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On Rhexoxylon, Bancroft-A Triassic Genus of Plants Exhibiting a Liane-Type of Vascular Organisation

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IV—On *Rhexoxylon*, Bancroft—a Triassic Genus of Plants exhibiting a Liane-Type of Vascular Organisation.*

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Communicated by Prof. A. C. SEWARD, *F.R.S.*

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(PLATES 5 AND 6.)

PART I.—INTRODUCTORY.

In 1913 Dr. BANCROFT instituted the generic name *Rhexoxylon* for a portion of a petrified stem sent by Dr. ROGERS, Director of the Geological Survey of South Africa, to Prof. SEWARD for investigation. The specimen was handed over to Dr. BANCROFT, who, in a communication to the Linnean Society of London,† gave a full account of its anatomy. *Rhexoxylon*, as represented by the type-specimen, may be briefly described as follows:—

The fragment of stem exhibits "parts of two more or less concentric series of vascular structures surrounding a large pith and embedded in a parenchymatous ground-mass," which contains sclerotic nests and small vascular strands. The pith, in addition to sclerotic nests and small vascular strands, contains other structures, which are most probably of an anomalous nature. There is an inner ring or series of vascular structures, which were called, for convenience in description, "steles"; each consists of two portions of secondary wood, one centrifugal and the other centripetal, separated by a narrow zone of obliterated cells. The "steles" branch and rarely anastomose. Traces were described separating from the sides of the centripetal portions of the "steles" and taking a centrifugal course. Outside and opposite each member of this inner series is a mass of centrifugally-developed secondary wood, on the inner margin of which are numerous small protoxylem groups. The tracheids have bordered pits, arranged typically in two alternating series; the pits are flattened and in contact. The medullary rays are uniseriate. Tissue external to the xylem was described as phloem.

The genus was placed in the *Medulloseae* by Dr. BANCROFT on account of the resemblance, in the apparent polystelic nature of the stem, to many members of that group. It should be noticed, however, that Dr. BANCROFT describes the occurrence of Coniferous secondary wood in conjunction with the Medullosean arrangement of

* A preliminary account of this work was given by the writer to Section K, British Association, Hull, 1922.

† 'Trans. Linn. Soc. Lond.,' 2nd series, Bot., vol. 8, Part II (1913).

"steles" as a feature of particular interest. Another distinction, evident on examination of the type-specimen, is that in *Rhexoxylon* the outer masses of entirely centrifugal wood are always opposite the members of the inner series; while in the *Medulloseae* the members of one series may alternate with those of another series, lying either internally or externally to them.

By the discovery of several less incomplete and better preserved specimens in beds of known horizon it has been possible to extend our knowledge of this interesting plant genus, at least as far as concerns the structure of the stem and its geological age. It is found that the specimens from these sources can be divided into three sets, each of which have characteristic features by which they may be distinguished from the others.

In a recent paper by Prof. SEWARD and Mr. HOLTTUM* an account is given of a collection of fossil plants from Rhodesia. This collection, which included several stems (one of which reached a diameter of 25 cm.), had been submitted to the senior author for description. The stems were recognised as specimens of *Rhexoxylon* and were reserved for more complete treatment in a subsequent communication. In the brief description given, the authors mention the resemblance these stems bear in the distribution of their woody tissue to lianes found growing at the present day. These Rhodesian specimens are apparently of one type and belong to the species *Rhexoxylon africanum*, BANCROFT. They will be described in the second set, B.

While engaged in investigating this material, which was very kindly entrusted to me for description by Prof. SEWARD, I had the opportunity of showing some of the preparations to Dr. KIDSTON, who generously suggested that I should undertake the investigation of material of a somewhat similar type which had been sent to him by Dr. DU TOIT, of the Irrigation Department, Pretoria.

As there is no doubt about the horizon of the beds in which Dr. DU TOIT's specimens were found, they afford important evidence of the geological age of *Rhexoxylon*. One of the specimens from this source belongs to *R. africanum*, BANCR., while the rest are assigned to a new species, *R. tetrapteridoides*, and will be described in the first set, A. A fragmentary specimen, undoubtedly a part of a *Rhexoxylon* axis, was found among some coniferous woods in the Botany School collection at Cambridge. These woods, from the Molteno beds at Dordrecht, Cape Province, South Africa, were sent to Prof. SEWARD by Dr. ROGERS.

The third set described consists of a single specimen, originally described by Prof. SEWARD in 1914, and named by him *Antarcticoxylon priestleyi*. This stem may now be placed, with considerable certainty, in the genus *Rhexoxylon*. It is a specimen of great interest, as it was found on a moraine on the Priestley Glacier on the journey of the northern party of Capt. SCOTT's second expedition. The sandstone boulder in which it was found was probably derived from the upper portion

* SEWARD and HOLTTUM (1921).

of the Beacon Sandstone Series, a series of considerable thickness and including strata belonging to more than one geological period.

The division of the specimens into three sets is determined by certain distinctive features, shown in the arrangement and number of the "steles" and in the relative dimensions of the stems. The three groups may be briefly summarised as follows :—

A. *Rhexoxylon tetrapteridoides*, sp. nov.—Specimens A 1, A 2, ? A 3.
Smaller stems than *R. africanum*, with a simpler system of "steles."

B. *Rhexoxylon africanum*, BANCROFT.—Specimens B 1, B 2.
Larger stems, with a more complex system of "steles."

C. *Rhexoxylon priestleyi* (SEWARD).—Specimen C 1.
A small stem with an almost unbroken ring of outer centrifugal wood. The inner series probably not so well developed or wanting. (The preservation is bad in the central portion of the type specimen.)

The localities and stratigraphical positions of the specimens, as far as is known, are given in Table I, which shows the subdivisions of the Karroo formation, while the geological sketch-map, fig. I, shows the position of some of the localities.

Table I.

Horizon.	Specimen.	Species.	Locality.
		AFRICA, CAPE PROVINCE AND NATAL.	
Stormberg Series—			
Drakensberg Volcanics . . .			
Cave Sandstone			
Red Beds	B 3	*R. africanum*	Lady Grey, Aliwal (Cape).
Molteno Beds	A 1	*R. tetrapteridoides* . . .	Ipolela (Natal).
. . . .	A 2	*R. tetrapteridoides* . . .	Elliot (Cape).
Beaufort Series—			
Burghersdorp Beds	A 3	*R.* ? . . .	Aliwal (Cape).
Middle Beaufort			
Lower Beaufort			
		AFRICA, SOUTHERN RHODESIA.	
?	B 1	*R. africanum*	Willoughby's Gwelo (Rhodesia).
?	B 2	*R. africanum*	
		ANTARCTICA, S. VICTORIA LAND.	
Beacon Sandstone Series—			
Upper (?) Beacon Sandstone .	C 1	*R. priestleyi*	Priestley Glacier (S. Victoria Land).

Before the different species are described in detail the outstanding features of the genus, based on fuller knowledge derived from a study of the additional material, may be briefly summarised.

It has already been pointed out* that *Rhexoxylon africanum*, BANCROFT, shows a

* SEWARD and HOLTTUM, *loc. cit.*, p. 44 (1921).

close resemblance in the distribution of woody tissue to some modern lianes, and when the fossils are examined histologically the most remarkable similarities to these

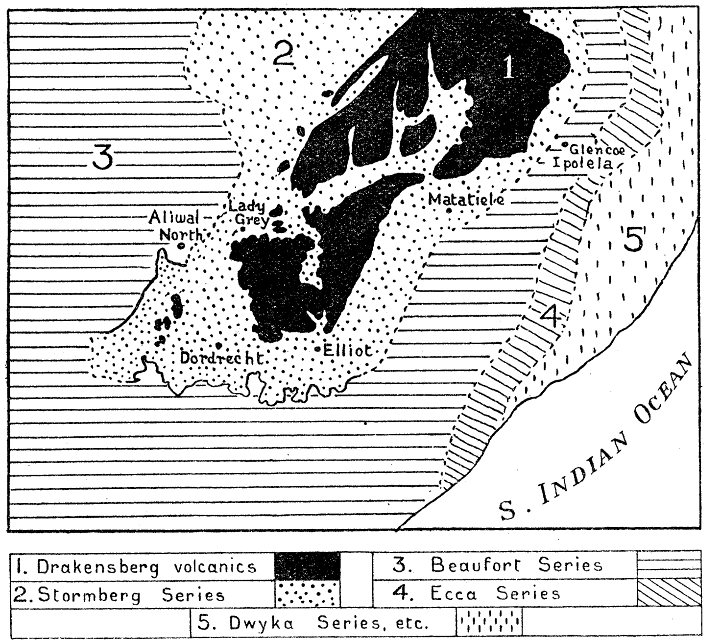


Fig. I.—South African Localities.

plants become evident. It is interesting to recall that some species of *Medullosa** reveal features which, it has been suggested, indicate that the plants had the liane habit of growth. Thus the "Plattenringen" of *Medullosa stellata*, Cotta, have been compared† with the external rings of wood formed by cambial activity in the pericycle of the recent liane *Serjania*, sp. It is noteworthy that the perimedullary "steles" of *Rhexoxylon* resemble these pericyclic developments of *Serjania* in an even greater degree. The division of the main mass of secondary wood into narrow sectors by local cessation of cambial activity in the formation of xylem is especially characteristic of lianes (*cf. Tetrapteris guilleminiana*, Juss.).‡ In many specimens of *Rhexoxylon* this is a very characteristic feature (*cf. Tetrapteris*, sp., fig. IV, 5, with *Rhexoxylon*, fig. II, 3).

Another most interesting phenomenon is that caused by a parenchymatisation and disruption of the secondary wood with the formation of new zones of cambial activity. *Banisteria hassleriana*, Chod.,§ is an example of a recent plant in which the secondary wood is split up tangentially by dilatation of the living parenchyma in the wood and also radially by dilatation of the cells of the secondary medullary rays. It

* *E.g.*, *M. stellata* and *M. leuckarti*, Seward, vol. 3, p. 87 (1917).

† Göppert and Stenzel, p. 8 (1881).

‡ Schenk, Fig. 62, Taf. VI (1893).

§ Chodat, p. 181, and Figs. 154–156 (1917).

appears that this meristematic activity may be succeeded by the differentiation of bast within these tissues.

As we shall see in *Rhexoxylon* the secondary xylem in the outer centrifugal sectors, or segments which correspond to Dr. BANCROFT'S "partial steles," is split tangentially along lines coinciding approximately with the first-formed wider elements in the growth-zones. It is possible that this splitting is due to a resuscitation of meristematic activity in living cells (*e.g.*, wood parenchyma) which lie somewhere in the region near the boundary between the zones of the larger and smaller tracheids. The gap between the masses of disrupted xylem is found to be filled with parenchymatous cells among which occur small fan-shaped developments of xylem, obviously produced by "tertiary,"* meristems in the parenchymatous tissue. Radial splitting also occurs, and is probably initiated by meristematic activity of the cells in the secondary medullary rays. Thus, instead of bast alone being formed by renewed meristematic growth, as in some modern lianes, in *Rhexoxylon* we find the production of new vascular tissue containing xylem and a tissue probably analogous to phloem, represented by crushed cells in the fossils. These small vascular developments in the parenchymatous gaps between the disrupted xylem are especially characteristic of *Rhexoxylon*. The changes produced by this disruption are considerable, and, as will be seen later, modify the distribution of the tissue in the axis so that, as in many lianes, the primary arrangement is lost. As there are no specimens of very young axes one cannot obtain any satisfactory evidence for supposing that the outer wood formed a complete ring at one stage in the development of the axis, and that by interrupted cambial development and subsequent disruption the system of sectors was formed. In many of the African examples, and in *Rhexoxylon priestleyi*, the flanks of the main outer portions of secondary xylem are fringed with small cuneate developments of xylem produced in the same manner as those of *Bignonia*, sp.,† by growth at the sides of the main wedge due to relict cambial layers. It is assumed that these fossil plant axes are stems (some, as we shall see, are straight and measure 10 feet in length). That they are aerial stems is not quite so certain, for dilatation and disruption are not always characteristic of aerial stems; thus, in *Dicella nucifera*, CHOD.,‡ the aerial portion shows none of these peculiarities which are restricted to the underground portions, and are therefore probably correlated with the formation of a parenchymatous storage-tissue.

* WORSDELL, p. 610 (1896).

† SCHENK, *loc. cit.*, fig. 161 (1893).

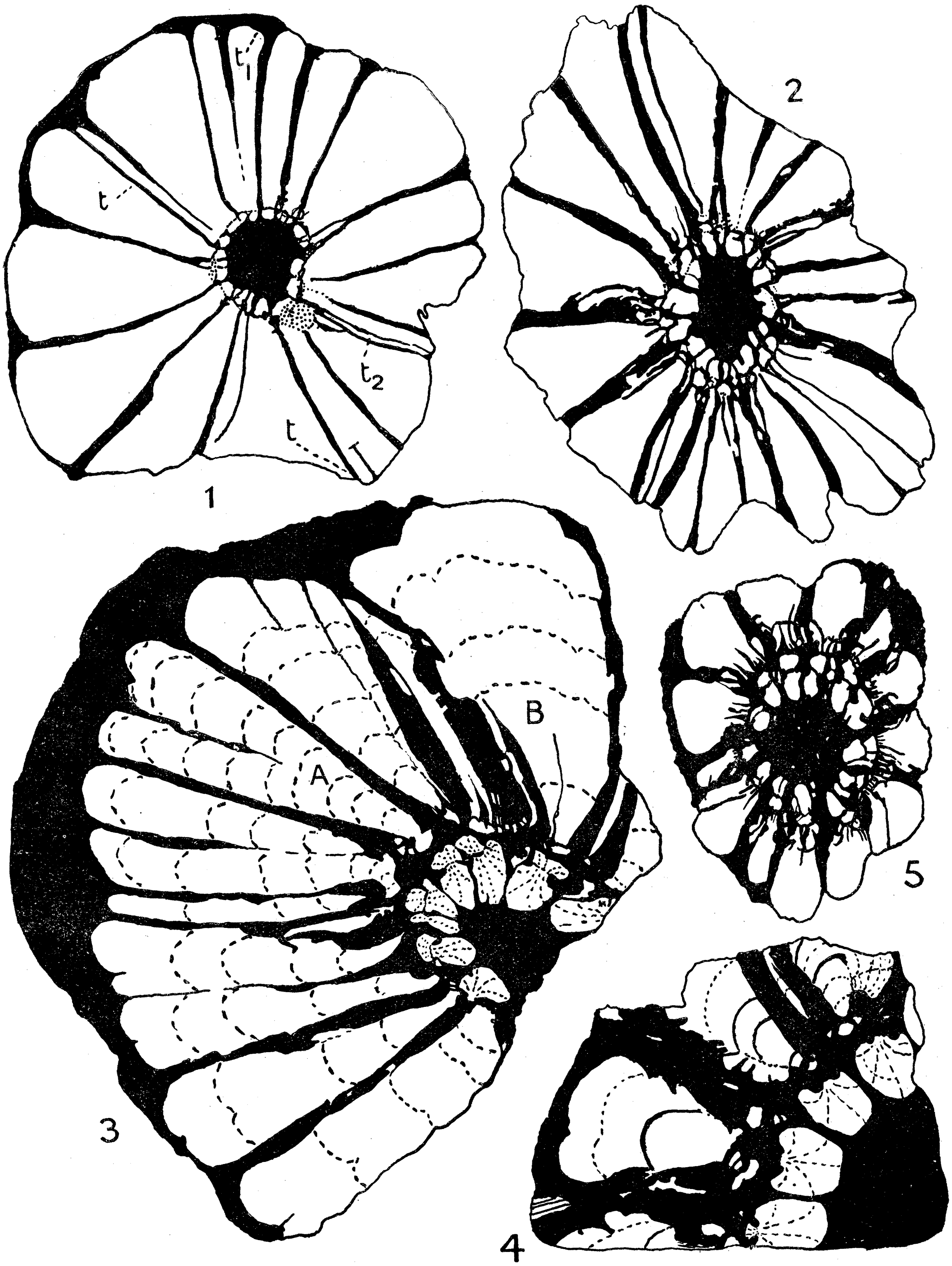
‡ CHODAT, *loc. cit.*, p. 174 (1917).

PART II.—DESCRIPTION OF THE SPECIMENS.

Set A.—Specimen A 1. *Rhexoxylon tetrapteridoides*, sp. nov.

This specimen was discovered by Dr. A. L. DU TOIT in the Molteno Beds (see Table I) at Glencoe, Umkomazaan Valley, Ipolela County, Natal (fig. I). It consisted apparently of a considerable length of axis as samples were taken from different parts of the stem to show the variation in the structure (fig. II, 1, 2, 3, 4, 5, and Plate 5, 1). It is impossible, on account of the incompleteness of the material provided, to ascertain the position and sequence of emission of leaf-traces, or the relative positions of any appendages to the axis. The samples give indications, however, that the plan of the conducting tissue, and probably the thickness of the axis, varied very considerably at different levels. In three of the samples (fig. II, 1, 2 and 5), the entire central part of the stem is represented, and the greater part of the main wedges of secondary wood. Only a very small portion of the tissue external to the secondary wood is exhibited in any of the samples (fig. II, 3, shows more than the rest). The preservation, generally speaking, is not good, but enough is shown to indicate that this outer tissue consisted of parenchymatous cells, some of which probably had a secretory function, many sclerotic nests, and, in one or two places, small collateral vascular strands, the orientation of which is quite irregular. At fig. II, 1, t_2, a strand is seen passing out from one of the broad rays of loosely-packed tissue between the main masses of secondary wood and taking a tangential course to the side; it is possibly the vascular supply to some appendage. In Sample 6, Plate 5, 1, there are several vascular strands in the external tissue at *a* (see Plate 5, 1, 2), and in the broad rays between the main masses of secondary wood (*y*, Plate 5, 1). In the small strand at *a* (Plate 5, 1), the tracheids are seen to have a scalariform, or spiral thickening (Plate 5, 2), but this, as we shall see later, is no criterion of primary tissue, as in *Rhexoxylon priestleyi* similar tracheids occur in tissues which are, without doubt, entirely secondary. A larger strand is seen more than half-way up the gap of parenchymatous tissue at *b* (Plate 5, 1). In a similar strand shown in another section from the same sample, secondary wood is present, for muriform medullary rays can be seen where the strand is cut tangentially. Near the outermost limits of the secondary wood the external tissues are crushed and unrecognisable. Occasionally, these crushed tissues show indications of radial arrangement which suggest that they have been formed by the cambium which produced the secondary wood.

The centre of the stem is occupied by a relatively large pith (8 mm. by 12 mm. in Sample 1, fig. II, 1), consisting of a parenchymatous ground tissue with numerous sclerotic nests, secretory ducts, and a few irregularly scattered vascular strands similar in detail to the small strands found in the external tissue. When seen in transverse section the xylem in these strands is in the form of a sector of a



TEXT-FIG. II.—*R. tetrapteridoides*, sp. nov.
1 to 5. Diagrams of Samples 1 to 5 of Specimen A 1. (Xylem left white. Nat. size.)

circle. The first formed elements are situated at the apex and crushed tissue, no doubt representing phloem, is seen outside the curved boundary of the xylem sector. These strands are often cut lengthwise in a transverse section of the stem, so that they must have followed a sinuous course in the pith. There is no indication of any correlation between the strands and the canals which are found in the pith. The canals may be short and are probably of the nature of reservoirs rather than ducts. At the part of the axis from which Sample 4 (fig. II, 4) was taken, the diameter of the pith is greater than in Sample 1, for example. As we shall see later, this may be explained as a result of cell division and secondary growth in the medullary and perimedullary region.

The Secondary Xylem.

The main masses of secondary xylem in transverse section, fig. II, 1, 2, 3, 4, 5, appear as sectors, with truncated apices, arranged in a circle round the axis. They vary very much in size and shape in the different samples. Some are lobed so deeply that they appear as separate sectors. This lobing, seen clearly in various stages in Sample 3 (fig. II, 3), originated as an interruption in the cambium at an earlier stage in the development of the sector, as can be proved by examining the contours of the growth rings (fig. II, 3, A, and Plate 5, 1, *c*), at the point at which the interruption occurred. In most cases it appears to have occurred quite early, and in most of the sections it is evident that complete separation at the base of the two lobes has been effected subsequently, and that what were originally lobes of one sector now form the outer portion of what appear distinct sectors. The sectors show frequent irregular splits which, in some cases, start from the inner end of the sector and extend centrifugally (fig. II, 3). There are indications of local cambial activity on the flanks of the lobes where small irregular fan-shaped developments of xylem are seen in some of the sections (fig. II, 4). The tangential pressure due to this growth might be sufficient to account for the splitting apart of the lobes.

There are sclerotic nests and parenchymatous tissue and other crushed unrecognisable elements in the bays between the lobes, also where the bay has been enlarged by disruption. The xylem of the sectors has been developed from a line of small separate protoxylem initials seen at the smaller truncated apex of the sector, and presenting much the same appearance as the protoxylems of the Permo-Carboniferous species *Dadoxylon pedroi*, ZEILL.,* or the inner margin of one of the "partial steles" in *Rhexoxylon africanum*, BANCR.,† with which the sectors are certainly homologous. The medullary rays between the strips of tracheids extending radially from the protoxylems have undergone dilatation with the result that sometimes the strips are widely separated by parenchymatous tissue.

* ZEILLER, p. 619 (1895).

† BANCROFT, *loc. cit.*, Plate 11, fig. 2 (1913).

This gives the sector of secondary wood a frayed appearance at its truncated narrow end (fig. II, 5, and fig. III, 6). In Sample 6 (Plate 5, 1) there is in the radial crack at *d* some xylem which has been split into strips and the interspaces filled with parenchymatous tissue (Plate 5, 6). It is interesting to compare this straining of the secondary tissues in *Rhexoxylon* with a similar phenomenon found in the "Dictyoxylon cortex"* of *Lyginopteris*, where the secondary growth of the stem has produced a tangential strain in the parenchymatous cells in the meshes of the fibrous cortical network,† as a result of which they are elongated tangentially.

In fig. II, 4, and Plate 5, 1, tangential cracks can be seen in the main sectors. These coincide, when they are present, with the zones of thinner-walled "spring" elements of the wood. Small strands of xylem (Plate 5, 3, 4, 5) are found here and there in the cracks of Sample 6 (Plate 5, 1), which are elsewhere filled with what is apparently a loose parenchymatous tissue. The first formed elements of these small strands abut directly on the surface of the secondary wood (Plate 5, 4) and the development of the xylem in the strands is either centrifugal or centripetal, depending on whether the strand is next to the wood on the adaxial or to that on the abaxial side of the crack. These strands are of an entirely secondary nature, as will be shown conclusively in the description of one of the other specimens. It seems possible that the tangential cracking is partly influenced by growth stresses in the stem, and that the parenchymatous filling tissue is formed by proliferation of living cells in the wood either of medullary-ray cells or of xylem parenchyma. It is known definitely that the medullary-ray cells do proliferate where dilatation is occurring (*cf.* Plate 5, 8). On the other hand, the cracking may be due to growth pressure exerted by living cells situated in the secondary wood along the line of the split.

The secondary wood consists of radially seriated tracheids with uniseriate medullary rays. It is compact, with well marked growth zones. In this specimen it is not well preserved, but enough can be made out to show that it is of essentially the same character as that of other better preserved specimens to be described later. It will be noticed that tangential splitting occurs at the same level in the three lobes shown in Plate 5, 1. This suggests that the production in the secondary wood by the cambium of the cells through which the tangential cracks tend to pass is influenced by some seasonal factor.

The Perimedullary System.

Surrounding the medullary region is a ring of vascular structures. The greater part of each of these consists of centripetally developed secondary xylem, with or without a smaller centrifugal development in contact with it, on its abaxial side

* Solms-Laubach, 1891, p. 218.

† Williamson and Scott, 1895.

(fig. II, 1–5; fig. III, 6, 7). These masses of xylem have no protoxylems such as are found at the inner extremities of the outer sectors. Their first formed tracheids are smaller than the normal tracheids of the secondary wood.* In possessing these features they resemble the small xylem developments found in the tangential cracks of Sample 6 (Plate 5, 1). The centripetal part is usually separated from the centrifugal part by a gap or definite line of discontinuity, but occasionally they constitute a single, mesarch development (fig. III, 7, A). In addition to this ring of secondary xylem developments there are frequently smaller centripetal developments closely abutting on the protoxylems of the main sectors (fig. III, 6 and 7), but always separated by a gap or discontinuity. There is considerable variation in the size and shape of these perimedullary structures (*e.g.*, fig. III, 7). Their occurrence and development suggest that they are probably the products of some anomalous perimedullary meristem similar to that which is found in some specimens of the carboniferous fossil *Lyginopteris*† or in the recent species *Wilbrandia verticillata*, COGN. (Cucurbitaceæ). It would be a difficult problem to supply a satisfactory explanation of the form and arrangement of the perimedullary developments in terms of stelar groups of a Medullosean vascular system (*cf.* WORSDELL).‡ The shape of the xylem masses in fig. II, 4, is worthy of notice. It will be seen that the initial regions of the perimedullary centripetal developments correspond with the protoxylem regions of the outer sectors. Now, from the shape of the two large outer sectors in the upper half of the fig. II, 4, it is strongly suggested that they were originally lobes of one sector, which has been split right to the base. In order that the two corresponding centripetal developments should have their symmetrical shape, they must have had room to expand, so that in all probability their development did not begin before the separation of the outer sector into two portions.

Specimen A 2.

From the point of view of the physiological anatomy of *Rhexoxylon*, this specimen is the most interesting, as its superior preservation enables one to interpret with greater precision many of the phenomena peculiar to these plants. In transverse section (fig. III, 1, 2) only a portion of the axis is seen. There is a relatively large, well-preserved medullary region, with a considerable number of small vascular strands, secretory ducts (fig. IV, 3), and sclerotic nests, with a ground-tissue of thin-walled parenchyma, with dark inclusions inside the cells (Plate 5, 7). At one point a strand of vascular tissue, cut lengthwise, is seen passing from the medullary

* In some lianes (e.g., *Bignonia unguis*) the vessels in the adventitious vascular strands are stated to be of smaller size than those in the normal secondary wood (*cf.* HOVELACQUE, p. 84 (1888)).

† WILLIAMSON and SCOTT, 1895.

‡ WORSDELL, 1896.

region between the perimedullary secondary xylem developments, VII and VIII (fig. III, 2).

Portions of representatives of the outer sectors of secondary centrifugal wood, described in the other specimens, are seen at the periphery of the block. They are much broken up by dilatation, particularly at their inner extremities, where they are split up into strips, and present a ragged appearance when examined under slight magnification. They are also winged laterally with cuneate developments of xylem (fig. III, 1, 2, *e.g.*, the outer sectors exterior to VII and VIII in 1). The tissue between the xylem masses is not well preserved. Surrounding the growing faces of the xylem there is a considerable amount of crushed tissue, which doubtless represents the remains of meristematic tissue and of the tissue exterior to the cambium, but the preservation is not good enough to reveal its structure. In addition to this there are frequent indications that there was a ground-tissue of much the same character as that which is found in the medullary region, only it is impossible to say whether it was primary or secondary.

There are well developed masses of centripetal xylem (I to XIII, fig. III, 1 and 2) in the perimedullary zone which show growth zones, and one (fig. III, 1 and 2, III) shows in the different sections the course of a disruptive action, by which a small cylindrical piece is cut out near the middle. The preservation is fairly good at this point, and the dilatation parenchyma shows up clearly. In sections of a portion near the periphery of the block (external to IV) the dilatation parenchyma is seen dividing the tracheids into small groups* (Plate 5, 8). One finds groups of sclerotic cells differentiated by secondary thickening from cells in the dilatation parenchyma. In a longitudinal section of some xylem in a similar condition (Plate 5, 9) one of these groups of sclerotic cells (fig. IV, 4) was seen in the parenchyma between the disrupted tracheids.

Another interesting feature is the presence in the lumen of the tracheid of structures, indicating that the fully differentiated tracheids were not dead, empty cells, but contained organic matter, or probably living cells. The tracheids shown in Plate 5, 9, *t*, contain structures which resemble in thickness, as well as in other respects, the walls of the parenchyma outside, and the tracheids thus appear irregularly septate. The structure seen in several sections is suggestive of the occurrence inside the tracheids of separate cells (tyloses?), each with a complete wall of its own. The presence of these living inclusions in the tracheids seems to be correlated with active dilatation action. The manner of origin of these cells inside the tracheids is difficult to imagine, but it is conceivable that they arose by secondary septation of the tracheid before the loss of its living contents. It is also possible that they may have grown into the lumen of the tracheid, either through a pore, as in normal tylosis of coniferous wood,† or through a broken end of a tracheid

* *Cf.* CHODAT, 1917, *Banisteria hassleriana*, p. 189, fig. 156.

† CHRYSLER, 'Tyloses of Tracheids in Conifers,' etc., 1908; also GOTHAN, 1910.

ruptured by dilatation. In addition, these cross walls seem to have been formed subsequently to the normal secondary cellulose thickening of the tracheid, and in some places the vertical wall of the inner cell (tylose) can be seen distinct from that of the tracheid in longitudinal section. The very close resemblance of the *Rhexoxylon* tracheids, with their included and apparently once living cells, to tracheids with tyloses in certain fossil conifers tends to confirm this hypothesis.

In one or two places, where the amount of dilatation parenchyma is considerable, there is a definite zone of meristematic cells which resembles a cambial layer. Between the two masses of secondary xylem (I and II, fig. III, 2) such a meristematic zone has arisen (Plate 6, 10). This has produced parenchymatous cells* which, on examination, in both longitudinal and transverse section, are seen to be tabular in shape and regularly seriated (Zone *a*, Plate II, 10). Some of these have dark inclusions, while in others the lumen is clear. Further out from this cambial layer are sclerotic nests (Zone *b*, Plate 6, 10), probably formed by secondary thickening of some of the parenchymatous cells.

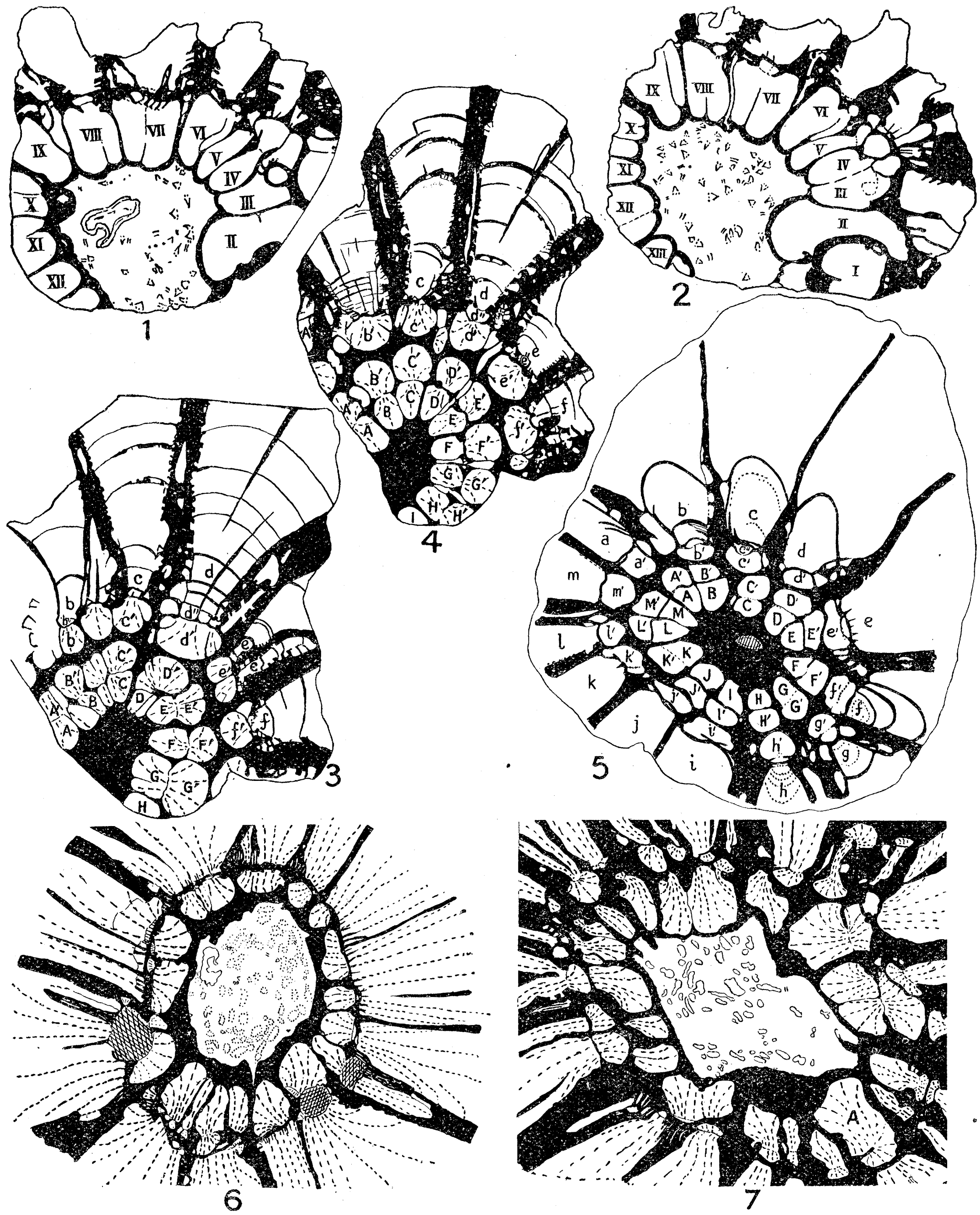
If this parenchymatisation were not so common—it occurs in many of the xylem masses—one would perhaps be inclined to regard it as a traumatic phenomenon. Considering, however, the anatomical similarity shown by the stem of *Rhexoxylon* to lianes, one is justified in assuming that here we have the formation of tissues from anomalous growth processes affording another example of the liane type of physiological anatomy in an earlier, distinct phylum of plants.

Another interesting feature about this axis is that in the medullary region in some of the transverse sections prepared (fig. III, 1), all of which were cut from a portion not more than 2 cm. long, there appears a ring consisting of regularly arranged cells similar in appearance to the tissue described as "periderm" in *Rhexoxylon africanum*, BANC.† Inside this is another tissue containing sclerotic nests, parenchyma and canals, differing only from the outside tissue in having no vascular strands. This peculiar structure does not appear in all sections (*e.g.*, fig. III, 2); it is most probably of no morphological significance, and has arisen in response to certain physiological conditions attendant on the position of a large mass of living cells at the centre of a large axis. Immediately outside this ring of cells (*e.g.*, in fig. III, 1) there is secondary tissue, similar to that already described, between the perimedullary xylem masses I and II (fig. III, 2), which consists of sclerotic nests and regularly seriated parenchymatous cells. It seems rather doubtful whether or not the ring itself consists of a periderm tissue; it might be of the nature of secondary parenchyma, or even a zone of actively dividing cells.

Although the preservation is poor, and cellular structure is only shown in a few places, there is a certain amount of evidence furnished by longitudinal sections as to the nature of the secondary wood. The medullary rays are uniseriate, and up to

* *Cf.* WILLIAMSON and SCOTT, 'Secondary parenchyma in *Lyginopteris*,' p. 722 (1895).

† BANCROFT, p. 89, Plate 11, figs. 7, 8 (1913).



TEXT-FIG. III.

(Xylem left white; crushed and unrecognisable tissues black.)

1, 2. Cross-sections of specimen A 2. I–XIII. Perimedullary developments, with corresponding portions of normal secondary xylem sectors above. Medullary region left white, and strands indicated by V or II when cut transversely or longitudinally respectively. The point of the V is where tracheid formation was begun. Dots represent crushed tissue (phloem) accompanying strands. Approx. nat. size.

3, 4. Diagrams of cross-sections of specimen B 1. The series of xylem sectors and perimedullary developments are designated by letters, so that centripetally developed portions of inner series of perimedullary groups are A, B, C, etc.; centrifugal portions A′, B′, C′, etc. Correspondingly main outer sectors are labelled *a*, *b*, *c*, etc.; and developments opposite them *a*′, *b*′, *c*′, etc. In outer series there are often additional centripetal portions labelled *b*″, *d*″, etc. About $\frac{1}{4}$ nat. size.

5. Diagram of cross-section of B 3. *a*, *b*, *c*, etc., main sectors, many of which show tangential cracks. A′, B,′ C′, etc., and *a*″, *b*″, *c*″, etc., centripetal developments. "Periderm" ring in medulla. $\frac{2}{3}$ nat. size.

6 and 7. Enlarged diagrams of perimedullary region of samples 1 and 2, specimen A 1 (Text-fig. II, 1, 2). The larger sclerotic nests are indicated in the medulla. 2·5 times nat. size.

six or seven cells high. There appears to be one large simple pit in the "field."* The pits on the radial walls of the tracheids are usually biseriate, alternate and compressed, and sometimes uniseriate.

Diagnosis: Rhexoxylon tetrapteridoides, sp. nov.

Fragments of stems from the Molteno Beds of the Stormberg Series, South Africa.

They are portions of axes smaller than *R. africanum*, BANCROFT, and the perimedullary system of secondary xylem masses is less developed. Sometimes there is only a single ring of centripetal developments inside the "normal" ring of centrifugal wood. Traces are given off from near the perimedullary region; these pass out through the gaps between the large sectors of the normal wood, which are deeply lobed.

The medullary region contains parenchyma, sclerotic nests, and a variable number of vascular strands, which are not orientated in any particular fashion.

The wood is compact, and consists of tracheids with uniseriate or biseriate alternate pits. The pitting in the field is not well shown, but seems to consist typically of one large simple pit. The medullary rays are uniseriate, typically 5–7 cells high. Anomalous growth processes are exhibited in all specimens so far examined, recalling similar processes in the modern lianes.

Set B: Specimen B 1. *Rhexoxylon africanum*, BANCROFT.

Locality.—Willoughby's, near Gwelo, Southern Rhodesia.

Description.—This specimen consists of a large, roughly weathered and chipped block, with a maximum diameter of 28 cm. and a length of 50 cm. No tissues are preserved outside the main sectors of centrifugally developed xylem, all of which are incompletely represented (fig. III, 3, 4, and Plate 6, 12). The wood masses were probably arranged in nearly concentric series; the outer sectors have small centripetal developments opposite their narrow ends, and form one series; there is also an inner series consisting of a similar arrangement, with an approximately equal development of centrifugal and centripetal xylem.

This differs from the arrangement in Dr. BANCROFT's type-specimen, in which there was an outer ring of centrifugal masses of wood, "partial steles" (described above in *R. tetrapteridoides* as the outer sectors), an inner ring of "steles," consisting of a centrifugal and a centripetal portion. From the centripetal portion "traces" were given off. In Specimen B 1 (fig. III, 3, 4) there is an outer series of large sectors (which in Dr. BANCROFT's specimen were only represented by the small centrifugal partial steles at the periphery of the block); interior to these sectors there is a series of centripetal developments, *b′*, *c′*, *d′*, *e′* (sometimes two to each of the outer sectors, as at *d′*, *d″* (fig. III, 4, and Plate 6, 13, *d′*, *d″*)), which correspond possibly to the centripetal portions of the inner ring of "steles" in

* SEWARD, vol. 4, p. 138 (1919).

Dr. BANCROFT'S specimen. In addition, there is a complete inner series of complete "steles," AA′, BB′, CC′, etc., not represented in Dr. BANCROFT'S specimen. In this specimen there is no indication of the formation of traces from members of any of the inner series of "steles."

An important feature to notice is that the xylem groups are also in radial series (*e.g.*, *d*, *d″*, *d′*, D′, D). This is a definite distinction from all Medullosean types of axis so far described, in which the steles are not thus arranged (*cf. M. solmsi*, which shows greater similarity than most in other respects). The members of the inner series show signs of dividing up by radial fission, and it is noteworthy that this fission is often accompanied by a corresponding separation in the outer series.

Thus in fig. III, 3, the group lying between BB′ and CC′ corresponds to that between *bb′* and *cc′*, but in 4 both have disappeared as they have probably joined up with CC′ and *cc′*. The groups *b* and *c* and the mass lying between in all probability formed a continuous arc of wood when the axis was younger: they have been split apart subsequently (*cf.* the outer sectors, Specimen A 1, seen in fig. III, 6). At several places there are horizontally-running strands seen in the gaps between the outer sectors between the centripetal portions of the outer series, and between the groups of the inner series. It has not been demonstrated whether the portions of xylem lying between DD′ and EE′, fig. III, 4, ultimately pass out between or anastomose with members of the outer system *bb′*, *ee′*, *ff′*, etc.,* or whether they fuse up again with the masses between which they lie. The preservation is very poor and no structure, apart from the xylem, can be made out in the tissue. There are no indications of any extensive system of small strands in the medullary region or of any "periderm" developments.

The outer main sectors are much broken up by dilatation, and in many places, in the tangential cracks especially, there are adventitious productions of xylem. These are clearly shown in the outer tangential cracks in the outer sector, *c*, in all the diagrams in fig. III, 3, 4, and Plate 6, 13, *x*. The outer sectors (*b*, *c*, *d*, *e*, *f*) are fringed on the flanks with small fan-shaped xylem groups (fig. III, 3, 4, and Plate 6, 12 and 13, *z*).

The Secondary Wood. (*Note on Methods of Examination.*)

In the Rhodesian specimens, which are all silicified, the preservation is such that in thin sections the material is too homogeneous and transparent to show trustworthy histological detail. The use of colour-screens and polarised light did not give any appreciable assistance. Crystallisation obscures the cellular structures and, in addition, the matrix in the lumina of the tracheids often exhibits the banded structure characteristic of agates.† It was noticed, however, that on one of the sides of the large specimen, where it had recently been fractured, the grain of the wood showed up where the split was radial-longitudinal, and in some places the course of the medullary rays was evident. It was found

* *Cf.* GNETUM, La Rivière, Ann. Jard. Bot. de Buitzenzorg, vol. 30, 2nd ser., XV.

† SEWARD and HOLTTUM, *loc. cit.*, p. 42 (1921).

that a satisfactory way of examining such a surface was to use a Leitz-Wetzlar vertical illuminator, with a $\frac{1}{6}$-inch objective. The pitting on the tracheids could then be seen quite definitely. Collodion film impressions were also used, but they were found to give less satisfactory results, and of course were liable to introduce artefacts. This method was therefore regarded as less trustworthy than direct observation with the vertical illuminator.

Another method was used which gave even better results with transparent homogeneous material. Small flakes of rock from one of the surfaces revealing the grain of the wood were placed on a slide, with the grained surface uppermost, on a drop of balsam (solution in xylol) sufficiently fluid to flow in the space between the flake and the slide and to expel all air from the interspace. No balsam was allowed to get on to the grained surface. If the flake was thin and sufficiently transparent its upper surface could be examined easily by transmitted light under a $\frac{1}{6}$-inch objective. The balsam, being of about the same refractive index as the siliceous rock, the irregularities of the under-surface immersed in the balsam were eliminated optically and did not interfere with the examination of the grained surface (fig. IV, 6*a* and *b*).

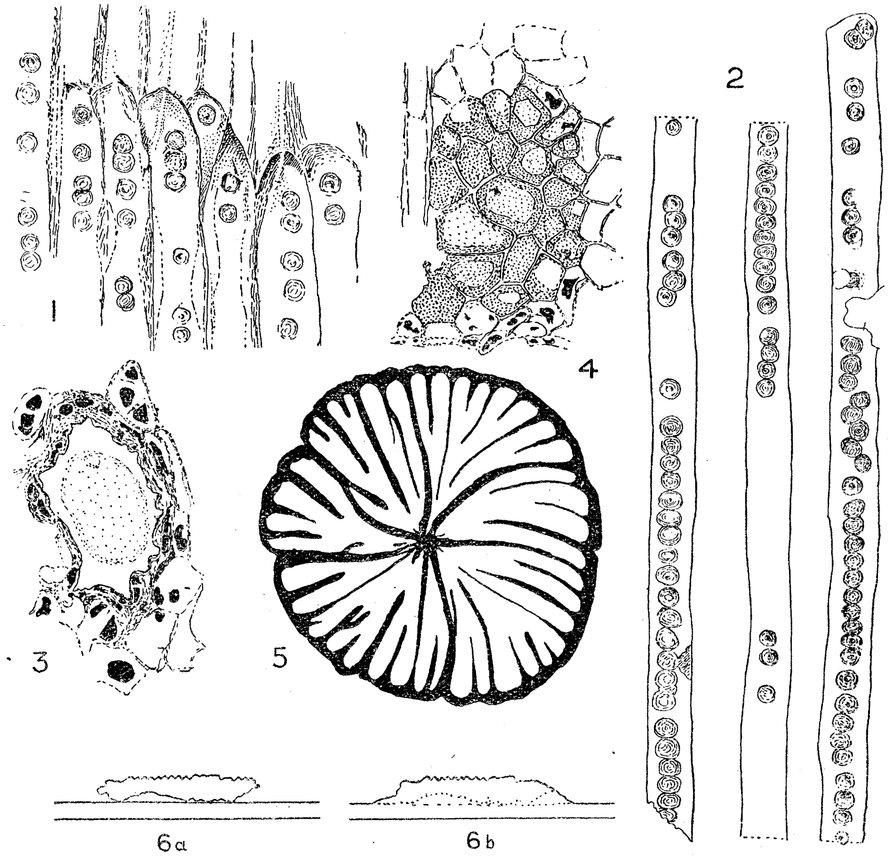
Better preparations (Plate 6, 14 and 15) of this type are made by first fixing the flake, with the grained surface downwards, on to a slide by means of fused balsam, allowing it to cool, and then grinding off sufficient rock from the back of the flake to render it thin and transparent. The thinned flake is then removed from the slide by heating, the balsam dissolved away, and the flake washed in alcohol and then mounted as before on balsam with the grained side uppermost. If the balsam, or any liquid, is allowed to get on to the grained surface practically all trace of structure disappears, and the preparation gives as little indication of structure as an ordinary thin section of this material.

Structure of the Tracheids and Medullary Rays.

The best results were obtained with a sample of the secondary wood from one of the outer sectors (fig. III, 4, *e*). The appearance of a fractured radial surface thus prepared is illustrated by Plate 6, 14, 15. Such preparations are equivalent to a relief map. The tracheids are seriated radially and the pits (diameter 20 μ), which occur only on the radial walls, as far as one can make out from these preparations or from any transverse sections showing structure, are bordered and have a centric circular pore (diameter 6 μ) (fig. IV, 1, 2). The arrangement of the pits varies greatly; they may be uniseriate and widely separated, and circular (Plate 6, 15), or they may be in contact and flattened (fig. IV, 2). They are often biseriate and alternate, and flattened on the sides of contact. The ends of the tracheids are blunt (fig. IV, 1) and there are no indications of perforations, the bordered pits occurring at the ends being of the normal type. The average diameter radially of a tracheid is 52 μ, and tangentially 56 μ. The whole length of some tracheids was observable in one preparation and was 4 mm.

The cells of the medullary rays form a single vertical series, as may be seen from a tangential section of wood in which dilatation has not occurred. In radial section the rays are seen to be one to seventeen cells deep (in Plate 6, 14, rays one, five, and six cells deep are represented). The length of a medullary-ray cell was found to be about 120 μ. The breadth, determined from flake preparations, was about 27 μ.

The pits which occur in the "field" of the ray cells and the tracheids vary considerably; generally they are large and circular to elliptical, the greatest diameter being usually parallel to the direction of the ray, but in some cases it is inclined, giving the pit an oblique orientation. The maximum diameter is about 20 μ, and the minimum is 14 μ in the larger pits. Sometimes there were smaller circular pits, whose diameter was approximately 14 μ. Occasionally two or three of these smaller



TEXT-FIG. IV.—*R. africanum.*

1 and 2. Drawings of tracheids exposed on radially fractured surface of B 1; 2 is of one tracheid, shown for convenience in three portions.

R. tetrapteridoides.

3. Secretory cavity from medullary region of A 2.
4. Sclerotic nest differentiated from dilatation parenchyma in A 2.

Tetrapteris sp.

5. Transverse section after SCHENK.

R. africanum.

6. *a*, flake mounted dry on a glass slide; *b*, after adding balsam. (Note that one irregular surface has been eliminated optically.)

pits were found in the field, and sometimes one small pit and one larger, oblique, elliptical pit. The arrangement of the pit suggests the possibility that the larger ones have in the course of descent been derived from a fusion of smaller ones. There was no sign of any border to these pits, and, in view of the fact that the pores in the tracheids are clearly preserved, one is led to believe that they were probably simple. The pits were possibly similar to the "eiporen" found in the genus *Pinus.*

The secondary wood is compact and coniferous in type, except where dilatation has taken place. There are well-marked growth rings, due to the difference in size of the lumen of the tracheids formed at different seasons.

Specimen B, 2 : *Rhexoxylon africanum*, BANC.

Locality.—Willoughby's, Gwelo, Southern Rhodesia.

This specimen consists of a roughly cylindrical block, 11 cm. in height and 12 cm. maximum diameter (Plate 6, 16).

Sections cut from one end* revealed a very complicated structure. Probably only a small portion of the whole axis is represented; externally, at one side, there is a large scar (*s*, Plate 6, 16), representing the point of attachment of a lateral axis. The vascular tissue of the scar had been weathered out, and consisted probably of a ring of wood sectors with a centric medullary region (*q*, Plate 6, 16). The complexity of the vascular strands in this specimen is in all probability connected with the departure of a lateral axis from the main system.

An interesting feature in a transverse section cut from the top of the block is that at one part of the secondary xylem, in one of the wood masses, there has been apparently a cessation of cambial activity, and this has occurred just after the formation of the larger tracheids in the growth ring. This stoppage has occurred only in one part of the growth ring, and elsewhere there is no discontinuity of growth. The further growth of the wood, opposite the part where the cessation has occurred, has been resumed at separate points, giving the appearance of a series of protoxylem groups. The radial series of tracheids, formed centrifugally from these initials, broaden out, and finally compact wood of the normal Rhexoxylon type has been again produced.

This specimen is attributed to *R. africanum*, as the shape of the xylem masses and their size correspond very closely to those of that species.

Specimen B, 3 : *Rhexoxylon africanum*, BANC.

Locality.—Lady Grey, Aliwal North Commonage, Cape Province.

Horizon.—Red Beds. Stormberg Series.

Only a small portion of the original fossil trunk was available for examination. The original specimen, as it was found in the field, is thus described by Dr. DU TOIT in a letter to Dr. KIDSTON : ". . . It is some 10 feet in length, coming to a point at what I take to be the distal end, swells out to about 7 inches in the centre, contracts to only 2 inches, and then thickens to nearly 4 inches. The curious feature of the stem is the eccentric arrangement of the group of steles throughout the whole length; presumably the cortex has disappeared. Leaf traces are visible on the exterior of the stem, which is both fluted and crossed by transverse wrinklings."

* SEWARD and HOLTTUM, *loc. cit.* (1921).

Fig. III, 5, represents diagrammatically the arrangement of the xylem. The tissues are badly preserved, and no trace of primary wood is to be found in the gap between the centrifugal and centripetal portions of any of the inner series of "steles."

This axis resembles Dr. BANCROFT'S specimen in the arrangement of the xylem groups a, b, c, etc., and a', b', c', etc. It will be seen that lateral wings of secondary xylem become detached and pass outwards from the series a', b', c', etc., and i', k', g'. Members of the series (*e.g.*, i', k' and g') show different stages in this process, which has already been described for *Rhexoxylon africanum*, BANC.* There is another set of "steles" inside which do not take part in any such activity. The system g', g resembles "Stele 5" (Plate 10, fig. 3, stele 5).† The preservation of the pith is sufficiently good to show several vascular strands of rather larger size than those which appear in *R. tetrapteridoides;* there are also indications of sclerotic nests, secretory canals, and a considerable amount of large-celled parenchyma. In addition to the larger structure indicated near the centre of the medullary region in fig. III, 5, there is another smaller one of apparently the same nature (not shown in the diagram). These structures correspond to the "periderm" developments mentioned above.

The specimen is obviously very similar to the one described by Dr. BANCROFT and only differs in having the additional inner ring of "steles," and in showing more of the outer system of sectors. The surface of the block shows also the same transverse and longitudinal ridging, and altogether there is no doubt that this is a specimen of *R. africanum*, BANC.

Emended Diagnosis: Rhexoxylon africanum, BANCROFT.

Large stems from the Stormberg Series, South Africa; some with a minimum diameter of 25 cm. The vascular system of the stem consists of a normal ring of centrifugal xylem, which has been broken up, and occupies a peripheral position. In addition, there are systems of secondary vascular structures in the perimedullary region. These may take the form of centrifugal or centripetal fans of xylem (in transverse section) or may be endarch developments in themselves. There is a large medullary region with scattered vascular strands. The xylem of the normal ring is compact, with uniseriate rays of from 1–17 cells high. The tracheids are pitted on the radial walls. Uniseriate pitting, distant or in contact, is characteristic of the narrower tracheids, while in the wider elements biseriate alternating pitting is the rule. Anomalous growth processes are a marked feature. The normal wood is split radially and tangentially, and intercalations in these cracks of small strands of xylem are frequent. The sides of the sectors into which the normal ring is split are fringed with small strands of xylem of an adventitious nature. There is one example of a branching axis.

* BANCROFT, *loc. cit.*, p. 91 (1913).

† *Id. op.*

Specimen C, 1: *Rhexoxylon priestleyi* (SEWARD) (= *Antarcticoxylon priestleyi*, SEWARD).

Locality.—Priestley Glacier, South Victoria Land. Antarctica. From the Beacon Sandstone.

This interesting stem, which has already been thoroughly investigated,* shows peculiarities which can now be interpreted in terms of phenomena characteristic of *Rhexoxylon*.

Unfortunately, the preservation of the medullary and perimedullary regions is very imperfect, but there are indications of what were probably masses of centripetal xylem in the perimedullary zone (Plate IV, 24; Plate VIII, 44, x', 46; SEWARD). This xylem was thought to be "primary," but we shall see later that similar tracheids occur in the tangential cracks of the secondary wood, where they must be considered "tertiary."†

The main secondary xylem consists of an almost complete ring when examined in transverse section, but shows a few of the narrow radial gaps so characteristic of the other types of *Rhexoxylon* (Plate IV, 24; SEWARD). The tangential cracks are represented towards the outer part of the axis. The structure of the wood, as described by Prof. SEWARD, agrees closely with what we know of *Rhexoxylon tetrapteridoides*, in that two rows of alternate pits are frequently found on the tracheids.

The axis has been compressed laterally, probably after fossilisation, as the tangential cracks are not closed up even where they run perpendicular to the direction of compressions, as one would have expected from their parenchymatous nature in *Rhexoxylon*. If Plate IV, 23 (SEWARD), is looked at obliquely from one side, one gets an idea of the shape of the axis before this compression occurred, and the general distribution of tissues recalls that of *R. tetrapteridoides*. The light bands, supposed to have been formed partly by the destruction of the secondary wood, must be of the same nature as those appearing in *Rhexoxylon*, the small portions of xylem "connecting the two sides" (*cf.* Plate 6, fig. 11 (WALTON)), being the small adventitious developments described above for *Rhexoxylon*, which in this case have spanned the gap. There are also small cuneate growths at the sides of the radial gaps.

A curious feature of this specimen is the excellent preservation of the small adventitious strands. In several places the scalariform or spiral nature of the xylem development in the cracks is evident. These strands are obviously identical in origin with those which occur in *R. tetrapteridoides* and *R. africanum*, the adventitious strands of which are therefore probably composed of similar elements. In the specimen of secondary wood from Dordrecht (see p. 80) there is a small crack in

* SEWARD, 1914.

† In the sense used by WORSDELL, 1896.

which tracheids of precisely the same nature occur. All these facts lead up to the inevitable conclusion that *Rhexoxylon* and *Antarcticoxylon* are generically the same, and this leads to a consideration of the contrast in the relative sizes and developments of their medullary and perimedullary regions. In *Antarcticoxylon*, with its small pith, it is difficult to credit the existence of a series of well-developed centripetal secondary wood masses such as occurs in the other specimens of *Rhexoxylon*. On the other hand, it may represent a young axis in which the perimedullary growth has not started.

Diagnosis: Rhexoxylon priestleyi, SEWARD.

Small stem from the Beacon Sandstone Series, South Victoria Land, Antarctica. Geological age uncertain, possibly Triassic.

It resembles *R. tetrapteridoides* in that the medullary system was less developed than in *R. africanum*. The traces given off formed a spiral sequence, as was clearly shown on the specimen (SEWARD, *loc. cit.*, text-fig. III). Adventitious xylem developments occur in tangential cracks in the normal ring of secondary wood, which is not so much lobed and split as in *R. tetrapteridoides*. The adventitious strands in the cracks consisted of tracheids with a close spiral thickening on the cell wall.

A fragmentary and badly preserved specimen of silicified wood from the Burghersdorp Beds of the Beaufort Series at Aliwal, Cape Province, shows features which are undoubtedly those of *Rhexoxylon*, and possibly *R. tetrapteridoides*, but it is impossible to obtain sufficient data on which to base a definite determination.

Emended Diagnosis of the Genus Rhexoxylon, BANCROFT.

Plant stems with secondary growth of an anomalous character.

The normal ring of secondary xylem is developed centrifugally by a cambium starting from a ring of small protoxylem initials, which surround a pith, which at a later stage consists of large-celled parenchyma, secretory ducts, and small collateral vascular strands. This normal ring is generally broken up by narrow bays, extending from the outside towards the centre. In addition to the normal ring of xylem, additional masses of considerable size are formed in the perimedullary region in radial series with segments of the normal ring, and may take the form of fan-shaped centrifugally or centripetally developed masses, or may be composed partly of centrifugal and partly of centripetal xylem. The normal wood may be split up radially or tangentially, the cracks being filled with parenchymatous tissue, in which small fan-shaped developments of xylem are produced. The normal secondary wood is pycnoxylic* and consists of tracheids and medullary rays, and shows well-marked growth rings. The tracheids have usually uniseriate or biseriate bordered pits; when uniseriate the pits may be distant and circular, or in contact and slightly flattened;

* See SEWARD, vol. 4, p. 128 (1917).

when biseriate the pits are alternate and slightly flattened. The medullary rays are uniseriate and muriform, one to seventeen cells deep. The pits in the "field" are simple and vary from one to three in number. Often there is one large slightly oblique pit in the "field."*

The tracheids of the small xylem developments in the cracks of the normal secondary wood have a close spiral or scalariform thickening band on the walls.

Horizontally-running vascular strands occur in the tissue between some of the segments of the normal ring.

Genus Rhexoxylon, BANCROFT (syn. *Antarcticoxylon*, SEWARD); *R. africanum*, BANCROFT; *R. tetrapteridoides*, sp. nov.; *R. priestleyi* (SEWARD).

Discussion.—In most of the specimens of *Rhexoxylon* there are radially directed strands of xylem in some of the gaps between the large xylem sectors, but, owing to the fragmentary nature of the samples, it has been impossible to find out the order of emission of these nearly horizontally-running strands, which are possibly leaf-traces. In addition to this, the adventitious xylem developments produced after the disruption of the secondary xylem and the small xylem wedges, formed from delayed cambial layers on the sides of the main xylem sectors, are so similar to them in appearance and structure that uncertainty as to the nature of these strands is considerably increased. In *R. africanum* there is evidence that the secondary xylem of the perimedullary was continuous with outgoing strands.

The apparent polystely of *Rhexoxylon* at once suggested a possible relationship with the *Medulloseae*. The material on which the first description of the genus was based was not sufficiently complete to indicate any of the curious secondary growth phenomena which have been revealed by study of the recently found specimens described above. It was thought that the perimedullary developments ("steles") were comparable to the steles of the *Medulloseae*, but that the central primary wood (partial pith) of the Medullosean stele was missing in *Rhexoxylon*, being represented by parenchyma.

If we examine the outer sectors of the series *Rhex. africanum*, *R. tetrapteridoides*, and *R. priestleyi*, we see that in *R. africanum* they are fairly widely separated, in *R. tetrapteridoides* they are very close together in some cases, while in *R. priestleyi* they form an almost complete cylinder. It is also noticeable that with this wider separation there is a corresponding larger development of the perimedullary systems, and, as already pointed out, the evidence indicates that in all three types the outer sectors formed an almost closed cylinder, which in *R. africanum* and *R. tetrapteridoides* was ruptured by secondary growth processes. It is supposed that this outer centripetal wood was the normal xylem of the stem, and that the perimedullary developments arose internally to the protoxylems of the normal xylem by anomalous

* See SEWARD, vol. 4, p. 128 (1917).

cambiums similar to those which are found in *Lyginopteris** and *Cycadoxylon*,† and in the recent plant *Wilbrandia verticillata*, Cogn. (Cucurbitaceæ).‡ That this supposition is not unreasonable will be allowed when the evidence in favour of the theory that *Rhexoxylon* had the habit of a liane is reviewed.

The division of the main mass of wood formed by cambial activity into lobes or sectors is an exceedingly widespread character among many of the families which show the liane type of vascular structure. It has been suggested that it is correlated with the flexibility of the axis, just as a steel cable is more flexible than a steel rod of the same length and weight. This lobing is effected by the cessation in the formation of xylem at certain points of the normal cambium. By subsequent growth at the side of these lobes small lateral wings of xylem are formed, which give a very characteristic§ fringed appearance to the main masses of xylem. The splitting-up of the secondary wood by a resumption of growth and division by living cells included in the wood is characteristic of many lianes (*cf. Banisteria hasleriana*).‖ The ground tissue in many lianes expands and increases by cell division, forming a large amount of parenchymatous tissue (dilatation parenchyma), in which meristems may form new and permanent tissues (xylem or phloem). Owing to the expansion and increase in amount of this parenchymatous tissue, the primary permanent tissues are pushed apart and their original distribution plan is modified (*cf. Tetrapteris*, sp.).¶ Anomalous meristems originating in the cortex may form large developments of vascular tissue (*e.g.*, Serjania, spp.).**

When we examine the genus *Rhexoxylon*, we find many peculiarities which are undoubtedly instances of processes parallel to those which occur in the lianes. The stem of *R. tetrapteridoides* bears a very close resemblance in the general plan of the secondary wood distribution, and in particular in its deep lobing, to species of *Tetrapteris* and *Wilbrandia*. The large masses of xylem are fringed with small wings or fans of xylem. *R. africanum* shows this feature in a very striking degree. There has undoubtedly been considerable splitting up of the secondary wood in *R. africanum* and *R. tetrapteridoides*. The medulla shows signs of meristematic activity, and since the splitting apart of the main outer sectors, there has been considerable secondary growth in the perimedullary xylem masses.

In addition to this, the discovery of a specimen of *Rhexoxylon*, 10 feet long and from 2 to 7 inches in diameter, is highly suggestive when we consider the external form of a typical liane.

When we realise that all these peculiar features are repeated in modern lianes,

* Williamson and Scott, p. 722 (1895).
† Seward, p. 72 (1897).
‡ Schenk, *op. cit.*, fig. 101, *x*.
§ Schenk, *op. cit.*, figs. 161, 163, and others.
‖ Chodat, *loc. cit.*, fig. 156 (1917).
¶ Schenk, *loc. cit.*, fig. 66*c*.
** Schenk, *loc. cit.*, fig. 54.

there seem to be very good grounds for supposing that *Rhexoxylon* agrees with the lianes in the general scheme of secondary thickening of the axis.

The evidence forthcoming from the comparative study of the three species of *Rhexoxylon* tends to show that there was originally a solid ring of secondary centrifugal wood, which was ruptured by a considerable development of secondary tissues in the perimedullary region. The critical point is whether this secondary growth was centred round primary groups or not, in other words, whether the perimedullary developments are steles or mere excrescences of secondary tissues. The evidence seems to be in favour of the latter hypothesis. First, there is no evidence of any mixed pith in the perimedullary "steles"; secondly, there is evidence in favour of the view that they were formed subsequently to the outer wood sectors; thirdly, there is a marked variability in different parts of the same stem (*R. tetrapteridoides*); and fourthly, there is a very close resemblance in structural features, *e.g.*, the centripetal "partial steles" (Plate 6, 13, *d′*, *d″*) and the adventitious strands, *x*, are very much alike. If we assume that *Rhexoxylon* is a case of parallel evolution of liane stem structure, then other facts support the hypothesis that the perimedullary "steles" are entirely secondary structures. As already mentioned, in *Wilbrandia*, meristems arising in the perimedullary region do give rise to secondary xylem. CHODAT* also describes adventitious vascular strands in the perimedullary region of *Doxantha* (*Bignonia*) *unguis*. It is interesting not only to note that in *Doxantha* the adventitious strand is in close relation with the protoxylem of the normal wood, but to compare its position with the position of the small centripetal strands on the inner faces of the main sectors in *R. africanum* (text-fig. III, 1, 2, 3 and 4). The shape of the inner series of perimedullary developments in *R. africanum* resembles very closely indeed the pericyclic developments in *Paullinia*.

The question of the nature of the strands passing out between the sectors is one that cannot be settled until better preserved material is forthcoming, and even, given better preserved material, it would be extremely difficult to distinguish the primary structure in an axis in which so many secondary changes have occurred. It would be an almost impossible problem for an investigator, given a mature stem of a liane, to distinguish the typical dicotyledonous primary arrangement.

A Reconsideration of the Affinities of Rhexoxylon.

When *Rhexoxylon africanum* was first described, the occurrence of what appeared to be polystely was put forward as evidence of Medullosean affinities.† But now, in spite of newly described features, which in themselves would seem to lend support to this view (*e.g.*, the occurrence of secretory canals, and of small vascular strands in

* CHODAT, *loc. cit.*, p. 268, figs. 219, 220 (1917).

† BANCROFT, *loc. cit.*, 1913.

the tissue external to the main xylem ring), other facts have come to light which cause one to reconsider the relationships of *Rhexoxylon*.

(i) *The Secondary Wood.*

In the first place, as Dr. BANCROFT states,* the secondary xylem differs very considerably from that of any *Medulloseae* of which the structure of the xylem is known. The wood is distinctly compact or pycnoxylic, as opposed to the manoxylic† wood of the *Medulloseae* generally. The character of the medullary rays is different, being uniseriate except where dilatation is occurring. The pitting of the tracheids is decidedly coniferous in character, and there are well defined zones of growth due to the regular alternation of different types of tracheids. This type of wood structure is found closely paralleled in specimens of wood designated as *Dadoxylon*‡ from the Rio Grande do Sul in Brazil, from the Iraty Black Shales of the Passa Dois Series, which series has been correlated with the Beaufort Series of South Africa.§ These specimens of *Dadoxylon* were found associated stratigraphically with *Dadoxylon pedroi*, ZEILL. Unfortunately, they represent portions of secondary wood only, and no idea of the medullary regions is given. The only considerable difference is in the pitting of the medullary-ray cells in the field. In one, *Dadoxylon nummularium*, WHITE, and in another, *D. meridionale*, a uniseriate type of tracheal pitting prevails, and the pits are usually a little distant but sometimes contiguous (*cf.* fig. IV, 1, 2, *Rhexoxylon africanum*), and while in *D. meridionale* the pores of the bordered pits are oblique elliptical, in *D. nummularium* they are circular as in *Rhexoxylon africanum*. These woods are of interest in this connection, as showing the presence of a similar type of secondary wood organisation in the same (Gondwana) botanical province in South America and South Africa, and from not widely separated horizons. Of greater interest in this connection are *Dadoxylon bengalense*, HOLDEN, and *D. indicum*, HOLDEN,‖ two other examples of Gondwana *Dadoxyla*. They show some important features in common with *Rhexoxylon*. In the first place, there are distinct growth rings in both; *D. indicum* has a large pith with secretory cells. The occurrence between the vascular cylinder and the pith proper of a "jacket" of cells of smaller diameter than the other cells in the pith is extremely suggestive. "Longitudinal sections reveal their characteristically reticulate tracheoidal markings." Miss HOLDEN adds further: "For strictly comparable structures, we must go to *Antarcticoxylon*."

Other stems closely allied to these forms have been described by HALLE¶ from the

* BANCROFT, *loc. cit.*, p. 97, 1913.

† SEWARD, Definition of Manoxylic in "Fossil Plants," vol. 3, p. 7, 1917.

‡ WHITE, I. C., p. 573, Plates 13 and 14, 1908.

§ *Ibid.*, p. 381.

‖ HOLDEN, R., 1917.

¶ HALLE, T. G., 1911.

Falkland Islands. *Dadoxylon lafoniense*, HALLE, has the same kind of pith and primary bundle arrangement.

The writer, thanks to the kindness of Prof. SEWARD, has had the opportunity of investigating some fossil wood from the Falkland Islands. This wood, *Dadoxylon bakeri*, SEW. and WAL.,* is closely related to HALLE's species.† The interesting feature about it is that the radial pitting of the tracheids is very variable. In the narrow "summer" elements there are uniseriate distant pits, while in the wide spring elements the pitting varies from uniseriate to triseriate. The commonest arrangement is biseriate, when the pits are in contact and compressed, with a polygonal outline. There are frequently star-groups of pits in the wider tracheids. The character of the wood is somewhat similar to that of *Callixylon oweni*, ELKINS and WIELAND,‡ from the Upper Devonian of Indiana, U.S.A. In *Callixylon* the pits are arranged in large groups and a biseriate opposite arrangement occurs quite frequently.

Some of the South African *Dadoxyla*§ show features in the organisation of the secondary wood which indicate a certain amount of affinity with the type represented by *Rhexoxylon*. There was evidently at this period a widespread group of plants whose secondary wood has been designated by the term *Dadoxylon*, but which differ from the typical *Dadoxylon* in the tendency to have uniseriate pitting in the tracheids (although biseriate Araucarian pitting does occur) and in the tendency of the pits to be separate and circular. Of these *Dadoxyla* several have been mentioned, viz., *D. nummularium*, *D. meridionale*, and *D. pedroi*.

It is also worthy of remark that HALLE‖ observes that the structure of the pith of the *Dadoxyla* from Gondwanaland does not support the view that they are allied to the Cordaitean group, but rather by their large pith, and sometimes by the occurrence of secretory cells and canals,¶ to a Cycadean stock.

In secondary wood characters *Callixylon*, *Dadoxylon lafoniense*, *D. bengalense*, *D. indicum*, *D. pedroi*, *Rhexoxylon*, and others form a series in which there is a tendency to a reduction by fusion of the pits in the "field."

(2) *Primary Structure.*

It might be said that the nature of the protoxylems of the main outer secondary wood resembled the xylem cylinders in the modern cycads. So it does, but this type of secondary wood development from a large number of small endarch protoxylem developments is not necessarily Cycadean or Medullosean. *Dadoxylon pedroi*,

* SEWARD and WALTON. Read at a meeting of the Geological Society, 1923.

† The state of preservation of HALLE's specimens was not good enough to show the pitting on the tracheids except at one or two points.

‡ ELKINS, M. G., and WIELAND, G. R., 1914.

§ WARREN, E., 1912.

‖ HALLE, T. G., p. 178, 1911.

¶ HALLE, p. 177, 1911.

ZEILLER,* has very similar protoxylems. The only feature in which the secondary wood of *Rhexoxylon* differs from that of *Dadoxylon pedroi*, to any considerable extent, is in the pitting of the medullary-ray cells.

One feature that should be mentioned is that in *D. indicum*, HOLDEN, two strands go out from the margin of the pith separated by an intercalary bundle. Miss HOLDEN† compares this arrangement with that which occurs in *Ephedra*. Is it possible that in the outgoing strands of secondary wood of *Rhexoxylon*, which leave the centripetal portions of the perimedullary systems (which, it should be noticed, lie nearest the protoxylems of the normal ring in Dr. BANCROFT's specimen and in Specimen B. 3, pp. 96–97, above) we have an indication of the same primary bundle arrangement? In other words, does the group of small protoxylems at the apex of the outer sector represent the intercalary bundle of *D. indicum*? It is possible that this outgoing secondary xylem has been developed in conjunction with the trace that left the margin of the pith at that point at the same time that the main portions of the perimedullary systems were developed in relation to the other primary bundles, cauline or other, which did not pass out as traces. However, it will not be possible to answer these questions until younger stems, with the primary arrangement less modified by secondary growth, are discovered.

(3) *Anomalous Growth Processes.*

Having regard to the secondary nature of the small xylem developments in the cracks and the other peculiar growth phenomena exhibited by these plants, and to the similarity which these processes bear to many found in modern lianes, it seems impossible to avoid coming to the conclusion that the perimedullary masses of xylem are also entirely composed of secondary tissue. This is supported by the failure to observe any primary xylem in association with these developments. Hence the appearance of polystely would seem to be quite fortuitous, and a search for allied types, not among the *Medulloseae*, but among such plants as the Gondwana *Dadoxyla*, appears to be more promising.

The Geological Significance of the Occurrence of a Species of the Genus Rhexoxylon *in the Antarctic Continent.*‡

The occurrence in the Upper Beacon Sandstone, Antarctica, of a plant obviously closely related to the Rhexoxyla of South Africa is highly significant, in view of the confirmatory evidence it affords of a close relationship between these two continents at a period probably corresponding to the Triassic Age in Europe.

* ZEILLER, M. R., 1895.

† HOLDEN, R., p. 317, 1917.

‡ The reader is referred for a statement of the geological aspect of the question to DEBENHAM, F., "Brit. Antarctic Expd., 1910," 'Geology,' vol. 1, No. 4*a*, British Museum (Natural History).

SUMMARY.

I. A new species of *Rhexoxylon* is described and named *R. tetrapteridoides*, on account of the similarity in the appearance of the cross section of the stem to that of members of the genus of South American lianes, *Tetrapteris*. The specimens on which the description and diagnosis are based were found in the Molteno Beds of the Stormberg Series in the Cape Province, South Africa.

II. Some specimens of *Rhexoxylon africanum*, BANCROFT, are described, and the original diagnosis of the species is emended, in view of some new structural details exhibited by these specimens. They are, with one exception, from beds of uncertain horizon in Southern Rhodesia. One is described from the Red Beds of the Stormberg Series in the Cape Province. A method of examining very transparent silicified wood is described.

III. A comparison is made between these species of *Rhexoxylon* with *Antarcticoxylon priestleyi*, SEWARD, and reasons are given for referring the Antarctic stem to the genus *Rhexoxylon*.

IV. The diagnosis of the genus *Rhexoxylon* is modified so as to include the species *R. priestleyi* (SEWARD) with other emendments, based on our increase in knowledge of the genus as a whole.

V. Reasons are given for regarding the vascular organisation of *Rhexoxylon* as different from anything that is found in the Medulloseae.

It is shown that there is considerable agreement in character in the development and structure of the secondary tissues between *Rhexoxylon* and some of the modern lianes, and that in *Rhexoxylon* the course of formation of the adult structure is altogether unlike anything that occurs in any other fossil plants so far described.

VI. The affinities of the genus are reconsidered, and reasons are given against a relationship with the Medulloseae. It is pointed out that there seem to be many points of connection between *Rhexoxylon* and certain *Dadoxyla* of the Southern or Gondwana Province.

VII. The geological significance of the recognition of the generic identity of *Antarcticoxylon* and *Rhexoxylon* is discussed.

In conclusion, I express my warmest thanks to Prof. SEWARD, who, throughout the course of this work gave much useful advice, and by whose kindness a large part of the investigation was made possible. I have also to thank Dr. KIDSTON for a great deal of the material and for many sections from which a large number of my descriptions and figures are made. I am also indebted to Dr. A. W. ROGERS and Dr. DU TOIT, who are responsible for the discovery of many of the specimens, and for notes on the localities and the circumstances under which they were found. I also thank Mr. R. E. PRIESTLEY for specimens and sections of his Antarctic material.

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DESCRIPTION OF PLATES.

Plate 5.

Rhexoxylon tetrapteridoides, sp. nov.

Fig. 1.—Photograph of transverse section of A 1, Sample 6. *a*, *b*, small strands (see p. 84); *c*, point at which a forking of one of the outer sectors has occurred; *d*, radial crack in sector. Nat. size.

Fig. 2.—Small vascular strand in the tissues external to the sectors at *a*, fig. 1; *x*, tracheids cut transversely. (×120.)

Fig. 3.—Area at the base of the fork in sector at *c*, fig. 1. *a*, *b*, small adventitious strands. (×16.)

Fig. 4.—The adventitious strand, *a*, in fig. 3 from another section. Upper part of photo. represents a portion of the normal secondary wood bordering on the crack in which the strand occurs. Note fan-shaped arrangement of seriated tracheids, developed centripetally with crushed tissue on the adaxial face. (×120.)

Fig. 5.—Photomicrograph of a similar strand. Note the close association between the elements of the strand and the normal wood. (×120.)

Fig. 6.—Photomicrograph of radial crack at *d*, fig. 1. Note radial strips of tracheids separated by dilatation parenchyma. (×30.)

Fig. 7.—Transverse section of specimen A 2. Portion of medulla with secretory cavities *m*, and large-celled parenchyma. (×30.)

Fig. 8.—Transverse section of specimen A 2. Portion of secondary xylem undergoing disruption. Separated strands of tracheids with dilatation parenchyma in between. The dense black patches are sclerenchymatous elements. (×30.)

Fig. 9.—Radial longitudinal section of specimen A 2. Portion of secondary xylem undergoing dilatation. *l*, dilatation parenchyma; *t*, tracheids with tyloses. (×64.)

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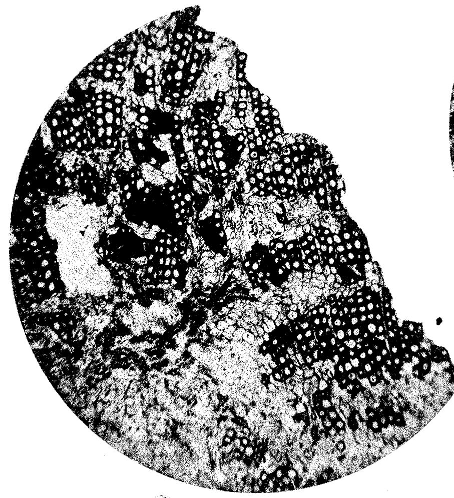

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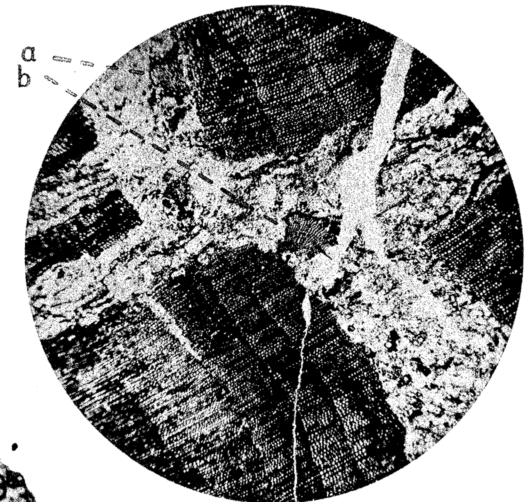

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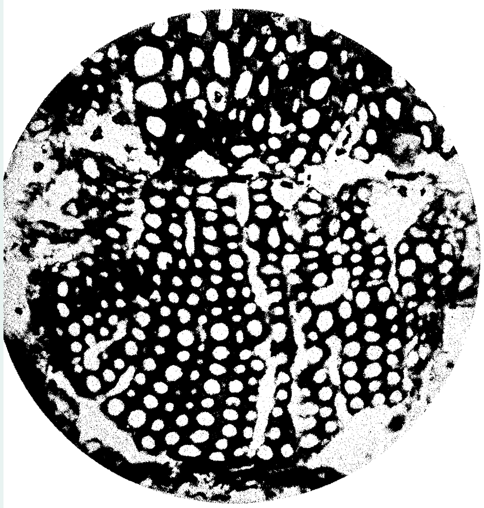

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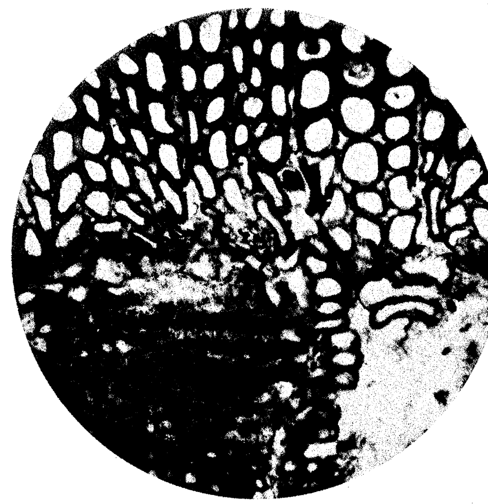

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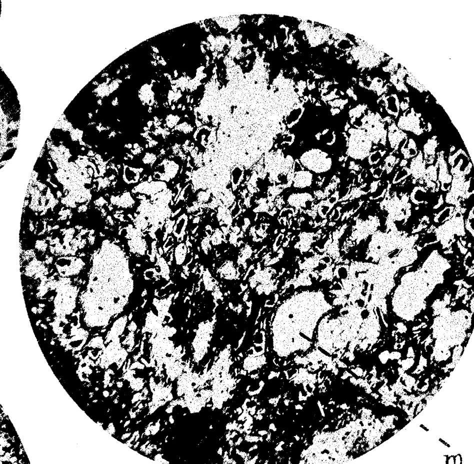

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Rhexoxylon tetrapteridoides.

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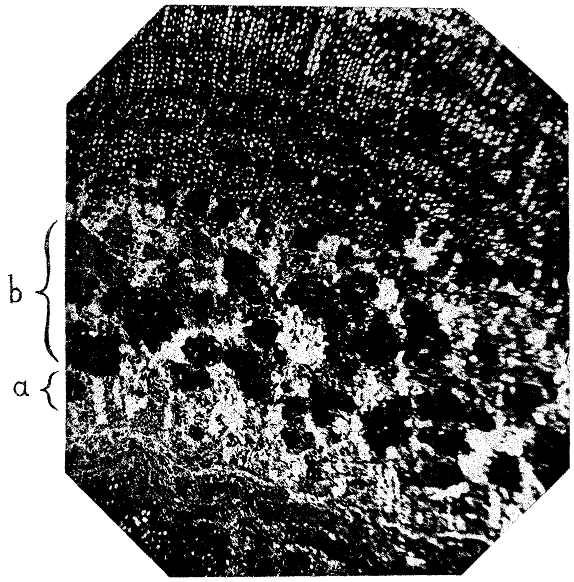

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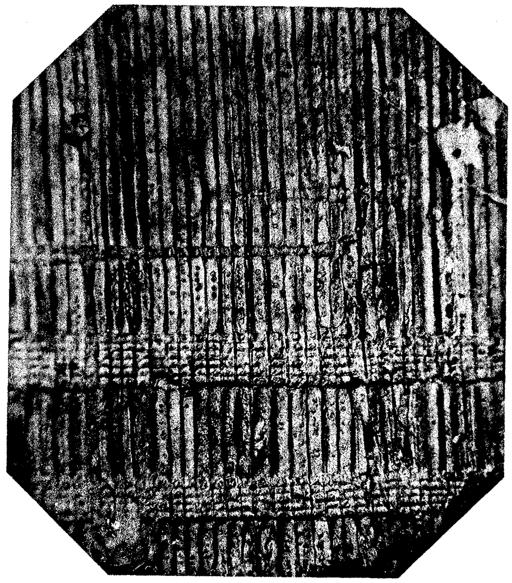

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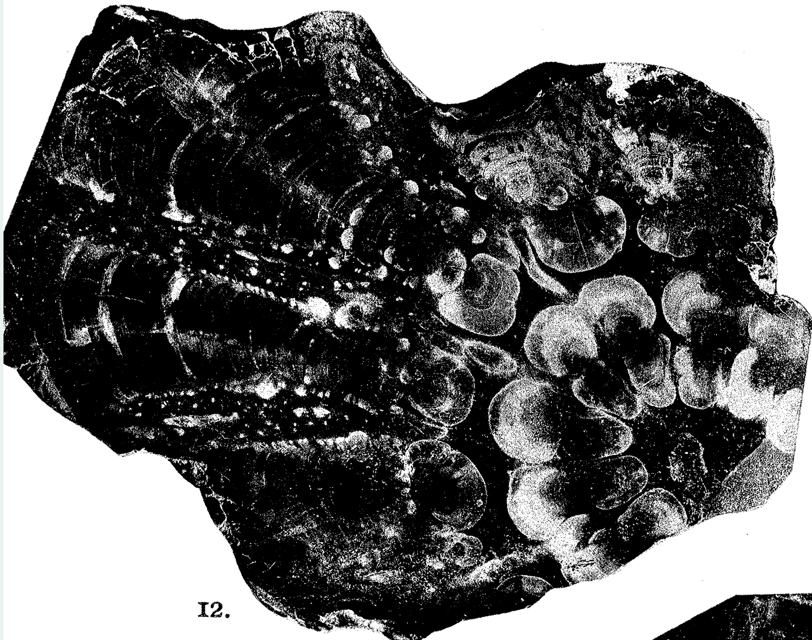

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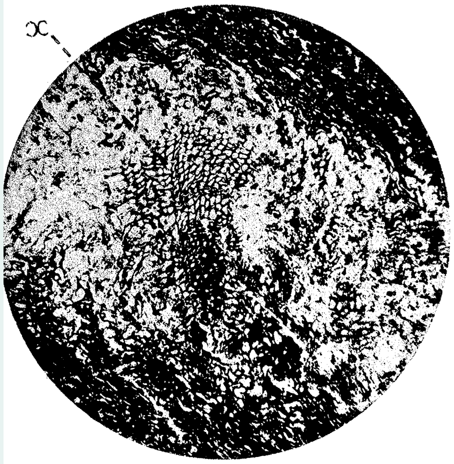

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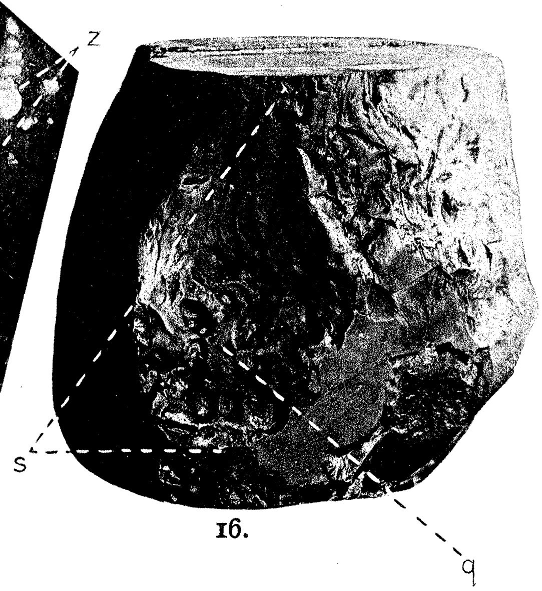

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Fig. 10. Rhexoxylon tetrapteridoides. Fig. 11. R. priestleyi. Figs. 12—16. R. africanum.

Plate 6.

Rhexoxylon tetrapteridoides, sp. nov.

Fig. 10.—Transverse section of split between I and II (text-fig. III, 2). *a*, zone of radially seriated cells; *b*, zone with sclerotic nests. (×30.)

R. priestleyi, Seward sp.

Fig. 11.—Transverse section of tangential crack with small adventitious strand, *x*. (×30.)

R. africanum, Bancr.

Fig. 12.—Transverse section of specimen B 1. $\frac{2}{5}$ nat. size.

Fig. 13.—Enlarged from 12. *d′d″*, centripetal developments of outer, perimedullary series. *x*, adventitious strands in a tangential crack. *z*, adventitious strands on the flank of the sector of normal xylem. Approx. nat. size.

Fig. 14.—Photo. of a fractured surface of the secondary wood, exhibiting two large and two small medullary rays crossing the tracheids. (×64.)

Fig. 15.—Enlarged from 14 to show bordered pits. (×250.)

Fig. 16.—Photo. of B 2. *s*, branch scar; *q*, medullary region of branch surrounded by depressions representing the weathered out vascular structures of the branch. $\frac{2}{5}$ nat. size.

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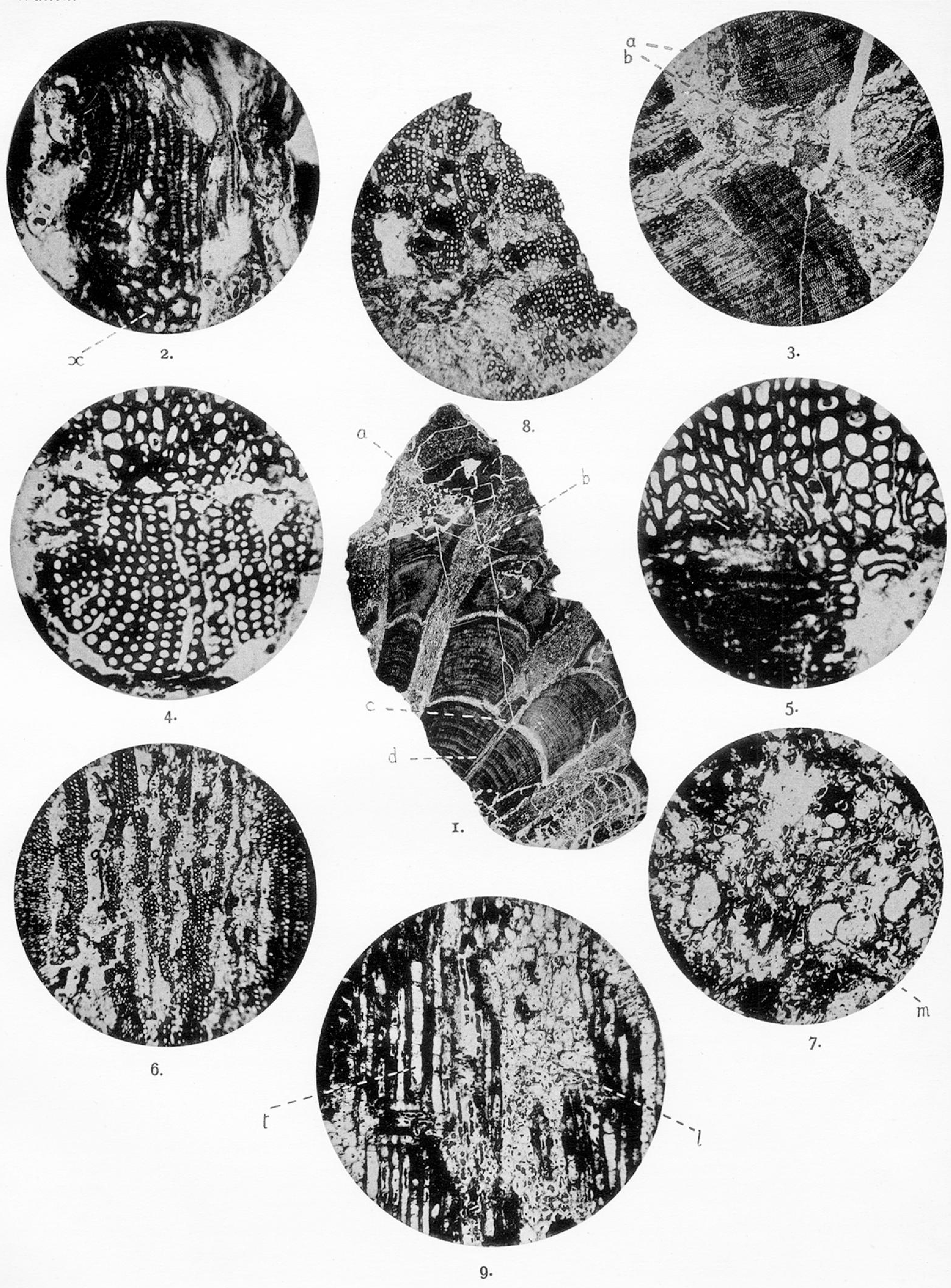

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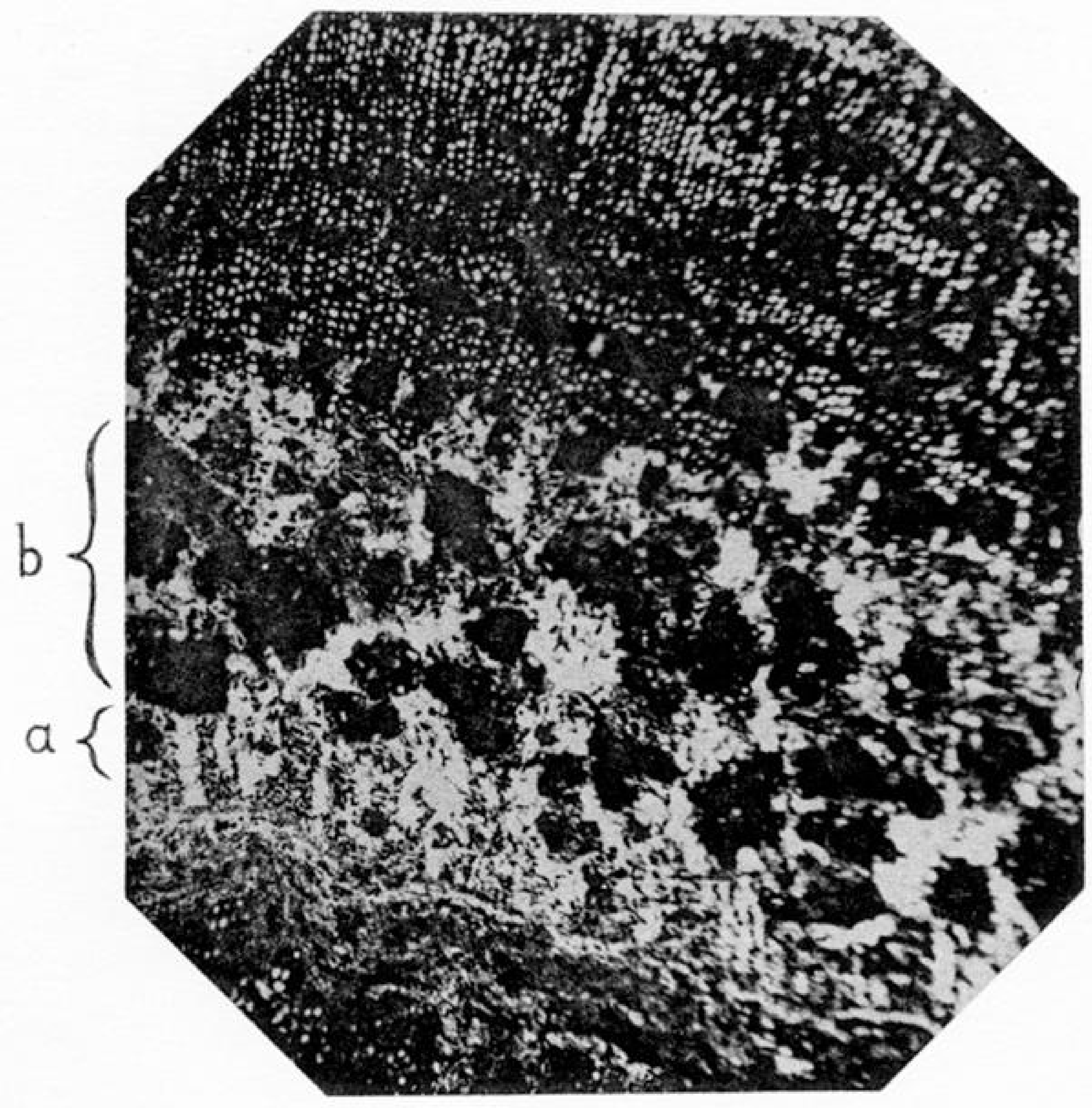

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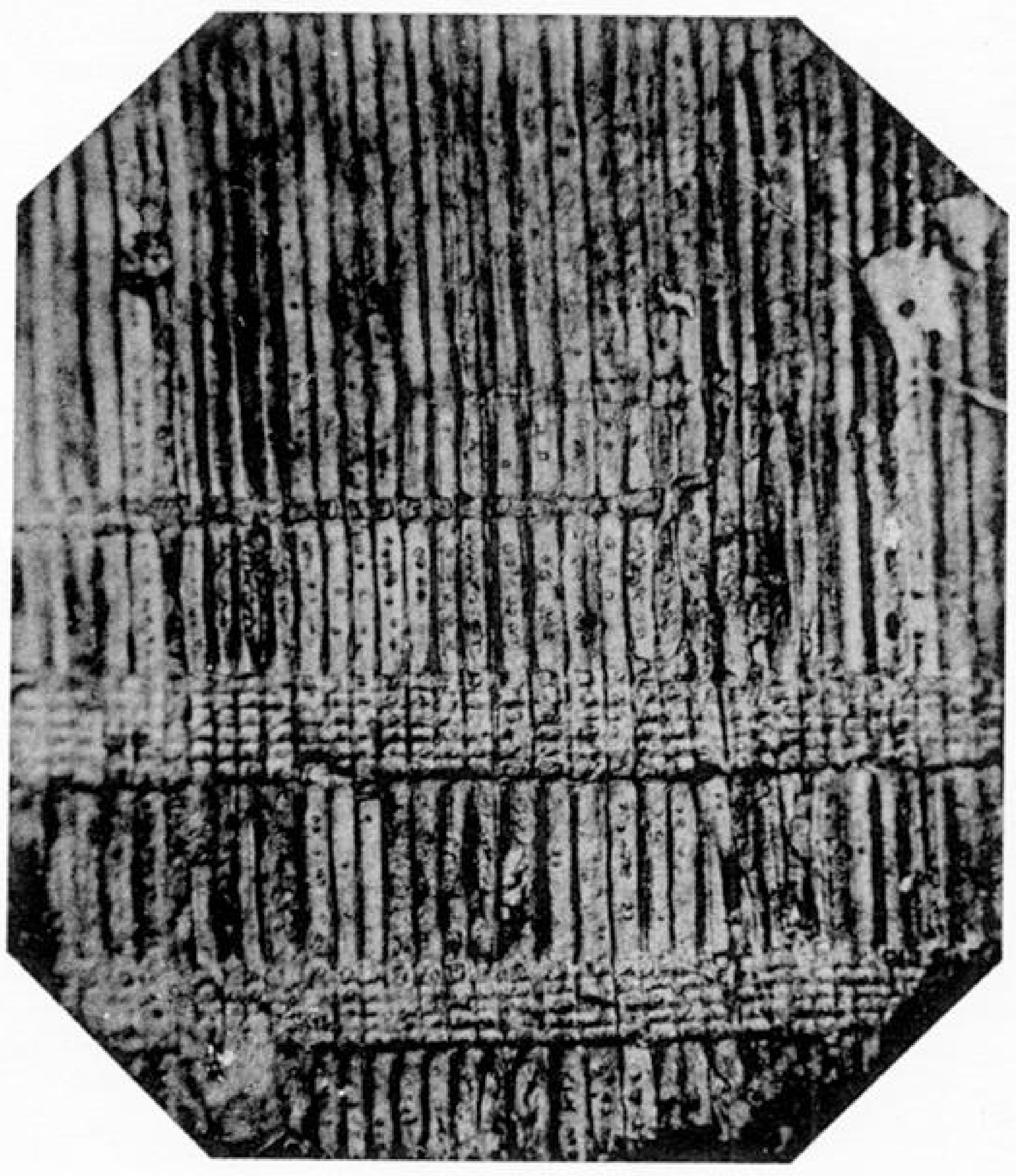

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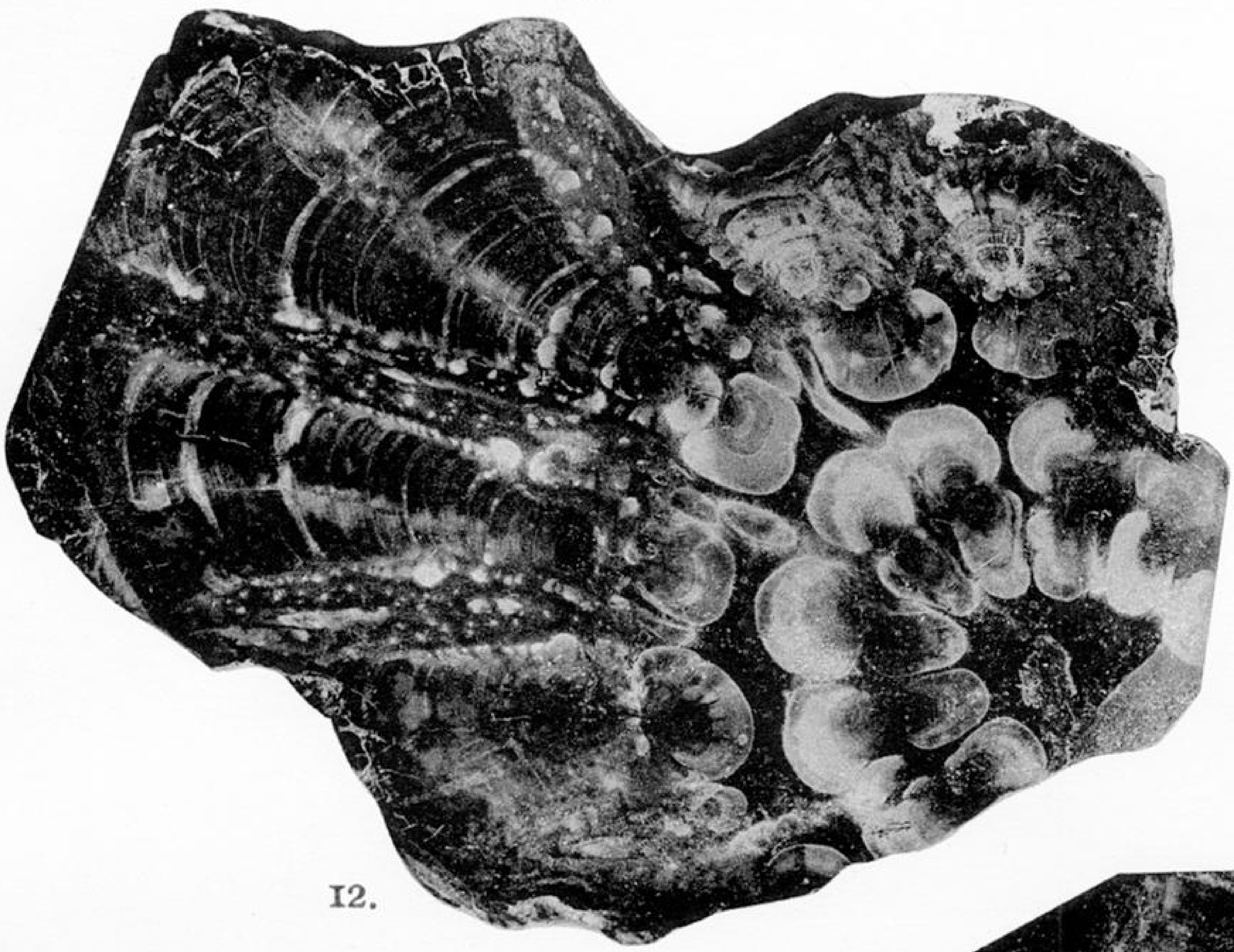

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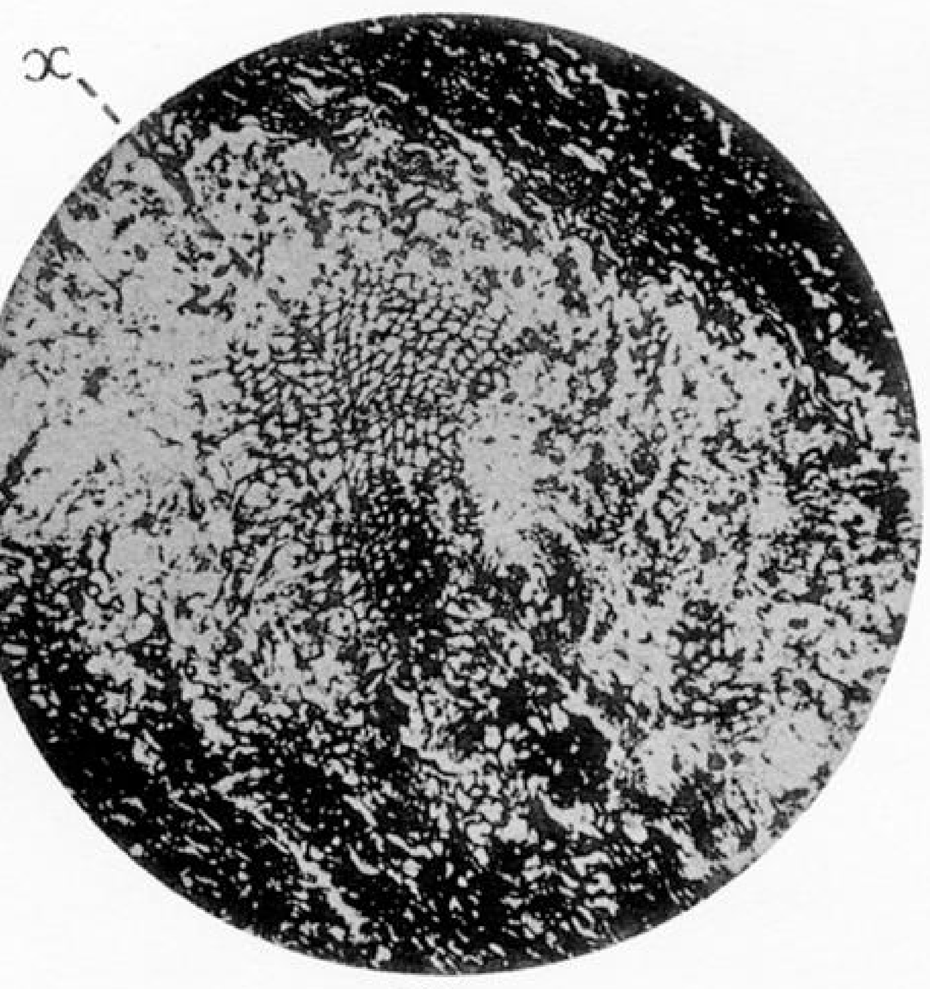

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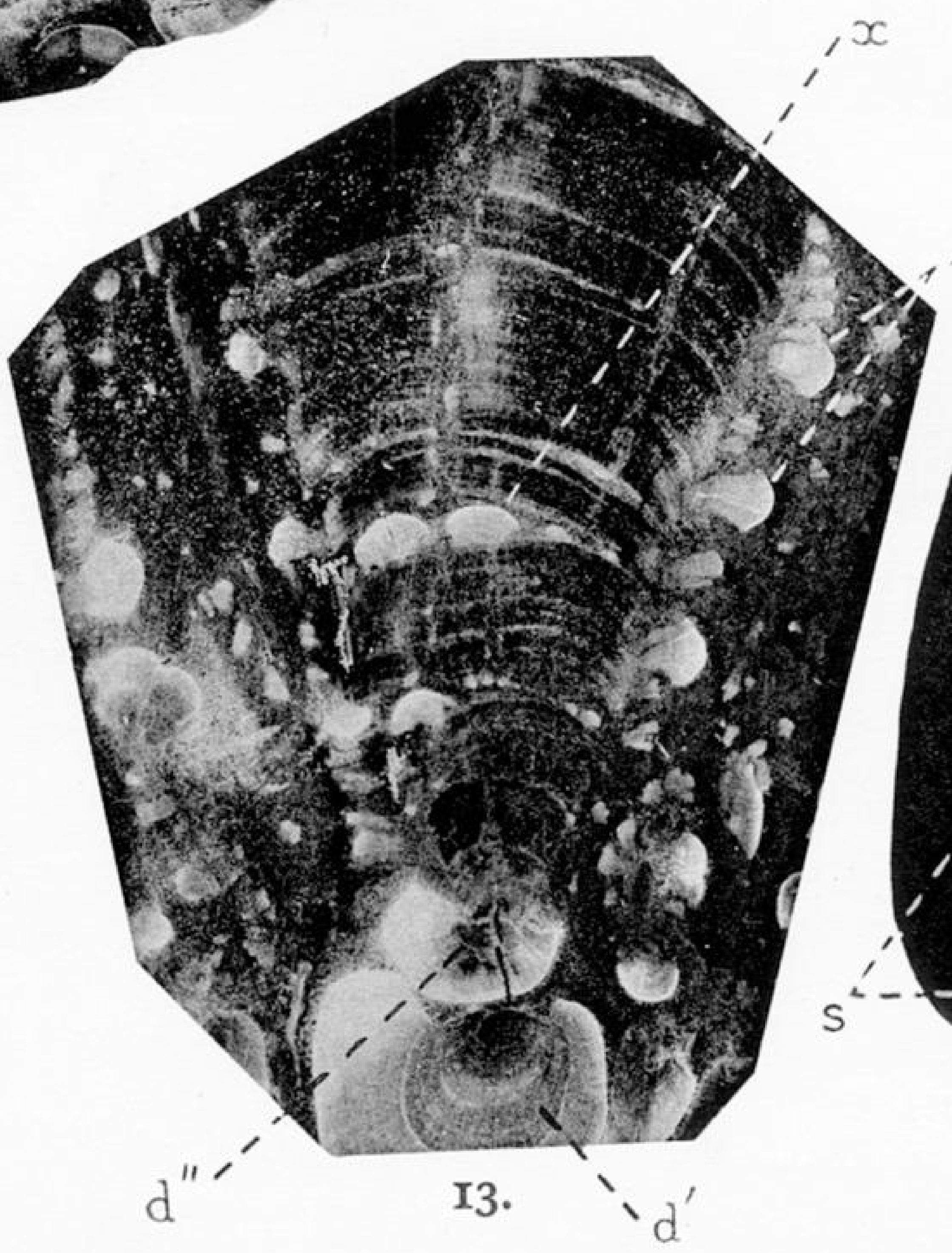

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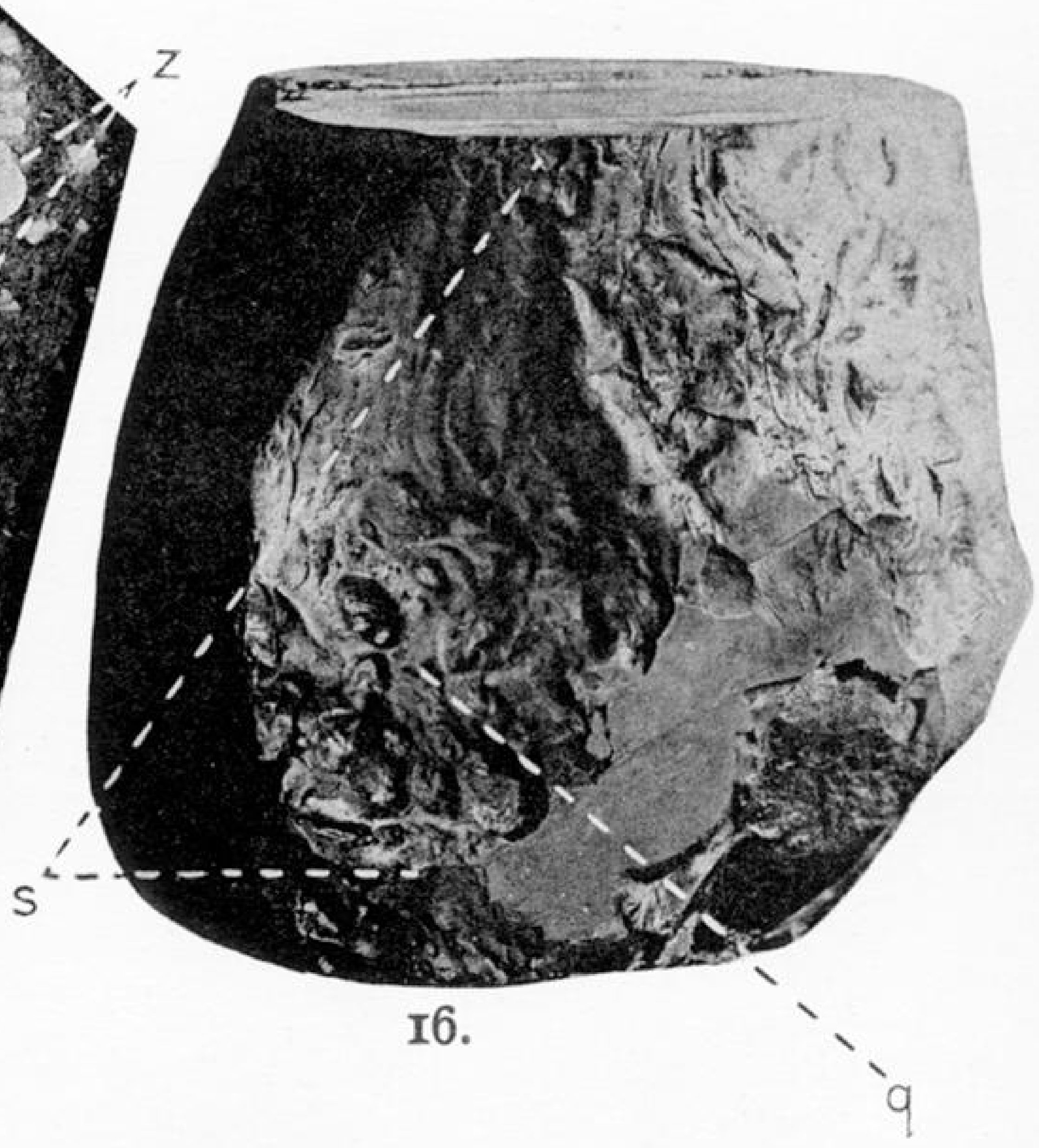

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