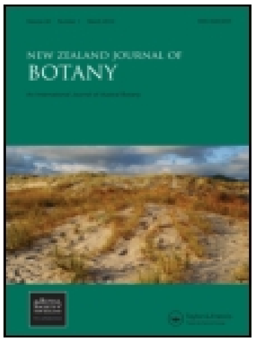

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RESEARCH ARTICLE

First extra-Patagonian record of Podocarpaceae fossil wood in the Upper Cenozoic (Ituzaingó Formation) of Argentina

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The main objective of the present paper is to describe a new genus and species of Podocarpaceae fossil wood from the Upper Cenozoic Ituzaingó Formation, Paraná Basin, Argentina, based on a detailed description of the secondary xylem. This specimen, *Prumnopityoxylon gnaedingerae* Franco & Brea gen. nov. & sp. nov., is the first fossil wood referable as coniferous from northeastern Argentina. This fossil resembles extant *Prumnopitys* Phil. (Podocarpaceae), sharing the following anatomical features: slightly distinct growth rings; the absence of axial parenchyma; uniseriate and homocellular rays; uniseriate or biseriate, opposite or sub-opposite, separate or contiguous tracheid pitting; and cupressoid or taxodioid cross-field pitting. The presence of this Podocarpaceae fossil from the Ituzaingó Formation indicates that the distribution of this family was more widespread and probably continuous in South America in the past. It also provides new evidence for the hypothesis of its wide distribution in northeastern Argentina during the Cenozoic.

Keywords: Argentina; Ituzaingó Formation; Podocarpaceae; *Prumnopitys* Phil.; Upper Cenozoic

Introduction

Gymnosperms are woody plants, either shrubs, trees or, rarely, vines (Taylor et al. 2009; Earle 2013). Living gymnosperms are distributed worldwide (excepting Antarctica), with a majority in temperate and subarctic regions, particularly the conifers (Earle 2013). Extant conifers are typically placed in seven families consisting of 60 genera and 650 species (Taylor et al. 2009). In the Southern Hemisphere today, conifers reach their greatest abundance in wet forests (Hill & Brodribb 1999). The concentration of conifers in wet forests left them vulnerable to the climate changes which occurred in the late Cenozoic, and decreases in diversity have occurred since the Paleogene in all regions for which fossil records are available.

In Argentina, the gymnosperms have an excellent fossil record in the western region and in Patagonia (Conwentz 1885; Gothan 1908; Barreda et al. 2007; Gnaedinger 2007; Herbst et al. 2007; Pujana 2008). However, in the north central region, the gymnosperm macro fossil record is very scarce and the presence of conifers was only inferred from palynological studies (Anzótegui 1975; Anzótegui & Garralla 1986).

This paper is part of a series of contributions that aim to study and identify fossil wood from the Upper Cenozoic deposit of the Ituzaingó Formation. Previous studies described fossil material assigned to *Astroniumxylon bonplandianum* Franco and *Astroniumxylon parabalansae* Franco & Brea of the Anacardiaceae, *Soroceaxylon entrerriensis* Franco of the Moraceae, *Microlobiusxylon paranaensis* Franco & Brea, *Menendoxylon vasallensis* Lutz, *Anadenantheroxylon villaurquicense* (Brea, Aceñolaza & Zucol) emend. Franco & Brea, *Prosopisinoxylon americanum* Franco and Brea and

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Gleditsioxylon paramorphoides Franco & Brea of the Fabaceae, *Curtiembreoxylon poledrii* Franco and *Laurinoxylon artabeae* (Brea) Dupéron-Laudoueneix & Dupéron of the Lauraceae, *Palmoxylon yuqueriense* Lutz and *Palmoxylon* sp. of the Arecaceae and *Guadua zuloagae* Brea & Zucol and *Guadua morronei* Brea, Zucol & Franco of the Bambusoideae (Brea & Zucol 2007; Franco 2009, 2010, 2012, 2014; Franco & Brea 2010, 2013; Brea et al. 2013).

In this study, a new gymnosperm genus and species is erected. This taxon confirms, for the first time, the presence of coniferous fossil wood in the Upper Cenozoic of northeastern Argentina.

Geographical and geological settings

The Ituzaingó Formation (De Alba 1953) is an important fluvial deposit of the Paleoparaná River, and its outcrops are widely distributed in the western riverside cliff of the Paraná River, from the north of Corrientes Province (c. 27°S, 56°W) to the south to near Paraná City in Entre Ríos Province (c. 31°S, 60°W), Argentina (Herbst 1971, 2000; Iriondo 1980; Anis et al. 2005; Brea & Zucol 2011). This unit is mainly composed of consolidated and poorly consolidated quartz sandstones. The sands are occasionally whitish, yellowish and brown-reddish. Dark-grey and greenish clay lens intercalations are common among the sands (Aceñolaza & Sayago 1980; Herbst & Santa Cruz 1985; Iriondo et al. 1998; Herbst 2000; Franco 2011). The most frequent sedimentary structures are tangential cross-bedding, troughs and planar bedding. Low-angle ripple cross-laminations of fluvial origin are also recognised (Anis et al. 2005).

The age of the Ituzaingó Formation has no consensus, mainly due to the scarcity of fossils and the inability to use current numerical methods of dating because of the successive re-transport of its sediments (Franco et al. 2013). For this reason, its estimated age has fluctuated in the literature between the Miocene and the Quaternary (Frenguelli 1920; Herbst 1971; Bidegain 1993; Iriondo 1994; Torra 2001; Brunetto et al. 2013).

The palaeobotanical records of the Ituzaingó Formation are based on studies of palynomorphs (Anzótegui 1975; Caccavari & Anzótegui 1987; Garralla 1987; Anzótegui & Acevedo 1995), fossil leaves and cuticles (Anzótegui 1980), fossil woods, palm trunks and grass culms (Lutz 1979, 1991; Brea & Zucol 2007; Franco 2009, 2010, 2011, 2012, 2014; Franco & Brea 2010, 2013; Brea et al. 2013; Franco et al. 2013), found in various fossiliferous localities in the Entre Ríos and the Corrientes Provinces, Argentina.

All these data suggest that during the deposition of the Ituzaingó Formation, elements linked with the Gran Chaco Region, riparian forests and components of Seasonally Dry Tropical Forest (SDTF) were well represented in the study area (Franco 2011 and references therein). The Ituzaingó Formation responds to subtropical to tropical dry climate with some species adapted to wet environments (Franco 2011).

Material and methods

The material was collected in the El Brete fossiliferous locality of the Ituzaingó Formation, located in Paraná City, Entre Ríos Province, Argentina (c. 31°42′S; 60°27′W; Fig. 1). The specimen was preserved by siliceous permineralization, and thin-sections (transversal, radial longitudinal and tangential longitudinal) were prepared using standard petrographic techniques.

The anatomical terms used in this paper follow the recommendations of the IAWA List of Microscopic Features for Softwood Identifications (IAWA Committee 2004). The fossil material was identified using classical descriptions of extant and fossil plants (Phillips 1941; Greguss 1955; Patel 1967; García Esteban et al. 2002, 2004; Greenwood 2005; Gnaedinger 2007; Philippe & Bamford 2008; Tortorelli 2009; Vásquez Correa 2010; Vásquez Correa et al. 2010). The gymnosperm database electronic page for descriptions, distributions and bibliography of extant species was consulted (Earle 2013).

The quantitative values in the anatomical description are averages of 25 measurements. In all cases, the average is cited first, followed by the minimum and maximum values, which are given in parentheses.

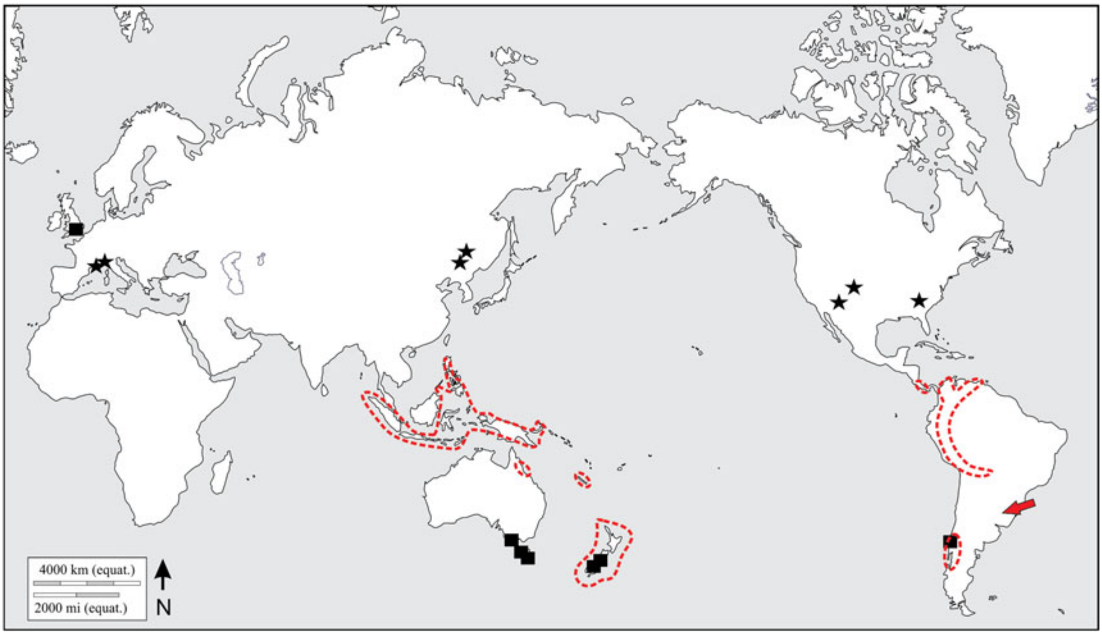

Figure 1 Map showing the distribution of the genus *Prumnopitys* Philippi (enclosed by dashed line), El Brete fossiliferous locality (arrow), fossils of *Prumnopitys* (■) and putative *Prumnopitys*-like species (★). Modified from de Laubenfels (1988) and Greenwood et al. (2013).

The specimen was studied with a Nikon Eclipse E200 light microscope, and photomicrographs were taken with a Nikon Coolpix S4 digital camera. The material was prepared for scanning electron microscopy (SEM) by cutting a 1 cm^3 block of wood that was mounted on SEM stubs without coating and then observed in a low vacuum using a SEM LEO 1450VP at the Universidad Nacional de San Luis, San Luis, Argentina.

Growth rings of the fossil wood were analysed from polished blocks and measured to the nearest 0.01 mm Essex using digital callipers. The growth ring parameters measured were: number of rings, mean ring width, the width of the narrowest ring and widest ring. The age of the fossil trees was estimated using the relationship between the stump radius and growth-ring widths (Frangi 1976; Pole 1999).

The fossil specimen is deposited in the Museo de Ciencias Naturales y Antropológicas ‘Profesor Antonio Serrano’, Paraná, Entre Ríos Province, Argentina, labeled as MASPALEOBOT380, and the slides are deposited at the Laboratorio de Paleobotánica, CICYTTP-CONICET, Entre Ríos Province, Argentina, labeled as CIDPALBO-MIC 1044.

Systematic paleobotany

Subclass Pinidae Cronquist, Takht. & Zimm.
Order Araucariales Gorozh. Family Podocarpaceae Endl.
Genus Prumnopityoxylon Franco & Brea gen. nov.
(Figs. 2–4)

Derivation of name

The generic name denotes the resemblance of the wood to extant *Prumnopitys* Phil.

Type species

Prumnopityoxylon gnaedingerae Franco & Brea

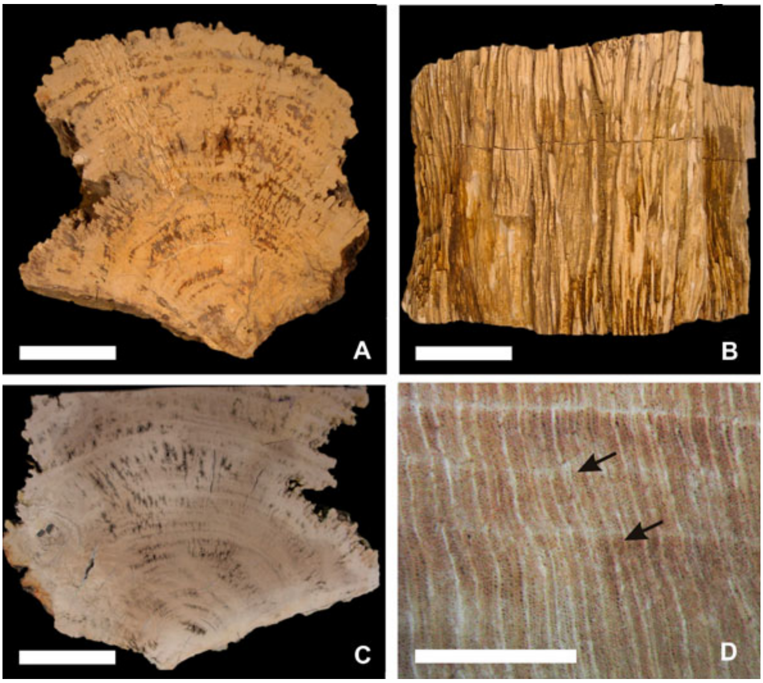

Figure 2 *Prumnopityoxylon gnaedingerae* Franco & Brea sp. **A,** Cross section of the fossil wood; **B,** longitudinal section of the fossil wood; **C,** polished cross section view with growth rings slightly demarcated; **D,** detail of the cross section of the fossil wood to show growth rings (arrows). Scale bars: A–C = 40 mm; D = 2 mm.

Diagnosis

Coniferous wood with slightly distinct or indistinct growth rings; absence of axial parenchyma; uniseriate and homocelullar rays; uniseriate or biseriate, opposite or sub-opposite, separate or contiguous tracheid pitting; taxodioid or cupressoid cross-field pitting, with 1–5 bordered pits per field.

Prumnopityoxylon gnaedingerae Franco & Brea sp. nov.

(Figs. 2–4)

Derivation of name

The specific epithet is dedicated to Dr Silvia C. Gnaedinger for her important studies on gymnosperm wood fossils of Argentina.

Holotype

MASPALEOBOT380, CIDPALBO-MIC 1044.

Type locality and horizon

El Brete, Paraná, Entre Ríos, Argentina. Ituzaingó Formation (Upper Cenozoic).

Diagnosis

As for the genus.

Description

The fossil specimen consists of a 9 cm long and 12.5 cm wide fragment and is in a very good state of preservation (Fig. 2A–C). In cross section, the growth rings are slightly demarcated and the transition from earlywood to latewood is gradual (Fig. 2C–D). Five to two rows of cells comprise the latewood. The earlywood is made up of 16 to 50 rows of tracheids. The specimen has 29 growth rings, and their mean width is 2.08 mm. The width of the narrowest ring is 0.69 mm, and that of the widest is 9.57 mm.

The age of the trees was estimated using the radius of the stump and the average width of

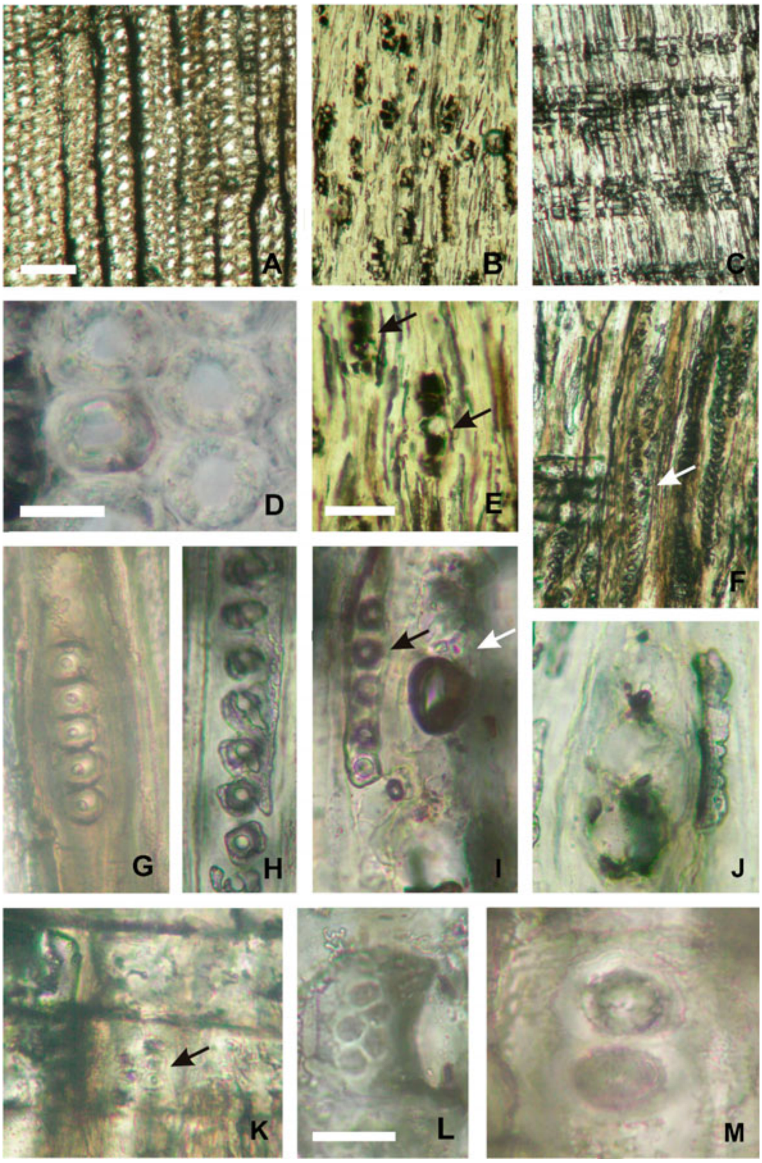

Figure 3 *Prumnopityoxylon gnaedingerae* Franco & Brea sp. **A,** general view in cross section showing the tracheids; **B,** general view in longitudinal tangential section showing the height and distribution of uniseriate rays; **C,** general view in longitudinal radial section showing homocellular rays; **D,** detail of round to slightly polygonal tracheids; **E,** uniseriate rays (arrows); **F,** biseriate tracheid pitting in longitudinal radial section (arrow); **G,** detail of contiguous tracheid pitting in longitudinal radial section; **H,** detail of separate tracheid pitting in longitudinal radial section; **I,** detail of tracheid pitting (black arrow) next to a ray (white arrow) in longitudinal tangential section; **J,** uniseriate ray; **K,** cross-field (arrow); **L,** detail of a cross-field with five bordered pits; **M,** detail of a cross-field with two bordered pits. Scale bars: A–C = 200 µm; D = 30 µm; E–G = 100 µm; H–K = 30 µm; L–M = 10 µm.

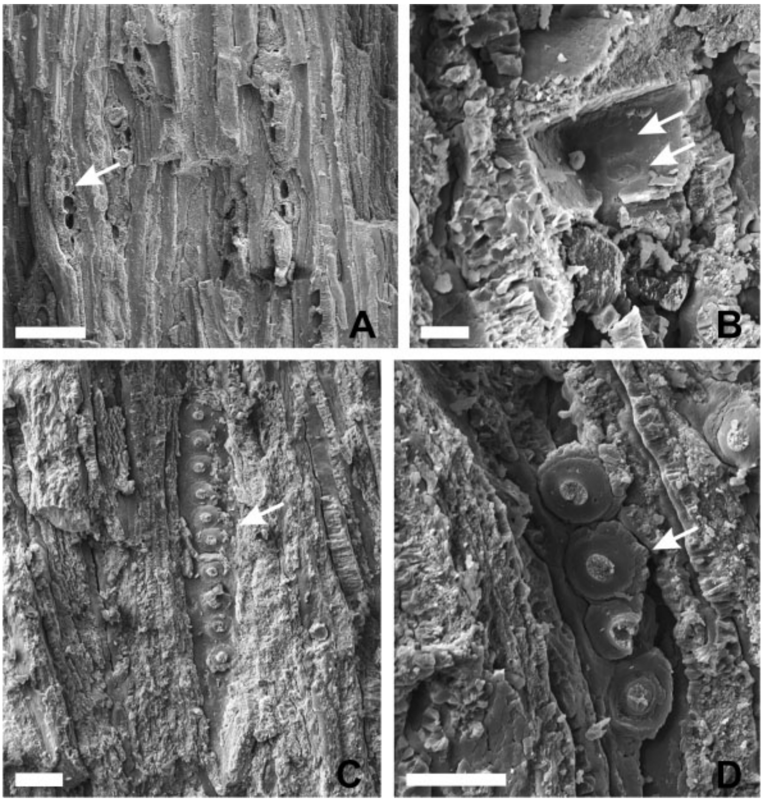

Figure 4 *Prumnopityoxylon gnaedingerae* Franco & Brea sp. All SEM. **A,** general view in longitudinal tangential section showing uniseriate rays; **B,** detail of a cross-field with two bordered pits; **C,** separate tracheid pitting; **D,** detail of contiguous tracheid pitting. Scale bars: A = 100 µm ; B = 10 µm ; C = 30 µm ; D = 20 µm.

growth rings (Frangi 1976; Pole 1999). The ring width indicates an average annual growth rate in the order of 2.08 mm and the radius of the stump is 121 mm. This implies that the tree may have been a minimum of 58 years old. The tracheids are round to slightly polygonal (square) (Fig. 3A, D). The mean tangential diameter of the tracheids is 54 (35–65) µm; the mean radial diameter is 50 (35–75) µm, and the wall thickness is 12 (8–15) µm in earlywood. Latewood tracheids have a mean tangential diameter of 46 (35–60) µm, a mean radial diameter of 30 (20–40) µm and a wall thickness of 10 (8–13) µm. They are thick-walled (Fig. 3D). No intercellular spaces between tracheids were observed (Fig. 3D). The rays are separated from each other by one to five rows of tracheids, with an average of three rows (Fig. 3A). Dark contents are observed inside the ray cells, probably attributable to resins. Axial parenchyma cells are not observed (Fig. 3A).

In the radial longitudinal section, the tracheid pittings are frequently uniseriate and rarely biseriate. The bordered pits are circular, opposite or sub-opposite, with a separate or contiguous arrangement (Figs 3F–H, 4C–D). Pits are 15 (13–17) µm in radial or horizontal diameter and 12 (10–14) µm in tangential or vertical diameter. Pits pores are circular in outline and have a diameter of 6 (3–8) µm. The rays are homocellular, without tracheids, comprised solely of ray parenchyma, composed of procumbent cells with horizontal and transverse smooth walls (Fig. 3C, K). The ray cells have a radial diameter of 142 (85–190) µm, and vertical diameter of 31 (25–45). The cross-fields are of the cupressoid and taxodioid type, with one to five bordered pits per field, separated from each other or not, presenting a rounded shape with a diameter of 6 (3–9) µm (Figs 3L–M, 4B).

In the tangential longitudinal section, the radial system is homogeneous and consists of exclusively uniseriate and homocellular rays (Figs 3B, E, J, 4A). The rays have a mean height of 127 (45–250) µm or 4 (2–8) cells and a mean width of 33 (20–50) µm. The mean number of rays per linear millimeter is 5 (4–7). In this section, it is possible to observe pits in tracheids with a diameter of 11 (9–12) µm (Fig. 3I).

Discussion and conclusions

Comparison with extant species

The absence of vessels and the predominance of simple tracheids with circular pits indicate that the fossil is a gymnosperm. Among the conifers, the material has greatest affinity with members of the Podocarpaceae family. The fossil shares the following features with Podocarpaceae: uniseriate and homocellular rays with thin smooth walls that are five to six cells long, but occasionally longer; tangential walls of tracheids with bordered pits and radial walls of tracheids with simple pits, uniseriate and biseriate, opposite pits; helical thickenings absent; resin canals absent, cupressoid cross-field pitting with a single pit and taxodioid cross-field pitting with several minute pits, and axial parenchyma sometimes absent (Phillips 1941; Greguss 1955; IAWA Committee 2004).

The absence of axial parenchyma is important as an initial element of differentiation of the large groups of conifers of the Southern Hemisphere and some genera of the Northern Hemisphere (*Juniperus* L., *Cupressus* L., *Tetraclinis* Mast.) from the rest of the conifers (García Esteban et al. 2002, 2004). Podocarpaceae species that exhibit this characteristic are: *Dacrydium elatum* (Roxb.) Wall. ex Hook., *Lepidothamnus intermedius* (Kirk) Quinn, *Manoao colensoi* (Hook.) Molloy, *Microcachrys tetragona* (Hook.) Hook.f., *Phyllocladus aspleniifolius* (Labill.) Hook.f., *Phyllocladus trichomanoides* D.Don, *Podocarpus brasiliensis* de Laub., *Podocarpus elongatus* (Aiton) L'Hér. ex Pers., *Prumnopitys harmsiana* (Pilg.) de Laub., *Prumnopitys taxifolia* (Sol. ex D.Don) de Laub., *Prumnopitys andina* (Poepp. ex Endl.) de Laub. and *Sciadopitys verticillata* (Thunb.) Siebold & Zucc. (Phillips 1941; Greguss 1955; Acevero Mallque & Kikata 1994; De Paula et al. 2000; García Esteban et al. 2002; Vásquez Correa 2010; Vásquez Correa et al. 2010). The comparison between these Podocarpaceae species and the fossil wood studied here is shown in Table 1.

Dacrydium Sol. ex Lamb., emend. de Laub. and *Prumnopitys* Phil. are two of the most closely resembling genera. Important diagnostic features of *Dacrydium* are: tracheids square to rounded, axial parenchyma generally present, growth rings distinct to indistinct, ray height of 1–16 cells and uniseriate rays with bordered pits on tangential tracheid walls rarely present, cross-fields with one to two bordered pits per field, and uniseriate or biseriate tracheid pitting (Phillips 1941; Greguss 1955; Greenwood 2005). *Dacrydium elatum* (Roxb.) Wall. ex Hook., is the only species of the genus in which the axial parenchyma is absent, but differs from the fossil studied here because it only has up to two bordered pits per cross-field (Table 1).

The anatomical features of the fossil material more closely resemble the genus *Prumnopitys*. A clear distinction between *Podocarpus* and *Prumnopitys* is not easy based only on wood. Nevertheless, the genus *Prumnopitys* shares the following characters with the fossil wood: slightly distinct growth rings; absence of axial parenchyma; uniseriate and homocellular rays, ray height varying from 15 to 450 µm; tracheids with a tangential diameter of 18 to 71 µm; uniseriate or biseriate tracheid pitting; cupressoid and taxodioid type cross field-pitting, with 1–5 bordered pits per field (Phillips 1941; Greguss 1955; Acevero Mallque & Kikata 1994; García Esteban et al. 2002; Vásquez Correa 2010; Vásquez Correa et al. 2010). The fossil wood described in this paper differs from *Podocarpus* in the presence of cupressoid and taxodioid type cross-field pitting, with one to five bordered pits per field.

Table 1 Comparative table among Podocarpaceae species without axial parenchyma and the fossil wood studied.

				Tracheids						Rays					Cross-fields		
			Growth ring	Section		Tangential wall		Radial wall									
Taxa	Geographical distribution	Axial Parenchyma	Distinct	Round	Square	Pit.	Diam. (µm)	Rows	Diam. (µm)	Type	Cell height	Cell width.	Height (µm)	Width (µm)	Type	N° of pits	Pits diameter (µm)
Prumnopityoxylon gnaedingerae Franco & Brea nov. gen. & nov. sp.			X	X	X	X	11 (9–12)	1–2	15 (13–17)	Ho	4 (2–8)	1	127 (45–250)	33 (20–50)	C–T	1–6	6 (3–9) µm
Dacrydium elatum (Roxb.) Wall. ex Hook.	China		_		X	X	10–12	1–2	16–17	Ho	1–10 (17)	1			C	1–2	13
Lepidothamnus intermedius (Kirk) Quinn	New Zealand	X													T		
Manoao colensoi (Hook.) Molloy	New Zealand				X	X	7–8	1	11–14		1–12 (18)	1			T	1–2	16–24
Microcachrys tetragona (Hook.) Hook.f.	Australia	X	X		X	X	7–8	1–2	12–14	Ho	1–8 (12)	1–2			T	1–2	10–16
Phyllocladus aspleniifolius (Labill.) Hook.f.	New Zealand	X														1–3	
Phyllocladus trichomanoides D.Don	New Zealand		X					1	10–18		1–10 (22)	1				1–2	12–16
Podocarpus brasiliensis de Laub.	Brazil, Venezuela		X					1					97–127	11–18			
Podocarpus elongatus (Aiton) L'Hér. ex Pers.	South Africa		_	X	X	X	11–13	1	12–13	Ho	1–6 (7)	1			C	1–2	6–8
Prumnopitys taxifolia (Sol. ex D.Don) de Laub.	New Zealand	X	X					1				1–2			C–T	1–6	
Prumnopitys andina (Poepp. ex Endl.) de Laub.	Argentina and Chile	X	_		X	X	7–8	1–2	13–16	Ho	1–6 (10)	1			C	1–2	7–11
Prumnopitys harmsiana (Pilg.) de Laub.	From Venezuela to Bolivia		X		X	X	12 (8–13)	1	14 (12–15)	Ho	7 (1–28)	1–2	124 (21–462)		C–T	1–2	13 (11–15)
Sciadopitys verticillata (Thunb.) Siebold & Zucc.	Japan		X			X	9–13	1–2	13–15	He	1–7 (10)	1–2				1–2	15–22

References: Phillips (1941); Greguss (1955); Acevero Mallque & Kikata (1994); de Paula et al. (2000), García Esteban et al. (2002); Vásquez Correa (2010); Vásquez Correa et al. (2010).

Abbreviations: –, uncommon; C, cupressoid; Diam., diameter of the pits in tracheids; He, heterocellular; Ho, homocellular; T, taxoid; X, present.

Comparison with fossil species

The material studied here is the first fossil wood with affinity to *Prumnopitys*. Although this extant genus was described in 1861, it was not separated or distinguished from the genus *Podocarpus* between 1861 and 1978, and today, many authors still do not differentiate between them (Mill & Quinn 2001). For this reason, *Prumnopityoxylon gnaedingerae* Franco & Brea is here compared with fossil species of *Podocarpoxylon* Gothan and *Podocarpus* L'Hér. ex Pers taxa described for the Cenozoic of Gondwana (Table 2).

The species of *Podocarpoxylon* without axial parenchyma are: *P. aparenchymatosum* Gothan, *P. dusenii* Kräusel, *P. sahnii* Ramanujam, *P. tiruvakkaraianum* Ramanujam and *P. latrobensis* Greenwood.

Podocarpoxylon aparenchymatosum has one to three seriate pitting in tracheid radial walls, one to two bordered pits per cross-field and higher rays (1–20 cells in height) than those of *P. gnaedingerae* (Table 2; Gothan 1908; Pujana et al. 2014). *Prumnopityoxylon gnaedingerae* differs from *P. dusenii* because the latter has resin plates, one to two bordered pits per cross-field and uni-biseriate rays up to 40 cells in height (Table 2; Kräusel 1924). *Podocarpoxylon sahnii* has only uniseriate tracheid pitting in radial walls, bi and triseriate rays and one to two bordered pits per cross-field, but these were not observed in the Argentinean Podocarpaceae wood (Table 2; Ramanujam 1953; Trivedi & Srivastava 1989). Characters such as resin plates, rays up to 50 cells high and only one pit per cross-field are present in *P. tiruvakkaraianum*, but they differ from those of the Ituzaingó Formation fossil wood which has rays up to eight cells high, lacks resin plates and cupressoid and taxodioid type cross-field pitting, with one to five bordered pits per field (Table 2; Ramanujam 1953; Trivedi & Srivastava 1989). *Podocarpoxylon latrobensis* is the most similar fossil species, but differs from the fossil wood described in this contribution in the number of bordered pits per cross-field (Table 2; Greenwood 2005).

Phytogeography and fossil record of the Podocarpaceae family

The Podocarpaceae are the second largest extant conifer family in terms of number of genera and they exhibit the greatest amount of morphological diversity. Despite this, their ecological and environmental range is not as large as that of either the Araucariaceae or Cupressaceae. They are almost entirely restricted to rainforest or wet montane environments (Hill & Brodribb 1999; Farjon 2008).

The present distribution of the Podocarpaceae, a characteristic family of the Antarctic flora, is in the Southern Hemisphere, Central America, and Mexico. Despite this, megafossil evidence, together with scattered Northern Hemisphere reports of pollen, suggest that some of the members of this group may have been more cosmopolitan in their distribution (Taylor et al. 2009).

Fossils attributed to the Podocarpaceae are known from the Lower Permian and extend throughout the Mesozoic and Cenozoic (Hill & Brodribb 1999; Crisafulli & Herbst 2008; Taylor et al. 2009). However, there has been an obvious decline in diversity since peaking in the Early Oligocene (Hill & Brodribb 1999; Taylor et al. 2009). In the Cenozoic, the Podocarpaceae macrofossil record is extensive in Australia, where most of the extant genera have been found (Hill & Brodribb 1999). However, in South America, it is still very scarce.

In Argentina, the oldest Podocarpaceae fossil is *Podocarpoxylon indicum* (Bhardwaj) Bose & Maheshwari from the Solca Formation (Lower Permian), La Rioja Province, Argentina (Crisafulli & Herbst 2008). However, the most abundant and diverse records of this family are from the Cretaceous of Patagonia (Del Fueyo et al. 2007).

The genus Prumnopitys

There are ten living species of *Prumnopitys*, among which nine are currently placed in section *Prumnopitys*, and a single species, *Prumnopitys amara*, is placed in section *Sundacarpus* (de Laubenfels 1978; Knopf et al. 2012; Greenwood et al. 2013; Earle 2013). The species in section *Prumnopitys* are found as follows: in South and Central America, *P. andina* (Poepp. ex Endl.) de

Table 2 Comparative table among some selected *Podocarpoxylon* Gothan and *Podocarpus* L'Hér. ex Pers taxa described for the Cenozoic of Gondwana.

							Rays	
Fossil species	Age	Locality	Pitting in radial walls	Axial parenchyma	Resin plates	Cross-fields	Width	Cells height
Prumnopityoxylon gnaedingerae Franco & Brea nov. gen & nov. sp.	Pliocene–Pleistocene	El Brete, Entre Ríos, Argentina	1–2 seriate, opposite or sub–opposite, separate or contiguous	Absent	Absent	1–6	Uniseriate	2–8
Podocarpoxylon aparenchymatosum Gothan (1908)	Tertiary	Antarctica.	1–3 seriate	Absent	Absent	1–2	Uniseriate	1–20
P. dusenii Kräusel (1924)	Tertiary	Río Negro, Argentina	1–2 seriate; separate	Absent	Present	1–2	Uni-biseriate	1–20 (40)
P. mazzonii (Petriella) Müller-Stoll & Schultze-Motel (1990)	Paleoceno	Chubut, Argentina	1 (2) seriate, separate, opposite	Rare	?	1–2	Uni-biseriate, rarely triseriate	1–38
P. speciosum (Ramanujam) Trivedi & Srivastava (1989)	Miocene–Pliocene	Tamil Nadu, India	1–2 seriate, opposite or sub-opposite	Abundant	Present	2–4	Uni-biseriate	1–18
P. mahabalei (Agashe) Trivedi & Srivastava (1989)	Miocene–Pliocene	Tamil Nadu, India	1 seriate; separate or contiguous	Present	Present	1	Uniseriate	1–30
P. schmidianum Sahni (1931)	Miocene–Pliocene	Tamil Nadu, India	1–2 seriate, opposite	Scanty	Absent	1–2	Uni-biseriate	2–100
P. sahnii (Ramanujam) Trivedi & Srivastava (1989)	Miocene–Pliocene	Tamil Nadu, India	1 seriate; separate or contiguous; opposite	Absent	Absent	1(2)	Uni-biseriate (triseriate)	1–20
P. tiruvakkaraianum (Ramanujam) Trivedi & Srivastava (1989)	Miocene–Pliocene	Tamil Nadu, India	1–2 seriate, opposite	Absent	Present	1	Uniseriate	3–50
P. latrobensis Greenwood (2005)	Miocene	Victoria, Australia	1 (2)	Unusual or absent	Absent	1 (2)	Uniseriate	2–18
Podocarpus sp. Wijninga (1996)	Pliocene	Bogota, Colombia	1 seriate	Present	Absent	1	Uniseriate	1–7

Modified from Gnaedinger (2007). References: Gothan (1908); Kräusel (1924); Sahni (1931); Ramanujam (1953, 1955); Agashe (1969); Petriella (1972); Trivedi & Srivastava (1989); Wijninga (1996); Greenwood (2005); Gnaedinger (2007), Brea et al. (2011); Pujana et al. (2014).

Laub, *P. exigua* de Laub., *P. harmsiana* (Pilg.) de Laub., *P. montana* (Humb. & Bonpl. ex Willd.) de Laub. and *P. standleyi* (J. Buchholz & N.E. Gray) de Laub.; New Caledonia, *P. ferruginoides* (Compton) de Laub.; New Zealand, *P. ferruginea* (G.Benn. ex D. Don) de Laub., *P. taxifolia* (Sol. ex D. Don) de Laub. *Prumnopytis ladei* (F. M. Bailey) de Laub. grows in north-eastern Queensland, but extends to New Guinea, parts of Indonesia and the southern Philippines (Fig. 1; de Laubenfels 1978; Earle 2013; Greenwood et al. 2013). The monospecific section *Sundacarpus* extends across Malesia from Sumatra and the Philippines to New Ireland and northern Queensland (Fig. 1; de Laubenfels 1978). This list of species extends the genus *Prumnopitys* from the Asian tropics through New Zealand to America, where it is found from Costa Rica and Venezuela to southern Chile (de Laubenfels 1978).

Prumnopitys fossils are very little known and *Prumnopityoxylon gnaedingerae* Franco & Brea is the first fossil wood that resembles *Prumnopitys*. In Australia, several fossil *Prumnopitys* leaves have been described: *P. tasmanica* (Townrow) Greenw. ex Mill & Hill (2004) from the Eocene of Tasmania and Victoria (Townrow 1965; Greenwood 1987), *P. portensis* Pole and *P.* sp. "cf. *P. montana*" of Pole from the Eocene of Tasmania (Pole 1992); *P. opihiensis* Pole, *P. limaniae* Pole, *P.* sp. "Mt Somers" and *P. taxifolia* from the Paleocene and Miocene of New Zealand (Pole 1997a,b, 1998) and *P. anglica* Greenwood, Hill & Conran from the Eocene of England (Fig. 1; Greenwood et al. 2013). *Prumnopityoxylon gnaedingerae* Franco & Brea is the first fossil resembles this genus in South America. Its presence in the Upper Cenozoic of the Paraná Basin, Argentina shows that the Podocarpaceae were more widespread.

Recent molecular phylogenetic analysis for Podocarpaceae suggests that the major clades within the family differentiated during the Cretaceous and Palaeogene (Greenwood et al. 2013). 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, giving a probable late Cretaceous origin for the genus (Greenwood et al. 2013).

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