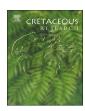
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First Lower Cretaceous record of Podocarpaceae wood associated with dinosaur remains from Patagonia, Neuquén Province, Argentina



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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 - Podocarpoxylon prumnopityoides - is proposed based on features that include the presence of abietinean wood type (tracheid radial pitting), plus podocarpoid (cupressoid type) and some dacrydioid (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-Dacrydioid" 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).

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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-Dacrydioid" 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 *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 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 Valaginian-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 familiy Podocarpaceae. The fossils represent a new species — *Podocarpoxylon 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 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; 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, Lycophyta 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

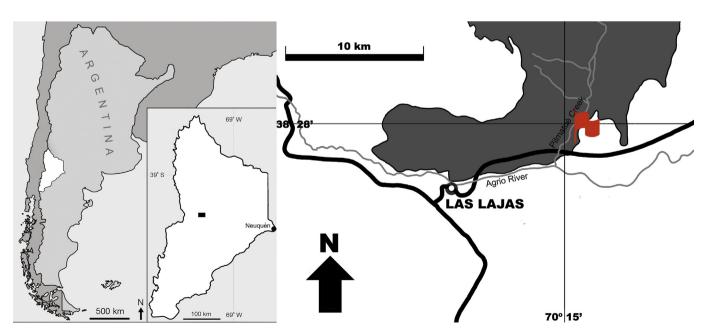


Fig. 1. Map showing the locality of Pilmatué. Red flag depicts location of the fossils. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

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