Rhexoxylon brunoi Artabe, Brea et Zamuner, *sp. nov.*, a new Triassic corystosperm from the Paramillo de Uspallata, Mendoza, Argentina

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Abstract

A new species of *Rhexoxylon* from the Upper Triassic of Argentina is described. The material was collected at El Paramillo de Uspallata area and comes from Los Colorados Formation. There is a big buried specimen and scattered material which is preserved by silicification, corresponding to an adult eccentric, oval trunk, whose diameter is 71 × 58 cm. Three zones can be distinguished: pith, vascular (with perimedullar bundles and centrifugal wedges of secondary xylem) and cork layer. *Rhexoxylon brunoi* Artabe, Brea et Zamuner, *sp. nov*. has a heterogeneous pith with parenchyma cells and idioblasts. Perimedullar bundles make up two cycles; the first one is complete constituted by double collateral bundles, facing each other, with secondary growth. The second one is incomplete, showing just the centripetal xylem sector. Peripheral centrifugal secondary xylem wedges show extensive development, reaching up to 38 cm of thickness. The tracheids of secondary xylem have opposite uni- to biseriate bordered radial pitting, and crossfields with one or two simple, slanted lenticular pits. Outside of the xylem a cork layer of about 2 cm persists conforming a longitudinally and transversely fractured rhytidome-like zone. *Rhexoxylon brunoi* shows a morpho-structural pattern determined by high activity of normal cambium, moderate activity of supernumerary cambium and scarce activity of remanent cambium.

Keywords: paleobotany; systematic; corystosperms; *Rhexoxylon*; Upper Triassic; Argentina

1. Introduction

In the province of Mendoza, the Cuyana Basin (sensu Kokogian and Mancilla, 1989) includes six main subbasins of Triassic continental sediments, among which is that of Las Peñas, approximately 2000 m thick. To the west of the latter, in the outcrop area identified as Villavicencio–Paramillo de Uspallata, the Uspallata Group with five formations (Río Mendoza, Las Cabras, Potrerillos, Cacheuta and Río Blanco) was recognized by Stipanicic (1979) (Fig. 1). At El Paramillo de Uspallata, in the zone comprised by the San Bartolo Range and Los Colorados Hill, the sedimentary sequence includes four units: the Paramillo, Agua de la Zorra, Portezuelo Bayo and Los Colorados formations (Harrington, 1971), which are correlatable with the middle and

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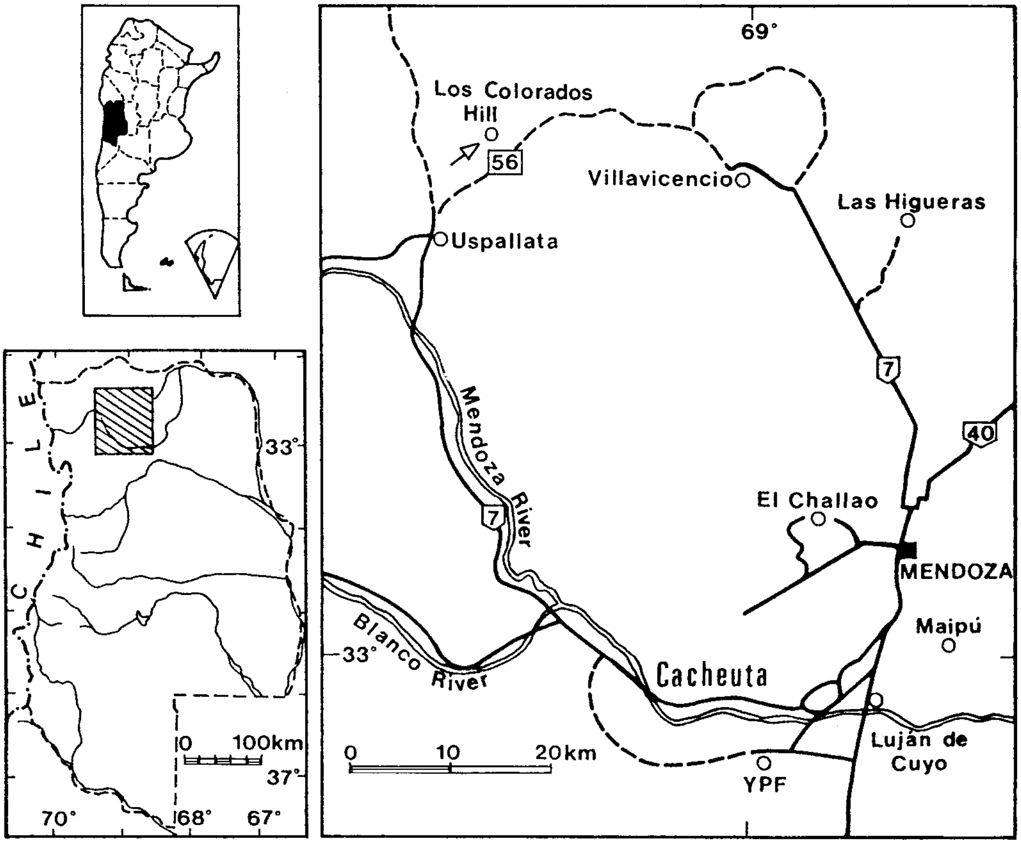


Fig. 1. Geographic location of the fossiliferous locality.

upper parts of the Uspallata Group (Fig. 2; Strelkov and Alvarez, 1984; Ramos, 1993).

The Paramillo de Uspallata area has been the object of several geological studies (Harrington, 1971; Strelkov and Alvarez, 1984; Massabie, 1985; Massabie et al., 1985; Kokogian and Mancilla, 1989; Linares and Gonzáles, 1990; Ramos and Kay, 1991; Ramos, 1993; Kokogian et al., 1993). Little is known as to its paleontological content (Conwentz, 1885; Stappenbeck, 1910; Kurtz, 1921; Du Toit, 1927; Groeber, 1939; Windhausen, 1941; Harrington, 1971; Stipanicic et al., 1996) even though Darwin (1846) noted the existence of a petrified forest, fossilized in situ (assigned to *Araucarites*).

Because of these reasons, and within the CONICET (National Research Council of Argentina) Proyect PID 330/92, the outcrops of the El Paramillo, Agua de la Zorra and Los Colorados formations, in the Agua de la Zorra zone, were revised. The paleofloristical content is currently being studied and is the object of the doctoral thesis of one of the authors (Brea, 1995). On the Los Colorados Formation (sensu Harrington, 1971), material assignable to a new species of *Rhexoxylon* Bancroft emend Archangelsky et Brett, 1961 (Artabe et al., 1994) has been found. The aim of this work is the description of this taxon and the comparison with previously described species.

2. Materials and methods

The studied material comes from the Los Colorados Formation (sensu Harrington, 1971) cropping out in El Paramillo de Uspallata zone, on Los Colorados Hill, situated at 32ºS, 68ºW, at approximately

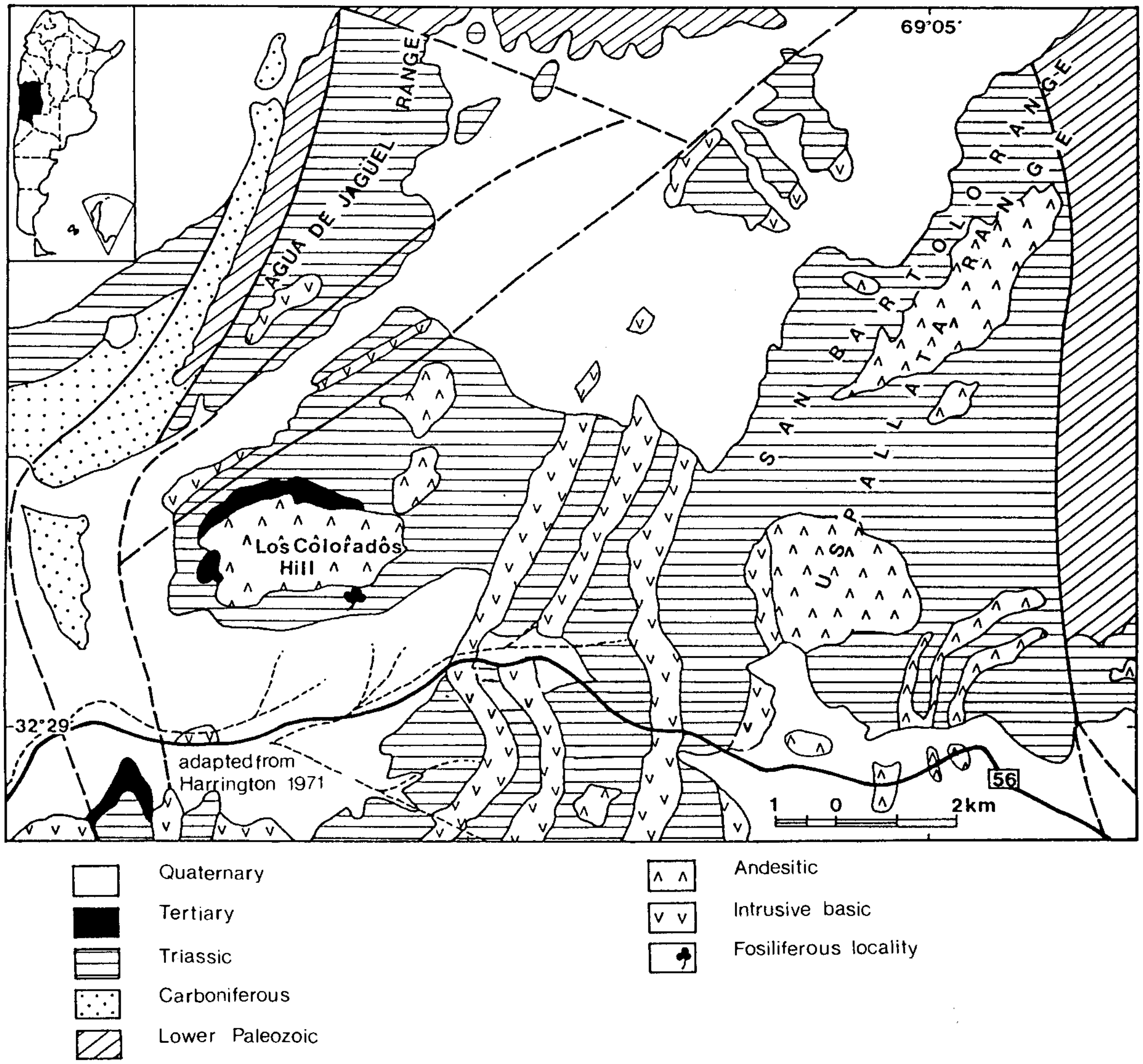


Fig. 2. Geological map of the region showing Triassic units of El Paramillo de Uspallata (modified from Harrington, 1971).

15 km from the city of Uspallata, Mendoza, Argentina (Figs. 1 and 2). It was collected by two of the authors (A.A. and M.B.) during a fieldwork in 1994. The specimens were found in deep red sandstone, with medium grain size, compact and solid, stratified in thick beds.

Specimens are silicified trunks which are deposited in the Paleobotanical collection of the La Plata Museum, under the acronym LPPB. The samples correspond to scattered material and to a large, partially buried specimen, whose exposed part is approximately 3 m long. The dimensions of the buried trunk made transportation impossible, thus hand drawing of a complete transversal section (Fig. 4) was made on the specimen, in the field. Samples of each of the zones recognized in the stem were collected. Surface polishing and thin sections were done using traditional techniques. The material was studied with light microscopy (Iroscope YZ6 and Wild M11) and camera lucida (Wild M5).

3. Systematics

Class GYMNOSPERMOPSIDA
Order PTERIDOSPERMALES
Family CORYSTOSPERMACEAE Thomas, 1933

Genus ***Rhexoxylon*** Bancroft emend. Archangelsky et Brett, 1961

Type: Rhexoxylon africanum Bancroft, 1913 emend. Walton, 1923

Rhexoxylon brunoi Artabe, Brea et Zamuner, *sp. nov.* (Plates I and II; Figs. 3–6)

Holotype: LPPB 12960–12974, LPPBpm 1556-1561.
Paratypes: LPPB 12975–12984.
Repository: Paleobotany Department, La Plata Museum, U.N.L.P. Argentina.
Stratigraphic and geographic origin: Los Colorados Formation (Upper Triassic), Villavicencio–Uspallata Subbasin, Los Colorados hill, Mendoza province.
Etymology: This species is dedicated to the late Dr. Bruno Petriella, an outstanding Argentinian paleobotanist, who made important advances in the knowledge of the Corystospermaceae family.
Diagnosis: Mature columnar stem, up to 71 cm in diameter, differentiated into pith, vascular cylinder and cork layer. Small oval, heterogeneous pith with parenchyma cells and idioblasts. The vascular cylinder comprises two cycles of perimedullar bundles and a peripheral zone of centrifugal secondary xylem wedges. The first cycle of perimedullar bundles made up of 16 collateral double bundles, facing each other, constituted of centripetal–centrifugal secondary xylem, oval-rounded, contiguous, separated by very thin medullary rays; second cycle (incomplete) showing only centripetal secondary xylem. Zone of centrifugal wood wedges 38 cm thick; wedges of xylem related to perimedullar bundles, each one separated from the contiguous one by narrow parenchymatous rays up to 1 cm wide; having fan-like form; radial and cross fragmentation produced by dilatation parenchyma. Radial intervascular bordered pitting contiguous uniseriate, with occasional opposite biseriate, and crossfields show one or two simple, slanted and lenticular pits. Tracheids show simple or double spiral tertiary thickenings. Cork layer of 2 cm persists conforming a longitudinally and transversely fractured rhytidome-like zone.
Description: The trunk is eccentric, of oval shape with a major diameter of 71 cm and a minor one of 58 cm. It is differentiated into pith, vascular zone and cork layer (Plate I, 1). The pith is 2.4 × 1.7 cm; it is oval and heterogeneous (Plate I, 2), with spheroidal parenchymatous cells of 105 × 110 μm and polygonal isodiametric idioblasts, with dark contents of 115 × 110 μm. The vascular zone presents two rings of perimedullar bundles 2.1 cm thick (Plate I, 2; Fig. 3) above described. The peripheral sector of centrifugal wedges up to 38 cm thick (Plate II, 1, 2; Fig. 4) develops around the second ring of perimedullar bundles and is related with it. Each wedge is separated from the contiguous one by parenchymatous rays up to 1 cm wide; they are fan-like and fragment at different levels by means of parenchymatous rays of different radial length. The tangential dilatation parenchyma, which frequently fragments secondary xylem wedges, measures between 0.01 and 0.1 cm, exceptionally up to 0.3 cm. Tracheids measure 60 × 74.7 μm. The bordered pits are approximately 30 μm in diameter and are contiguous uniseriate or partially opposite biseriate (Fig. 5a). Crossfields present one or two simple, slanted lenticular pits 41.15 × 17.14 μm (Fig. 5b).

The cork layer is 2 cm thick with quadrangular or rectangular suberized cells 16 μm wide × 23 μm high; this tissue persists over the trunk conforming longitudinally and transversally fractured rhytidome-like zone (Plate II, 3, 4).
Discussion and comparisons: Rhexoxylon Bancroft, 1913 emend. Archangelsky et Brett, 1961 was created for permineralized specimens with a distinctive secondary xylem distribution. All the species assigned to these genus are characterized by a pith surrounded by a secondary vascular cylinder composed of two zones; the inner with one or more cycles of strands of secondary xylem that are either centripetal or both centripetal and centrifugal (perimedullar zone); and the outer with wedges of centrifugal secondary xylem separated by parenchy-

PLATE I

Rhexoxylon brunoi Artabe, Brea et Zamuner, *sp. nov*.
1. General aspect of trunk showing the pith and vascular zone.
2. Detail of the pith and the zone of perimedullar bundles.

PLATE I

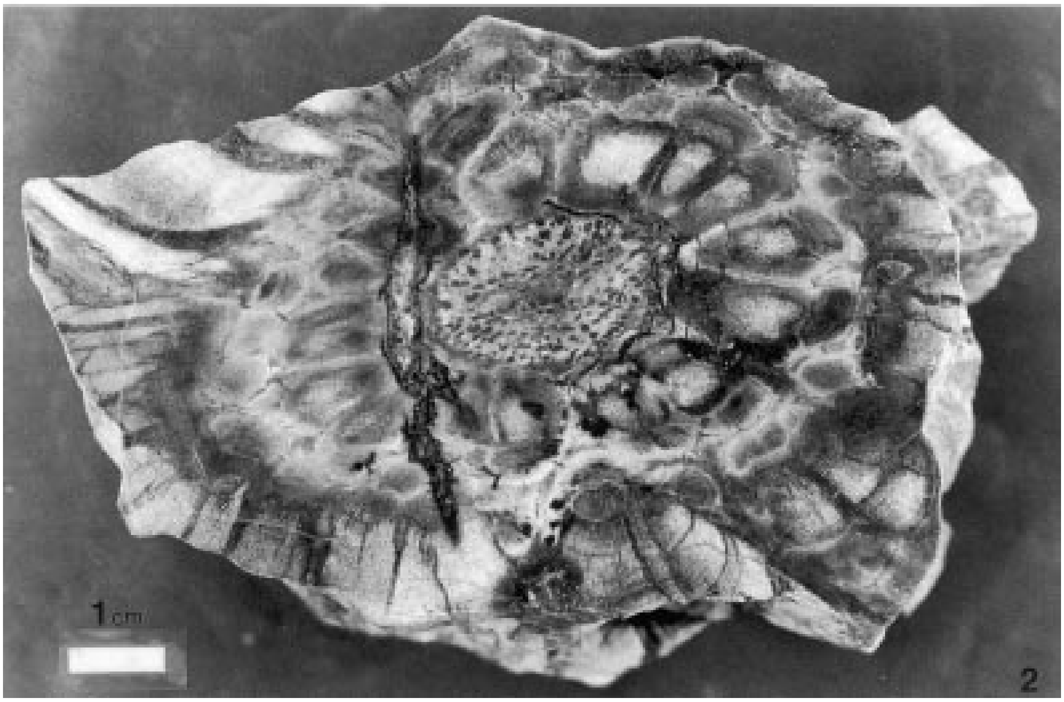
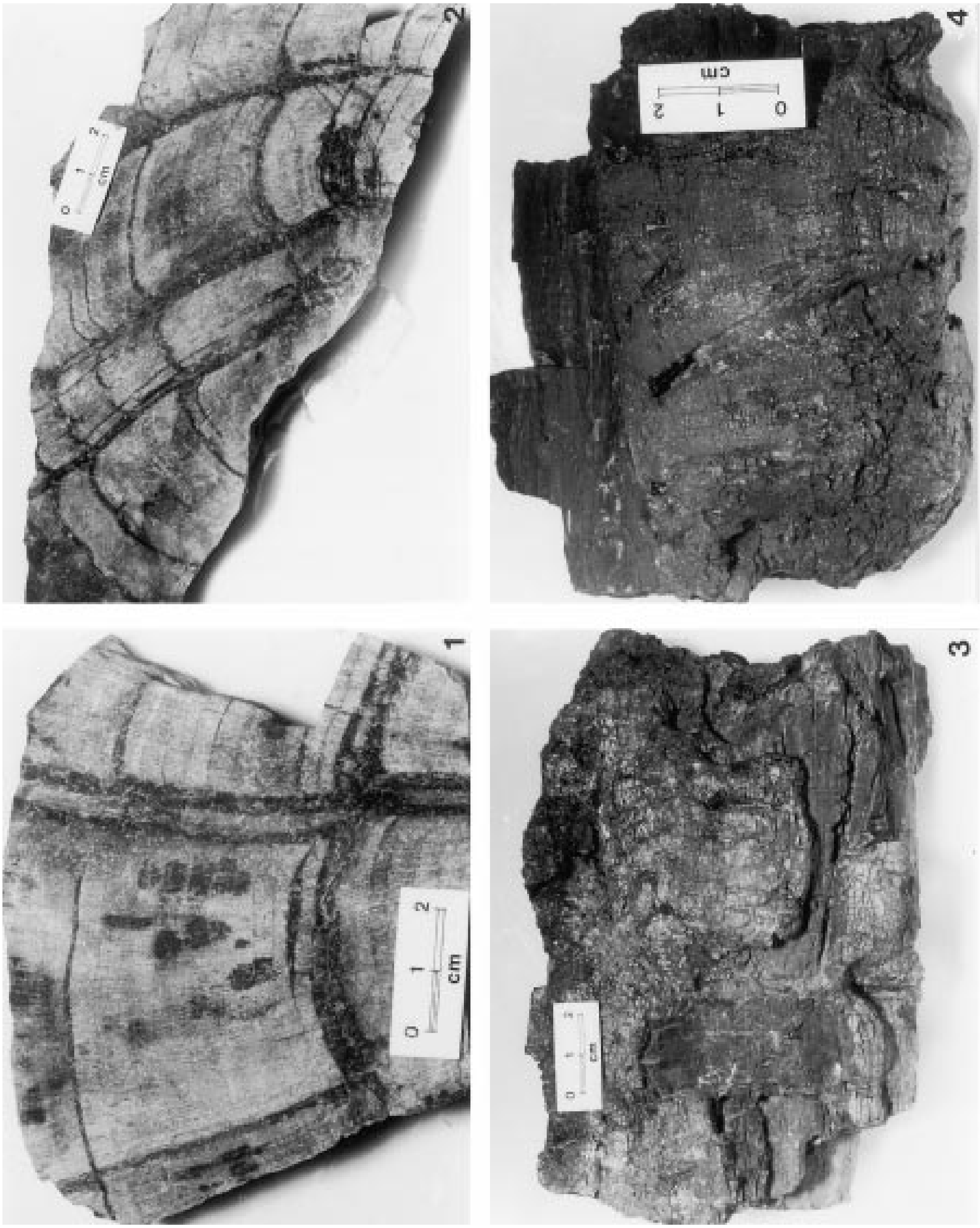


PLATE II



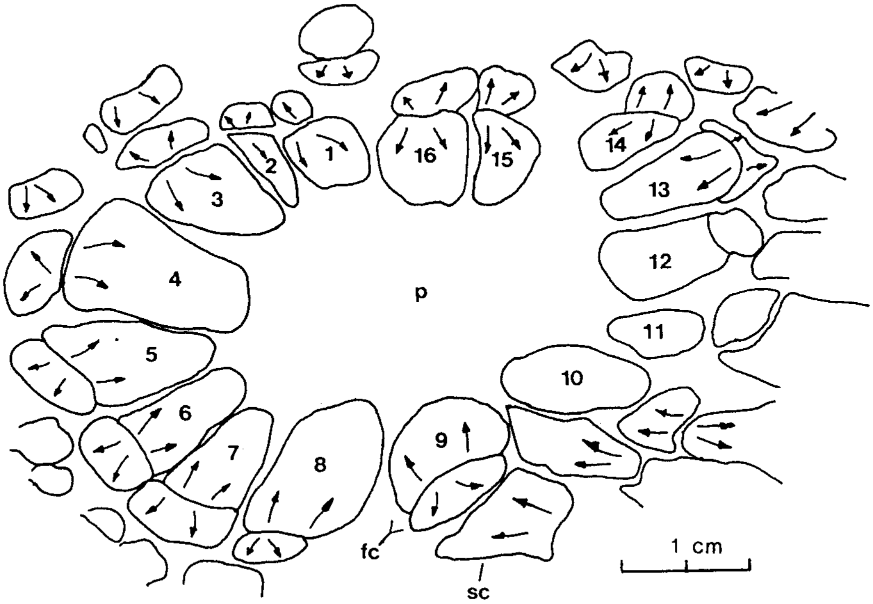


Fig. 3. *Rhexoxylon brunoi* Artabe, Brea et Zamuner, *sp. nov*. Diagram of the perimedullar zone and detail of cycles of vascular bundles. *p* = pith; *fc* = first cycle of perimedullar bundle made up 16 collateral double bundles, constituted of centripetal–centrifugal secondary xylem; *sc* = second cycle (incomplete) showing only centripetal secondary xylem.

matous rays. The anatomy of *Rhexoxylon* has been interpreted as a consequence of an unusual secondary growth (Brett, 1968; Zamuner, 1992). A parenchymatic and xylematic proliferation within perimedullar zone and peripheral centrifugal xylem wedges triggers a mechanism of vascular fragmentation (remanent and supernumerary cambial activity; Zamuner, 1992). This has been called 'dilatation parenchyma' or 'adventitious parenchyma' because it dilates or separates the xylem (Walton, 1923; Obaton, 1960; Archangelsky and Brett, 1961; Bonnamain et al., 1963; Herbst and Lutz, 1988).

Up to now two species have been recognized from South Africa, *R. africanum* Bancroft emend. Walton, 1923 and *R.tetrapteridoides* Walton emend. Archangelsky et Brett, 1961, because *R.waltonii* Kräusel, 1956 was synonymized by Archangelsky and Brett (1961) with *R.africanum*. In South America three species of this genus have been found. *R. piatnitzkyi* Archangelsky et Brett, 1961, described from the Ischigualasto Formation, province of San Juan, Argentina (Archangelsky and Brett, 1961; Archangelsky, 1968; Brett, 1968), *R. brasiliensis* found in the Caturrita Formation, Rio Grande do Sul, Brasil (Herbst and Lutz, 1988) and a new species preliminarily described from the Barreal Formation, province of San Juan, Argentina (Lutz and Herbst, 1992).

In Antarctica, Taylor (1992) described a portion of a stem as *Rhexoxylon* sp. because of the secondary wood in the form of wedges and the parenchymatous ground tissue.

Comparing histological characters of the pith, secondary xylem and cortex of the different species of the genus (Table 1), the pith shows sclerotic nests, secretory cavities and vascular strands in every taxon. *R. brunoi* is the only species with a parenchymatous pith with idioblasts. Secondary xylem in *R.tetrapteridoides*, *R.africanum*, *R.piatnitzkyi* and *Rhexoxylon sp*. (Taylor, 1992) consists of tracheids with uni- to biseriate alternate bordered pitting and crossfields with 1 to 4 simple pinoid pits. *R. brunoi* has uni or partially biseriate opposite bordered radial

PLATE II

Rhexoxylon brunoi Artabe, Brea et Zamuner, *sp. nov*.
1, 2. Detail of centrifugal secondary xylem wedges.
3, 4. General aspect of cork layer.

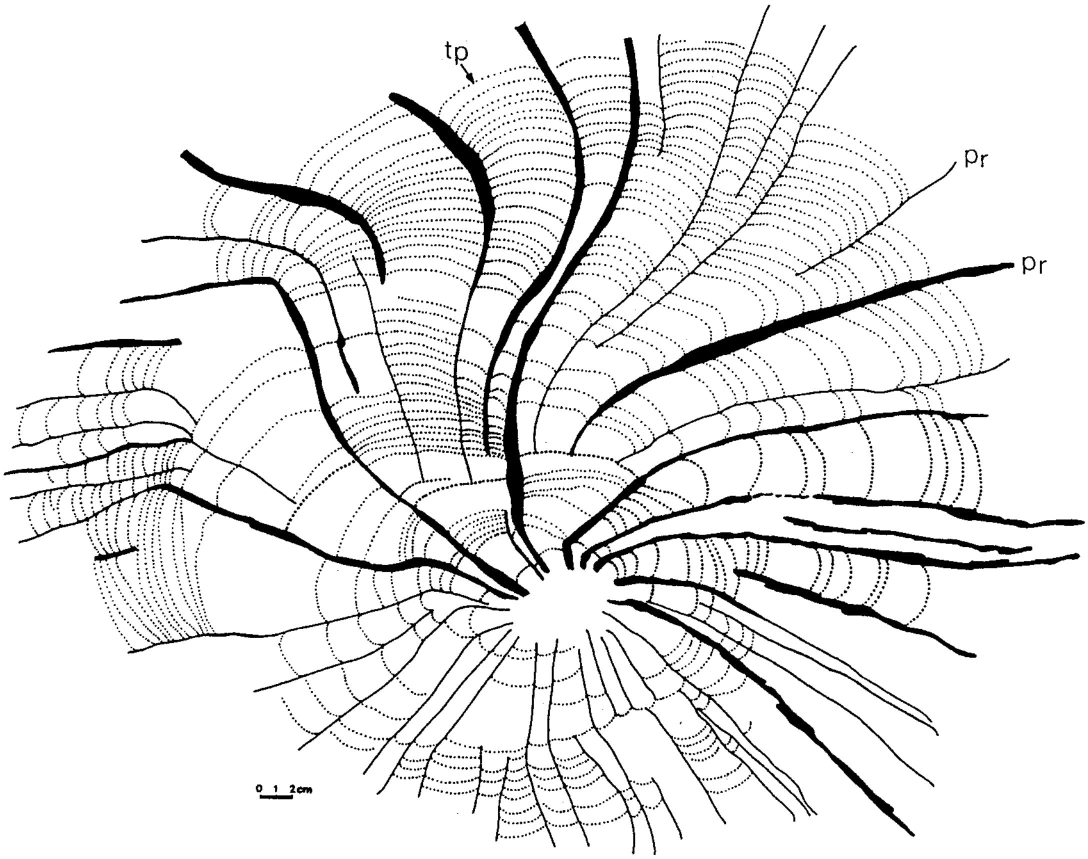


Fig. 4. *Rhexoxylon brunoi* Artabe, Brea et Zamuner, *sp. nov*. Diagram of the peripheral zone of centrifugal secondary xylem divided into wedges by parenchymatous rays (*pr*) and tangential dilatation parenchyma (*tp*).

pitting and crossfields with 1 or 2 simple, elliptical slanted pits. The cortex is generally parenchymatous with idioblasts and sometimes with sclerotic nests and vascular strands. A distinctive cork layer has only been described in *Rhexoxylon* sp. and *R. brunoi* (Petriella, 1978; Taylor, 1992). The antarctic specimen develops a cork layer that reach a millimetre in thickness whereas in the argentinian material is about 2 cm.

Studies on developmental anatomy carried out by Zamuner (1992) demonstrated that in *Rhexoxylon* wood secondary structure is produced by the simultaneous action of three cambia: normal, supernumerary and remanent. The normal one, located at the distal ends of perimedullar bundles, produces a differential development of their centrifugal part generating the secondary xylem wedges. The remanent cambium favours the formation of abundant dilatation parenchyma unchaining the fragmentation of centrifugal wedges and perimedullar bundles. Finally, the supernumerary one (located in the parenchymatic zone of the perimedullar bundles and in the parenchymatic inner zone of xylematic wedges), activates the production of inverse xylem, originating bundles and centripetal polyxyly. The capacity for developing inverse xylem appeared sporadically in some Paleozoic Pteridosperms and was established as a character in the Medullosans, persisting during the Mesozoic in Corystosperms and Cycadales. In Cycadales has been cited in stems and seedlings of extant and fossil genera: *Macrozamia*, *Lepidozamia*, *Encephalartos*, *Cycas*, *Bowenia*, *Lepidozamia*, *Fascivarioxylon* and *Worsdellia* (Worsdell, 1896, 1906; Jain, 1962; Artabe et al., in press).

Differential activity of the cambia generates the different morpho-structural patterns found in the

Table 1
Comparison of histological characters of the pith, secondary xylem and cortex of the different species of the genus *Rhexoxylon*: *R. africanum* Bancroft emend. Walton, 1923; *R. tetrapteridoides* Walton emend. Archangelsky et Brett, 1961; *R. piatnitzkyi* Archangelsky et Brett, 1961; *R. brasiliensis* Herbst et Lutz, 1988; *R.* sp. Lutz et Herbst, 1992; *R.* sp. Taylor, 1992; and *R. brunoi*

	R.africanum	*R. tetrapteridoides*	*R. piatnitzkyi*	*R. brasiliensis*	*R.* sp.	*R.* sp.	*R. brunoi*
Pith							
Sclerotic nets	×	×		×		?	
Vascular strands	×	×	×		×	?	
Idioblasts			×			?	×
Secretory cavities	×	×	×	×	×	?	?
Secondary xylem							
Radial pitting	1–3 seriate alternate	1–3 seriate alternate	1–2 seriate alternate	2 seriate?	1 seriate	1–2 seriate alternate	1–2 seriate opposite
Cross field pits	1–3 circular elliptical	1 circular	1–3 circular elliptical	?	?	2–4 circular elliptical	1–2 oblique lenticular
Ray width	1 seriate	1 seriate	1 seriate	?	?	1–2 seriate	?
Cortex							
Only parenchymatic					×		
Sclerotic nets	?	×					
Vascular strands	?	×	×				
Idioblasts	?		×				
Cork layer	?		×			×	×

species of *Rhexoxylon*. Thus, supernumerary cambial activity is scarce in *R. tetrapteridoides*, *R. piatnitzkyi* and *Rhexoxylon* sp. (Lutz and Herbst, 1992), moderate in *R. brasiliensis* and *R. brunoi*, and abundant in *R. africanum* producing up to three cycles of perimedullar bundles. Remanent cambial action is scarce in *R. tetrapteridoides*, *R.* sp. (Lutz and Herbst, 1992) and *R. brunoi*, moderate in *R. piatnitzkyi*, *R. brasiliensis* and *Rhexoxylon* sp. (Taylor, 1992), and quite abundant in *R. africanum*. Finally, cambium activity produces scarce radial and tangential parenchyma in *R. tetrapteridoides*, *R. piatnitzkyi*, *Rhexoxylon* sp. (Lutz and Herbst, 1992) and *R. brunoi*, and abundant parenchyma in *R. africanum* and *R. brasiliensis*.

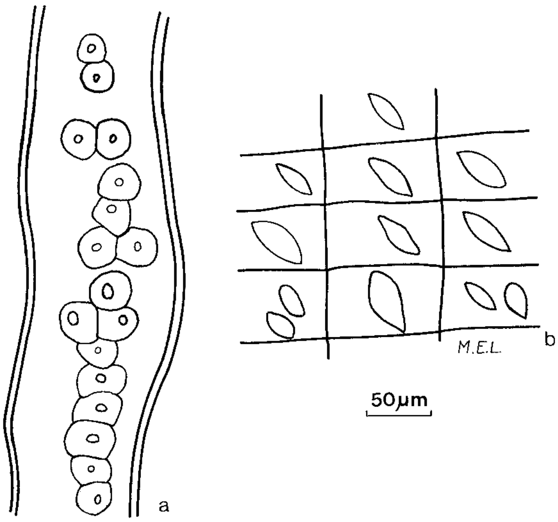


Fig. 5. *Rhexoxylon brunoi* Artabe, Brea et Zamuner, *sp. nov*. (a) Tracheid showing uni- or partially biseriate opposite bordered radial pitting. (b) Crossfields with 1 or 2 simple, elliptical slanted pits.

In mature stems, differential action of the cambia, added to the pith, perimedullary bundles and peripheral xylem wedges diameters, determines the different degrees of manoxyly/picnoxyly characteristic of each species (Table 2). Thus, *R. africanum* would represent the most manoxylic form within the group, with high activity of supernumerary and remanent cambia, abundant radial and tangential parenchyma in xylematic wedges and wide pith. *Rhexoxylon tetrapteridoides* and *R. brunoi* are the most picnoxylic forms. The first, with scarce supernumerary and remanent cambial activity, scarce radial and tangential parenchyma and small pith; the second, with moderate supernumerary cambial activity, scarce development of remanent cambia, high

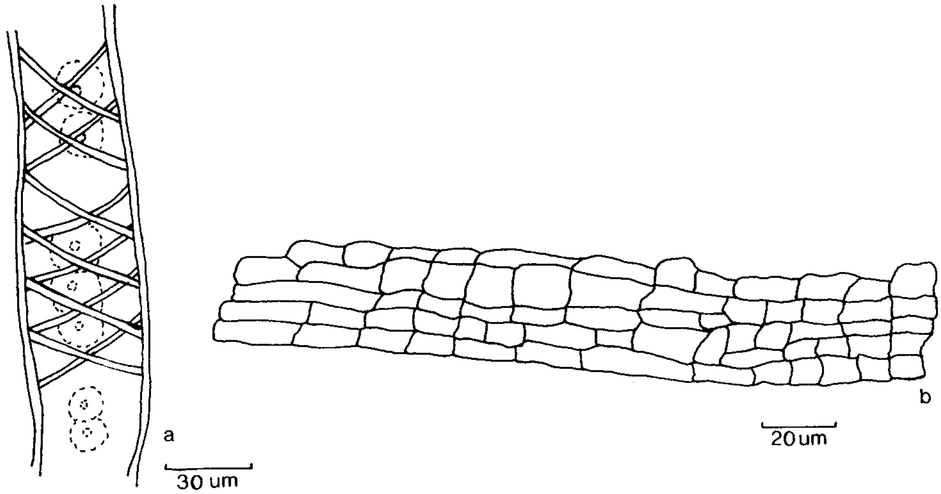


Fig. 6. *Rhexoxylon brunoi* Artabe, Brea et Zamuner, *sp. nov*. (a) Tracheid showing the double spiral tertiary thickenings. (b) cork layer.

activity of normal cambium with highly developed wedges with scarce radial and tangential parenchyma and a small pith.

The remaining stem genera assigned to the corystosperms, *Antarcticoxylon* Seward, 1914, *Kykloxylon* Meyer-Berthaud et al., 1993 and one stem (stem A) recently described (Brea, 1995), are characterized by a vascular organization different from that of *Rhexoxylon*. Stem A presents a normal development of primary xylem, with endarch protoxylem. The absence of double perimedullar bundles with centripetal–centrifugal xylem, implies the lack of development of inverse xylem. The distribution of secondary xylem is ordered according to four cycles of wedges separated by circular bands of tangential dilatation parenchyma. Contiguous wedges in each cycle are separated by the development of secondary parenchymatous rays. In this case, the activity of remanent cambium is restricted to tangential dilatation parenchyma separating the cycles of wedges and to that developing within them. A regular morpho-structural pattern thus originates, unlike what happens in *Rhexoxylon*. *Antarcticoxylon* is based only on one specimen and one species alone, *A.*

Table 2
Relation between pith, perimedullary strands, secondary xylem and amount of parenchyma of the different species of the genus *Rhexoxylon*: *R. africanum* Bancroft emend. Walton, 1923; *R. tetrapteridoides* Walton emend. Archangelsky et Brett, 1961; *R. piatnitzkyi* Archangelsky et Brett, 1961; *R. brasiliensis* Herbst et Lutz, 1988; *R.* sp. Lutz et Herbst, 1992; *R.* sp. Taylor, 1992; and *R. brunoi*

	Diameter			Ring of perimedullary strands	Wedges of secondary xylem (cm)	Amount of parenchyma	Cambium activity	
	Total (cm)	Pith (cm)	Pith + perimedullary strands (cm)				remanent	supernumerary
R. africanum	50	6	24	1 or 2 complete 1 incomplete	14	abundant	great	great
R. tetrapteridoides	18	2	6.6	1 complete	5.5	scarce	scarce	scarce
R. piatnitzkyi	100	6.5	12	1 complete	25	scarce	moderate	scarce
R. brasiliensis	43	7 × 5	16	1 complete 1 incomplete	14	abundant	moderate	moderate
R. sp.	60	3.2 × 1.3	5.3	1 incomplete	6	scarce	scarce	scarce
R. sp.	35	?	?	?	?	?	moderate	?
R. brunoi	76	2.4 × 1.7	6.6	1 complete 1 incomplete	38	scarce	scarce	moderate

priestleyi, possibly of Permian age of Antarctica (Seward, 1914; Meyer-Berthaud and Taylor, 1991). According to Archangelsky and Brett (1961) *Antarcticoxylon* has a small diameter, scarcely divided vascular cylinder, endarch protoxylem, and shows no evidence of cambial activity at the perimedullar region. Finally, *Kykloxylon* has been found associated to leaves assigned to *Dicroidium fremouwensis* Pigg, 1990 (Meyer-Berthaud et al., 1992, 1993). This species consists of stems up to 2 cm in diameter with endarch primary xylem and normal undivided secondary xylem.

Corystospermic woods show an organization of primary and secondary tissues determined by typical and atypical cambial activity.

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