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

Silvia Gnaedinger a, *, Rodolfo A. Coria b, Eva Koppelhus c, Silvio Casadío d, Maisa Tunik d, Philip Currie c

* CONICET-Centro de Ecología Aplicada del Litoral, Área de Paleontología (CECOAL- CCT-CONICET Nordeste-UNNE), Facultad de Ciencias Exactas y Naturales y Agrimensura, Universidad Nacional del Nordeste (FaCENA-UNNE), Ruta 5, Km 2.5, Casilla correo 291, 3400, Corrientes, Argentina
* CONICET-Subsecretaría de Cultura de Neuquén — Museo Carmen Funes, Av. Córdoba 55 (8318), Plaza Huincul, Neuquén, Argentina
b University of Alberta, CW405 Biological Sciences Building, Edmonton, Alberta, T6G 2E9, Canada
c CONICET-Instituto de Investigación en Paleobiología y Geología. Universidad Nacional de Río Negro, Av. Roca. 1242 (8332), General Roca, Río Negro, Argentina

corresponding author.

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A B S T R A C T

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 — Podocarpoxylon prumnopityoides — is proposed based on features that include the presence of abietinean wood type (tracheid radial pitting), plus podocarpoid (cressuproid type) and some dacyroid (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 “Podocarpoideae-Dacrydoid” 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, 1983; 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 “Podocarpoideae-Dacrydoid” 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.,

E-mail addresses: sgcnaed@hotmail.com (S. Gnaedinger), rcoria@unn.edu.ar (R.A. Coria), ebk@ualberta.ca (E. Koppelhus), scasadio@unn.edu.ar (S. Casadío), mtunik@unn.edu.ar (M. Tunik), pcurrie@ualberta.ca (P. Currie).

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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 Podocarpoxylon 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 Agathoxylon (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 Fuego, 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 Podocarpoxylon 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 — Podocarpoxylon prumnопityoides. 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 Huincul; 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; Deliаe et al., 1978; Volkheimer and Musacchio, 1981; Prámparo et al., 1995; Quattroccio 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, Lycophyta and Pteridophyta, and coenobia from Chlorophyta (Volkheimer, 1980; Ottone, 2009). Also, specimens of the fern Tempskiy 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. 2. Geological section showing the provenance of *Podocarpoxylon prumnopityoides* sp. nov. (MCF-PBP-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-finishing with tangential or trough cross-stratification; c) beds of massive or parallel-bedded sandstone, possibly merging into packstone and intraclasts, arranged in lenses with an erosional base; d) massive or laminated greenish to purplish pelites of massive or parallel-bedded sandstone, possibly merging into pelites, clayey sands and polymictic sabulites with tangential cross-stratification. 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 channelized 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 Pilmatué 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 Colorada 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 silified logs was collected in the Pilmatué locality of the Mulichinco Formation, Neuquén Province, Argentina (Figs. 1 and 2). Standard petrographic thin sections were prepared 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; Guggess, 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; Guggess, 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.** Pilmatü, 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 (dacrydioid 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.
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 types with elliptical aperture and border weakly marked or reduced (podocarpoid type sensu Gothan, 1905) and some taxodioid pits with circular aperture and border reduced (dacrydioid 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 podocarp type (sensu Gothan, 1905) and some dacrydioid 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 dacrydioid/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 (Philips, 1941; Krausel, 1949; Greguss, 1955, 1972; Bouraeu, 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, dacrydioid, piceoid) and simple pits (oapores, phyllocladoid and cipipore). Following the same criteria, the IAWA Committee established (Richter et al., 2004), as diagnostic characteristic, 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 Ramford (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 “dacrydioid” 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 (dacyrdoid type sensu Patel, 1967) pits (white arrow). M. Uniseriate rays (black-white arrow). Scale bars = 15 µm.
Table 1
Comparison between species of Podocarpaceae from Gondwana sharing the character: axial parenchyma. (1/2: rays uniseriate partially biseriate; in parenthesis – character with occasional condition).

<table>
<thead>
<tr>
<th>Species</th>
<th>Characters</th>
<th>Horizon/Country</th>
<th>Radial walls pits</th>
<th>Axial parenchyma</th>
<th>Cross-field</th>
<th>Rays Width/Height</th>
</tr>
</thead>
<tbody>
<tr>
<td>P. paralatifolium Voizenin-Serra and Grant-Mackie, 1996</td>
<td>Upper Triassic New Zealand</td>
<td>Uniseriate, contiguous</td>
<td>Scarce</td>
<td>1–2 (3): podocarpoid (eye-shaped or slit-like aperture), dacyroid and circopore</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>P. atuaensis Gnaedinger et al., 2015</td>
<td>Lower Jurassic Argentina</td>
<td>Uniseriate (biseriate); separate (contiguous), opposite (alternate)</td>
<td>Abundant pairs</td>
<td>1–2 (4): cupressoid (–podocarpoid)</td>
<td>1–12</td>
<td></td>
</tr>
<tr>
<td>P. austroamericanum Gnaedinger, 2007</td>
<td>Middle Jurassic Argentina</td>
<td>Uniseriate, (biseriate); separate-contiguous; opposite (alternate)</td>
<td>Scarce</td>
<td>1–4: cupressoid (–podocarpoid); some circopore</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>P. gangtensis Rai et al., 2016</td>
<td>Middle Jurassic India</td>
<td>Uniseriate (biseriate); separate-contiguous; alternate-opposite</td>
<td>Scarce</td>
<td>2–5: small to large; oval to circular, bordered</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>P. dunstani (Sahn) Kraussel (1949)</td>
<td>Jurassic. Australia</td>
<td>Uniseriate (biseriate), crassulae</td>
<td>Present</td>
<td>3–6 or more: simple</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>P. trinchopoliense (Varma) Bose and Maheshwari, 1974</td>
<td>Cretaceous India</td>
<td>Uniseriate; separate (contiguous)</td>
<td>Scarce</td>
<td>1–2: podocarpoid (fusiform obliquely placed pits)</td>
<td>2–6,10</td>
<td></td>
</tr>
<tr>
<td>P. prumnopityoides (This Work)</td>
<td>Lower Cretaceous Argentina</td>
<td>Uniseriate (biseriate); separate-contiguous, opposite</td>
<td>Scarce diffuse</td>
<td>1–2 (3–4): podocarpoid and some dacyroid</td>
<td>2–9</td>
<td></td>
</tr>
<tr>
<td>P. haburesulis Guleria and Shukla, 2008</td>
<td>Lower Cretaceous India</td>
<td>Uniseriate (biseriate); separate-opposite-subopposite.</td>
<td>Present</td>
<td>Not seen</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>P. cf. sahnii Ramanujam (In Bamford and Corbett, 1994)</td>
<td>South Africa</td>
<td>Uniseriate (biseriate); separate-contiguous, opposite. Bars of Sanio.</td>
<td>Present</td>
<td>1 (2): large, elliptic in shape with pointed ends (i.e. fusiform).</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>P. woburnense (Stopes) Seward (In Bamford and Corbett, 1994)</td>
<td>Lower Cretaceous South Africa</td>
<td>Uniseriate; separate-contiguous</td>
<td>Very rare</td>
<td>1: simple, oval-rounded</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>P. cf. woburnense (Stopes) Seward (In Bamford and Corbett, 1994)</td>
<td>Lower Cretaceous South Africa</td>
<td>Uniseriate (biseriate); separate-contiguous, opposite</td>
<td>Present</td>
<td>1–2: simple, rounded-oval</td>
<td>1–15,35</td>
<td></td>
</tr>
<tr>
<td>P. stokesii Thayn and Tidwell (In Bamford and Corbett, 1994)</td>
<td>Lower Cretaceous South Africa</td>
<td>Uniseriate; separate-contiguous</td>
<td>Present</td>
<td>1: rounded, elliptical aperture (Podocarpoid); circular aperture (dacyroid)</td>
<td>1–28,48</td>
<td></td>
</tr>
<tr>
<td>P. cf. stokesii Thayn and Tidwell (In Bamford and Corbett, 1994)</td>
<td>South Africa</td>
<td>Uniseriate (biseriate); separate-contiguous, opposite</td>
<td>Scarce 1–3: small</td>
<td>1 (1/2)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>P. cf. umzambense Schultz-Motel (In Bamford and Corbett, 1995)</td>
<td>Lower Cretaceous South Africa</td>
<td>Uniseriate (biseriate); separate-contiguous, opposite. Bars of Sanio.</td>
<td>Scarce</td>
<td>1: ovate rounded</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>P. umzambense Schultz-Motel, 1966</td>
<td>Upper Cretaceous South Africa</td>
<td>Uniseriate (biseriate); separate-opposite. Bars of Sanio.</td>
<td>Scarce</td>
<td>1–2: elliptical pits (podocarpoid)</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>P. garciae Del Fuego, 1998</td>
<td>Upper Cretaceous Argentina</td>
<td>Uniseriate; separate</td>
<td>Present</td>
<td>1–2: circular, not preserved aperture</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>P. garciae Del Fuego (in Varella et al., 2015)</td>
<td>Upper Cretaceous Argentina</td>
<td>Uniseriate (biseriate); separate-contiguous, opposite- alternate. Bars of Sanio</td>
<td>Scarce-diffuse</td>
<td>1–2: cupressoid</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>P. chapmana Poole and Cantrill, 2001</td>
<td>Upper Cretaceous Antarctica</td>
<td>Uni-biseriate (triseriate); contiguous-opposite (alternate)</td>
<td>Scarce to absent</td>
<td>1–4: circular to obliquely elliptical apertures</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>P. communis Poole and Cantrill, 2001</td>
<td>Lower and Upper Cretaceous Antarctica</td>
<td>Uniseriate (biseriate); contiguous-opposite (alternate); Bars of Sanio.</td>
<td>Abundant</td>
<td>1–3 (4): podocarpoid, circular-oval pits, large oval aperture</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>P. mazzoni (Petriella) Müller-Stoll and Schultz-Motel (Brea et al., 2011)</td>
<td>Paleocene Argentina</td>
<td>Uniseriate (biseriate); opposite</td>
<td>Scarce</td>
<td>1–2: cupressoid</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>P. palaeoschizopodioides Nishida, 1984</td>
<td>Eocene Chile</td>
<td>Uniseriate; spaced</td>
<td>Scarce</td>
<td>1 (2–3)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>P. palaeoschizopodioides Nishida, 1984</td>
<td>Eocene, Patagonia</td>
<td>Uniseriate (biseriate)</td>
<td>Abundant</td>
<td>1–2 elliptical or thick, lenticular pit apertures</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>P. speciosum (Ramanujan) Trivedi and Srivastava, 1989</td>
<td>Miocene-Pliocene India</td>
<td>Uni-biseriate; opposite-subopposite</td>
<td>Abundant</td>
<td>2–4: podocarpoid</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>P. mahabalei (Agashe) Trivedi and Srivastava, 1989</td>
<td>Miocene - Pliocene India</td>
<td>Uniseriate; separate-contiguous.</td>
<td>Abundant</td>
<td>1: podocarpoid</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>P. kutchensis Lakhanpal et al., 1975</td>
<td>Pliocene India</td>
<td>Uniseriate (biseriate); separate, opposite-subopposite</td>
<td>Present</td>
<td>1–2: small, circular, oval, bordered – podocarpoid to taxodioid</td>
<td>1–18,41</td>
<td></td>
</tr>
</tbody>
</table>
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 dacyroid; Prumnopitys generally has podocarpoid but rarely dacyroid pits; and both Dacrycarpus and Retrophyllum frequently have dacyroid, 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 (dacyroid) 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 (P. andina and P. ferrugineoides) 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 Podocarpus 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. ferrugineoides) 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; Patiel, 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- like structures are assigned to Podocarpaceae. They are mostly distinguished by the types of pits in the cross-fields: Circropaxonyl Kräusel is circropore; Microachryxylon Torres, Courtinat, Méon with one or two large pits, irregular in shape, which occupy the whole field; Dacrydioxylon Greguss has dacyroid pits; Phyllocladoxylon Gothan has the phyllocladoid type, and Podocarpyoxylon 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 fossil taxon is identified as Podocarpyoxylon (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 Podocarpyoxylon 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 dacyroid type pits in the cross-field are Podocarpyoxylon paralatifolium, P. stokesii and Podocarpoxylon sp (Terada et al., 2006). P. prumnopityoides nov. sp. differs from P. paralatifolium 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 Thayn and Tidwell, from the Lower Cretaceous Cedar Mountain Fm of Utah and Colorado (Thayn 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 Podocarpoxylon 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, Podocarpyoxylon prumnopityoides indicates that it is closely related to Podocarpyoxylon. However, it also shows affinities with the extant genus of Prumnopitys, particularly with P. andina.

The presence of the fossil wood Podocarpyoxylon prumnopityoides sp. nov. in the Valanginian rocks of northern 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 Podocarpoideae-Dacyroid 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 Podocarpyoxylon 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 diplocodoid 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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