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Studies on Triassic Fossil Plants from Argentina. I. Rhexoxylon from the Ischigualasto Formation

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STUDIES ON TRIASSIC FOSSIL PLANTS FROM ARGENTINA
I. *RHEXOXYLON* FROM THE ISCHIGUALASTO FORMATION

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[Plates 1 and 2]

CONTENTS

A new species, *Rhexoxylon piatnitzkyi* is described and illustrated. It is a small stem showing the primary organization of the vascular cylinder and has enabled the authors to present a new interpretation of the development of the complex mature stem structure of *Rhexoxylon*. Together with further specimens of larger stems described provisionally as *Rhexoxylon* sp.A the material has revealed new anatomical details.

The diagnosis of *Rhexoxylon* and of *R. tetrapteridoides* Walton are emended. *R. waltonii* Kräusel is reduced to a synonym of *R. africanum* Bancroft. *R. priestleyi* (Seward) Walton is restored to *Antarcticoxylon* Seward because of differences judged to be of generic value. The affinities of *Rhexoxylon* are discussed.

The present record from Triassic strata in north-west Argentina is the first occurrence of *Rhexoxylon* outside Africa and supports a stratigraphical correlation of the beds (Ischigualasto Formation) with the Stormberg Series of South Africa.

Introduction

The specimens of *Rhexoxylon* described in this article were collected by one of us (S.A.) during the 1958 Ischigualasto Expedition undertaken by the Palaeontological Section of the Lillo Institute.

The new material consists of: a small, fairly young stem which we have described as *R. piatnitzkyi* n.sp., and fragments of larger stems described as *Rhexoxylon* sp.A. These larger stems appear to differ from all other species of the genus but are too fragmentary for a new species to be based on them.

The great interest of this material is in the small stem, which provides completely new information on the primary organization of the complex vascular system. The generally good preservation of all the material has made possible a considerable revision of histological details, particularly of the secretory structures, secondary wood and the phloem.

All the specimens are silicified and in most cases have yielded good cellulose acetate peel sections using the technique of Joy, Willis & Lacey (1956).

R. piatnitzkyi was found in the same formation as *Rhexoxylon* sp.A but at a distance of 100 m. The fragments of *Rhexoxylon* sp.A were scattered over several metres, partially exposed on the surface.

RHEXOXYLON PIATNITZKYI N.SP.

(Figures 1 to 5, and 10 to 12, 14 to 17, 19 to 21, plate 1.)

Diagnosis. Small stem reaching a diameter of 7 to 8 cm. Externally are rhomboidal leaf bases among which are branch scars surrounded by small scale-leaves. The broad medulla of 2 to 3 cm diameter, contains an irregular anastomosing system of small vascular strands, and numerous large spherical cysts; the latter are also abundant in the cortex. The vascular cylinder is dissected by gaps associated with the origin of leaf traces, and forms a system of anastomosing vascular strands 7 to 8 mm in radial extent. The xylem of this vascular cylinder consists of a centrifugal and a centripetal part separated by a narrow zone of parenchymatous tissue. Leaf traces are connected to both margins of the gaps, and divide in the inner cortex. Each leaf is supplied by traces from several gaps. The vascular system in the leaf base consists of 7 or 8 strands arranged in a semi-circle, each strand comprising two or more vascular bundles concentrically disposed.

Holotype: LIL 2152; slide preps. 134–146.

Horizon: Ischigualasto Formation (Trias).

Locality: La Rioja Province, Argentina.

The name of the new species honours Alexander Piatnitzky, a pioneer in Patagonian geology, who died in Buenos Aires on 27 December 1959, aged 80 years.

Anatomical description. The several fragments represent a length of stem of about 15 cm which at its largest end is 7 or 8 cm wide, tapering to 4 or 5 cm. The vascular system shows a corresponding decrease in size and complexity at the smaller end. There is, however, a decrease only in the number of vascular bundles; the size of the individual bundles and the amount of secondary xylem is not at all different. Our inference is that the smaller end of the stem is a narrower, basal region.

Although weathered and deformed by compression, much of the outer surface of the stem is preserved and shows rhomboidal leaf bases, among which are several branch scars surrounded by small scale-leaves (figure 10, plate 1). One of these scars, more exposed than most and suggesting an unexpanded bud, is shown in figure 1 and also in figure 12, plate 1.

The internal anatomy of the stem is complicated, but reference to figure 2, a diagram of the transverse section, will make clear our use of descriptive terms.

Medulla

At the lower end of the stem the medulla is 2 cm wide and about 3 cm at the upper end. There is an irregular anastomosing medullary system of vascular strands which originates in the basal region of the stem from small curved strands connected to the centripetal portion of the main vascular cylinder. Higher up the stem where the medulla is broader,

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the vascular strands are larger and much more numerous, and have a clearly defined cambium. The larger medullary strands appear in transverse section as narrow, more or less curved strips (figure 11, plate 1). The system is also increased by new small strands connected to the vascular cylinder (figure 17, plate 1). Apart from the protoxylem, the tracheids of the medullary strands are pitted.

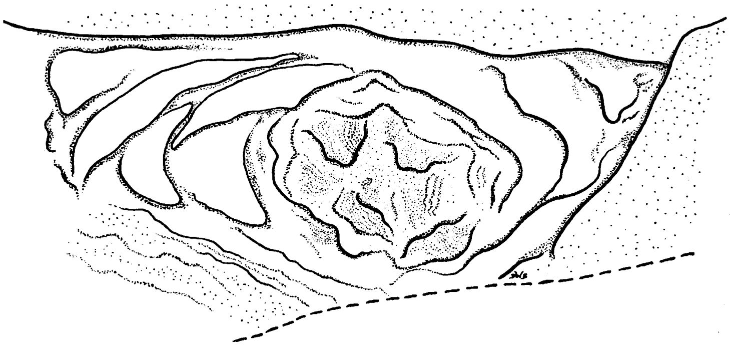

FIGURE 1. *Rhexoxylon piatnitzkyi*: sketch of the exposed bud surrounded by scale-leaves, also illustrated in figure 12, plate 1. The discontinuous line indicates the fractured side of the specimen. The surface is very badly weathered and histological details are lacking. The areas shown with a wavy grain in the centre are more translucent and may be vascular tissue (× 6.)

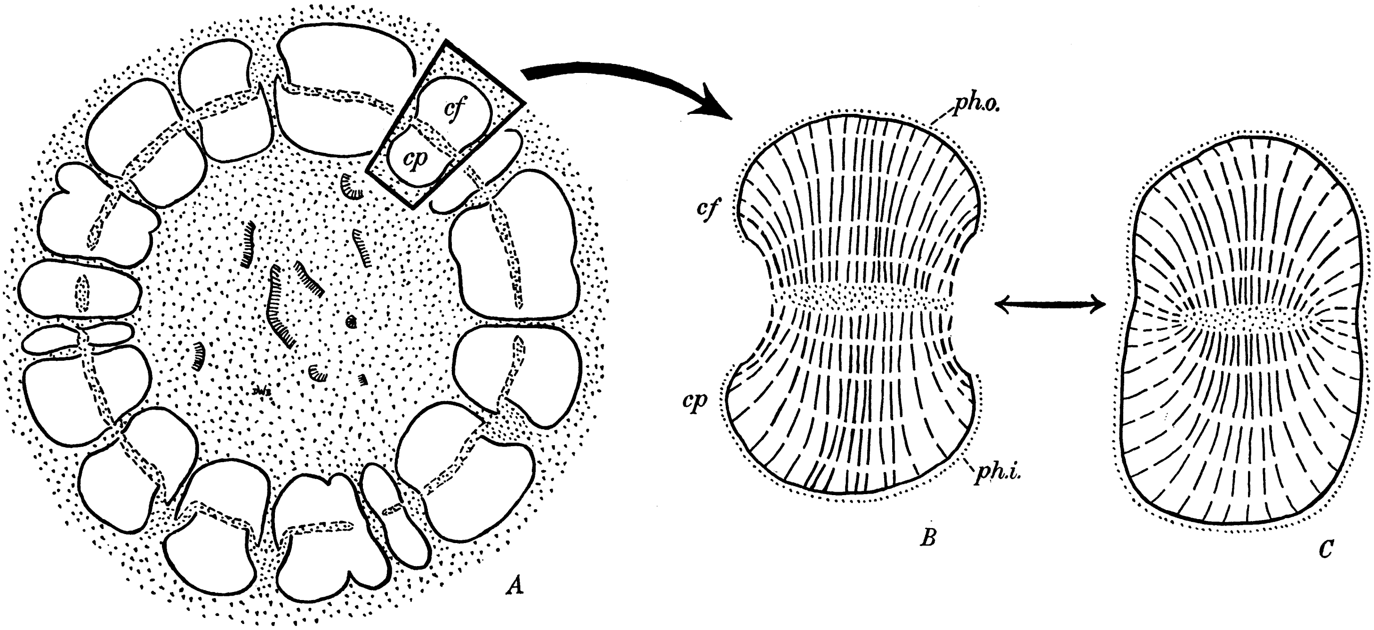

FIGURE 2. *Rhexoxylon piatnitzkyi*: diagram of the transverse section. *A*. The vascular cylinder surrounds a broad medulla, in which are smaller strands of vascular tissue. The vascular cylinder is dissected by leaf gaps and so appears as a ring of vascular bundles (the leaf traces are omitted for simplicity). *B*, *C*, represents the two extremes in the construction of the vascular bundles. *B*, is a double collateral bundle with more or less equal centrifugal and centripetal development; the two protoxylems are separated by parenchyma. The position of the outer and inner phloem and cambium is shown by line of dots. *C*, is a concentric bundle with the protoxylems surrounding the small parenchyma zone. The cambium completely encircles the bundle but most development is centrifugal and centripetal. *cf*, centrifugal; *cp*, centripetal portion of vascular bundle; *ph.o.*, *ph.i.*, outer and inner phloem, respectively.

The medulla consists of several kinds of cells. Most are thin-walled parenchyma, about 80 to 100 μ wide. There are also many scattered cells of about the same size but with dark contents, usually contracted away from the walls. There are large spherical cells which we call cysts. These are relatively few but conspicuous. They occur at about 150/cm^2 and are about 250 to 300 μ wide. They are surrounded by rather flattened parenchyma cells usually with dark contents (figures 14, 17, plate 1). Within the cyst wall, generally some little distance from it, is a concentric and hollow crystalline sphere. Enclosed in the small centre and showing up clearly the shape of the inwardly projecting crystals, is a dark amorphous substance. There is often also a darker zone surrounding the crystalline sphere.

There are many irregular cavities which may have been formed in life by tissue breakdown or local failure in fossilization. Some of these cavities are surrounded by thin-walled parenchyma cells.

No cells recalling typical stone cells occur in the medulla and there are no solid blocks of thick-walled cells.

Cortex

The cortex is over a centimetre broad in places but is mostly badly squashed. No cells apart from those of vascular bundles can be made out, but numerous cysts similar to those in the medulla can be seen, particularly in the tangential sections where their circular form is still retained.

Vascular cylinder

In transverse section the vascular cylinder consists of a number of vascular bundles separated to a greater or lesser extent by broad primary rays of parenchymatous tissue. The bundles are of very variable form, and are seen in stages of fusion or division. This is caused by the departure of leaf traces at different levels around the vascular cylinder.

The primary structure of the bundles is mesarch, in that differentiation has proceeded both centrifugally and centripetally. However, there are two protoxylems, separated from one another by a narrow zone of parenchymatous tissue. Secondary development of the vascular tissue has taken place by means of two independent cambiums, each giving rise to phloem and xylem: the one differentiating centrifugally towards the cortex, the other differentiating centripetally towards the medulla.

The tissue separating the centrifugal and centripetal xylems is composed of large cells like those of the medulla. There are many spaces in this tissue, and almost all the cells which have resisted decay have dark contents.

The first formed xylem, both centrifugal and centripetal, consists of narrow tracheids with irregular spiral thickenings or with scalariform pitting. In the secondary xylem (figures 15, 16, plate 1), the tracheids have either a single or two alternating rows of bordered pits in the radial walls, the borders being about 20 μ wide and flattened where they are in contact. The pit apertures are small, circular or slightly elliptical, 3 to 4 μ wide. A typical tracheid is 35 μ wide with a thick wall and rounded lumen, and the wall shows oblique bands of thickening (tertiary spiral).

There is a periodicity in the radial growth of the secondary xylem, and the tracheids are wider at the commencement of the growth increments.

The xylem rays are uniseriate and up to twenty-two cells high in the tangential section. The ray cells are elongated radially and are 2 or 3 times as long as they are high. Pitting from the ray cells to the tracheids consists most commonly of either a single large pit, up to 25 μ wide and resembling the large pits of *Pinus*, or two pits in the cross-field. Less often there are three pits. The rays are six per millimetre in the latest formed xylem.

There is no wood parenchyma.

The cambium and phloem around the margins of the xylem are very poorly preserved except for the phloem fibres, which are mainly present in a diffuse band in the secondary phloem.

Leaf gaps and traces

When followed through a series of transverse sections taken from below upwards, the broad ray or gap originates by tangential division of a vascular bundle (figure 3, 1). The margins of the centrifugal xylem turn outwards into the gap and a bundle is organized towards the middle of the gap. This is a leaf trace. It is as a rule connected with the centrifugal xylem alone but occasionally shows a slight connexion with the centripetal xylem. At the same time the margins of the centripetal xylem are extended outwards as projections which embrace the innermost centrifugal xylem (figures 3, 2; figure 19, plate 1). Succeeding sections show the leaf trace further to the outside of the gap towards the cortex, and the margins of the vascular bundles on each side of the gap become closed by the extended centripetal xylem which joins with the free edge of the centrifugal xylem (figure 3, 3; figure 20, plate 1). Above this the gap is closed by the fusion of the neighbouring vascular bundles along these margins.

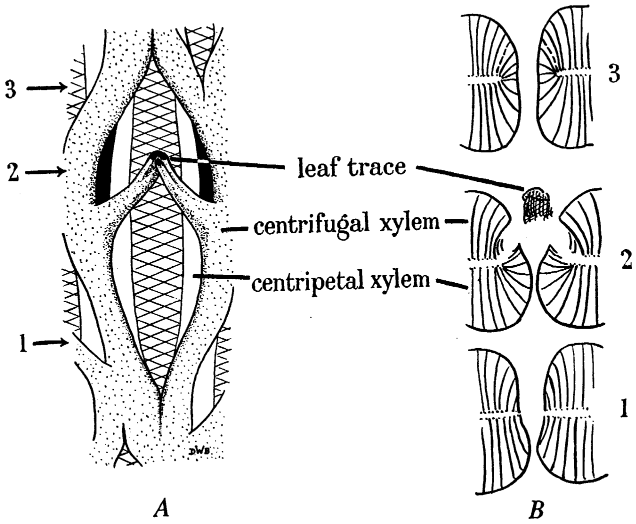

FIGURE 3. *Rhexoxylon piatnitzkyi*. *A*, reconstruction of the leaf gap seen from the cortex. The leaf trace is formed from two small strands connected to the centrifugal (outer) xylem (stippled), one on each side of the gap. The centripetal xylem (solid white) divides with the centrifugal xylem at the bottom of the gap but is not directly connected to the leaf trace. Parenchyma (solid black) is exposed between the centrifugal and centripetal xylem above the origin of the leaf trace. The medulla is cross-hatched. *B*, diagram to show the leaf gap in transverse section at the three corresponding levels in *A*. For full explanation, see text.

When leaf traces depart at about the same level from neighbouring gaps, the vascular bundle between these gaps is more or less symmetrical. In serial transverse sections the appearance of the bundle changes as follows. Below the origin of the traces, the bundle is a double collateral bundle with the protoxylems of the centrifugal and centripetal xylems facing each other across the narrow zone of parenchyma (figure 2*B*). At the point of origin of the traces the centripetal portion has lateral projections which embrace the centrifugal portion. Above this level, the centrifugal and centripetal portions are united completely along the margins of the gaps (figure 2*C*). The bundle is thus concentric for a short distance before the two gaps are closed by fusion of the bundle with its neighbours.

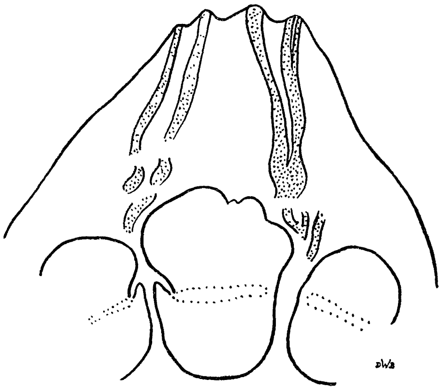

FIGURE 4. *Rhexoxylon piatnitzkyi*: line drawing showing the course of the leaf traces from two adjacent gaps in the vascular cylinder.

The original trace divides further in the cortex. In the example illustrated (figure 4), traces from adjacent gaps each divide into two in the inner cortex. The two pairs of traces converge towards the leaf base and appear as four, almost equidistant, tiny projections on the weathered surface.

The leaf trace never consists of single bundles but of groups of two or more cuneate or crescentic bundles concentrically disposed.

In a tangential section through the outer cortex 7 or 8 groups of bundles are seen to be disposed in a broad semi-circle (figure 5*B*). Further out in the leaf base this arrangement suggests a broad multi-stranded arc, open towards the adaxial side, with a larger median strand situated in this opening, (figure 5*A*, *C*).

Thus each leaf is supplied by traces from at least three or four gaps, some at different levels in the vascular cylinder.

In the cortex beneath a branch scar there is a number of small vascular bundles disposed in an ellipse. We are unable to give any further details of the vascular supply of these branches.

RHEXOXYLON SP.A

(Figure 18, plate 1; figures 22 to 32, plate 2)

Description. The first set of specimens we include in this species consists only of medulla and parts of the vascular cylinder (figures 22, 23, plate 2). They are from stems larger than that described as *R. piatnitzkyi*, being 7 cm across.

Medulla

The medulla consists of several kinds of cells. Most are large parenchyma cells with moderately thin walls, not obviously pitted. Many of these parenchyma cells are misshapen. This is due both to natural compression of the medulla by the development of secondary vascular tissue and parenchyma, and also to collapse by decay. Some of the parenchyma

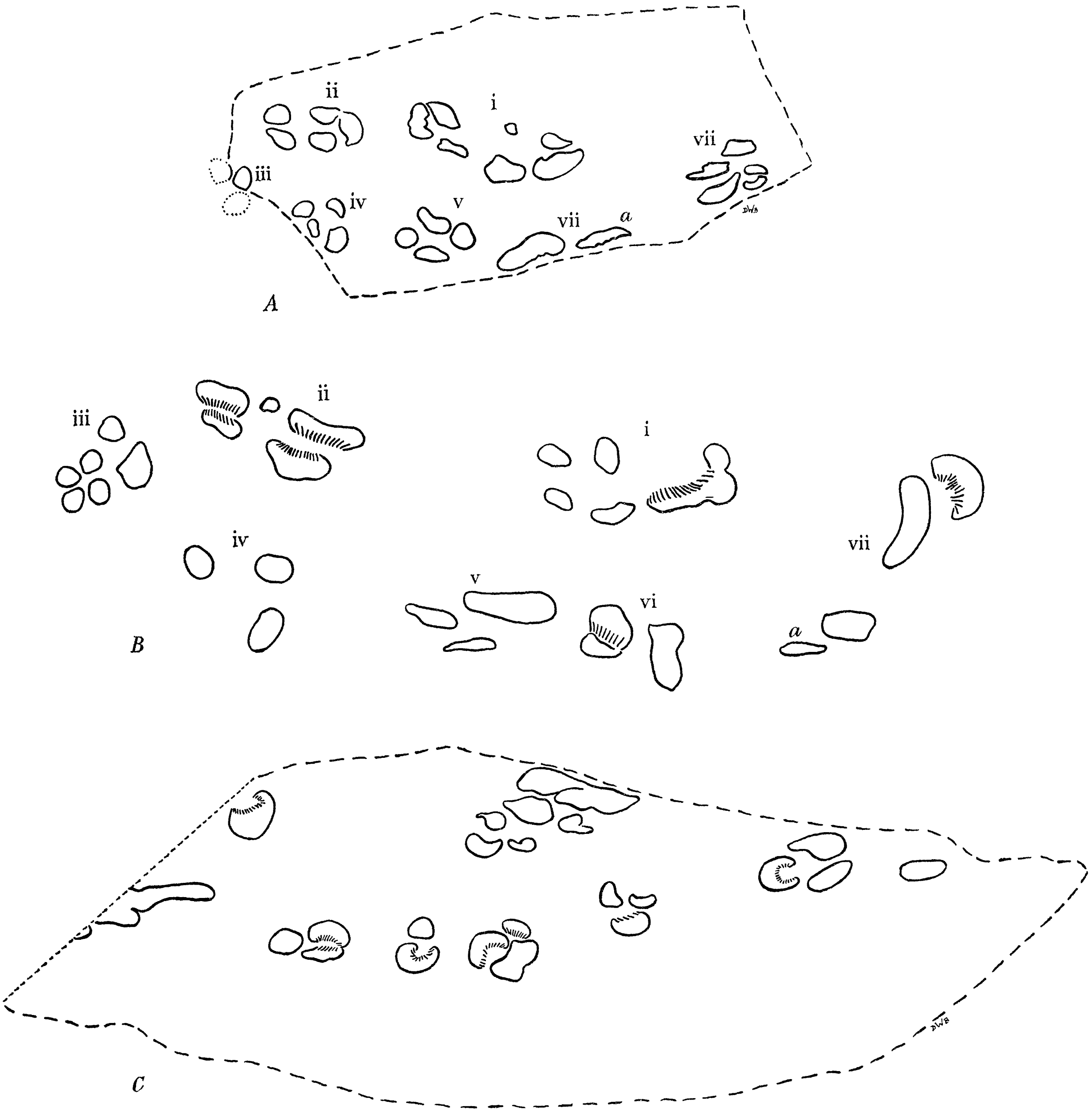

FIGURE 5. *Rhexoxylon piatnitzkyi*: disposition of the vascular bundles in the leaf base and cortex. *A* and *B* are drawn from the same example at different levels. *B* is the inner level showing the groups of small bundles in the outer cortex as they begin to converge towards the base of the leaf. *A* shows the same groups of bundles in the leaf base. The two small bundles represented by dotted lines in (iii) were encountered a little below the general level owing to the uneven weathering of the surface. *C* is drawn from another leaf base. (All × 5.)

cells have dark contents which has shrunk away from the walls. There are also rather thicker walled cells, much less distorted in shape, which tend to form groups, and often surround cavities which may have been produced in fossilization. In some of these cells the inner layers of the wall have contracted from the primary wall. These cells are possibly of the nature of stone cells, but if so their walls are very much thinner than those of the cortical stone cells.

Spherical cysts filled with a crystalline substance, are scattered throughout the medulla, less than 10/cm².

Numerous vascular strands occur in the medulla. Many of them are very small but a few larger strands have a definite cambium and broad phloem zone. The first-differentiated tracheids in these strands are spirally thickened but the tracheids of the later formed xylem have bordered pits and are identical to the tracheids of the xylem of the vascular cylinder.

In most specimens there are large irregular secondary bodies in the medulla, and there may be more than one of these in a transverse section. The flat shape and regular seriation of the cells composing these bodies give the appearance of callus tissue. Occasionally another callus surrounds the first concentrically. The tissue enclosed within the callus is partly unaltered medulla with crystal cysts. In two specimens, however, there is a small area of frass, 2 to 3 mm across, within the callus body, suggesting that the secondary development is traumatic, sealing off an insect boring. In one specimen where this secondary tissue has the form of a cylinder it is 5 mm wide and continuous through a vertical distance of at least 4 cm, the specimen being broken at both ends. In another specimen the callus body is of about the shape and size of an almond kernel.

Vascular cylinder

As in *R. piatnitzkyi* the innermost vascular tissue has developed centripetally from a cambium, and in one specimen there is also part of the outer centrifugal xylem. In this specimen, however, there is no sign of protoxylem. The region between the centrifugal and the centripetal xylem has become dilated by a secondary development of parenchyma, and the inner margins of both xylems have become frayed by the expansion of this parenchyma between the radial rows of tracheids. The parenchyma shows many instances of local meristematic activity. It is assumed therefore that the protoxylem has been obliterated.

The secondary xylem, both centrifugal and centripetal, resembles the secondary xylem of *R. piatnitzkyi*, but most of the tracheids are a little wider. The diameter of the tracheids in transverse section is from 30 to 75 μ (average 50 μ). The pitting is identical (figures 25 to 28, plate 2).

Wood parenchyma cannot be distinguished from the tracheids in the transverse sections but it is abundant. The vertical strands are conspicuous in all longitudinal sections. The individual cells are mostly about 0·1 mm high and often have dark contents.

Around the inner face of the centripetal xylem, the phloem which has developed from the same cambium as the centripetal secondary xylem, extends for a considerable distance towards the medulla. The sieve cells are well preserved and have lateral sieve areas (figures 29 to 31, plate 2). Often a more or less continuous band of fibres occurs in the newly formed phloem, while in the older phloem large parenchyma cells are present. These parenchyma cells have obviously developed subsequently and their enlargement has disarranged the phloem. In the transverse section the parenchyma appears in bands of varying widths between crushed phloem cells, whilst in the radial section the parenchyma presents an appearance similar to that of broad rays in tangential section since it has developed in lenticular masses (figure 18, plate 1). The results of recent cell divisions are still clearly visible.

Some other fragmentary specimens were found close by those of the previous set. Although they consist mainly of an external vascular tissue and dilation parenchyma, there is no reason to regard them as different. The structure of the wood is alike and the cortex is very similar to the ground tissue of the medulla of the previous set.

The largest specimen of this set is a fragment consisting mostly of a single large-lobed mass of xylem embedded in parenchyma of secondary origin (figure 24, plate 2). At each side of the xylem, at a distance of one to two centimetres from it, are the edges of other xylem masses. The lobed xylem mass is bounded along the outer margin and sides by a continuous zone of cambium and phloem. Along the narrow inner margin however, the xylem is split apart by dilation parenchyma and tails off into a multitude of short radial rows of tracheids dispersed through the parenchyma. A wedge of parenchyma almost cuts the xylem mass into two. The structure of the xylem corresponds closely to the structure of the secondary xylem of the previous specimens.

The dilation parenchyma consists of cells varying greatly in shape and size, and often with dark contents. Stone cells are abundant, particularly in clusters forming sclerotic nests, although isolated stone cells are also present. Sclerotic nests are of irregular shape and size and reach 2·5 mm in length (figure 32, plate 2). Many of the stone cells in the centre of the nests are poorly preserved, probably as a result of imperfect fossilization: hence the sclerotic nests often appear as a hollow ball of stone cells. Numerous vascular strands occur in the parenchyma. Some consist solely of tracheids and have obviously been detached from the larger masses of xylem through the development of the dilation parenchyma. Others have well-preserved cambium between xylem and phloem, and in these the tracheids are almost all of the spirally thickened or scalariform pitted types: these tracheids are adventitious developments.

Material studied: LIL 2140–2151 (slides 119–133); LIL 2153–2159 (slides 147–155).
Horizon: Ischigualasto Formation (Trias).
Locality: La Rioja Province, Argentina.

REVIEW OF THE GENUS *RHEXOXYLON* BANCROFT

We have emended the diagnosis of the genus in the light of the new information provided by our South American specimens, and in accordance with our revision of the species.

GENUS *RHEXOXYLON* BANCROFT EMEND

Diagnosis. Stems attaining a large diameter through secondary growth processes involving prolific adventitious meristematic activity, splitting of the vascular cylinder by proliferation of parenchyma cells and growth of adventitious vascular tissue in the interstices. There is a large medulla containing numerous secretory structures and accessory vascular strands. The double, centrifugal-centripetal, vascular cylinder of the young stem is dissected by broad primary rays or gaps associated with the origin of leaf traces. These broad primary rays are perpetuated in the older stems which are characterized by a peripheral cylinder of broad wedges of centrifugal vascular tissue, and to the inside of this are one to several concentric perimedullary series of centripetal or double, centrifugal-centripetal, vascular strands.

The tracheids of the first-formed xylem have spiral thickenings and scalariform pitting; xylem rays are uniseriate, and the cross-fields have 2 or 3 elliptical pits. The tracheids of the secondary xylem have alternate 1 or 3 seriate-bordered pitting; the rays are almost exclusively uniseriate, and cross-field pitting consists of 1 to 3 large circular or elliptical pits. Vertical strands of parenchyma are also common in the secondary xylem. The sieve cells of the secondary phloem have numerous lateral sieve areas; fibres are present in the phloem.

Foliage and fructifications are not known.

Age: Lower Mesozoic (Triassic).

Geographical distribution: South Africa, South America.

Discussion. The genus *Rhexoxylon* with its one species *R. africanum*, was established by Bancroft (1913) for a single specimen of fossil plant exhibiting a novel type of vascular organization.

Walton (1923) described several additional specimens attributed to Bancroft's *R. africanum*, and to a new species, *R. tetrapteridoides*. He included *Antarcticoxylon priestleyi* Seward (1914) in the genus *Rhexoxylon*, and the diagnosis of *R. africanum* and of the genus were emended. In 1925 Walton described another specimen of *R. priestleyi* (Seward), this time from South Africa, and in 1956 recorded some further specimens of *Rhexoxylon* from South Africa. Kräusel (1956) established a new species, *R. waltonii* Kr. which he based on some of the specimens attributed by Walton to *R. africanum*.

Antarcticoxylon priestleyi Seward was considered to be a species of *Rhexoxylon* (Walton 1923, 1925, 1956) on account of a tendency for the otherwise compact woody cylinder to be split, and the presence of adventitious developments of xylem consisting of tracheids with spiral thickenings. The better preserved specimen described by Walton in 1925 reveals some details of the anatomy which do not support this view. Whilst *Rhexoxylon* has cross-field pitting consisting of a single or at most three large pits, *Antarcticoxylon* has six to eight small pits in the field. Furthermore, this latter genus has none of the really characteristic features of vascular organization to be found in *Rhexoxylon*. All known species of *Rhexoxylon* possess a ring of vascular bundles comprised of both centrifugal and centrifugal xylem and phloem, and development continues centrifugally and centripetally by means of cambiums. *Antarcticoxylon*, in common with some *Dadoxylon* spp. which it more nearly resembles, has a small amount of centripetally developed xylem (primary metaxylem?) in the perimedullary region: there is no evidence of a persistent cambium or of any phloem here. We consider *Antarcticoxylon* to be a distinct genus unrelated to *Rhexoxylon*.

REVIEW OF THE SPECIES OF *RHEXOXYLON*

We have examined available specimens including the types of species assigned to the genus by previous authors. Together with new facts about the general organization of the stem provided by our small stem *R. piatnitzkyi* n.sp., this study has led to our recognition of certain criteria which have enabled a more precise delimitation of the other species, *R. africanum* and *R. tetrapteridoides*. The diagnoses are given below.

RHEXOXYLON AFRICANUM BANCROFT

(Figure 6)

Diagnosis. Large stems, the woody cylinder attaining a diameter of over 50 cm. There is a broad medulla, 6 cm in diameter in the largest known specimens, with nests of stone cells, spherical cysts, and vascular strands. Meristematic activity in the medulla commonly results in the enclosure of portions of the medulla within hollow bodies of secondary tissue.

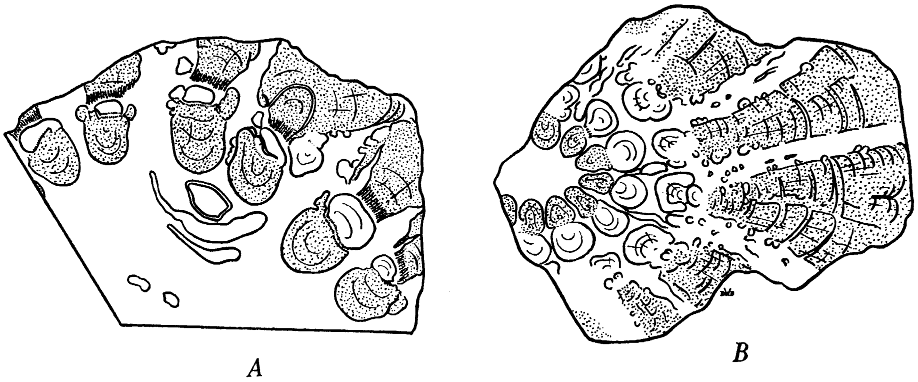

FIGURE 6. *Rhexoxylon africanum. A.* (From a photograph of the type specimen in Bancroft 1913). Xylem developed from the original vascular bundles is stippled. The inner margins of the centrifugal xylem sectors is frayed, and new adventitious xylem has arisen against the outer edges of the centripetal xylem. (× 1.) *B.* (From a photograph in Walton 1923). The greatly separated original centrifugal and centripetal xylem is stippled. (× 1/5.)

In transverse section the sectors of centrifugal secondary xylem may be over 12 cm in radial extent, and at their broadest over 5 cm. Between the medulla and the inner margin of the main centrifugal wood are one or more concentric series of double vascular strands consisting of a centrifugal and a centripetal part. The innermost series may be over 5 cm in radial extent. Adventitious vascular developments are very abundant in the outer cylinder of centrifugal wood.

Holotype: V 12561–3 and slide preparations V 12556–60 in coll. British Museum (Nat. Hist.); other preps. Kidston coll. no. 2311–2, Botany School, Cambridge no. 613–7.

Horizon and locality: unknown.

Observations: other material studied.

(i) Hunterian Museum Pb188; BM (NH) V21295; BM (NH) V15896, V15898, V31896, Cambridge Botany School, unregistered block and fragments of same specimen as these, slide preps. J. Walton coll. 50–4, Kidston coll. 2789.

Locality: Willoughby's, 12 miles south-west of Gwelo, Southern Rhodesia.

Horizon: unknown.

(ii) BM (NH) V 15899.
Locality: Samabula Flats, Gwelo, Southern Rhodesia.
Horizon: unknown.

(iii) Hunterian Museum Pb 189, slide preps, J. Walton coll. 428–9.
Locality: between Chimpandu and Zimbawe, Portuguese East Africa.
Horizon: Upper Sandstone (Triassic).

(iv) South African Museum 4359 (block not seen), slide preps. Kidston coll. 2790–6, J. Walton coll. 49.
Locality: Aliwal North (Lady Grey), Cape Province.
Horizon: Red Beds (Stormberg Series).

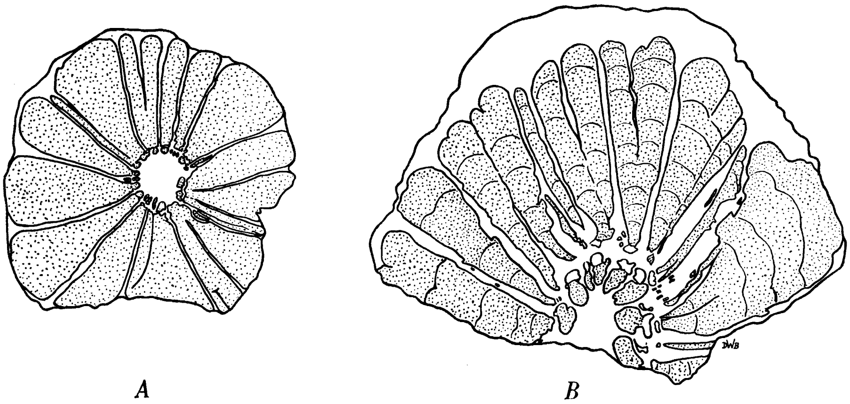

FIGURE 7. *Rhexoxylon tetrapteridoides* (From drawings in Walton 1923, ½ size). *A*. In this small stem the centrifugal and centripetal xylem sectors have not become widely separated, although considerable centrifugal growth has occurred and some of the centrifugal sectors are split. *B*. An older stem in which the centrifugal xylem is much more disrupted particularly on the inside where it has been separated from the centripetal xylem.

RHEXOXYLON TETRAPTERIDOIDES WALTON EMEND

(Figure 7)

Diagnosis. Stems with woody cylinder attaining the diameter of 16 cm in the largest known specimen. The medulla up to 2 cm in diameter, contains spherical cysts, a few small vascular strands, and numerous large nests of stone cells which form a high proportion of the medullary tissue. In transverse section the sectors of centrifugal secondary xylem are not more than 6 cm in radial extent and mostly less than 2 cm broad. Between the medulla and the inner margin of the main centrifugal wood is a single ring of vascular strands which may be double (centrifugal-centripetal) or consist solely of centripetally developed tissue, and not more than about 1 cm in radial extent. There is very little adventitious development of vascular tissue in the outer cylinder of centrifugal wood. The cortex contains sclerotic nests and vascular traces.

Syntypes: no. 433, 434u, 436u, 437u in South Africa Museum (blocks not seen); slide preps. from these, Kidston coll. 2780–6, 2847–50; J. Walton coll. 57–60.

Horizon: Molteno Beds (Stormberg Series; Triassic).

Locality: Glencoe, Umkomazaan Valley, Ipolela County, Natal.

Observation: slide preparation Kidston coll. 2774 seems to belong to this species. It is from South Africa Mus. 124u, from Matatiele Commonage, Cape Province.

R. tetrapteridoides Walton was based on specimens from two localities (Walton's specimens A1 and A2). The stem is of smaller diameter than most specimens of *R. africanum*. The largest transverse section figured by Walton (1923, text-fig. II, 3) is of a stem of some 17 cm in diameter. From the series of transverse sections belonging to a single specimen (A1) we may characterize this species as having a woody cylinder which is much more compact than that of *R. africanum*. The medulla is small and the inner ring of vascular bundles much less developed. In the smaller specimens the inner ring consists only of small centripetal fans which arise from points on the same radii as the sectors into which the centrifugal wood is divided, and the numerous centrifugal sectors are separated by only very narrow zones of parenchyma. In the larger specimens this separation is more marked and the sectors are further split, both radially and tangentially, by dilation parenchyma. There is, however, rarely any adventitious development of vascular tissue within the centrifugal xylem. In this respect the appearance is quite different from that of *R. africanum*, although there may be additional centripetal developments on the inner edge of these sectors (figures 6, 7).

Two sections accepted by Walton as being of the same specimen (A1), however, differ from the rest. One of these (Walton 1923, text-fig. II, 4, sample 4) is from part of a specimen with a very broad medulla surrounded by large fan-shaped centripetal xylem masses, and rather larger sectors of centrifugal xylem separated by broad parenchyma zones. The centrifugal xylem is both much less in radial extent and also less compact than in any other specimen of *R. tetrapteridoides*. There are also numerous adventitious developments of xylem from the sectors of centrifugal wood, as in *R. africanum*. Sample 5 also differs slightly from the other samples of *R. tetrapteridoides*, the centrifugal xylem again being less developed.

The second specimen included by Walton in his description of *R. tetrapteridoides* (specimen A2) consists of little else but a medullary region with a ring of centripetal vascular bundles, and outside this only very small portions of a few of the centrifugal sectors of wood. The specimen does not therefore show the major specific difference between this species and *R. africanum*, which we have noted above. The medulla is rather broader than in the other specimen (A1) and the centripetal bundles are rather larger. The small portions of the outer sectors present are split by dilation parenchyma, and have numerous small wedge-shaped developments of xylem. They recall the specimen A1 sample 4 described above, and in some other features, notably the structure of the medulla, again recall *R. africanum*.

We consider these specimens (A1, sample 4; A2) too fragmentary to permit a specific determination. (The material studied by us is in the slide preps. Kidston coll. no. 2775–9, and in J. Walton coll. no. 61–4).

The medulla provides criteria of diagnostic value. The narrow medulla of *R. tetrapteridoides* has many large sclerotic nests forming a high proportion of the cross-sectional area. The wider medulla of *R. africanum* and Walton's specimen A2, has a much smaller proportion of sclerotic tissue and a large number of small vascular strands, in addition to which there is commonly present an irregularly shaped body of secondary origin ('periderm' of Bancroft). Spherical cysts are present in both.

Except for a small sector of an outer zone of centrifugal wood, frayed and split by dilation parenchyma, Bancroft's original specimen, the type of *R. africanum*, consists only of medulla and a ring of vascular bundles composed of both centrifugal and centripetal elements (figure 6*A*). The new, larger specimens described by Walton (1923, 1956) have more of the outer woody cylinder preserved and a much greater development of fan-shaped adventitious xylem masses, including an additional centripetal development from the inner margin of each outer sector (figure 6*B*).

Kräusel's new species, *R. waltonii* (Kräusel 1956), was segregated from *R. africanum sensu* Walton. It was based on specimens with a compact fan of centripetal xylem arising from the inner margin of the outer sectors of centrifugal wood in addition to one or more inner series of centrifugal-centripetal bundles; *R. africanum sensu* Kräusel being characterized by the presence of a fringe of rows of tracheids (Fransenxylem) along the inner edge of the outer sector which he homologizes with the centripetal wood in the perimedullary region in *Antarcticoxylon priestleyi* Seward. The 'Fransenxylem' seen in some specimens of *R. africanum* is not, however, centripetal xylem, but is merely the margin of the centrifugal wood sector which has become frayed by the expansion of dilation parenchyma. In our opinion, Walton's specimens resemble the type sufficiently to justify their inclusion in the species with slight emendation of the diagnosis. Anatomically they are quite similar, and differ only, as Kräusel has noted, in the detail of the disposition of the centripetal xylem developments between the inner ring and the outer sectors of centrifugal wood. In *R. africanum* there is a great amount of variation in the development of centrifugal and centripetal wood elements in this zone between the inner ring and the outer cylinder of centrifugal wood. In large specimens where the zone is wide, there is usually a fan-shaped growth of centripetal wood from the inner margin of the outer sectors. But in some specimens this centripetal development may be quite irregular or even lacking on individual sectors (Hunt. Mus. PB188). The situation is similar in *R. tetrapteridoides* where the different types or stages of development may often be seen in a single transverse section. It is wrong therefore to base a species on such a character, and *R. waltonii* Kräusel, is synonymous with *R. africanum* Bancroft.

The complex stem structure of *Rhexoxylon* may now be interpreted from the point of view of development.

R. piatnitzkyi shows clearly the primary vascular organization of the stem. It has a ring of double collateral vascular bundles, each bundle consisting of a centrifugal and a centripetal part (figure 2). Walton's view that the mature stem structure resulted from the splitting of a 'normal' cylinder of centrifugal wood together with the development of perimedullary centripetal wood (Walton 1923 and later), cannot therefore be supported.

The vascular organization of *R. tetrapteridoides* is in its early stages, essentially similar to that of *R. piatnitzkyi*. The only obvious difference is the relatively greater centrifugal development of the xylem in *R. tetrapteridoides*, which may be correlated with the much smaller medulla (figure 7). An early stage of *R. africanum* with its broader medulla, would presumably have a structure closely similar to *R. piatnitzkyi*. An unidentified stem of *Rhexoxylon* from the Burghersdorp Beds, Cape Province, having a broad intact medulla (Walton 1923, p. 99; South African Museum no. 2944) may be a young *R. africanum* (figure 13, plate 1).

It appears most probable from the antomy of *R. piatnitzkyi* that, from the very earliest stage of vascular differentiation, there are two protoxylems, centrifugal and centripetal, separated by a very small amount of parenchyma. The development of xylem and phloem is continued both centrifugally and centripetally by the cambium.

In the larger specimens of *R. tetrapteridoides* and *R. africanum* the centrifugal and centripetal parts of the vascular bundles have become pushed apart by proliferation of the parenchyma in and between the primary xylems and new adventitious growths of xylem (probably phloem too) have appeared along the inner margins of the separated primary xylems. This results in a considerable increase in the diameter of the tissues within the ring of centrifugal xylem sectors. In *R. africanum* these sectors of centrifugal xylem, apart from radial extension due to normal cambial activity, are further parted and split radially and tangentially by development of dilation parenchyma and adventitious vascular tissue (figure 6).

Eventually in both *R. africanum* and *R. tetrapteridoides*, separation of the original xylem from the new growth occurs by a process similar to that which separated the original primary xylems. In this way two or more concentric rings of double bundles arise. These lie along the radii of the original double bundles of which the centripetal parts still remain next to the medulla (figures 6*B*, 7*B*).

Our knowledge of the new *Rhexoxylon* sp.A is incomplete but the evidence available suggests that the centrifugal xylem sectors are separated to a much greater extent by dilation parenchyma than in either of the other two species (figure 24, plate 2).

Affinities of *Rhexoxylon*

Bancroft (1913) included the genus *Rhexoxylon* in the family Medullosaceae. Walton (1923) on the other hand compared the genus with some southern hemisphere *Dadoxylon* spp. with which there is a resemblance in the character of the secondary wood except for the cross-field pitting. The single pits in *Rhexoxylon* he regarded as a result of fusion of the numerous smaller pits in *Dadoxylon*, a tendency traceable through such species as *D. pedroi*.

Histologically there is much general agreement between *Medullosa* and *Rhexoxylon* except for the details of tracheidal pitting. The tendency for adventitious meristematic activity, proliferation of parenchyma, new vascular structures, cambial zones giving rise to periderm-like tissue in the pith, are common to certain species of the two genera. Other features include a medullary vascular system, an abundance of secretory structures, and the presence of fibres in the phloem. Some of these similarities were noted by Bancroft and she also emphasized the 'distinct points of difference between them' in the histology of the wood so far as it was known for *Medullosa*. But her comparison rested chiefly on the apparent 'polystelic' condition of the new stem fragment and of the medullosean alliance.

We are now able to consider the evidence provided by the primary organization of the vascular cylinder in *R. piatnitzkyi*. Although greatly complicated by being double, with an outer (centrifugal) and inner (centripetal) component, the vascular cylinder is a dictyostele.

This interpretation of stelar organization in *Rhexoxylon* differs fundamentally from that suggested to Bancroft by the small fragmentary specimen on which the genus was based. The appearance of 'polystely', in the sense in which that term has been used for the Medullosaceae, was in *R. africanum* a result of the considerable secondary development which had already occurred. There is, however, still a good case for regarding the Medullosaceae, particularly the Permian forms, as having affinity with *Rhexoxylon*. The stelar organization of the Permian Medullosae may be compared with that of *R. piatnitzkyi*. The peripheral 'plate-rings' of these forms constitute a more or less unbroken cylinder of vascular tissue surrounding the central medullary region in which are found smaller vascular strands. The plate-ring vascular cylinder consists of an outer (centrifugal) and an inner (centripetal) plate of xylem, and between the two a narrow zone of parenchyma and tracheids, the so called 'partial-pith'. Around the xylem masses is a cambium and broad phloem zone. By homology with the earlier Medullosae, such as *M. anglica*, the main centrifugal and centripetal xylem masses are generally described as *secondary*, and the narrow zone of mixed tracheids and parenchyma considered as the *primary* xylem.

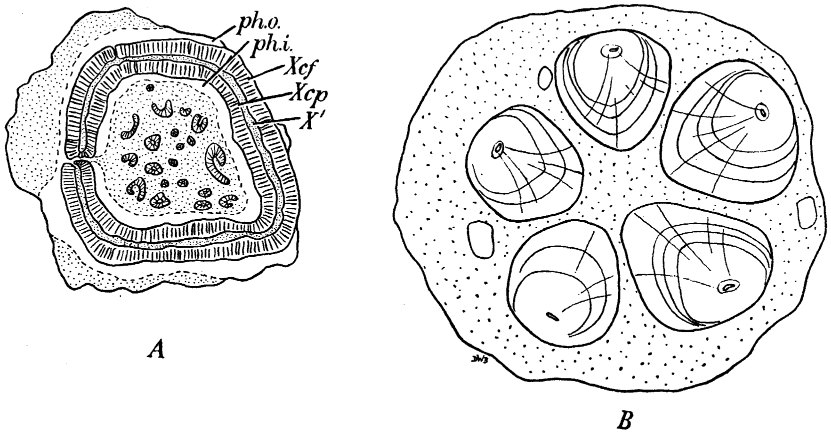

Figure 8. *A*. Transverse section of *Medulla porosa* (from a drawing in Weber & Sterzel 1896). *Xcf*, *Xcp*, centrifugal and centripetal 'secondary' xylem. *X'*, primary xylem ('partial pith'). *ph.o.*, *ph.i.*, outer and inner phloem. *B*. Transverse section of *Pentoxylon* stem showing the 5 concentric vascular bundles (from a photograph in Sahni 1948). (× 11.)

Throughout these forms however can be detected a trend towards a reduction in this primary xylem zone until the amount of tracheidal tissue is very little. This may be illustrated by reference to *M. porosa* (figure 8*A*). In this species the vascular cylinder bears a most striking resemblance to that of *Rhexoxylon piatnitzkyi*, although in the latter there are no tracheids in the narrow parenchyma zone. The centrifugal and centripetal xylem in both instances commences around the margin of this zone with very small tracheids suggestive of protoxylem, which in *R. piatnitzkyi* have spiral bands of thickening. In view of these facts and the commonly precocious appearance of 'secondary' xylem in the earlier Medullosae it appears as if there has been a gradual takeover in function and time of development of the original primary xylem, and what we see as protoxylem in the later forms of *Medullosa* and in *Rhexoxylon* originated as a secondary venture which has eventually been incorporated into the primary body.

It is unfortunate that so little is known of the histological details of the Permian Medullosae since this prevents any closer comparison with our Triassic fossil. However, in transverse section the wood of the two is very similar in appearance. Unlike the Carboniferous species, the Permian Medullosae had a more compact wood with mostly uniseriate rays and fairly narrow tracheids, as in *Rhexoxylon*.

In the detailed anatomy of the wood, the Indian Jurassic stem *Pentoxylon* (Sahni 1948) seems to be almost identical with *Rhexoxylon*. The more or less independent vascular strands of this stem (figure 8*B*) may well be the product of a similar line of stelar evolution. They are constructed on a similar plan with mainly centripetal and centrifugal development, but the cambium completely encircles the strand. An interesting comparison may be made with the concentric strand of *Rhexoxylon piatnitzkyi* as it appears just above the origin of a leaf trace (figure 21, plate 1).

Despite the similarities, it must be remembered that *Rhexoxylon* and *Medullosa* are far apart both stratigraphically and geographically. And there are also sufficient important morphological differences, such as the nature of the leaf traces and consequent dissection of the vascular cylinder, to justify their separation. The leaves of *Rhexoxylon* are unknown but they are unlikely to be either *Alethopteris* or *Neuropteris*, the type borne on the earlier Medullosae. The main associated gymnosperm leaves are *Dicroidium* and *Xylopteris*. When the foliage and the reproductive organs of *Rhexoxylon* are found, and the Permian Medullosae better known, systematic relationship may become more evident. Meantime *Rhexoxylon* remains isolated taxonomically from all other genera of plants, living and fossil. There may be justification for regarding it as a taxon of ordinal rank.

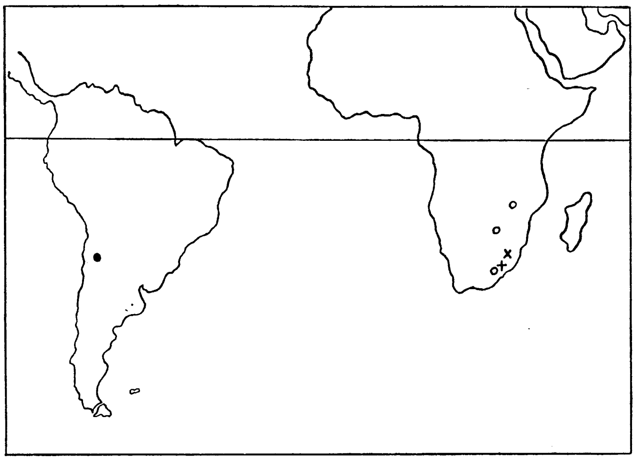

FIGURE 9. Map showing the geographical distribution of the species of *Rhexoxylon* ○, *R. africanum*; ●, *R. piatnitzkyi* and *Rhexoxylon* sp.A.; ×, *R. tetrapteridoides*; +, *Rhexoxylon* sp.

OCCURRENCE OF *RHEXOXYLON*

All the specimens of *Rhexoxylon* described by previous authors came from several localities in Africa—Cape Province, Natal, Rhodesia, Nyasaland and Portuguese East Africa. In each case the age has been determined as Upper or Middle Triassic (Molteno and Red Beds of the Stormberg Series). The new material we have described is from the Ischigualasto Formation in Northern Argentina.

Ischigualasto is a semi-desert which lies exactly on the border between La Rioja and San Juan Provinces of the Argentine Republic, and the series of sediments represented in the region comprises, from oldest to youngest, The Ischichuca, Los Rastros, Ischigualasto and Los Colorados formations. The second and the third formations are the most fossiliferous, and from them has been described a rich flora, consisting of odontopteroid leaf impressions. The specimens of *Rhexoxylon* come from the uppermost horizon of the Ischigualasto formation. A few metres below is another plant-bearing horizon which has yielded a mummified material with well-preserved cuticles.

The very rich fauna is a remarkable feature of the Ischigualasto formation. The abundance of cynodonts, some of them identical with the South African *Scalenodontoides*, led at first to a correlation with the Upper Beaufort Beds. But later, the presence of rhynchosaurians (*Cephalonia*) and numerous pseudosuchian techodonts was reported, and palaeozoologists now correlate the Ischigualasto formation with the Molteno and Red Beds of the Stormberg Series (O. A. Reig, personal communication).

We should like to record our thanks to Professor J. Walton, to Professor T. M. Harris, F.R.S. and Dr S. Williams for helping during the course of this work, and to Dr H. Hamshaw Thomas, F.R.S. and Mr F. M. Wonnacott for making available for study specimens from the University Museum, Cambridge and British Museum (Nat. Hist.), respectively. We are also indebted to the British Council for a scholarship which has made possible our collaboration in these studies.

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DESCRIPTION OF PLATES 1 AND 2

PLATE 1

FIGURE 13. *Rhexoxylon* sp.
FIGURE 18. *Rhexoxylon* sp.A.
Others. *Rhexoxylon piatnitzkyi.*

FIGURE 10. External view of largest fragment showing two scars among the distorted leaf bases. (×1.) (LIL 2152.)

FIGURE 11. Transverse surface of the same specimen showing the incomplete cortex, the vascular cylinder, and medulla with small vascular strands. (×1.)

FIGURE 12. View of another fragment showing the exposed bud illustrated in figure 1. (A little over natural size.)

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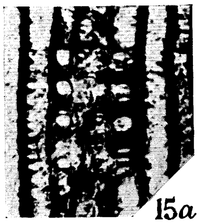

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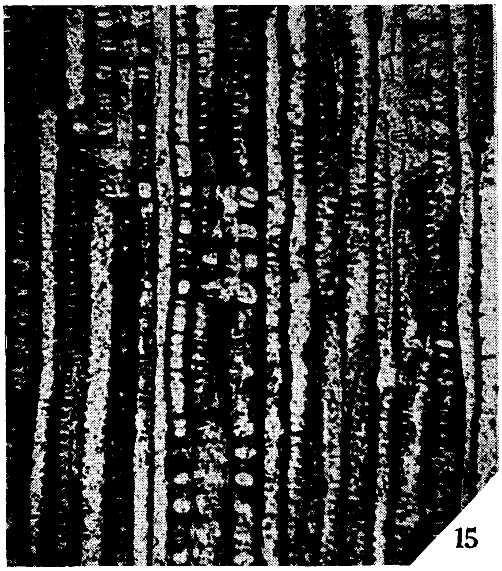

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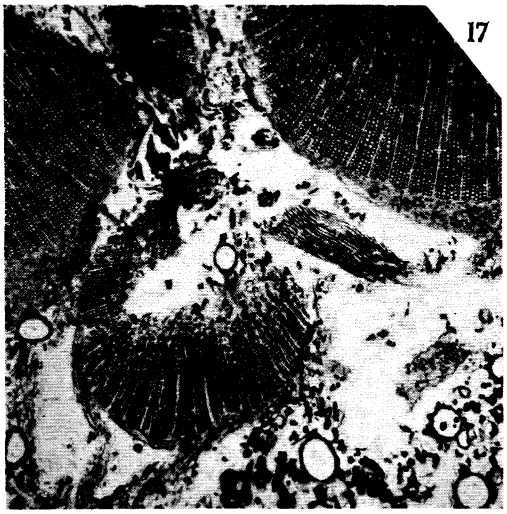

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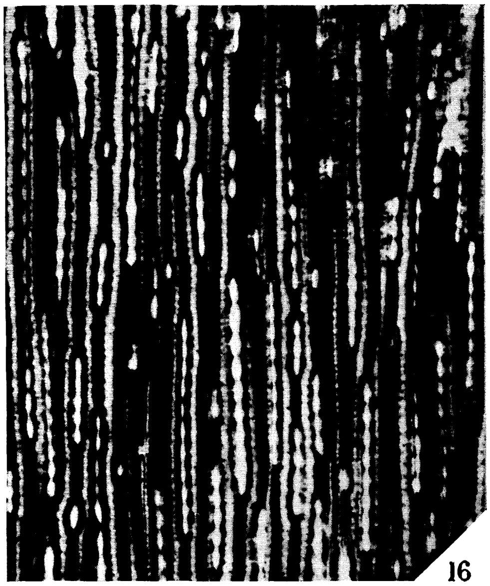

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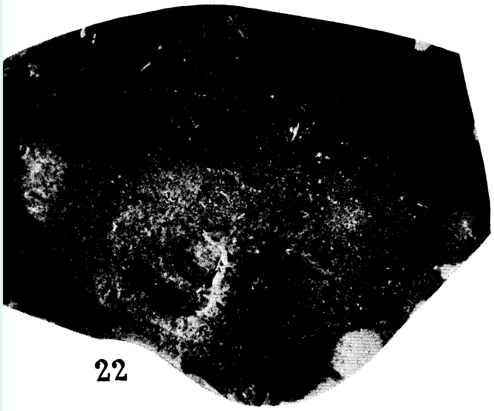
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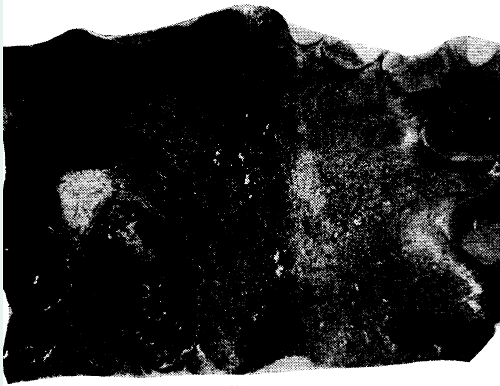
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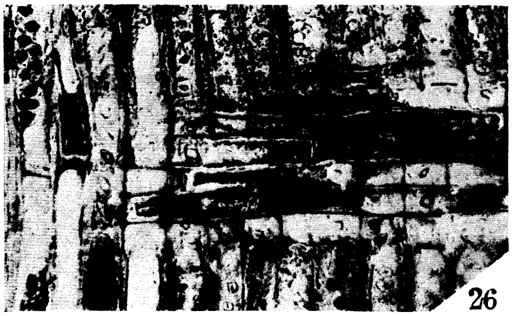
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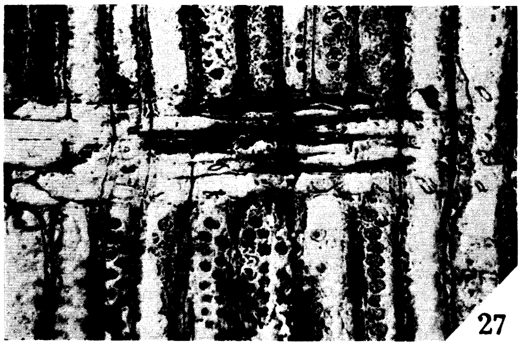
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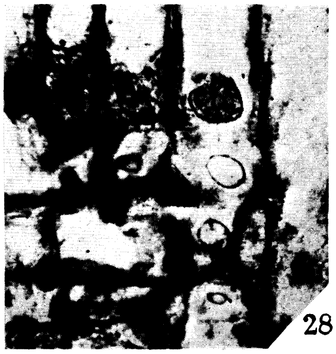
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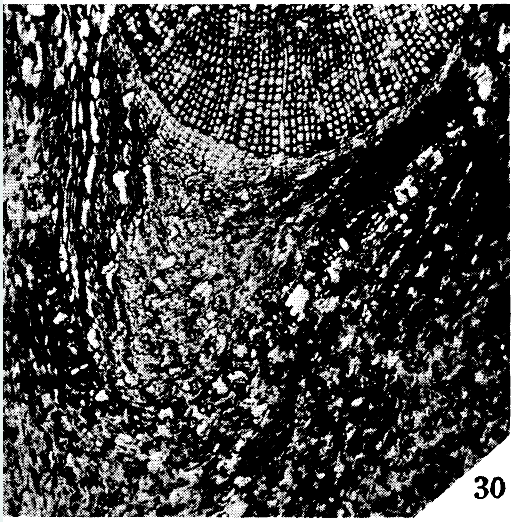
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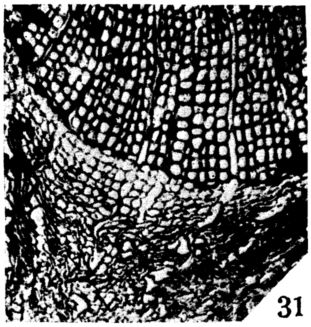
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FIGURE 13. Transverse section of stem showing great similarity to *R. piatnitzkyi* in vascular organization, and presumed to be young stage of a type such as *R. africanum*. (Slightly reduced.) (Kidston coll. 2787.)

FIGURE 14. Radial section of cysts in the medulla with dark centre which reveals the outline of projecting material (× 65.) (Slide 135.)

FIGURES 15, 15*a*. Radial section of xylem to show cross-field (ray to tracheid) pitting. (× 100.) (Slide 135*a*.)

FIGURE 16. Tangential section of xylem showing the variation in height of the rays. (× 65.) (Slide 136.)

FIGURE 17. Transverse section showing the origin of a medullary vascular strand from the peripheral cylinder. (× 12.) (Slide 145.) Cysts are here seen in t.s.

FIGURE 18. Radial section of phloem zone with dilation parenchyma. (× 70.) (Slide 119.)

FIGURES 19, 20. Transverse sections illustrating stages in the departure of leaf traces from the vascular cylinder.

19. Trace just before leaving the gap, the margins of the bundles bordering the gap are still 'open', as projections of the centripetal portions begin to embrace the centrifugal portions of the bundles.

20. A slightly later stage seen in the adjacent gap. Here the margins of the bundles have become 'closed' by a continuous cambium as the trace is about to leave the gap. (Both × 12.) (Slide 145.)

FIGURE 21. The vascular bundle seen in part between the two gaps illustrated in the previous figures. It is almost completely enclosed by cambium. The slight periodicity in the xylem is also shown here. (× 12.) (Slide 145.)

PLATE 2

Rhexoxylon sp.A.

FIGURES 22, 23. Whole transverse sections consisting almost entirely of medulla with part of the centripetal xylem and inner phloem. In the medulla are some vascular strands and the larger secondary bodies ('periderm') showing dark against the ground tissue. (× 1.) (22, slide 125; 23, slide 127.)

FIGURE 24. Whole transverse section showing the lobed mass of xylem and secondary parenchyma with large sclerotic nests. The xylem is disrupted by dilation parenchyma. (× 1.) (Slide 149.)

FIGURE 25. Radial section of xylem showing the uniseriate and biseriate bordered pits of the tracheids, and the ray cells. (× 70.) (Slide 119.)

FIGURES 26, 27. As figure 25 (× 110.) (Slide 151.)

FIGURE 28. Radial section: detail of ray showing cross-field (ray to tracheid) pitting. (× 270.) (Slide 119.)

FIGURE 29. Radial section of the inner phloem showing the numerous lateral sieve areas on the walls of the sieve cells. (× 270.) (Slide 119.)

FIGURE 30. Transverse section of the inner phloem and centripetal xylem of a vascular bundle. Towards the outer edge of the phloem tissue is a zone with fibres. (× 22.) (Slide 126.)

FIGURE 31. Detail from figure 30 (× 30.)

FIGURE 32. Sclerotic nest from the ground tissue showing fine pitting and concentric lamellae of the secondary cell walls. (× 110.) (Slide 154.)


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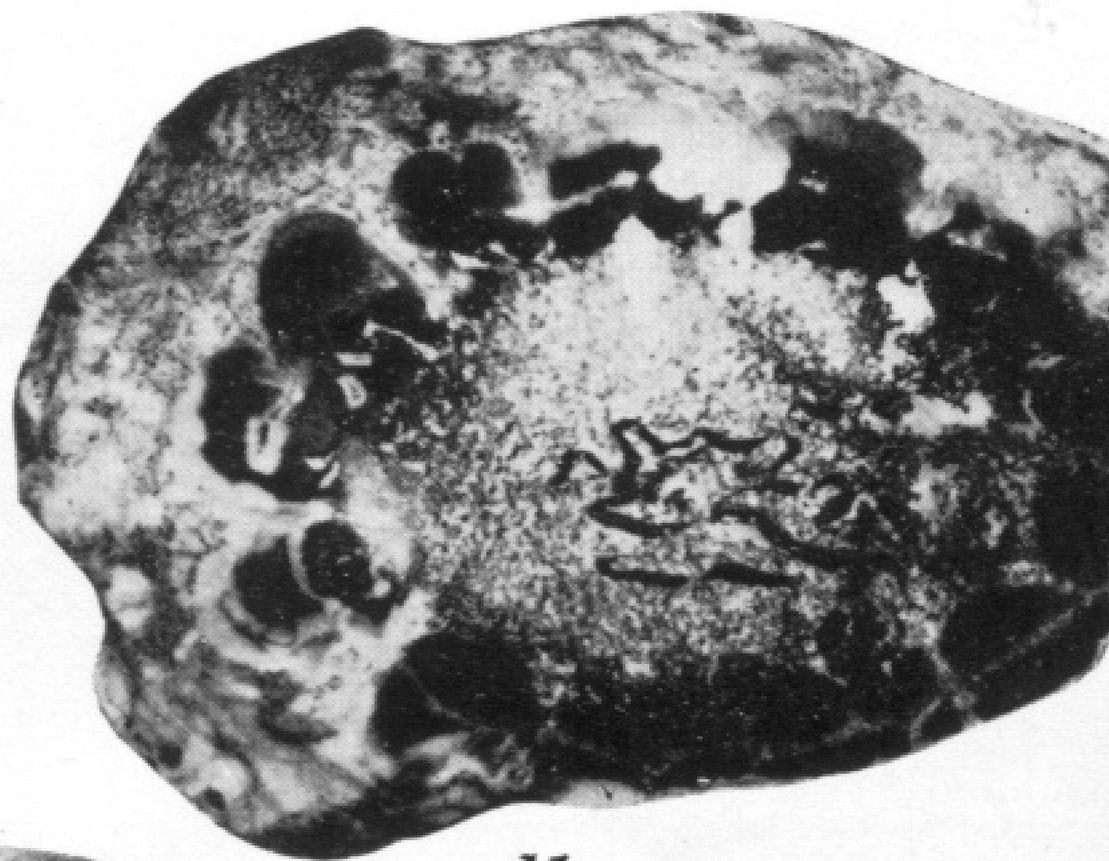
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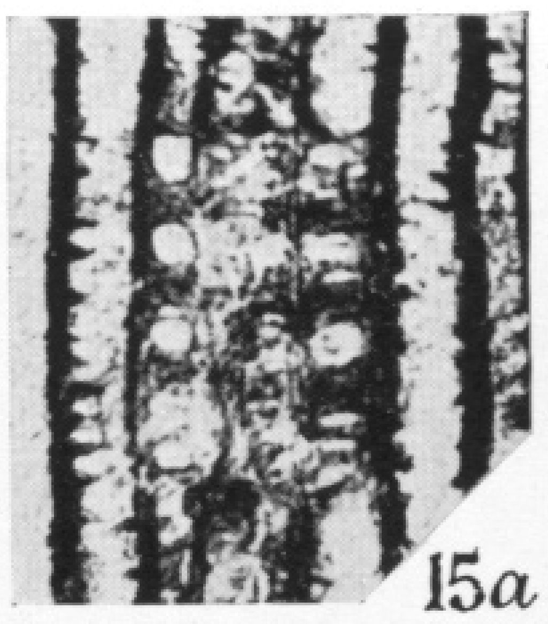
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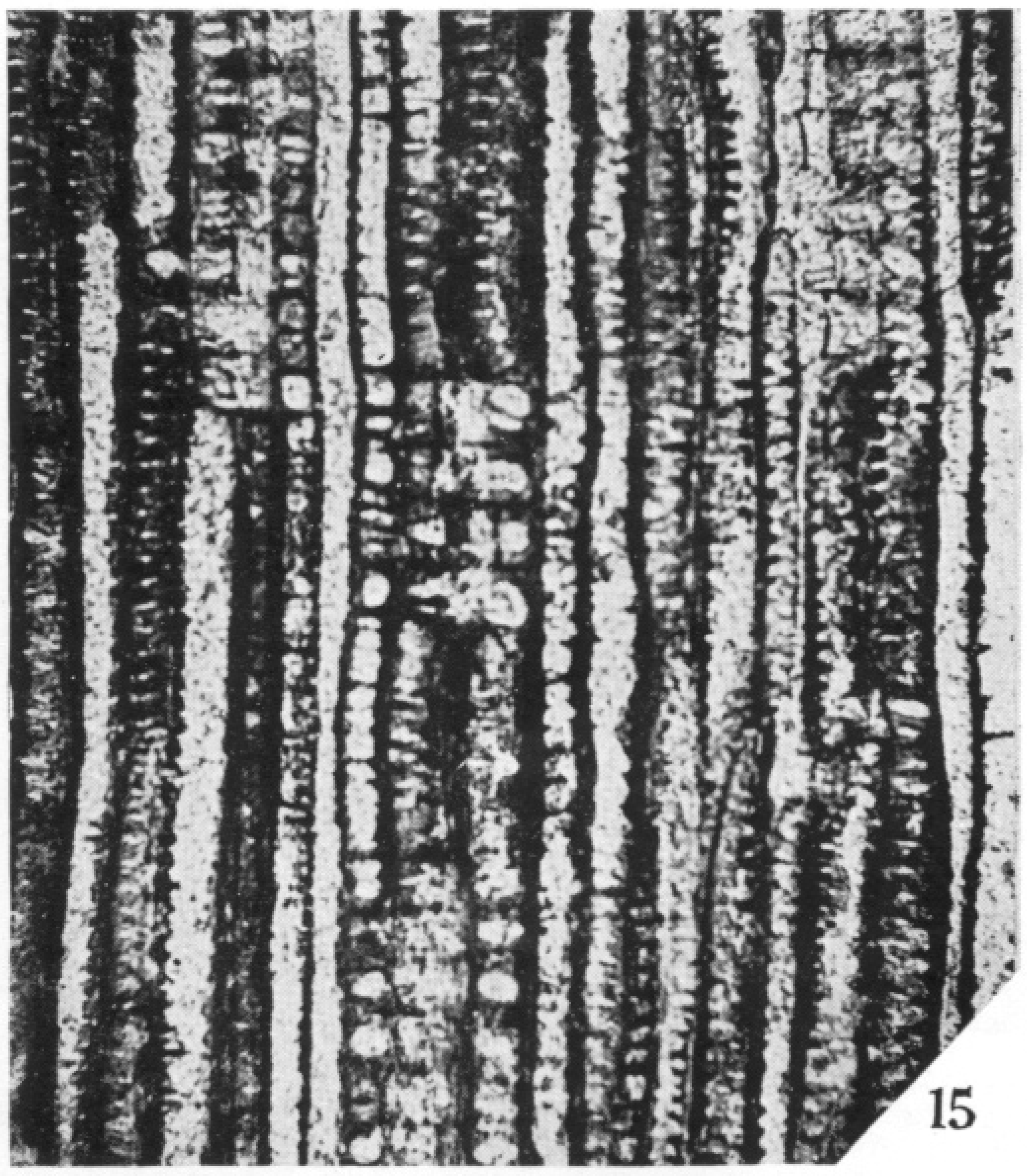
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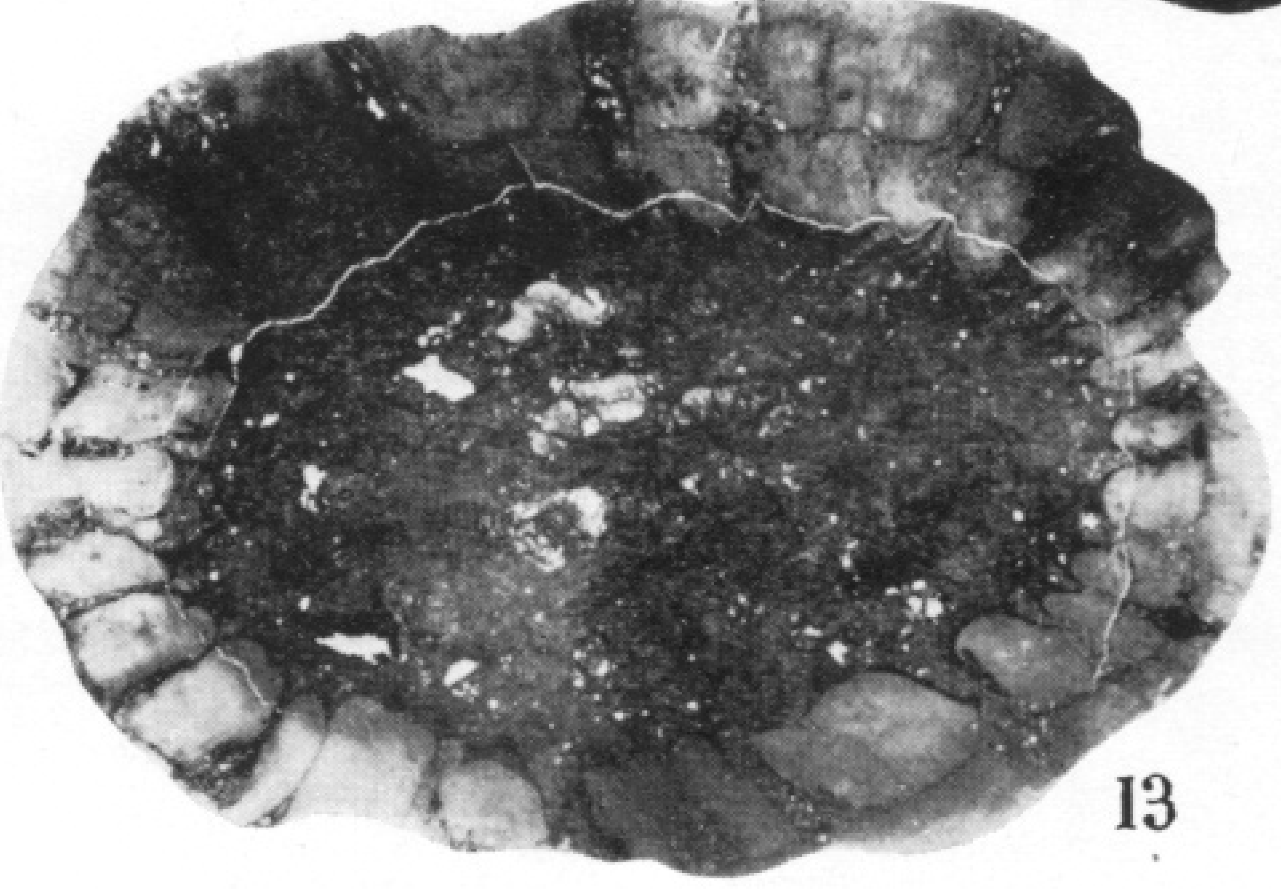
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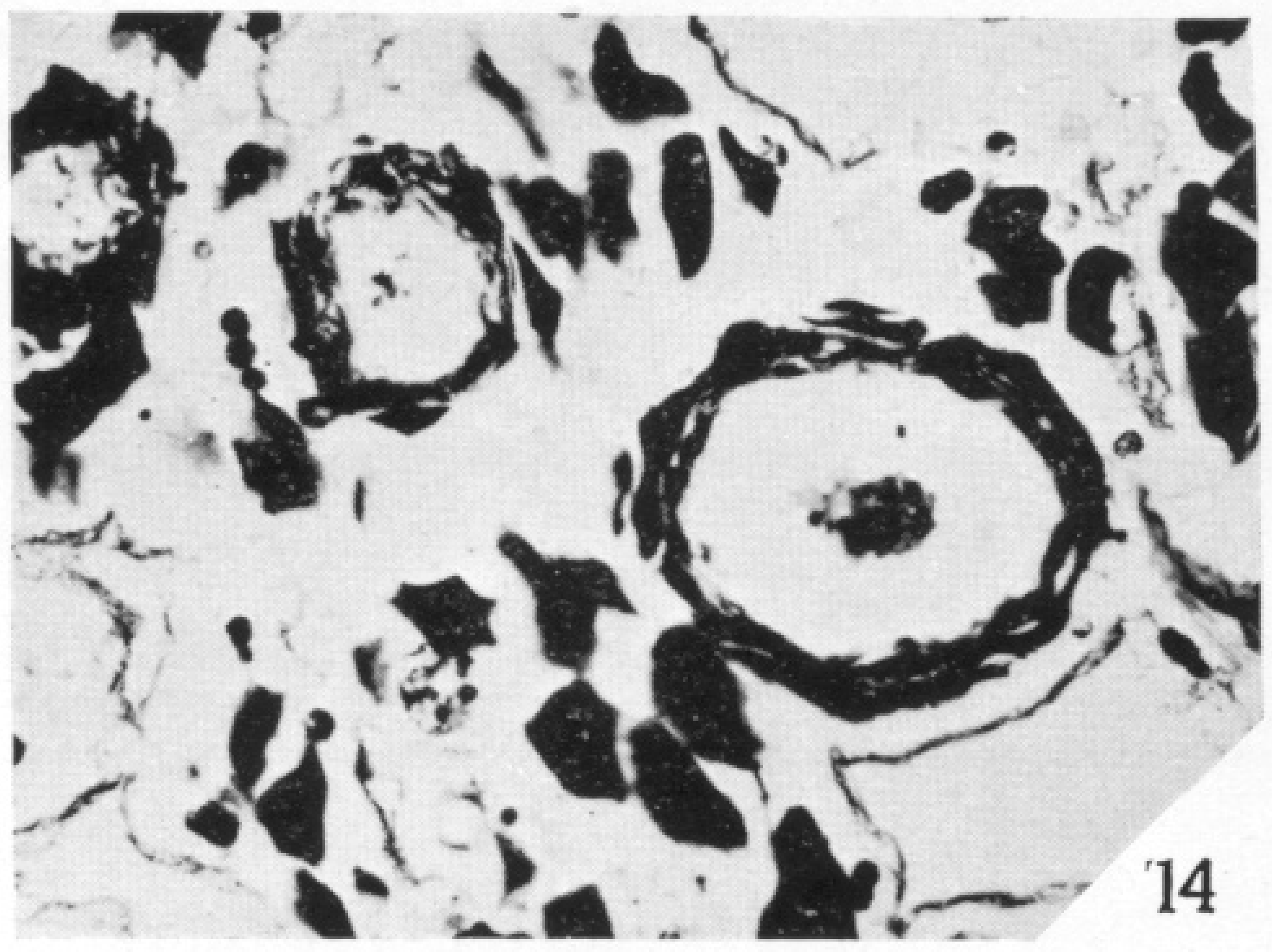
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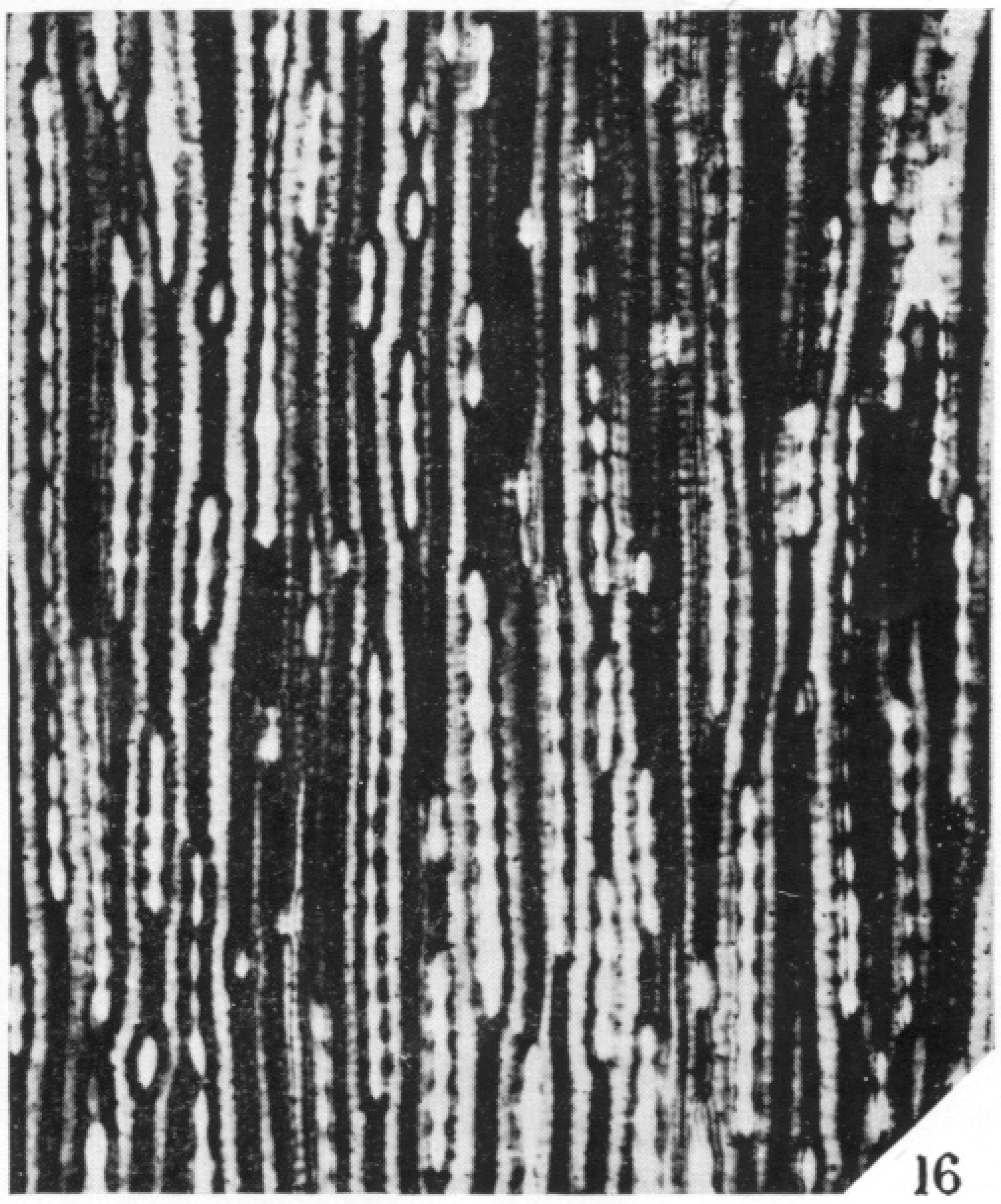
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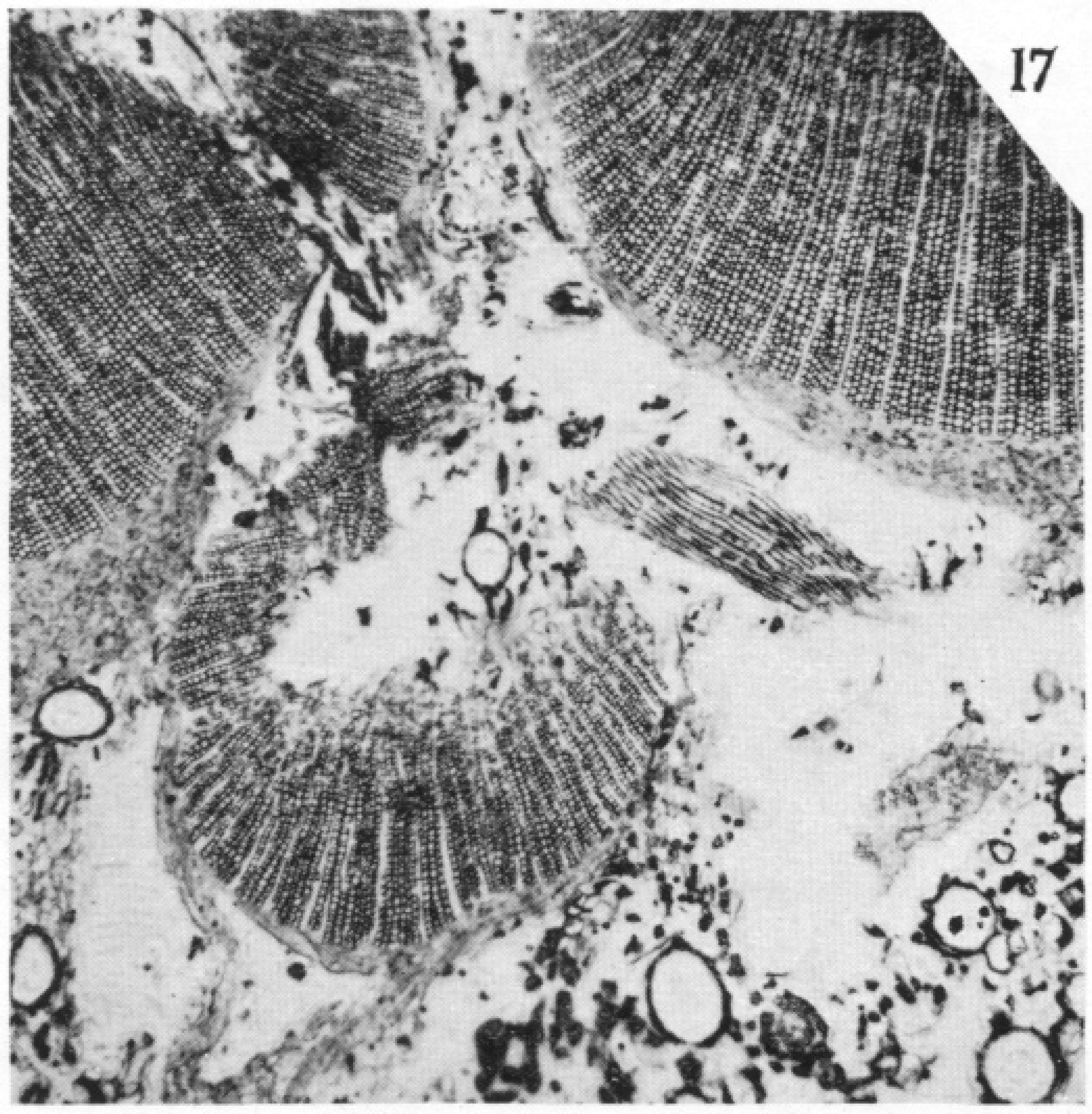
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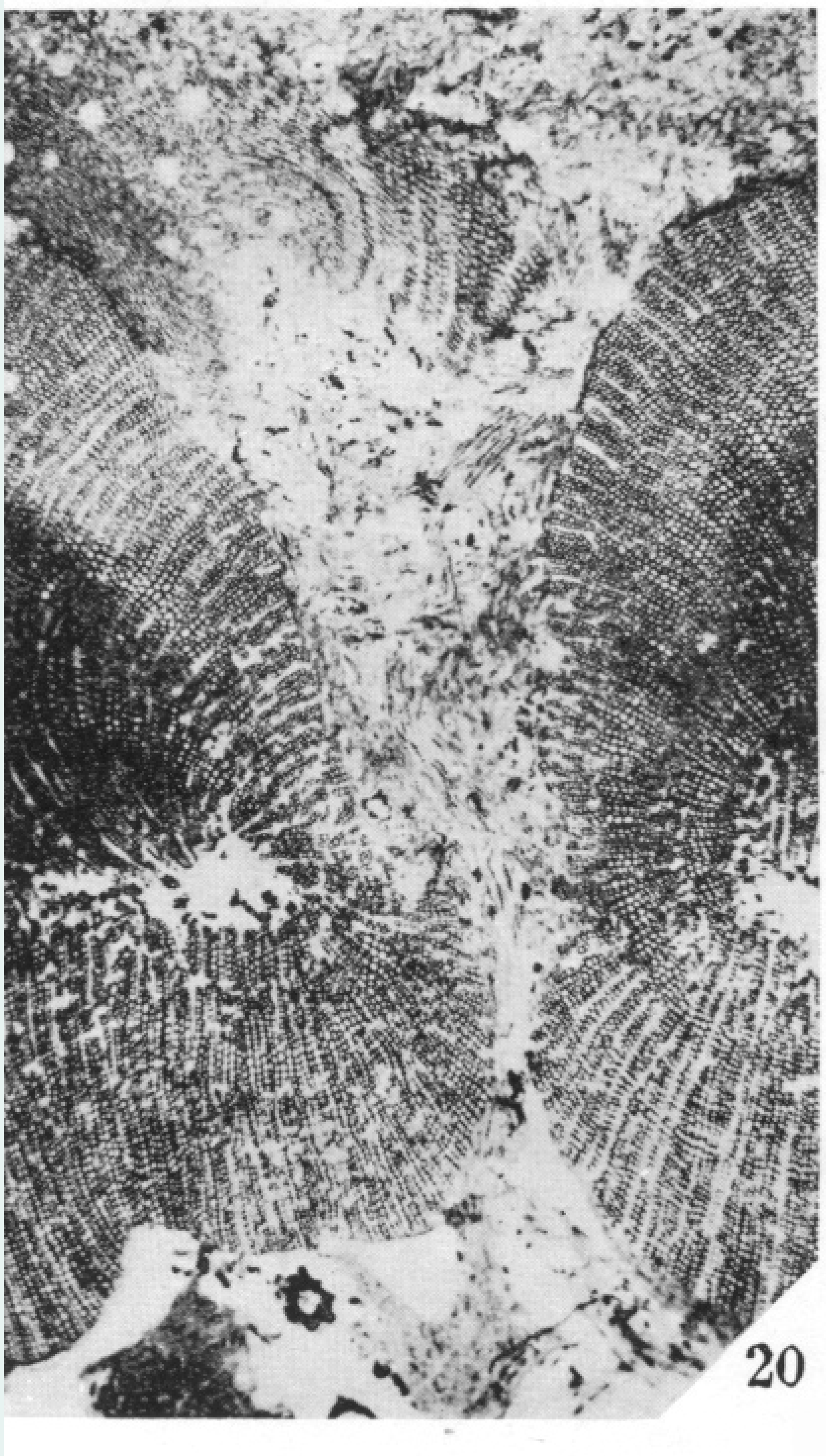
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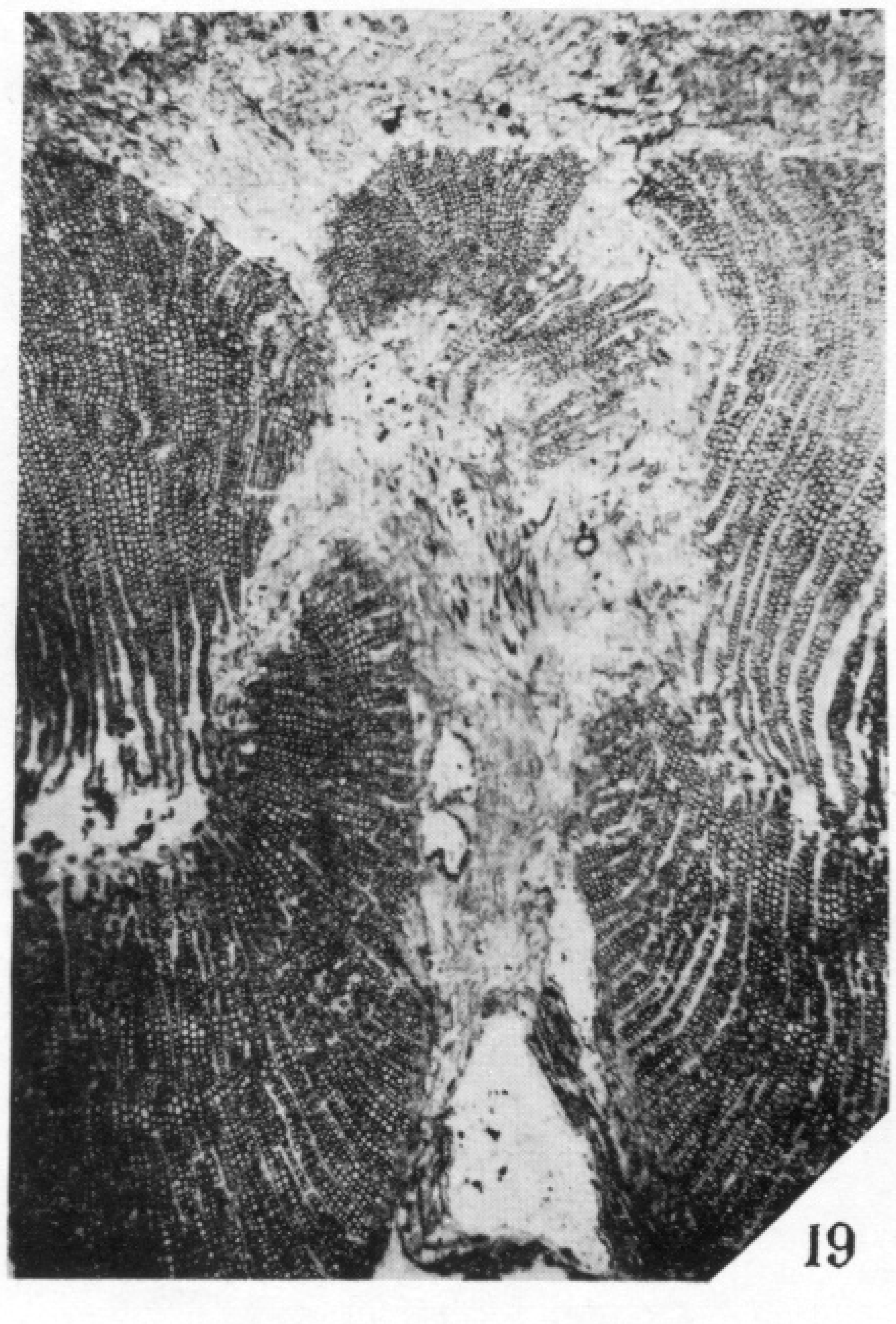
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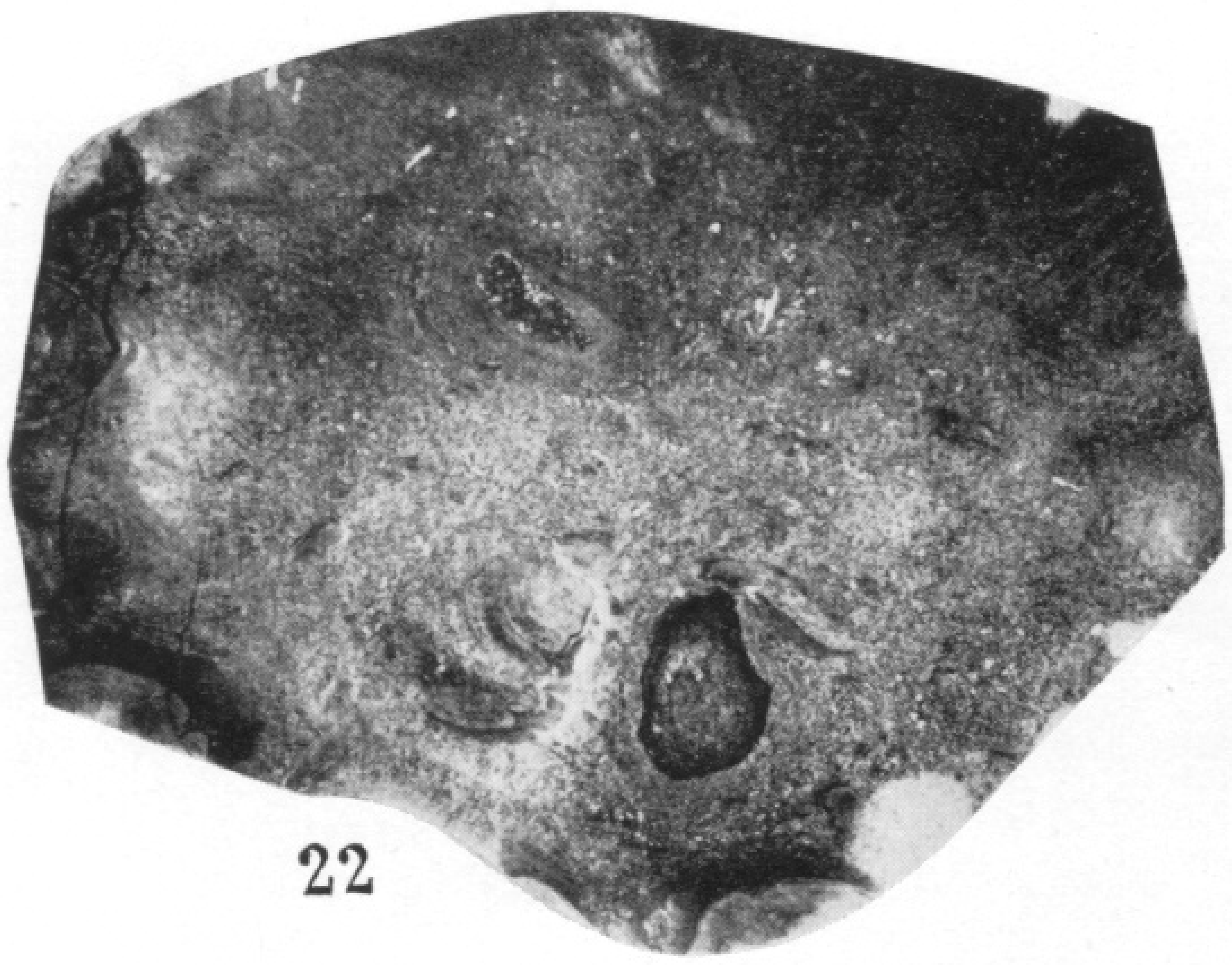
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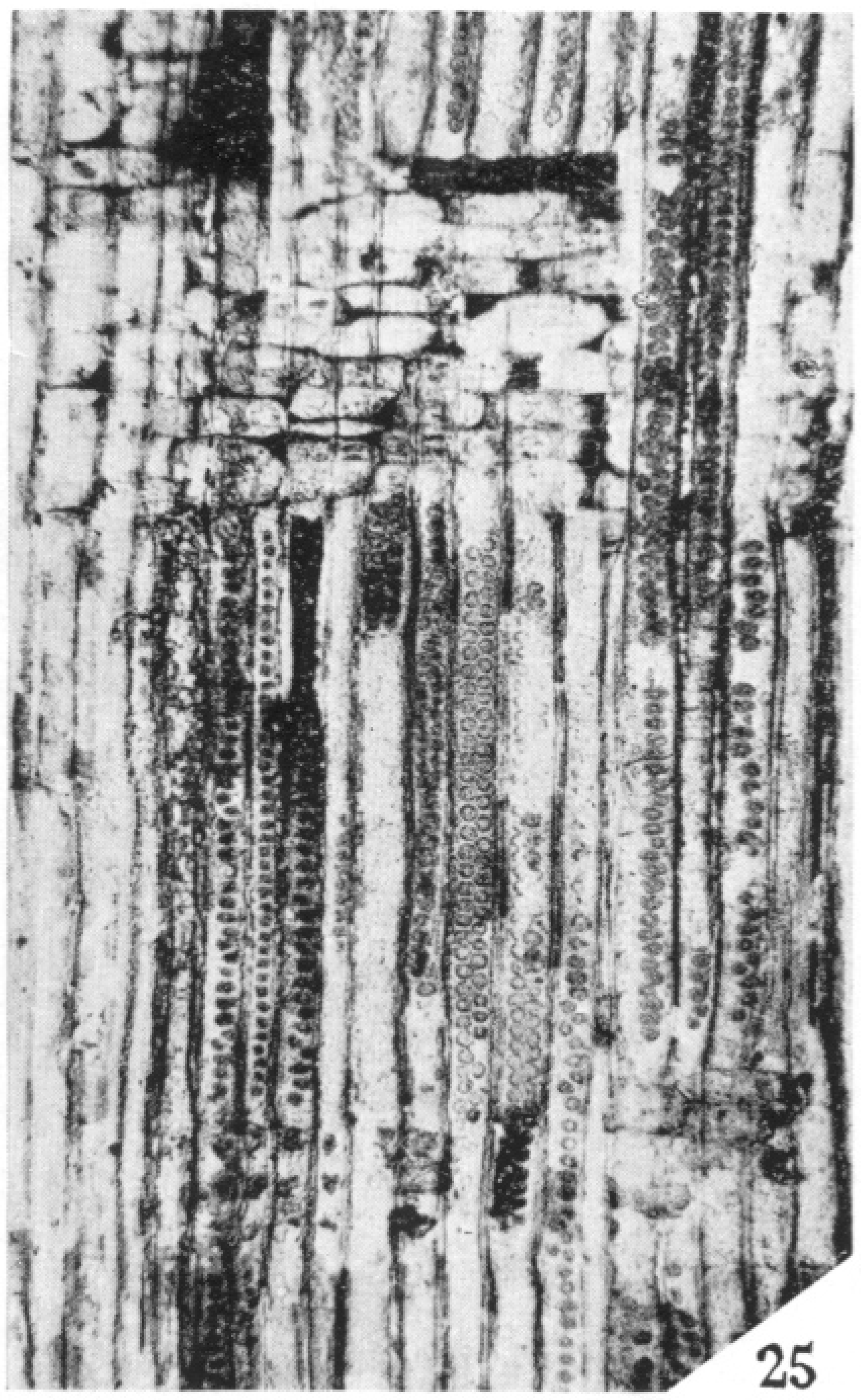
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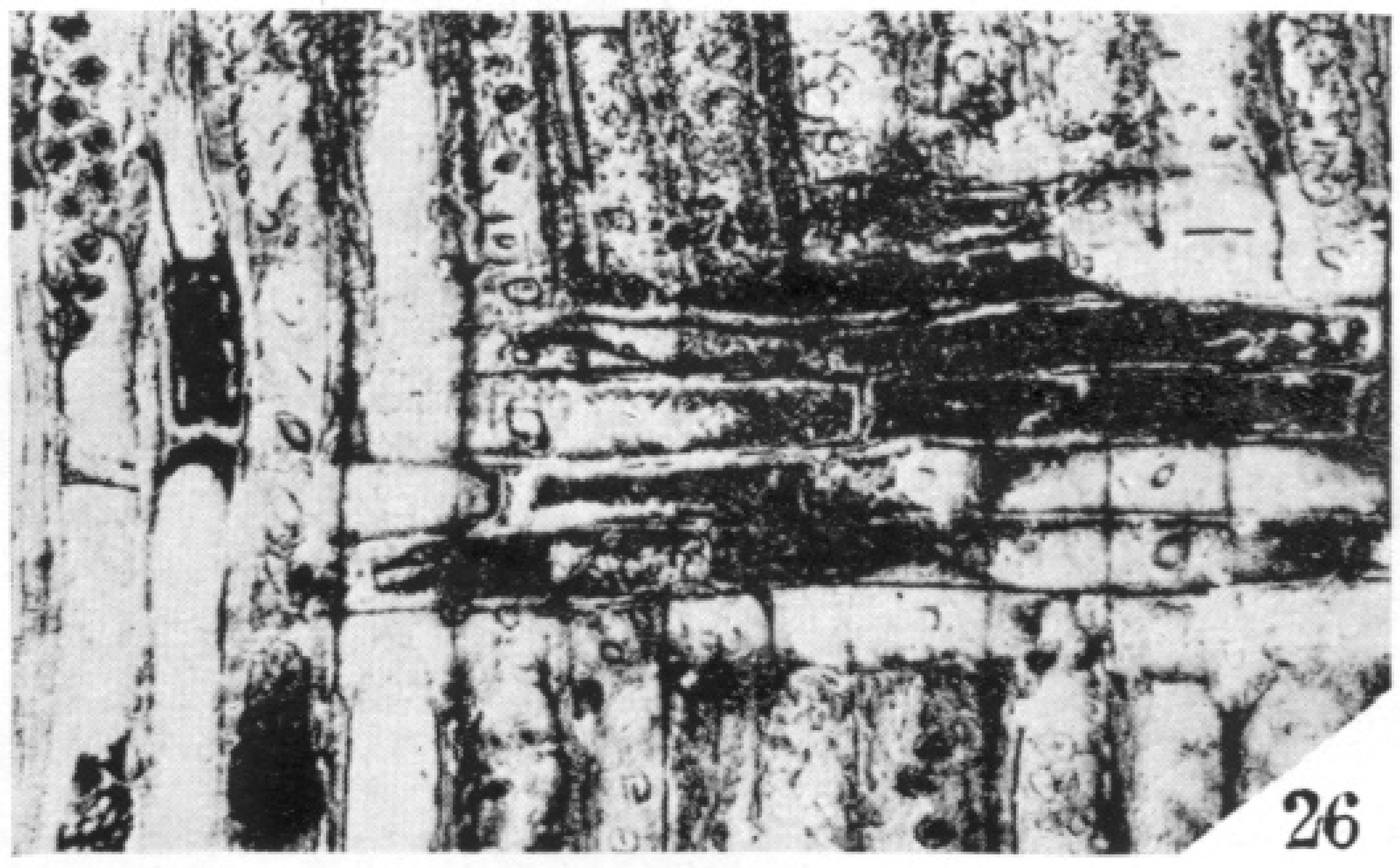
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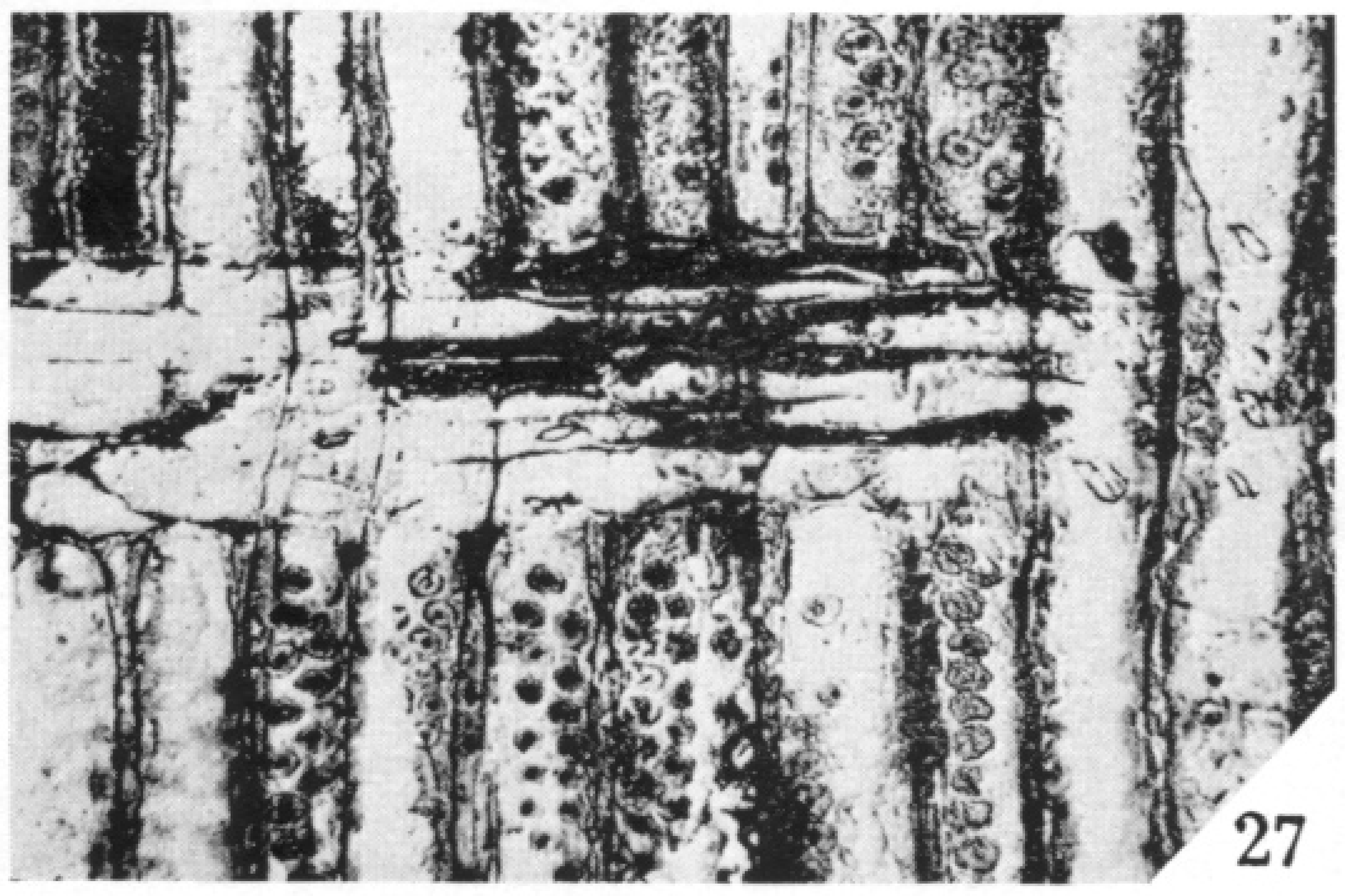
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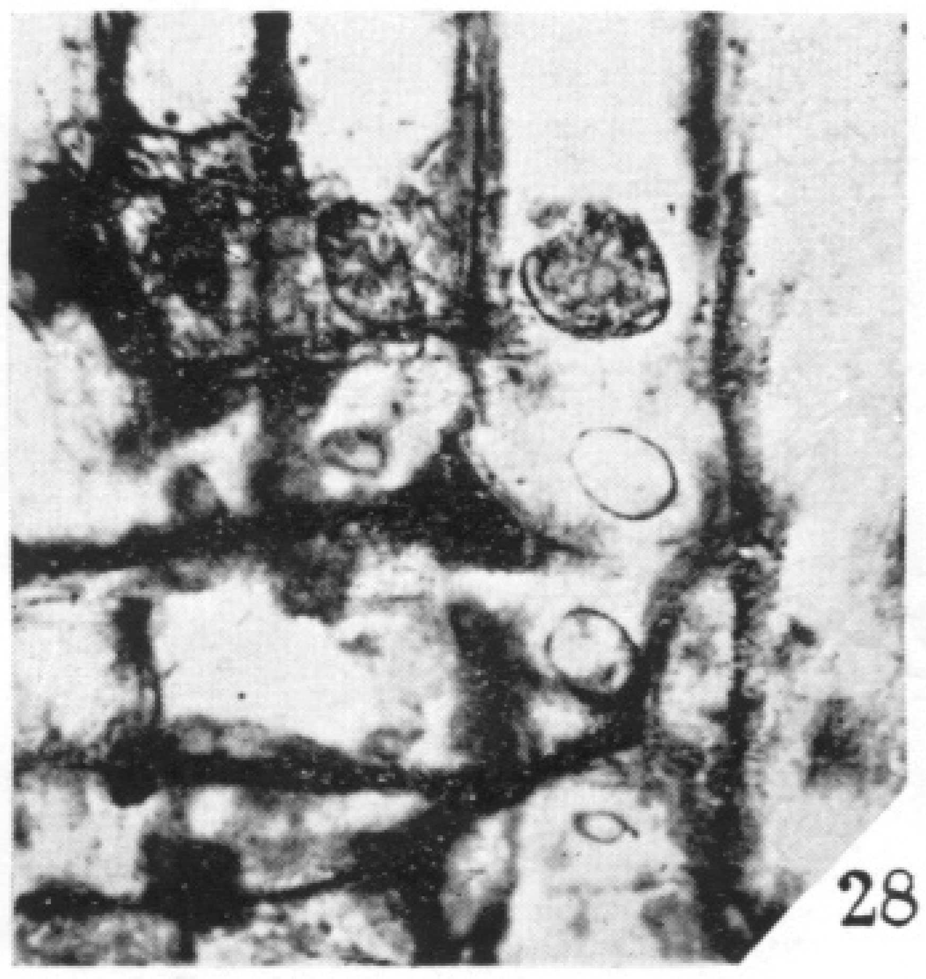
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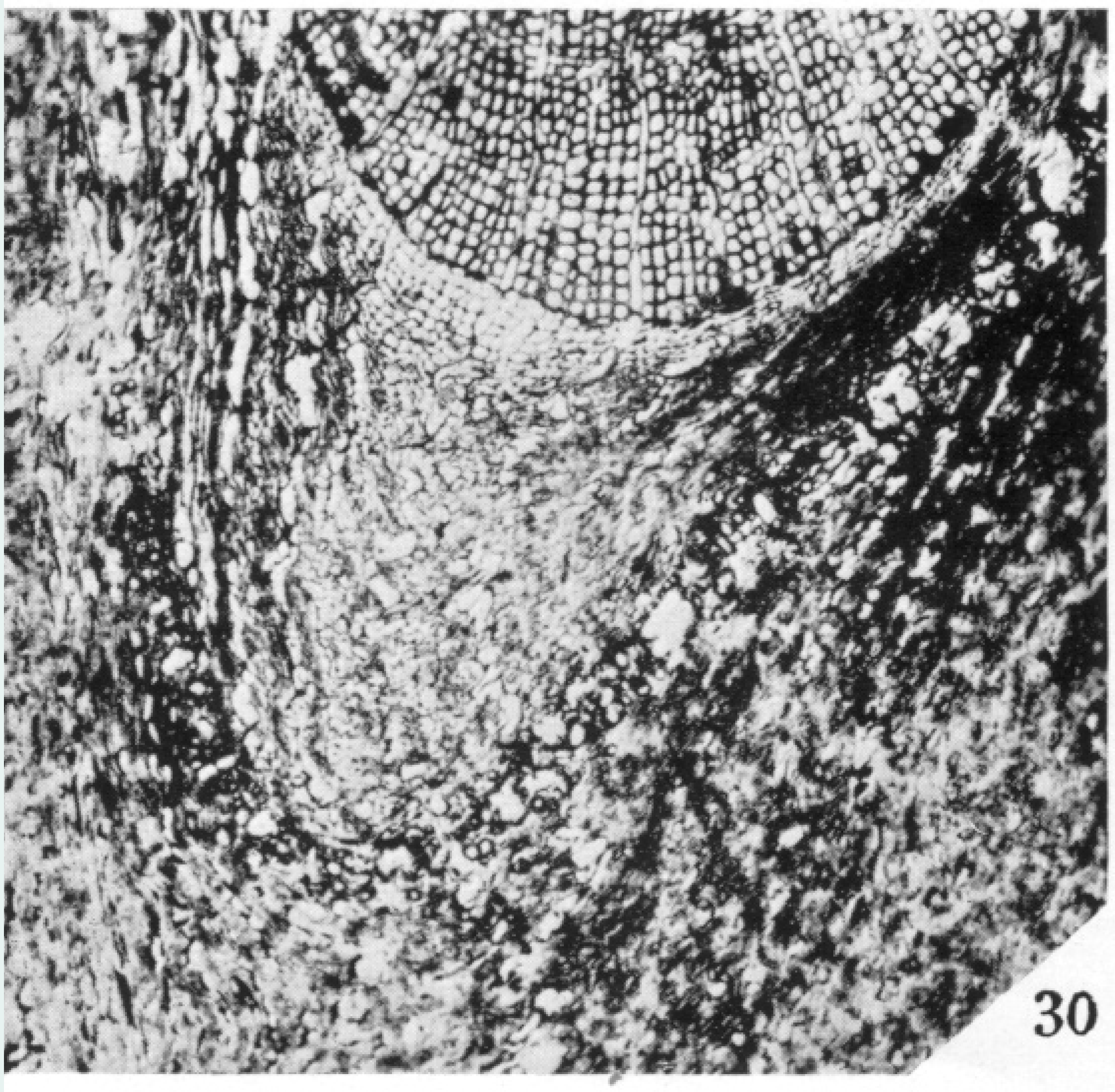
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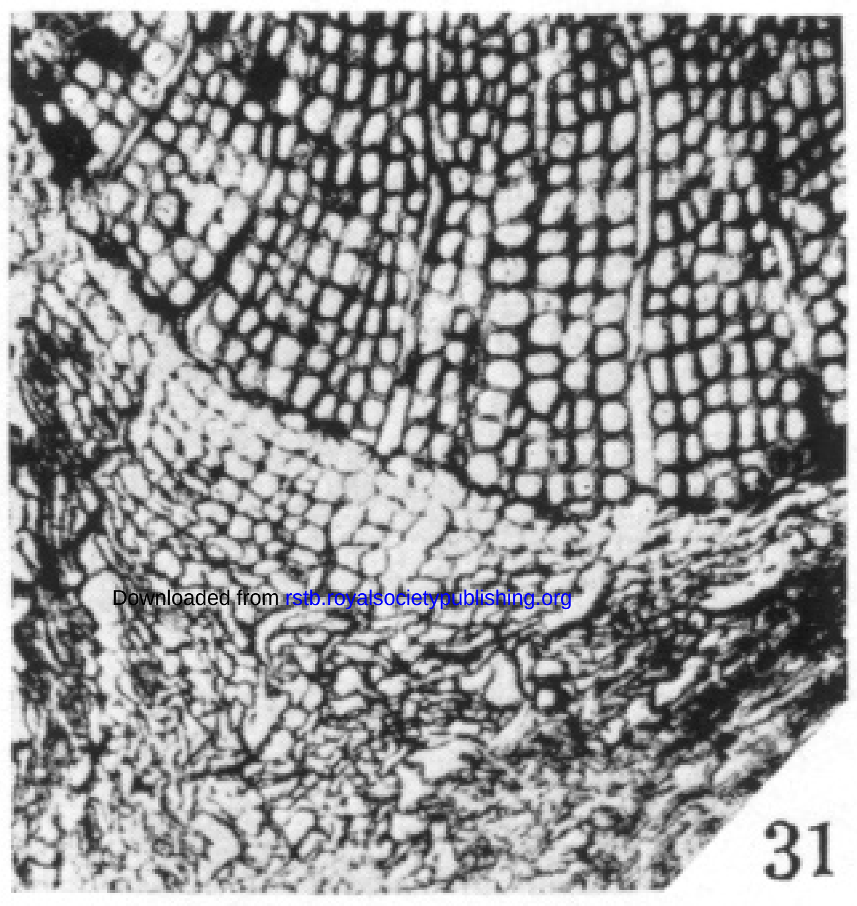
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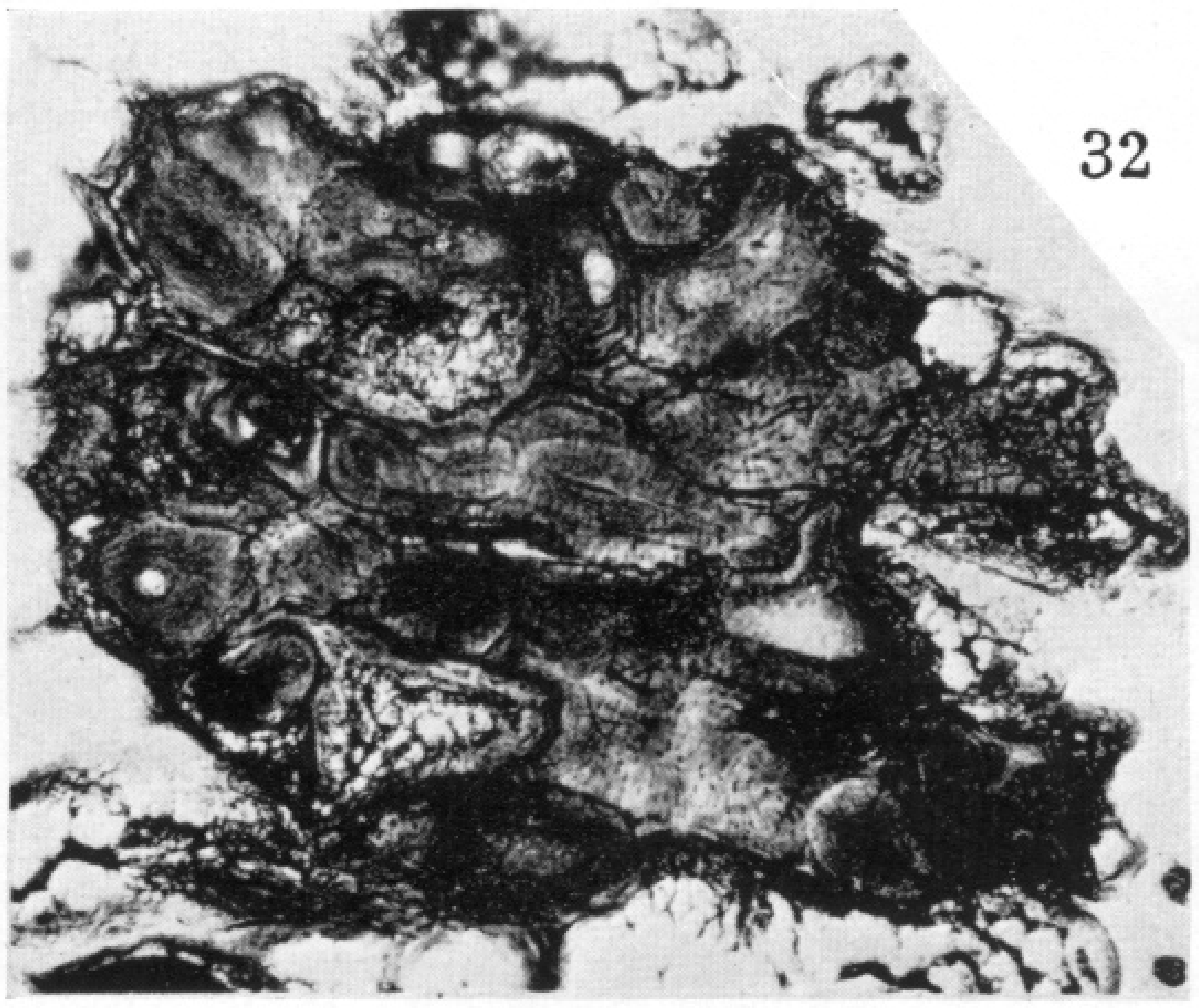
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