# STUDIES ON TRIASSIC FOSSIL PLANTS FROM ARGENTINA III. THE TRUNK OF *RHEXOXYLON*

*by* DONALD W. BRETT

ABSTRACT. The occurrence of plant fossils in the Ischigualasto region in north-west Argentina is discussed in relation to the geology of the area. Specimens of large trunks of *Rhexoxylon piatnitzkyi* from the Ischigualasto formation are described and the peculiar secondary growth processes of the plant are discussed with reference to this new material.

THE Triassic fossiliferous beds of north-western Argentina have long been known as a source of fossil plants, many of which have been described by the Argentine palaeobotanist J. Frenguelli and others. A full bibliography is given in Archangelsky 1965.

Extensive exposures occur in Mendoza and San Juan provinces and over an area of some 1,750 km.$^2$ centred on Ischigualasto in the Sierra del Valle Fertíl along the boundary between the provinces of San Juan and La Rioja (approximately lat. 30° S., long. 68° W.).

In the two preceding papers of this series, petrified stems of *Rhexoxylon* and *Michelillo*a, a cycad, were described from Ischigualasto (Archangelsky and Brett 1961, 1963). The occurrence of *Rhexoxylon* in Argentina is of special interest since along with recent finds of vertebrate remains in the same beds (Reig 1959, Romer and Cox 1962, Cox 1965) it suggests a correlation of the Ischigualasto formation with the Molteno and Red Beds of the Stormberg Series in Africa from which *Rhexoxylon* had been described previously (Archangelsky and Brett 1961). In 1961 the present author accompanied Drs. Sergio Archangelsky and Rafael Herbst on expeditions to the several Triassic exposures and collected additional material of both petrified and carbonized plants. At Ischigualasto a detailed record was kept of localities and stratigraphical position of the fossils and some relevant data is included in the present report.

### *Fossiliferous localities at Ischigualasto*

The concordant series of Triassic sediments exposed in the Ischigualasto region has been referred to as the 'Ischichuca-Ischigualasto Series'. Since both these names are used separately for formations it is proposed to call the series the Agua de la Peña series, and so avoid possibility of confusion (Archangelsky, personal communication).

The Agua de la Peña series comprises four formations attaining a total thickness of some 1,300 m. (Groeber and Stipanicic 1953).

| | |
|---|---|
| Los Colorados | 150 m. |
| Ischigualasto | 550 m. |
| Los Rastros | 400 m. |
| Ischichuca | 200 m. |

The strata have been little affected by tectonic movements. Over the whole area they dip 7–10° to the north-east. All four formations are fossiliferous but only in Los Rastros and the Ischigualasto are the fossils abundant and reasonably well preserved.

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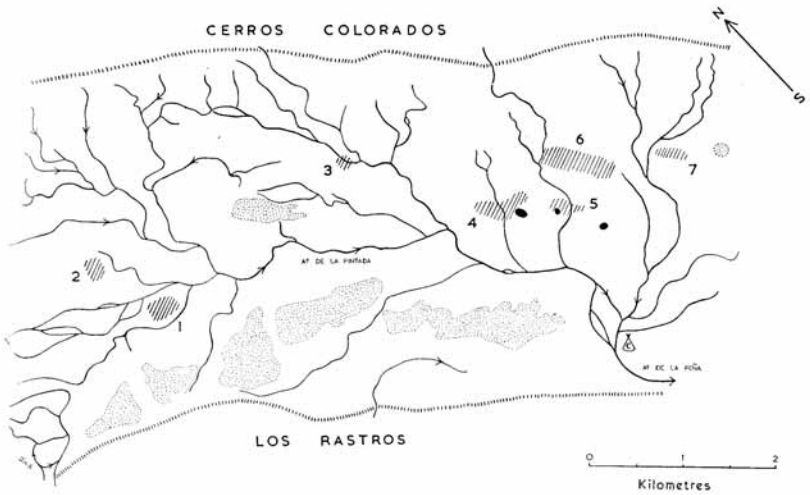
The Ischigualasto formation consists mostly of sandstones, fine conglomerates, and tuffs in rhythmic successions. It is separated from Los Rastros formation in the Agua de la Peña region by a thick bed of coarse conglomerate (La Peña Conglomerate), but this bed thins out westwards until the two formations intergrade. There is likewise an insensible transition between the uppermost Ischigualasto beds and the red sandstones of Los Colorados formation.

The Ischigualasto sediments are exposed in a desert basin (map) dominated by the cliffs of the more resistant strata of Los Rastros and Los Colorados formations. The fossil




MAP. Part of the Ischigualasto basin showing the main fossiliferous areas in the Ischigualasto formation numbered 1 to 7. For further account of these see text. Stippled areas indicate the major terraces, and the smaller black areas sand dunes. The camp site near the Agua de la Peña is indicated by the wigwam symbol. (Map based on plane table survey prepared under the direction of Rogelio Bellman.)

plants occur in a medium- to coarse-grained limonitic sandstone, and in a soft grey shale which usually underlies the sandstone. These facies are lenticular and do not always contain many fossils. The fossil vertebrates are not confined to these facies.

Seven localities where fossil plants are abundant are shown on the map of the Ischigualasto basin. The localities are numbered according to their stratigraphical succession from the lowest upwards.

In the lower beds only carbonized leaves were found, but these are plentiful. At 1 the fossiliferous beds attain a thickness of over one metre. At both 1 and 2 they consist of compact layers of black plant compressions in a sandstone matrix and are conspicuous from a distance because where they outcrop they show as dark and yellowish bands across the grey detritus.

At the remaining localities 3, 4, 6, and 7, both compressions and petrifactions occur, often closely associated. No great differences have been found in the assemblages of carbonized remains (compressions) at any locality except 5 where they are exclusively

equisetalean. The carbonized leaves will be described by S. Archangelsky in the following paper in this series.

Many large trunks occur at locality 4 and fewer at 3, 6, and 7. Most of the trunks are of *Rhexoxylon* and, usually, it is the broad basal part which is exposed on the surface, the rest of the trunk being buried owing to the dip of the rock.

At 4, 6, and 7 some of the trunks were found on microscopic examination to be of a conifer-type, though *not* araucarioid. (Similar trunks occur at Uspallata near Mendoza in the Potrerillos formation.)

At locality 6, along with the large specimens of *Rhexoxylon*, were found additional fragments of *Rhexoxylon piatnitzkyi* Arch. and Brett and of the cycad *Michelilloa waltonii* Arch. and Brett.

Los Rastros and Los Colorados formations appear to be of less importance as sources of petrified plants, although carbonized leaves have been described from Los Rastros by Frenguelli. These are found in grey shales, in sandstones, and in thin coaly layers exposed in the gorge of the Rio de la Peña. They are mostly fragmentary, however, and a few petrifactions that I have seen are too poorly preserved for adequate description.

Los Colorados formation is almost barren and no plant fossils have previously been recorded from these strata. There are several large silicified trunks, some reaching a length of 12 m., on the plateau overlooking the Ischigualasto basin. The wood, although not well preserved, is seen on microscopic examination of flakes to be araucarioid. Bonaparte (1960) has described fossil vertebrates from this formation.

*The trunk of Rhexoxylon*

Although the peculiar arrangement of the woody tissue in *Rhexoxylon* resembles that of certain extant lianes (Walton 1923) the size of some of the African specimens has made it clear that the adult plants had large upright trunks which could not have belonged to climbing plants (Walton 1956). Some of the largest fragments of *R. africanum* that have been described have a woody cylinder about 50 cm. across while the wood of *R. tetrapteridoides* is known to have attained a diameter of 16 cm. in the largest specimen figured by Walton (1923, text-fig. II, 3). The general features of these large stems are shown in text-fig. 1.

The numerous trunks at Ischigualasto amply confirm Walton's conclusion that *Rhexoxylon* was a tree. Partial excavation of one specimen revealed 5–6 m. of trunk that was still about 30 cm. across at the upper end. *Rhexoxylon* is thus proved to have been a large tree and it was obviously an important if not dominant plant in the vegetation of an extensive swampy area in mid-Triassic times.

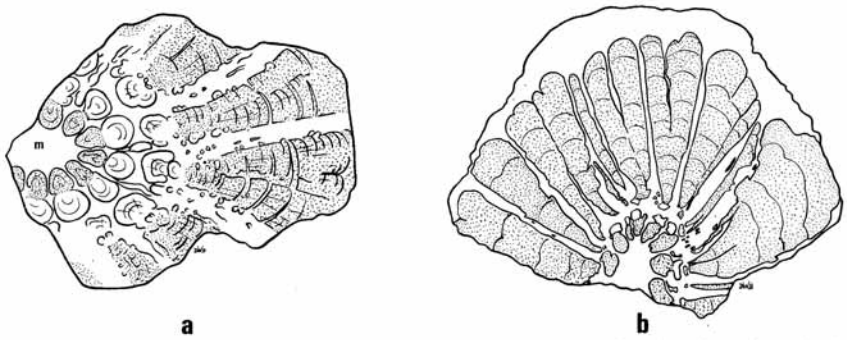
The separation of the sectors of woody tissue in the stem by broad rays of softer tissue has resulted in the fossils acquiring a fluted shape. The fossil trunks have lost most of the tissues external to the woody cylinder so there is no firm evidence that they were not terete in life. Nevertheless the trunk splayed out at the base where the woody sectors become more widely separated and it is possible that the tree was buttressed as are many present day trees.

The trunk base described below has a maximum width of about 48 cm. but this represents little more than half the full width of the woody cylinder. In life the trunk must have been at least one metre wide at a height above ground level of about a metre.

Veins of gypsum in the Ischigualasto fossils give them a tendency to fragment on

cutting so the specimen was embedded in a concrete mix with a 1-cm. aggregate before cutting was attempted. The approximate positions of the cuts are indicated on the photograph of the specimen before embedding reproduced as Plate 44, fig. 1.

The original slices are deposited in the Hunterian Museum (University of Glasgow) no. Pb 3906a–f. Cellulose acetate 'peel' sections prepared from the surfaces are in the Museo de La Plata, Argentina. Text-figs. 2–6 were prepared from the surfaces a–e in Plate 44, fig. 1 and the drawings are labelled accordingly. There is a great similarity between the arrangement of wood in the sections illustrated in text-figs. 4–6 and in the section of *R. africanum* (text-fig. 1). Comparison with sections taken from close to the



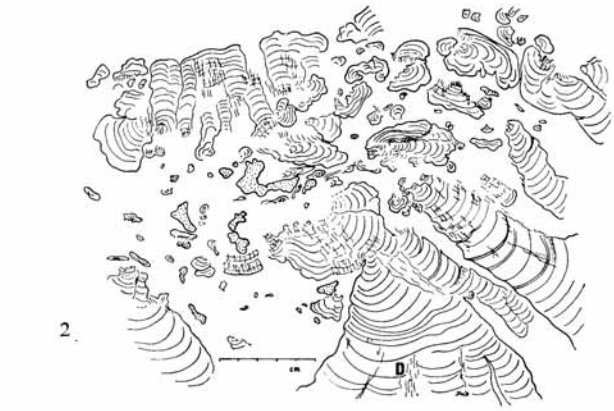

TEXT-FIG. 1. Disposition of xylem in adult stems; the separated centrifugal and centripetal xylem sectors are stippled. Both from Archangelsky and Brett 1961. (*a*) *Rhexoxylon africanum* (×0·2), m, medulla. (*b*) *R. tetrapteridoides* (×0·5).

trunk base (text-figs. 2 and 3), which show a very confused distribution of wood, makes it clear that the regular arrangement of xylem sectors around the medulla is a feature of the upper parts of the trunk.

The major outer sectors of wood in these lower sections (labelled D in text-figs. 2 and 3) probably indicate the position of buttresses or the tops of large divergent roots. Text-fig. 2 shows very little of the outer xylem. This lowest section passes through the centre of the base of the stem in between the diverging roots or buttresses.

The structure of the trunk base leads one to expect higher levels of the trunk to have a regular arrangement of xylem sectors, not complicated by the root connexions, and, of course, in a condition in which much less secondary growth has taken place. The section shown in text-fig. 7 was taken from the narrower part of the trunk of a different specimen (Peel sections Pb 3908 in Hunterian Museum, from specimen deposited in the Museo de La Plata). The outer (centrifugal) wood sectors are here much more compact yet are quite distinctly separated from one another by the parenchyma rays. In one place (marked r in text-fig. 7) the characteristic radial splitting of the centrifugal xylem has occurred; this is brought about by local cessation of regular cambial activity. In other places (t in text-fig. 7) tangential bands of parenchyma have developed between the growth rings in the centrifugal wood. These secondary growth processes are discussed in more detail later on.

The medulla of this specimen is narrower than the medulla in the lower part of the trunk and is in fact not much broader than the medulla in the very small stem *Rhexoxylon*



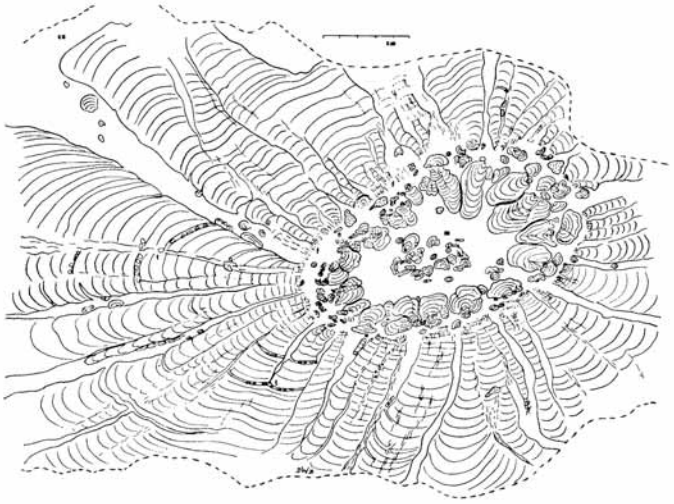


TEXT-FIGS. 2–6. *R. piatnitzkyi*. Disposition of xylem in transverse sections of trunk. Figs. 2–6 prepared from sections *a–e* of trunk base. (Fig. 7 is from the upper region of another trunk.) 5-cm. scale on each figure. Only a few of the well-defined growth rings are represented; these indicate the changes in the cambial arc that have occurred during development. Likewise many of the smaller fragments of vascular tissue and adventitious strands have been omitted for the sake of clarity. Where much frayed xylem occurs among dilatation parenchyma this is indicated by short radial lines.

The expanded mass of centrifugal xylem at top left of fig. 2 corresponds to the innermost part of the sector labelled D in that position in fig. 3. Most of the large sector labelled D at bottom left of fig. 3 is not represented in the lower section. Stippling in these lower sections indicates the corky bodies.

co, cortex; f, frayed xylem, especially the inner fringe ('Fransenxylem'); m, medulla; r, radial splitting of centrifugal xylem; t, tangential splitting of centrifugal xylem. D, centrifugal xylem diverging at trunk base into roots or buttresses.

Explanation of the secondary growth processes is given in the text.



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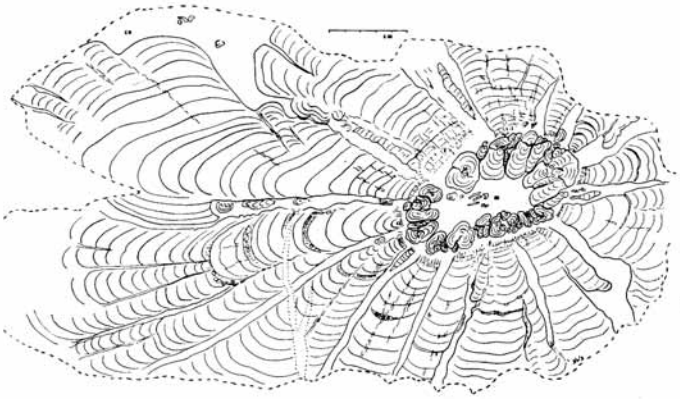

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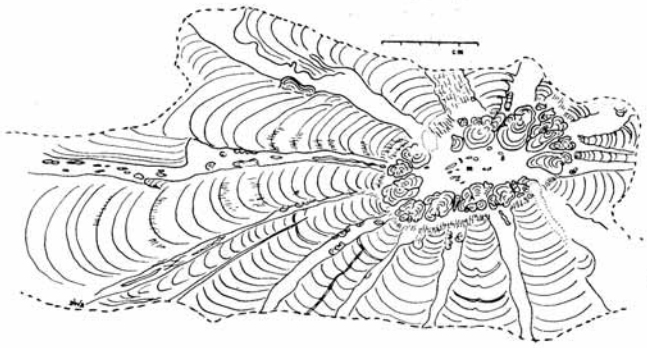

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*piatnitzkyi* Archangelsky & Brett (1961). The inner (centripetal) xylem sectors are small and regularly disposed around the medulla on the same radii as their centrifugal counterparts. They are, however, separated from the latter by additional small patches of xylem. These appear to have developed centripetally, that is with their cambiums away from the protoxylems of the outer sectors.

The small fragments described by Archangelsky and Brett (1961) as '*Rhexoxylon* sp. A' are from the large trunks. Histological details were given in that account (loc. cit., pp. 6–9) so there is no need to repeat them here. There are no anatomical differences between the material described by Archangelsky and Brett and the trunks described in the present contribution to suggest that the Ischigualasto *Rhexoxylon* is not a single species. The material is therefore referred to *Rhexoxylon piatnitzkyi*. This species now comprises both the small stem and the adult trunks: an emended diagnosis follows.

*Emended diagnosis of* R. piatnitzkyi *Archangelsky and Brett* 1961. Small stem 7–8 cm. diameter: surface with rhomboidal leaf bases and branch scars or buds surrounded by small scale leaves; medulla, 2–3 cm. diameter, containing anastomosing system of vascular strands and spherical cysts (250–300 $\mu$); cysts also abundant in cortex. Vascular cylinder dissected by gaps associated with origin of leaf traces; vascular strands 7–8 mm. in radial extent. Xylem of vascular cylinder comprising centrifugal and centripetal parts separated by narrow zone of parenchyma. Leaf traces connected to both margins of gaps, dividing in inner cortex; leaf supply of traces from several gaps; 7–8 vascular strands in leaf base arranged in semicircle, each strand comprising two or more bundles concentrically disposed.

*Trunk of adult plant.* Woody cylinder attaining 80 cm. diameter, medulla 8 cm., towards base of stem. Sclerotic nests and irregular secondary bodies in medulla and secondary parenchyma; centrifugal and centripetal xylem sectors separated by adventitious vascular developments and secondary parenchyma, and fragmented by proliferation of parenchyma and adventitious vascular tissue. Regular arrangement of centrifugal and centripetal xylem lost in lowest parts of trunk; broad wedges of centrifugal xylem diverge into large roots or buttresses; centre of stem occupied by confused mixture of vascular strands and secondary parenchyma.

### *The secondary development of* Rhexoxylon *stems*

Archangelsky and Brett (1961) suggested a course of development that could lead from the structure seen in the young stem (*R. piatnitzkyi*) to the complex structure of *R. africanum*. The xylem of the vascular cylinder in *R. piatnitzkyi*, as seen in transverse section was shown to consist of a centrifugal and a centripetal part separated by a narrow parenchyma zone and dissected by leaf gaps into about fifteen bundles. A similar arrangement was also demonstrated in the younger stems of *R. tetrapteridoides* and in an unidentified stem from Africa which was taken to be a young *R. africanum*.

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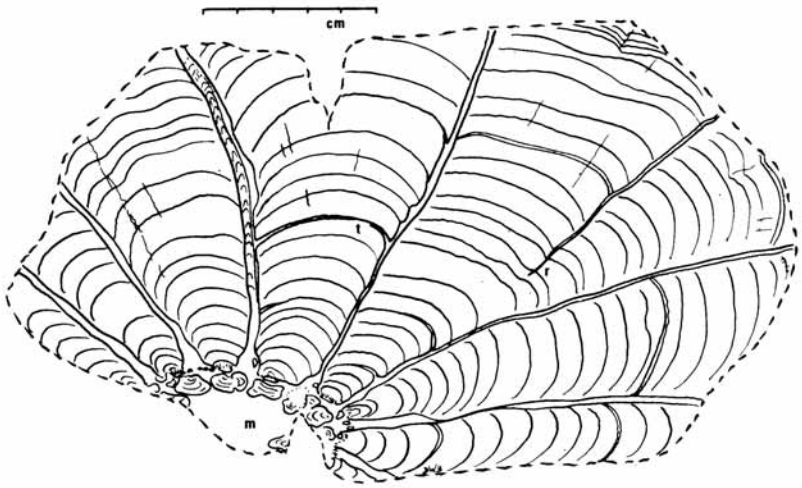
EXPLANATION OF PLATE 44

Fig. 1. The trunk base before embedding in concrete. This view includes the 'upper' and 'right-hand' sides of the sections and their approximate locations are shown a–e (text-figs. 2–6); the base of the specimen is to the right of the photograph.

Fig. 2. Part of section from cut surface opposite that shown in text-fig. 5. Natural size. The photograph is thus a mirror image of the diagram.

Secondary development in *R. africanum* and *R. tetrapteridoides*, according to their interpretation, results in the separation of the two parts of the double bundles: the outer (centrifugal) parts form the main bulk of the wood of the trunk and become split up due to the proliferation of parenchyma and growth of adventitious vascular tissue; the inner (centripetal) parts remain as a ring around the medulla. The separated parts are indicated by the stippling in text-fig. 1, the new vascular tissue formed from extra cambiums is left clear in the drawing.




TEXT-FIG. 7. *R. piatnitzkyi.* Transverse section of trunk. Peel section HM Pb 3908. Full explanation in text.

It is now possible to consider the secondary development of *Rhexoxylon* with reference to young and mature specimens of *R. piatnitzkyi* from the one locality. The present investigations have confirmed the general interpretation put forward by Archangelsky and Brett.

*Centrifugal xylem.* Within the individual sectors the radial extent of the secondary xylem is increased through the regular activity of the cambium in the normal manner. The tangential width of the sectors is increased through the normal broadening of the cambial arcs but this is associated with a 'splitting' of the cambium in places. This results in the formation of new broad rays of mixed tissue, mainly parenchyma. These rays are not formed by the cambium which ceases regular activity at this point (r in text-fig. 7). Some residual cambial activity occurs intermittently in the rays, however, and radially arranged groups of cells and patches of xylem occur frequently in the rays. This xylem does not appear to have been 'detached' from the margins of the xylem sectors.

In addition to the xylem arising along with the parenchyma in these rays, renewed meristematic activity at a later stage produces the characteristic fan-shaped adventitious growths of vascular tissue which develop from small cambiums along the margins of

the xylem sectors in the broad rays. Similar adventitious growths also arise within the xylem sectors but probably only after the appearance there of dilatation parenchyma in which the new vascular tissue then develops. Dilatation parenchyma proliferates along certain of the growth-ring boundaries attaining in some places a radial extent of 2–3 mm. separating adjacent growth rings (t in text-figs. 4, 7). Usually adventitious vascular tissue is seen only in the broader bands of parenchyma (t in text-fig. 4).

At a late stage of secondary thickening such as that represented by the sections from the trunk base (text-figs. 2–6), a considerable amount of dilatation parenchyma proliferates from the vascular rays in the xylem sectors. This splits the wood and gives rise to irregular tracts of mixed tissue containing many short radial strings of tracheids detached from the main masses of xylem (f in text-figs. 4 and 5). This occurs especially as a fringe along the inner margins of the centrifugal xylem sectors and corresponds to the 'Fransenxylem' of Kräusel (Kräusel 1956, Archangelsky and Brett 1961). There is no essential difference between the frayed xylem of the inner zone and that appearing further out in the secondary xylem.

*Centripetal xylem and the separation zone.* The variation in the appearance of the vascular bundles of the small stem is related to the origin of the leaf traces (Archangelsky and Brett 1961). This variation no doubt accounts for much of the variation seen in the bundles of the inner ring in the adult stems. Only where the cambium of the primary bundle was continuous around both centrifugal and centripetal xylem (i.e. the bundle was concentric) will the eventual separation of the two parts have involved actual rupture of the primary xylem and innermost secondary xylem. The point of separation is presumably determined by the location of production of dilatation parenchyma.

Adventitious cambiums arise in the parenchyma between the separated primary xylems and also along the newly exposed margins of the secondary xylem of the inner sectors. These new cambiums may be orientated so as to produce xylem either centripetally or centrifugally. In the former case the new tissue appears as fan-shaped developments along the frayed xylem of the outer sectors. Activity of both the original and the new cambiums soon closes up the primary faces of the inner xylem sectors resulting in the irregular, more or less concentric, bundles of the inner ring surrounding the medulla (text-figs. 4–6). The orientation of the first adventitious vascular tissue to arise during the separation process seems to be variable or at least to differ according to the region of the trunk. In the section from the upper region of the trunk (text-fig. 7) the first adventitious xylem is centripetal. In the base of the trunk however there is little evidence of centripetal adventitious xylem in the zone of separation although the bundles of the inner ring are all completely closed. Archangelsky and Brett (1961) noted the variation in the orientation of the adventitious vascular tissue of this zone in *R. africanum* in which centripetal xylem may also be lacking in some specimens. There is evidence that the first growth may be centrifugal in *R. africanum* (loc. cit., fig. 6A). In sections of *R. tetrapteridoides* (Kidston Coll., Univ. Glasgow, 2780–81) the first adventitious cambiums in some sectors have produced centripetal xylem, in other sectors both centripetal and centrifugal fan-shaped masses are equally well developed.

The extent of the centripetal development of the inner ring bordering the medulla is variable in the base of the trunk: there is a much greater development of xylem on one side of the medulla (text-figs. 3–5). The opposite side of the trunk however has the clearly defined outer sectors of wood which diverge into the large roots or buttresses and are

separated by very broad parenchyma rays. The differences between the two sides of the trunk are particularly shown in text-fig. 3. I infer from this that the tree was inclined at an angle to the vertical in life and that this resulted in the centripetal reaction wood on one side and the buttresses on the opposite side.

*Medulla.* The small spherical cysts present in the medulla and cortex are a primary feature. In the medulla of the small stem they occur at about 150/cm.$^2$ but their frequency is reduced to 10/cm.$^2$ in the expanded medulla of the adult trunk (Archangelsky and Brett 1961); a maximum count of 22/cm.$^2$ was obtained in the section of the new material shown in text-fig. 6. The additional tissue of the enlarged medulla is secondary in origin and consists of dilatation parenchyma and adventitious vascular tissue. Sclerotic nests are developed in all the secondary parenchyma of *Rhexoxylon* and are common in the medulla. At the very base of the trunk the primary medulla loses its identity and in the large areas of parenchyma secondary bodies of cork-like tissue develop. These are seen in text-figs. 2 and 3, and were first described by Bancroft (1913) in her original account of *R. africanum*.

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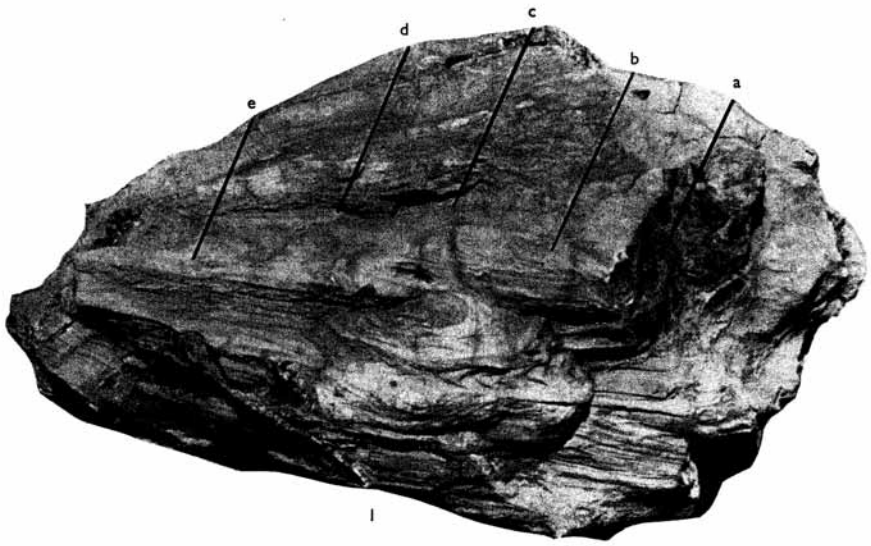


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BRETT, Trunk of *Rhexoxylon*