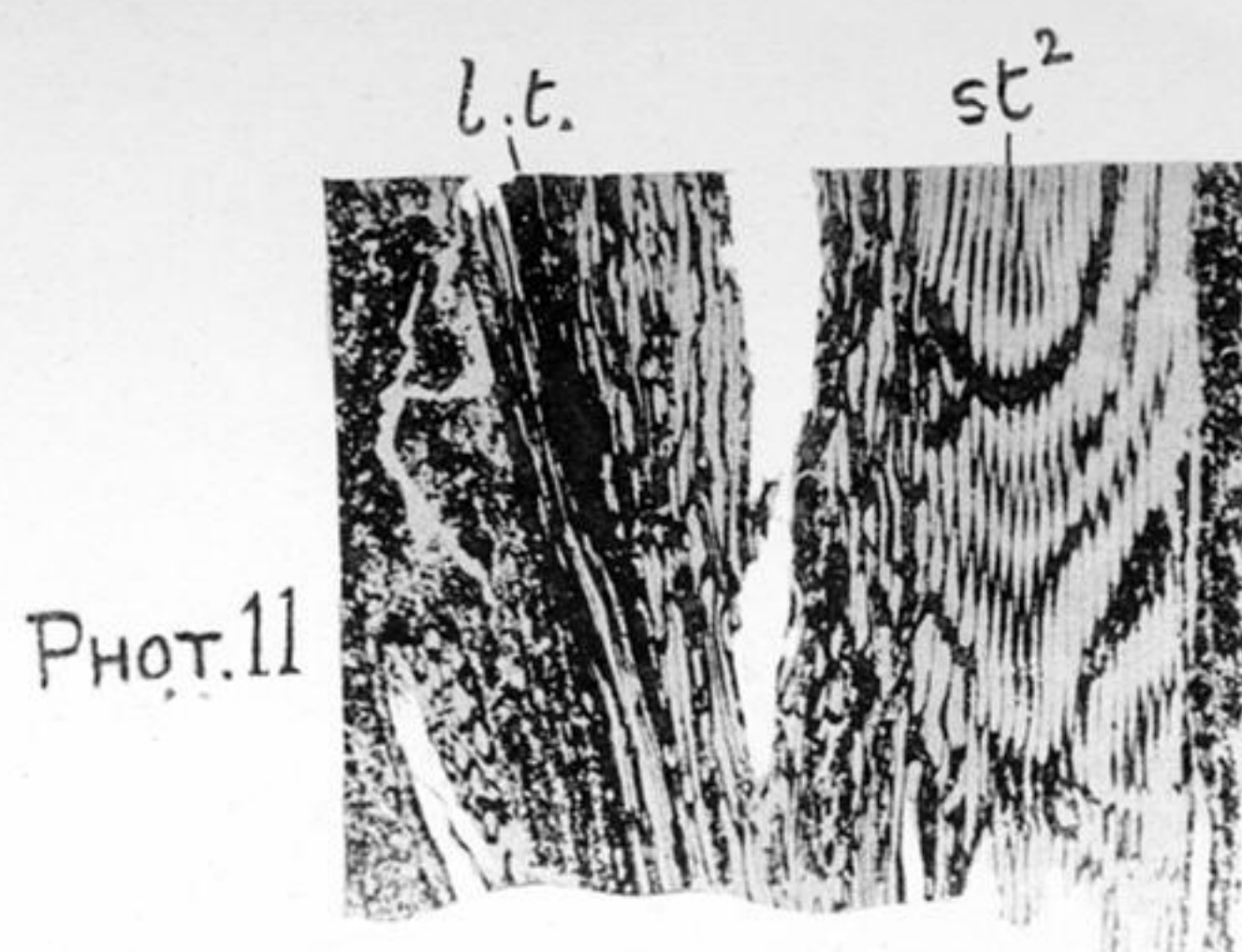
Phot. 8 (Specimen I.). Parts of steles 1 and 2 in transverse section; primary and secondary wood evident, and phloem of stele 2 partly preserved.  $l.t.^1$ , leaf-trace beginning to detach itself from stele 2;  $l.t.^2$ , large leaf-trace already free. Other leaf-traces are shown.  $\times 10$ . S. 581. (See pp. 92 and 94).

Phot. 9 (Specimen I.). The same part, from a section about 1 centim. higher up the stem. The leaf-trace,  $l.t.^1$ , is here just free from its stele;  $l.t.^2$  is beginning to divide. Other leaf-traces shown.  $\times 10$ . S. 579. (See pp. 92 and 94).

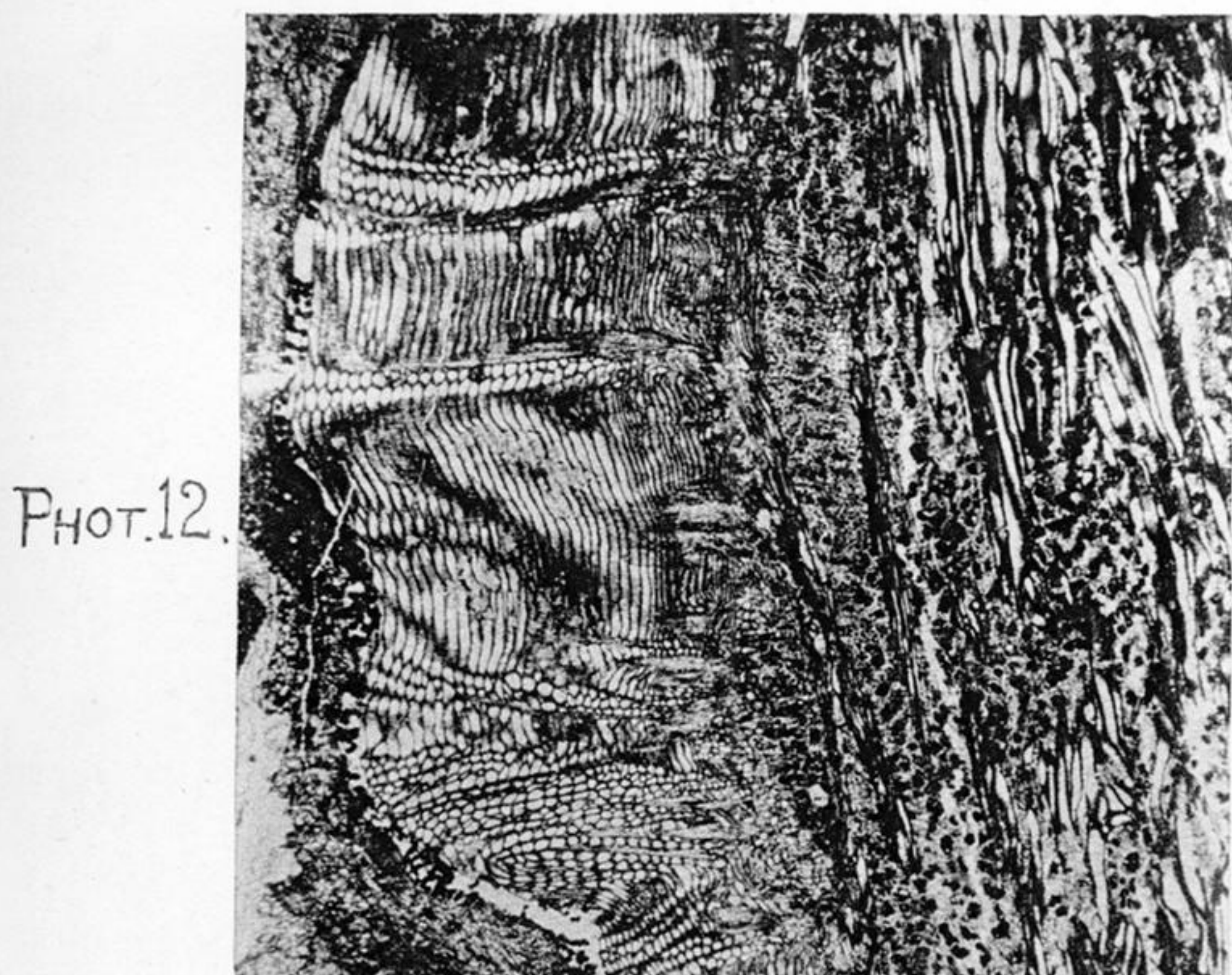




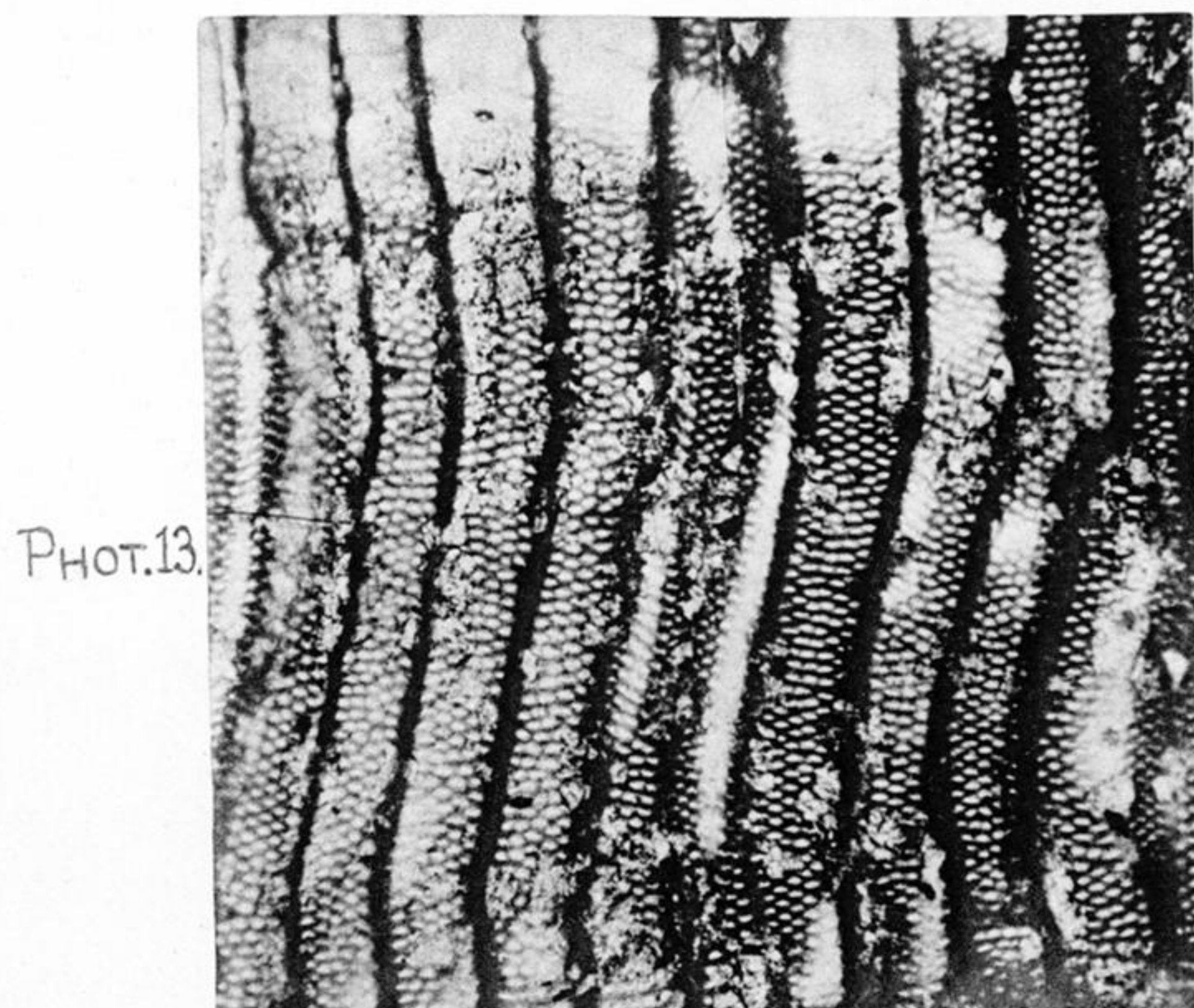
PHOT.10.



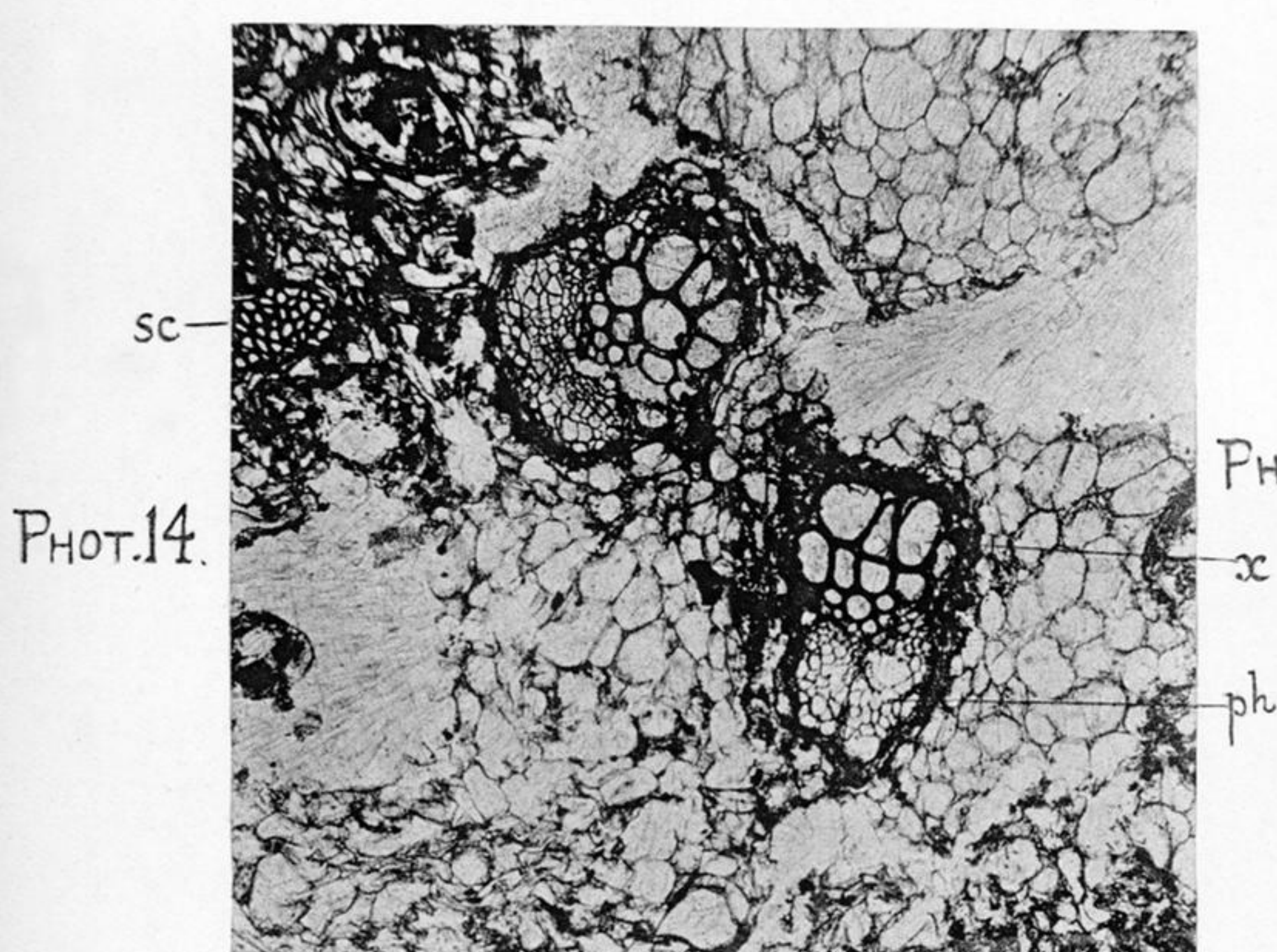
PHOT.11



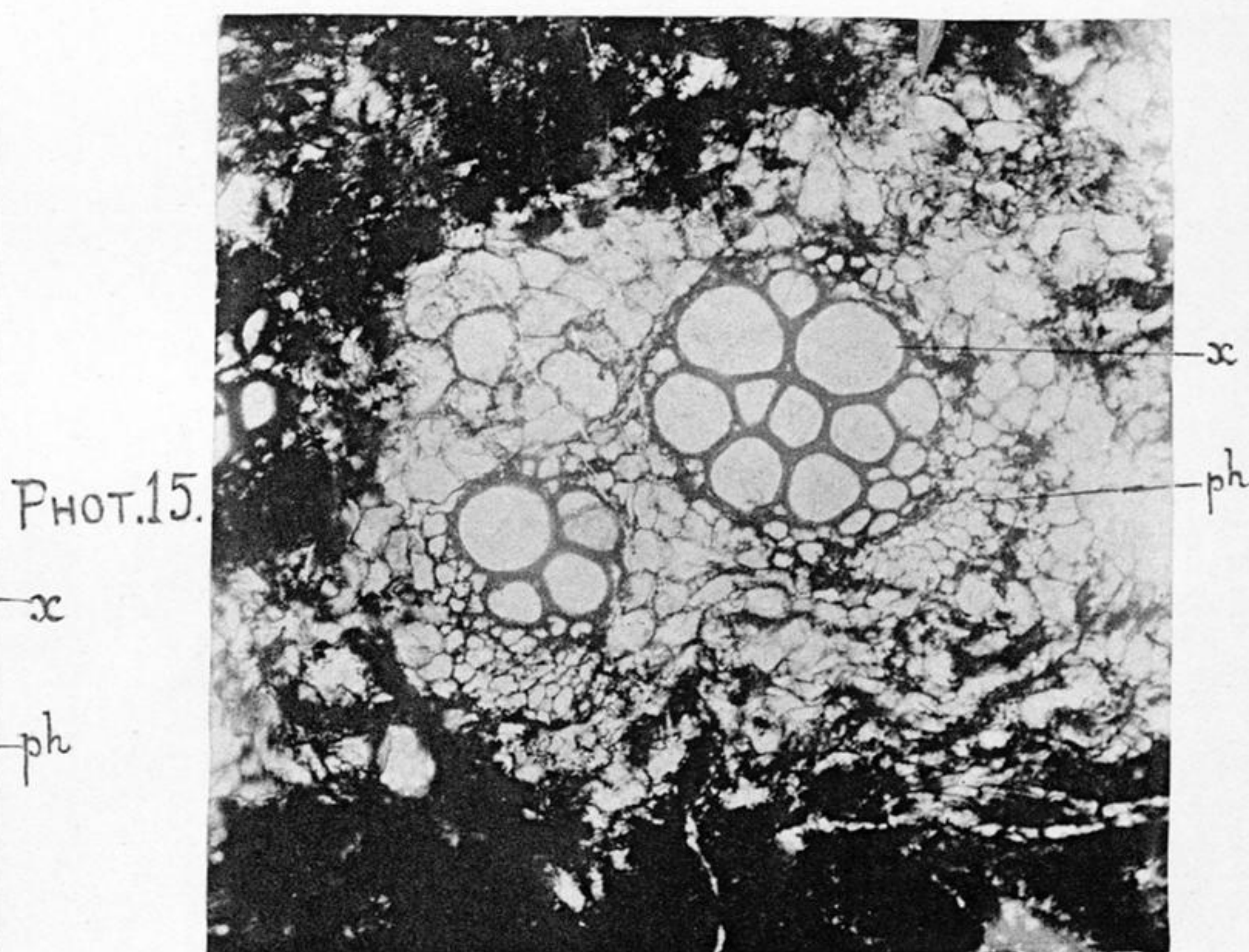
PHOT.12.



PHOT.13.



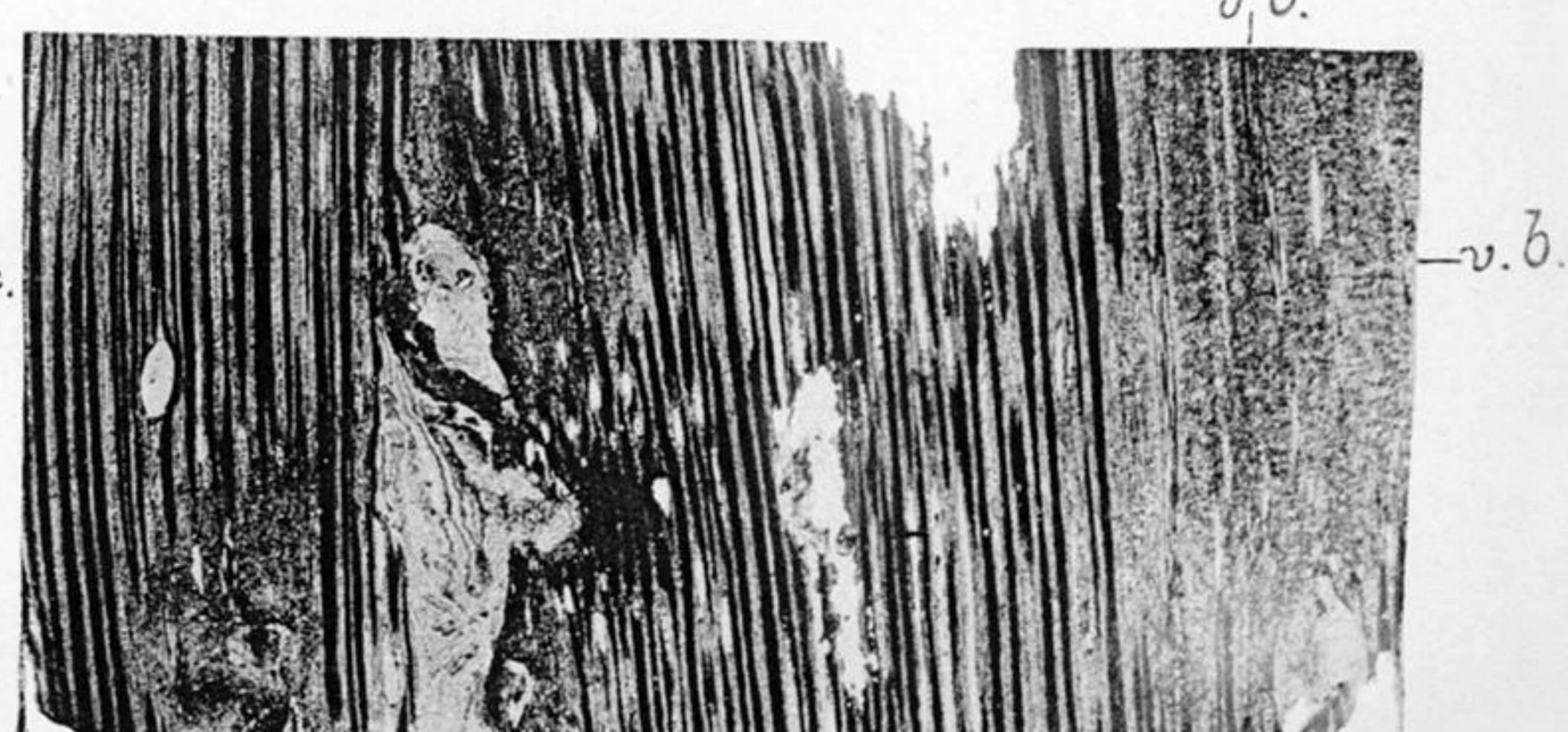
PHOT.14.



PHOT.15.



PHOT.16.



PHOT. 17.

Medullosa Anglica.

## PLATE 7.

Phot. 10 (Specimen I.). Radial section from a series cut a little below the transverse sections figured in Plate 6, crossing steles 1 and 2 at right angles.  $st.^1$ , shown in tangential section through the secondary wood;  $st.^2$ , shown in radial section. Leaf-traces are seen in the cortical tissue on either side.  $\times 3$ . S. 596. (See p. 95.)

Phot. 11. From an adjacent section to the preceding, showing part of stele 2 in radial section, with a leaf-trace,  $l.t.$ , passing out from the stele.  $\times 4$ . S. 595. (See p. 93.)

Phot. 12 (Specimen I.). Part of a longitudinal section, from a series cut between transverse sections 578 (phot. 4) and 226 (phot. 2), parallel to long axis of stele 1, a part of which is shown in radial section.  $x$ , primary wood, showing the strands of tracheides and conjunctive tissue;  $x^2$ , secondary wood in radial section. The arrow marks the limit between the two.  $\times 10$ . S. 576. (See p. 88.)

Phot. 13. Secondary tracheides from the same radial section, to show bordered pits.  $\times 90$ . (See p. 90.)

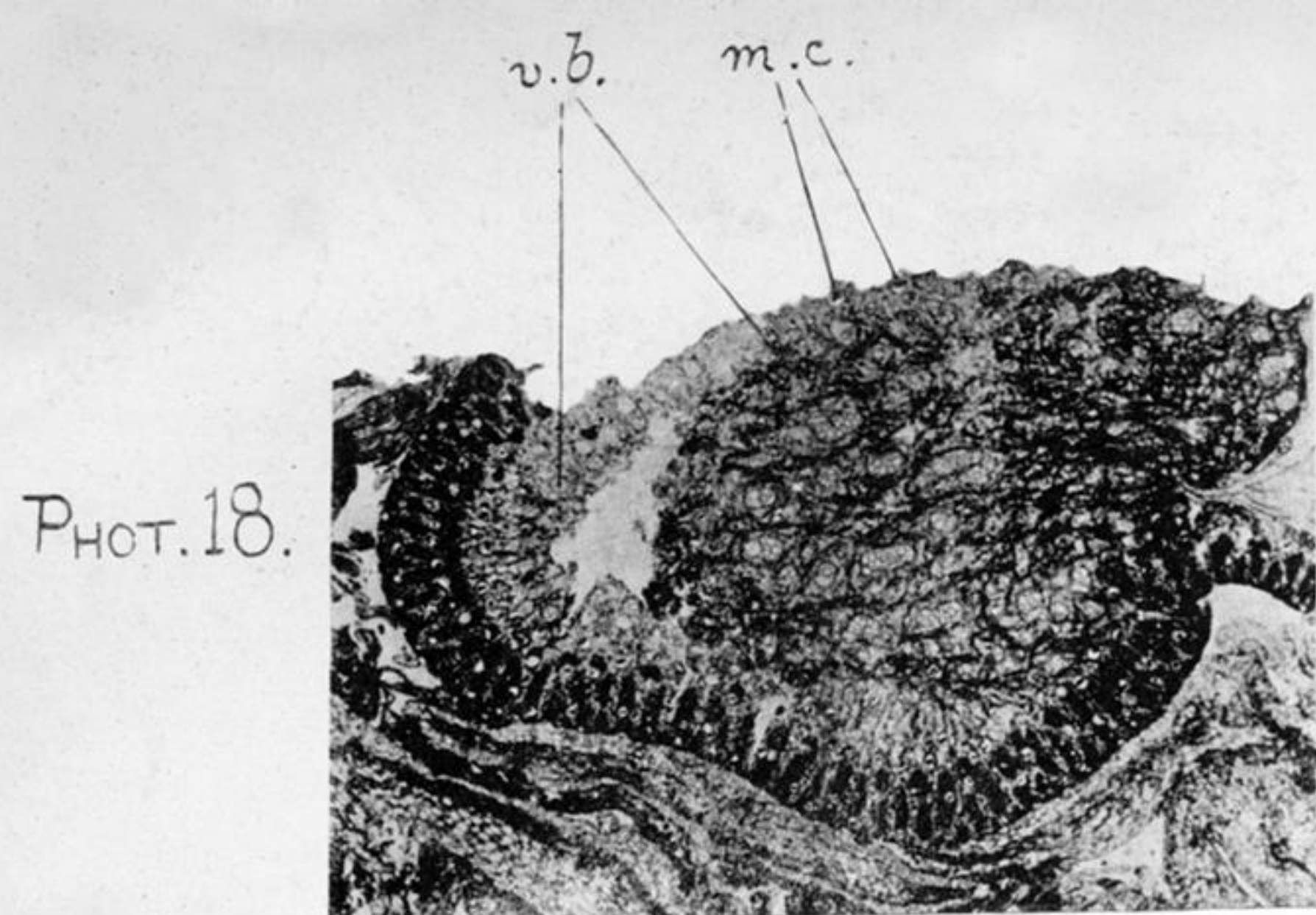
Phot. 14 (Specimen I.). Part of the transverse section 579, to show the two collateral leaf-trace bundles marked  $v.b.$  in phot. 5.  $x$ , xylem of one of the bundles, with its protoxylem towards the phloem,  $ph$ ; cortical tissue of stem and a fragment of internal sclerenchyma ( $sc.$ ) also shown.  $\times 35$ . (See p. 94.)

Phot. 15 (Specimen I.). Two similar bundles from the base of a leaf.  $x$ , xylem;  $ph$ , phloem of one of the bundles.  $\times 55$ . S. 581. (See p. 95.)

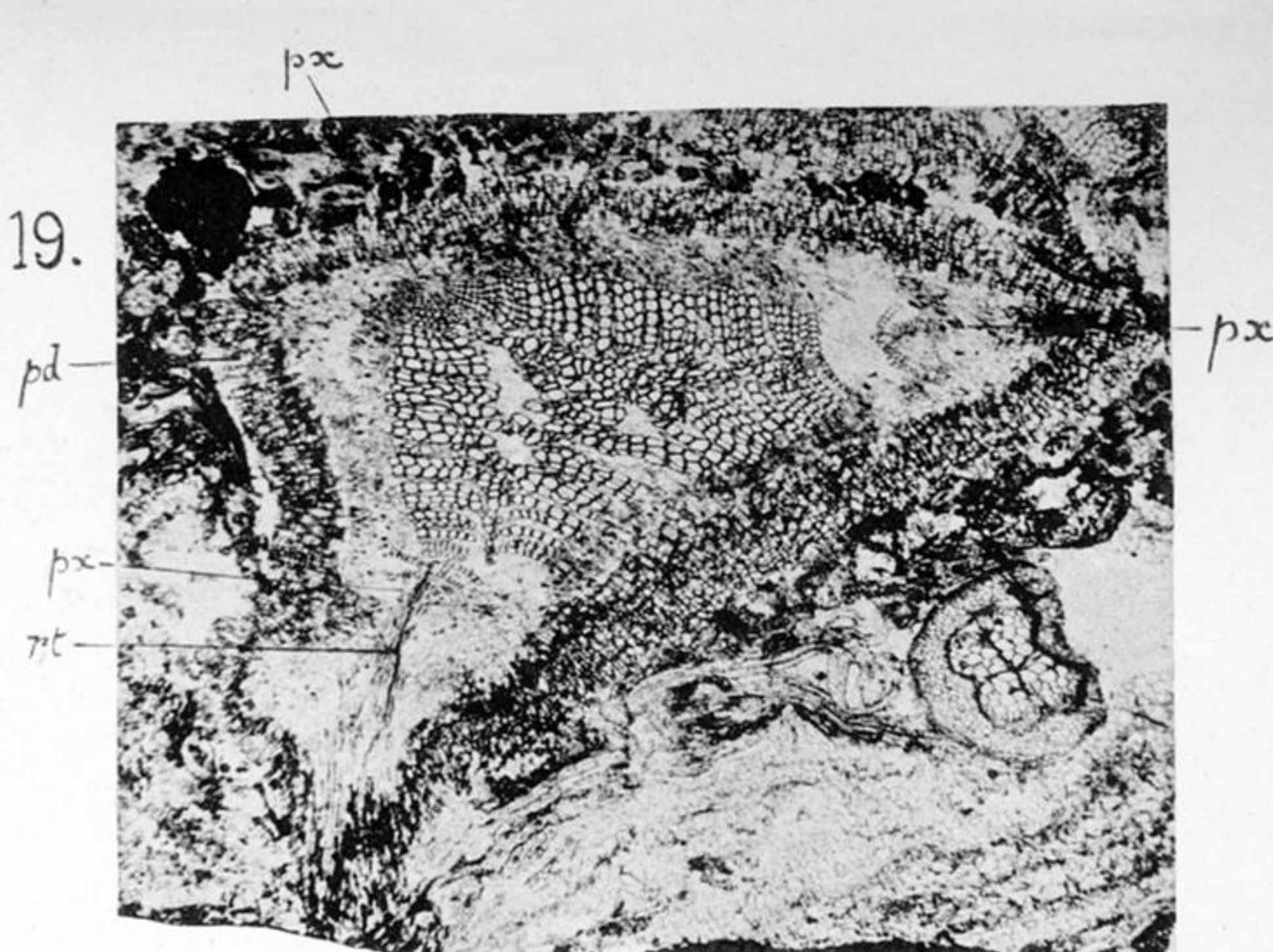
Phot. 16. Part of a transverse section from a detached piece of stem, probably forming part of Specimen IV., showing the axil of a leaf.  $st.$ , part of a stele;  $pd.$ , periderm of stem;  $o.c.$ , hypoderma, in oblique section, continuous with the torn hypoderma of the petiole,  $pet.$   $\times 1\frac{1}{10}$ . S. 792. (See p. 100.)

Phot. 17 (Specimen II.). Tangential section, from a longitudinal series, cut immediately above the level 4 at top of fig. 1, Plate 9, and parallel to the free surface of specimen. The section passes chiefly through the hypoderma, showing "*Sparganium*" structure and gum-canals. To the right it cuts more deeply into the tissues, showing the parenchyma and vascular bundles ( $v.b.$ ) of a leaf-base.  $\times 1\frac{3}{4}$ . S. 742. (See p. 99.)

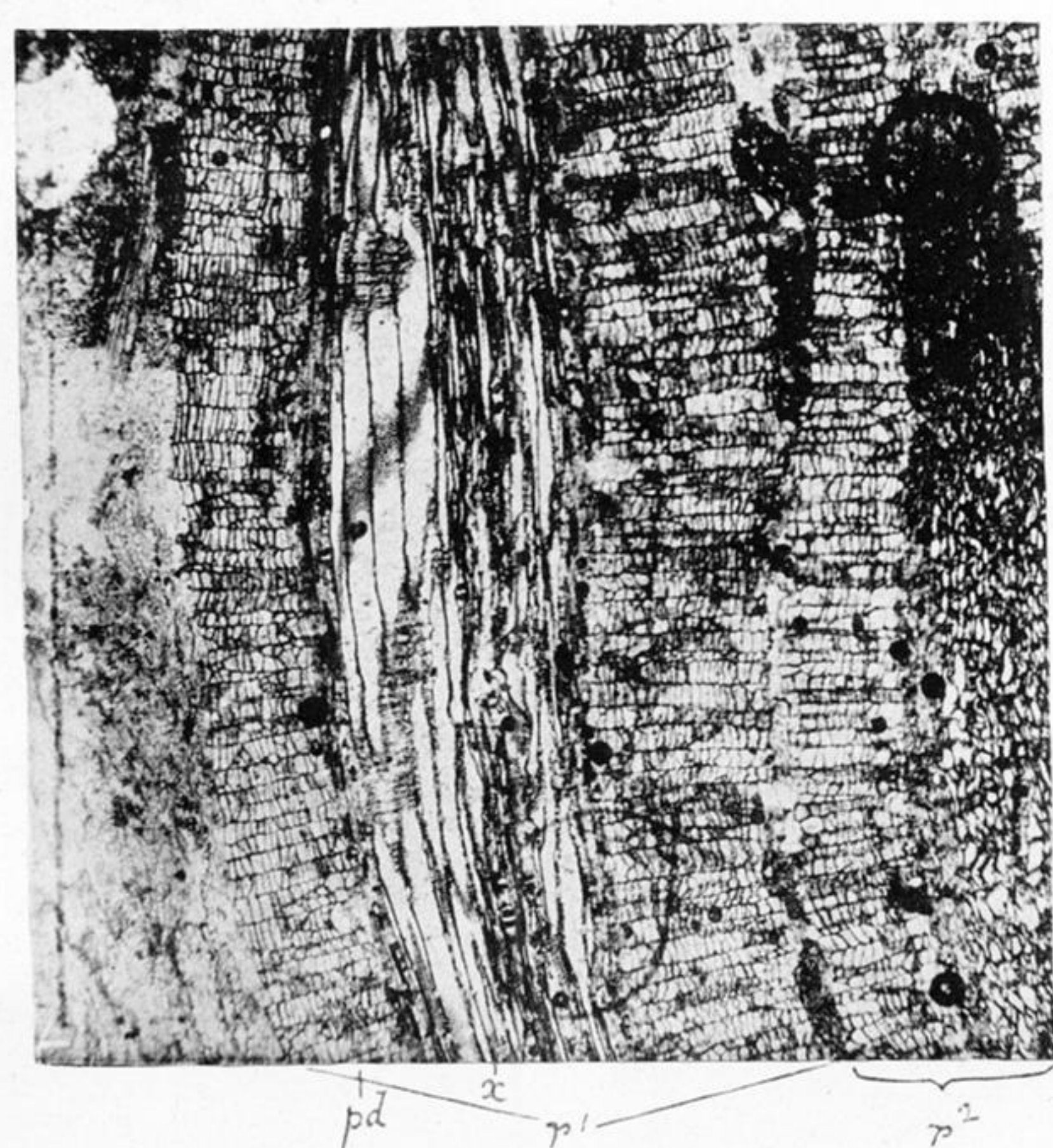




PHOT. 18.

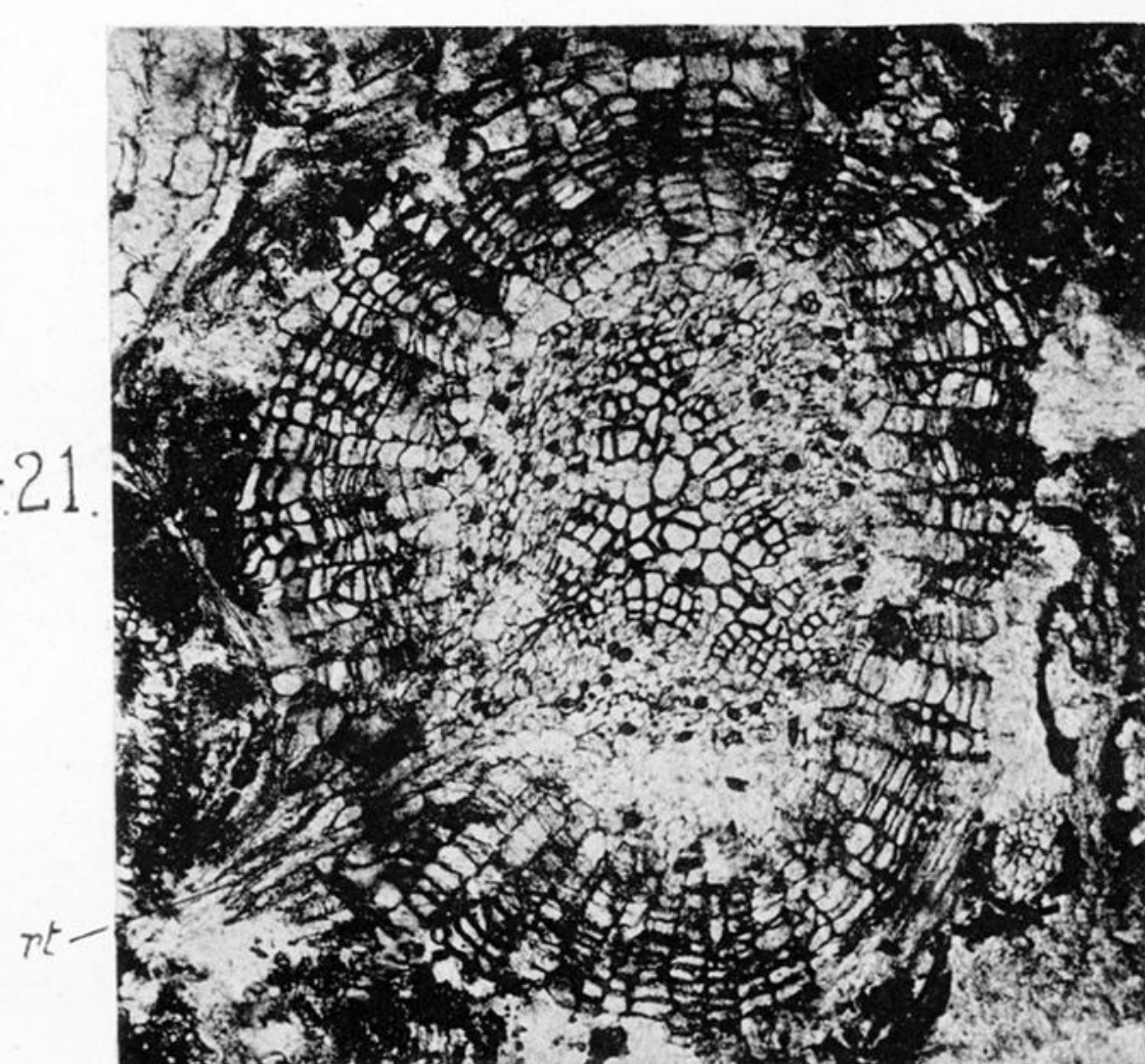


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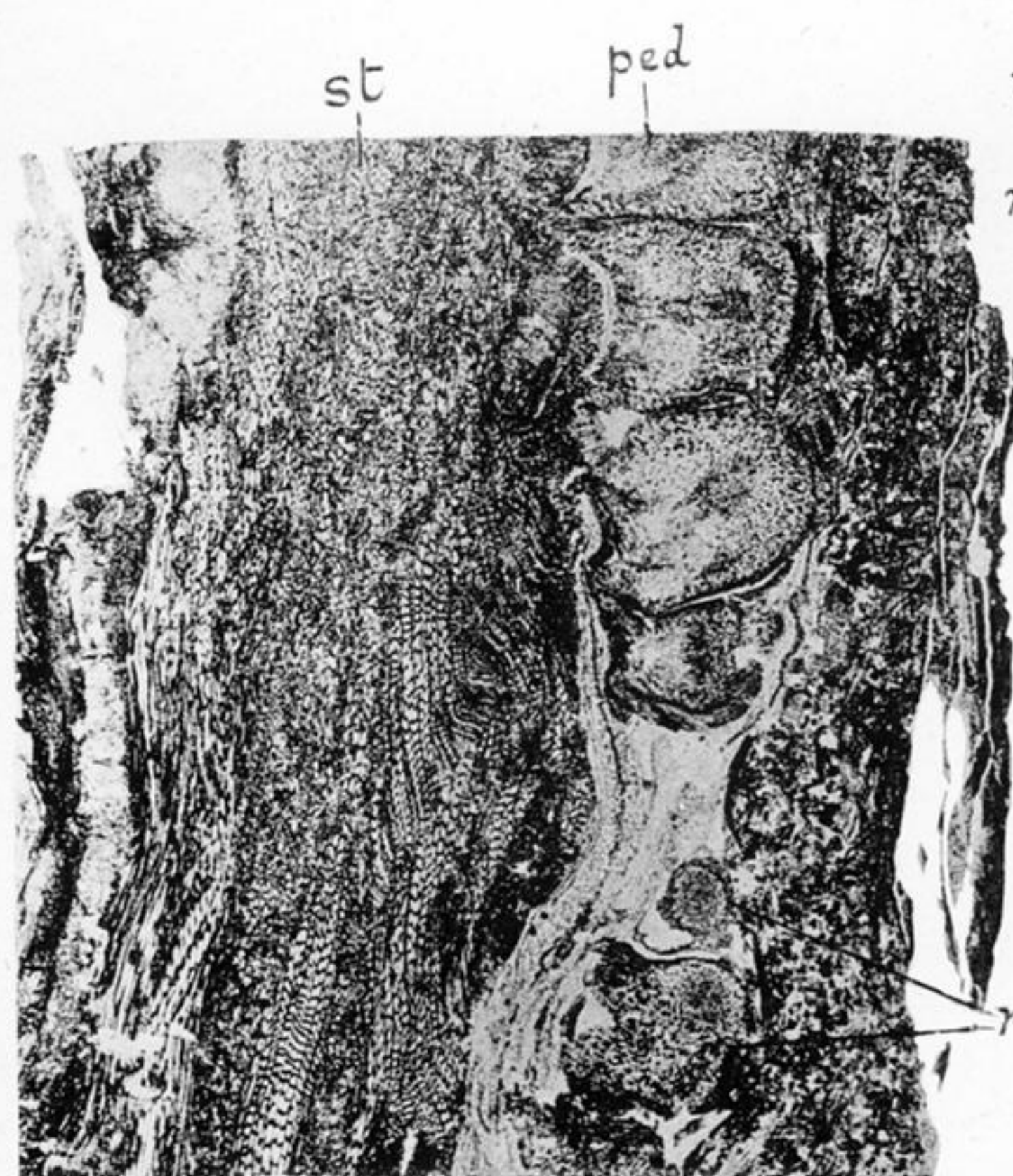


PHOT. 20.

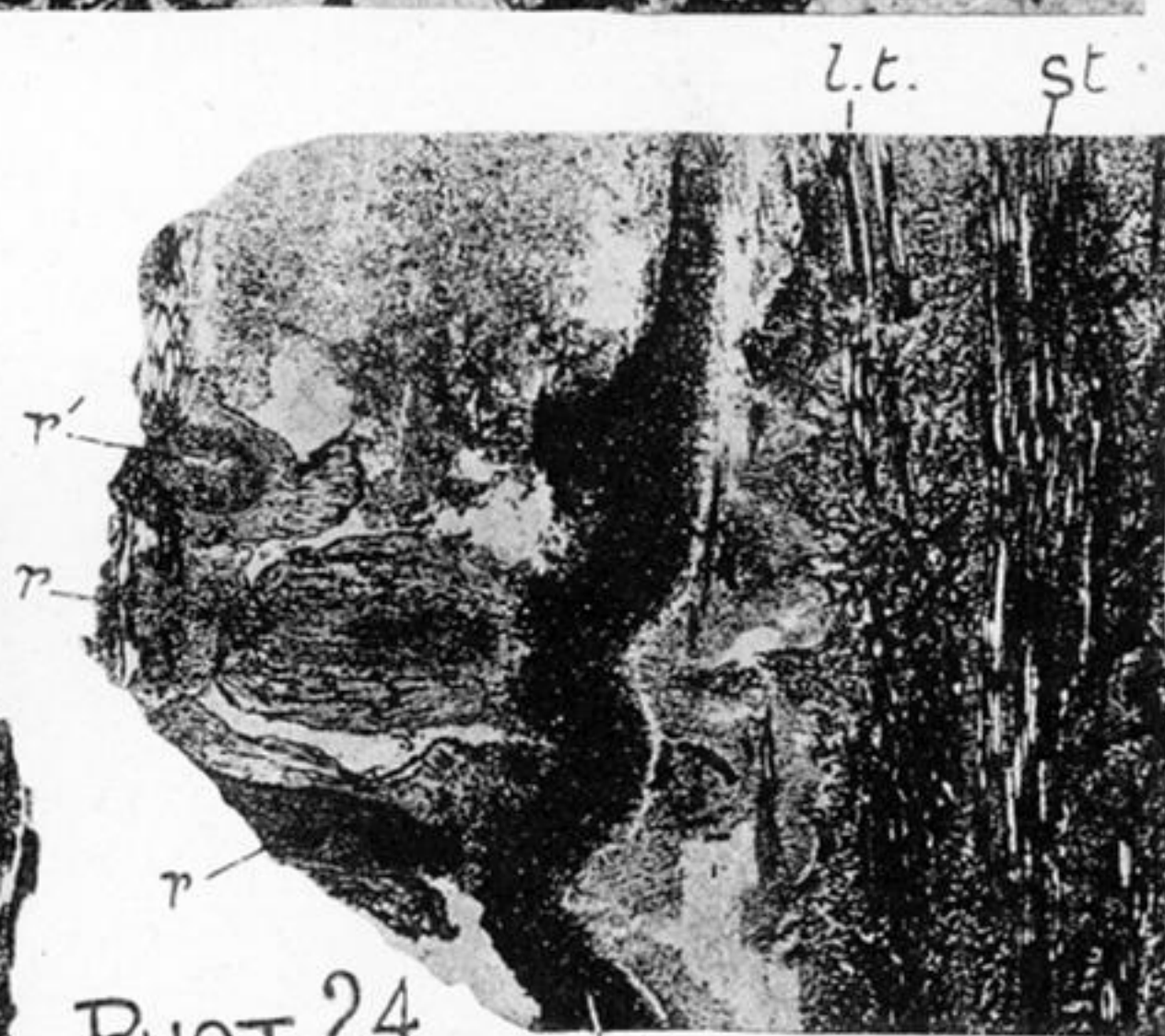
PHOT. 21.



PHOT. 22.

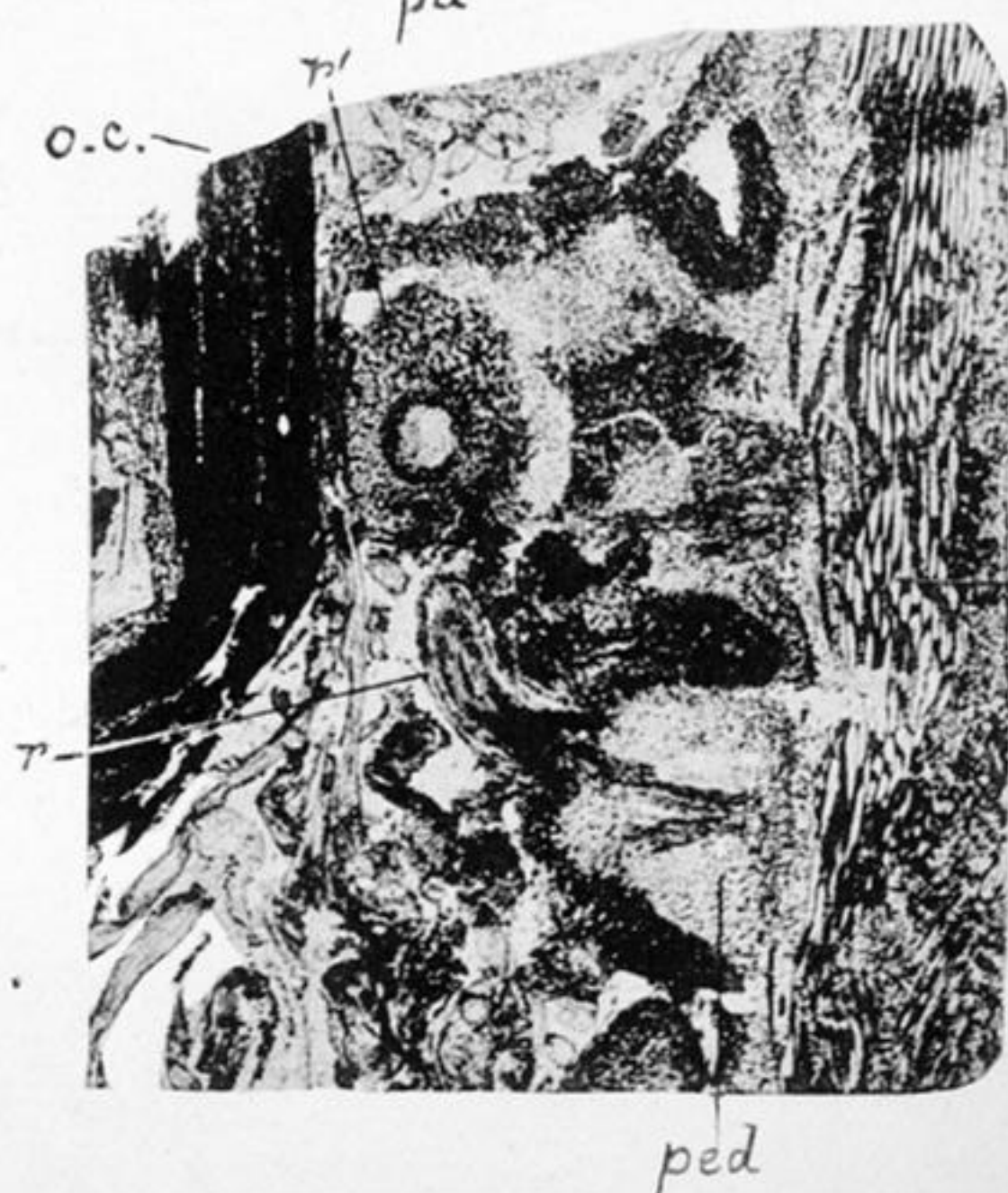


PHOT. 23.



PHOT. 24.

PHOT. 25.



Medullosa Anglica.

# PLATE 8.

- Phot. 18. Partial transverse section of a free petiole from the same block as Specimen I. Structure as in *Myeloxylon Landriotii*, REN. *m.c.*, gum-canals, also conspicuous in hypoderma. *v.b.*, collateral vascular bundles.  $\times 4$ . S. 685. (See p. 101.)
- Phot. 19. Transverse section of a large triarch root. *px.*, the three prominent protoxylem-angles, two of which have broken away from the stele. In the middle is the primary wood, with secondary wood and bast between the protoxylem-groups. *rt.*, vascular strand of rootlet, connected with *px.*; *pd.*, periderm.  $\times 8$ . S. 567. (See p. 102.)
- Phot. 20. Longitudinal section of two roots, *r.*<sup>1</sup> and *r.*<sup>2</sup>, the former complete, but somewhat compressed. *pd.*, periderm; *x.*, wood of root. The secondary wood is partly in radial section, showing pits and medullary rays.  $\times 20$ . S. 569. (See p. 103.)
- Phot. 21. Transverse section of triarch rootlet, showing the stele, with primary and secondary xylem, phloem-groups, pericycle, phellogen, and broad zone of periderm. At *rt* a lateral rootlet branches off, opposite one of the protoxylem-angles.  $\times 50$ . S. 569. (See p. 104.)
- Phot. 22. Tangential section from a fragment of stem, showing the bases of four adventitious roots (*r.*<sup>1</sup>-*r.*<sup>4</sup>). *M.c.*, cortex, with *Medullosa* structure, connected with the roots on either side.  $\times 2$ . From outermost section of Mr. WILD's specimen, lent by him. (See p. 105.)
- Phot. 23. Part of another tangential section of Mr. WILD's specimen, cut further to the interior. *st.*, a stele of the stem, with which the roots *r.*<sup>1</sup>-*r.*<sup>4</sup> in phot. 22 have united; *ped.*, series of root-pedicels, in oblique section; *r.*, two young roots, one free, the other attached to a pedicel. These roots are shown on a larger scale in Plate 13, fig. 21.  $\times 3\frac{1}{4}$ . S. 720. (See p. 106.)
- Phot. 24. Part of a radial section from Specimen IV. of *Medullosa anglica*, to show insertion of adventitious roots. *st.*, a stele of the stem; *lt.*, leaf-trace bundle connected with stele by radial system of tracheides; *pd.*, periderm; *r.*, young roots in tangential section, connected with cortex; *r.*<sup>1</sup>, free root.  $\times 4$ . S. 782. (See p. 107.)
- Phot. 25. From another radial section of Specimen IV. *st.*, part of a stele; *ped.*, root-pedicel in median section, showing bifurcating bundle; *r.*, young root borne on pedicel; *r.*<sup>1</sup>, larger root, in transverse section, shown on an increased scale in Plate 13, fig. 22; *o.c.*, sclerenchyma of a leaf-base.  $\times 4$ . S. 783. (See p. 107.)



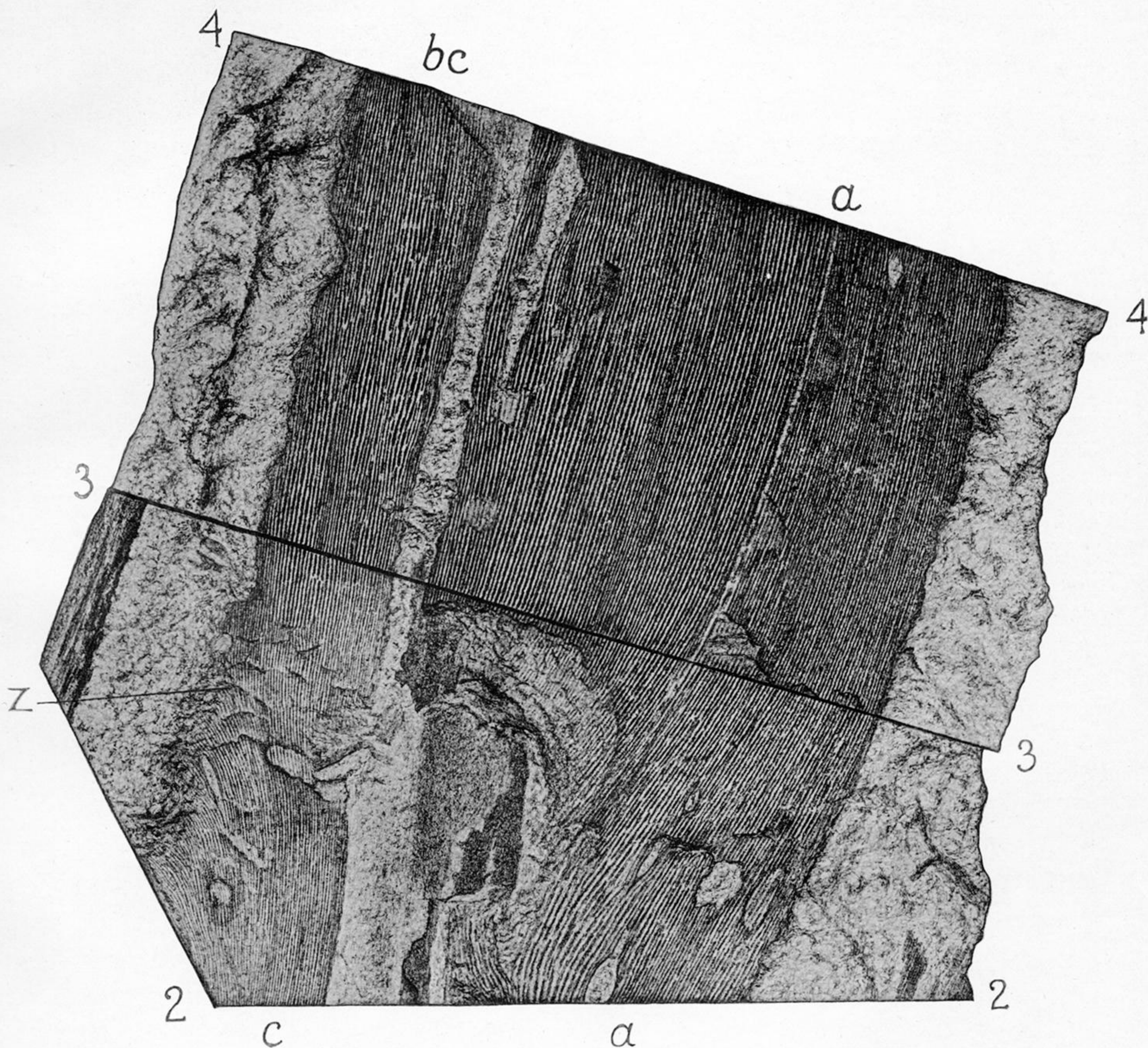


Fig. 1.

Medullosa Anglica.

PLATE 9.

Fig. 1. External view of Specimen II., showing all that part of the block in which the surface of the *Medullosa* is exposed. 2, 3, 4, planes from which transverse sections have been prepared. Phot. 1 is from a section cut at the top of the lowest piece (not shown), immediately below the plane 2. The longitudinal sections were cut just above 4, from a piece not shown. *a.*, external surface of a leaf-base which extends the whole length of specimen (*cf.* phot. 1). In the upper part it is much flattened out by pressure. *c.*, inner concave surface of another leaf-base, *c.*, which had split away (see crack in phot. 1). Note the finer striation of the internal sclerenchyma. Between *a.* and *c.*, at the bottom, the inner cortex is exposed. *bc.*, a new leaf-base, which appears about at the line Z; its external surface is *convex*. This leaf-base is shown in transverse section, at the plane 3, in phot. 3. The leaf-base, *b*, shown in photograph 1, is not seen here, as it lies at the back of the specimen. Natural size. (See p. 84.)



Fig. 2.

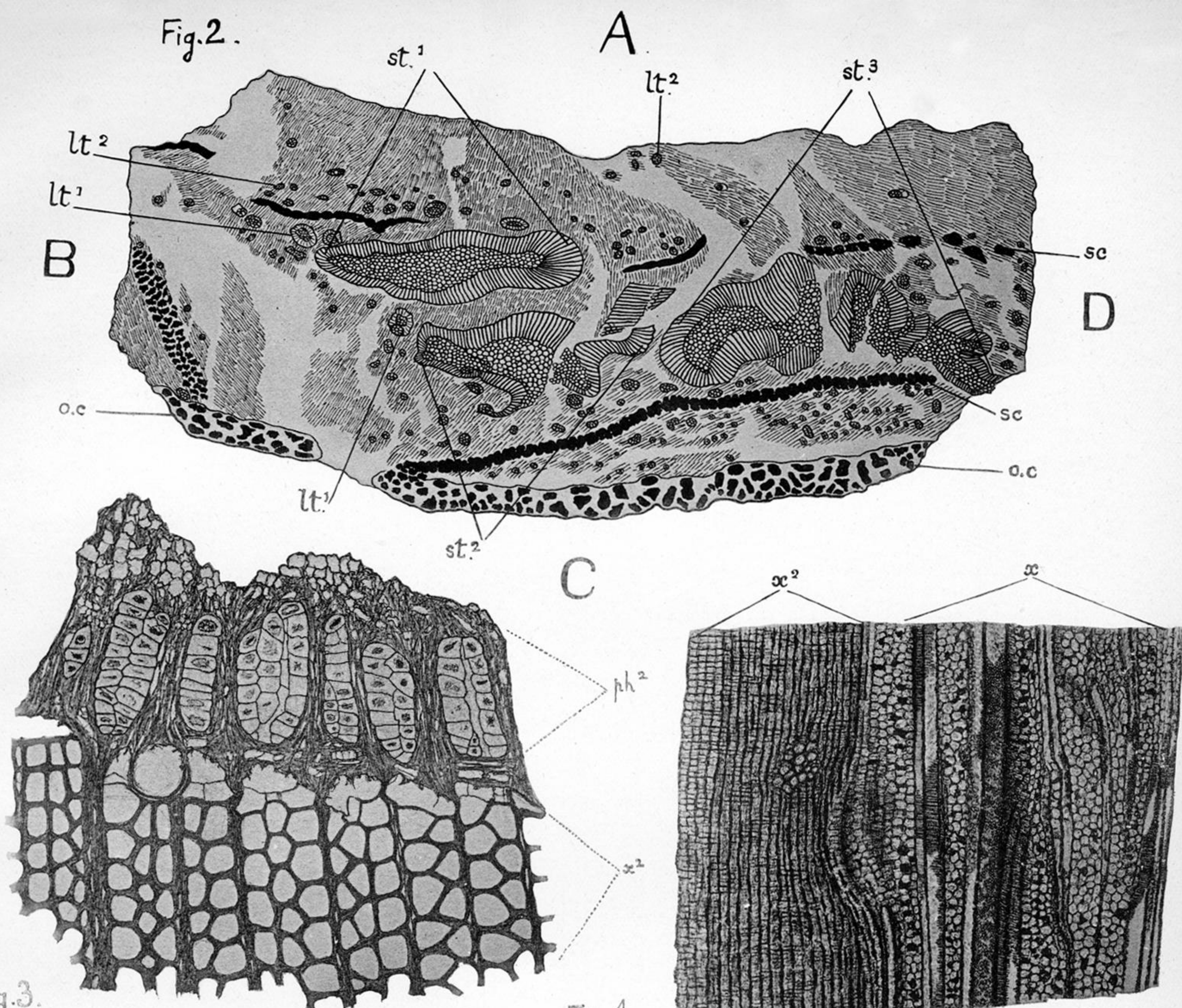


Fig. 3.

Fig. 4.

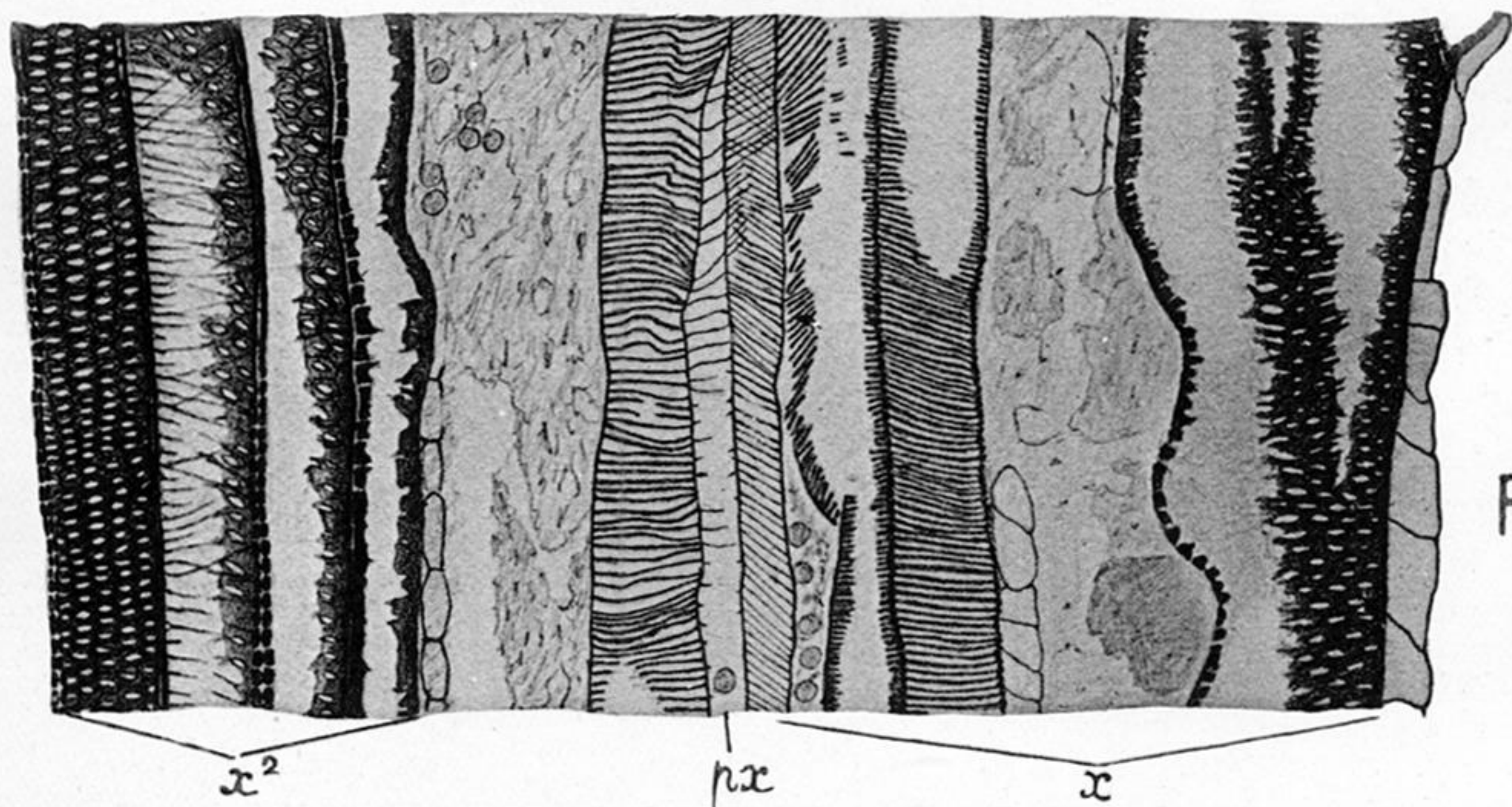


Fig. 5.

Fig. 6.

Fig. 7.

Medullosa Anglica.

## PLATE 10.

Fig. 2. Diagrammatic transverse section of Specimen I., at a level just below that of phot. 5. *st.*<sup>1</sup>, *st.*<sup>2</sup>, and *st.*<sup>3</sup>, the three steles, as shown in detail in phot. 5. *lt.*<sup>1</sup>, large undivided leaf-trace bundles; *lt.*<sup>2</sup>, smaller leaf-traces after sub-division; many of both kinds are shown. *o.c.*, hypoderma; *sc.*, internal sclerenchyma. The triangular space between *o.c.* and *sc.* (towards C) is part of a leaf-base, identical with the petiole shown, at a higher level, in phot. 2. On the side A the hypoderma is lost, but the ground-tissue better preserved. On the side B is a part of another leaf-base. The ground-tissue is shaded, where preserved.  $\times 2$ . S. 580. (See p. 86.)

Fig. 3 (Specimen I.). Transverse section of secondary wood and bast of stele 3. *x.*<sup>2</sup>, secondary wood; *ph.*<sup>2</sup>, secondary phloem, the larger elements probably the sieve-tubes; slight remains of cambium are present between wood and phloem.  $\times$  about 50. S. 578. (See p. 89.)

Fig. 4 (Specimen II.). Radial section through part of the primary and secondary wood of a stele. *x.*, primary wood, with tracheides and abundant parenchyma. One primary tracheide is pitted, the rest spiral or scalariform. *x.*<sup>2</sup>, secondary wood, showing medullary rays.  $\times 35$ . S. 751. (See p. 89.)

Fig. 5 (Specimen I.). Radial section through part of the primary and secondary wood of stele 1. *px.*, spiral elements of protoxylem; *x.*, inner part of primary wood; some tracheides pitted; parenchyma only partly preserved; *x.*<sup>2</sup>, secondary wood; bordered pits of tracheides shown in places.  $\times$  about 110. S. 597. (See p. 89.)

Fig. 6 (Specimen II.). Part of periderm of stem in radial section, with phellogen and cells of primary cortex to the left. The transverse section is quite similar.  $\times 43$ . S. 747. (See p. 96.)

Fig. 7 (Specimen III.). Small portion of periderm of stem, in tangential section.  $\times 43$ . S. 770. (See p. 96.)



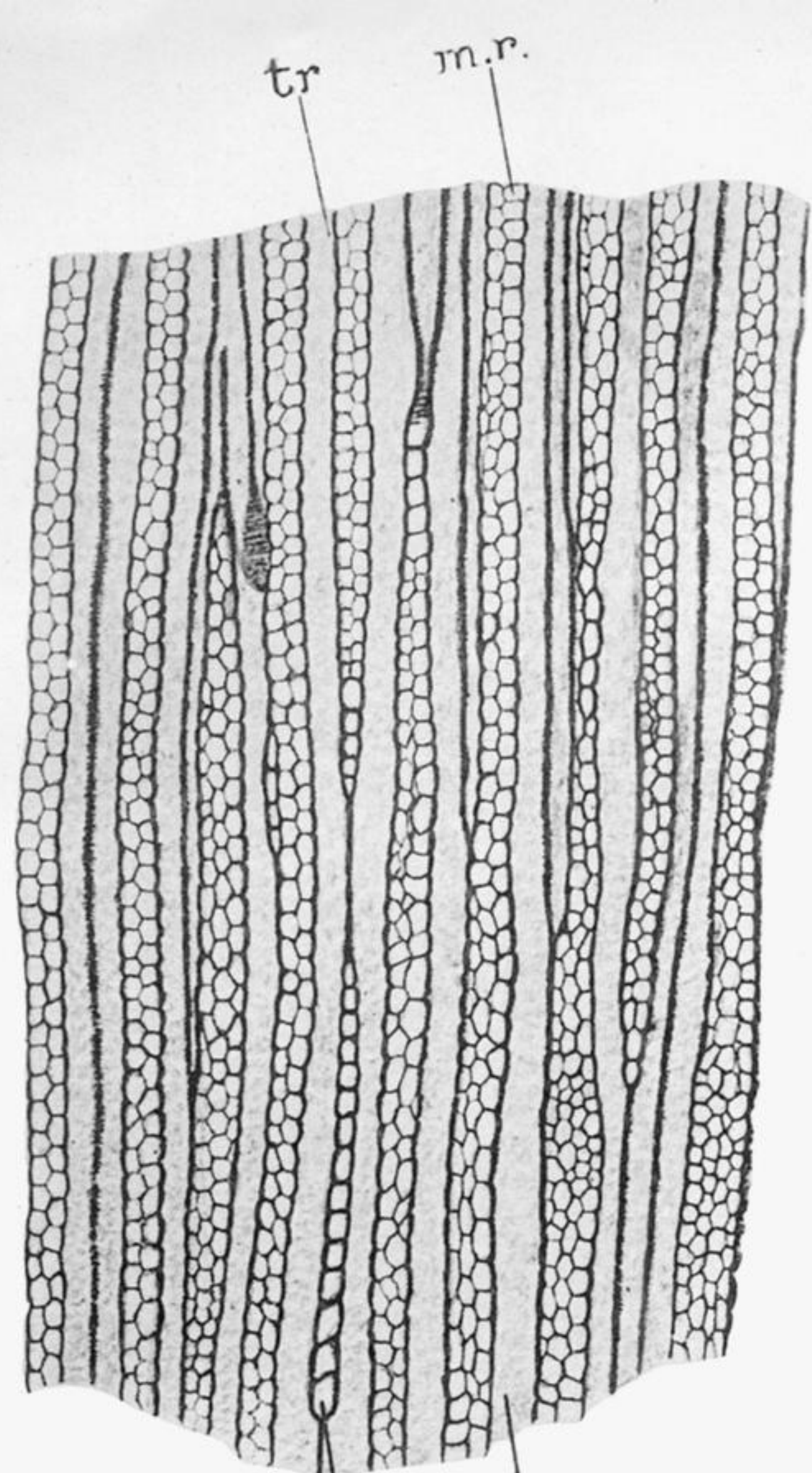


Fig. 8.

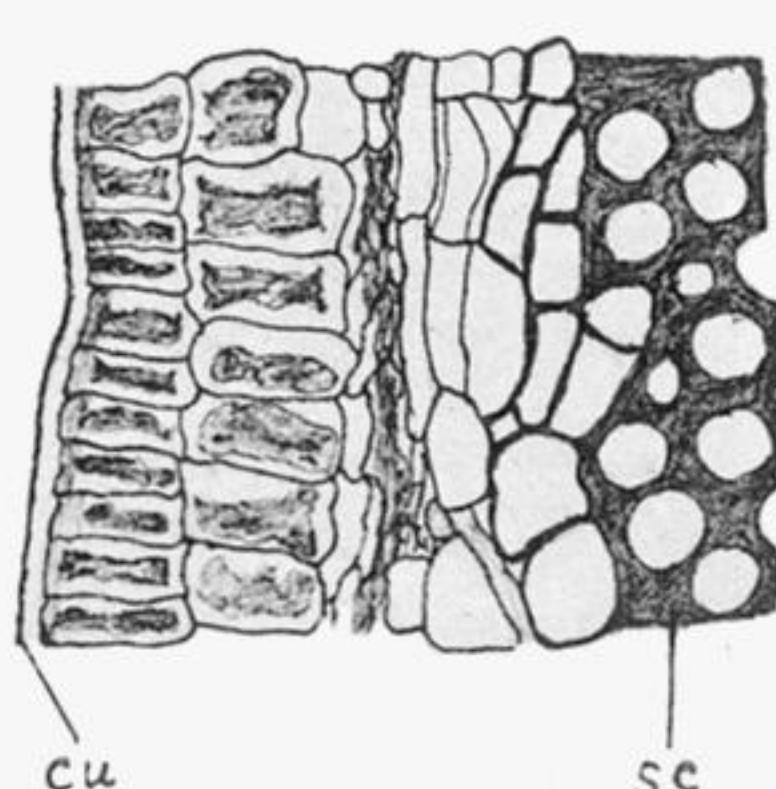


Fig. 13.

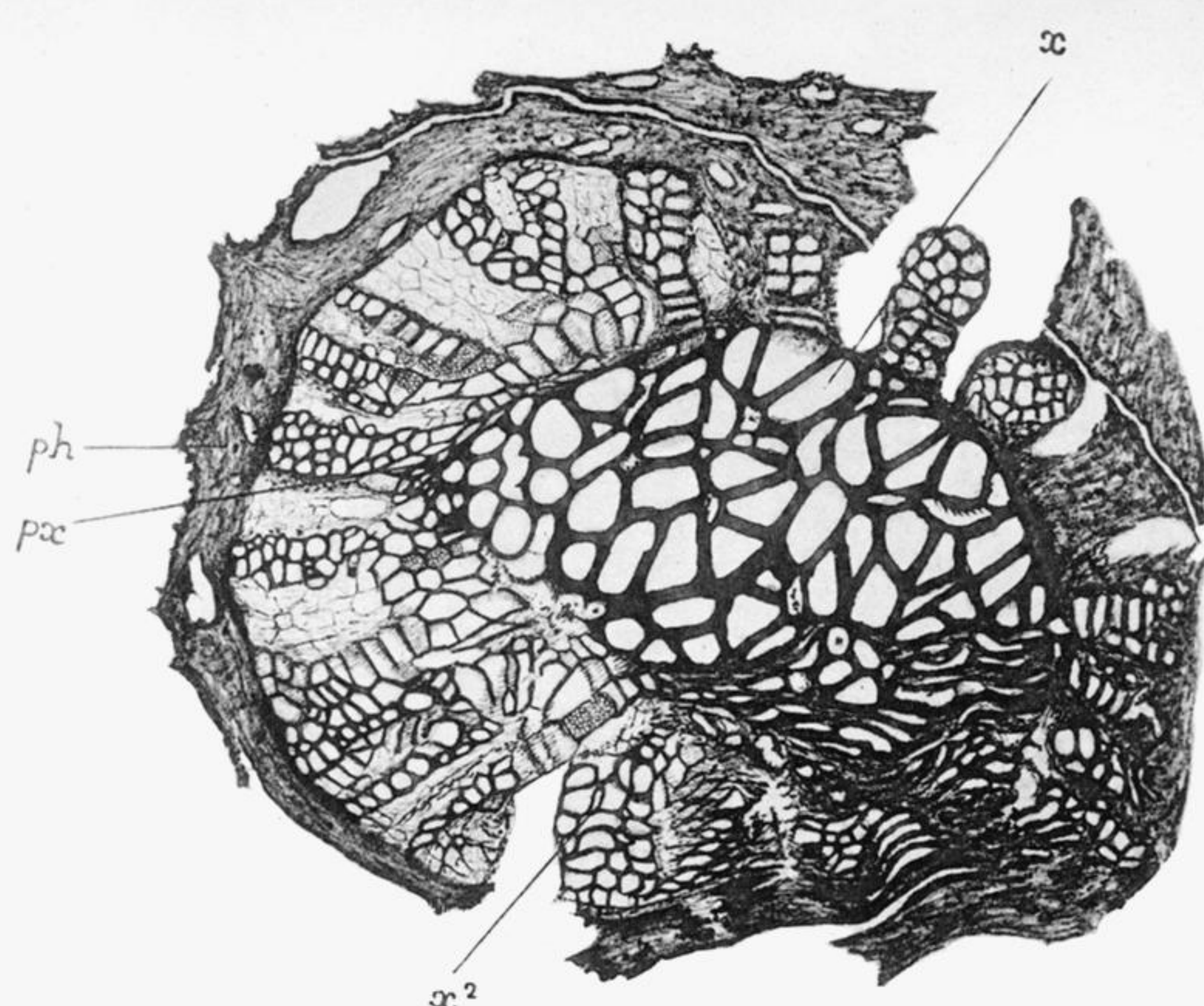


Fig. 10.

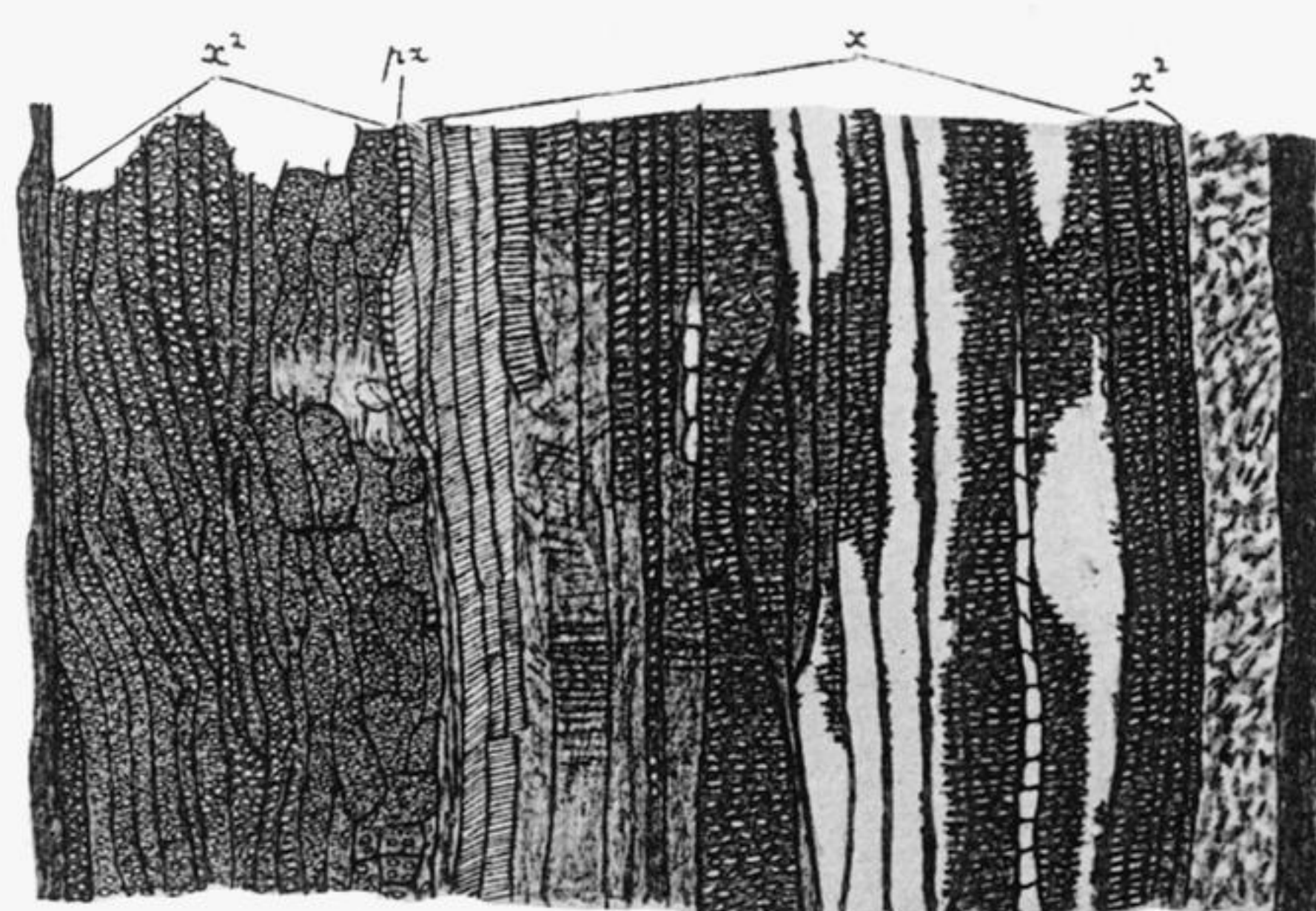


Fig. 11.

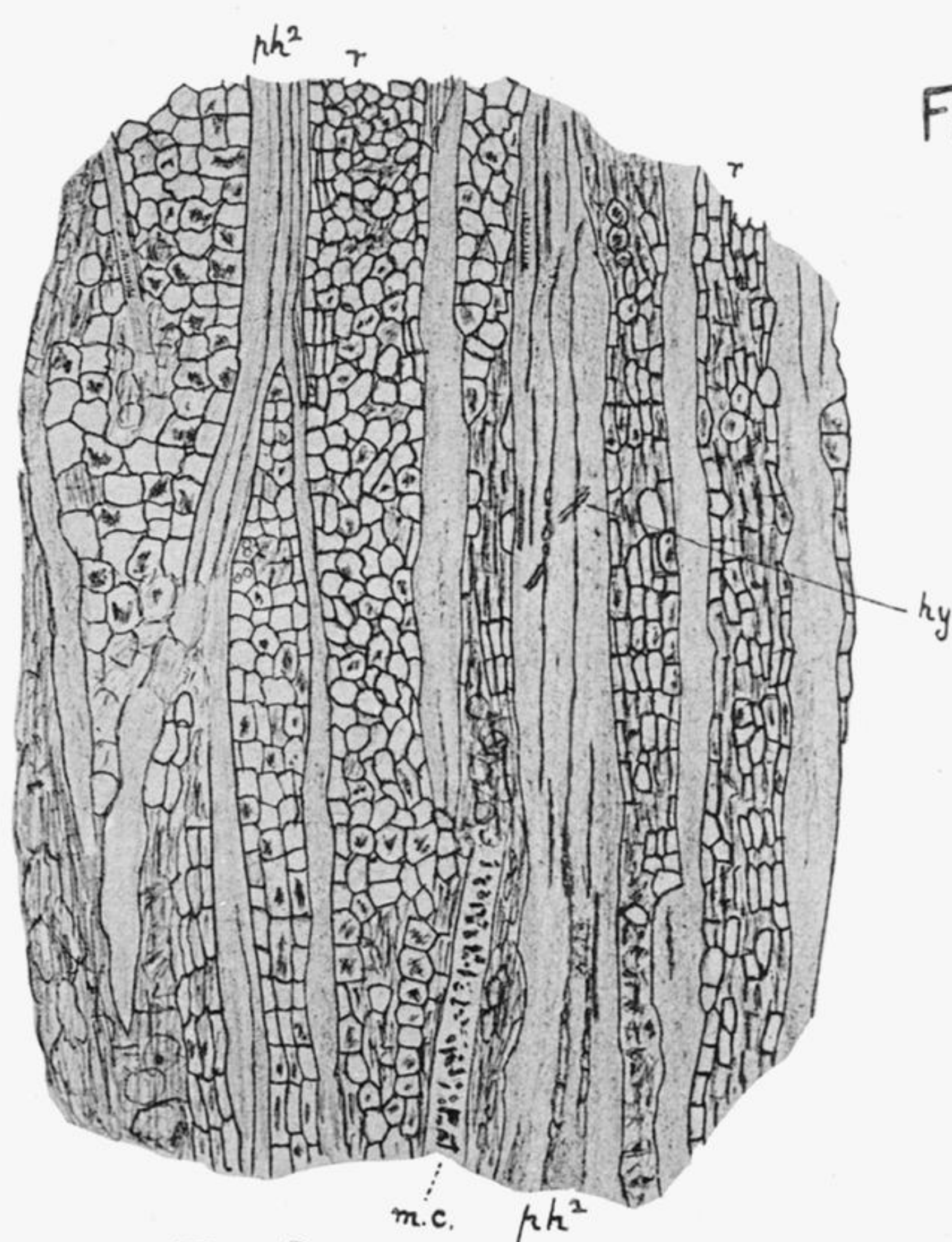


Fig. 9.

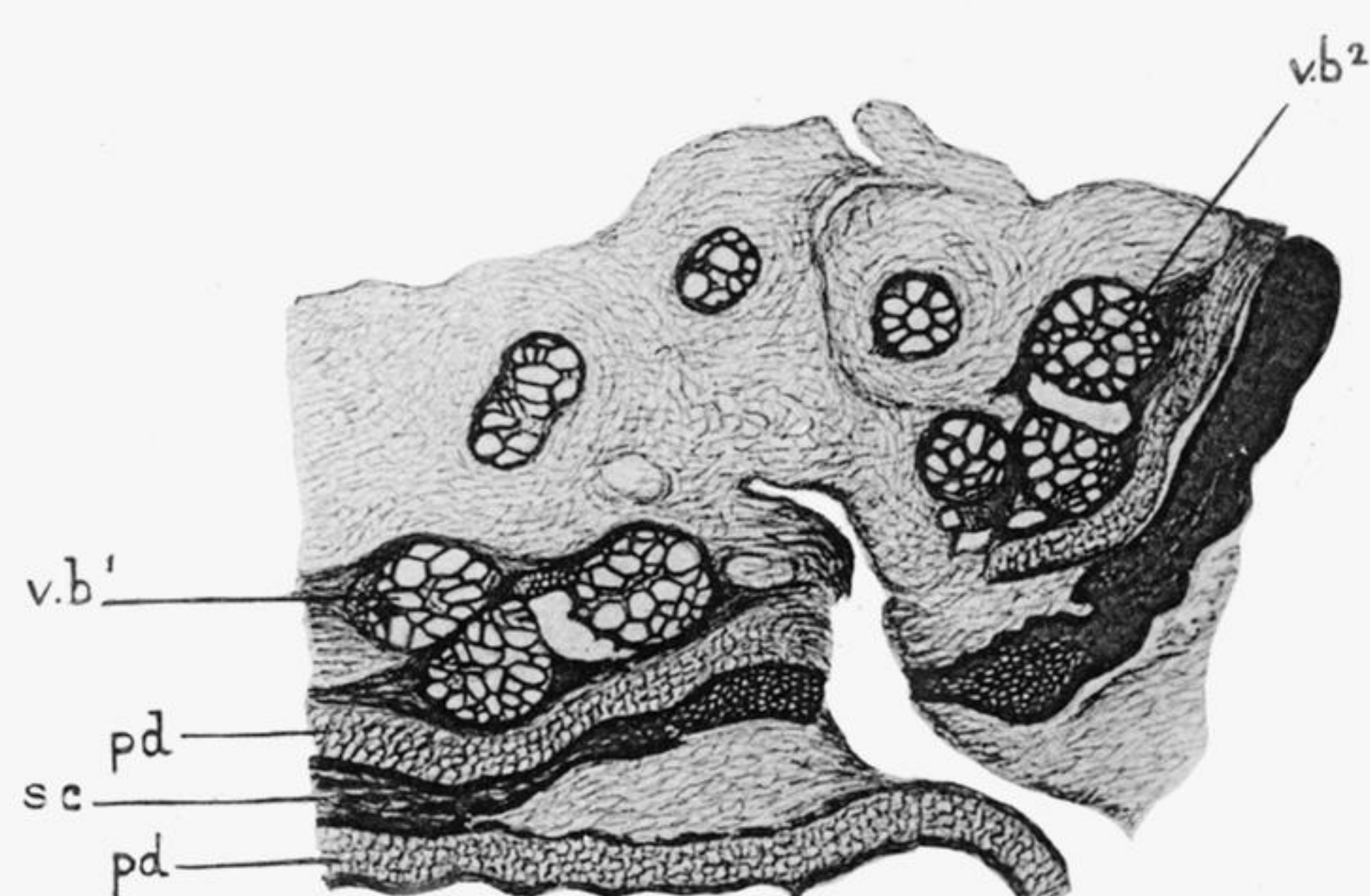


Fig. 12.

Medullosa Anglica.

# PLATE 11.

Fig. 8 (Specimen II.). Tangential section of secondary wood. *tr.*, tracheides; *m.r.*, medullary rays.  $\times 44$ . S. 750. (See p. 89.)

Fig. 9 (Specimen I.). Tangential section of phloem from stele 1. *ph.*<sup>2</sup>, strands of sieve-tubes in secondary phloem; *r.*, phloem-rays; *m.c.*, gum-canals in pericycle (?); *hy.*, fragments of fungal hyphae.  $\times 40$ . S. 595. (See p. 90.)

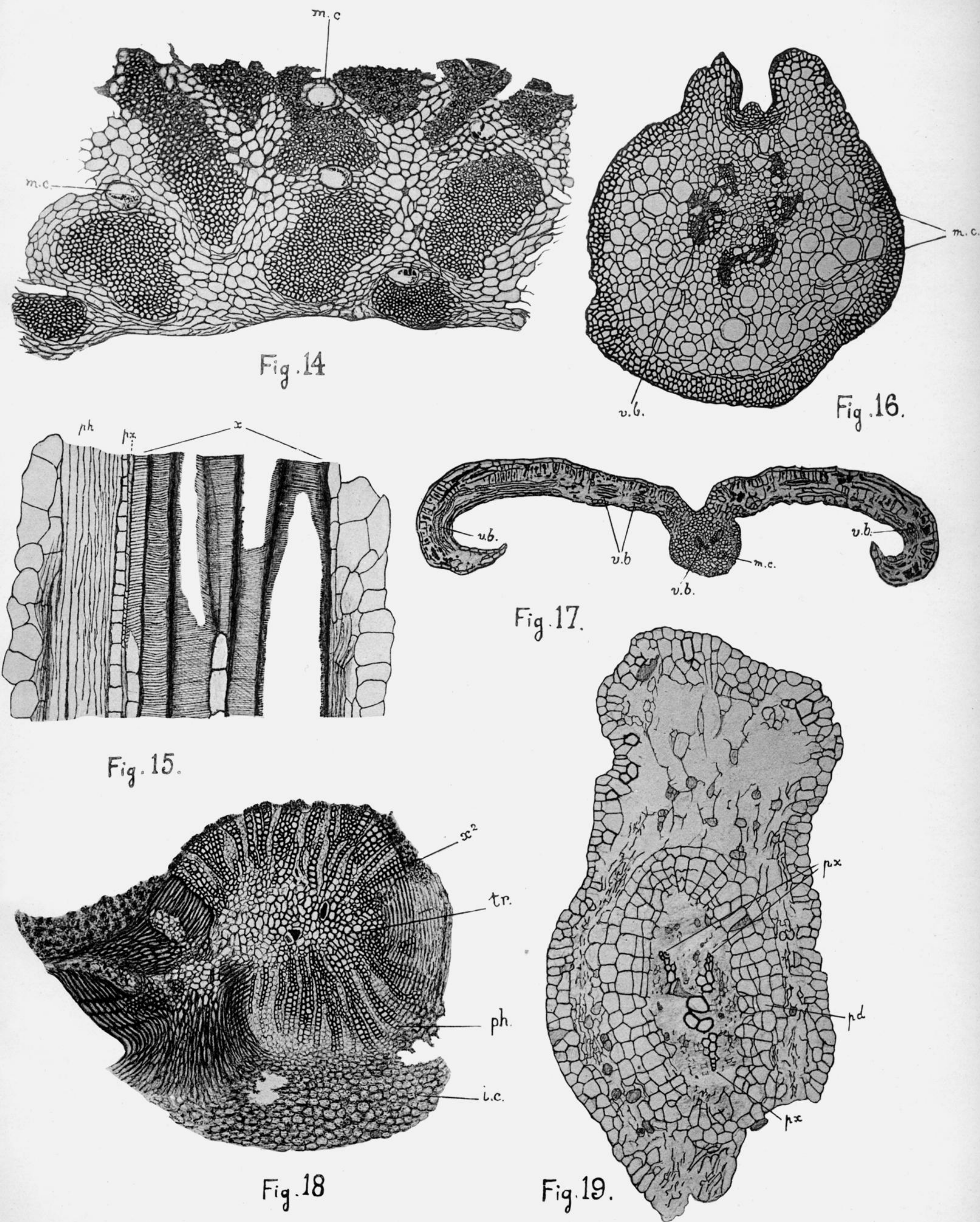
Fig. 10 (Specimen I.). Transverse section of a large undivided leaf-trace bundle, given off from stele 1. *x.*, primary xylem, consisting of large tracheides, with a little conjunctive parenchyma; *px.*, protoxylem; *x.*<sup>2</sup>, secondary wood, extending all round, except for accidental ruptures. On the border of primary and secondary wood, the pitted walls of short tracheides are seen. *ph.*, phloem, imperfectly preserved.  $\times 50$ . S. 582. (See p. 92.)

Fig. 11 (Specimen I.). Radial section of the large leaf-trace, *lt.*<sup>2</sup>, shown in transverse section in photos. 8 and 9. *x.*, primary wood of leaf-trace, consisting chiefly of pitted tracheides, becoming scalariform and spiral towards the protoxylem, *px.*; *x.*<sup>2</sup>, secondary wood, of very unequal thickness on the two sides. Towards the left many short tracheides are shown.  $\times$  about 45. S. 601. (See p. 93.)

Fig. 12 (Specimen I.). Transverse section, showing a number of small leaf-trace bundles, probably belonging to a leaf-base, as they lie outside the internal sclerenchyma, *sc.* The two groups *v.b.*<sup>1</sup> and *v.b.*<sup>2</sup> each arise from the subdivision of a single strand. *pd.*, double layer of periderm enclosing part of the sclerenchyma.  $\times 12$ . S. 580. (See p. 94.)

Fig. 13 (Specimen I.). Small portion of the external tissue of a leaf-base, in transverse section. *cu.*, probably cuticle. The epidermis and next layer have palisade form. *sc.*, part of hypodermal sclerenchyma.  $\times 88$ . S. 735. (See p. 99.)





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PLATE 12.

Fig. 14 (Specimen I.). Transverse section of the hypodermis of a leaf-base. The outer surface (from which the external tissues have perished) is directed upwards. The fibrous strands and intermediate parenchyma are obvious. *m.c.*, gum-canals.  $\times 23$ . S. 580. (See p. 99.)

Fig. 15 (Specimen I.). Radial section of a collateral vascular bundle from a leaf-base. *x.*, xylem, containing scalariform and spiral tracheides only; *px.*, protoxylem; *ph.*, phloem.  $\times$  about 85. S. 588. (See p. 95.)

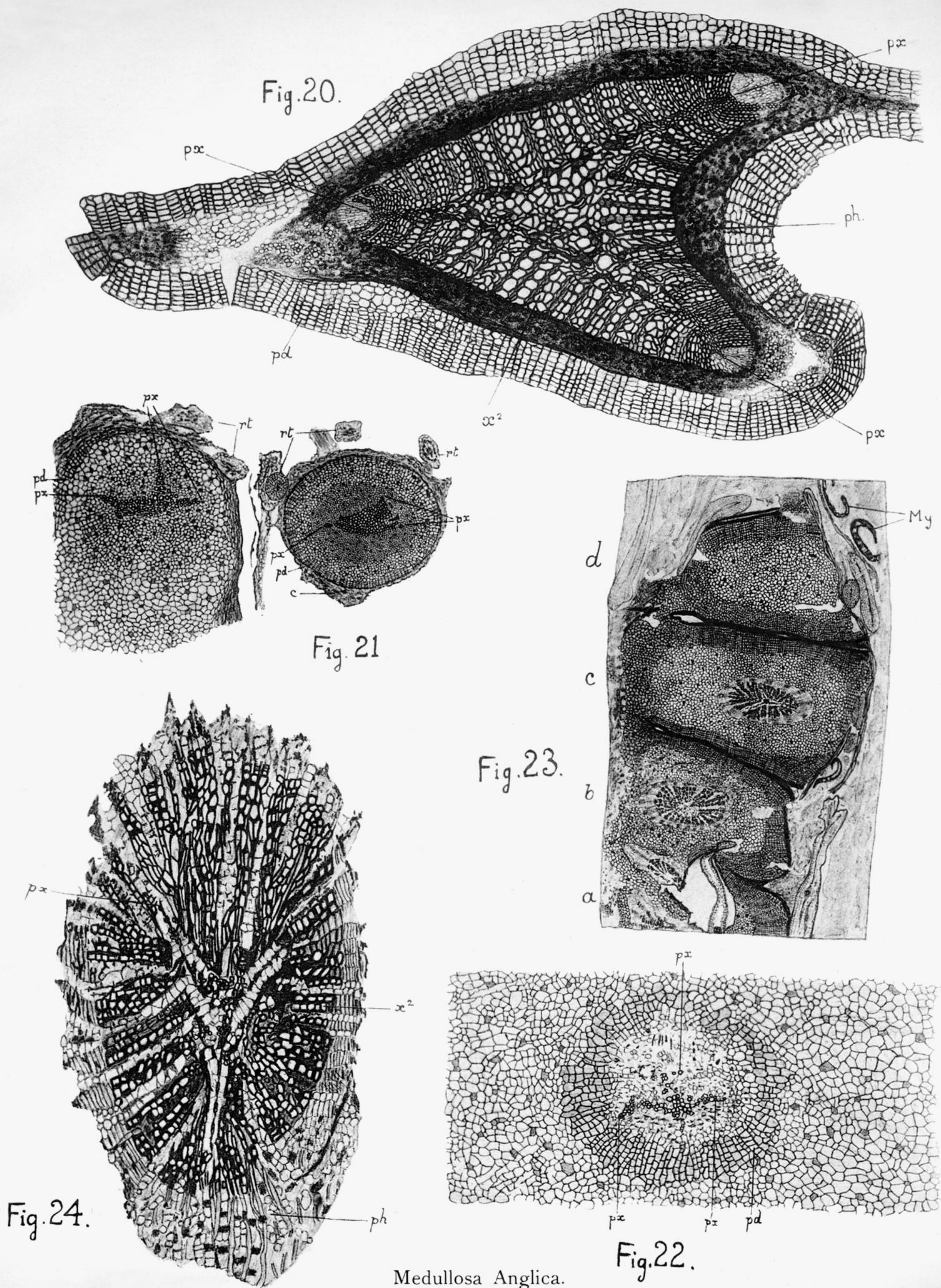
Fig. 16. Transverse section of the rachis of a pinna, from same block as Specimen I. Note the wings on upper surface; *v.b.*, vascular bundles, forming a ring, with phloem outwards, around a gum-canal; *m.c.*, other gum-canals. The hypodermis is almost continuous.  $\times$  about 50. S. 687. (See p. 101.)

Fig. 17. Transverse section of a leaflet (associated with rachis, petioles and stem of Specimen I.). *v.b.*, vascular bundles. The two in the midrib have their phloem directed laterally; those in the lamina are in longitudinal or oblique section. Note the palisade tissue towards upper surface.  $\times 36$ . S. 691. (See p. 101.)

Fig. 18 (Specimen II.). Accessory vascular strand from a transverse section of the stem, cut at the level 2 (*cf.* Plate 9, fig. 1). *tr.*, tracheides in the central parenchyma. *x.<sup>2</sup>*, secondary wood; some of the tracheides are horizontal. *ph.*, remains of phloem and cambium; *i.c.*, inner cortex.  $\times 28$ . S. 738. (See p. 98.)

Fig. 19. Transverse section of small rootlet. *px.*, the three protoxylem-groups. *pd.*, pericyclic periderm beginning to develop. Beyond this are the endodermis and primary cortex, as described in text.  $\times 90$ . S. 696. (See p. 104.)





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PLATE 13.

Fig. 20. Transverse section of a large triarch root, associated with Specimen I. *px.*, the three protoxylem-angles. To the interior is the primary wood. *x.<sup>2</sup>*, secondary wood, interrupted opposite the protoxylem-groups; *ph.*, phloem; *pd.*, periderm.  $\times 25$ . S. 731. (See p. 102.)

Fig. 21. From Mr. WILD's specimen, showing the two roots marked *r.* in phot. 23. One root is free, the other is still seated on its pedicel, which forms part of the cortex of the stem. *px.*, the three protoxylem groups of the two triarch roots. (The long axis of the xylem is vertical in nature.) *pd.*, periderm; *c.*, primary cortex of the free root, partly cast off; *rt.*, rootlets. (In the free root the parenchymatous cells are shown rather too small and numerous.)  $\times 19$ . S. 720. (See p. 106.)

Fig. 22 (Specimen IV.). Part of the root marked *r.<sup>1</sup>* in phot. 25, in transverse section. *px.*, the three protoxylem-groups of the asymmetric wood. In the natural position the long axis is vertical. *pd.*, internal periderm. Beyond this is primary cortex, with "secretory sacs."  $\times 36$ . S. 783. (See p. 107.)

Fig. 23. Section of Mr. BUTTERWORTH's specimen, showing four root-pedicels, *a*, *b*, *c*, *d*. In *b*, the stele has an apparent pith; in *c* it is triarch. The pedicels are coated by periderm, and united at their bases. *My.*, associated *Myeloxylon* leaflets.  $\times 4\frac{2}{3}$ . (See p. 108.)

Fig. 24. Stele of pedicel *c* in the last figure, shown in obliquely transverse section. *px.*, one of the three protoxylem-angles of the triarch primary xylem; *x.<sup>2</sup>*, secondary wood; *ph.*, phloem.  $\times$  about 30. (See p. 108.)