

This article was downloaded by: [Dr Mariana Brea]

On: 05 June 2012, At: 12:35

Publisher: Taylor & Francis

Informa Ltd Registered in England and Wales Registered Number: 1072954 Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK



Alcheringa: An Australasian Journal of Palaeontology

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/talc20>

A new approach to Corystospermales based on Triassic permineralized stems from Argentina

Analía Artabe ^a & Mariana Brea ^b

^a Departamento Científico Paleobotánica, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Paseo del Bosque SN, 1900, La Plata, Argentina E-mail:

^b Centro de Investigaciones Científicas, Diamante (CICYTTP-CONICET), Matteri y España SN, Diamante (3105), Entre Ríos, Argentina E-mail:

Available online: 22 Feb 2011

To cite this article: Analía Artabe & Mariana Brea (2003): A new approach to Corystospermales based on Triassic permineralized stems from Argentina, Alcheringa: An Australasian Journal of Palaeontology, 27:3, 209-229

To link to this article: <http://dx.doi.org/10.1080/03115510308619353>

PLEASE SCROLL DOWN FOR ARTICLE

Full terms and conditions of use: <http://www.tandfonline.com/page/terms-and-conditions>

This article may be used for research, teaching, and private study purposes. Any substantial or systematic reproduction, redistribution, reselling, loan, sub-licensing, systematic supply, or distribution in any form to anyone is expressly forbidden.

The publisher does not give any warranty express or implied or make any representation that the contents will be complete or accurate or up to date. The accuracy of any instructions, formulae, and drug doses should be independently verified with primary sources. The publisher shall not be liable for any loss, actions, claims, proceedings, demand, or costs or damages whatsoever or howsoever caused arising directly or indirectly in connection with or arising out of the use of this material.

A new approach to Corystospermales based on Triassic permineralized stems from Argentina

ANALÍA ARTABE AND MARIANA BREA

ARTABE, A.E. & BREA, M., 30.9.2003. A new approach to Corystospermales based on Triassic permineralized stems from Argentina. *Alcheringa* 27, 209-229. ISSN 0311 5518.

Anatomically preserved mature stems of late Middle Triassic corystosperms from the Paramillo Formation of Argentina are described and assigned to *Cuneumxylon spallettii* gen. nov. et sp. nov. The silicified specimens show features of the pith, primary xylem and successive rings of secondary xylem and phloem. The most striking characteristic is the anomalous secondary growth, represented by secondary xylem bounded by arcs of secondary phloem probably derived from successive repositioned cambia. *Cuneumxylon* has two kinds of unusual centrifugal secondary growth. The first shows unequal activity of different portions of the cambium on the circumference of the axes; the consequent restriction of cambial activity to certain restricted areas develops wedged stems, which often split. The second produces polyxylic stems following supernumerary cambial activity. As in extant plants growing in arid regions, the included phloem and the associated parenchyma may have had functional value avoiding desiccation of the outer tissues of the stem during droughts. Anatomical features of other Corystospermaceae were used to determine systematic affinities and to establish relationships among medullosans, corystosperms and cycads.

Analia Artabe [aeartabe@satlink.com.ar], Departamento Científico Paleobotánica, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Paseo del Bosque SN, 1900 La Plata, Argentina and Mariana Brea [cidmbrea@infoaire.com.ar] Centro de Investigaciones Científicas, Diamante (CICYTTP-CONICET), Materi y España SN, Diamante (3105), Entre Ríos, Argentina; received 11.4.2002, revised 15.1.2003.

Key words: Argentina, Middle Triassic, Paramillo Formation, Corystospermaceae, fossil wood, *Cuneumxylon*.

THE CORYSTOSPERMS, a characteristic family of the Triassic floras of Gondwanaland, were first described by Thomas (1933) from Triassic beds of Natal, South Africa. The group was reconstructed based on detached but closely associated *Dicroidium* Gothan (*emend.* Townrow 1957) leaves, pollen and ovulate organs (*Pteruchus* Thomas [*emend.* Townrow 1962] and *Umkomasia* Thomas, 1933). Cuticular similarities and the occurrence of similar pollen grains (*Alisporites* Daugherty, 1941, *Falcisporites* (Leschik) Klaus 1963 and *Pteruchipollenites* Couper, 1958) in *Pteruchus* pollen sacs and *Umkomasia* ovules supported this association. Although attached organs have not been found, corystosperms have been considered a natural

group. The supposed attachment of the *Dicroidium* leaf to the axis reported by Axsmith *et al.* (2000) could be questioned because the single attached leaf has a seam of sediment between the petiole and axis. Its orientation is opposite that of the associated short shoots, in contradiction to the rule that all leaves and shoots grow toward the light. Furthermore the short shoots with their abundant leaf bases have not a single leaf attached.

Among genera based on permineralized axes, *Rhexoxylon* Bancroft (*emend.* Archangelsky & Brett 1961) and *Tranquiloxyton* Herbst & Lutz, 1995, exhibit anomalous development of the secondary xylem and liana-like anatomy. Proliferation of parenchyma cells divided the secondary xylem into sectors, suggesting that

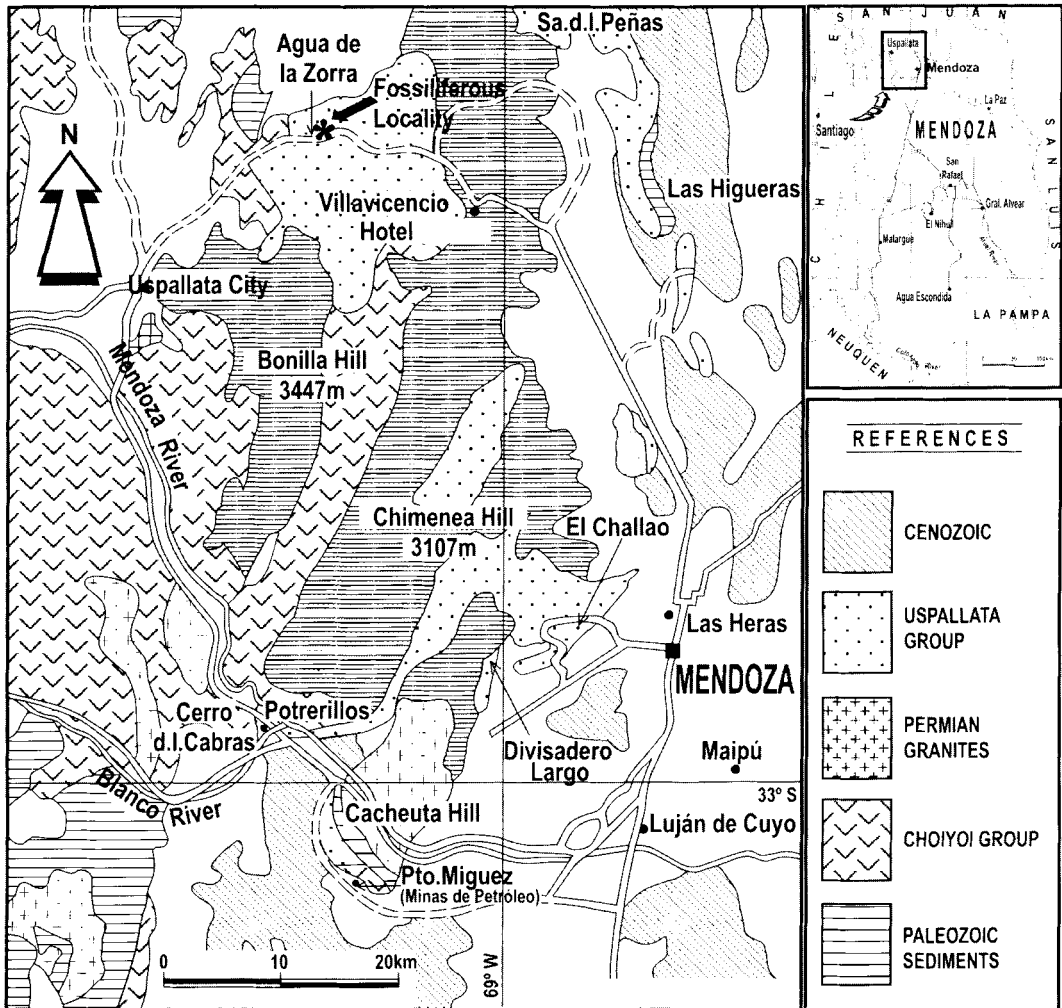


Fig. 1. Geographical and geological map of the studied region showing the Triassic units of the Paramillo de Uspallata (Harrington 1971) and the fossiliferous locality (from Stipanovic *et al.* 1996).

these cells retained their capacity to divide as a remnant cambium. *Rhexoxylon* includes six species (Bancroft 1913; Walton 1923, 1925; Archangelsky & Brett 1961, Brett 1968, Herbst & Lutz 1988, Zamuner 1991, Artabe *et al.* 1999) and shows a wide distribution in southwest Gondwanaland (Argentina, Brazil, South Africa) and Antarctica (Taylor 1992). *Tranquiloxyton*, with only one species, is found in Argentina and Chile (Herbst & Lutz 1995, Chong Diaz *et al.* 1997, Spalletti *et al.* 1999).

Unlike *Rhexoxylon* stems, the Antarctic axis *Kykloxyton* Meyer-Berthaud, Taylor & Taylor,

1993, has an undivided solid cylinder of secondary xylem (Meyer-Berthaud *et al.* 1992, 1993; Taylor 1996) and was assigned to the corystosperms because the attached foliar bases are similar in size and structure to *Dicroidium fremouwensis* Pigg, 1990. The axes and leaves were found at the same locality and the leaf traces derive from different sympodia as in *Rhexoxylon* (Meyer-Berthaud *et al.* 1993).

A new late Middle Triassic genus of Corystospermaceae based on stem fragments is described in this paper. The new corystosperm stems assigned to *Cuneumxyton spallettii* gen. et

sp. nov. and *Araucarioxylon protoaraucana* Brea, 1997 represent the dominant larger members of the *in situ* stumps of a permineralized forest. The fossil stumps were first described as a monotypic forest of *Araucarites* by Charles Darwin (1846), but are here reinterpreted on the basis of sedimentological, paleobotanical and spatial analyses (Brea 1995, 1997, 2000; Brea & Artabe 1999, Spalletti *et al.* 1999).

Materials and methods

The fossil stems described here are derived from the El Sauce and Darwin localities in the Paramillo Formation (=lower section of the Potrerillos Formation), Mendoza province, 24 km from Uspallata city (Fig. 1).

At these sites the Paramillo Formation is 140 m thick and consists of orthoconglomerate, pebbly sandstone, tuffaceous sandstone and mudstone. The permineralized stems occur in fossiliferous strata IV and V (Brea 1995). The sediments were deposited in a high sinuosity fluvial system, in which channel-filling sand bodies are associated with mud-dominated floodplain deposits.

Following the paleobotanical biozonation by Spalletti *et al.* (1999) for the continental Triassic of Argentina, *Cuneumxylon spallettii* is located in the oldest Biozone of the Cortaderitian Stage (*Yabeiella mareyesiaca*-*Scytophyllum bonettiae*-*Protocircoporoxylon cortaderitaensis* Assemblage Biozone), which corresponds to the late Middle Triassic.

The material was preserved by siliceous cellular permineralization. Thin sections and cellulose acetate peels were prepared for microscopic examination. The standard terminology of Greguss (1955, 1968), Boureau (1956), Tortorelli (1956, 1963), Cozzo (1964), Fahn (1990) and Stevenson (1990) was used to describe the fossil woods. The specimens and microscopic slides are deposited in the Departamento Científico de Paleobotánica, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata (LPPB and pmLPPB).

Systematic paleobotany

Class GYMNOSPERMOPSIDA Stewart & Rothwell, 1993

Order CORYSTOSPERMALES Petriella, 1981

Family CORYSTOSPERMACEAE Thomas, 1933

***Cuneumxylon* gen. nov.**

Type species. Cuneumxylon spallettii sp. nov.

Etymology. The name *Cuneumxylon* refers to the cross section structural pattern, characterized by the unusual distribution of the secondary conducting tissue dissected into triangular wedges.

***Cuneumxylon spallettii* gen. nov. and sp. nov.** (Figs 2-5)

Type material. Holotype specimen LPPB 12690 pmLPPB 1511-1517; paratypes LPPB 12688, pmLPPB 1518-1520; LPPB 12715, pmLPPB 1524-1525; LPPB 12714, pmLPPB 1526-1527; LPPB 12689, pmLPPB 1521-1525.

Type locality. Agua de la Zorra, Uspallata, Mendoza. The material comes from the Paramillo Formation (= lower section of the Potrerillos Formation), at the El Sauce and Darwin localities (69° 12' W, 32° 30' S; Fig. 1) at Agua de la Zorra (Fig. 1), 24 km NE of Uspallata city, Mendoza province, Argentina.

Stratigraphic horizon. Paramillo Formation (Harrington 1971).

Age. Late Middle Triassic (Spalletti *et al.* 1999).

Etymology. The specific epithet, *spallettii*, is dedicated to the Dr. Luis A. Spalletti, an outstanding sedimentologist who has studied the Triassic sequences of Argentina.

Diagnosis. Mature, columnar, terete and eccentric gymnospermous stems, 30–90 cm in diameter, showing features of the pith, primary xylem, secondary xylem and secondary phloem. Heterogeneous pith with parenchyma cells and polyhedral sclerenchyma cells. The primary xylem strands surrounding the pith composed of endarch

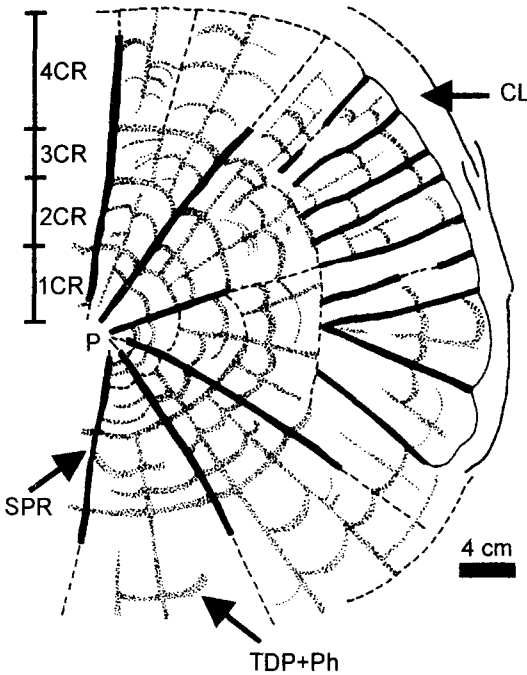


Fig. 2. *Cuneumxylon spallettii* sp. nov. (LPPB 12690). Diagram of wood transverse section showing secondary xylem pattern. The specimens consist of one concentric normal ring of secondary vascular tissue (1CR) and additional concentric rings (2CR, 3CR, 4CR) of abnormal secondary vascular tissue, developing a polyxylic stele; TDP+Ph, the included secondary phloem is associated with tangential dilatation parenchyma; SPR, secondary parenchymatous rays; CL, cork layer with no structurally preserved anatomy.

protoxylem and centrifugal metaxylem, with tracheids in radial files and a gradual transition from primary xylem to first-formed secondary xylem. The anomalous development of secondary growth includes two kinds of deviations with respect to the common type. The first shows unequal activity of different portions of the cambium on the circumference of the axes, so the reduction of cambial activity to certain restricted areas develops wedged stems, which often split. Secondary wood is divided into radial wedges by large parenchymatous rays. The second one produces polyxylic stems following supernumerary cambial activity. First vascular ring is embraced by three additional rings developing a polyxylic stele.

Fig. 3A-B. *Cuneumxylon spallettii* (LPPB 12690). A, primary xylem strands surrounding the pith are composed of endarch protoxylem (ep), centrifugal metaxylem (cm) and secondary xylem (sx). B, heterogeneous pith shows collapsed parenchyma cells and polyhedral sclerenchyma cells. C, radial section of wood showing ray with simple pits in the cross-fields. D, tracheids in radial section with intervascular pitting. [see page 213].

Each vascular ring integrated by internal secondary xylem and external secondary phloem imbricates in bands of tangential parenchyma. The secondary xylem shows ring-like growth, often dissimilar from with the contiguous wedges and false rings.

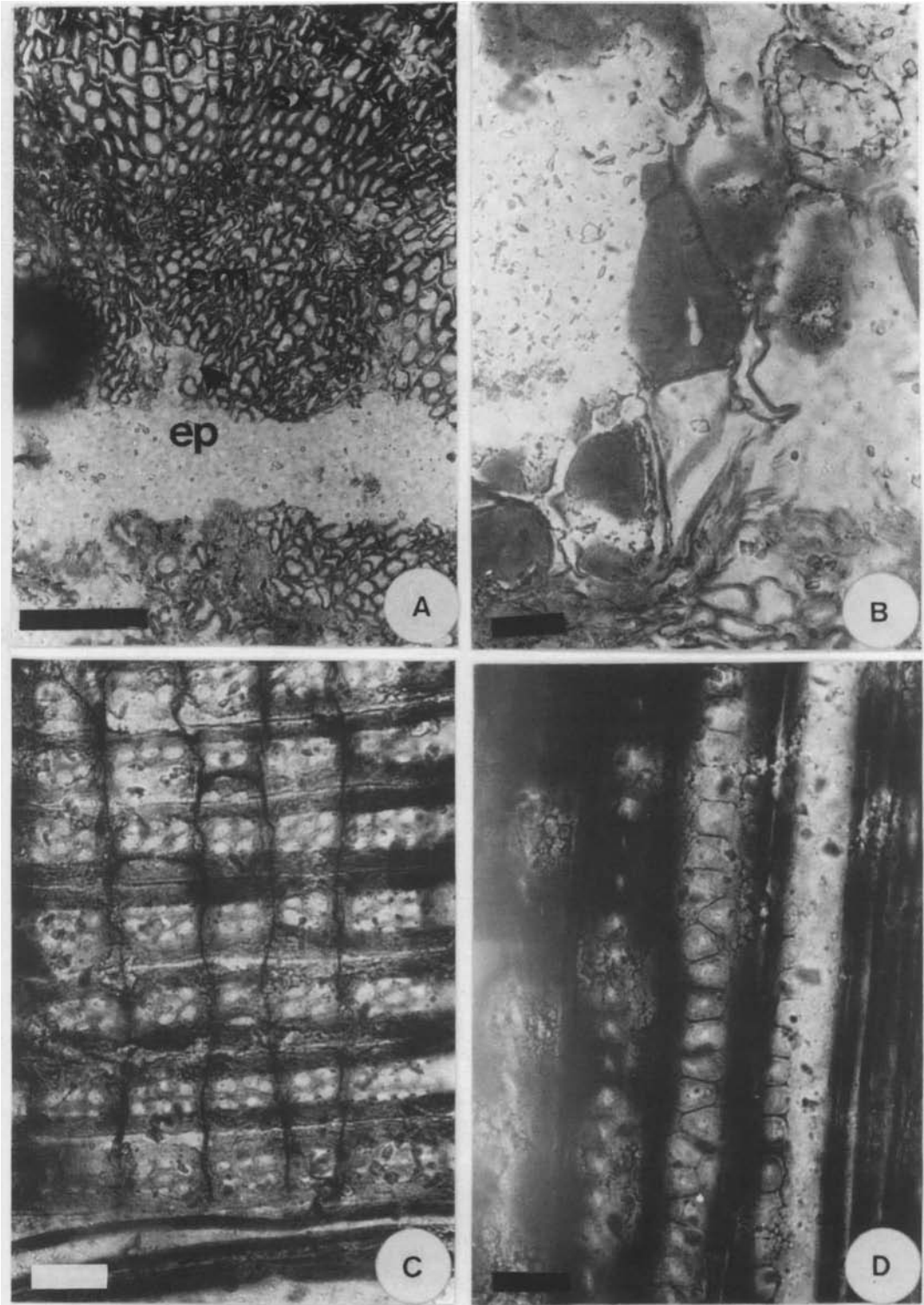
The secondary xylem tracheids are narrow and quadrangular, each with an oval lumen. The tracheid pitting is restricted to radial walls and uniseriate, uniseriate with biseriate portions and biseriate. The rays are short, uniseriate, and typically homocellular, and sparsely heterocellular. Cross-fields have 2-13 circular or oval simple pits in irregular or, in some cases, vertical arrangement. The secondary phloem is poorly preserved and consists of parenchyma, fibers and sieve cells.

Description. The trees are fossilized in growth position (30–90 cm in diameter at the base) or as fallen logs up to ca. 12 m long. The fossil represents mature gymnospermous woods, with eccentric and circular trunks. The specimens are characterized by the presence of pith, primary xylem, four cycles constituted by secondary xylem and secondary phloem, and an external layer, presumably cork, with no structurally preserved anatomy (Fig. 2).

The pith is 2-3 mm in diameter, heterogeneous, with parenchyma cells and polyhedral sclerenchyma cells with a diameter of 35-146 (mean 68) μm (Fig. 3B).

The primary xylem strands surround the pith and are composed of endarch protoxylem and centrifugal metaxylem with a gradual transition from primary xylem to first-formed secondary xylem. Protoxylem is present in small isolated groups, composed of about 3-4 more or less terete isodiametric tracheids. Metaxylem tracheids are isodiametric with a diameter of 4.6-16.9 (mean 13.9) μm ; the wall is 2-4 μm thick (Fig. 3A).

The specimens belong to a large trunk with anomalous development of secondary growth. The vascular tissue includes two kinds of deviations with respect to the common type of secondary



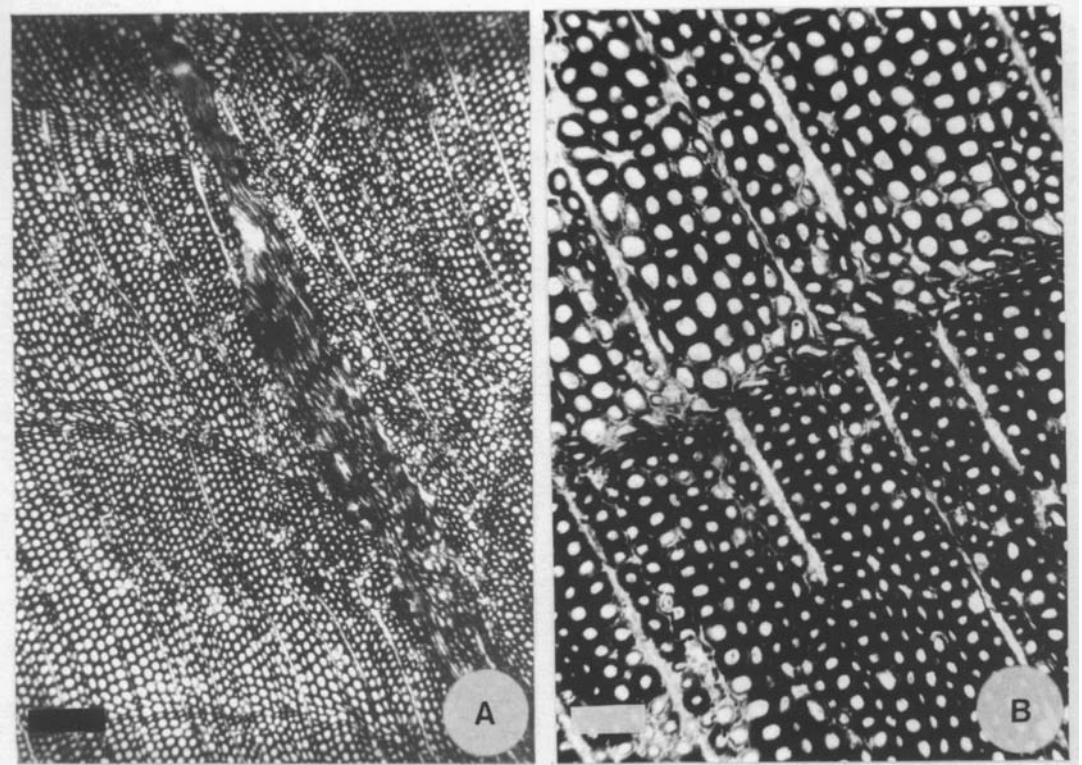


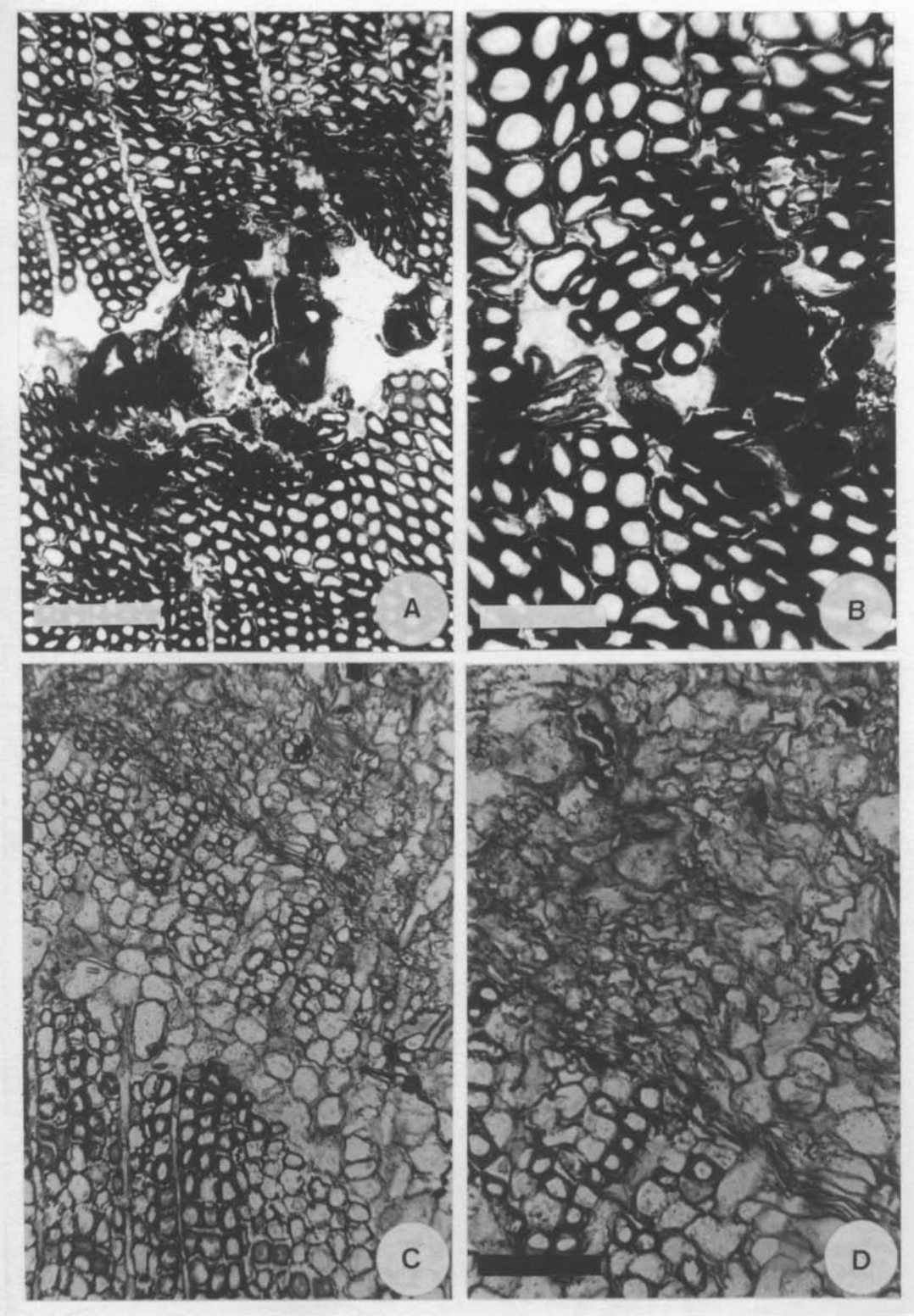
Fig. 4A-B. *Cuneumxylon spallettii* (LPPB 12690). A, B, ring-like growth developed inside the wedges. The ring-like growth boundaries are very often dissimilar from the contiguous radial wedges and constitute false rings. Parenchymatic rays do not run properly between ring-like growth, showing a little shifting.

growth. Firstly, unequal activity of different portions of the cambium on the circumference of the axes is evident. The confinement of cambial activity to restricted areas develops wedged stems, which often split. Neighboring wedges are separated by the development of large secondary parenchymatous rays (2–3.6 mm thick; Fig. 4A) and inside each wedge, secondary parenchymatous rays may develop, dividing and splitting some wedges. Secondly, polyxylic stems may develop following supernumerary cambial activity. Polyxylic anatomy consists of concentric rings of secondary vascular tissue in which each ring is composed of a xylem cylinder surrounded externally by a phloem cylinder. Thus, the stem has a pith surrounded by alternating bands of xylem

and phloem. The first-formed ring of secondary vascular tissue is 6 cm wide and there are three additional concentric rings with mean widths of 5.2, 4.4 and 9.6 cm wide respectively, encircling the first one (Fig. 2). Each vascular ring is composed of internal secondary xylem and external secondary phloem intercalated with bands of tangential parenchyma (4–6 mm wide). Within the four major rings, incomplete supernumerary rings covering two or three wedges could also be recognized (Fig. 2). The two unusual kinds of growth add anomalies in the distribution of peripheral secondary tissues (Fig. 2).

Ring-like growth developed inside the wedges. The ring-like growth boundaries are very

Fig. 5A-D. A-B, secondary phloem in *Cuneumxylon spallettii* (LPPB 12690) showing phloem parenchyma, phloem fibres and probable sieve cells (badly preserved). C-D *Rhexoxylon piatnitzkyi* (LPPB 7950 LPPm 1731), showing tissue described before as dilatation parenchyma. Because the radial arrangement of the parenchymatic elements it is interpreted here as secondary included phloem, consisting mainly of parenchymatic elements and phloem fibres either solitary or in clusters. [see page 215].



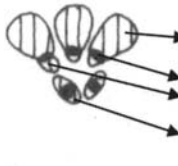
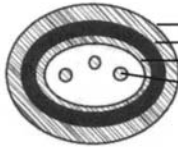
ANOMALOUS DEVELOPMENT OF SECONDARY XYLEM		
	CUNEUMXYLOID LINEAGE Centrifugal polyxyly	RHEOXXYLOID LINEAGE Centrifugal and centripetal polyxyly
TRIASSIC CORYSTOSPERMALES	<p><i>Tranquiloxyton</i> <i>Cuneumxyton</i></p> <p>Cylindrical vascular system</p> <ul style="list-style-type: none"> - Centrifugal secondary xylem dissected in wedges - Endarch primary xylem - Lack of centripetal xylem - Absence of centripetal-centrifugal perimedullar bundles 	<p><i>Rhexoxyton</i></p>  <p>Cylindrical vascular system</p> <ul style="list-style-type: none"> - Centrifugal secondary xylem dissected in wedges - Mesarch primary xylem - Centripetal xylem <p>Medullar vascular system</p> <ul style="list-style-type: none"> - Centripetal-centrifugal perimedullar bundles
LATE PALEOZOIC MEDULLOSALES	<p><i>Medullosa</i></p>  <p>Cylindrical vascular system</p> <ul style="list-style-type: none"> - Centrifugal secondary xylem - Mesarch primary xylem - Centripetal xylem <p>Medullar vascular system</p> <ul style="list-style-type: none"> - Medullar bundles 	

Fig. 6. According to Worsdell (1906) in the Permian medullosans, two vascular systems exist: cylindrical and medullar; both are variations of a single system. The first is primitive and gives rise to the second one. Corystosperms are described using this terminology.

often dissimilar from the contiguous radial wedges and they sometimes constitute false rings (Figs 4A-B). Further, parenchymatic rays do not run properly between ring-like growths, showing a little dislocation (Fig. 4B).

Secondary xylem tracheids are narrow and quadrangular, each with an oval lumen. Tracheids lack pitting on tangential walls but uniseriate, uniseriate with portions biseriate and biseriate pitting on radial walls (Fig. 3D). In the uniseriate tracheids, the bordered pits are circular, with separate or contiguous arrangement; in the biseriate examples, the bordered pits are circular or hexagonal, with separated or compressed arrangement, with alternated and sometimes subopposite pit rows. Pit pores are circular or lenticular enclosed. The uniseriate bordered pits are 7.7-18.5 (mean 15.4) μm in diameter, with pores 1.5-4.6 (3.1) μm in diameter; the biseriate bordered pits are 12.3-18.5 (mean 16.9) μm , with pores 3.1-6.16 (mean 4.6) μm in diameter. The tangential

diameter of tracheids is 20.8-46.2 (mean 33.1) μm ; the radial diameter of tracheids is 22.6-39.3 (mean 30) μm (Fig. 4B). The thickness of the double wall between two tracheids is 6.2-20 μm in the 'early wood' and 9.7-17 μm in the 'late wood'.

Rays are parenchymatous, uniseriate, usually homocellular and homogeneous, sometimes heterocellular and heterogeneous. The rays are short with rectilinear trajectory, and vary from 48-846 (mean 243) μm in height and 1-15 (mean 5.5) cells high. They are composed of oval or rectangular parenchyma cells with thin walls. Axial parenchyma is absent. Radial tracheids are absent.

Cross-fields with 2-13 simple pits with circular or oval outline, 18-42 (mean 27) μm in diameter, disposed irregularly or uncommonly in vertical rows (Fig. 3C).

This secondary phloem zone is about 480 μm thick and consists of phloem parenchyma, phloem fibres and probably sieve cells, which are badly preserved and difficult to identify.

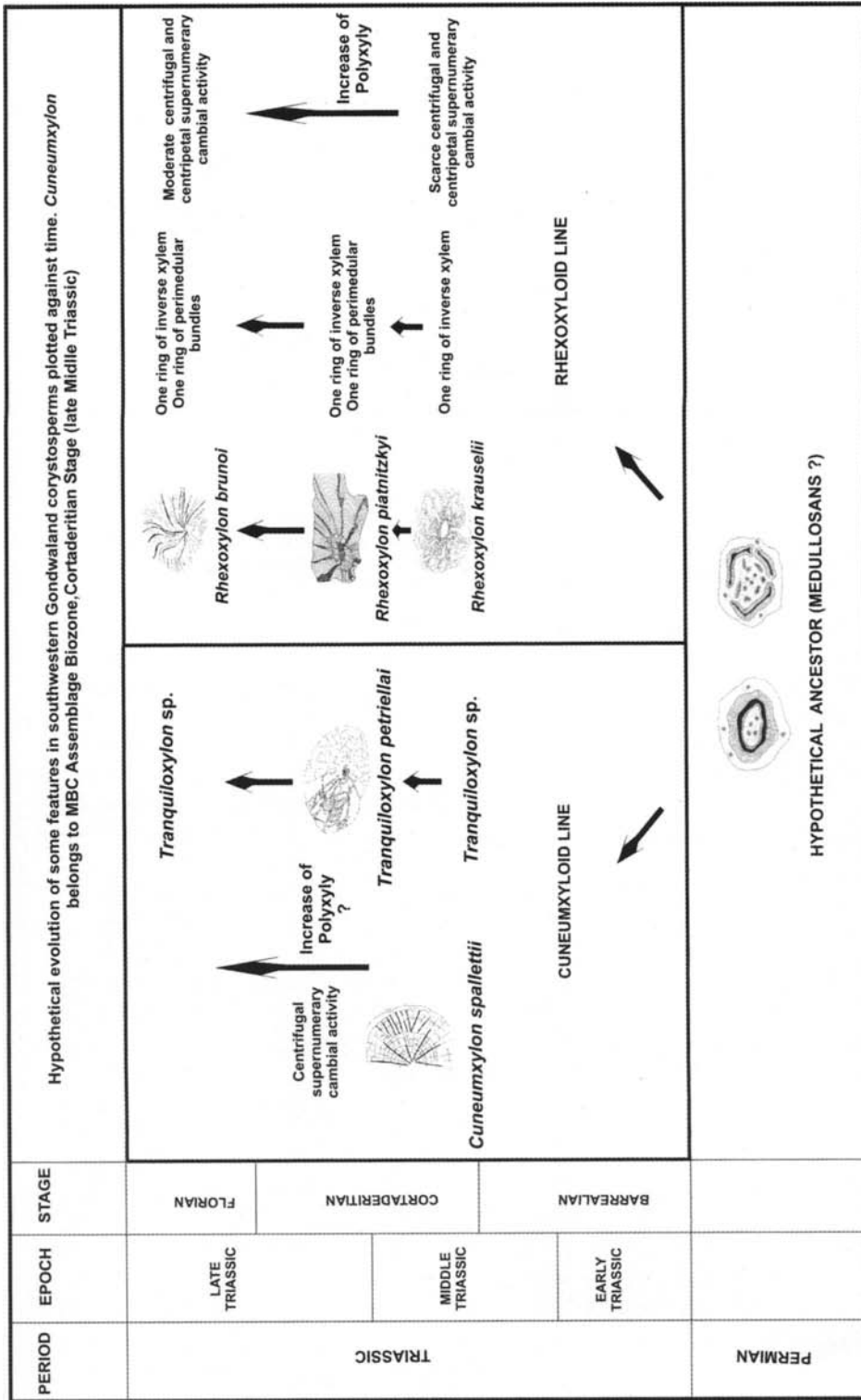


Fig. 7. Biostratigraphic distribution of corystosperm stems in Argentina and hypothetical evolutionary lineages. *Cuneumxylon spallettii* belongs to MBC Assemblage Biozone, Cortaderitian stage (late Middle Triassic).

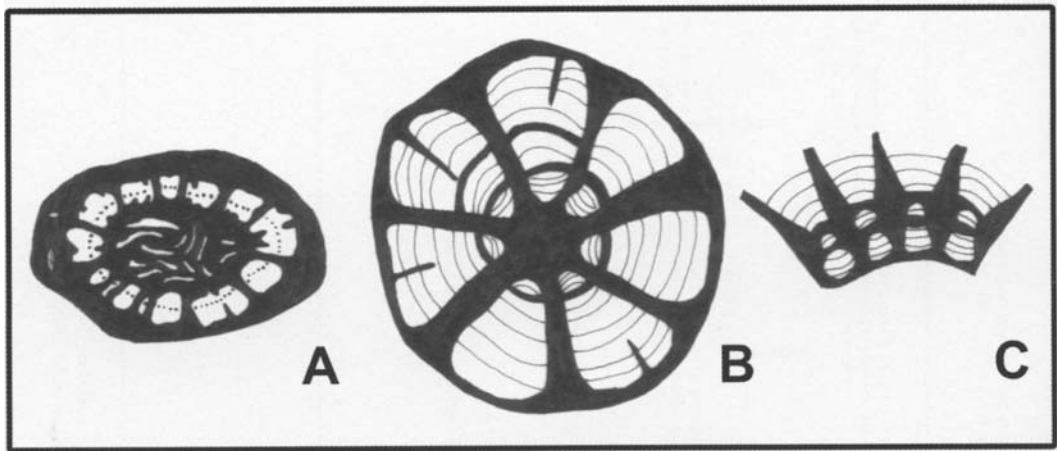


Fig. 8A-C. A, early stage of development of *Rhexoxylon* showing a polyxylic stem; two discontinuous cambial rings give rise to the centrifugal secondary xylem and centripetal secondary xylem of the cylindrical vascular system. B, the discontinuous cambial rings produce a differential development of their centrifugal part generating the secondary xylem wedges (the unusual secondary growth of centrifugal xylem is better explained in figures 9A and 9B). C, the formation of adventitious parenchyma between the centripetal-centrifugal secondary xylem separates both sectors triggering a mechanism of bundle fragmentation and due to supernumerary activity new bundles appear giving rise to the medullar system.

Phloem fibers are abundant, rectangular in cross section; they are 27-67 μm in radial width and 40-47 μm in tangential width with narrow lumens (Figs 5A-B). Primary phloem is not visible. The external layer, presumably cork, is crushed and does not yield cellular details.

Comparisons and discussion

The Corystospermaceae are generally interpreted as an isolated group of 'pteridosperms' probably allied more closely with peltasperms. Petriella (1981) concluded that Corystospermaceae are an independent order (Corystospermales) within the Pteridospermopsida, and indicated that the greatest corystosperm affinities are with the Peltaspermales, with which they constitute the subclass Peltaspermidae. Meyen (1987) placed the Corystospermaceae in his order Peltaspermales (Class Ginkgoopsida) along with the Cardiolepidaceae, Peltaspermaceae, and Trichopitiaceae. In cladistic analysis of seed plants, Crane (1985) linked the Corystospermales to anthophytes (Bennettitales, Pentoxylales, Gnetales and angiosperms) as their direct sister taxon, whereas Doyle & Donoghue (1986) placed the Corystospermales in a sister group to the anthophytes along with Cycadales,

Peltaspermales, Caytoniales and Glossopteridales (see Crane 1988). Against the major gondwanan corystosperm distribution, some authors point out an extragondwanan origin for the group (Petriella 1981, Retallack 1977, Meyen 1987) whereas others, like Archangelsky (1996), thought that *Botrychiopsis* Kurtz, 1895 probably belonged to an ancestral stock of pteridosperms from which Mesozoic plants, perhaps corystosperms, evolved. Insufficient paleobotanical information is available to clarify relationships between the late Paleozoic gondwanan pteridosperms and the Mesozoic corystosperms. Although some morphological frond characters and the few known fructifications are comparable, *Botrychiopsis* stems have not been found yet.

Corystosperm stems share some anatomical features with medullosans and cycads (Archangelsky & Brett 1961, Archangelsky 1996). In these groups there are deviations from the typical pattern of secondary growth and development of anomalous secondary growth.

The cauline vascular system in medullosans differs from typical seed plants only in the position of the secondary vascular tissue. The secondary xylem surrounds each segment of primary xylem as a complete cylinder (Namboudiri & Beck 1968,

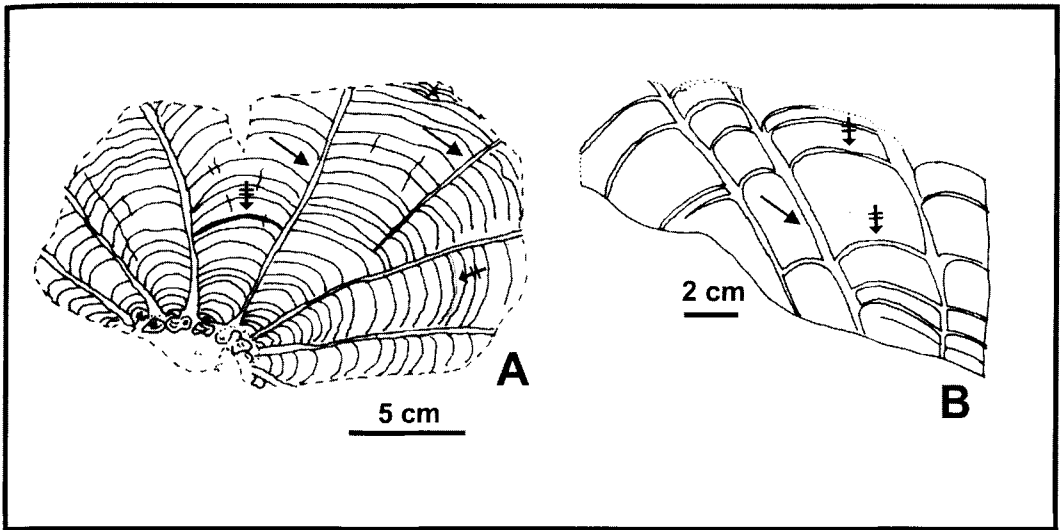


Fig. 9A-B. Unequal activity of different portions of the cambium on the circumference of the axes. The reduction of cambial activity to certain areas results in the formation of wedged stems, which often split (simple arrow). A-B, periodically cambial activity ceased and was repositioned as evidenced by the presence of secondary xylem with included phloem (arrow with bars). In *Rhexoxylon piatnitzkyi* the successive cambia form short arches whilst in *R. brunoii* they form incomplete entire rings.

Basinger *et al.* 1974) developing centrifugal and centripetal portions. Worsdell (1896, 1906) suggested that cycads were derived from medullosans by progressive loss of the centripetal secondary xylem in the stele ring. Comparing medullosans and cycads, a conspicuous regression in the degree of the character expression is observed, which is relict in extant genera (Worsdell 1906).

The appearance of medullar bundles is a feature probably related to the existence of centripetal xylem. According to Worsdell (1906) Permian medullosans have two vascular systems – cylindrical and medullar – both being variations of a single system. The same author pointed out that the former is plesiomorphic and the medullar system is derived. This hypothesis seems to be corroborated in corystosperms and fossil cycads (Artabe & Stevenson 1999) in which inverse, peripheral pith bundles grow and split at the inner part of the first vascular ring.

In *Rhexoxylon* several vascular segments comprise the cylindrical system. Each segment has primary bodies, usually with two axial sympodia per segment, and centrifugal-centripetal secondary xylem (Archangelsky & Brett 1961). The centrifugal

portions develop great amounts of secondary xylem towards the cortex (centrifugal wedges), whereas the centripetal sections give rise to discrete quantities of inverted xylem. Inside the primary body, the formation of adventitious parenchyma separates both centrifugal-centripetal secondary xylem, triggering bundle fragmentation and, by further activity, new medullar bundles appear towards the pith (Walton 1923, Archangelsky & Brett 1961, Brett 1968, Herbst & Lutz 1988, Zamuner 1991, Artabe *et al.* 1999).

The cycles of perimedullar bundles of *Rhexoxylon* can be compared with the medullar system of Medullosales and Cycadales. However, in corystosperm stems, the vasculature develops according to a regular pattern which, depending on the species, produces from one to several cycles of additional perimedullar bundles. This pattern of growth, unique among gymnosperms, can be defined as centripetal polyxyly. In this group, the main vascular system gives rise to the medullar system and develops a centripetal polyxyly in stems and a cable structure in rhizomes (Zamuner 1991).

The lack of centripetal xylem results in the absence of perimedullar bundles in *Cuneumxylon spallettii*, which could have important phylogenetic

implications as it suggests that the corystosperm stele evolved along two principal lineages (rhexoxyloid and cuneumxyloid) from a medullosan or similar precursor (Figs 6-7). The rhexoxyloid line is characterized by: mesarch primary xylem, centrifugal wedges of secondary xylem, centripetal secondary xylem (inverted xylem) and perimedullar bundles. The southwestern Gondwanaland species seem to fit into a developmental series: *R. sp* (*R. krauselii?*), *R. piatnitzkyi* Archangelsky & Brett, 1961 and *R. brunoi* Artabe, Brea & Zamuner, 1999. The series shows an increase of the anomalous vascular tissue development with formation of successive cycles of medullar bundles inside the trunk and the progressive acquisition of bigger stems by an increase in the amount of centrifugal secondary conducting tissues (Figs 6-7).

Cuneumxylon and *Tranquiloxyton* characterize the cuneumxyloid line. These taxa show anomalous vasculature only in the form of centrifugal secondary xylem because they do not produce centripetal xylem or perimedullar bundles (Figs 6-7).

Rhexoxylon was based on South African permineralized stems with distinctive anatomy (Bancroft 1913) produced by unusual secondary growth (Archangelsky & Brett 1961, Brett 1968, Zamuner 1991). Evidence from studies of developmental anatomy (Archangelsky & Brett 1961, Zamuner 1991) of several well-dated species (Herbst & Lutz 1988, Lutz & Herbst 1992, Herbst & Lutz 1995, Artabe *et al.* 1999) including the new genus described herein permits interpretation of generalized pathway in the evolution of Corystosperm vasculature.

Rhexoxylon is considered a polyxylic stem because all species possess two discontinuous cambia rings, which start developing centrifugal secondary xylem and centripetal secondary xylem around the mesarch primary xylem bundles (Fig. 8A). The adult stems have two principle components to their vascular systems: cylindrical and medullar. The first consists of several segments of vascular tissue, each with centrifugal wedges of secondary xylem, mesarch primary xylem bundles, and centripetal secondary xylem (inverted xylem). Perimedullar

bundles represent the second component. As mentioned above, the formation of adventitious parenchyma between the centrifugal and centripetal secondary xylem serves as a mechanism of bundle fragmentation. New bundles appear by supernumerary activity, thus giving rise to the medullar system. This phenomenon has been shown in *R. tetrapteridoides* Walton (*emend.* Archangelsky & Brett 1961), *R. piatnitzkyi* and *R. africanum* Bancroft (*emend.* Walton 1923) (Archangelsky & Brett 1961, Brett 1968) and is illustrated in Figs 8B-C. Each new cycle of centrifugal-centripetal perimedullar bundles adds two cambia rings to the stele by the mechanism detailed above; consequently, one species with two cycles of perimedullar bundles can be said to have added four supernumerary cambia rings.

The centrifugal wedges of Corystospermaeae also have two types of unusual secondary growth. The first is expressed by differential cambial activity around the circumference of the axes, and splitting of the stem along zones of reduced cambial activity. It is likely that there are cambium strands, which only produce ray-parenchyma, so the whole secondary wood is divided by large parenchymatous rays. In *Rhexoxylon*, *Tranquiloxyton* and *Cuneumxylon*, inside the large parenchymatous rays a remnant cambial activity favours the formation of abundant dilatation parenchyma. Brett (1968) stated that 'within the individual wedges of *Rhexoxylon* the radial extent of secondary xylem increased through the regular activity of the cambium. The tangential width of the wedges is increased through the normal broadening of the cambial arcs but this is associated with splitting of the cambium in places'. Large parenchymatous rays may also develop locally within the xylem wedges (Fig. 9A). Therefore, wedges in turn are divided by the same mechanism. This phenomenon also takes place in certain extant plants like *Aristolochia* (Fahn 1990).

The second type of unusual centrifugal secondary growth is the appearance of secondary xylem with included phloem. In *Cuneumxylon*, the first normal ring shows well developed secondary

	Diameter			Primary xylem	Secondary xylem	
	total	pith	Pith + perimedullary bundles	type	Medullar vascular system	Cylindrical vascular system (cm)
<i>R. africanum</i>	50	6	24	Mesarch	1 or 2 complete and 1 incomplete	14
<i>R. tetrapteridoides</i>	18	2	6.6	Mesarch	1 complete	5.5
<i>R. piatnitzkyi</i>	100	6.5	12	Mesarch	1 complete	25
<i>R. brasiliensis</i>	37x4 3	7.5	16	Mesarch	1 complete and 1 incomplete	14
<i>R. sp. 1</i>	60	3.2x1.3	5.3	Mesarch	1 incomplete	6
<i>R. brunoi</i>	76	2.4x1.7	6.6	?	1 complete and 1 incomplete	38
<i>R. sp. 2</i>	35	?	?	?	?	?
<i>K. fremouwensis</i>	1x1.5	0.5 (portion apical) 1.8x2.6 (largest stem)	----	Endarch	Absent	----
<i>T. petriellai</i>	26-30	0.7x3.3	4	?	Absent	24-28
<i>C. spallettii</i>	90	0.2-0.3	----	Endarch	Absent	25

Table 1. Comparison of the anatomical characteristics of pith, primary xylem and secondary xylem of *Rhexoxylon*, *Klykoxylon*, *Tranquiloxyton* and *Cuneumxylon* species: *R. africanum* Bancroft (*emend.* Walton 1923); *R. tetrapteroides* Walton (*emend.* Archangelsky & Brett 1961); *R. piatnitzkyi* Archangelsky & Brett, 1961; *R. brasiliensis* Herbst & Lutz, 1988; *R. sp. 1* (*R. krauselii* ?) Lutz & Herbst (1992); *R. brunoi* Artabe *et al.*, 1999; *R. sp. 2* Taylor 1992; *K. fremouwensis* Meyer-Berthaud *et al.*, 1993; *T. petriellai* Herbst & Lutz, 1995 and *C. spallettii*, this paper.

xylem followed by phloem, which largely consists of phloem parenchyma cells and only a few sieve elements and phloem fibres. The supernumerary rings encircle the first ring band in concentric pattern. Although secondary xylem with included phloem has not been described in *Rhexoxylon* or *Tranquiloxyton*, it seems likely that centrifugal supernumerary cambial activity exists. The 'dilatation parenchyma' described in *Rhexoxylon piatnitzkyi* seems to support this idea for although the tissue consists mainly of parenchymatic elements, it shows radial arrangement with phloem fibers either isolated or in clusters (Figs 5C-D).

The successive cambia form short arches restricted to one wedge in *R. piatnitzkyi* or form incomplete rings, as in *R. brunoi* (Figs 9A-B). In most cycads the growth of woody zone is continuous, but in *Cycas*, *Macrozamia*, *Lepidozamia* and *Encephalartos* the growth of the woody zone ceases, and after a time a new cambium appears in the cortex. This kind of anomalous secondary growth also appears in Chenopodiaceae, where the successive cambia produce irregularly or spirally arranged phloem. In this family the additional cambia generate zones of secondary tissue ranging from short arches to more

or less entire rings (Fahn 1990).

The species of *Rhexoxylon* show a remarkable similarity in vascular pattern; differences may be due to the simultaneous differential action of three cambia: the normal, the supernumerary and the remnant ones (Artabe *et al.* 1999).

Rhexoxylon africanum and *R. tetrapteridoides* have been recognized in South Africa (Table 1). The stem of *R. africanum* has pith with sclerotic nets, vascular strands and secretory cavities. The cylindrical vascular system includes several segments, each with well-developed centrifugal wedges of secondary xylem with very abundant adventitious developments, mesarch primary xylem, and centripetal secondary xylem (inversed xylem). The medullar system contains one or more concentric series of centrifugal-centripetal vascular bundles. The innermost series may be over 5 cm in radial width (Archangelsky & Brett 1961) (Tables 1-2).

In *R. tetrapteridoides* the pith contains spherical cysts, a few small vascular strands, and numerous large nests of stone cells, which form a high proportion of medullar tissue. The cylindrical vascular system incorporates compact centrifugal wedges of secondary xylem with little adventitious

parenchyma (Archangelsky & Brett 1961) and centripetal secondary xylem (inverse xylem) towards the medulla. The medullar system may appear if the centrifugal xylem is separated from its original position by adventitious parenchyma; after that, a new strand develops by supernumerary cambial activity (Tables 1-2).

Four species of this genus have been described in South America: *R. piatnitzkyi*, Ischigualasto Formation, San Juan province, Argentina (Archangelsky & Brett 1961, Archangelsky 1968, Brett 1968, Zamuner 1991); *R. brasiliensis* Herbst & Lutz, 1988, Caturrita Formation, Rio Grande do Sul, Brasil; *R. sp. (R. krauselii?)*, Cortaderita Formation, San Juan province, Argentina (Lutz & Herbst 1992); and *R. brunoi*, Los Colorados Formation, Mendoza province, Argentina (Artabe *et al.* 1999; Table 1-2).

Rhexoxylon piatnitzkyi shows pith with an irregular anastomosing system of small vascular strands and numerous large spherical cysts. The dissected, cylindrical vascular system consists of several segments with centrifugal-centripetal secondary xylem separated by a narrow zone of parenchymatous tissue (Archangelsky & Brett 1961). A complete ring of centrifugal-centripetal bundles constitutes the medullar system (Table 1-2).

Rhexoxylon brasiliensis has a pith with smaller parenchyma cells, few spherical cysts, some sclerotic nests and isolated or grouped fibers. The cylindrical vascular system incorporates a ring of 12 centrifugal-centripetal segments. The secondary centrifugal xylem is divided into wedges separated by parenchymatous rays, which also contain isolated or grouped fibers and opaque cells (Herbst & Lutz 1988). The medullar system is represented by a complete ring of centrifugal-centripetal bundles (Tables 1-2).

Rhexoxylon sp. (R. krauselii ?) shows a pith with isolated or grouped fibers, secretory cavities and a cylindrical vascular system composed of a cycle of segments with centripetal-centrifugal secondary xylem; the centrifugal xylem forms large lobed wedges separated by parenchyma (Lutz & Herbst 1992, tables 1-2).

Rhexoxylon brunoi differs in its pith, vascular

cylinder and cork architecture. The pith is heterogeneous with parenchyma cells and idioblasts. The cylindrical vascular system comprises segments with centrifugal-centripetal secondary xylem (wedges and the inverse xylem). The medullar system has a complete cycle of 16 centrifugal-centripetal medullar bundles (Artabe *et al.* 1999; Tables 1-2).

A specimen with *Rhexoxylon*-like secondary anatomy was reported from the Triassic of Antarctica; the specimen is characterized by a cylinder of secondary xylem divided into sectors by large wedges of parenchyma and the development, within the pith, of some strands of secondary xylem that are either centripetal or both centripetal and centrifugal (Taylor 1992; Tables 1-2).

Another genus assigned to Corystospermaceae is *Antarcticoxylon* Seward, 1914. The original species description (*A. priestleyi*), founded on one sample from Antarctica, was improved by Walton (1923, 1925) based on better preserved material from South Africa. Based on additional specimens from the Irati Formation of Brazil, Mussa (1980) reinterpreted the *Antarcticoxylon* anatomy. Walton's (1925) proposal to synonymise *Antarcticoxylon* with *Rhexoxylon* was rejected by Archangelsky & Brett (1961), Herbst & Lutz (1995), Meyer-Berthaud & Taylor (1991) and Meyer-Berthaud *et al.* (1993). These last authors recommended maintaining *Antarcticoxylon* as a form genus including only one valid representative, the specimen found in the Beacon Sandstone (Permian), Antarctica. They suggested that the South African material, though decisively not a *Rhexoxylon*, could be assigned to Corystospermaceae, based on the features of the pith and secondary xylem. A comparison of the available anatomical features of *Antarcticoxylon* and *Cuneumxylon* indicates that these taxa have pycnoxylic secondary xylem, uni- or biseriate pitting on the radial walls of the tracheids and bordered pits with a circular, sometimes slightly elliptical, aperture.

The small Antarctic axes assigned to *Kykloxylon* by Meyer-Berthaud *et al.* (1992) found in close association with *Dicroidium fremouwensis*

is regarded as the distal twigs of a 'Dicroidium plant' (Pigg 1990, Meyer-Berthaud *et al.* 1992, 1993; Yao *et al.* 1995, Axsmith *et al.* 2000). It shows endarch primary xylem and normal undivided secondary xylem and resembles *Rhexoxylon* in its form of leaf trace departure (Tables 1-2). There is not enough information to include *Antarcticoxylon* and *Kykloxylon* into the phylogenetic lineages schematized in Fig. 7.

The most recently established genus and species of this group, *Tranquiloxydon petriellai* (Herbst & Lutz, 1995), from the Upper Triassic of Santa Cruz province, Argentina, is characterized by a parenchymatous pith with opaque cells surrounded by a continuous ring of primary xylem; the eccentric pycnoxylic wood is composed of closely packed wedge-shaped sections of secondary xylem with well marked growth rings, separated by radial parenchymatic rays. The xylem bears uniseriate araucarioid bordered pits, cross-fields with simple pits and complex leaf-trace forming structures (Herbst & Lutz 1995; Tables 1-2). This genus has been also recognized in Triassic sediments of northern Chile (Chong Díaz *et al.* 1997).

In relation to other interesting evolutionary features present in vegetative structure, Stewart & Rothwell (1993) recognized two main patterns in gymnospermous leaf trace departure. In *Lyginopteris* Potonié, 1897, *Callistophyton* Delevoryas & Morgan, 1954 and many conifers, the five sympodia of the eustele give rise to leaf traces in a 2/5 spiral sequence. The division of the only sympodium that originates the leaf trace and an axial bundle is tangential. After formation, the leaf trace dichotomizes to form two to several bundles that reunite in the cortex to form a simple trace in the petioles.

In medullosans, cycads and corystosperms, leaf traces arise from few sympodia and form a complex leaf bases. *Medullosa* Cotta, 1832 has large petioles with numerous vascular bundles. Leaf traces arise from the sympodia in an irregular sequence. Leaf traces are derived from different levels of the same sympodium or different sympodia may supply the same leaf trace (Stewart & Rothwell 1993). In cycads, leaf traces are differentiated into numerous small

radial traces as well as large traces that partially girdle the stem through the cortex before entering the leaf base. There are usually two such girdling traces in addition to a number of smaller radial traces that supply a petiole. Smoot *et al.* (1985) suggested that the girdling configuration was the evolutionary result of stem length reduction, which may correlate with growth in drier habitats. On the other hand, Stevenson (1980) linked this character with the primary thickening meristem (PTM) activity responsible for the development of radial growth and pachycaulous habit in several extant Cycadales. As the shoot grows, the leaf traces are displaced with reference to the center of the apex as a consequence of PTM. The girdling trace is a derived character in the group and, as Stevenson suggests, is related to the change in habit, providing the plant with an additional mechanism of support.

In *Rhexoxylon* leaf traces arise from four different sympodia and two pairs of traces converge towards the leaf base. Leaf traces consist of groups of two or more cuneate or concentric bundles concentrically disposed (Archangelsky & Brett 1961). *Kykloxylon* has a solid vascular cylinder of secondary xylem without centripetal wood and is related to corystosperms because, among other characteristics, it has a comparable pattern of trace departure (Meyer-Berthaud *et al.* 1993).

Another feature of phylogenetic importance is axillary branching. In the eusteles of *Lyginopteris* and *Callistophyton* one sympodium gives rise to the leaf trace and the adjacent sympodium divides to provide the primary vascular system of the axillary branch or bud. In Medullosales, axillary branching is an unusual feature only described in *Medullosa endocentrica* Baxter, 1949 (Hamer & Rothwell 1983). Among cycads with aerial trunks, branching mechanisms are not well developed (Jones 1993). Axillary buds do not exist but branching may occur following damage to a trunk or from specialized structures (Stevenson 1980, 1990). Forking or dichotomous branching of the trunk apex is generally rare whereas adventitious branching is more common; the

latter results from the development of bulbils (offsets) on the subaerial portion of the trunk and suckers on that part of the trunk, which is below the ground. These growths arise as adventitious buds produced from the callus or the parenchyma tissue of the leaf bases. Much attention has been paid to the presence of axillary buds in *Rhexoxylon* and *Kykloxylon* (Archangelsky & Brett 1961, Meyer-Berthaud *et al.* 1993) but evidence presented so far does not confirm axillary branching in corystosperms (Axsmith *et al.* 2000).

Adaptive features

Inferences about corystosperm autecology are complicated by the tendency of stems and leaves to be fossilized independently in a range of depositional environments. Therefore, interpretations are based on a few organs rather than on the whole plant. The concept of the 'Dicroidium plant' was recently expanded to include not only the *Dicroidium-Rhexoxylon* alliance of South Africa and South America but also the *Dicroidium-Dadoxylon* association of Antarctica (Meyer-Berthaud *et al.* 1992).

The Antarctic plant, based on material from Fremouw Peak, consists of axes with dense, pycnoxylic wood of the *Dadoxylon* type bearing leaves of *Dicroidium* type, and was interpreted as a large deciduous tree (Meyer-Berthaud *et al.* 1993, Taylor 1996). New data regarding the overall growth habit of corystosperms were provided by cupulate organs (*Umkomasia uniramia* Axsmith, Taylor, Taylor & Cúneo 2000) and a leaf (*Dicroidium odontopteroides* [Morris] Gothan 1912) supposedly attached to long shoot that also bore short shoots, which indicate that the plant had a habit similar to *Ginkgo biloba* (Axsmith *et al.* 2000).

Assuming *Rhexoxylon* as the stem of *Dicroidium*, two plant reconstructions have been made for this group in southwest Gondwanaland. The first suggests that '*Umkomasia granulata*' was probably a woodland deciduous tree that dominated seasonally waterlogged floodplains of extensive lowlands in the Cape region of South

Africa (Retallack & Dilcher 1988). Taylor (1996) reconsidered this interpretation because in South Africa, *Rhexoxylon* stems are not associated with megafossil floras (Anderson & Anderson 1983).

The second provides a reasonably accurate reconstruction of '*Dicroidium*' with a palm-like tree habit, and bearing *Pteruchus* pollen organs and *Umkomasia* ovulate structures (Petriella 1978). It was based on consistent association of *Dicroidium zuberi-Rhexoxylon piatnitzkyi* found in Ischigualasto Formation, Argentina (Archangelsky & Brett 1961, Archangelsky 1968, 1970).

Ecological features such as the stature of an individual plant have been used to infer both autecology and height of the vegetation (Wing & DiMichele 1992). Trunk diameter to height ratios observed in living trees allow estimation of the original stature of the fossil plants based on the basal diameters of stumps and long segments of tree stems (Mossbrugger *et al.* 1994, Niklas 1994, Brea 1995). In spite of the anomalous, liana-like structure of *Rhexoxylon* and *Cuneumxylon*, they typically attain moderate (28 m) to very large size (59 m) (Lutz & Herbst 1992, Brea 1995, Artabe *et al.* 1999). As stature is the major factor controlling canopy position, the deduced height of *Rhexoxylon* and *Cuneumxylon* suggests that the forested landscape of late Middle Triassic was dominated by corystosperms and by coniferophytes, with other corystosperms, peltasperms, cycadophytes, and ferns prevalent in the understorey. Corystosperms are interpreted as having constituted the largest emergent (uppermost) or canopy (second) stratum of the *in situ* mixed forests found in the Cortaderita and Paramillo Formations (Brea 1995, Spalletti *et al.* 1999).

Based on the morpho-anatomical traits evident in the roots, leaves and stems, Petriella (1985) suggested that Corystospermaceae are meso-xeromorphic plants exhibiting morpho-structural adaptations to seasonal water stress (monsoonal climates).

Rhexoxylon and *Cuneumxylon* bark tends to be thick and rough (Artabe *et al.* 1999). This kind of covering usually appears in xerophytes whilst

	Pith				Secondary xylem				Cortex			
	Sclerotic nets	Vascular strands	Idioblasts	Secretory cavities	Radial pitting	Cross field pits	Ray width	Only parenchymatic	Sclerotic nets	Vascular strands	Idioblasts	Cork layer
<i>R. africanum</i>	P	P	A	P	1-3 seriate alternate	1-3 and circular, elliptical, simple	1-seriate	----	----	----	----	----
<i>R. tetrapteroides</i>	P	P	A	P	1-3 seriate alternate	1 and circular, simple	1-seriate	----	P	A	A	A
<i>R. piatnitzkyi</i>	A	P	P	P	1-2 seriate alternate	1-3 and circular, elliptical, simple	1-seriate	----	P	P	P	P
<i>R. brasiliensis</i>	P	A	A	P	2 seriate?	?	?	?	----	----	----	----
<i>R. sp. 1</i>	A	P	A	P	1 seriate	?	?	P	----	----	----	----
<i>R. brunoi</i>	A	A	P	?	1-2 seriate opposite	1-2 and oblique lenticular, simple	?	----	----	----	----	P
<i>R. sp. 2</i>	?	?	?	?	1-2 seriate alternate	2-4 and circular, elliptical, simple	1-2 seriate	----	----	----	----	P
<i>K. fremouwensis</i>	P	A	A	P	1-3 seriate opposite or alternate	3-9 oval-horizontal, simple	1-seriate	----	P	----	----	----
<i>T. petriellai</i>	A	P	P	A	1-2 seriate subopposite	1 and simple	1-2 seriate	----	----	----	----	----
<i>C. spalletii</i>	A	P	P	A	1-2 seriate alternate and sometimes subopposite	2-13 circular or oval, simple	1-seriate	----	----	----	----	----

Table 2. Comparison of anatomy characters of the pith, secondary xylem and cortex of the species of *Rhexoxylon*, *Klykoxylon*, *Tranquiloxyton* and *Cuneumxyton*: *R. africanum* Bancroft (emend. Walton 1923); *R. tetrapteroides* Walton (emend. Archangelsky & Brett 1961); *R. piatnitzkyi* Archangelsky & Brett, 1961; *R. brasiliensis* Herbst & Lutz, 1988; *R. sp. 1* (*R. krauselii* ?) Lutz & Herbst (1992); *R. brunoi* Artabe et al., 1999; *R. sp. 2* Taylor 1992; *K. fremouwensis* Meyer-Berthaud et al., 1993; *T. petriellai* Herbst & Lutz, 1995 and *C. spalletii* (this paper).

to medullosans. The rhexoxyloid line is characterized by centrifugal wedges of secondary xylem, mesarch primary xylem, centripetal secondary xylem and perimedullar bundles. The cuneumxyloid line only shows anomalous growth in the centrifugal secondary xylem because it does not produce centripetal xylem and its consequence: perimedullar bundles.

Although corystosperm polyxyly is comparable to that present in some cycads and medullosans, the development of pycnoxylic wood is a synapomorphy for the corystosperms, differentiating them from groups such as the manoxylic medullosans and cycads. Further, the corystosperm polyxyly is not only related to habit but also to habitat. By comparison with extant plants growing in arid regions, the included phloem and associated parenchyma in Corystospermaceae stems may be an important adaptive strategy to avoid water stress.

Acknowledgments

We are grateful for financial support provided by the *Consejo Nacional de Investigaciones Científicas y Técnicas* (Project PID-CONICET 0912/98) and the *Agencia Nacional de Promoción Científica y Tecnológica* (PICT 07-08467). The authors want to express their acknowledgement to Luis Spalletti, Eduardo Morel and Alba Zamuner for cooperation in field work, as well as for the important exchange of opinions and ideas during the investigations. We especially thank the reviewers for the critical revision of the paper which improve the original manuscript.

References

- ANDERSON, J.M. & ANDERSON, H.M., 1983. *Palaeoflora of Southern Africa Molteno Formation (Triassic)*. Volume I, Parts 1-2. Introduction: *Dicroidium*. A.A. Balkema, Rotterdam, 227 p.
- 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., 1970. *Fundamentos de Paleobotánica*. Facultad de Ciencias Naturales y Museo, Universidad Nacional de la Plata. Serie técnica y Didáctica 10, 347 p.
- 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 London* 706B (244), 1-19.
- ARTABE, A.E. & STEVENSON, D.W., 1999. Fossil Cycadales of Argentina. *The Botanical Review* 65, 219-238.
- 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.
- AXSMITH, B.J., TAYLOR, E.L., TAYLOR, T.N. & CÚNEO, R.N., 2000. New perspectives on the Mesozoic seed fern Order Corystospermales based on attached organs from the Triassic of Antarctica. *American Journal of Botany* 87, 757-768.
- BANCROFT, N., 1913. *Rhexoxylon africanum*, a new Medullosean stem. *Transactions of the Linnean Society of London (Series 2, Botany)* 8, 87-103.
- 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.
- BAXTER, R.W., 1949. Some pteridosperm stems and fructifications with particular reference to the medullosae. *Annals of Missouri Botanical Garden* 36, 287-352.
- BIERHORST, D.W., 1971. *Morphology of vascular plants*. McMillan, New York, 560 p.
- BREA, M., 1995. *Estudio de la paleoflora de la secuencia triásica de Agua de la Zorra, provincia de Mendoza*. Tesis Doctoral 642, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, 202 p. Inédita.
- BREA, M., 1997. Una nueva especie fósil del género *Araucarioxylon* Kraus 1870 emend. Maheshwari 1972 del Triásico de Agua de la Zorra, Uspallata, Mendoza, Argentina. *Ameghiniana* 34, 485-496.
- BREA, M., 2000. Paleoflora triásica de Agua de la Zorra, Uspallata, provincia de Mendoza, Argentina: Lycophyta y Filicophyta. *Ameghiniana* 37, 199-204.
- BREA, M. & ARTABE, A.E., 1999. Apocalamitaceae (Sphenophyta) triásicas de la Formación Paramillo, Agua de la Zorra, provincia de Mendoza, Argentina. *Ameghiniana* 36, 389-400.
- BOUREAU, E., 1956. *Anatomie Végétale*. Tome 2. Presses Universitaires de France, Paris, 333-503.
- BRETT, D.W., 1968. Studies on Triassic fossil plants from Argentina. III The trunk of *Rhexoxylon*. *Palaeontology* 11, 236-245.
- CHAMBERLAIN, C.J., 1911. The adult cycad trunk. *Botanical Gazette* 53, 1-19.
- CHAMBERLAIN, C.J., 1935. *Gymnosperms: Structure and evolution*. University of Chicago Press, 483 p.

- CHAMBERLAIN, C.J., 1965. *The living cycads*. (Reprint of 1919 ed.) Hafner, New York, 172 p.
- CHONG DÍAZ, G., ZAMUNER, A.B. & LAMELLI HERRERA, C., 1997. Primer hallazgo de flora triásica en Quebrada Guanaueros, Sierra de Almeida, Alta Cordillera de la Segunda Región de Antofagasta, Chile. *X Simposio Argentino de Paleobotánica y Palinología, Resúmenes*, 17. Mendoza.
- COTTA, C.B., 1832. *Die Dendrolithen in Beziehung auf ihren inneren Bau*. Dresden & Leipzig, Arnoldische Buchhandlung, 89 p.
- COUPER, R.A., 1958. British Mesozoic microspores and pollen grains. A systematic and stratigraphic study. *Palaeontographica* 103B, 75-179.
- COZZO, D., 1964. Glosario de términos empleados en anatomía de maderas. Traducido y comentado por D. Cozzo. *Revista de la Facultad de Agronomía y Veterinaria Universidad de Buenos Aires* 16, 33-79.
- CRANE, P.R., 1985. Phylogenetic analysis of seed plants and the origin of angiosperms. *Annals of Missouri Botanical Garden* 72, 716-793.
- CRANE, P.R., 1988. Major clades and relationships in the "Higher" Gymnosperms. In *Origin and Evolution of Gymnosperms*, C. B. BECK, ed., Columbia University Press, New York, 218-272.
- DARWIN, C., 1846. *Geological observations on South America. Being the third part of the Geology of the voyage of the Beagle, during the years 1832 to 1836*. Smith, Elder & Co., London, 279 p.
- DAUGHERTY, L.J., 1941. The Upper Triassic Flora of Arizona. *Carnegie Institute of Washington, Publications* 526, 108 p.
- DELEVORIAS, T. & MORGAN, J., 1954. A new pteridosperm from Upper Pennsylvanian deposits of North America. *Palaeontographica* 96B, 12-23.
- DOYLE, J.A. & DONOGHUE, M.J., 1986. Seed plant phylogeny and the origin of angiosperms: An experimental cladistic approach. *Botanical Review* 52, 321-341.
- FAHN, A., 1990. *Plant anatomy*. Pergamon Press, 588 p.
- GOTHAN, W., 1912. Über die Gattung *Thinnfeldia* Ettingshausen. *Abhandlung der Naturhistorische Gesellschaft zu Nürnberg* 19, 67-80.
- GREGUSS, P., 1955. *Identification of Gymnosperms on the basis of xylotomy*. Akadémiai Kiadó, Budapest, 263 p.
- GREGUSS, P., 1968. *Xylotomy of the Living Cycads, with a description of their leaves and epidermis*. Akadémiai Kiadó, Budapest, 260 p.
- HAMER, J.J. & ROTHWELL, G.W., 1983. The vegetative structure of *Medullosa endocentrica* (Pteridospermopsida). *Canadian Journal of Botany* 66, 375-87.
- HARRINGTON, H.J., 1971. *Descripción geológica de la hoja 22c, "Ramblón" provincias de Mendoza y San Juan*. Carta Geológica - Económica de la República Argentina Escala 1:200.000. Ministerio de Industria y Minería Subsecretaría de Minería, Dirección Nacional de Geología y Minería, Boletín 114, 87 p.
- HERBST, R. & LUTZ, A.I., 1988. *Rhexoxylon brasiliensis* n. sp. (Corystospermaceae, Pteridospermales) from the Upper Triassic Caturrita Formation, Brazil, with comments on biology and environment. *Mededelingen rriks Geologische Dienst* 42, 21-28.
- HERBST, R. & LUTZ, A.I., 1995. *Tranquiloxyton petriellai* nov. gen. et sp. (Pteridospermales) from the Upper Triassic Laguna Colorada Formation, Santa Cruz province, Argentina. *Ameghiniana* 32, 231-236.
- JONES, D. L., 1993. *Cycads of the world*. Smithsonian Institution Press, Washington, D.C., 312 p.
- KLAUS, W., 1963. Sporen aus dem südalpinen Perm (Vergleichsstudie für sie Gliederung nordalpinen Salzserien). *Jahrbuch der Geologischen Bundesanstalt* 106, 229-361.
- KURTZ, F., 1895. Contribución a la Palaeophytología Argentina. II. Sobre la existencia del Gondwana inferior en la República Argentina (Plantas fósiles del Bajo de Velis, provincia de San Luis). *Revista del Museo de La Plata* 6, 125-139.
- LUTZ, A.I. & HERBST, R., 1992. Una nueva especie de *Rhexoxylon* del Triásico de Barreal, San Juan, Argentina. 7º *Simposio Argentino de Paleobotánica y Palinología* (Corrientes 1991), Publicación Especial 2 Asociación Paleontológica Argentina, 73-76.
- MEYEN, S.V., 1987. *Fundamentals of Palaeobotany*. Chapman & Hall, 432 p. London.
- MEYER-BERTHAUD, B. & TAYLOR, T.N., 1991. A probable conifer with podocarpacean affinities from the Triassic of Antarctica. *Review of Palaeobotany and Palynology* 67, 179-198.
- MEYER-BERTHAUD, B., TAYLOR, E.L. & TAYLOR, T.N., 1992. Reconstructing the Gondwana seed fern *Dicroidium*: evidence from the Triassic of Antarctica. *Geobios* 25, 341-344.
- MEYER-BERTHAUD, B., TAYLOR, T.N. & TAYLOR, E.L., 1993. Petrified stems bearing *Dicroidium* leaves from the Triassic of Antarctica. *Palaeontology* 36, 337-356.
- MILLER, W.L., 1919. Polyxylic stem of *Cycas media*. *Botanical Gazette* 68, 208-220.
- MOSSBRUGER, V., GEE, C.T., BELZ, G. & ASHRAF, A.R., 1994. Three-dimensional reconstruction of in-situ Miocene peat forest from the lower Rhine Embayment, northwestern Germany- new methods in palaeovegetation analysis. *Palaeogeography, Palaeoclimatology, Palaeoecology* 110, 295-317.
- MUSSA, D., 1980. Ocurrência do genero *Antarcticoxylon* Seward, Na Formação Irati (Permiano) do Estado de São Paulo, Brasil. 2nd *Congreso Argentino de Paleontología y Bioestratigrafía y 1st Congreso Latinoamericano de Paleontología* (Buenos Aires, 1978), Actas 4, 139-155.
- NAMBOODIRI, K.K. & BECK, CH.B., 1968. A comparative study of the primary vascular system of Conifers. III. Stelar evolution in Gymnosperms. *American Journal of Botany* 55, 464-472.
- NIKLAS, K.J., 1994. Predicting the height of fossil plant remains: an allometric approach to an old problem. *American Journal of Botany* 81, 1235-1242.
- NORSTOG, K.J. & NICHOLLS, T.J., 1997. *The Biology of the Cycads*. Cornell University Press, Ithaca, 363 p.

- PETRIELLA, B., 1978. La reconstrucción de *Dicroidium* (Pteridospermopsida, Corystospermaceae). *Obra del Centenario del Museo La Plata* 5, 107-110.
- PETRIELLA, B., 1981. Sistemática y vinculaciones de las Corystospermaceae H. Thomas. *Ameghiniana* 18, 221-234.
- PETRIELLA, B., 1985. Caracteres adaptativos y autoecología de las Corystospermaceae. 3° Congreso Latinoamericano de Paleontología (Mexico, 1984), Simposio Floras Triásico, Memoria, 53-57.
- PIGG, K.B., 1990. Anatomically preserved *Dicroidium* foliage from the central Transantarctic Mountains. *Review of Palaeobotany and Palynology* 66, 129-145.
- POTONIÉ, H., 1897. *Lehrbuch der Pflanzenpalaeontologie*. Berlin, parts 1-2, 208 p.
- RETALLACK, G.J., 1977. Reconstructing Triassic vegetation of eastern Australasia: a new approach for the biostratigraphy of Gondwanaland. *Alcheringa* 1, 247-277 plus fiche I, G1 - J17.
- RETALLACK, G.J. & DILCHER, D.L., 1988. Reconstructions of selected seed ferns. *Annals of the Missouri Botanical Garden* 75, 1010-1057.
- SEWARD, A.C., 1914. Antarctic fossil plants. *British Museum (Natural History), British Antarctic (Terra nova) Expedition (Geology) 1*, 1-49.
- SMOOT, E.L., TAYLOR, T.N. & DELEVORYAS, T., 1985. Structurally preserved fossil plants from Antarctica. I. *Antarcticycas*, gen. nov., a Triassic cycad stem from the Beardmore Glacier Area. *American Journal of Botany* 72, 1410-1423.
- SPALLETTI, L.A., ARTABE, A.E., MOREL, E.M. & BREA, M., 1999. Biozonación paleoflorística y cronoestratigrafía del Triásico Argentino. *Ameghiniana* 36, 419-451.
- STEVENSON, D.W., 1980. Radial growth in the cycadales. *American Journal of Botany* 67, 465-475.
- STEVENSON, D.W., 1990. Morphology and systematics of the Cycadales. *Memoirs of the New York Botanical Garden* 57, 8-55.
- STEWART, W.R. & ROTHWELL, G. W., 1993. *Paleobotany and the evolution of plants*. Cambridge University Press, 521 p.
- STIPANICIC, P.N., HERBST, R. y BONETTI, M.I.R., 1996. Floras Triásicas. In *Revisión y actualización de la obra paleobotánica de Kurtz en la República Argentina*. P.N. STIPANICIC & M.A. HÜNICKEN, eds, *Actas de la Academia Nacional de Ciencias*, 11, 127-184.
- TAYLOR, E.L., 1992. The occurrence of a *Rhexoxylon*-like stem in Antarctica. *Courrier Forschungsinstitut Senckenberg* 147, 183-189.
- TAYLOR, E.L., 1996. Enigmatic gymnospermous? Structurally preserved Permian and Triassic seed ferns from Antarctica. *Review of Palaeobotany and Palynology* 90, 303-318.
- TAYLOR, T.N. & TAYLOR, E.L., 1993. *The Biology and Evolution of fossil plants*. Prentice Hall, 982 p.
- TERRAZAS, T., 1991. Origin and activity of successive cambia in *Cycas* (Cycadales). *American Journal of Botany* 78, 1335-1344.
- THOMAS, H. H., 1933. On some Pteridospermous plants from the Mesozoic rocks of South Africa. *Philosophical Transactions of the Royal Society London* 222B, 193-254.
- TORTORELLI, L.A., 1956. *Maderas y Bosques Argentinos*. Ed. ACME, Buenos Aires, 910 p.
- TORTORELLI, L.A., 1963. Glosario de términos usados en anatomía de maderas. Traducido al castellano por L.A. Tortorelli. *Revista de Investigación Forestal* 4, 3-32.
- TOWNROW, J.A., 1957. On *Dicroidium* probably a pteridospermous leaf, and other leaves now removed from this genus. *Transactions of the Geological Society of South Africa* 60, 21-56.
- TOWNROW, J.A., 1962. On *Pteruchus*, a microsporophyll of the Corystospermaceae. *Bulletin of the British Museum of Natural History (Geology)* 6(2), 287-320.
- WALTON, J., 1923. On *Rhexoxylon* Bancroft, a Triassic genus of plants exhibiting a liane-type of vascular organisation. *Philosophical Transactions of the Royal Society of London* 212B, 79-109.
- WALTON, J., 1925. On some South Africa fossil woods. *Annals of the South African Museum* 22, 1-26.
- WING, S. & DIMICHELE, W.A., 1992. Ecological characterization of fossil plants. In *Terrestrial ecosystems through time: evolutionary paleoecology of terrestrial plants and animals*. A. BEHRENSMEYER, J. DAMUTH, W. DIMICHELE, R. POTTS, H.D. SUES & S. WING, eds, The University of Chicago Press, Chicago, 327-416.
- 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.
- YAO, X., TAYLOR, T.N. & TAYLOR, E.L., 1995. The corystosperm pollen organ *Pteruchus* from the Triassic of Antarctica. *American Journal of Botany* 82, 535-546.
- ZAMUNER, A.B., 1991. *Estudio de una tafoflora de la localidad tipo de la Formación Ischigualasto (Neotrias), Provincia de San Juan*. Tesis Doctoral N° 583 Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, 97 p, inédita.