



First Lower Cretaceous record of Podocarpaceae wood associated with dinosaur remains from Patagonia, Neuquén Province, Argentina



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ABSTRACT

The first Podocarpaceae wood record is described from the Mulichinco Formation (Valanginian, Lower Cretaceous), Neuquén Basin, Argentina. The specimen was directly associated with a middle caudal vertebra of a diplodocid sauropod dinosaur. A new species – *Podocarpoxyylon prumnopityoides* – is proposed based on features that include the presence of abietinean wood type (tracheid radial pitting), plus podocarpoid (cupressoid type) and some dactyloid (taxodioid type) cross-field pits, diffuse axial parenchyma and low rays. This combination of anatomical characters is comparable to both *Prumnopitys* and *Podocarpus*, whereas the type of pits in the cross-fields resembles some members of the extant *Prumnopitys*. This is the first unequivocal record of the Family Podocarpaceae in the Valanginian of South America and confirms the hypothesis that the divergence between the “Podocarpoid-Dactyloid” and “Prumnopityoid” clades occurred earlier than the Early Cretaceous.

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1. Introduction

The modern family Podocarpaceae comprises 19 genera (including *Phyllocladus* Rich. ex Mirb.) of evergreen trees and shrubs. They are almost entirely restricted to rainforest or wet montane environments, but occasionally occur in lowland forests (Farjon, 2008, 2010; Cernusak et al., 2011). This family is mainly distributed in tropical and subtropical regions in the southern hemisphere and extends north to Japan, Central America and the West Indies (Hill and Brodribb, 1999; Farjon, 2008, 2010; Cernusak et al., 2011). Five of the genera occur in South America: *Lepidothamnus* Phil., *Podocarpus* Labill., *Prumnopitys* Phil. *Retrophyllum* C.N. Page and *Saxegothaea* Lindl. (sometimes treated as the separate family Saxegothaeaceae; Mill and Stark Schilling, 2009) (de Laubenfels, 1985; Kelch, 1997, 1998; Farjon, 2001, 2008, 2010).

Podocarpaceae is the oldest extant conifer family and is placed as the sister clade of Araucariaceae based on paleontological and molecular analyses (Chaw et al., 1997; Hill and Brodribb, 1999; Farjon, 2008; Rai et al., 2008; Biffin et al., 2011). Molecular phylogenies of Podocarpaceae genera are supported as monophyletic, with the exception of *Prumnopitys*, which includes *Sundacarpus* (*Prumnopitys sensu lato*). Current phylogenetic analyses suggest that the major clades within Podocarpaceae differentiated during the Late Cretaceous and Paleogene, and most modern genera are already known by the late Paleogene (Biffin et al., 2011; Greenwood et al., 2013; Quiroga et al., 2015). Nevertheless, the cladogenesis of the “Podocarpoid-Dactyloid” from the “Prumnopityoid” clade probably occurred between the mid-Jurassic and mid-Cretaceous (145 (99–194) Ma or 101 (67–135) Ma) (Biffin et al., 2011; Leslie et al., 2012; Greenwood et al., 2013; Quiroga et al., 2015). The dates for the divergence of *Prumnopitys* suggest a mean stem age of 80 (64–121) Ma and a crown age of 64 (40–91) Ma, indicating a likely Late Cretaceous origin for the genus (Biffin et al., 2011; Leslie et al., 2012; Greenwood et al., 2013; Quiroga et al., 2015). However, although a phylogenetic analysis of the Podocarpaceae (Biffin et al.,

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2012) suggests that the group began to diversify between the mid-Jurassic and mid-Cretaceous, other analyses indicate that some of the extant genera originated in the Early Cretaceous whereas others appeared during the Paleogene. Most podocarpacean genera would have appeared and diversified during the Cenozoic.

The Gondwanan Lower Cretaceous coniferous woods include representatives related to the families Araucariaceae, Cheirolepidiaceae, Cupressaceae and Podocarpaceae. The fossil wood record shows that the *Podocarpoxyylon* dominated in the winter wet zone (southern South America, southern Africa except for the south and east coasts, central Madagascar and western India), whereas in most other regions there is a clear dominance by *Agathoxyylon* (Fig. 1 in Philippe et al., 2004).

Whereas the Argentinean record of Podocarpaceae wood is extensive during Triassic, Jurassic and Late Cretaceous times (Zamuner and Artabe, 1994; Del Fueyo, 1998; Gnaedinger, 2007; Herbst et al., 2007; Martínez and Lutz, 2007; Crisafulli and Herbst, 2011; Gnaedinger et al., 2015), coniferous woods from the Early Cretaceous are scarce and mostly attributed to the Araucariaceae (Herbst et al., 2007).

At present, the Valanginian-Hauterivian record of the Family Podocarpaceae is restricted to *Circoporoxylon* sp. from Antarctica (Philippe et al., 1995; Torres et al., 1997) and *Podocarpoxyylon* from Chile (Philippe et al., 2000).

In this contribution, we present the first record of wood remains from the Valanginian Mulichinco Fm (Lower Cretaceous, Neuquén Basin, Argentina) assigned to the family Podocarpaceae. The fossils represent a new species – *Podocarpoxyylon prumnopityoides*. Remarkably, the permineralized remains of this new form were collected in direct association with a sauropod dinosaur fossil.

Institutional Abbreviations: MCF-PBPH, Museo Carmen Funes, Paleobotánica de Plaza Huinçul; MLL-PV, Museo Municipal de Las Lajas, Paleontología de Vertebrados; UNRN, Universidad Nacional de Río Negro.

2. Paleontological background of the Mulichinco Formation

The Cretaceous rocks from the Neuquén Basin are known worldwide because of their paleontological contents, which consist

mainly of vertebrates (see Gasparini et al., 2007 and references therein). The Valanginian rocks of the Mulichinco Formation, although typically formed by marine sediments, bear extensive terrestrial sediments at the Pilmatué locality. There, well preserved dinosaur remains – including partial skeletons of ornithopods, theropods and sauropods – have been found (Coria et al., 2013).

The paleobotanical record of the Mulichinco Formation is essentially based on palynological data. The record refers in part to the zone of *Cyclusphaera psilata*-*Classopollis* sp. of late Valanginian-? Barremian age (Volkheimer, 1980), which includes pollen, spores and phytoplankton (Archangelsky, 1977, 1980; Dellapé et al., 1978; Volkheimer and Musacchio, 1981; Prámparo et al., 1995; Quattrocchio et al., 1999, 2002, 2003; Ottone, 2009). This biozone is dominated by Araucariaceae (*Araucariacites australis* and *Cyclusphaera psilata*) and Cheirolepidiaceae (*Classopollis* sp.) pollen, with a subordinate presence of Podocarpaceae (*Podocarpidites* sp.), spores of Bryophyta, Lycophta and Pteridophyta, and coenobia from Chlorophyta (Volkheimer, 1980; Ottone, 2009). Also, specimens of the fern *Tempskya* Corda have been reported from Mulichinco Fm levels at Pilmatué and other localities (Martínez et al., 2012; Martínez and Olivo, 2015).

3. Geological setting and associated biota

The Mulichinco Formation is a stratigraphic unit widely exposed in the Neuquén Basin. It shows great vertical and lateral facies variations that represent marine, continental and transitional environments (Schwarz and Howell, 2005 and references therein). These facies changes are also reflected in the fossil content of this unit, which includes ammonite zones indicating an early Valanginian age (Aguirre Urreta et al., 2005) and also dinosaur remains (Coria et al., 2013).

The plants described in this paper come from a section of the Mulichinco Formation in the area around Arroyo Pilmatué, located 9 km northeast the city of Las Lajas, central Neuquén Province (Figs. 1 and 2). This section is located within the Austral Region proposed by Schwarz (2003) for the basin.

In this area, terrestrial sediments attributed to the middle section of the Mulichinco Fm are extensively exposed. The section was

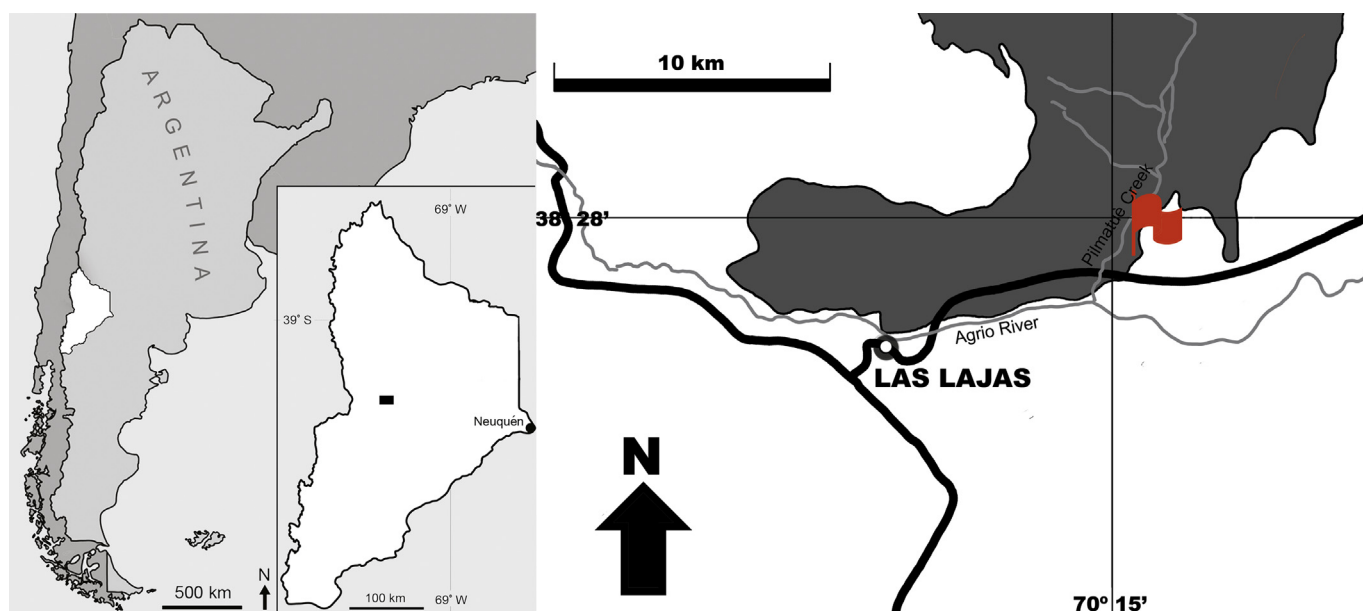


Fig. 1. Map showing the locality of Pilmatué. Red flag depicts location of the fossils. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

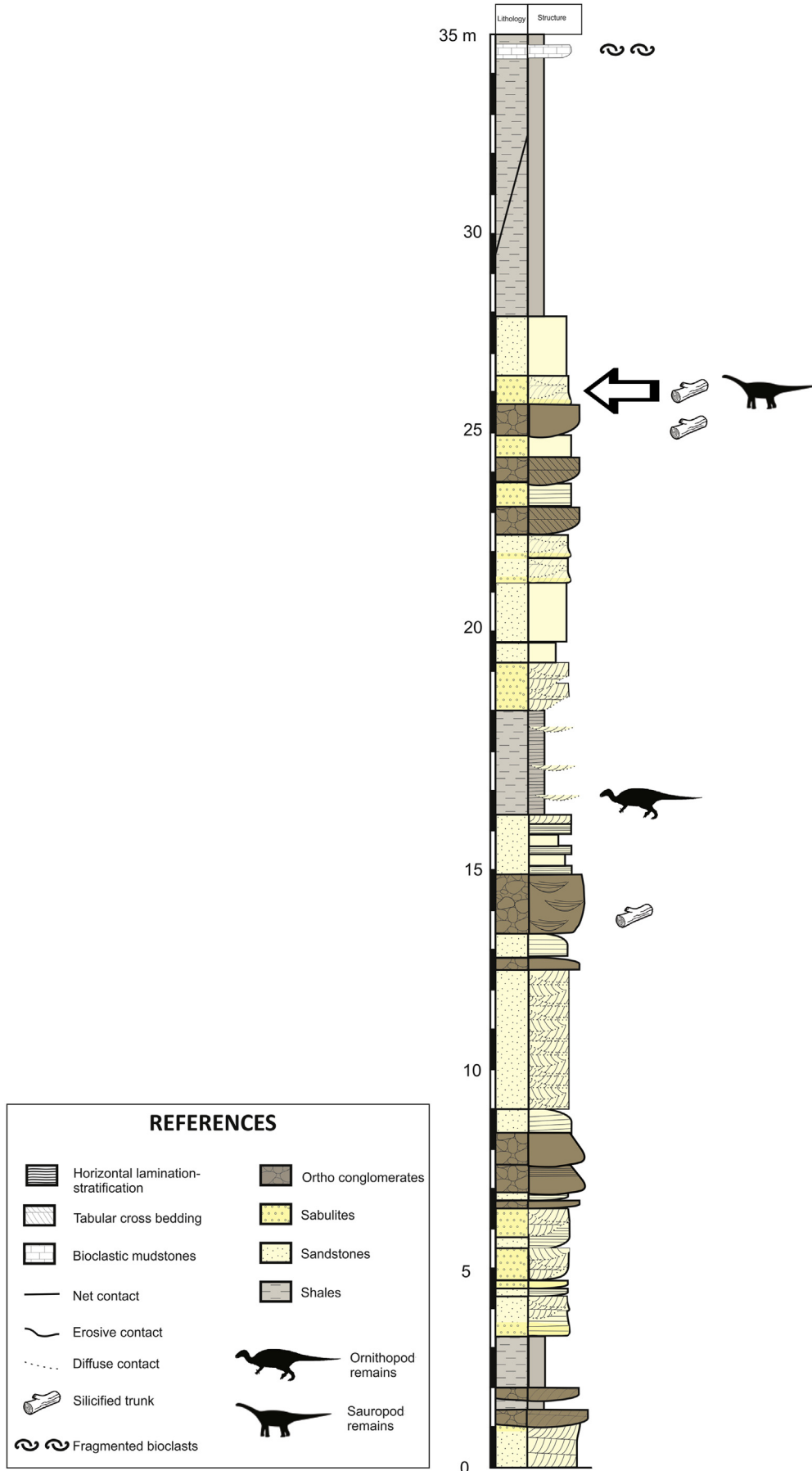


Fig. 2. Geological section showing the provenance of *Podocarpoxylon prumnopyoides* sp nov. (MCF-PBPH-223) and *Diplodocidae* indet (MLL-PV-013). Fossil-bearing level indicated by the arrow.

measured bed-by-bed. The description of the section includes lithology, sedimentary structures, and shape and arrangement of the beds. The sands and finer-grained fractions were systematically sampled for petrographic characterizations. The top 35 m were analyzed and four sedimentary facies were identified; a) massive sands and polymictic sabulites with tangential cross-stratification in tabular beds, one layer of which yielded ornithopod remains; b) well-sorted, fine conglomerates with abundant well-rounded quartz clasts and intraclasts, arranged in lenses with an erosional base and upward-fining with tangential or trough cross-stratification; c) beds of massive or parallel-bedded sandstone, possibly merging into packs up to 3 m thick; d) massive or laminated greenish to purplish pelites that under X-ray diffraction analysis reveal the presence of chlorite, illite and interstratified illite-smectite in the clay fraction ($<2 \mu\text{m}$). Layers in facies b have produced sauropod remains and abundant silicified trunks. Petrographically, the sandstones are lithoarenites with variable percentages of quartz, whether mono- or polycrystalline. The most abundant lithic fragments are clasts of volcanic rocks, but also abundant flexured mica and accessory minerals.

The facies association recognized in this sector of the basin suggests the development of a fluvial system with channel deposits and bar migration on a poorly developed floodplain, associated with flooding and spillover events. The channeled and flat-bedded sandstone and conglomerate facies predominate over pelitic beds. The general arrangement of the section is upward-coarsening until the uppermost 10 m. Although the upper section is partly covered, greenish-grey pelitic beds intercalate with beds carrying abundant fragments of oysters and other bivalves.

Since 2009, a multidisciplinary and international team has been conducting systematic exploration and collection. As a result of this work, remains of sauropod, theropod and ornithopod dinosaurs have been recovered and are currently under study (Coria et al., 2013). The dinosaur remains include isolated, semiarticulated and articulated specimens that are preserved in two fossil-bearing levels. The higher of these two levels has more abundant fossils. At that level, sauropods include eroded postcranial remains of possible titanosauriformes, and *in situ* fossils of dicraeosaurids and diplodocids. Among the latter, one complete mid-caudal vertebra was collected at the top of the section exposed on the left bank of Pilmatue creek, north of the bridge of National Route 40. The Podocarpaceae described in this paper was associated with this caudal vertebra (MLL-PV-013, Fig. 3). However, the specimen was only seen underneath the centrum when the fossil bone was being prepared in the laboratory. The vertebra was exposed on its heavily weathered right side. However, the opposite side is well preserved. The neural spine is complete, and the transverse process is reduced, which identifies it as a mid-caudal vertebra. A deep longitudinal cavity excavates the ventral side of the vertebra, which also has well developed ventrolateral ridges. These features, and a vertebral centrum that is anteroposteriorly almost twice the dorsoventral height of the whole vertebra, have been considered as features shared by several diplodocid species (Salgado and Bonaparte, 2007; Mannion et al., 2012; Tschopp and Mateus, 2012). Cretaceous diplodocids from the underlying Bajada Colorado Fm include *Leinkupal laticaudata* (Gallina et al., 2014). The holotype of this species includes a mid/distal caudal vertebra that has a longitudinal ventral cavity comparable with that of MLL-PV-013. A proportionally longer centrum of the specimen from Pilmatué (Fig. 3) might be an indication of a more distal position in the tail.

4. Materials and methods

The fragment of silicified logs was collected in the Pilmatué locality of the Mulichinco Formation, Neuquén Province, Argentina (Figs. 1 and 2). Standard petrographic thin sections were prepared

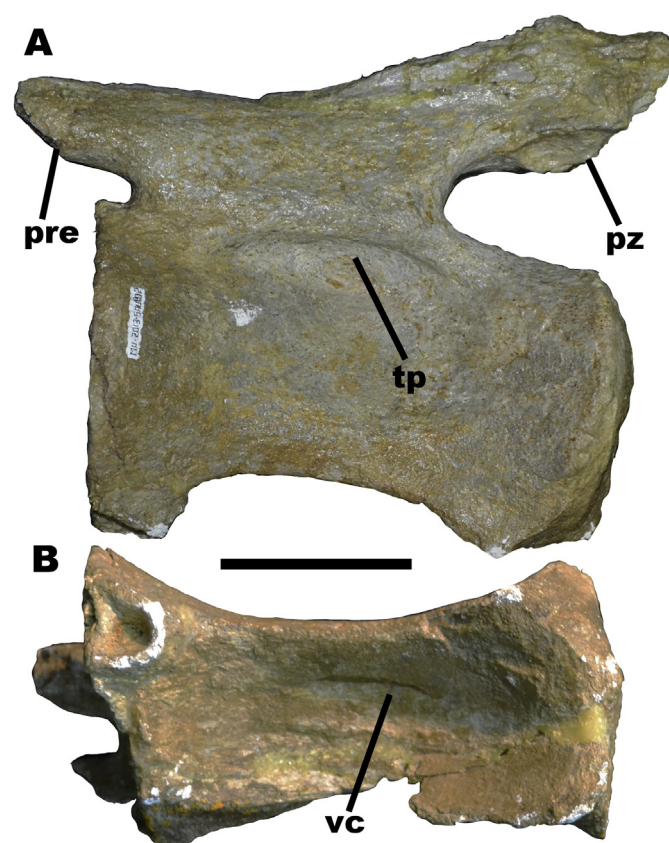


Fig. 3. Caudal vertebra of *Diplodocid* indet. MLL-PV-013 in A. left lateral and B. ventral views. Abbreviations: prz, prezygapophysis; pz, postzygapophysis; tp, transverse process; vc, ventral cavity. Scale bar: 10 cm.

with the wood fragments oriented along three planes – transverse section (TS), radial longitudinal section (RLS), and tangential longitudinal section (TLS). These thin sections were studied in detail with a Leica microscope (DM500) and photomicrographs were taken using a digital camera (Leica ICC50). The present description of the specimen is based essentially on observations under a scanning electron microscope (SEM Jeol 5800LV) from the Universidad Nacional del Nordeste (Corrientes, Argentina). The sample is described and identified following Richter et al. (2004) and others (Phillips, 1941; Greguss, 1955; García Esteban et al., 2002, 2003, 2004). The terminology of the wood fossil types (secondary structure) and radial pitting of the tracheids follows the considerations given in Gnaedinger et al. (2015). The measurements follow standards established by Chattaway (1932). At least 20 individual measurements of the various anatomical elements were recorded, giving values for average, minimum and maximum. The specimen was identified and compared using descriptions of extant and fossil woods (Phillips, 1941; Greguss, 1955, 1972; Patel, 1967; García Esteban et al., 2002, 2004; Greenwood, 2005; Gnaedinger, 2007; Philippe and Bamford, 2008; Tortorelli, 2009; Vásquez Correa et al., 2010; Franco and Brea, 2015; Gnaedinger et al., 2015). The nomenclature system of the fossil genus follows Philippe and Bamford (2008).

The paleobotanical material is housed in the Paleontological Collection of the Museo Municipal “Carmen Funes”, Plaza Huincul, Neuquén Province, Argentina under the prefix MCF-PBPH.

5. Paleobotanical systematics

Order Araucariales *Gorozhankin, 1904* (ex Coniferales) *sensu Christenhusz et al., 2011*

Family Podocarpaceae Endlicher, 1847

Genus *Podocarpoxylon* Gothan, 1905

Type species: *Podocarpoxylon juniperoides* Gothan, 1905 in Gagel, 1906, p. 272

Podocarpoxylon prumnopityoides nov. sp.

Figs. 4–7

Derivation of name. Refers to the similarities with the “*Prumnopityoid*” clade of the extant Podocarpaceae Family

Holotype. MCF-PBPH-223.

Type locality. Pilmatué, 9 km northeast Las Lajas City, Neuquén province, Argentina. (GPS coordinates are available upon request from the author RAC)

Stratigraphic horizon. Mulichinco Formation (Valanginian).

Diagnosis. The secondary wood type (tracheid radial pitting) is abietinean (close to 91.5% of the abietinoid type pits: separate pits).

Pits are bordered, circular, predominantly uniseriate, some uniseriate with biseriate sections, and rarely biseriate. Pits are predominantly separate, or sometimes contiguous. Biseriate pits are mainly opposite, rare opposite-alternate, or alternate. Cross-fields 1–2 cupressoid pits, with elliptical aperture and border weakly marked or reduced (podocarpoid type *sensu* Gothan, 1905) and some taxodioid pits with circular aperture and border reduced (dactrydioid type *sensu* Patel, 1967; Philippe, 1995). In some marginal cross-fields, 3–4 pits can be observed. Radial system homogeneous, rays uniseriate and low. Axial parenchyma diffuse and scarce.

Description. The fossil specimen consists of a 20 cm long and 1.6 cm wide fragment (Figs. 4A–B; 6A). The secondary xylem is pycnoxylic, with quadrangular-polygonal tracheids. Early wood consists of tracheids with a mean radial diameter of 43 μm (33–54 μm) and late wood tracheids with a mean radial diameter of 16 μm

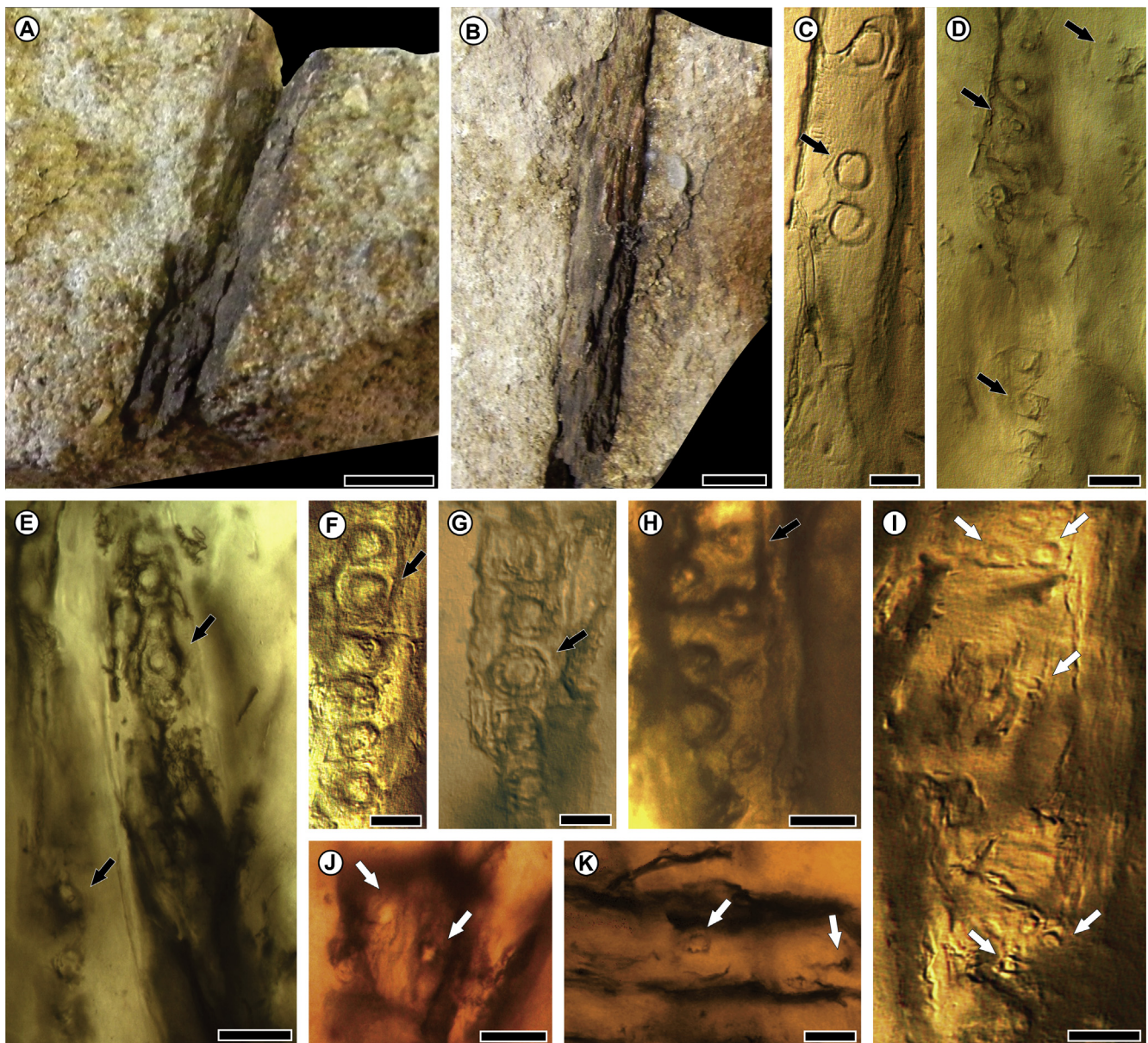


Fig. 4. *Podocarpoxylon prumnopityoides* sp. nov. A–B. General view of the petrified wood. C–H. RLS, showing detail pits on tracheids: C–G, uniseriate pits, C–D: abietinoid pits; F–G araucarioid pits; H, alternate biseriate pits (black arrow). I–K, RLS, detail of cross-field pits (white arrow): I–J, cupressoid (podocarpoid type *sensu* Gothan, 1905); K, taxodioid (dactrydioid type *sensu* Patel, 1967). Scale bars = 1 cm in A–B; 15 μm in C–L.

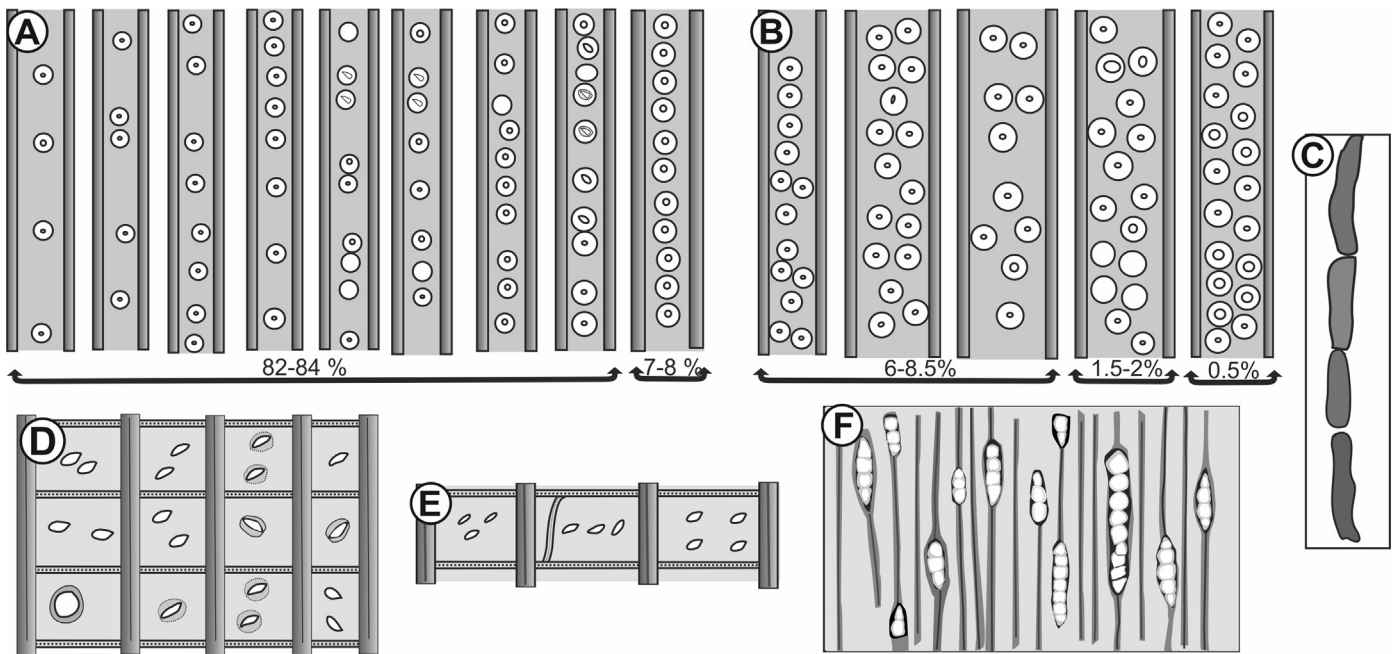


Fig. 5. *Podocarpoxylon prumnopityoides* sp. nov. Line drawings. **A–B.** Tracheid radial pitting: uniseriate separate or contiguous; biseriate opposite, opposite-alternate and alternate pits. **C.** Cross-field pitting with cupressoid (podocarpoid type *sensu* Gothan, 1905) and taxodioid (dactrydioid type *sensu* Patel, 1967) pits. **D.** Marginal cross-field pitting. **E.** Axial parenchyma. **F.** Uniseriate rays.

(14–24 μm) (Fig. 6E). The secondary wood (tracheid radial pitting) is abietinean (91.5% of the pits are abietinoid type and 8.5% of them are araucarioid type). Pits are bordered, circular (close to 100%). The tracheids have predominantly uniseriate radial pitting (89–92%), separate (82–84%) or contiguous (7–8%); some uniseriate with biseriate sections (6–8%), and biseriate pits (2–3); opposite (6–8.5%), opposite-alternate (1.5–2%), or rarely alternate (close to 0.5%) (Figs. 4D–I; 5A–B; 6B–D; 7A–J). Pits are 11–17 μm in diameter, occupy only a portion of the tracheid radial walls and have circular or oval-elliptic apertures (3–7 μm in diameter) (Figs. 4D–I; 5A–B; 6B–D; 7A–J). Cross-fields 1–2 cupressoid pits, with elliptical aperture and border weakly marked or reduced (podocarpoid type *sensu* Gothan, 1905) and some taxodioid pits with circular aperture and border reduced (dactrydioid type *sensu* Patel, 1967; Philippe, 1995): measure 8–9 μm in diameter. In some marginal cross-fields, 3–4 cupressoid type pits can be observed (Figs. 4J–L; 5C–D; 6B–D; 7K–L). The radial system is homogeneous with homocellular, uniseriate and low rays that are 2–9 cells in height (Figs. 5F; 7I, M). The central cells are rectangular, 21–29 μm high and 15 μm wide. Marginal cells are triangular to elliptic, 18 μm in height and 12 μm in width and central cells are ovoid rectangular, 21–29 μm high and 15 μm wide (Figs. 5F; 7M). The axial parenchyma is diffuse and scarce, measure 133–242 μm in height and 24 μm wide, might have smooth walls (Figs. 5E; 7A–D).

6. Remarks

6.1. Similarities with extant taxa

The anatomical features of the described specimen indicate that the fossil is a conifer with abietinean wood secondary structure, which is present in the families extant Cupressaceae (including Taxodiaceae), Pinaceae, Podocarpaceae and Sciadopityaceae. The cross-field pitting is crucial to the identifications of coniferous woods at the family level, and requires an understanding of the

frequency, arrangement, form, size and/or position of the aperture relative to the borders of the pits (Richter et al., 2004). The presence of both podocarpoid type (*sensu* Gothan, 1905) and some dactrydioid type (*sensu* Patel, 1967; Philippe, 1995) pits in the cross-field suggest that the new fossil is related with the Family Podocarpaceae. These characters are only present in woods of this Family (Greguss, 1955, 1972; García Esteban et al., 2002, 2003, 2004; Richter et al., 2004).

In extant Podocarpaceae wood, different terms have been used to identify pits in cross-fields: podocarpoid (preferable), phyllocladoid and dactrydioid/taxodioid (Gothan, 1905; Greguss, 1955, 1972; Patel, 1967; Rancusi et al., 1987; Tortorelli, 2009). The terminology used to establish differences between genera and species varies among authors (Philipps, 1941; Krausel, 1949; Greguss, 1955, 1972; Boureau, 1956; Patel, 1967). In an effort to standardize terminology, Marguerier and Woltz (1977) proposed the following names for pits in the cross-field: oculipore pits (podocarpoid, cupressoid, taxodioid, dactrydioid, piceoid) and simple pits (oopore, phyllocladoid and circopore). Following the same criteria, the IAWA Committee established (Richter et al., 2004), as diagnostic character, three types of cross-field pitting in the podocarpaceae wood: cupressoid, taxodioid and window-like.

Gothan (1905) defined “podocarpoid” pits as an oculipore with a narrow slit-like sub-vertical aperture. In turn, IAWA compendium (Richter et al., 2004) considers as diagnostic the form, size and position of the aperture in the pits of the cross field. Philippe and Bamford (2008, p. 187), in their review of fossil genera, interpreted that the features originally used by Gothan (1905) to distinguish “podocarpoid” from “cupressoid” crossfield pits (i.e. narrow slit-like subvertical aperture) are considered in the IAWA compendium to fall with the variation range of the latter, making, “podocarpoid” a synonym of “cupressoid” (Gerards et al., 2007, fig. 8b–c).

In the same way, Patel (1967) defined “dactrydioid” pits as an circular, weakly bordered oculipores. In the IAWA Committee (Richter et al., 2004), are included as taxodioid pits (it only includes

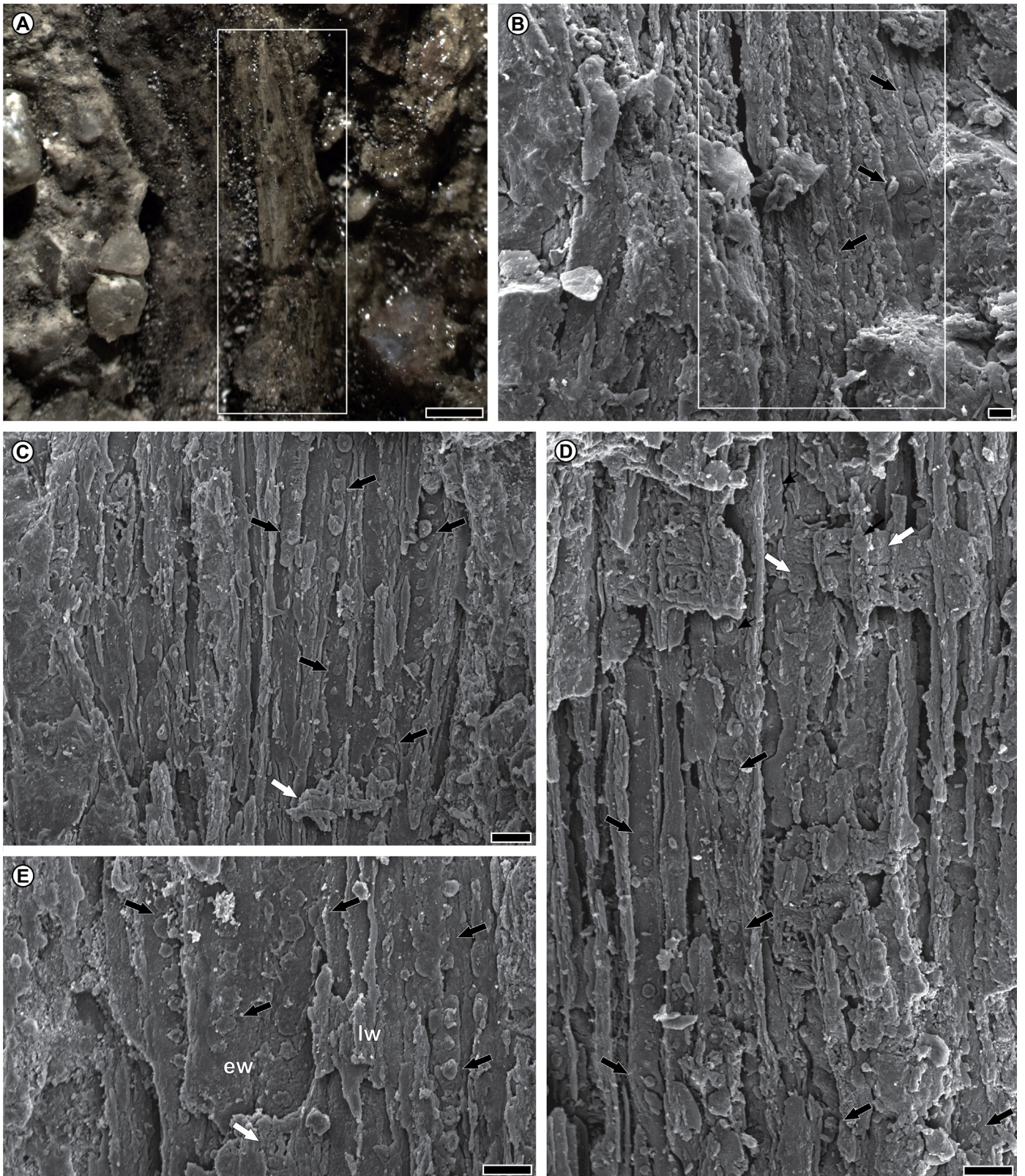


Fig. 6. *Podocarpoxylon prumnopityoides* sp. nov. SEM images. **A.** General view of the observed section in SEM. **B–D.** General view in radial longitudinal section, showing radial pitting (black arrow) and cross-field (white arrow). **E.** detail of the tracheids, ew = earlywood; lw = latewood. Scale bars 30 μm, except A = 1 mm.

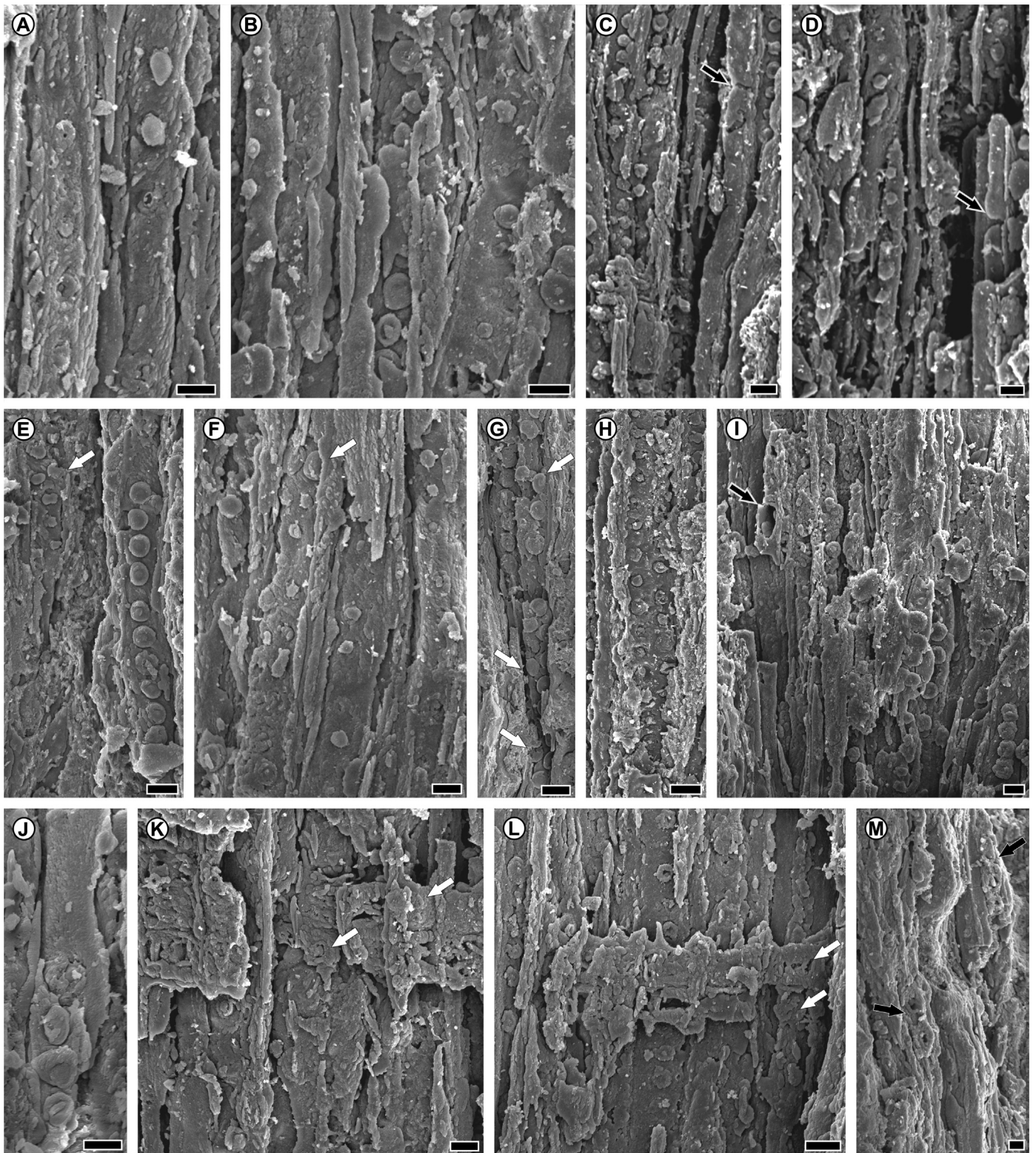


Fig. 7. *Podocarpoxylon prumnopityoides* sp. nov. SEM images. **A–D.** RLS, showing tracheids with separate or contiguous uniseriate pits and axial parenchyma (black–white arrow). **E–G.** RLS, showing tracheids with uniseriate pits and opposite biseriate portions (white arrow). **H.** Radial longitudinal section, showing tracheids with alternate biseriate pits. **I.** Longitudinal section, showing tracheids with separate or contiguous uniseriate pits and rays (black–white arrow). **J.** Detail of the aperture pits. **K–L.** Cross-field pitting with cupressoid (podocarpoid type *sensu* Gothan, 1905) and taxodioid (dactrydioid type *sensu* Patel, 1967) pits (white arrow). **M.** Uniseriate rays (black–white arrow). Scale bars = 15 μ m.

pits that have large circular apertures; each aperture exceeds the width of the border at its widest point).

The types of cross-fields present in the specimen of *Podocarpoxylon prumnopityoides* nov. sp. have podocarpoid (cupressoid, with elliptical aperture and border weakly marked or reduced) and

some dacrydioid (taxodioid, with circular aperture and border reduced) pits, which are also observed in some species of *Dacrycarpus dacrydioides*, *Podocarpus* (e.g. *P. glomeratus*, *P. madagascariensis*, *P. milanjanus*, *P. oleifolius* and *P. totara*.), *Prumnopitys* (*P. andina*, *P. ferrugineus*, *P. ferruginoides*, *P. montana*) and

Table 1
Comparison between species of *Podocarpoxylon* from Gondwana sharing the character: axial parenchyma. (1/2: rays uniseriate partially biseriolate; in parenthesis = character with occasional condition).

Species	Characters				
	Horizon/Country	Radial walls pits	Axial parenchyma	Cross-field	Rays Width/Height
<i>P. parlatifolium</i> Vozenin-Serra and Grant-Mackie, 1996	Upper Triassic New Zealand	Uniseriate, contiguous	Scarce	1–2 (3): podocarpoid (eye-shaped or slit-like aperture), dacrydioid and circopore	1 1–12
<i>P. atuelensis</i> Gnaedinger et al., 2015	Lower Jurassic Argentina	Uniseriate (biseriolate); separate (contiguous), opposite (alternate)	Abundant pairs	1–2 (4): cupressoid (=podocarpoid)	1 2–10
<i>P. austroamericanum</i> Gnaedinger, 2007	Middle Jurassic Argentina	Uniseriate, (biseriolate); separate-contiguous; opposite (alternate)	Scarce	1–4: cupressoid (=podocarpoid), some circopore	1 (1/2) 1–14
<i>P. gangtaensis</i> Rai et al., 2016	Middle Jurassic India	Uniseriate (biseriolate); separate-contiguous; alternate-opposite	Scarce	2–5: small to large; oval to circular, bordered	1 (1/2) 3–8,18
<i>P. dunstani</i> (Sahni) Kräusel (1949) (= <i>Cupressinoxylon dunstani</i> Sahni)	Jurassic. Australia	Uniseriate (biseriolate), crassulae	Present	3–6 or more: simple	1 5–10,20
<i>P. kraeuselii</i> Rajanikanth & Sukh-Dev (1989)	Jurassic. India	Uniseriate	Present	4–5: elliptic and grouped	1 2–28
<i>P. trichinopoliense</i> (Varma) Bose and Maheshwari, 1974	Cretaceous India	Uniseriate; separate (contiguous)	Scarce	1–2: podocarpoid (fusiform obliquely placed pits)	1 2–6,10
<i>P. prumnopityoides</i> (This Work)	Lower Cretaceous Argentina	Uniseriate (biseriolate); separate-contiguous, opposite.	Scarce diffuse	1–2 (3–4): podocarpoid and some dacrydioid	1 2–9
<i>P. habuensis</i> Guleria and Shukla, 2008	Lower Cretaceous India	Uniseriate (biseriolate); separate, opposite -subopposite.	Present	Not seen	1 3–10
<i>P. cf. sahnii</i> Ramanujam (In Bamford and Corbett, 1994)	Lower Cretaceous South Africa	Uniseriate (biseriolate); separate-contiguous, opposite. Bars of Sanio.	Present	1 (2): large, elliptic in shape with pointed ends (i.e. fusiform).	1 (1/2) 3–30
<i>P. woburnense</i> (Stopes) Seward (In Bamford and Corbett, 1994)	Lower Cretaceous South Africa	Uniseriate; separate-contiguous	Very rare	1: simple, oval-rounded	1 (1/2) 2–15,25
<i>P. cf. woburnense</i> (Stopes) Seward (In Bamford and Corbett, 1994)	Lower Cretaceous South Africa	Uniseriate (biseriolate); contiguous, opposite	Present	1–2: simple, rounded-oval	1 (1/2) 1–15,35
<i>P. stokesii</i> Thayne and Tidwell (In Bamford and Corbett, 1994)	Lower Cretaceous South Africa	Uniseriate; separate-contiguous	Present	1: rounded, elliptical aperture (Podocarpoid); circular aperture (dacrydioid)	1 (1/2) 1–28,48
<i>P. cf. stokesii</i> Thayne and Tidwell (In Bamford and Corbett, 1994)	Lower Cretaceous South Africa	Uniseriate (biseriolate); separate, (contiguous), opposite	Scarce	1–3: small	1 (1/2) 2–47
<i>P. cf. umzambense</i> Schultze-Motel (In Bamford and Corbett, 1995)	Lower Cretaceous South Africa	Uniseriate; separate	Scarce	1: oval to rounded	1 3–18
<i>P. umzambense</i> Schultze-Motel, 1966	Upper Cretaceous South Africa	Uniseriate (biseriolate); separate, opposite. Bars of Sanio.	Scarce	1–2: elliptical pits (podocarpoid)	1 1–25
<i>P. garcie</i> Del Fueyo, 1998	Upper Cretaceous Argentina	Uniseriate; separate	Present	1–2: circular, not preserved aperture	1 1–15
<i>P. garciae</i> Del Fueyo (in Varela et al., 2015)	Upper Cretaceous Argentina	Uniseriate (biseriolate); separate-contiguous, opposite- alternate. Bars of Sanio	Scarce-diffuse	1–2: cupressoid	1 2–17
<i>P. chapmanae</i> Poole and Cantrill, 2001	Upper Cretaceous Antarctica	Uni-biseriate (triseriate); contiguous-opposite (alternate)	Scarce to absent	1–4: circular to obliquely elliptical apertures	1 1–42
<i>P. communis</i> Poole and Cantrill, 2001 (= <i>Podocarpoxylon</i> sp. 2 Falcon-Lang and Cantrill, 2001)	Lower and Upper Cretaceous Antarctica	Uniseriate (biseriolate); contiguous-opposite (alternate). Bars of Sanio.	Abundant	1–3 (4): podocarpoid, circular-oval pits, large oval aperture	1 1–32
<i>P. mazzonii</i> (Petriella) Müller-Stoll and Schultze-Motel (Brea et al., 2011)	Paleocene Argentina	Uniseriate (biseriolate); opposite	Scarce	1–2: cupressoid	1(2–3) 4–24
<i>P. palaeoandinum</i> Nishida, 1984	Eocene Chile	Uniseriate; spaced	Scarce	Large, ovoid simple and elliptical to lenticular	1 1–6, 13
<i>P. palaeosalignum</i> Nishida, 1984	Eocene. Patagonia	Uniseriate (biseriolate)	Abundant	1–2: elliptical or thick, lenticular pit apertures	1 1–5,10
<i>P. speciosum</i> (Ramanujan) Trivedi and Srivastava, 1989	Miocene-Pliocene India	Uni-biseriate; opposite-subopposite	Abundant	2–4: podocarpoid	1–2 1–18
<i>P. mahabalei</i> (Agashe) Trivedi and Srivastava, 1989	Miocene -Pliocene India	Uniseriate; separate-contiguous.	Abundant	1: podocarpoid	1 1–30
<i>P. kutchensis</i> Lakhanpal et al., 1975	Pliocene India	Uniseriate (biseriolate); separate, opposite - subopposite	Present	1–2: small, circular, oval, bordered = podocarpoid to taxodioid	1 (2) 1–18,41

Retrophyllum minor (Greguss, 1955, 1972; Patel, 1967; Marguerier and Woltz, 1977; Greenwood, 2005; García Esteban et al., 2004; Farjon, 2010; Christenhusz et al., 2011). For the Podocarpaceae genera mentioned, Greenwood (2005, Table 1) points out that *Podocarpus* can be either podocarpoid or dactyroid; *Prumnopitys* generally has podocarpoid but rarely dactyroid pits; and both *Dacrycarpus* and *Retrophyllum* frequently have dactyroid, and sometimes podocarpoid pits. Within this framework, the new taxon is reminiscent of the condition in *Prumnopitys* by the presence of the cupressoid (podocarpoid) and some taxodioid (dactyroid) pits in the cross-field.

Further characters shared by the new taxon with the Podocarpaceae include the presence of uniseriate and homocellular rays; uniseriate and biseriate pits in the radial walls of tracheids with opposite pits; and the occasional presence of axial parenchyma (Phillips, 1941; Greguss, 1955; Richter et al., 2004).

Diffuse axial parenchyma is known in different genera and species of the Podocarpaceae, including *Podocarpus* with smooth transversal walls (15 species) or with smooth or slightly nodular walls (2 species); in two species of *Prumnopitys* (*P. andina* and *P. ferruginoides*) that have smooth to slightly nodular walls, and in one species (*Prumnopitys taxifolia*) in which parenchyma is either absent or scarce. Finally, *Retrophyllum minus* has a spaced distribution of parenchyma with smooth transversal walls (Greguss, 1955; Richter et al., 2004; García Esteban et al., 2002, 2004).

The presence of uniseriate and opposite biseriate radial pitting as in *Podocarpoxyton prumnopityoides* nov. sp., is observed in extant species of *Podocarpus* (among them *P. madagascariensis*, *P. oleifolius*, *P. totara*), in species of *Prumnopitys* (*P. andina*, *P. ferruginoides*) and in *Retrophyllum minus*. Furthermore, the presence of alternate biseriate radial pitting (araucarioid type) is occasionally mentioned in *Prumnopitys andina* and *Podocarpus madagascariensis*, as in the fossil wood of Neuquén (Greguss, 1955; Patel, 1967; García Esteban et al., 2002, 2004; Vásquez Correa et al., 2010). *Podocarpus madagascariensis* is also characterized by the presence of crassula in the pits, which is not present in the new species.

The anatomical features described in the fossil material more closely resemble the genus *Prumnopitys*, particularly *P. andina*, which grows in the foot hills of Argentina and Chile. *Prumnopitys andina* (= *Podocarpus andinus*) shares the following characters with the fossil wood: presence of axial parenchyma with smooth to slightly nodular walls; uniseriate or biseriate opposite tracheid radial pitting, the occasional presence of alternate biseriate pits; cupressoid and some taxodioid types of cross field-pitting, with 1–2 bordered pits per field and homocellular and uniseriate rays (Phillips, 1941; Greguss, 1955; García Esteban et al., 2002; Vásquez Correa et al., 2010).

6.2. Comparisons with fossil taxa

In the Mesozoic record, diverse genera with secondary abietinean structures are assigned to Podocarpaceae. They are mostly distinguished by the types of pits in the cross-fields: *Circoporoxylon* Kräusel is circopore; *Microcachryxylon* Torres, Courtinat, Méon with one or two large pits, irregular in shape, which occupy the whole field; *Dacrydioxyton* Greguss has dactyroid pits; *Phyllocladoxyton* Gothan has the phyllocladoid type, and *Podocarpoxyton* has the podocarpoid type of pitting *sensu* Gothan, 1905 (Gothan, 1905; Kräusel, 1949; Greguss, 1967; Philippe, 1995; Torres et al., 1995; Bamford and Philippe, 2001; Gnaedinger, 2007; Philippe and Bamford, 2008).

Based on the high frequency of cupressoid pits (=podocarpoid type *sensu* Gothan, 1905: with elliptical aperture and border weakly marked or reduced) the cross-field, the new taxon fossil is identified as *Podocarpoxyton* (Philippe, 1995; Bamford and Philippe, 2001;

Greenwood, 2005; Gnaedinger, 2007; Philippe and Bamford, 2008; Gnaedinger et al., 2015; Franco and Brea, 2015).

Table 1, shows species of *Podocarpoxyton* with axial parenchyma from Gondwana landmasses for the Mesozoic and Cenozoic (Gnaedinger, 2007; Franco and Brea, 2015; Rai et al., 2016). From these species, those that have dactyroid type pits in the cross-field are *Podocarpoxyton parlatifolium*, *P. stokesii* and *Podocarpoxyton* sp. (*Terada et al., 2006*). *P. prumnopityoides* nov. sp. differs from *P. parlatifolium* Vozenin-Serra and Grant-Mackie (Lower Triassic from New Zealand) because the latter has uniseriate radial pitting and one to two pits per cross-field. Unlike *P. prumnopityoides* nov.sp., *P. stokesii* Thayne and Tidwell, from the Lower Cretaceous Cedar Mountain Fm of Utah and Colorado (Thayne and Tidwell, 1984) and from the Lower Cretaceous of Namaqualand/South Africa (Bamford and Corbett, 1995) has only uniseriate separate, rarely contiguous radial pitting, abundant axial parenchyma, one pit per cross-field, and uni-biseriate rays up to 48 cells in height. *P. prumnopityoides* nov. sp. is more closely comparable to the Chilean specimen of *Podocarpoxyton* sp. (*Terada et al., 2006*), but differs in the absence of the axial parenchyma.

7. Conclusions

The anatomical structure of the new species described here, *Podocarpoxyton prumnopityoides* indicates that it is closely related to *Podocarpoxyton*. However, it also shows affinities with the extant genus of *Prumnopitys*, particularly with *P. andina*.

The presence of the fossil wood *Podocarpoxyton prumnopityoides* sp. nov. in the Valanginian rocks of northwestern Patagonia indicates that the family was already established in the Southern Hemisphere during the Early Cretaceous. This supports the hypothesis by Biffin et al. (2012) that the origin for the genus was during the Early Cretaceous, and the divergence of the *Podocarpoid-Dacrydioid* clade from the *Prumnopityoid* clade could have occurred earlier.

The fluvial system facies described for the fossil bearing section of Mulichinco Fm is coherent with the environmental conditions attributed to *Podocarpoxyton* and related forms.

The stratigraphical association of dinosaur and plant fossil remains is unusual in Patagonian outcrops. Thus, although it is not possible to determine if there was a trophic relationship between the diplodocid sauropods and the podocarpaceans from the Mulichinco Fm, the associated biota that is being currently collected and under study (Coria et al., 2013) suggest the existence of a complex ecological scenario for the Valanginian of northern Patagonia.

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