

Rhexoxylon cortaderitaense (Menéndez) comb. nov., a species of permineralized stems newly assigned to the Corystospermaceae, from the Triassic of Argentina

JOSEFINA BODNAR

BODNAR, J., June, 2008. *Rhexoxylon cortaderitaense* (Menéndez) comb. nov., a species of permineralized stems newly assigned to the Corystospermaceae, from the Triassic of Argentina. *Alcheringa* 32, 171–190. ISSN 0311-5518.

Anatomically preserved stems of Late Triassic corystosperms from the upper Cortaderita Formation in San Juan province, Argentina are described and assigned to *Rhexoxylon cortaderitaense* (Menéndez) comb. nov. These specimens were originally attributed to conifers, a group not closely related to corystosperms. The silicified axes preserve features of the cortex, pith, and secondary vascular system. Like all *Rhexoxylon* species, these axes have two discontinuous cambial rings that develop centrifugal secondary xylem (normal secondary xylem) and centripetal secondary xylem (inverted secondary xylem). Both types of xylem are separated by a band of parenchymatous tissue developed by a remnant cambium. The centrifugal xylem is divided by parenchymatous rays following differential cambial activity. The secondary xylem is pycnoxylic with uniseriate rays; tracheids have mainly biseriate and alternate bordered pits on radial and tangential walls, and one simple oval pit in cross-fields. The distinctive feature of *R. cortaderitaense* is the conspicuous amount of centripetal secondary vascular tissues not forming perimedullar bundles, this being interpreted as an apomorphic trait. This interpretation of the character modifies previous hypothesized phylogenetic relationships of corystosperm wood taxa.

Josefina Bodnar [jbodnar@fcnym.unlp.edu.ar] División Paleobotánica, Facultad de Ciencias Naturales y Museo. Paseo del Bosque S/N B1900FWA La Plata, Buenos Aires, Argentina and Consejo Nacional de Investigaciones Científicas y Técnicas. Received 7.12.2006; revised 14.5.2007.

Key words: Argentina, Late Triassic, upper Cortaderita Formation, Corystospermaceae, fossil wood, *Rhexoxylon*.

CORYSTOSPERMS are a Mesozoic seed-fern family that dominated most Gondwanan Triassic palaeofloras. First described from the Molteno Formation (Natal Beds) of South Africa (Thomas 1933), the group was reconstructed based on detached but closely associated *Dicroidium* Gothan, 1912 emend. Townrow, 1957 leaves, *Pteruchus* Thomas, 1933 emend. Townrow, 1957 pollen organs and *Umkomasia* Thomas, 1933 ovulate organs. Cuticular similarities and the occurrence of similar pollen grains [*Alisporites* Daugherty, 1941; *Falcisporites* (Leschik 1956) Klaus, 1963;

Pteruchipollenites Couper, 1958] in *Pteruchus* pollen sacs and *Umkomasia* ovules confirm this association (Artabe & Brea 2003). Vegetative and reproductive remains are well known both from permineralized specimens and from compression/impression fossils (Artabe & Zamuner 2007).

Seven genera of Corystospermaceae stems have been described based on permineralized axes. *Rhexoxylon* Bancroft, 1913 emend. Archangelsky & Brett, 1961 (Argentina, Brazil, South Africa and Antarctica), *Tranquiloxyton* Herbst & Lutz, 1995 (Argentina and Chile), *Cuneumxyton* Artabe & Brea, 2003 (Argentina) and *Elchaxyton* Artabe & Zamuner, 2007 (Argentina) exhibit anomalous development of the

secondary xylem and liana-like anatomy (Archangelsky & Brett 1961, Brett 1968, Herbst & Lutz 1995, Chong Díaz *et al.* 1997, Artabe & Brea 2003, Artabe & Zamuner 2007). On the other hand, *Kykloxylo*n Meyer-Berthaud, Taylor & Taylor, 1993 (Antarctica) and *Jeffersonioxylo*n Del Fueyo, Taylor, Taylor & Cúneo, 1995 (Antarctica) have a normal cylinder of secondary xylem (Del Fueyo *et al.* 1995, Meyer-Berthaud *et al.* 1992, 1993, Taylor 1996). *Kykloxylo*n was assigned to corystosperms based on the presence of attached foliar bases similar in size and structure to *Dicroidium* (Meyer-Berthaud *et al.* 1992, 1993, Taylor 1996), whereas *Jeffersonioxylo*n was considered to belong to this group based on its association with *Dicroidium* foliage (Taylor 1996, Cúneo *et al.* 2003). Another genus assigned to Corystospermaeae is *Antarcticoxylo*n Seward, 1914 (Antarctica, South Africa and Brazil). Walton's (1925) proposal to synonymize *Antarcticoxylo*n with *Rhexoxylo*n was rejected by Archangelsky & Brett (1961), Plumstead (1964), Mussa (1980), Meyer-Berthaud & Taylor (1991), Meyer-Berthaud *et al.* (1993), and Herbst & Lutz (1995). These authors recommended maintaining *Antarcticoxylo*n as a morphogenus including exclusively the specimen found in the Beacon Sandstone (Permian), Antarctica. The South African and Brazilian materials were suggested to be referable to Corystospermaeae as they share features of the pith and secondary xylem with *Rhexoxylo*n and *Cuneumxylo*n (Archangelsky & Brett 1961, Mussa 1980, Meyer-Berthaud & Taylor 1991, Meyer-Berthaud *et al.* 1993, Herbst & Lutz 1995, Artabe & Brea 2003). However, *Antarcticoxylo*n does not show anomalous secondary growth (Seward 1917, Archangelsky & Brett 1961, Mussa 1980).

*Rhexoxylo*n trunks have a pycnoxylic wood derived from a unique mode of secondary vascular tissue production that results in centripetal and centrifugal

polyxylic stems. Secondary xylem is commonly used to describe the whole secondary vascular cylinder, as in these stems the secondary xylem is more conspicuous and has more chance of preservation, than secondary phloem. All the species assigned to this genus are characterized by a pith surrounded by a secondary vascular cylinder composed of two zones: (1) an inner zone with one or more cycles of secondary xylem strands that are either centripetal or both centripetal and centrifugal, i.e., the perimedullar vascular zone or medullar vascular system; and (2) an outer zone with wedges of centrifugal secondary xylem separated by parenchymatous rays, i.e., the peripheral vascular zone or cylindrical vascular system (Archangelsky & Brett 1961, Artabe *et al.* 1999, Artabe & Brea 2003). Seven species have been attributed to *Rhexoxylo*n: *R. africanum* Bancroft, 1913 emend. Walton, 1923, *R. tetrapteridoides* Walton, 1923 emend. Archangelsky & Brett, 1961, *R. piatnitzkyi* Archangelsky & Brett, 1961 emend. Brett, 1968, *R. brasiliense* Herbst & Lutz, 1988, *Rhexoxylo*n sp. Lutz & Herbst (1992 = *R. kraeuselii* Spalletti, Artabe, Morel & Brea *nomen nudum*; see systematic palaeobotany section below), *Rhexoxylo*n sp. Taylor (1992) and *R. bruno*i Artabe, Brea & Zamuner, 1999. This genus shows a wide distribution in southwest Gondwana (Argentina, Brazil and South Africa) and Antarctica (Taylor 1992).

A species newly assigned to *Rhexoxylo*n is described in this paper. The material comes from the upper Cortaderita Formation exposed at La Tinta Creek, Barreal area, San Juan, Argentina. These stems were first described by Menéndez (1956) and named as *Protophyllocladoxylon cortaderitaense*. He assigned it to the conifer genus *Protophyllocladoxylon* Kräusel, 1939 based on secondary xylem characters (pycnoxylic wood, uniseriate rays, cross-fields with one simple oval to circular pit, tracheids with alternate and slightly hexagonal bordered

pits). However, corystosperm axis anatomy was poorly known at the time of Menéndez' (1956) work. Comprehension of their complex anatomy advanced in subsequent years via the contributions of Archangelsky (1968), Archangelsky & Brett (1961), Brett (1968), Petriella (1981, 1983), Herbst & Lutz (1988, 1995), Zamuner (1991), Meyer-Berthaud *et al.* (1993), Brea (1995), Artabe *et al.* (1999), Artabe & Brea (2003), and Artabe & Zamuner (2007). Moreover, corystosperm trunks have pycnoxylic wood resembling that of primitive conifers. In particular, Kräusel (1949) recognized a strong similarity between the secondary xylem of *Rhexoxylon* and the *Protophyllocladoxylon*-type wood. Consequently, it is very difficult to distinguish the wood of these groups if only isolated secondary xylem is found. Menéndez (1956), in spite of having a complete trunk, merely studied, described and illustrated the secondary xylem of the specimens, this situation resulting in later authors' failure to notice the corystospermaceous nature of these fossils. *Protophyllocladoxylon cortaderitaense* has also been mentioned as a primitive conifer by Schultze-Motel (1961), Vogellehner (1965), and Serra (1966). Lepekhina (1972) considered *P. cortaderitaense* and the whole genus as gymnosperm morphotaxa, not necessarily coniferous.

The species was later revised and included in the family 'Protopinaceae' by Vogellehner (1967), who recombined it as *Protocircoporoxylon cortaderitaense*. Furthermore, several revisions of the Barreal palaeoflora were carried out by Bonetti (1963), Stipanovic (1972, 1979), Artabe *et al.* (1995, 2001, 2003), and Zamuner *et al.* (1999, 2001). These authors pointed out the occurrence of conifer trunks in the palaeoflora based on Menéndez' (1956) descriptions and illustrations.

Lutz & Herbst (1992) were the first investigators to mention the presence of *Rhexoxylon* trunks in the Barreal zone, but

their description was preliminary. Previously, Archangelsky (unpublished annotation on the collection label dated 1990) had reviewed the *Protocircoporoxylon cortaderitaense* type material and noticed that it probably belonged to *Rhexoxylon*. That supposition was confirmed by Bodnar (2006). Actually, the *Protocircoporoxylon cortaderitaense* type material corresponds to the informally named *Rhexoxylon* species cited by Lutz & Herbst (1992) and has unique features within the genus.

Materials and methods

The studied fossil stems were found in the upper Cortaderita Formation at La Tinta creek, 8 km east of Barreal city, situated in the southern Precordillera, San Juan province, western Argentina. The type material was collected by Menéndez (1956) at the southern limit of that creek (69° 23' W, 31° 40' S; Fig. 1). It consists of fragments, branches, and sprouts belonging to a larger silicified trunk buried in rose-coloured siltstones and sandstones with a high proportion of pyroclastic material. Complementary samples were later collected from the same locality and unit during a field trip carried out by the *División Científica de Paleobotánica* of the *Museo de La Plata*. The stems were preserved parallel to bedding, in very fine red conglomerates (sabulites) with a high proportion of pyroclastic material and silcrete development (Fig. 2). The sediments were deposited in a sandy to gravelly braided fluvial system (Spalletti 2001). This species is also very abundant in the lower Cortaderita Formation (Middle to Late Triassic). Conspecific specimens of *Rhexoxylon* were erroneously ascribed to the Barreal Formation by Lutz & Herbst (1992), whereas they certainly derive from the lower Cortaderita Formation.

Stems were preserved by siliceous cellular permineralization. Preservation of all the material is poor. Polished surfaces were

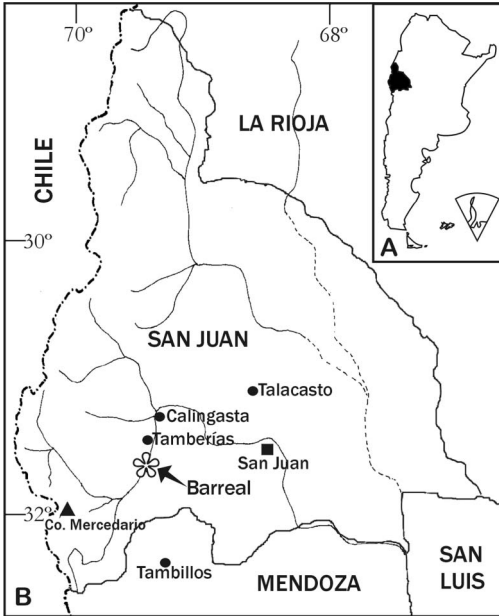


Fig. 1. Location map of Barreal area, San Juan province, Argentina. A, Geographical map of Argentina showing the location of San Juan province. B, Geographical map of San Juan province showing Barreal fossiliferous locality.

obtained from new specimens. The three types of thin-sections (transverse, radial and tangential) were prepared from these fossils for microscopic examination and also from the type material, because some of Menéndez' (1956) original slides are lost. The standard terminologies of Greguss (1955), Boureau (1956), Fahn (1990) and IAWA Committee (2004) were used to describe the fossil woods. The complementary material enabled improvement of the original diagnosis and description of the species.

The specimens and their microscopic slides are deposited in the Paleobotanical National Collection, *Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia'* (BAPb and BAPbPm), and Paleobotanical Collection, *División Científica de Paleobotánica, Museo de La Plata, Universidad Nacional de La Plata* (LPPB and pmLPPB).

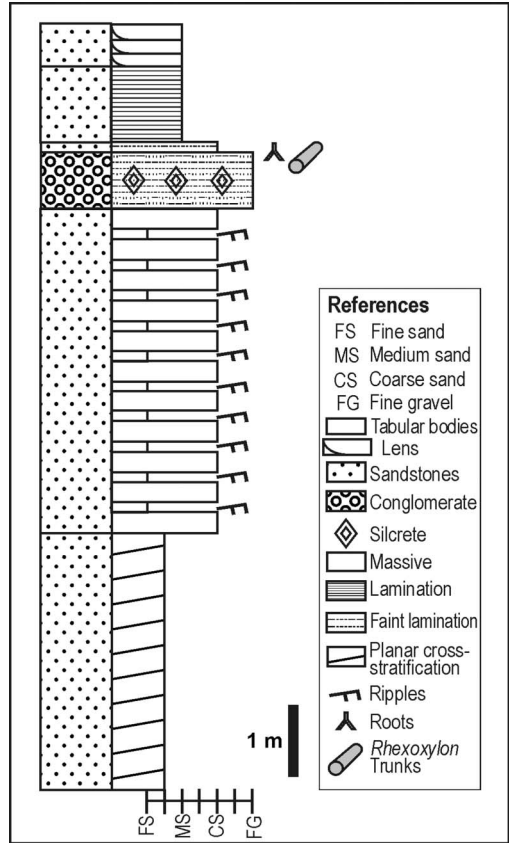


Fig. 2. Sedimentary log of the upper section of Cortaderita Formation at La Tinta Creek including the fossiliferous level with silicified trunks.

Systematic palaeobotany

Class GYMNOSPERMOPSIDA Stewart & Rothwell, 1993

Order CORYSTOSPERMALES Petriella, 1981

Family CORYSTOSPERMACEAE Thomas, 1933

Rhexoxylon Bancroft, 1913 emend. Archangelsky & Brett, 1961

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

Rhexoxylon cortaderitaense (Menéndez, 1956) Bodnar comb. nov. emend. (Figs 3–7)

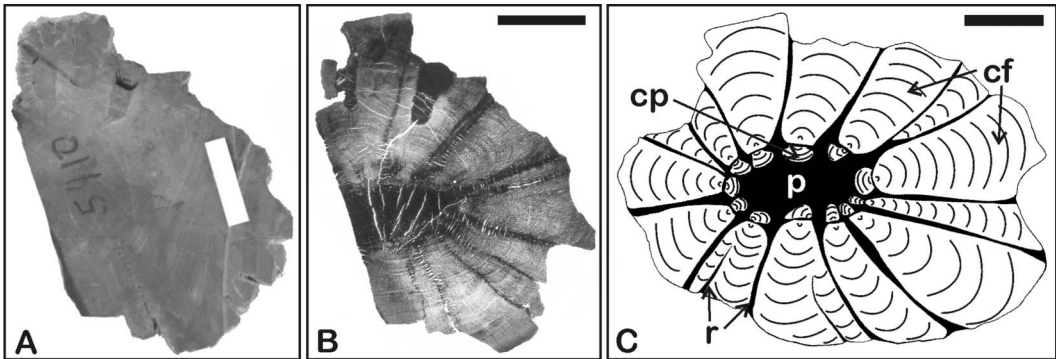


Fig. 3. *Rhexoxydon cortaderitaense* (Menéndez) Bodnar comb. nov. **A**, Polished surface showing the general aspect of the stem in transverse section, BAPb 5410 (lectotype). Scale bar: 2 cm. **B**, Transverse section of the same stem showing secondary vascular cylinder pattern, BAPbPm 5410 (lectotype). Scale bar: 2 cm. **C**, Diagram of the same stem showing the secondary vascular cylinder organization: pith (p), centripetal secondary xylem (cp), centrifugal secondary xylem (cf) and parenchymatous rays (r), BAPb 5410 (lectotype). Scale bar: 2 cm.

Basionym. *Protophyllocladoxylon cortaderitaense* Menéndez, 1956, p. 274, pls. I–II.

Synonymy

1967 *Protocircoporoxylon cortaderitaense* Vogellehner, p. 41.

1992 *Rhexoxydon* sp. Lutz & Herbst, p. 74–76, fig. 1.

1999 *Rhexoxydon kraeuselii* Spalletti, Artabe, Morel & Brea, *nomen nudum*.

2001 *Rhexoxydon* sp. A (*R. kraeuselii*?) Lutz & Herbst in Zamuner, Zavattieri, Artabe & Morel, p. 163, fig. 6.21.

2001 *Rhexoxydon kraeuselii* Morel, Artabe, Zavattieri & Bonaparte, *nomen nudum*.

2003 *Rhexoxydon kraeuselii* Artabe & Brea *nomen nudum*.

2003 *Rhexoxydon* sp. (*R. kraeuselii*?) Lutz & Herbst in Artabe & Brea, p. 11.

Type material. Lectotype specimen BAPb 5410; BAPbPm 5410, 505, 506, 507 and 520. Paralectotypes BAPb 5372, 5378, 5382 and 5417; BAPbPm 5433; LPPB 13083, 13084, 13085, 13086, pmLPPB 1358, 1359, 1360, 1361, 1362, 1363, 1364.

Additional material. LPPB 13087, 13088, 13089, 13090.

Type locality. La Tinta Creek, Barreal, San Juan; upper Cortaderita Formation, Late Triassic (Spalletti *et al.* 1999).

Emended diagnosis. Columnar, eccentric, and polyxylic gymnospermous stems, 10–45 cm in diameter. Oval and heterogeneous pith, 3–4 cm × 1.4–3.2 cm in diameter, with parenchyma cells, polyhedral idioblasts, sclerotic nests, and secretory cavities. Vascular secondary system with centripetal and centrifugal xylem and phloem, divided in wedges by parenchymatous rays 0.07–0.45 cm wide. Conspicuous and thick centripetal secondary xylem, separated by a thin band of parenchymatous tissue from centrifugal secondary xylem. Secondary xylem tracheids rectangular to pentagonal in cross-section, with mainly biseriate and alternate bordered pits on radial and tangential walls. Cross-fields with one simple and large pit, circular to oval in shape. Rays uniseriate, 1–15 cells high. Axial parenchyma and ray tracheids absent. Cortex with an inner zone of vascular strands and a poorly preserved outer zone composed of centrifugal secondary phloem and cork.

Description. The trunks are eccentric and oval in cross-section with a major diameter

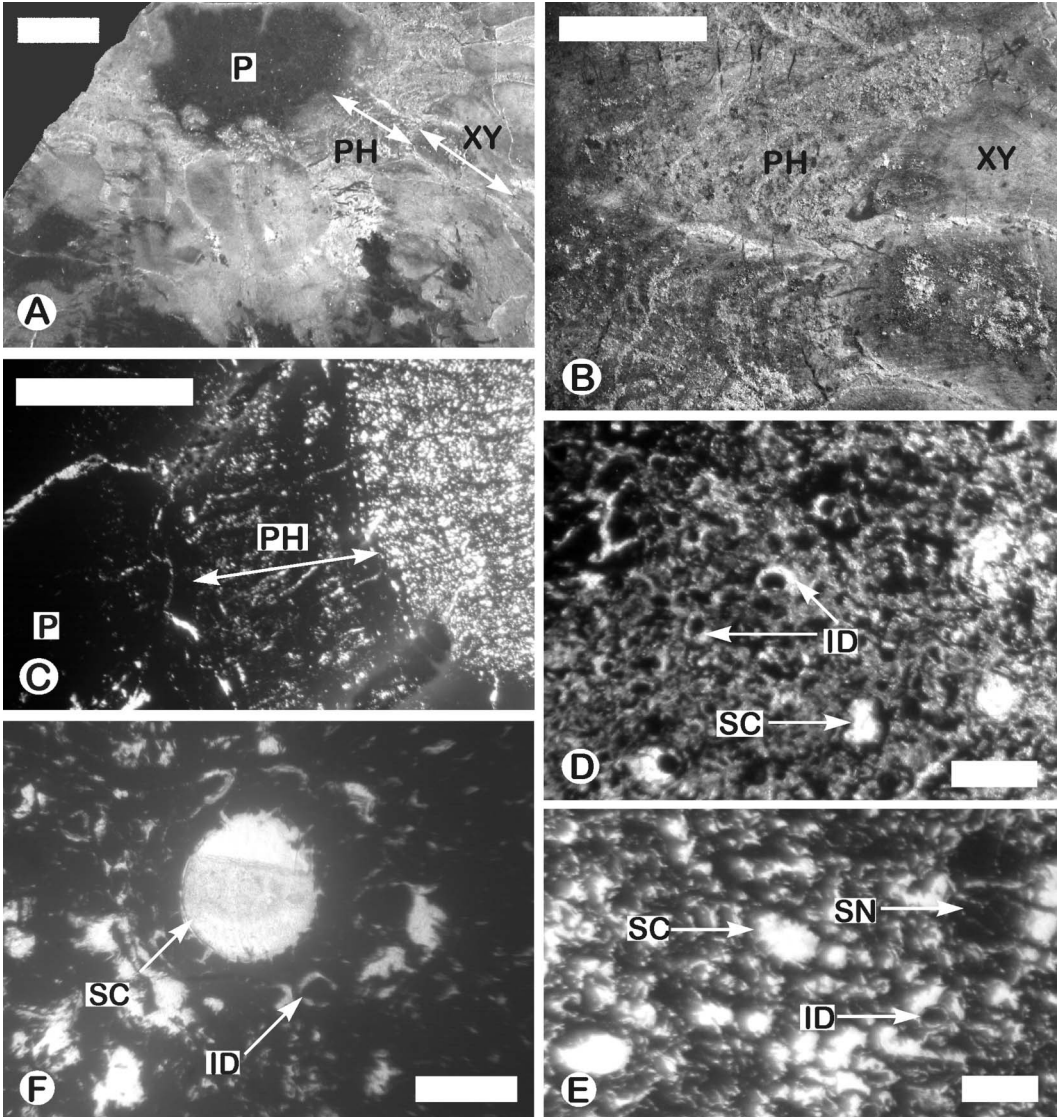


Fig. 4. *Rhexoxylon cortaderitaense* (Menéndez) Bodnar comb. nov. **A**, Perimedullar region of a mature stem, showing the pith (P) and centripetal secondary vascular tissues: centripetal phloem (PH) and centripetal xylem (XY), LPPB 13083 (paralectotype). Scale bar: 10 mm. **B**, Detail of centripetal phloem (PH) and centripetal xylem (XY) in the same stem, LPPB 13083 (paralectotype). Scale bar: 5 mm. **C**, Cross-section showing less developed centripetal phloem (PH) towards the pith (P) in an immature stem, BAPbPm 5410 (lectotype). Scale bar: 1 mm. **D**, Cross-section of the pith with polyhedral idioblasts (ID) and secretory cavities (SC), pmLPPB 1358 (paralectotype). Scale bar: 300 μ m. **E**, Radial section of the pith with polyhedral idioblasts (ID), secretory cavities (SC) and sclerotic nests (SN), BAPbPm 5410 (lectotype). Scale bar: 300 μ m. **F**, Detail of a secretory cavity (SC) surrounded by idioblasts (ID) in radial section, BAPbPm 5410 (lectotype). Scale bar: 250 μ m.

of 10–30 cm and a minor diameter of 8–24 cm. Some specimens reach 45 cm in diameter (Menéndez 1956). The specimens

are characterized by the presence of pith, secondary xylem, secondary phloem, and cortex. This trunk is polyxylic because of

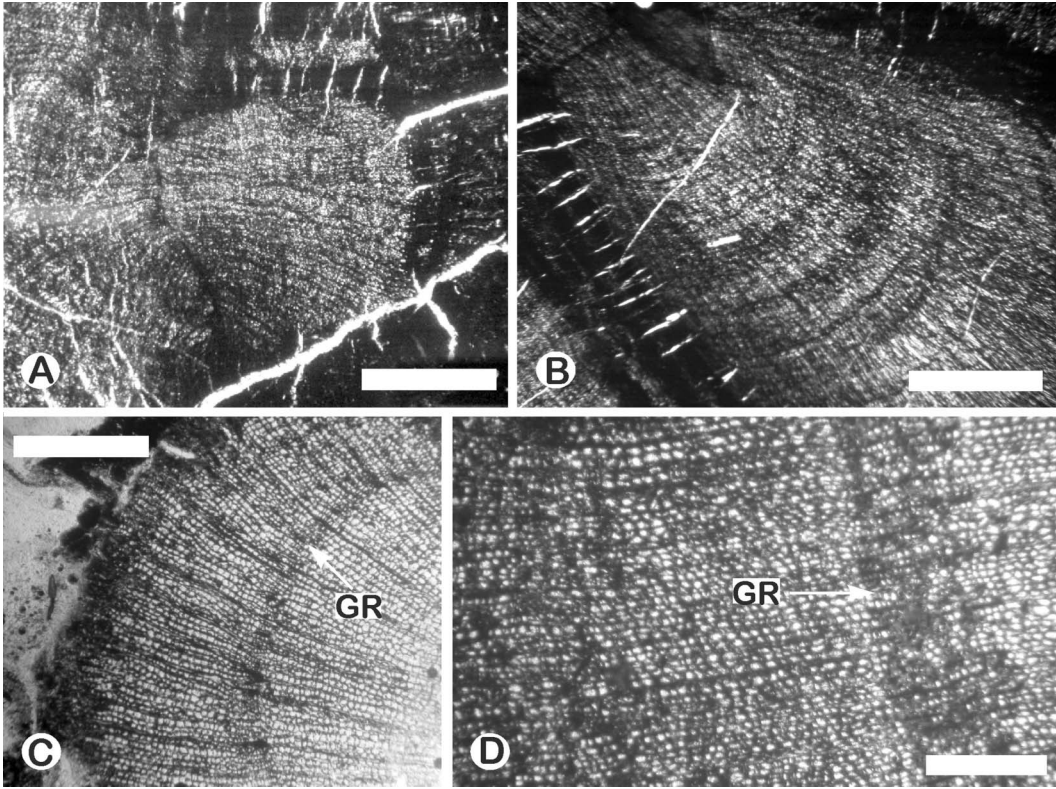


Fig. 5. *Rhexoxylon cortaderitaense* (Menéndez) Bodnar comb. nov. **A**, Segment of centripetal secondary xylem in cross-section. BAPbPm 5410 (lectotype). Scale bar: 2 mm. **B**, Centrifugal secondary xylem wedge in cross-section. BAPbPm 5410 (lectotype). Scale bar: 4.5 mm. **C**, Ring-like growth developed inside the centripetal xylem. GR symbolizes the ring-like boundary. pmLPPB 1358 (paralectotype). Scale bar: 1 mm. **D**, Ring-like growth developed inside the centrifugal xylem wedges. GR symbolizes the ring-like boundary. pmLPPB 1361 (paralectotype). Scale bar: 400 μ m.

two discontinuous anomalous cambial rings that start developing centripetal secondary xylem and phloem towards the pith and centrifugal secondary xylem and phloem towards the cortex (Figs 3A, B, C; 4A, B, C).

The pith is 3–4 cm \times 1.4–3.2 cm in diameter, oval and heterogeneous (Figs 3B, C; 4A), with spherical parenchyma cells, polyhedral idioblasts with dark contents, sclerotic nests, secretory cavities, and probably vascular strands (Fig. 4D, E, F).

Centripetal secondary phloem is 0.1–(0.65)–1.1 cm thick. Owing to its poor preservation, anatomical features of the phloem cannot be determined in detail. However, it seems to include phloem

parenchyma, phloem fibres and sieve cells. Phloem fibres are clustered in groups separated by bands of crushed and deformed cells (Fig. 4A, B, C).

Centripetal secondary xylem is 0.24–(1.05)–1.4 cm thick. Each centripetal xylem segment is 0.37–(0.94)–1.3 cm wide and is separated from centrifugal secondary xylem by parenchymatous tissues of cells similar to those of the medulla (=tangential parenchyma) arising from a remnant cambium (Fig. 5A).

Primary xylem, which should be located between centripetal and centrifugal secondary xylem, is not discernible. Despite this, it can be inferred to be mesarch.

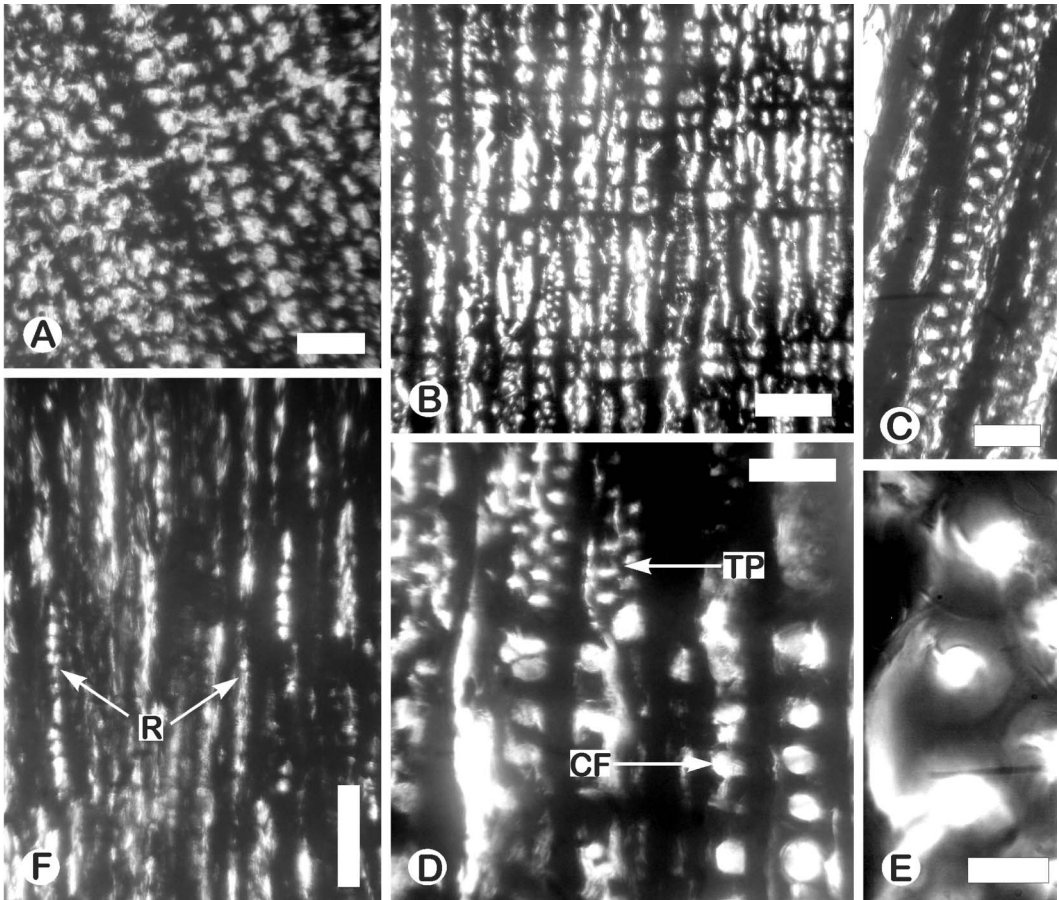


Fig. 6. *Rhexoxydon cortaderitaense* (Menéndez) Bodnar comb. nov. A, Detail of tracheids in transverse section, BAPbPm 505 (lectotype). Scale bar: 200 μm . B, General view of secondary xylem in radial section, pmLPPB 1359 (paralectotype). Scale bar: 100 μm . C, Biseriate radial pitting of tracheids, BAPbPm 506 (lectotype). Scale bar: 30 μm . D, Fenestriform cross-fields (CF) and triseriate radial pitting of tracheids (TP), pmLPPB 1359 (paralectotype). Scale bar: 40 μm . E, Detail of biseriate radial pitting of tracheids showing its slightly hexagonal shape and circular pore, BAPbPm 506 (lectotype). Scale bar: 10 μm . F, Uniseriate homocellular rays (R) of secondary xylem in tangential section, pmLPPB1363 (paralectotype). Scale bar: 150 μm .

Centrifugal secondary xylem is 3.3–(5.73)–11.5 cm thick (Fig. 5B). It is arranged in wedges as a result of differential cambial activity around the circumference of the axes. There are cambium strands that only produce ray-parenchyma, so the whole secondary wood is divided by parenchymatous rays. Such rays may also develop locally within the xylem wedges (Figs 3B, C; 5B). Each centrifugal xylem wedge is 1.1–(2.81)–6.5 cm wide. Parenchymatous

rays are 0.07–(0.19)–0.45 cm wide and consist of tissues similar to those of the medulla. In addition, tangential fragmentation inside xylem wedges is evident in some specimens. It is a consequence of remnant cambial activity, which produces parenchymatous tissue (=tangential parenchyma).

Ring-like growth is developed inside the centripetal and centrifugal secondary xylem, with an abrupt diminution of the radial diameter of tracheids towards the ring's

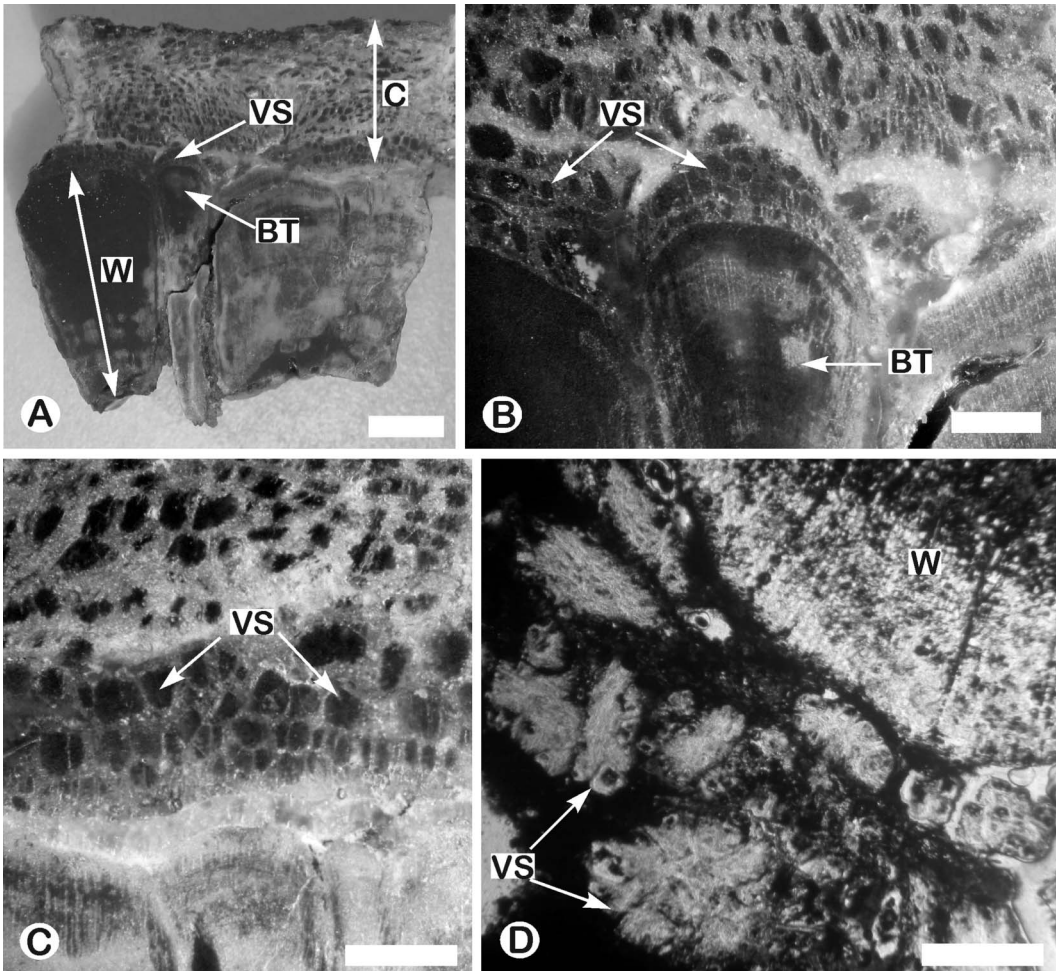


Fig. 7. *Rhexoxydon cortaderitaense* (Menéndez) Bodnar comb. nov. **A**, General view of the outer zone of centrifugal xylem wedges (W) and cortex (C), its inner zone composed of vascular strands (VS). A probable branch trace (BT) is also visible departing from centrifugal xylem, LPPB 13086 (paralectotype). Scale bar: 10 mm. **B**, Detail of the branch trace (BT) and the inner cortex zone composed of vascular strands (VS), LPPB 13086 (paralectotype). Scale bar: 5 mm. **C**, Detail of cortex vascular strands (VS), LPPB 13086 (paralectotype). Scale bar: 3 mm. **D**, Cross-section of the outer zone of centrifugal xylem wedges (W) and cortex vascular strands (VS), pmLPPB 1364 (paralectotype). Scale bar: 600 μm .

outer margin (Fig. 5C, D). This ring-like growth does not constitute true continuous rings because the boundaries are interrupted by the parenchymatous rays; this results in unconformity with those of the adjacent xylem wedges. The 'latewood' band is 1–3 cells thick. Secondary xylem tracheids are rectangular to pentagonal in transverse section. The radial diameter of tracheids is

16.33–(37.11)–65.31 μm and the tangential diameter of tracheids is 28.57–(40.77)–58.77 μm (Figs 5D, 6A). The thickness of the double wall between two tracheids is 4.16–(7.99)–24.49 μm in radial section and 4.16–(7.70)–20.41 μm in tangential section. Tracheids show mainly biseriate, less commonly triseriate and uniseriate, bordered pits on both radial and tangential walls

(Fig. 6B, C, D, E). Tangential pits are very poorly preserved. Pits are circular or slightly hexagonal, with contiguous or compressed arrangement in alternate pit rows. Pit pores are circular or elliptical (Fig. 6E). On both radial and tangential tracheid walls, pits are 10.40–(13.67)–18.72 μm high and 11.44–(14.10)–22.88 μm wide. Cross-fields have one, sporadically two, simple pits with circular or oval outline, 10.4 \times 14.56 μm –(16.89 \times 23.44 μm)–29.7 \times 33 μm in diameter, placed in vertical rows (Fig. 6B, D).

Secondary xylem rays are homocellular; uniseriate, rarely biseriate (Fig. 6F). The rays are short with rectilinear trajectory, and are 48.98–(198.65)–448.98 μm and 1–(mode 3; mean 5.78)–15 cells high. They are composed of rectangular parenchyma cells with thin walls, and 20.41–(31.31)–42.9 μm high and 12.24–(24.96)–36.73 μm wide. Ray cell length cannot be measured because of poor preservation. Axial parenchyma and ray tracheids are absent.

The cortex is 1–3 cm wide and consists of two zones (Fig. 7A). The inner zone shows continuity with centrifugal secondary and parenchymatous tissues (Fig. 7B, C). It consists of numerous vascular strands surrounded by parenchyma cells, polyhedral idioblasts and probably sclerotic nests (Fig. 7D). The outer zone is poorly preserved and consists of centrifugal secondary phloem and cork. Primary phloem is not preserved.

Remarks. A lectotype (BAPb 5410) was chosen from the syntypes described by Menéndez (1956). The specimen assigned as lectotype is the most complete and best preserved of Menéndez' samples. Two original slides (transverse and radial) of BAPb 5410 material are identified by the collection number: BAPbPm 5410. The new slides prepared from BAPb 5410 specimen are labelled with the collection numbers: BAPbPm 505, 506, 507, and 520. Menéndez' other specimens (BAPb 5372, 5378, 5382

and 5417; BAPbPm 5433) are indicated as paralectotypes. Some of the complementary materials (LPPB 13083, 13084, 13085, 13086) were essential for the emended diagnosis, and so they are also considered paralectotypes. The rest of the complementary fossils are indicated as additional material (LPPB 13087, 13088, 13089, 13090).

Rhexoxylon cortaderitaense is also abundant in the lower Cortaderita Formation (Artabe *et al.* 1995). It is the same species that Lutz & Herbst (1992) described as *Rhexoxylon* sp. and erroneously ascribed to the Barreal Formation. After the original description of the species, several authors mentioned it under different names: *Rhexoxylon kraeuselii* and *Rhexoxylon* sp. A (*R. kraeuselii?*); based on the intention of Lutz & Herbst (1992) to dedicate this species to Dr Richard Kräusel. *Rhexoxylon kraeuselii* is a *nomen nudum* because it was published without a description or diagnosis (ICBN, McNeil *et al.* 2006). On the other hand, *Rhexoxylon* sp. A (*R. kraeuselii?*) is not an appropriate reference to the species because such a citation is applied to a taxon doubtfully ascribed to the legitimately named species between parentheses, this not being the case here.

Comparisons and discussion

Corystospermaceae stems share some anatomical features with medullosans and cycads (Archangelsky & Brett 1961, Archangelsky 1996). Deviations from the typical pattern of secondary growth are present in these groups. Each segment of primary xylem in the vascular system of medullosans is surrounded by a complete cylinder of secondary xylem (Namboodiri & Beck 1968, Basinger *et al.* 1974), which has centrifugal and centripetal portions developed by normal and inverted cambium, respectively. The presence of two

discontinuous anomalous cambial rings is considered as polyxyly.

Recently, Césari *et al.* (2005) described Late Carboniferous stems from Argentina with anomalous secondary xylem completely surrounding each segment of primary xylem, which is the first record of this kind of axis for the Palaeozoic of Gondwana.

Permian medullosans have a more complex vascular cylinder with two distinct systems: a cylindrical one or 'Plattenringe', and medullar one or 'Sternringe' (Weber & Sterzel 1896, Worsdell 1906, Bancroft 1914). Both systems, also present in cycad and corystosperm stems, are considered to be homologous, as the medullar arrangement is interpreted to derive from the cylindrical one (Worsdell 1906, Artabe & Stevenson 1999, Artabe & Brea 2003, Artabe *et al.* 2005). Within medullar and cylindrical systems, there may be more than one cycle of secondary vascular tissues produced by supernumerary cambia.

Most Permian medullosans show an increase in complexity and regularity of cylindrical system. They have one or two cycles of centripetal–centrifugal secondary xylem and secondary phloem segments, which constitute an almost complete ring by tangential fusion (Weber & Sterzel 1896, Bancroft 1914, Petriella 1981). Consequently, some species of *Medullosa* Cotta, 1832 have been observed to possess included phloem (Weber & Sterzel 1896). The cylindrical system in cycads shows a progressive loss of the centripetal secondary xylem, which becomes relictual in extant genera (Worsdell 1896, 1906). Centripetal secondary xylem is also absent in the cylindrical system of some corystosperm genera (Artabe & Brea 2003).

As mentioned above, the medullar system develops from centripetal secondary xylem of the cylindrical system (Worsdell 1906, Artabe & Stevenson 1999, Artabe & Brea 2003, Artabe *et al.* 2005). Centripetal xylem splits from the cylindrical system,

and subsequently, centrifugal xylem begins to grow at the outer edge leading to perimedullar bundle formation. The medullar system in medullosans and cycads consists of many concentric and double (centripetal–centrifugal) bundles with an irregular arrangement (Weber & Sterzel 1896, Worsdell 1896, 1906, Bancroft 1914). In contrast, corystosperms have perimedullar double bundles organized in a regular pattern (Artabe & Brea 2003).

Although medullosans and cycads share structural features with corystosperms, their secondary xylem histology differs from each other, since, in the first two groups, it is manoxylic and in the last one, pycnoxylic. The presence of anomalous secondary xylem production yielding pycnoxylic wood is unique within gymnosperms.

Within the Corystospermaceae, *Kyklaxylon*, *Jeffersonioxylon* and *Antarcticoxylon* possess a normal solid secondary vascular cylinder equivalent to the cylindrical system described above. *Tranquiloxylon* and *Cuneumxylon* only show an anomalous vasculature in the form of polyxylic centrifugal secondary xylem dissected by parenchymatous rays. They do not produce centripetal xylem or perimedullar double bundles, so they lack a medullar system (Herbst & Lutz 1995, Artabe & Brea 2003). *Elchaxylon* has an undivided cylindrical system, but it is a polyxylic stem because it possesses both centrifugal and centripetal secondary xylem around the mesarch primary xylem; however, it does not develop perimedullar bundles (Zamuner 1991, Artabe *et al.* 1999, Artabe & Brea 2003, Artabe & Zamuner 2007).

Rhexoxylon shows the most complex vascular cylinder pattern within corystosperms. It has a polyxylic stem owing to the presence of a centrifugal (normal) cambium and a centripetal (inverted) cambium. These stems can develop more than one centrifugal cambium, generating a centrifugal polyxylic anatomy composed of secondary

xylem and phloem concentric rings in the cylindrical system. In addition, the medullar system develops from more than one cambium, i.e. centripetal polyxyle, characterized by one or more cycles of perimedullar bundles. Each perimedullar bundle consists of a centripetal vascular section (xylem + phloem) towards the pith and a centrifugal portion (xylem + phloem) towards the cortex. The formation of tangential parenchyma (from a remnant cambium) separates both centrifugal–centripetal secondary xylems triggering bundle fragmentation. In brief, *Rhexoxylon* stems have two secondary vascular systems: cylindrical or peripheral and medullar or perimedullar. Most of the species of *Rhexoxylon* express variations on the pattern described above.

In *R. tetrapteridoides* (Molteno Formation, Stormberg Group, Middle to Late Triassic; Natal, South Africa), the cylindrical vascular system incorporates quite compact centrifugal secondary xylem wedges with a small quantity of parenchymatous tissues (tangential parenchyma and parenchymatous rays) and scarce development of centripetal secondary xylem towards the medulla (Archangelsky & Brett 1961). The medullar system is composed of one complete ring of centripetal–centrifugal bundles (Archangelsky & Brett 1961, Artabe & Brea 2003). In these bundles, the centripetal xylem is significantly thicker than the centrifugal xylem (Zamuner 1991).

In *R. piatnitzkyi* (Ischigualasto Formation, Agua de La Peña Group, early Late Triassic; San Juan province, Argentina), the dissected, cylindrical vascular system consists of several centrifugal xylem segments with a discrete quantity of centripetal secondary xylem separated by a narrow zone of tangential parenchyma (Archangelsky & Brett 1961, Archangelsky 1968, Brett 1968, Zamuner 1991). Parenchymatous tissues are abundant. The medullar system is more conspicuous than in *R. tetrapteridoides*. It is constituted by one complete ring of

centripetal–centrifugal bundles, in which centrifugal parts show a more marked development than in the *R. tetrapteridoides* medullar system.

Rhexoxylon brasilense (Caturrita Formation, Rosário do Sul Group, Late Triassic; Rio Grande do Sul, Brazil) possesses a cylindrical vascular system with a ring of centripetal–centrifugal wedges, in which centripetal xylem is thicker than in previously mentioned species and is closely associated with the medullar system (Herbst & Lutz 1988). The medullar system has a complete ring of centripetal–centrifugal bundles.

In *R. brunoi* (Los Colorados Formation, Uspallata Group, Late Triassic; Mendoza province, Argentina), the cylindrical vascular system comprises wedges with centripetal–centrifugal secondary xylem, and the centripetal xylem is also closely linked to the medullar system. The medullar system has a complete cycle of 16 centripetal–centrifugal bundles and one cycle of centripetal xylem (Artabe *et al.* 1999).

The stem of *R. africanum* (lower Elliot Formation? or ‘red beds’, Stormberg Group, Late Triassic to Early Jurassic?, Cape Province, South Africa) possesses a cylindrical vascular system with well-developed centrifugal wedges of secondary xylem and centripetal secondary xylem. The medullar system contains one or more concentric series of centripetal–centrifugal bundles (Bancroft 1913, Walton 1923, Kräusel 1956, Archangelsky & Brett 1961).

The specimen with *Rhexoxylon*-like secondary anatomy from the Triassic of Antarctica is characterized by a cylinder of secondary xylem divided into sectors by large parenchymatous rays and the development, within the pith, of some secondary xylem strands of uncertain structure (Taylor 1992). As the medullar system arrangement is unknown, this stem is not included in the following discussion and phylogenetic considerations.

In the seventh species of the genus, *R. cortaderitaense*, the cylindrical vascular system is composed of one cycle of large wedges of centrifugal secondary xylem separated by tangential parenchyma from one cycle of centripetal secondary xylem and secondary phloem. The medullar vascular system is not developed, since *R. cortaderitaense* lacks perimedullar bundles, but centripetal tissues are very well developed, and they could be described as a 'perimedullar vascular zone' for practical purposes. Despite this, *R. cortaderitaense* shows a strong resemblance to *R. tetrapteridoides* as the secondary vascular cylinder of smaller *R. tetrapteridoides* specimens is composed of only one cycle of centrifugal–centripetal xylem, without perimedullar centripetal–centrifugal bundles (Archangelsky & Brett 1961, Zamuner 1991).

Ontogenetic and phylogenetic considerations

The cauline vascular system ontogeny of three species of *Rhexoxylon* was studied: *R. tetrapteridoides*, *R. piatnitzkyi*, and *R. africanum* (Archangelsky & Brett 1961, Zamuner 1991). Developmental features expressed within these species can be extrapolated to other species within the genus (*R. brunoii*, *R. brasiliense*). In the juvenile axes, the secondary vascular cylinder consists of only one centrifugal–centripetal xylem cycle, with uniform development of both parts (Fig. 8A). In the following stages, cambium activity becomes differential with more prominent growth of centrifugal tissues than of centripetal tissues (Fig. 8B). Later, the centripetal xylem splits from the centrifugal one due to parenchyma development between them (Fig. 8C). In the late phases, centrifugal xylem begins to grow at the outer edge of the centripetal one, this leading to the double (centripetal–centrifugal) bundle formation. Furthermore, a discrete quantity of centripetal xylem is

developed on the inner edges of centrifugal wedges. These three processes, centripetal xylem growth, separation of centrifugal and centripetal parts, and double bundle formation, may take place more than once. Consequently, the mature trunk of *Rhexoxylon* has a vascular cylinder with a cycle of perimedullar centripetal–centrifugal bundles and a cycle of centrifugal–centripetal peripheral wedges (Fig. 8D). On the other hand, when the first centripetal xylem splits from centrifugal xylem in *R. cortaderitaense* axes (Fig. 9A, B), a new centrifugal xylem is not generated at the outer edge. Conversely, more centripetal tissues continue to develop (Fig. 9C). This is a distinctive feature (= autapomorphy) of this species, and the differences in xylem production have important phylogenetic implications.

It was suggested that the corystosperm secondary vascular cylinder evolved along two principal lineages (rhexoxyloid and cuneumxyloid) from a medullosan or similar precursor (Artabe & Brea 2003, Artabe & Zamuner 2007). *Cuneumxylon* and *Tranquiloxylon* characterize the cuneumxyloid line. These taxa show anomalous vasculature only in the centrifugal secondary vascular tissues because they do not produce centripetal xylem or perimedullar bundles. The rhexoxyloid line includes *Rhexoxylon* and *Elchaxylon* and is characterized by: mesarch primary xylem, centrifugal wedges of secondary xylem, centripetal secondary xylem and perimedullar bundles. According to Artabe & Brea (2003), the Argentinean species of *Rhexoxylon* fit into a developmental series (*R. cortaderitaense*, *R. piatnitzkyi*, and *R. brunoii*) showing an increase in anomalous vascular tissue development with formation of successive cycles of perimedullar bundles inside the trunk and the progressive acquisition of larger stems by an increase in the amount of centrifugal secondary conducting tissues. *Elchaxylon* represents a branch that initiates with *R. cortaderitaense* (Artabe & Zamuner 2007).

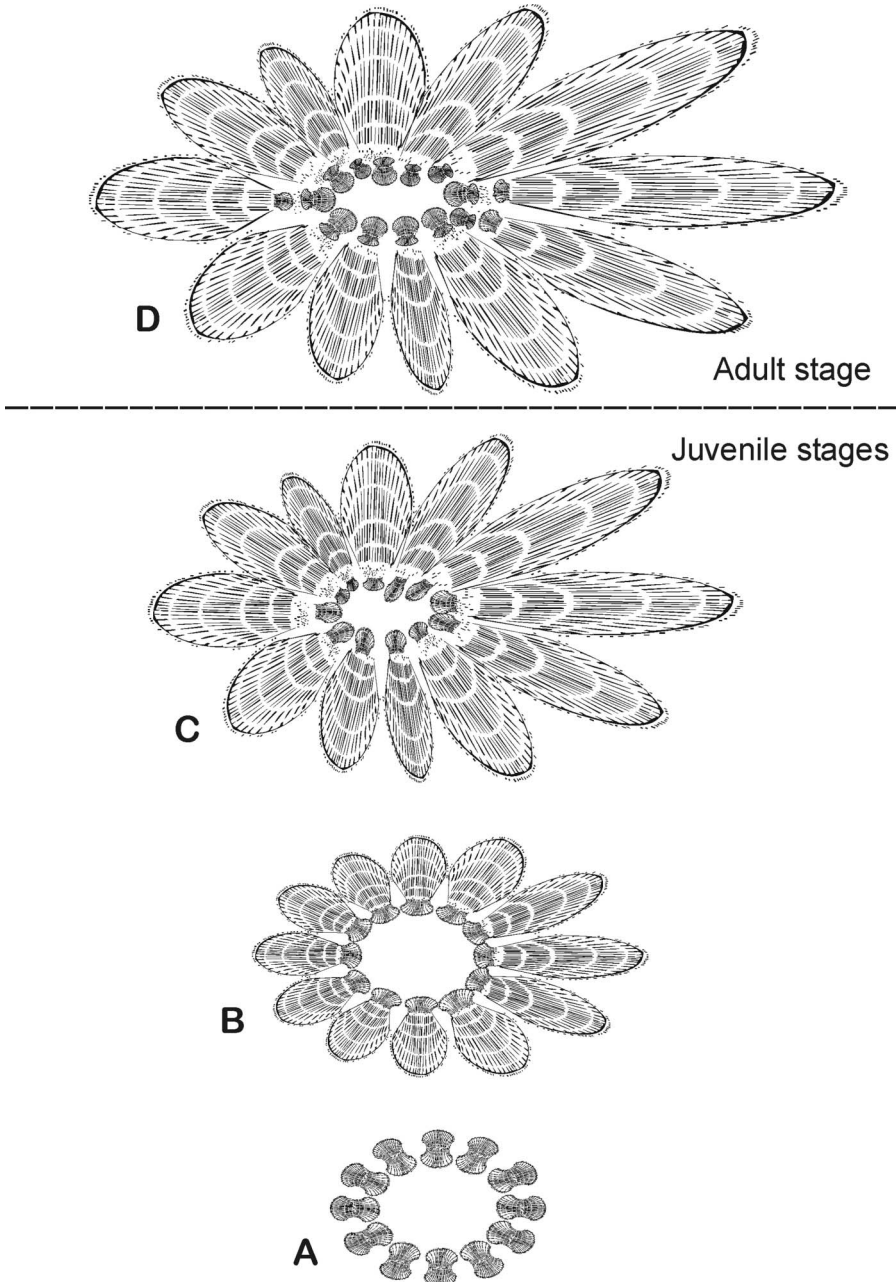


Fig. 8. Development sequence of secondary vascular system in *R. tetrapteridoides*. Lined pattern represents secondary xylem; dotted pattern symbolizes tangential parenchyma and secondary phloem. At the first stage (A), two discontinuous cambial rings give rise to equal amounts of centrifugal secondary xylem and centripetal secondary xylem around primary xylem. At the next phase (B), cambial rings show preferential development of their centrifugal part. In late stages, centripetal xylem splits from centrifugal xylem due to parenchyma development between them (C). At the adult phase of *R. tetrapteridoides* (D), centrifugal xylem grows at the outer edge of centripetal xylem generating a cycle of double (centripetal-centrifugal) bundles. Furthermore, centripetal xylem is developed in the inner edges of some centrifugal wedges.

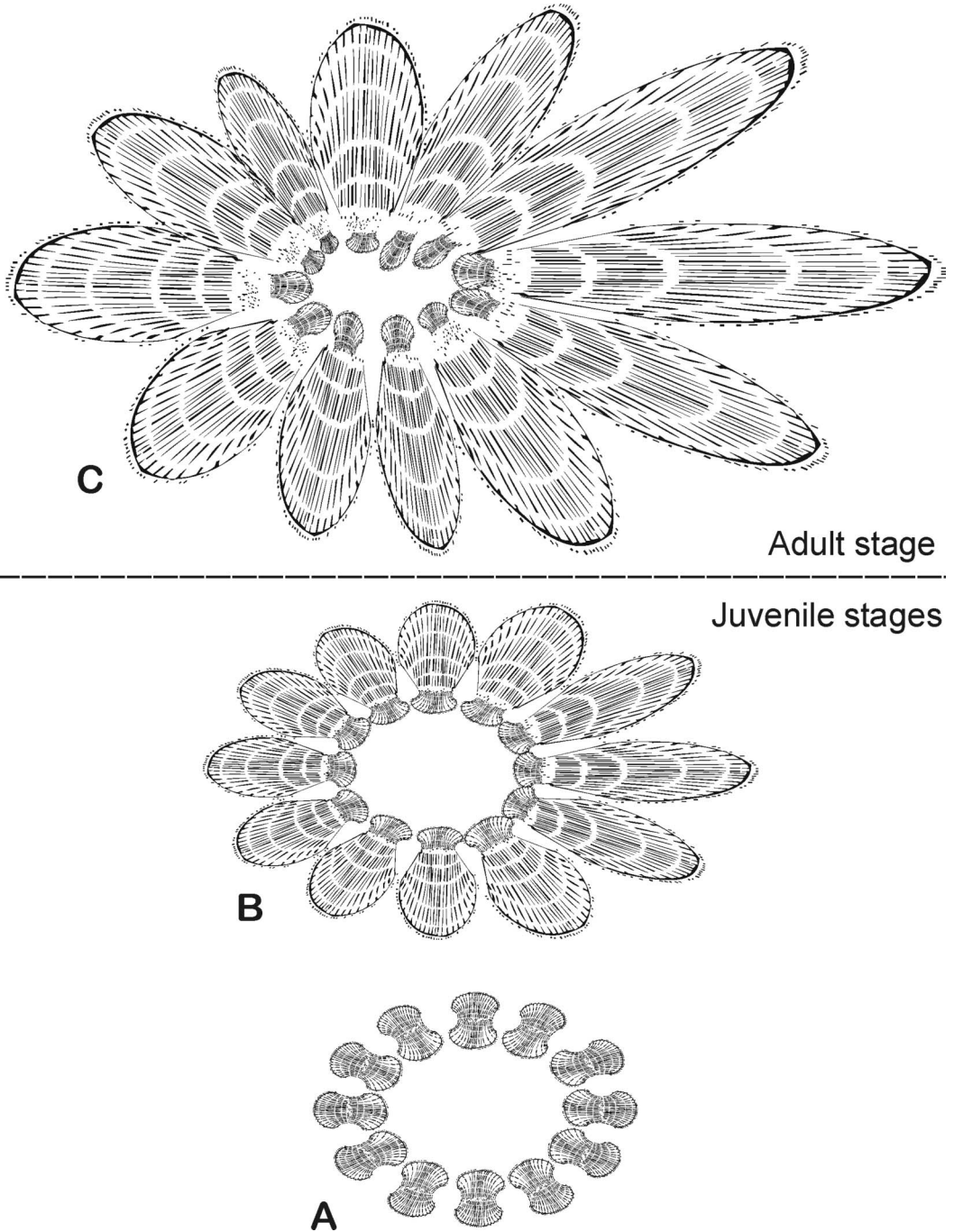


Fig. 9. Development sequence of secondary vascular system in *R. cortaderitaense*. Lined pattern represents secondary xylem; dotted pattern symbolizes tangential parenchyma and secondary phloem. The two early stages (A and B) are the same as those of *R. tetrapteridoides*. In later stages, centripetal xylem splits from centrifugal xylem due to parenchyma development between. At the adult phase of *R. cortaderitaense* (C), centripetal xylem keeps on growing towards the pith.

Elchaxylon, like this last species, has centripetal secondary xylem but does not produce perimedullar bundles (Fig. 10A).

An alternative phylogeny to the Artabe & Brea (2003) model can be hypothesized by incorporating the characters of the

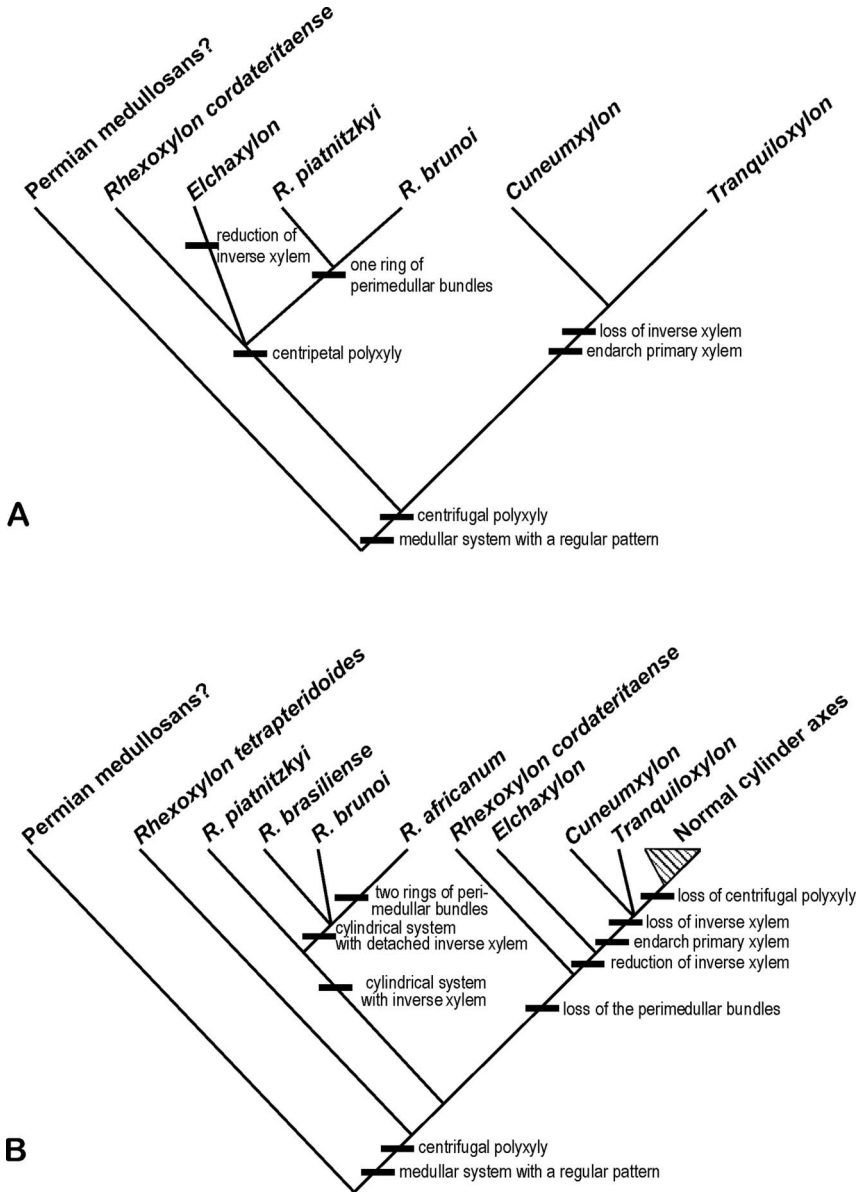


Fig. 10. Conjectural phylogenetical trees showing the hypothesized relationships between corystosperm stem taxa. **A**, Hypothesized relationships between Argentinean corystosperm stem taxa considering the lack of a medullar system primitive (adapted from Artabe & Brea 2003; Artabe & Zamuner 2007). **B**, Hypothesized relationships between all the corystosperm axis morphotaxa considering the lack of a medullar system derived (as suggested in this paper).

non-Argentinean taxa and interpreting all the characters from a different point of view. If Permian medullosans are considered as the probable ancestor of corystosperms, then all their stem features must be assumed as plesiomorphic in the corystosperm axis phylogenetic analysis. Thus, the rhexoxyloid lineage, characterized by traits present in Permian medullosans (mesarch primary xylem, centrifugal wedges of secondary xylem, centripetal secondary xylem, and perimedullar bundles) is not a natural group. On the other hand, the cuneumxyloid lineage could be a monophyletic group, given that its diagnostic characters (endarch primary xylem, loss of medullar system) are apomorphic. *Rhexoxylon tetrapteridoides* is proposed as basal in the corystosperm axis phylogeny, given that it has perimedullar bundles in the adult stage showing, at the same time, the simplest vascular pattern, features that are reiterated in the ontogeny of most of *Rhexoxylon* species and Permian medullosans. The other species of the genus could be arranged in a lineage that shows a trend towards increasing anomalous vascular tissue development: *R. tetrapteridoides*, with one complete ring of centripetal–centrifugal bundles; *R. piatnitzkyi*, with a more conspicuous ring of centripetal–centrifugal bundles and a discrete quantity of centripetal xylem in the cylindrical system; *R. brasilense* and *R. brunoi*, with a complete ring of centripetal–centrifugal bundles and a thicker centripetal xylem in the cylindrical system closely linked to the medullar system; and *R. africanum*, with two complete rings of perimedullar bundles. In contrast, *R. cortaderitaense* and *Elchaxylon* would be placed closer to the cuneumxyloid line, because they lack a medullar system and show a reduction of the centripetal (inverse) xylem (Fig. 10B). In this hypothesis, corystosperm stems with normal secondary vascular cylinder (*Kykloxylon*, *Jeffersonioxylon*, and *Antarcticoxylon*) should be related to the cuneumxyloid group

given that the acquisition of a non-anomalous vascular cylinder is secondary. However, until a thorough phylogenetic analysis is carried out with a character matrix analyzed by a cladistic software program, these relationships remain largely untested.

Conclusions

A species of Corystospermaceae, *Rhexoxylon cortaderitaense*, is described from the Late Triassic upper Cortaderita Formation of Argentina. As *R. cortaderitaense* had been originally described as the ‘protopinacean’ conifer *Protophyllocladoxylon* (= *Protocircoporoxyylon*) *cortaderitaense*, the new combination has important implications for the composition and biostratigraphy of the southwestern Gondwanan Triassic flora, taking into account that *Protocircoporoxyylon cortaderitaense* has been considered a biostratigraphic index characterizing one of the Assemblage Biozones proposed for the Triassic of Argentina (Spalletti *et al.* 1999).

The anatomically preserved stems, like all *Rhexoxylon* species, have a polyxylic anatomy with two discontinuous anomalous cambial rings, which develop both centrifugal secondary xylem and centripetal secondary xylem. *Rhexoxylon cortaderitaense* adult stems have conspicuous amounts of centripetal tissues that do not constitute centripetal–centrifugal perimedullar bundles. This character is considered apomorphic, placing *R. cortaderitaense* in a derived position within the corystosperm stem phylogeny. This new interpretation of the character modifies the previous hypothesized phylogenetic relationships of corystosperm axis morphotaxa.

Acknowledgements

I acknowledge Sergio Archangelsky, Georgina del Fueyo and Luis Lezama for the loan of specimens from Paleobotanical National

Collection and allowing the preparation of new slides. I thank Analía Artabe, Eduardo Morel, Ari Iglesias and Daniel Ganuza for their cooperation during fieldwork, and for the important exchange of opinions and ideas during the investigation. I am most grateful to Amanda Zamuner for improving the English version of the manuscript. I especially thank the reviewers for their constructive comments. This work was supported by the *Agencia Nacional de Promoción Científica y Tecnológica* (PICT 07-08467).

References

- ARCHANGELSKY, S., 1968. Studies on Triassic fossil plants from Argentina IV. The leaf genus *Dicroidium* and its possible relation to *Rhexoxylon* stems. *Palaeontology* 11, 500-512.
- ARCHANGELSKY, S., 1996. Aspects of Gondwana paleobotany: gymnosperms of the Paleozoic–Mesozoic transition. *Review of Palaeobotany and Palynology* 90, 287-302.
- ARCHANGELSKY, S. & BRETT, D., 1961. Studies on Triassic fossil plants from Argentina. 1. *Rhexoxylon* from the Ischigualasto Formation. *Philosophical Transactions of the Royal Society of London B* 244, 1-19.
- ARTABE, A.E. & BREA, M., 2003. A new approach to Corystospermales based on Triassic permineralized stems from Argentina. *Alcheringa* 27, 209-229.
- ARTABE, A.E. & STEVENSON, D.W., 1999. Fossil Cycadales of Argentina. *The Botanical Review* 65, 219-238.
- ARTABE, A.E. & ZAMUNER, A.B., 2007. *Elchaxylon*, a new corystosperm based on permineralized stems of the Late Triassic of Argentina. *Alcheringa* 31, 85-96.
- ARTABE, A.E., ZAMUNER, A.B., GANUZA, D.G. & SPALLETTI, L.A., 1995. Novedades en la tafoflora triásica de la quebrada de la Cortaderita, Barreal, provincia de San Juan, Argentina. *Actas de la 2ª Reunión sobre el Triásico del Cono Sur*, Bahía Blanca, 10–12 August 1995, 7.
- ARTABE, A.E., BREA, M. & ZAMUNER, A.B., 1999. *Rhexoxylon brunoi* Artabe, Brea et Zamuner, nov. sp., a new Triassic Corystosperm from the Paramillo de Uspallata, Mendoza, Argentina. *Review of Palaeobotany and Palynology* 105, 63-74.
- ARTABE, A.E., MOREL, E.M. & SPALLETTI, L.A., 2001. Paleocología de las floras triásicas argentinas. In *El Sistema Triásico en la Argentina*, A.E. ARTABE, E.M. MOREL & A.B. ZAMUNER, eds., Fundación Museo de La Plata 'Francisco Pascasio Moreno', La Plata, 199-225.
- ARTABE, A.E., MOREL, E.M. & SPALLETTI, L.A., 2003. Caracterización de las provincias fitogeográficas triásicas del Gondwana extratropical. *Ameghiniana* 40, 387-405.
- ARTABE, A.E., ZAMUNER, A.B. & STEVENSON, D.W., 2005. A new genus of Late Cretaceous cycad stem from Argentina, with reappraisal of known forms. *Alcheringa* 29, 87-100.
- BANCROFT, N., 1913. *Rhexoxylon africanum*, a new Medullosean stem. *Transactions of the Linnean Society of London, Series 2 (Botany)* 8, 87-103.
- BANCROFT, N., 1914. Pteridosperm anatomy and its relation to that of the cycads. *New Phytologist* 13, 41-68.
- BASINGER, J.F., ROTHWELL, G.W. & STEWART, W.N., 1974. Cauline vasculature and leaf trace production in medullosan pteridosperms. *American Journal of Botany* 61, 1002-1015.
- BODNAR, J., 2006. Nueva interpretación del material tipo de *Protocircoporoxylon cortaderitaense* (Menéndez) Vogellehner, leño fósil del Triásico Superior de Barreal, San Juan, Argentina. *Resúmenes del 9º Congreso Argentino de Paleontología y Bioestratigrafía*, Córdoba, 18–22 September 2006, 123.
- BONETTI, M.I.R., 1963. *Contribución al conocimiento de la flora fósil de Barreal (Depto. de Calingasta) Prov. de San Juan*. Tesis Doctoral, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad de Buenos Aires, 257 pp., 40 pl. (Unpublished).
- BOUREAU, E., 1956. *Anatomie Végétale. Tome 2*, Presses Universitaires de France, Paris, 170 pp.
- BREA, M., 1995. *Estudio de la paleoflora de la secuencia triásica de Agua de la Zorra, provincia de Mendoza*. Tesis Doctoral No. 642, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, 202 pp. (Unpublished).
- BRETT, D.W., 1968. Studies on Triassic fossil plants from Argentina. III. The trunk of *Rhexoxylon*. *Palaeontology* 11, 236-245.
- CÉSARI, S.N., ARCHANGELSKY, S. & VEGA, J.C., 2005. Anatomy of a new probable pteridosperm stem from the Late Carboniferous of Argentina. *Revista del Museo Argentino de Ciencias Naturales, n.s.* 7, 7-15.
- CHONG DÍAZ, G., ZAMUNER, A.B. & LAMELLI HERRERA, C., 1997. Primer hallazgo de flora triásica en Quebrada Guanaqueros, Sierra de Almeida, Alta Cordillera de la Segunda Región de Antofagasta, Chile. *Resúmenes del X Simposio Argentino de Paleobotánica y Palinología*, Mendoza, 29–31 October 1997, 17.
- COTTA, B., 1832. *Die Dendrolithen in Beziehung auf ihren inneren Bau*. Arnoldische Buchhandlung, Dresden and Leipzig, 89 pp.
- COUPER, R.A., 1958. British Mesozoic microspores and pollen grains. A systematic and stratigraphic study. *Palaeontographica* 103B, 75-179.
- CÚNEO, N.R., TAYLOR, E., TAYLOR, T. & KRINGS, M., 2003. In situ fossil forest from the upper Fremouw Formation (Triassic) of Antarctica: paleoenvironmental setting and paleoclimate analysis. *Palaeogeography, Palaeoclimatology, Palaeoecology* 197, 239-261.

- SEWARD, A.C., 1914. Antarctic fossil plants. *British Museum (Natural History), British Antarctic (Terra Nova) Expedition (Geology) 1*, 1-49.
- SEWARD, A.C., 1917. *Fossil Plants. Vol. 3*, Cambridge University Press, Cambridge, 656 pp.
- SPALLETTI, L.A., 2001. Modelo de sedimentación fluvial y lacustre en el margen pasivo de un hemigraben: el Triásico de la Precordillera occidental de San Juan, República Argentina. *Revista de la Asociación Geológica Argentina* 56, 189-210.
- SPALLETTI, L.A., ARTABE, A.E., MOREL, E.M. & BREA, M., 1999. Biozonación paleoflorística y cronoestratigrafía del Triásico Argentino. *Ameghiniana* 36, 419-451.
- STEWART, W.R. & ROTHWELL, G.W., 1993. *Paleobotany and the Evolution of Plants. Vol. 3*, Cambridge University Press, Cambridge, 521 pp.
- STIPANIC, P., 1972. Cuenca triásica de Barreal. In *Geología Regional Argentina*, A.F. LEANZA, ed., Academia Nacional de Ciencias, Córdoba, 537-566.
- STIPANIC, P., 1979. El Triásico del valle del Río de Los Patos (provincia de San Juan). In *Geología Regional Argentina*, J.C.M. TURNER, ed., Academia Nacional de Ciencias, Córdoba, 695-744.
- TAYLOR, E.L., 1992. The occurrence of a *Rhexoxylon*-like stem in Antarctica. *Courier Forschungsinstitut Senckenberg* 147, 183-189.
- TAYLOR, E.L., 1996. Enigmatic gymnosperms? Structurally preserved Permian and Triassic seed ferns from Antarctica. *Review of Palaeobotany and Palynology* 90, 303-318.
- THOMAS, H.H., 1933. On some pteridospermous plants from the Mesozoic rocks of South Africa. *Philosophical Transactions of the Royal Society London B* 222, 193-254.
- TOWNROW, J.A., 1957. On *Dicroidium* probably a pteridospermous leaf and other leaves now removed from this genus. *Transactions Geological Society South Africa* 60, 21-56.
- VOGELLEHNER, D., 1965. Untersuchungen zur Anatomie und Systematik der verkieselten Hölzer aus dem fränkischen und südhüringische Keuper. *Erlanger geologische Abhandlungen* 59, 1-76.
- VOGELLEHNER, D., 1967. Zur anatomie und phylogenie mesozoischer Gymnospermenhölzer, 5: Prodomus zu einer Monographie der Protopinaceae. 1. Die protopinoiden Hölzer der Trias. *Palaeontographica* 124B, 125-162.
- WALTON, J., 1923. On *Rhexoxylon* Bancroft, a Triassic genus of plants exhibiting a liane-type of vascular organization. *Philosophical Transactions of the Royal Society London B* 212, 79-109.
- WALTON, J., 1925. On some South African fossil woods. *Annals of the South African Museum* 22, 1-26.
- WEBER, O. & STERZEL, J.T., 1896. Beiträge zur Kenntnis der Medulloseae. *Bericht der Naturwissenschaftlichen Gesellschaft zu Chemnitz* 13, 1-102, 9 pl.
- WORSDELL, W.C., 1896. The anatomy of the stem of *Macrozamia* compared with that of other genera of Cycadaceae. *Annals of Botany* 10, 601-620.
- WORSDELL, W.C., 1906. The structure and origin of the Cycadaceae. *Annals of Botany* 20, 129-155.
- ZAMUNER, A.B., 1991. *Estudio de una tafoflora de la localidad tipo de la Formación Ischigualasto (Neotriás), Provincia de San Juan*. Tesis Doctoral No. 583, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, 97 pp., 25 pl. (Unpublished).
- ZAMUNER, A.B., ARTABE, A.E. & GANUZA, D.G., 1999. A new peltasperm (Gymnospermopsida) from the Middle Triassic of Argentina. *Alcheringa* 23, 185-191.
- ZAMUNER, A.B., ZAVATTIERI, A.M., ARTABE, A.E. & MOREL, E.M., 2001. Paleobotánica. In *El Sistema Triásico en la Argentina*, A.E. ARTABE, E.M. MOREL & A.B. ZAMUNER, eds., Fundación Museo de La Plata 'Francisco Pascasio Moreno', La Plata, 143-184.