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On the Structure of Zygopteris primaria (Cotta) and on the Relations between the Genera Zygopteris, Etapteris and Botrychioxylon

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II. *On the Structure of* Zygopteris primaria (Cotta) *and on the Relations between the genera* Zygopteris, Etapteris *and* Botrychioxylon.

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

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[Plates 6–8.]

Contents.

Introduction.

Just a hundred years ago Bernhard von Cotta described, in one of the earliest works dealing with the internal structure of silicified plants, the Permian tree-fern now known as *Zygopteris primaria*. The general belief is that only one specimen was ever discovered; our knowledge of the structure is thus confined to the petiole, and that, too, as we shall see, is defective. It was therefore a pleasant surprise when, during a visit to Berlin in September, 1929, I came across a magnificent specimen with the centre occupied by a fairly well-preserved protostelic stem. Round the stem the persistent

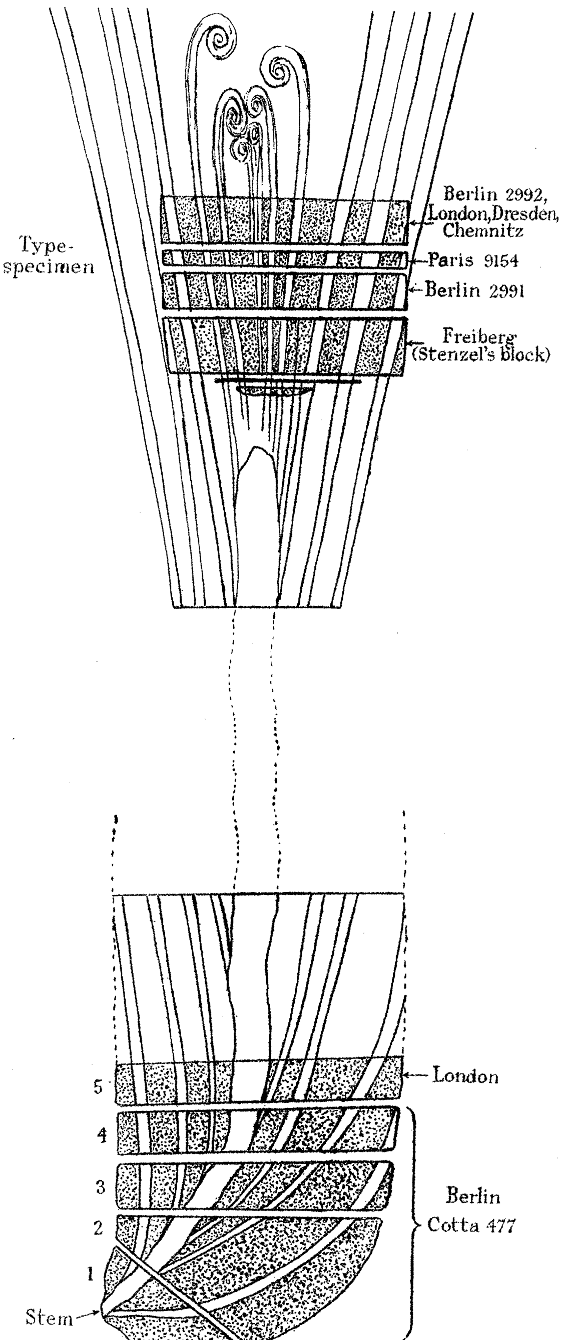

FIG. 1.—Diagram to show the relation between the type-specimen and the Berlin specimen. The topmost slab has been theoretically reconstructed from several fragments of which the interrelations are not exactly known; the thickness of the Paris slab is drawn from memory; the remaining seven slabs are shown roughly to scale. About 1/5 natural size.

leaf-bases revealed all the stages, hitherto unknown, in the leaf-trace sequence, while the outermost petioles were identical in structure with those of the type-specimen, leaving no doubt whatever of a specific identity. Between the petioles were numerous adventitious roots, also previously unknown.

While this improved acquaintance with one of the first-known Zygopterids is welcome in itself, the facts now brought to light are of a very unexpected nature. For, as I have ascertained beyond doubt, and as will be seen from what follows, *Z. primaria had typical Etapteris petioles, borne upon a stem having the Botrychioxylon type of stele; the leaf-trace sequence and root-structure were also essentially as in B. paradoxum.* Had the Berlin specimen been known earlier, neither the genus *Botrychioxylon* (SCOTT, 1912) nor *Etapteris* (BERTRAND, 1907) would ever have been founded. Indeed, the creation of the latter genus was entirely due to an error of observation, for even in the type-specimen the petiolar bundles are typically *Etapteris*-like, as COTTA showed a century ago, and not ≻-≺-shaped with hooked antennæ, as we have been accustomed to believe, after PAUL BERTRAND, since 1909.

The object of this paper is firstly to give a brief description of the new facts and then to discuss their bearings upon the question of nomenclature and relationships within the Zygopterideæ.

Concerning the history of the Berlin specimen, all we know definitely is that it formed part of the old Cotta Collection, purchased by the Museum für Naturkunde in 1895. But there seems hardly any doubt that it is the identical specimen which was said to have been discovered by Professor KLUGE in 1862* (GOEPPERT, 1864), and to which brief references were made by GOEPPERT and later by STENZEL. The fossil, when it was shown to me by Dr. JULIUS SCHUSTER in September, 1929, had already been cut transversely into four pieces. In the British Museum (August, 1930) I found a fifth piece, no doubt cut from the top end of the same specimen, fig. 1 and fig. 8, Plate 6.

I owe it to Dr. SCHUSTER's extraordinary kindness, for which I wish to express my warmest thanks, that the investigation of this valuable specimen was entrusted to me. I also wish to thank him and the following gentlemen for permission, during my tours, to examine the various fragments of the type-specimen, now scattered over several museums in Europe: Dr. W. D. LANG and Mr. W. N. EDWARDS (London), Professor COSTANTIN and Dr. A. LOUBIÈRE (Paris), Professor K. WANDERER (Dresden), Dr. E. STRAUSS (Chemnitz), Professor F. SCHUMACHER and Professor R. SCHREITER (Freiberg i, S.). To Professor SCHUMACHER I am specially grateful for permission to cut further sections from STENZEL's original. As a considerable part of this work was done while touring about on the Continent during the years 1929 and 1930, I am indebted for laboratory facilities and other kindnesses to Professor W. GOTHAN (Berlin), Professor SUZANNE LECLERCQ and Professor C. FRAIPONT (Liége), Professor C. BOMMER (Brussels), Professor Dr. B. KUBART (Graz), and to Professor F. X. SCHAFFER, Professor J. PIA, Dr. TRAUTH and Frl. LOTTE ADAMETZ (Vienna). To Professor A. C. SEWARD, F.R.S., and Dr. D. H. SCOTT, F.R.S., I am, as on previous occasions, grateful for their able criticism and for valuable opportunities of discussion.

I am further indebted to Dr. A. LOUBIÈRE, of Paris, for a tracing of the Paris slab (No. 9154) of the Type Specimen; also to Mr. W. N. EDWARDS and Professor H. S. HOLDEN for help in connexion with the slides of *Botrychioxylon paradoxum* in the British Museum (Scott Collection).

With the exception of the large section A, fig. 2, which was prepared at the Sorbonne, all the thin sections were made by hand in my laboratory by Messrs. SHANKAR and R. S. SHARMA.

Previous Work.

The early history of *Z. primaria* will be seen at a glance from the synonymy on p. 39. The old genus *Zygopteris*, CORDA (1845), once included all fossil ferns having an H- or X-shaped foliar bundle, but in 1909 P. BERTRAND reduced it to the single species *Z. primaria* under the (mistaken) belief that the structure of the foliar bundle was unique. The remaining plants referred to this once extensive genus are now assigned to the independent genera *Etapteris*, *Ankyropteris*, *Diplolabis* and *Metaclepsydropsis*.

Our knowledge of *Z. primaria* is due to the works of COTTA (1832), STENZEL (1889),

* See GOEPPERT (1864), p. 43; STENZEL (1889), p. 26.

and BERTRAND (1909). COTTA's figure of the petiolar bundle is essentially correct, but his description has now only an historical interest. STENZEL's account is by far the fullest and most accurate. Like COTTA, he correctly shows (see his *fig.* 45, *Plate V*) that the typical form of the bundle is H-shaped, but his detailed sketch (*fig.* 47, *Plate V*)

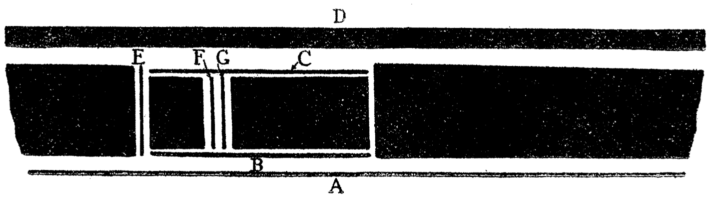

FIG. 2.—Diagram to show the way in which slab 3 of the Berlin specimen was sectioned. The letters A to G indicate the thin sections, except D, which is an unground slice. One $\frac{1}{2}$ nat. size.

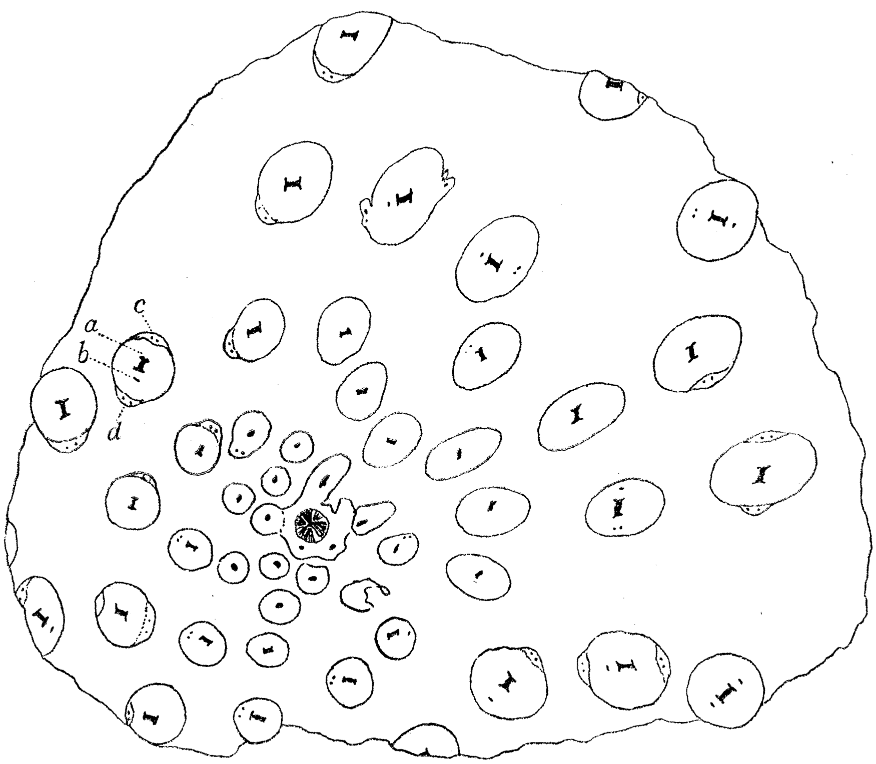

FIG. 3.—Diagram (partially restored) of lower polished face of slab 3 (Berlin specimen), *drawn as if seen from above.* The petioles on the right-hand side are cut obliquely (see fig. 1 and compare the thin section A, Plate 7, fig. 23, which was prepared from this face of the slab). The interstitial roots and pinna-lobes have been omitted. *a–d* as in fig. 5. About $\frac{2}{3}$ nat. size.

was not based upon a typical bundle, for the antennæ are here shown inclined outwards. According to STENZEL, the supply to each pinna arises as a single initial strand which, after the usual forking, passes into the appendage. The present work shows that there are two initial strands; these, however, immediately fuse into a single strand which then forks as described by STENZEL.

PAUL BERTRAND, unfortunately relying upon a single poorly preserved rachis, and probably misled by STENZEL'S fig. 47, describes a bundle shaped thus ≻–≺, with hooked antennæ, and states that the pinna-traces arise in pairs by the nipping off of the hooks. He accordingly re-defines *Zygopteris* in a much restricted sense, retaining under it the solitary species *Z. primaria*. As I hope to show, BERTRAND'S account is essentially wrong; the petiolar structure in both the specimens being typically as in his genus *Etapteris* (BERTRAND, 1907), which now proves to have been created under a misapprehension.

Till the discovery, or, rather, the re-discovery, of the Berlin specimen now to be described, nothing was known of the stem stele, leaf-trace changes or roots.

Description.

Habit.—There seems no doubt that, contrary to the view expressed by STENZEL, the plant was a tree-fern of very considerable size. I have attempted to show very diagrammatically in fig. 1 the relative positions of the type-specimen and the Berlin specimen. At the lower end the petioles are rather sharply curved to one side, showing that the Berlin specimen represents either the ascending base of a lateral branch or the juvenile part of the main stem gradually assuming an erect posture. The relatively slender axis, with a leaf-spiral of about 3/8, lies somewhat eccentrically, supported by the thick armour of leaf-bases and interstitial roots. In the type-specimen, on the other hand, there is no trace either of roots or of the stem*: a number of stout erect petioles lie in their natural positions round the crushed remains of a central bunch of young leaves, the phyllotaxis (*ca.* 3/8) being undisturbed. All the petioles, young and old, with their numerous aphlebiæ, are packed in a dense ramentum of scales, while roots are entirely absent. Evidently, as STENZEL says, this specimen represents the basal part of the crown of leaves, just beyond the stem apex. At the base the petioles are only 6–7 mm. thick; in the highest parts available (Dresden fragment, see STENZEL'S figs. 48, 49) they attain a diameter of 20 mm. This affords some idea of the size of frond they must have supported.

Stem.—The stem, excluding the decurrent leaf-bases, is barely 1·5 cm. in diameter, of which as much as 7 mm. is occupied by the stele.

As seen in cross-section, the xylem has the form of a pentagon with well-rounded angles (almost a perfect circle), enclosing a thin stellate core. The great development of secondary wood is a striking feature in common with *Botrychioxylon* (SCOTT, 1912, fig. 7, Plate 38), although the stele as a whole is much larger in our plant. The radial

* The actual leaf-bearing stem is not seen in any of the fragments of the type-specimen, all of which I have recently examined at Freiberg, Chemnitz, Dresden, Berlin, London and Paris; not even at the base of STENZEL'S large block, which has now been cut (fig. 10, Plate 6).

seriation of the cells is very obvious throughout the greater part of the stele,* but the preservation is too poor to show any cambium. The primary wood is apparently confined to the central patch, barely a millimetre in diameter; it has tracheids of the narrow elongated type, with a fine scalariform pitting which may become multiseriate in the larger elements (fig. 6). No spiral or annular thickenings have been noticed, even in the narrowest tracheids. The preservation is too poor to show whether there was any mingled parenchyma. The cross-section (figs. 13, 15, Plate 6,) shows a number of thick-walled elements scattered in a groundwork of crushed, apparently more delicate, tissue; but the exact nature of this crushed tissue remains obscure; the longitudinal section throws no light on this point. The secondary tracheids are much wider and relatively short, although not exactly of the parenchymatous type; the pitting is scalariform and multiseriate, exactly as figured by Dr. SCOTT in *Botrychioxylon* (SCOTT, 1912, fig. 21, Plate 41).

The phloem and associated layers form a thin crushed border to the stele. The cortex is very thin compared to that in *Botrychioxylon*; there is no sclerenchyma; the most prominent feature is the large secretory sacs, similar to those described by STENZEL in the petiole.

Leaf.

(*a*) *Leaf-trace and Petiolar Strand.*—The sequence of changes in the leaf-trace, as seen in cross-section, is shown in figs. 24–34, Plates 7 and 8. These figures should be compared with the radial and tangential sections in figs. 16–18, Plate 7. Each leaf-trace originates in one of the rays of the stellate primary xylem. The ray at first passes horizontally outwards through the secondary wood of the stele (figs. 16–18, Plate 7); then it is continued obliquely upwards as the core of the leaf-trace, which on leaving the stele takes away a thick sheath of secondary xylem. At this stage the leaf-trace is an elliptical strand measuring about 2 by 3 mm. (fig. 24, Plate 7), and *consisting mostly of secondary tracheids*; the only primary tissues are the few small tracheids in the centre, derived from the ray, which no doubt include the protoxylem, although the details are not preserved. Before the bundle enters the free part of the rachis the protoxylem has already forked, and for a time the diverging protoxylems remain connected together by a row of small tracheids in the tangential plane. This "protoxylem bridge" sometimes extends for a considerable distance up into the petiole (fig. 31, Plate 8), and it afforded the first clue to the fact (confirmed only after further sections had been cut) that initially there is a single centrally placed protoxylem, as in *Asterochlænopsis* (SAHNI, 1930, p. 63, and figs. 16–23, Plate 51).

At its very base the free petiole contains an elliptical bipolar strand; this is of a more

* The possibility should, however, be kept in view that the part of the peripheral zone immediately round the stellate core may be of primary origin. The radial arrangement of the cells, so evident in the outer region, becomes less obvious as we pass towards the inner border.

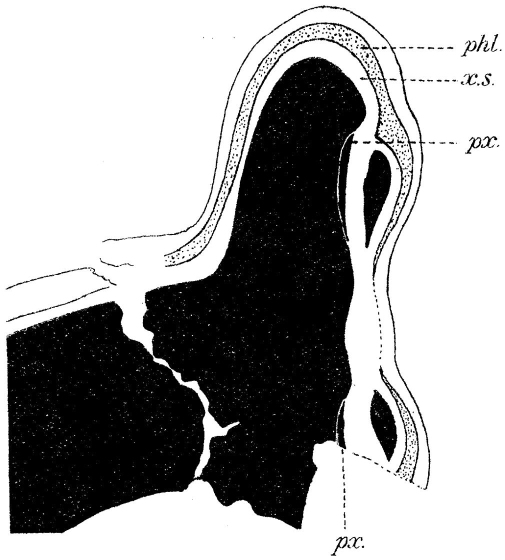

FIG. 4.—Outline sketch of part of a petiolar bundle showing origin of vascular supply to a pinna. Xylem black, phloem dotted. All along the dotted region *phl.* large empty cells, presumably sieve-tubes, are visible; *px.* protoxylem; *x.s.* xylem sheath. × about 36.

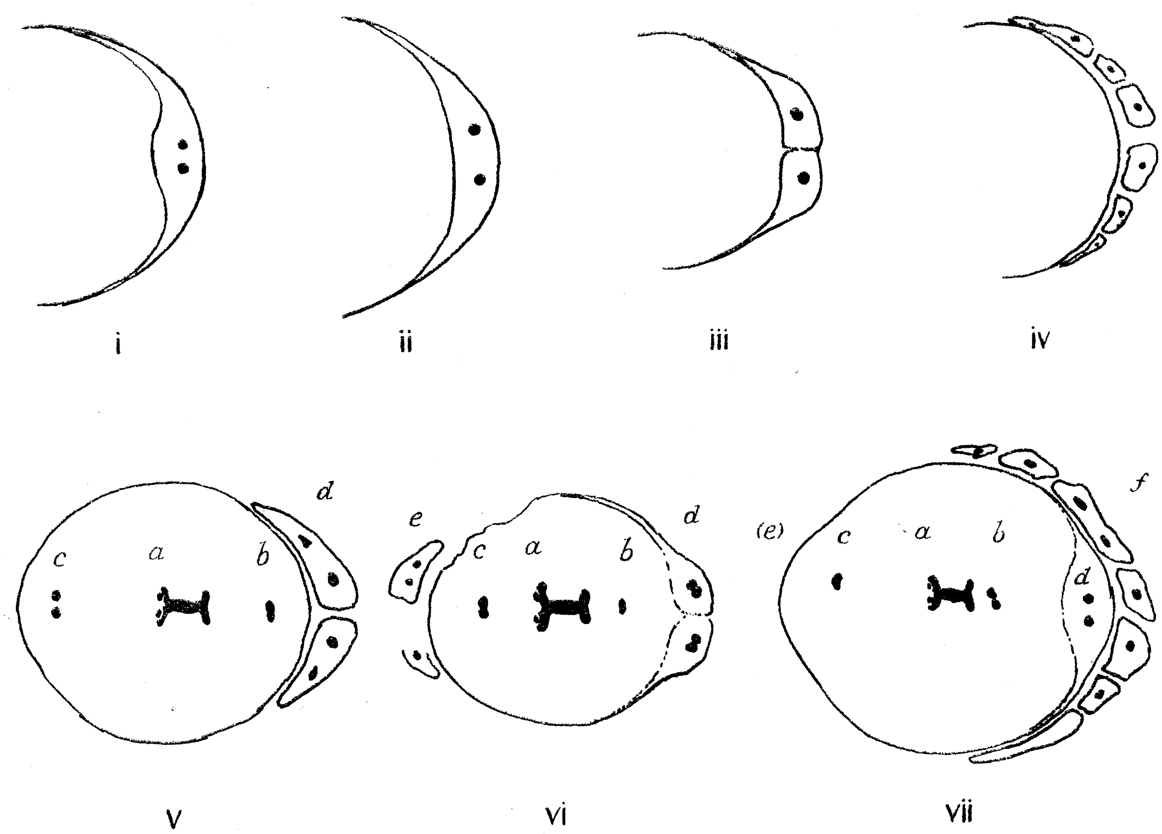

FIG. 5.—Outline sketches of petiolar cross-sections to show mode of branching of pinnæ and their vascular strands; *a–f.* successive stages, from below upwards, in the course of the pinna strands. i—iv, Branching of pinnæ. All from STENZEL's original; somewhat diagrammatic. All *ca.* × 2.

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or less swollen shape, according to the amount of secondary xylem round it. The strand shown in fig. 27, Plate 7, is nearly circular,* and shows no curvature, but as a rule the form is not so full, and there is a slight curvature which makes the bundle look somewhat reniform, the concavity facing outwards. At this stage a root-trace frequently comes off from one of the protoxylems on its abaxial side. The protoxylems lie at each focus of the ellipse, but this immersed position does not necessarily mean that they are mesarch, because at least in some well-preserved strands (figs. 25, 26, Plate 7) the tracheids over the protoxylems are radially arranged and are probably of secondary origin. In some other cases, it is true, a radial seriation is not in evidence, and the strand recalls the transient curved phase in *Ankyropteris*, especially as the protoxylems also become stretched antero-posteriorly. This resemblance with *Ankyropteris* is, however, only superficial, for the loop of tracheids is never actually closed (figs. 22, 28, Plate 7, and fig. 29, Plate 8).

As the bundle ascends the petiole, the curve straightens out, the secondary xylem rapidly disappears, the " protoxylem bridge " has also vanished, and the two protoxylems come to lie clearly on the surface, at either end of a thick barrel-shaped *Dineuron*-like strand. From the four corners of the apolar blunt processes are now thrown out *at right angles* and the characteristic ⊢⊣ form of the bundle is gradually moulded. Meanwhile the two protoxylems become extended at right angles to the plane of the apolar, and each of them immediately divides into two. This quadripolar condition is the permanent one; each protoxylem lies along the outer face of the antenna, midway between the apolar and the extreme tip, fig. 4. In undisturbed petioles the antennæ are never inclined outwards in the way described by BERTRAND (fig. 27, Plate 7, and figs. 32–34, Plate 8).

(*b*) *Origin of the Pinna-traces.*—Pinna-traces already begin to come off from the lower part of the petiolar bundle, long before it has acquired its final form. In fig. 28 (right), Plate 7, a pair of lateral strands is seen just coming off from one end of a slightly curved primary bundle. The two lateral strands are still attached to the parent bundle by their outer ends, beyond which the arms of the foliar bundle are just beginning to grow out. Fig. 31, Plate 8, shows a slightly later stage, both in the development of the foliar bundle and in the process of pinna-trace emission. The elongated strand lying off the right end of the main bundle appears to have just been formed by the fusion of the two initial strands. On the opposite side of the same rachis, far out in the cortex, there is a pair of small circular strands (no doubt the resultants of a dichotomy) already preparing to enter the base of a pinna.

In the fully formed bundle the process is essentially the same (figs. 32–37, Plate 8, and figs. 3–5). The two initial strands lie in one plane, parallel to the vertical bar from which they have just come off. There is no indication that they are hook-like processes

* Partly owing to the section being oblique. The correct form will be obtained if this photograph is viewed obliquely from the top end.

detached from the ends of the bar, as BERTRAND supposed. Very soon after their origin they unite to form one elongated bundle, but only to separate again almost immediately. In fact, *the whole process, down to the details, is like that in the form-genus Etapteris* as originally defined by BERTRAND.*

(*c*) *Form and Structure of the Pinnæ.*—There is little to add to STENZEL'S description of the pinnæ, except to elucidate their mode of branching, which was left in doubt. STENZEL suggests that the pinnæ branched in one of the two following ways: either there was a median axis from which segments came off in two lateral rows, as in a pinnate leaf, or the pinnæ were flabellate organs, with the segments diverging from the base. The latter view is no doubt nearer the truth. Examination of the material (including STENZEL'S original specimen) leads to the conclusion that the mode of

FIG. 6.—Two tracheids from a petiolar strand in the Berlin specimen (section E). A similar kind of pitting is seen in the stem and root wood. × *ca.* 185.

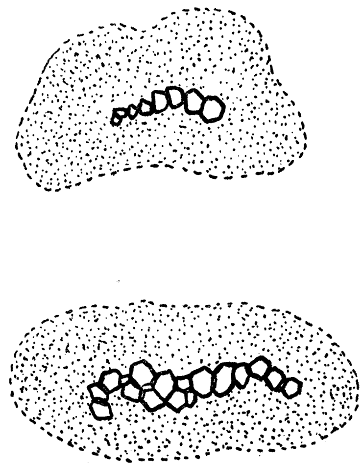

FIG. 7.—Strands of free aphlebia-lobes from the section cut at the base of STENZEL'S block. The dotted region is a thick dark-brown zone of crushed tissue. × *ca.* 185.

branching was a sort of modified repeated dichotomy, the basal segments clasping the rachis. Each pinna is deeply cleft down the middle, this first dichotomy being already initiated in the vascular supply long before it emerges from the petiolar cortex. The further branching of the two halves is not so regular, the segments towards the outer side tending to become thinner and also more and more confluent, sometimes forming continuous expanses of lamina, as STENZEL has already pointed out. It would be difficult to reconstruct the exact form of a pinna without examining a close series of sections, but the available facts seem to indicate that the basal segments of the two

* No case has yet been observed where a definite peripheral loop is formed such as we now know in several species of this genus, namely, in *E. Tubicaulis* (BERTRAND, 1909, p. 144), *E. Bertrandi*, SCOTT (POSTHUMUS, 1923), *E. Renieri* (LECLERCQ, 1929, 1931), *E. Scotti* (LECLERCQ, 1932).

halves branched in a pedate manner* while the finer branches were again dichotomous. The pedate type of branching is strongly suggested by the basal (clasping) segments in fig. 5, while the forked branching of the distal lobes is frequently witnessed among the numerous fine segments lying freely between the petioles.

The ground tissue of the segments is thin-walled, there being no suggestion of a spine-like development such as Dr. Scott describes in *Botrychioxylon*. The vascular bundle in the best preserved lobes is a thin, slightly curved arc of tracheids, surrounded by a dark brown zone of crushed thin-walled tissue, fig. 7.

(*d*) *Ramentum*.—The structure of the ramentum is not clearly preserved, but there is no doubt that it consists of scales a single layer of cells thick. They seem to be attached both to the young rachises and to the pinnæ (or ? aphlebiæ); there are no emergencies of any other kind.

Root.

The roots are mostly 1–2 mm. thick, and sometimes arise directly from the stem, sometimes from the leaf-base. The stele is usually diarch, sometimes triarch, and often shows a great development of secondary wood. The appearance of the xylem as seen in cross-section is very peculiar, resembling a butterfly with expanded wings; the body of the insect being represented by the primary xylem plate, the wings by two large triangular or hatchet-shaped masses of secondary wood (figs. 19, 24, Plate 7). Apparently the cambium was active only along a very restricted line on either flank of the primary wood. A curious point of resemblance with *Botrychioxylon paradoxum* is the unusually large size of the outer tracheids (Scott, 1912, p. 382, fig. 16, Plate 40), which may have served, as Scott suggests, for the storage rather than conduction of water.† The thickenings are like those in the secondary xylem of the stem, even the protoxylem elements being scalariform.

As a rule the cortex is badly crushed, and no root-hairs can be made out. Fig. 21, Plate 7, shows a young diarch root, with only primary tissues; there is a wide parenchymatous cortex, with a dark zone near the periphery. The same kind of cortex is seen in many roots with secondary growth like those described above (fig. 20, Plate 7).

Diagnosis.—In view of the facts now described we may re-define the genus *Zygopteris* as follows:—

Genus *Zygopteris*, Corda, *emend*. Sahni.

Stele cylindrical, with a stellate core of primary xylem and a thick outer zone of secondary wood. Leaf-trace at first mesarch, with a complete sheath of secondary wood (which may extend into the petiole); then a tangentially extended band with a

* The Matoniaceous resemblance here strongly hinted need not be seriously considered till we know the facts better.

† Diarch roots, with steles almost identical in structure with those here shown in figs. 19, 24, Plate 7, are to be seen in slides 2158 and 2550 of the Scott Collection (Brit. Mus.).

temporary abaxial curvature and two lateral protoxylems: final form and mode of branching as in *Etapteris*. Pinnæ biseriate, deeply forked. Roots with well-developed secondary wood. The sporangia are known in *Etapteris Lacattei,* which is probably a *Zygopteris*, as the genus is here defined.

Zygopteris primaria (Cotta), Corda.

1828. *Endogenites Solenites* p.p., Sprengel, " Commentatio de Psarolithis," p. 32.
1832. *Tubicaulis primarius* Cotta sp., " Dendrolithen," p. 19, Plate 1, figs. 1, 2.
1845. *Tubicaulis primarius*, Unger, " Synops. Plant. Foss.," p. 108.
1845. *Zygopteris primæva*, Corda, " Beitr. Flora Vorwelt," p. 81.
1850. *Zygopteris primæva,* Unger, " Gen. Spec. Plant. Fossil," p. 200.
1852. *Zygopteris primæva,* Goeppert, " Foss. Flora Uebergangsgeb," p. 136.
1869. *Zygopteris primæva,* Schimper, " Traité de Paléont. Végét.," p. 696.
1889. *Zygopteris primaria,* Stenzel, " Die Gattung Tubicaulis," p. 26, Plate 5, figs. 45–47, Plate 6, figs. 48, 49.
1909. *Zygopteirs primaria,* P. Bertrand, " Études sur la fronde des Zygopt.," pp. 136, 212, Plate 15, figs. 102, 103.
1910. *Zygopteris primaria,* Seward, ' Foss. Plants,' vol. II, p. 443 ff.
1920. *Zygopteris primaria,* Scott, ' Studies,' vol. I, p. 319.
1927. *Zygopteris primaria,* Hirmer, " Handb. d. Palæobot," p. 504.

Diagnosis.—Large tree-ferns with a trunk at least 20 cm. in diameter. Leaf-bearing axis barely 1·5 cm. in diam, devoid of sclerenchyma, held erect by a stout armour of petioles and adventitious roots. Stele about 7 mm. thick, including a core of primary xylem barely 1 mm. across, which sends out rays through the thick zone of secondary wood. Primary tracheids narrow, finely scalariform, ? with mixed parenchyma; secondary tracheids wider, multiseriate scalariform. Petioles cylindrical, up to 20 mm. thick, pinnae biseriate, deeply forked, the segments further dissected. Leaf-traces traversing the secondary wood of the stele at a wide angle, at first monarch and mesarch with a complete sheath of secondary wood, which persists into the free petiole-base, finally ⊢⊣-shaped, giving off pinna-traces in an *Etapteris*-like manner. Ramentum, scaly. Roots mostly 1–2 mm. thick, usually diarch, often showing a great development of secondary wood which forms two lateral hatchet-shaped masses of unusually wide (? water-storing) tracheids; rarely triarch. Fertile organs unknown.

Age.—Lower Permian (Oberer oder Zeisigwalder Porphyrtuff des Mittleren Rotliegenden).* *Locality.*—Flöha, near Chemnitz, Saxony.

Theoretical considerations.

The discovery that *Z. primaria* combined *Etapteris*-like petioles with a stele, leaf-trace and root structure of the *Botrychioxylon* type raises questions of nomenclature and relationships which demand a brief discussion.

* See " Geologische Specialkarte von Sachsen, dritte Auflage " (1908), Erläuterungen, p. 31.

Relation with Etapteris.

It is clear that if the petiolar structure of *Z. primaria* had been correctly understood in 1907 the genus *Etapteris* would not have been created, and the various species of detached petioles now referred to it would have been assigned to *Zygopteris*. The question arises whether *Etapteris* should now be merged in CORDA's genus or whether it should be maintained for the detached petioles. At present we have no reason to doubt that most of the known *Etapteris* petioles were borne upon plants of the *Zygopteris* type, as now defined. But until this connexion is proved it seems advisable to keep up *Etapteris* as a form genus, because recent experience has shown that petioles of an identical type may sometimes have belonged to distinct genera of Zygopterideæ.*

Relation with Botrychioxylon.

A comparison with *Botrychioxylon* also reveals a very interesting situation. With this genus, too, the resemblances are so striking that *B. paradoxum* may after all be only a species of *Zygopteris sens. str.*† Had the structure of the Berlin specimen of *Z. primaria* been known in 1912 the genus *Botrychioxylon* would probably never have been founded.

The cylindrical stele, with its great development of secondary wood, and with the primary tissues reduced to a narrow stellate core, is essentially similar in the two plants. The leaf-trace in both species carries with it a sheath of secondary wood; in *Z. primaria* this extends some little distance into the petiole, in *Botrychioxylon* it stops short. In both plants the leaf-trace passes through an abaxially curved phase, with a temporary "protoxylem bridge"; in both, the lateral sinuses are open, peripheral loops being absent. The root structure was also very similar, even in matters of detail, such as the large size of the secondary tracheids. The thickenings of the xylem were almost identical in the two plants.

In view of these fundamental resemblances in the structure, it is remarkable how distinct the two plants were in habit. *Z. primaria* was no doubt a tree-fern of large size. In comparison, *Botryoxylon paradoxum* was a slender plant, with the leaves placed at long intervals on a branched, probably creeping, rhizome.‡ Other points of difference lay in the size of the stele, the structure of the cortex, the position of the roots and the aphlebiæ.

* For example, clepsydroid petioles having essentially the same structure were present both in "*Clepsydropsis*" *australis* and in *Asterochlænopsis*; see SAHNI (1930), p. 463, fig. 4; pp. 465–467.

† SCOTT (1912, p. 380) mentions a petiole of *Etapteris Scotti* associated with the *Botrychioxylon*, but adds that there is also an *Ankyropteris*. The latter, however, can scarcely have belonged to the *Botrychioxylon*. The facts now brought forward make this all the more unlikely, and at the same time enhance the possibility that *Etapteris Scotti* was the petiole of *B. paradoxum* (which may thus ultimately have to be re-named *Zygopteris Scotti*). But no one would assert this without further evidence.

‡ In a stem of this habit the great development of secondary wood is difficult to explain physiologically; perhaps it is a useless legacy from some erect ancestor.

On the whole, the resemblances far outweigh the differences: no doubt the two plants were very closely allied, if not co-generic. The difference in habit, however striking, is not inconsistent with generic identity*; the other points are also of minor significance, being partly related to the habit. Of course, the suspected connexion of *Botrychioxylon* with *Etapteris*, if confirmed, would set all doubt at rest; but until then it is best to keep up *Botrychioxylon* as an independent genus. For there is just a possibility that we have here a case parallel to that of *Ankyropteris scandens* and "*Clepsydropsis*" *australis*, two zygopterids having an identical stelar structure, but possessing petioles of two distinct types. SAHNI (1928).

We are certainly faced with an intriguing situation. We know that both *Etapteris*† and *Botrychioxylon* are firmly linked with *Zygopteris*, the former through the petiolar structure, the latter through the stele, leaf-trace and root. It would be surprising if the petiole of *B. paradoxum* should eventually prove to be of a type distinct from *Etapteris*, or if *Etapteris* petioles should later be found attached to stems essentially unlike those of *Z. primaria* or of *B. paradoxum*. And yet, in both cases, recent experience within the Zygopterideæ warns us against a merging of the genera.

Nevertheless, the probabilities are that the old and once extensive genus *Zygopteris*, recently dismembered and all but demolished, will finally emerge as the largest genus of the family, and the most widely distributed both in space and time. But it would be a pity if, on grounds of priority, the name *Botrychioxylon* should ever have to be abandoned: it is so expressive of the Ophioglossaceous affinities, long suspected, but first clearly demonstrated by Dr. SCOTT.

Comparison with other genera.

After *Botrychioxylon*, *Diplolabis* and *Metaclepsydropsis* are perhaps the nearest genera. The latter agrees with *Z. primaria* in the cylindrical form of the stele and in the presence of secondary xylem, although only as an occasional feature (GORDON, 1911*a*, Plate 4, fig. 46).‡ In *Diplolabis*, too, the stele is cylindrical and shows "a strong suggestion of radial arrangement" in its outer tracheids (GORDON, 1911, Plate 1, figs. 1–4; Plate 2, figs. 17–20), suggesting secondary growth. But the region of the cambium, if one was present at all, is badly preserved. GORDON states that there is no secondary xylem; but the resemblance with the condition in *Z. primaria* is very close, the main

* For example, *Ankyropteris* includes both creeping as well as climbing species. *Tubicaulis Solenite* was a tree-fern, and *T. Sutcliffii* was also erect, while *T. Berthieri* is commonly seen as an epiphyte among the roots of *Psaronius*. Both *Grammatopteris Rigolloti* and *G. Baldaufi* were small tree-ferns, but in the Dresden museum I have seen among the roots of a *Psaronius* a small epiphytic plant with a stele very similar to that of *G. Baldaufi*. I hope at a later date to describe some of these epiphytes on *Psaronius*.

† The various species of *Etapteris* range from Western Europe to Silesia, and in geological age from Lower Carboniferous to Lower Permian.

‡ A less marked radial seriation of the tracheids is seen as a normal occurrence.

difference being the thickness of the outer zone. Both the genera differ from *Z. primaria* in habit; the leaf-trace is devoid of secondary xylem, and the petiolar strand is also quite distinct, although that of *Diplolabis* stands somewhat nearer to *Zygopteris*. There can be no question of any near affinity, although all three genera belong to the group with foliar bundles devoid of peripheral loops.

The only other zygopterid at present known to possess secondary wood is *Ankyropteris corrugata* (Scott, 1912, pp. 376, 382), recently described in detail by Holden, 1930, Plate 7, figs. 4 and 5; Plate 8, fig. 18*a*.* Scott (*loc. cit.*, p. 384) drew attention to several points of resemblance with *Botrychioxylon*, and some of these apply also to *Z. primaria:* the "mixed pith" (somewhat doubtful in our species), the temporary abaxial curve in the leaf-trace, and the presence of secondary xylem in both stem and root (only occasionally in *A. corrugata*). An uncommon feature described by Holden (1930, p. 85) is the presence of traumatic secondary wood in the petiole of *A. corrugata*,† recalling a character which is normal in *Z. primaria*. But in spite of all these facts the closed peripheral loops of *Ankyropteris* remain a serious obstacle to any close affinity with *Zygopteris*, as with *Botrychioxylon*.

There is no other genus of Zygopterids, sufficiently well known, with which *Z. primaria* can be even remotely compared.

Summary.

Zygopteris primaria (Cotta) Corda was one of the first known Zygopterideæ, originally described over a century ago, but our knowledge of it was hitherto confined to the petiole, and that too was defective. In the present paper the structure of the stem, leaf-trace and root is described for the first time, from an old specimen in the Cotta Collection at Berlin, which had been overlooked for many years. At the same time, the type-specimen has been re-examined and the structure and mode of branching of the petiolar strand, hitherto obscure, has been elucidated.

In habit, *Z. primaria* was a large tree-fern; the slender leaf-bearing axis was held erect by a thick supporting armour of petiole-bases and adventitious roots. The young leaves and aphlebiæ were clothed in a dense ramentum of scales.

The investigation of the anatomy has revealed facts of a very unexpected nature. It has been ascertained beyond doubt that *Z. primaria had typical Etapteris petioles, borne upon a stem having the Botrychioxylon type of stele; the leaf-trace sequence and root-structure were also essentially as in B. paradoxum.* Had the Berlin specimen been

* I am here leaving out of consideration the epiphytic axis, with a *Botrychioxylon*-like stele, found among the roots of "*Clepsydropsis*" *australis;* the affinities of this plant being still uncertain (Sahni, 1928, pp. 25–26, pl. 6, figs. 50, 51).

† Holden suggests that the sporadic occurrence of secondary wood in the stem of this plant may likewise be a traumatic character, *loc. cit.*, p. 108; see also Holden (1931).

known earlier, neither of the genera *Botrychioxylon* (SCOTT, 1912) and *Etapteris* (BERTRAND, 1907) would have been founded. Indeed, the creation of the latter genus was due entirely to an error of observation, for even in the type-specimen the petiolar bundles are typically *Etapteris*-like, as COTTA showed a century ago, and not ≻–≺-shaped with hooked antennæ, as we have been accustomed to believe, after PAUL BERTRAND, since 1909. The mode of branching of the petiolar strand is also identical in every respect with that of *Etapteris*.

These facts raise questions of nomenclature and relationships which are briefly discussed. Both *Etapteris* and *Botrychioxylon* are no doubt firmly linked with *Zygopteris;* and in ordinary circumstances would be merged in CORDA's much older genus. But recent experience within the Zygopterideæ imposes caution against a merging of the genera at the present stage. For while, on the one hand, petioles of an identical type have actually been found attached to stems of two different genera ("*Clepsydropsis*" *australis* and *Asterochlænopsis kirgisica*), on the other, stems having an almost identical stelar structure are known to have borne petioles of two distinct types (*Ankyropteris Grayi* or *A. scandens* and "*Clepsydropsis*" *australis*).

At the same time, although, as a precautionary measure, the genera *Botrychioxylon* and *Etapteris* may for the present be maintained, the author believes that it would be surprising if the petiole of *B. paradoxum* should eventually prove to be of a type distinct from *Etapteris*, or if *Etapteris* petioles should later be found attached to stems essentially unlike those of *Z. primaria* or *B. paradoxum*.

Thus the old and once extensive genus *Zygopteris*, after many vicissitudes, will probably once more emerge as the largest and most important of the Zygopterideæ.

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EXPLANATION OF PLATES 6–8.

Abbreviations.—*a*, *b*, *c*, *d*, successive stages in emission of pinna-traces ; *ant.*, antenna ; *app.*, appendages of petiole (pinnæ or ? aphlebiæ) ; *app. tr.*, vascular supply of appendages ; *i.c.*, *o.c.*, inner, outer cortex ; *i.l.t.*, incipient leaf-trace ; *l.t.*, leaf-trace ; *p.r.*, ray of primary xylem ; *px*, protoxylem ; *px. br.*, protoxylem bridge ; *r*, root ; *r.t.*, root-trace ; *ram.*, ramental scales ; *s.s.*, secretory sacs ; *x*1, primary xylem (? with mixed parenchyma) ; *x*2, secondary xylem.

(For fig. 8 the author is indebted to Professors Fraipont and Leclercq of Liége ; for figs. 9 and 37 to Professor C. Bommer of Brussels.)

(All the figures, except fig. 8, are from untouched photographs.)

Plate 6.

Fig. 8.—Berlin specimen, external view, taken before thin sections were made. The top slab (sketched on the negative) is in the Brit. Mus., the rest belongs to the Mus. f. Naturkunde, Berlin. The slice between slabs 2 and 3 was made into the thin section A ; compare text-fig. 1. $\times \frac{2}{7}$.

Fig. 9.—Berlin specimen, polished lower face of slab 4. $\times$ *ca.* $\frac{1}{2}$.

Fig. 10.—Type-specimen (Freiberg). Cross-section at lower end of Stenzel's original (*cf.* text-fig. 1 and Stenzel's fig. 45) to show the apical bunch of crushed young leaves, the pinnæ or aphlebiæ, and the phyllotaxis. The cross marks the point directly over the stem apex. Nat. size.

Fig. 11.—Part of the same section, showing aphlebiæ packed in ramentum. $\times 8\frac{3}{4}$.

Fig. 12.—Berlin specimen cross-section C (from upper end of slab 3) to show stele and phyllotaxis. The large elliptic leaf-trace to the left of the stele is further enlarged in Plate 7, fig. 24. A root is arising abaxially from one of the petioles. The arrow indicates a root further enlarged in fig. 22. $\times 1\frac{3}{7}$.

Fig. 13.—Stele from the same section, with an incipient root-trace (top left) and a leaf-trace (top right), both passing out almost horizontally. $\times 10\frac{1}{2}$.

Fig. 14.—Part of stele from polished face shown in fig. 9 (photographed with strong reflected light). $\times 11\frac{1}{2}$.

Fig. 15.—Central part of stele shown in fig. 13. $\times 36$.

Plate 7.

Fig. 16.—Median longitudinal section (G) of stem from slab 3. On the right, a leaf-trace, originating in the primary xylem and carrying away a sheath of secondary wood. The origins of other leaf-traces are seen in oblique section, making the primary xylem look zig-zag. $\times 2\frac{4}{5}$.

Fig. 17.—Horizontal ray from bottom right-hand part of the same section. $\times 38\frac{2}{5}$.

Fig. 18.—Tangential section (F) of the same stem as in fig. 16, showing origins of four leaf-traces in a vertical series. The section is slightly oblique ; the lower end being nearer the central axis, shows the bottom leaf-trace cut nearer the core, the top one nearer the surface. The longitudinally cut strand at the top seems to be the same as the one seen in cross-section near it. $\times 3\frac{5}{6}$.

Fig. 19.—Berlin specimen, diarch root-stele with secondary growth, from section A (lower end of slab 3). $\times 63$.

Fig. 20.—Triarch root from the same section ; dark zone in outer cortex. $\times$ *ca.* 19.

Fig. 21.—Berlin specimen. Young roots without secondary growth, from longitudinal section (E) (slab 3) ; dark zone in outer cortex. $\times$ *ca.* 19.

Fig. 22.—Diarch stele of root marked with an arrow in fig. 12 (section C, at upper end of slab 3). $\times$ *ca.* 46.

FIG. 23.—Berlin specimen ; part of section A (lower end of slab 3). The numerals refer to figures where some of the foliar bundles are shown in detail. × $2\frac{1}{9}$.

FIG. 24.—Leaf-trace from the section (C) shown in Plate 6, fig. 12. × 19.

N.B.—*In this and all subsequent figures the abaxial side is shown facing downwards.*

FIGS. 25–27.—Strands of free or almost free petiole-bases from section A (*cf.* fig. 23). × 19.

FIG. 28.—Strand of free petiole-base from the polished face of slab 4, shown in fig. 9 (photographed in reflected light). × *ca.* 19.

PLATE 8.

FIG. 29.—Strand of free petiole-base (see fig. 23). × *ca.* 14.

FIG. 30.—Free petiole (see fig. 23). × *ca.* 16.

FIG. 31.—Strand of free petiole (see fig. 23). × 19.

FIG. 32.—Berlin specimen. Branching petiolar strand from the polished upper surface of slab 4 (photographed in reflected light). × 19.

FIG. 33.—Another branching petiolar strand from the same face as fig. 32. × 19.

FIG. 34.—Type-specimen (STENZEL's Freiberg block). Fully formed petiolar strand of a rachis shown in fig. 10 (bottom). × 19.

FIG. 35.—Berlin specimen. Petiole from section A (lower end of slab 3). The same petiole is shown more clearly in text-fig. 3 (left). × *ca.* $3\frac{1}{6}$.

FIG. 36.—The same petiole cut at a level 2–3 mm. below fig. 35. Photographed in reflected light from the polished face before the slice was ground. As the section was mounted upside down the right and left sides of the petiole have been interchanged. × *ca.* $2\frac{2}{3}$.

FIG. 37.—Berlin specimen. Another petiole from section A. × *ca.* $3\frac{1}{4}$.

ERRATA.

Page 36, line 14, *for* figs. 22, 28 *read* fig. 28.

,, lines 24–25, *delete the words* " fig. 27, Plate 7, and "

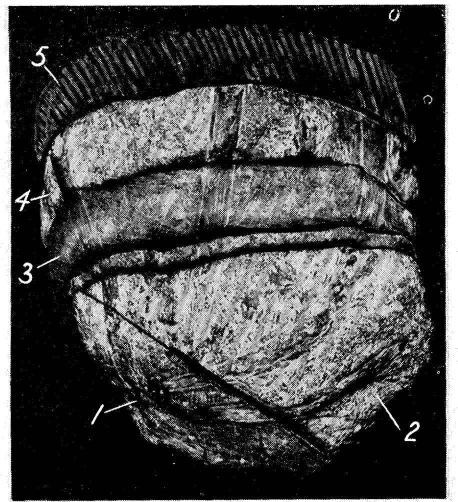
Page 38, line 20, *for* figs. 19, 24, *read* figs. 19, 22.

Page 40, line 13 from below, *for* " *Botryoxylon* " *read* " *Botrychioxylon.*"

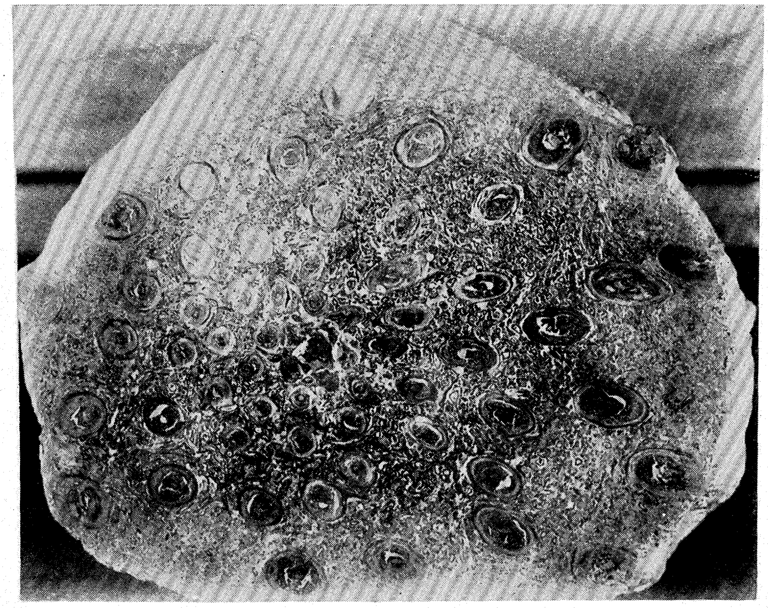
Page 41, line 8 from below, *for* " *Solenite* " *read* " *Solenites.*"

In fig. 23, Plate 7, the inset numerals 18, 19, 20, 22, 23, 24 *should read respectively*, 25, 26, 27, 29, 30, 31.

8

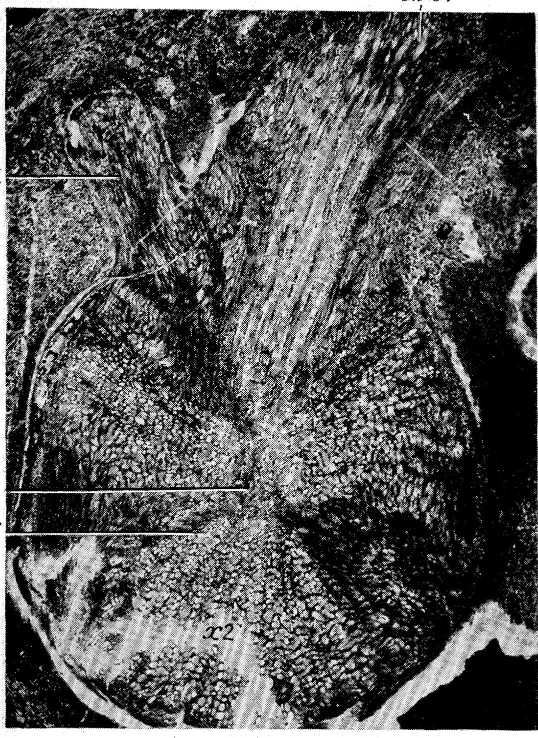


× 2/7



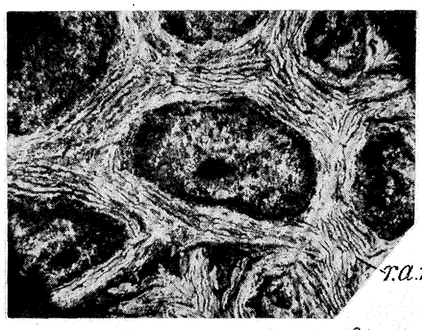
9

× ca. ½



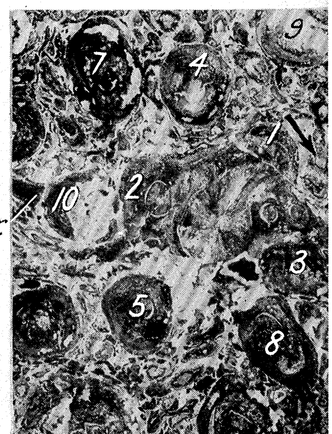
13

× 10½



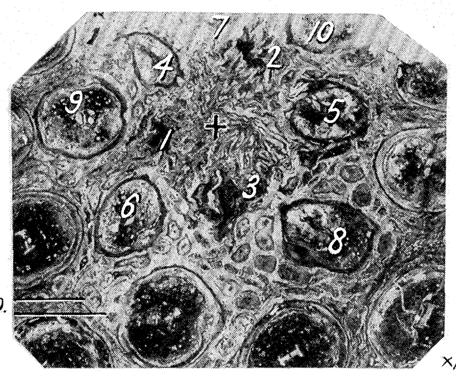
11

× 8¾



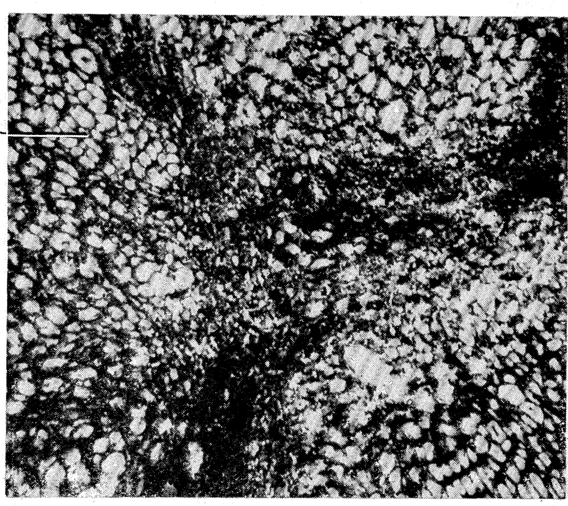
12

× 1 3/7



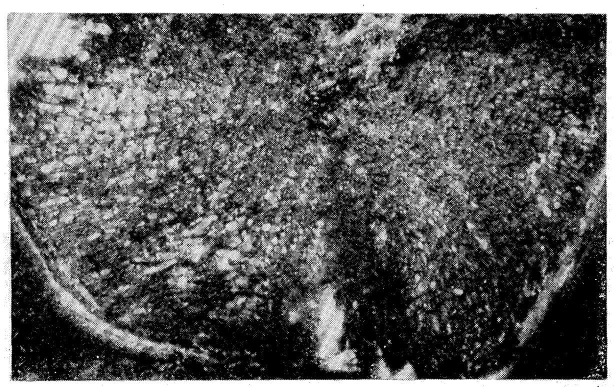
10

× 1



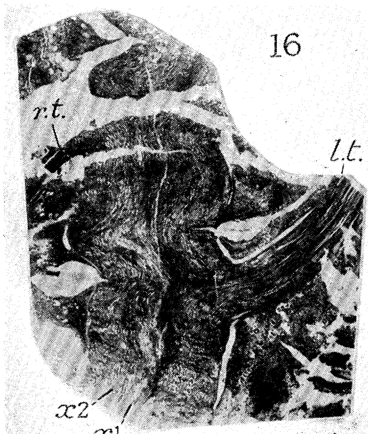
15

× 36

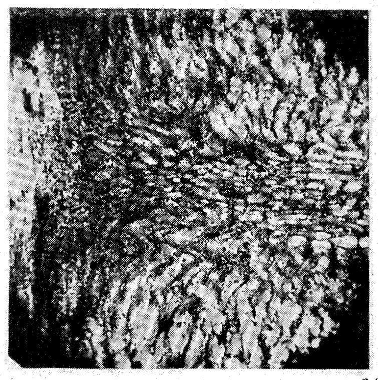


14

× 11½

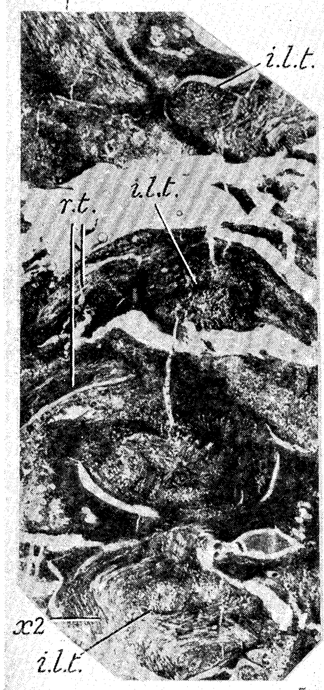


16 ×2 4/5

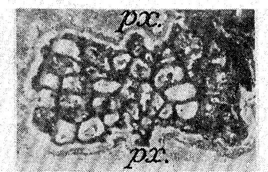


17 ×38 2/5

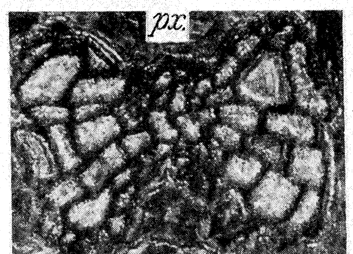
23 ×2 1/3



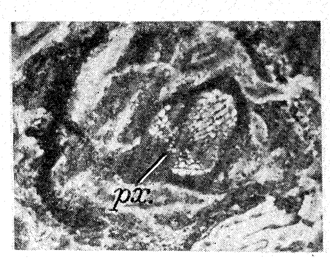
18 ×3 5/6



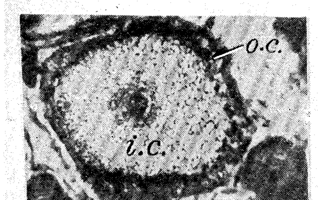
22 ×ca. 46



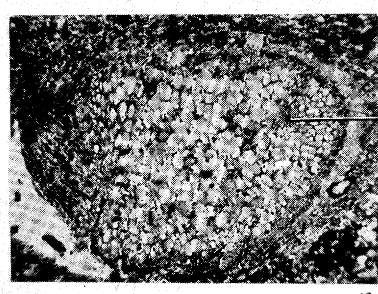
19 ×63



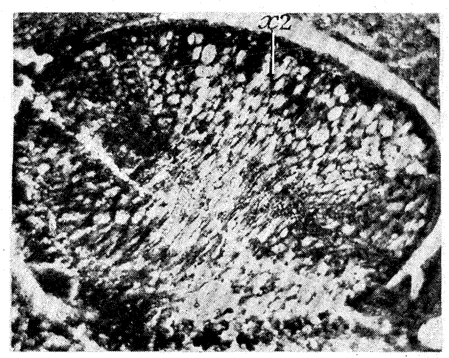
20 ×ca. 19



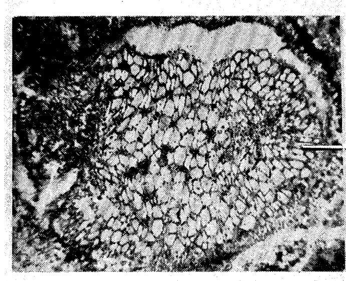
21 ×ca. 19



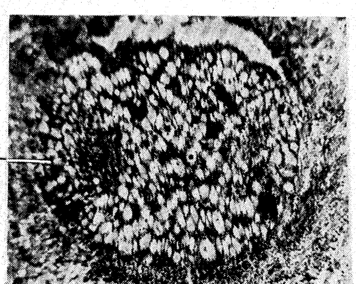
25 ×19



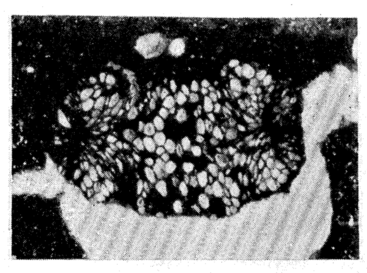
24 ×19



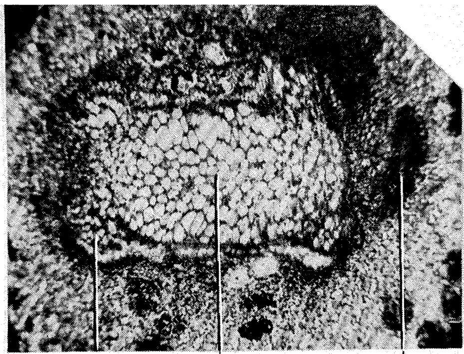
26 ×19



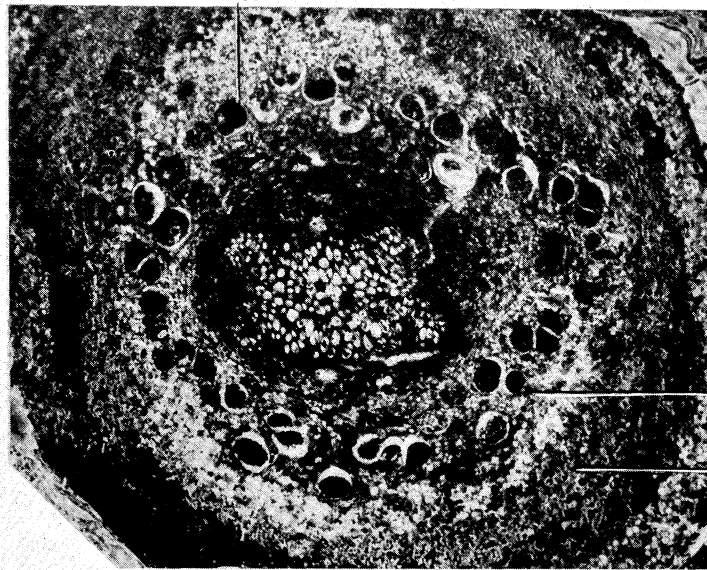
27 ×19



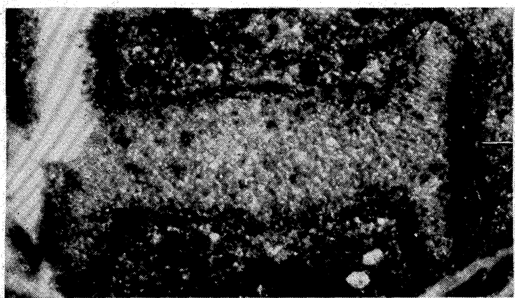
28 ×ca. 19



31 ×19

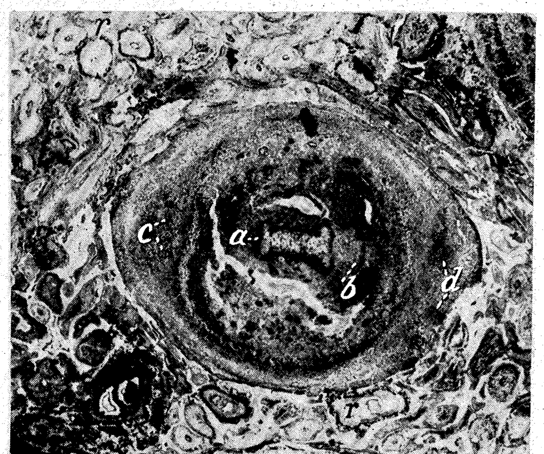


30 ×ca. 16

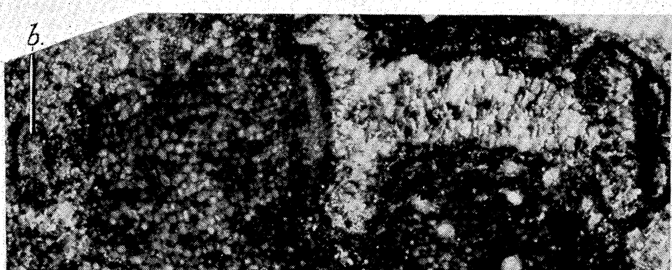


33 ×19

36 ×ca. 2⅔

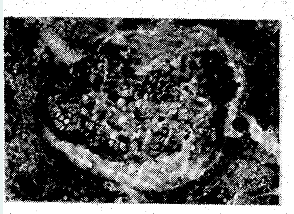


35 ×ca. 3⅙

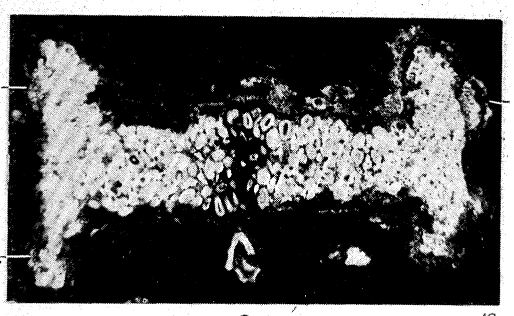


32 ×19

37 ×ca. 3¼



29 ×ca. 14



34 ×19

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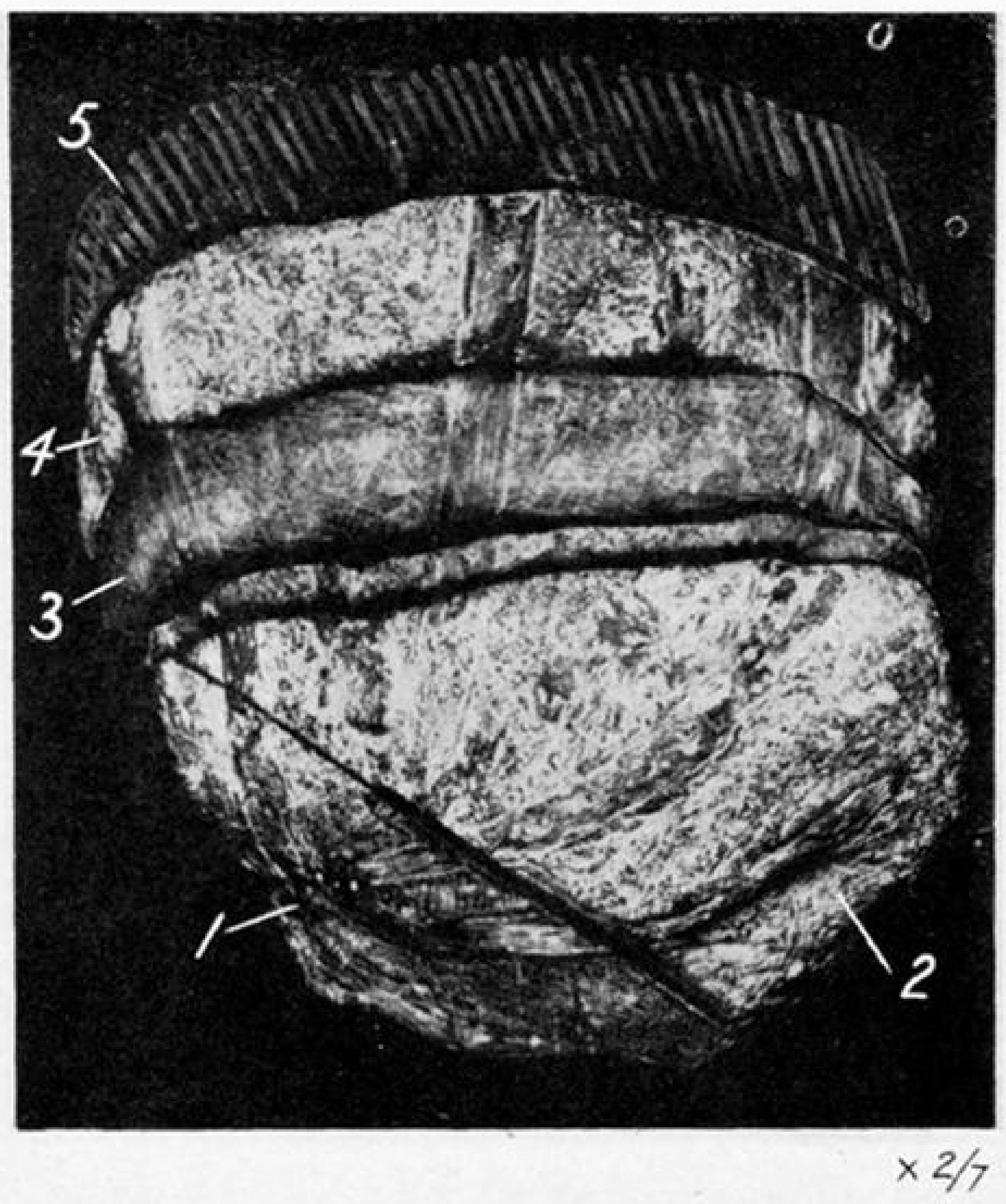

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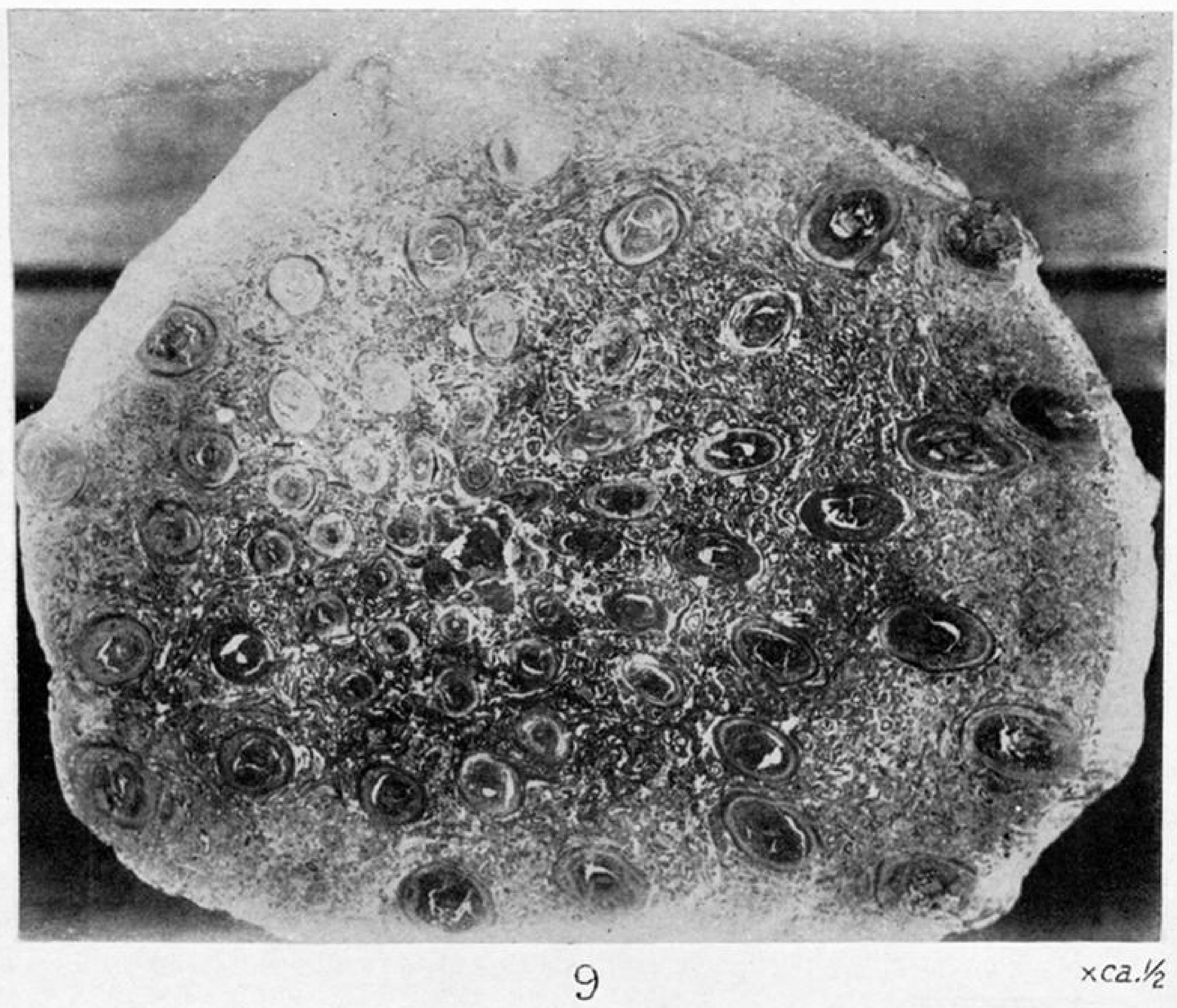

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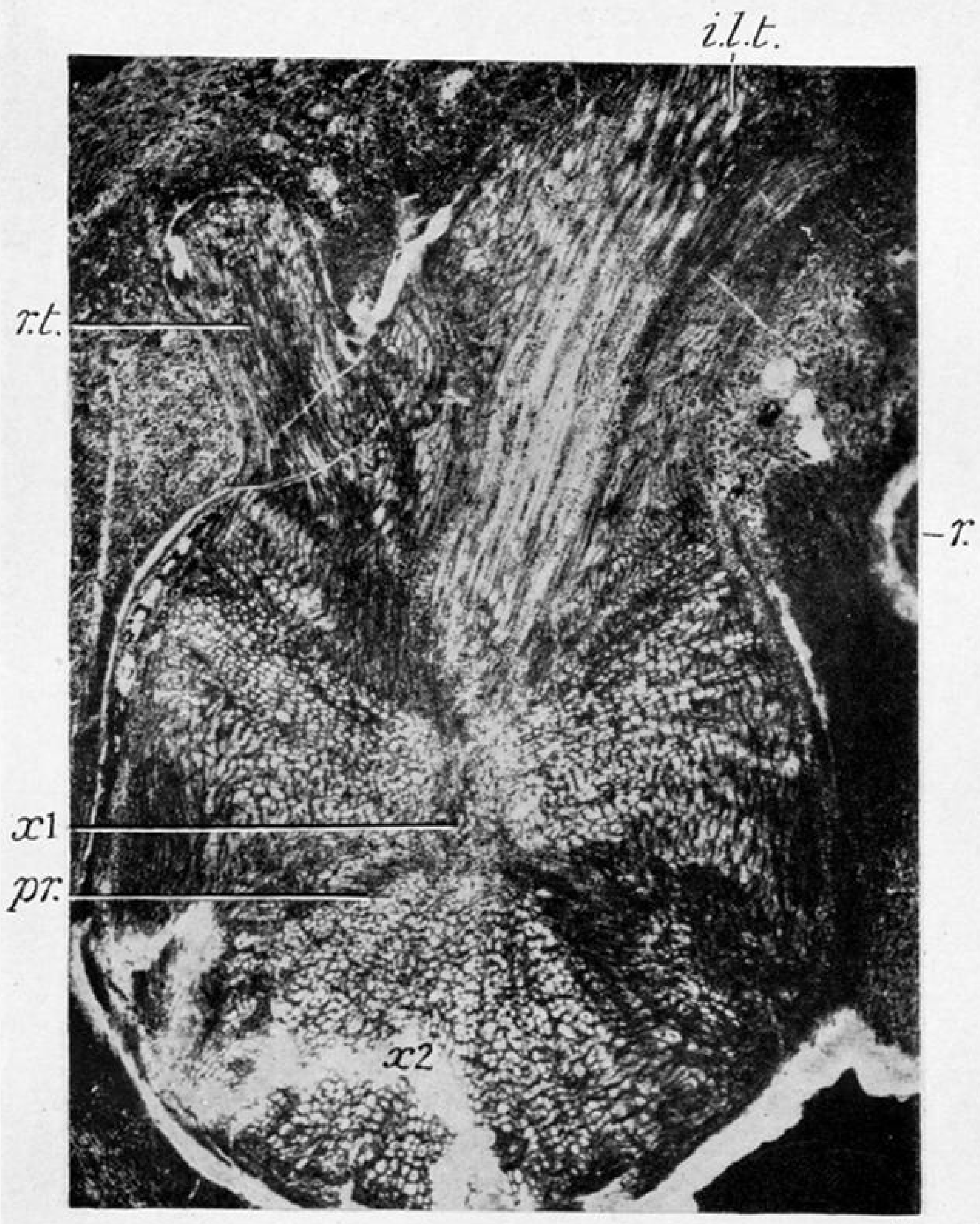

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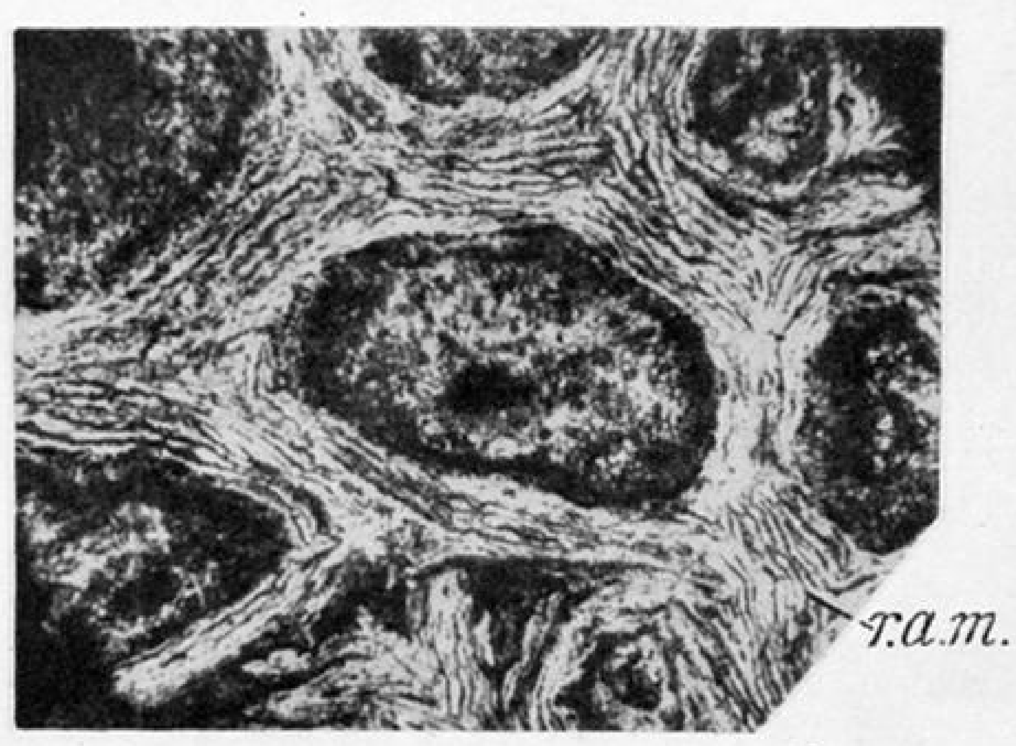

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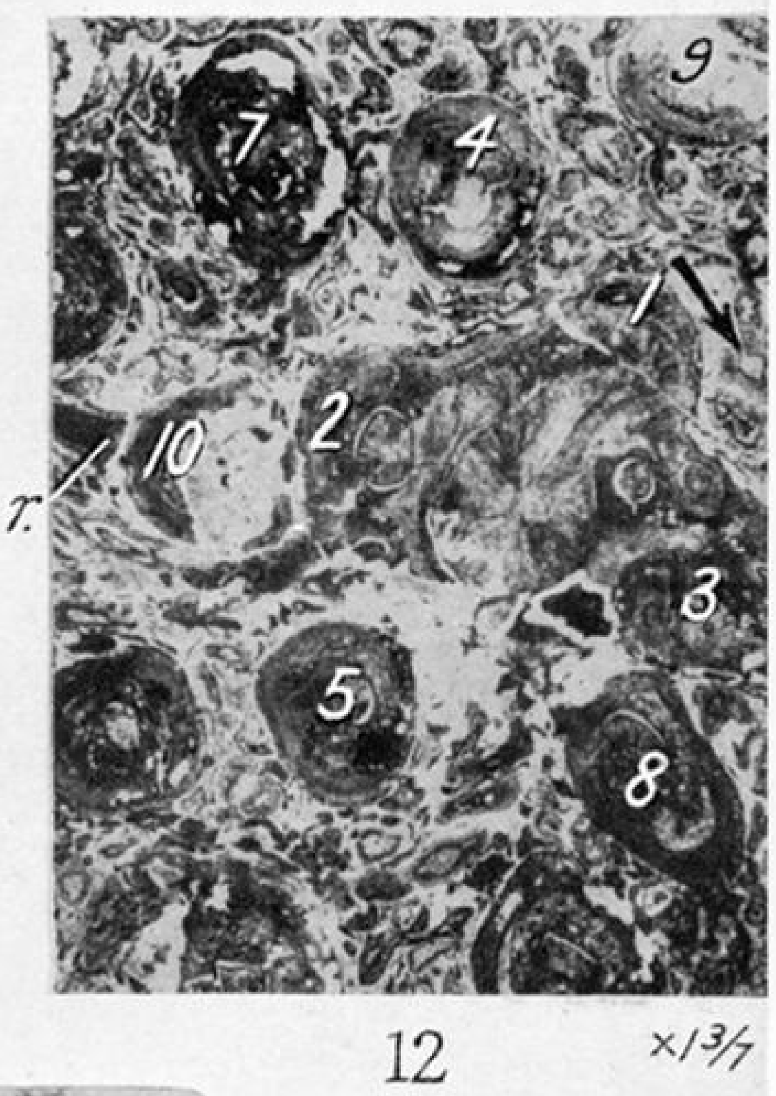

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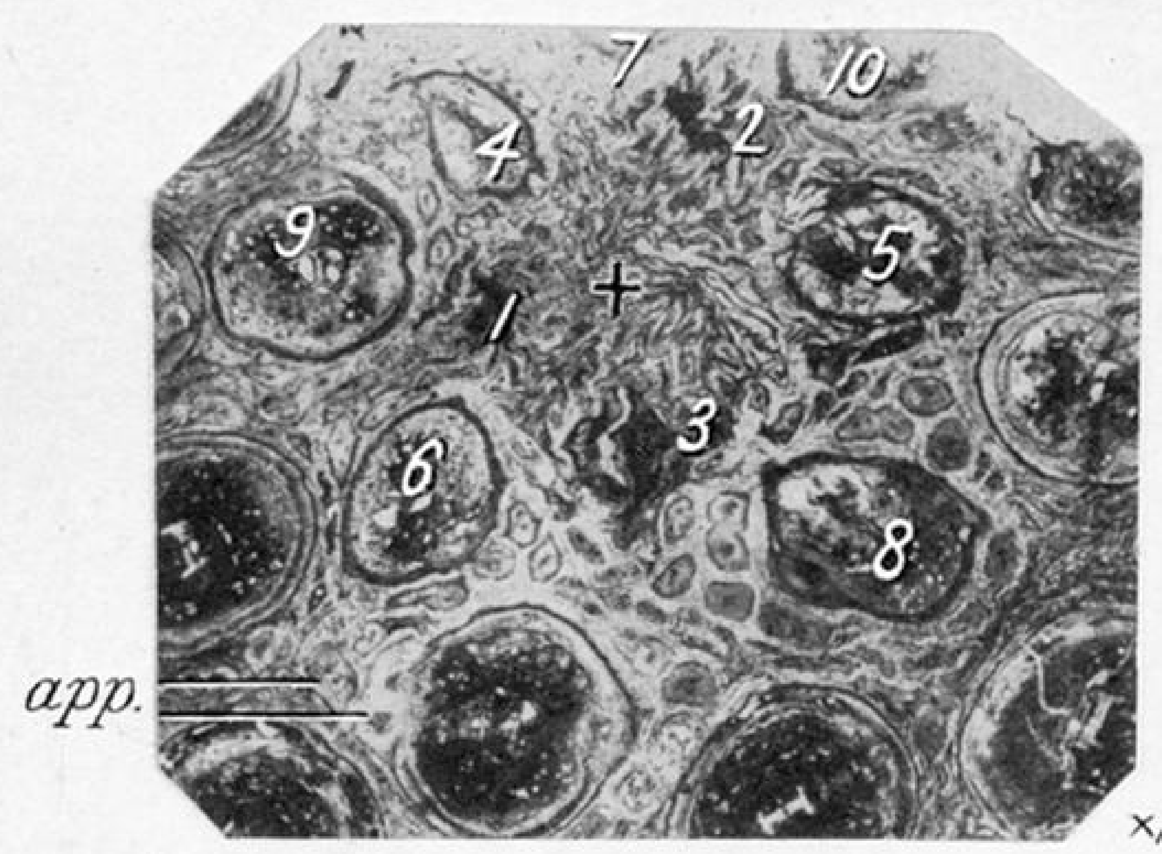

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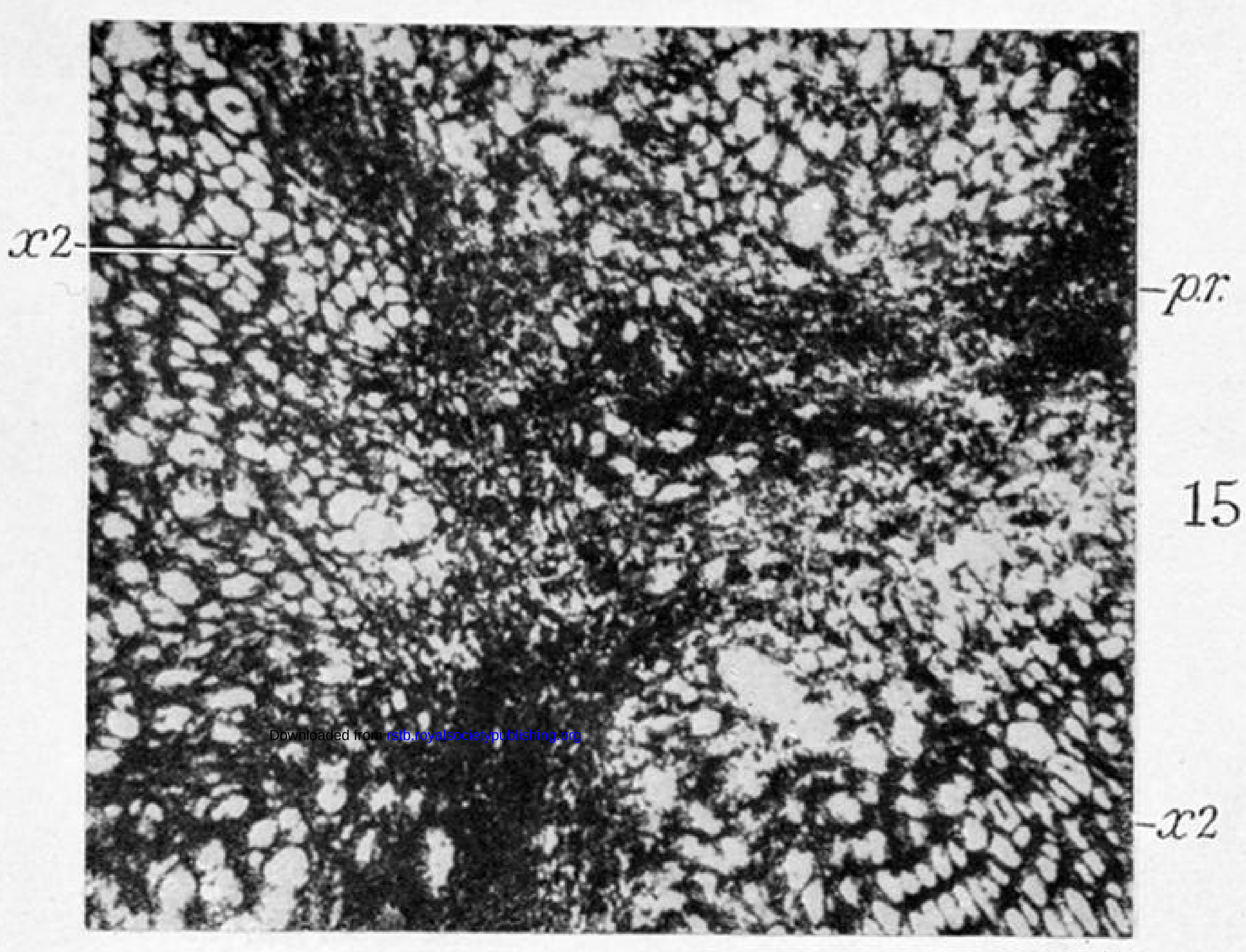

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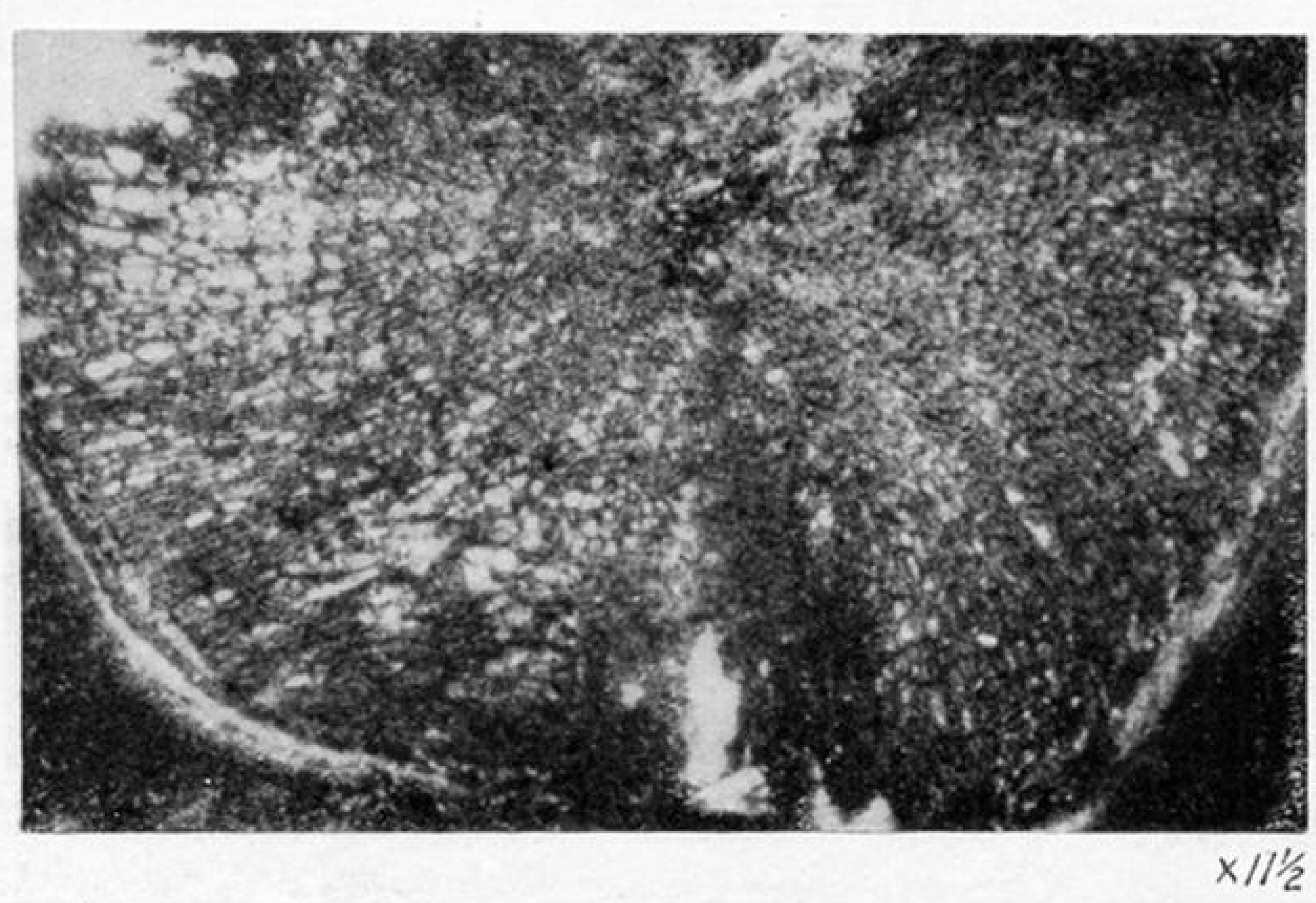

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PLATE 6.

FIG. 8.—Berlin specimen, external view, taken before thin sections were made. The top slab (sketched on the negative) is in the Brit. Mus., the rest belongs to the Mus. f. Naturkunde, Berlin. The slice between slabs 2 and 3 was made into the thin section A; compare text-fig. 1. $\times \frac{2}{7}$.

FIG. 9.—Berlin specimen, polished lower face of slab 4. $\times$ *ca.* $\frac{1}{2}$.

FIG. 10.—Type-specimen (Freiberg). Cross-section at lower end of STENZEL's original (*cf.* text-fig. 1 and STENZEL's fig. 45) to show the apical bunch of crushed young leaves, the pinnæ or aphlebiæ, and the phyllotaxis. The cross marks the point directly over the stem apex. Nat. size.

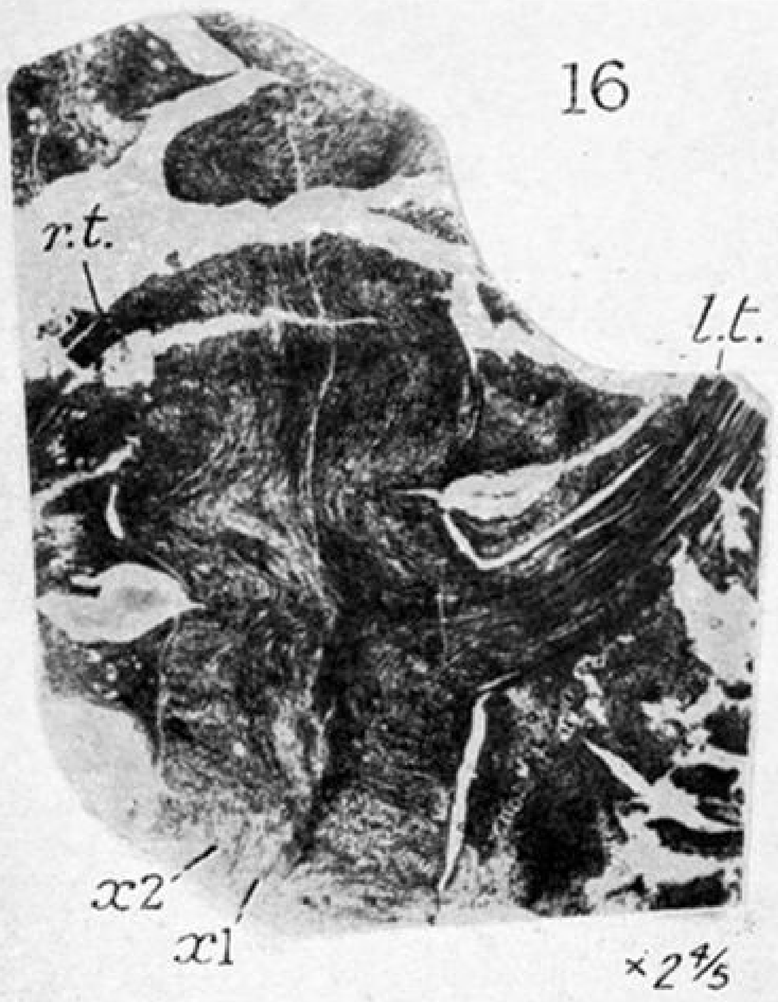
FIG. 11.—Part of the same section, showing aphlebiæ packed in ramentum. $\times 8\frac{3}{4}$.

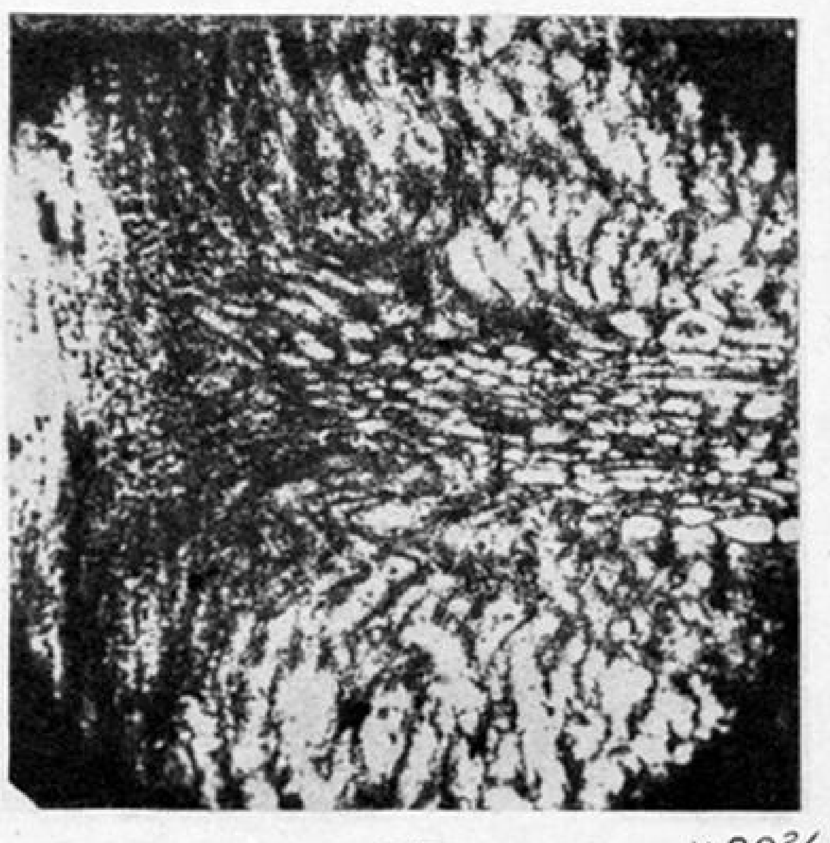
FIG. 12.—Berlin specimen cross-section C (from upper end of slab 3) to show stele and phyllotaxis. The large elliptic leaf-trace to the left of the stele is further enlarged in Plate 7, fig. 24. A root is arising abaxially from one of the petioles. The arrow indicates a root further enlarged in fig. 22. $\times 1\frac{3}{7}$.

FIG. 13.—Stele from the same section, with an incipient root-trace (top left) and a leaf-trace (top right), both passing out almost horizontally. $\times 10\frac{1}{2}$.

FIG. 14.—Part of stele from polished face shown in fig. 9 (photographed with strong reflected light). $\times 11\frac{1}{2}$.

FIG. 15.—Central part of stele shown in fig. 13. $\times$ 36.





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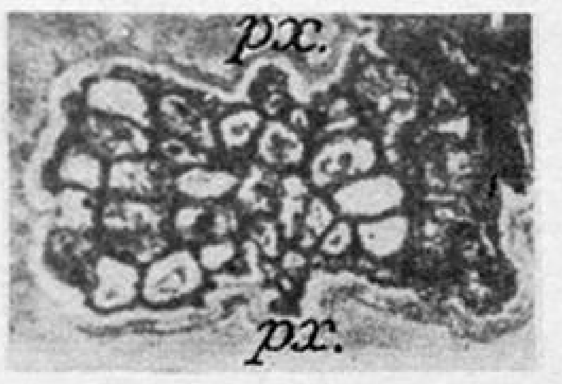

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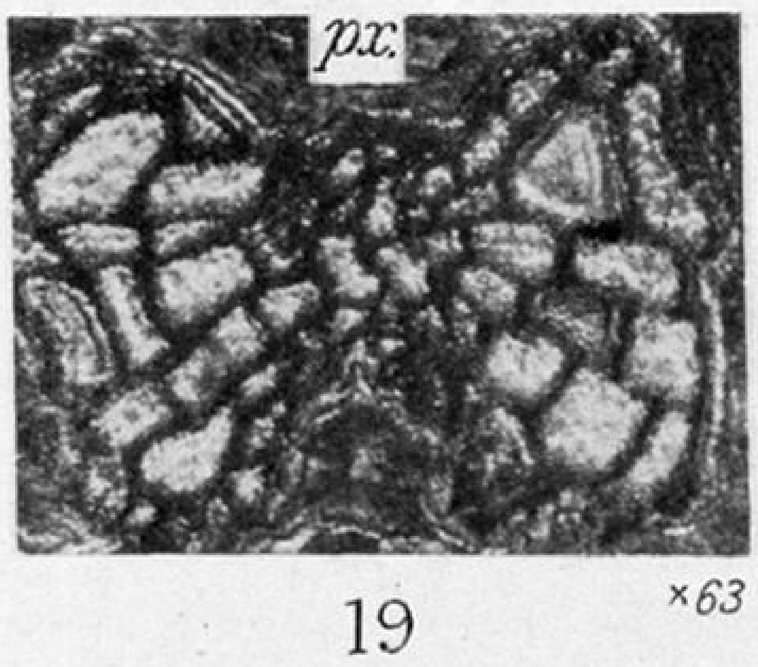

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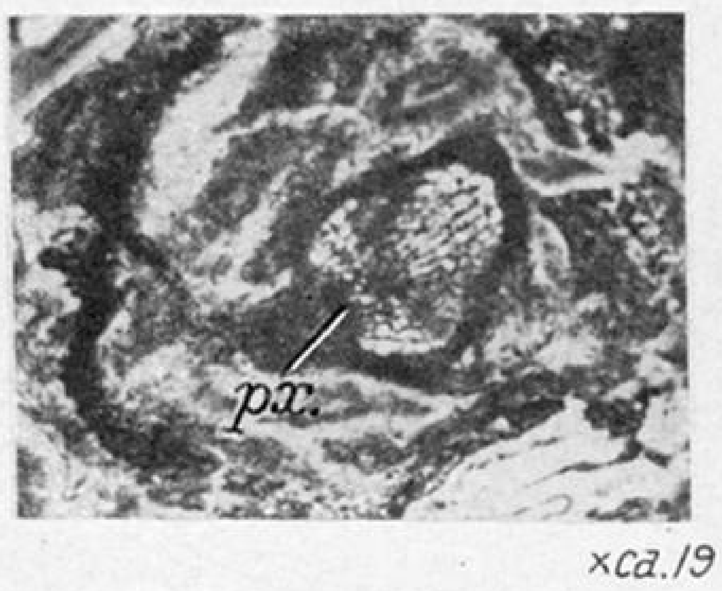

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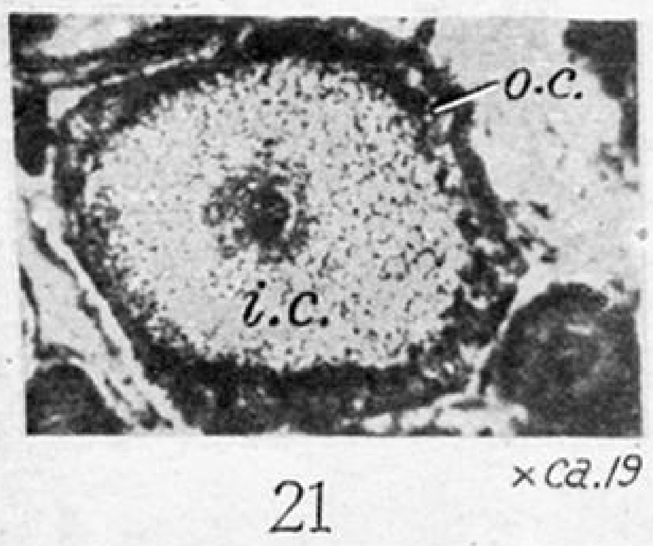

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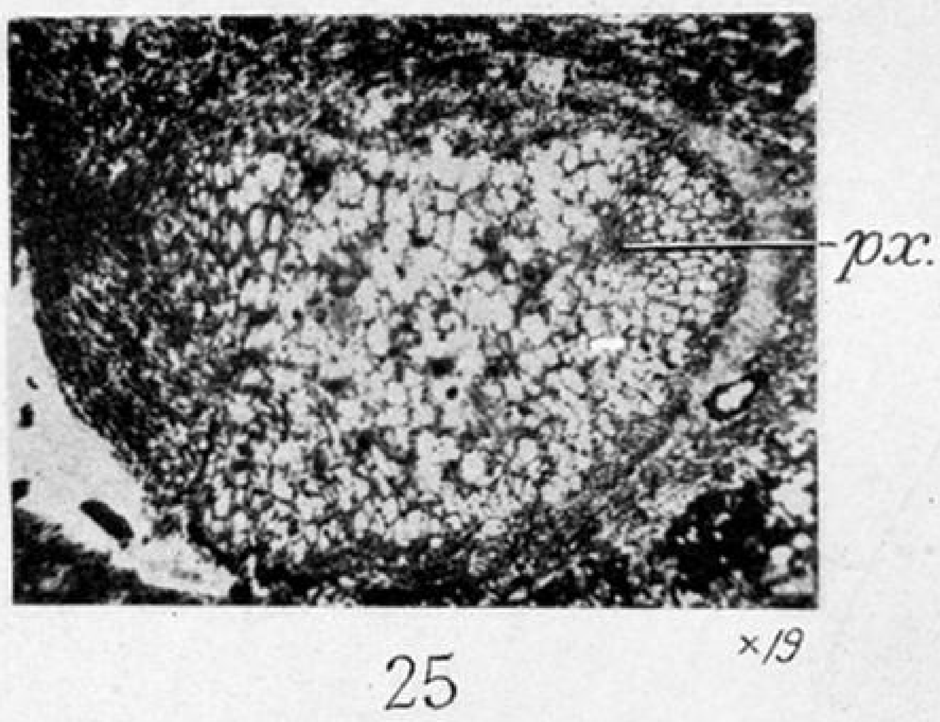

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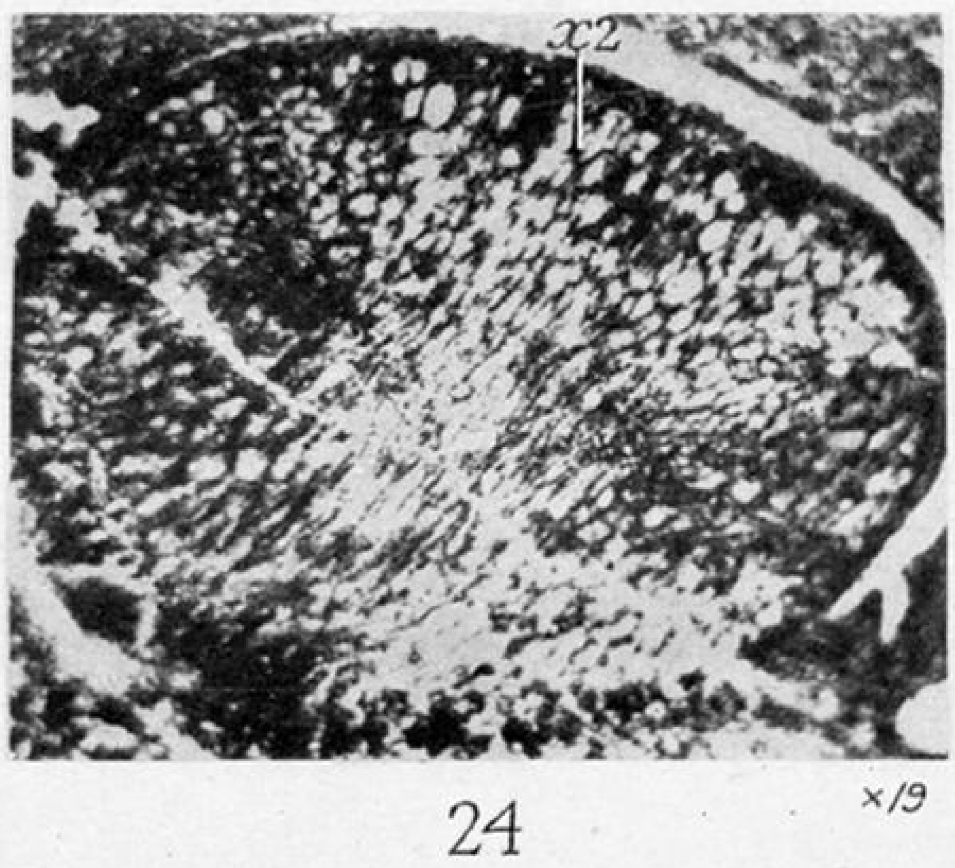

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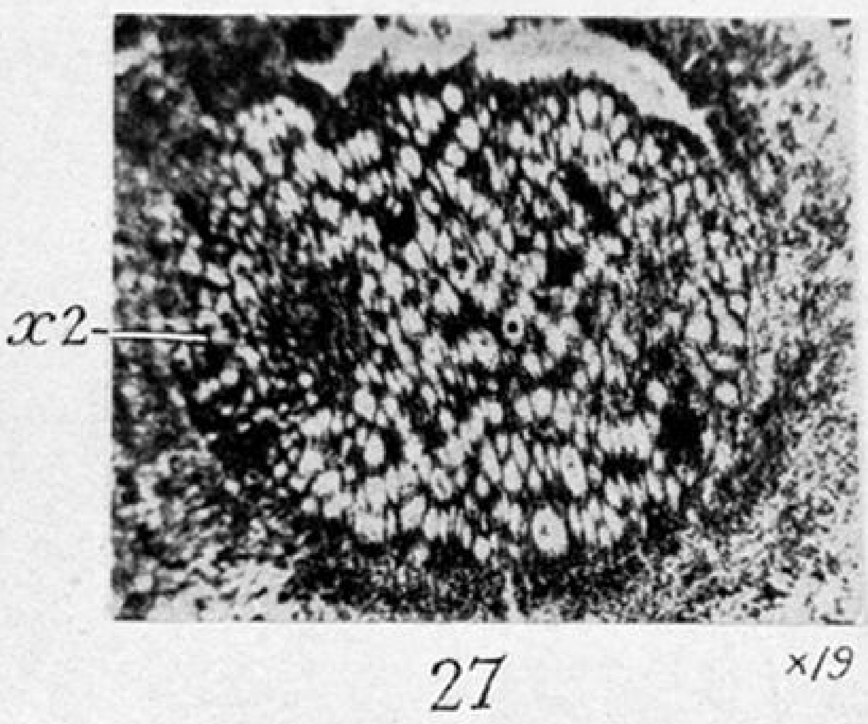

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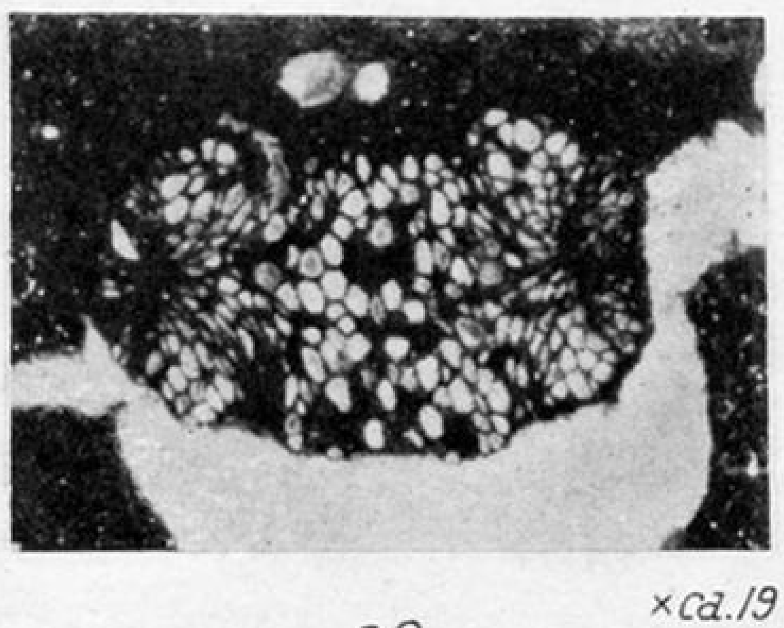

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PLATE 7.

FIG. 16.—Median longitudinal section (G) of stem from slab 3. On the right, a leaf-trace, originating in the primary xylem and carrying away a sheath of secondary wood. The origins of other leaf-traces are seen in oblique section, making the primary xylem look zig-zag. $\times 2\frac{4}{5}$.

FIG. 17.—Horizontal ray from bottom right-hand part of the same section. $\times 38\frac{2}{5}$.

FIG. 18.—Tangential section (F) of the same stem as in fig. 16, showing origins of four leaf-traces in a vertical series. The section is slightly oblique; the lower end being nearer the central axis, shows the bottom leaf-trace cut nearer the core, the top one nearer the surface. The longitudinally cut strand at the top seems to be the same as the one seen in cross-section near it. $\times 3\frac{5}{6}$.

FIG. 19.—Berlin specimen, diarch root-stele with secondary growth, from section A (lower end of slab 3). $\times$ 63.

FIG. 20.—Triarch root from the same section; dark zone in outer cortex. $\times$ *ca.* 19.

FIG. 21.—Berlin specimen. Young roots without secondary growth, from longitudinal section (E) (slab 3); dark zone in outer cortex. $\times$ *ca.* 19.

FIG. 22.—Diarch stele of root marked with an arrow in fig. 12 (section C, at upper end of slab 3). $\times$ *ca.* 46.

FIG. 23.—Berlin specimen; part of section A (lower end of slab 3). The numerals refer to figures where some of the foliar bundles are shown in detail. $\times 2\frac{1}{3}$.

FIG. 24.—Leaf-trace from the section (C) shown in Plate 6, fig. 12. $\times$ 19.

N.B.—*In this and all subsequent figures the abaxial side is shown facing downwards.*

FIGS. 25–27.—Strands of free or almost free petiole-bases from section A (*cf.* fig. 23). $\times$ 19.

FIG. 28.—Strand of free petiole-base from the polished face of slab 4, shown in fig. 9 (photographed in reflected light). $\times$ *ca.* 19.

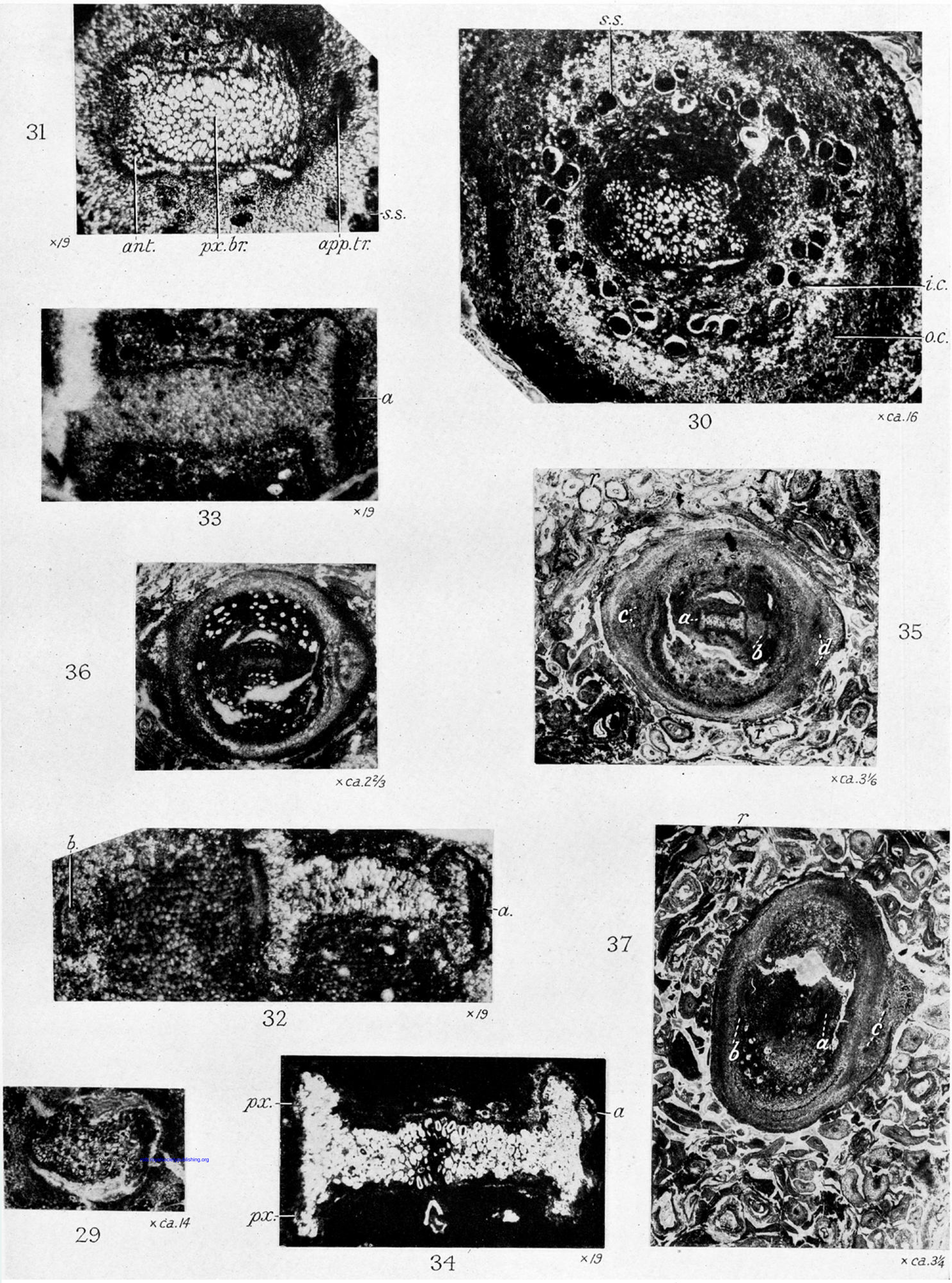

PLATE 8.

FIG. 29.—Strand of free petiole-base (see fig. 23). × *ca.* 14.

FIG. 30.—Free petiole (see fig. 23). × *ca.* 16.

FIG. 31.—Strand of free petiole (see fig. 23). × 19.

FIG. 32.—Berlin specimen. Branching petiolar strand from the polished upper surface of slab 4 (photographed in reflected light). × 19.

FIG. 33.—Another branching petiolar strand from the same face as fig. 32. × 19.

FIG. 34.—Type-specimen (STENZEL'S Freiberg block). Fully formed petiolar strand of a rachis shown in fig. 10 (bottom). × 19.

FIG. 35.—Berlin specimen. Petiole from section A (lower end of slab 3). The same petiole is shown more clearly in text-fig. 3 (left). × *ca.* $3\frac{1}{6}$.

FIG. 36.—The same petiole cut at a level 2–3 mm. below fig. 35. Photographed in reflected light from the polished face before the slice was ground. As the section was mounted upside down the right and left sides of the petiole have been interchanged. × *ca.* $2\frac{2}{3}$.

FIG. 37.—Berlin specimen. Another petiole from section A. × *ca.* $3\frac{1}{4}$.

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