PHILOSOPHICAL TRANSACTIONS.

I. *On* Clepsydropsis australis, *a Zygopterid Tree-fern with a* Tempskya-*like False Stem, from the Carboniferous Rocks of Australia.*

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(*Communicated by Prof.* A. C. Seward, *F.R.S.*)

Received January 16,—Read June 14, 1928.)

(Plates 1–6.)

Contents.

The material which forms the subject of the present communication was recently discovered at two different localities in New South Wales, and was received for investigation partly from Prof. Sir Edgeworth-David through Prof. A. C. Seward, F.R.S., partly from Mr. G. D. Osborne, Lecturer in Geology at the University of Sydney. The two localities are (1) near Mt. Tangorin, Hunter River District, (2) Lyndon, S. of Eccleston, Allyn River.

The six specimens from the first locality were all found *in situ* by Mr. G. D. Osborne, in a fresh-water conglomerate belonging to the Kuttung Series of rocks, at an horizon

[Published July 20, 1928.

at least 2,000 feet above the base of the series.* The single specimen from the second locality was found as a loose pebble, but although the exact horizon is unknown the fossil probably also belongs to the Kuttung Series.

This system of rocks is the younger of the two series of the Carboniferous as developed in New South Wales. The older beds, known as the Burindi Series, have yielded a small but well-preserved flora, in which *Lepidodendron* preponderates ; opinion seems to be agreed upon a Lower Carboniferous age for these beds. The overlying Kuttung Series, from which our material is derived, has yielded a very different flora, in which *Rhacopteris* is by far the most prominent genus, both owing to its abundance and to the number of species. The homotaxial relations of the Kuttung Series are still an open question.†

Dr. A. B. WALKOM‡ tentatively compares the flora with others known from the lower portion of the Westphalian (Middle Carboniferous) and adds—" From the present knowledge of the flora it does not appear possible to say how high up in the Middle Carboniferous the Kuttung Series may be extended." It may even range into the base of the Upper Carboniferous, but at any rate it seems clear that the flora represents a phase of vegetation distinct from and older than the *Glossopteris* flora of the overlying " Permo-Carboniferous " rocks, which succeeded an era of very widespread glaciation in the southern hemisphere.

The circumstances in which the material here described came into my hands may be briefly stated. In March, 1926, I heard from Prof. W. N. BENSON, of Dunedin, New Zealand, that some large specimens of a Zygopterid had been discovered near Mt. Tangorin in the Hunter River District of New South Wales. In the same vicinity a small fragment of *Clepsydropsis* had been found several years ago,§ and as any fresh discovery of material was likely to be of some importance, I wrote to Prof. BENSON expressing a desire to examine a specimen. In November, 1926, I was gratified by receiving from Mr. OSBORNE a silicified block, kindly sent by him at the suggestion of Prof. BENSON.

The fossil was at once recognised as *Clepsydropsis australis*, a plant previously known only from two small fragments ; it proved to be a specimen of more than ordinary interest. For it showed the existence, in this southern member of the family, of a type of stem-organisation such as had not, to my knowledge, been suspected before in any Palæozoic plant. The polished face showed that the plant must have had *a composite or false stem, formed of a number of weak leaf-bearing axes rising vertically, close together, leaves and stems being all bound together by means of adventitious roots into a single erect trunk.*

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* G. D. OSBORNE (1926), p. 394.

† A full discussion, with reference to previous literature, is given by SÜSSMILCH and DAVID (1920) ; see also G. D. OSBORNE (1926).

‡ Appendix I in SUSSMILCH and DAVID (1920), pp. 285–287.

§ SAHNI (1918), p. 375 ; (1919).

It was evident that the extraordinary mode of growth seen in the Cretaceous fern *Tempskya* had already been anticipated, in principle, by this Palæozoic fern. This being a result worth following up in detail, I wrote in December, 1926, to Prof. SEWARD, drawing attention to the main features of my specimen ; at the same time I sent him a few sketches and a slice of the block, for I had learned from Mr. OSBORNE that he had also sent him a specimen, and it was possible that a comparison of the two would bring out further facts. Prof. SEWARD'S specimen, which was much larger than mine, not only confirmed the general comparison with *Tempskya*, but also yielded fresh points of interest concerning the structure and mode of growth of this remarkable southern Zygopterid.

That the investigation of this valuable material was entrusted to me is entirely due to Prof. SEWARD'S great kindness, of which I have had ample proof in the past, and for which I find it difficult adequately to thank him. He not only made over to me the whole of the block in his possession, but also a splendid transverse section* and a longitudinal section which had already been prepared on his instructions. At a later date several other specimens were received from Mr. OSBORNE, so that eventually the entire collection was made available for this investigation.

I gladly take this opportunity of recording my hearty thanks to Mr. OSBORNE for the generous way in which he placed these specimens at my disposal. Some of them had already been presented to different institutions, but he very kindly secured their loan to me ; I am thus indebted also to the authorities of the Australian Museum, Sydney, the Mining Museum of the New South Wales Department of Mines, and the Museum of Geology at the University of Sydney. Lastly, I must express my thanks to Prof. BENSON for having originally written on my behalf to Mr. OSBORNE.

A description of the Mt. Tangorin collection was nearly ready when I received (in June, 1927) several sections as well as a piece from another specified specimen which was picked up near Lyndon, south of Eccleston, N.S.W. The exact horizon of the fossil is unknown, but it most probably belongs, like Mr. OSBORNE'S specimens, to the Kuttung Series. It was handed over by Prof. Sir T. W. EDGEWORTH-DAVID, F.R.S., to Prof. A. C. SEWARD, F.R.S., who very kindly suggested that I should incorporate a description in this paper. I must thank Dr. A. B. WALKOM, who originally had these sections under examination, for his willingness to place them at my disposal. The excellent preservation of some parts of this specimen cleared up several doubtful points in the anatomy of the root and rachis, but no well-preserved stems are included.

Apart from the sections received from Prof. SEWARD, a number of fresh ones were prepared in Lucknow from several of the specimens. As most of the sections were of large size and the work had to be done by hand, the process was slow and laborious, besides demanding skill. I thus owe a great deal of help to my attendant Shankar, whom I had trained to cut the slices with a wire-bow, and to my laboratory assistant Ram Singh Sharma, who did the grinding and mounting.

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* This section was unfortunately damaged in transit.

It may perhaps be useful to add that in dealing with large specimens, when the rock-cutting machine frequently presents difficulties, the hand-worked wire bow never fails, and that from uniformly hard blocks it has been possible to obtain large orientated slices which before grinding were no thicker than a millimetre. In the absence of large enough coverslips, photographic plates, ground thin on one side, were used, the ground surface becoming quite invisible in contact with the Canada balsam.

Summary of Previous Work.

Clepsydropsis australis is the only member of the Zygopterid ferns so far known from the southern hemisphere.* Both from the structural point of view and from that of geographical distribution the Australian species is a type of great interest; but our knowledge of the plant was confined to two small fragments. One of these was briefly described without figures in a preliminary report by Mrs. E. M. OSBORN† in 1915; the other was figured and described in some detail by myself a few years later.‡ The specimens were found within a few years of each other, at localities about 150 miles apart, both in New South Wales.

The first specimen, discovered near Barraba,§ is described as including three closely associated leaf-bearing stems, of which a length of a few centimetres is preserved. The stem anatomy is of the *Ankyropteris Grayi* type, with a 2/5 phyllotaxis but without axillary branches. The leaf-traces, given off as closed rings, soon become clepsydroid and retain this form. The association of this simple form of leaf-trace with the highly developed *Ankyropteris* type of stele is important. In her necessarily brief account Mrs. OSBORN does not give the relative dimensions of the petioles and of the stems upon which they were borne, a relation which as we shall see is of some importance in a reconstruction of the plant. But it is significant that she compared the habit with that of the massive tree-fern *Todea barbara*. This discovery of a Zygopterid fern in the southern hemisphere afforded proof of an unsuspectedly wide distribution of the family in Devono-Carboniferous times.

The second specimen, which through the kindness of Prof. SEWARD I was able to examine in 1917,|| was picked up near Mt. Tangorin in the Hunter River District, N.S.W., not far from the place where the specimens described in the present paper

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* Elsewhere the genus has been recorded only from Central Europe (UNGER, 1856, p. 165) and Siberia (STENZEL, 1889, p. 20; SCHENK, 1889, p. 353); further references in SAHNI (1919), pp. 82–3.

† OSBORN (1915), pp. 727–728.

‡ SAHNI (1919), pp. 81–92, Plate 4, and text-figs. 1, 2.

§ This fossil was at first supposed to have been found *in situ* in rocks regarded as probably Upper Devonian, but it is not impossible that it was derived from younger strata (see SAHNI, 1926, p. 237, footnote).

|| A brief account was read before the Cambridge Philosophical Society on February 19, 1917, but the full paper was not published till 1919 (SAHNI, 1919; see also SAHNI, 1918). The original specimen, now in several pieces, as well as the sections made from it, is in the collection of the Queensland Geological Survey, Brisbane.

were discovered. Although not found *in situ* the fossil bore no signs of transport, and the colour and mode of preservation were so nearly identical with that of the newly discovered specimens that it might very well have been a fragment of one of these. There now seems scarcely any doubt that it belongs to the same geological horizon. In this specimen the stem was not preserved, but a dozen finger-thick petioles, embedded in a packing of adventitious roots, had their bundles rather regularly orientated; it was concluded that the leaves had been preserved in their natural positions with respect to the missing "stem," which no doubt was erect. The facts suggested, at the time, the picture of a tree-fern of medium size with a *single* central axis surrounded by a thick zone of leaf-bases in several cycles. The fossil was apparently a part of this peripheral zone.

From an examination of this specimen, which is the only one yet figured or fully described, it thus seemed obvious that *C. australis* was "a fair-sized tree-fern resembling the fossil Osmundaceæ."* This, I believe, has been the commonly accepted view as to the constitution of the stem in this plant; and this view was strengthened by a comparison with *Asterochlæna* and with the Siberian form *C. kirgisica* of which STENZEL† figured a cross-section showing part of an apparently solitary central axis surrounded by a thick zone of petioles. However, as already stated, the stem-organisation as revealed by the newly discovered specimens was in reality very different from that of an ordinary tree-fern.

The only plant with which a comparison (in general organisation) suggested itself at the time was the Cretaceous fern *Tempskya*.‡ But on following up this comparison in the literature it was found that a rather similar kind of structure had also been described in some living ferns, for example, in *Hemitelia crenulata* METT. and in *Todea barbara* MOORE.§ It was then that I first realised the significance of a remark made by Mrs. E. M. OSBORN in her preliminary note. As she wrote, her specimen consisted of "three closely associated stems, each surrounded by roots and petiolar bases *rather suggesting a habit similar to that of Todea barbara*." From the passage here quoted by me in italics it is clear that she also had suspected the existence of a false stem, although she does not appear to have attached much importance to this peculiarity.

It is a pity that Mrs. OSBORN'S specimen was not figured or more fully described, for this suggestive comparison with *Todea*, which was worth following up, was lost sight of. It is also unfortunate that the fragment described by me shortly afterwards gave rise to such a misleading, though at the time perfectly natural, view as to the constitution of the stem. The picture of a monopodial trunk suggested by the latter specimen seemed at the time so convincing that it was accepted without reserve, and, so far as I know, has never been questioned, even by Mrs. OSBORN. It will appear from the description

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* SAHNI (1919), p. 86.

† BERTRAND (1911); STENZEL (1889), Plate 4, fig. 38.

‡ KIDSTON and GWYNNE-VAUGHAN (1911), pp. 1–20, Plates 1–3; STOPES (1915), pp. 9–21; SEWARD (1924), pp. 485–507, Plates 16, 17.

§ SCHOUTE (1906), pp. 198–207, Plates 18, 19.

given below that the comparison with *Todea barbara* cannot be carried so far as that with *Tempskya*, but it must be admitted that it was nearer the truth than the view which has for several years passed unchallenged.

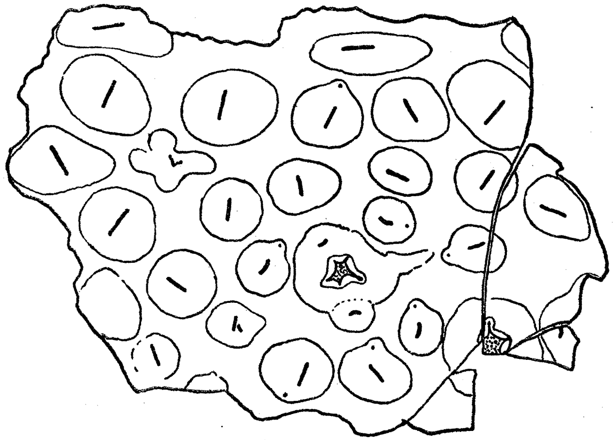
Description.

Gross Features.

A rough idea of the material may be gained from the list of specimens given below, where the gross features are briefly described. All the specimens are relatively small fragments of a trunk of considerable size, but the smallest of them is larger than the two specimens previously described.

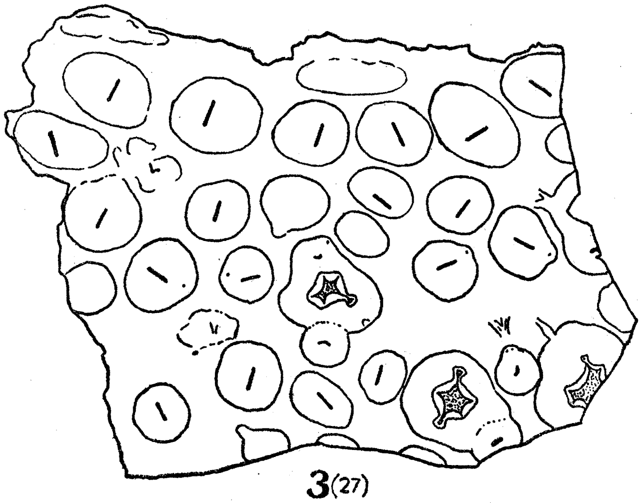
Locality 1.—*About* 4 *miles N.N.E. of Mt. Tangorin, Hunter River District, N.S.W. Found* in situ *by Mr. G. D.* Osborne, *in a decomposed fresh-water conglomerate at least* 2,000 *feet above the base of the Kuttung Series.* Horizon, *Carboniferous.*

Specimen 1 (Plate 2, fig. 2, Plate 3, figs. 10–12, Plate 4, figs. 18–25 ; text-figs. 1–8.—Received from Mr. Osborne, November, 1926).—A roughly transverse slab, about



1(9)

2(12)



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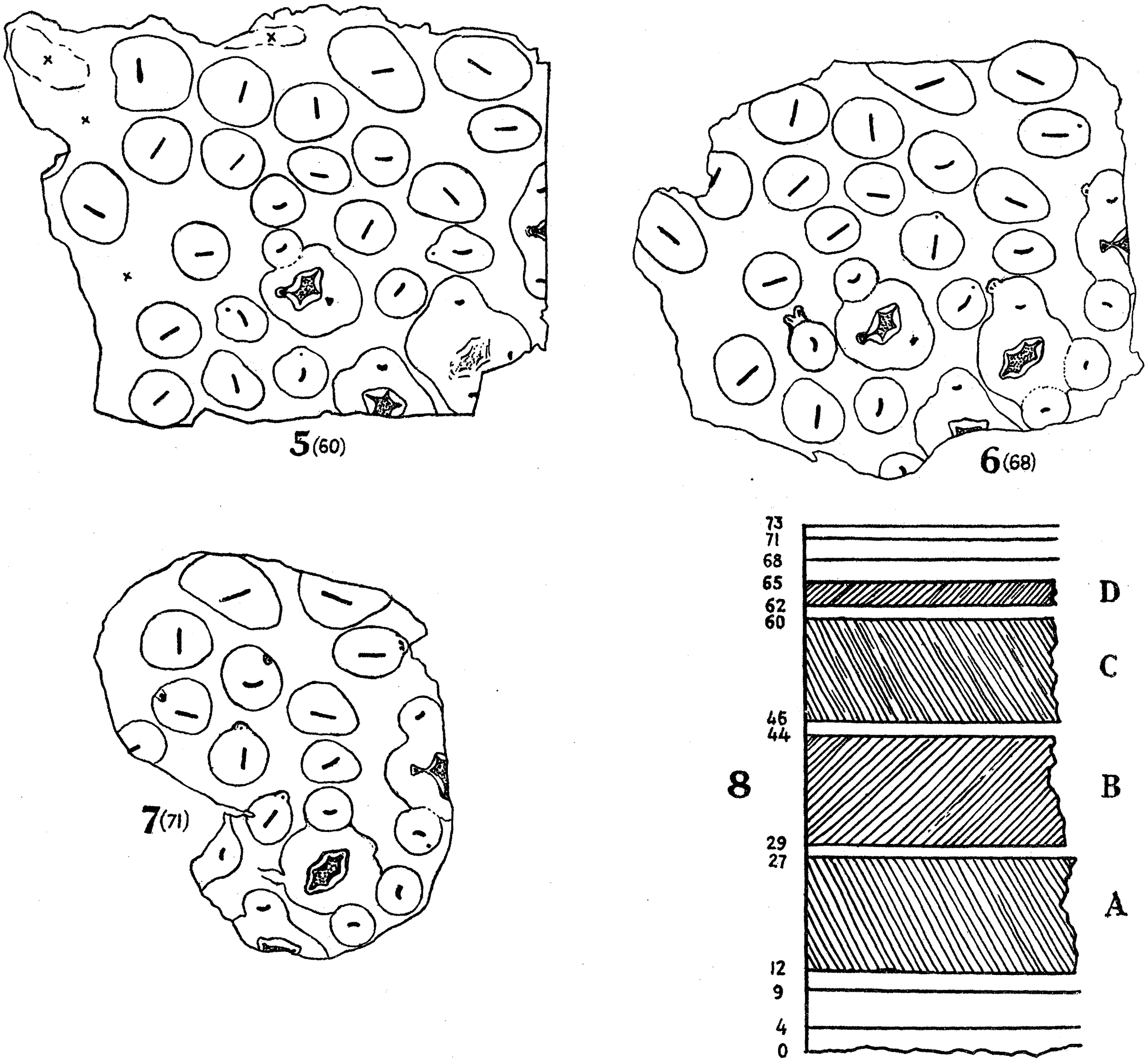


Text-Figs. 1–8.—The natural-size diagram (fig. 8) indicates the way in which specimen 1 was sectioned. The original is now in four blocks, A, B, C, D, and five thin sections, cut at the levels 4, 9, 68, 71, 73, besides one longitudinal section. The levels of the transverse sections, as well as of the upper and lower faces of the blocks, are indicated by numbers which give their heights in millimetres from the lower end (zero) of the fossil.

Figs. 1–7 are from direct tracings of some of these sections and polished faces, *all drawn as if viewed from the upper side*. (Conventions as in text-fig. 9.) All 3/4 nat. size.

7½ cm. thick, representing so much of the length of the false stem. This was cut into a series of transverse sections and slabs as shown in text-fig. 8, besides one longitudinal section. The cross-section of the upper end, measuring 10 by 7½ cm., includes four relatively slender leaf-bearing stems and about two dozen petioles, the stems and petioles being all embedded in a packing of adventitious roots and aphlebiæ; in their distal parts the petioles almost equal the stems in diameter. Three of the stems are only partially preserved, but enough is seen to make it certain that each bore leaves spirally on all sides. The stems, petioles and aphlebiæ are all cut transversely. There is thus no doubt that the composite trunk stood erect.

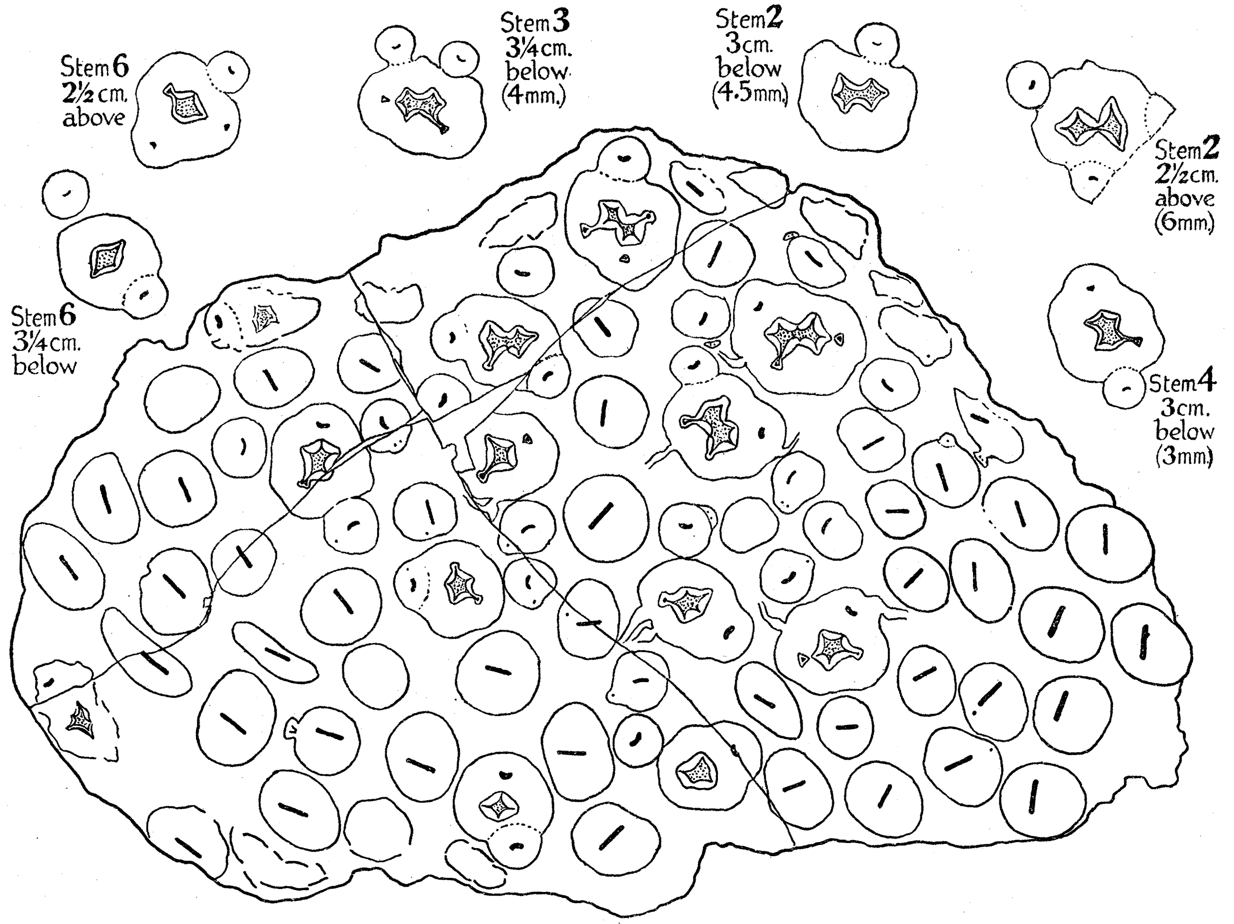
The leaf-traces are nipped off in 2/5 order from 5-rayed steles of the *Ankyropteris Grayi* type. One of the stems has a six-angled stele ; this is an early preparation for a dichotomy of the stele, but no actual branching is seen. Clearly the fossil is a relatively small fragment of a trunk of large size, which no doubt included many more leaf-bearing stems than are preserved in the specimen. The corner round which the four leaf-bearing stems are grouped (text-fig. 5) is evidently more central than the remaining parts, including only roots and the stouter petioles (with their aphlebiæ) which together must have formed a thick peripheral zone to the trunk.

A general comparison with the " false stem " of *Tempskya* is at once suggested, although the large number of persistent petioles in the *Clepsydropsis* form a striking point of difference. A conspicuous feature, which is common to all the specimens, is the large number of roots found as intrusions in the petioles. There is scarcely a petiole without such intrusions, and there are frequently as many as 20 in one petiole. But it is curious that the stems as well as the attached parts of the leaf-bases are invariably free from intruded roots.

Specimen 2 (Plate 1, fig. 1, Plate 2, fig. 2, Plate 3, figs. 4–9, 13, 14, Plate 4, figs. 15–17, 19–22 ; text-figs. 9–11.—Received from Prof. SEWARD, March, 1927).—A large block with a cross-section 20 by 14 cm. and a thickness (length) of about 9 cm. This is the most complete of all the specimens, including as many as 13 leaf-bearing axes, four of which show bifurcating steles. Text-figs. 9 and the natural-size photograph in Plate 1 are from a complete transverse section. A full description will be given later, but the topography of the section may be explained here.

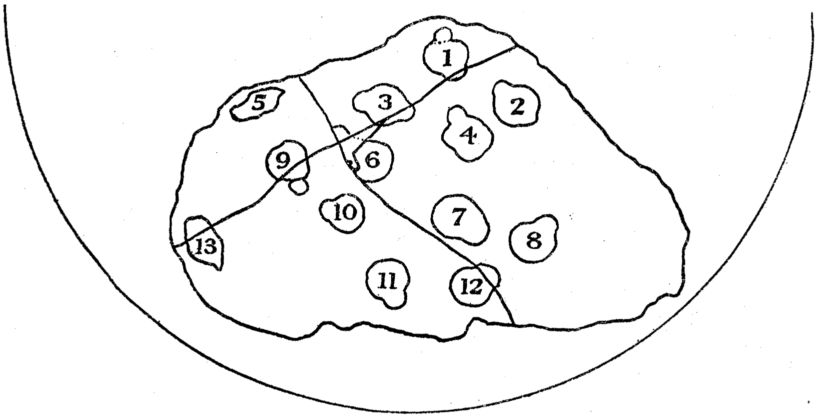
Assuming that the cross-section of the complete trunk was circular, the specimen represents a rough sector including a little less than one-third of the circle (see text-fig. 10). The top of the figure, where the bifurcating stems are grouped, probably lies not far from the centre of the false stem ; the right and left ends of the section, occupied by the stoutest petioles and by roots mostly running vertically, form parts of the peripheral zone. The actual exterior of the trunk is not preserved.

An important fact is the difference in the size and orientation of the petioles between the central and peripheral parts of the trunk. In the central part, to which the leaf-bearing stems are almost confined, the petioles are on the whole of small diameter and have their vascular bundles orientated with regard to their respective parent axes ; viewed apart from their parent stems, therefore, the

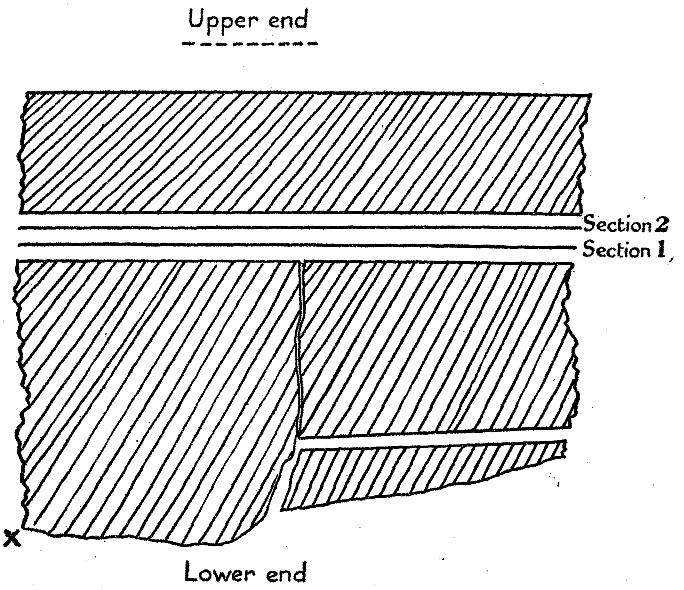


Text-Fig. 9.—Diagrammatic tracing of section 1, specimen 2, 3/4 nat. size, showing the outline of the stems and petioles (*the section is drawn as seen from below*). In the stem stele the "mixed pith" is dotted, the xylem is left blank. The foliar bundles are indicated mostly as dashes, the aphlebia-traces as dots. This diagram should be compared with the natural-size photograph in Plate 1. In the text the 13 leaf-bearing stems are referred to by means of numbers assigned to them in text-fig. 10.

The six small diagrams show some of the stems as seen in sections taken at the different levels indicated, above or below the level of the large section. Thus, stem 6 is shown at a level $2\frac{1}{2}$ cm. above, stem 2 at a level 3 cm. below, the large section. It will be noted that in the forking steles the interstelar distances increase only very gradually from below upwards; the figures within brackets give the interstelar distances in the sections figured. All 3/4.



Text-Fig. 10.—Diagram to indicate the numbers by which the 13 leaf-bearing stems in specimen 2 are referred to in the descriptions. The crossing lines indicate cracks in the section, and are useful as landmarks.



TEXT-FIG. 11.—Diagram 3/4 nat. size, of part of specimen 2 to show the approximate levels at which the different transverse sections were cut. Only the middle portion of the specimen is shown. The broken line at the top shows the highest point at the upper end of the specimen ; the vertical double line along the middle marks a crack in the lower block. The cross indicates the approximate level of the section shown in Plate 4, fig. 16.

petiolar traces in this central part, taken as a whole, show an irregular orientation. In the outer zone, on the contrary, the petioles are stouter and their bundles are placed tangentially *as if the leaves were borne in several cycles round a single central stem.*

In the central part, moreover, the roots ramify in all directions, whereas in the outer zone they mostly run vertically (Plate 1, fig. 1) ; and there are indications that the false stem was covered by a root-felt. Intruded roots are on the whole more common in the peripheral leaves, which represent the more distal parts of the petioles, than in the central leaves, which are seen cut in their narrower basal parts.

A notable feature is the tetrarch instead of the usual pentarch steles of two of the stems. In all the bifurcating stems also the resulting steles are 4-angular ; the presumption is that the two separate stems with 4-angular steles are recent products of dichotomy, although they may not be sister axes. This tetrarch condition persists for a considerable distance upwards before giving place to the typical 5-angled form (see text-fig. 9, stem No. 6). Associated with each dichotomy is an inevitable disturbance of the normal 2/5 phyllotaxis ; this is, however, restored higher up, though very gradually. This and other questions relating to the phyllotaxis will be discussed at a later stage.

Another remarkable fact is the extremely small angle of divergence in the bifurcating stem. This is clearly indicated by the serial sections drawn in text-fig. 9 ; the sister axes lie almost parallel to each other, that is, practically vertical, like the parent stem. These are facts of importance in a reconstruction of the plant, and are more fully considered below.

(Three sections have been prepared, two transverse and one longitudinal.)

Specimen 3 (No. 1089, Museum of Geology, University of Sydney).—This is the largest specimen in the collection, with a cross-section 20 × 15½ cm. and a length of about 13½ cm. It includes 11 leaf-bearing stems, two of which show signs of bifurcation. The upper end has been cut level and polished, but no transparent sections have been made. This specimen is not figured.

Specimen 4 (text-fig. 13. No. 18568, Australian Museum, Sydney).—A fragment including a length of 6½ cm. ; the polished upper end of the block, 14 × 6¼ cm., shows four complete stems and portions of several others. Two of the complete stems (text-fig. 13, B) are of unusually small size and are lying in contact with each other ; they are the result of a recent dichotomy. The parent axis, as seen at the lower end of the block, is drawn in text-fig. 13, A. The steles of the resulting axes are tetrarch, as in specimen 2 ; the angle of divergence is very small.

Specimen 5 (No. 20364, Mining Museum, Department of Mines, Sydney).—An irregular piece including half a dozen stems ; not figured.

Specimen 6 (private collection of Mr. G. D. OSBORNE).—This small fragment, in a cross-section of 10 × 12½ cm., includes as many as 12 leaf-bearing axes.

(Specimens 3–6 were received from Mr. OSBORNE in June, 1927.) Locality 2. *Lyndon, S. of Eccleston, Allyn River, N.S.W. Found as a loose pebble, probably from the Kuttung Series ; exact horizon unknown.*

Specimen 7 (Plate 5, figs. 26–38 ; Plate 6, figs. 39–51—Received in June, 1927, from Prof. SEWARD, to whom it had been handed over by Sir EDGEWORTH DAVID).—A black silicified specimen about 9½ × 6½ cm. in cross-section. This is the best preserved of all the specimens but does not include a single clearly preserved stem. The origin of the pinna-trace is well shown in two of the petioles ; the roots are mostly seen in true transverse section, their anatomy being very clearly shown ; root-hairs are present in large numbers, and are seen even on the intruded roots. Caught among the root-hairs a number of tetrahedral spores of three different sizes have been found, but there is no evidence that they belong to *Clepsydropsis*.

(Three transverse and four longitudinal sections have been prepared.)

From the above brief description the reader will have gained a fair idea of the construction of the false stem. Unfortunately, nothing is known of the foliage or of the fertile organs. It is therefore difficult to form an adequate picture of the plant as it appeared in life, but a partial restoration based upon the available data will be attempted after a full description of the material has been given.

Detailed Description.

In a previous account the anatomy of the root and of the petiole, including that of its vascular trace, was described in some detail. The preliminary forms assumed by the leaf-trace, as well as the stelar anatomy, had already been outlined by Mrs. Osborn. These points will now be illustrated and described in full; at the same time the structure and arrangement of the aphlebiæ, which are still rather obscure, will be elucidated as far as the available sections allow.

(i) *The Stem.*

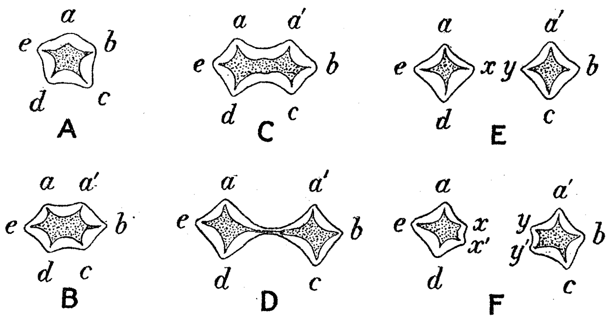
The leaf-bearing stem is ordinarily not much thicker than the distal parts of the petioles which it bears. The daughter axes immediately above the dichotomy may even be thinner than an average petiole in its distal part (text-fig. 13, B).

The cortex is in two zones, the outer sclerenchymatous, the inner wider, of larger thin-walled cells. The epidermis is not clearly differentiated, and no stomata have been seen; one would scarcely expect to find them on stems which are packed among roots. Of course, if the young shoots projected freely at the top of the false stem, which is quite possible or even likely, they may have possessed stomata; but if this was so, no trace of them appears to have been left on the older parts.

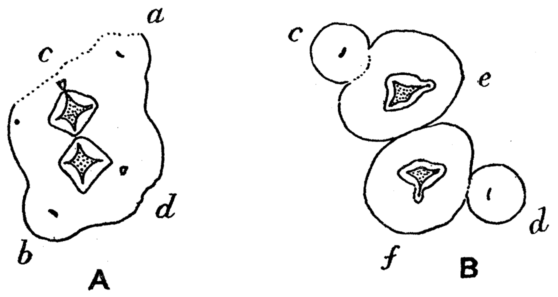
Multicellular emergences are frequently seen on the stems and petioles. In shape some of them recall prickles (figs. 23, 24, Plate 4), but their tips are not sharp, and at least in a few cases appear to be incomplete, as if something had been broken off from them. Fig. 41, Plate 6 (from a petiole), suggests a capitate gland; near it one or two spherical cell-masses (possibly detached glandular heads) are seen. These are, however, the only observed instances suggestive of secretory organs; as a rule one sees only the bluntly pointed and slightly curved stalks, attached by a broad base (Plate 4, fig. 24; Plate 6, fig. 42). In the brief preliminary account of her specimen Mrs. E. M. Osborn speaks of "external glands or hairs" (*loc. cit.*, p. 728). The prickle-like organs seen in my specimens may be only the hardened stalks of capitate glands which were functional in the younger freely exposed parts. A final expression of opinion on this point must, however, be reserved for the future.

The stele, as stated by Mrs. Osborn, is mainly of the *Ankyropteris Grayi* type. The stellate "pith" sends its thin rays far into the arms of the stele, from the ends of which the leaf-traces are nipped off in 2/5 order. The "pith" is, however, so poorly preserved that the parenchyma and tracheides composing it are barely visible. The xylem cylinder is always much thinner at the angles than at the bays, where it thickens out by bulging into the "pith." At the bays the tracheides are also wider and sometimes appear to be radially serrated, as if formed by cambial activity (Plate 4, fig. 15). Although no clear evidence of secondary growth has yet been found in the present instance, the possibility is to be kept in mind. The tracheides, even the narrowest of them, are scalariform. A narrow band of crushed cells closely investing the xylem probably represents the phloem.

The newly formed stems resulting from a dichotomy are, as stated, thinner than the ordinary stem ; their tetrarch steles are of a correspondingly small diameter, but they steadily enlarge as the stem gradually assumes the normal size.[*] Anatomically these tetrarch steles are similar to the 5-rayed type, although, of course, the phyllotaxis is different. The characteristic 5-rayed form as well as the normal 2/5 phyllotaxis is gradually restored higher up.



TEXT-FIG. 12.—Diagrams to show the stelar changes during a dichotomy. B, formation of a six-rayed stele (presumably by the forking of one of the rays). D, E, formation of two four-rayed steles. E, re-establishment of the five-rayed stele. The figures are not drawn from actual sections, but all the stages are represented in the sections examined and some have been figured elsewhere in this paper. No attempt has been made to mark the rays in their natural sequence, as it has not been possible to determine the transitional phyllotaxis. × 1.



TEXT-FIG. 13.—A forking stem from specimen 4, cut at the lower (A) and upper (B) ends of the block. The vertical distance between the two sections is 6 cm. A certain regularity is noticeable in the arrangement of the leaf-traces, which can be grouped into pairs according to "age," *a*, *b* : *c*, *d* : *e*, *f*. The members of each pair are, however, only approximately of equal "age." × 1.

Mode of Branching.—We have seen that the individual stems, with leaves borne spirally on all sides, were mostly grouped in the central part of the trunk, and passed vertically or almost vertically up through the matrix of intertwined roots. Although they may for a time follow a slightly oblique course, none of them are sufficiently inclined from the vertical to suggest that any of them projected as lateral branches

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[*] The stelar diameter varies from 5 to 8 mm., the diameter of the stems from 13 to 20 mm. In the rachis the corresponding sizes are 2·5 to 6·5 mm. (long axis of strand in cross-section) and 8 to 16 mm.

from the false stem. It seems the older branches ultimately strayed into the peripheral zone and there ended in a crushed state, among the stumps of the older petioles, but they retained their vertical position to the last.

In all the specimens the size of the leaf-bearing stems is of the same order, varying but slightly. There is no question of a main axis of which the numerous stems could be branches. The only mode of branching observed is equal dichotomy. The different stages in the process, so far as the stele is concerned, are shown diagrammatically in text-fig. 12 (see also text-figs. 2–7, 9, 13). Although the basal parts of the plant are unknown, it seems highly probable that the numerous axes in the false stem were the result of repeated forking of a single original axis, as was shown by Prof. SEWARD to be characteristic of *Tempskya*.

Phyllotaxis.—Two types of leaf-trace spiral are seen: (1) the normal 2/5 order, shown by the 5-rayed steles, and (2) the one associated with the tetrarch steles belonging to stems recently formed by dichotomy. The latter is difficult to describe in exact terms as it appears to vary a good deal, passing distally into the first type. Sufficient lengths of stem are not available to show clearly the way in which the normal pentarch stele, with 2/5 phyllotaxis, gives rise to the pair of tetrarch steles, and especially how the disturbance in the phyllotaxis caused by the dichotomy is restored in the branches.

During a scrutiny of the different stems for ascertaining the phyllotaxis I observed a difference in the *direction* of the leaf-spiral which it has been impossible to explain. Thus in the large section shown in Plate 1 most of the stems show a clockwise spiral, while one of them (No. 7) shows a counter-clockwise one.* Of the 11 stems in specimen 3 four show clockwise spirals, five the reverse. If all the stems have arisen from a single original axis, it is a puzzling question how the difference in direction first appeared. The irregularities associated with the dichotomy are probably concerned with this, but it is difficult to know in what way.

(ii) *The Leaf.*

Nothing is yet known of the distal part of the leaf; the only parts available are the lower part of the rachis, and the aphlebiæ. There is no trace of an absciss-layer in any of the petioles. Concerning the anatomy of the rachis and of the fully formed leaf-trace, there is not much to add to what was said in my earlier paper. While in its upper part the rachis may be as much as 16 mm. in diameter, thus almost equalling an average-sized stem, at its point of attachment to the stem it is generally not more than 8 mm. across. Multicellular emergences, sometimes large and blunt, at other times short and almost spine-like, have been noticed on the rachis; so far as observed there is nothing glandular about them (except in the solitary instance shown in Plate 4, fig. 41), but it may be that glandular heads have been broken off from their tips, as suggested above. Stomata have not been observed. The outer cortex, of small thick-

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* The section is figured as seen from below. The description in all cases refers to the appearance as seen from above.

walled cells, is about 1 mm. wide; it grades off into the inner cortex (consisting of larger thin-walled cells), which is much wider and includes scattered cells with dark contents (fig. 30, Plate 5). No trace has been preserved of the phloem, pericycle or endodermis.

The chief points remaining to be dealt with are (*a*) the origin of the leaf-trace and the changes it undergoes in ascending through the petiole and (*b*) the structure and arrangement of the pinna-traces and aphlebiæ.

The Leaf-Trace.—The origin of the leaf-trace and the changes it undergoes may be outlined in Mrs. OSBORN's words, while referring to figures in the present paper. "Leaf-traces leave the stele in the same order and manner as in *Ankyropteris Grayi*. As each departs it is of a triangular shape with rounded angles (Plate 3, figs. 5, 6, 10) the apex of the triangle being the point of attachment to the stem [stele]. This bundle soon becomes flattened tangentially (Plate 3, fig. 5, on the left) so that before it leaves the cortex it has the appearance of a flattened ring, slightly curved, with the convexity of the curve on the adaxial side. As the trace passes outwards it becomes still more flattened and tangentially elongate (Plate 5, figs. 30, 31, 34, 35), until when a little above the base of the petiole it appears as a long band-shaped xylem-mass, without curvature, rather constricted in the middle and with a peripheral loop at each end" (Plate 3, fig. 8, on the left; Plate 4, fig. 19; Plate 5, figs. 32, 33).

Each peripheral loop is bounded by a row or two of small tracheides. Within the loops the delicate parenchyma, including a few narrow tracheides, is faintly preserved in a few traces (Plate 5, fig. 30). For some time before the trace assumes its final shape the parenchyma forms a connecting bridge between the two loops (Plate 5, figs. 30, 34, 35); then for a short distance upwards the place of the parenchymatous bridge is taken by a row or two of small tracheides (Plate 5, fig. 31). Even after the characteristic form has been arrived at the leaf-trace continues to increase in size, thus keeping pace with the increase in diameter of the petiole.

The Pinna-Trace.—From P. BERTRAND's work* we know that in *C. antiqua* the pinna-traces are nipped off as closed rings alternately from the two ends of the petiolar bundle. In *C. australis* the process is the same. Several traces in various stages of formation were figured in my earlier paper.† In the present material the best preserved trace is the one shown in Plate 5, figs. 32, 33, where an earlier stage in the formation of a pinna-trace is seen. A later stage is represented in Plate 5, fig. 36. It is a curious fact that while pinna-traces have frequently been seen, no pinnæ have yet been found; nor have any pinna-traces been observed detached from the petiolar bundle.

The Aphlebiæ.—Very little was previously known of these organs in *C. australis* and several points concerning them are still obscure. It seems fairly certain that they are the proximal homologues of the pinnæ, for their relation to the primary rachis and probably also the mode of origin of their vascular supply are essentially the same.

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* BERTRAND (1911, *a*), pp. 15–18.

† SAHNI (1919), p. 87, text-fig. 2.

In 1919 I figured (*loc. cit.*, p. 87) a detached ring-like strand, placed at an angle near one end of a petiolar bundle, as a probable aphlebia-trace, but no aphlebiæ were then made out. In the better preserved material now available aphlebiæ occur in large numbers, both attached to the rachis and in the detached condition, packed among the adventitious roots (Plate 2, fig. 3; Plate 3, figs. 11, 12; Plate 4, fig. 18; Plate 5, figs. 26, 29; Plate 6, fig. 40). In transverse sections of the false stem they are invariably cut transversely, showing that they grew vertically upwards. Each aphlebia, directly it leaves the rachis, forks into two equal lobes which lie tangentially to the rachis and closely applied to it. The two lobes then fork repeatedly, producing finer and finer segments, each with a single slender strand; the ultimate segments are minute, almost filiform (Plate 5, fig. 26). The mode of branching of the aphlebiæ is very evident in some sections (for example, those shown in Plate 3, figs. 11, 12; Plate 5, fig. 29), where the segments are undisturbed in position and may still be seen in pairs. Sometimes the aphlebia-lobes of two or more neighbouring petioles may be seen packed together in a sort of mosaic (Plate 3, figs. 11, 12).

The anatomy of the aphlebia is fairly well preserved (Plate 4, fig. 18; Plate 6, fig. 40); the segments are generally lenticular in cross-section, bounded by a well-defined epidermis of small regular dark cells; no stomata are seen. The large-celled mesophyll includes scattered cells with dark contents; it encloses a slender stele consisting of a few very narrow tracheides surrounded by several layers of equally narrow thin-walled cells.

Actual aphlebia-traces have not been observed in the present material, but their position and outward course through the petiolar cortex are marked by cavities in the tissues. Their exact points of origin from the leaf-trace are uncertain, but they seem to come off from the actual margin of the leaf-trace, as do the pinna-traces. Their outward course through the cortex is usually dorso-lateral, as in *Asterochlæna*.*

I have suggested above that the aphlebiæ are probably the basal homologues of the pinnæ. Whether the part of the rachis bearing the aphlebiæ was separated by an interval from the lowest pinnæ is a question; quite possibly the more distal aphlebiæ passed by gradual transitions into pinnæ. Sufficient lengths of individual leaves have not been serially sectioned to decide the point. It is true that the aphlebia-traces usually come off in the region of the petiolar base, where the leaf-trace still shows a slight curvature, and sometimes even lower down, while the leaf-trace is still in the stem cortex. But both aphlebia-traces and aphlebiæ have also been observed on higher parts of the rachis, where the leaf-trace is fully formed (see the peripheral zone of the false stem shown in text-fig. 9, to the right.)

It is noteworthy that the first dichotomy of the aphlebia-trace frequently occurs before the aphlebia has become free from the rachis. In such cases the pair of strands

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* Bertrand (1911), Plate 4, fig. 22, a photograph which, except for the single leaf-bearing axis, shows some striking points of resemblance with *C. australis*.

lying in the tangential plane within the petiolar cortex shows a striking resemblance to the condition seen in the Dineuroideæ, suggesting that the distinction between that sub-family and the Clepsydroideæ is after all not a very sharp one.

It is a pity that we know nothing of the more distal part of the leaf. No pinnæ or even detached pinna-traces have yet been observed.

(iii) *The Root.*

As already observed, the roots in the central part of the false stem ramify in all directions, forming a packing round the stems and petioles; while those in the outer zone usually follow a vertical course, and appear to have formed a sort of felt round the trunk.

Roots have been seen attached to the decurrent leaf-bases but never to the free part of the leaf-axis. A few appear to come off from the stem in the neighbourhood of leaf-bases. But no root-traces are preserved, hence their actual point of origin is uncertain.

Anatomy.—The best preserved roots are seen in the Lyndon specimen (No. 7). They vary in diameter from less than 1 mm. to as much as 3 mm. The stele is invariably diarch and usually well developed; only scalariform tracheides have been observed, even in the protoxylem. The phloem consists of two or three layers of thin-walled elements, of which the larger ones may be sieve-tubes. A pericycle is clearly marked off by its slightly thicker-walled cells and comparatively dark colour. The endodermis forms a well-defined dark zone, round which, in the best preserved roots, three distinct layers of the cortex are visible. Of the latter the middle zone is prominent in the photographs as a dark narrow band. The root-hairs are unusually well preserved; they are straight and unbranched, often standing out radially like the bristles of a bottle-brush. No root-caps have been seen.

Intrusions.

The numerous roots found as intrusions in the petioles raise interesting points for discussion, and are best considered separately.* They recall the way in which Stigmarian rootlets commonly occur in many of the English coal-ball petrifactions. There cannot, however, be much doubt that the intrusions here described all belong to the *Clepsydropsis* itself, although a continuity has not been observed between any of the intruded roots and those outside the petioles. The number of intrusions is sometimes so large that the greater part of the petiolar cross-section is occupied by

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* It is well known that in some species of *Lycopodium* cross-sections of the stem often show a number of roots embedded in the cortex of the stem. These roots originate near the stem-apex and pass downwards through the stem-cortex, often for long distances, before they emerge. There is, however, no real comparison between these roots and those intruded into the petioles of *Clepsydropsis*.

them; the result is that while the thin-walled tissues of the rachis have been badly crushed, the petiolar strands have been pushed out of position and distorted. As many as two dozen intrusions have been counted in some petioles (Plate 5, fig. 27). Roots have even been found enclosed in other root-intrusions (but never in the free roots); fig. 36 shows three invading roots lying one inside the other in concentric fashion; in such cases usually the only parts preserved are the outer cortex and the diarch xylem-plate, of which the two poles are generally seen a little distance apart, the intervening centripetal tissue, not yet lignified, having been crushed (see Plate 5, fig. 31, in which the steles of both roots are visible). Occasionally two roots lie side by side in the cortical sheath of a third root.

The xylem in the intruded roots (which are all at an early stage of development) is invariably feebly developed, and the middle zone of the cortex is not differentiated. In other respects the structure is similar to that of the roots outside. It is remarkable how well the root-hairs have been preserved, even in the intrusions (Plate 5, figs. 27, clearly seen with a lens, 28; Plate 6, figs. 41, 43, 46), a fact which suggests that they continued to function as well as in the roots outside.

The invading roots almost invariably run lengthwise through the petiole. Whether they grew downwards or upwards, or some in one direction and others in another, is a question which will be discussed presently. A noteworthy fact about the distribution of the intruded roots is that they are commonest in the large petioles towards the periphery of the trunk (see Plate 1), becoming gradually rarer in the thinner petioles towards the interior.

As the large outer petioles are those of the older leaves cut at a higher level, while the inner petioles are younger but cut nearer the base, where they are thin, one is inclined to suspect that the roots grew downwards through the leaf-axis. In spite of the number of petioles examined, intruded roots were invariably absent from the very base of the leaf, where it is attached to the stem; nor are such roots found in any of the stems, although the latter are literally packed among roots. Moreover, not a single root has been observed piercing the sclerenchymatous sheath of a rachis, whether from within or without. These facts, combined with the almost invariably longitudinal course of the intruded roots, would seem to show fairly conclusively that the roots made their way into the leaves from above.

Such an entry they can have effected in one of the two following ways: Either they may have penetrated the living tissues of the leaves in their younger parts, which being presumably devoid of sclerenchyma would offer less resistance to their entry; or, what seems far more probable, they entered through the decaying upper ends of old rachis-stumps.

If it is supposed that they made their way into the younger distal parts of the leaves before the latter became elongated, there would be at least two difficulties to be explained. In the first place (to put it crudely), there seems to be no reason for the roots of a plant to penetrate its own living parts. Secondly, one would have to assume that when the leaves elongated, as they must have done fairly rapidly and to a very considerable height, the external parts of these roots were carried up with them, stretching in order to keep pace with the growth of the leaves. One has only to imagine such a hypothesis in order to dismiss it at once as untenable.

On the other hand, it is quite natural to suppose that many of the roots in the peripheral zone, in their normal downward course, would find themselves entering the open ends of old rachis-sheaths. Once having gained an entry, they coursed downwards through the decaying softer tissues of the rachis, confined within the sclerenchymatous sheaths of the latter, till their growth was arrested by the live tissues of the leaf-base. This conjecture appears quite likely, for the crushed upper parts of several rachis-stumps have been observed, full of intruded roots, and with their sclerenchymatous sheaths flattened, indented or fractured. The clearest example was seen in the small specimen originally received from Mr. OSBORNE. It is shown photographed in fig. 24, Plate 4, and in text-figs. 1–4. The sclerenchymatous sheath has been invaginated and ruptured in several places, while the vascular bundle is seen bent upon itself. The photograph shows a section taken at a level 9 mm. from the lower end of the block. At 27 mm. (text-fig. 3) and 29 mm. the rachis was in a still more crushed state ; at 44 mm. (text-fig. 4) scarcely a trace of it was left. In text-fig. 5 its place is marked by a cross. Another rachis in the same specimen, already showing signs of disintegration at 9 mm., was similarly traced upwards through the block, becoming more and more decrepit, till it ended at about 60 mm. In this way several other rachis-stumps were followed up to their ends, or almost up to their ends, in the large specimen received from Prof. SEWARD.

Diagnosis of Clepsydropsis australis *E. M. Osborn sp. (in M.S.)*[*] (1).

Large tree-ferns with a tall and erect, probably unbranched, false stem at least a foot in diameter and covered externally by a root-felt. The false stem is composed of numerous repeatedly forked leaf-bearing axes and relatively stout, erect petioles, the stems and petioles being all bound together by and embedded in a packing of adventitious roots and aphlebiæ. Individual stems about 12–20 mm. in diameter ; petioles cylindrical, about 8 mm. in diameter at the base, distally increasing to a diameter almost equalling that of the stem. Multicellular emergences (? capitate glands) are present on both stems and rachis.

Cauline stele of the *Ankyropteris Grayi* type, but without axillary branches. The newly formed branches of a dichotomy have a tetrach stele, but the normal pentarch stele is restored higher up. Leaf-traces usually arise in 2/5 order as closed rings, which at first become tangentially flattened, then develop a slight abaxial curvature and ultimately become clepsydropsoid.

The fully formed petiolar strand is distinct in shape from that of the other species,

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[*] See SAHNI (1919), p. 82.

C. antiqua and *C. kirgisica*; "it is proportionately thinner, has pointed instead of truncated ends, and the internal contour of the peripheral loops is fusiform instead of elliptical."* Pinna-traces nipped off as closed rings at long intervals, alternately from the two ends of the petiolar trace. Pinnæ unknown. Aphlebiæ distant, arising in two alternating series, repeatedly forked, segments linear, mostly lenticular in cross-section, ultimately filiform. Roots diarch, many intruded into old rachises.

Occurrence.—Specimens have been discovered on four different occasions at the following localities, all in New South Wales :—

(*a*) In the bed of the Manilla R., 12 miles west of Barraba, N.S.W. Originally supposed to have been found *in situ* in shales and tuffaceous agglomerates of the Barraba series, and regarded as of uppermost Devonian age ; probably derived from younger strata.†

(*b*) Near Mt. Tangorin, Hunter R. District, N.S.W. Not found *in situ*, but regarded as probably of Carboniferous age.‡

(*c*) Four miles N.N.E. of Mt. Tangorin in the Hunter River District, N.S.W. Found *in situ* in a decomposed fresh-water conglomerate of the Kuttung Series at a horizon at least 2,000 feet above the base of the series. According to Sir EDGEWORTH DAVID the horizon is probably Lower Carboniferous. (In all probability (*b*) also belongs to the same horizon.)

(*d*) Lyndon, south of Eccleston, Allyn River, N.S.W. Not *in situ*, but probably from the Kuttung Series (Carboniferous).

Reconstruction.

No really satisfactory picture of the habit of a plant can be formed without some acquaintance with the foliage. But with the facts at our disposal it is none the less worth while to attempt such a reconstruction.

We have seen that the false stem was probably of large diameter and that it stood erect. The formation of such a composite stem, with a peripheral zone consisting of petioles and roots, would enable the individual leaf-bearing stems to attain a much greater height than they could have done had they stood independently. Nor could leaf-bearing stems of such modest dimensions have supported by themselves leaves of the size suggested by the petioles alone (even apart from the question of the weight of a lamina, whose existence we have, I think, no reason to doubt).

The petioles in the peripheral zone of the trunk have their bundles placed tangentially, as if the leaves were borne in several cycles round a single central stem. It is clear that if only the peripheral zone had been found preserved no one would seriously have

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* SAHNI (1919), p. 88.

† This was the first specimen to become known (OSBORN, 1915, pp. 727–728).

‡ SAHNI (1919), p. 81.

doubted that there was only a single parent axis. But now that the facts are known, a symmetrical disposition of the peripheral leaves, irrespective of their origin from one central axis or from several centrally grouped ones, is not only found to be possible, but is even to be expected on mechanical and physiological grounds. Although the foliage is not preserved, there is scarcely a doubt that round the top of the "false stem" these leaves of mixed origin formed what may be called a "false crown."

A little consideration will show that no twist in the petioles is needed to reduce their irregular disposition in the central part to the orderly arrangement at the periphery of the trunk. All that is necessary is a slight radially outward inclination of each petiole during its ascending course through the matrix of roots. Sufficient lengths of the "false stem" are not available to allow one to follow a rachis from the centre to the periphery; but knowing the extremely small angle of inclination, we can say that a petiole arising from a stem near the centre of the trunk probably did not reach the surface before a height of several feet from the base was attained. This fact alone gives some idea of the height which the entire leaf may have reached.

Fortunately it is also possible to form a rough minimum estimate of the height of the trunk. In the large section figured in Plate 1 there are 13 stems, four of which show bifurcating steles. Considering that this specimen represents less than one-third of the entire trunk, the number of stems in the complete cross-section at this level must have been well over 40. This would mean that the original axis must have undergone at least six successive dichotomies previously to the one actually seen. This fact is of great use in a reconstruction of the false stem, for, if we knew the minimum vertical distance required for the completion of a dichotomy, till the next one is initiated, we could form at least a rough idea of the height of the trunk at the level of the section.

TEXT-FIG. 14.—Restoration of *Clepsydropsis australis*.

We know that the process of bifurcation was extremely slow. The natural size drawings in text-figs. 2–7, 9 and 13 show some of the forking stems cut at different levels. The vertical distances between the sections, as well as the interstelar distances (as measured from centre to centre of the paired steles) are given in millimetres in the table below, where also the calculated angles of bifurcation are stated :—

Sections.	Vertical distance between lowest and highest section.	Interstelar distance.		Angle of bifurcation.
		In lower section.	In higher section.	
Specimen 1 (stem in corner) (text-figs. 2–7)	59	3	Under 4	59′
Specimen 2 (text-fig. 9)—				
Stem 2	55	4·5	6	1° 35′
Stem 3	32·5	4	4	0
Stem 4	30	3	3·75	1° 26′
Specimen 4 (text-fig. 13)	60	6·5	11	4° 17′

In one of the stems, as we see, the axes of the sister steles ran quite parallel for a distance of 32·5 mm. ; in the other cases they diverged at angles varying from only 59′ to 4° 17′. The length required for a complete dichotomy of such a stem can best be realised by actually drawing one of the dichotomies to scale.

Even at the level where the two stems just become free from each other they will not be ready for a fresh dichotomy, for the normal size and pentarch stele would not be acquired till several inches higher up (to judge by the only observed case, namely, stem No. 6 in specimen 2). This stem shows a tetrarch stele at both ends of the block, 9 cm. apart ; at the level shown in the small separate figure (text-fig. 9) the stele is only just beginning to acquire the five-rayed shape. Without entering into further detail it may safely be agreed that the average length of a complete dichotomy was at least 1½ to 2 feet (45–60 cm.), which would give the height of the " false stem " at the level of the section shown in Plate 1 as at least 9 to 12 feet (2·74 to 3·66 metres). This is a modest estimate, and of course the section is not necessarily taken from near the top of the false stem.

It is unprofitable to attempt an exact estimate of size on data of the kind available, but one may say without fear of exaggeration that *Clepsydropsis australis* was a tree fern exceeding in size of trunk and probably approaching in height some of the largest tree-ferns of the present day. The trunk, so far as we know, was unbranched, and no doubt stood upright, perhaps recalling that of a large columnar cycad more than any tree-fern known.

An intriguing problem is the presence of such large numbers of apparently active and healthy roots inside the older petioles. Viewing the facts as they are, and they have been sufficiently discussed above, we may conclude that these invading roots entered only the stumps of fallen or decayed leaves, and that they grew downwards till their progress was arrested by the living cells of the leaf-base. The xylem strands of the leaf-stumps might still have conducted a feeble stream of water, while possibly the humified remains of the softer tissues may have provided the roots with assimilable food materials. Thus it is not inconceivable that this Palæozoic tree-fern actually reared itself, in part at least, " upon its own ashes."

The likelihood that there was a root-felt over the false stem has already been mentioned. The predominantly downward course of the roots enhances the probability that the root-felt was thicker round the lower parts of the false stem ; here, indeed, such a thick supporting structure would be more in demand than higher up. Considering that at the very base there was probably only a single leaf-bearing stem, which only by gradual degrees gave rise to the system of dichotomising axes, it is probable on mechanical grounds that as the sporeling grew into a tree-fern the basal parts became enclosed in a root-felt of ever-increasing thickness, which not only fixed the whole stem to the soil, but formed a broad base for the support of the column. In the upper parts of the false stem the root-felt, if there was any, would be thinner so that the stumps of old leaves could project from the surface, only to become subsequently invaded by the younger roots and eventually enclosed in the increasing thickness of the root-felt.

There is no indication that any of the leaf-bearing stems projected as lateral branches from the false stem. But at the apex of the trunk, the young free shoots each bearing a few erect circinately coiled leaves probably grew up vertically for a short distance from among a tangle of fresh roots. Between them were a few older leaves variously orientated and, surrounding the whole apex, the " false crown " of oldest leaves. Owing to the almost vertical position of the rachises the crown would probably have the form of a narrow inverted cone.

Speculations as to the Nature of the Frond.

Unfortunately our knowledge of the distal parts of the leaf of *C. australis*, indeed of the Zygopterideæ as a whole, is scanty. Although no lamina has yet been discovered it is difficult to picture these large tree-trunks as carrying merely a bunch of sticks, like the rachises to which our knowledge is almost confined. The size of the rachises alone suggests a large lamina, but there is at present no evidence as to the nature of the frond.

Among the fern-like leaves occurring in the rocks of the Kuttung Series species of *Rhacopteris* are by far the commonest, but of course without further evidence it cannot be asserted that any of them belonged to *Clepsydropsis*. In reply to a letter suggesting this possibility Mr. G. D. OSBORNE wrote (March 22, 1927), " Unfortunately the material comes from a conglomerate where fern fronds would not have much chance of being preserved. I have noticed, however, that wherever one gets *Rhacopteris* in the Carboniferous, there one finds numerous small stems preserved. These are of a brown colour and possess a smooth surface."

In a more recent letter (June 20, 1927) Prof. SEWARD said, " I wondered whether the fronds may be of the *Rhacopteris* type, but I think Walton in his recent paper figures the comparatively small rhizome bearing some *Rhacopteris* fronds." Apparently these fronds belong to a plant of a very different habit and smaller size. *Rhacopteris*, however, is an artificial genus, and the possibility is not excluded that some other species of the genus, hitherto not found attached, were borne on the stem of *C. australis*. *C. australis* was apparently not such a rare species in the Carboniferous flora of New South Wales; one may therefore be led to entertain hopes of a discovery that will settle the question, but considering the habit of the plant the chances of finding attached fronds in the expanded condition are probably remote.

Other Plant-Remains found preserved in the False Stem.

In the course of investigation the remains of several other plants, as well as tetrahedral spores of unknown origin, were found in the false stem.

(i) *Tetrahedral Spores* (Plate 6, figs. 47–49).—These are seen in considerable numbers in the Lyndon specimen. They are of three different sizes, about 68 μ, 31 μ and 8·7 μ in diameter respectively. The commonest are those of the smallest size: mostly isolated and scattered among the root-hairs, they are sometimes found in masses of as many as a dozen or more in pockets among the roots. Of the largest spores only a few were met with. The triradiate mark is clearly visible on all three types of spore; in the two smaller kinds the exine shows a sculpturing of very fine dots. Many of the spores have opened along the triradiate mark, which is seen agape (figs. 47, 49, Plate 6), but it is doubtful if this has anything to do with functional dehiscence. No undoubted germinating spores have been met with.

The only way in which the spores could have reached the interior of the trunk would be by falling on to the stem apex and later becoming enclosed by the growing roots and other organs.

The attribution of the spores is purely a matter of conjecture. Being of three sizes they may either belong to different species or, possibly, they may be heterospores, a feature not so far observed in the Zygopterideæ; they may even be " homospores " of variable size.* There is no proof that any of the spores belong to the *Clepsydropsis*, although the frequent occurrence of one kind in masses may indicate that they do; moreover, it would be easier for such relatively heavy spores to fall on to the stem-apex

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* Considerable variation in the size of spores has been observed in other vascular plants in which true heterospory has not been proved. Prof. BOWER (1923, p. 264) records it in *Notholæna affinis*) and J. M'L. THOMPSON (1917, p. 161, figs. 12–14) figures in *Platyzoma microphyllum* spores of three different sizes. As Prof. BOWER (*loc. cit.*) states, " These facts suggest initial heterospory, but they have not yet been tested by cultivation of the prothalli."

from leaves held above it, than for them to be blown over to that height from a different plant, unless the latter was also a tree-fern. On the other hand, we have to keep in view the possibility that some of the spores may belong to a vascular cryptogam growing as an epiphyte upon the *Clepsydropsis,* a view suggested by certain facts presently to be described.

(ii) *Fungus* (Plate 4, figs. 20, 21).—The intercellular mycelium of a fungus shown in Plate 4, figs. 20, 21, was found in a stem in one of the Mt. Tangorin specimens (specimen 2). Similar hyphæ are of frequent occurrence in several other specimens. It has not been possible to ascertain whether the mycelium is septate. No haustoria have been recognised, but this may be due to the exigencies of preservation; it is therefore impossible to say whether the fungus was a parasite or a saprophyte. Certainly, the presence of the fungus is not associated with hypertrophy or any other kind of distortion in the tissues in which it is found.

Towards the top of fig. 20 (to the right) are seen a number of spherical bodies of variable size, a few of which are enlarged in fig. 22. They may at first sight be taken to be resting spores, produced singly in spherical sporangia, but in all probability they are of inorganic origin. They have never been found attached to the mycelium and are not always found even associated with it. The thin-walled sacs appear to be merely precipitation membranes formed round nuclei of soluble matter.* Similar deceptive appearances have been seen in all the Mt. Tangorin specimens.

(iii) *Axis of an unknown Vascular Plant* (Plate 5, fig. 26; Plate 6, figs. 50–51). —Among the peripheral transversely cut roots of the *Clepsydropsis* there is, in the Lyndon specimen, a cylindrical axis with a stele showing well-developed secondary wood. The axis is only slightly larger than the surrounding *Clepsydropsis* roots, and the structure of the cortex is very similar to theirs, so that at first sight the organ might be taken for a larger *Clepsydropsis* root with secondary growth. Unfortunately, the only material available is two transverse sections; one of these is seen in section 3, but is very oblique and badly preserved; the other, seen in section 1, is described here in some detail (see Plate 6, figs. 50–51). It is a pity that no longitudinal section is available; the description is therefore incomplete.

The stele is solid, the xylem consisting entirely of tracheides. All the walls are provided with bars of thickening which are rather distant and usually multiseriate, so that the pitting cannot be described as typically scalariform. The centre of the stele is occupied by the primary xylem, but neither the position nor the number of the protoxylem strands can be made out. The surrounding secondary xylem, radially about half a dozen cells deep, is devoid of all parenchyma, like the primary wood; there are no medullary rays. The tracheides of the secondary wood appear to be of short length, like parenchymatous tracheides, to judge by the frequency of the horizontal walls, which also show the rather characteristic sculpturing. In each radial series the

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* SAHNI (1919), p. 88.

elements increase steadily in size from the centre outwards, those next the cambium being wider tangentially than radially.

When undisturbed the stele must have been circular in section, but in our photograph it is incomplete on one side, where it is giving off the supply to a lateral organ. The outline of the main xylem is marked on the photograph (fig. 51) by a black line. The tracheides shown in Indian ink opposite the gap represent the vascular supply to the lateral organ. Farther out in the cortex on the same side (fig. 51, top, right) is a large branch organ with a cortex of its own, and containing a pair of small xylem strands. Apparently both these lateral appendages are of endogenous origin, and must have arisen one above the other. The appearance of the section suggests that similar lateral appendages arose along the opposite side of the axis.

The cambium and the zone of tabular cells formed by it are absent on the side where the stele is interrupted. The phloem cannot be definitely recognised as such. Two or three layers of thin-walled cells form a dark sheath (? endodermis) to the whole stele, and this sheath bulges out in front of the emerging lateral organ (see fig. 50). The marked thickening of the sheath on the opposite side is possibly related to the recent exit of an appendage.

The cortex, except for indications of a periderm on one side (fig. 50, Plate 6), is very similar in appearance and structure to that of the surrounding *Clepsydropsis* roots. There are the same three zones, of which the middle one is prominent as a narrow dark band; scattered in the inner cortex are the same dark-coloured cells as in *Clepsydropsis*.

These facts suggest that the organ may after all be a large *Clepsydropsis* root with secondary growth—a parent root to many others given off distichously, as hinted above. But if this be so it is strange that among the numerous roots examined there is not one which shows a trace of periderm or secondary wood. No root-hairs are seen, but this may be because the organ is packed among the surrounding roots. On the other hand, there is the possibility that the organ in question belongs to some delicate plant which grew as an epiphyte on the false stem, somewhat like *Ankyropteris scandens* on a Permian *Psaronius*, or *Tmesipteris*, *Trichomanes* and other delicate plants on the trunks of modern tree-ferns.

In the absence of further data it is impossible to express an opinion as to the nature of the organ. Comparison with such diverse objects as *Botrychioxylon paradoxum** and the root of *Sphenophyllum*† were tried, but the evidence is insufficient. It is hoped that at a later date further material may become available.

It is interesting to observe that in describing a section of the petiole of *C. antiqua* P. BERTRAND‡ mentions the occurrence of a stem of *Sphenophyllum insigne* as an intrusion into the inner cortex.

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* Compare, for example, SCOTT (1912), Plate 37, figs. 1, 3; Plate 38, fig. 7.

† The resemblance with the root of *Sphenophyllum* as seen in transverse section is in some respects very close; *e.g.*, *cf.* SCOTT (1920), p. 87, fig. 43.

‡ BERTRAND (1911 *a*), p. 8.

General Observations.

(i) *Comparison with Tempskya and other "False Stems."*—The Cretaceous fern *Tempskya** affords perhaps the nearest analogy with the condition seen in *C. australis*, although there are important points of difference in the structure. In both, the false stem consists of relatively weak repeatedly forked leaf-bearing axes embedded in a matrix of adventitious roots. But whereas in *Clepsydropsis* the numerous persistent petioles form a considerable part of the transverse section, in *Tempskya* by far the greater part of the section is occupied by the transversely cut roots. A significant point of agreement between the two types is the small number of root-origins observed —a fact which indicates that the roots were of great length. In *Clepsydropsis* the only root-origins seen are in the central part of the false stem, whence they appear to have grown out towards the peripheral zone before they turned downwards.

Another feature in common between the two genera is the presence of numerous roots invading other organs of the plant to which they themselves belong. In *C. australis*, so far as observed, the invading roots are confined to the petioles; but in *Tempskya Knowltoni*, as Prof. SEWARD has shown,† even the stems are not free from them. In both plants the indications are that the organs were invaded after decay had set in, and the suggestion that the burrowing roots drew nourishment from the disorganised tissues would apply equally to the two ferns. Indeed, it would be no surprise to find that in the later stages of growth the proximal (oldest) parts of false stems like those of *Tempskya* and *C. australis* consisted chiefly or even entirely of decayed stems and petioles riddled with intruded roots. Of about 24 stems figured by Prof. SEWARD‡ in a section of *T. Knowltoni* taken about 8 inches from the basal end, only one had its tissues intact and was free from invading roots. On the other hand, in the specimen described as *T. rossica* by KIDSTON and GWYNNE-VAUGHAN,§ which no doubt represents a more distal part of the trunk, the stems are all intact and there is no trace of intrusions.

As Prof. SEWARD suggests (*loc. cit.*, pp. 498, 504), the two species may well be identical, *T. rossica* representing the erect distal part of a false stem, which at its base (*T. Knowltoni*) was obliquely ascending and for the most part subterranean. Even apart from the question of specific identity the facts do not seem to conflict with the view that as the " false stem " grew in height the older parts gradually decayed from below upwards and became invaded by roots, eventually forming a sort of pedestal of ruins upon which the younger parts of the plant were raised.

Whether the false stem of *Tempskya* was erect from the first, as shown in the restoration drawn by KIDSTON and GWYNNE-VAUGHAN and subsequently published by

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* KIDSTON and GWYNNE-VAUGHAN (1911); STOPES (1915), p. 9; SEWARD (1924).

† SEWARD (1924), p. 490, Plate 17, fig. 25.

‡ SEWARD (1924), p. 490, text-fig. 2.

§ KIDSTON and GWYNNE-VAUGHAN (1911).

Dr. MARIE STOPES* or whether it only gradually attained a vertical position, as suggested by Prof. SEWARD, there seems no reason to doubt that the juvenile stem of *C. australis* was erect. The radial organisation of the individual stems of *Clepsydropsis*, in contrast with the dorsiventral axes of *Tempskya*, would alone suggest this view. Be that as it may, it is interesting to find that the problem of raising the photosynthetic organs into a position of advantage was solved in essentially the same unusual manner in two ferns of widely different affinities at remote geological epochs.

I know of no other fossil ferns possessing a false stem, but among recent ferns there are several instances, *e.g.*, *Hemitelia crenulata* METT. (*Alsophila crenulata* METT.)† and *Todea barbara* MOORE, where a conglomeration of branching stems and adventitious roots results in the formation of a single trunk. In these species the individual stems agree with those of *C. australis* in their radial organisation, but there are several important points of difference in the way in which the false stem is constructed. In the *Hemitelia* the numerous individual axes are lateral branches of a single mother axis, and (according to KIDSTON and GWYNNE-VAUGHAN, *loc. cit.*, p. 18) are derived from adventitious buds produced on the leaf-bases, while in the *Clepsydropsis*, as in *Tempskya*, they are the result of repeated dichotomies. The lateral branches in the *Hemitelia*, moreover, first grow out horizontally through the root-matrix till they reach the surface, and then turn upwards, later becoming enveloped by the growing roots. In habit, too, the fossil genera must have been very different from *H. crenulata*, whose trunk attains massive dimensions and supports at its top the free individual stems for a height of 10 feet or more. *Tempskya*, we know, was built on a much slenderer scale, while in *Clepsydropsis*, too, although no complete sections of the trunk are available, the indications are clearly in favour of a relatively stout, but nevertheless tall, columnar axis of cycadean or palm-tree habit.

In *Todea barbara*,‡ again, we have an extraordinarily massive trunk, of very considerable girth but of no great height, which must include an enormous number of individual stems. The mode of formation of the false stem still needs elucidation, but it is clear that the comparison with *C. australis* cannot be pushed very far. The individual stems may be the result of repeated forking (a point which needs to be ascertained), but many of them emerge as lateral branches from the sides of the trunk.

(ii) *Possible Existence of a " False Stem " in C. antiqua and C. kirgisica.*—The discovery of a complex type of stem-organisation in *C. australis* naturally raises the question as to what was the nature of the stem in the European and Siberian species, *C. antiqua* and *C. kirgisica*. There can be no doubt that they were also tree-ferns. The leaf-bearing axes of these forms are still unknown, but the structure of the outer zone of the trunk, with its persistent petioles, aphlebiæ and interstitial adventitious roots,

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* STOPES (1915), p. 15, text-fig. 5.

† SCHOUTE (1906).

‡ SEWARD and FORD (1903), p. 239 ; CHRIST (1897), p. 333 ; CHRIST (1910), pp. 247–248, 259.

is essentially the same* as in the Australian species; whether a "false stem" existed in these species or whether the stem was simple, as in the Osmundaceæ, can only be shown by the discovery of more complete specimens.

(iii) *Geographical Distribution.*—One of the most interesting facts about *C. australis* is its isolated geographical position, which extends the range of distribution, not only of the genus but of the family Zygopterideæ, far away into the southern hemisphere. FEISTMANTEL'S† comprehensive work on the fossil flora of Eastern Australia, followed by that of several recent authors, has proved the existence, in the Carboniferous rocks of New South Wales, of a considerable flora showing clear affinities with European types of a corresponding age. Similar evidence of a fundamental uniformity of the earlier Carboniferous flora has gradually accumulated from several other directions in the southern hemisphere.‡ The discovery of an Australian species of *Clepsydropsis*, a genus previously known only from allied species in Central Europe and Siberia, affords further testimony that before the advent of the *Glossopteris* flora, towards the close of the Carboniferous period, there was no barrier to prevent the free migration of land plants between the northern and the southern hemispheres.

(iv) *The probable Habitat of C. australis.*—Incidentally we may add that if the habit and structure of a plant can be relied upon as an index of its natural surroundings, we would probably have to picture both *Tempskya* and *C. australis* characteristically as inhabitants of dense and humid forests, similar to the native haunts of our modern tree-ferns. The peculiar device adopted by these weak-stemmed plants, in order to bring their large leaves into an elevated position, would thus find a natural explanation. A like observation would apply to *Ankyropteris scandens,* which compensated for a similar handicap by adopting the climbing habit.

(v) *Affinities.*—At present the most reliable single criterion of affinities within the family is the permanent form of the foliar bundle. But the combination of the simple *Clepsydropsis* leaf-trace with the complex *Ankyropteris* type of stele shows that these two genera are not so distinct as was formerly believed, although to unite them in one genus, as I suggested some years ago,§ is perhaps going too far. As Dr. SCOTT|| observes, "It is remarkable that the more complex types of stem structure have so far been found among the biseriate Zygopterids. This may perhaps be correlated with their more crowded leaves, but in any case it shows that the Clepsydroideæ were an advanced group." The intricate general organisation of the "stem" now revealed in the Australian species adds point to this observation, which is further supported

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* I wish to thank the Director of the Mineralogical Museum, Dresden, for very kindly sending at my request a slice from STENZEL'S type-specimen of *C. kirgisica* for comparison with the Australian species. I hope, at a later date, to publish an account of the type-specimen, which deserves to be more fully described.

† FEISTMANTEL (1890).

‡ For a summary of the literature see SAHNI (1926).

§ SAHNI (1918), p. 376.

|| SCOTT (1920), p. 337.

by the precocious dichotomy of the aphlebia-trace, recalling the Dineuroid condition. Fig. 12, Plate 3, of the present paper is very suggestive of one of the Dineuroideæ. It cannot be denied that instances of this kind tend to break down the distinction between the "biseriate" and "quadriseriate" forms, however convenient such a classification may be for practical purposes. The quadriseriate condition is fundamentally biseriate and must be regarded as derived; such leaves are far from radially symmetrical in any true sense, as Dr. P. BERTRAND, as well as KIDSTON and GWYNNE-VAUGHAN* have justly pointed out.

The known history of the Zygopterideæ, with their elaborate and often fantastic leaf-trace forms, and the remarkable diversity exhibited in their habit and stelar anatomy, scarcely justifies their being ranked among the "primitive ferns." This view is in agreement with those expressed by Prof. SEWARD,† by KIDSTON and GWYNNE-VAUGHAN‡ and by Dr. D. H. SCOTT.§ Much more probably they represent a blindly ending side line of evolution, itself derived from a more distant stock which may have been ancestral to the modern ferns.

Summary.

Clepsydropsis australis is the only member of the Zygopterideæ known from the southern hemisphere. Several large specimens recently discovered in Carboniferous rocks of the Kuttung Series in New South Wales are here described; they are the first figured specimens showing the leaf-bearing axis, and reveal an unexpected and extraordinary type of stem-organisation, comparable in general lines with that of Corda's genus *Tempskya*.

The main results of the investigation may be summarised as follows :—

(1) *C. australis* was a large tree-fern of which the upright trunk was at least a foot in diameter, it probably attained a height of at least 9–12 feet (2·74 to 3·66 metres) and supported a heavy crown of foliage.

(2) The trunk was a "false stem" composed of numerous relatively weak, repeatedly forked leaf-bearing axes which, along with the stout erect petioles borne upon them, were embedded in a dense matrix of adventitious roots and aphlebiæ. The roots in the interior of the trunk were irregularly intertwined, while those in the peripheral parts grew parallel with the trunk and probably formed a thick felt round its lower parts. In cross-sections of the false stem the individual axes, petioles and, in the peripheral parts of the trunk, even the roots, are all cut more or less transversely.

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* KIDSTON and GWYNNE–VAUGHAN (1910), p. 474.

† SEWARD (1910), p. 433.

‡ *Loc. cit.*, p. 474.

§ SCOTT (1920), p. 364; (1924), p. 169.

(3) The individual leaf-bearing stem is erect and radially symmetrical, with leaf-traces arising in 2/5 order from a stele of the *Ankyropteris Grayi* type. There are no axillary branches ; the only mode of branching is equal dichotomy. The cortex shows no specially marked development of mechanical tissue such as would be expected in a thin stem which was to stand erect by itself. Multicellular emergences (some of them possibly capitate glands) are present on both stem and rachis.

(4) The leaf-trace is nipped off as a closed ring which soon becomes flattened, with a slight convexity facing the stele. The trace enters the rachis in this curved form, but soon straightens out, at the same time increasing in size with the enlarging diameter of the petiole. A slight median constriction gradually gives it the definitive clepsydroid form. The peripheral loops are lined by small tracheides and surround a delicate tissue with similar tracheides scattered in it.

(5) The pinna-traces are closed rings, nipped off from the ends of the peripheral loops, alternately on the two sides, apparently at long intervals. They have never been seen detached ; nor have any pinnæ been found, the outline of the rachis opposite the pinna-trace being undisturbed.

(6) The aphlebiæ are repeatedly forked in the tangential plane, with their linear segments standing vertically alongside the rachis. They arise at fairly long intervals, from the decurrent leaf-bases and from the proximal parts of the petiole, in two alternating rows. The first dichotomy of the aphlebia occurs immediately the aphlebia becomes free from the rachis. The aphlebia-trace often bifurcates in the petiolar cortex, and the twin strands, lying in the tangential plane, strikingly resemble the paired " pinna "-traces (of tertiary order) in Dineuroideæ.

(7) The roots arise from the decurrent leaf-bases, possibly also from the stem near the leaf-bases. The majority of them form a sort of packing in which the individual stems and petioles are embedded ; but many are seen intruded into the old, partially decayed petioles. These intruded roots are invariably of smaller diameter and, judging from their steles, of which usually only the protoxylems are lignified, appear to be younger than the roots outside. All the roots are diarch ; well preserved root-hairs are seen, even on the intruded roots.

(8) Nothing is known of a leaf-lamina.

(9) Numerous well-preserved tetrahedral spores have been found, caught among the root-hairs or lying in irregular masses in pockets between the roots ; whether any of them belonged to the *Clepsydropsis* or not is an open question.

(10) The vegetative mycelium of a fungus is rather abundant in several of the specimens.

(11) Among the transversely cut roots in one specimen there is a small cylindrical axis (root or stem) with a stele showing well-developed secondary wood, and traces of a periderm in the outer cortex. Except for the periderm, the cortical structure is almost identical with that of the *Clepsydropsis* roots, but the stele is very different. In the absence of further material the nature and attribution of the organ remain a

mystery; one of the possibilities is that it is the root or rhizome of some delicate vascular cryptogam which grew as an epiphyte upon the tree-fern.

(12) An attempted restoration of *C. australis* is given on p. 21. It is considered probable that the natural habitat of the plant was similar to that of modern tree-ferns, namely, a moist and relatively dense forest.

(13) *C. australis* forms an important and interesting addition to the known pre-Gondwana flora of Australia, and provides a further link with the contemporaneous European flora.

BIBLIOGRAPHY.

BERTRAND, P. (1909). "Etudes sur la Fronde des Zygoptéridées." Lille.

BERTRAND, P. (1911). "Structure des Stipes d'*Asterochlæna laxa* Stenzel." 'Mém. Soc. Géol. du Nord,' vol. 7, (i), pp. 1–72. Lille.

BERTRAND, P. (1911 *a*). "Nouvelles remarques sur la fronde des Zygoptéridées." 'Mém. Soc. d'Hist. Nat. d'Autun,' vol. 25 (année 1912), pp. 1–38. Autun.

BOWER, F. O. (1923). 'The Ferns (Filicales).' Vol. 1. Cambridge.

BOWER, F. O. (1926). 'The Ferns (Filicales).' Vol. 2. Cambridge.

CHRIST, H. (1897). 'Die Farnkräuter der Erde.' Jena.

CHRIST, H. (1910). 'Die Geographie der Farne.' Jena.

DAVID, Sir T. W. EDGEWORTH- (1920). See SÜSSMILCH and DAVID.

FEISTMANTEL, O. (1890). "Geological and palæontological relations of the coal- and plant-bearing rocks of Palæozoic and Mesozoic age in Eastern Australia and Tasmania." 'Mem. Geol. Surv. New South Wales, Palæont. No. 3.' (Dept. of Mines.) Sydney.

KIDSTON, R., and GWYNNE-VAUGHAN, D. T. (1910). "The Fossil Osmundaceæ. Part IV." 'Trans. Roy. Soc. Edinb.,' vol. 47, Part iii, No. 17.

KIDSTON, R., and GWYNNE-VAUGHAN, D. T. (1911). "On a new species of *Tempskya* from Russia." 'Verhandl. d. Russ. Mineralog. Gesellschaft,' Bd. 48, pp. 1–20, Plates 1–3. St. Petersburg.

OSBORN, E. M., Mrs. (1915). "Preliminary observations on an Australian Zygopteris." 'Annual Report, Brit. Assoc. (Manchester),' pp. 727–738.

OSBORNE, G. D. (1926). "Stratigraphical and Structural Geology of the Carboniferous Rocks in the Mt. Mirannie and Mt. Dyrring districts, near Singleton, New South Wales." 'Proc. Linn. Soc., N.S.W.,' vol. 51, pt. 3, pp. 387–407.

SAHNI, B. (1918). "The Branching of the Zygopteridean Leaf, and its relation to the probable Pinna Nature of *Gyropteris sinuosa* Goepp." 'Ann. of Bot.,' vol. 32, pp. 369–379.

SAHNI, B. (1919). "On an Australian specimen of *Clepsydropsis*." 'Ann. of Bot.,' vol. 33, pp. 81–92, January 1919.

Sahni, B. (1926). "The Southern Fossil Floras : a study in the Plant-geography of the past." 'Proc. 13th Ind. Sci. Congress (Bombay).' Presidential Address to Geology Section. Pp. 229–254, Asiat. Soc. of Bengal, Calcutta.

Schenk, A. (1889). "Ueber *Medullosa* Cotta und *Tubicaulis* Cotta." 'Abh. k. Sächs. Ges. Wiss. (Math.-phys. Kl.).,' vol. 15, pp. 523–557. Leipzig.

Schoute, J. C. (1906). "Eine neue Art der Stammbildung im Pflanzenreich." 'Ann. Jard. Bot. Buitenzorg,' Sér. 2, vol. 5, pp. 198–207, Plates 18, 19.

Scott, D. H. (1912). "On *Botrychioxylon paradoxum* sp. nov., a Palæozoic fern with secondary wood." 'Trans. Linn. Soc. Lond. ; 2nd Ser. Bot.,' vol. 7, pt. 17, pp. 373–389.

Scott, D. H. (1920). 'Studies in Fossil Botany.' 3rd Edit., Part I.

Scott, D. H. (1924). 'Extinct Plants and Problems of Evolution.' London.

Seward, A. C., and **Ford**, S. O. (1903). "The Anatomy of *Todea,* with notes on the Geological History and Affinities of the Osmundaceæ." 'Trans. Linn. Soc. London ; 2nd Ser., Botany,' vol. 6, pt. 5, pp. 237–260.

Seward, A. C. (1910). 'Fossil Plants.' Vol. 2. Cambridge.

Seward, A. C. (1924). "A New Species of *Tempskya* from Montana." 'Ann. of Bot.,' vol. 38, pp. 485–507, Plates 16, 17.

Stenzel, K. G. (1889). "Die Gattung *Tubicaulis* Cotta." 'Bibliotheca Botanica,' Heft 12, pp. 1–50, Plates I–VII. Cassel.

Stopes, M. C. (1915). "The Cretaceous Flora, Part II." 'British Museum Catalogue of Mesozoic Plants,' pp. 9–21.

Süssmilch, C. A., and **Edgeworth-David**, T. W. (1920). "Sequence, Glaciation, and Correlation of the Carboniferous Rocks of the Hunter River District, New South Wales." 'Journ. and Proc. Roy. Soc., N.S.W.,' vol. 53, pp. 246–338 (with appendices by A. B. Walkom and W. R. Browne). Sydney.

Thompson, J. M'L. (1917). "A Further Contribution to the Knowledge of *Platyzoma microphyllum.*" 'Trans. Roy. Soc. Edinb.,' vol. 52, pt. 1 (No. 7), pp. 157–165.

Unger, F. (1856). In "Richter u. Unger, Beitrag zur Palæontologie des Thüringer Waldes." 'Denkschr. kais. Akad. Wiss. Wien (Math.-Nat. Klasse),' vol. 11, pp. 53–100. Wien.

Walkom, A. B. (1920). "Note on the Correlation of the Fossil Floras of the Carboniferous Rocks." Appendix I, pp. 282–287 in "**Süssmilch** and **David**" (1920).

EXPLANATION OF PLATES 1–6.

PLATE 1.

FIG. 1.—Natural-size photograph, from an untouched negative, of a transverse section of a part of the "false stem" (specimen 2, section 1). The level at which the section was taken is shown in text-fig. 11. The 13 leaf-bearing stems preserved in this section are referred to in the text by means of numbers, as shown in text-fig. 10. *The photograph shows the section as seen from below.*

PLATE 2.

(Both the figures are from untouched photographs.)

FIG. 2.—Part of the section shown in Plate 1, fig. 1, slightly enlarged. Of the 13 leaf-bearing stems the following 10 are here seen :—1–4 (with the bifurcating steles), 6–10, 12. × 1·28.

FIG. 3.—Transverse section of specimen 1, taken at level 9 in text-fig. 8. In the centre, a stem with characteristic five-rayed stele (2/5 phyllotaxis). The matrix in which the stems and petioles are embedded is composed of roots (*rt.*), and numerous aphlebiæ (*aphl.*) mostly showing a lenticular cross-section and containing either one or two strands. *O.c.* outer cortex ; *em.* emergences ; *pet. str.* petiolar strand ; *aphl. tr.* aphlebia-trace ; *intr. rt.* intruded root. × 3·25.

PLATE 3.

(All the figures are from untouched photographs.)

FIG. 4.—Exterior of a part of specimen 2, showing a petiole (*pet.*) and roots (*rt.*) weathered out on the surface. × 1.

FIG. 5.—Stem No. 2 of the section shown in Plate 1, fig. 1 ; the bifurcating stele, with three leaf-traces (*l. tr.*) in the inner cortex ; *o.c.* outer cortex. × 3.

FIG. 6.—Stem No. 1 of the same section. × 3.

FIG. 7.—Bifurcating stele of stem No. 2 as seen in section 2, specimen 2 ; *phl.* phloem., *p.r.* "pith"-ray. The "mixed pith" is scarcely preserved at all. In places the arrangement of the xylem elements suggests cambial activity. × 8·5.

FIG. 8.—Stem No. 6 and two petioles from section 1, specimen 2. The stem shows the origin of a root (*r.t.*) (on the upper side) and a four-rayed stele. The smaller petiole, with a slightly curved strand, and an aphlebia-trace on the upper side, have just come off from the stem. The larger petiole shows the characteristic permanent form of the petiolar strand, and includes several intruded roots. × 2·8.

FIG. 9.—Stem No. 13 in section 1, specimen 2. The stem is badly crushed, but the stele is recognisable (×) and on the upper side a tangentially elongated leaf-trace is seen. × 1·8.

FIG. 10.—Origin of a leaf-trace (specimen 1, section cut at level 68 in text-fig. 8). This photograph was taken with the section inclined at an angle of over 35°, in order to correct the obliquity of the section. The "pith"-ray (*p.r.*) is still in continuity with the central tissue of the leaf-trace, which tissue is produced into two processes. The smallest tracheides (*s.tr.*) are at the right and left ends of the trace (*phl.* phloem). × *ca.* 17.

FIG. 11.—A petiole with an aphlebia-trace on the right, and numerous sections of aphlebiæ packed together in a sort of mosaic. Specimen 1, section at level 71, text-fig. 8. × 4·5.

FIG. 12.—The same petiole, cut 2 mm. higher up. The aphlebia-trace has divided into two before the aphlebia has become detached, thus showing the "dineuroid condition." Specimen 1, section at level 73, text-fig. 8. × 4·5.

FIG. 13.—A petiolar strand showing the origin of a pinna-trace (on the right). Near the pinna-trace a portion of the inner cortex is preserved. Below, an intruded root. Section 2, specimen 2. × 8·2.

FIG. 14.—Scalariform tracheides from a stem stele in specimen 2. × 129.

PLATE 4.

(All the figures are from untouched photographs.)

FIG. 15.—Stele of stem No. 9 (specimen 2, section 2). × 7·3.

FIG. 16.—Part of a cross-section of specimen 2 taken in the region of stem No. 13 at the level × in text-fig. 11. The large white patch indicates the position of the crushed stem. Numerous closely packed roots, all transversely cut, forming part of a probable root-felt. × 1·4.

FIG. 17.—Transverse section of a petiole near its base. The petiolar strand still shows a slight curvature (the intruded root is on the abaxial side); the peripheral loops are still connected together by the tangential bridge. On the right, abaxially, an aphlebia-trace. Small-celled outer cortex, grading into the larger-celled inner cortex. Specimen 2, section 2. × 8·1.

FIG. 18.—An aphlebia-lobe in cross-section, with two meristeles, each delimited from the cortex by a well-marked endodermis of small regular cells; the stele on the left shows a group of small tracheides in the centre. *Ep.* epidermis; the cortex includes scattered cells with dark contents, especially around the meristeles. Specimen 1, section at level 73 in text-figs. 8. × 36.

FIG. 19.—Petiolar strand of the larger of the leaves shown in Plate 3, fig. 8 (specimen 2, section 1). The same leaf is seen natural size in the centre of fig. 1, Plate 1. × 9.

FIG. 20.—Longitudinal section of a stem in specimen 2, showing towards the lower end the mycelium of a fungus and towards the top what may at first sight be regarded as the reproductive bodies of the fungus, but which are probably of inorganic origin. × 52·5.

FIG. 21.—The same section, showing the mycelium. × *ca.* 200.

FIG. 22.—The same section, showing some of the dark resting-spore-like bodies enclosed in spherical thin-walled sacs. × *ca.* 200.

FIG. 23.—Longitudinal section of specimen 1. On the right, part of a stem with four spine-like emergences; on the left, part of a diarch root. The tip of one of the emergences is frayed, indicating that something has been broken off from there (see p. 12, and compare Plate 6, fig. 41). × 19.

FIG. 24.—Transverse section of a peripheral part of specimen 1, taken at level 9 in text-fig. 8. (Compare the top left-hand corner of text-fig. 1.) In the centre the tip of an old rachis-stump in cross-section, invaded by roots; the outer cortical sheath has been invaginated and the petiolar strand (*pet. str.*), as seen in section, has been bent upon itself. Several of the petioles show invading roots; the petiole on the extreme left bears several emergences. × 2·6.

FIG. 25.—A petiole from the same section, showing over a dozen invading roots, some of which have pushed the petiolar strand out of shape. The large intruded root on the lower side contains a copious fungal mycelium of the same type as in figs. 20, 21, clearly visible if the photograph is examined with a lens. × 3·66.

PLATE 5.

(All the figures are from untouched photographs.)

FIG. 26.—Transverse section of part of the Lyndon specimen (specimen 7, section 3). The arrows point towards what are probably two very badly crushed stems. At other places the preservation is excellent. Two of the leaves are shown enlarged in figs. 27, 28, 34. The cross indicates the enigmatical axis described on p. 25 (shown also in figs. 50, 51, Plate 6); *em.* emergences (enlarged in Plate 6, fig. 41). Numerous well-preserved roots and aphlebiæ are present (examine with a lens, especially at *aphl.*, where a group of several very minute terminal segments of aphlebiæ are seen). At *br. aphl.* are seen the two lobes of an aphlebia forked at its very base. × 1.

FIG. 27.—Transverse section of the same specimen 2–3 mm. above fig. 26. Petiole with numerous intruded roots, one of the latter with another root intruded into itself. The thin-walled tissue of the inner cortex, including numerous cells with dark contents, has been pressed against the petiolar strand, of which the " waist " has been crushed. × *ca.* 3·3.

FIG. 28.—The same petiolar strand ; small tracheides line the peripheral loops. × *ca.* 14.

FIG. 29.—Part of specimen 7, section 1, showing three petioles, roots and aphlebiæ. The petiole on the left shows the origin of a pinna-trace, further enlarged in fig. 36 ; that on the right has not yet attained the permanent form (further enlarged in fig. 31) ; on the left it bears emergences, enlarged further in fig. 37. The spores shown in Plate 6, figs. 47–49, were all found entangled in root-hairs at the spot marked *sp.* × *ca.* 3·3.

FIG. 30.—Another petiole from the same section, showing the outer cortex (*o.c.*) of narrow cells ; inner cortex (*i.c.*) of wider cells, many of them with dark contents ; two intruded roots on the abaxial side of the slightly curved petiolar trace, in which the tissues of the peripheral loop and the tangential bridge are preserved. × *ca.* 12.

FIG. 31.—Another petiole from the same section, showing a slightly later phase of the strand ; tangential bridge of small tracheides. On the adaxial side two intruded roots lying one inside the other ; *rt. st.* the steles of the two roots (see fig. 29, petiole to the right) ; *i.c.* inner cortex (crushed). × *ca.* 12.

FIG. 32.—A fully developed petiolar strand from section 2, specimen 7, surrounded on all sides by intruded roots. The peripheral loop on the left has been deformed ; that on the right is about to give off a pinna-trace. × *ca.* 12.

FIG. 33.—Part of the same strand, to show the incipient pinna-trace, and small tracheides lining the peripheral loop. The delicate parenchyma is not preserved. × *ca.* 24.

FIG. 34.—The same petiolar trace as the one shown in fig. 30, 2–3 mm. distally to that figure. × *ca.* 12.

FIG. 35.—The same trace, 2–3 mm. still higher up. × *ca.* 12.

FIG. 36.—The trace of the petiole at the left of fig. 29. The upper peripheral loop has formed a pinna-trace. On the right, two intruded roots, one inside the other ; on the left, three such roots, placed in a concentric manner. Under the microscope the steles of all the roots are clearly seen. × *ca.* 12.

FIG. 37.—Unusually large emergences on the petiole shown at the right in fig. 29. The nature of the oval or elliptic dark bodies on the right is unknown ; they do not seem to be spores. × *ca.* 37.

FIG. 38.—Peripheral part of the petiole shown in fig. 30, showing the unusual presence of an irregular zone of horizontally and radially elongated cells immediately outside the outer cortex (*o.c.*). × *ca.* 37.

PLATE 6.

(All the figures except fig. 51 are from untouched photographs.)

FIG. 39.—Scalariform tracheides from a root (specimen 7). × *ca.* 80.

FIG. 40.—An aphlebia-lobe, *cf.* fig. 18, Plate 4 (section 1, specimen 7). × *ca.* 12.

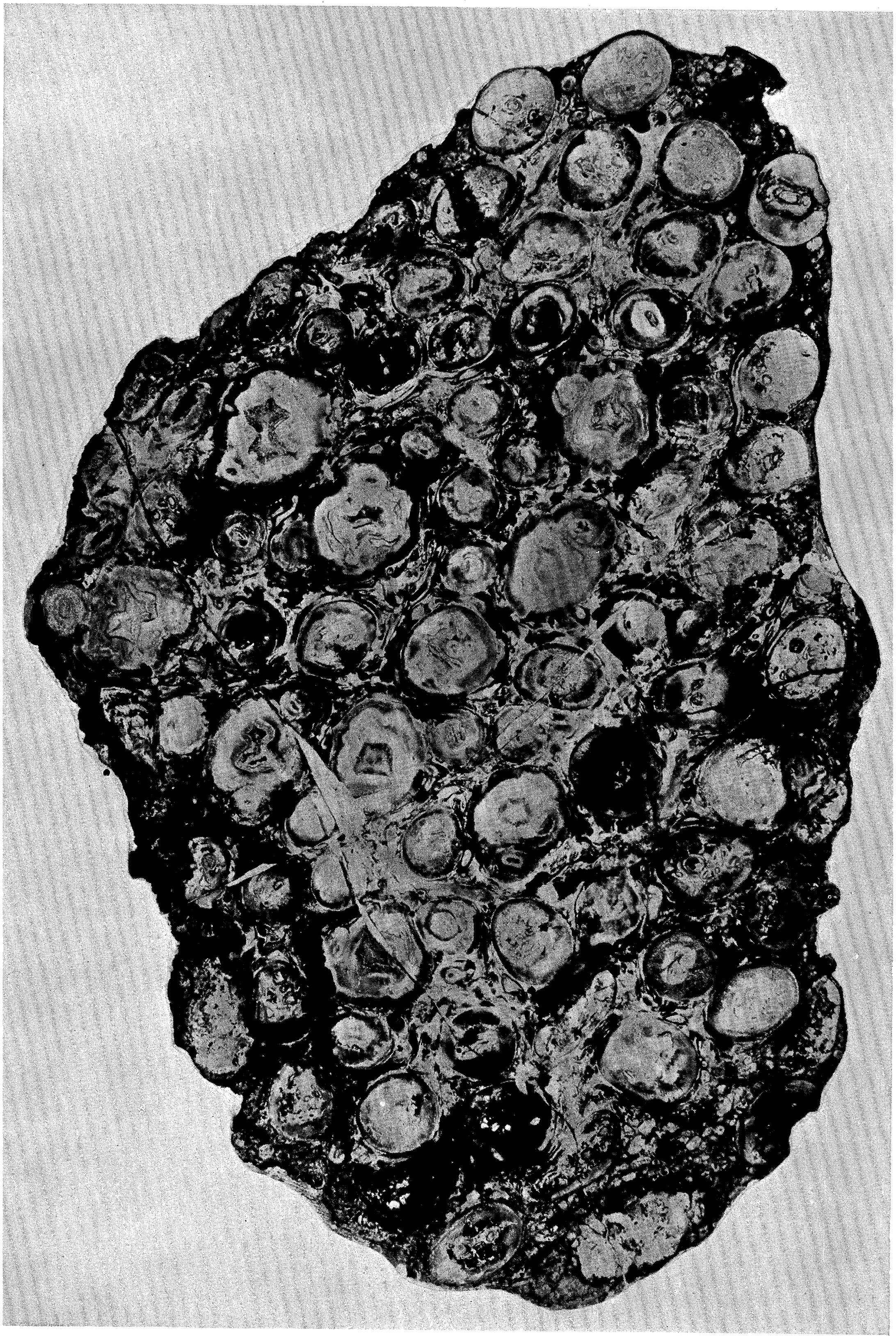
FIG. 41.—Emergences on the large petiole to the extreme left of fig. 26, Plate 5. One of the emergences (the one on the right) appears to terminate in a mass of cells which may be a glandular head ; similar detached masses of cells are lying near by ; well-preserved root-hairs are seen on the three roots. The exact spot which this figure represents is indicated in fig. 26 by the reference line (*em.*) on the left. × *ca.* 16·5.

FIG. 42.—A well-preserved root from section 2, specimen 7 (seen also in fig. 27, Plate 5). The petiole on the left shows (near the root) over half a dozen emergences. × *ca.* 6.

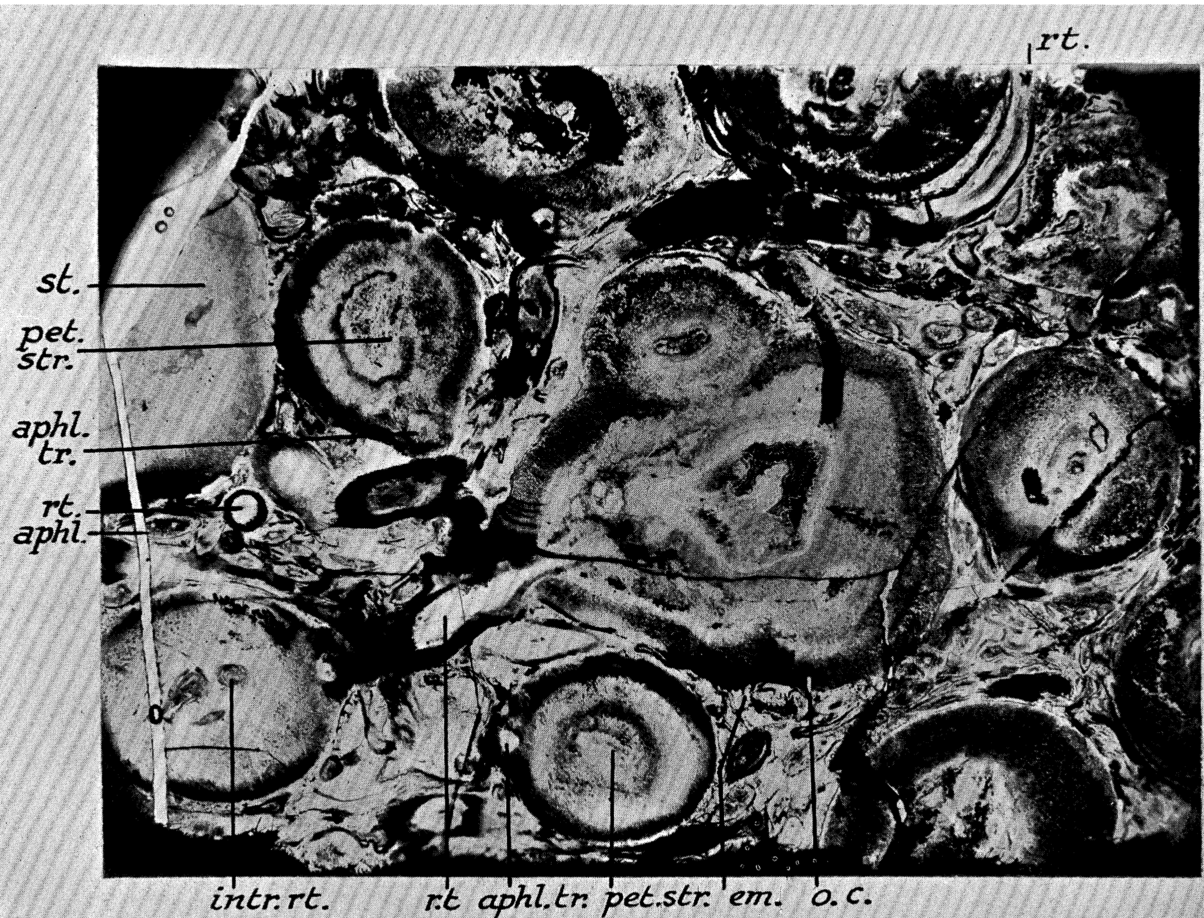
FIG. 43.—The same root, showing the diarch xylem-plate, phloem (*phl.*), pericycle (*per.*), endodermis (*end.*), inner, middle and outer cortex (*i.c.*, *m.c.*, *o.c.*) ; *rh.* root-hairs. × *ca.* 30.

FIG. 44.—Xylem and part of the phloem (*phl.*) of the root shown in the middle of fig. 50. In the xylem the middle lamella is clearly visible. × *ca.* 66.

FIG. 45.—Part of the cortex and crushed stele of one of the roots intruded into the petiole shown in figs. 27, 28. The same root is seen at the bottom of the latter figure. The diarch xylem plate is seen in two pieces, as the middle part of the plate, not yet lignified, has been destroyed. The crushed inner cortex surrounds the stele. × *ca.* 77.



Clepsydropsis australis.



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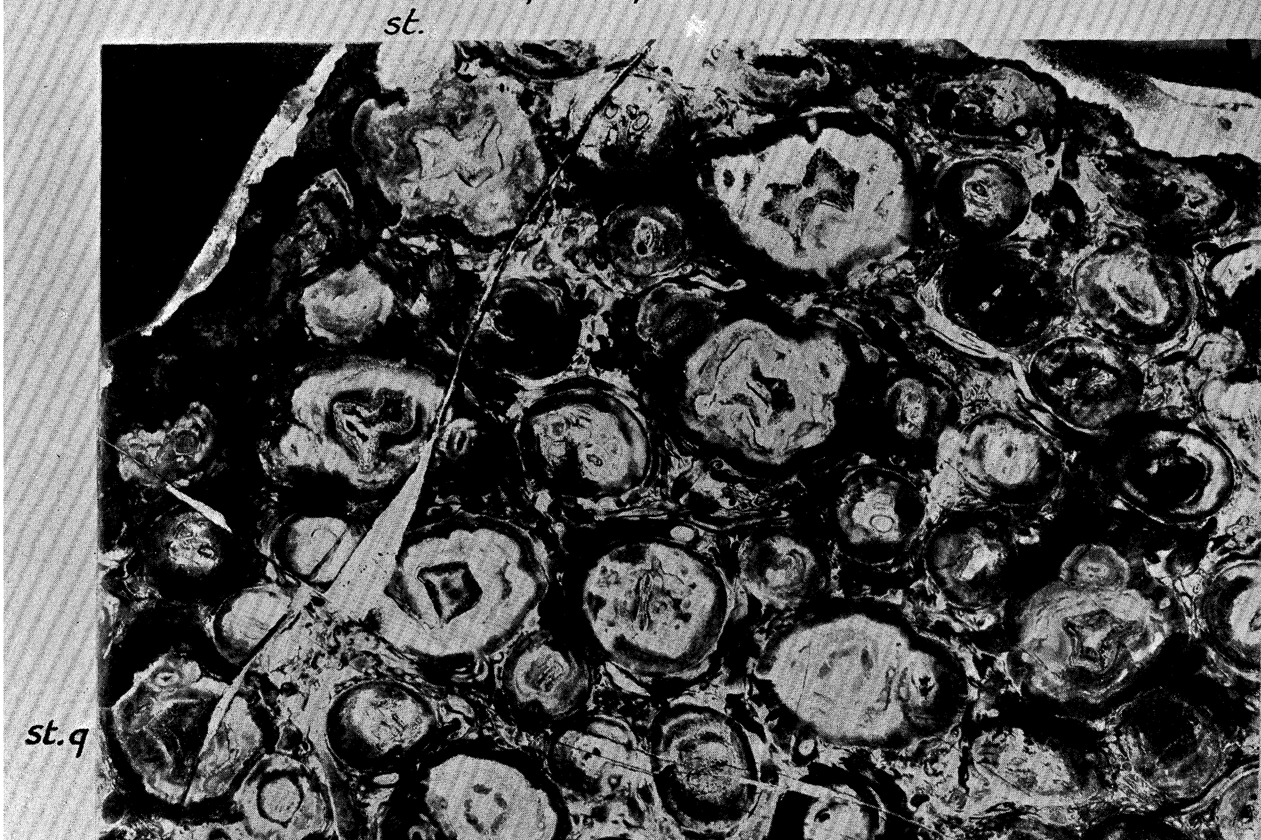

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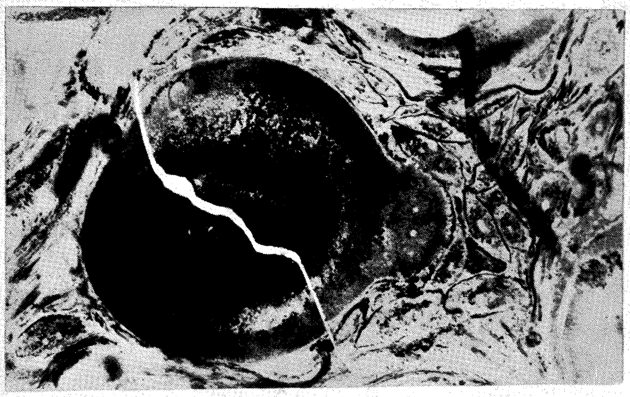
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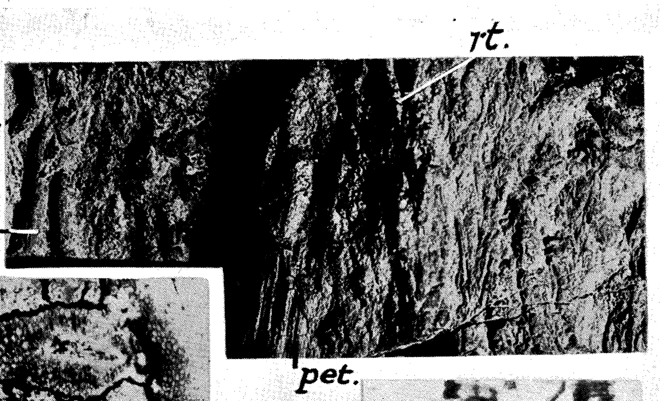
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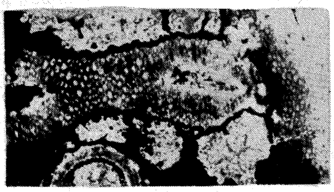
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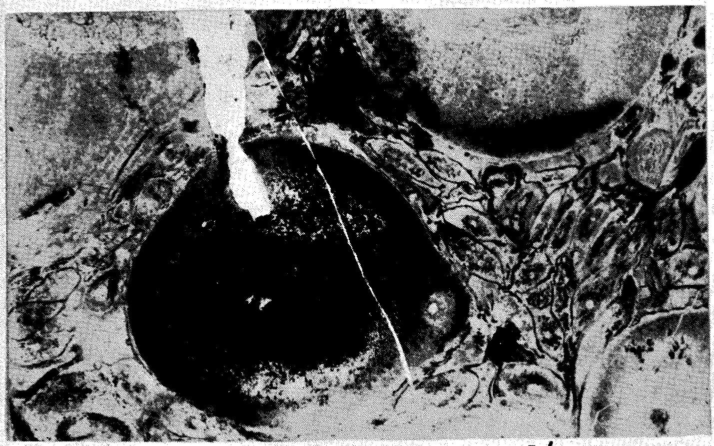
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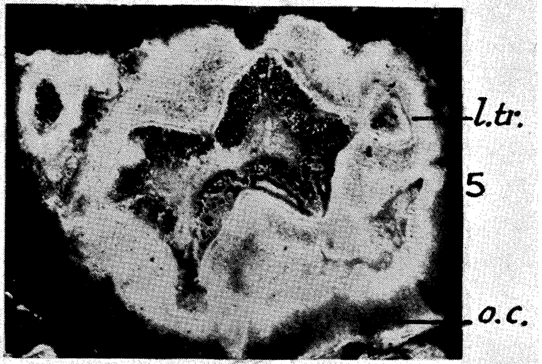
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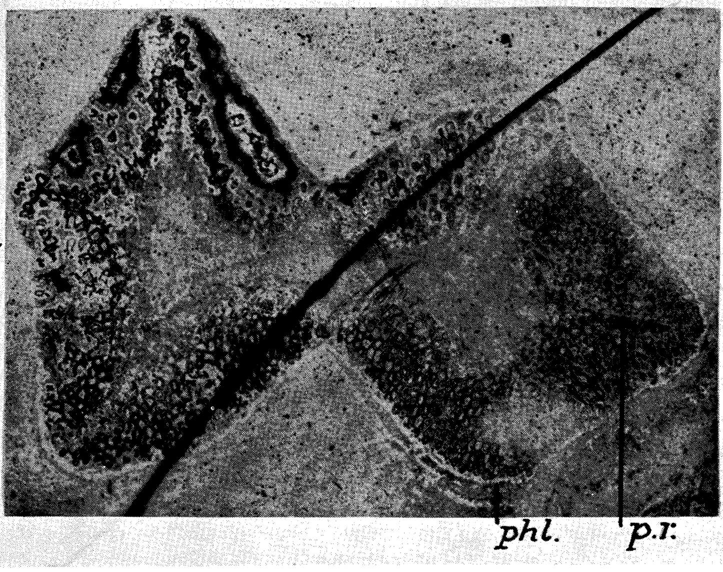
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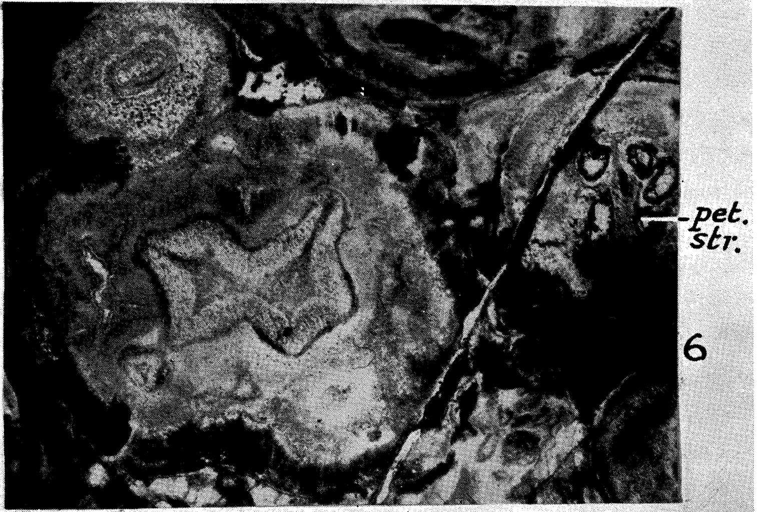
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Clepsydropsis australis.

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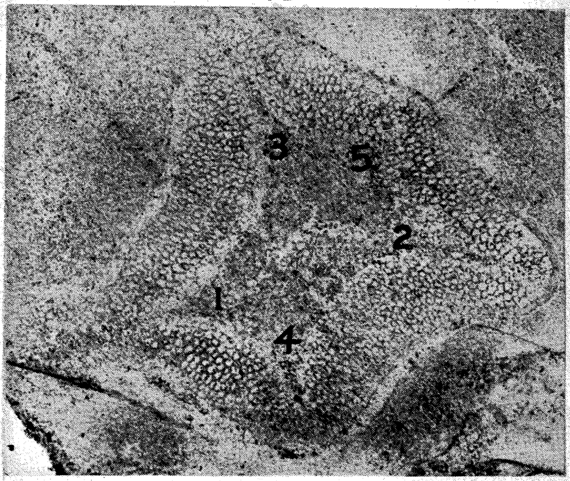

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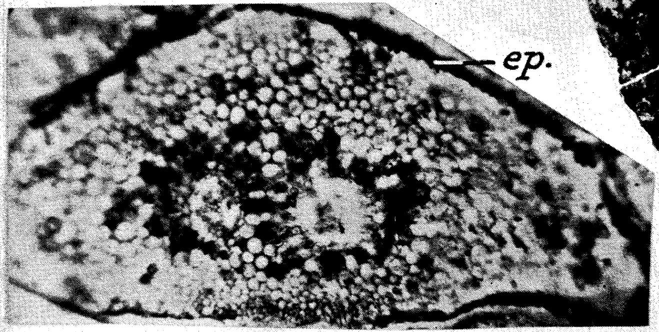

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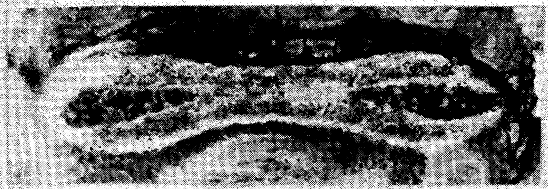

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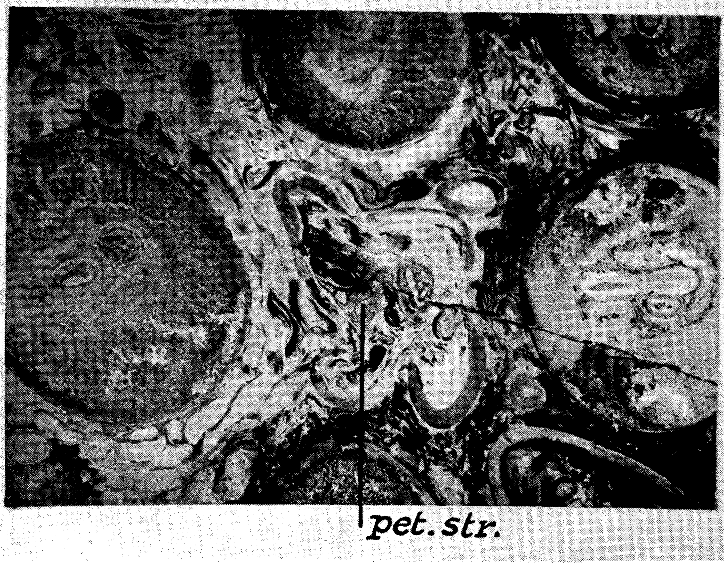

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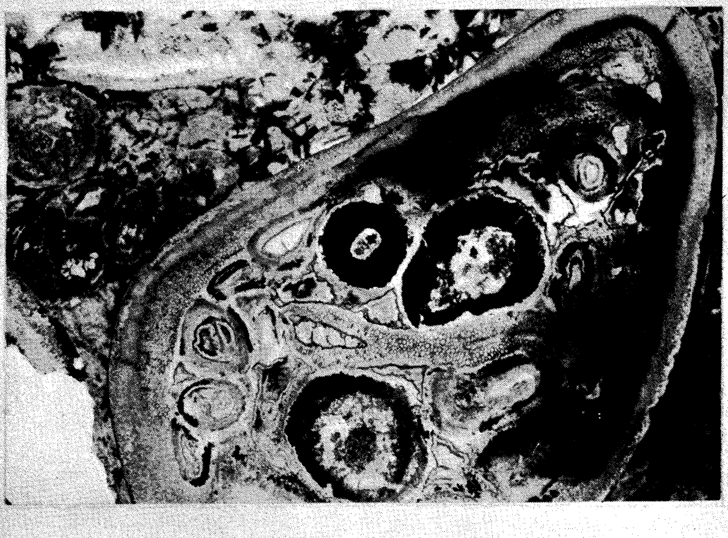

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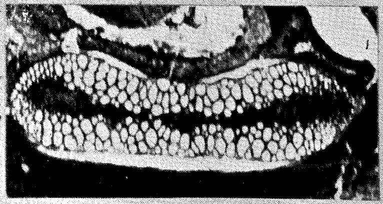

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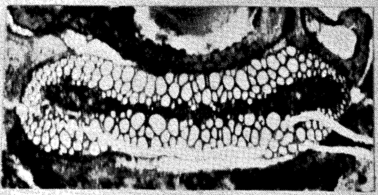

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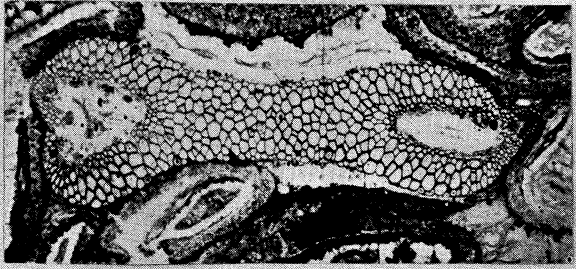

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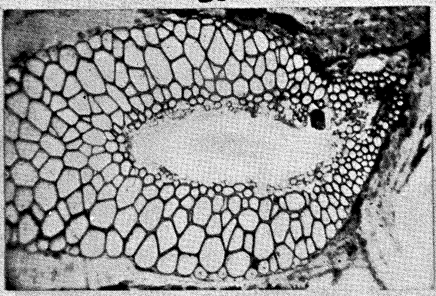

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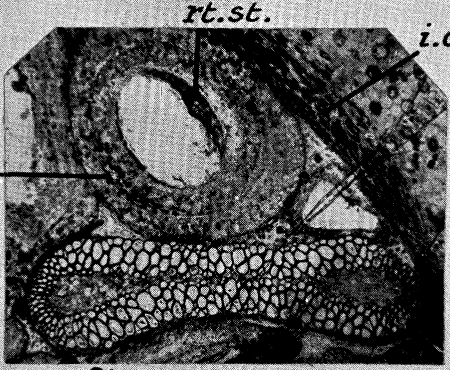

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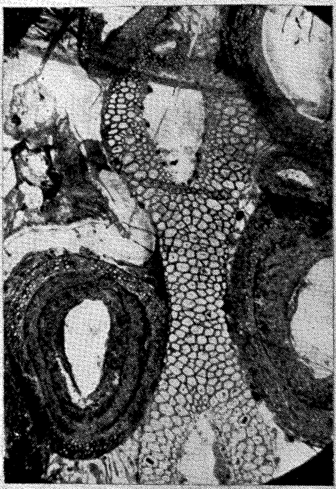

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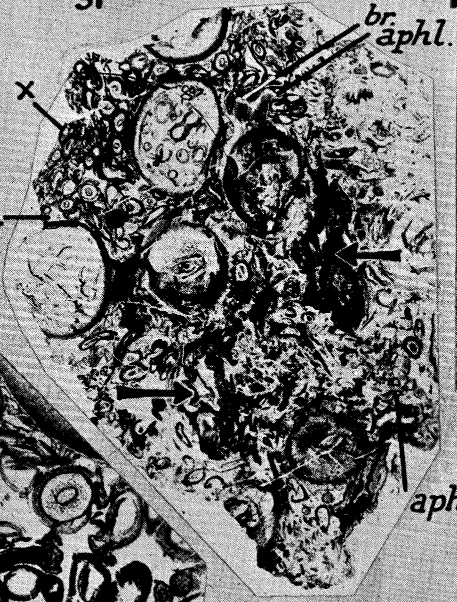

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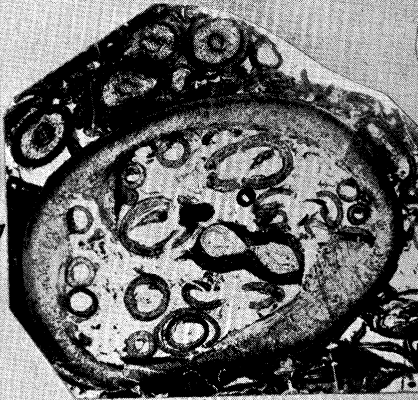

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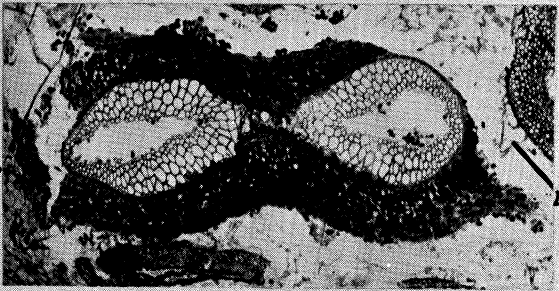

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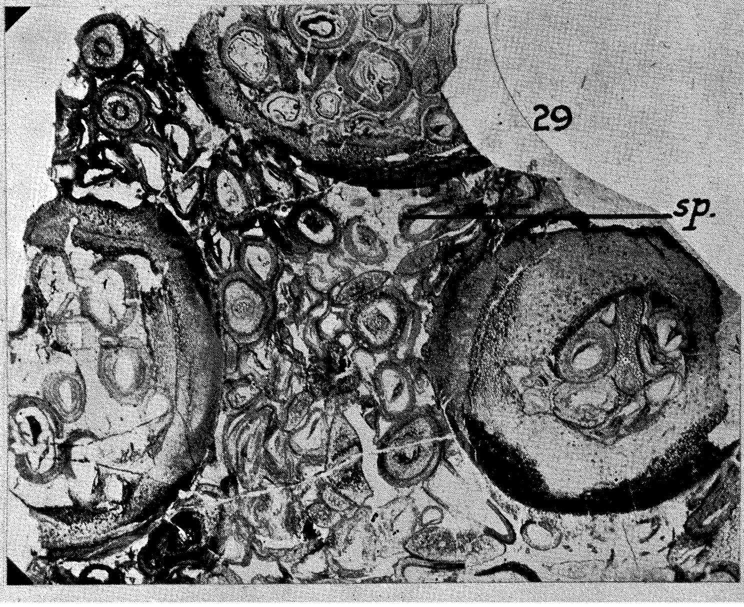

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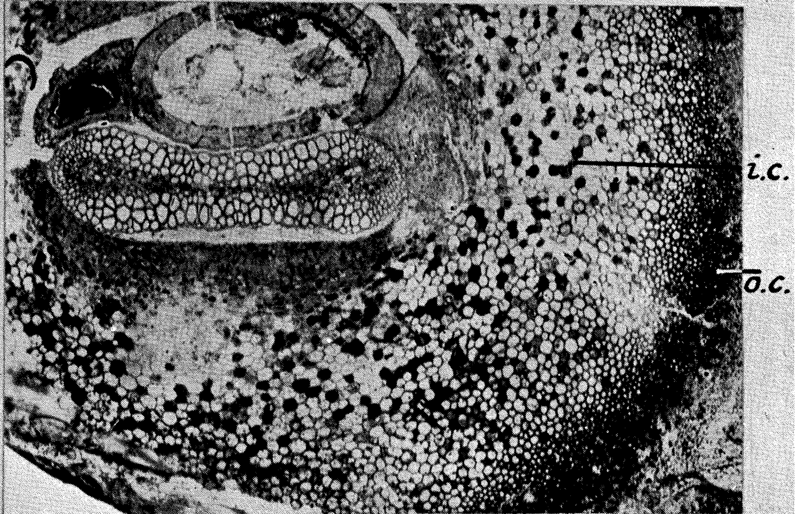

Clepsydropsis australis.

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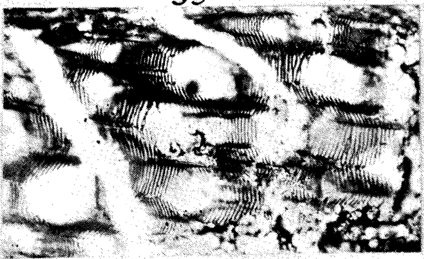

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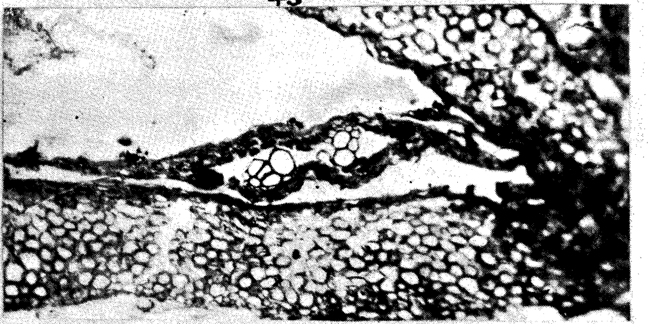

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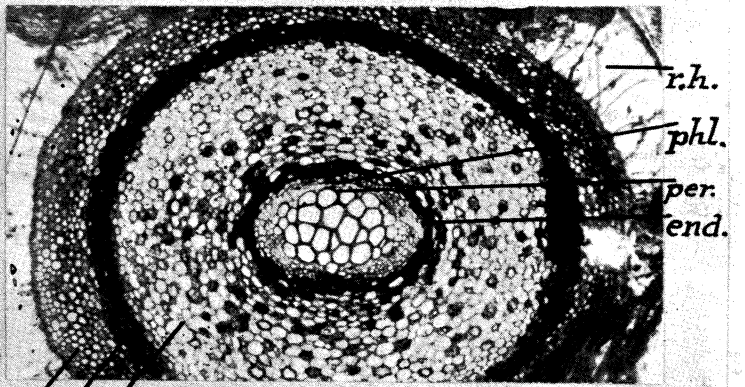

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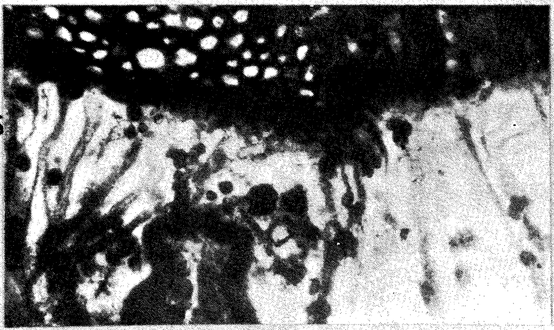

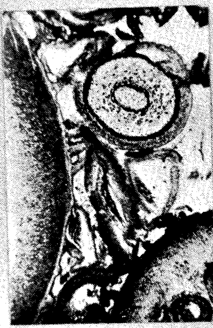

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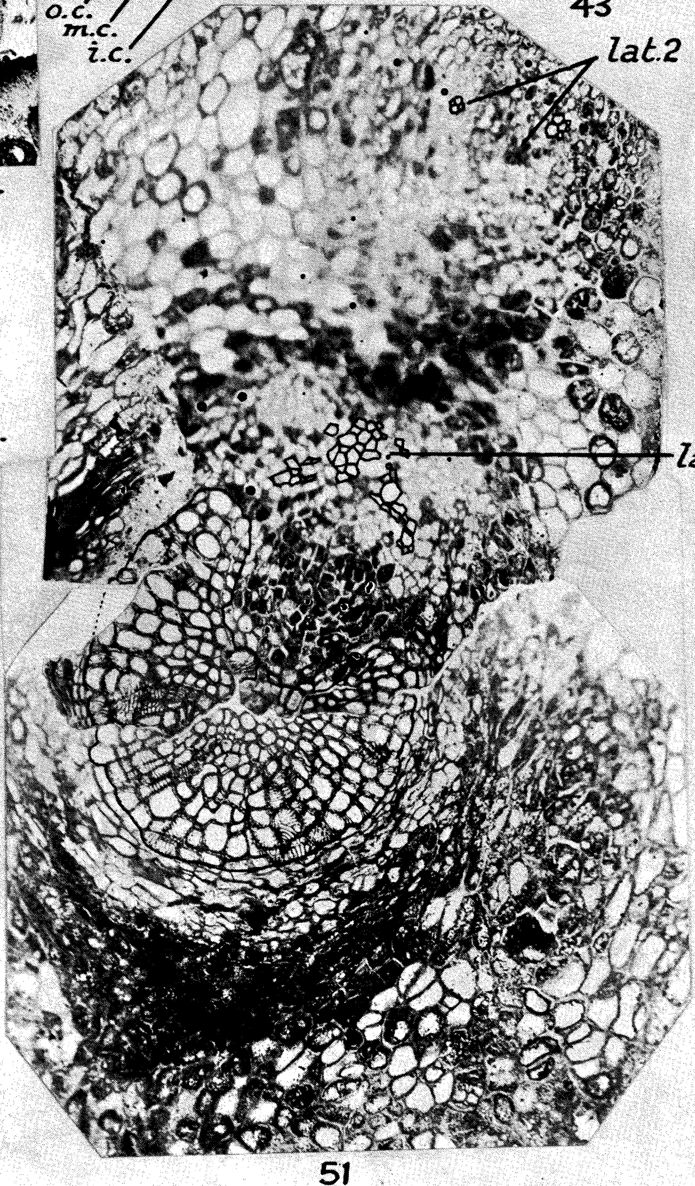

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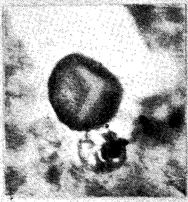

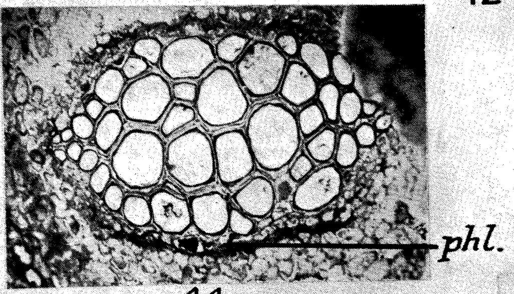

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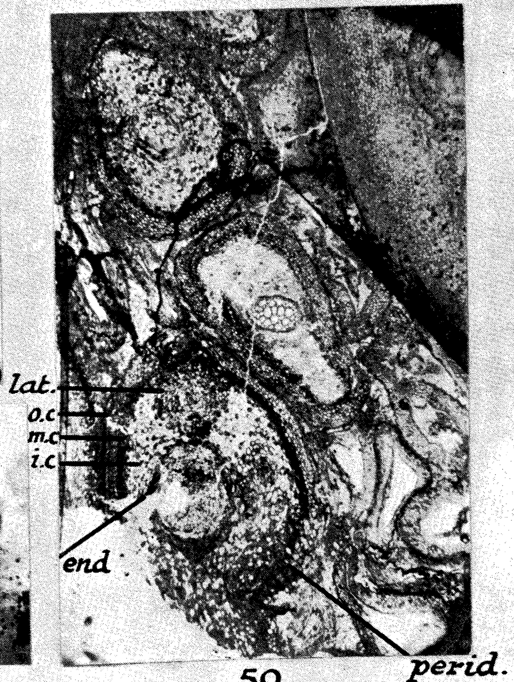

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Clepsydropsis australis.

FIG. 46.—Spores of various sizes caught among the root-hairs (specimen 7, section 1). × 82·5.

FIGS. 47 to 49.—Tetrahedral spores of three different sizes, all magnified exactly in the same proportion. The spore (of medium size) in fig. 47 has opened along the triradiate mark. In fig. 48 the small upper figure with two spores is only a darker print of part of the lower figure, reproduced to show more clearly the triradiate mark in the spore on the right. The large spore in fig. 49 has also burst along the triradiate mark; the black round body in the opening is extraneous. All × *ca.* 340.

FIG. 50.—Part of section 1 of specimen 7 (Lyndon) showing several roots of the *Clepsydropsis*, part of a petiole (in the top right-hand corner, with an intruded root), and, in the bottom left-hand corner, the better-preserved of the two sections of the enigmatical axis (stem or ? root) containing a partially preserved stele with well-developed secondary wood; *perid.* traces of a periderm; *lat.* lateral organ in cortex; *o.c.*, *m.c.*, *i.c.*, outer, middle, inner cortex; *end.* ? endodermis. × *ca.* 10.

FIG. 51.—Part of the same axis, further magnified. After the photograph in fig. 50 had been prepared the section was unfortunately further damaged. Fig. 51 was prepared by piecing together four different parts which had to be photographed separately at the same magnification; *lat.* 1, *lat.* 2 vascular supply to the two lateral organs (inserted in Indian ink with the help of a camera lucida). × *ca.* 60.

Clepsydropsis australis.

PLATE 1.

FIG. 1.—Natural-size photograph, from an untouched negative, of a transverse section of a part of the "false stem" (specimen 2, section 1). The level at which the section was taken is shown in text-fig. 11. The 13 leaf-bearing stems preserved in this section are referred to in the text by means of numbers, as shown in text-fig. 10. *The photograph shows the section as seen from below.*

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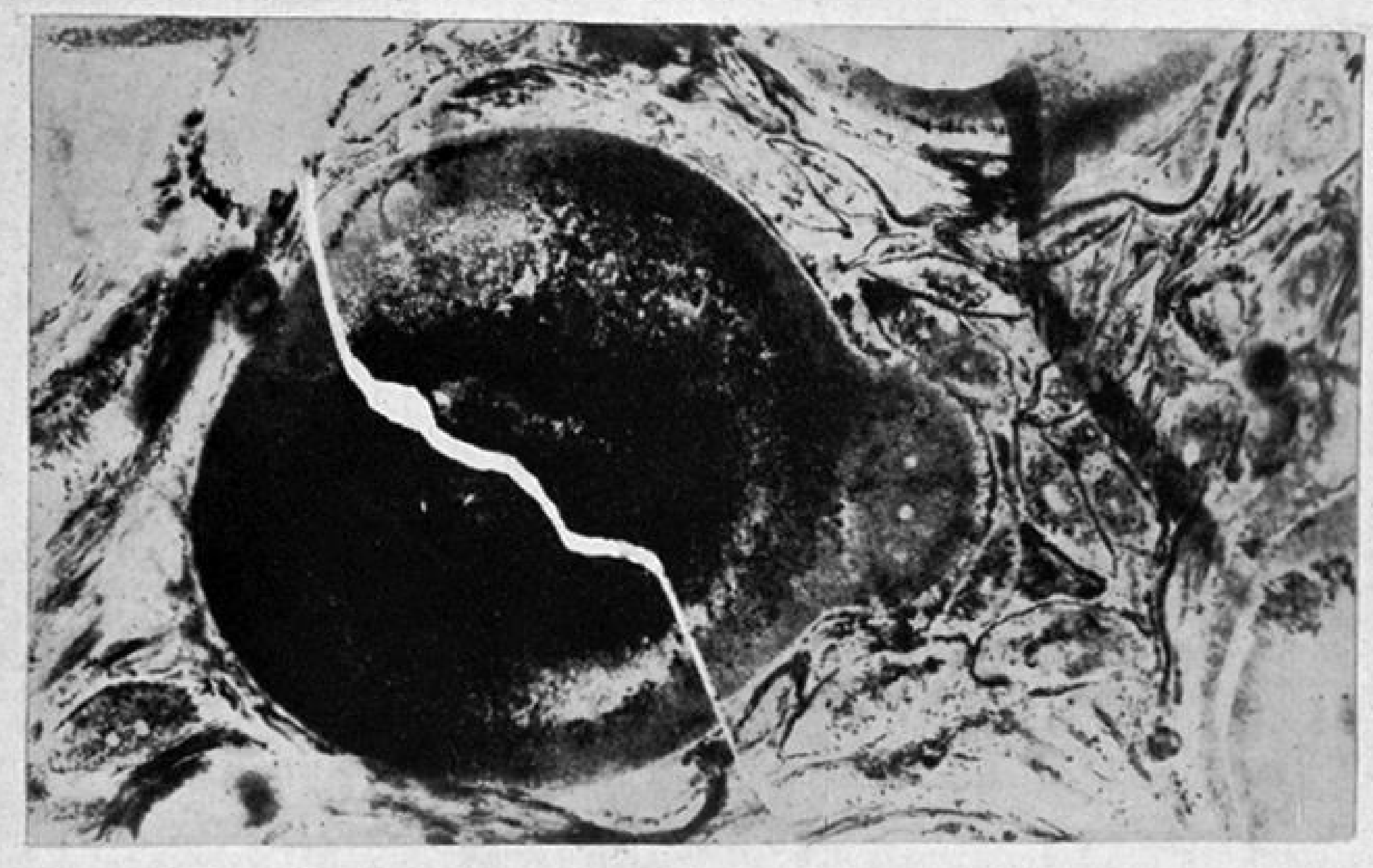
Clepsydropsis australis.

PLATE 2.

(Both the figures are from untouched photographs.)

FIG. 2.—Part of the section shown in Plate 1, fig. 1, slightly enlarged. Of the 13 leaf-bearing stems the following 10 are here seen :—1–4 (with the bifurcating steles), 6–10, 12. × 1·28.

FIG. 3.—Transverse section of specimen 1, taken at level 9 in text-fig. 8. In the centre, a stem with characteristic five-rayed stele (2/5 phyllotaxis). The matrix in which the stems and petioles are embedded is composed of roots (*rt.*), and numerous aphlebiæ (*aphl.*) mostly showing a lenticular cross-section and containing either one or two strands. *O.c.* outer cortex ; *em.* emergences ; *pet. str.* petiolar strand ; *aphl. tr.* aphlebia-trace ; *intr. rt.* intruded root. × 3·25.



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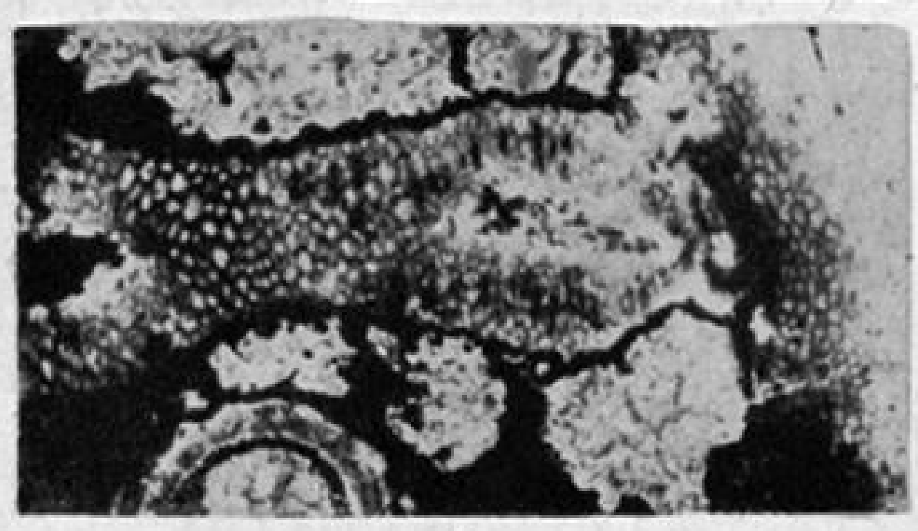

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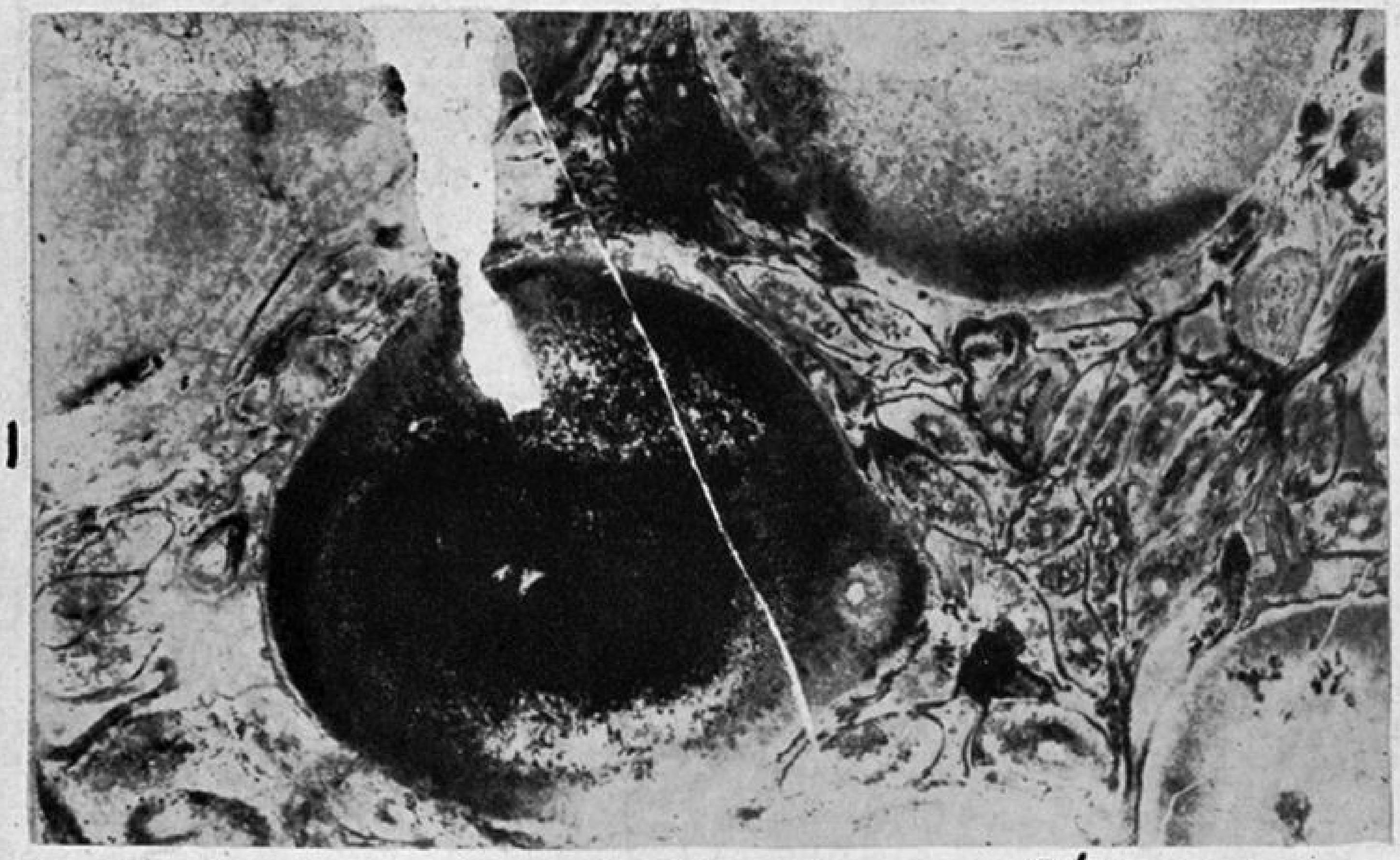

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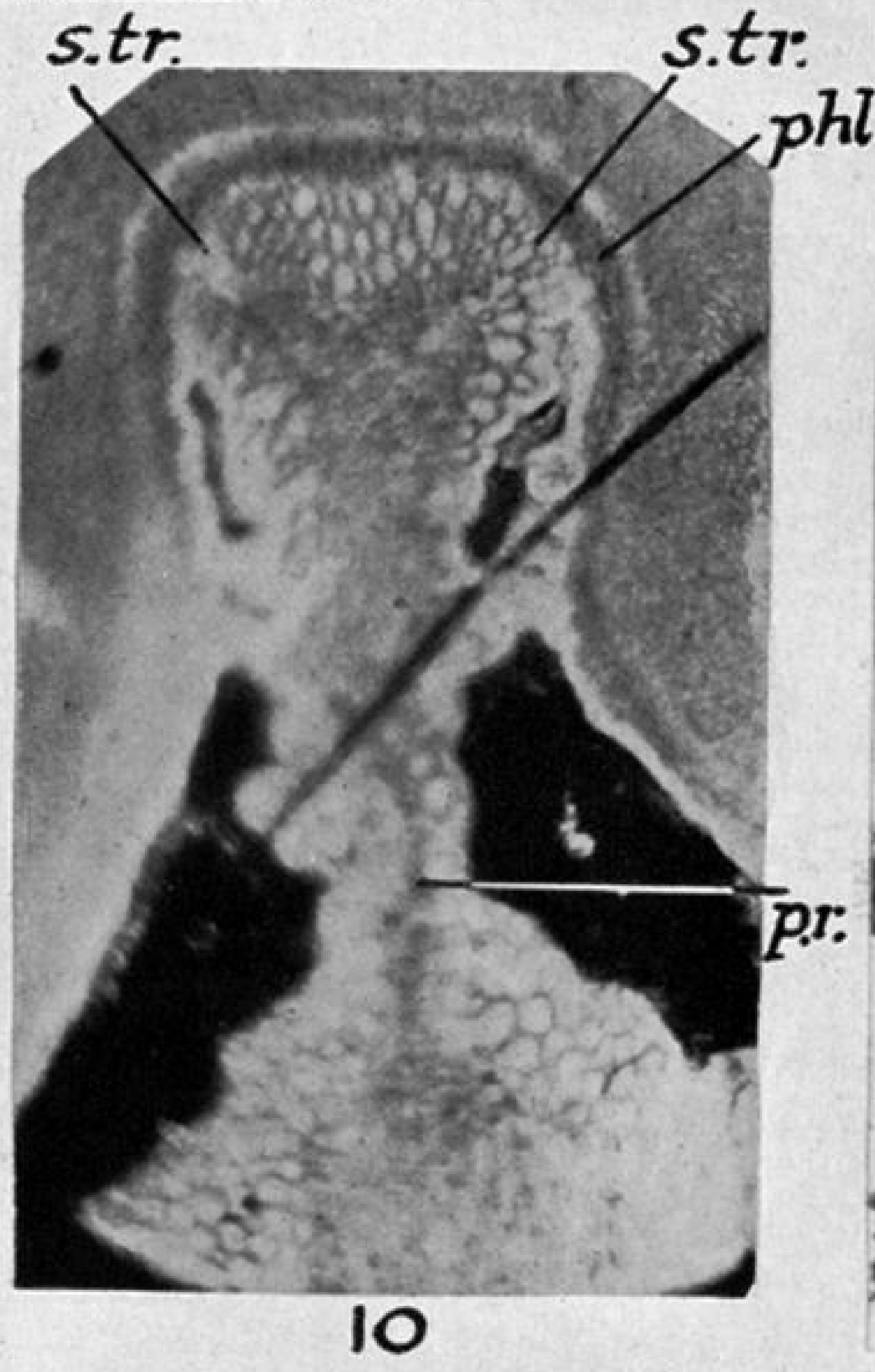

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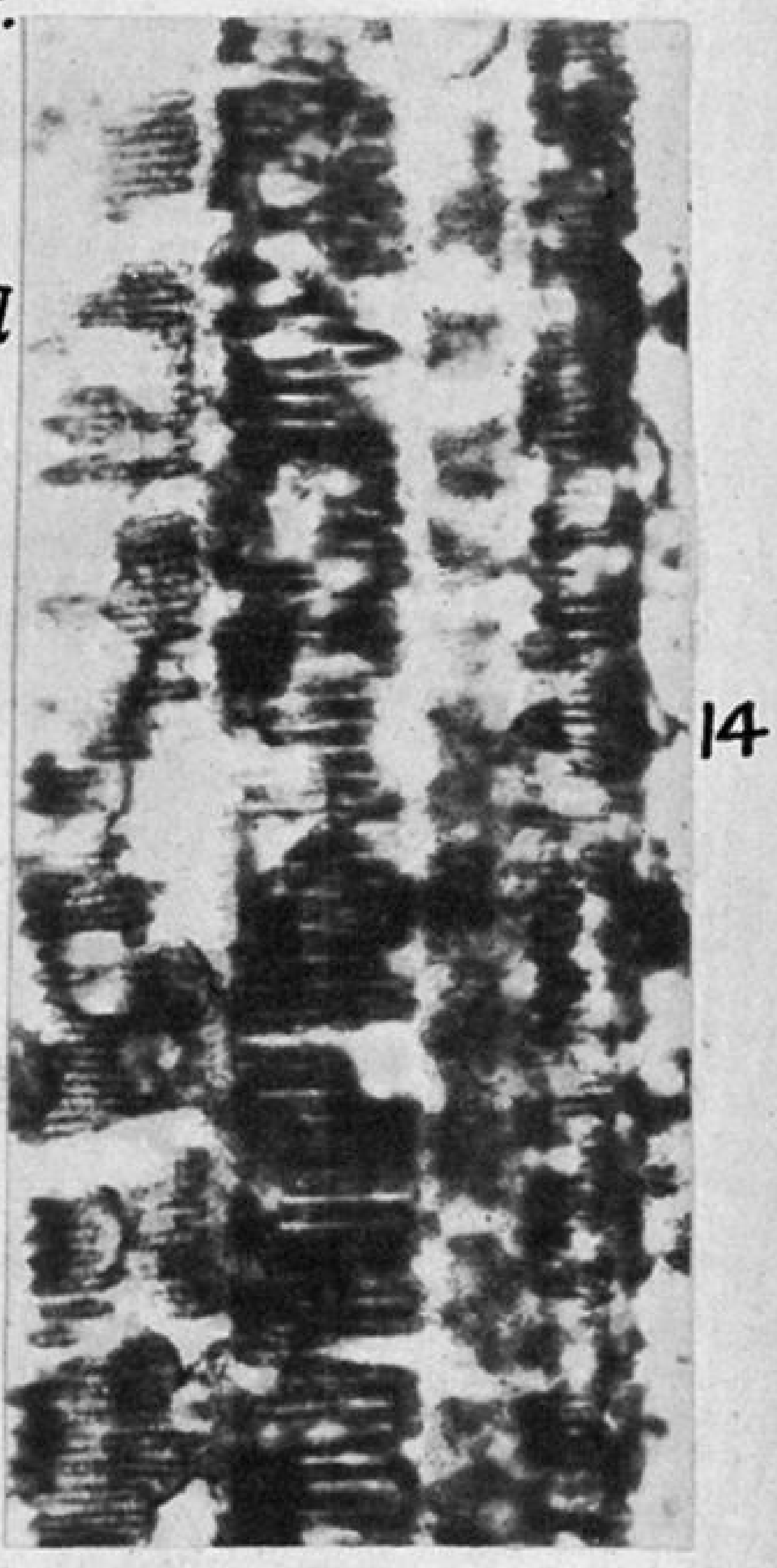

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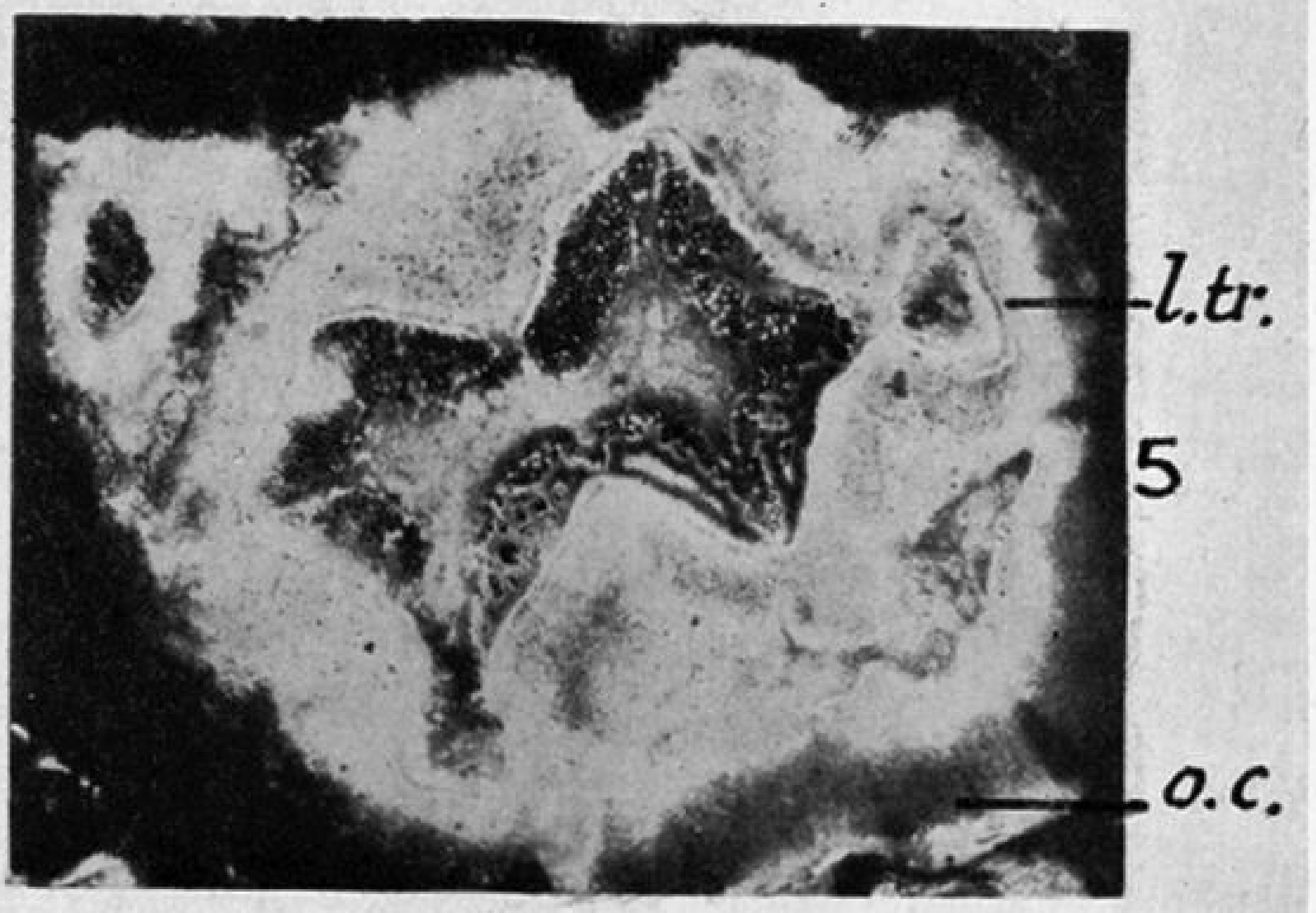

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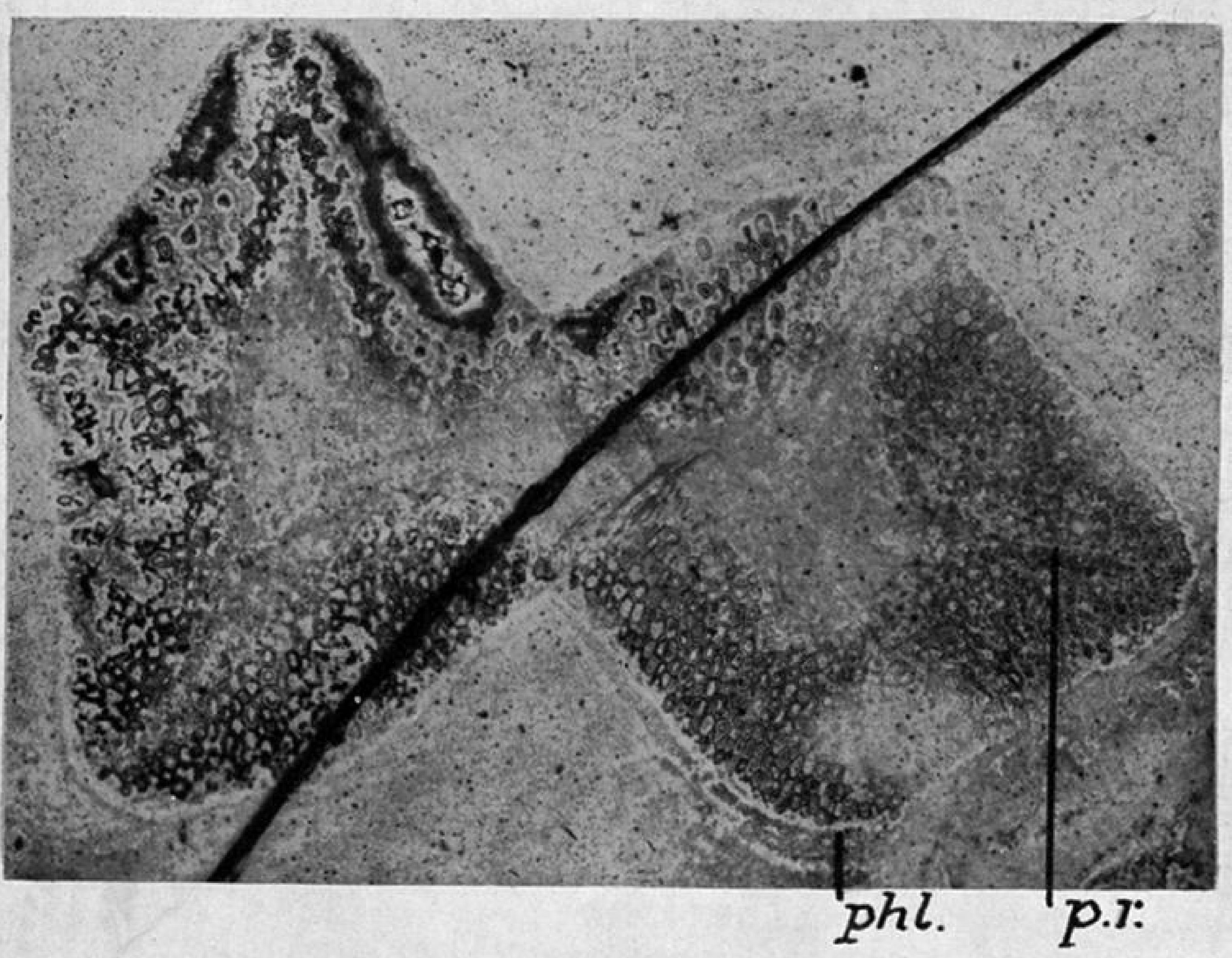

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Clepsydropsis australis.

PLATE 3.

(All the figures are from untouched photographs.)

FIG. 4.—Exterior of a part of specimen 2, showing a petiole (*pet.*) and roots (*rt.*) weathered out on the surface. × 1.

FIG. 5.—Stem No. 2 of the section shown in Plate 1, fig. 1; the bifurcating stele, with three leaf-traces (*l. tr.*) in the inner cortex; *o.c.* outer cortex. × 3.

FIG. 6.—Stem No. 1 of the same section. × 3.

FIG. 7.—Bifurcating stele of stem No. 2 as seen in section 2, specimen 2; *phl.* phloem., *p.r.* " pith "-ray. The " mixed pith " is scarcely preserved at all. In places the arrangement of the xylem elements suggests cambial activity. × 8·5.

FIG. 8.—Stem No. 6 and two petioles from section 1, specimen 2. The stem shows the origin of a root (*r.t.*) (on the upper side) and a four-rayed stele. The smaller petiole, with a slightly curved strand, and an aphlebia-trace on the upper side, have just come off from the stem. The larger petiole shows the characteristic permanent form of the petiolar strand, and includes several intruded roots. × 2·8.

FIG. 9.—Stem No. 13 in section 1, specimen 2. The stem is badly crushed, but the stele is recognisable (×) and on the upper side a tangentially elongated leaf-trace is seen. × 1·8.

FIG. 10.—Origin of a leaf-trace (specimen 1, section cut at level 68 in text-fig. 8). This photograph was taken with the section inclined at an angle of over 35°, in order to correct the obliquity of the section. The " pith "-ray (*p.r.*) is still in continuity with the central tissue of the leaf-trace, which tissue is produced into two processes. The smallest tracheides (*s.tr.*) are at the right and left ends of the trace (*phl.* phloem). × *ca.* 17.

FIG. 11.—A petiole with an aphlebia-trace on the right, and numerous sections of aphlebiæ packed together in a sort of mosaic. Specimen 1, section at level 71, text-fig. 8. × 4·5.

FIG. 12.—The same petiole, cut 2 mm. higher up. The aphlebia-trace has divided into two before the aphlebia has become detached, thus showing the " dineuroid condition." Specimen 1, section at level 73, text-fig. 8. × 4·5.

FIG. 13.—A petiolar strand showing the origin of a pinna-trace (on the right). Near the pinna-trace a portion of the inner cortex is preserved. Below, an intruded root. Section 2, specimen 2. × 8·2.

FIG. 14.—Scalariform tracheides from a stem stele in specimen 2. × 129.

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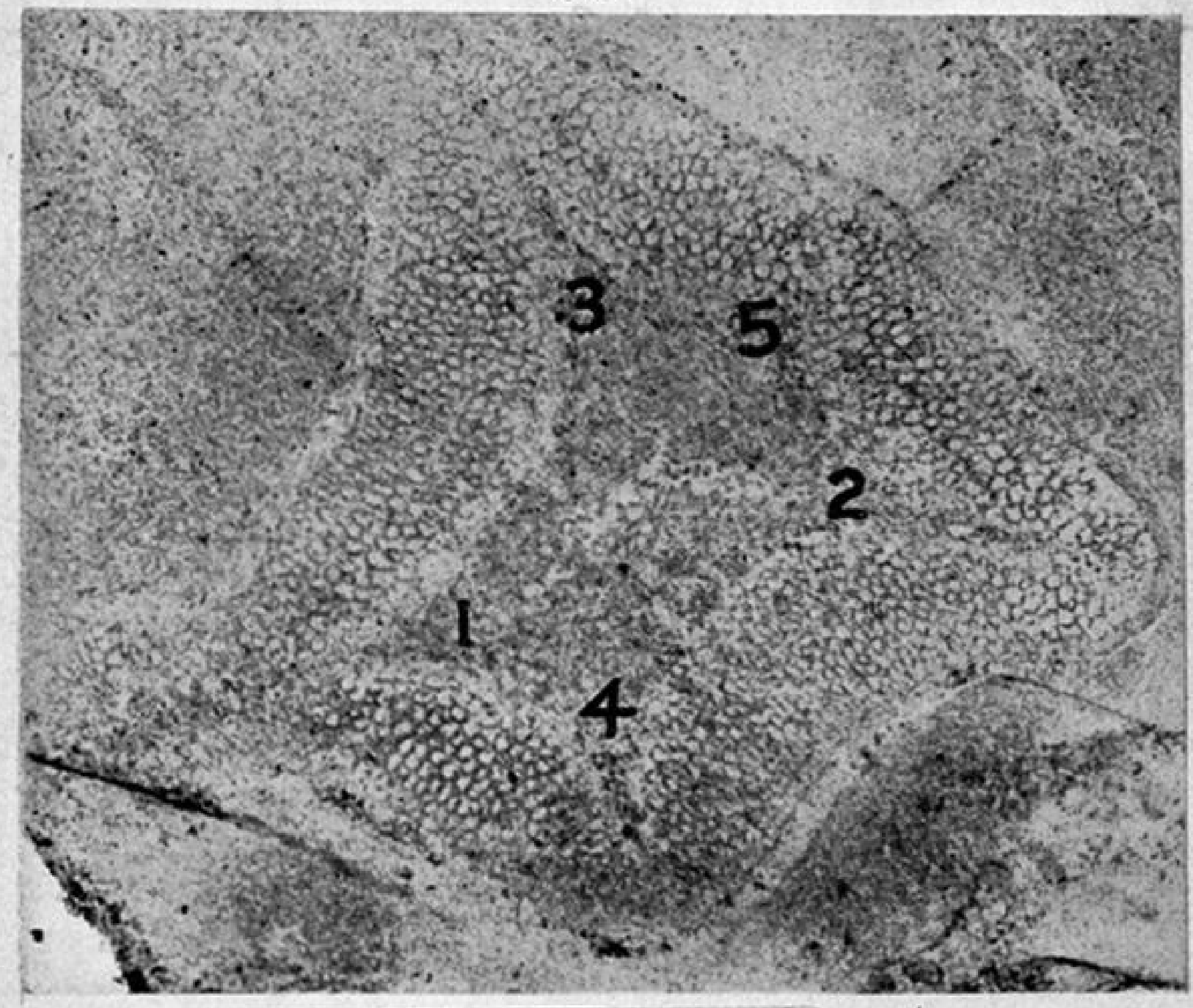

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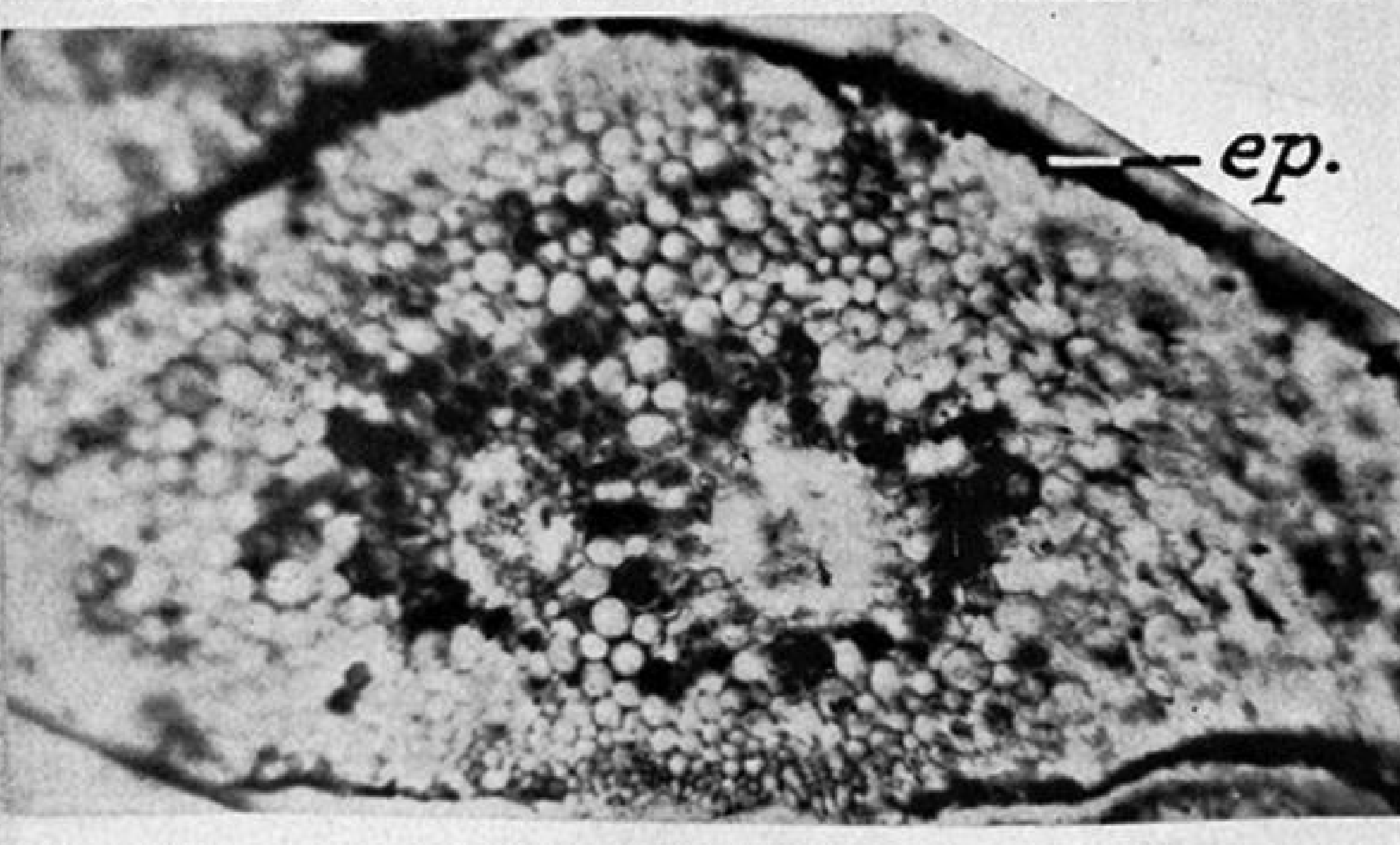

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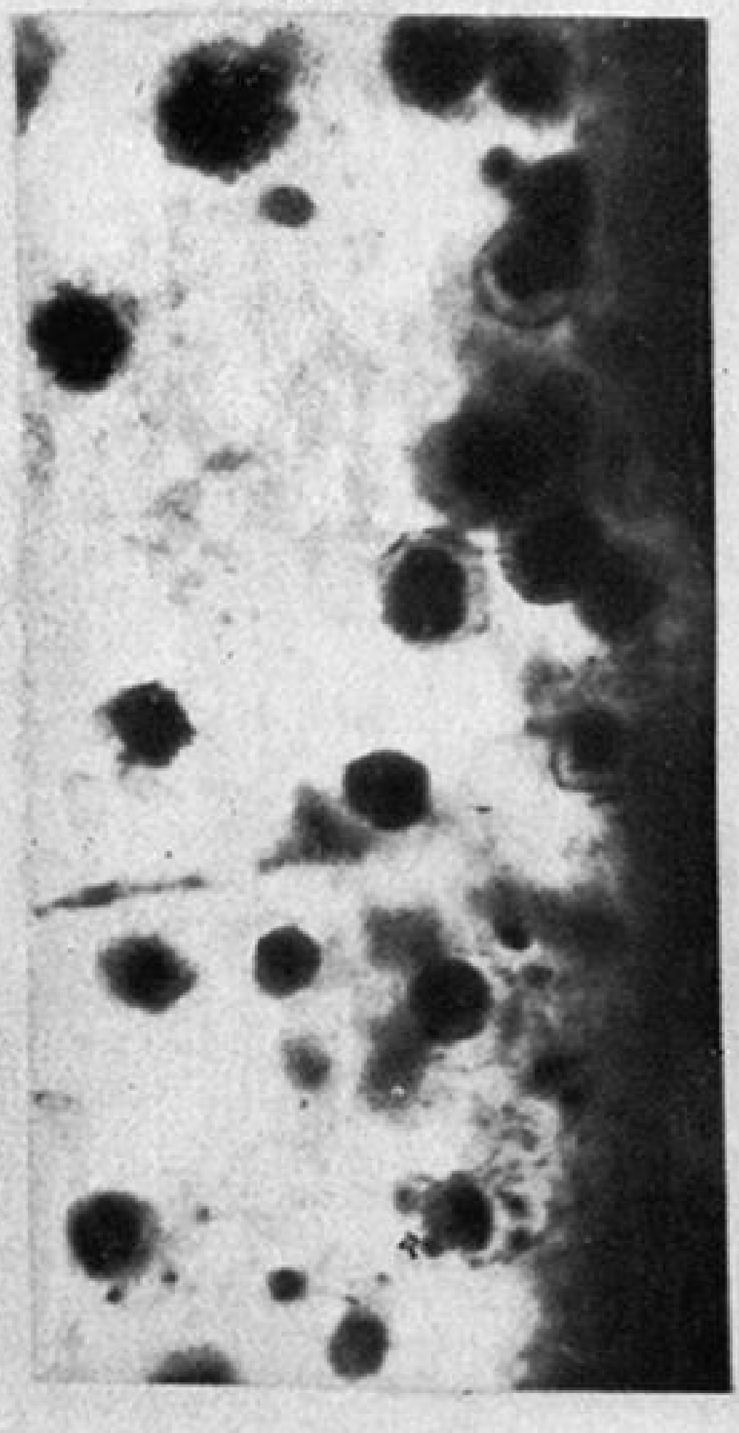

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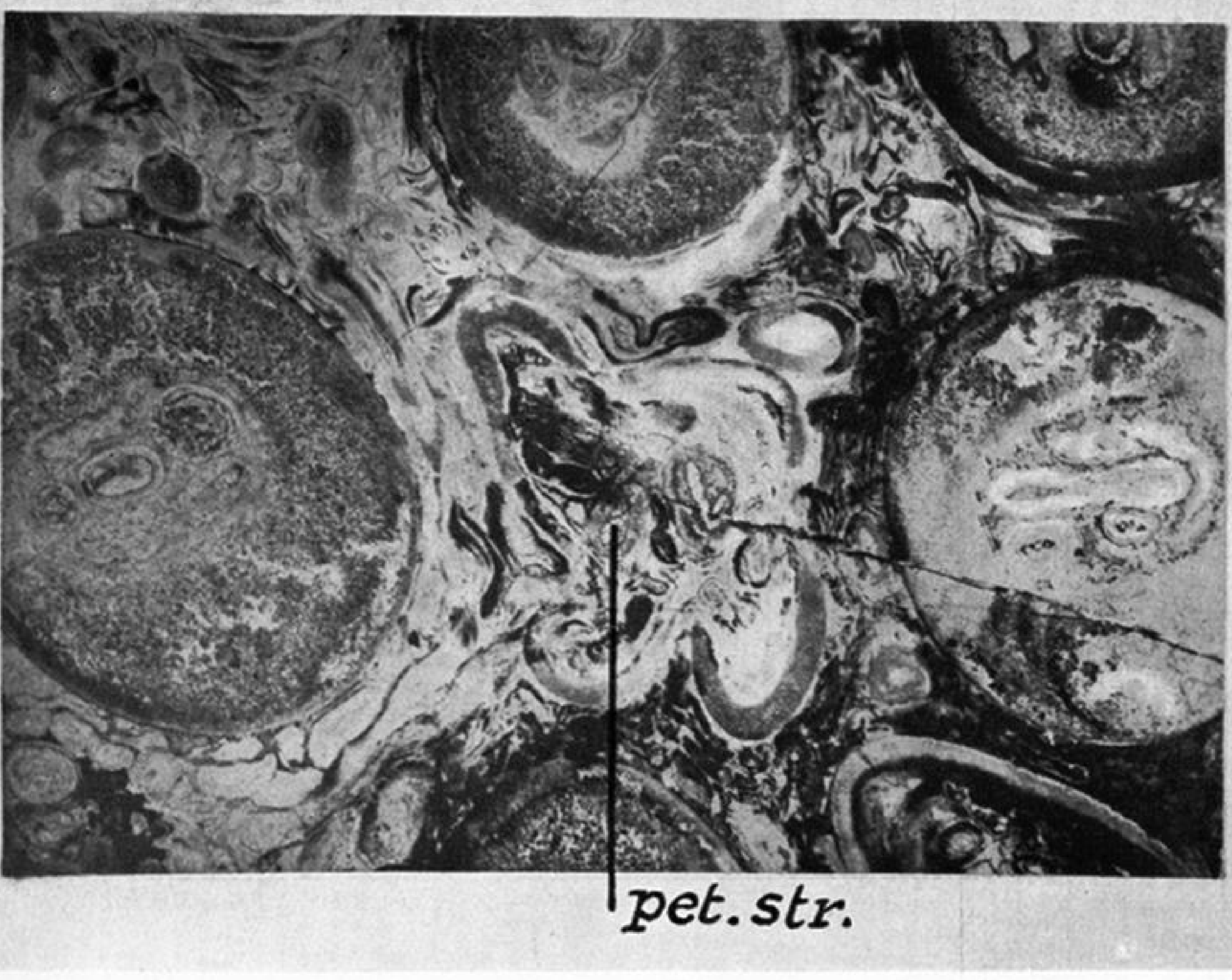

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Clepsydropsis australis.

PLATE 4.

(All the figures are from untouched photographs.)

FIG. 15.—Stele of stem No. 9 (specimen 2, section 2). × 7·3.

FIG. 16.—Part of a cross-section of specimen 2 taken in the region of stem No. 13 at the level × in text-fig. 11. The large white patch indicates the position of the crushed stem. Numerous closely packed roots, all transversely cut, forming part of a probable root-felt. × 1·4.

FIG. 17.—Transverse section of a petiole near its base. The petiolar strand still shows a slight curvature (the intruded root is on the abaxial side); the peripheral loops are still connected together by the tangential bridge. On the right, abaxially, an aphlebia-trace. Small-celled outer cortex, grading into the larger-celled inner cortex. Specimen 2, section 2. × 8·1.

FIG. 18.—An aphlebia-lobe in cross-section, with two meristeles, each delimited from the cortex by a well-marked endodermis of small regular cells; the stele on the left shows a group of small tracheides in the centre. *Ep.* epidermis; the cortex includes scattered cells with dark contents, especially around the meristeles. Specimen 1, section at level 73 in text-figs. 8. × 36.

FIG. 19.—Petiolar strand of the larger of the leaves shown in Plate 3, fig. 8 (specimen 2, section 1). The same leaf is seen natural size in the centre of fig. 1, Plate 1. × 9.

FIG. 20.—Longitudinal section of a stem in specimen 2, showing towards the lower end the mycelium of a fungus and towards the top what may at first sight be regarded as the reproductive bodies of the fungus, but which are probably of inorganic origin. × 52·5.

FIG. 21.—The same section, showing the mycelium. × *ca.* 200.

FIG. 22.—The same section, showing some of the dark resting-spore-like bodies enclosed in spherical thin-walled sacs. × *ca.* 200.

FIG. 23.—Longitudinal section of specimen 1. On the right, part of a stem with four spine-like emergences; on the left, part of a diarch root. The tip of one of the emergences is frayed, indicating that something has been broken off from there (see p. 12, and compare Plate 6, fig. 41). × 19.

FIG. 24.—Transverse section of a peripheral part of specimen 1, taken at level 9 in text-fig. 8. (Compare the top left-hand corner of text-fig. 1.) In the centre the tip of an old rachis-stump in cross-section, invaded by roots; the outer cortical sheath has been invaginated and the petiolar strand (*pet. str.*), as seen in section, has been bent upon itself. Several of the petioles show invading roots; the petiole on the extreme left bears several emergences. × 2·6.

FIG. 25.—A petiole from the same section, showing over a dozen invading roots, some of which have pushed the petiolar strand out of shape. The large intruded root on the lower side contains a copious fungal mycelium of the same type as in figs. 20, 21, clearly visible if the photograph is examined with a lens. × 3·66.

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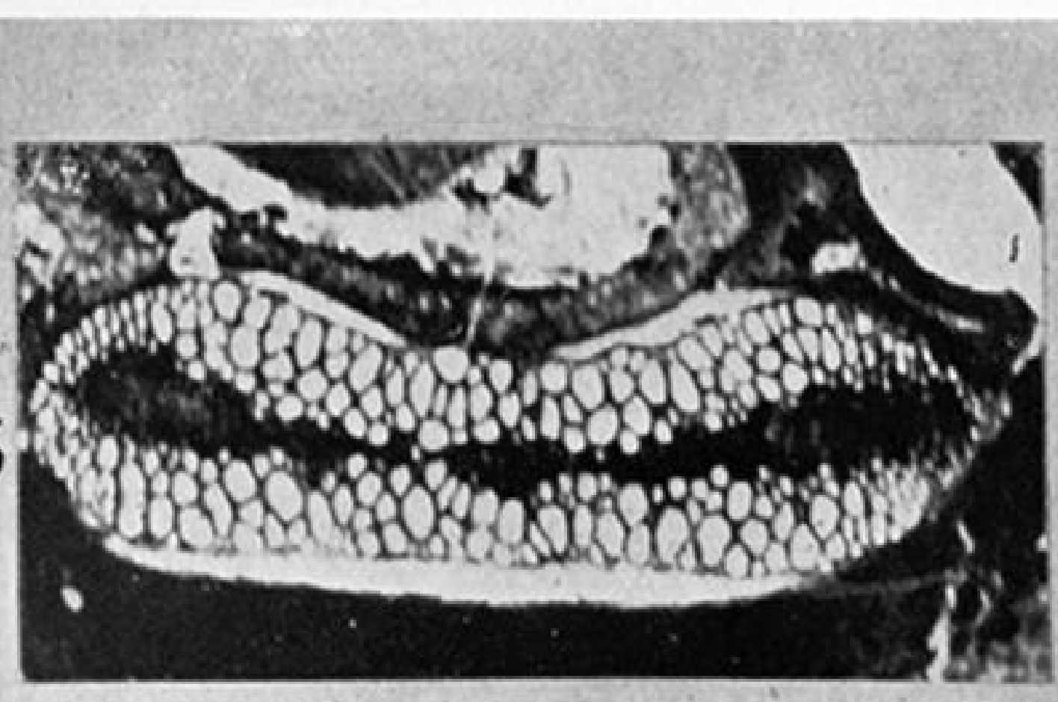

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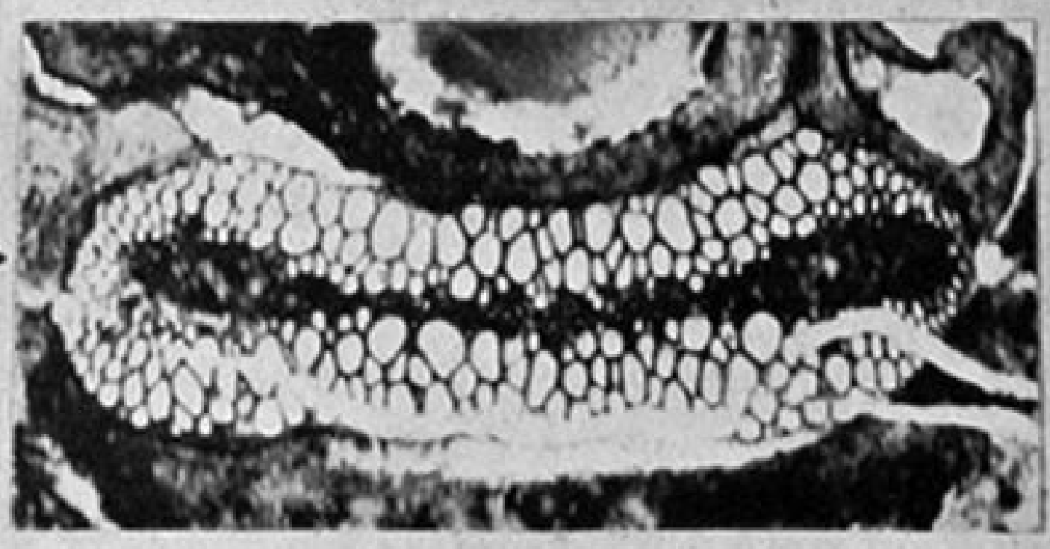

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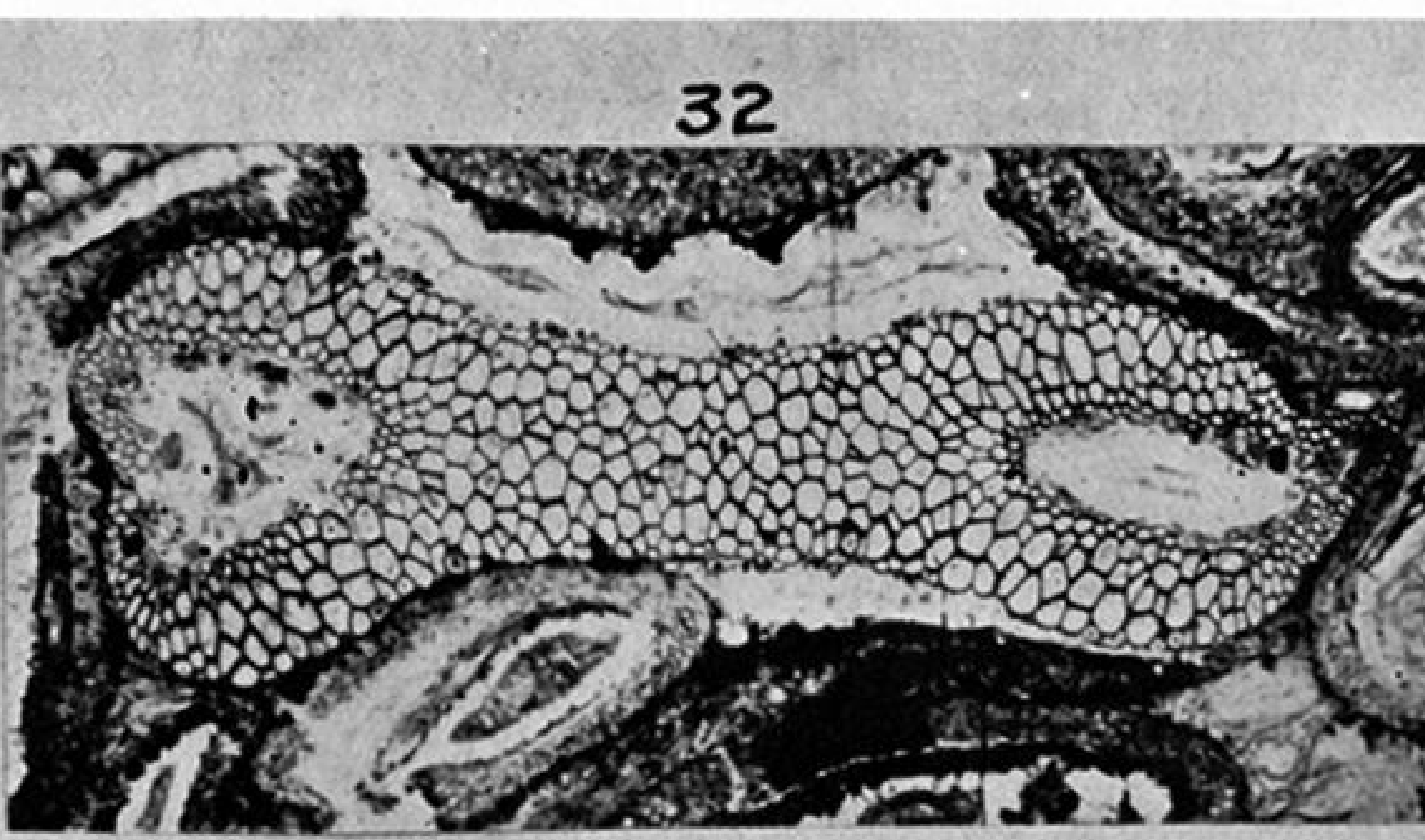

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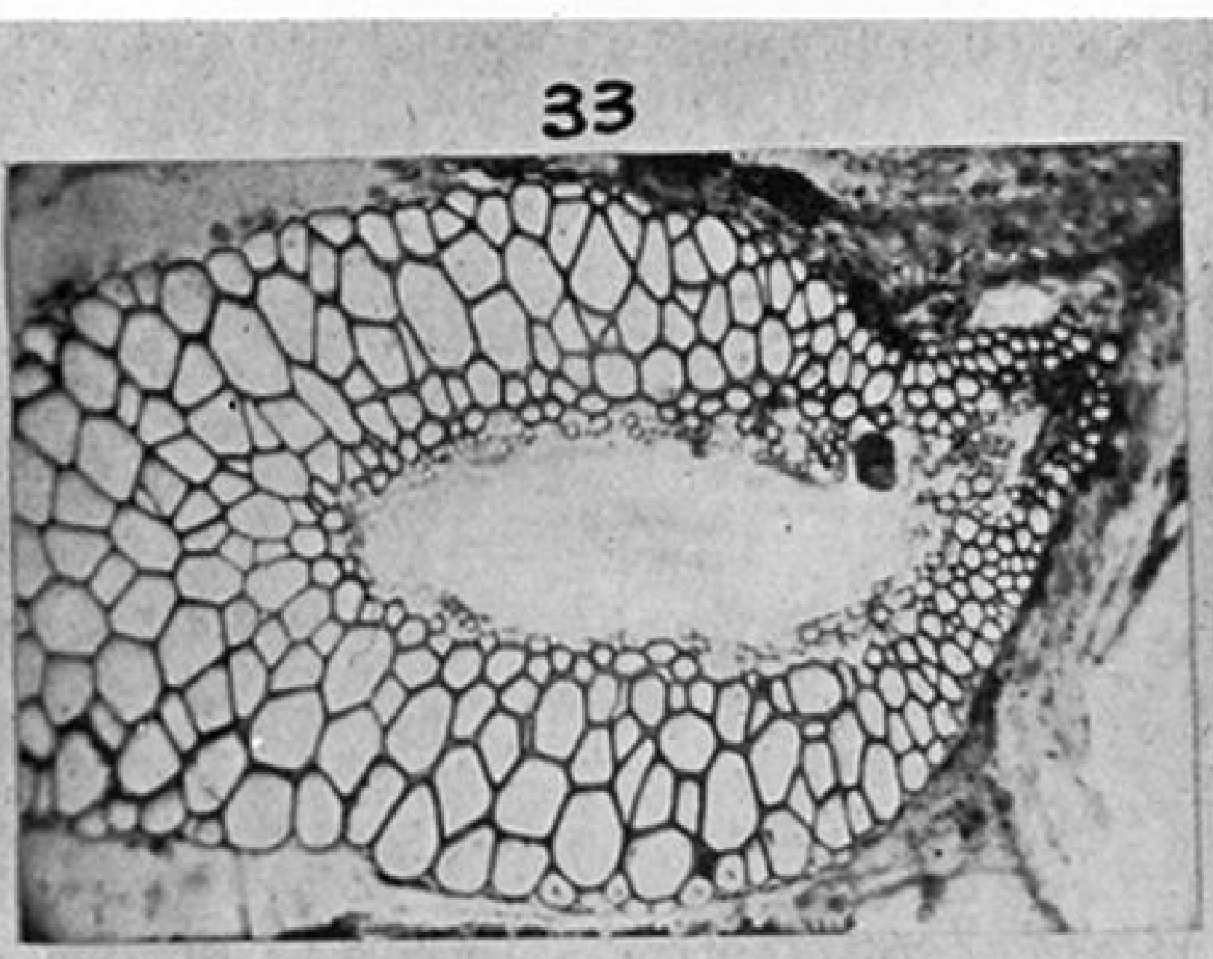

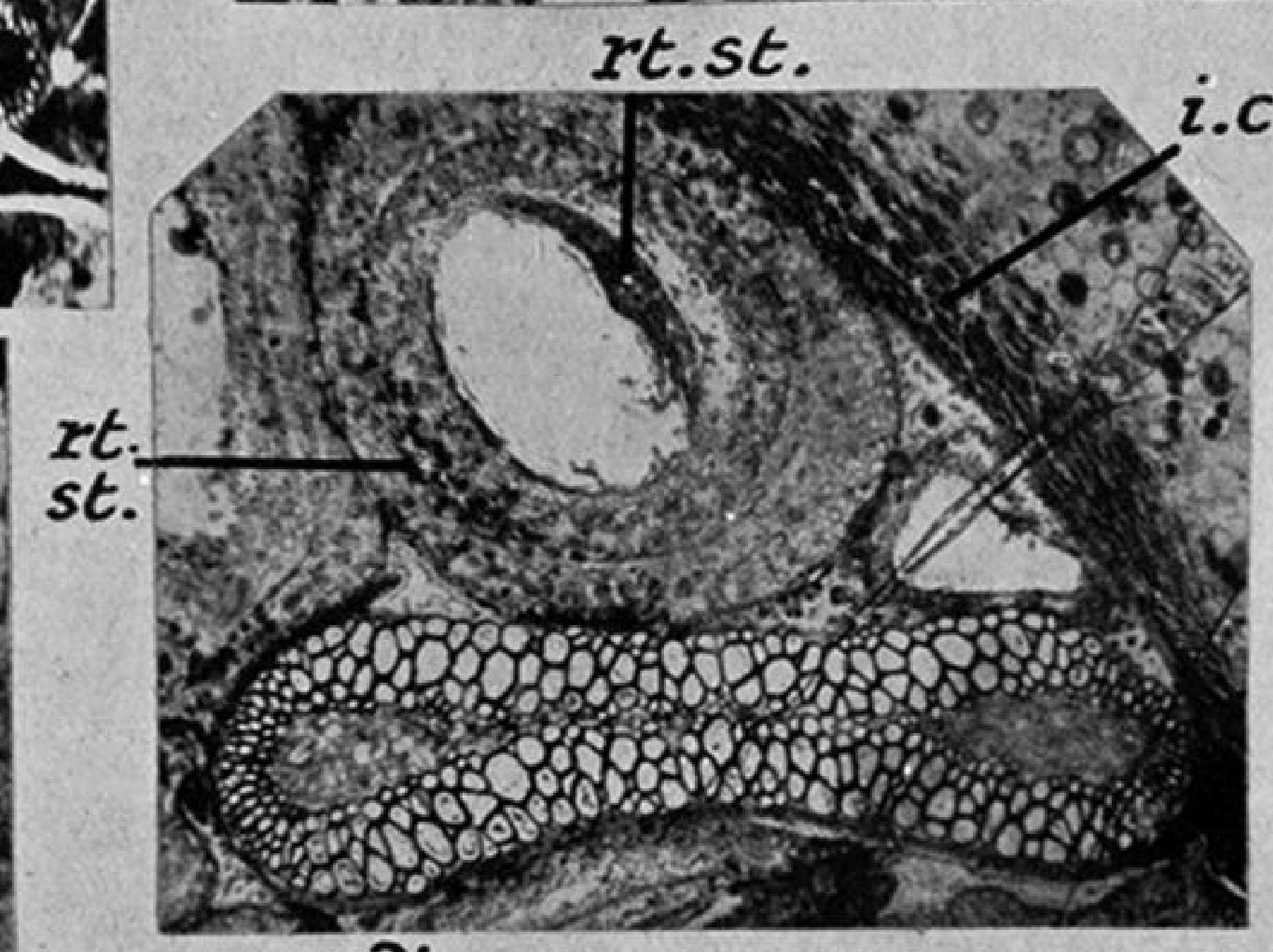

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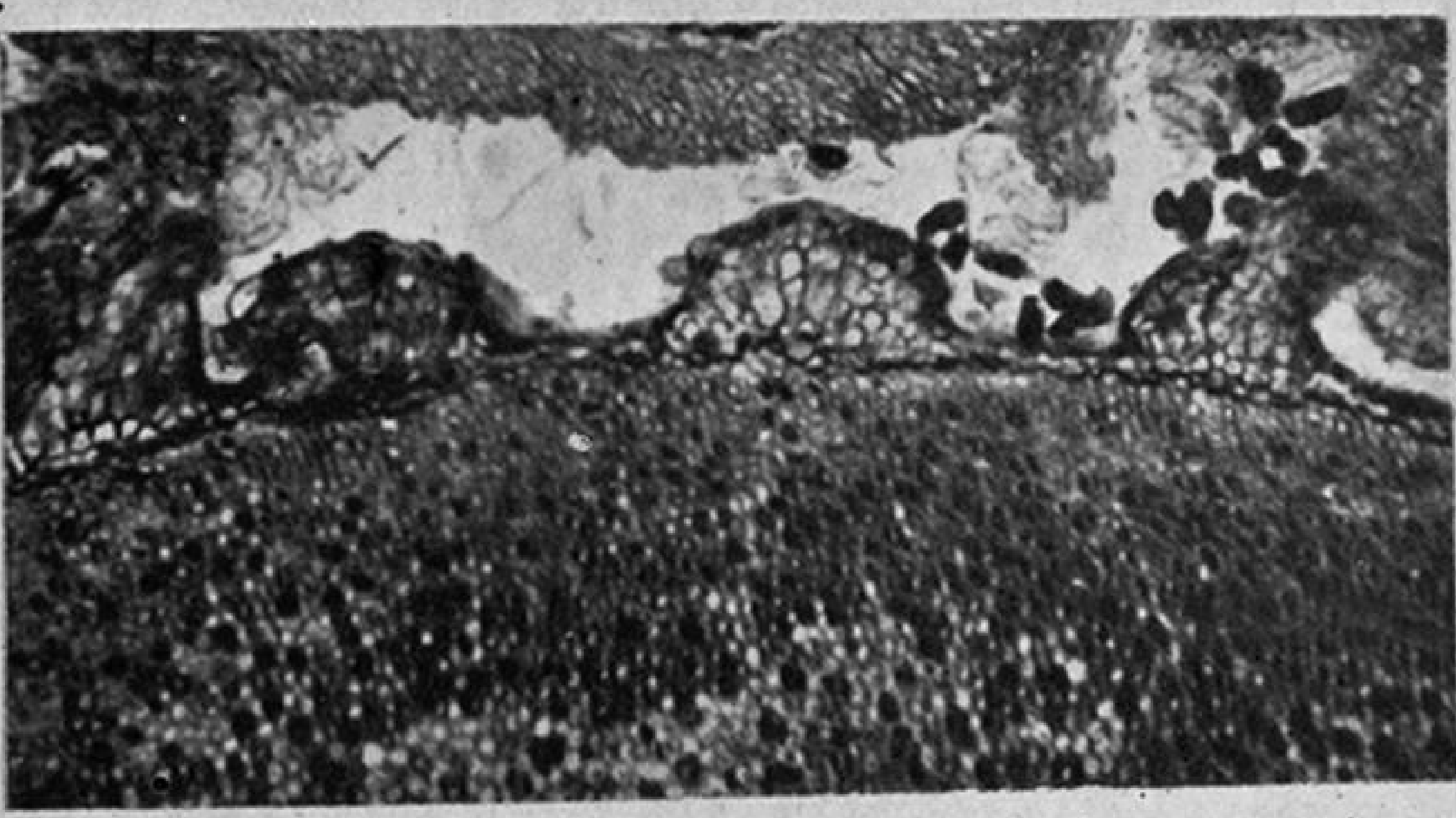
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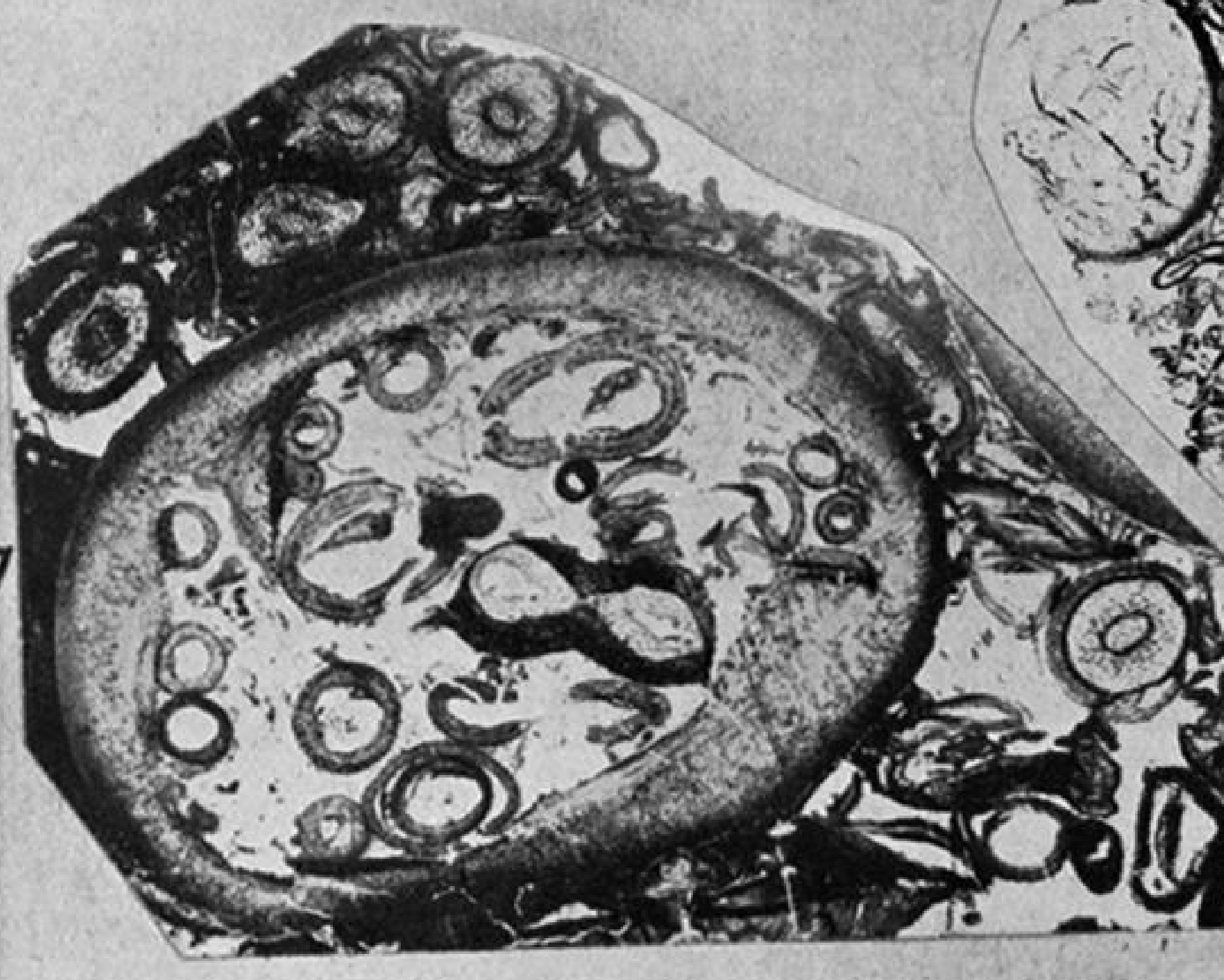

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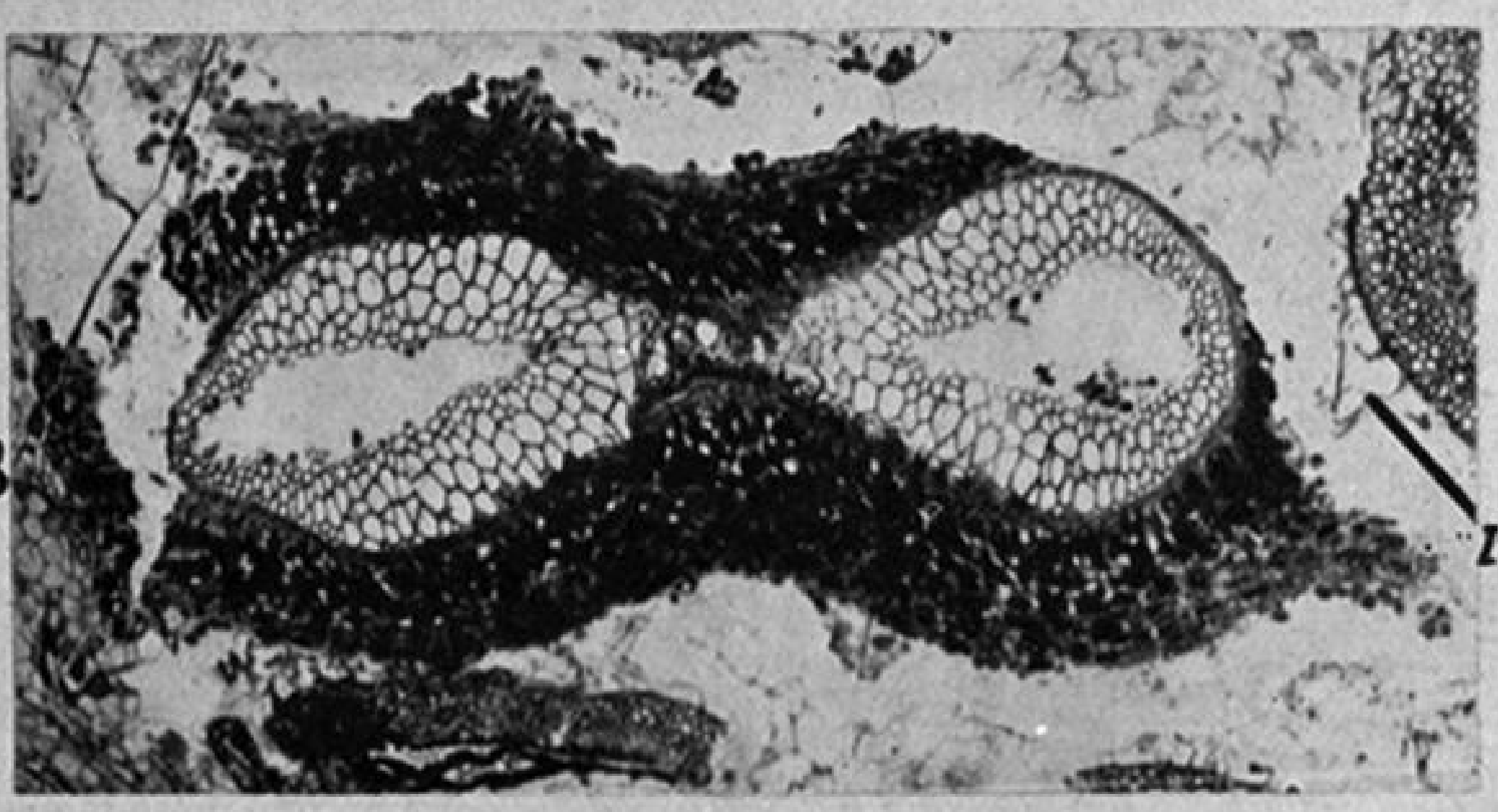

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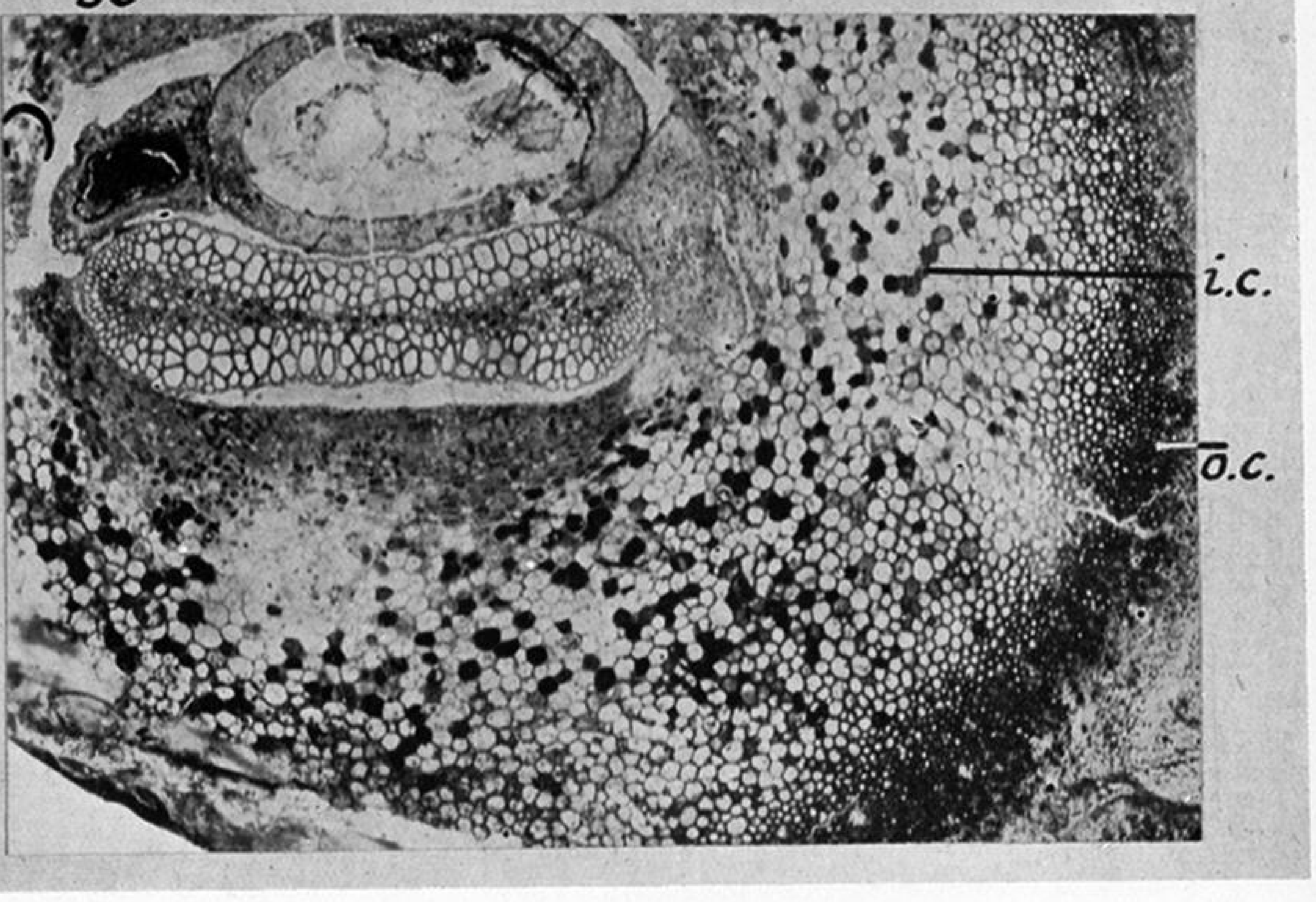

Clepsydropsis australis.

PLATE 5.

(All the figures are from untouched photographs.)

FIG. 26.—Transverse section of part of the Lyndon specimen (specimen 7, section 3). The arrows point towards what are probably two very badly crushed stems. At other places the preservation is excellent. Two of the leaves are shown enlarged in figs. 27, 28, 34. The cross indicates the enigmatical axis described on p. 25 (shown also in figs. 50, 51, Plate 6); *em.* emergences (enlarged in Plate 6, fig. 41). Numerous well-preserved roots and aphlebiæ are present (examine with a lens, especially at *aphl.*, where a group of several very minute terminal segments of aphlebiæ are seen). At *br. aphl.* are seen the two lobes of an aphlebia forked at its very base. × 1.

FIG. 27.—Transverse section of the same specimen 2–3 mm. above fig. 26. Petiole with numerous intruded roots, one of the latter with another root intruded into itself. The thin-walled tissue of the inner cortex, including numerous cells with dark contents, has been pressed against the petiolar strand, of which the "waist" has been crushed. × *ca.* 3·3.

FIG. 28.—The same petiolar strand; small tracheides line the peripheral loops. × *ca.* 14.

FIG. 29.—Part of specimen 7, section 1, showing three petioles, roots and aphlebiæ. The petiole on the left shows the origin of a pinna-trace, further enlarged in fig. 36; that on the right has not yet attained the permanent form (further enlarged in fig. 31); on the left it bears emergences, enlarged further in fig. 37. The spores shown in Plate 6, figs. 47–49, were all found entangled in root-hairs at the spot marked *sp.* × *ca.* 3·3.

FIG. 30.—Another petiole from the same section, showing the outer cortex (*o.c.*) of narrow cells; inner cortex (*i.c.*) of wider cells, many of them with dark contents; two intruded roots on the abaxial side of the slightly curved petiolar trace, in which the tissues of the peripheral loop and the tangential bridge are preserved. × *ca.* 12.

FIG. 31.—Another petiole from the same section, showing a slightly later phase of the strand; tangential bridge of small tracheides. On the adaxial side two intruded roots lying one inside the other; *rt. st.* the steles of the two roots (see fig. 29, petiole to the right); *i.c.* inner cortex (crushed). × *ca.* 12.

FIG. 32.—A fully developed petiolar strand from section 2, specimen 7, surrounded on all sides by intruded roots. The peripheral loop on the left has been deformed; that on the right is about to give off a pinna-trace. × *ca.* 12.

FIG. 33.—Part of the same strand, to show the incipient pinna-trace, and small tracheides lining the peripheral loop. The delicate parenchyma is not preserved. × *ca.* 24.

FIG. 34.—The same petiolar trace as the one shown in fig. 30, 2–3 mm. distally to that figure. × *ca.* 12.

FIG. 35.—The same trace, 2–3 mm. still higher up. × *ca.* 12.

FIG. 36.—The trace of the petiole at the left of fig. 29. The upper peripheral loop has formed a pinna-trace. On the right, two intruded roots, one inside the other; on the left, three such roots, placed in a concentric manner. Under the microscope the steles of all the roots are clearly seen. × *ca.* 12.

FIG. 37.—Unusually large emergences on the petiole shown at the right in fig. 29. The nature of the oval or elliptic dark bodies on the right is unknown; they do not seem to be spores. × *ca.* 37.

FIG. 38.—Peripheral part of the petiole shown in fig. 30, showing the unusual presence of an irregular zone of horizontally and radially elongated cells immediately outside the outer cortex (*o.c.*). × *ca.* 37.

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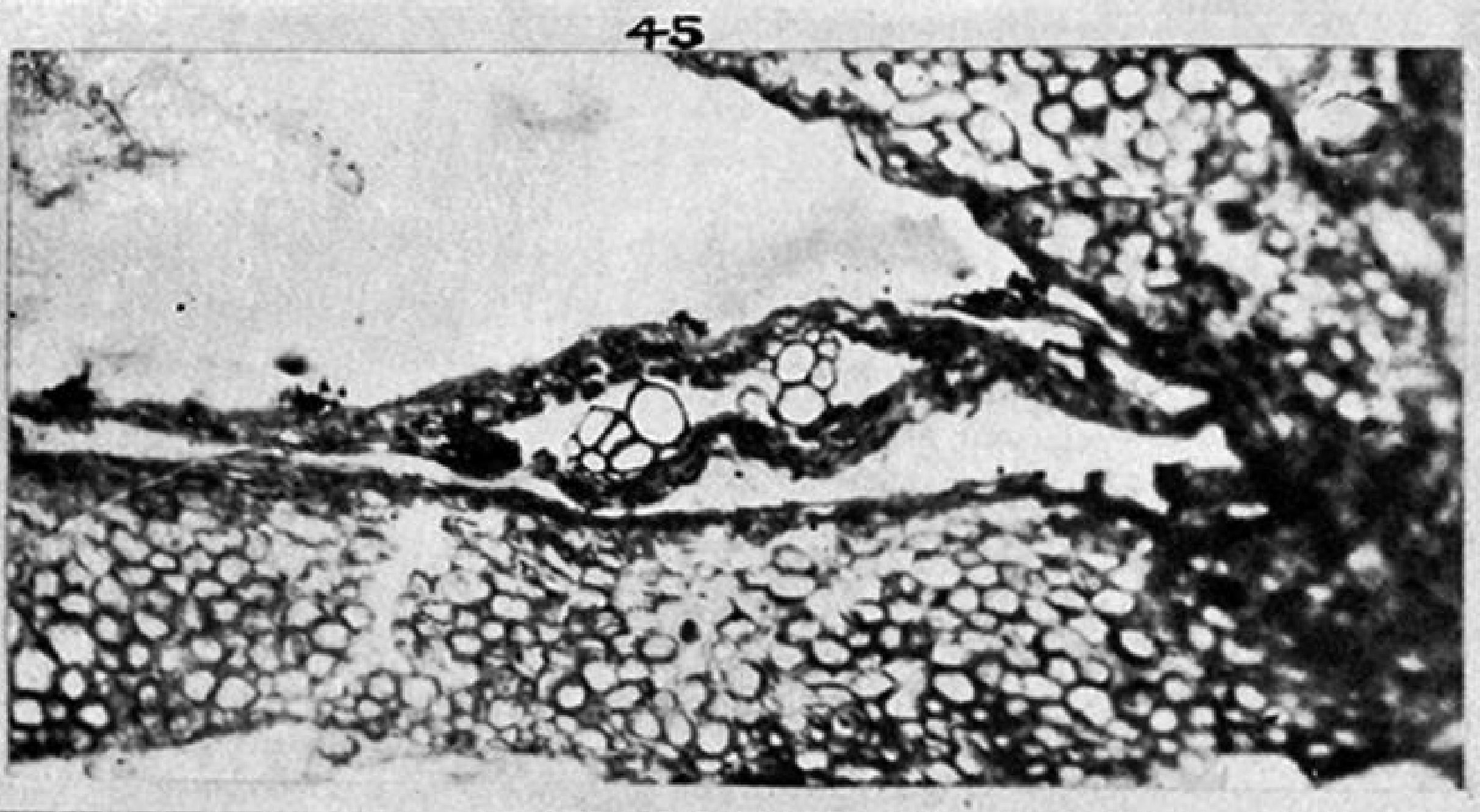

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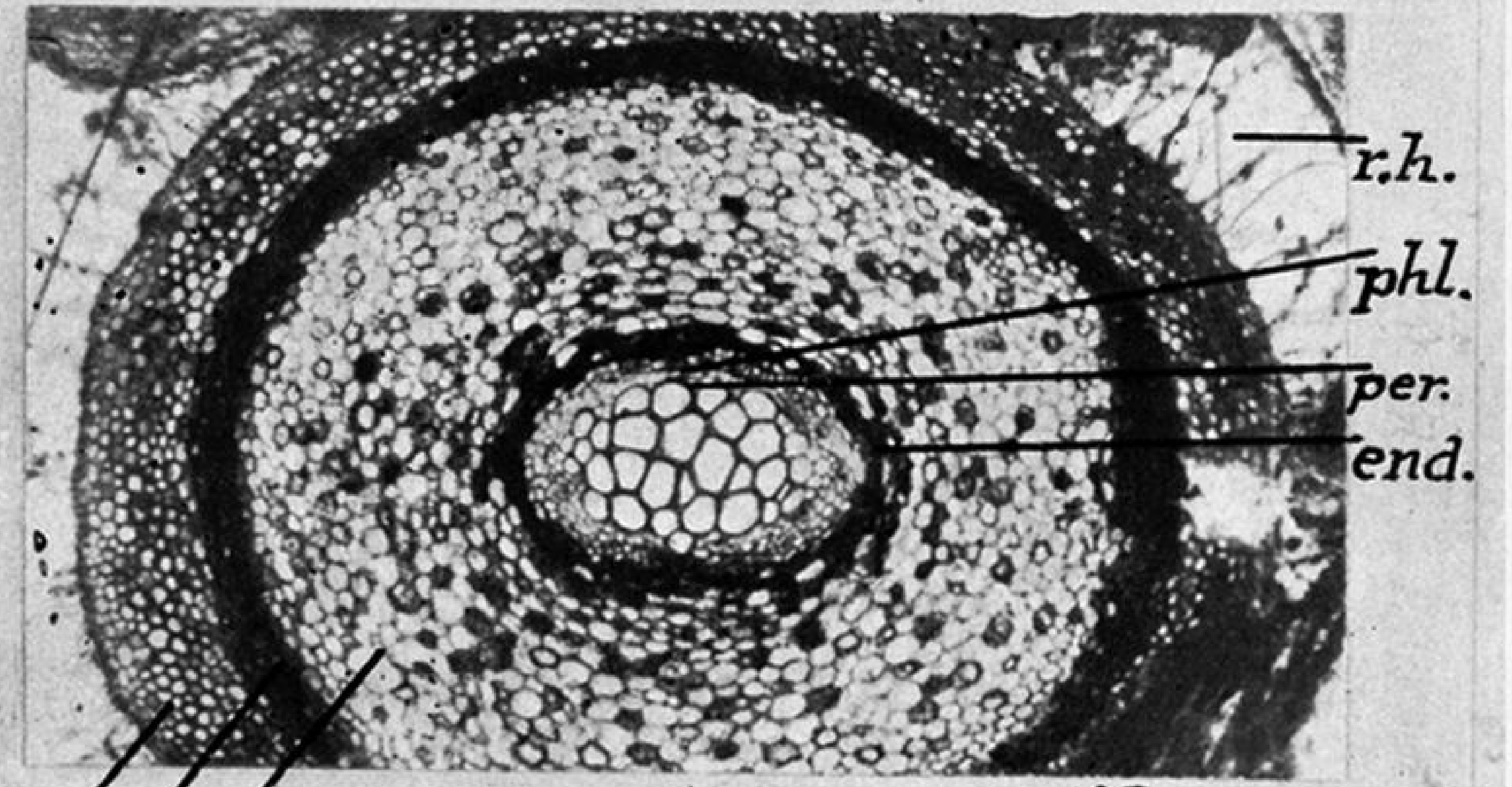

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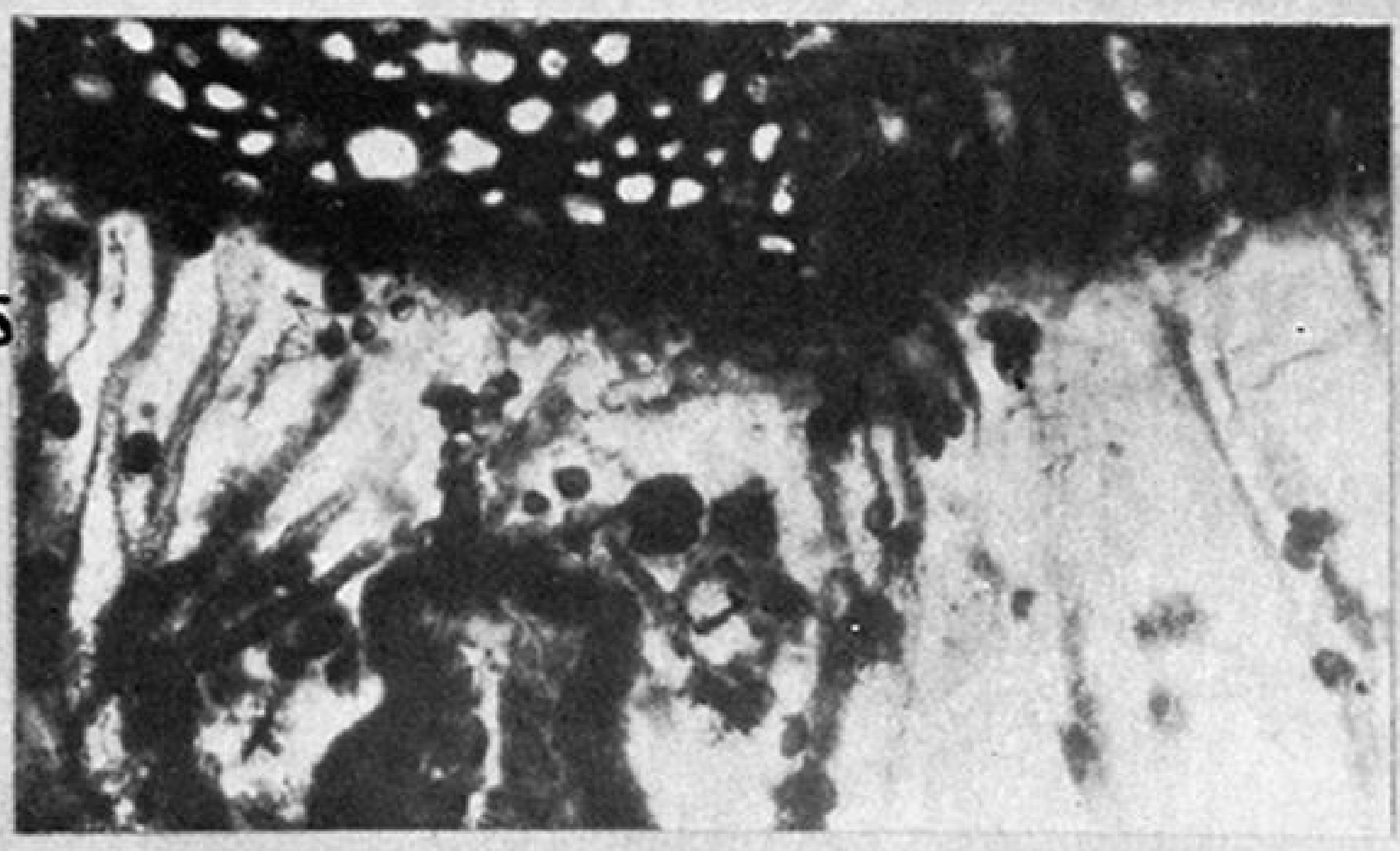

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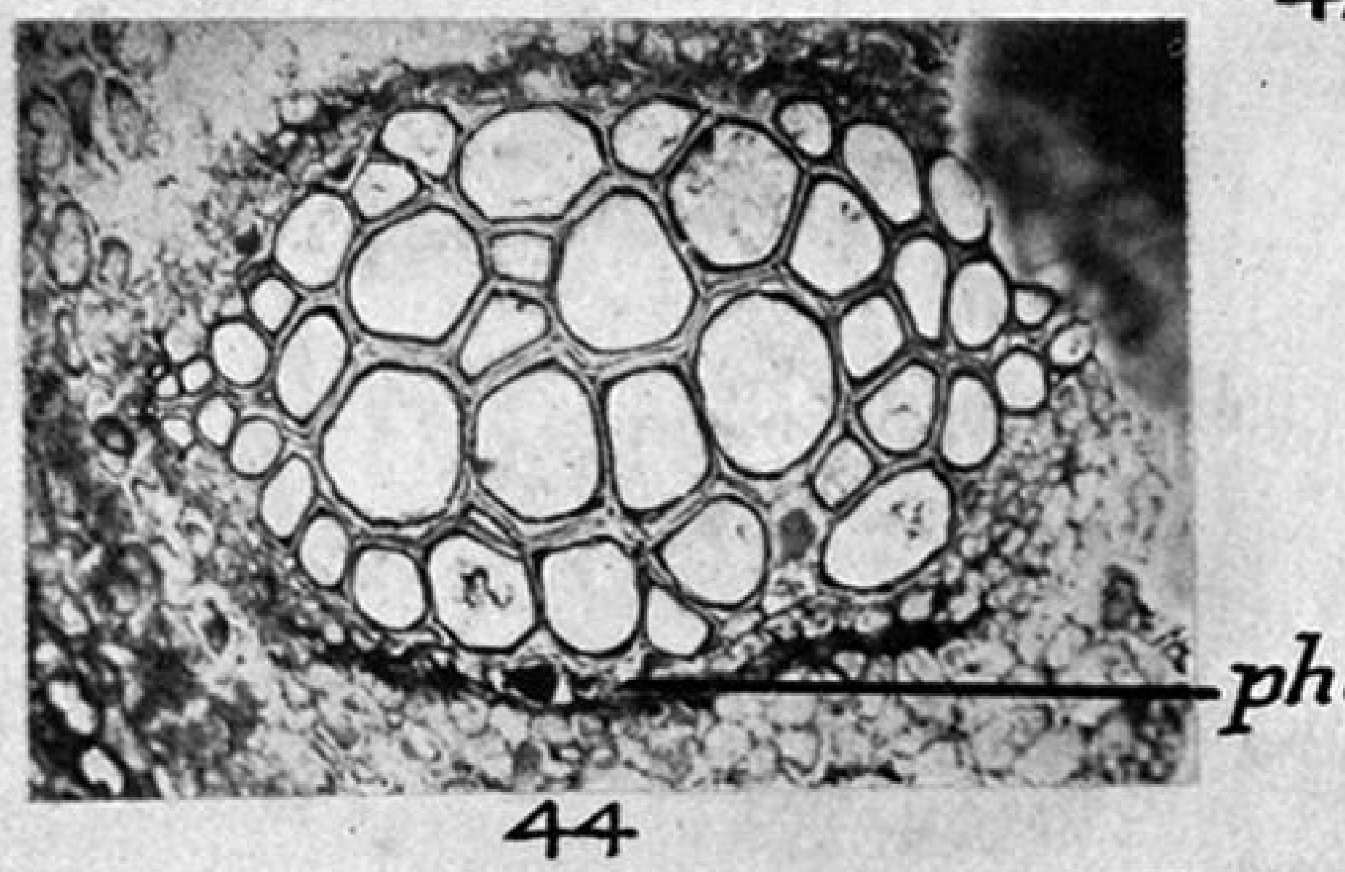

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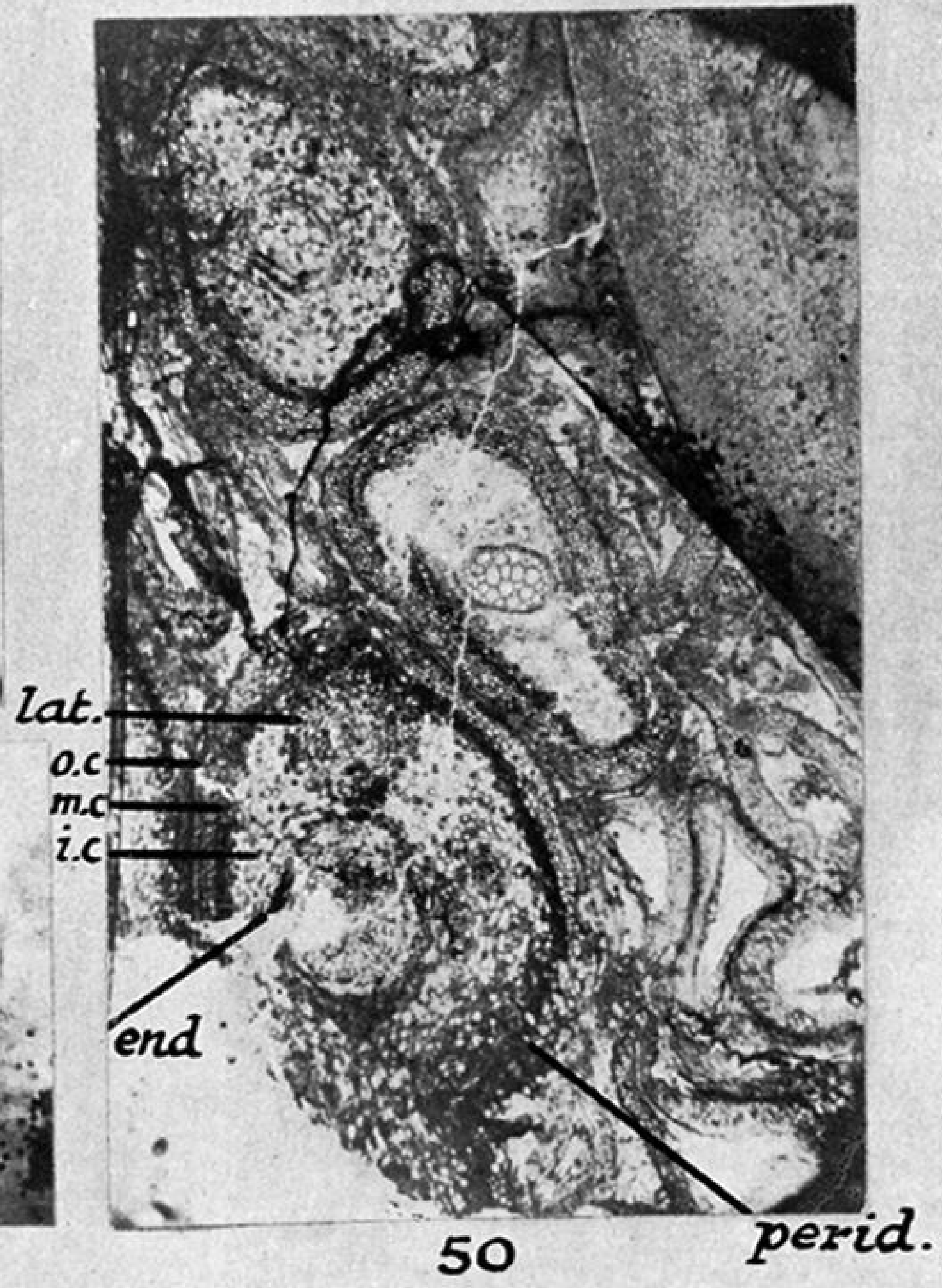

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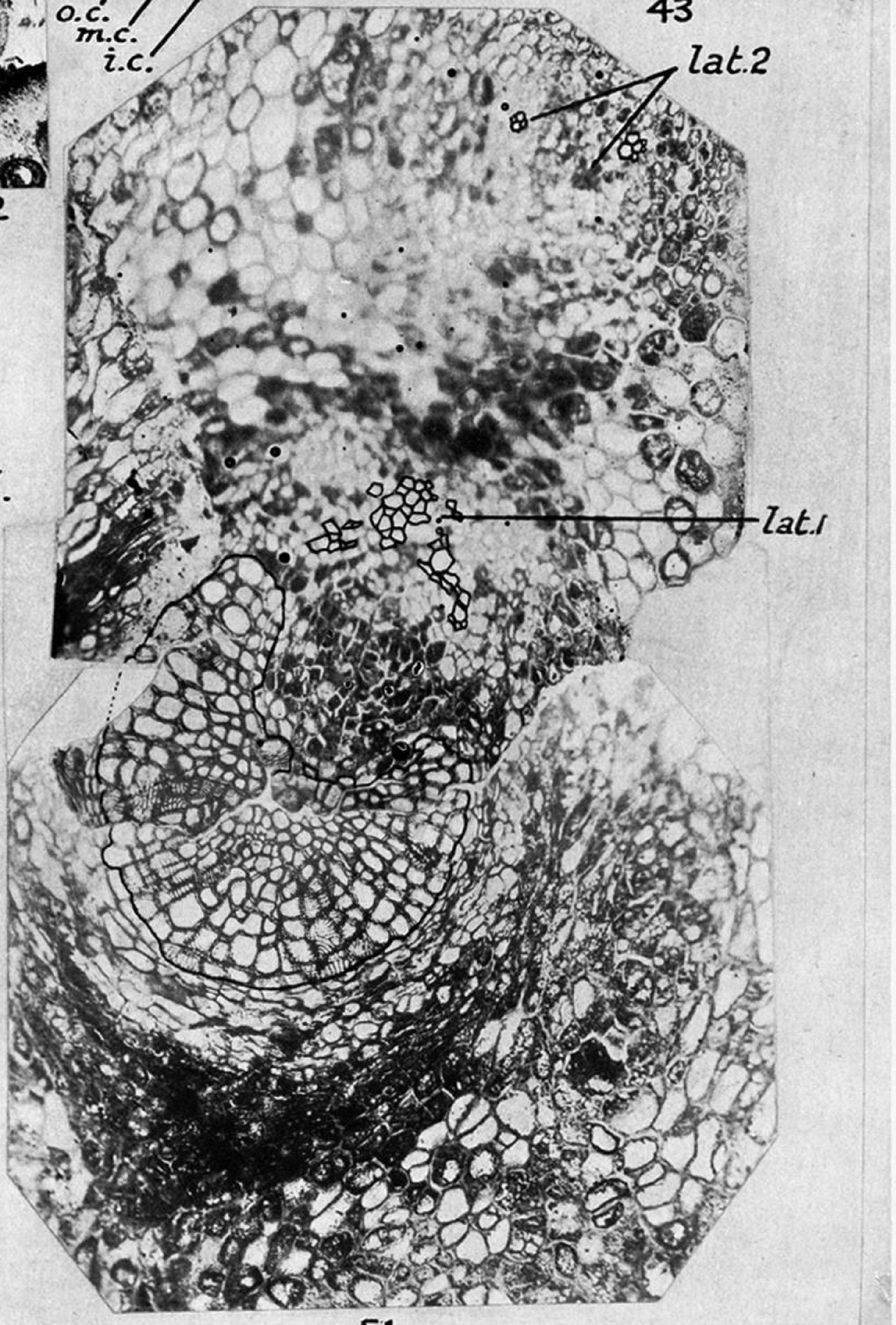

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Clepsydropsis australis.

PLATE 6.

(All the figures except fig. 51 are from untouched photographs.)

FIG. 39.—Scalariform tracheides from a root (specimen 7). × *ca.* 80.

FIG. 40.—An aphlebia-lobe, *cf.* fig. 18, Plate 4 (section 1, specimen 7). × *ca.* 12.

FIG. 41.—Emergences on the large petiole to the extreme left of fig. 26, Plate 5. One of the emergences (the one on the right) appears to terminate in a mass of cells which may be a glandular head; similar detached masses of cells are lying near by; well-preserved root-hairs are seen on the three roots. The exact spot which this figure represents is indicated in fig. 26 by the reference line (*em.*) on the left. × *ca.* 16·5.

FIG. 42.—A well-preserved root from section 2, specimen 7 (seen also in fig. 27, Plate 5). The petiole on the left shows (near the root) over half a dozen emergences. × *ca.* 6.

FIG. 43.—The same root, showing the diarch xylem-plate, phloem (*phl.*), pericycle (*per.*), endodermis (*end.*), inner, middle and outer cortex (*i.c.*, *m.c.*, *o.c.*); *rh.* root-hairs. × *ca.* 30.

FIG. 44.—Xylem and part of the phloem (*phl.*) of the root shown in the middle of fig. 50. In the xylem the middle lamella is clearly visible. × *ca.* 66.

FIG. 45.—Part of the cortex and crushed stele of one of the roots intruded into the petiole shown in figs. 27, 28. The same root is seen at the bottom of the latter figure. The diarch xylem plate is seen in two pieces, as the middle part of the plate, not yet lignified, has been destroyed. The crushed inner cortex surrounds the stele. × *ca.* 77.

FIG. 46.—Spores of various sizes caught among the root-hairs (specimen 7, section 1). × 82·5.

FIGS. 47 to 49.—Tetrahedral spores of three different sizes, all magnified exactly in the same proportion. The spore (of medium size) in fig. 47 has opened along the triradiate mark. In fig. 48 the small upper figure with two spores is only a darker print of part of the lower figure, reproduced to show more clearly the triradiate mark in the spore on the right. The large spore in fig. 49 has also burst along the triradiate mark; the black round body in the opening is extraneous. All × *ca.* 340.

FIG. 50.—Part of section 1 of specimen 7 (Lyndon) showing several roots of the *Clepsydropsis*, part of a petiole (in the top right-hand corner, with an intruded root), and, in the bottom left-hand corner, the better-preserved of the two sections of the enigmatical axis (stem or ? root) containing a partially preserved stele with well-developed secondary wood; *perid.* traces of a periderm; *lat.* lateral organ in cortex; *o.c.*, *m.c.*, *i.c.*, outer, middle, inner cortex; *end.* ? endodermis. × *ca.* 10.

FIG. 51.—Part of the same axis, further magnified. After the photograph in fig. 50 had been prepared the section was unfortunately further damaged. Fig. 51 was prepared by piecing together four different parts which had to be photographed separately at the same magnification; *lat.* 1, *lat.* 2 vascular supply to the two lateral organs (inserted in Indian ink with the help of a camera lucida). × *ca.* 60.