On the Structure and Affinities of Ankyropteris corrugata.*

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Communicated by D. H. Scott, *F.R.S.*

(Received June 29.—Read November 7, 1929.)

(Plates 7—10.)

Ankyropteris corrugata is a small zygopterid fern found in the calcareous nodules of the Lower Coal Measures of Lancashire and Yorkshire. It was first discovered by Williamson (46, *b*), who included it in his comprehensive genus *Rachiopteris*, giving it the specific name *corrugata* on account of the fact that the external surface of the stem in his specimen was thrown into a series of irregularly transverse, round-topped ridges. The petioles were also described by him (46, *c*) under the name *Rachiopteris insignis ;* Williamson recognised, however, that the petioles he had described as *R. insignis* were those of *R. corrugata*, although he never actually published the fact (39).

Rachiopteris corrugata was later included in Corda's genus *Zygopteris* (15), in common with other palæozoic ferns, the petioles of which were " characterised by a vascular strand having the form of an H in transverse section " (41). It owes its present generic name to Dr. Paul Bertrand, who, in his important memoir on the petiole-anatomy of the zygopterid ferns (4), has revived, in a limited and more rigidly defined sense, the name employed by Stenzel (42) in his sub-division of Corda's genus.

In addition to Williamson's account a relatively brief description of the structure of the stem and petiole is given by Prof. Seward (41) and by Prof. Tansley (44), whilst a somewhat more extended account is given in the latest edition of Dr. Scott's " Studies " (39).

The present investigation was undertaken at Dr. Scott's suggestion and I am indebted to him, not only for his kindly interest and advice throughout the progress of the work, but also for his transfer to me of the detailed notes he had made on the material in the Williamson Collection. Quite apart from the information thus supplied, these notes were of inestimable value in indicating the method of investigation which he had pursued, and in suggesting further lines of study.

The account now submitted is largely based upon a study of the slides of *Ankyropteris corrugata* in the Williamson and Scott Collections, both of which are housed in the Geological Department of the British Museum (Natural History), and upon those in the Kidston and Nottingham (University College) Collections. In addition to these, I have examined the relevant slides in the collections of University College, London, and of the

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* I am indebted to the Royal Society for a grant towards the expenses incurred in connection with this investigation.

[Published January 22, 1930.

Victoria University of Manchester. Although there are still a number of details about which some uncertainty prevails, the collation of the considerable body of material indicated above has rendered it possible to ascertain most of the essential features of the anatomy and morphology.

The Stem.

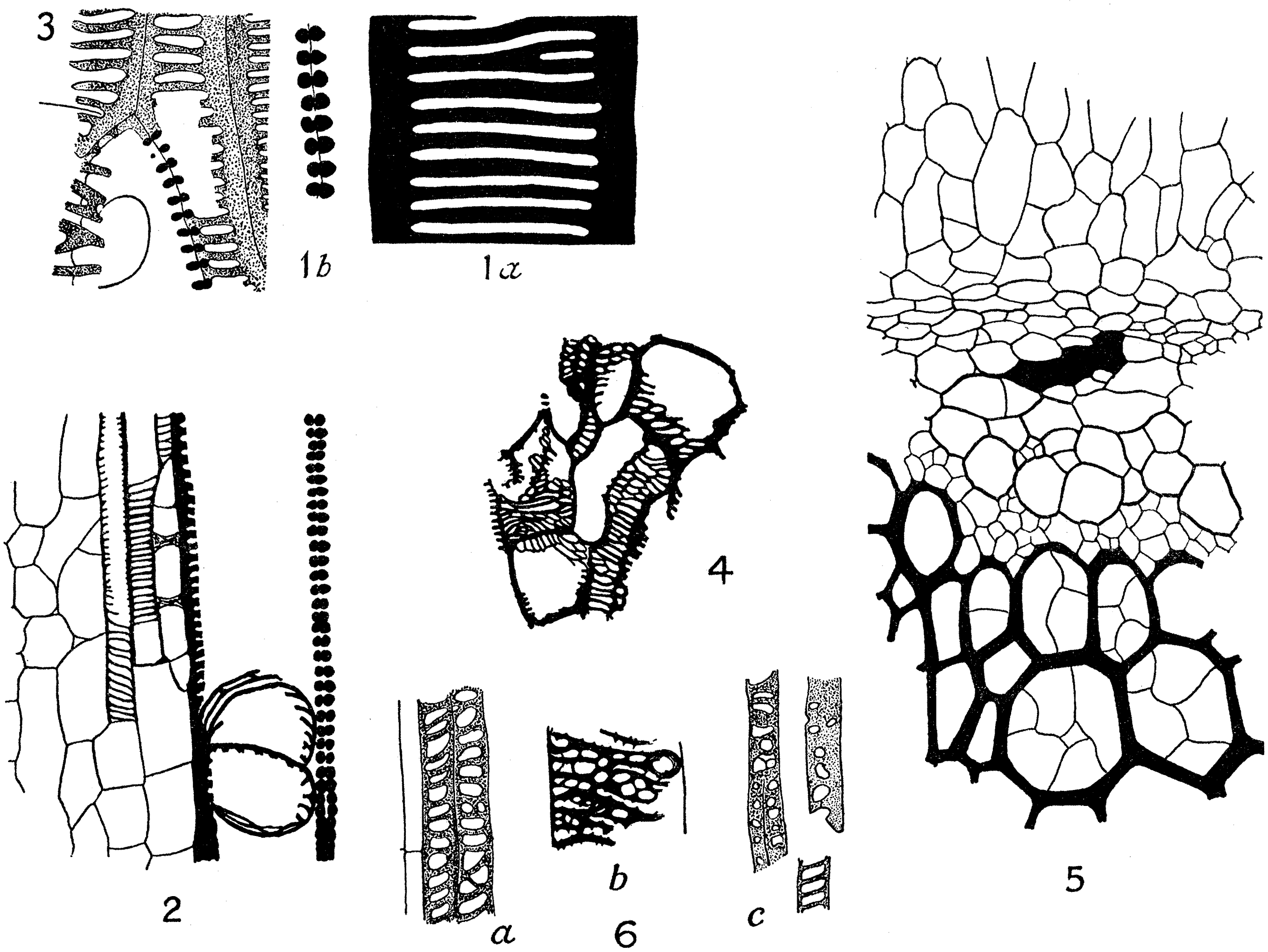
The stem of *Ankyropteris corrugata* is relatively small. Its centre is occupied by a stele, which is cylindrical or slightly ovoid (Plate 7, fig. 1), except where its symmetry is affected by the emission of vascular strands to lateral members. Quite frequently the xylem core alone is preserved and measurements of this in a number of specimens show that it ranges from 1·8 mm. to 3·4 mm., those with a diameter of a little over 2 mm. being commonest.

Xylem.—As in *Ankyropteris Grayi*, the xylem is differentiated into a peripheral region which is homogeneous and consists of relatively large tracheids with scalariform pitting (text-fig. 1), and a central region which consists of a parenchymatous ground mass which is traversed by scattered tracheids of smaller calibre. In the majority of the specimens I have examined the tracheids of the central region are elongated and have pointed ends and, apart from their much smaller diameter, appear to resemble closely those of the peripheral region (see, for example, Slides 256 and 260, Williamson Collection). They vary considerably in number, some stems, such as the Williamson specimen, showing relatively few with a marked preponderance of parenchyma, whilst in others they are abundant. Occasionally they approach those of the peripheral region in diameter, and a specimen of this kind is shown in Plate 7, fig. 2.

It is interesting to note that in certain parts of the stem the narrow elongated type of tracheid may be wholly replaced by a short type with truncated ends, which bears considerable resemblance to the medullary tracheids seen in *Lepidodendron selaginoides.* In such modified tracheids the pitting is no longer scalariform ; the pits are frequently short and irregularly ovoid and the thickening, in many cases, is reticulate (39, 41). This condition is illustrated in Plate 7, fig. 3, which is from a longitudinal section through a dichotomising stem. The region from which the photograph is taken is immediately below the dichotomy, and it is a point of interest to note that tracheids of a similar type are developed in the concavity formed at the point of divergence of the two daughter axes, these, of course, lying *outside* the homogeneous tracheidal system. It is probable that this external group of modified tracheids is of secondary origin, and further reference will be made to it later.

Tracheids of this nature are usually regarded as a water-storing device and their occurrence in the neighbourhood of the dichotomy is a feature which, perhaps, supports this interpretation. It may be noted in passing that where the preservation is sufficiently good, the middle lamella may be frequently detected both in the central and peripheral xylem elements (text-fig. 1, *b*), thus leaving no doubt as to their tracheidal nature (2, 19).

The protoxylem consists of narrow, spirally thickened tracheids lying near the periphery of the mixed " pith," and usually separated from the outer zone of tracheids by one or two parenchymatous elements (text-fig. 2). It appears to be distributed discontinuously round the whole of the medullary region.



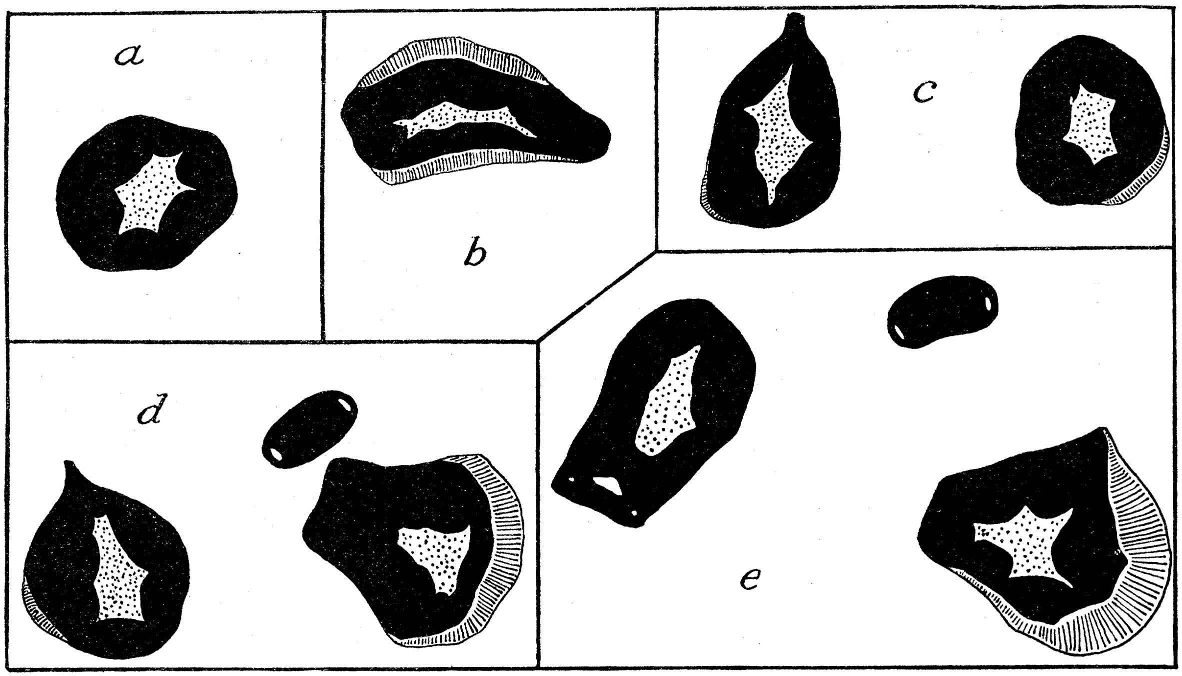
TEXT-FIGS. 1–6.—1, *a*. Small portion of a typical metaxylem tracheid in longitudinal section, to show the scalariform pitting. × 600. U.C.N. Coll. B84. 1, *b*.—Section showing the persistent middle lamella between the xylem bars. × 600. U.C.L. Coll. K610. 2.—Portion of a longitudinal section of the stem showing a metaxylem tracheid on the right occluded by two lignified tyloses and, to the left, part of a protoxylem element with spiral thickening. × 400. U.C.L. Coll. K610. 3.—Longitudinal section of a group of tracheids at the junction of stem and root. Note the wider pits and the narrower xylem bars. × 500. U.C.L. Coll. K610. 4.—Small group of tracheids with reticulate thickening from the central region of a dichotomising stem. × 400. S. Coll. 2692. 5.—Transverse section of part of a stem showing metaxylem tracheids with tyloses, phloem, and adjacent cortex. × 300. Will. Coll. 245. 6.—*a*, *b*, *c*. Sieve tubes. × 300. *a*, *b*, U.C.L. Coll. K602. *c*, M.U. Coll. Q71.

The xylem elements are frequently occluded by parenchymatous ingrowths (text-fig. 5), so frequently, indeed, that the feature is almost characteristic of the species. They were interpreted by WILLIAMSON as tyloses (46, *b*), and although their actual nature has given rise to some discussion (20, 28, 45), there can be little doubt that WILLIAMSON'S view is the correct one, since numerous examples are now known in which the walls of these intrusions have undergone reticulate, or spiral-reticulate, tracheid-like lignification (20). An example of this kind is shown in text-fig. 2, taken from a longitudinal section of the stem in which two adjacent ingrowths show this peculiarity.

Phloem.—The sieve tubes which constitute the bulk of the phloem are relatively large cells, separated from the xylem by a narrow zone of smaller parenchymatous elements. They form a more or less continuous series completely surrounding the xylem, and constitute a layer varying in width from one to four cells (text-fig. 5). Associated with the large sieve tubes are a number of smaller ones which appear to be structurally identical. In both types of element the sieve-plates which, as in other ferns, are situated on the vertical walls (text-fig. 6, *a*, *b*, *c*), are frequently closely crowded, and, in the case of the larger sieve tubes, are very similar to those of *Stauropteris oldhamia* figured by BERTRAND (4). Beyond the phloem is a further zone of small-celled parenchyma bounded, in the most perfectly preserved specimens, by a fairly well-defined layer, which may be interpreted as the endodermis, although it does not stand out clearly like the endodermis of the majority of existing ferns. The primary structure may be modified as a result of cambial activity, this leading to the production of secondary elements of rather a peculiar type. The radial arrangement of the parenchyma adjacent to the primary xylem is occasionally suggestive of an incipient secondary meristem, and I have been fortunate enough to obtain two sections through an internode in which a clearly defined cambium is present, though in this instance it has not produced any secondary vascular tissue (Plate 7, fig. 4). The most remarkable case of this kind, however, is one associated with a stem dichotomy and merits detailed description. It consists of a series of transverse sections in the Scott Collection, Nos. 2713–2720, cut from above downwards. Of these Nos. 2716 and 2717 are cut at the same level, the former alone containing the specimen with which we are concerned.

In the lowest section of the series (No. 2720) the stem, which is a small one with a stele some 1·8 mm. in diameter, appears to be perfectly normal, and has an approximately circular outline. The central mixed tissue is small in amount relative to the total diameter of the stele (text-fig. 7, *a*). Parts of the cortex are well preserved, though somewhat obscured by pyrites, and in it, to the right of the stele, is a radial fissure 1·5 mm. in length, which is flanked on both sides by a wound meristem, several cells in depth, composed of cambiform elements.

In slide No. 2719, which is evidently cut some distance above the previous one, the stele has an irregularly ovoid outline (text-fig. 7, *b*), and measures 3 mm. along its major diameter. On both the longer sides there is a well-marked zone of secondary xylem, which consists chiefly of short tracheids with reticulate thickening, many of these showing elongation in the transverse plane. In the region of the junction with the outer primary tracheidal system there is a considerable admixture of parenchyma, especially on the right of the stem. There is no indication of secondary phloem, a feature which is characteristic of the whole series.



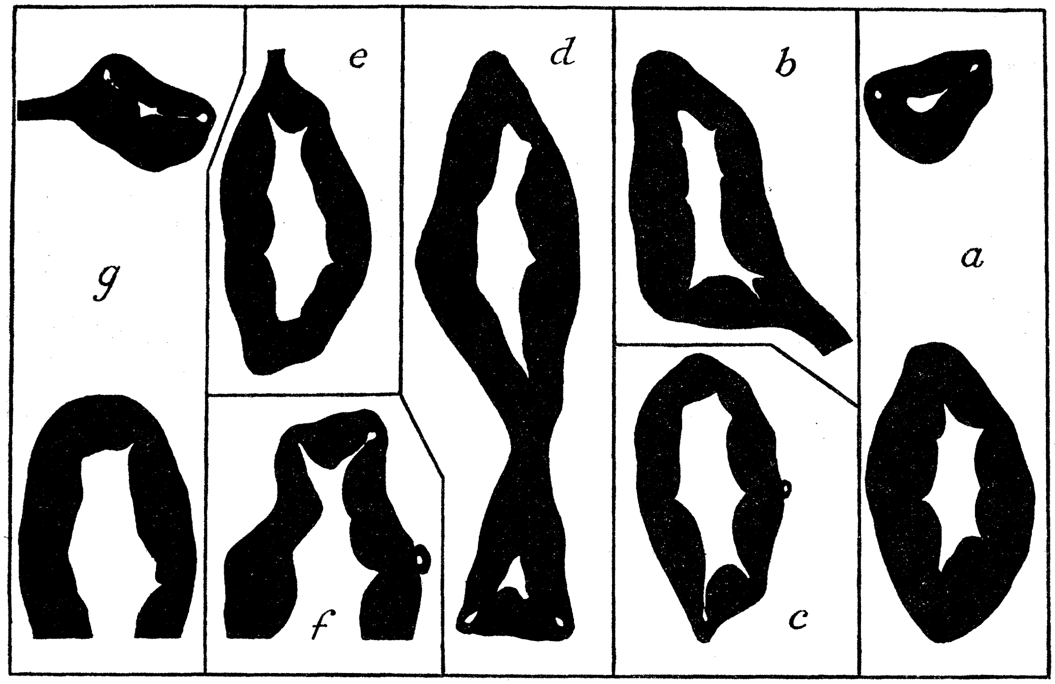
TEXT-FIG. 7, *a–e*.—Camera-lucida silhouettes of a dichotomising stem showing secondary thickening. The outer primary xylem is shown in solid black, the secondary xylem by close-set lines. S. Coll. 2720, 2719, 2716, 2715, 2714.

In slide No. 2718 the stele has bifurcated, and one of the daughter steles has been much damaged, so that it is represented only by a circular outline enclosing a small isolated group of tracheids. The two steles are about 1 mm. apart at this level. The intact stele shows a small patch of secondary tracheids on the side remote from the injured stele. The cortex in this and the following slides is badly preserved and disrupted, though evidences of injury can be detected here and there.

In the next slide (No. 2716) the steles are still less than 2 mm. apart. The stele which was imperfectly shown in the previous slide shows a little secondary xylem on its lower side, a similar patch occurring on the uninjured stele (text-fig. 7, *c*).

Slide 2715 is one which has already been figured by SCOTT (38, 39). The stele to the left showing secondary xylem in the previous section is essentially unchanged, but has an ovoid outline, whilst the other is roughly pear-shaped. The broader end shows a wide strip of secondary tissue (text-fig. 7, *d*, and Plate 7, fig. 5). Where this makes contact with the primary xylem (here curiously thinned) the secondary tissues consist almost entirely of parenchyma for a depth of about eight cells, these being arranged in radial series. Beyond this zone is a homogeneous strip of the peculiar reticulately thickened tracheids, also radially arranged and mostly of small calibre, from eight to twelve cells in depth in the middle, but thinning out at each margin.

The steles are 3 mm. apart in No. 2714, and that which is normal has cut off the central tissue destined for the petiole trace by a tracheidal bridge. The other stele shows a remarkable condition. It is still approximately pear-shaped, and shows the base of a stout root at one side. The meristematic region is very wide, and consists in the main of radially arranged parenchyma, interspersed here and there with small groups of tracheids. Along both margins the parenchyma is wholly replaced by tracheids, the individual cells of which are much larger than those among the parenchyma. In this and in the following slide the thinning out of the primary xylem in this region is remarkable, and certainly suggests traumatic arrest (text-fig. 7, *e*).



TEXT-FIG. 8, *a–g*.—Camera-lucida silhouettes of a series of sections showing a stem giving off three petiole traces, two to the left and one to the right. U.C.N. Coll.

The last slide of the series (No. 2713) shows the steles 5 mm. apart, and at this level the normal stele has given off its petiole trace, whilst the other exhibits a meristematic zone extending three-fifths of the way round its circumference. This is differentiated into an inner belt of radially arranged parenchyma, six to eight cells in width, beyond which is a zone of small tracheids of the type previously described.

In view of its unique character it is to be regretted that the series is such a short one, but the fortunate chance of its preservation serves at least to illustrate a somewhat unexpected potentiality in this species.

Reference has already been made (p. 80) to a mass of tracheids of somewhat similar type, which occupies the concavity between the two shanks of a dichotomising axis, and it is this similarity, together with their position, which renders it probable that they too are of secondary origin. It should be noted, however, that bifurcation of the axis, which is the normal method of branching, is not necessarily accompanied by cambial activity, and it seems reasonable to suppose that the relatively large development of secondary tissues in the stem described above is due in part to traumatic stimulus, since the cortex, though somewhat ill-preserved, shows very clear evidence of injury.

The view that traumatic stimulus may have played a part in inducing so considerable a secondary development is supported by the occurrence of secondary xylem in injured petioles. It is hoped to describe these more fully in a subsequent paper, but it is interesting to note that in these cases also the secondary tracheids are short, and frequently show reticulate thickening. On the other hand, it should be stated that injury does not invariably lead to the development of secondary vascular tissue, and it is probable that a number of other factors are involved, such, for example, as the age of the axis when wounded, the nature and extent of the actual injury, and the humidity or otherwise of the habitat. In the case of the particular axis under discussion it seems likely that the association of the dichotomy with the traumatic stimulus has played a major part in inducing exceptional secondary growth.*

Cortex and Epidermis.—Beyond the limiting layer of small cells, to which reference was made earlier, lies a wide cortex, which is generally poorly preserved, and is indeed frequently missing. This cortex is almost entirely parenchymatous, apart from modifications associated with the development of the lateral members, and consists of irregular, somewhat loosely packed cells, much larger than those of the phloem parenchyma. Towards the periphery the cells undergo division, giving rise to a thin periderm (*cf.* text-fig. 9). The epidermis and, in many cases, the cortical cells immediately subjacent for a depth of from two to four cells, show a very characteristic lamellose thickening of the walls, which is frequently so pronounced that the cell lumen is reduced to very small dimensions. The bulk of the thickening material is usually laid down on the outer and lateral (radial) walls of each cell, but is apt to be somewhat unequally distributed, and may occasionally involve all the walls (*cf.* text-fig. 10). The surface of the stem bears stout hairs which, where the preservation is sufficiently good, appear to be present in considerable numbers. Each hair is pointed, and, for the greater part of

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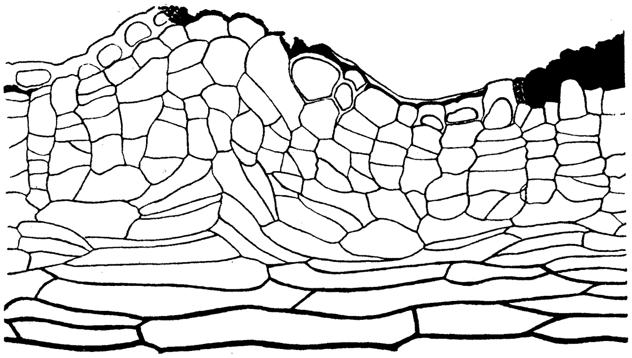
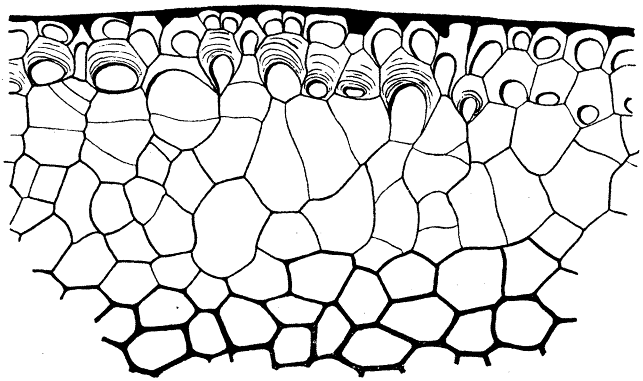
* The anatomical features shown by the stem described above recall the somewhat similar characters shown by branching axes of *Helminthostachys*. These have been fully described by LANG (26), who has also drawn attention to many other points of resemblance between the zygopterids and the Ophioglossaceæ. SCOTT has also stressed this resemblance in the first volume of the " Studies " (39).

The branching axes of *Helminthostachys* do not, however, provide an exact parallel to that of our specimen, since the branching itself is a traumatic response in the existing fern, whilst it is a normal feature of the extinct one, and one which is not usually accompanied by secondary thickening. It should also be noted that secondary thickening due to trauma may occur quite apart from branching.

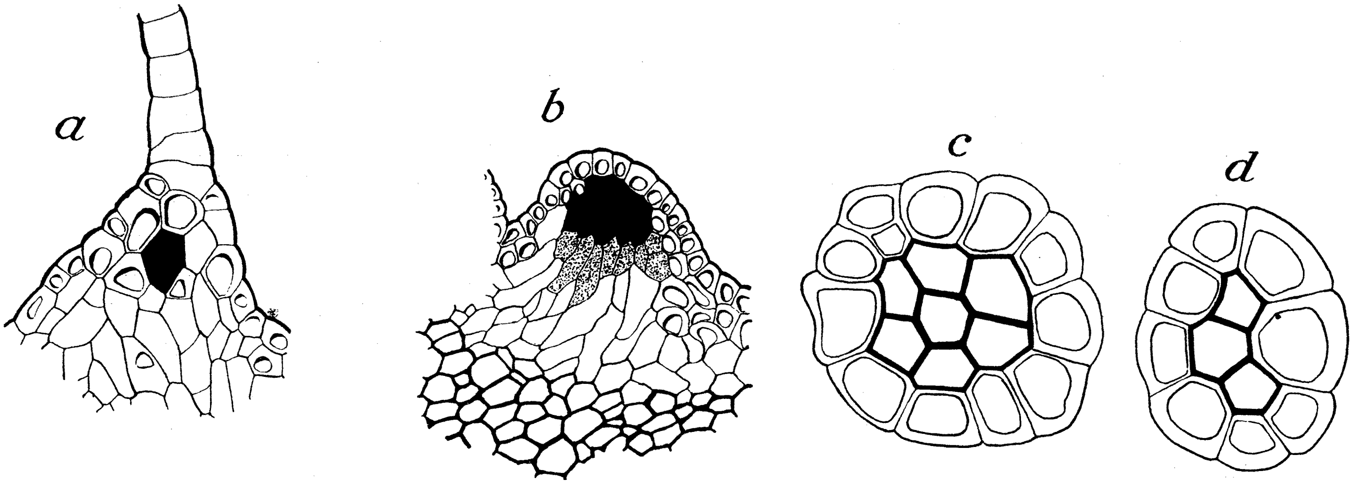
its length, consists of a single row of cylindrical cells. Towards the base, however, it is several cells in width, the constituent cells being grouped symmetrically and forming the core of a bluntly conical process composed of the thick-walled epidermal and sub-epidermal cells described above (*cf.* text-fig. 11, *a–d*).



TEXT-FIG. 9.—Part of a longitudinal section through the base of a petiole, showing periderm. × 300. M.U. Coll. Q71.



TEXT-FIG. 10.—Part of a transverse section of a petiole a little way above the base, showing the lamellose thickening of the outer cells and occasional divisions in the subjacent parenchyma. × 400. U.C.L. Coll. K602.



TEXT-FIG. 11, *a–d*.—Sections through the stout hairs occurring on the stem and petiole; *a* and *b* are oblique sections cutting the base of the hair tangentially; *c* and *d* are transverse sections cut near the base and at a slightly higher level respectively; *a*, *b*, × 200. *c*, *d*, × 600. *a*, S. Coll. 2725. *b*, S. Coll, 2727. *c* and *d*, S. Coll. 2726.

The Petiole Trace.

The petiole traces are given off in two rows, being produced at relatively short intervals alternately from the right and left sides of the parent axis. This distichous arrangement is in striking contrast to the condition obtaining in the remaining species of *Ankyropteris*, of which the stem is known, and was so surprising that, although such an interpretation appeared probable as a result of a close study of the material in the Williamson and Scott Collections, it was not until a longer sequence of transverse stem-sections, cut for me by Mr. W. HEMINGWAY, of Derby, was available that the matter was placed beyond dispute. A selection of camera-lucida silhouettes from this series is shown in text-fig. 8, which illustrates stages in the emission of three traces, two on the left and one on the right. Mr. HEMINGWAY informs me that the sections figured represent a length of about two inches of the original stem.

The first indication of the emission of a petiole trace is provided by the lateral extension of the stem stele, this being followed by the development of two prominent ridges, so that the stele first becomes ovoid and then roughly pentagonal, as seen in transverse section (Plate 7, figs. 6, 7). The tissues occupying the centre of the stele keep pace with the extension of the outer tracheidal system and project into the angles formed by the two ridges mentioned above, to such a degree that the outer tracheids form a short narrow arch only two or three tracheids in width, the tracheids of which are of smaller calibre than those of the main mass. This stage is followed by the development, behind the projecting portion of the stele, of a bridge of large tracheids which separates the central tissue into two portions, the smaller one having the form of a shallow gutter and being destined for the developing petiole trace, whilst the larger main mass forms the core of the parent stele (Plate 7, fig. 8). The tracheidal bridge thickens and its outer portion constitutes the adaxial moiety of the petiole trace which is then slowly nipped off as a stele of triangular outline with rounded angles (Plate 8, fig. 10), whilst its inner portion serves to maintain the continuity of the peripheral part of the stem stele.

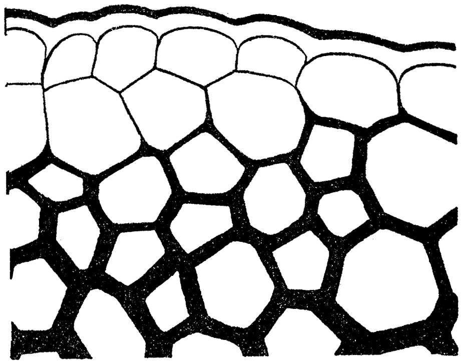
The stage in the formation of the petiole trace at which the tracheidal bridge is initiated varies within wide limits. In some few cases (Plate 7, fig. 2) it is practically completed before the transverse extension of the stele has proceeded very far, whilst in others its development is relatively leisurely (Plate 7, fig. 7), so that the connection between the inner tissues of petiole trace and axis is maintained for a considerable interval. The tracheids which constitute the bridge are peculiarly modified at the point of separation of the xylem of the petiole trace from that of the axis, many of them being U or V-shaped, with one arm in the axial and the other in the petiolar segment. They are admirably shown in No. 2692 (Scott Collection), and are figured in Plate 7, fig. 9. The phloem of the petiole trace completely surrounds the xylem, and, on the adaxial and abaxial faces, consists of an arc of large sieve tubes, two or three cells in width, with their accompanying small-celled parenchyma. The large sieve tubes are linked round the ends of the trace by smaller but otherwise similar elements (Plate 9, fig. 22).

It will be clear from the above description that the departure of the petiole trace is typically protostelic, and involves no break in the continuity of the stelar tissues of the stem. The angle of departure of the petiole trace is very acute, so that the various stages in its modification can be readily seen in serial transverse sections. As a rule the stage showing a triangular outline is short-lived, the angles becoming more rounded and the stele assuming an elongate ovoid form (Plate 8, fig. 11). There is, however, considerable variation in this respect, as may be seen from a comparison of fig. 11 (Plate 8) and fig. 22 (Plate 9), which represent approximately equivalent stages in different stems. At this stage the first indications of the abaxial concavity, which is so characteristic a feature of the petiole trace in *Ankyropteris*, become apparent, and the peripheral arches of smaller tracheids, with their enclosed groups of intrastelar parenchyma which occupy the two extremities of the trace, are also more evident (Plate 8, fig. 13).

The fate of the group of small tracheids and parenchyma which is situated in the central region of the departing trace is of some interest. At the level of separation of the trace from the parent stele it often takes the form of a thin, more or less continuous, plate of tissue, showing a median dilatation and linking up at either end with the parenchymatous inclusions immediately subjacent to the peripheral loops (Plate 8, fig. 10). It soon loses contact with these, and may become subdivided into a number of small separate groups, of which the central one is the largest (Plate 8, fig. 11). The smaller groups dwindle rapidly and disappear, to be followed at a somewhat later stage by the larger central one, so that from this point onwards the bulk of the petiole trace consists of a homogeneous system of tracheids (Plate 8, fig. 13). Apart from an increase in the size of the peripheral loops, accompanied by a flattening of the parenchyma which they enclose, no further change of importance takes place in the character of the trace during its passage through the stem cortex, though its symmetry may undergo considerable disturbance as a consequence of the attachment of root traces.

The giving off of the petiole trace is accompanied by a characteristic change in the outer cortical region of the stem immediately opposite to it. This takes the form of the development of a curved strip of thick-walled cells, the concavity of which is adaxial and which forms a gutter-like structure, towards the centre of which the petiole trace passes (Plate 9, fig. 21). Meanwhile the two free edges of the gutter curve inwards behind the outgoing trace, and unite to form the sclerised outer cortex of the petiole proper, the enclosed parenchyma being continuous with the inner petiolar cortex. Occasionally the sclerenchymatous sheath is incomplete on the adaxial side at the level of separation, but the gap is rapidly filled in such cases at a slightly higher level. At its base the sclerenchyma is surrounded by a sheath several cells in thickness, which is continuous with and similar in character to the superficial tissues of the stem. Thus the epidermal cells and those immediately underlying them show the pronounced and somewhat unequally distributed stratified thickening of the walls to which reference has already been made, whilst below this layer the parenchyma has undergone division to form a well-defined periderm (text-figs. 9, 10).

The stout hairs characteristic of the stem occur here also, frequently in considerable numbers, and at somewhat higher levels the dark cells which constitute the shaft of the hair and which traverse the core of the basal papilla appear to be continuous with the sclerised cells of the outer cortex (text-figs. 11, *a–d*). Traced in an upward direction the parenchyma and periderm steadily decrease in amount (text-figs. 9, 10) and ultimately disappear, so that at higher levels the cortical sclerenchyma of the petiole is either directly in contact with the epidermis or is merely separated from it locally by small shallow patches of parenchyma from one to four cells in width (text-fig. 12).



TEXT-FIG. 12.—Transverse section of a part of the outer tissues from the middle of a petiole. × 400. S. Coll. 2724.

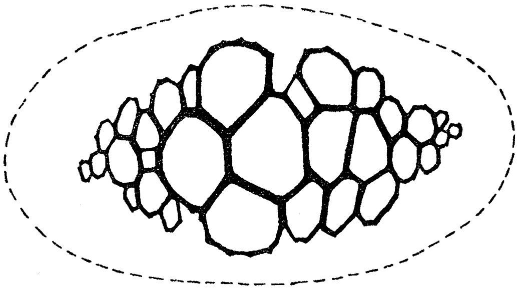
Although we may, at this point, conveniently defer the further study of the petiolar anatomy and that of its associated structures until the relationship of the roots and aphlebiæ to the stem has been considered, reference may be made to an exceptional type of petiole trace which has occasionally been met with during the course of this study. It is characterised by the fact that, instead of becoming elongated tangentially and developing the characteristic abaxial curvature, it assumes a stout symmetrical ovoid outline very like that of Dineuron. A petiole of this type in which the median protoxylem and parenchyma are still present is shown in Plate 9, fig. 28, *a*, whilst a more advanced stage is shown in fig. 28, *b*, on the same plate. It is naturally impossible to assign these aberrant petioles with certainty to *Ankyropteris corrugata*, and whilst personally considering this assignation probably correct, the possibility of their belonging to some closely allied species must be borne in mind.

The Root System.

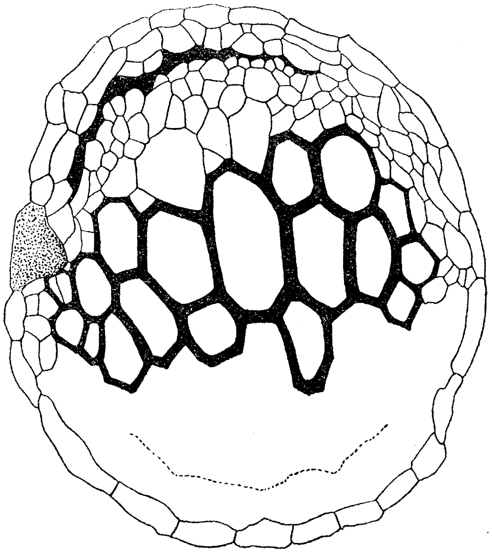
The root system of *Ankyropteris corrugata* is adventitious, the majority of the roots arising from the stem. It is not uncommon, however, to find a stout root arising from the petiole trace during its passage through the stem cortex, this causing a pronounced local disturbance of symmetry, which is emphasised by the character of the tracheids in the region of fusion. This association of petiole and root trace may possibly represent a foreshadowing of the condition normally obtaining in the majority of the recent and fossil Osmundaceæ (22). It may be noted in this connection that, in the allied *Asterochlaena laxa*, the roots are of two types, some arising on the flanks of the arms of the markedly stellate stele, whilst others are developed in symmetrical pairs, constantly associated with the petiole traces (6). The roots vary considerably in size, the major diameter of the steles of the larger ones ranging from about 0·7 mm. to 1 mm., whilst those of the smaller ones have a diameter of about 0·25 mm. They traverse the stem cortex at various angles, some growing diagonally forward towards the stem apex, some towards the base, and others again growing out more or less transversely (Plate 8, fig. 14). Normally they do not branch at this stage, but two cases have been noted in which a root has produced a number of laterals during its passage through the stem tissues. These are shown in No. 2687 (Scott Collection) and No. 345. 20 (U.C.N. Collection).

and in both it is quite evident that the branching is monopodial, a feature which appears to be constant in the material I have examined. The tracheids which occur at the region of fusion between root and stem and root and petiole trace are so distinctive as to be unmistakable. They are short square-ended or obliquely truncated elements, frequently irregularly bent, with relatively wide somewhat unequal pits, often of a reticulate or semi-reticulate character (Plate 8, fig. 15).

The stele of the root is invariably diarch, and its major axis at the point of origin is at right angles to that of the stem, thus conforming to the usual cryptogamic type. Although it is difficult, owing to the varying angle at which the root stele makes contact with that of the stem, to obtain precise structural details of the early stages, it is clear that these are accompanied by an outward extension of the tracheido-parenchymatous central tissue and, in some cases at least, by the development of small groups of parenchyma among the normally homogeneous outer tracheidal system. The diarch root plate at this stage consists of a thin, frequently discontinuous group of tracheids enclosed by parenchyma. When free from the stem xylem, however, it is a relatively robust stele of the osmundaceous type, and in the larger roots closely resembles that of some species of Osmundites (e.g., *O. Kolbei*) (text-fig. 13).



TEXT-FIG. 13. Xylem of a root in transverse section, showing its osmundaceous character. × 240. S. Coll. 2721.



TEXT-FIG. 14.—Transverse section of the stele of a young root showing the xylem, phloem, and endodermis. The structureless layer is probably the protophloem. × 400. S. Coll. 2681.

The xylem is flanked on either side by phloem and phloem parenchyma. The protophloem can be recognised in the young root before the primary xylem plate is completely differentiated, as a narrow tangential strip of small-celled tissue, but in older roots its position is marked by a dark band in which no structure is visible (text-fig. 14). The stele is bounded externally by a clearly defined endodermis composed of flattened cells which stand out boldly on account of the dark nature of their cell-contents.

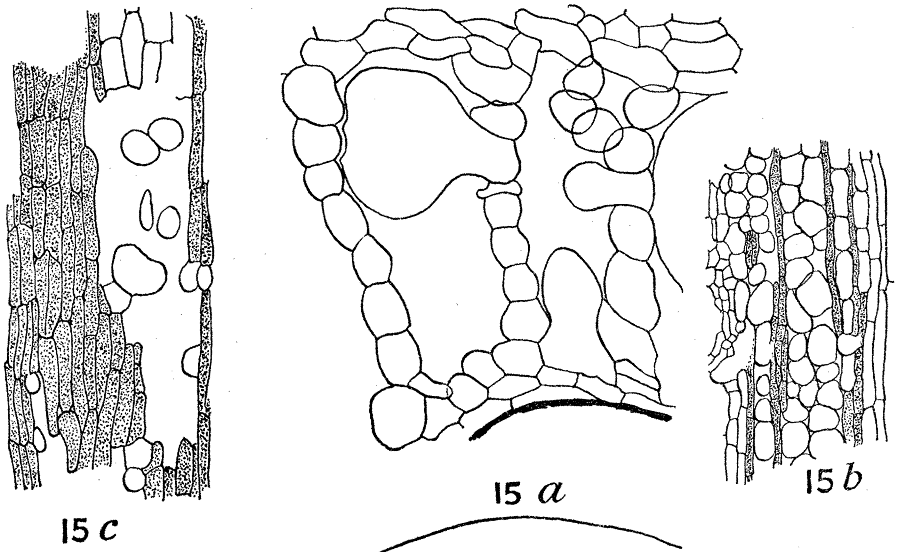
The root does not develop an independent cortex until it has passed well out into the stem, and in some cases, notably in the Williamson specimen, there is a curious inter-digitation of the cortical cells with those of the stem at and near its origin. The tardy development of a separate root cortex is a further feature which finds a parallel among the fossil Osmundaceæ, the majority of the species studied by KIDSTON and GWYNNE-VAUGHAN showing this character (22).

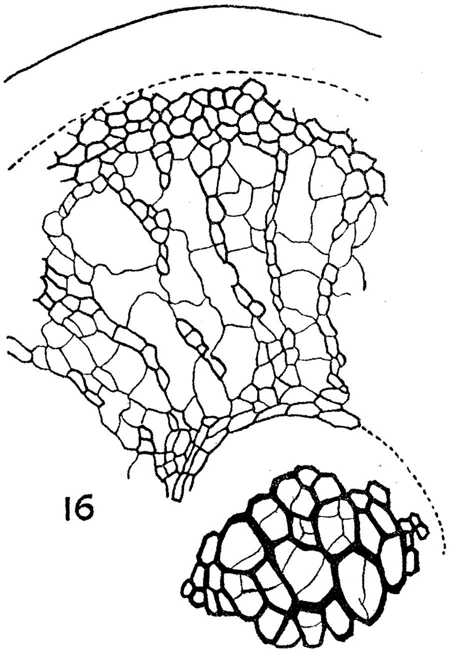
When first developed the root cortex consists of homogeneous parenchyma, but before emergence from the stem tissues the first indications of differentiation are seen, these consisting in the development of an internal zone of small rounded cells surrounded by a zone, some six to eight cells wide, in which the constituent cells are much more closely set. Immediately the root is free from the stem further cortical differentiation occurs, this, in the external zone, taking the form of a slight, but quite definite, thickening of the two or three innermost layers of cells, whilst the inner zone gives rise to a cylinder of simple parenchyma, three or four cells wide, in contact with the endodermis, beyond which is a lacunar middle region.

The lacunar middle cortex is composed of radial plates of tissue, one cell wide except at their extremities, separated by relatively wide intercellular cavities (Plate 8, fig. 16). The general appearance of the cortex at this stage is very similar to that of the stem of *Myriophyllum spicatum* or of the smaller roots of Calamites. A series of secondary changes is, however, initiated, usually, as far as one can judge, whilst the root is still quite young, which leads to considerable modification of the middle and outer regions. The cells of the outer cortex undergo division, giving rise to a well-marked periderm, this, apart from its superficial origin, not being specially noteworthy.

The changes in the lacunar middle cortex are more striking. The first stages are the result of the development of vesiculate outgrowths from the parenchymatous cells constituting the radial plates of tissue (text-fig. 15, *a*, and Plate 8, fig. 17). These increase both in size and number until the lacunæ are, in many cases, completely occluded (text-figs. 15, *b*, *c*). Further increase in the size of the outgrowths results in the disruption of the radial plates. A stage is shown in text-fig. 16, in which the displaced remnants of these plates are still recognisable, but in older roots all trace of them appears to be lost, so that the middle cortex then consists entirely of irregular, somewhat open-textured parenchyma (Plate 8, fig. 18, *a*). Secondary thickening, which occurs only in exceptional cases in the stem, is a characteristic feature of the root. As SCOTT has stated (39), a considerable amount of secondary xylem may be developed towards the base of the root, but it is not confined to this region, and I have observed it even in roots of relatively small diameter at some distance from the point of origin. Two particularly fine examples of roots showing secondary thickening occur in the Nottingham and Manchester collections respectively, and the former of these is illustrated in fig. 18, *a* (Plate 8).

It is a remarkable fact that the nature of the pitting of the secondary tracheids, especially those which form the radiating series surrounding the protoxylem poles, is quite different from that of the primary metaxylem, the pits being short and in some cases irregular, so that a reticulate appearance results. The precise nature of the pitting is, however, probably of physiological rather than phylogenetic interest (Plate 8, fig. 18, *b*).

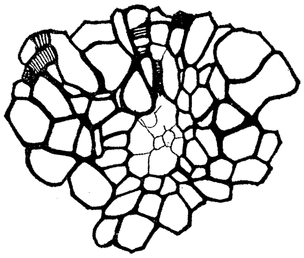




Text-figs. 15–16.—15, *a*.—Part of a transverse section through the lacunar cortex of a young root showing the development of vesiculate outgrowths from the constituent cells. × 320. S. Coll. 2726. 15, *b*.—Tangential section through the radiating lamellæ of the middle cortex, showing the intercellular spaces occluded by vesiculate outgrowths. × 200. S. Coll. 2702. 15, *c*.—Radial section through a lamella. × 240. S. Coll. 2682. 16.—Transverse section through a root, showing disintegration of the still recognisable radial lamellæ as a result of the further growth of the vesicles. × 240. S. Coll. 2726.

Aphlebia Traces and Aphlebiæ.—In addition to the large pointed hairs to which reference has already been made, the surface both of the stem and petiole bore numbers of flattened scale-like aphlebiæ, which were traversed by small concentric vascular bundles. The vascular supply to a stem aphlebia is initiated by an outward extension of the central stelar tissue, accompanied by the development of a bulge composed of small tracheids at the periphery of the stem xylem (Plate 7, figs. 1 and 6, *aph*). The central tissue penetrates into the small superficial group of tracheids which thus, in transverse section, has the form of an arc. The adaxial edges of this arc unite and the small circular trace, including a central group of parenchyma, passes into the cortex surrounded by a narrow strip of phloem. The enclosed parenchyma has, in many cases, a striking resemblance to the cavity-parenchyma which characteristically replaces the protoxylem in the petioles of many existing ferns, although its real nature is totally different (text-fig. 17).

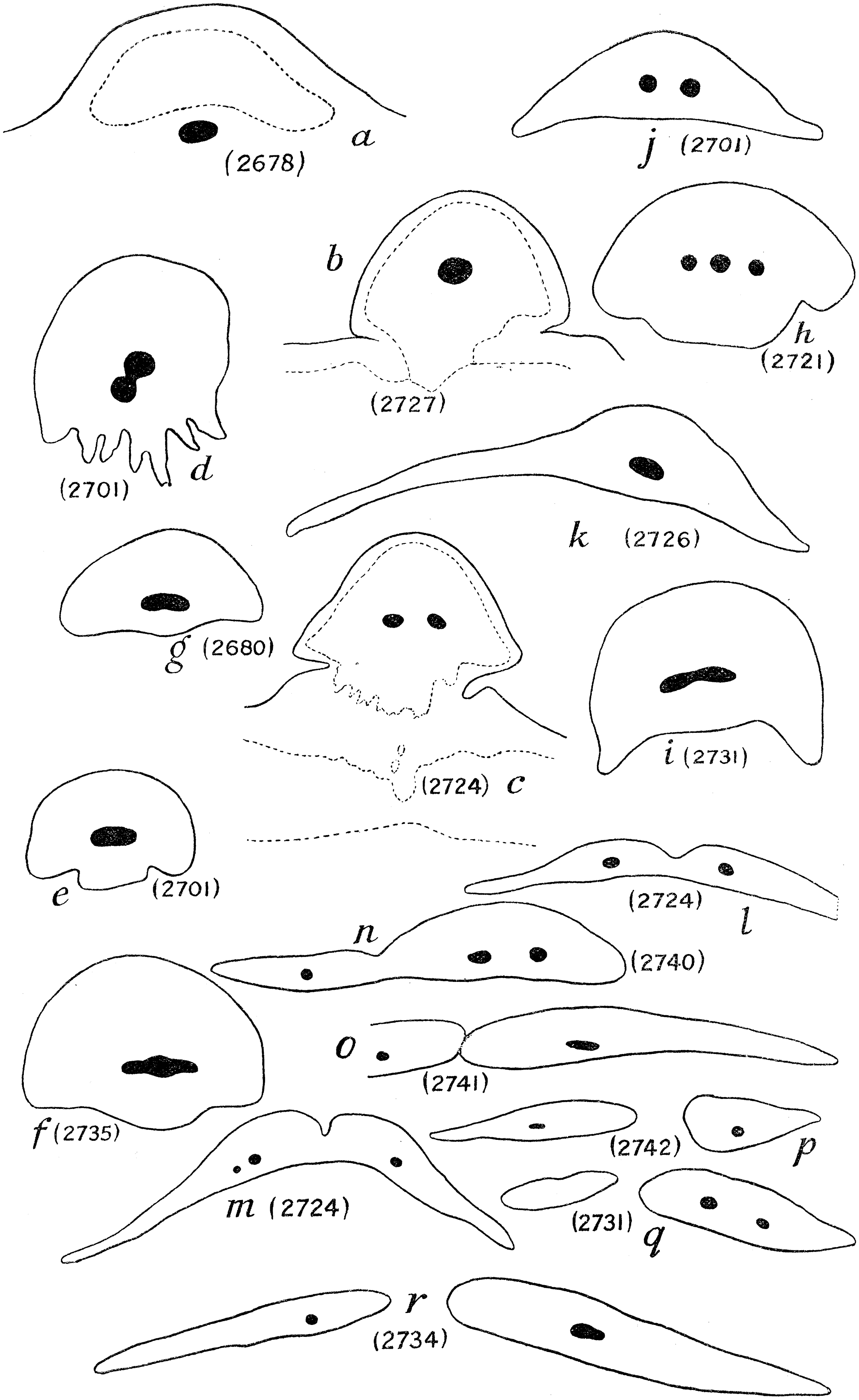
The aphlebia trace passes out through the cortex at a steep angle, but owing to the rarity with which this tissue is preserved intact it is almost impossible to trace the strand from its origin to its entry into the structure it is destined to supply. As a rule it enters the aphlebia as a single strand, but occasionally it may dichotomise immediately before doing so. The development of a small hump of thick-walled tissue in the outer cortex marks the base of the aphlebia itself, and the vascular strand penetrates into the centre of this, carrying with it a narrow parenchymatous sheath.



TEXT-FIG. 17. — Transverse section of a large aphlebia strand in the stem cortex. × 300. S. Coll. 2704.

The free aphlebia at the region just above its junction with the stem is biconvex in transverse section, with the more convex side abaxial. It may be surrounded by a thin sheath of periderm and thick-walled epidermal and sub-epidermal tissue at its base, but this is soon lost. Its superficial tissues are frequently lacking, but in the most perfectly preserved specimens an investment of delicate hairs of a peculiar type is developed. These are slender and the majority show dichotomous branching, though trichotomy is also common (text-fig. 31, *a*, *b*). Their close setting and complex branching produce a felted appearance when they are present in quantity (Plate 8, fig. 19).

Apart from the narrow sheath of parenchyma surrounding the vascular system, the tissues of the aphlebia are thick-walled, and these outgrowths must have been scabrid in character. Soon after they become free they may develop a median adaxial ridge (text-fig. 18), although this is not always the case. A short distance from the base they develop a wing-like expansion on either side, which is composed of thick-walled cells similar to those constituting the bulk of the cortex, but growing in a direction at right angles to them (Plate 8, fig. 20). At the same time the bundle may divide further, so that the aphlebia contains from three to five bundles. When traced towards their extremities the lateral wings become reduced in size and disappear, while the tip of the



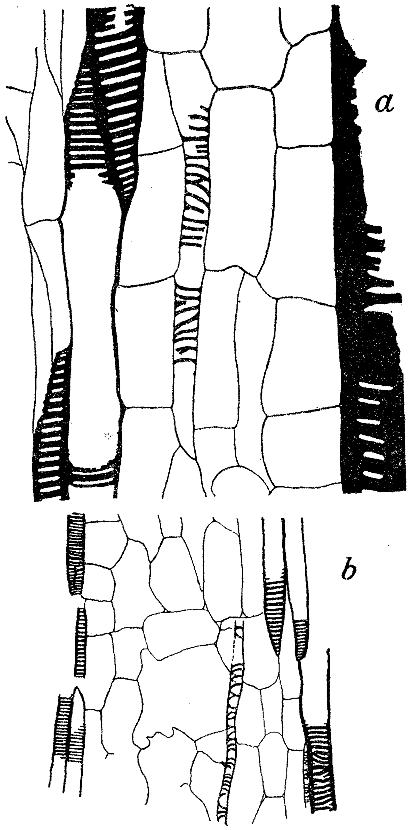
Text-fig. 18, *a–r*.—Series of camera-lucida outlines of stem aphlebiæ, all from slides in the Scott Collection; *a–d* represent the early stages in the development and separation of the aphlebia; *e–h* show the variable character of the adaxial ridge and vascular strands; *i–k* the development of the wing; *l–n* the beginning of bifurcation near the apex; *o–r* divided apices; *n*, *o* and *p* are probably sections of the same aphlebia. The numbers in brackets are those of the slides upon which they occur.

aphlebia, which consists of somewhat thinner-walled cells than the rest, flattens out and bifurcates, and may occasionally divide into three (text-fig. 18). The separate portions of the aphlebia are frequently unequal, one containing a single bundle whilst the other contains two (text-fig. 18).

There seems no doubt that these structures, with their surface hairs and resistant tissues, constituted a system of scales which afforded some measure of protection to the delicate tissues of the rhizome.

The Petiole.

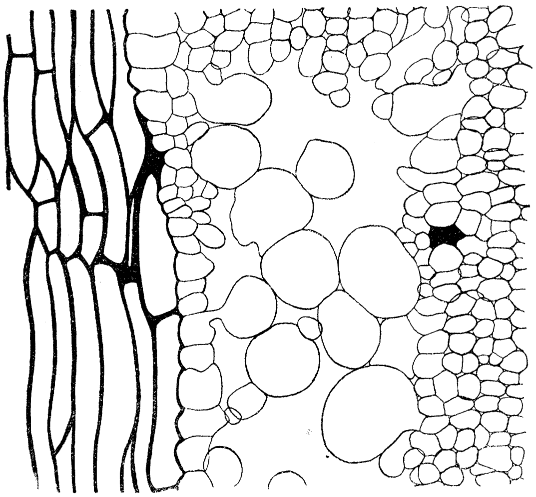
The petiolar strand at its base consists of a well-defined central bar (BERTRAND'S " Apolaire "), showing a slight abaxial concavity and composed of large scalariform tracheids, at either end of which the short antennæ are just beginning to be clearly defined (Plate 9, fig. 23). The adaxial antennæ, even at this level, are much stronger than the abaxial ones, and in both the distal portion is narrower than the proximal portion owing to the progressive diminution in the size of the constituent tracheids. Their tips are bent outwards and united by the convex band of uniformly small scalariform tracheids which constitute the peripheral loop or filament. These filaments, in contradistinction to those of the quadriseriate zygopterids (Dineuron, Metaclepsydropsis, Etapteris), are permanently closed. The enclosed parenchyma, in the most perfectly preserved specimens, shows, generally at and near its outer margin, small groups of tracheids and single tracheids distributed along the whole length of the filament, which I think must be interpreted as protoxylem. In the few cases where they are cut in longitudinal section they show the characteristic lax spirals typical of the first formed xylem elements, and, as will be seen subsequently, other collateral evidence is available which supports this interpretation (text-fig. 19, *a*, *b*).



TEXT-FIG. 19, *a*, *b*.—Longitudinal sections of parts of petiole between antenna and peripheral loop, showing protoxylem elements in the enclosed parenchyma. 19, *a*. × 350. U.C.L. Coll. K602. 19, *b*. × 150. S. Coll. 2728.

The phloem and phloem parenchyma follow the contours of the xylem, both sides of the central bar being flanked by a single row of large sieve tubes, which generally show some degree of collapse (Plate 9, figs. 23–27). These gradually decrease in size as they pass along the inner sides of the antennæ, at the tips of which they unite with the smaller phloem elements lying outside the filaments. As in the stem the large sieve tubes have smaller ones adjoining them on both their inner and outer faces. Where the preservation is adequate there is a row of small regular cells delimiting the stele, this probably being the endodermis. It is quite clear that the dark structureless layer figured by WILLIAMSON as such (46, *c*, Plate 9, fig. 22), and which he compares to the endodermis of *Woodwardia orientalis*, is simply the result of the collapse of the large sieve tubes, to which reference has been made above. The material examined in connection with the present paper shows every stage from the row of practically normal elements to the condition in which they are represented by a dark heavy line similar to that figured by WILLIAMSON (*cf.* Plate 9, figs. 22–27).

The stele is surrounded by a wide parenchymatous inner cortex of loose texture, the cells of which, especially in the region immediately surrounding the stele, frequently possess dark brown contents, which suggest that they contained some kind of secretory material when alive. Not uncommonly the cells of the cortical parenchyma are found to have collapsed, and in this condition they form radiating plates of tissue uniting the stele with the outer cortex. I have no doubt that this, in the majority of instances, is a *post-mortem* effect, but it is not invariably the case. The loose nature of the tissues appears to have led quite commonly to the development of radial fissures during life, and their subsequent occlusion by the development of tylosis-like outgrowths from the parenchyma bordering the cavity. A portion of a series of such fissures is shown in tangential section in Plate 10, fig. 32, in which the process of occlusion has not yet commenced, whilst Plate 9, fig. 30, shows a portion of a petiole in transverse section in which the fissures have undergone complete closure. Occasionally a happy accident has preserved for us a stage in between these extremes. Text-fig. 20 illustrates a case of this kind. It will be seen from the figure that the cortical lacuna is in process of elimination, as a result of the development of numbers of vesiculate outgrowths from the neighbouring cells, and that the whole process bears a distinct resemblance to the blockage of effete xylem elements.


TEXT-FIG. 20.—Portion of the cortex of a petiole in longitudinal section, showing partial occlusion of a cortical fissure by vesiculate outgrowths from neighbouring cells. × 300. U.C.L. Coll. K602.

The inner cortex, as has already been stated, is surrounded by a somewhat narrower zone of thick-walled cells, which are much longer and which frequently have pointed ends. Although it is probable, from analogy with recent ferns, that the thickened walls were lignified, it is a point of some interest to note that they must have retained their protoplasmic contents, since wounded specimens occur in which these cells have undergone one or two divisions in an attempt to produce a healing meristem.

Apart from the gradual loss of the sheath of periderm and its replacement by a typical epidermis, reference to which has already been made, no further change takes place in the more superficial tissues of the petiole. In the bundle itself, however, there is a progressive increase in the prominence of the antennæ, so that when fully developed the resemblance of the bundle to a double anchor (which has given the genus its name) is quite evident (Plate 9, fig. 26). It would be more apt, perhaps, to compare the appearance of the bundle in the median region of the petiole to a double pick-axe head rather than to an anchor, in the case of *Ankyropteris corrugata*, since the inward flexure of the antennæ towards the sagittal plane is relatively slight compared with that of *A. westphaliensis*. The latter species also differs in the much greater abaxial curvature of the central bar, this in our species being relatively slight. Both species resemble one another, however, in the fact that the abaxial antennæ are invariably shorter than the adaxial ones.

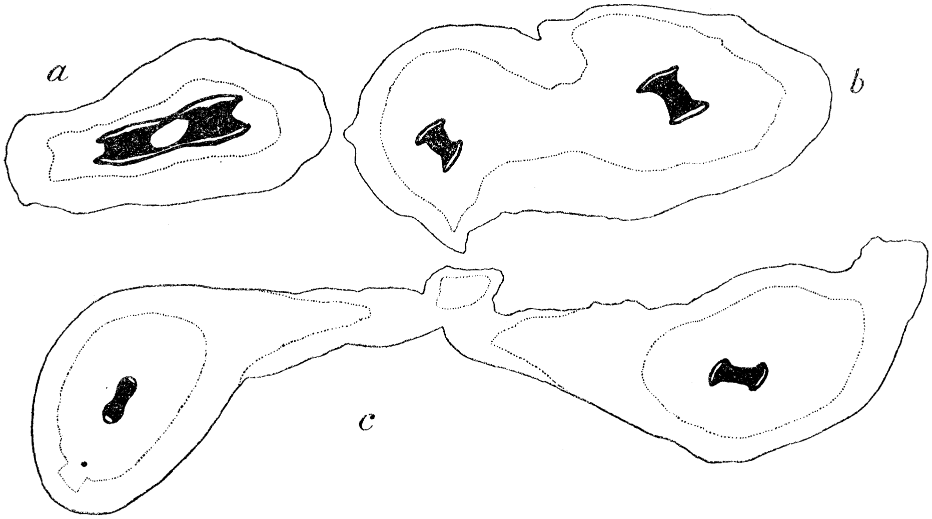
There appear to be two extreme varieties of petiolar strand, one of which has a relatively stout central bar with an abaxial curvature which is extremely slight (Plate 9, fig. 26) and with rather stumpy antennæ, whilst the other has a slenderer, more curved central bar, with sometimes longer more strongly flexed antennæ (44, fig. 8). It is possible that these variants may represent two closely related species, but in view of the large number of petioles of intermediate character which link the two extremes, this does not seem likely.

The strands also vary considerably in size, the central bar in some cases consisting of as many as from 36 to 40 tracheids in transverse section, whilst in others it may consist of as few as 8 or 9. One of the smaller forms is figured by BERTRAND (4—Plate 12, fig. 34), and Slide No. 1333 (Scott Collection) is very similar. Both this section and the one figured by BERTRAND show a peculiarity which, though not common, occurs in several instances in this species. This consists of the separation of the base of the antenna from the central bar by a thin strip of parenchyma, which thus links the phloem with the parenchyma normally isolated in the space between the antennæ and the filaments. Either the abaxial or adaxial antenna, or both, may be affected in this way. A further example from the Scott Collection is shown in fig. 27 (Plate 9).

The branching of the petiole, in strong contrast to that of allied zygopterids, is dichotomous, the bifurcation in the specimens I have seen taking place in the plane at right angles to that of the central bar. Three petioles illustrating progressive stages in dichotomy of this type are shown in text-fig. 21. Judging by the paucity of specimens showing dichotomy the branching must have been relatively infrequent.

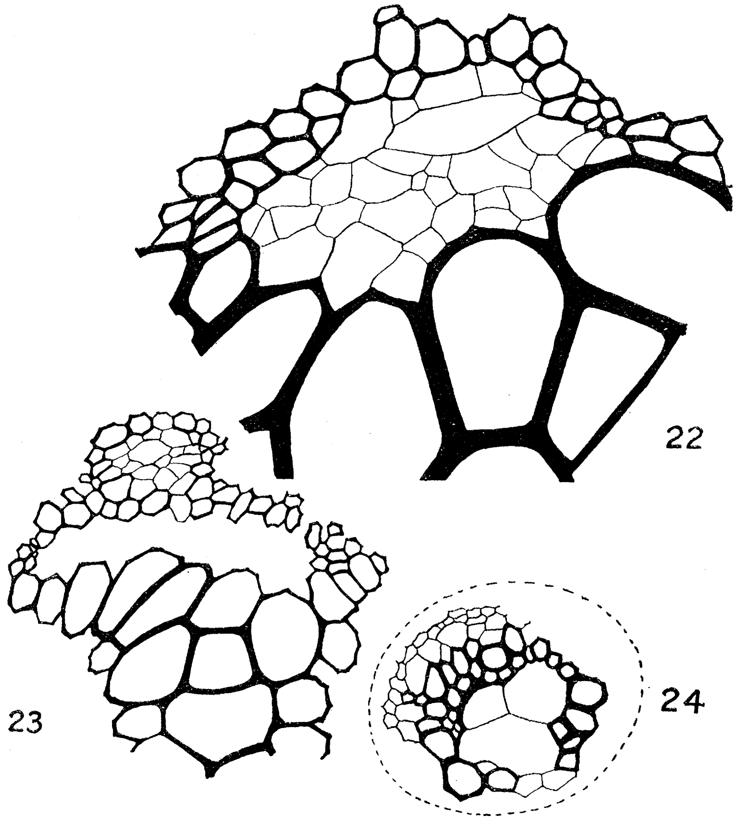
Like the stem, the petioles bear a number of stout aphlebiæ, which are developed in two series, one on either flank. Their arrangement differs from that of the majority of the zygopterids in that they are produced, so far as one can judge, alternately on the right and left sides of the petiole. Structurally they are identical with those borne on the stem.

The vascular supply of a petiolar aphlebia is initiated as a small tracheidal bulge, which arises slightly on the adaxial side of the middle line of the filament. This is nipped off as a small annular trace surrounded by a narrow sheath of phloem and, as in the corresponding traces in the stem, the xylem ring is somewhat thicker on the abaxial side (text-figs. 22–25). There is some evidence that the trace is accompanied by a small amount of protoxylem (text-fig. 25). Generally it pursues a steeply oblique course through the cortex and so into the base of the aphlebia, but in a few cases its path is almost horizontal near its point of origin, and again as it leaves the petiole, so that it has a sigmoid character. Unlike that of the stem, the petiolar aphlebia strand commonly divides in the outer cortex, this division as a general rule being dichotomous (text-fig. 26), but there are a number of instances (Plate 10, fig. 36) in which there appears to be a continuous main bundle with a lateral strand on either side. This may, of course, be due to the modification of an initially dichotomous mode of branching, but unfortunately the close seriation of sections which alone would provide conclusive evidence upon this point is lacking.

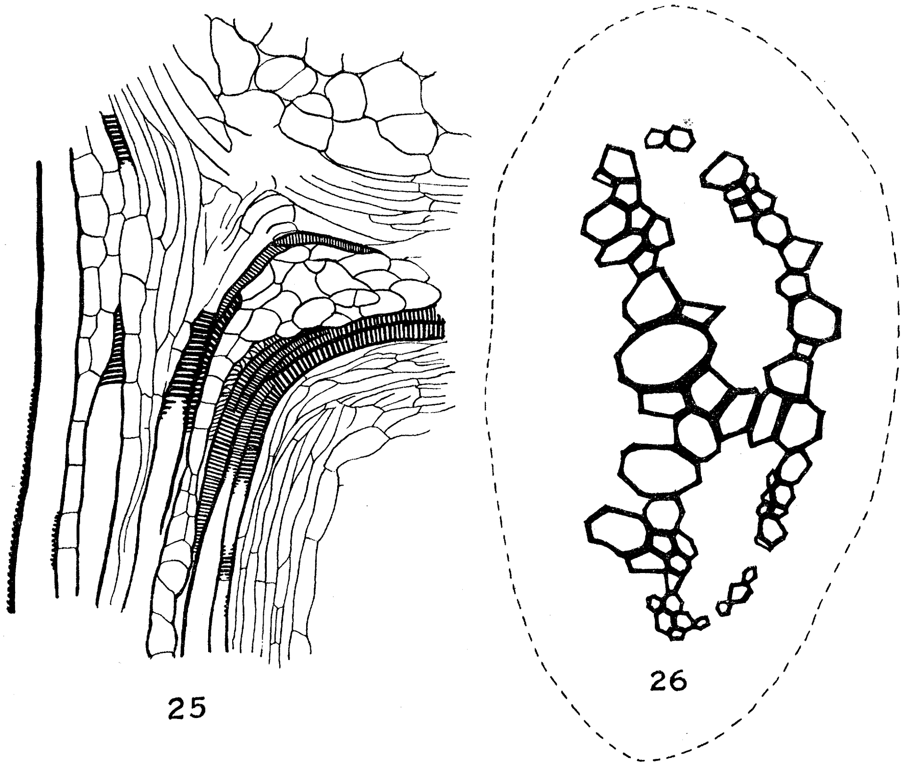


Text-fig. 21, *a*, *b*, *c*.—Successive stages in the dichotomy of the petiole. × 20. *a*, K. Coll. 2030. *b*, K. Coll. 2271. *c*, K. Coll. 2271.

The aphlebiæ themselves vary considerably in size, and the base of a particularly large one with three vascular strands is shown in Plate 9, fig. 29. The initiation of the aphlebia strand is marked by the development of a groove on the inner face of the sclerised cells of the outer cortex. This becomes progressively deeper during the passage of the aphlebia bundle through the inner cortex, and forms a parenchyma-filled trench into which the strand passes. The groove soon closes in behind the strand, which thus has a sheath of parenchyma. At the point of exit of the strand the sclerised



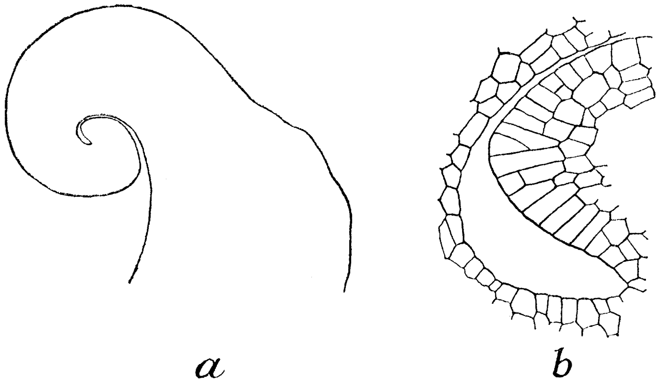
Text-figs. 22–24. 22.—Initiation of an aphlebia trace from the peripheral loop. × 480. S. Coll. 2687. 23.—Aphlebia trace completed, but still attached to the peripheral loop. × 200. S. Coll. 2730. 24.—Aphlebia trace in cortex. × 200. S. Coll. 2741.



Text-figs. 25–26. 25.—Semi-diagrammatic sketch showing the departure of an aphlebia trace in longitudinal section ; a spiral element is shown. × 225. U.C.L. Coll. K602. 26.—Xylem of a dichotomising aphlebia trace. × 450. S. Coll. 2706.

elements undergo a characteristic modification, which often results in the development of a system of intercellular spaces, and a similar modification has been noted in connection with the aphlebiæ of *Ankyropteris westphaliensis*. It is possible that this modification serves the purpose of the aërating system which BOWER (11) has shown to exist in the petioles of existing ferns, though in the absence of more detailed knowledge this suggestion must be regarded as purely tentative.

I am in full agreement with the conclusion of KIDSTON and GWYNNE-VAUGHAN (22) that there is no evidence whatever of the development of true pinna-traces in this fern. The probabilities are that the petioles were totally devoid of flattened pinnules and that, apart from the bristle-like hairs and aphlebiæ, they were quite naked. Further evidence upon this point is provided by two sets of very fine sections of the apical parts of the petiole, which are included in the Kidston and University College (London) Collections respectively. In one of the former (Kidston Collection, No. 1985) a section of the actual apex is available, this being circinately coiled, as in modern ferns (text-fig. 27, *a*). As BOWER has already shown, the tip is occupied, so far as one can judge from an isolated section, by a single apical cell (text-fig. 27, *b*).



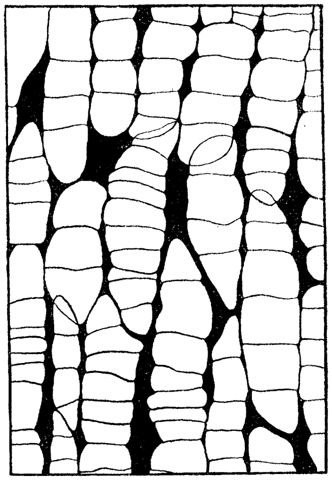
TEXT-FIG. 27, *a*, *b*. *a*.—Outline of circinately coiled apex of petiole. × 30. K. Coll. 1985. *b*.—Median section of apical meristem of petiole (after Bower). × 265. K. Coll. 1985.

Now if an apical section of the immature, still coiled, frond of a fern is examined the developing pinnæ are recognisable as a series of conical outgrowths, developing acropetally a little way behind the apical cell itself, and it is reasonable to suppose that if, in *Ankyropteris corrugata*, lateral pinnæ were present, a similar configuration would result. In actual fact there are no indications whatever of lateral structures suggesting developing pinnæ, and the coiled apex is perfectly smooth (text-fig. 27, *a*).

The remaining sections of the immature apical region of the frond are transverse, or nearly so, the Kidston specimens being cut somewhat nearer the apex than those in the University College (London) Collection. In neither case is there any evidence of the occurrence of flattened pinnæ, although in view of the delicacy of the tissues actually preserved one would have expected them to be present had they existed (Plate 10, figs. 33, 34).

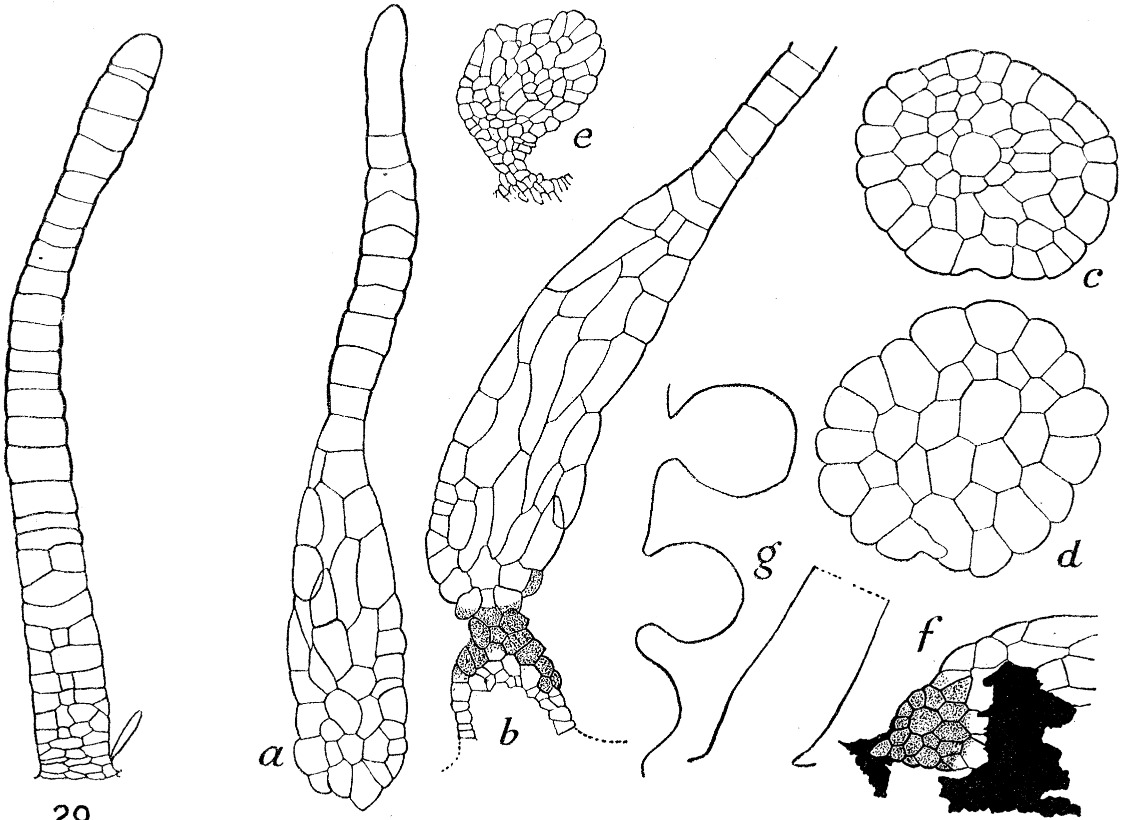
The bundle conforms in type to that of the middle of the petiole (Plate 10, fig. 31), the antennæ being well developed. Slide No. K606A (U.C.L.) is of exceptional interest, since it shows the direction of development of the xylem. Although apart from one small area the parenchyma enclosed by the filaments has collapsed, leaving a cavity, the outer margin in each case is fringed by lignified tracheids, among which spiral protoxylem elements can be detected. The tracheids constituting the antennæ and the central bar, on the other hand, consist of immature, relatively thin-walled elements, so that differentiation was evidently from without inwards (Plate 10, fig. 31), a feature which SCOTT (38) has shown to be characteristic of Botrychioxylon also.

The cortex consists of homogeneous parenchyma, the cells of which are arranged in radial series, and a companion section (Slide No. K606B, U.C.L.) reveals the fact that these cells are still meristematic and form small spindle-shaped groups, the ends of which dovetail into one another (text-fig. 28). The epidermis itself consists of small regular cells, but is remarkable for the development of large numbers of hairs of a most peculiar and specialised type. Those present in the Kidston slides (text-fig. 29) are smaller and less highly differentiated than those of the University College specimens (text-fig. 30), but in both the hairs consist of a long finger-shaped multicellular lower portion, the apex of which bears a stout pointed portion consisting for the greater part of its length of a single row of large cells. These last are identical in character with those composing the stout hairs occurring on the stem and lower parts of the petiole. The base, in the somewhat older University College specimen, is relatively much longer, and consists of a proximal part composed of very small cells (text-fig. 30, *c*), and a distal portion composed of larger somewhat more irregular ones (text-fig. 30, *d*). It seems probable that the explanation of the difference between the two specimens lies in the fact that in the one case we are dealing with fully developed examples whilst in the other they are immature. In both they form a dense thatch, the apical parts of the lower ones overlapping the bases of those higher up the petiole (Plate 10, fig. 35). In addition to the specialised hairs the Kidston specimen has an investment of what are undoubtedly rather flattened aphlebiæ, which appear to have functioned in the manner of bud scales, and which bore upon their basal parts a felted mass of fine branching hairs identical in type with those occurring on the aphlebiæ at lower levels (Plate 10, fig. 34, and text-fig. 31, *a–d*).



TEXT-FIG. 28. — Tangential section of actively growing cortex of young petiole. × 450. U.C.L. Coll. K606B.

No reference has been made to sporangia, since, although examples showing the usual zygopterid characters frequently occur associated more or less closely with the various parts of our plant, in no case have these been discovered in actual organic connection. Apart from the reproductive organs, however, we are now in a position to obtain a good



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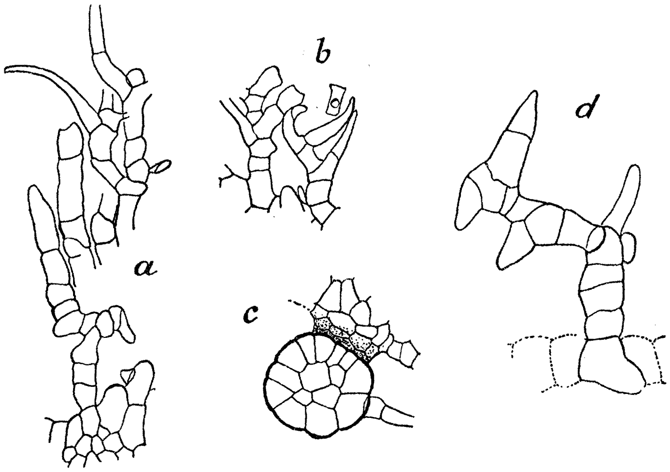
Text-figs. 29, 30, *a–g*. 29.—Immature stout hair from apical part of petiole. × 400. K. Coll. 1983. 30, *a–g*.—Various sections of similar mature hairs : *a* and *b* are longitudinal sections, *c* is a transverse section near the base, *d* is a similar section nearer the middle, *e* and *f* are superficial sections, *g* is a diagram showing region of attachment to petiole. *a–f* × 400. *g* × 200. U.C.L. Coll. K606B.



Text-figs. 31, *a–d*.—Fine branching hairs from aphlebiæ. *a* and *c*.—K. Coll. 1893. *b*.—K. Coll. 1895 (all × 320). *d*, × 450. U.C.L. Coll. K602. *c* shows the base of a stout hair with a fine hair growing from it.

general idea of the appearance of *Ankyropteris corrugata* as it lived and grew. The stem branched dichotomously at infrequent intervals, and the fact that it bore both aphlebiæ and hairs superficially strongly suggests that it was aerial rather than subterranean, whilst the large size of the petioles and their distichous arrangement indicate that it was prostrate, a view which receives some support from the parenchymatous nature of its cortex and from the irregular direction of growth of the roots. The petioles themselves were devoid of pinnæ and bore two rows of aphlebiæ, one on either side, in addition to stiff scattered hairs which were generally distributed. They branched dichotomously, and their circinately coiled apices and the parts immediately below were protected by a dense covering of large stout hairs, whilst the actual tips were hooded over and enclosed by a system of aphlebiæ.

The whole plant must therefore have differed widely in externals from any existing fern, though its peculiarities appear to have been shared, in some measure at least, by a number of its contemporaries, very few of which have yielded evidence of the possession of the delicate expanded pinnæ which characterise most modern Filicineæ.

The Aphlebiæ.—Whilst the present investigation has shown that, in *Ankyropteris corrugata* at least, the function of the aphlebiæ was largely a protective one, it has only served to render their precise homologies more obscure. They were originally interpreted by RENAULT (30) and by STENZEL (42) as reduced leaves, but a fuller knowledge of their distribution has rendered this view untenable, and more recently BERTRAND (4) has suggested that they were equivalent to secondary petioles (*i.e.*, pinna traces). SCOTT (37), whilst tentatively accepting this interpretation, points out that their vascular system, consisting as it does of a number of strands, differs from that of the normal pinnæ, which was monodesmic. It should be noted, however, in this connection that our present knowledge indicates that the pinna did not develop a flat lamina, and that as a consequence a monodesmic strand would meet its requirements, whilst in the flattened scale-like aphlebiæ the initially monodesmic strand may readily be conceived to have branched in response to a need for a wider distribution of vascular tissue. The occurrence of aphlebiæ in *Ankyropteris Grayi* on the stem, as well as the leaf bases, is a further point of difficulty, which SCOTT (37) meets by suggesting that they have "spread downwards on to the stem" from the leaf bases.

A survey of their distribution in the zygopterids as a whole, however, renders acceptance of BERTRAND's view difficult. Within the genus Ankyropteris itself we have considerable variation. Thus in *A. Grayi*, and apparently in the closely allied *A. scandens* (42), those associated with the petiole traces were borne in four series, two from each peripheral loop, whilst others were stem-borne. In *A. corrugata*, on the other hand, they appear to have been borne commonly upon the stem without relation to those developing in connection with the petiole traces. In the latter they were in two series, produced alternately from the filaments of the right and left sides of the trace. Finally in *A. westphaliensis*, in which the stem is unknown, the only aphlebia traces which I have observed are, like the ones diagrammatically figured by BERTRAND (4), given off from the secondary petiole itself.

We may summarise their distribution in the remaining genera in which they are recorded as follows :—

Clepsydropsis australis.—Apparently absent from the stem, arising "at fairly long intervals, from the decurrent leaf-bases and from the proximal parts of the petiole, in two alternating rows" (35).

Botrychioxylon paradoxum.—Present both on the stem and the petiole traces (38).

Asterochlaena laxa.—Absent from the stem, given off in two series from the petiole traces (5).

Diplolabis Romeri.—Absent from the stem and primary petiole trace, given off from the margins of the tertiary traces (17).

Metaclepsydropsis duplex.—As in Diplolabis Romeri (18).

Stauropteris oldhamia.—Stem unknown, given off from the secondary, tertiary and quaternary traces (4).

From the foregoing summary it will be seen that within the group the aphlebia traces exhibit a wide variation as to source of origin, ranging from stem to ultimate pinnule traces, and from general to localised distribution. Both source of origin and type of distribution serve to render any attempt to determine their homologies peculiarly difficult, if not impossible. In the present state of our knowledge it seems soundest to record the facts, and to defer interpretation until these facts are more numerous and capable of closer co-ordination.

Affinities.—*Ankyropteris corrugata* exhibits obvious affinities with the remaining plants comprising the zygopterid alliance, sharing with them the stem stele, differentiated into peripheral and central regions, and the monodesmic bipolar petiole trace, with its characteristic type of symmetry and its protostelic method of departure. Within that alliance the correctness of its assignation to the genus Ankyropteris is, I think, undoubted. The structure of the petiolar stele, with its abaxially curved central bar and its abaxial and adaxial antennæ linked by a permanently closed filament of smaller tracheids (39, 41, 46), is in close agreement with that of the remaining species of the genus, the differences being merely differences of proportion. The stelar structure, with its core of mixed tracheids and parenchyma, is also shared by those members of the genus in which the stem has been preserved, though it should be noted that this feature is one which is also common to a number of zygopterid genera (*e.g.*, Asterochlaena, Botrychioxylon, Clepsydropsis and Metaclepsydropsis). In habit it evidently differed widely from the type illustrated by *Ankyropteris Grayi* and *A. scandens,* since these were radially organised plants with a crowded petiole insertion, showing a two-fifths divergence, whilst *A. corrugata,* though not possessing long internodes, exhibited bilateral symmetry with a distichous petiole insertion. Similar differences of habit are not, however, infrequent among existing ferns, and a remarkably close parallel to the condition obtaining in the species of Ankyropteris has been recently illustrated by BOWER (11) for Dryopteris, in which *D. Filix-mas* illustrates the type of habit characterising *Ankyropteris Grayi,* whilst *Dryopteris Linneana* shows the prostrate dichotomising axis and distichous petiolar arrangement of *Ankyropteris corrugata.* A deeper-seated difference appears to exist, however, in the mode of branching of the petiole, which is dichotomous in *A. corrugata* whilst it is monopodial in *A. westphaliensis,* the only other species in which we have any knowledge of the secondary rachis. The branching is also monopodial in the case of the closely allied genus Clepsydropsis (35). It may be noted in passing that in the dichotomous method of branching of its petiole, *Ankyropteris corrugata* cuts across the suggested division of the Zygopterideæ into biseriate and quadriseriate groups.

A further difference from both *A. Grayi* and *A. scandens* lies in the nature of the branching of the axis. In *A. corrugata* this, as has already been stated, takes the form of relatively infrequent dichotomies, which do not appear to bear any relation to the insertion of the leaves, whilst in the other two species the branching is axillary. If BOWER's view as to the primitiveness of dichotomy within the Filicales is accepted (10, 11), then *A. corrugata* has retained the primitive method of branching, both in petiole and axis, accompanied by a loss of radial organisation, whilst the remaining species have retained the radial organisation of the axis but have evolved a more advanced type of branching. It may be noted in this connection that *Clepsydropsis australis,* with which Ankyropteris has much in common, has retained an upright radial type of organisation, accompanied by a repeatedly dichotomising axis and an absence of axillary branches (35). It seems certain that, whatever the primitive mode of stem-branching in the ferns may have been, axillary branching was evolved at an early period in their phyletic history, and has, in fact, been considered by LANG (26) to be a primary feature of the organisation of the Ophioglossaceæ, a group showing a considerable number of structural similarities to the Zygopterideæ. LANG, indeed, appears to regard the case for the primitiveness of axillary branching in ferns as stronger than that for dichotomy (27).

Our views as to the relative primitiveness of these two forms of branching must obviously affect our interpretation of the structure of the petiole trace in *Ankyropteris corrugata.* There can be little doubt that this strand is wholly homologous with what SCOTT (37) has termed the " common trace " of *A. Grayi.* It has the same general form, and shares with it both a median and polar groups of protoxylem. Whilst, however, in *A. Grayi* the central protoxylem, with the adjacent metaxylem tracheids surrounding it, becomes detached as the stele of the axillary branch, that of *A. corrugata* dwindles and disappears. If we regard axillary branching as the derived condition, then the median protoxylem of the petiole trace in *A. corrugata* represents its rudimentary expression, whilst if, on the other hand, we consider that the zygopterids were primitively monopodial in construction, then the median protoxylem in our species can only be regarded as vestigial.

It is possible that the third protoxylem, termed by BERTRAND the "pôle résiduel," which is recorded by him as occurring in the Fribourg specimen of *Asterochlaena laxa* (6), and which lies between the two xylem poles destined for the petiole trace, may also be significant in this connection. It is regarded by BERTRAND—theoretically, at any rate—as the source of the corresponding foliar trace at a higher level, the original connection having been obliterated by the subsequent development of the metaxylem. It may, however, represent the inception, or last vestige, of an axillary branch.

With regard to the evolution of the type of stem stele characteristic both of Ankyropteris and many other zygopterids, two diametrically opposed views have been put forward. The one most generally accepted (11, 22, 39, 44) regards the stelar archetype as consisting of a homogeneous protostele with immersed protoxylem groups, from which the forms possessing a continuous sheath of relatively large tracheids enclosing a core of mixed tracheids and parenchyma have evolved. BERTRAND (6, 8), on the other hand, has suggested that the evolutionary sequence is one in which, starting with a stellate form possessing a differentiated central portion, or even with a number of separate steles grouped in a stellate manner, a system of condensation and simplification has occurred, this producing a homogeneous cylindrical stele as its final term.

The absence of juvenile stages of the fossil types unfortunately deprives us of any ontogenetic clue as to developmental sequence, but if the collateral evidence yielded by the young stages of the Ophioglossaceæ and other ferns be admitted, the traditional view is decidedly strengthened. It seems probable that BERTRAND was influenced, in part at any rate, by the occurrence in strata as early as the Devonian of Asteropteris, with its elaborately stellate contour, and by his view (since abandoned) that Clepsydropsis was the petiole of Cladoxylon (5, 8).

One point, which has apparently received scant attention in considering the development of intrastelar parenchyma, is that in the petiole trace of certain genera the development of inclusions of thin-walled tissue at the poles of the trace preceded the development of the "mixed pith." Such polar inclusions are present in the case of Asteropteris, and, judging by the somewhat ill-preserved sections available, in the imperfectly known *Zygopteris Kidstoni* also (Plate 10, fig. 37). They can therefore hardly be regarded as due to an extension of the axial parenchyma into the petiole trace, and where the two are continuous, as in Ankyropteris, this must be interpreted as a later evolutionary feature. It may be, as BERTRAND and others (8) have suggested, that the petiole represents a specialised type of axis derived originally from a stem branch—that is, that it is the bipolar equivalent of a multipolar and radially symmetrical stem. Its parenchymatous inclusions could then be interpreted as precociously developed features, homologous with the axial "mixed pith;" but this can be nothing more than an interesting speculation.

Whilst it seems clear that a group of ferns such as the Zygopterideæ are derived from a common stock, and whilst we can indicate tentatively the primitive structural features of any given genus, it is becoming increasingly unfashionable to attempt to draw up phylogenetic schemes indicating the exact relationships of the various genera and species within the group. This seems largely due to a recognition of the fact that the rate of evolution of the different structural units (features, biocharacters) (43) within the group varies from genus to genus, so that a relatively advanced type of petiole may be associated with a relatively primitive axis, and *vice-versa* (*cf.* 39, p. 309). It appears more logical to consider that stem, petiole and root exhibit a number of characteristic evolutionary tendencies or potentialities, the rate of progress towards the highest expression of each such tendency in any one genus being more or less independent of the remainder (3, 23, 24, 43). In the zygopterid stem the chief structural tendencies are towards medullation, though a wholly parenchymatous pith is never realised, and towards a stellate stelar outline. In addition there is a tendency, expressed sporadically in a few genera and only becoming well marked in Botrychioxylon, towards the development of secondary wood. The available evidence seems to indicate also that the ancestral mode of branching was by dichotomy, with an early adoption of the monopodial habit in some cases.

Our knowledge of the structure of the various petioles is more complete, and their seriation has been attempted with a fair measure of success by KIDSTON and GWYNNE-VAUGHAN (22). The ovoid bipolar trace has strong claims to be regarded as the ancestral type. Probably it too was originally dichotomous in its mode of branching, and, becoming monopodial, gave rise to the biseriate clepsydroid series, on the one hand, and the quadriseriate dineuroid series on the other. The permanently closed filaments of the biseriate forms, enclosing parenchyma throughout which the protoxylem is distributed in small groups, appear to be less specialised than the quadriseriate forms with their more modified secondary and tertiary traces, and their more strictly localised protoxylem groups.

Beyond these general statements, in the present state of our knowledge, it seems to the writer unwise to go, since though the continued study of fossil plants is giving us a clearer conception of their anatomy and its peculiarities, many gaps still remain to be bridged by further research.

Summary.

1. *Ankyropteris corrugata* was a small fern with, probably, a prostrate habit.
2. Its stem, which is protected by hard-textured scales (aphlebiæ), branches dichotomously, the branches having no apparent relation to the leaf-insertion.
3. The petioles show a distichous arrangement and are borne at short intervals.
4. They also branch dichotomously, and bear aphlebiæ in two alternating series.
5. There is no evidence that they bore expanded pinnæ similar to those of modern ferns.
6. The young apices of the petioles are coiled, as in existing ferns, and are enclosed and protected by an overlapping system of aphlebiæ.

7. Both stem and petiole bear stout, probably hispid, hairs, a specially modified type of these being abundant in the apical region.

8. The bases of the aphlebiæ are covered by a close felt of delicate branching hairs.

9. The roots are borne mainly on the stem, though some are attached to the petiole traces near their origin. Their branching is monopodial.

10. The centre of the stem is occupied by a single cylindrical stele, composed of a core of small tracheids and parenchyma, towards the periphery of which the protoxylem is situated. This is surrounded by a homogeneous sheath of larger tracheids, which in turn is enclosed by phloem and phloem-parenchyma.

11. The cortex is mainly parenchymatous and its sub-epidermal layers produce a thin periderm.

12. The petiole trace, the giving off of which does not disturb the continuity of the stelar tissues of the stem, is triangular in transverse section with rounded angles.

13. It contains three main groups of parenchyma, one median and two lateral, continuous with that in the centre of the stem. The petiolar protoxylem groups are situated in these.

14. The median group of parenchyma and its associated protoxylem dwindle and disappear, but the lateral groups are persistent.

15. The petiole trace rapidly loses its angular contour and becomes ovoid, at the same time developing a slight but distinct abaxial curvature.

16. The poles flatten and the first indications of the development of the antennæ are evident before the petiole trace leaves the stem cortex.

17. The stem cortex becomes modified, forming an arc of sclerenchyma on the abaxial side of the outgoing petiole trace, and later, by the incurving and fusion of the free margins behind the trace, forms the sclerised outer cortex of the petiole.

18. The antennæ become more strongly developed in the free petiole, the adaxial ones being longer than the abaxial ones. They are linked by a permanently closed filament of small tracheids.

19. The aphlebia traces are annular, and are nipped off from the outer margin of the stem stele, or, in the petiole, from the filament. They may bifurcate or divide into three before the aphlebia becomes free.

20. The roots are diarch with a stele of osmundaceous type. When young they are surrounded by a parenchymatous cortex, the middle region of which consists of radiating plates of tissue separated by large intercellular spaces.

21. In older roots a superficial periderm is developed and the structure of the middle cortex is modified, owing to the disruption of the plates by the development of vesiculate outgrowths.

22. Many of the roots show secondary thickening.

23. Secondary thickening also occurs sporadically in the stem and in the petiole. In the latter it is traumatic and may be due to wounding in the stem also.

24. *Ankyropteris corrugata* is considered to be a relatively primitive species of the genus to which it belongs.

I am much indebted to Dr. A. Smith Woodward, F.R.S., Dr. F. Bather, F.R.S., and Dr. W. D. Lang, successively Keepers of the Department of Geology, British Museum (Natural History), for facilities for studying the material in the Williamson and Scott Collections ; to Prof. M. Drummond, of Glasgow University, for similar facilities in the case of the Kidston Collection ; and to Prof. F. W. Oliver, F.R.S., and Prof. F. E. Weiss, F.R.S., for the loan of slides from the collections of which they have charge. To my friends, Mr. W. N. Edwards, of the British Museum, and Dr. S. Williams, of Glasgow University, I am specially grateful for innumerable kindnesses during the course of the investigation.

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Explanation of Plates 7–10.

All the figures are from untouched negatives. Figures 1, 21, 22, and 27 are from negatives by Mr. L. A. Boodle: Figure 36 is from a negative by Dr. S. Williams, Glasgow. Examination with a hand lens will be found helpful in many cases.

Plate 7.

Fig. 1.—Transverse section of stem stele through an internode. Note small calibre of central tracheids and aphlebia traces at *aph.* and *aph.* 1. × 30. Will. Coll. 264.

Fig. 2.—Transverse section of stem stele through an internode. Note relatively large calibre of central tracheids compared with those in fig. 1. Phloem is shown on left. An early stage in emission of a petiole trace is shown at bottom of figure. × 40. U.C.N. Coll. 345.5.

Fig. 3.—Longitudinal section of a stem stele just below a dichotomy, showing short irregular tracheids with reticulate thickening. × 20. S. Coll. 2692.

Fig. 4.—Transverse section of part of stem stele, showing well developed cambium on right. × 40. U.C.N. Coll. 442.23.

Fig. 5.—Transverse section of a stem stele, showing a zone of secondary tissue at upper end. Note thinning of primary xylem below this. × 40. S. Coll. 2715.

Fig. 6.—Transverse section of a stem stele, showing initiation of a petiole trace at upper end. Note aphlebia trace to right. × 30. U.C.N. Coll. 345.20.

Fig. 7.—A similar section, showing a stele in which initiation of tracheidal bridge is delayed. Note root at bottom to right. × 16. U.C.N. Coll. 345.5.

Fig. 8.—Later stage in emission of petiole trace. Note three protoxylem groups. × 30. U.C.N. Coll. 345.14.

Fig. 9.—Longitudinal section, showing U and V-shaped tracheids at junction of stem and petiole. × 40. S. Coll. 2692.

PLATE 8.

FIG. 10.—Transverse section of petiole trace just free from stem stele. Note triangular outline and general similarity to that of *Ankyropteris Grayi*. × 40. M.U. Coll. R448.

FIG. 11.—Transverse section of petiole trace a little way out in the stem cortex. Note irregular distribution of intrastelar parenchyma and slight abaxial curvature. × 20. U.C.N. Coll. 261.69.

FIG. 12.—Transverse section of stem and petiole trace. × 15. U.C.N. Coll. 345.18.

FIG. 13.—Transverse section of the petiole trace shown in fig. 12. Note elimination of median protoxylem group and small tracheids of the peripheral loops. × 40. U.C.N. Coll. 345.18.

FIG. 14.—Transverse section of a large stem, showing the emission of two stout roots. × 15. U.C.N. Coll. 261.69.

FIG. 15.—Longitudinal section, showing union of stem and root. The characteristic tracheids in region of union are well shown. × 40. U.C.L. Coll. K610.

FIG. 16. Transverse section of a young root, to show lacunar middle cortex. × 100. S. Coll. 2687.

FIG. 17.—Transverse section of a slightly older root, showing development of vesiculate outgrowths in middle cortex. × 100. S. Coll. 2725.

FIG. 18, *a*.—Transverse section of an old root, showing superficial periderm, modified middle cortex, and secondary xylem. × 60. U.C.N. Coll. 261.74.

FIG. 18, *b*.—Transverse section of stele of an old root, to show type of pitting in secondary xylem. × 80. U.C.N. Coll.

FIG. 19.—Transverse section of an aphlebia, showing investment of fine branching hairs and, to left, hairs of stouter type. × 50. K. Coll. 1985.

FIG. 20.—Transverse section of a winged aphlebia. × 30. U.C.L. Coll K603a.

PLATE 9.

FIG. 21.—Transverse section of stem and petiole trace, showing the arc of sclerenchyma developed behind outgoing petiole trace. A root is seen to right. × 10. S. Coll. 2725.

FIG. 22.—Transverse section of a petiole trace just losing its triangular outline. The three protoxylem groups are well shown, also large sieve tubes on lower side of trace. × 50. Will. Coll. 252.

FIG. 23.—Transverse section of petiole trace (stout type), showing its appearance at base of petiole. The antennæ are now evident, the stronger adaxial ones being to right of figure. Note dark line produced on either side of central bar by collapse of sieve tubes. × 40. U.C.N. Coll. 442.9.

FIG. 24.—Transverse section of a petiole trace at a slightly higher level. Abaxial curvature is well shown. Note collapsed sieve tubes, as in last figure. × 30. U.C.L. Coll. K600.

FIG. 25.—Transverse section of a similar petiole to that shown in fig. 24. Large sieve tubes flanking central bar are clearly shown. Note also tyloses filling tracheids. × 40. K. Coll. 1672.

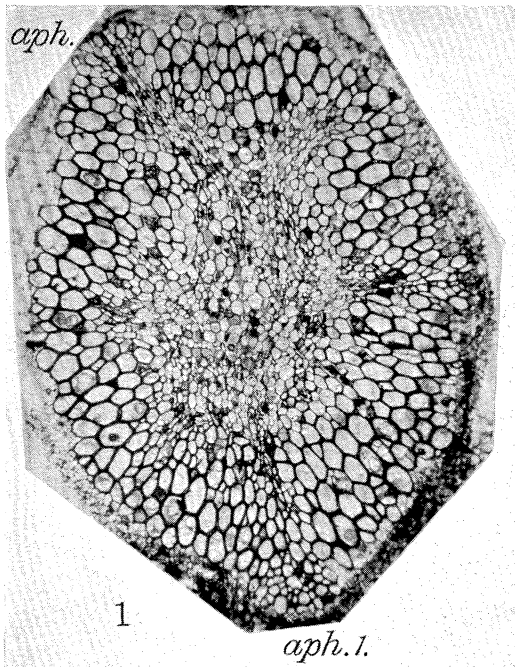
FIG. 26.—Transverse section of fully developed petiole trace (stout type). × 40. U.C.N. Coll. 261.1

FIG. 27.—Transverse section of petiole trace (slender type) showing discontinuity between xylem of central bar and that of right adaxial antenna. × 30. S. Coll. 2729.

FIG. 28, *a*, 28, *b*.—Transverse sections of petiole traces of unusual stout ovoid type, recalling petiole trace of Dineuron. In fig. 28, *a*, the central protoxylem is still present, but has disappeared in fig. 28, *b*. Both × 30. Fig. 28, *a*. U.C.N. Coll. 345.A2. Fig. 28, *b*. U.C.N. Coll. 261.50.

FIG. 29. Transverse section of base of stout aphlebia with three vascular bundles. × 100. K. Coll. 1984.

FIG. 30.—Transverse section of part of cortex of petiole showing complete occlusion of fissures. × 100. U.C.N. Coll.



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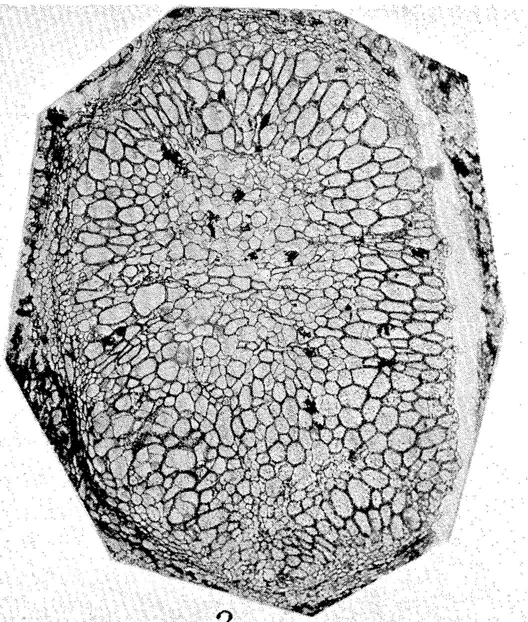

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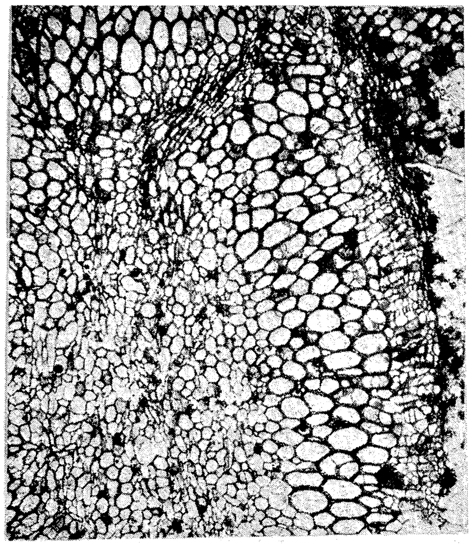

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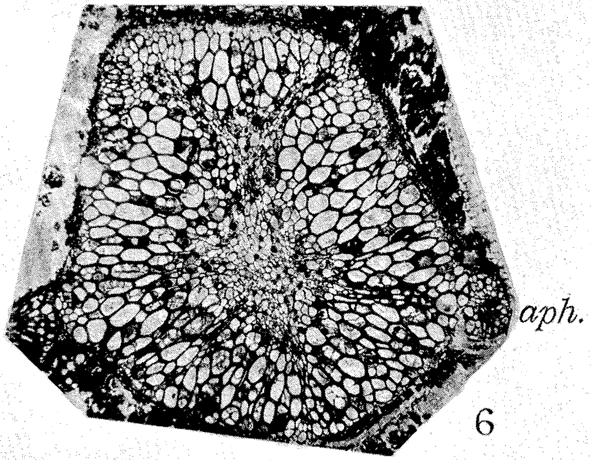

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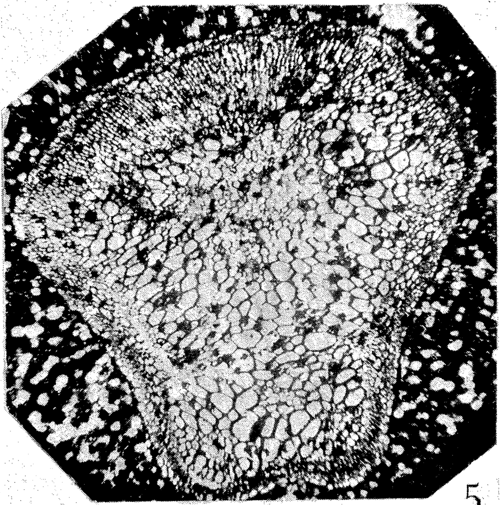

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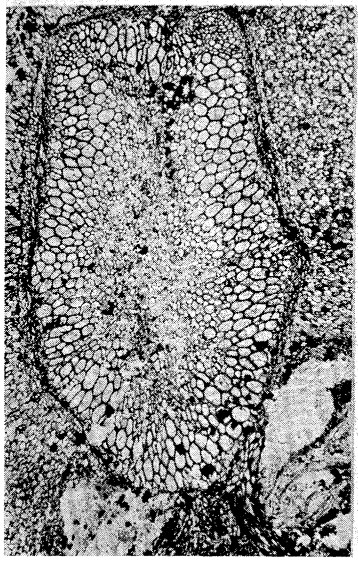

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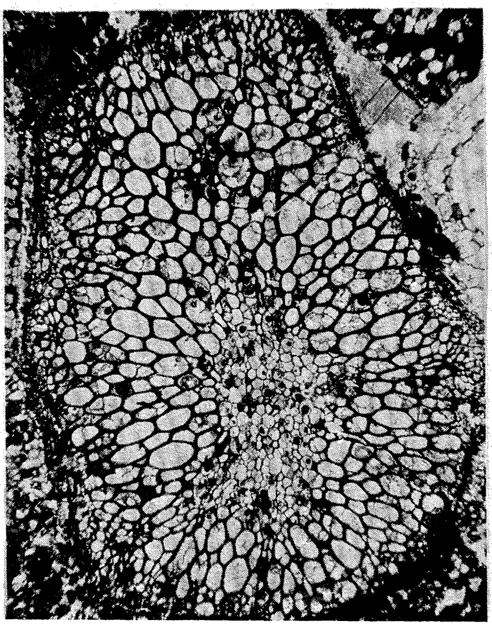

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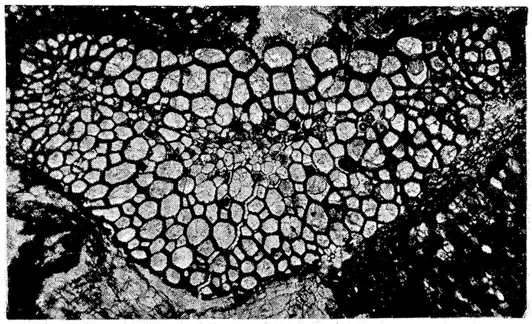
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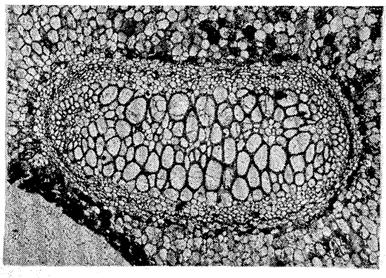
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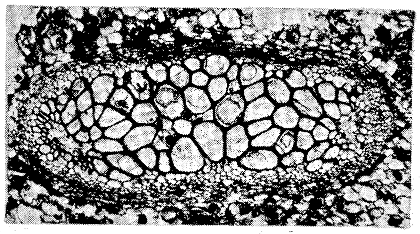
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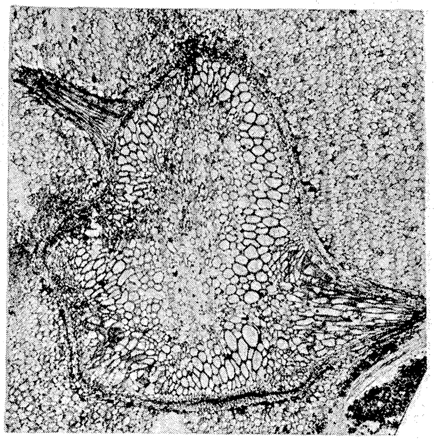
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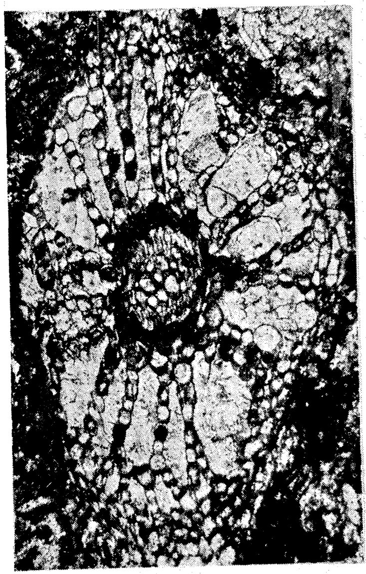
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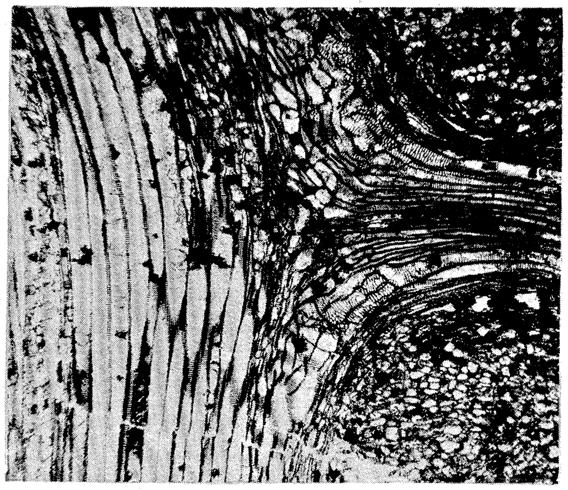
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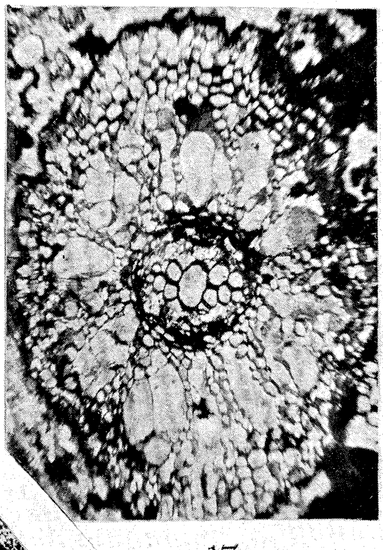
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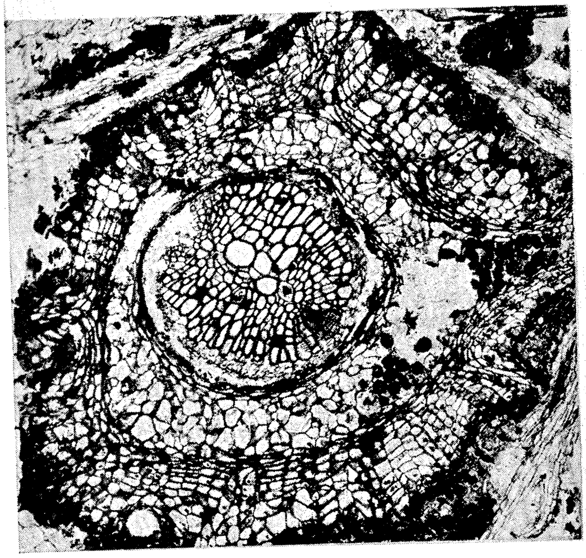
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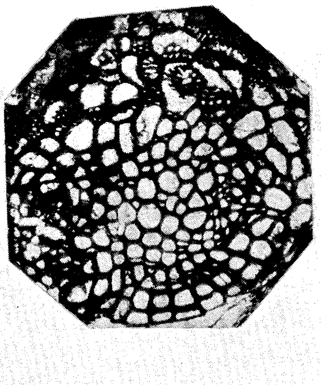
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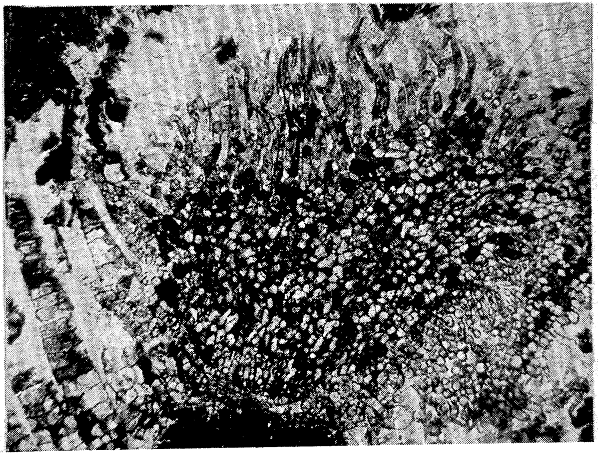
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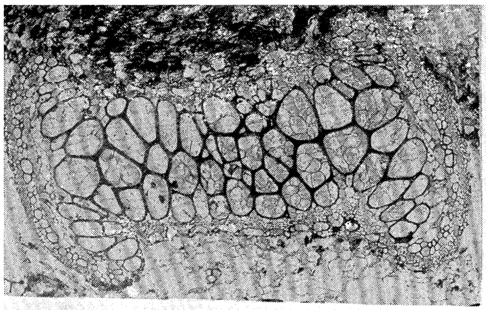

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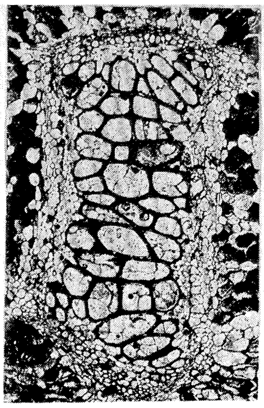

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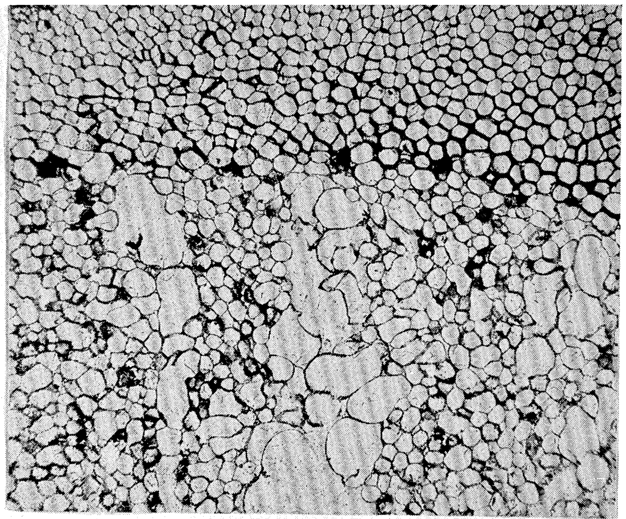

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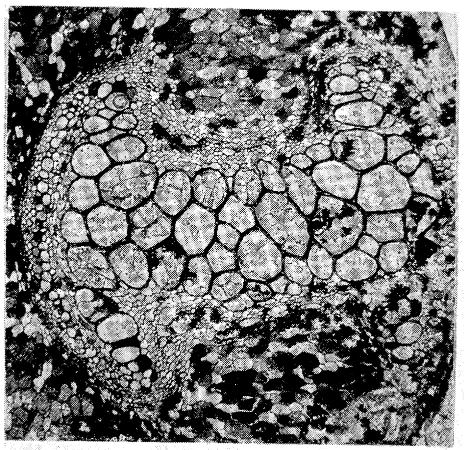

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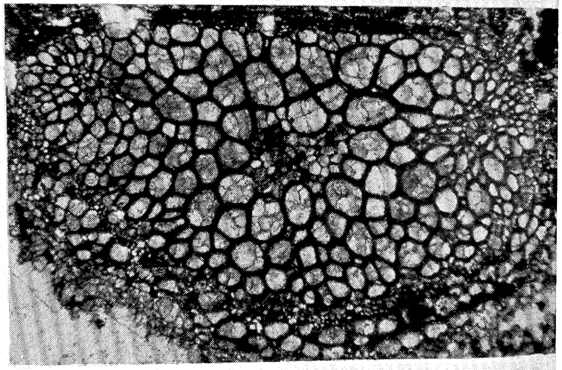

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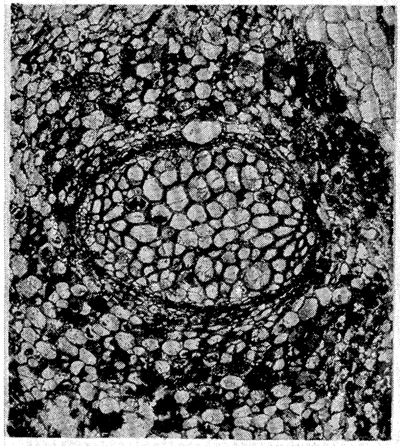

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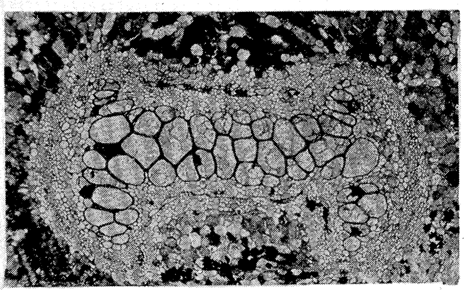

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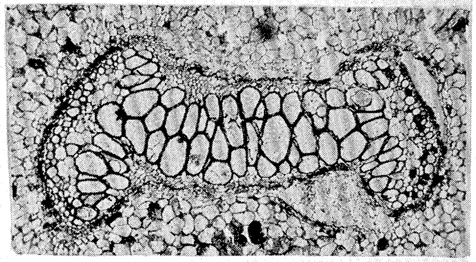

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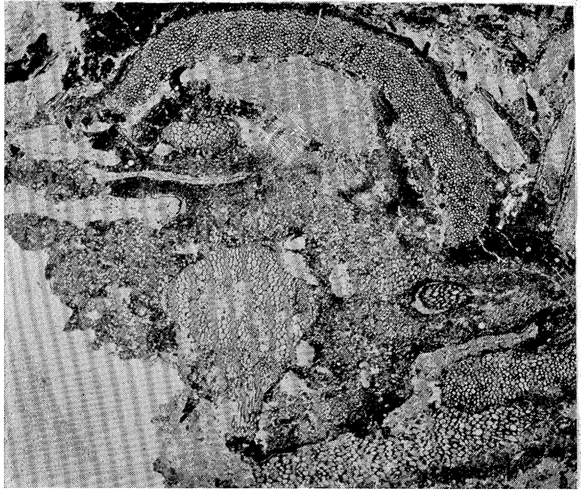

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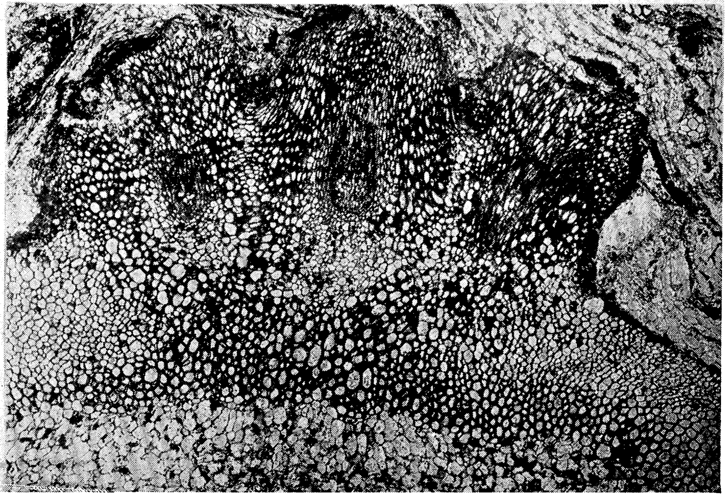

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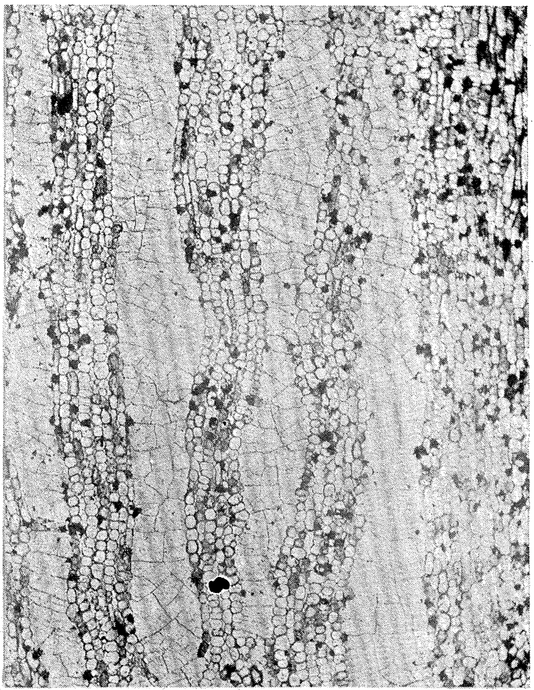

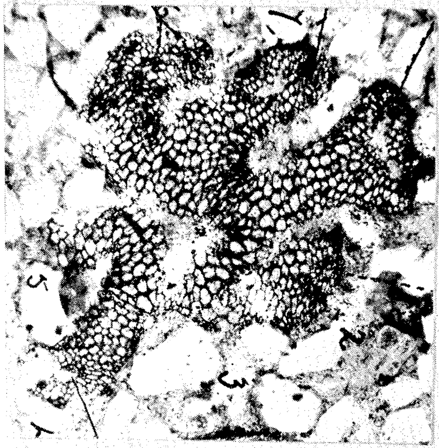

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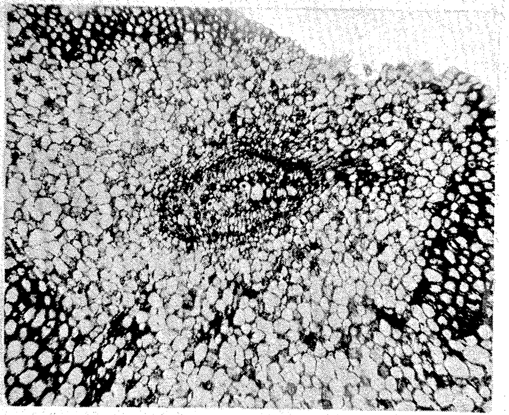
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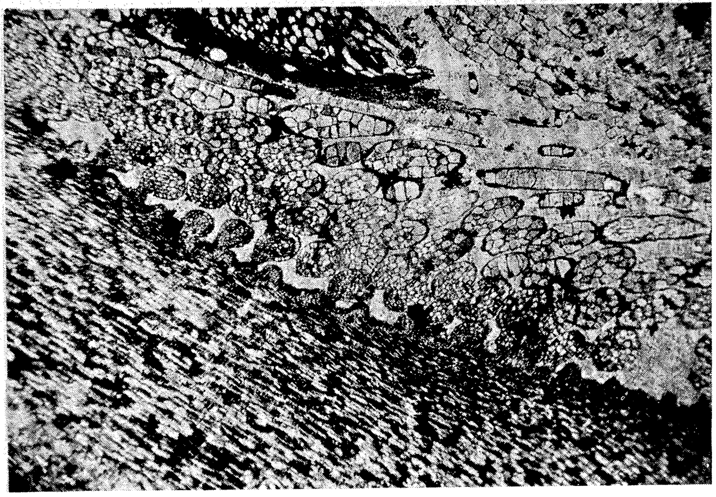


PLATE 10.

FIG. 31.—Transverse section of young petiole. The large sieve tubes flanking the immature central bar are well shown. Note also radial arrangement of wholly parenchymatous cortical cells. × 60. U.C.L. Coll. K606a.

FIG. 32.—Tangential section through cortex of a petiole, showing radial fissures in cortex. × 100. K. Coll. 1453.

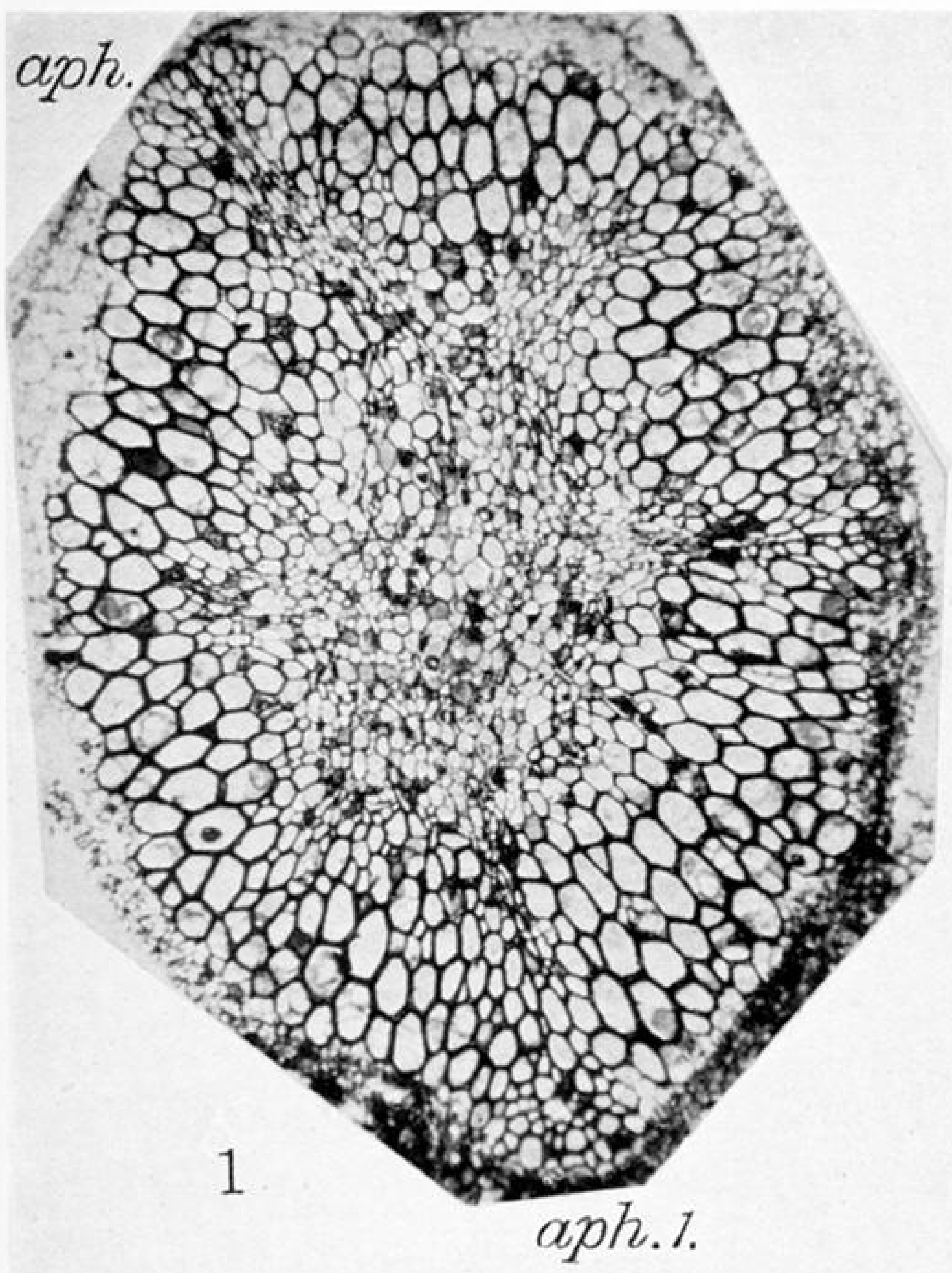
FIG. 33.—Transverse section of young petiole, showing investment of stout hairs. × 30. K. Coll. 1985.

FIG. 34.—Transverse section of a similar petiole, showing both stout hairs and investment of aphlebiæ. × 30. K. Coll. 1982.

FIG. 35.—Part of a longitudinal section through young petiole, showing mature condition of stout hairs, which are cut in various planes. × 60. U.C.L. Coll. K606b.

FIG. 36.—An aphlebia trace with its parenchymatous sheath passing through outer cortex of petiole × 100. U.C.N. Coll. 261.91.

FIG. 37.—Transverse section of stem of *Zygopteris Kidstoni*. K. Coll. 719b.



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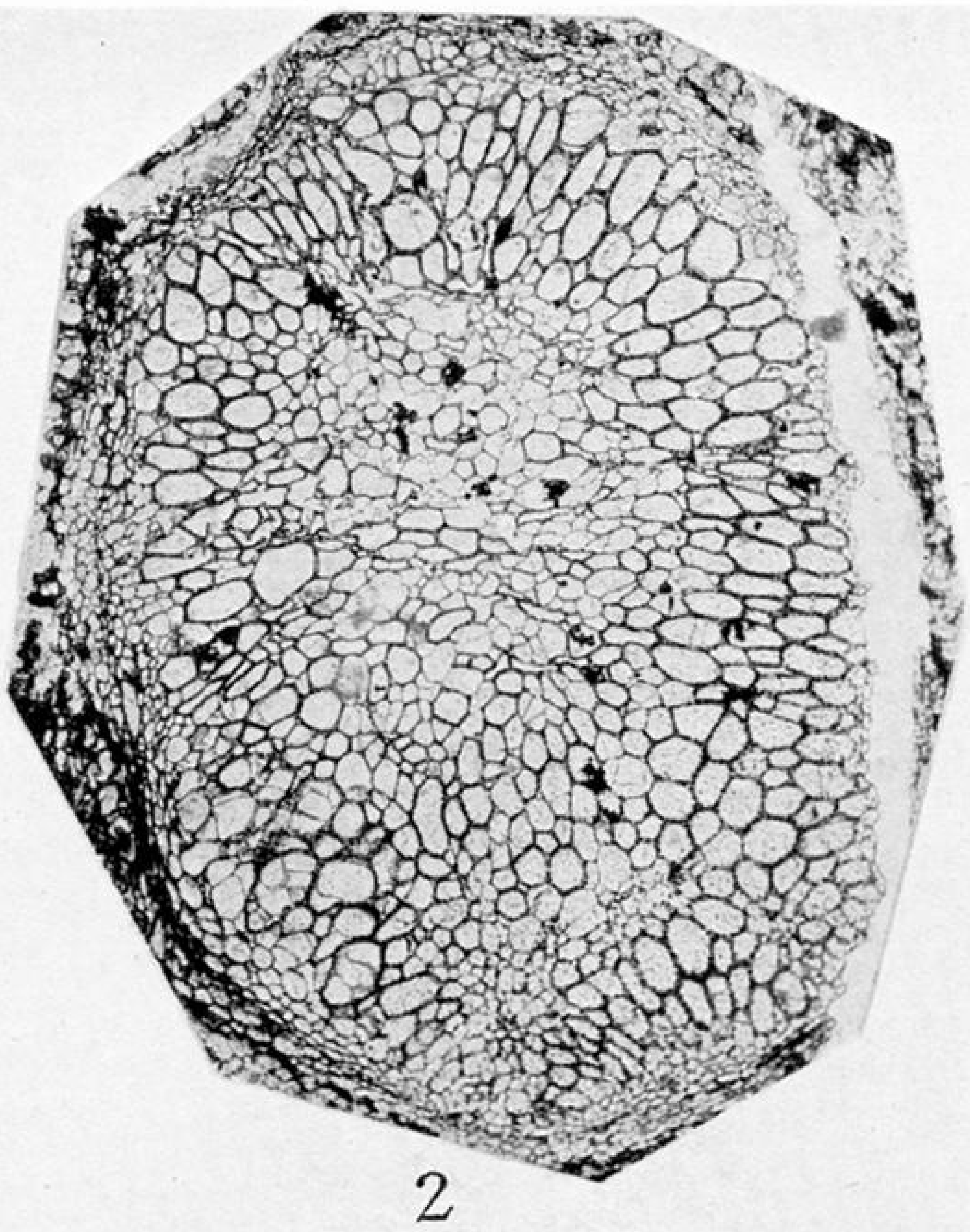

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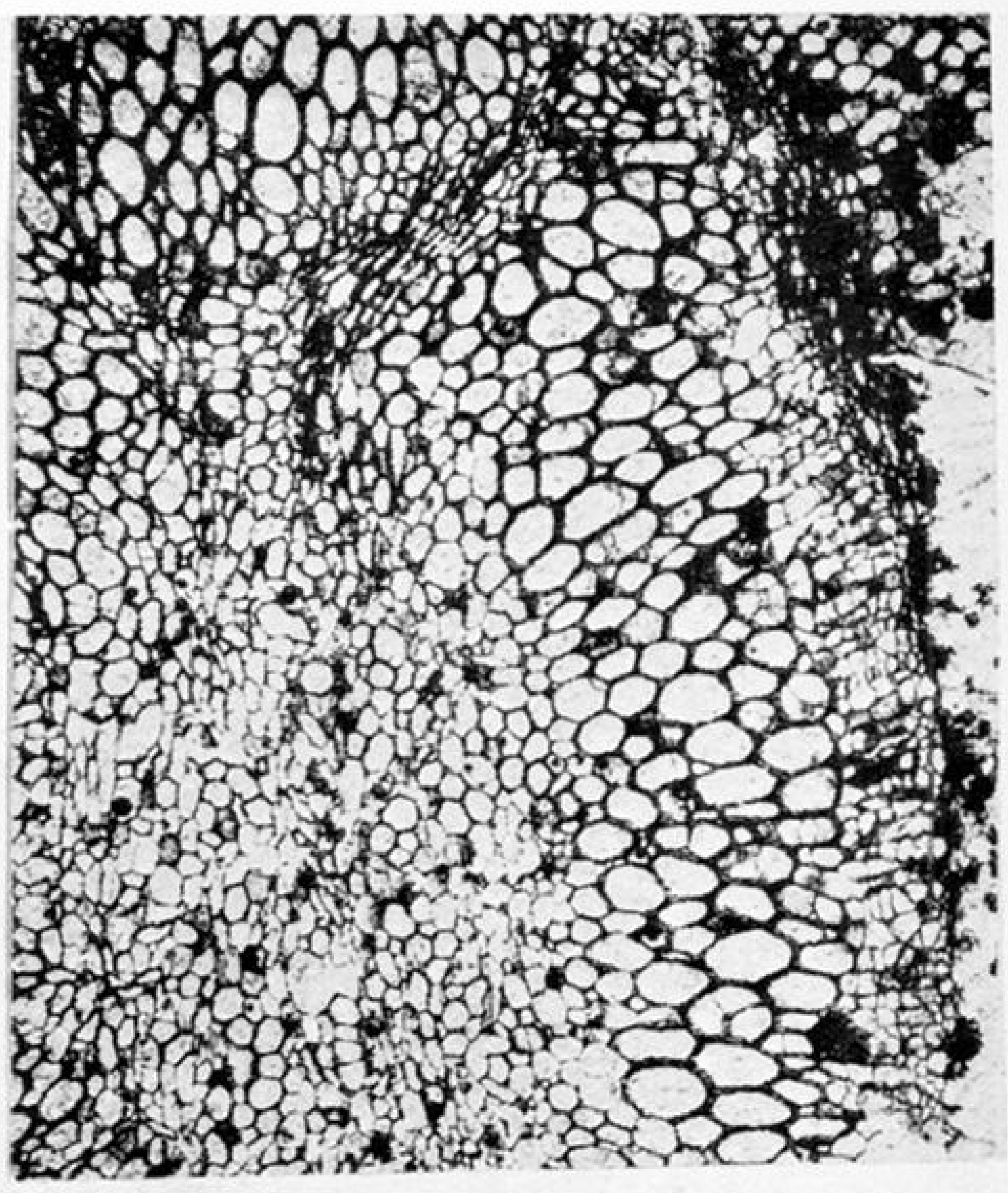

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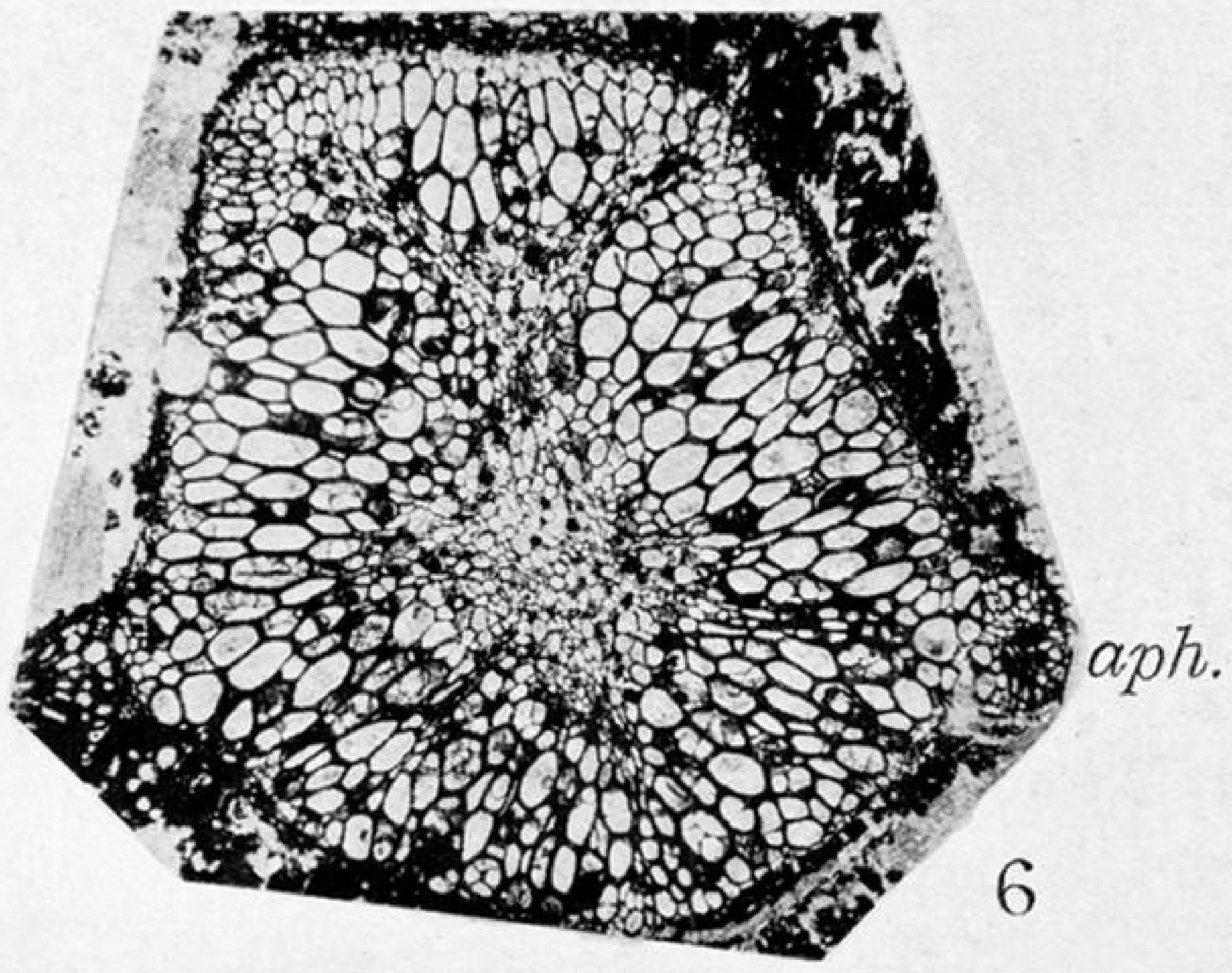

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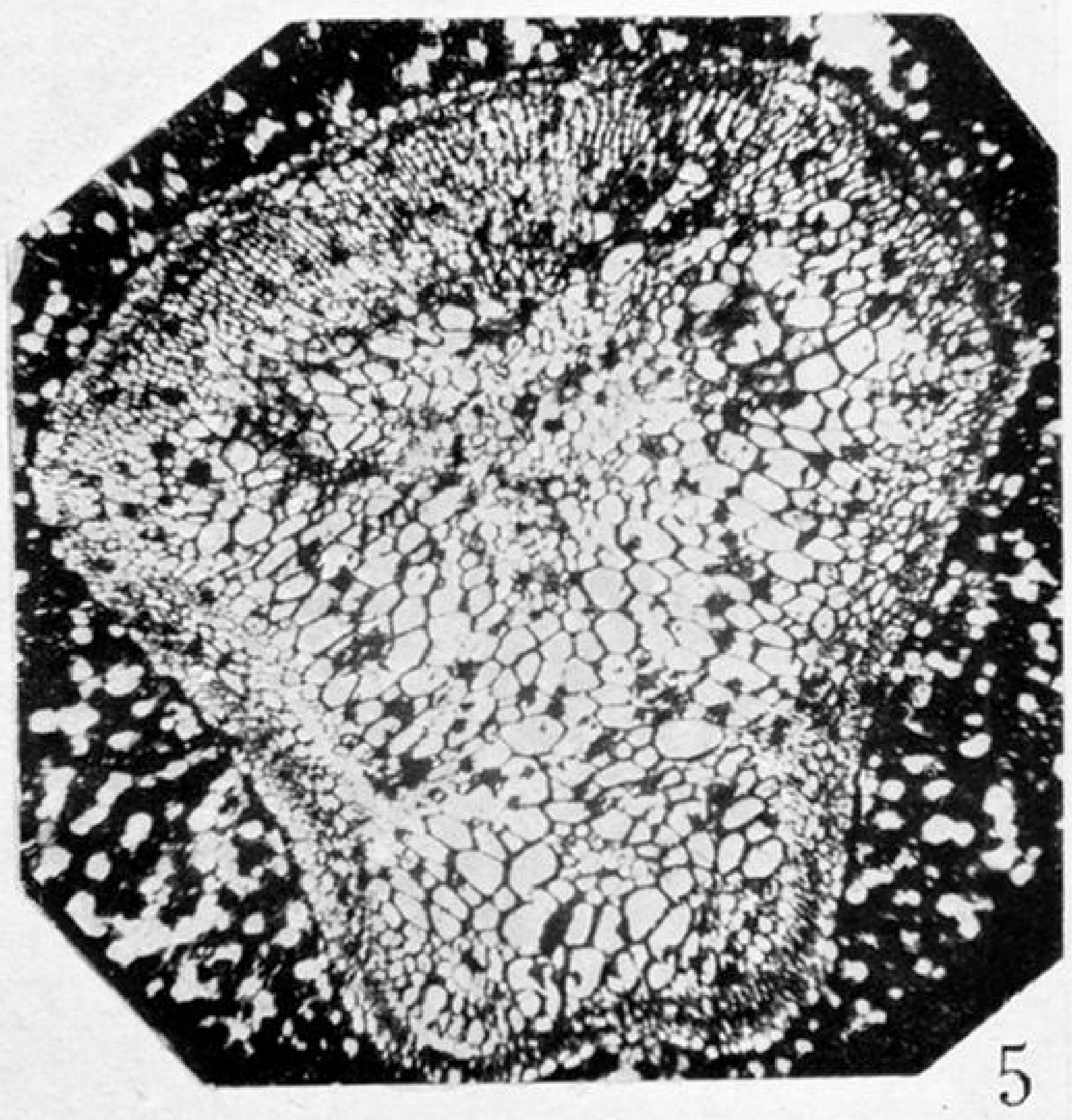

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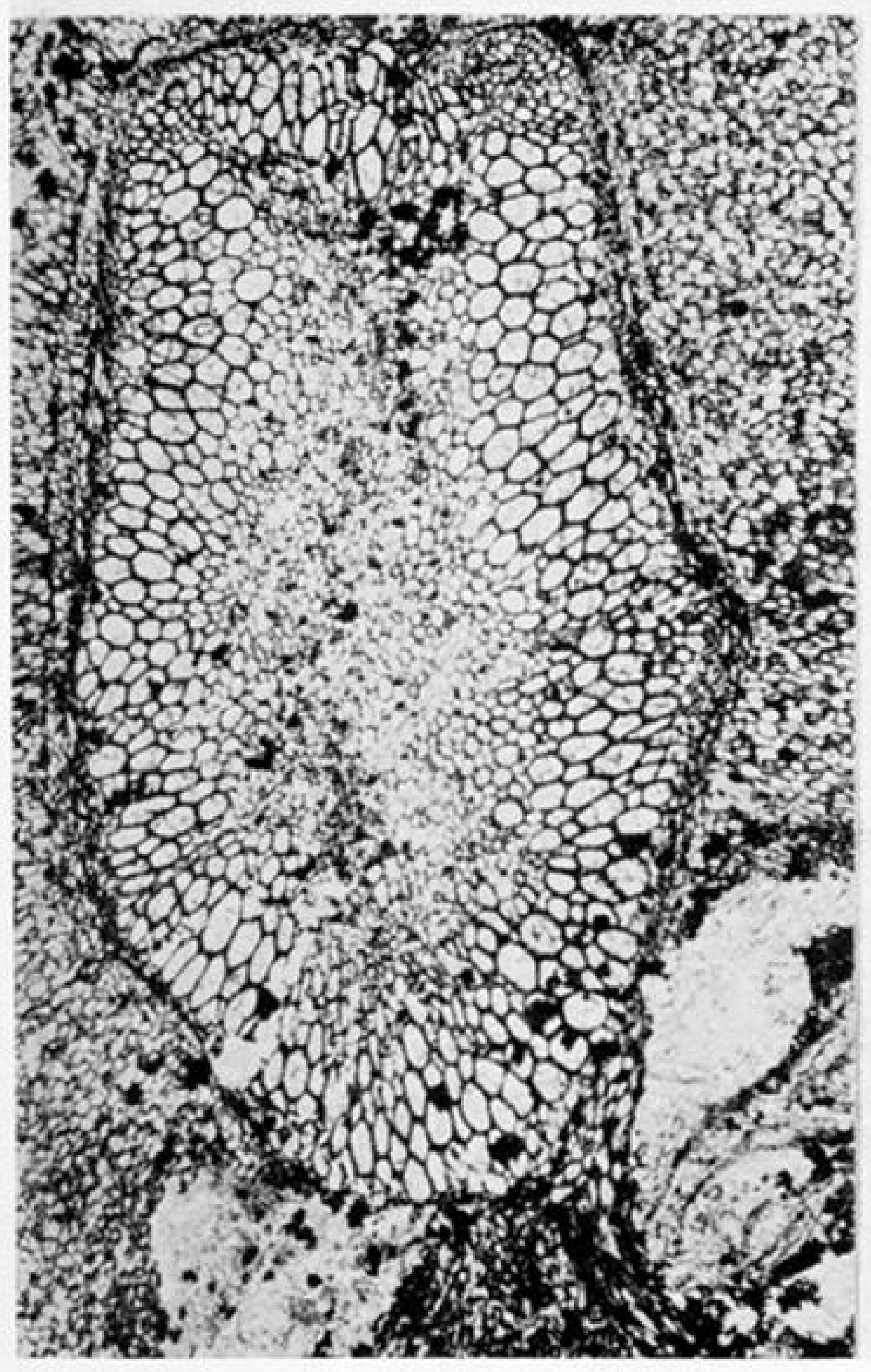

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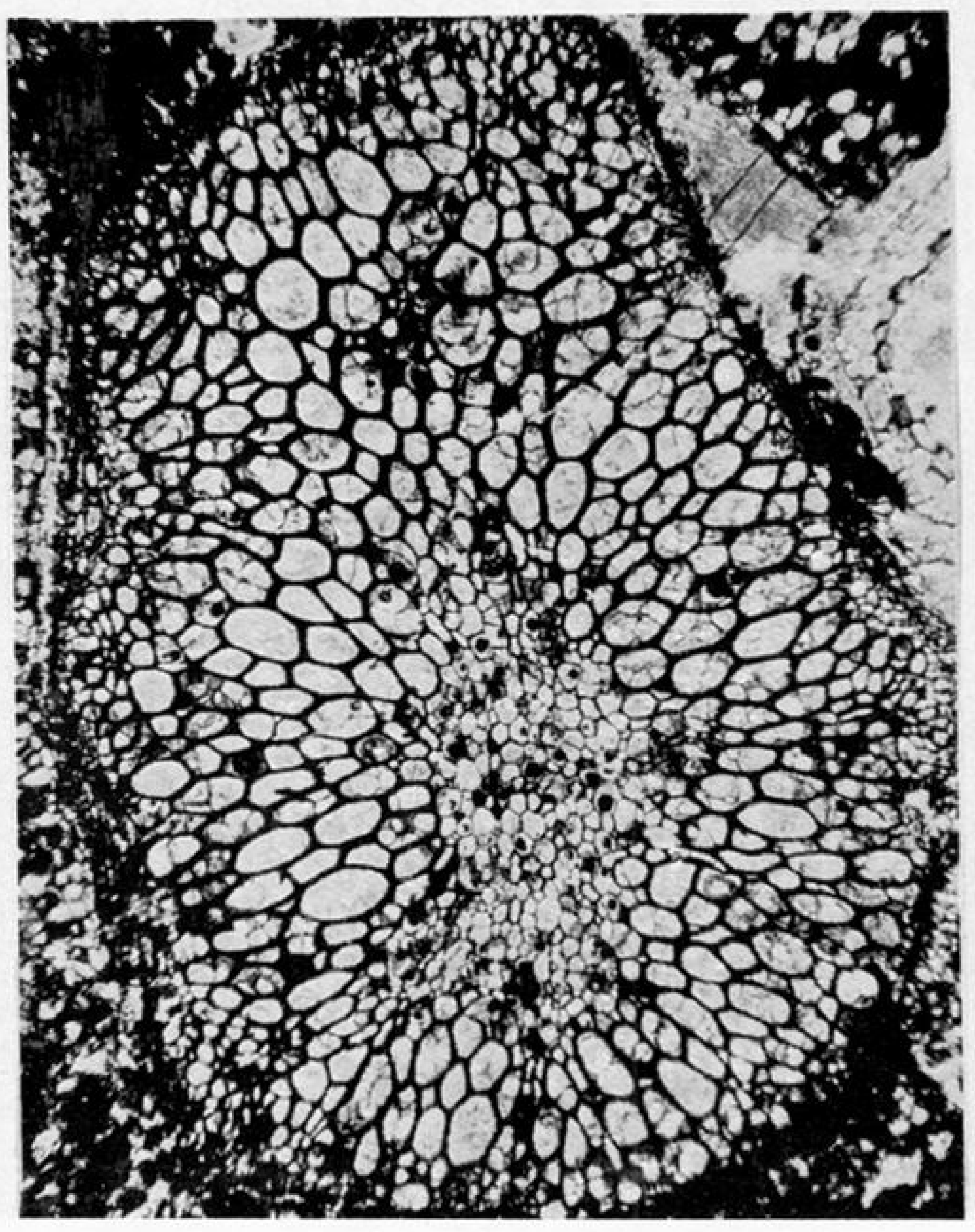

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PLATE 7.

FIG. 1.—Transverse section of stem stele through an internode. Note small calibre of central tracheids and aphlebia traces at *aph.* and *aph.* 1. × 30. Will. Coll. 264.

FIG. 2.—Transverse section of stem stele through an internode. Note relatively large calibre of central tracheids compared with those in fig. 1. Phloem is shown on left. An early stage in emission of a petiole trace is shown at bottom of figure. × 40. U.C.N. Coll. 345.5.

FIG. 3.—Longitudinal section of a stem stele just below a dichotomy, showing short irregular tracheids with reticulate thickening. × 20. S. Coll. 2692.

FIG. 4.—Transverse section of part of stem stele, showing well developed cambium on right. × 40. U.C.N. Coll. 442.23.

FIG. 5.—Transverse section of a stem stele, showing a zone of secondary tissue at upper end. Note thinning of primary xylem below this. × 40. S. Coll. 2715.

FIG. 6.—Transverse section of a stem stele, showing initiation of a petiole trace at upper end. Note aphlebia trace to right. × 30. U.C.N. Coll. 345.20.

FIG. 7.—A similar section, showing a stele in which initiation of tracheidal bridge is delayed. Note root at bottom to right. × 16. U.C.N. Coll. 345.5.

FIG. 8.—Later stage in emission of petiole trace. Note three protoxylem groups. × 30. U.C.N. Coll. 345.14.

FIG. 9.—Longitudinal section, showing U and V-shaped tracheids at junction of stem and petiole. × 40. S. Coll. 2692.

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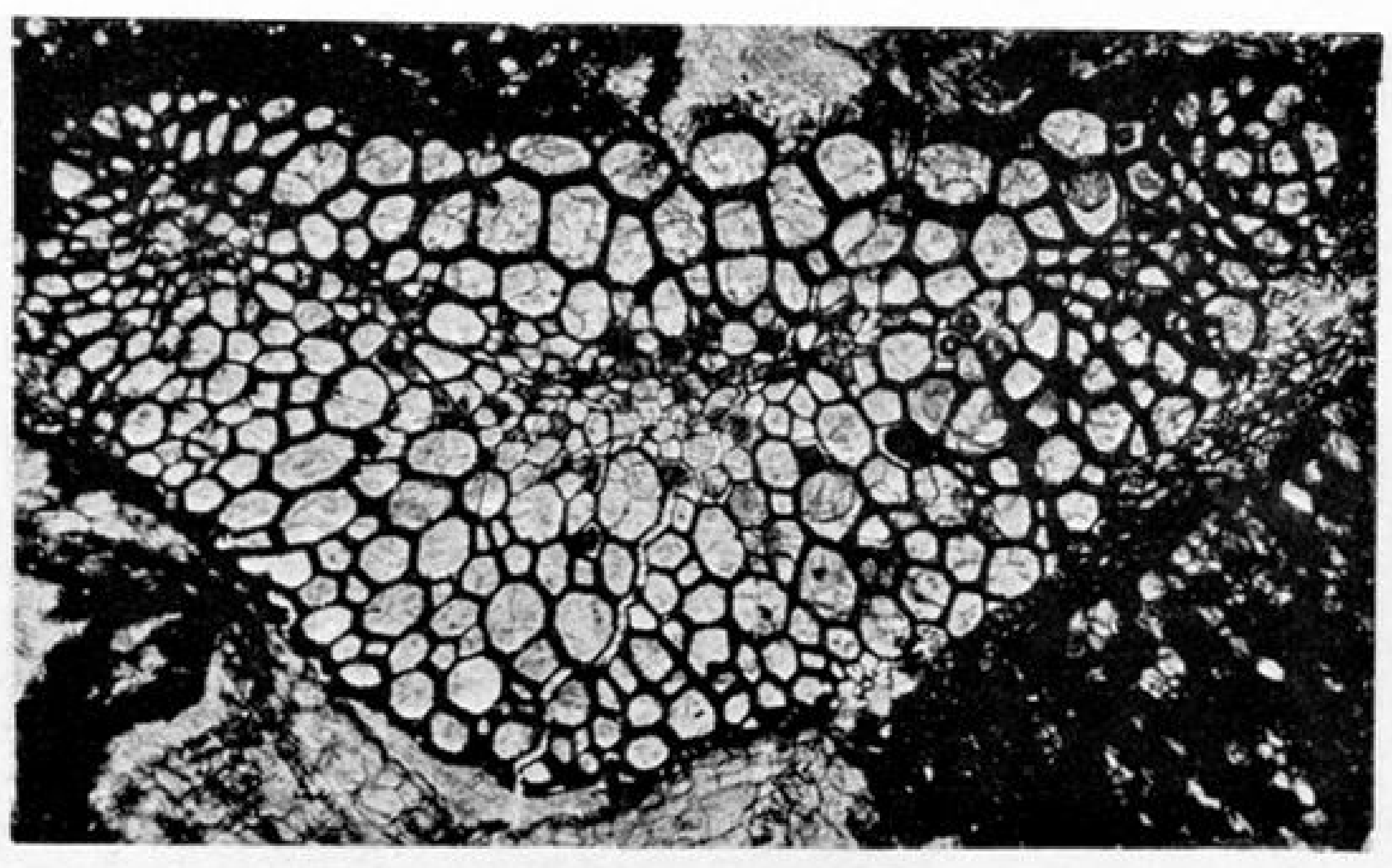

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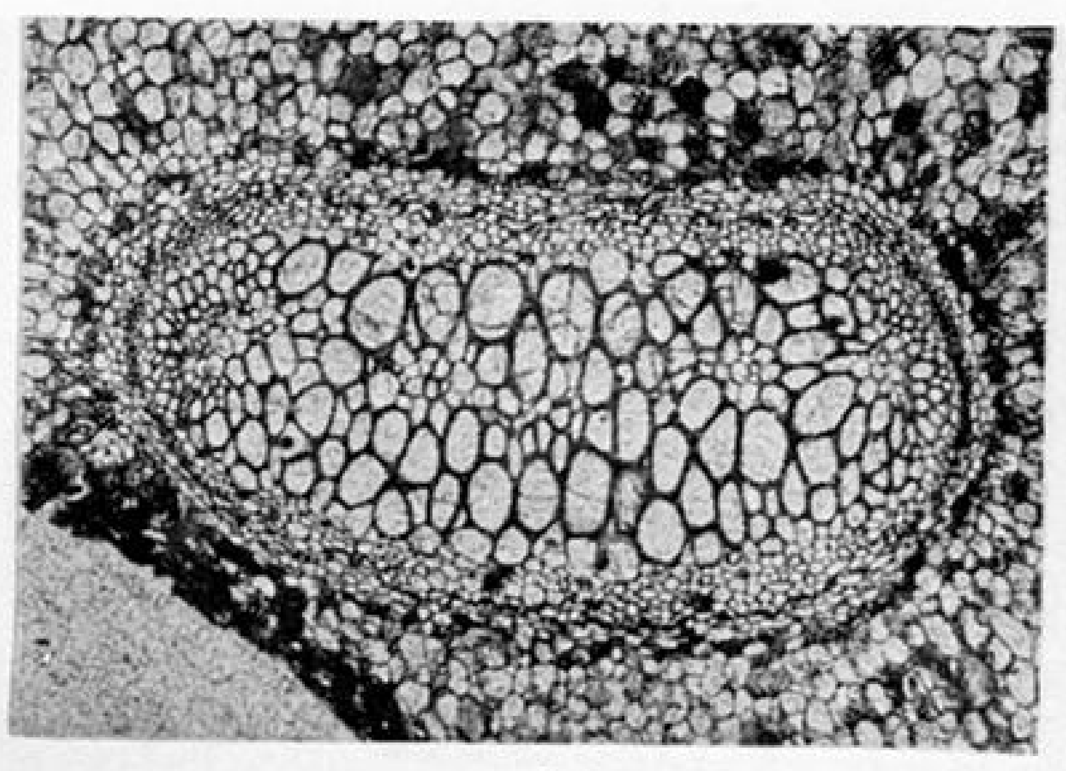

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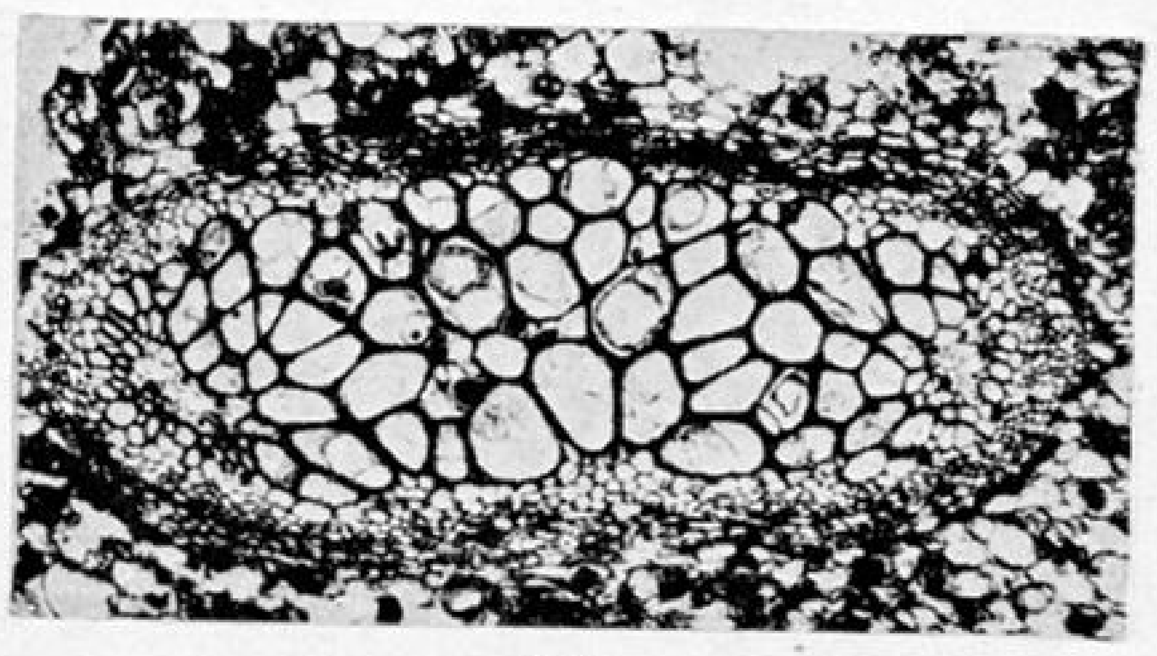

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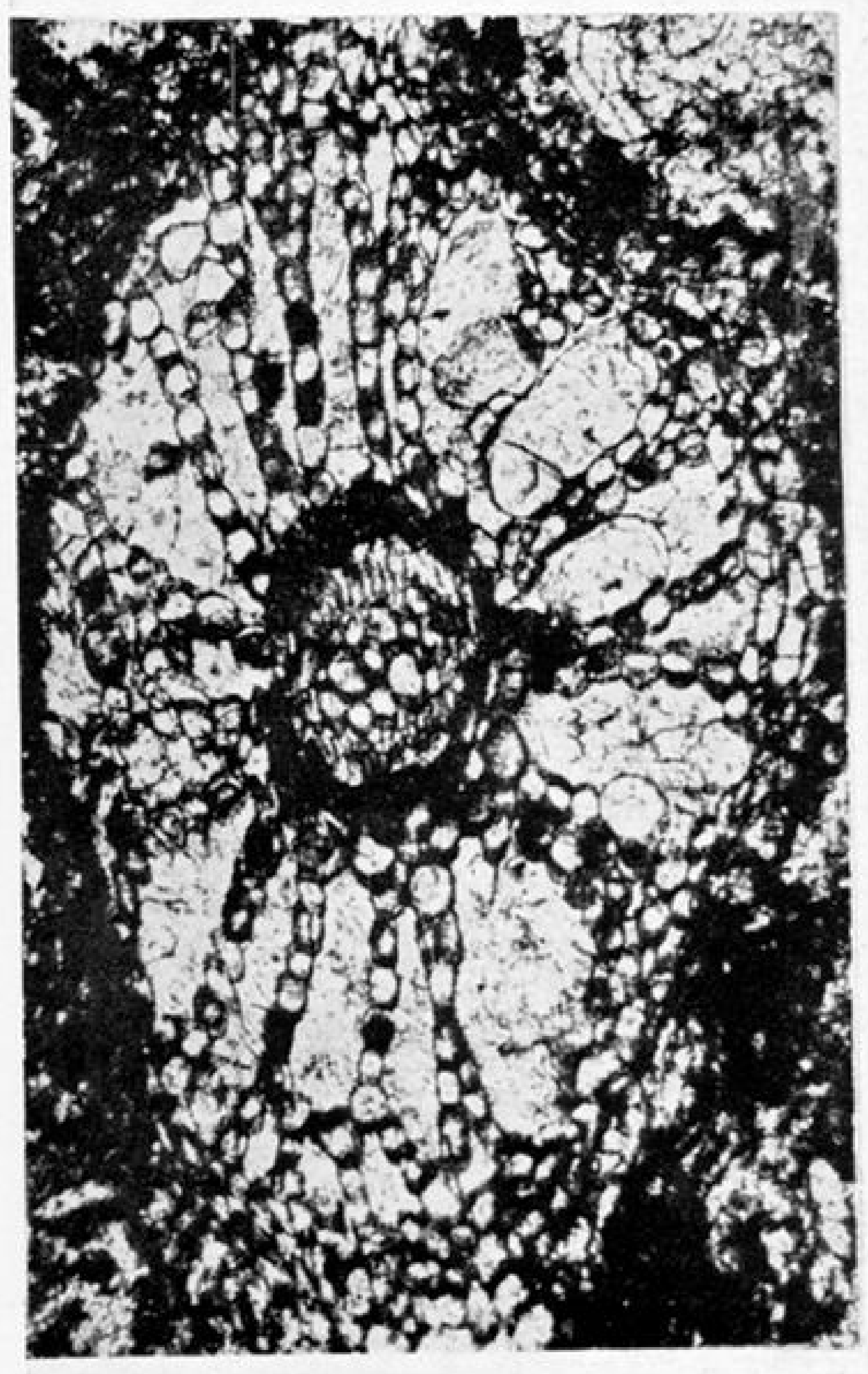

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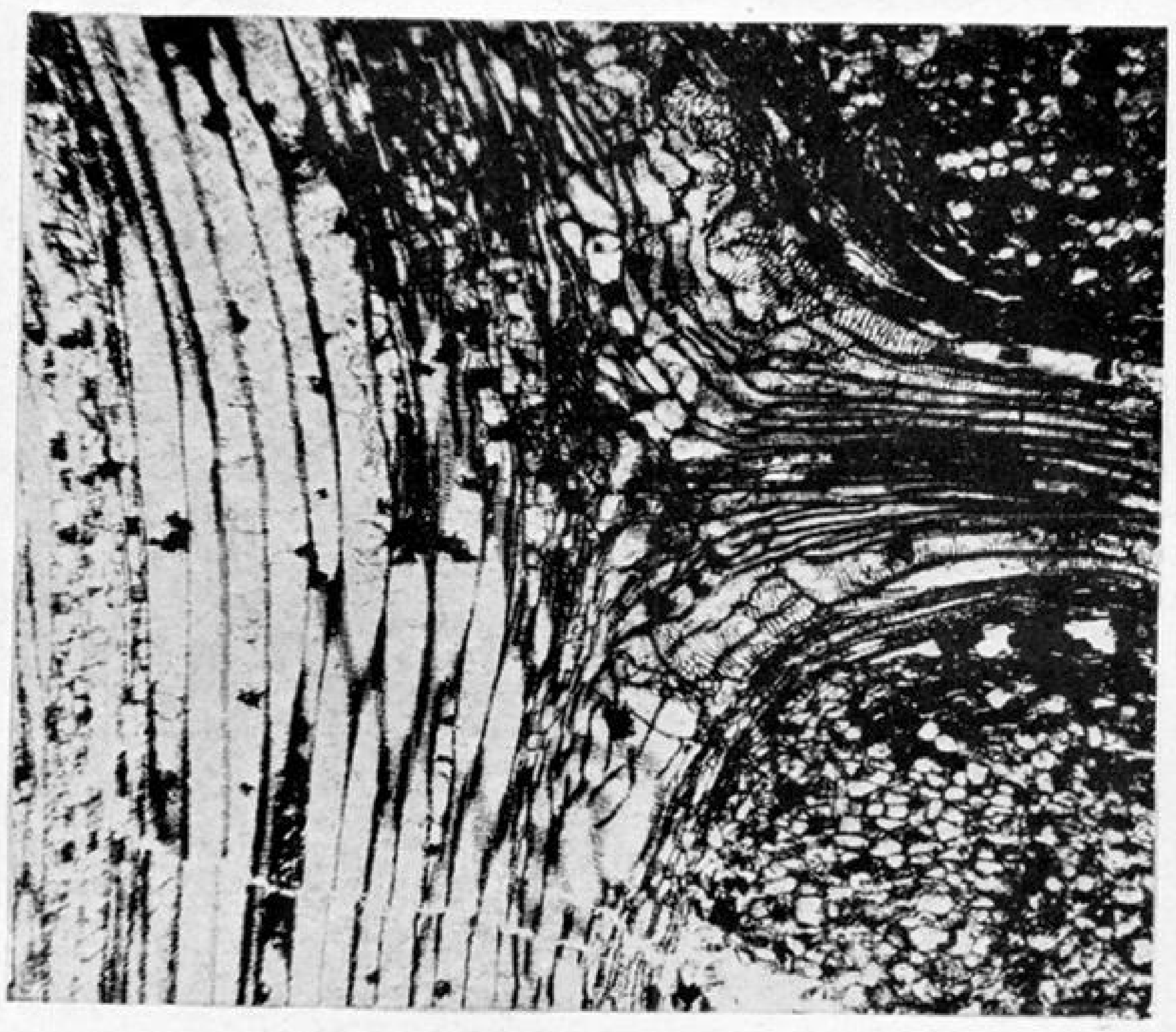

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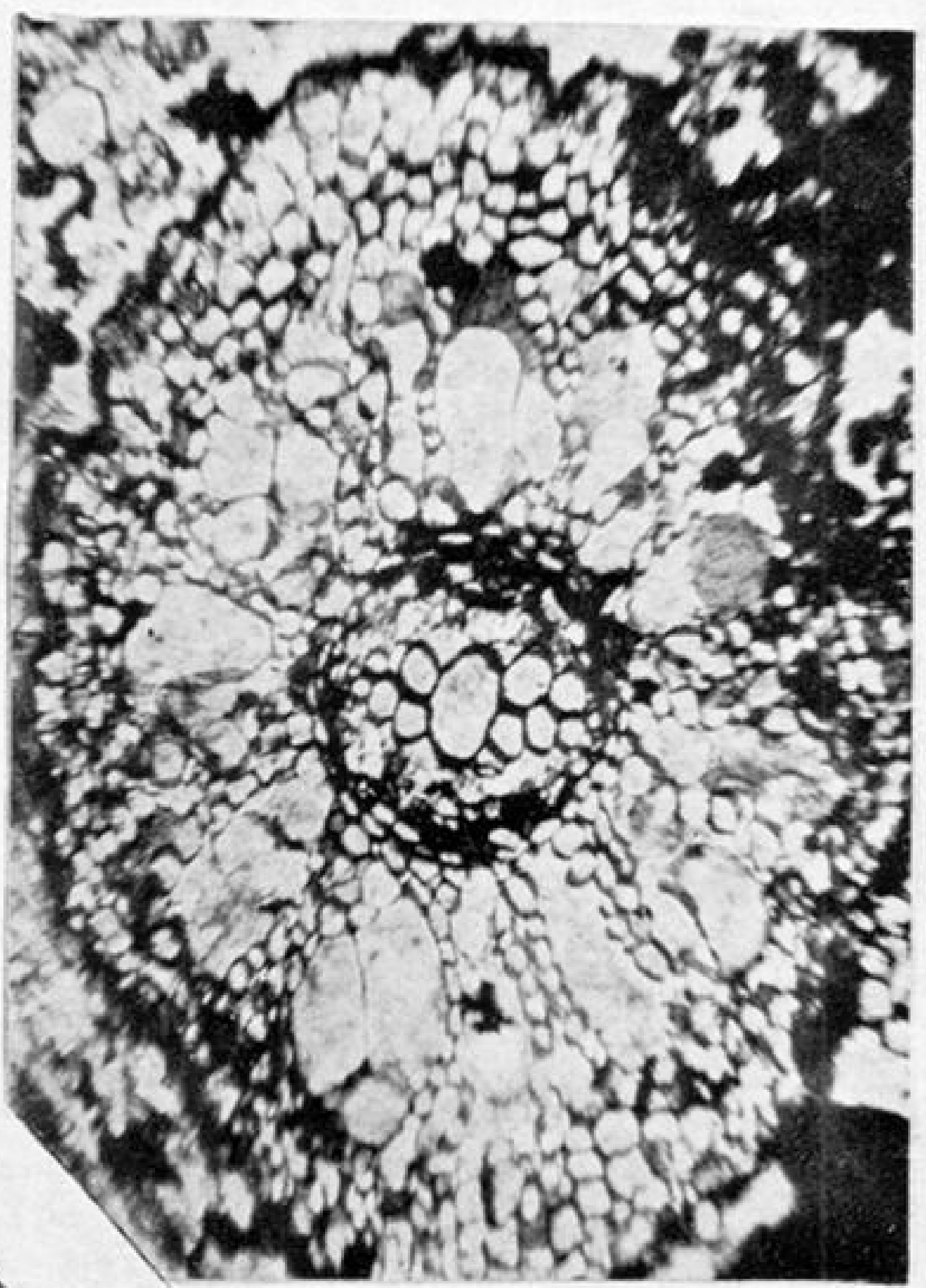

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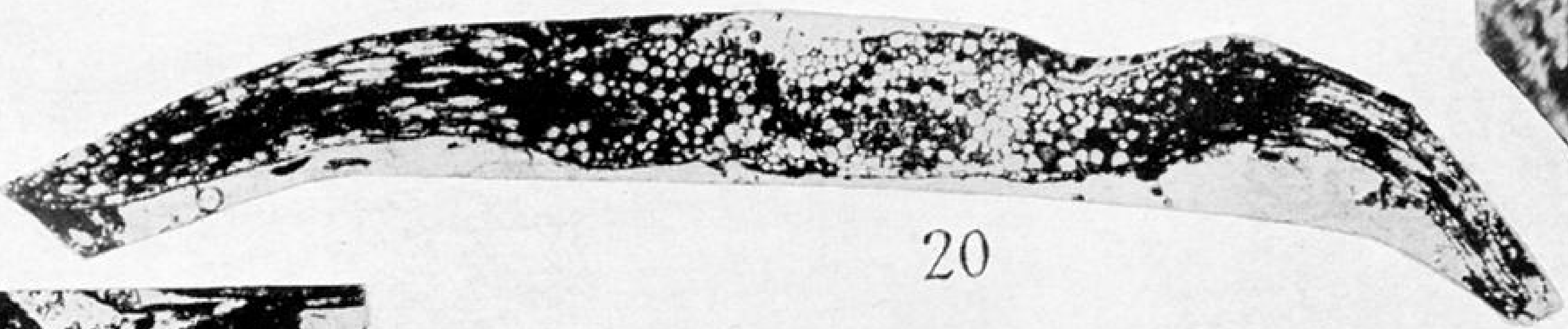

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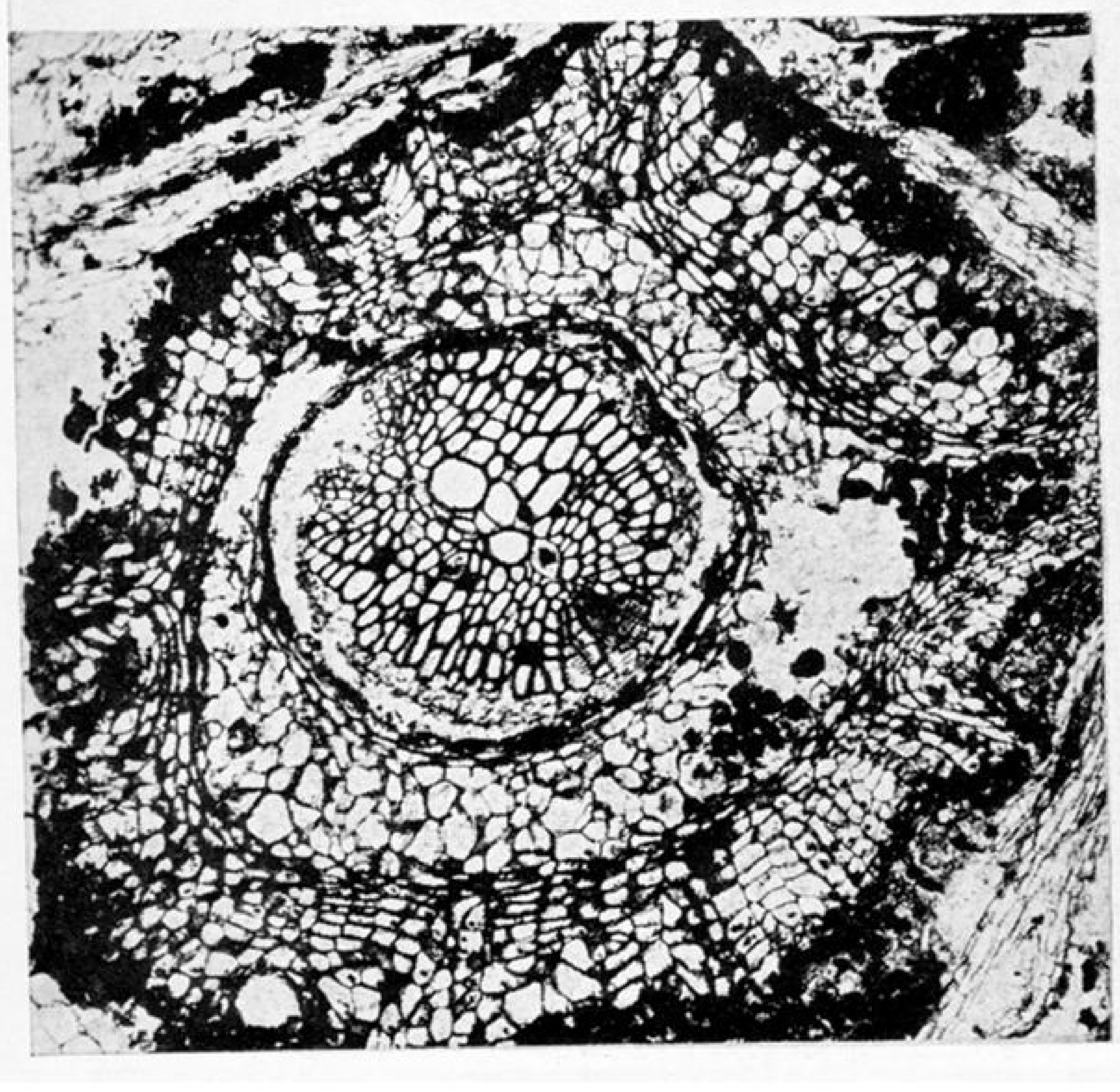

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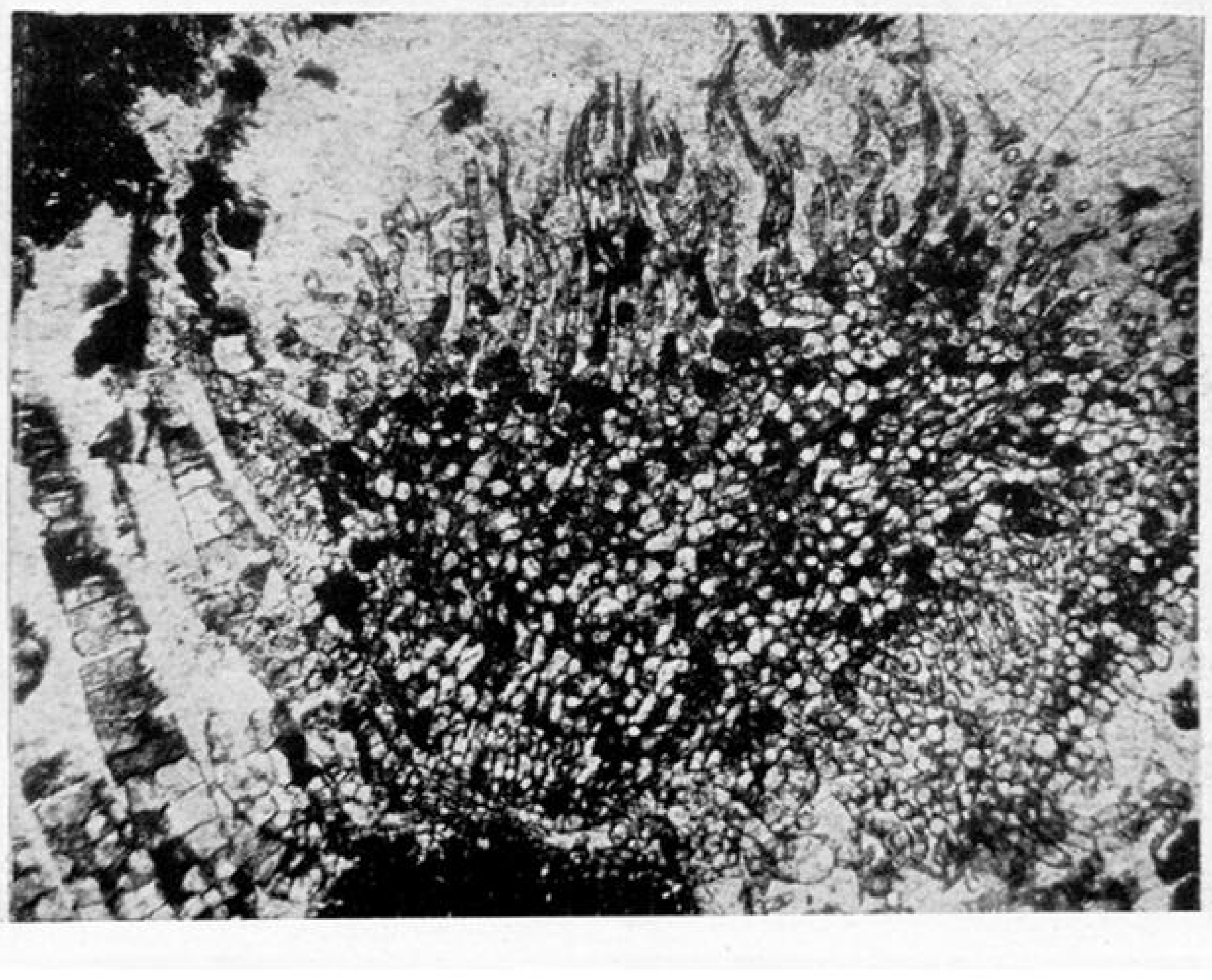

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PLATE 8.

FIG. 10.—Transverse section of petiole trace just free from stem stele. Note triangular outline and general similarity to that of *Ankyropteris Grayi*. × 40. M.U. Coll. R448.

FIG. 11.—Transverse section of petiole trace a little way out in the stem cortex. Note irregular distribution of intrastelar parenchyma and slight abaxial curvature. × 20. U.C.N. Coll. 261.69.

FIG. 12.—Transverse section of stem and petiole trace. × 15. U.C.N. Coll. 345.18.

FIG. 13.—Transverse section of the petiole trace shown in fig. 12. Note elimination of median protoxylem group and small tracheids of the peripheral loops. × 40. U.C.N. Coll. 345.18.

FIG. 14.—Transverse section of a large stem, showing the emission of two stout roots. × 15. U.C.N. Coll. 261.69.

FIG. 15.—Longitudinal section, showing union of stem and root. The characteristic tracheids in region of union are well shown. × 40. U.C.L. Coll. K610.

FIG. 16. Transverse section of a young root, to show lacunar middle cortex. × 100. S. Coll. 2687.

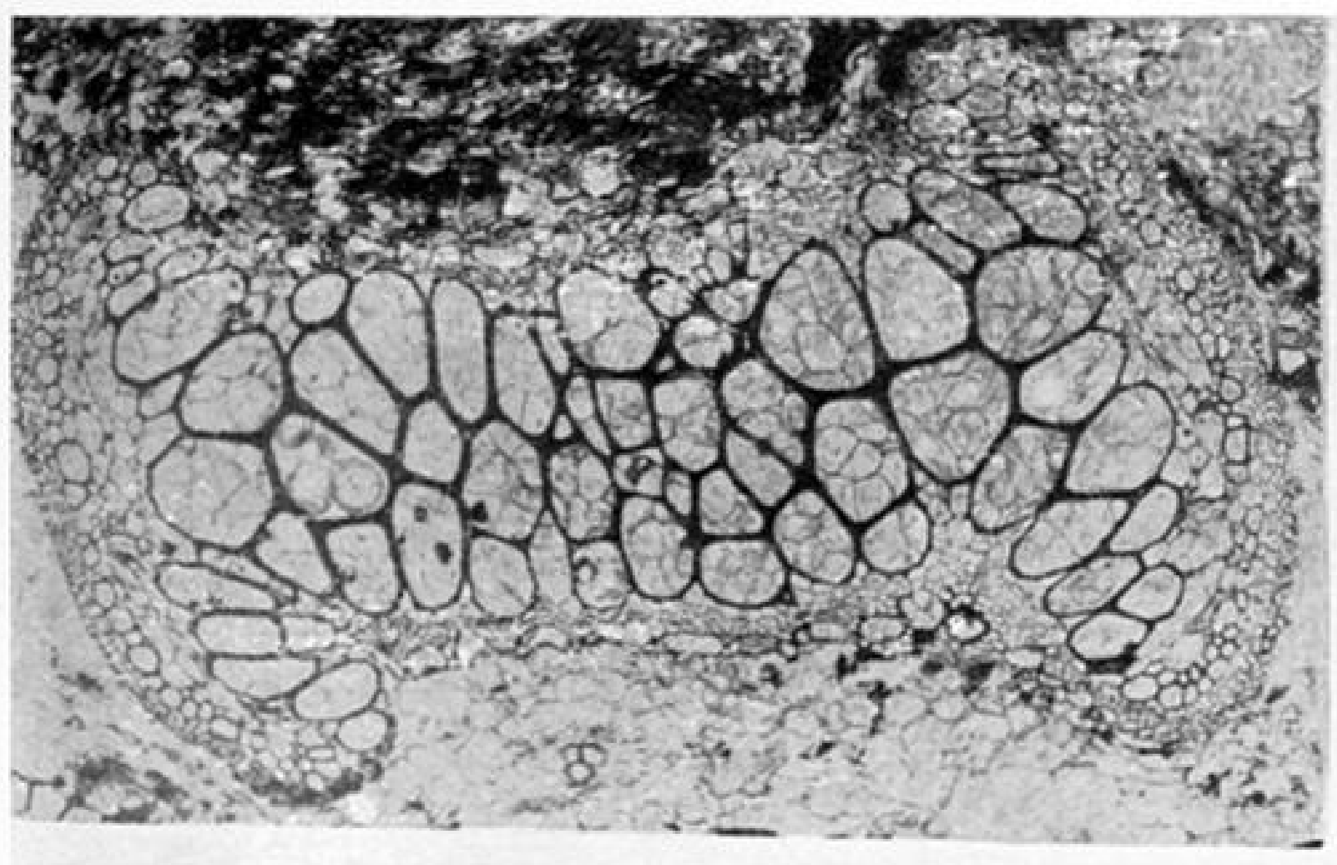
FIG. 17.—Transverse section of a slightly older root, showing development of vesiculate outgrowths in middle cortex. × 100. S. Coll. 2725.

FIG. 18, *a*.—Transverse section of an old root, showing superficial periderm, modified middle cortex, and secondary xylem. × 60. U.C.N. Coll. 261.74.

FIG. 18, *b*.—Transverse section of stele of an old root, to show type of pitting in secondary xylem. × 80. U.C.N. Coll.

FIG. 19.—Transverse section of an aphlebia, showing investment of fine branching hairs and, to left, hairs of stouter type. × 50. K. Coll. 1985.

FIG. 20.—Transverse section of a winged aphlebia. × 30. U.C.L. Coll K603a.



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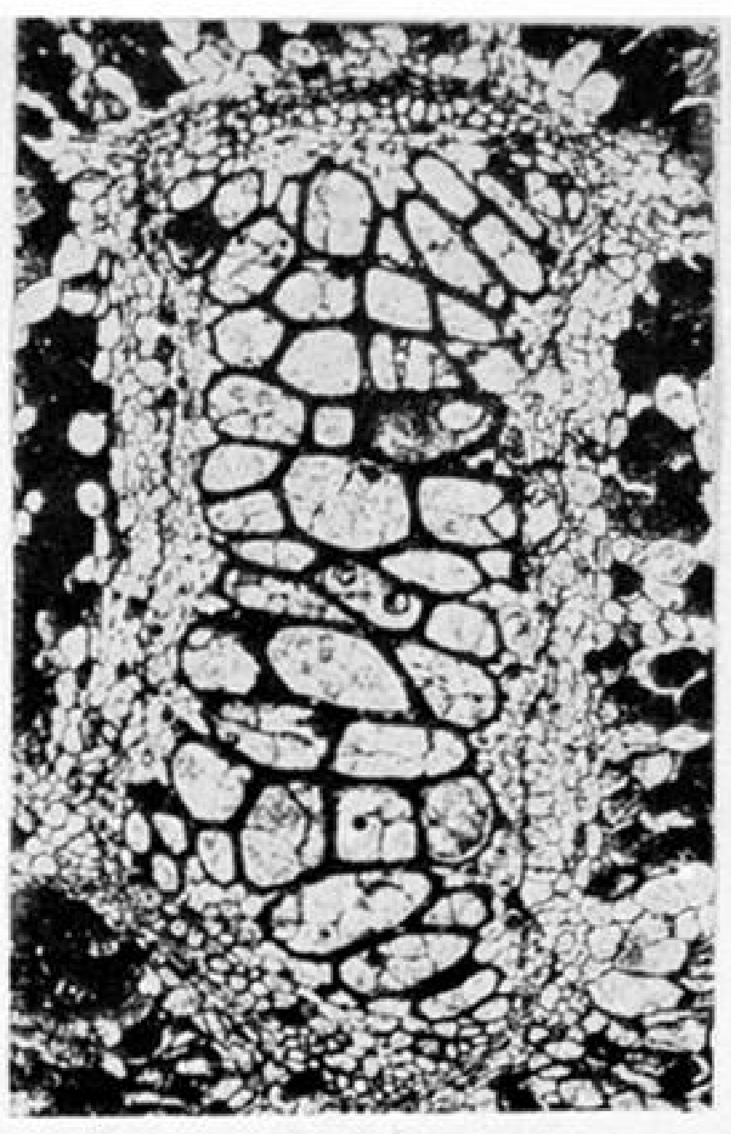

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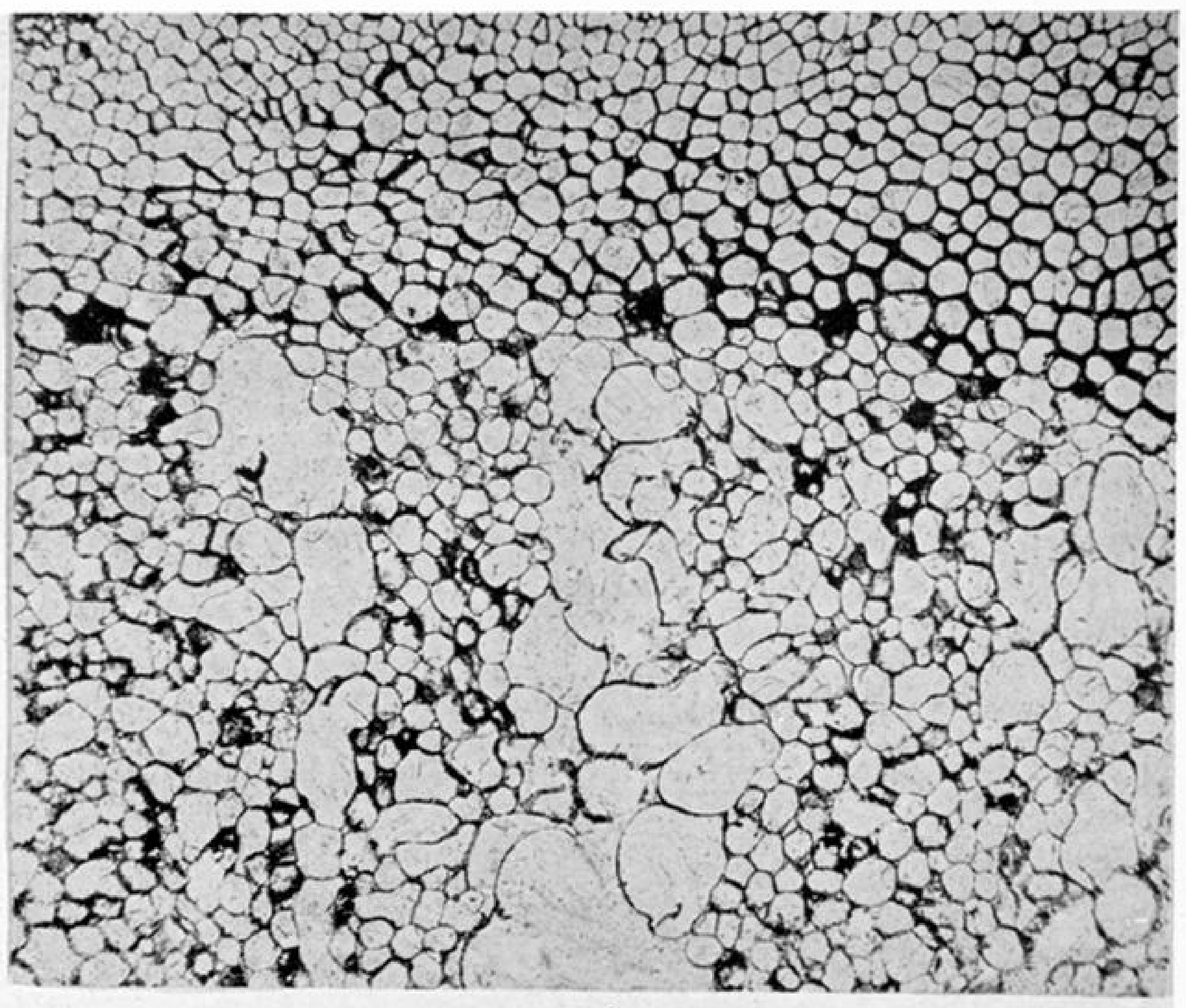

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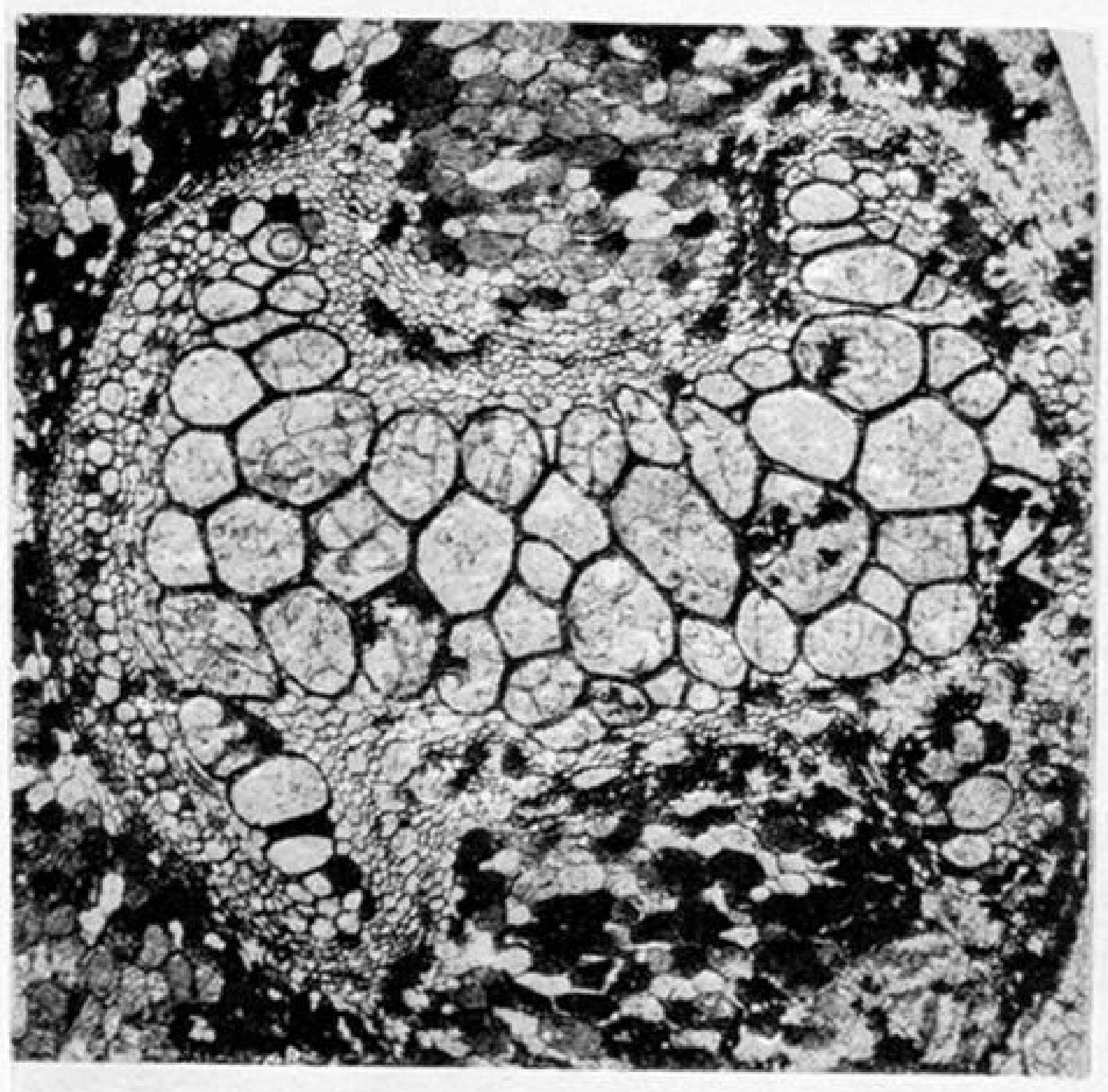

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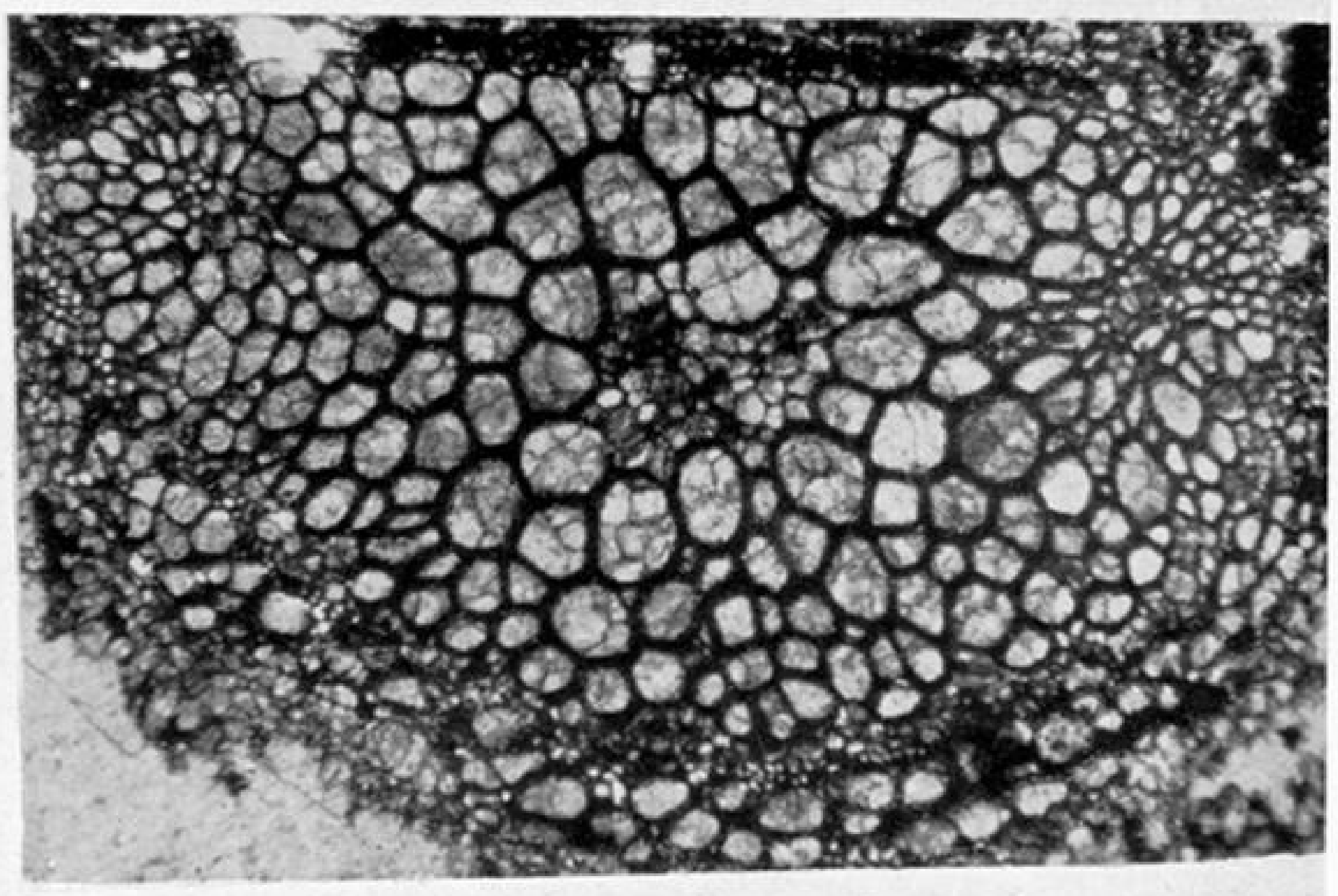

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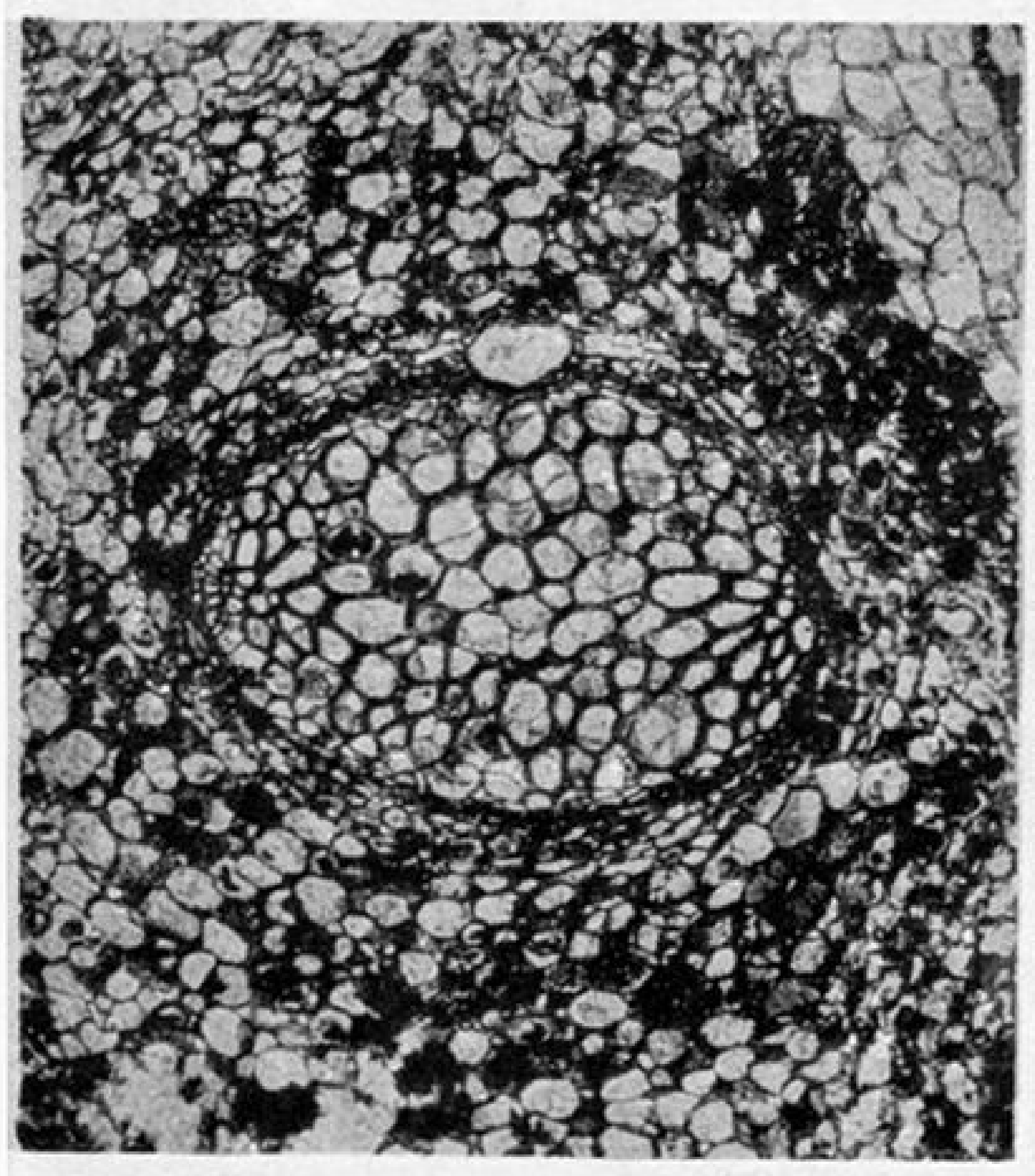

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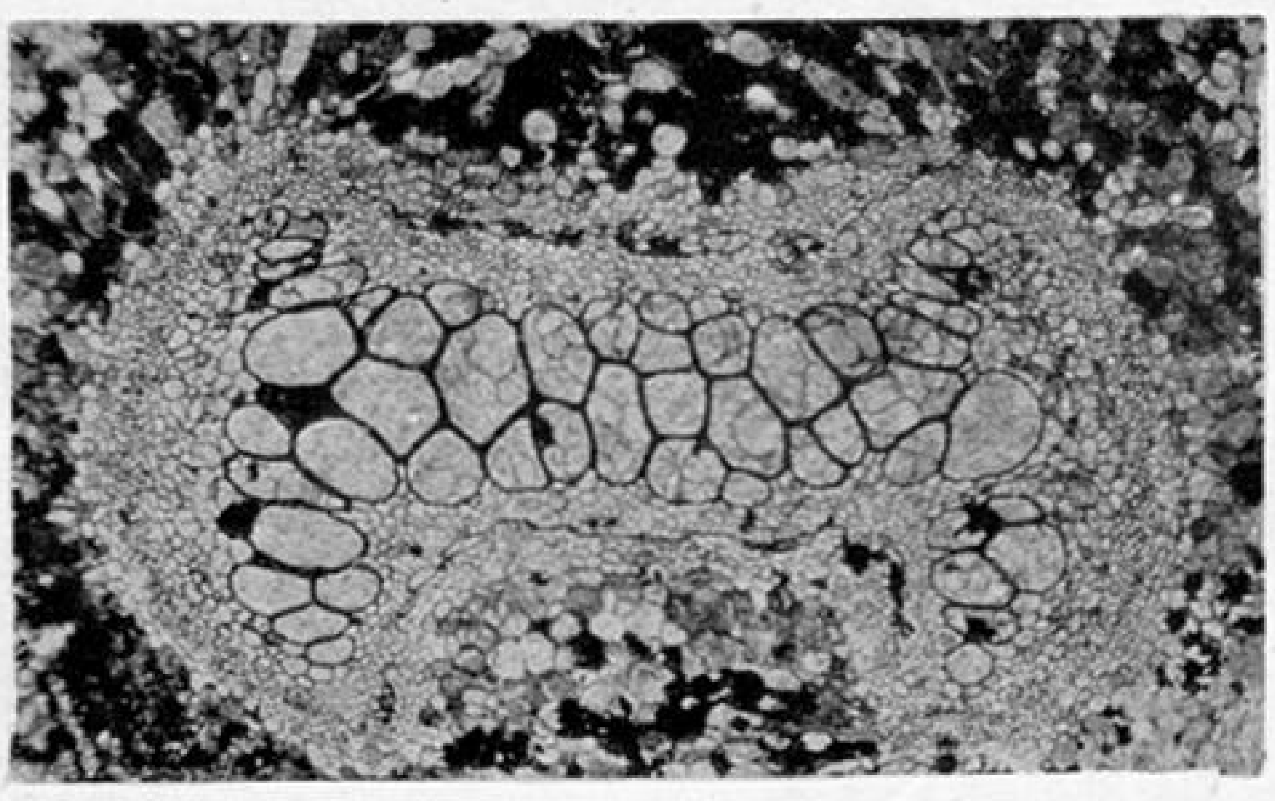

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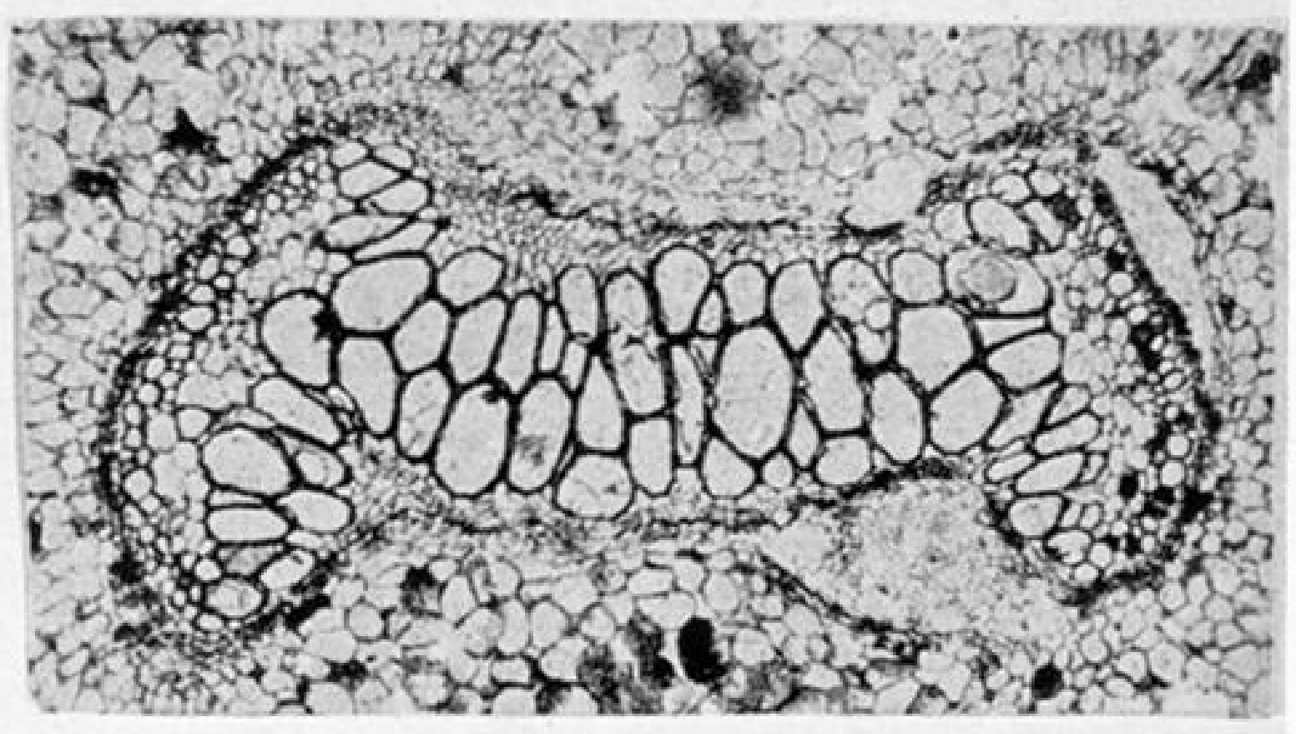

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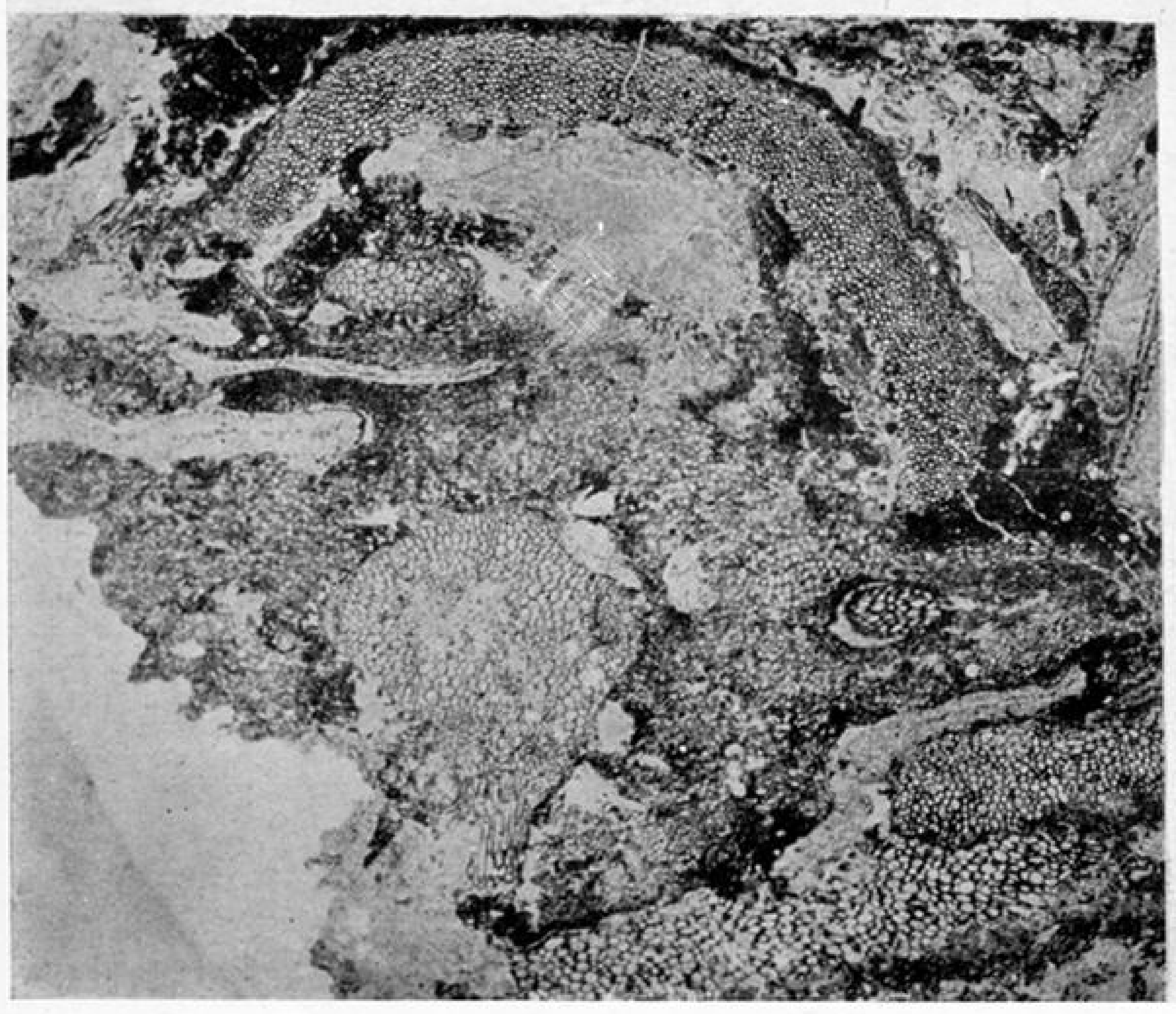

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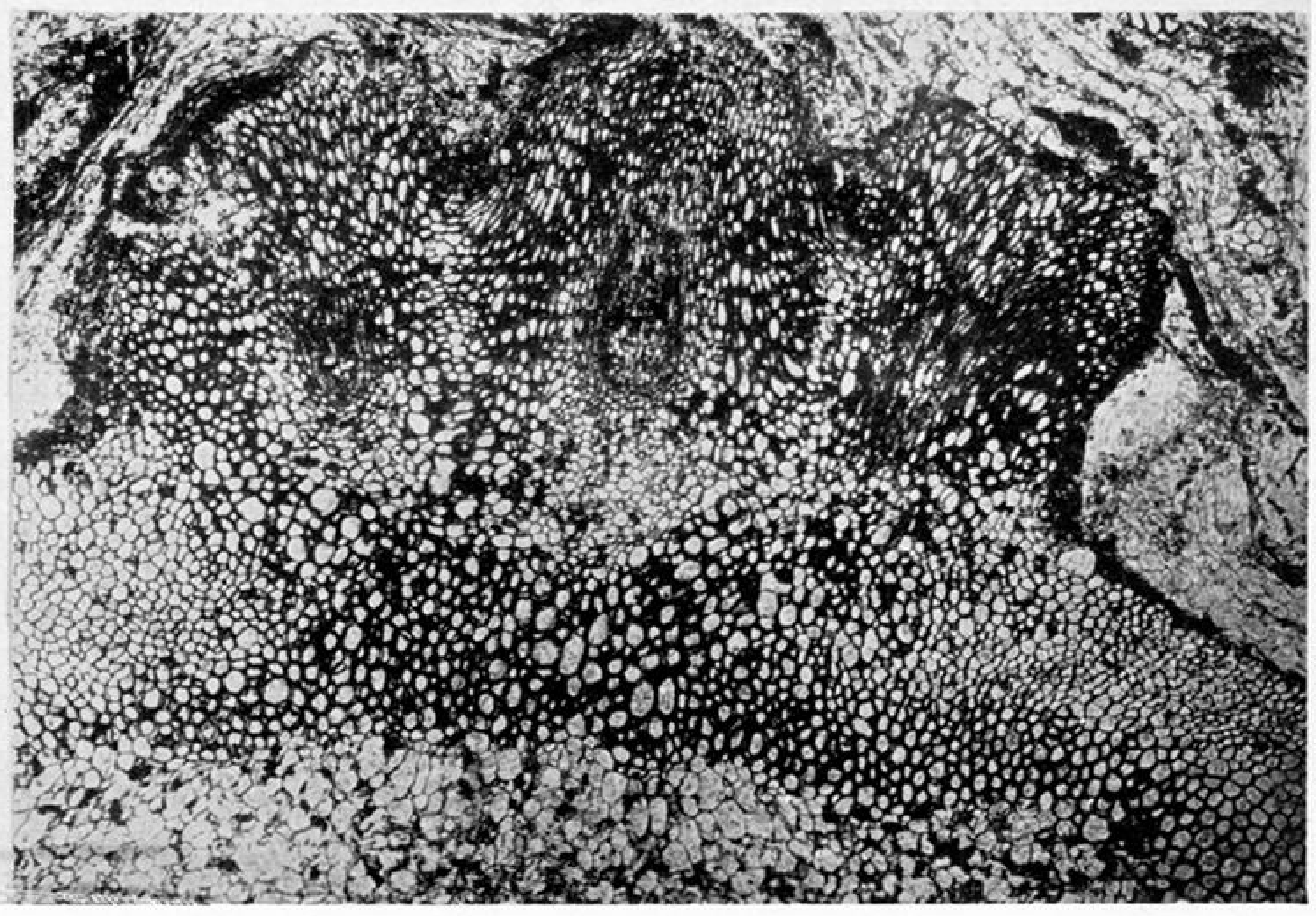

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PLATE 9.

FIG. 21.—Transverse section of stem and petiole trace, showing the arc of sclerenchyma developed behind outgoing petiole trace. A root is seen to right. × 10. S. Coll. 2725.

FIG. 22.—Transverse section of a petiole trace just losing its triangular outline. The three protoxylem groups are well shown, also large sieve tubes on lower side of trace. × 50. Will. Coll. 252.

FIG. 23.—Transverse section of petiole trace (stout type), showing its appearance at base of petiole. The antennæ are now evident, the stronger adaxial ones being to right of figure. Note dark line produced on either side of central bar by collapse of sieve tubes. × 40. U.C.N. Coll. 442.9.

FIG. 24.—Transverse section of a petiole trace at a slightly higher level. Abaxial curvature is well shown. Note collapsed sieve tubes, as in last figure. × 30. U.C.L. Coll. K600.

FIG. 25.—Transverse section of a similar petiole to that shown in fig. 24. Large sieve tubes flanking central bar are clearly shown. Note also tyloses filling tracheids. × 40. K. Coll. 1672.

FIG. 26.—Transverse section of fully developed petiole trace (stout type). × 40. U.C.N. Coll. 261.1

FIG. 27.—Transverse section of petiole trace (slender type) showing discontinuity between xylem of central bar and that of right adaxial antenna. × 30. S. Coll. 2729.

FIG. 28, *a*, 28, *b*.—Transverse sections of petiole traces of unusual stout ovoid type, recalling petiole trace of Dineuron. In fig. 28, *a*, the central protoxylem is still present, but has disappeared in fig. 28, *b*. Both × 30. Fig. 28, *a*. U.C.N. Coll. 345.A2. Fig. 28, *b*. U.C.N. Coll. 261.50.

FIG. 29. Transverse section of base of stout aphlebia with three vascular bundles. × 100. K. Coll. 1984.

FIG. 30.—Transverse section of part of cortex of petiole showing complete occlusion of fissures. × 100. U.C.N. Coll.

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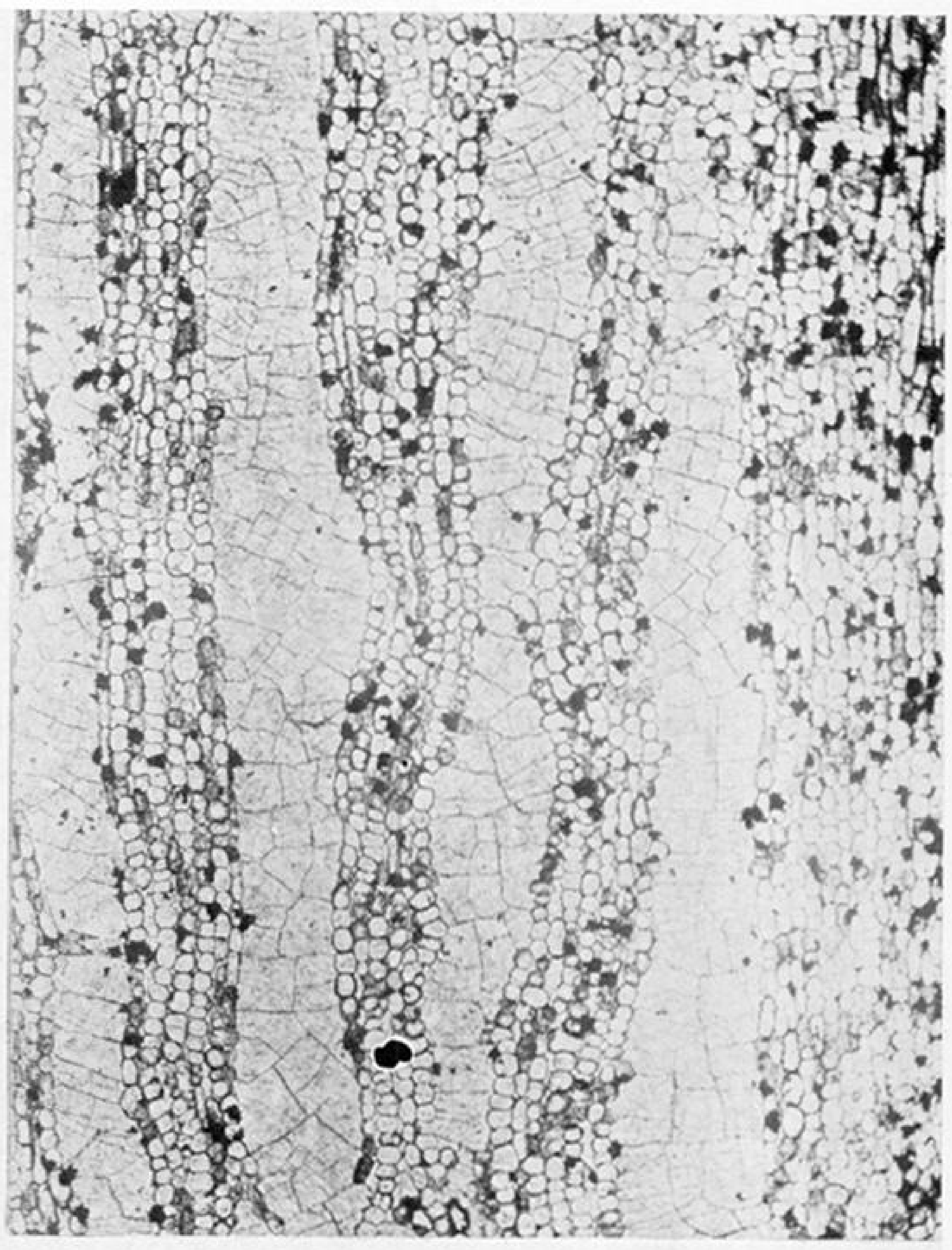

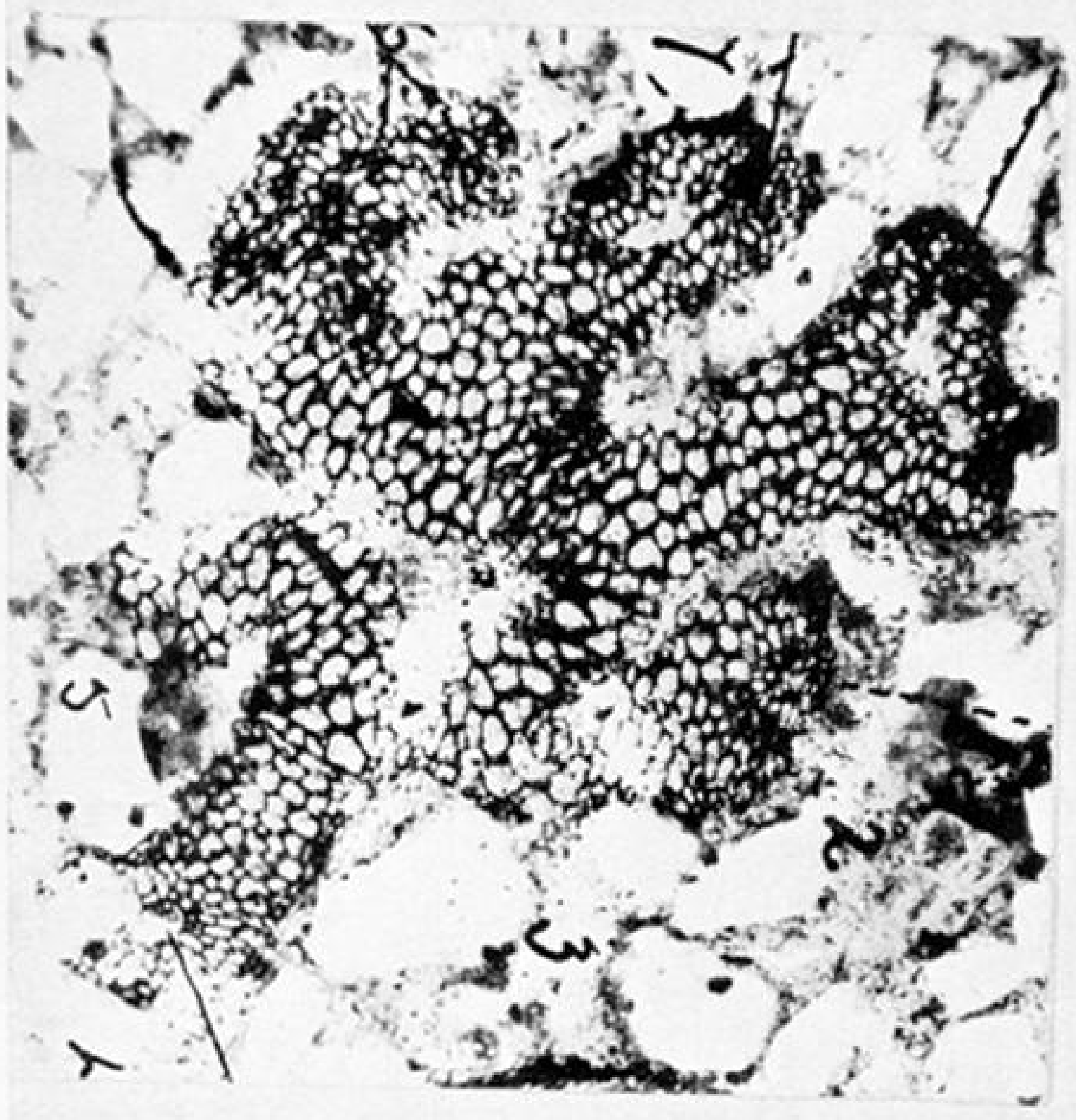

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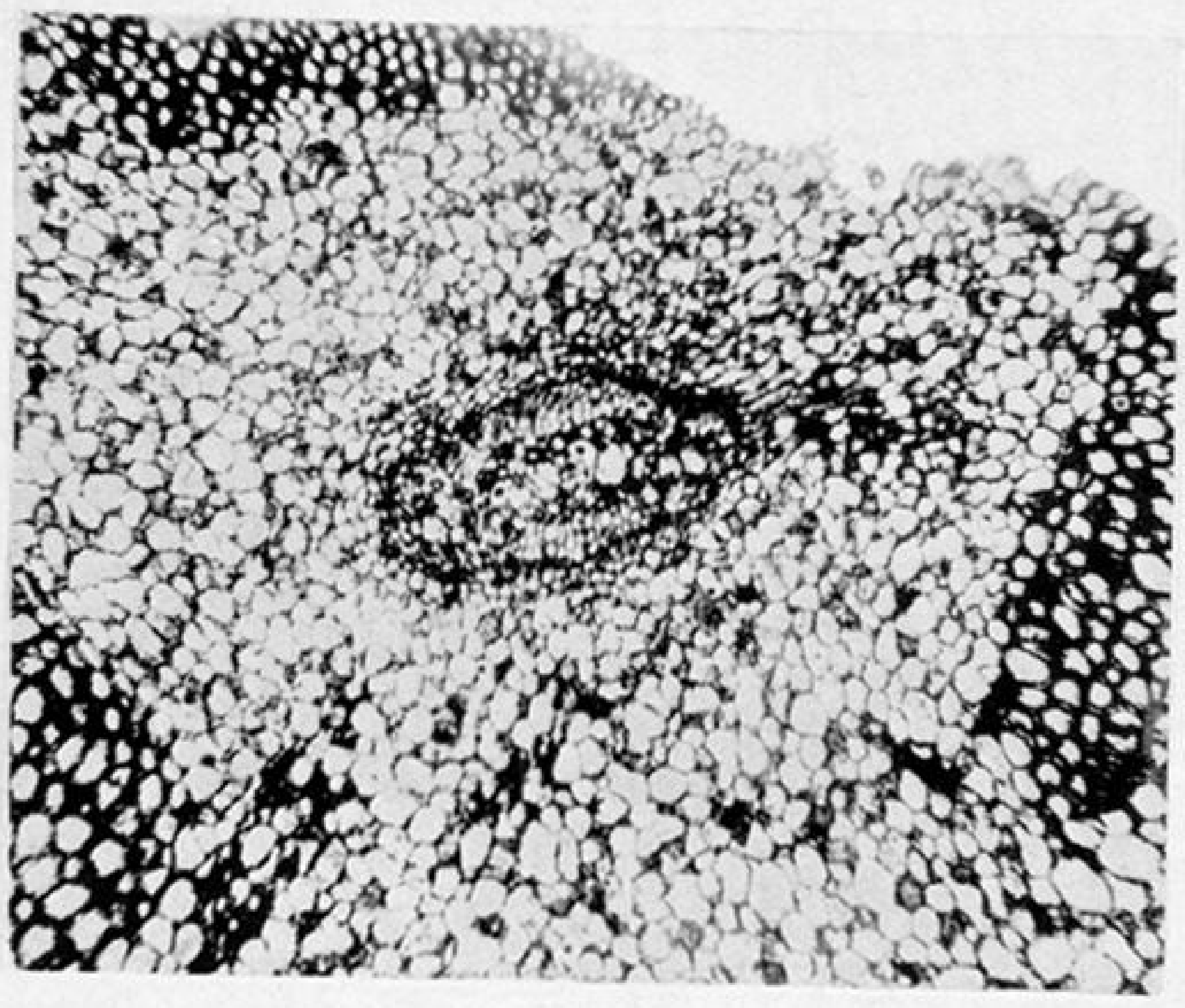

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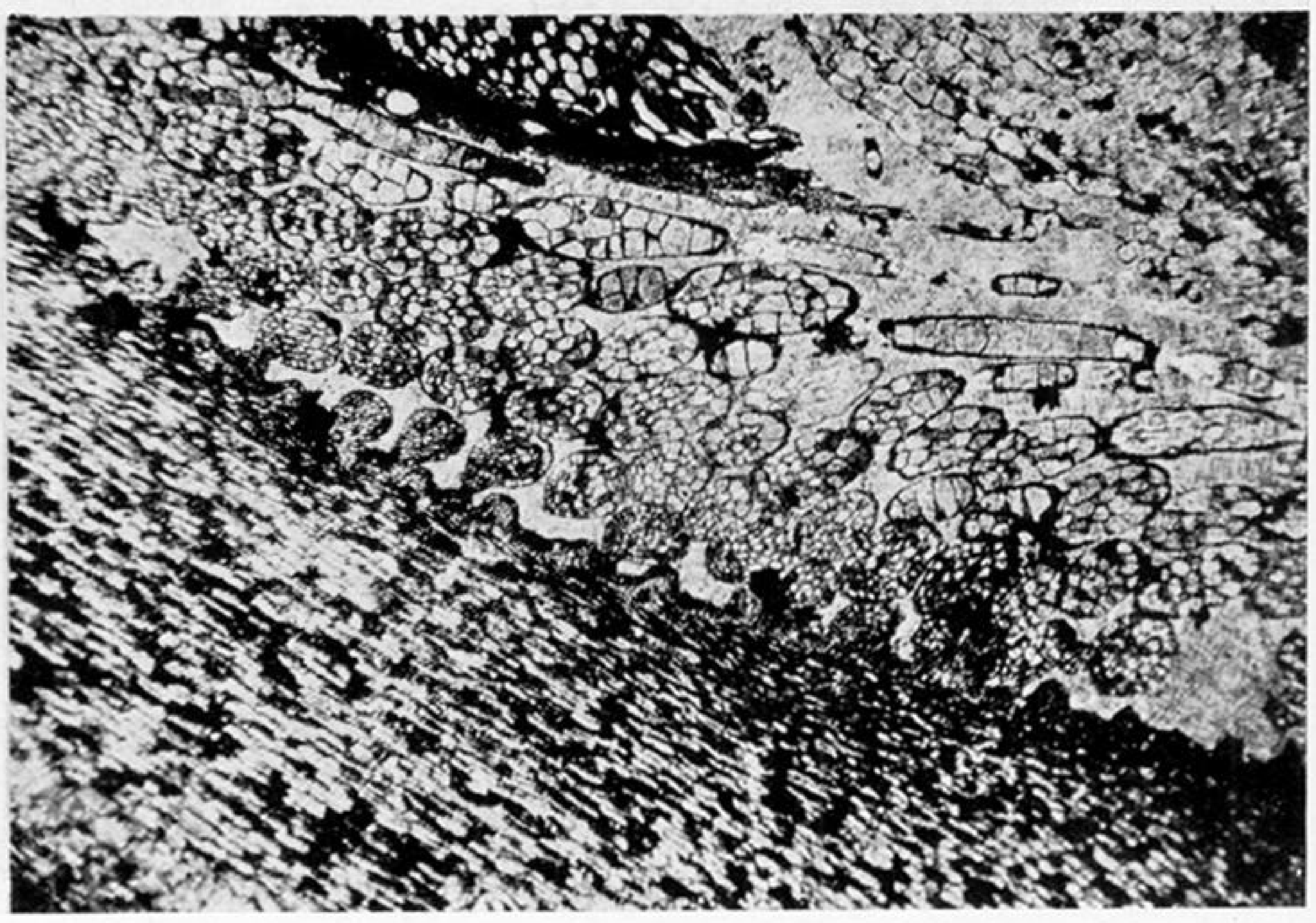

PLATE 10.

FIG. 31.—Transverse section of young petiole. The large sieve tubes flanking the immature central bar are well shown. Note also radial arrangement of wholly parenchymatous cortical cells. × 60. U.C.L. Coll. K606a.

FIG. 32.—Tangential section through cortex of a petiole, showing radial fissures in cortex. × 100. K. Coll. 1453.

FIG. 33.—Transverse section of young petiole, showing investment of stout hairs. × 30. K. Coll. 1985.

FIG. 34.—Transverse section of a similar petiole, showing both stout hairs and investment of aphlebiæ. × 30. K. Coll. 1982.

FIG. 35.—Part of a longitudinal section through young petiole, showing mature condition of stout hairs, which are cut in various planes. × 60. U.C.L. Coll. K606b.

FIG. 36.—An aphlebia trace with its parenchymatous sheath passing through outer cortex of petiole × 100. U.C.N. Coll. 261.91.

FIG. 37.—Transverse section of stem of *Zygopteris Kidstoni*. K. Coll. 719b.