

***Elchaxylon*, a new corystosperm based on permineralized stems from the Late Triassic of Argentina**

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Anatomically preserved stems of Late Triassic corystosperms from the Río Blanco Formation of Argentina are described and assigned to *Elchaxylon zavattieriae* gen. et sp. nov. The polyxylic gymnospermous axes have two discontinuous cambial rings, which develop centrifugal secondary xylem and centripetal secondary xylem around the mesarch primary xylem bundles. The centrifugal undivided pycnoxylic secondary xylem incorporates uniseriate rays, uni- to biseriate radial pitting either alternate or opposite, and one or two simple pits in each cross-field. Atypical secondary growth is restricted to localized development of centripetal secondary xylem (inverted xylem). *Elchaxylon* could represent a basal member of the rhexoxyloid lineage. This basal clade is characterized by limited centripetal secondary xylem, lack of perimedullar bundles, and modest development of centrifugal xylem.

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THE CORYSTOSPERMACEAE represent one of the most distinctive and widely distributed groups of Triassic gymnosperms in Gondwana. The group, first described by Thomas (1933) from Triassic beds of Natal, South Africa, was reconstructed based on detached but closely associated *Dicroidium* Gothan *emend.* Townrow, 1957 leaves, microsporophylls (*Pteruchus* Thomas *emend.* Townrow 1962), and ovulate organs (*Umkomasia* Thomas 1933). Although convincing attached organs have not been found, corystosperms have been considered a natural group because of cuticular similarities between dispersed organs and the occurrence of similar pollen grains [*Alisporites* Daugherty, 1941; *Falcisporites* (Leschik) Klaus, 1963; *Pteruchipollenites* Couper, 1958]

in *Pteruchus* pollen sacs and *Umkomasia* ovules. Vegetative and reproductive remains are well known, both from permineralized specimens and from compression/impression fossils. Despite most stems and leaves being fossilized independently in diverse depositional environments, the reconstruction of the whole plant (Retallack & Dilcher 1988) is based on a few organs and does not take into account the full diversity of stem genera assigned to the Corystospermaceae.

Assuming *Rhexoxylon* Bancroft *emend.* Archangelsky & Brett, 1961 is the stem of *Dicroidium*, two plant reconstructions have been made for this group in southwestern Gondwana (Petriella 1978, Retallack & Dilcher 1988). The most accurate reconstruction was based on the consistent association of *Dicroidium zuberi* and *Rhexoxylon piatnitzkyi* in the Ischigualasto Formation, Argentina (Archangelsky & Brett

1961, Archangelsky 1968, 1970). *Rhexoxylon* is a pycnoxylic wood associated with a unique mode of secondary xylem production that results in centripetal or/and centrifugal polyxylic stems. *Tranquiloxyton* Herbst & Lutz, 1995 and *Cuneumxyton* Artabe & Brea, 2003 are axes with slightly different growth forms but are affiliated with the Corystospermaceae because of their anatomical resemblance to *Rhexoxylon*. The anomalous development of the secondary xylem and liana-like anatomy indicate close relationships between these genera. *Rhexoxylon* currently includes six species (Bancroft 1913, Walton 1923, 1925, Archangelsky & Brett 1961, Brett 1968, Herbst & Lutz 1988, Zamuner 1991, Lutz & Herbst 1992, Artabe *et al.* 1999) and shows a wide distribution in southwestern Gondwana (Argentina, Brazil, South Africa) and Antarctica (Taylor 1992). *Tranquiloxyton*, with only one species, was found in Argentina and Chile (Herbst & Lutz 1995, Chong Díaz *et al.* 1997, Spalletti *et al.* 1999). The monospecific *Cuneumxyton* has been recorded only in Argentina.

The concept of the 'Dicroidium plant' was expanded to include not only the *Dicroidium-Rhexoxylon* association of South Africa and South America but also the *Dicroidium-Dadoxylon* association found in Antarctica (Meyer-Berthaud *et al.* 1992). The Antarctic plant, based on material from Fremouw Peak, consists of axes with dense, pycnoxylic wood of *Dadoxylon* type associated with leaves of *Dicroidium* (Meyer-Berthaud *et al.* 1993, Taylor 1996). 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 (Meyer-Berthaud *et al.* 1993). Additionally,

the silicified wood *Jeffersonioxyton* Del Fueyo *et al.* 1995 found at Gordon Valley, Antarctica, and previously assigned to the Podocarpaceae, is considered to belong to the Corystospermales (Taylor 1996, Cúneo *et al.* 2003) because *Dicroidium*-type foliage is associated with the stumps.

New pycnoxylic stumps with anomalous growth from Late Triassic Río Blanco Formation at Cerro Cacheuta (Fig. 1), near the town of Potrerillos, Argentina, are described in this paper and represent a new genus of Corystospermaceae. The anatomy, pattern of secondary growth, and polyxyly development of *Elchaxylon zavattieriae* gen. et sp. nov. emphasize the broad diversity of growth forms within the rhexoxyloid lineage. The new plants are preserved in a large, monotypic, *in situ* petrified forest.

Materials and methods

The fossil stems were found in the lower levels of the Río Blanco Formation at La Elcha Mine (near Cacheuta Hill), situated in the southern Precordillera, Mendoza province, western Argentina (69° 09' 24.3" W and 33° 03' 36.8" S; Fig. 1). More than 150 stems in living position are preserved in an area 550 m long and 340 m wide. The new corystosperm stems assigned to *Elchaxylon zavattieriae* gen. et sp. nov. constitute a monotypic community. Field observations reveal that all of the trees with good preservation have the same anatomical features and are assigned to a single species; six specimens were selected for anatomical study. Following the palaeobotanical biozonation by Spalletti *et al.* (1999) for the continental Triassic of Argentina, the taphocoenosis is located in the younger Biozone of the Florian Stage (DLM Assemblage Biozone), which corresponds to the latest Triassic.

Stems were preserved by siliceous cellular permineralization. Thin-sections were

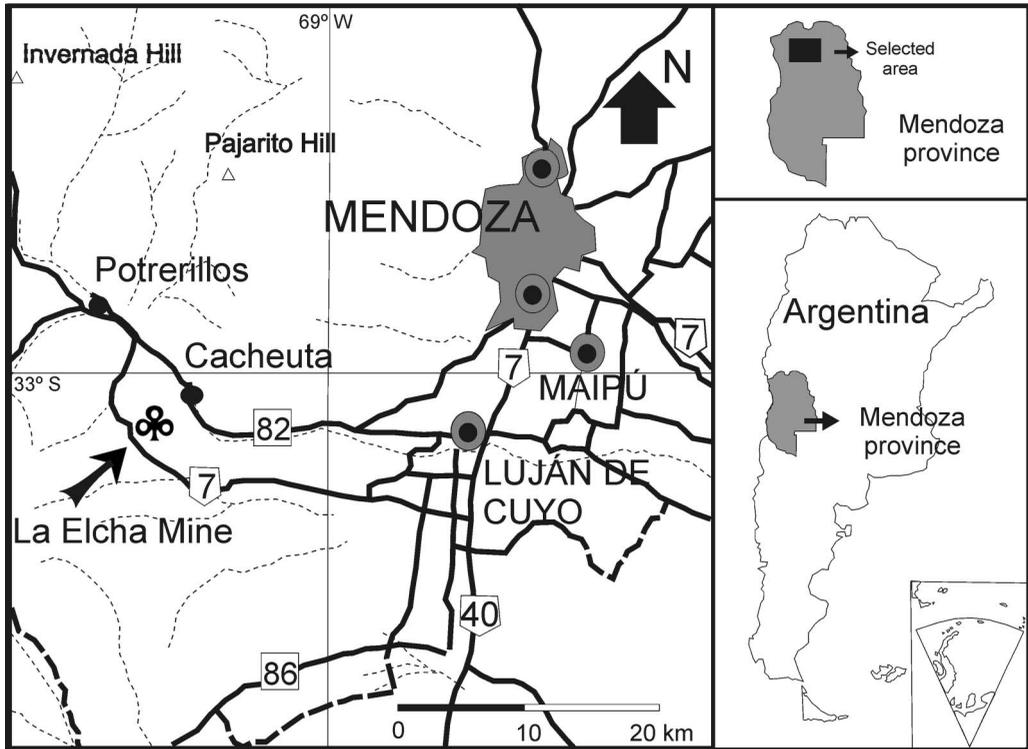


Fig. 1. Map showing the La Elcha Mine locality, Medoza province, Argentina, where the fossil forest is preserved.

prepared for microscopic examination. The standardized terminology of Greguss (1955, 1968), Boureau (1956), Tortorelli (1956, 1963), Cozzo (1964), Fahn (1990), and Stevenson (1990) are used to describe the fossil woods.

The specimens and their microscopic slides are deposited in the Paleobotanical Collection, División Paleobotánica, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata (LPPB and pmLPPB), and the Museo Municipal Moyano of Mendoza city (MCNAM-PB).

Systematic palaeobotany

Class GYMNOSPERMOPSIDA Stewart & Rothwell, 1993

Order CORYSTOSPERMALES Petriella, 1981

Family CORYSTOSPERMACEAE Thomas, 1933

Elchaxylon gen. nov.

Type species. Elchaxylon zavattieriae sp. nov. from Río Blanco Formation, Mendoza province, Argentina, Late Triassic (Spalletti *et al.* 1999).

Etymology. The generic name refers to the place (La Elcha Mine) near which the genus was discovered.

Diagnosis. Oval and slightly eccentric polyxylic gymnospermous stems with pith, primary and secondary xylem. Cortex not preserved. Homogeneous pith with polyhedral parenchyma cells. Cylindrical vascular system with several discrete vascular

segments, usually with few axial sympodia per segment; two discontinuous cambial rings developing great amounts of undivided pycnoxylic centrifugal secondary xylem and small quantities of centripetal secondary xylem around mesarch primary xylem bundles. Secondary xylem shows definite growth rings. Pits on radial walls of the tracheids are uni- to biseriate, alternate or opposite. Rays are uniseriate and low; cross-fields include 1-3 oval or round simple pits. Axial parenchyma is scanty.

Elchaxylon zavattieriae sp. nov. (Figs 2–4)

Type material. Holotype: MCNAM-PB1495, LPPB 13236, pmLPPB 1740-1745; paratypes: MCNAM-PB1496, LPPB 13237, pmLPPB 1746; MCNAM-PB1497, pmLPPB 1747-1750; MCNAM-PB1498, LPPB 13238, pmLPPB 1751-1756; LPPB 13239, pmLPPB 1757; LPPB 13240, pmLPPB 1758.

Type locality. Mina La Elcha, Potrerillos, Mendoza.

Stratigraphic horizon. Río Blanco Formation (Fossa Mancini 1937).

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

Etymology. The specific epithet, *zavattieriae*, is dedicated to Dr. Ana María Zavattieri, an outstanding palynologist who has studied the Triassic sequences of Argentina and found (together with Augusto Menéndez) the *in situ* forest.

Diagnosis. Polyxylic gymnospermous stems, 5-58 cm in diameter. Small homogeneous pith with polyhedral parenchyma cells up to $56.1 \times 72.6 \mu\text{m}$. Cylindrical vascular system containing several discrete segments, usually with a few axial sympodia per segment, and centrifugal-centripetal secondary xylem. Mesarch primary xylem composed of clusters of small tracheids up to $9.9 \mu\text{m}$ in

diameter. Centripetal secondary xylem up to $2458 \mu\text{m}$ wide. Centrifugal secondary xylem with distinct true growth rings of variable thickness and common false rings; radial wall tracheids with bordered pits uni- to biseriate either alternate or opposite, $8.3\text{-}14.6 \mu\text{m}$ in diameter; 1-3 simple, circular to oval, $8.3 \times 10.4 \mu\text{m}$ to $14.6 \times 20.8 \mu\text{m}$ diameter pits in cross-fields; rays uniseriate, 19.8×99 to $26.6 \times 204.6 \mu\text{m}$ and 1-20 cells high (mode 3; mean 5.3). Axial parenchyma is scanty.

Description. The stumps are fossilized in growth position. The stems are 5-58 cm in basal diameter, with oval or circular outline. Among the trunks studied, only one has poorly preserved pith, all of them being decorticated (Fig. 2A). The compressed pith measures $12 \times 2 \text{ mm}$ in width (Fig. 2A) and is homogeneous, with polyhedral parenchyma cells 26.4×33 to 56.1×72.6 (mean 53.7×42.2) μm (Fig. 2B). The cylindrical vascular system has several segments, each with a few axial sympodia and centrifugal-centripetal secondary xylem (Fig. 2C). The mesarch primary xylem strands are composed of isolated groups of small isodiametric tracheids of $9.9\text{-}16.5 \mu\text{m}$ in diameter (Figs 2D-F) surrounded by small amounts of centripetal secondary xylem towards the pith and a large amount of centrifugal xylem towards the cortex. The centripetal secondary xylem measures $458.9\text{-}984.4$ (603.2 mean) μm in thickness and $524.5\text{-}2458.5$ (1163.7 mean) μm in width (Figs 2A, D-F) and their tracheids up to $33 \times 49.5 \mu\text{m}$. Atypical centrifugal secondary growth shows hourglass-like zones of xylem tissue without proliferation of parenchyma cells (Figs 3A-B); these areas range between 262.2 and $426.1 \mu\text{m}$ wide and between 131.1 and $1147.3 \mu\text{m}$ in radial thickness.

Secondary xylem tracheids are quadrangular with an oval lumen. Tracheids have uniseriate, irregularly biseriate or fully biseriate pitting on radial walls (Figs 4A-B, D). When uniseriate, the bordered pits are

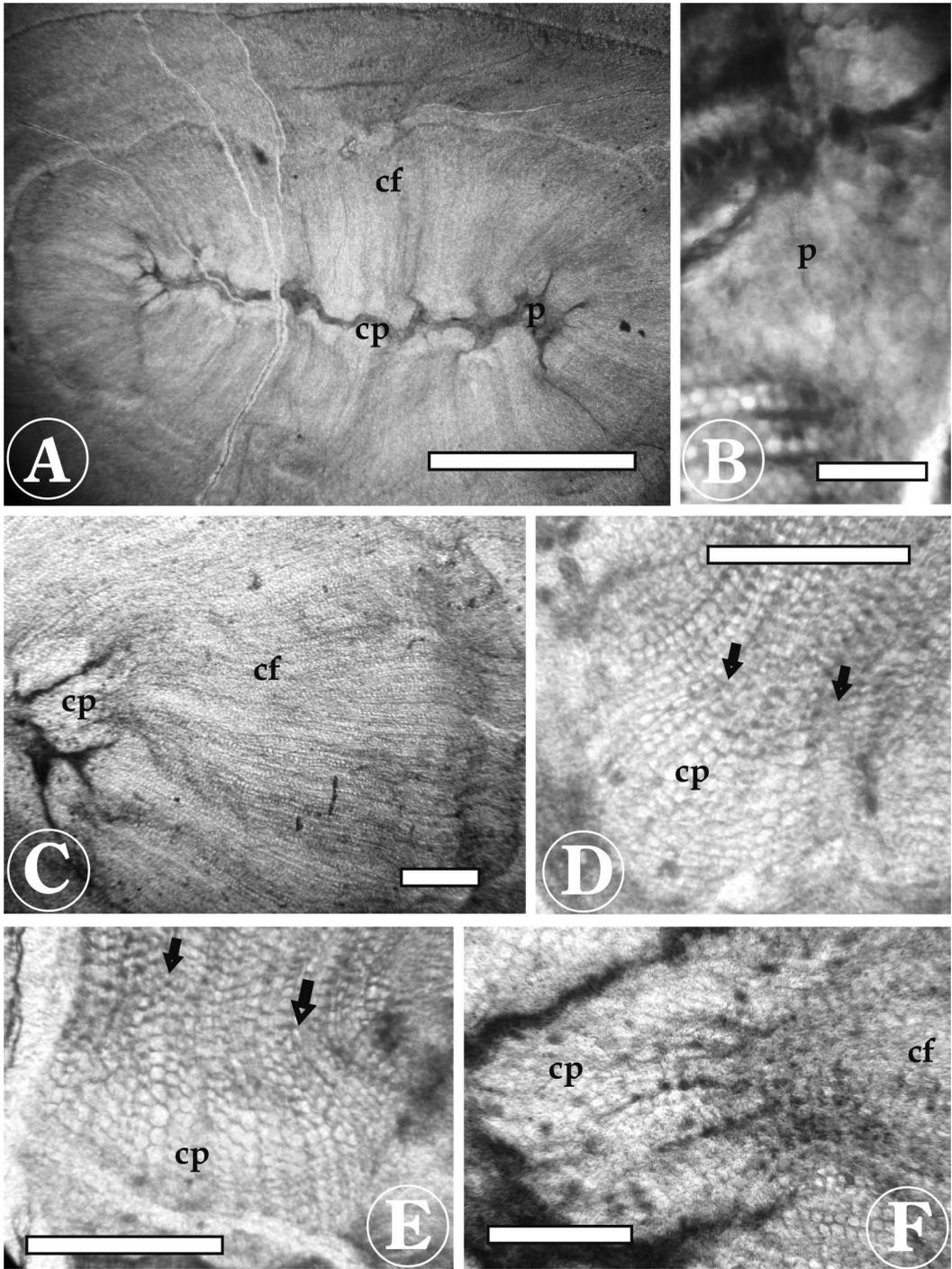


Fig. 2. *Elchaxylon zavattieriae* sp. nov. MCNAM-PB1495, LPPB13236, pmLPPB1740, 1741: A, transverse section showing the central part of the stem: (p) pith, (cp) centripetal secondary xylem, (cf) centrifugal secondary xylem; B, parenchyma cells of the pith; C, detail of A. D, E, F, centripetal secondary xylem; arrows show mesarch protoxylem (bar-scales A, 5 mm; B, 150 μ m; C, 1 mm; D, E, F, 500 μ m).

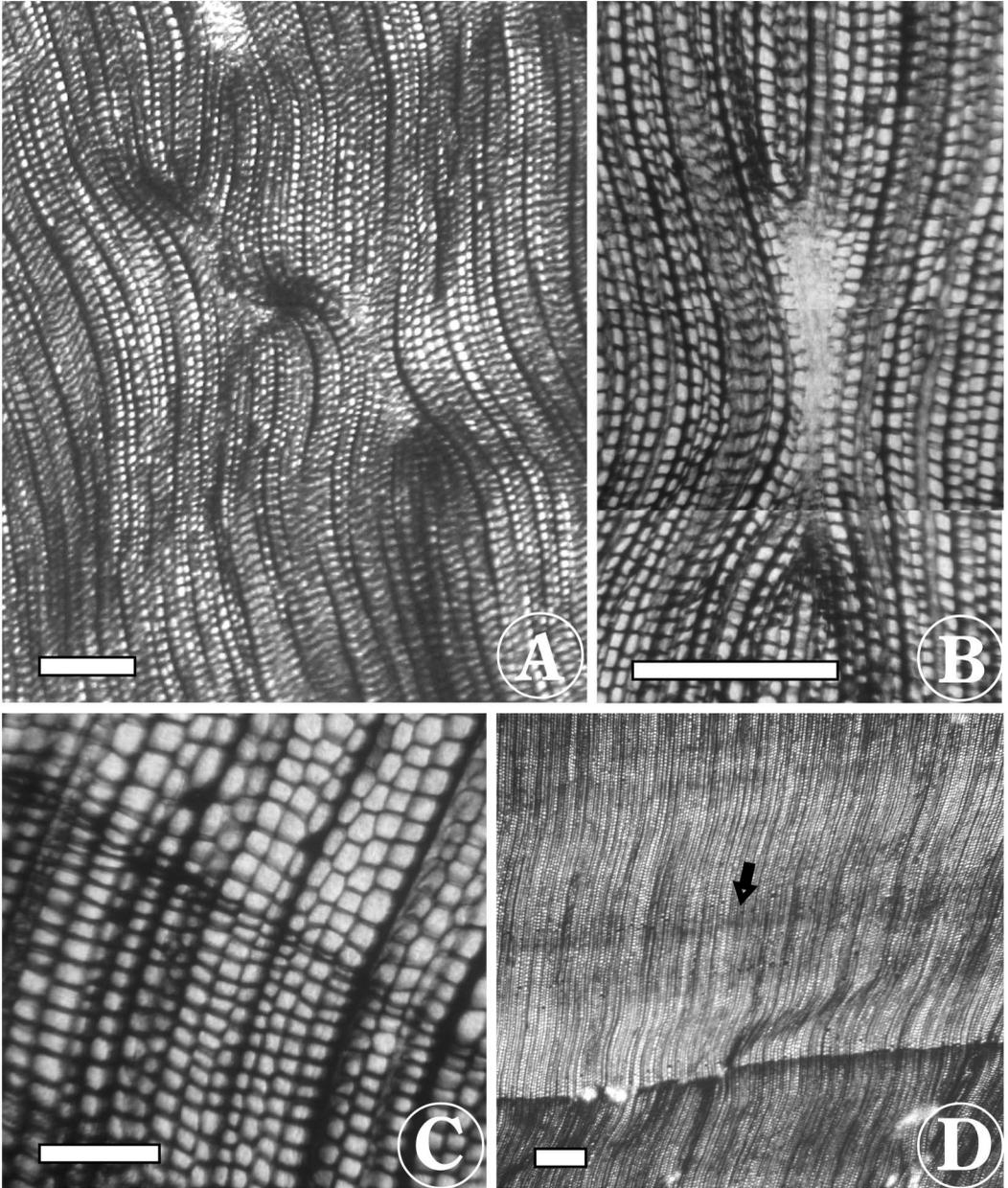


Fig. 3. *Elchaxylon zavattieriae* sp. nov. LPPB13239, pmLPPB1757. A, transverse section of wood showing the hourglass-like xylem structures; B, detail of hourglass-like structures; C, transverse section of wood showing a true growth ring; D, transverse section of wood; arrow shows a false ring (bar-scales A, B, D, 500 μ m; C, 250 μ m).

circular or oval, with slightly separate or contiguous arrangement (Figs 4A-B); in biseriata examples, the bordered pits are circular or vaguely hexagonal, either sepa-

rated or compressed, with alternate or opposite arrangement (Figs 4B-C). Pit pores are circular and enclosed. The uniseriate and biseriata bordered pits are

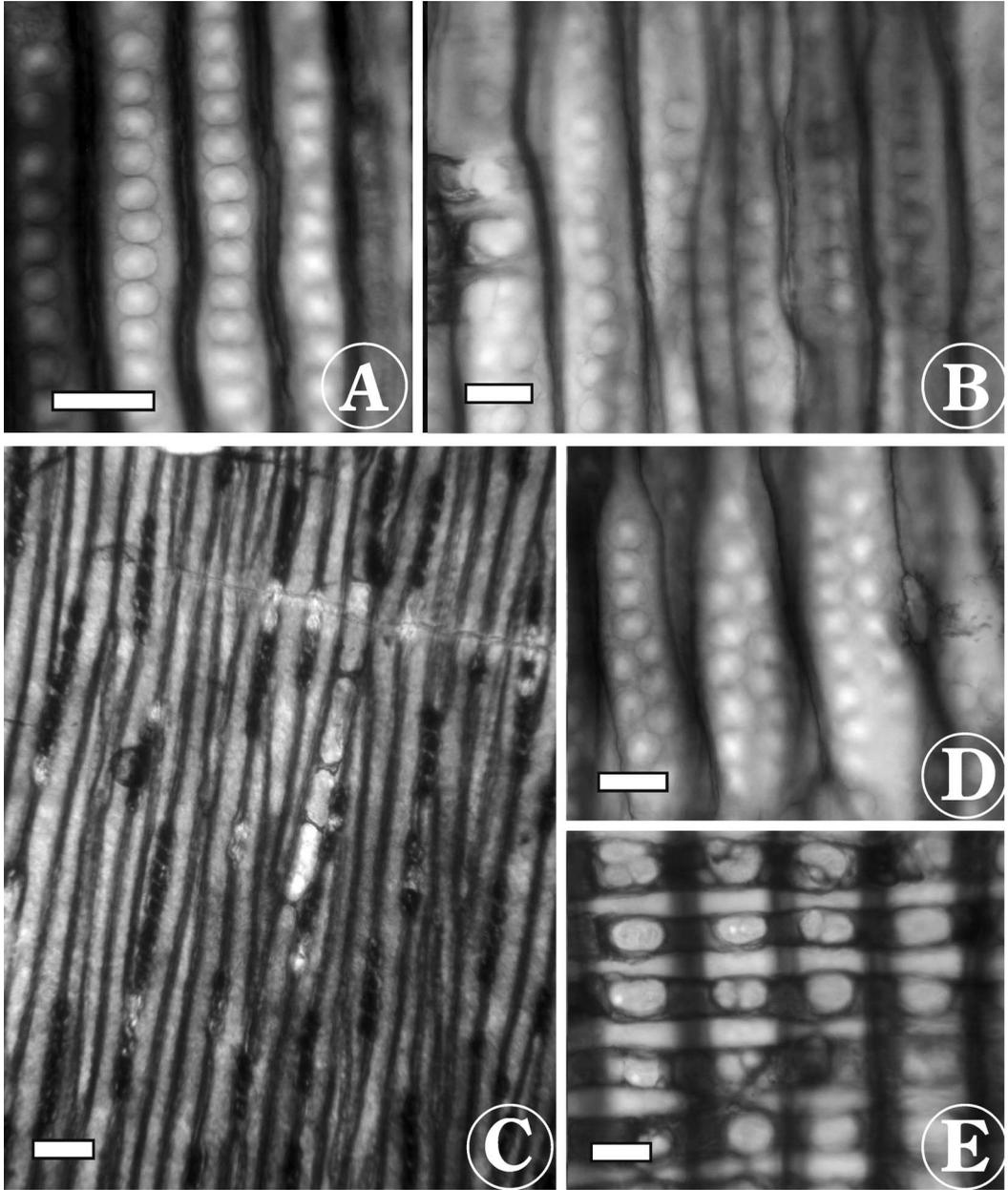


Fig. 4. *Elchaxylon zavattieriae* sp. nov. MCNAM-PB1498, LPPB13238. A, B, D, tracheids in radial longitudinal section showing uni- to biseriate radial pitting (pmLPPB 1755); C, tangential longitudinal section of wood showing uniseriate rays and axial parenchyma (pmLPPB1753); E, radial longitudinal section of wood showing ray with simple pits in the cross-fields (pmLPPB 1755) (bar-scales A, B, D, E, 25 μm ; C, 100 μm).

8.3-14.6 (mean 12.5) μm in diameter, with pores 3.1-4.16 μm in diameter. The tangential diameter of tracheids is 36.3-56.1 (mean

45.2) μm ; radial diameter is 39.6-66 (mean 48.6) μm in early wood and 13.2-23.1 (mean 16.8) μm in latewood (Fig. 4B). The

thickness of the double wall between two tracheids is 3.3 μm in the early wood and 6.6 μm in the latewood.

Rays are parenchymatous, uniseriate, homocellular, and homogeneous. The rays are short and vary from 33 to 592 (mean 157.8) μm in height and from 1 to 20 (mean 5.3; mode: 3) cells high (Fig. 4C). They are composed of oval or rectangular parenchyma cells with thin walls. In radial section, parenchyma cells measure 19.8 \times 0.99 to 26.6 \times 204.6 (mean 19.8 \times 23.1 \times 144.2) μm . Axial parenchyma is scanty and tends to form tangential rows (Fig. 4C).

Cross-fields commonly have one, rarely two or three simple circular to oval pits 8.3 \times 10.4 to 14.6 \times 20.8 (mean 10.4 \times 16.8) μm in diameter (Fig. 4E).

The secondary xylem shows distinct true growth rings. In a radial section, nine series of growth rings were counted. The growth ring width is very variable ranging from 0.27 to 8.94 mm, with a mean of 3.4697 mm. The early/latewood transition is gradual. One to three cell rows of latewood (Fig. 3C) abruptly terminate the season's growth. The earlywood cells are commonly crushed and, in certain cases, extensively distorted. There are regions where wood takes on a zigzag pattern due to compression of the tracheids. False rings are abundant (Fig. 3D); sparse incomplete rings are evident.

Comparisons and discussion

Pycnoxylic wood associated with a unique mode of secondary xylem production that results in polyxylic stems, relates *Rhexoxylon*, *Tranquiloxyton*, *Cuneumxyton* and *Elchaxyton* to the Corystospermaceae. *Elchaxyton* is considered a polyxylic stem because the stem possesses two discontinuous cambial rings, which start developing centrifugal secondary xylem and centripetal secondary xylem around the mesarch pri-

mary xylem bundles. As in *Rhexoxylon*, the new genus is characterized by: mesarch primary xylem, centrifugal secondary xylem, and centripetal secondary xylem (inverted xylem). However, it does not develop the perimedullar bundles and centripetal polyxyly of *Rhexoxylon* (Zamuner 1991, Artabe *et al.* 1999, Artabe & Brea 2003). *Cuneumxyton* and *Tranquiloxyton* have endarch primary xylem, i.e. they do not produce centripetal xylem or perimedullar bundles (Artabe & Brea 2003). However, like *Rhexoxylon*, they have two kinds of unusual centrifugal secondary growth. First, they show unequal activity of different portions of the cambium on the circumference of the axes; consequently, the reduction of cambial activity to certain restricted areas develops wedged, commonly split stems. Second, secondary xylem develops with 'included phloem' producing centrifugal polyxylic stems (Artabe & Brea 2003). *Elchaxyton* generates a different kind of abnormality in the centrifugal secondary xylem producing an hourglass-like xylem pattern without proliferation of parenchyma cells. These zones may be due to compression of xylem into pockets generated by fungal or insect attack. The unusual xylem growth found in some Triassic pycnoxylic gymnosperm woods of Antarctica (probably related to Podocarpaceae or Corystospermaceae) have been considered as evidence of mechanical wounding and wound responses (Putz & Taylor 1996). The anomalous morphological feature present in *Elchaxyton* may not be a consequence of wounding because there is commonly no evidence of scars (Putz & Taylor 1996), although sharply truncated cell boundaries are evident in the centre of some 'hourglass zones' (Fig. 3B). Because corystosperms commonly produce anomalous secondary growth, the hourglass-like structures could be generated by this process. The origin of these ambiguous anatomical structures remains unclear. Their

derivation awaits study of better preserved material.

Wood characters relate *Elchaxylon* to *Rhexoxylon* and *Tranquiloxyton*. They have uni- to triseriate radial pitting and cross-fields with 1-4 simple pits and secondary rays mainly uniseriate. In contrast, *Cuneumxyton* has cross-fields with 2-13 simple pits. Consistent characters in *Rhexoxylon* that are absent in *Cuneumxyton* and *Tranquiloxyton* are the presence of sclerotic nests (*R. africanum*, *R. tetrapteridoides*, *R. brasiliensis*) and secretory cavities (*R. africanum*, *R. tetrapteridoides*, *R. piatnitzkyi*, *R. brasiliensis*, *Rhexoxylon* sp.) in the pith.

Another genus assigned to Corystospermaceae is *Antarcticoxyton* 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. Walton's (1925) proposal of a synonymy between *Antarcticoxyton* and *Rhexoxylon* was rejected by Archangelsky & Brett (1961), Mussa (1980), Herbst & Lutz (1995), and Meyer-Berthaud *et al.* (1993). Although *Antarcticoxyton* shares some features of the secondary xylem with *Rhexoxylon* (uni- to biseriate, alternate, radial pitting and mainly uniseriate rays), Archangelsky & Brett (1961) and Mussa (1980) argued that *Antarcticoxyton* has no centripetal secondary xylem. This stem appears to be endarch with pycnoxylic secondary growth and does not show anomalous secondary xylem (Seward 1917, Archangelsky & Brett 1961).

The small Antarctic axes assigned to *Kykloxyton* by Meyer-Berthaud *et al.* (1992) found in close association with *Dicroidium fremouwensis* are regarded as the distal twigs of a 'Dicroidium plant' (Pigg 1990, Meyer-Berthaud *et al.* 1992, 1993, Yao *et al.* 1995, Taylor 1996, Axsmith *et al.* 2000). Unlike *Rhexoxylon* stems, *Kykloxyton* has endarch primary xylem and an undivided solid cylinder of secondary xylem; hence its

corystospermalean affiliations remain equivocal.

The silicified wood *Jeffersonioxyton* found at Gordon Valley, Antarctica, originally assigned to the Podocarpaceae, was also later considered to belong to the Corystospermales (Taylor 1996, Cúneo *et al.* 2003) because the foliage associated with the stumps is of the *Dicroidium* type. Cúneo *et al.* (2003) proposed that *Jeffersonioxyton* represented the trunk and *Kykloxyton* the distal twigs of a large tree with gymnospermous wood and axillary branching that bore seasonal deciduous *Dicroidium* leaves (Taylor 1996), or that it might represent another taxon linked to *Dicroidium* foliage (Cúneo *et al.* 2003). Like these forms, *Elchaxylon* has an undivided solid cylinder of centrifugal secondary xylem, but differs in developing discrete quantities of centripetal secondary xylem around mesarch primary xylem bundles. In relation to the histological features of the secondary xylem, *Kykloxyton* has uni- to triseriate radial pitting, cross-fields with 3-9 simple pits, and uniseriate rays, whereas *Jeffersonioxyton* has uni- to biseriate radial pitting, with 1-2 oval pits in the cross-fields and uniseriate rays.

It seems clear that *Elchaxylon* has anomalous secondary growth like *Rhexoxylon*, *Cuneumxyton* and *Tranquiloxyton*. The presence of centripetal secondary xylem could be phylogenetically important. Artabe & Brea (2003) suggested that the corystosperm stele evolved along two principal lineages (rhexoxyloid and cuneumxyloid) from a medullosan or a similar precursor. *Rhexoxylon* characterizes the rhexoxyloid line and shows: mesarch primary xylem, centrifugal wedges of secondary xylem, centripetal secondary xylem (inverted xylem), and perimedullar bundles. The southwestern Gondwana species seem to fit into a developmental series: *R.* sp. [*R. krauselii*? (Lutz & Herbst 1992)] → *R. piatnitzkyi* Archangelsky & Brett 1961 → *R. brunoi*

Artabe *et al.* 1999. The series shows an increase in the anomalous vascular tissue development with formation of successive cycles of medullar bundles inside the trunk and the progressive acquisition of larger stems by an increase in the amount of centrifugal secondary conducting tissues.

Cuneumxylon and *Tranquiloxylo*n 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.

Elchaxylon may represent a basal branch of the rhexoxyloid line close to *Rhexoxylo*n sp. (*R. krauselii*). *Elchaxylon* has features akin to *Rhexoxylo*n sp. (*R. krauselii*) such as centripetal secondary xylem, but it does not produce perimedullar bundles. As in the rhexoxyloid line, *Elchaxylon* shows a degree of pycnoxyly, but anomalous centripetal xylem growth is more restricted.

Conclusions

A new genus and species, *Elchaxylon zavattieriae*, of anatomically preserved corystosperm stems is described from the Upper Triassic Río Blanco Formation of Argentina. Similar to *Rhexoxylo*n, the new genus is characterized by: mesarch primary xylem, centrifugal secondary xylem, centripetal secondary xylem (inverted xylem), but it does not develop perimedullar bundles. Anatomical evidence suggests that corystosperm vascular anatomy diverged into two lineages from hypothetical precursors similar 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, consequently, develops no perimedullar bundles. *Elchaxylon* may represent a basal branch of the

rhexoxyloid lineage. This clade has a degree of pycnoxyly in the centrifugal xylem but does not produce perimedullar bundles.

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