III. Rhexoxylon africanum, *a new Medullosean Stem.*

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(Plates 10 & 11.)

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I. INTRODUCTION.

THE specimen which forms the subject of this paper was sent to Prof. Seward by Dr. A. W. Rogers, the Director of the South African Geological Survey, as an unusual type of petrified stem-structure. The block was sent to Dr. Rogers without any information as to its locality or associations, but in his letter in reference to the fossil he writes:—"I have no doubt that the specimen came from the Cape." He adds: "It probably came from the Karroo rocks."

Since the Karroo Series ranges from the Dwyka boulder-beds and shales to the Stormberg Series—*i. e.*, in terms of European geological chronology, from the Upper Carboniferous (approximately) to the Rhætic or Lower Jurassic (5, pp. 233–243)—the exact age of the specimen must be left in doubt, so far as concerns evidence other than that supplied by the structural features themselves.

II. DESCRIPTION OF THE SPECIMEN.

(a) *External Characters.*

The specimen is silicified, and represents what is evidently a portion of a stem, the outer layers of which are absent. The length of the specimen before cutting was about 6·5 cm. and the diameters 7·2×5·7 cm., the structure being somewhat elliptical in transverse section (Pl. 10. fig. 1; Pl. 11. fig. 8).

Externally the fossil has an irregularly ribbed appearance, with vertical and alternating bands of varying width and of two different textures. The more outstanding bands consist apparently of a fairly porous and loose ground-tissue, while the alternate bands show fine vertical striations and are very compact (Pl. 11. fig. 1, *a* & *st*). These correspond to the irregular masses of compact texture which are seen on the transverse surface of the stem (Pl. 10. fig. 12), and which are evidently vascular structures.

The cut transverse surface shows general ground-tissue, more compact towards the interior of the stem than at the outer parts, where here and there it is very porous (Pl. 11. fig. 8). Embedded in this ground-tissue, mainly at the periphery of the block, are the masses of compact tissue mentioned above. Each of these is presumably a stele

or part of a stele, and each of the complete steles is more or less heavily outlined by a dark brown coloration of the adjacent tissues (Pl. **11.** figs. 3, 7, & 8).

Since it is impossible to know how much of the outer layers of the stem is lacking, the precise arrangement of the "steles"* must remain undetermined, although apparently one or more series were originally arranged peripherally. In addition to these, the central ground-tissue contains irregular isolated patches of tissue of the same compact structure and of varying size and shape. Situated near two steles belonging to what is considered as the inner series is an irregularly arched mass of the same tissue, consisting of two distinct parts (Pl. **10.** figs. 1, 8, 9, & 11; Pl. **11.** figs. 7 & 8).

A comparison of the cut and rough transverse sections of the block considered in connection with the outer surface-features shows that the masses of compact tissue run fairly regularly through the short length of stem without changing their position to any great extent, hence apparently without much branching or anastomosing. The cut vertical surface figured (Pl. **10.** fig. 13) shows the straight and independent course of two of the steles. The irregular arched mass mentioned above slightly changes its relative position with regard to the members of the inner series of steles.

(b) *Internal Structure.*

Several transverse sections were cut from one end of the block, one of them being practically complete. This will be referred to as Section A. Three incomplete sections were taken from the same original thick section as this, and are therefore in approximately the same plane. These, with another incomplete transverse section, cut about a centimetre higher, do not reveal any facts as to change of position, branching, or anastomosing of the steles. An almost complete section (referred to as Section B) cut from the other end of the block, its position being about 4 cm. below the first complete section, shows no change in general arrangement of the steles, and very little change in their individual outlines. The central arched mass is more irregular and broken up; while one of the steles of the inner series (stele 5; see Pl. **10.** figs. 3 & 10; Pl. **11.** figs. 7 & 8) assumes a different form, possibly in relation to the separation of a trace. It also moves slightly away from stele 4 towards stele 6 in passing from the level of Section A to that of Section B. All the sections give the same details of structure.

Section A, corresponding approximately to the cut surface of the block shown in diagram (*cf.* Pl. **10.** fig. 1 and Pl. **11.** fig. 8), shows eight complete steles (1–8) embedded in the ground-mass, one almost entire (9), and parts of four others (10–13), all belonging to what is termed the "inner series." In addition to these there are seven groups of vascular tissues (*a–g*), evidently parts of steles which are not completely represented. These seem to belong to an outer series. Here and there amongst the steles, and more or less in connection with them, particularly in the case of the inner series, are groups of xylem elements, possibly representing a leaf-supply system (Pl. **10.** fig. 1; Pl. **11.** figs. 3, 7, & 8). Finally, in the central ground-tissue are patches of vascular elements

* The term "stele" is used provisionally for convenience in describing the structure of the stem. See footnote to p. 48 of Dr. Scott's monograph on *Sutcliffia insignis*.

varying in size and form. In this central system is included the irregularly arched group of vascular elements mentioned above, the group as a whole consisting of two *distinct* parts separated by a thin line of ground-tissue. In the description of the individual masses of vascular tissue this will be referred to as the "central stele."

Pl. 11. fig. 7, a photograph of Section B from the opposite end of the block, shows the steles lettered and numbered as in Pl. 11. fig. 8 and Pl. 10. fig. 1.

Structure of the Ground-tissue.

Silicification has rendered the material so homogeneous and transparent that it is impossible to determine definitely the structure of the ground-tissue in which the steles are embedded. It seems, however, to have been composed of moderately large parenchymatous cells, not generally very compactly arranged, though the apparent loose structure is probably to some extent due to the shrinking together of the cells and the consequent production of large spaces. A similar process is described by Weber and Sterzel for *Medullosa* (13, p. 74). As before mentioned, the ground-tissue at the periphery of the block appears more porous than at the centre. This may be due to more marked shrinking and destruction of the cells in the outer tissues.

In the curve of the central "stele" is an irregularly oval mass of fairly compact ground-tissue surrounded by a band of varying width of what appears to be periderm (Pl. 10. figs. 1, 8, 9, & 11; Pl. 11. figs. 7 & 8). Here and there the cells of the band are seen to be tabular in transverse section and radially arranged (Pl. 11. fig. 6). The mass of tissue enclosed by the band of periderm varies in area at different levels, according apparently to the variation of the curve of the central stele (*cf.* Pl. 11. figs. 7 & 8; also Pl. 10. figs. 1, 8, 9, & 11). Other more or less circular or irregular bands occur here and there, as shown in Pl. 11. figs. 7 & 8, *pd*.

In Section B the band of periderm encloses a mass of ground-tissue containing scattered and erratic xylem elements; some of these are cut obliquely, some transversely, but the majority are seen in longitudinal section (Pl. 10. fig. 11, xy^b). The band of periderm itself encloses here and there patches of xylem elements transversely cut. There is no trace of accompanying phloem (Pl. 11. fig. 6, xy^a). A similar enclosure of xylem elements by periderm is figured by Dr. de Fraine (1, p. 1050, text-fig. 16) in the case of two leaf-trace bundles in a stem of *Sutcliffia*. The author suggests that the abnormal condition may be due to injury perhaps by fungal growth. It is difficult to account for the formation of xylem enclosed by periderm in the present case. In the parenchymatous ground-mass are occasional groups of sclerotic cells, these occurring particularly in the neighbourhood of the steles (Pl. 10. figs. 3, 7, 10, & 16; Pl. 11. fig. 4). There is no certain evidence as to the presence of secretory cells or gum-canals, although here and there are cells with dark contents which may possibly represent secretory elements.

Briefly, then, the ground-tissue consists, as far as may be determined, of large-celled parenchyma, with sclerotic nests and bands of periderm in the neighbourhood of some of the steles.

Structure of the Steles.

These are irregular in nature, in some respects recalling the plate-rings of certain Medulloseæ. The stele 3 of the inner series, as seen in Section A, is a fairly typical example (Pl. **10.** fig. 2; Pl. **11.** fig. 3). At first sight, the impression is given of a somewhat elliptical mass or bundle, apparently a single complete structure. On closer examination, however, this is seen to consist of two closely-developed though *distinct* parts, the inner being much larger than the outer. These are presumably the product of two cambiums, one giving rise to normally, the other to inversely, orientated elements. The fact that the outer and inner, or normal and inverse, parts are independent structures is demonstrated by a slight space between them, and by the lateral discontinuity of the brownish elements, which are considered to represent crushed cambium and phloem (Pl. **10.** fig. 2). The crushed tissue between the two masses shows here and there traces of vascular elements, and may represent a much reduced "partial pith" such as shown definitely in *Medullosa stellata*, Cotta, or *M. porosa*, Cotta (13, Taf. vii. figs. 1 & 4; p. 64, fig. 9), or it may represent ordinary ground-tissue with transfusion-cells, such as occurs in *Cycas*, between the normal and inverse bundles of the stem. On to this tissue abut what appear to be the protoxylems of the two masses (Pl. **10.** figs. 2 & 15). The inverse group shows a lateral projection, probably a leaf-trace about to separate. The direction of the xylem elements is here slightly oblique (Pl. **10.** fig. 2, *ob*; Pl. **11.** fig. 3). In the diagram the dark line marking the external borders of the xylem represents the brown crushed cells, probably the remains of cambium and phloem. In the case of stele 3 nothing could be determined with regard to the form and arrangement of these cells. In Section B stele 3 shows very little change in form and structure; a slight interruption in the continuity of the radial series of elements appears in the inverse part, which is larger in proportion to the whole stele than in Section A (Pl. **11.** fig. 7, *cf.* fig. 8).

A structure such as stele 3 may be compared with the plate-rings of *Medullosa stellata*, Cotta, which, it will be remembered, consist of a "partial pith" surrounded by secondary vascular tissues. In stele 3 the partial pith may be regarded as either much reduced in amount or crushed by subsequent secondary growth; while the lateral portions of the complete ring may have remained undeveloped by discontinuity of the cambium at these points. In this way a stele, consisting apparently of two distinct parts, may be derived from a complete ring of the *Medullosa stellata* type. Worsdell (14) considers that the so-called anomalous vascular structures in *Cycas* may be derived from Medullosean steles by local suppression of cambiums*, and the type of structure possessed by this South African stem may also have been produced in the same manner. Weber and Sterzel's figures (13, Taf. viii. fig. 3; Taf. iii. fig. 5) of *M. Solmsii*, Schenk, indicate a similar condition in some of the steles of that form, partial pith being reduced or practically absent, while there is also a smaller lateral development of the secondary tissues of the rings.

* See also Chodat ("Les Ptéridopsides des temps paléozoiques; étude critique," Arch. des Sci. phys. et nat. t. xxvi. 1908) and Matte ('Recherches sur l'appareil libéro-ligneux des Cycadacées': Caen, 1904) on this point.

Stele 4 (Pl. 10. fig. 3; Pl. 11. fig. 8) in Section A shows a very irregular type of development. Smaller normal and larger inverse parts (α and β) are present as before, but at one side these are so closely in contact as to appear almost continuous, the lateral break being less evident than in the case of stele 3. At the opposite side, however, the break is marked (Pl. 10. fig. 3). The position and arrangement of the xylem elements marked γ suggest that they belong to β, the inverse xylem; the apparent separation may be due to a break in cambial activity, such as mentioned by Dr. Scott for *Medullosa anglica* (7, p. 90). At the side of the inversely developed xylem is a small group of obliquely running elements, possibly a leaf-trace. The crushed tissue external to stele 4 shows no trace of structure; while between the normal and inverse parts, which, as the diagram shows (Pl. 10. fig. 3), are very closely in contact, the tissue is obliterated.

In Section B (Pl. 11. fig. 7) stele 4 still shows the break in the development of the inverse xylem. The inverse and normal parts show no distinct separation laterally, the elements swinging round and appearing oblique and confused.

Stele 5 (Pl. 10. fig. 3; Pl. 11. fig. 8) presents in Section A the same arrangement of normally and inversely developed elements, the product of two independent cambiums. The inverse group apparently consists of two parts, β and γ; the continuity of the medullary rays at one point, however, suggests that β and γ are not really independent, although the arrangement of the xylem elements shows evidences of a slight disturbance. At the other side, however, there is a distinct break in the continuity of the medullary rays and of the radial series of elements, owing perhaps to a change of direction of the cambium at that point, or to a temporary cessation of cambial activity. At the left-hand side, the inverse group shows a separating trace; and at the right, further towards the periphery of the stem, is a separate trace, of interest on account of a few well-preserved cells in the crushed tissue accompanying it on its external border. These cells have delicate walls, and show evidences of having been arranged originally in a radiating series. Their nature and position suggest that they are phloem-cells. Traces of similar cells occur in the crushed tissue in connection with the outer normal part of stele 5. No partial pith is present between the closely-developed normal and inverse parts of the stele. In section B, stele 5 (Pl. 11. fig. 7; Pl. 10. fig. 10) shows a considerable amount of change in form and structure. The normal part is much reduced and, like the inverse, shows discontinuity of development. The elements of both groups are more or less oblique in section. The inverse part shows a large limb, possibly a trace, bending round towards the partial stele *d*, the direction of the elements being usually oblique. On the inner edge of the limb, closely approximating partial stele *d*, the elements run horizontally and show spiral thickenings on their walls. They are evidently the protoxylem of the limb.

Stele 6, which in Section A shows a structure very similar to that of stele 3 (Pl. 10. fig. 4; Pl. 11. fig. 8), is considerably changed in form at the level of Section B (Pl. 10. fig. 10; Pl. 11. fig. 7). The inverse part shows the break in development as before, and at the left-hand side (towards stele 5) is a large, much broken-up limb or trace with scattered sclerotic nests between the groups of xylem elements. This trace approaches

the normal part of stele 5 very closely. It is impossible to say whether the two steles 5 and 6 are really distinct, for the appearances almost suggest an anastomosis between them. In stele 6, as in 5, the elements are mostly oblique in direction.

Stele 7 is more suggestive of a complete stele than any of the others shown in Section A. The break in continuity of development at the left-hand side is very slight, the chief evidence of it being a confusion of direction of the xylem elements here (Pl. **10.** fig. 5). It seems as if the outer and inner cambiums had almost joined at this point. At the right-hand side, however, where a trace is evidently about to separate from the inner mass, separation of the normal and inverse parts is very distinct. As usual, the structure of the tissues external to the xylem and between the two groups is obliterated. The transverse section from the opposite end of the stem-fragment includes only a small portion of this stele; its straight course, indicating but slight change of position or form, is shown by the vertical cut surface figured in Pl. **10.** fig. 13.

The other steles of the inner series, as shown in Section A, do not present any new points of structure (see diagrams of steles 8 and 9, Pl. **10.** figs. 6 & 7). In Section B, stele 9 shows the same outlines as in the first, 7 and 8 are incompletely represented, but their straight course and unbroken contours are shown in the diagram (Pl. **10.** fig. 13). The position of steles 6, 7, 8, 9, and 10 in Section B appears slightly closed in towards the interior of the stem as compared with their position in Section A (*cf.* Pl. **11.** figs. 7 & 8). Stele 10 is complete in Section B. It is much smaller than the others, consisting of a comparatively large, fan-shaped, inversely orientated part and a very small normal part. There is a slight indication of a partial pith, and both parts of the stele possess much of the brown phloem-like tissue (Pl. **11.** figs. 7 & 4).

Immediately external to the inner steles, at the periphery of the stem-fragment, are several portions of large masses of normally orientated xylem (Pl. **10.** fig. 1; Pl. **11.** figs. 7 & 8, *a–g*), representing presumably a second series of steles. They are evidently the product of independent cambiums, which, so far as can be judged from the form of the incomplete masses, must have had a more or less arched course, as in the case of the cambiums of the inner series of steles. The first-formed xylem elements of these masses are sometimes almost in contact with the inner steles; in every case the ground-tissue between the two series of vascular structures is crushed.

The members of the second series of xylem groups correspond to the small parts of the inner ring, having no inversely orientated groups pairing with them. They are thus, in terms of the inner series, "partial steles." Partial steles *c*, *d*, and *e*, as seen in Section A, show breaks in the xylem, the medullary rays and radial series of elements being discontinuous along certain lines, although the general direction of development remains the same after the break as before (Pl. **10.** fig. 3). This indicates a cessation of cambial activity for a time; or a new cambium may actually have arisen.

In association with the majority of these partial steles are patches and strands of xylem elements. In the case of *b* a large strand is seen in actual connection; but their nature, and in most cases their origin also, is extremely problematical. They may be developed by abnormal extensions of the cambium, or they may be ultimately connected

with the leaf-supply, although nothing could be decided on this point owing to the absence of the external layers of stem.

It is interesting to note that the direction of the xylem elements in these strands is very varied, for though the main masses in transverse section usually show transverse sections of the individual elements, the elements of the strands often run obliquely or horizontally, owing possibly to the extreme abnormality of the cambial growth (Pl. **10.** figs. 3 & 10). Crushed tissue occurs with some of the lateral strands, showing occasionally thin-walled radially arranged cells, as in the case of some of the inner steles. Portions of partial steles *a*, *b*, *c*, and *d* are shown in Section B (Pl. **11.** fig. 7). *a*, *b*, and *c* present practically the same appearance as in Section A. Partial stele *d*, however, shows great irregularity in structure (Pl. **10.** fig. 10). The xylem is much broken up and the direction of the individual elements frequently varies from vertical to horizontal within a small area. The appearances suggest that the stem has been locally injured, causing abnormality in the development of the neighbouring tissue. In one place a band of periderm-like tissue borders the outer margin of the main mass of xylem (Pl. **10.** fig. 10, *pd.*). Preservation is not sufficiently good to give any idea as to the formation of this tissue. It may be of the same nature as that described by Holden for *Myeloxylon* (3, p. 253). External to this is a band of badly preserved ground-tissue with sclerotic nests (*s*) and an isolated group of inversely orientated vacular elements (*vb*). Beyond this is a group of irregular xylem elements, apparently inversely developed, for a band of brown crushed tissue showing here and there traces of radial arragement appears on the *inner* edge of the group. The rest of the tissues of the partial stele are mostly oblique and show occasional breaks in development. A large trace appears at the left-hand side separated from the "trace" of stele 5 by a band of sclerotic nests. In the ground-tissue between the normal part of stele 5 and partial stele *d* are sclerotic cells and groups of variously orientated xylem elements accompanied by crushed tissue.

Other Vascular Structures of the Stem.

The central arched stele in Section A consists of two parts separated by rather more of the crushed and structureless tissue than occurs in the case of the inner steles (Pl. **10.** fig. 8). The larger part of the stele shows a change from vertically running elements at one extremity to horizontal elements in the thin elongated limb at the other. This limb swings round in a hook-like manner, the elements maintaining their horizontal course. In the smaller part of the stele (that towards the centre of the stem) the elements are more or less oblique in direction throughout. The crushed tissue considered as representing phloem outlines the external margins of the two parts. In the thin hooked limb of the larger, where the elements run horizontally, this tissue becomes twisted from the inner side of the hook to the outer side (Pl. **10.** fig. 8).

In one of the incomplete sections, slightly *above* the level of the complete Section A, only a trace of this hook is to be seen (Pl. **10.** fig. 9); while no trace of it appears on the cut surface of the block, which is slightly *below* the level of the section (Pl. **10.** fig. 1). Nor does the hook occur at the level of the section taken from the opposite end of the

stem-fragment, although there is a slight swinging round of the elements (Pl. 10. fig. 11). The break indicated in the smaller part of the stele in the complete Section A becomes more marked in passing through the stem to the opposite end of the block (*cf.* Pl. 10. figs. 8, 1, & 11). A break also appears in the larger portion of the stele. At the level of Section B the elongated limb beyond the break is fairly strongly marked, the xylem elements running more or less horizontally throughout its length. In the main part of the stele the xylem elements are oblique (Pl. 10. fig. 11).

The appearance of the central stele at the different levels indicates a probable sinuous and irregular course in a vertical direction.

It is interesting to note that opposite the ends of the central stele there are larger spaces than usual between the steles of the inner series; this is seen particularly in Section A (Pl. 11. fig. 8; Pl. 10. fig. 1). Whether or not it has any significance connected with the separation of traces from the central stele cannot be determined. Besides this structure the central ground-mass, particularly at the level of Section B, contains small isolated patches of xylem and crushed phloem arranged collaterally (Pl. 11. figs. 7 & 8) *. The course of the constituent elements varies from vertical to horizontal, the variation owing, no doubt, to the abnormality of cambial formation and growth indicated throughout the whole vascular system of the stem. It is difficult to estimate the significance of these bundles; they may be the remnants of a cauline vascular system, representing the "star-rings" of some Medulloseæ.

Structural Details.

In all the transverse sections the wood is seen to be compact and coniferous in type, resembling that of Cordaitean and Araucarian stems (Pl. 11. figs. 3 & 4). The steles and partial steles consist of radiating rows of tracheides, with uniseriate medullary rays, both primary and secondary, occurring at intervals. The number of rows of tracheides between the medullary rays varies from three to eight or nine. The tracheides are closely arranged and polygonal in shape; the lumen of each element is filled with layered siliceous material, this being less compact towards the centre (Pl. 10. figs. 14 & 15). In one or two cases the middle lamella may be seen (Pl. 10. fig. 14, *ml*).

The xylem masses are apparently endarch in structure; stele 3, for example, shows probable protoxylems in both normal and inverse parts at the extreme inner margins. The other steles of the inner series do not show the first-formed tracheides clearly. The partial steles of the second series, however, clearly show endarch structure (Pl. 11. fig. 2) and at their inner margins the medullary rays seem to widen slightly, although they apparently still consist of one row of cells.

In Section A the horizontally running elements of the limb of the central stele are spirally thickened in the majority of cases; a few have bordered pits. In Section B, where the limb is much larger, most of the elements show a double series of bordered pits (Pl. 11. fig. 5).

* See page 89, reference to enclosure of xylem in periderm.

The lack of structure in the tissue immediately external to the xylem has already been commented upon in dealing with the separate steles. Only here and there are indications of radial rows of thin-walled cells, presumably representing the phloem.

The longitudinal sections add very little to the facts already obtained from the transverse sections. The evidence of the latter with regard to the loose parenchymatous nature of the ground-tissue is confirmed; gum-canals or secretory sacs cannot be distinguished, but patches of sclerotic cells are fairly abundant, especially near the steles. The masses of xylem in longitudinal section show little evidence of branching or anastomosing (*cf.* steles 7 and 8 on cut surface, Pl. 10. fig. 13). In some cases small branches or traces, such as occur in the transverse sections, are seen separating. The brown tissue outlining the xylem is crushed and structureless, as seen in longitudinal sections.

The structure of the xylem may be determined only occasionally in the longitudinal sections. The tracheides have large bordered pits on their radial walls, typically in two alternating series (Pl. 10. fig. 17 *a*; Pl. 11. fig. 5), although here and there only one series, and in one or two cases three series, are present (Pl. 10. fig. 17 *b*). The pits are always in contact and are usually flattened, resembling those of the Cordaiteæ and Araucarieæ. Where the wood is cut tangentially sections of the bordered pits are seen, but the middle lamella is not definitely distinguishable in any of the cases noted. The medullary rays, as seen in tangential section, are fairly high, consisting of three or four to fifteen cells in a vertical series. Their uniseriate nature is clearly shown (Pl. 10. fig. 18).

In the main masses of vascular tissue there are no indications of protoxylem in longitudinal section, but in the ground-mass between two of the steles is a strand of xylem consisting almost entirely of spiral elements.

(c) *Summary of Structure.*

(1) The stem-fragment under consideration shows parts of two series of vascular structures embedded in a parenchymatous ground-mass, which also contains a central arched stele and many isolated patches of vascular elements; sclerotic nests and bands of periderm occur irregularly in the ground-tissue.

(2) Each of the "steles" of the inner series consists of two parts, the outer small and normally orientated, the inner larger and inversely orientated. The two parts are almost in contact, the tissue between being more or less obliterated.

(3) The members of the second series consist of normally orientated xylem only; they are therefore termed "partial steles."

(4) The steles pursue a fairly straight course through the short length of stem, apparently with little branching or anastomosing. Here and there traces are seen separating from the inverse portions of the inner series; while the lateral portions of the partial steles are much broken and irregular.

(5) The xylem is compact and coniferous in type, having the protoxylem elements at the inner margin of the masses.

(6) The xylem elements have bordered pits arranged typically in two alternating series. The pits are flattened and in contact, as in the Cordaiteæ and Araucarian conifers.

(7) The medullary rays, both primary and secondary, are uniseriate.

(8) The tissue accompanying the xylem-masses externally is much crushed, but occasionally shows traces of thin-walled cells, radially arranged. It is considered as representing phloem.

III. Affinities and Reference of the Specimen.

In many respects the stem-fragment shows an approach to certain members of the fossil group Medulloseæ, the structure of which is well known from the researches of Göppert and Stenzel (2), Weber and Sterzel (13), Solms-Laubach (11), Scott (7, 8, 9), and other authors. The forms included under the genus *Medullosa* have been arranged by Weber and Sterzel in form-cycles, each form-cycle being represented by a typical species with varieties which may or may not be quite distinct. The principal form-cycles are those of *M. stellata*, Cotta, *M. porosa*, Cotta, *M. Solmsii*, Schenk, and *M. Leuckarti*, Göpp. & Stenz. Evidently belonging to the same Medullosean family or plexus are forms from different horizons and showing certain differences in structure and histology from *Medullosa* itself. Such genera are *Steloxylon*, *Sutcliffia*, and *Colpoxylon*. The Cladoxyleæ are a distinct group showing certain points of resemblance to the Medulloseæ. The South African stem agrees most closely in general appearance, at least, with *M. Solmsii*. The characters of this form-cycle may be briefly summarised as follows (see 13, p. 73; Taf. iii. figs. 1–5; Taf. viii. fig. 3):—*M. Solmsii* shows typically two series of plate-rings, each ring representing a stele, and appearing to consist of a normally orientated and an inversely orientated mass of secondary tissue, the lateral portions of the ring being often poorly developed (see 13, Taf. iii. fig. 5; Taf. viii. fig. 3). In variety *typica* the normal and inverse parts of the external rings are equally strongly developed; var. *incrassata* has the normal part most strongly developed; and, lastly, in var. *lignosa* there are several zones of secondary wood and bast outside the two zones of plate-rings. In many cases the "partial pith" containing primary tracheides, and typically occupying the central part of a ring, is practically absent (13, Taf. iii. fig. 5; Taf. viii. fig. 3). It may have been originally insignificant in amount, or it may have become crushed during the life of the plant or during fossilisation (13, p. 74). It seems to have entirely escaped preservation in the cases where a distinct space is seen in the interior of the ring. *Medullosa Solmsii*, according to these authors, has the closest xylem-structure known in the genus *Medullosa* (13, p. 114); nothing seems to be actually known of the type of pitting of the tracheides in *M. Solmsii*, though in the genus, as a whole, multiseriate bordered pits are the rule. Phloem is not recognisable; the dark-coloured tissue surrounding the steles is almost structureless. In the interior of the stem *M. Solmsii* shows very small star-rings, and in the cortex also are similar structures arising from the inner series of plate-rings.

The age of *Medullosa Solmsii* and of other Continental species is Permian (13, p. 48); the English species, *M. anglica*, however, is of Lower Coal Measure age (7, p. 84).

In the case of the South African stem, the general appearance and arrangement of the innermost series of steles recalls that of the plate-rings of *M. Solmsii*, except that in the African type the inverse part is much more strongly developed than the normal part, possibly because towards the centre of the stem there is more space for such development to proceed after the second zone of xylem-masses has begun to develop, cramping the normal parts of the first zone. It has been shown, however, that there is variation in the relative degrees of development of the normal and inverse parts of the rings in *M. Solmsii*; while in *M. porosa*, in the case of the outer bundles of the pith (13, p. 70) and sometimes in *M. anglica* (7, p. 89), there is greater development of xylem towards the central parts of the stem. Further, in the South African stem the outer plate-rings are not represented, unless the portions of normally orientated xylem at the periphery of the fragment correspond to these, the inverse parts being absent. Or, these masses may belong to an outer zone of normally orientated tissue, such as occurs in *M. Solmsii*, var. *lignosa*, although in this form the zone is more or less continuous. The outer plate-rings in this case would be entirely unrepresented.

The new stem shows agreement with *M. Solmsii*, and differs from *M. stellata* and *M. porosa*, in the extreme reduction or at least non-preservation of partial pith and primary tracheides. There is a marked difference from *M. anglica*, the steles of which show a large primary mass of tracheides and parenchyma (7, p. 88). The isolated irregularly orientated xylem-groups which occur in the South African stem may be vestigial star-rings, comparable with those very generally present in the central ground-mass of *Medullosa* stems.

The bundles arising from the inner ring of steles in the new type may be of the same nature as the leaf-traces, which in *Medullosa* typically arise from the inner plate-rings. Their ultimate fate, however, cannot be decided, as no cortex is present.

Secretory canals, which are present in the central ground-tissue of *M. Leuckarti* (13, p. 133) and in the ground-tissue and pericycle of the steles in *M. anglica* (7, p. 96), have not been distinguished in the South African stem, nor can they with certainty be shown to occur in species of *Medullosa* other than the two mentioned.

Sclerotic nests are present in the ground-tissue of the African stem; according to Weber and Sterzel, however, their presence in the species of *Medullosa* is uncertain (13, p. 115). Sclerenchymatous bands, isolated in the ground-tissue, are mentioned by Scott for *M. anglica* (7, p. 96; pl. x. fig. 2); while for the same species internal periderm is described (7, p. 96; pl. v. figs. 1 & 3; pl. vii. fig. 13; pl. x. figs. 6 & 7), occurring in a continuous though irregular zone. In the African stem isolated bands of periderm occur apparently without definite purpose.

Owing to the variability and wide range of structure shown by *Medullosa* stems, the only distinct points of difference between them and the South African stem lie in the compact wood of the latter, with its uniseriate medullary rays, and in the pitting of the tracheides. In the new specimen the biseriate pitting of the tracheides resembles that exhibited by the Cordaiteæ and Araucarieæ rather than the multiseriate type

occurring in the species of *Medullosa* and in Pteridosperms generally. It is unfortunate that, as mentioned above, nothing is known of the pitting in *M. Solmsii*, which shows an approach to the South African stem in the more compact nature of the xylem and also in the apparent reduction of "partial pith."

Steloxylon Ludwigii, a stem of doubtful Permian age, is another member of the Medullosean group. It was first somewhat superficially described by Göppert and Stenzel as *Medullosa Ludwigii* (2, Taf. xvii. figs. 18–20; see also 6, Taf. i. figs. 1–16; and 12, Taf. iii. figs. 6 & 9); it exhibits a homogeneous ground-tissue with usually roundish or elliptical steles. Some are, however, considerably elongated and arranged somewhat radially, instead of tangentially as in the case of the plate-rings of *Medullosa*. The structure of the ground-tissue is not clear, but appears to have been parenchymatous. The medullary rays of the wood are of varying heights, and are uni- or biseriate, separating groups of two or three series of tracheides. The tracheides bear roundish oval bordered pits in one or more rows. Phloem is not preserved; while the steles have a partial pith, the structure of which is not clear. *Steloxylon Ludwigii* differs from the species of *Medullosa* and from the South African stem in the arrangement of the steles. It approaches the new type in the pitting of the tracheides, but differs from it in the less constantly uniseriate nature of the medullary rays and in the definite presence of a partial pith (12, p. 552).

Sutcliffia insignis, from the Lower Coal Measures of Shore, is considered by Scott (8) to be a probable primitive type of Medullosean stem. The recent work of Dr. E. de Fraine indicates its affinities with *M. anglica*. It possesses a large central stele, very similar in structure to a single stele of *M. anglica*. From the main stele arise subsidiary steles at intervals. Phloem is well preserved, and the tracheides usually possess multiseriate bordered pits. *Sutcliffia* is not comparable with the South African stem, except through other members of the Medullosean group.

Colpoxylon, represented by the species *C. æduense*, Brongn., has been described by Renault as coming from the Permian of Autun (4, pl. 67, figs. 1 & 2). It is in agreement with regard to structure with some of the simpler Medulloseæ, but it is monostelic for some length of the stem. It is perhaps an aberrant *Medullosa*, and like *Sutcliffia* is only indirectly comparable with the South African stem.

The Cladoxyleæ are a group of forms (*Cladoxylon* and *Völkelia*) approaching the Medulloseæ in the possession of numerous steles. Solms described the structure of *Cladoxylon* in 1896 (10) and of *Völkelia* in 1910 (12). The group differs from the Medulloseæ in the arrangement of the steles, which are usually more or less radially disposed (cf. *Steloxylon*), and also in the minute structure of the wood, the tracheides usually having scalariform pits. The age of the group is Devonian or at least early Palæozoic. Scott concludes that the Cladoxyleæ and Medulloseæ have no intimate relation, but they probably present a case of parallel development, showing superficial resemblances to each other in the possession of many steles (8, p. 64; 9, p. 497).

Cladoxylon Kidstoni, however, deserves mention on account of an approach in certain characters to the South African fossil. It has been described by Solms-Laubach as coming from the Lower Carboniferous of Berwickshire (12, p. 537). As the stem-

fragment is very small (2·4 cm. × 2 cm. diam. and 1·3 cm. long), only four steles and part of two others being represented, it is impossible to determine the original arrangement of vascular structures. If anything may be judged from the position of those present, however, it would seem that they were more or less radially arranged—that is, the narrow partial pith lay in a radial direction. The steles are almost complete rings; only at one pole of the partial pith is the continuity of the secondary growth broken, and at this point, in the case of two of the steles, is attached a peculiar wing-like mass of secondary elements, probably representing a trace. In one instance, the wing is less closely in contact with the main stele and has divided into two parts (12, Taf. iii. fig. 5). At the other pole of the stele, secondary growth shows its greatest development. The partial pith is narrow and, like the phloem, usually not preserved: in one case its cellular nature may be determined (12, Taf. iii. fig. 11). The steles pursue a fairly straight course, so far as can be determined from the fragment. The wood is compact, with uniseriate rays separating groups of from two or three to eight or nine rows of tracheides (12, Taf. iii. fig. 11). In this there is agreement with the South African fossil. The chief feature of interest in *C. Kidstoni*, from the point of view of comparison of the two types, lies in the pitting of the tracheides. The radial walls possess typically a single series of elongate-elliptical bordered pits, giving a scalariform effect (*cf.* character of the group Cladoxyleæ). Here and there, however, often in the same tracheide with the single series, a double row of bordered pits occurs (12, Taf. iii. fig. 7) *, the pits being either alternate or opposite—they are always flattened and in contact. In the case of alternate pitting the appearance is very similar to that presented by the tracheides of the South African fossil. This cannot, however, be regarded as indicating any relationship between the two types, which show points of dissimilarity in other respects, such as stelar organisation. *C. Kidstoni* is interesting, in that the pitting of its tracheides points to a transition from a simpler more fern-like type to that exhibited by the South African fossil, Cordaiteæ, and Araucarieæ. The Cladoxyleæ need not be considered so far as the closer relationships of the new type are concerned, but must be mentioned with the Medulloseæ as representative of the plexus of polystelic types to which the stem under consideration is apparently referable.

With regard to the wider affinities of the new specimen, it is possible that the biseriate Araucarian type of pitting exhibited by its xylem elements indicates a point of contact more or less remote with the ancestral forms of the Araucarieæ. The combination of Araucarian pitting of the xylem elements with the Medullosean arrangement of steles is interesting, and the possibility is suggested that there may have existed other simpler or even monostelic forms, as yet unknown, also exhibiting Araucarian pitting, and that from these or their ancestral stock the Araucarieæ may have been derived either directly or indirectly. It is extremely unsafe to base any conclusions upon the pitting of the xylem elements, for how far such a character may serve as a criterion in the consideration of relationship between types is not as yet thoroughly understood, and the above suggestion is made with due regard to this fact. It is, however, interesting

* In Solms-Laubach's figures the bordering of the pits is not shown.

in that it provides a parallel case to that put forward by Miss de Fraine (1) for the Cycadaceæ, which she considers may have originated from a monostelic Medullosean form typified by *Sutcliffia* *, which shows a more Cycadean type of pitting.

The age of the South African specimen, as has been shown, is doubtful, but its structure justifies its reference to the Palæozoic era, while its agreement in general anatomy with the Continental Medulloseæ rather than with the earlier English types is consistent with reference to an Upper Permian horizon.

From early Palæozoic to Permian times there seems to have been a plexus of types showing polystelic structure, and the South African stem may be included as a member of this plexus. To recapitulate its probable affinities:—The stem seems to agree most closely with the genus *Medullosa*, which is recognised as showing considerable variation of stelar structure. It differs from the typical species †, however, in the extreme reduction of the partial pith, in the general coniferous texture of the xylem with its compact structure and uniseriate rays, as well as in the pitting of the elements, which in this respect resemble those of the Cordaiteæ or the Araucarian conifers. *Steloxylon* is approached chiefly in the type of pitting of the tracheides, but it differs in the less definite arrangement of the steles and in the presence of a partial pith—this being much reduced in the South African stem.

These differences, united to the facts that the horizon and locality of the stem-fragment are indefinite and that its associations are indeterminable, sufficiently isolate it from all hitherto-described types to render its reference to any one of them undesirable. Further, this fossil appears to be the first, and so far the only, specimen of a stem of this nature known from the Southern Hemisphere, so that it seems justifiable to institute a provisional genus for its reception and to include the genus in the family Medulloseæ.

The generic name *Rhexoxylon* ‡ is suggested as being descriptive of the broken-up nature of the vascular structures of the stem.

IV. Summary and Diagnosis.

(1) *Rhexoxylon africanum*, a stem-fragment of doubtful later Palæozoic age, from an unknown South African locality, is described and diagnosed as follows:—

Rhexoxylon, nov. gen.

Vascular system of the stem consisting of an inner ring of elliptical steles, each composed of a large inversely orientated part, from which traces are given off, and a small normal part; external to these a series of "partial steles" consisting only of normally orientated elements; the lateral margins of these partial steles often much broken by the separation of traces. Xylem compact, having spiral elements on the inner margin;

* *Cf.* Worsdell's views on the origin of Cycadean structures.

† *M. Solmsii* must be excepted. Note remarks on p. 96.

‡ Gr., ῥηγνυμι—I break up.

metaxylem elements typically with biseriate bordered pits. Medullary rays uniseriate. Ground-tissue parenchymatous, with scattered and irregular vascular strands, bands of periderm, and sclerotic nests.

R. AFRICANUM, nov. sp.
Characters of the genus.

(2) The general structure of *Rhexoxylon africanum* suggests relationship with the genera *Medullosa* and *Steloxylon*, and the new genus is included in the family Medulloseæ.

In conclusion, the writer's expressions of gratitude are due to Professor Seward for help and advice during the above investigation; and also to Dr. R. Kidston for slides of *Cladoxylon Kidstoni* which he kindly lent for comparison with the South African stem.

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EXPLANATION OF THE PLATES.

PLATE 10.

Figures 1–12 diagrammatic, figures 14–18 drawn with the aid of a camera lucida.

Fig. 1. Transverse surface of the stem, after cutting, showing the main features (*cf.* Pl. **11.** fig. 8, a photograph of the complete Section A, taken from this surface, and representing a level slightly higher in the stem): 1–13, steles of the inner series; *a–g*, partial steles of the outer series. Nat. size.

Figs. 2–8. Transverse sections of the vascular structures of the stem, drawn from the complete Section A, shown in Pl. **11.** fig. 8. Comparison should be made with this and with fig. 1 for the relative positions of the vascular masses of the stem. *tr* signifies transverse section of the xylem elements; *ob*, oblique section; and *lg*, longitudinal section. The shaded outlining of the steles indicates the brown crushed tissue.

Fig. 2, stele 3 of the inner series: *pm*, partial pith; *px*, protoxylem; at *ob* a trace is seen separating from the larger inverse part of the stele. Fig. 3, steles 4 and 5 of the inner series, and partial steles *c* and *d* of the outer series: α and β, normal and inverse xylem, respectively, of the inner steles; γ, xylem evidently belonging to β, but more or less separated from it by breaks in the continuity of the radial series of elements: similar breaks are seen in partial stele *c*; *s*, sclerotic nests. Figs. 4, 5, and 6, steles 6, 7, and 8, respectively. Fig. 7, stele 9, showing sclerotic nests in the crushed tissue at *s*. Fig. 8, central stele; *pd*, bands of periderm. Figs. 2–7, ×3; fig. 8, ×5.

Fig. 9. Central stele, at a slightly higher level than fig. 8. (From an incomplete Section.) ×5.

Figs. 10 & 11. Vascular structures at the level of Section B, shown in Pl. **11.** fig. 7. Fig. 10, steles 5 and 6 of the inner series, and partial steles *d* and *e* of the outer series: *vb*, isolated and irregular vascular strands; other lettering as before. ×3. (*Cf.* figs. 3 & 4.) Fig. 11, central stele: xy^a, xylem elements enclosed in periderm; xy^b, xylem elements scattered in ground-mass. ×5. (*Cf.* figs. 8 & 9.) For the position of the central stele as shown in figs. 8, 9, & 11, relative to that of the other vascular structures of the stem, refer to fig. 1 and Pl. **11.** figs. 7 & 8.

Fig. 12. Diagram showing the relation between the vertically striated bands of the outer surface of the stem (*cf.* Pl. **11.** fig. 1) and the vascular masses of the cut transverse surface. Nat. size.

Fig. 13. Portion of a tangential longitudinal surface, showing the straight course of two inner steles (7 and 8): *a*, ground-mass. Nat. size.

Fig. 14. Xylem elements, showing the layered siliceous filling of the cell-cavities (see also figs. 15 & 18). Note indication of middle lamella, *ml*. ×450.

Fig. 15. Protoxylem group of stele 3 (*cf.* fig. 2). ×450.

Fig. 16. Sclerotic nests in the crushed tissue of stele 9. ×90. (*Cf.* fig. 7, *s*, and Pl. **11**, fig. 4.)

Fig. 17. Pitting of the tracheides: *a*, typical; *b*, from the limb of the central stele. ×280. (*Cf.* Pl. **11.** fig. 5.)

Fig. 18. Tangential section of xylem, showing the uniseriate medullary rays. Note the layering of siliceous material in the cells of the rays. ×280.

Plate 11.

Fig. 1. A photograph of the decorticated stem-fragment, showing the external appearance: *a*, ground-tissue; *st*, stelar tissues. Nat. size.

Fig. 2. The inner margin of partial stele *b*, showing protoxylems (*px*) and uniseriate medullary rays (*mr*). × 70.

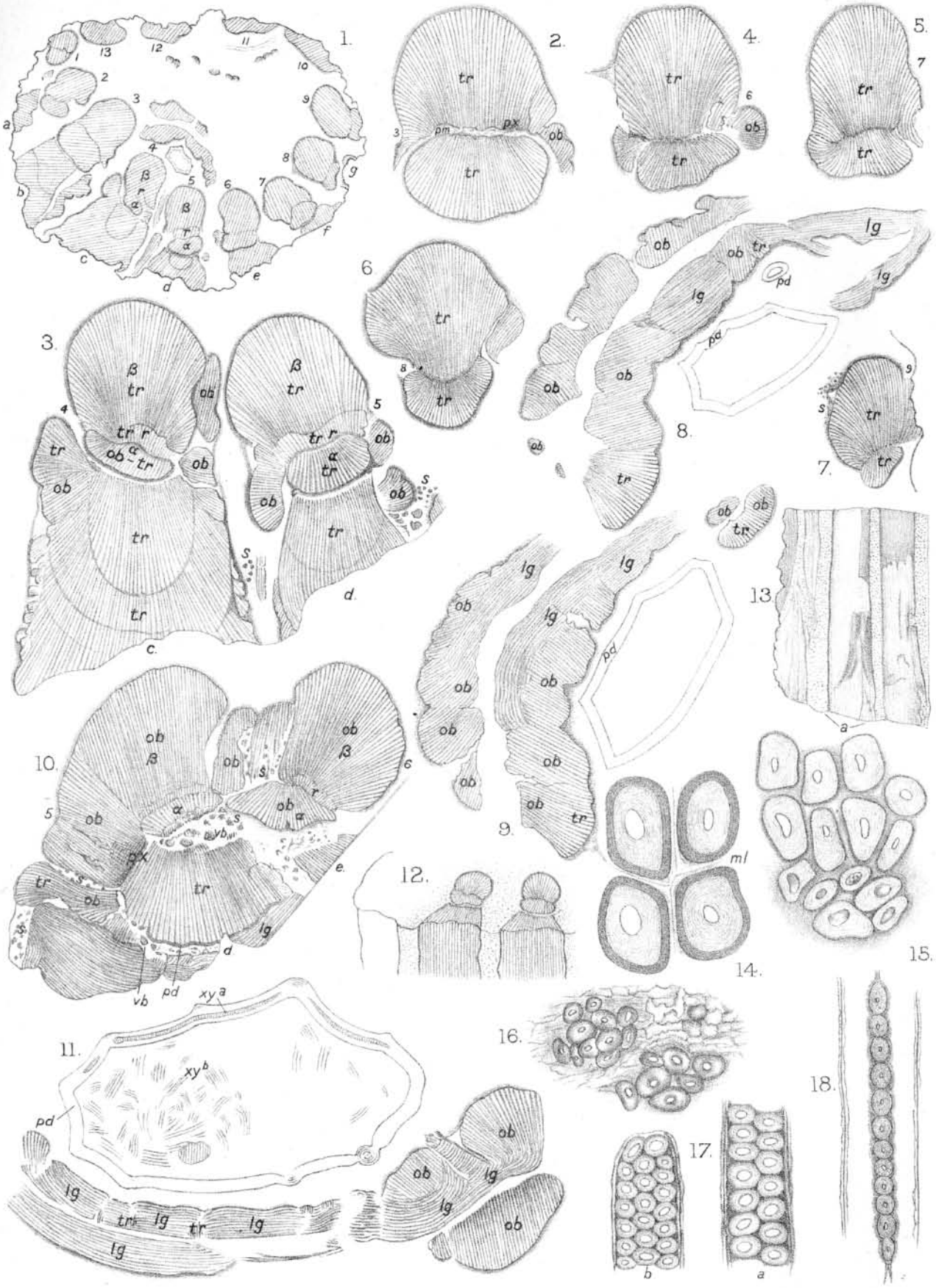
Fig. 3. Stele 3, from Section A (*cf.* fig. 8), a fairly typical example of an inner stele: *t*, trace; *pm*, partial pith. × 5. Note the arrangement of the xylem elements and the outlining of dark crushed tissue.

Fig. 4. Brown tissue of stele 10 (from Section B), showing radial arrangement of elements: *s*, sclerotic nests. × 70. Note the structure of the xylem, with uniseriate medullary rays.

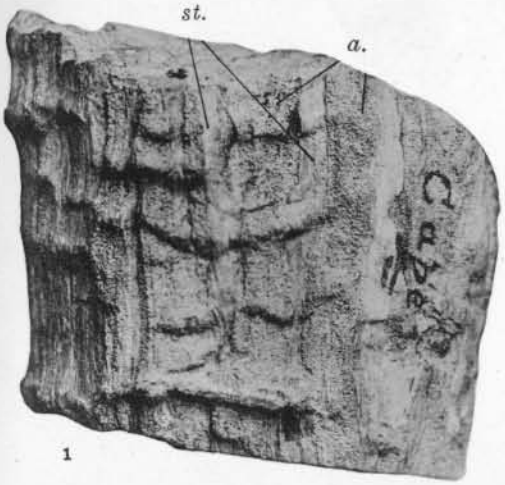
Fig. 5. Xylem elements, showing biseriate pitting. × 325.

Fig. 6. Portion of periderm band in arch of central stele (Section B). The periderm (*pd*) encloses a strand of xylem elements (xy^a). × 70. (*Cf.* Pl. **10**. fig. 11.)

Figs. 7 & 8. Sections B and A respectively. × 2. Steles and partial steles are numbered and lettered as in Pl. **10**. fig 1: *cs*, central stele; *pd*, epiderm bands; *vb*, isolated vascular strands.



RHEXOXYLON AFRICANUM.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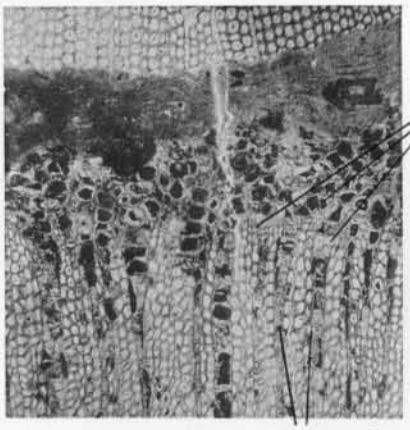
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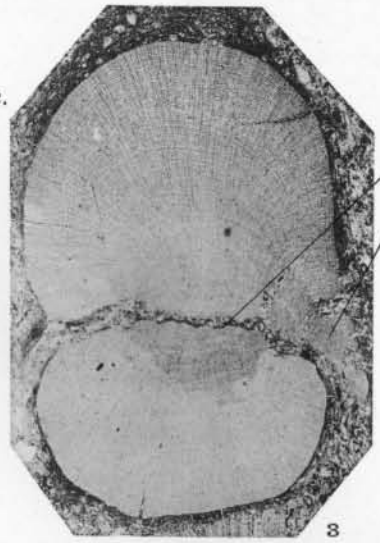
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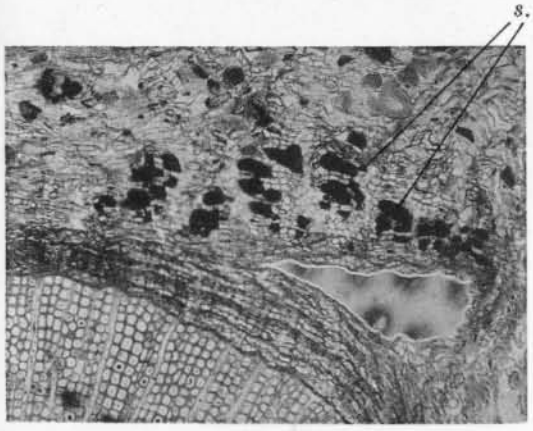
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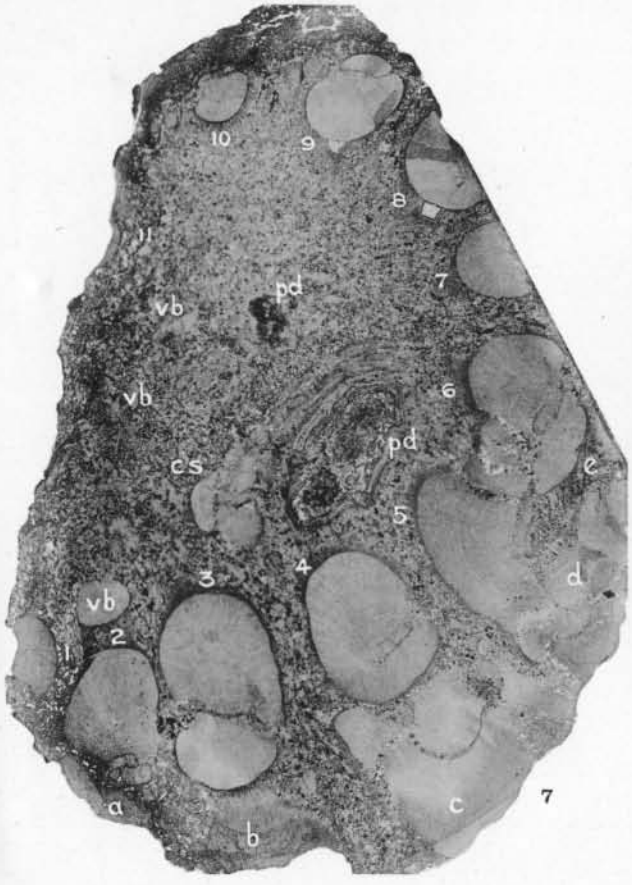
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