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

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

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[PLATES 15–17.]

Introduction.

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

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

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

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

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

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

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

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

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

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

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

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

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

Relation of Root and Stem.

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

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

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

‡ RENAULT et ZEILLER, 'Flore houillière de Commentry,' Part II., Plate 57, fig. 1.

§ WILLIAMSON and SCOTT, "Further Observations on the Organization of the Fossil Plants of the Coal-Measures," Part I., p. 899, 'Phil. Trans.,' B., 1894.

‖ WILLIAMSON, "Organization," Part IX., 1878, p. 319; Part XII., 1883, p. 459. HICK and CASH, "Flora of the Lower Coal-Measures of Halifax," Part III., 1881, and Part IV., 1884; published in 'Proc. Yorkshire Geological and Polytechnic Society,' vols. 7 and 8. Their specimens are named by them *Myriophylloides*; the question of the identification of the latter with *Astromyelon* will be considered below. See also RENAULT, "Végétaux fossiles du genre *Astromyelon*," 'Ann. des Sci. Géol.,' vol. 17, 1885.

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

** RENAULT, "Flore fossile du bassin houillier et permien d'Autun et d'Épinac," Part II., 1894; published in 'Études des Gîtes Minéraux de la France.' See especially Plates 42, 43, 44, 53, 54, 55, 59. The text of this memoir has not yet appeared.

Among our own specimens, which RENAULT regards as specifically distinct from his own, such evidence is scanty. In one case, however, we believe that the connection between root and stem is distinctly shown. The sections numbered C.N. 1351—C.N. 1355 (see Plate 15, photographs 1 and 2), in the WILLIAMSON Collection, were all cut from the same specimen. They are all approximately tangential sections of the wood of a main axis, on which lateral roots* are borne. Three of these roots are cut through transversely on their way out through the wood. Two of them are placed side by side, and appear in the same section (C.N. 1355). All three exhibit the typical structure of the larger specimens of *Astromyelon*—a considerable pith (which has been bored by Stigmarian rootlets, but was probably solid in life), a ring of centripetal xylem-groups (10 to 12 in number), and a zone of secondary wood, which is connected with that of the parent axis (see photograph 1).

There can be no doubt that the specimen shows the attachment of the roots to a main axis of some kind. The question to be solved is, whether this main axis was itself a root or a stem. This question appears to be decided by one of the sections (C.N. 1353; see Photograph 2), which distinctly shows three of those "lenticular organs," or enlarged medullary rays, which are so characteristic of the stem of *Calamites*, in its infranodal regions, but which, so far as we know, are entirely absent from the roots themselves.† At two points, also, the transverse sections of outgoing leaf-trace bundles can be distinguished. Photograph 2 shows one of the "lenticular organs," and one of the leaf-traces, which is especially clear. These facts demonstrate that the section passes through a node, and therefore that the axis is a stem. This conclusion is further strengthened by the fact that immediately above the node we find the base of a branch (probably abortive) which is thus in the normal position for branches of the stem of *Calamites*.‡

This specimen may therefore safely be regarded as affording additional evidence that organs with "*Astromyelon*" structure, were borne on Calamitean stems.

The nature of the organs hitherto known under the name of *Astromyelon*, is now so far established that we know them to have been appendages of the stem of *Calamites* (*Arthropitys* of the French authors). RENAULT has shown that very similar appendages, also showing the *Astromyelon* type of structure, were produced on the stems of *Bornia* and *Calamodendron*.§ So far as our English specimens of "*Astromyelon*" are concerned, we have no reason to doubt that they all belonged to the genus *Calamites*, though it is very probable that various species may be represented among them. The direct evidence of continuity applies only to the larger specimens, such as those originally described, in which there is a conspicuous pith.‖

* The proof that these organs are, morphologically, *roots*, will be fully given below.

† See our previous memoir, "Further Observations," &c., Part I., p. 887; also WILLIAMSON, "Organization," Part IX., p. 325.

‡ See our "Further Observations," Part I., pp. 890 and 893.

§ *Loc. cit.*, "Flore fossile d'Autun," Part II., Plates 42 and 43, 59 and 60.

‖ See WILLIAMSON, "Organization," Part IX, Plate 19, figs. 1–7.

The smaller specimens, such as those which were first described by HICK and CASH under the name *Myriophylloides*,* but have since been united with *Astromyelon*,† were no doubt branches of the larger organs, as will be shown below.

Structure of the Roots.

We have now to consider in detail the structure of these appendages, with special reference to those points by which their morphological nature has been established. That they were quite different from the ordinary branches of a Calamitean stem became obvious as soon as their organization was understood.‡ Their characteristic lacunar cortex, the entire absence of nodes, the usually solid pith, and the absence of canals accompanying the vascular bundles, all serve to distinguish them. That these organs were of the nature of *roots* could, however, only be established by a minute investigation of their structure and mode of development, so far as the latter could be ascertained. We hope that, by our observations, we have been able to add something to the evidence already brought forward by RENAULT, who recognizes most of these organs as true roots, though in certain cases he prefers to regard them as "stolons."§

The characters (likely to be traceable in petrified specimens) on which we have to depend in distinguishing a root from a stem, are the following:—

1. Centripetal development of the primary xylem.
2. Alternate arrangement of the primary groups of xylem and phloëm.
3. Endogenous mode of origin of the organ itself, and of its branches.
4. Absence of nodes.

Though no one of these characters is necessarily conclusive by itself, the sum of them is sufficient to determine with certainty the root-nature of the organ.

In describing the structure it will be best to begin with the typical specimens, possessing a well-marked medulla, such as those which have been found in direct connection with Calamitean stems. We will afterwards pass on to the more minute specimens, many of them destitute of any evident pith, which we regard as the rootlets, or finer branches, of the same organs.

The largest specimen in the collection is one figured in a previous memoir.‖ This is somewhat compressed, and measures, in its decorticated condition, about 25 millims. in greatest and 11 millims. in least diameter. The pith is hollow, and this is the only specimen in which, from the definite inner limit of the persistent peripheral portion of the medulla, it appears probable that the latter was really fistular during life. In

* *Loc. cit.*, 'Proc. Yorkshire Geol. and Polytechnic Soc.,' vol. 7, 1881.

† By WILLIAMSON, "Organization," Part XII., 1883.

‡ WILLIAMSON, *loc. cit.*, Parts IX. and XII.

§ *Loc. cit.*, "Flore fossile d'Autun," &c., Part II., Plates 55, 56, 57, 59, 60.

‖ WILLIAMSON, "Organization," Part IX., Plate 19, fig. 5; C.N. 1334.

all other specimens the pith is either solid, or, if hollow, there is every appearance of the cavity being due to decay or to the intrusion of Stigmarian rootlets.*

The pith varies enormously in size in the different specimens, and may only consist of three or four cells, as seen in transverse sections, while in the smallest rootlets it disappears altogether. Except in these extreme cases the structure is fairly uniform in all. The pith consists of rather large-celled parenchyma, and presents no peculiarities (see Plate 16, figs. 1, 2, and 3). It is surrounded by a ring of primary xylem-groups, varying in number from 25 downwards. When the pith is large the xylem-bundles are usually separated from one another by broad primary rays (see Plate 15, photographs 1 and 3); when it is small the bundles may be nearly in contact with one another, and in the latter case their limits may be somewhat difficult to trace. The presence, however, of these primary groups of xylem is absolutely constant, and their structure is always essentially the same. Each group, as seen in transverse section, has an approximately triangular form, with one angle directed outwards (see Plate 16, figs. 1 and 2).† It consists of a varying number of tracheides, of which there are often about 20. The elements become smaller towards the peripheral angle, and it is constantly at the angle itself that the most minute tracheide is situated (figs. 1 and 2, *px.*).

In accurately transverse sections, if the cells of the pith have rather thick walls, it may not be easy to distinguish them from the primary tracheæ. With care, however, this can always be done, in good preparations. Wherever the section is at all oblique, the primary tracheæ can be recognized with ease by the pits on their walls.

The arrangement of the tracheæ at once suggests, even from the inspection of transverse sections alone, that the development of each group of primary xylem was *centripetal,* the small tracheæ at the external angle representing the protoxylem, or first-formed elements. This conclusion is rendered certain by the examination of oblique and longitudinal sections, in which we find that the smallest and most external elements of the primary xylem are spirally thickened. This, for example, is beautifully shown in the radial section (C.N. 1317) a part of which is represented in fig. 3. The spiral protoxylem-tracheæ are quite unmistakable, both at the place figured, and at several other points in the section. Similar observations have been made by RENAULT, who has shown clearly that the development of the primary wood was centripetal in his specimens, which he refers to different species from ours.‡ We find that the spiral tracheides are few, and their spirals densely coiled, a peculiarity characteristic of the root in recent plants, and due to the shortness of its growing region. (See DE BARY, "Comp. Anat.," p. 352.)

* See WILLIAMSON, "Organization," Part IX., Plate 19, figs. 1–7; Part XII., Plates 27 and 28, figs. 2, 3, and 6; also Photographs 1, 3, 4, 6, and 7 in the present paper.

† See also WILLIAMSON, "Organization," Part I., Plate 25, fig. 16; Part XII., Plate 27, fig. 3.

‡ RENAULT, "Recherches sur les Végétaux fossiles du Genre *Astromyelon*," 'Annales des Sciences Géologiques,' vol. 17, 1885; see p. 12, Plate 8, fig. 8, &c.; 'Flore fossile d'Autun," Part II., Plate 57, fig. 7, &c.

The elements which adjoin the actual protoxylem on the inner side are often reticulated. Further towards the interior the primary tracheæ become considerably larger, and have pitted walls, the pits being often transversely elongated, so as to give a scalariform character to the thickening (fig. 3). Some of the pits show a slight border. The primary tracheæ have very oblique terminal walls, which are pitted like the lateral walls; there is no reason to doubt that these elements were closed tracheides, and not open vessels.

The primary xylem-groups, then, were evidently developed centripetally, and so far agree with those of recent roots.

The primary strands of *phloëm* can of course only be recognized in the most favourable preparations. A good example is represented in fig. 1, which is drawn from a section previously figured as a whole.* The specimen is the original one of "*Myriophylloides Williamsoni*," described by Hick and Cash in 1881, and another transverse section of it is figured in the memoir by those authors.† Neither of the former figures, however, show either the phloëm or the primary xylem. The details are remarkably clear in this specimen. The root has nine groups of primary wood, and shows the commencement of secondary growth; the secondary wood is as yet only three or four cells in thickness. Immediately outside the wood is a zone of very delicate tissue; opposite the protoxylem-groups this zone is excessively narrow —only two cells in thickness—and evidently represents the dividing cambium only. *Between* the groups of primary wood, however, the delicate tissue attains a thickness of about five cells; evidently phloëm is present at those places, to the outside of the cambial layer (fig. 1, *ph*, *ph*, on either side of the protoxylem, *px*). The alternation of the primary strands of xylem and phloëm is quite regular. Here, then, is another point, in which these organs conform to the typical structure of recent roots.‡

Secondary tissues, as is already well known, were formed in great abundance, and the various preparations show them at all stages of development—the wood, in the larger specimens, sometimes attaining a radial thickness of at least 60 elements.

* Williamson, "Organization," Part XII., Plate 28, fig. 2.

† Hick and Cash, *loc cit.*, 'Proc. Yorkshire Geol. and Polytechnic Soc.,' 1881.

‡ Hick and Cash describe the whole of this thin-walled zone as cambium, *loc. cit.*, p. 402. These authors have expressed doubts as to the identification of their *Myriophylloides* with *Astromyelon* (*loc. cit.*, 'Proc. Yorkshire Geol. and Polytechnic Soc.,' vol. 8, 1884, p. 375). They point out, quite justly, that the similarity in cortical structure is not by itself sufficient to prove identity. They go on, however, to state that the *axial* structure of *Astromyelon* bears "by no means a close resemblance to that of *Myriophylloides*." This is a mistake, arising from the fact that, at that time, the primary wood of *Myriophylloides* had not been recognised. The structure of the original specimen of *Myriophylloides* is in fact identical with that of *Astromyelon*. For example, there is no real difference, except in age, between the root shown in "Organization," Part XII., Plate 28, fig. 2 (*Myriophylloides*), and that shown in Plate 27, fig. 3 (typical *Astromyelon*). On comparing our own fig. 1 (*Myriophylloides*) with fig. 2, which is from a typical *Astromyelon*, the essential identity of structure becomes obvious. The question of the identification of the smallest pithless specimens presents greater difficulties, and will be discussed in the text.

The general structure of the secondary wood is identical with that of the stem of *Calamites.* The fascicular wood abuts directly on the external elements of the primary xylem (see fig. 2). The interfascicular wood is soon formed across the whole width of the primary rays, which, consequently, cannot be traced far outwards (see Plate 15, photographs 3, 6, and 7). In some cases the cells of the primary ray show tangential dilatation, exactly as we described in the case of the stem in our last paper.*

In these, as in other roots, the primary interfascicular rays are necessarily limited to the wood, for each of them corresponds in position to a strand of primary phloëm.

A characteristic feature of the secondary wood is the regular presence of a ray one or two cells in thickness, exactly opposite each protoxylem-angle (see Plate 16, fig. 2, *f.r.*). These rays, which often consist of cells rather broader than the tracheæ, can sometimes be traced for a long distance through the wood. In some cases they become subdivided by intercalated series of tracheæ. We may call them *fascicular* rays, to distinguish them from the broader *interfascicular* rays which lie between the bundles of primary xylem. The fascicular rays can be recognized in radial sections also, wherever the plane of section exactly passes through the protoxylem (see fig. 3, *f.r.*). They can also be distinguished in tangential sections which pass through the inner part of the wood. These rays were observed by RENAULT, in his *Astromyelon augustodunense*, in 1885.†

The formation of a ray opposite each protoxylem-group is a well-known phenomenon in recent roots.‡

The wood also contains numerous secondary rays of the ordinary type.§

The tracheæ agree in all respects with those of the stem. Their pits are usually limited to the radial walls, and are distinctly bordered, as can best be seen in good tangential sections.

Remains of the cambium and phloëm have been observed in several of the more advanced specimens, as well as in the younger roots already mentioned. Perhaps the best specimen in this respect is that illustrated in Plate 15, photograph 3, and in Plate 17, figs. 10 and 11. This root shows a distinct layer of phloëm (fig. 10, *ph.*), which has split away from the wood, and remains attached to the cortical zone. Here and there a tabular cambial cell is seen at the outer edge of the wood (*cb.*). We cannot be certain that the whole thickness of the phloëm remains; the part preserved is six or more cells in width, and its elements show traces of a radial arrangement. Most of this tissue, no doubt, belonged to the secondary phloëm; some more irregular groups in the outer part of the zone probably represent the primary phloëm.

The structure of the *cortex* has been fully described in former memoirs.‖ Only a

* "Further Observations," Part I., p. 884.

† *Loc. cit.*, "Nouvelles Recherches," p. 98.

‡ DE BARY, 'Comparative Anatomy of Phanerogams and Ferns,' Engl. ed., p. 474.

§ See WILLIAMSON, "Organization," Part IX., Plate 19, fig. 6, *c.*

‖ See especially "Organization," Part XII.

brief recapitulation, with the addition of one or two details, is needed here. The question of the presence of a distinct pericycle and endodermis will be postponed until the smaller rootlets have also been taken into consideration.

In all cases where the cortex is preserved, it consists of three well-marked zones: (1) an inner cortex, of continuous parenchyma, immediately surrounding the central cylinder; (2) a middle cortex, which is *lacunar*, consisting of radial plates of tissue, separated from one another by wide intercellular spaces; (3) an outer cortex, consisting, like the inner zone, of continuous parenchyma.* The relative thickness of the three zones varies considerably in different specimens, as is sufficiently shown in the figures cited. The lacunæ, however, are always arranged in a single circle only. The large root shown in photograph 3 has a somewhat peculiar cortex, which, at the first glance, appears to consist entirely of solid parenchyma. More careful examination, however, reveals the existence of a rather narrow lacunar zone (see Plate 17, fig. 11, *l.z.*) in the usual intermediate position. The trabeculæ have been crushed in upon the inner cortex, so as almost to obliterate the lacunæ between them.

The specimen shown, in transverse section, in photograph 4, has a cortex of the "*Astromyelon*" type, but differing considerably from the more usual form. It is, in all probability, specifically distinct from the more ordinary examples. The trabeculæ are much more numerous than usual, and the lacunæ between them are narrower in a corresponding degree. At some places the lacunæ are not empty, but contain large, irregular, rounded cells. Similar intralacunar cells have been found occasionally in other specimens; their nature will be discussed below (p. 693).

The structure of the trabeculæ is well shown in longitudinal or oblique sections, from which it is evident that they formed continuous vertical partitions, each of which was only one cell in thickness (see fig. 8; also "Organization," Part XII., Plate 31, fig. 4). The cells of which they are composed are cylindrical in shape, so that the partitions, as seen in tangential section, have a moniliform appearance. The inner cells of each trabecula are usually short, while those further to the exterior are often much elongated in the radial direction. Some further details as to the cortex will be given when the rootlets are considered.

The Rootlets.

Under the name "rootlets" we group those smaller specimens, which, while agreeing in other respects with the forms already described, differ from them in having little or no pith, and no primary rays, so that the groups of primary xylem either meet at the centre of the stele, or are, at least, laterally confluent. Specimens of this kind were included by HICK and CASH in their genus *Myriophylloides*,† the type-specimen of which, as we have seen, had a considerable pith and typical *Astromyelon*

* See the figures in "Organization," Part XII.

† *Loc. cit.*, 'Proc. Yorkshire Geol. and Polytechnic Soc.,' vol. 8, p. 377, 1884. See also RENAULT, "Nouvelles Recherches," p. 101, 1885.

structure. The pithless specimens, however, really differ conspicuously from the ordinary type of *Astromyelon*. Now that we know that *Astromyelon*, in its typical medullate form, is nothing but the root of *Calamites*, it becomes desirable to reconsider the evidence for the identification with it, of the minute pithless specimens. We believe we are able to prove that here also the identification is correct, and that the smallest specimens, without medulla, are, in fact, the finer branches, or rootlets, which were borne on the larger medullate organs. We shall, therefore, employ the word "rootlet" throughout the description, though, as we shall find, there is no sharp distinction between these finer branches and the larger medullate specimens which we term simply "roots."

The structure of the rootlets will first be described, after which we will discuss the evidence as to their nature.*

In some of them the middle of the central cylinder is entirely occupied by the primary xylem, and there is no pith whatever. Neither does there seem to be parenchyma of any kind among the primary tracheæ (see figs. 5, 7, and 8; also fig. 1 in "Organization," Part XII.). In other cases, a very few elements, with somewhat thinner walls, can be distinguished at the centre (see, for example, fig. 4). In such cases it is often impossible to make out for certain whether these elements are really parenchymatous cells or merely thin-walled tracheæ. In other specimens, however, there is no doubt of the existence of a very small pith.† In the remarkable branched specimen, figured in a previous memoir,‡ the rootlets seen in longitudinal section show no pith, while the branch, which is cut transversely, has a little thin-walled tissue within the primary wood.§

In all these rootlets the primary wood, whether actually reaching the centre of the stele or not, is perfectly continuous, so that the number of strands of which it is composed is indicated by the protoxylem-angles alone. The latter are often quite distinct, as, for example, in Plate 16, fig. 4, where the rootlet was evidently tetrarch. So also, no doubt, was the rootlet shown in Plate 15, photograph 5.‖

In the typical rootlets, with little or no pith, we have never found more than four

* The rootlets are illustrated in "Organization," Part XII., figs. 1, 5, and 7; and in photograph 5 and figs. 4, 5, 7, and 8 in the present paper.

† See, for example, the rootlet figured in "Organization," Part XV., Plate 3, fig. 23, which is almost certainly of the same nature. This rootlet occurs inside the stem of a *Lepidodendron selaginoides*, in the hollow zone left by the decay of the middle cortex. It is very probable that the rootlet had made its way, by its own growth, into the decaying stem, as so constantly happened in the case of the rootlets of *Stigmaria*.

‡ "Organization," Part XII., Plate 29, fig. 7.

§ Another very clear case of a minute pith (not figured) is C.N. 1348. Here the tetrarch rootlet has a perfectly distinct thin-walled medulla, consisting of three or four cells only, as seen in transverse section.

‖ See also WILLIAMSON, "Organization," Part XII., Plate 30, fig. 5, which shows another tetrarch rootlet.

groups of protoxylem; triarch and diarch specimens also occur. Thus our fig. 7 shows a triarch rootlet, and one of those figured in a previous memoir was probably also triarch.* We have figured a very characteristic *diarch* rootlet in fig. 5. Another rootlet (see fig. 8), itself probably tetrarch, bears a diarch branch. Minute diarch rootlets are excessively common in the preparations, but, as a rule, their structure is not sufficiently definite for us to be certain to what they belong. We have, however, figured one of these doubtful rootlets in fig. 9. It occurs in the same preparation as that shown in fig. 8, so it is very probable that it may be of the same nature as the diarch branch shown in the latter figure, borne upon a rootlet of the usual structure. Fig. 9 is in itself of considerable anatomical interest. The rootlet, which is very young, is seen in oblique section. The diarch xylem-plate is not yet completely lignified in the middle; the minute tracheæ of the protoxylem are clearly shown at either end of the plate. A branch, which is obviously of endogenous origin, is seen in median section. Its xylem is directly continuous with one of the protoxylem-strands of the parent rootlet. A more typical example of root-structure would be difficult to find; we have therefore thought the specimen worth figuring, though we cannot be quite certain that it is of the same kind as the other rootlets.

Returning to the typical specimens, we find that the rootlets, in some cases, possess the primary tissues only, while others have undergone a greater or less degree of secondary growth in thickness. Such differences are no doubt dependent simply upon age. Thus the rootlet shown in fig. 7 is destitute of any secondary tissues, while fig. 4 shows the first commencement of their formation. The diarch rootlet, represented in fig. 5, already has about five layers of secondary wood. A tetrarch rootlet, previously figured,† has a broad secondary zone, the wood of which is about ten layers thick. Other rootlets, with much thicker secondary wood, in one case amounting to sixty layers of tracheæ (C.N. 1309), are included in the collection. The structure of the wood of these rootlets is in all respects identical with that of the larger roots, except, of course, that in the former, owing to the absence of primary rays, the wood is not broken up into wedges.

Fascicular rays, corresponding to the protoxylem-groups, can often be distinguished in the rootlets, as well as in the larger roots.

Remains of the phloëm are frequent in the better-preserved rootlets (see figs. 4 and 5). The secondary phloëm does not seem to have attained any great thickness. The tetrarch rootlet, shown in transverse section in fig. 4, is very instructive. The position of the four protoxylem-groups (*px.*) is quite clear; at these four points no secondary growth had as yet taken place. In two cases the cell lying immediately outside the protoxylem has undergone a single tangential division; at the other two points there seems to have been no division, though it is possible that the delicate septa may have perished. Opposite the protoxylem-groups there is evidently an

* WILLIAMSON, "Organization," Part XII., Plate 27, fig. 1.

† "Organization," Part XII., Plate 30, fig. 5.

entire absence of phloëm, while between them four distinct bands of phloëm (*ph*) are shown. Thus the usual alternation, characteristic of roots, is maintained. Within each of the four bands of phloëm growth in thickness has commenced, and from three to four layers of secondary wood have already been formed in this position.

The rootlet shown in Plate 15, photograph 5, is essentially similar, but here the wood has already attained a somewhat greater thickness.*

We now come to the subject of pericycle and endodermis. The rootlet shown in Plate 16, fig. 4, has four rows of cells between the phloëm and the beginning of the lacunar zone. The two outer of these layers have intercellular spaces, and evidently form part of the inner cortex. The next layer, towards the interior (*en*, in fig. 4), consists of closely-fitting cells, and a slight thickening of their radial walls can be made out. This was almost certainly the functional endodermis. The innermost layer, abutting on the phloëm and protoxylem, consists of thin-walled cells. Now it is remarkable that these four layers of cells are arranged, on the whole, in radial series. The same is the case in the rootlet shown in Plate 15, photograph 5. The important point is that the layers which occupy the respective positions of pericycle and endodermis fit on to each other as if they had had a common origin. Traces of the same arrangement are found in other specimens, both rootlets and larger roots.† In some of the latter the thin-walled layer is two cells thick. Outside this comes the functional endodermis, and sometimes all three layers are in radial seriation. Too much stress must not be laid on these facts, which are not absolutely constant. At the same time they are not without interest, for we know that in the roots of *Equisetum* there is no pericycle, but a double endodermis, in which the outer layer alone has the typical endodermal structure, while the inner layer is thin-walled, and gives rise to the rootlets.‡ If the indications above mentioned are to be trusted it would appear that the same may have held good for the roots of *Calamites*, in which case we should have to speak of the thin-walled layer immediately surrounding the stele, not as pericycle, but as inner endodermis.

The cortex of the rootlets does not differ from that of the larger roots. We find the same three zones, of which the middle one is lacunar (see photograph 5, and figs. 4, 5, 7, and 8). Occasionally we find cells in the cortex which have rather thicker walls than their neighbours, and dark carbonised contents (see fig. 4). These may very probably have been secretory sacs of some kind. Similar cells also occur in the cortex of the largest roots (see fig. 11).

Attention has already been called to the occasional presence of irregular rounded cells within the lacunæ. This peculiarity appears both in the medullate roots and in

* *Cf.* "Organization," Part XII., Plate 30, fig. 5, which represents a similar rootlet at a more advanced stage of development.

† As for example in C.N. 1308.

‡ See, for example, VAN TIEGHEM et DOULIOT, "Origine des membres endogènes," 1889, p. 394, Plate 27, figs. 413–416.

the rootlets (see photographs 4 and 5, figs. 7 and 8). The specimens shown in photograph 5 and in fig. 8 throw great light on the origin of these intralacunar cells. It is evident that they arose as hernia-like outgrowths from the cells of the trabeculæ. An early stage of this process is shown in fig. 8; in photograph 5 the outgrowths have become larger and more numerous, while in the specimens represented in photograph 4 and in fig. 7 they have increased to such an extent as to block up some of the lacunæ. The process is evidently of the nature of *thylosis*, which is known to occur in the intercellular spaces of *Equisetum*.*

Wherever the outermost tissues of the cortex are preserved, whether in a rootlet, or in one of the larger roots, we find the surface protected by a special thick-walled layer of cells. The outer wall of this layer in some cases attains a great thickness, which may exceed the diameter of the cell-cavity. The thickened membrane often shows a distinctly laminated structure (see photograph 5, and figs. 5, 7 and 8).†

We propose to call this outer, protective layer of cells, the *epidermoidal* layer; it has the structure of a thick-walled epidermis, and appears to correspond in all respects with the epidermoidal layer‡ described by OLIVIER in many recent roots. It is probable that the epidermoidal layer in the roots of *Calamites* was not superficial in origin, for in some cases the remains of a layer of cells exterior to it can be traced. Most probably the actual absorptive epidermis of the young root was cast off, and the protective function was assumed by the cortical layer next below (the *exodermis* §), just as is the case in so many roots of recent plants.

In one of the larger roots the epidermoidal layer is evidently more than one cell thick (see fig. 11). It is possible that we here have the commencement of periderm-formation, such as was observed by RENAULT in one of his specimens.||

From the description already given, it is evident that the rootlets and the larger roots show a complete agreement in structure, except for the absence of pith and of primary rays in the former. In order, however, to prove decisively that the rootlets were really the minor branches of those roots which, as we know, belonged to *Calamites*, further evidence of two kinds is necessary. (1.) The most conclusive proof would be given, if we could find the small pithless rootlets borne as branches upon the typical medullate roots of *Calamites*. (2.) The point could also be proved by showing that an unbroken series of intermediate forms exists, connecting the smallest rootlets with the undoubted Calamitean roots.

The evidence available is chiefly of the latter kind, but we have some specimens which appear to show direct continuity between rootlet and root. It will therefore

* STRASBURGER, "Histologische Beiträge," vol. 3, p. 437.

† In "Organization," Part XII., fig. 5 (Plate 30), shows the layer in question at *e*, and it is also conspicuous in the rootlet figured in Part XV., Plate 3, fig. 23.

‡ OLIVIER, "Appareil tégumentaire des Racines," 'Ann. des Sci. Nat., Bot.,' sér. 6, vol. 11, 1881.

§ *Cf.* STRASBURGER, 'Das botanische Practicum,' 2nd ed., 1887, p. 181.

|| RENAULT, "Genre *Astromyelon*," 'Ann. des Sci. Géologiques,' vol. 17, 1885, Plate 7, fig. 2.

be well shortly to pass in review the principal specimens in which branching is shown, with special reference to the light which they throw upon this question.

Branching of the Roots.

Some examples of branched roots have been figured in previous memoirs,* while others are illustrated in the present paper (see photographs 6 and 7, figs. 6 and 8). Most of these specimens have no direct bearing on the question, for in some the branches, as well as the main root, have a distinct medulla,† while in others both the main axis and the branches are rootlets, with little or no pith (fig. 8).‡

The specimen shown in photograph 6 is of considerable interest. Here the principal root is probably hexarch, and has a perfectly well-defined, though small pith, 8 to 10 cells in diameter. Opposite two of the protoxylem-groups branches are given off, both of which are cut sufficiently near their median plane to show the continuity of their primary xylem with that of the main axis. In one branch there is no sign of any pith; in the other, one or two rows of parenchymatous cells can be distinguished. Such evidence is not conclusive, but the specimen certainly appears to show the bases of two rootlets, with little or no medulla, inserted upon a root, which, though small, has the typical internal structure of "*Astromyelon*," *i.e.*, of the Calamitean root.

Another specimen§ shows no less than four rootlets, in a tangential section of the main root, which, from its having distinct primary rays, was in all probability of the medullate type.

Plate 16, fig. 6, shows a tangential section (from another specimen) through the wood of a relatively main root, with a branch seen in approximately transverse section. Here the branch has a small pith.

The specimen represented in Plate 17, fig. 8, is interesting, for it proves very clearly that the branch rootlet is an *endogenous* appendage of the parent axis. In this case neither has any pith.

In Plate 15, photograph 7, we have illustrated a specimen which appears to deviate from the normal mode of branching. The main root, in its decorticated condition, is about 8 millims. in maximum diameter. It has a large pith, and no less than sixteen groups of primary xylem. The secondary wood is from fifteen to thirty elements in radial thickness. A branch, which is shown in nearly median section, lies exactly opposite one of the protoxylem-strands, but is separated from it by about fifteen layers of secondary wood. The inner extremity of the branch, in which both medulla and primary xylem are evident, ends quite sharply, and there is no

* WILLIAMSON, "Organization," Part IX., Plate 19, figs. 2 and 4; Part XII., Plate 29, fig. 7.

† As in "Organization," Part IX., Plate 19, figs. 2 and 4.

‡ So also in "Organization," Part XII., Plate 29, fig. 7. It seems that in this curious specimen the relatively main axis is that marked a', which is seen in longitudinal section.

§ C.N. 1321 (not figured).

appearance of obliquity. The base of the branch is embedded in a sheath of secondary xylem, which is not perfectly continuous with the normal wood upon which it is superposed. The peculiarity of this case lies in the want of connection between the base of the branch and the primary xylem of the parent root. As we have no other sections of the specimen, we cannot be absolutely certain that the actual base of the branch may not have passed obliquely inwards, and attached itself to the protoxylem of the main axis in another plane. The structure, however, shows no sign of such obliquity, and there is every appearance that the abrupt inner termination of the branch is its real base. If so, the branch must either have been an adventitious one, formed after secondary growth had already made some progress, or else it may have been a normal branch to begin with, which became separated from its place of origin by the intercalation of secondary wood. An analogous process is well known to happen in the case of "sleeping buds" in some recent trees, such as the beech.

We have examined a longitudinal section, from a different specimen, which shows essentially the same peculiarities.

The following conclusions may be drawn from the study of branched specimens.

1. The roots of *Calamites*, like those of the recent Equiseta and of vascular plants generally, branched endogenously.

2. The minute, pithless rootlets were, in some cases, borne on parent roots of the ordinary "*Astromyelon*" type, with a distinct pith.

3. In exceptional cases it appears that the base of the branch-root was separated from the primary xylem of the main axis by a zone of secondary wood.

Conclusion.

A general survey of the numerous specimens which we have investigated, shows conclusively that there is no sharp distinction between the small pithless rootlets and the large medullate roots. The extreme types are connected by an unbroken series of intermediate forms. As regards the number of primary xylem-strands, every number, from 2 up to 14, is represented; while we also find larger roots with 16 and 25 strands. As regards the size of the pith we find it of all dimensions, from a microscopic group of two or three cells, up to a diameter of nearly 2 centims.; nor is there any break in the series. We will only call attention here to two of the intermediate forms. In a previous memoir* a root is figured which at first sight one might take for a pithless rootlet. We have re-examined the specimen, and find that it has a perfectly distinct pith, about seven cells in diameter, surrounded by seven groups of primary xylem, which form an almost continuous ring. The root shown in photograph 6 has a slightly larger pith, eight to ten cells in diameter; its structure is probably hexarch, but as the primary xylem-strands are well separated from one another,

* "Organization," Part XII., Plate 28, fig. 6 (C.N. 1309).

there is a nearer approach to the original type of "*Astromyelon*" than in the specimen last considered. We might have added indefinitely to the list of intermediate forms, but it is unnecessary to do so. The secondary wood has precisely the same structure throughout, and so also has the cortex, wherever it is preserved.

There is thus no longer any doubt that the forms such as were first grouped together in Part XII. of the previous series of memoirs, under the name of "*Astromyelon Williamsonis*," really belong to the same plant, and that they consist of the roots and rootlets of various orders of branching of *Calamites*. The only form which seems to us strongly to suggest even a specific distinction from the rest, is that shown in photograph 4, in which, as already mentioned, the cortex has a somewhat peculiar character.

RENAULT speaks of some of his larger specimens as *stolons*, not roots. The organs to which he applies this name belong, some to *Calamites* (his *Arthropitys*), others to *Calamodendron*. The specimens in question are beautifully illustrated in his latest work,* and agree perfectly in structure with the larger roots such as we have described. We fail to see any reason for applying the name *stolon* to any of these organs. A stolon is a modified stem, and should show the structure characteristic of stems. In the organs, however, which RENAULT figures, the structure is distinctly that of a root, as is especially shown by the centripetal primary wood In the *stem* of *Calamites*, as we showed in our former paper, the primary wood is centrifugal.†

Our general results may be summed up as follows :—

1. The fossils hitherto described under the name of *Astromyelon Williamsonis* are the adventitious roots of *Calamites*.

2. Their structure is in all respects that characteristic of roots, as is proved by the centripetal primary wood, the alternating strands of xylem and phloëm, the endogenous mode of branching, and the absence of nodes.

3. The smallest specimens, with little or no medulla, represent the finest branches of the same roots, of which the large medullate forms are the relatively main axes.

EXPLANATION OF THE PLATES.

PLATE 15.

Photographs from the actual sections, taken by the late Mr. W. KIRMAN, *F.C.S.*

Photograph 1. Part of a tangential section through the wood of a stem, showing the base of a root, with "*Astromyelon*" structure, in transverse section. The

* *Loc. cit.*, "Flore d'Autun," &c., Part II., Plates 55, 56, 57, 59, and 60. The text of this work not having yet been published, we depend entirely on the figures and descriptions.

† "Further Observations," Part I. p. 872.

pith (P) of the root has been perforated by a Stigmarian rootlet. Eight strands of primary xylem are shown (as at X), around the pith; some are missing. The secondary wood (X^2) of the root is continuous with that of the stem on which it is borne. C.N. 1352. × about 10. (See p. 685.)

Photograph 2. Part of another tangential section from the same stem. One of the large infranodal rays or "lenticular organs" is shown (*M.R.*). Above this, and to the right, is the transverse section of an outgoing foliar bundle (*L.T.*). C.N. 1353. × about 16. (See p. 685.)

Photograph 3. Transverse section of a large corticated root. (For cortex and phloëm, see Plate 17, figs. 10 and 11.) Pith (P) perforated by a Stigmarian rootlet. Fourteen primary xylem-strands are shown (as at X); some are missing. The secondary wood (X^2) has a maximum thickness of about 50 cells. C.N. 1891. × about 10. (See p. 687.)

Photograph 4. Transverse section of a corticated root. Pith (P) solid, surrounded by about twelve strands of primary xylem. Secondary wood (X^2) only about three cells thick. Cortex (C—C) lacunar, with very numerous trabeculæ. Intralacunar cells (? thylosis) are seen. Possibly a different species from the other specimens. C.N. 1891A. × about 12. (See p. 690.)

Photograph 5. Transverse section of a tetrarch rootlet, without pith; CY, centre of cylinder. Formation of secondary wood has begun. The double endodermis (the inner layer of which is thin-walled) can be recognized (EN). The trabeculæ of the lacunar cortical zone show thylosis. The cortex (C) is limited externally by a thick-walled, epidermoidal layer (EP) C.N. 1890A. × about 25. (See p. 691.)

Photograph 6. Transverse section of a pentarch or hexarch root (decorticated), showing the bases of two branches. There is a small solid pith (P). Five primary xylem-strands (X) are plain. Opposite two of them are the branches (BR), which show little or no pith. Secondary wood of branches continuous with that of principal root. C.N. 1892A. × 22. (See p. 695).

Photograph 7. Part of transverse section of a root, showing the base of a branch (BR). The root had sixteen strands of primary xylem (X), of which four are shown, with part of the pith (P). The base of the branch-root is separated from the primary xylem, opposite which it arises, by about fifteen layers of secondary wood; X^2, limit between the two layers of secondary wood C.N. 1323. × 22. (See p. 695).

Plates 16 *and* 17 ; *figures from camera-lucida drawings, made by* *Mr.* GEORGE BREBNER.

PLATE 16.

Fig. 1. Part of a transverse section of a young 9-arch root, at the commencement of secondary thickening. C.N. 1308. × 100. (See p. 687.)

p, *p*, Cells of pith.

x, *x*, Primary xylem.

px, Protoxylem at the exterior of primary xylem.

x^2, x^2, Secondary wood, bordered externally by cambium.

ph, *ph*, Two groups of primary phloëm.

en, *en*, Probably the functional endodermis. The thin-walled layers within this may be either percycle or inner endodermis.

c, *c*, Cells of the inner cortex.

This figure represents part of the section figured by WILLIAMSON in "Organization," Part XII., Plate 28, fig. 2 (near *d''*), and is from the original specimen of "*Myriophylloides*," HICK and CASH.

Fig. 2. Part of a transverse section of a more advanced 9-arch root. C.N. 1314. × 100. (See p. 689.)

p, *p*, Cells of pith.

x, *x*, Strand of primary xylem.

px, Protoxylem.

x^2, Secondary wood.

f.r., Fascicular ray.

Fig. 3. Part of a radial section of a similar root. C.N. 1317. × 100. (See p. 687.)

p, *p*, Pith.

x, *x*, Primary xylem.

px, Protoxylem at the outer border of *x*, consisting of spiral tracheæ.

x^2, Secondary wood.

The parenchymatous tissue, *fr*, belongs to the fascicular ray.

Fig. 4. Transverse section of a tetrarch rootlet. The outer cortex (similar to that shown in photograph 5) was partly preserved, but is not represented. C.N. 1888. × 100. (See p. 691.)

px, The four protoxylem-groups of the primary wood, which probably reached the centre, though the central thin-walled cells perhaps represent a minute pith.

x^2, Secondary xylem, which is beginning to form between the protoxylem-groups. (Reference-line omitted.)

ph, Phloëm, of which there are four groups, alternating with the protoxylem.

en, Endodermis, which is evidently double.

c, *c*, Cells of inner cortex.

l.z. Part of lacunar zone. The dark cells may have been secretory sacs.

Fig. 5. Transverse section of a diarch rootlet. C.N. 1318. × 70. (See p. 692.)

px, *px*, The two protoxylem-groups of the primary xylem-plate.

About five layers of secondary wood have been formed.

ph, Remains of phloëm.

The endodermis has divided tangentially ; lacunar zone (*l.z.*) and epidermoidal layer are shown.

Fig. 6. Part of a tangential section of the wood of a root, showing the base of a lateral root. C.N. 1358. × 100. (See p. 695.)

x^2, Secondary wood of main root.

r, Secondary rays.

p, Pith of lateral root.

x, Primary, x'', secondary xylem of lateral root.

From the course of the tracheæ, we infer that the bottom of the figure is directed towards the organic base of the main root. *Cf.* STRASBURGER, 'Histologische Beiträge,' III., p. 136.

PLATE 17.

Fig. 7. Transverse section of a rootlet, probably triarch, without secondary wood. C.N. 1890. × 50. (See p. 692.)

l.z. Lacunar zone of cortex.

ep, Epidermoidal layer, which is especially clear.

One side of the cortex is omitted.

Fig. 8. Oblique section of a branching rootlet, probably tetrarch, with little or no secondary wood. C.N. 1892c. × 30. (See p. 692.)

l.z. Lacunar zone of cortex ; the trabeculæ show the commencement of thylosis.

ep, Epidermoidal layer.

br, Branch-rootlet, probably diarch, passing out through the cortex of the main rootlet.

Fig. 9. Oblique section of a branching diarch rootlet, from the same preparation as fig. 8. The xylem-plate is not yet lignified in the middle. C.N. 1892c, × 100. (See p. 692.)

px, *px*, The two protoxylem-groups, to one of which the xylem of the branch-rootlet, *br*, is attached.

en, Endodermis.

The endogenous origin of the branch is evident.

Fig. 10. Part of transverse section of the root shown in photograph 3. C.N. 1891. × 100. (See p. 689.)

x^2, Outer part of secondary wood.

cb, Cells of the cambium, adhering to the outer surface of the wood.

ph, Phloëm, separated from the wood by a gap, due to the tearing of the cambium.

en, Endodermis, probably double, including also the thin-walled cells adjacent to the phloëm.

Beyond *en*, a portion of the inner cortex is shown.

Fig. 11. A part of the cortex, from the same root, in transverse section. The whole thickness is shown. The inner cortex is thin-walled. C.N. 1891. × 40. (See p. 690.)

l.z. Lacunar zone of middle cortex; the lacunæ are obliterated by the crushing in of the trabeculæ.

ep, Epidermoidal layer, here multiseriate, probably owing to commencement of periderm-formation.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

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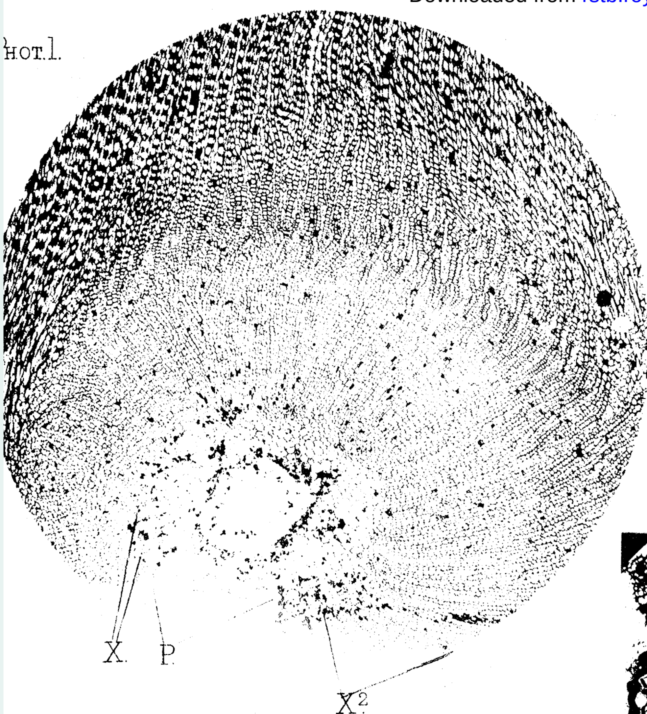

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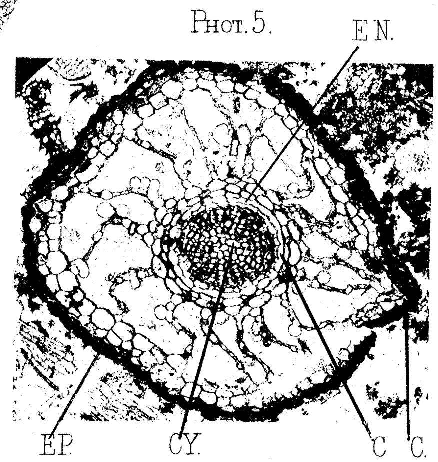

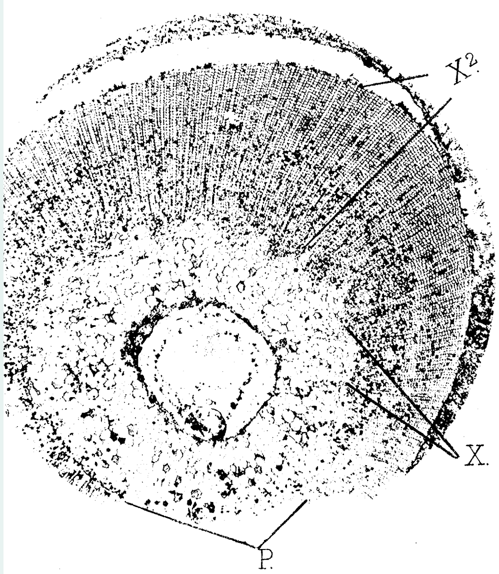

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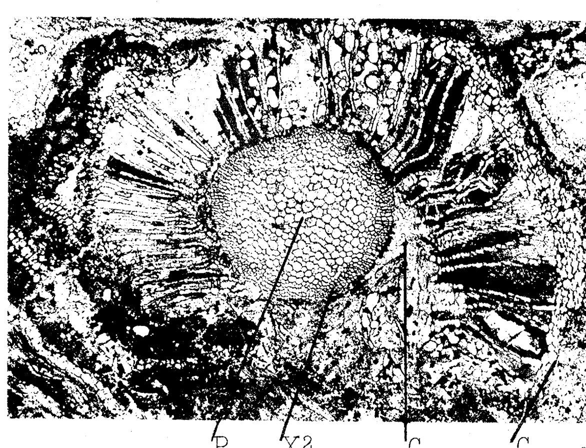

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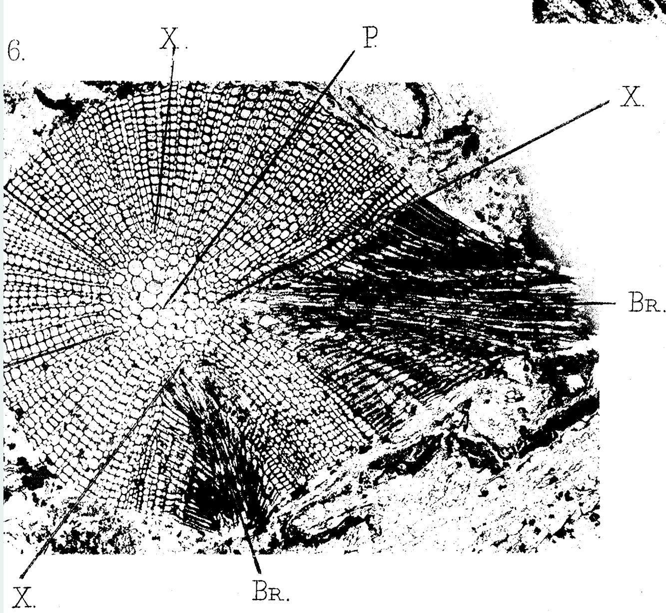

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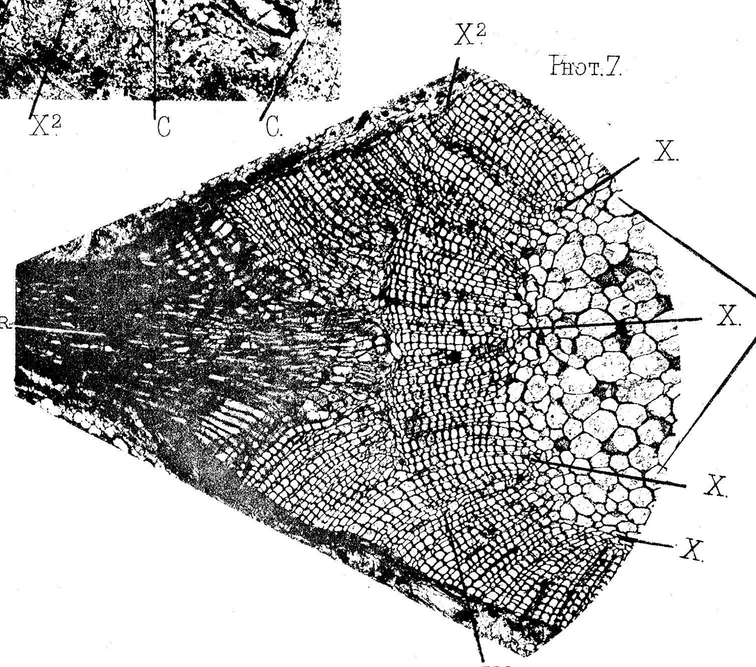

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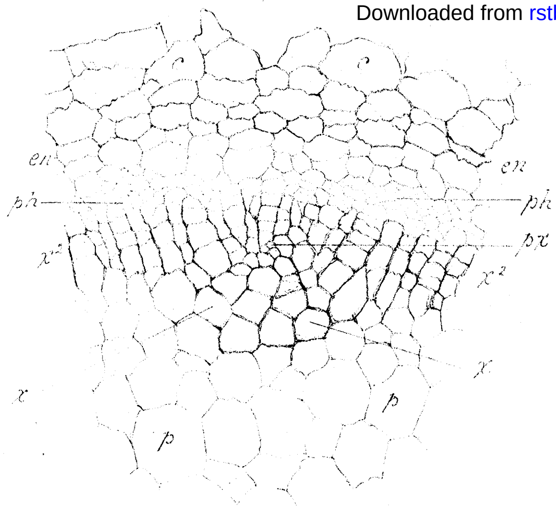

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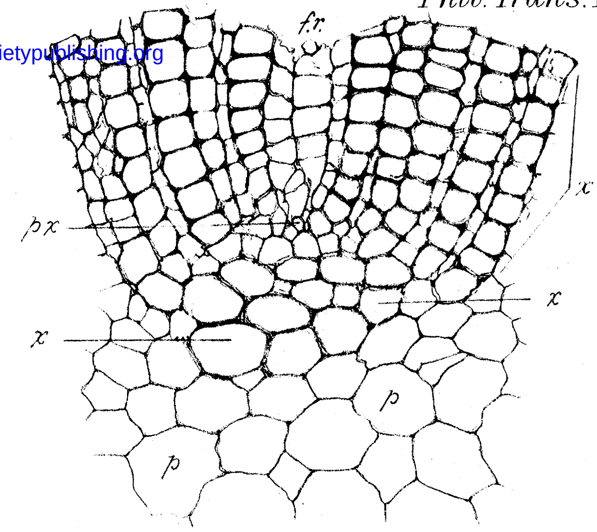

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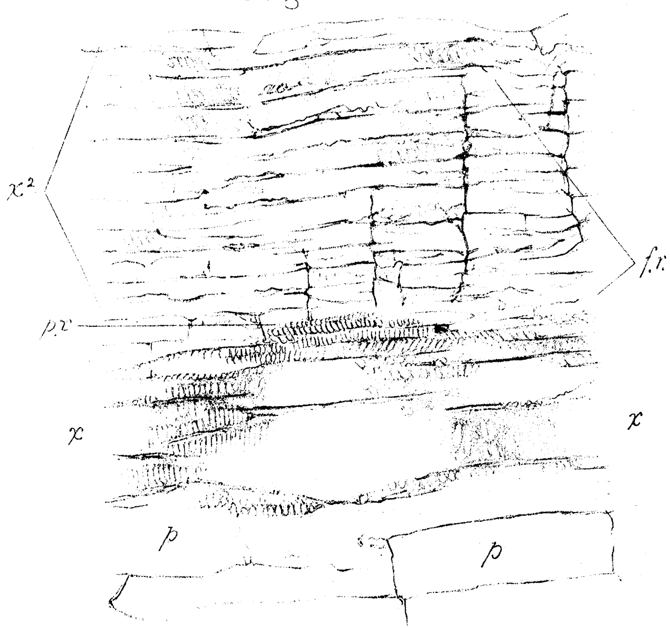

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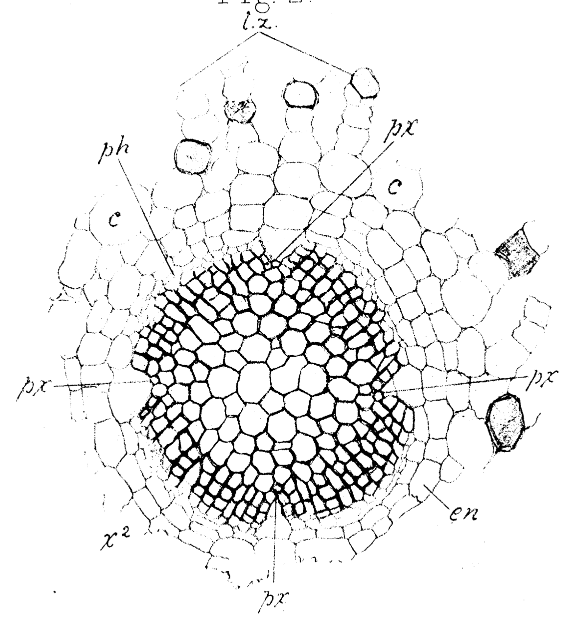

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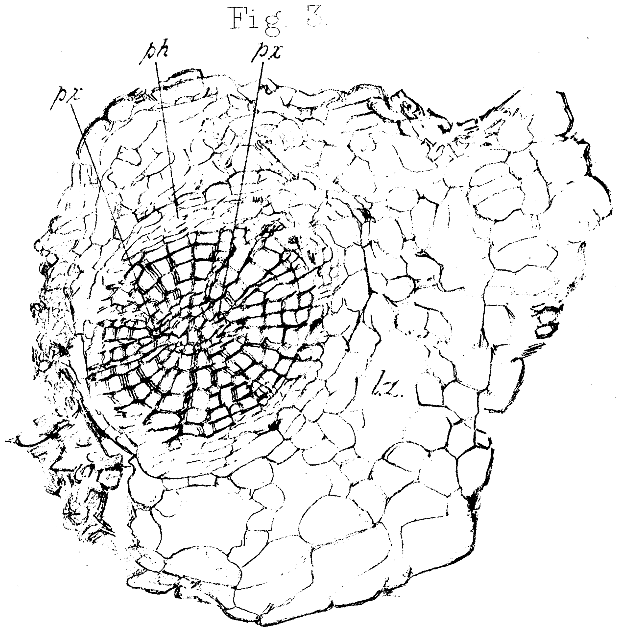

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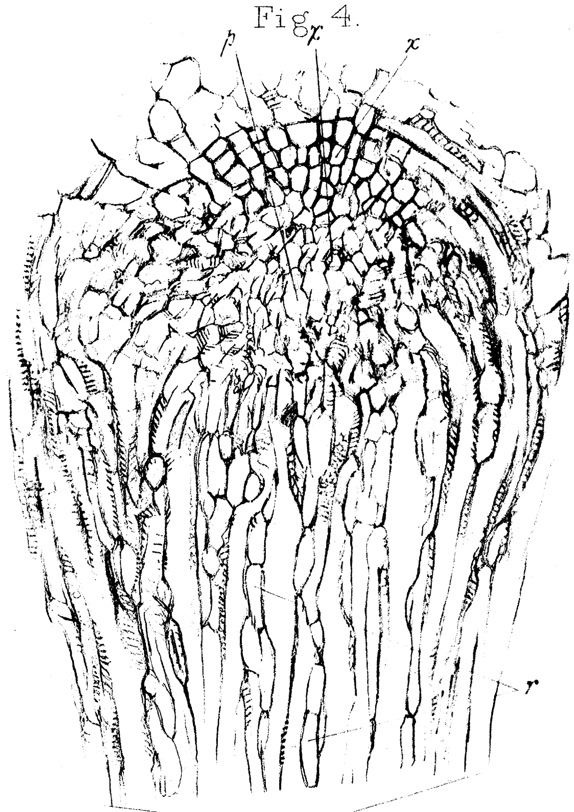

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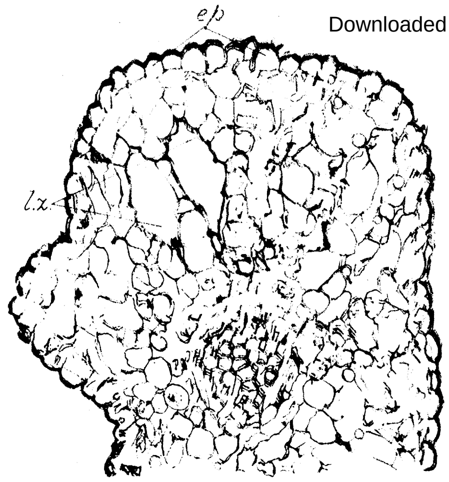
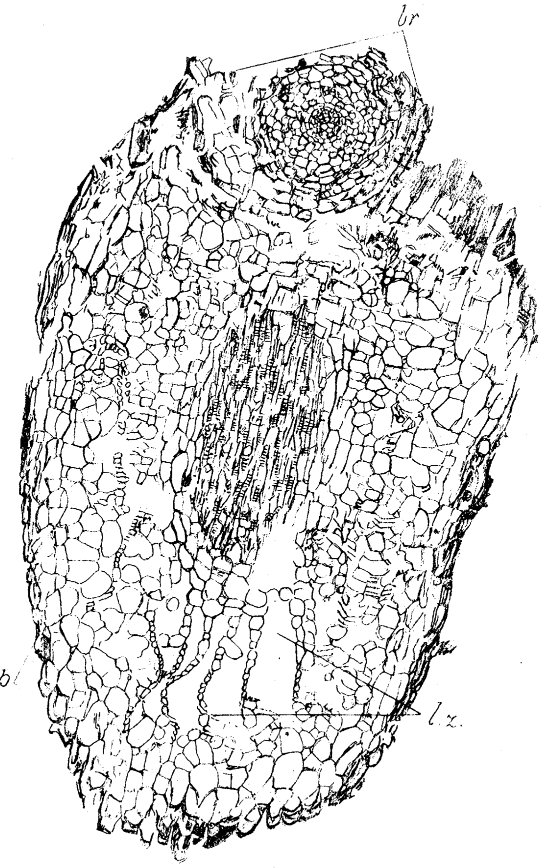


Fig. 7.



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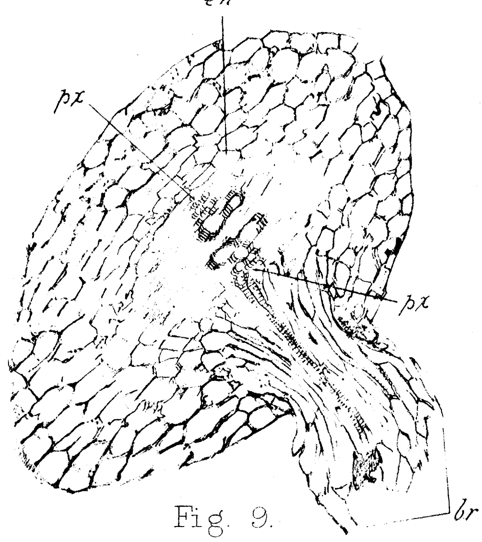

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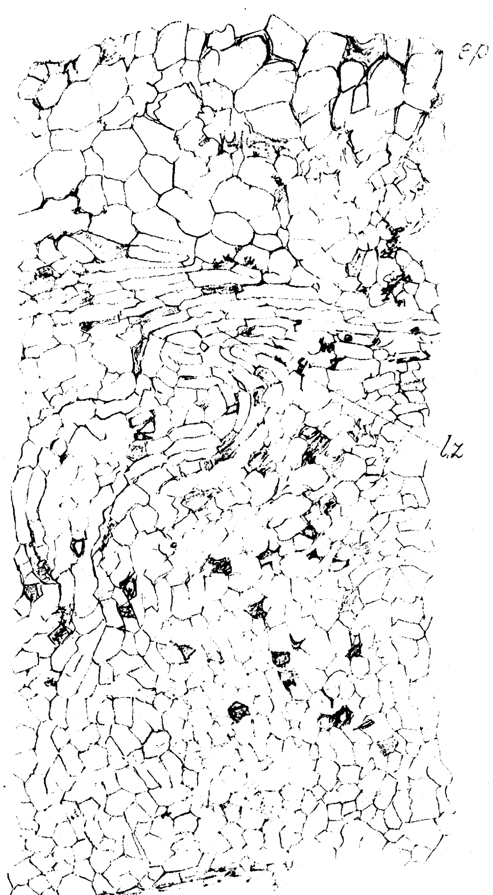

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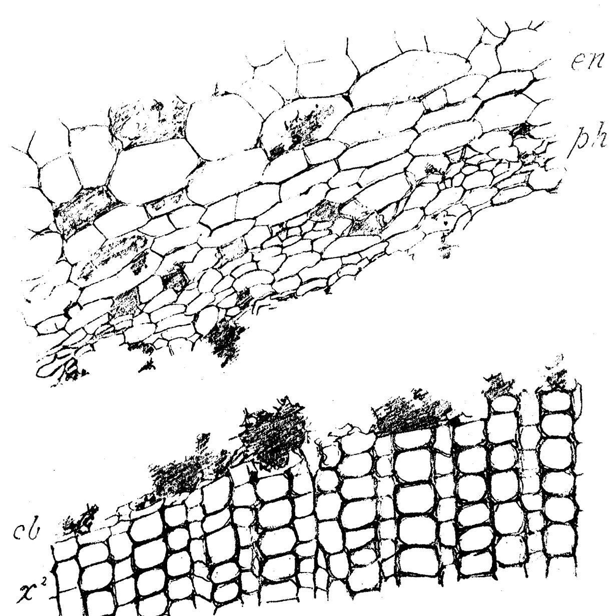

Fig. 10.

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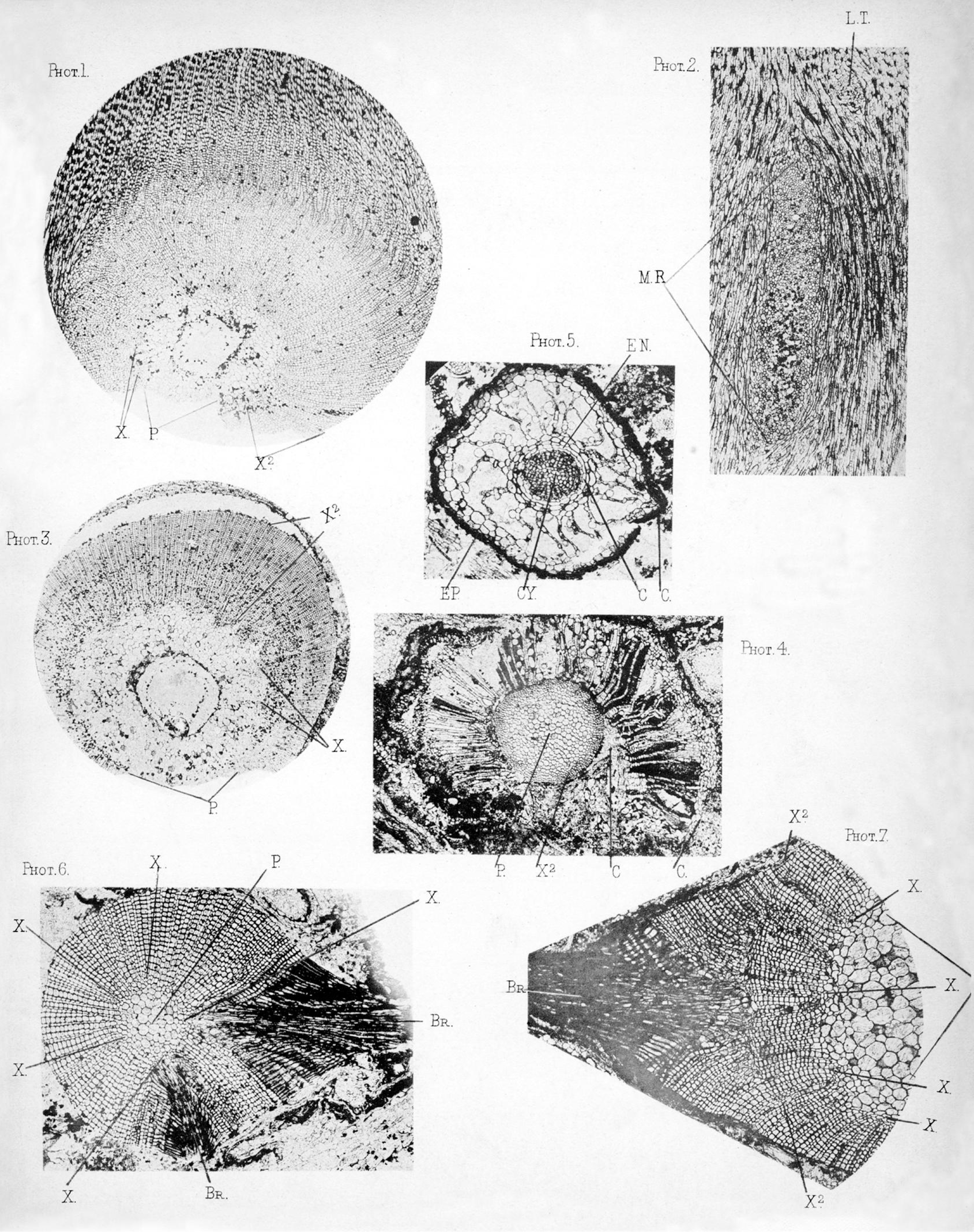

PLATE 15.

Photographs from the actual sections, taken by the late Mr. W. KIRMAN, *F.C.S.*

Photograph 1. Part of a tangential section through the wood of a stem, showing the base of a root, with "*Astromyelon*" structure, in transverse section. The pith (P) of the root has been perforated by a Stigmarian rootlet. Eight strands of primary xylem are shown (as at X), around the pith; some are missing. The secondary wood (X^2) of the root is continuous with that of the stem on which it is borne. C.N. 1352. × about 10. (See p. 685.)

Photograph 2. Part of another tangential section from the same stem. One of the large infranodal rays or "lenticular organs" is shown (*M.R.*). Above this, and to the right, is the transverse section of an outgoing foliar bundle (*L.T.*). C.N. 1353. × about 16. (See p. 685.)

Photograph 3. Transverse section of a large corticated root. (For cortex and phloëm, see Plate 17, figs. 10 and 11.) Pith (P) perforated by a Stigmarian rootlet. Fourteen primary xylem-strands are shown (as at X); some are missing. The secondary wood (X^2) has a maximum thickness of about 50 cells. C.N. 1891. × about 10. (See p. 687.)

Photograph 4. Transverse section of a corticated root. Pith (P) solid, surrounded by about twelve strands of primary xylem. Secondary wood (X^2) only about three cells thick. Cortex (C—C) lacunar, with very numerous trabeculæ. Intralacunar cells (? thylosis) are seen. Possibly a different species from the other specimens. C.N. 1891A. × about 12. (See p. 690.)

Photograph 5. Transverse section of a tetrarch rootlet, without pith; CY, centre of cylinder. Formation of secondary wood has begun. The double endodermis (the inner layer of which is thin-walled) can be recognized (EN). The trabeculæ of the lacunar cortical zone show thylosis. The cortex (C) is limited externally by a thick-walled, epidermoidal layer (EP) C.N. 1890A. × about 25. (See p. 691.)

Photograph 6. Transverse section of a pentarch or hexarch root (decorticated), showing the bases of two branches. There is a small solid pith (P). Five primary xylem-strands (X) are plain. Opposite two of them are the branches (BR), which show little or no pith. Secondary wood of branches continuous with that of principal root. C.N. 1892A. × 22. (See p. 695).

Photograph 7. Part of transverse section of a root, showing the base of a branch (BR). The root had sixteen strands of primary xylem (X), of which four are shown, with part of the pith (P). The base of the branch-root is separated from the primary xylem, opposite which it arises, by about fifteen layers of secondary wood; X^2, limit between the two layers of secondary wood C.N. 1323. × 22. (See p. 695).

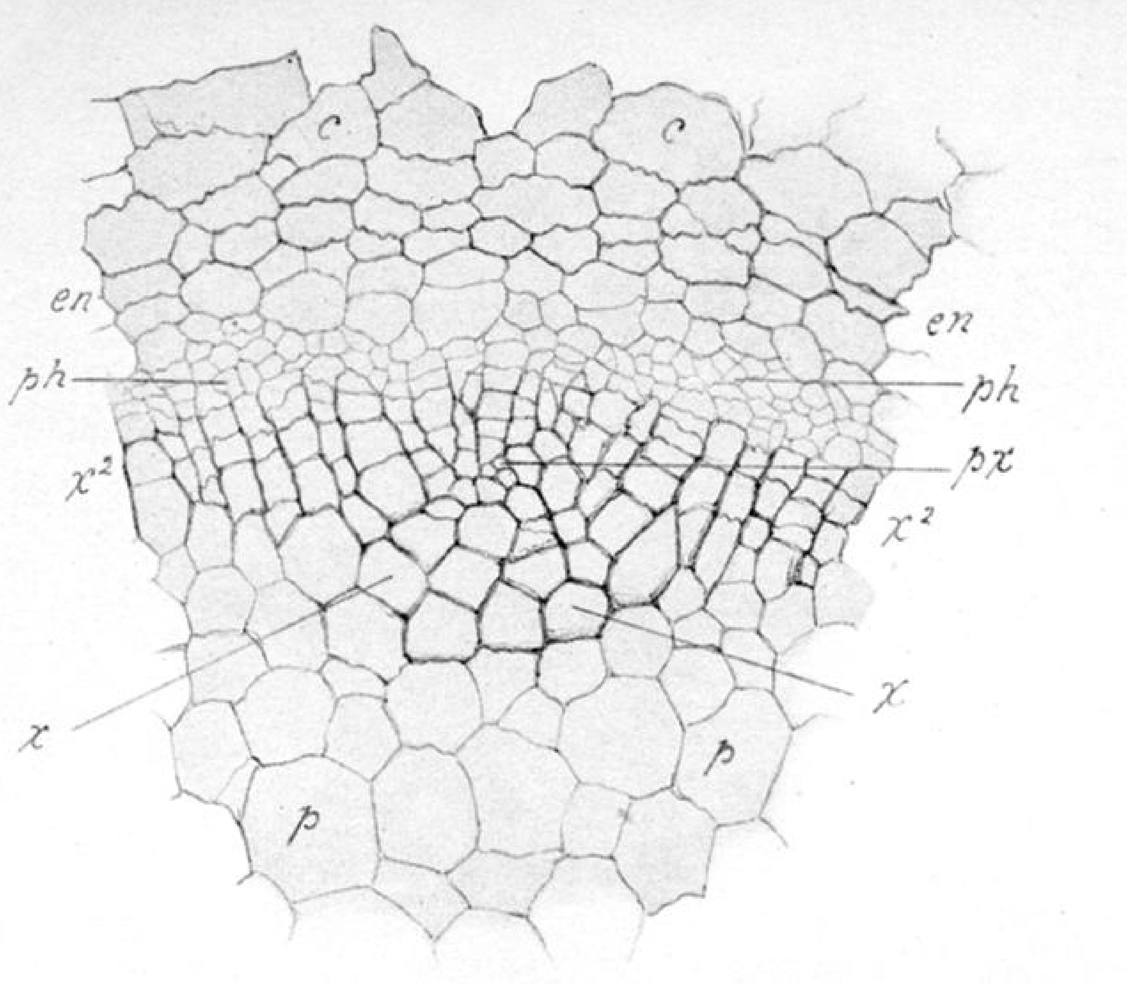

Fig. 1.

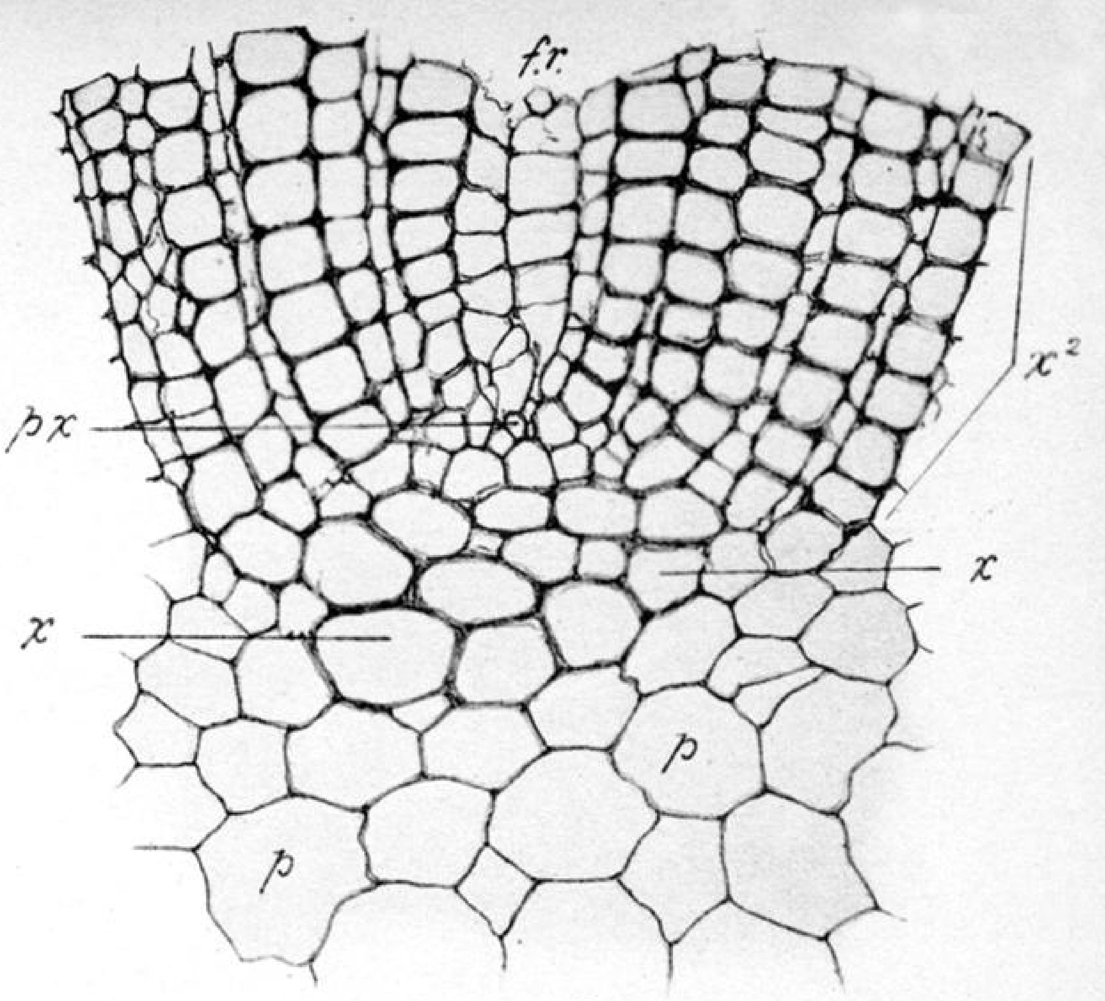

Fig. 2.

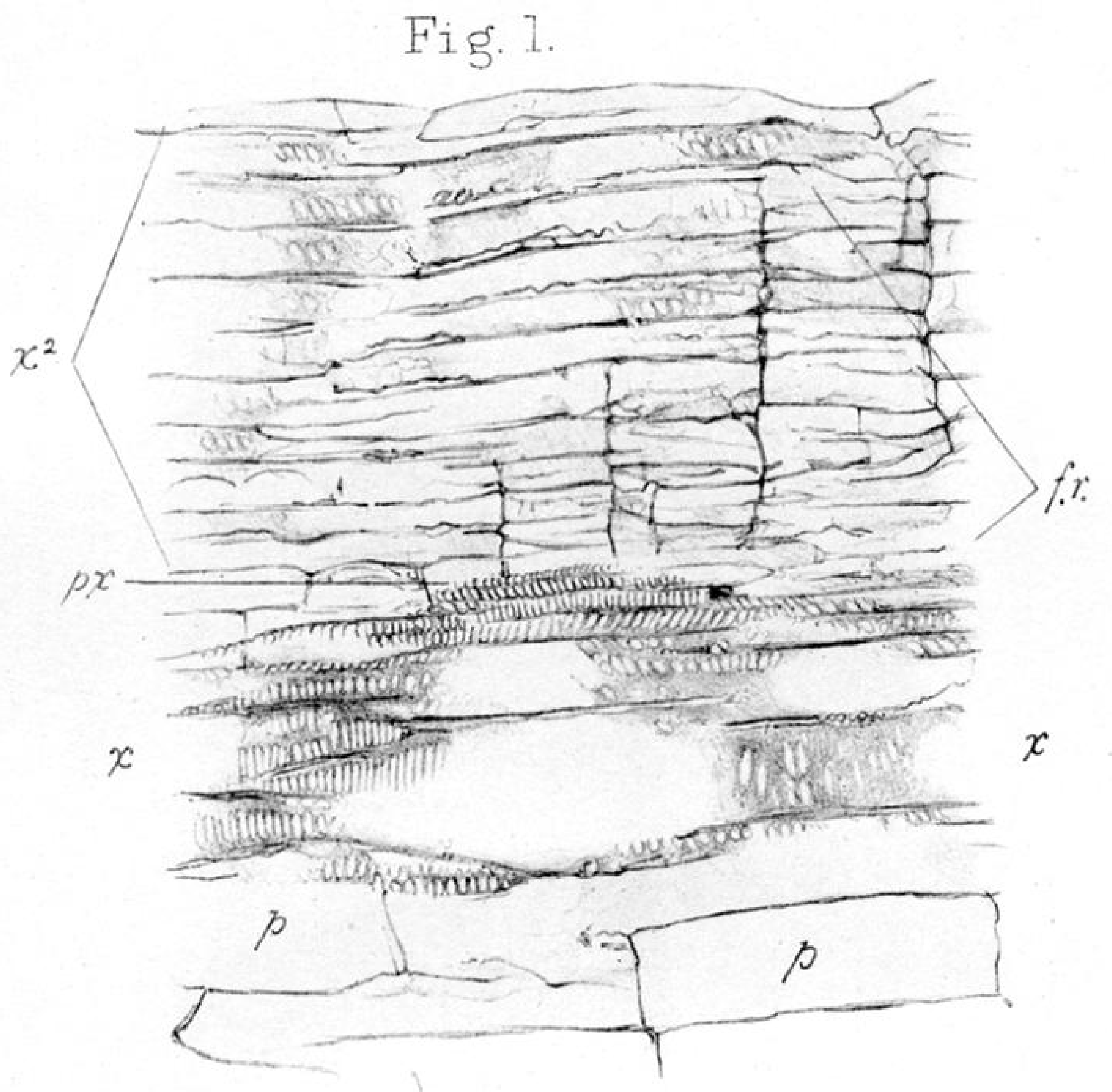

Fig. 3.

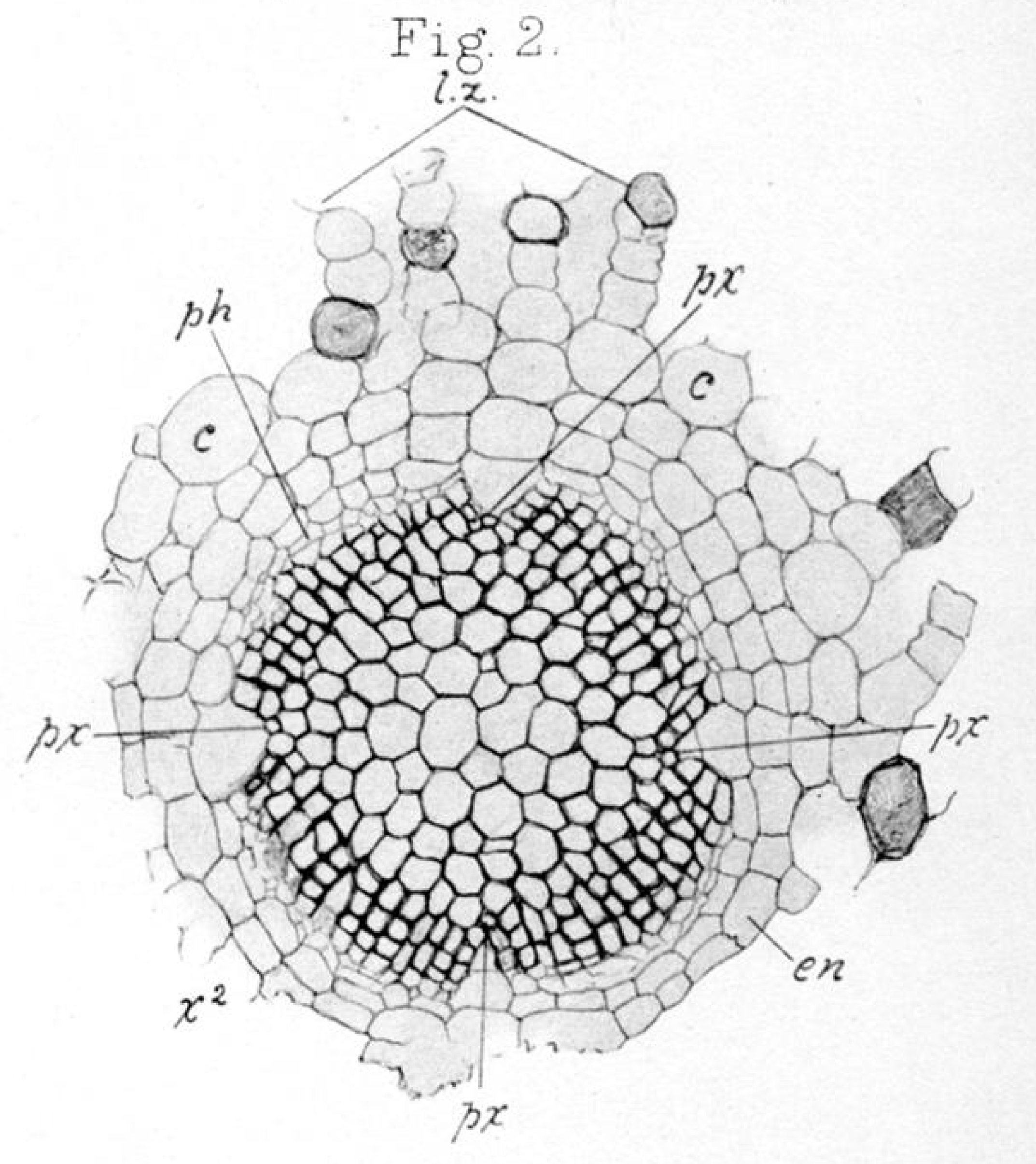

Fig. 4.

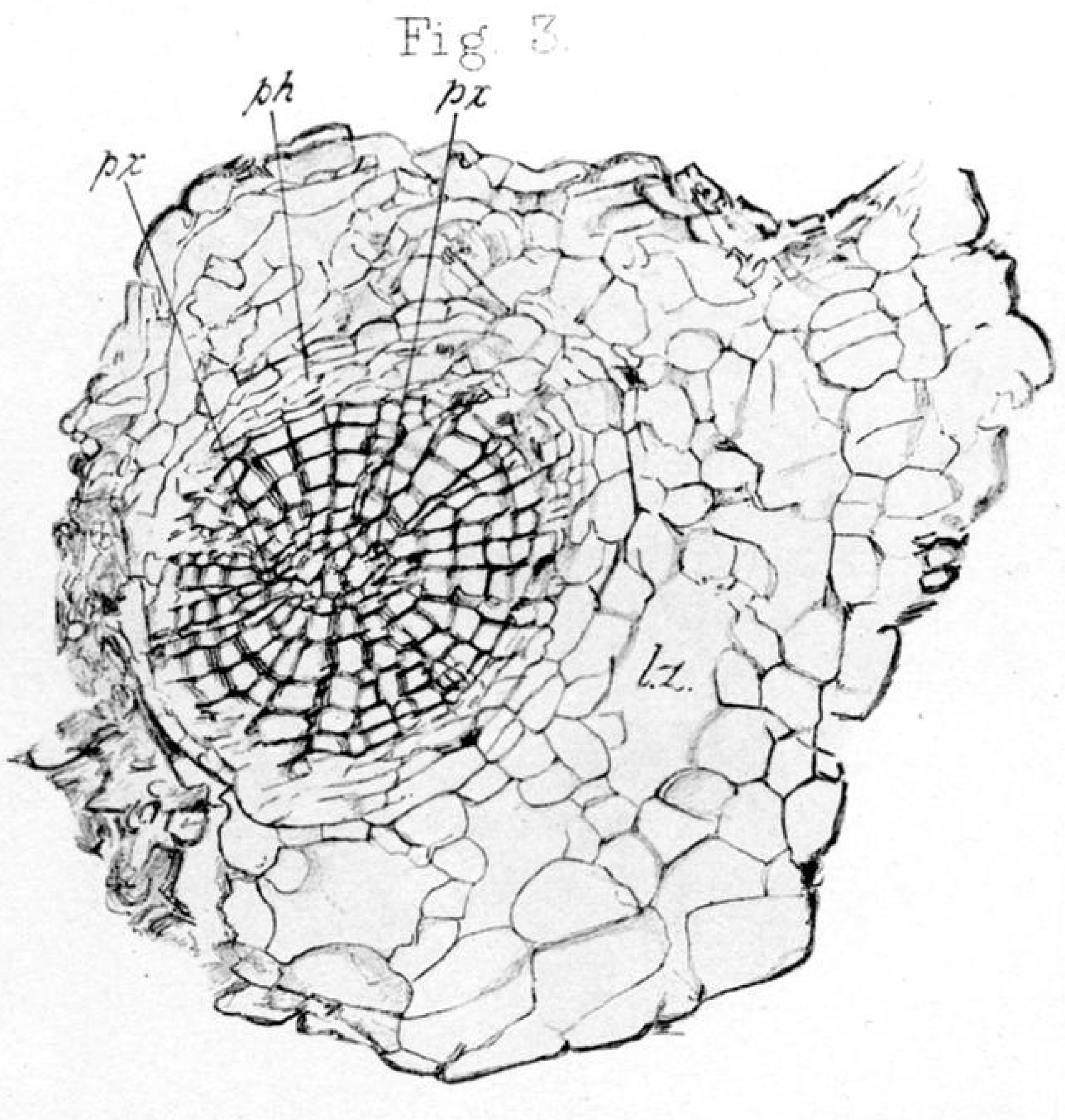

Fig. 5.

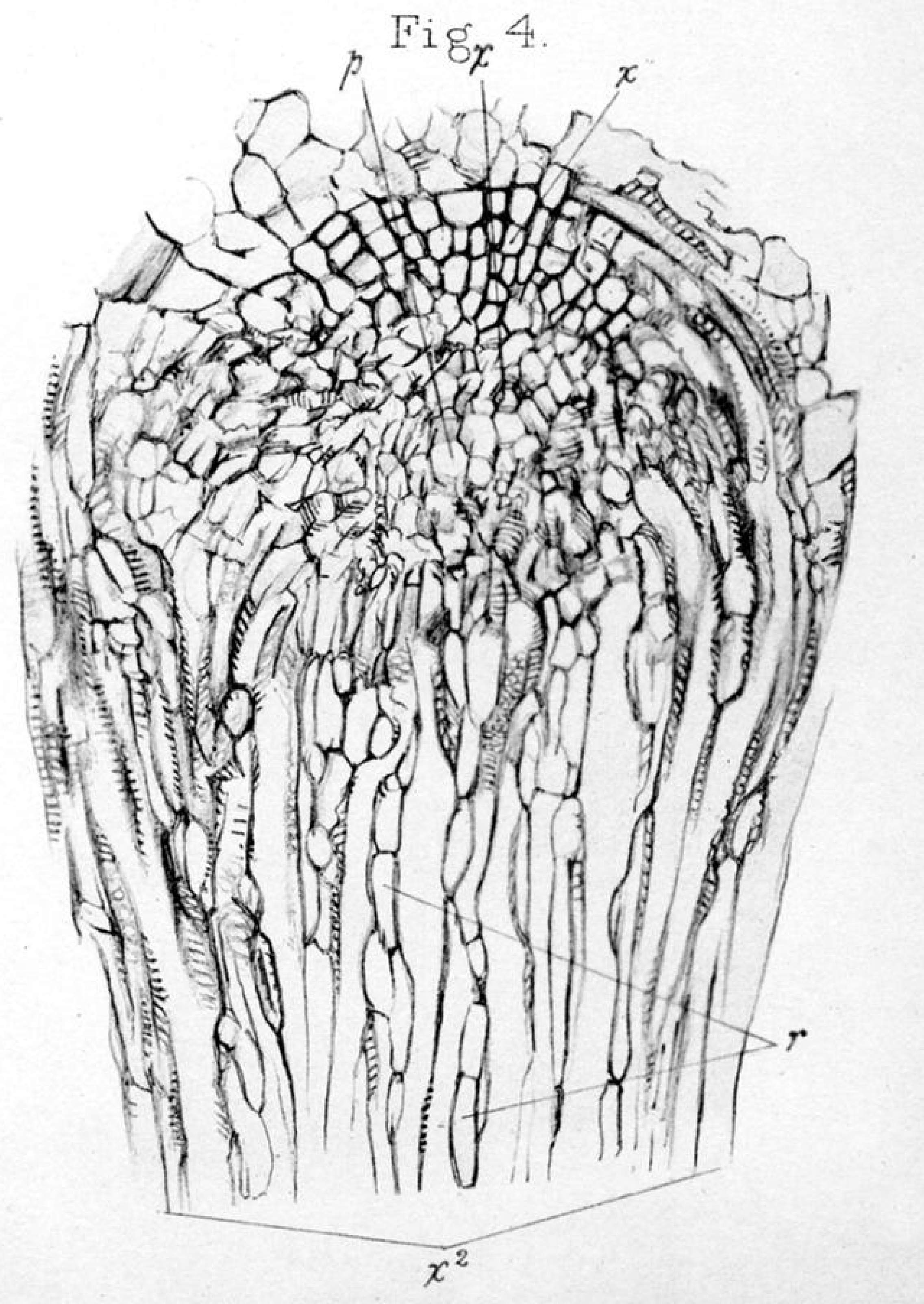

Fig. 6.

PLATE 16.

Fig. 1. Part of a transverse section of a young 9-arch root, at the commencement of secondary thickening. C.N. 1308. × 100. (See p. 687.)

p, p, Cells of pith.

x, x, Primary xylem.

px, Protoxylem at the exterior of primary xylem.

x^2, x^3, Secondary wood, bordered externally by cambium.

ph, ph, Two groups of primary phloëm.

en, en, Probably the functional endodermis. The thin-walled layers within this may be either pericycle or inner endodermis.

c, c, Cells of the inner cortex.

This figure represents part of the section figured by WILLIAMSON in "Organization," Part XII., Plate 28, fig. 2 (near *d''*), and is from the original specimen of "*Myriophylloides*," HICK and CASH.

Fig. 2. Part of a transverse section of a more advanced 9-arch root. C.N. 1314. × 100. (See p. 689.)

p, p, Cells of pith.

x, x, Strand of primary xylem.

px, Protoxylem.

x^2, Secondary wood.

f.r., Fascicular ray.

Fig. 3. Part of a radial section of a similar root. C.N. 1317. × 100. (See p. 687.)

p, p, Pith.

x, x, Primary xylem.

px, Protoxylem at the outer border of *x*, consisting of spiral tracheæ.

x^2, Secondary wood.

The parenchymatous tissue, *fr*, belongs to the fascicular ray.

Fig. 4. Transverse section of a tetrarch rootlet. The outer cortex (similar to that shown in photograph 5) was partly preserved, but is not represented. C.N. 1888. × 100. (See p. 691.)

px, The four protoxylem-groups of the primary wood, which probably reached the centre, though the central thin-walled cells perhaps represent a minute pith.

x^2, Secondary xylem, which is beginning to form between the protoxylem-groups. (Reference-line omitted.)

ph, Phloëm, of which there are four groups, alternating with the protoxylem.

en, Endodermis, which is evidently double.

c, c, Cells of inner cortex.

l.z. Part of lacunar zone. The dark cells may have been secretory sacs.

Fig. 5. Transverse section of a diarch rootlet. C.N. 1318. × 70. (See p. 692.)

px, px, The two protoxylem-groups of the primary xylem-plate.

About five layers of secondary wood have been formed.

ph, Remains of phloëm.

The endodermis has divided tangentially; lacunar zone (*l.z.*) and epidermoidal layer are shown.

Fig. 6. Part of a tangential section of the wood of a root, showing the base of a lateral root. C.N. 1358. × 100. (See p. 695.)

x^2, Secondary wood of main root.

r, Secondary rays.

p, Pith of lateral root.

x, Primary, *x''*, secondary xylem of lateral root.

From the course of the tracheæ, we infer that the bottom of the figure is directed towards the organic base of the main root. *Cf.* STRASBURGER, 'Histologische Beiträge,' III., p. 136.

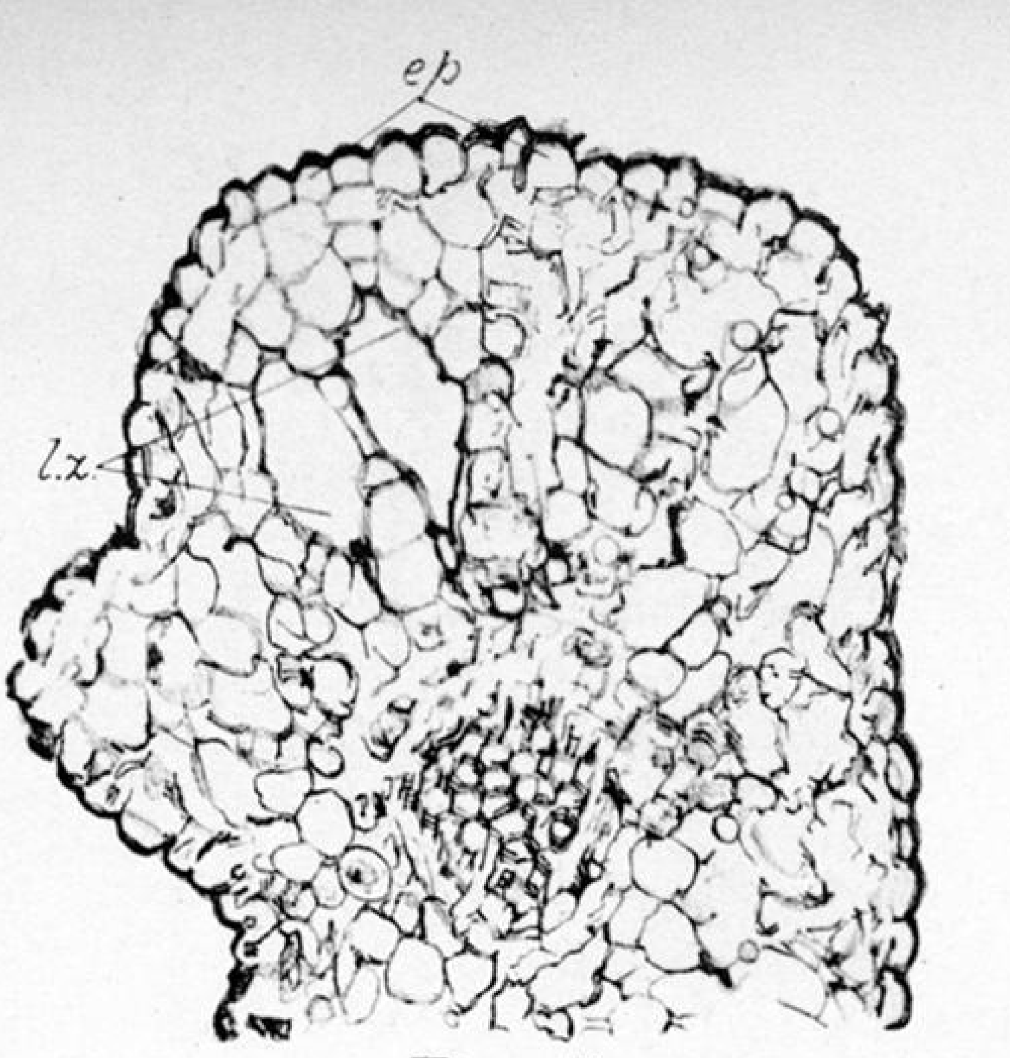

Fig. 7.

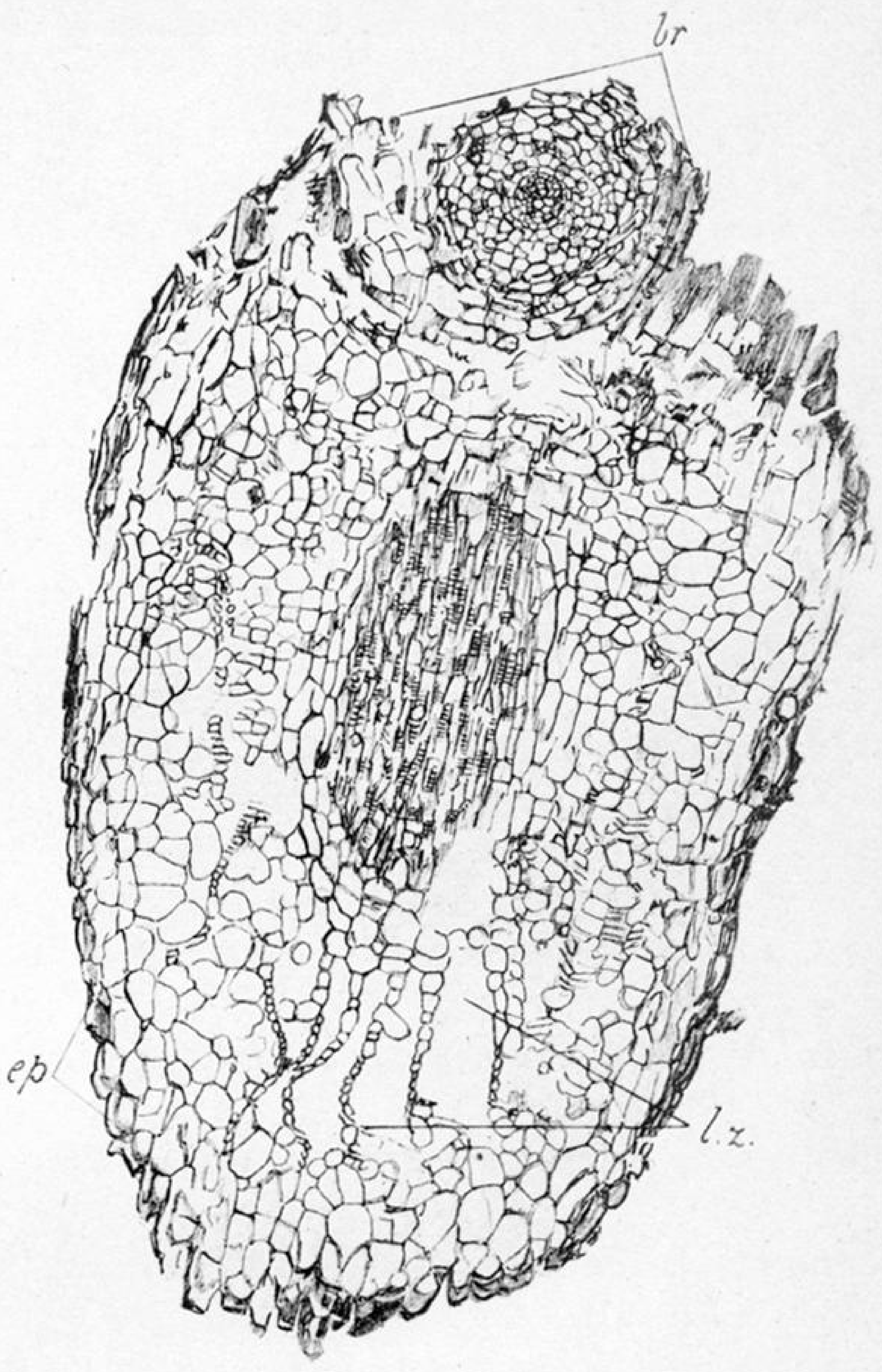

Fig. 8.

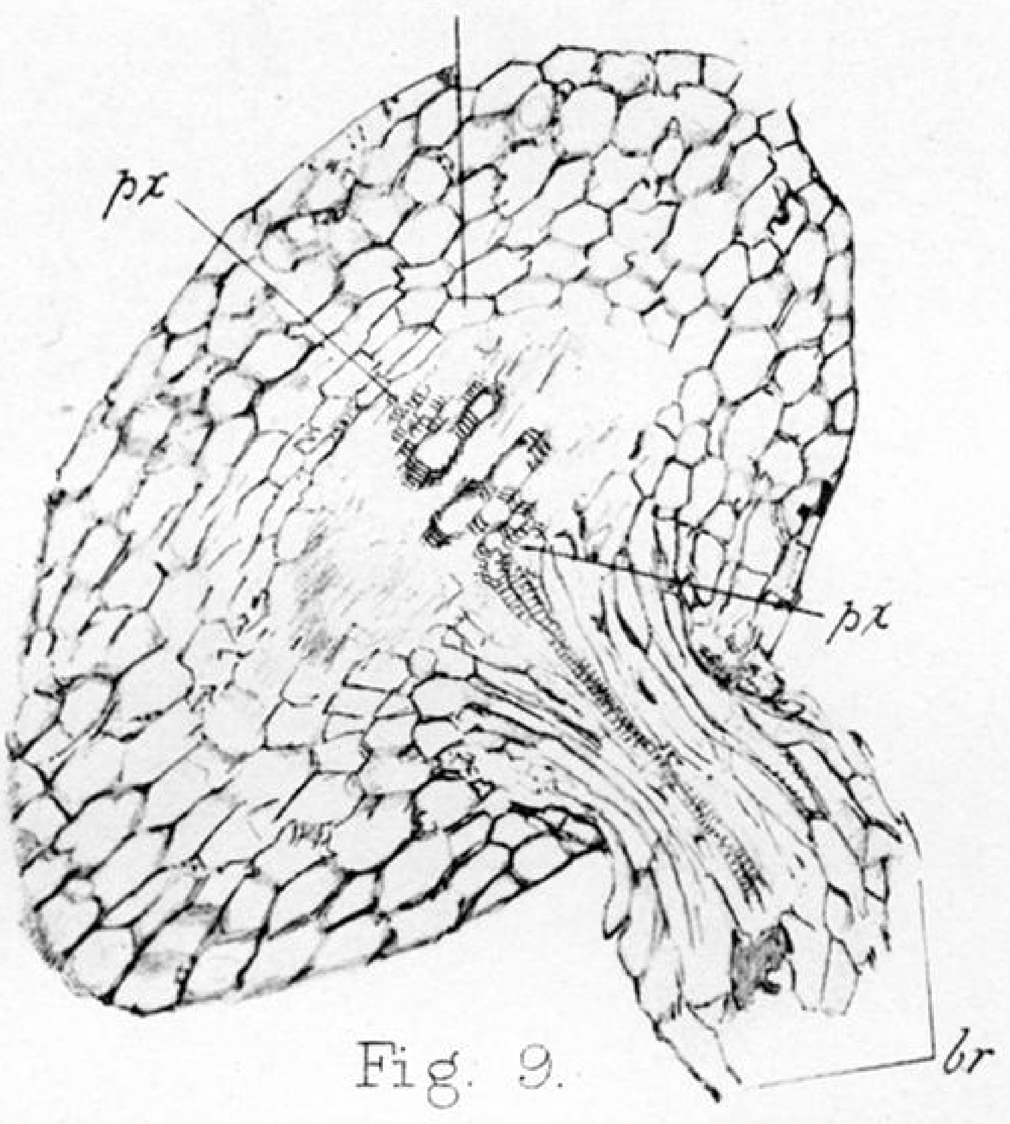

Fig. 9.

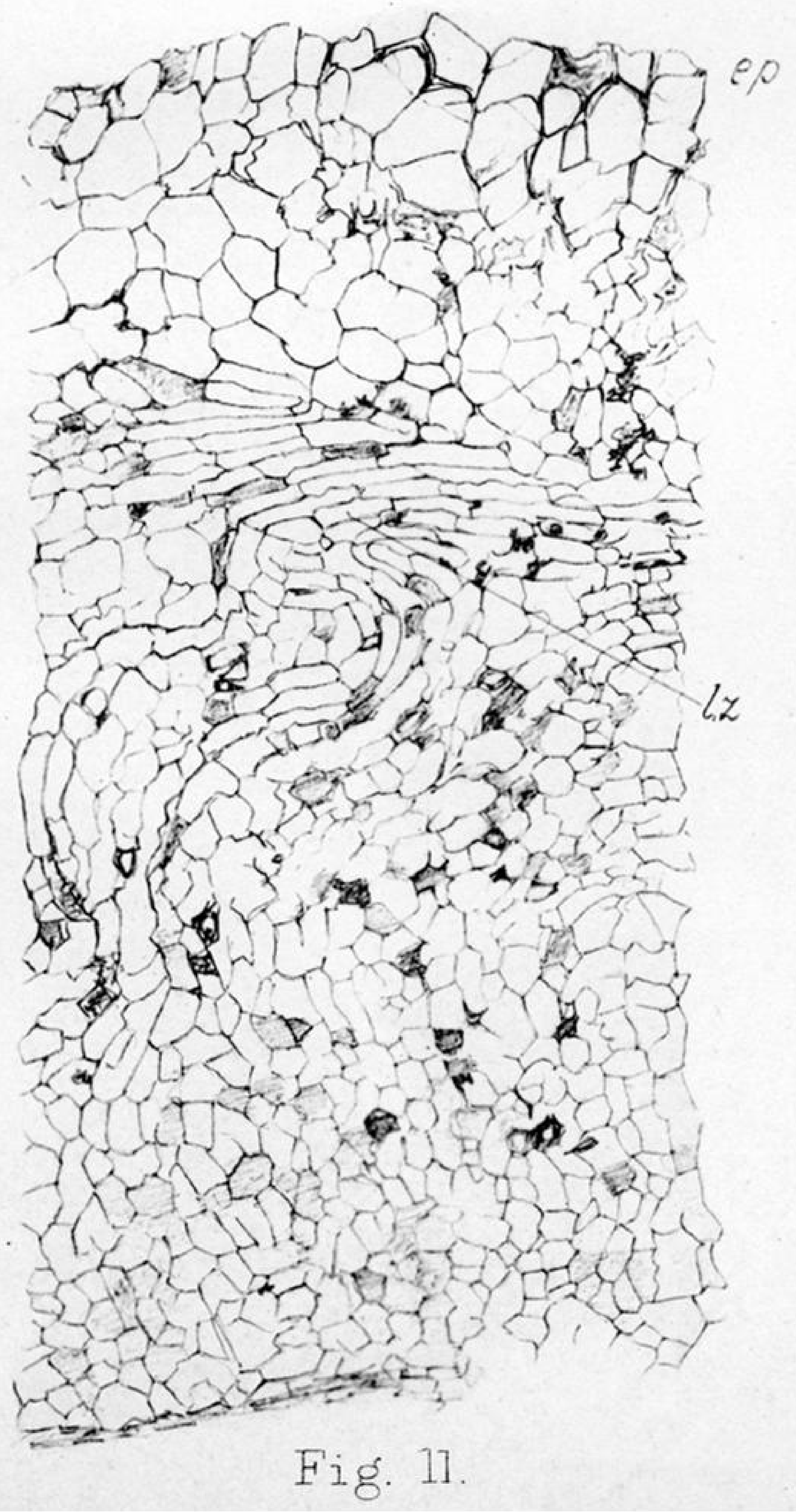

Fig. 11.

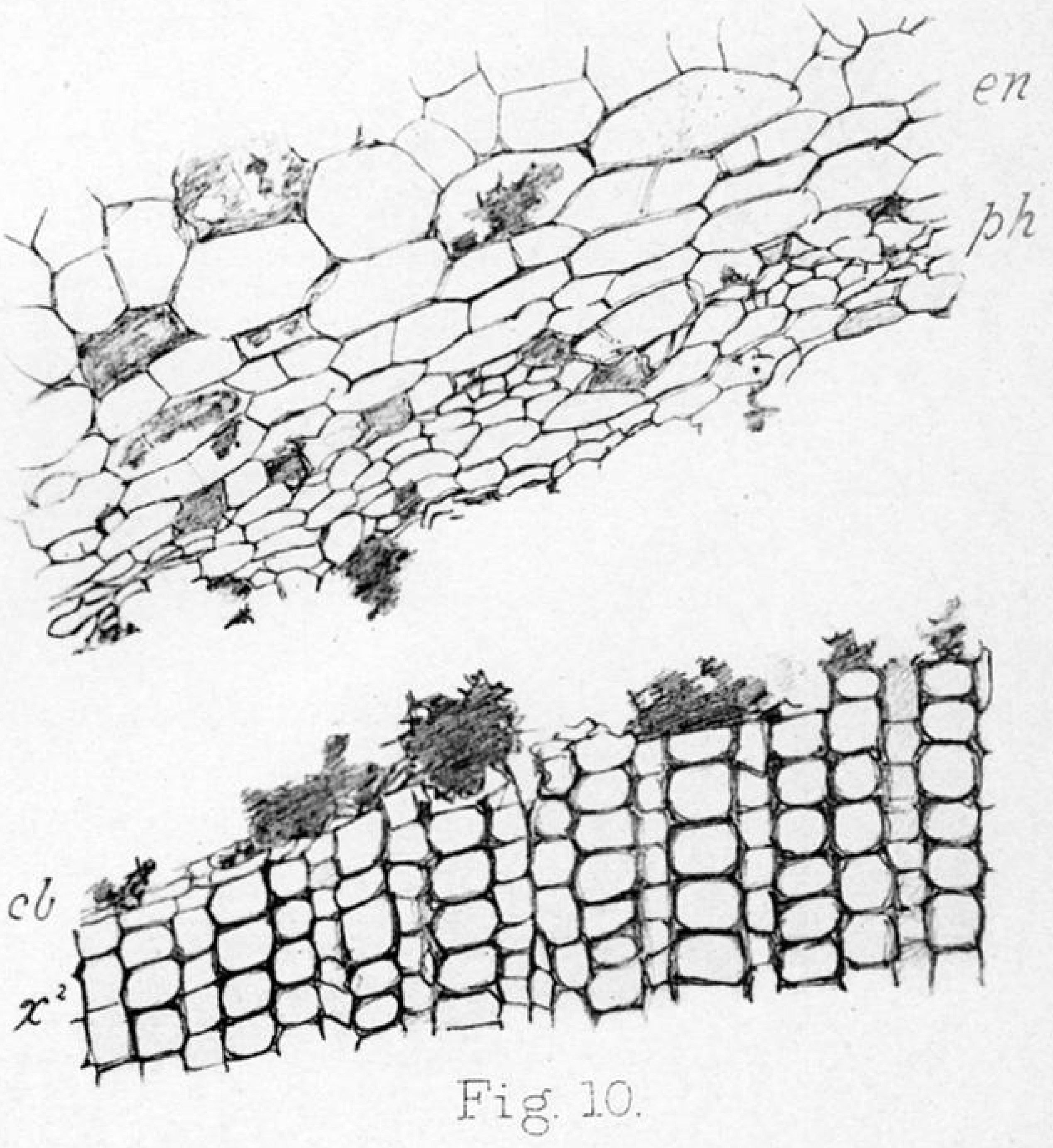

Fig. 10.

PLATE 17.

Fig. 7. Transverse section of a rootlet, probably triarch, without secondary wood. C.N. 1890. × 50. (See p. 692.)

l.z. Lacunar zone of cortex.

ep, Epidermoidal layer, which is especially clear.

One side of the cortex is omitted.

Fig. 8. Oblique section of a branching rootlet, probably tetrarch, with little or no secondary wood. C.N. 1892c. × 30. (See p. 692.)

l.z. Lacunar zone of cortex; the trabeculæ show the commencement of thylosis.

ep, Epidermoidal layer.

br, Branch-rootlet, probably diarch, passing out through the cortex of the main rootlet.

Fig. 9. Oblique section of a branching diarch rootlet, from the same preparation as fig. 8. The xylem-plate is not yet lignified in the middle. C.N. 1892c, × 100. (See p. 692.)

px, *px*, The two protoxylem-groups, to one of which the xylem of the branch-rootlet, *br*, is attached.

en, Endodermis.

The endogenous origin of the branch is evident.

Fig. 10. Part of transverse section of the root shown in photograph 3. C.N. 1891. × 100. (See p. 689.)

x^2, Outer part of secondary wood.

cb, Cells of the cambium, adhering to the outer surface of the wood.

ph, Phloëm, separated from the wood by a gap, due to the tearing of the cambium.

en, Endodermis, probably double, including also the thin-walled cells adjacent to the phloëm.

Beyond *en*, a portion of the inner cortex is shown.

Fig. 11. A part of the cortex, from the same root, in transverse section. The whole thickness is shown. The inner cortex is thin-walled. C.N. 1891. × 40. (See p. 690.)

l.z. Lacunar zone of middle cortex; the lacunæ are obliterated by the crushing in of the trabeculæ.

ep, Epidermoidal layer, here multiseriate, probably owing to commencement of periderm-formation.