On the Roots of Medullosa anglica.

BY

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With Plate XX.

THE first British specimens of *Medullosa*, a genus of Palaeozoic plants belonging to the Cycadofilices, were described by Dr. Scott[1] in a very interesting and complete memoir, published in 1899. Dr. Scott there gave the first account of the structure of the roots of a *Medullosa*.

A short time ago it was found that one of the petrifactions belonging to the Binney Collection in the Woodwardian Museum, Cambridge, contained a portion of a stem of *Medullosa anglica*, Scott, with which several roots were associated. No section of this specimen could be found[2], although the petrifaction had been cut previous to the presentation of the collection to the University in 1892. So far as I am aware, Binney did not refer to this specimen in any of his papers.

[1] Scott, Phil. Trans. Roy. Soc., Ser. B, vol. cxci, 1899, p. 81.

[2] A section of *Medullosa anglica* (S. 3533), formerly in the possession of Sir Joseph Hooker, and now in the General Collection of Sections of Fossil Plants in the Geological Department of the British Museum (Nat. Hist.), which was undoubtedly cut from a Binney specimen, may very possibly have been derived from the Cambridge specimen. I am indebted to Professor F. W. Oliver for calling my attention to this section.

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There is unfortunately no record of the locality from which the fossil was obtained. Mr. Lomax, however, who has recently made several excellent sections of the stem and the roots, tells me he is certain, from the appearance and preservation of the material, that it was originally obtained from the Lower Coal Measures of Hough Hill Colliery, Stalybridge, Lancashire; the same locality and horizon as the type specimens.

The examination of the structure of the stem, which in the Cambridge specimen is unfortunately incomplete, has added nothing of importance, with one exception, to the very complete account already given by Dr. Scott; which was founded on a study of several different specimens.

In association with the stem, and in one case in continuity with it, several exceptionally well-preserved roots occur. These agree very closely in structure with the roots previously figured [1], and they undoubtedly belong to *Medullosa anglica*. Some of these are the best-preserved specimens which have yet been found, for the more delicate tissues, especially the phloem, are almost perfect.

A photograph of a transverse section of one of these roots is shown on Pl. XX, Fig. 1 (compare also Fig. 6). The diameter is about 9 mm. The root is triarch, as are all the other roots of *Medullosa* which I have examined. The external tissue consists of a somewhat narrow but well-marked zone of radially seriate elements, the periderm (*p.d.*). As Dr. Scott [2] has pointed out, this periderm is developed centripetally from a phellogen (see Fig. 2, *ph.g.*) which lies on the inner side of this zone. It was also shown that this periderm is of deep-seated origin, arising, probably, in the pericycle [3].

Internal to the periderm, there is a somewhat broader zone of thin-walled tissue (*z*), with here and there very conspicuous cells, or groups of cells, with dark-coloured contents. This

[1] Scott, loc. cit., Pl. VIII, photos 19–25; Pl. XII, Fig. 19; Pl. XIII, Figs. 20–4.
[2] Scott, loc. cit., p. 102, Pl. VIII, photo 21.
[3] Scott, loc. cit., p. 104, Pl. XII, Fig. 19.

zone is exceptionally well preserved, and the evidence as to the nature of the tissues composing it is probably more complete than in the specimens which have previously been described. These tissues will be referred to presently in greater detail.

The rest of the root consists of an exceedingly regular triarch strand of xylem. The protoxylem-elements (*p.x.*) lie on the inner margins of three large bays or concavities, which occur at regular intervals in the almost circular outline of the strand. The elements of the primary wood can be seen extending from the protoxylem-groups to the centre of the root.

The secondary wood (x^2.) is formed of three large plates of radially disposed elements, with convex outer surfaces. The rays of woody elements composing the plates are generally one or two rows of tracheides, with multiseriate bordered pits on their radial walls. The medullary rays are often perfectly preserved. The parenchymatous cells of the ray are rounded, except where they have become elongated radially, probably as the result of stretching accompanying the increase in the dimensions of the secondary wood.

As a rule no secondary xylem-elements are formed opposite the protoxylem-groups. The vascular system of the secondary roots has, however, its origin in this position, and the xylem-strand, seen in one of the concavities (*r.x.*), is in connexion with a rootlet, which arises at some distance further along the root.

These roots differ somewhat in shape from some of those previously figured. The structure is, however, identical in both cases. Dr. Scott has made out in considerable detail the minute anatomy of the triarch strand, and I have nothing to add to our present very complete knowledge on this subject.

We may now consider in greater detail the structure of the zone of thin-walled tissue lying internal to the periderm, abutting on the convexities of the secondary xylem, and usually filling the concavities opposite the protoxylem-groups.

The Phelloderm and Pericycle.

A portion of a very thin transverse section is figured on Pl. XX, Fig. 2. It shows the thin-walled tissue opposite one of the protoxylem-groups (*p.x.*). The cells are fairly large, polygonal, or somewhat rounded parenchymatous elements, and are not very dissimilar in size or arrangement.

Towards the periphery of the section, in the lower part of the photograph, a small portion of the periderm (*p.d.*) can be seen. Immediately internal to the phellogen (*ph.g.*), some fairly large cells are shown lying on the same radii as the periderm-elements. This is no doubt phelloderm (*ph.d.*), produced by the activity of the phellogenetic meristem. In certain sections in which the preservation is particularly favourable, the origin of these cells can be clearly traced from divisions of the phellogen layer. The thickness of phelloderm is probably quite small. At a short distance from the phellogen the radial arrangement of the cells is lost.

Internal to the phelloderm, there occurs a fairly broad band of parenchymatous tissue (*p.c.*), the cells of which are irregularly arranged. These elements constitute the pericycle.

Conspicuous among the elements of the pericycle, single cells or groups of cells occur, with dark contents. These are regarded as 'secretory sacs[1].' They appear to be ordinary parenchymatous cells in all the sections of these roots which I have examined. They therefore differ in structure from the gum-canals, which are so abundant in the petiole of *Medullosa*[2]. The 'secretory sacs' occur not only in the pericycle, but among the parenchymatous elements in all parts of the root, including those of the phloem and the primary xylem, as is clearly seen in Figs. 1 and 6. The dark colour of the cells is no doubt due to some organic change which the cell-contents have undergone before, or at the time of, preservation. The distribution of these 'secretory sacs'

[1] The term is used in the same sense as in De Bary's Comparative Anatomy (Eng. edit.), 1884, p. 136.

[2] Scott, loc. cit., p. 99.

rather recalls that of the crystal-containing sacs of certain recent plants, e.g. *Solanum tuberosum*. There is, however, in this case no evidence that these 'secretory sacs' were of a similar nature. In a few cases the cell-contents were found to be much less altered than is usually the case, but even these afforded no clue to the nature of the original substance.

The parenchymatous tissue in the upper portion of the photograph, occupying the concavity on the inner side of which lies the protoxylem-group (*p.x.*), is the very broad main medullary ray (*m.r.*)[1]. Secondary xylem is usually absent in this position. The small xylem-strand (*r.x.*) seen in the photograph belongs to the xylem of a secondary root, which, as already mentioned, has its origin in this position.

The Phloem.

The photograph of a transverse section of a root, figured on Pl. XX, Fig. 3, shows a portion of the thin-walled zone of tissue opposite one of the xylem convexities. The tissues seen here include the phloem, which was of course not present in the section just described. At the lower end of the photograph, a few of the elements of the periderm (*p.d.*) and phelloderm are seen. Next comes a broad band of large-celled, irregularly disposed elements, the pericycle (*p.c.*). The 'secretory sacs' with dark contents form large groups in this section.

The upper half of the photograph shows a well-marked tissue, the elements of which are somewhat tangentially elongated. This is the phloem-zone (*b.z.*). The secondary phloem (b^2.) consists of radial groups of rather small cells, the sieve-tubes (*s.t.*), alternating with rays of much larger phloem-parenchyma (*b.p.*). The secondary bast as a whole has much the appearance of that of the stem of *Heterangium tiliaeoides*, Will.[2]. The groups of secondary phloem, corresponding to the groups of woody elements in the xylem-

[1] De Bary, loc. cit., p. 474.

[2] Williamson and Scott, Part III, Phil. Trans. Roy. Soc., Ser. B, vol. clxxxvi, 1896, p. 761, Pl. XXIX, Fig. 35.

plate, and separated by dilated parenchymatous rays, are characters common to these two plants. The sieve-tubes are also accompanied by a good deal of conjunctive parenchyma, as in *Heterangium*. In *Medullosa*, however, numerous 'secretory sacs' occur between the elements of the bast, and also among the cells of the parenchymatous rays, as is clearly seen in the photograph.

The sieve-tubes in the root of *Medullosa anglica* are, as far as I can ascertain, without the apparently thickened walls and narrow lumen, which are so characteristic of those of the stem [1]. But, like the sieve-tubes of the stem, they have lateral sieve-plates, similar to those of the phloem of most recent Ferns and Gymnosperms.

On Pl. XX, Fig. 4, a photograph of a drawing of highly magnified sieve-tubes from the *stem* of the Binney specimen is shown. The sieve-plates (*s.p.*) are clearly seen as little patches on the lateral walls.

In the *roots*, lateral sieve-plates also occur, as is shown in the drawing figured on Pl. XX, Fig. 5. It is only fair to add that Dr. Scott, who has examined the Binney sections, and most kindly given me the benefit of his opinion on several points in the anatomy of these roots, first recognized and pointed out to me the occurrence of lateral sieve-plates in the phloem of both stem and roots. I may therefore take this opportunity of expressing my thanks to Dr. Scott for much help in the examination of this material.

Lateral sieve-plates have been previously recognized in the phloem-elements of the stem of *Heterangium tiliaeoides* [2], and by Professor Renault [3] in the stem of *Poroxylon Edwardsi*, Ren. As far as I am aware, this is the first occasion in which they have been distinguished in the root of a fossil plant.

The external margin of the phloem-zone is composed of very tangentially elongated cells without any radial arrangement.

[1] Scott, loc. cit., p. 90, Pl. X, Fig. 3.

[2] Williamson and Scott, loc. cit., p. 762, Pl. XXIX, Figs. 37 and 38 *a*.

[3] Renault, Étud. Gîtes Minér. Bass. Houill. et Perm. d'Autun, 1896, p. 282, Pl. LXXIV, Fig. 11. Also Bertrand and Renault, Recherches sur les Poroxylons, Arch. Bot. N. France, 1886, Figs. 192–3.

This is no doubt the primary phloem (*b*[1].). It corresponds very closely to the primary phloem in the stem of *Heterangium tiliaeoides*[1]. In this section the primary phloem is very clearly marked off from the outer large-celled tissue, the pericyle.

The Secondary Roots.

The main points in the structure and origin of the secondary roots of *Medullosa* have been already described by Dr. Scott[2]. The examination of a large series of sections of a root contained in the Binney material has, however, resulted in the elucidation of a few additional details.

The transverse section of a root figured on Pl. XX, Fig. 6, shows the base of a rootlet or secondary root (*r.l.*). The structure of the root itself is precisely similar to that just described (Fig. 1). The particular rootlet shown in the photograph is, however, stunted and abnormal. The xylem-elements are very small, and much less developed than is usually the case, and probably the rootlet never functioned as a typical root.

The lateral roots arise in three rows on the roots, at points opposite the protoxylem-groups. There is apparently, in all the roots which I have examined, some little distance between successive lateral roots in the same row; and only one rootlet is given off in any one transverse plane. The ramification is therefore not so abundant as in certain roots of *Lyginodendron*[3].

The xylem-strand of the rootlet arises, as we have seen, opposite a protoxylem-group of the triarch root. It then passes outwards obliquely, and not at right angles to the stele of the root, as in *Lyginodendron*[4]. The parenchymatous tissues of the rootlet arise from the divisions of a group of meristematic cells, probably of pericyclic origin, which cause a protrusion of the periderm of the root at some little distance

[1] Williamson and Scott, loc. cit., p. 761, Pl. XXIX, Fig. 35.
[2] Scott, loc. cit., p. 103, Pl. VIII, photos 19 and 21.
[3] Williamson and Scott, loc. cit., p. 740.
[4] Ibid.

in front of the point of origin of the xylem-elements. This protrusion becomes more and more marked, until finally the rootlet becomes cut off, and a new growth of periderm completes the outer sheath of tissue of both the root and rootlet. For a short time after it has become free, the rootlet lies in a groove or inflection of the periderm of the root. One of these grooves can be seen in nearly every transverse section (Pl. XX, Figs. 1 and 6, *gr.*), opposite a protoxylem-group.

Conclusions.

The examination of the roots of *Medullosa* in the Binney specimen has resulted in a more complete knowledge of the thin-walled tissues which lie between the xylem and the periderm. The most noteworthy points are, the presence of a thin zone of phelloderm, the structure of the phloem, and the discovery of lateral sieve-plates on the phloem-elements of both the stem and roots. In the phloem of *Medullosa*, we have another point of agreement between *Medullosa* and *Heterangium*. The structure of the root of *Heterangium tiliaeoides* is at present unknown, but the phloem in the roots of *Medullosa anglica* closely resembles that of the stem in the former species.

EXPLANATION OF PLATE XX.

Illustrating Mr. Arber's paper on *Medullosa anglica*.

All the sections (A M 1-A M 29) are in the Woodwardian (Sedgwick) Museum, Cambridge. All the figures, except Figs. 4 and 5, are microphotographs from the actual sections by Mr. W. Tams, Cambridge. Some of these should be examined by means of a hand lens. Figs. 4 and 5 are photographs by Mr. Tams, from drawings by Mr. E. Wilson, Cambridge.

Fig. 1. Complete transverse section of a root. *p.d.*, periderm; *p.x.*, protoxylem; x^2., secondary xylem; *r.x.*, xylem of rootlet; *z.*, zone of thin-walled tissue, comprising phelloderm, pericycle, and phloem; *gr.*, groove in the periderm. × 11½. Section A M 18.

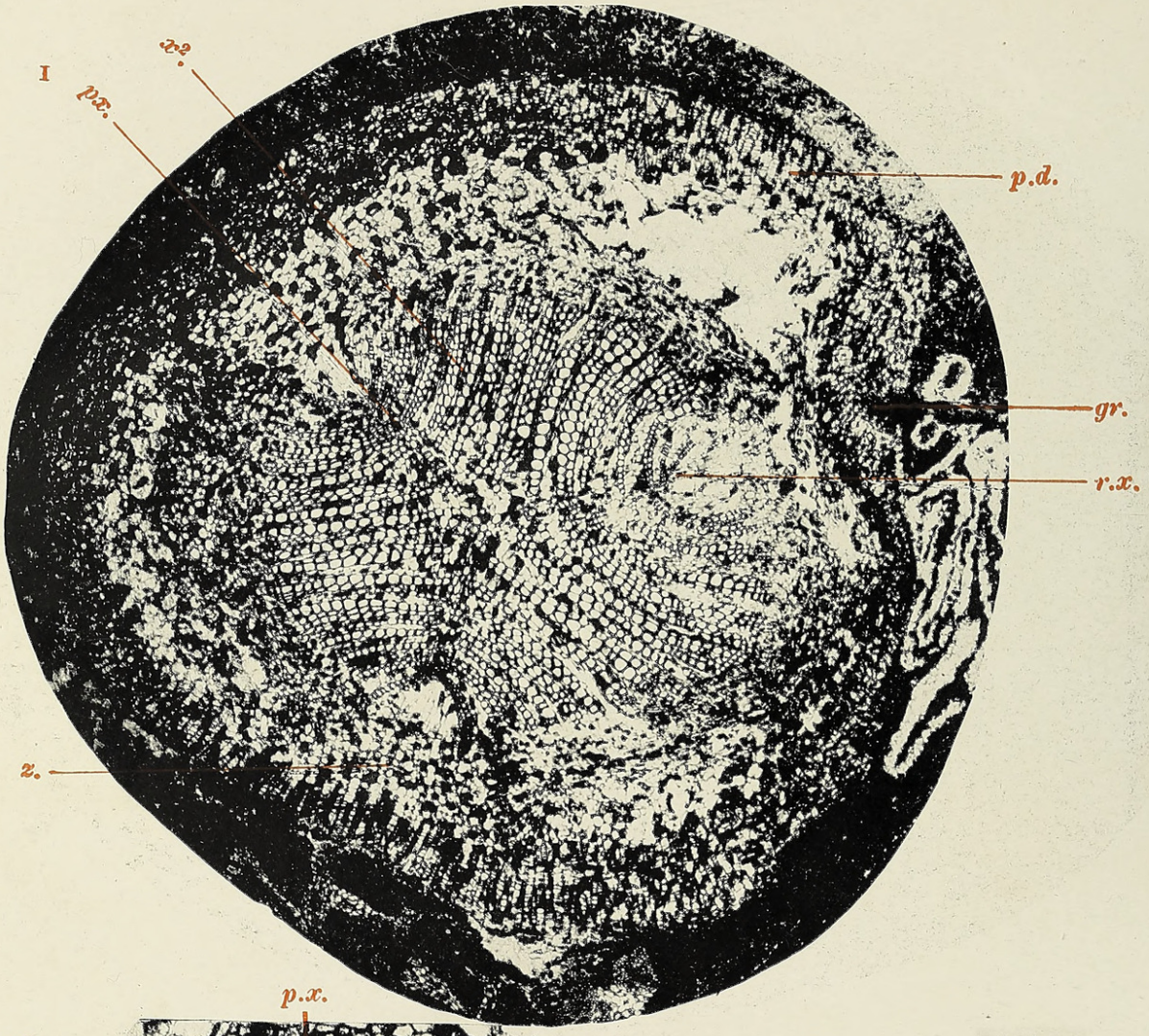
Fig. 2. Part of a transverse section of a root, internal to the periderm, and opposite a protoxylem-group. *p.d.*, periderm; *ph.g.*, phellogen; *ph.d.*, phelloderm; *p.c.*, pericycle; *m.r.*, main medullary ray; *p.x.*, protoxylem; *r.x.*, xylem of rootlet. × 75. Section A M 24.

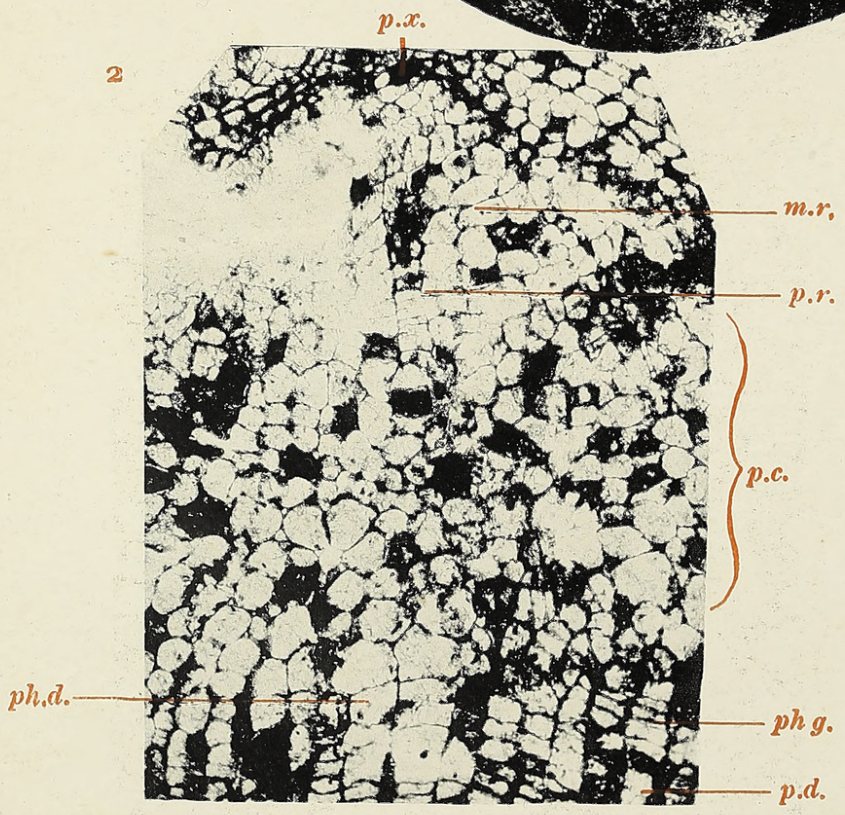
Fig. 3. Part of a transverse section of a root, internal to the periderm, and opposite one of the convexities of the secondary xylem. *p.d.*, periderm; *p.c.*, pericycle; *b.z.*, phloem-zone; b^2., secondary phloem; *s.t.*, sieve-tubes; *b.p.*, bast parenchyma; b^1., primary phloem. × 75. Section A M 15.

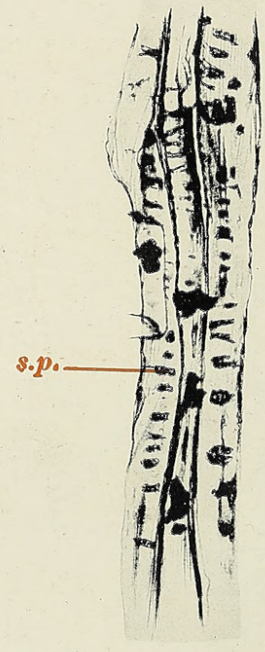
Fig. 4. Drawing of sieve-tubes as seen in a longitudinal section of the *stem* of *Medullosa anglica*. *s.p.*, sieve-plates. × 280 approximately. Section A M 9.

Fig. 5. Drawing of a sieve-tube as seen in a longitudinal section of a *root* of *Medullosa anglica*. *s.p.*, sieve-plates. × 430 approximately. Section A M 28.

Fig. 6. Complete transverse section of a root. *r.l.*, lateral root; *gr.*, groove in periderm. × 11½. Section A M 23.







W. Tams, Microphoto.

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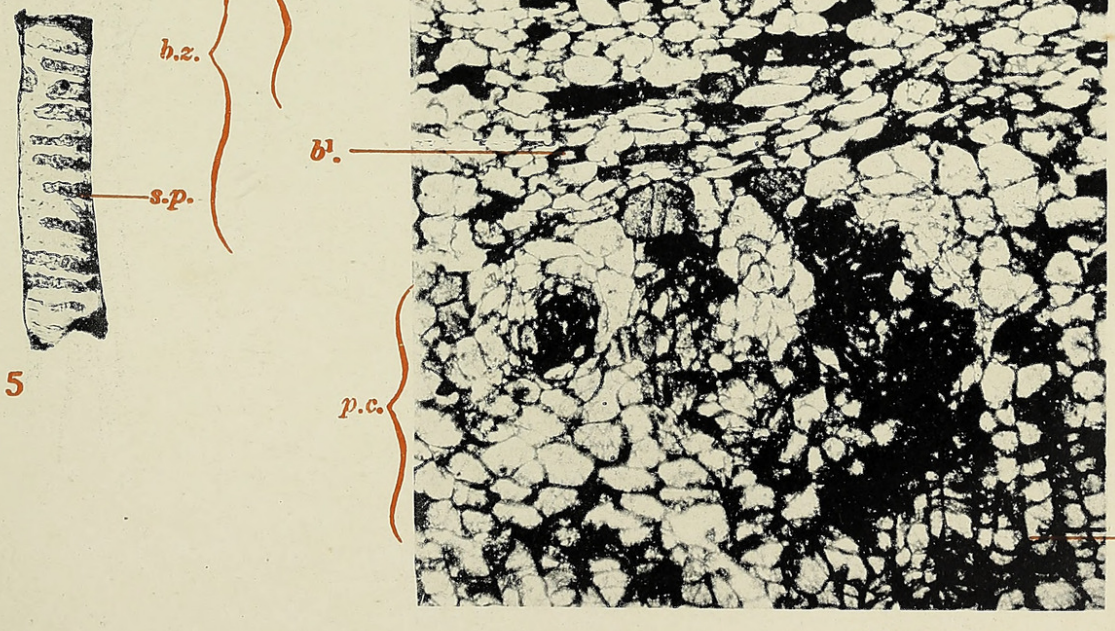

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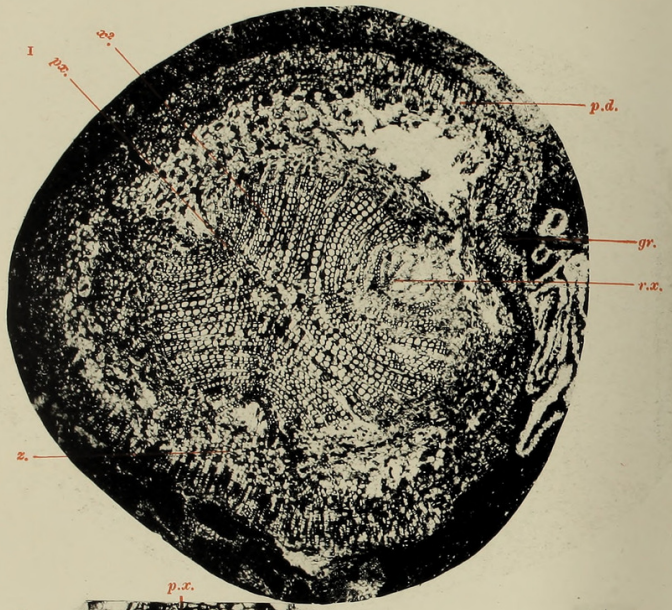

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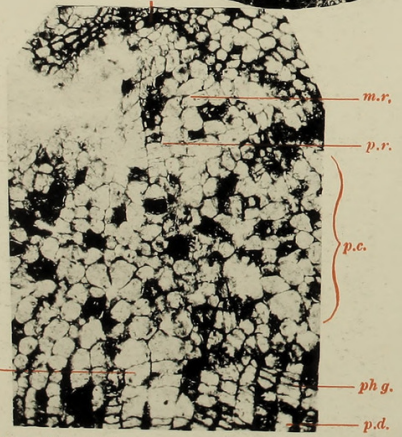

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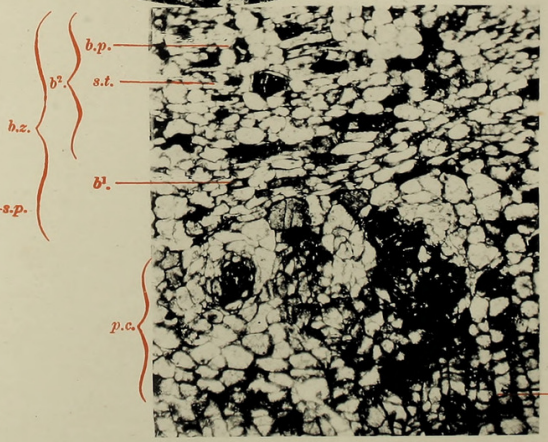

W. Tams, Microphoto.

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ARBER.—MEDULLOSA ANGLICA