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First record of fossil woods from the Mariño Formation (Miocene), Mendoza, Argentina and their palaeobiogeographical implications

MARÍA JIMENA FRANCO, MARIANA BREA and ANA MARÍA ZAVATTIERI

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The first Miocene records of silicified fossil woods from the Mariño Formation, Potrerillos area, Andes Precordillera, Mendoza province, Argentina are described. *Rhaphithamnoxylon artabeae* gen. et sp. nov. is described as the first fossil wood referable to Verbenaceae from Argentina. This new fossil species is related to extant *Rhaphithamnus* Miers, sharing the following anatomical features: diffuse porosity, distinct growth ring boundaries, numerous small to very small vessels, commonly in radial multiples, 1–3 seriate rays, and heterocellular and scarce paratracheal axial parenchyma. *Rhaphithamnus* contains only two extant species: *R. spinosus* (A.L. Juss.) Moldenke, which occurs in the Valdivian forests of Chile and Argentina, and *R. venustus* (Philippi) Robinson, which is endemic to the Juan Fernández Islands. Representatives of Verbenaceae are distributed predominantly in the Americas from Patagonia (Argentina) to Canada, and they are inferred to have originated in South America. The fossil wood described herein provides new age and geographical constraints on the raphithanoid lineage within Verbenaceae. Other fossil woods recorded from the Mariño level are retained under open nomenclature, as they possess a combination of mostly solitary broad vessels, and smaller vessels in radial multiples or in clusters, with numerous, vasicentric to confluent axial parenchyma, and heterocellular, high rays. Thus, they have features akin to dicotyledonous lianas or vine-like or small shrub species.

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Key words: Fossil woods, Mariño Formation, Miocene, Verbenaceae, Lianas or small shrubs, Argentina

THE NEOGENE MARIÑO FORMATION comprises a red-bed succession of mixed fluvial and eolian origin (Figs 1–3). Sedimentological evidence suggests that this unit was deposited in a low-gradient setting where arid or semi-arid conditions prevailed. The occurrence of strongly oxidized floodplain deposits and sandy fluvial sequences indicates deposition under ephemeral flow regimes along with the development of a thick succession of eolian deposits. These Neogene strata have yielded mammalian assemblages (Simpson *et al.* 1962, Pascual & Odreman Rivas 1971, 1973, Cerdeño *et al.* 2006, Cerdeño 2007) and have been dated radiometrically to *ca* 15.7–12.2 Ma age range (Marshall *et al.* 1986, Yrigoyen 1993, 1994).

Here we describe the first Miocene plant fossils from the middle member of the Mariño Formation at the south-southwestern extent of the Precordillera in Mendoza province. The fossils were recovered from the northern margin of the now-flooded Potrerillos Dam reservoir. Remarkably, these are the first plant remains

recorded from the Neogene Mariño Formation in Mendoza province.

One of the specimens collected from the Mariño Formation is assigned to Verbenaceae, which is mainly a New World family distributed in both temperate and tropical regions of America. Few genera are confined to the southern part of South America (Atkins 2004). This material is the first Verbenaceae fossil wood found in South America and the first record of the family in Argentina.

Geological setting

Thick Cenozoic non-marine red-beds are exposed at the south and southwestern extent of the Andes Precordillera at *ca* 33°S. The stratigraphy, sedimentology and vertebrate palaeontology of the synorogenic Neogene strata in northern Mendoza province have been investigated by several authors (Rolleri & Criado Roque 1970, Pascual & Odreman Rivas 1971, Rolleri & Fernández Garrasino 1979, Pascual & Bondesio 1981, Kokogían & Mancilla 1989, Legarreta *et al.* 1993, Yrigoyen 1993, 1994, Yrigoyen *et al.* 1995, 2000, 2002, Yrigoyen 1997).



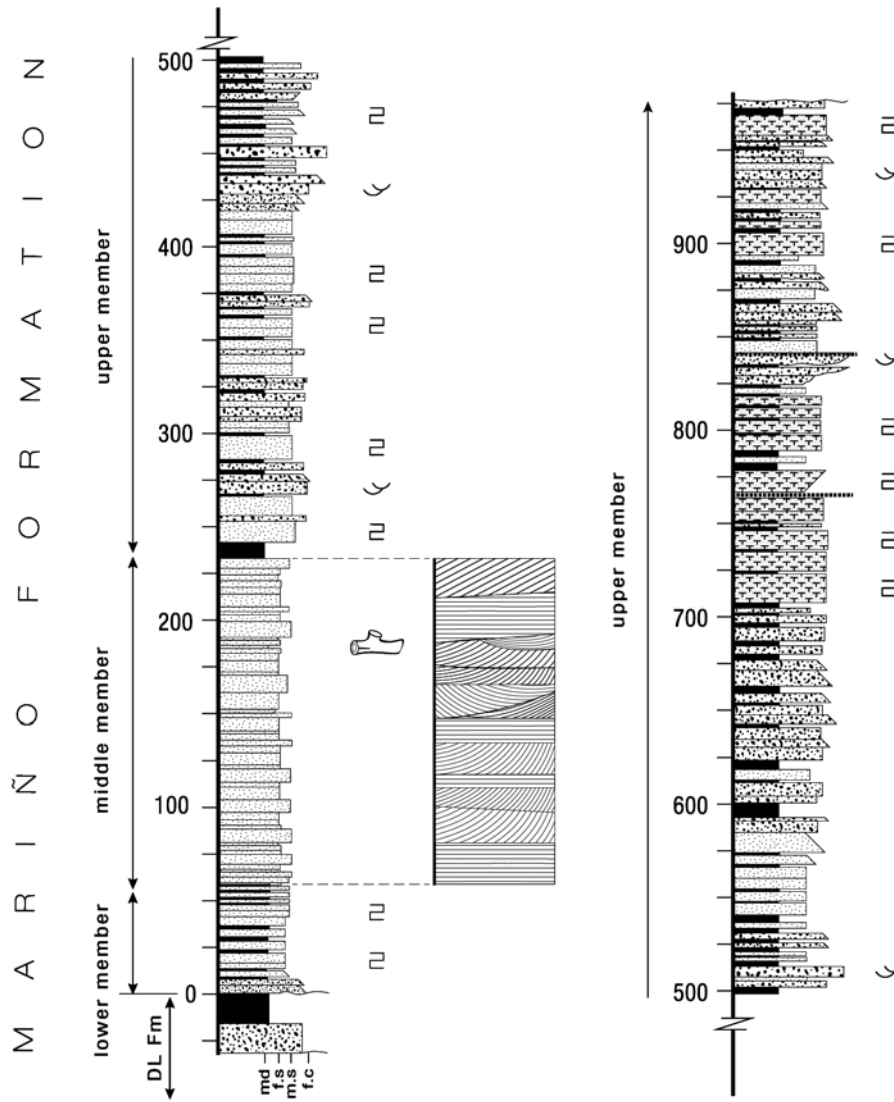
Fig. 1. Map of the Potrerillos Valley showing the fossil locality, Precordillera of Mendoza province, Argentina.

The stratigraphic nomenclature used in this contribution derives from Yrigoyen (1993). Detailed sedimentological descriptions, palaeoenvironmental interpretations, palaeoclimatic inferences, radiometric dating and magnetostratigraphic studies of the 3500 m thick well-exposed Neogene succession in the Cacheuta-Tupungato region were carried out by Irigoyen (1997) and Irigoyen *et al.* (1995, 2000, 2002).

According to these authors, the Miocene succession is divisible into four formations characterized by fluvial, eolian, alluvial and some volcanic deposits (see Fig. 1). At the southern end of the Precordillera, approximately 35 km southwest Mendoza city, mainly Triassic and Cenozoic continental strata are exposed (Figs 2, 3). In the study area, the oldest Palaeozoic rocks form Cacheuta Peak; the Cenozoic continental deposits unconformably overlie Middle to Upper Triassic non-marine strata of the Uspallata Group, which in turn onlap andesitic rocks of the volcanic and plutonic Permian–Triassic Choiyoi Group (Figs 2, 3).

The upper Eocene to lower Miocene Divisadero Largo Formation crops out in the Potrerillos Valley and surrounding areas between the eastern side of Cacheuta Peak and the Potrerillos locality (Figs 2, 3). Small exposures of sandstones with gypsum and anhydrite layers and varicoloured mudstones are exposed in the SSW foothills of Los Baños peak, and the formation is locally *ca* 35 m thick in the Cuchilla del Toscal section in the SSW foothills of Cacheuta Peak (Irigoyen *et al.* 2000, 2002). The middle Miocene Mariño Formation, described below in more detail, unconformably overlies the previous unit and crops out in the north but also more extensively in the southern areas of the Potrerillos Dam and on the western part of Cacheuta Peak (Fig. 2, 3). The upper Miocene (*ca* 11.7–9.0 Ma) La Pizona Formation (cf. Irigoyen 1997, Irigoyen *et al.* 2000, 2002) unconformably overlies the Mariño Formation (Yrigoyen 1993) and consists mainly of thick grey sandstones and conglomerates exposed in the west of the study area (Figs 1, 2).

TOSCAL DE MARIÑO and
CUCHILLA DEL TOSCAL SECTIONS



LEGEND

- | | | | |
|--|-----------------------------|--|---|
| | sandstone | | planar cross stratification |
| | fine grained conglomerate | | tangential or trough cross-stratification |
| | medium grained conglomerate | | horizontal stratification |
| | tuffaceous sandstone | | trough cross-stratification |
| | claystone and siltstone | | parallel lamination |
| | | | fossil wood |

Fig. 2. Schematic stratigraphic column of the Toscal de Mariño and Cuchilla del Toscal Section of the Mariño Formation, Mendoza, Argentina (Modified from Irigoyen 1997).

The Mariño Formation (Rolleri & Criado Roque 1970)

In the Potrerillos Valley, the Mariño Formation forms the highest topographic elevations, named ‘Tosca de

Mariño’ and ‘Cuchilla del Toscal’ (Fig. 1) where the typical succession is briefly described below (Fig. 2). This formation was subdivided into three members by

Yrigoyen (1993). Based on magnetic polarity stratigraphy and ash chronology, Irigoyen (1997) and Irigoyen *et al.* (2000, 2002) assigned the entire Mariño Formation to the interval *ca* 15.7–12.2 Ma (middle Miocene; Fig. 3). The following sedimentological descriptions correspond to the Toscal de Mariño and Arroyo Aguas Blancas sections (Irigoyen 1997).

Lower member ('Conglomerados violáceos': purple conglomerates). This member comprises two distinct packages occurring in isolated and discontinuous exposures in the study area. The lower part of the unit is characterized by purple and greenish fine conglomerates with sandstone matrix and planar-stratified sandstone beds that alternate with thinner intervals of massive grey tuffaceous sandstones and red mudstones

interpreted to represent channel-fill and floodplain deposits. The upper part consists of grey tuffaceous sandstone beds alternating with red mudstones. The lithofacies recognized in this member indicate that these deposits are of fluvial origin. The upper part of this member, characterized by the occurrence of mottled sandstone beds, abundant gypsum and carbonate-rich mudstone layers with sparse mud cracks, suggests semi-arid conditions where episodes of sandstone accumulation alternated with periods of floodplain mud deposition. This lower member attains a thickness of *ca* 50 m in the Tosca de Mariño section (Figs 2, 3).

Middle member ('Areniscas entrecruzadas': cross-bedded sandstones). This member typically crops out at the northern and southern margins of the Potrerillos

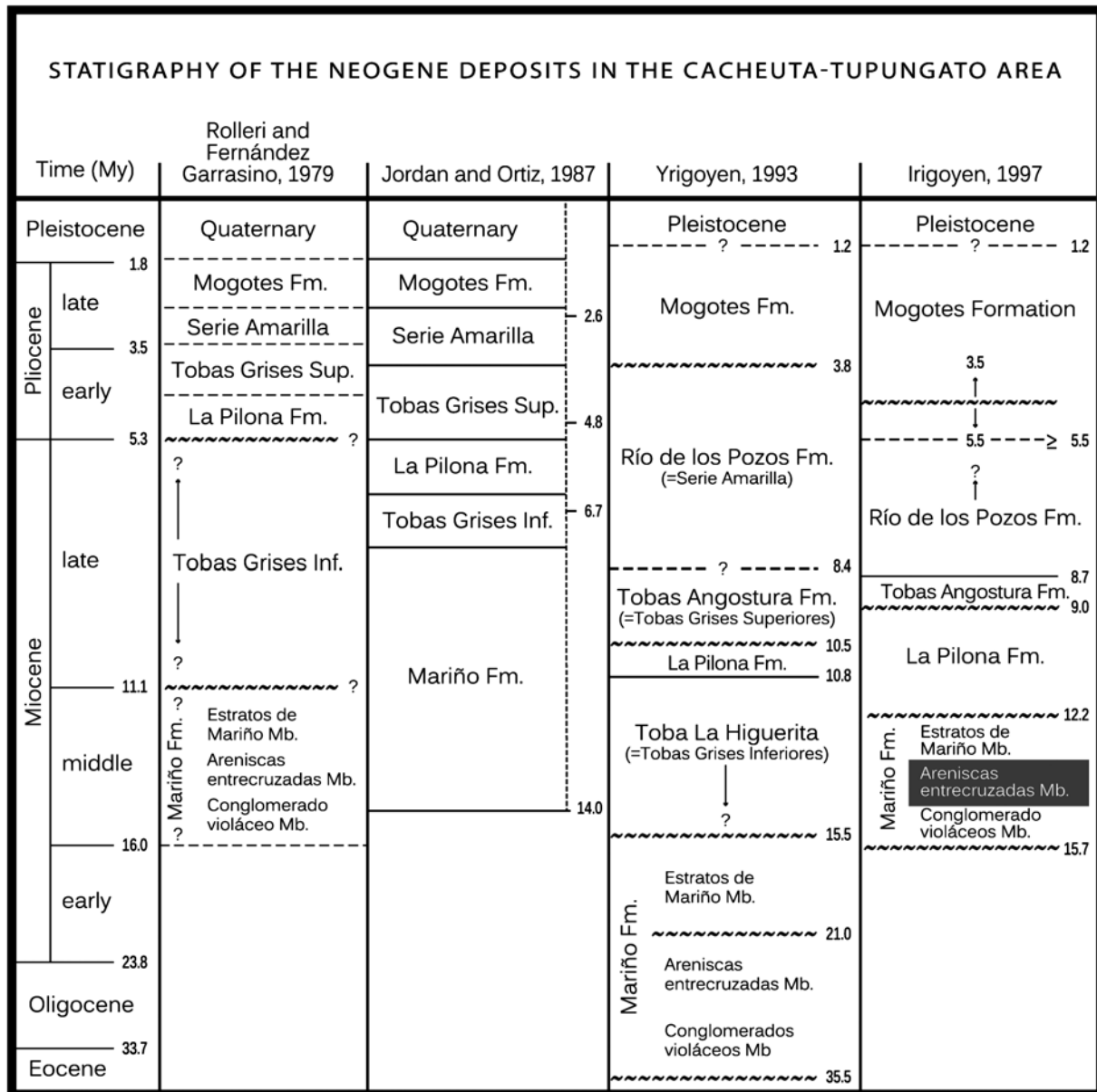


Fig. 3. Stratigraphy of the Neogene deposits in the Cacheuta-Tupungato area. Modified from Irigoyen (1997); Stratigraphic nomenclature from Yrigoyen (1993).

Dam reservoir. It comprises a distinctive *ca* 180 m thick monotonous fine- to coarse-grained and well-sorted succession of pale brown, parallel-laminated, cross-laminated or massive tuffaceous sandstone beds. This member has many sedimentological features of eolian origin, such as moderate- to high-angle cross-bedding forming wedge planar or tabular planar sets. Low-relief ripples occur on exposed forest surfaces. Large and medium-scale cross-beds are interpreted to represent dune facies. The occurrence of this lithofacies stratigraphically above fluvial sequences (deposited in semi-arid setting) suggests that fluvial input was progressively reduced favouring the development of an extensive dune field. The fossil twigs described below were probably reworked. A series of *in situ* undetermined vertebrate traces were also recorded in this member at the southern margins of the Potrerillos reservoir (ex Río Mendoza margins; Figs 2, 3).

Upper member ('Estratos de Mariño': marine strata). This member, more than 500 m thick, is well exposed at the southern end of the Río Mendoza Valley, on the highest hills of the area, the 'Toscal de Mariño' and 'Cuchilla del Toscal' (Figs 1–3). It consists of reddish sandstones and grey conglomerates alternating with red mudstones. The upper member is notable for the abundance of sandstone bodies and horizontally stratified conglomerates that show variable degrees of channelization; their sedimentary structures are indicative of braided stream deposits, under low flow conditions. The predominance of parallel-laminated sandstones, in conjunction with other sedimentological features, is suggestive of arid or semi-arid conditions in which sporadic and perhaps heavy rainfall favoured episodes of upper-flow-regime discharge (Irigoyen 1997).

Materials and methods

The fossil twigs were collected from exposures of the middle member of the Mariño Formation close to the northern margin of the Mendoza River, now flooded by the Potrerillos reservoir (32°57'36"S, 69°09'21"W; Fig. 1).

The fossil woods were preserved by siliceous permineralization. Transverse, tangential and radial thin-section of the woods were prepared for study using standard lapidary techniques.

Anatomical terms used in the descriptions follow the recommendations of the IAWA List of Microscopic Features for Hardwood Identification (IAWA Committee 1989). The identification of fossil woods was performed by consulting classical descriptions of extant and fossil plants, such as those of Metcalfe & Chalk (1950), Tortorelli (1956), Rancusi *et al.* (1987) and Roig & Vidal (2006). In order to compare the samples with extant and fossil species, the InsideWood website (InsideWood 2004–onwards) was used. The systematic classification follows the APG I (1998) and APG III

(2009), and the bibliography list is that of Gregory (1994) and Gregory *et al.* (2009). Authorities and references to extant taxa are available at the International Plant Names Index website: <http://www.ipni.org/>.

The quantitative values provided in the anatomical description are averages from 25 measurements. Minimum, maximum and average values are cited to the standard format of: minimum (average) maximum.

The fossil wood was studied with a Nikon Eclipse E200 light microscope, and the photomicrographs were taken with a Nikon Coolpix S4 digital camera. The studied fossil wood and microscope slides are registered in the 'Museo de Ciencias Naturales y Antropológicas Juan Cornelio Moyano' at Mendoza city, under the acronyms MCNAM-PB1393, MCNAM-PB1393 PR 1–3, MCNAM-PB1395, MCNAM-PB1395 PR 1–3 and MCNAM-PB1397, MCNAM-PB1397 PR 1–3.

Systematic palaeobotany

Order LAMIALES Bromhead, 1838

Family VERBENACEAE Saint-Hilaire, 1805

Rhaphithamnoxylon gen. nov. (Fig. 4A–K)

Diagnosis. Only secondary wood is preserved. Diffuse-porous wood; vessels predominantly solitary, sporadically in radial multiples of 2–4, in clusters, and in short tangential rows, small to very small in diameter, with simple perforation plates; intervessel pits alternate; axial parenchyma sparse and vasicentric; rays 1–3 seriate, weakly heterogeneous.

Etymology. The generic name denotes the woods resemblance to extant *Rhaphithamnus* Miers, 1870.

Type species. *Rhaphithamnoxylon artabeae* sp. nov.

Rhaphithamnoxylon artabeae gen. et sp. nov. (Fig. 4A–K)

Diagnosis. Growth rings distinct; septate and non-septate fibers present; rays heterocellular, composed of procumbent and upright or square cells, and uniseriate rays homocellular.

Etymology. The specific epithet is dedicated to Dr Analía E.E. Artabe for her important studies on the fossil floras of Argentina.

Material examined. Holotype MCNAM-PB1393, MCNAM-PB1393 PR 1–3.

Type locality. Northern margin of the now flooded Potrerillos reservoir (Río Mendoza Valley, between

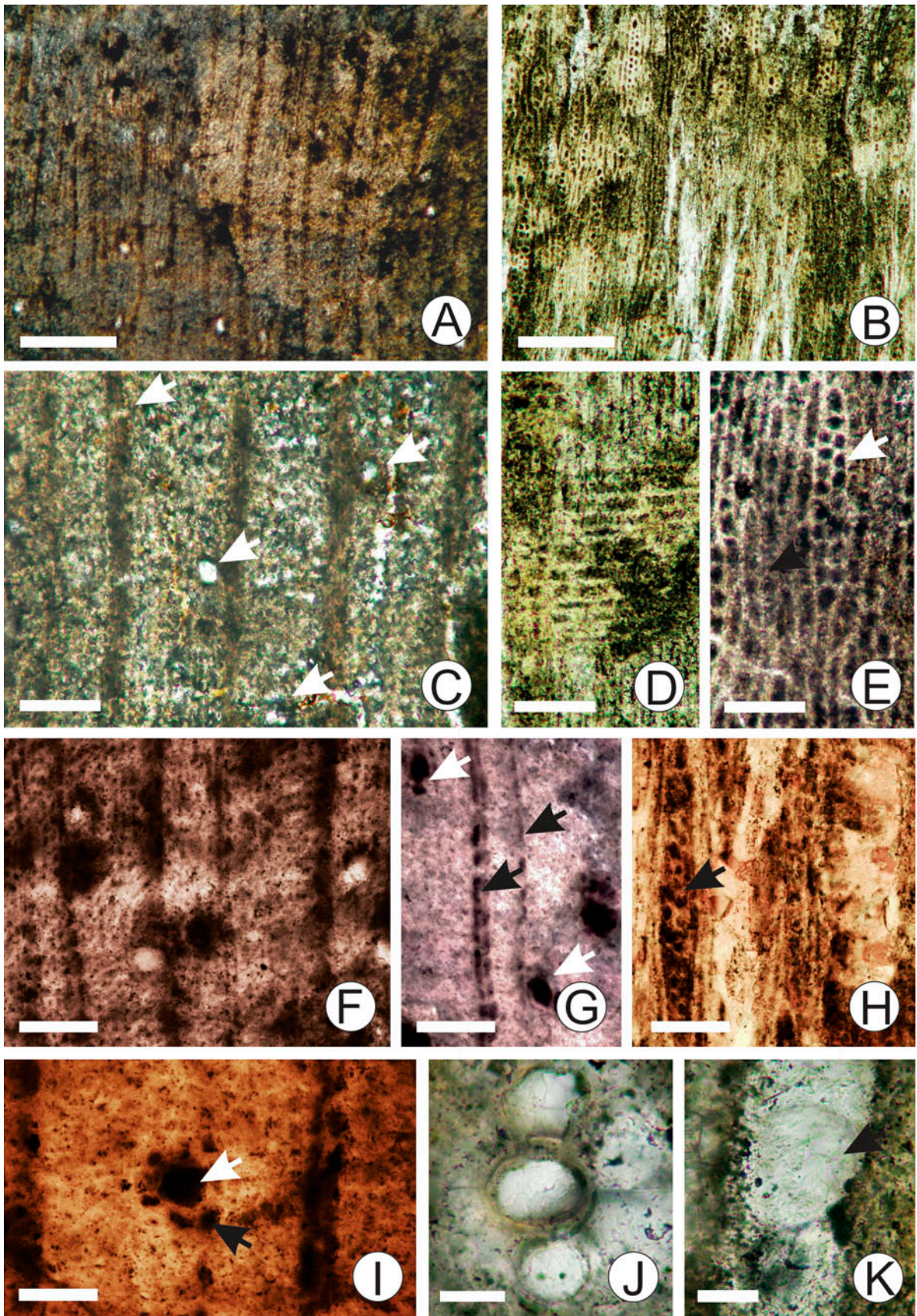


Fig. 4. *Rhaphithamnoxylon artabeae* gen. et sp. nov. (MCNAM-PB 1393). **A**, General view of transverse section. **B**, General view of longitudinal tangential section. **C**, Solitary vessels (arrows) in transverse section. **D**, Ray in radial longitudinal section. **E**, Biseriate (white arrow) and uniseriate (black arrow) rays in tangential longitudinal sections. **F**, **G**, Vessels (white arrows) and ray (black arrows) in transverse section. **H**, Triseriate ray (arrow) in tangential longitudinal section. **I**, Solitary vessel (white arrow) with sparse, vascentric parenchyma (black arrow) in transverse section. **J**, Multiple radial vessels in transverse section. **K**, Vessel with simple perforation plate (arrow) in tangential longitudinal section. Scale bars: A, B = 300 μ m, C–H = 100 μ m, I = 50 μ m, J, K = 30 μ m.

Cacheuta Peak and Potrerillos village), south-southwestern extent of the Precordillera, Mendoza Province, Argentina (32°57'36"S, 69°09'21"W).

Stratigraphic unit and age. Middle member ('*Areniscas entrecruzadas*': cross-bedded sandstones) of the Mariño Formation; middle Miocene.

Description. The species is based on a single fragment of secondary wood. The pith, primary xylem, cortex and secondary phloem are absent. In transverse section, the wood reveals distinct growth rings and diffuse porosity (Fig. 4A).

In cross-section, vessels are predominantly solitary (65%), but also occur sporadically in radial multiples of two (24%), three (6%), four (4%), in clusters (2%) and in short tangential rows (Fig. 4A, C, F, G, I, J). Solitary vessels are circular to oval in transverse section (Fig. 4I); they have tangential diameters of 17–(35)–60 µm and radial diameters of 22–(35)–53 µm; vessel density is 2–(5)–11 per mm². Vessels have straight end walls with simple perforation plates (Fig. 4K); intervessel pits very small to small (≤ 4 µm) and alternate; vessel-ray parenchyma pits are similar in size and shape to intervessel pits. Vessels 77–(133)–195 µm long.

Fibers are usually non-septate and rarely septate (Fig. 4E), arranged in radial rows (Fig. 4F), with diameters of 7–(14)–20 µm, and medium- to thick-walled: wall thicknesses of 2–(6)–8 µm. Axial parenchyma is scarce and vasicentric (Fig. 4I).

Rays are mostly biseriate (48%), or uniseriate (42%), rarely triseriate (10%; Fig. 4B, E, H); 6–(10)–12 per linear mm. Rays 38–(163)–470 µm high and 7–(26)–55 µm wide. Rays 1–(6)–17 cells high and 1–(2)–3 cells wide. Multiseriate rays are heterocellular, composed of procumbent, upright or square cells, and uniseriate rays are homocellular (Fig. 4D).

Comparisons with extant species. Verbenaceae is characterized by the following combination of anatomical features: distinct growth rings; very small vessels that are predominantly solitary, but also sparsely in radial multiples and in clusters; simple perforation plates; sparse and vasicentric axial parenchyma; and 1–3 seriate heterocellular to homocellular rays (Record & Hess 1941, Metcalfe & Chalk 1950).

The Mariño fossil wood was compared with various genera of Verbenaceae (Table 1) of which *Rhaphithamnus* shares the following features: diffuse-porous secondary xylem; distinct growth ring boundaries; vessels small (75 µm) to very small (30 µm), fairly numerous, commonly in short radial multiples, evenly distributed; rays 1–3 seriate, heterocellular, body ray cells procumbent with 1–7 rows of upright and/or square marginal

cells and uniseriate rays numerous and composed of upright or square cells; parenchyma sparsely paratracheal and in a narrow irregular band demarcating growth rings (Record & Hess 1941, Rancusi *et al.* 1987).

Using the InsideWood database, the following combination of features are shared with the Mariño fossil wood: 1p 2a 3a 4a 5p 6a 7a 8a 9a 13p 14a 19a 22p 24p 25p 30p 40p 41p 56a 65p 66p 75p 97p. With 0 allowable mismatches (see coding of IAWA Committee 1989), this yields only one species, *Rhaphithamnus spinosus*, with a compatible affinity to *Rhaphithamnoxylon artabeae* gen. et sp. nov.

Comparisons with fossil species. The fossil wood described herein was compared with other fossil species assigned to Verbenaceae (Table 2; Gregory *et al.* 2009): *Gmelina hubeiensis* Yang in Qi *et al.* 1997 (Neogene, China); *Gmelina tertiara* Bande, 1986 (Paleogene, India); *Gmelina wahanensis* Yang in Yang *et al.* 1993 (Neogene, China); *Tectonoxylon prambachense* Hofmann, 1944 (Oligocene, Austria); *Vitecoxylon aethiopicum* Lemoigne, 1978 (Miocene, Ethiopia); *Vitexoxylon africanum* Prakash, Awasthi & Legmoigne, 1982 (Mio-Pliocene, Ethiopia); *Vitexoxylon indicum* Ingle, 1972 (Cretaceous to Eocene, India); *Vitexoxylon miocenicum* Prakash & Tripathi, 1974 (Miocene, India); *Vitex* sp. cf. *V. simplicifolia* Oliver, 1875 (Mio-Pliocene, Ethiopia; Jolly-Saad & Bonnefille 2012).

Rhaphithamnoxylon artabeae differs from *Gmelina hubeiensis* and *Gmelina wahanensis* in the type of porosity and ray width. Abundant tyloses in vessels are characteristic of *Tectonoxylon prambachense*, *Vitecoxylon aethiopicum* and *Vitexoxylon africanum* but these were not observed in the Argentinean fossil wood (Table 2). Characters such as the size of vessels and the presence of metatracheal parenchyma or banded apotracheal parenchyma are present in *Vitexoxylon indicum* but they differ from those of the Mariño fossil specimen (Table 2). *Vitexoxylon miocenicum* has 4–10 seriate rays and larger vessels than those of *Rhaphithamnoxylon artabeae*. *Vitex* sp. cf. *V. simplicifolia* has wider rays than the fossil studied here. *Gmelina tertiara* is the most similar fossil species, but differs from the Mariño wood because it has larger vessels and aliform and confluent axial parenchyma (Table 2).

Order and family INCERTAE SEDIS

Mariño unknown dicot 1 (Fig. 5A–K)

Material examined. MCNAM-PB1395, MCNAM-PB1395 PR 1–3 and MCNAM-PB1397, MCNAM-PB1397 PR 1–3.

Locality. Northern margin of the now flooded Potrerillos reservoir (Río Mendoza Valley, between Cacheuta Peak and Potrerillos village), south-southwestern extent of the Precordillera, Mendoza Province, Argentina.

Genera	Distribution	Porosity	Growth rings	Rays			Fibers	
				Vessels	Type	Width		Axial parenchyma
<i>Rhaphithamnoxydon artabae</i> gen. et sp. nov.	Mendoza, Argentina	Diffuse	Distinct	Mostly solitary, also in radial multiples of 2–4 and in clusters. Tangential diameters 17–(35)–60 µm. 2–(5)–11 per mm ² . Perforations simple. Intervessel pits alternate.	Heterocellular multiseriolate rays and homocellular uniseriate rays	1–3 cells	Vascentric and scarce	Arranged in radial rows, thick walls
<i>Citharexylum</i> L.	Tropical–subtropical America	Ring porous in some cases	Distinct	Vessels solitary and in short radial multiples, small to medium size, diameter: 100–160 µm, few to numerous. Small intervessel pits. Solitary, in short radial series, rare long radial series. Small, diameter: 50–70 µm. Intervessel pits very small.	Heterogeneous	1–2 (4) cells	Scarce paratracheal and in some cases terminal	Septate or partially septate
<i>Duranta</i> L.	Tropical America	Diffuse	Distinct	Solitary, in short radial series, rare long radial series. Small, diameter: 50–70 µm. Intervessel pits very small.	Heterogeneous	1–3 cells	Scarce paratracheal	Septate
<i>Gmelina</i> L.	India, Pakistan, Sri Lanka	Diffuse	Distinct or indistinct	Short radial multiples and in clusters, diameter: 130–240 µm. 3–6(–12) vessels/mm ² . Tyloses present.	Homocellular	2–5 cells	Paratracheal vascentric and alliform	Septate
<i>Lantana</i> L.	Widely distributed in tropical and subtropical regions of the world	Diffuse ring porous in some cases	Distinct	Solitary. Medium to small, diameter: 50–160 µm. Mostly numerous. Small intervessel pits.	Heterogeneous	1–2 cells	Scarce paratracheal and in some cases vascentric and confluent	Some septate
<i>Lippia</i> L.	Africa and America, in tropical and subtropical regions	Commonly distinct	Commonly distinct	Solitary and in short radial series. Medium size, diameter: 120–180 µm. Few to numerous. Small intervessel pits.	Heterogeneous	1–3 (4) cells	Scarce paratracheal and in some cases terminal	With simple or bordered pits
<i>Petrea</i> L.	Tropical–subtropical America	Diffuse ring porous in some cases	Distinct	Solitary radial multiples of two	Of two sizes: uniseriate rays	1–8 (12) cells	Vascentric and confluent. Terminal	With bordered pits

(Continued)

Table 1. (Continued).

Genera	Distribution	Porosity	Growth rings	Vessels	Rays			Axial parenchyma	Fibers
					Type	Width	Fibers		
<i>Rhaphithamnus</i> Miers	South America	Diffuse ring porous in some cases	Distinct	elements or in clusters. Generally small, diameter: 60–125 µm. Mostly numerous. Very small intervessel pits. Solitary, radial multiples and in clusters. Small to very small, diameter: 75–30 µm. Numerous.	composed of cubic cells. Multiseriate rays formed by procumbent cells. Uniseriate rays composed of upright cells and multiseriate rays composed of procumbent and erect cells	1–3 cells	Scarce paratracheal and terminal, Apotracheal diffuse and scarce	Sparsely septate	

Table 1. Comparison of anatomical characteristics between *Rhaphithamnoxylon artabeae* gen. nov. and sp. nov. and most related genera of Verbenaceae.

Stratigraphic unit and age. Middle Member ('*Areniscas entrecruzadas*': Cross-bedded sandstones) of the Mariño Formation; middle Miocene.

Description. The fossil fragments consist of two pieces of permineralized twigs (*ca* 9 cm) with poorly preserved pith and well-preserved secondary xylem (Fig. 5A). Twigs are laterally compressed or flattened with large vessels, readily visible to the naked eye and eccentric pith in cross-section (Fig. 5A). Transverse sections reveal indistinct growth rings and diffuse-porous secondary xylem (Fig. 5A–C).

Vessels are predominantly solitary (70%), in radial multiples of two (18%), three (16%), four (1%) and up to 10 vessels (2%), and in clusters (1%; Figs 5A–G). Solitary vessels are circular in transverse section with tangential diameters of 83–(170)–253 µm and radial diameters of 31–(140)–220 µm; occurring at densities of 10–(15)–24 per mm². Solitary vessels are larger in diameter than in radial multiples or in clusters. Vessels have walls 9–(16)–27 µm thick. Vessel end walls are straight or oblique with simple perforation plates (Fig. 5I). Intervessel pits are alternate, very small (≤ 4 µm), with diameters of 3–(5)–7 µm (Fig. 5J); vessel-ray parenchyma pits not observed. Helical thickenings present only in some narrower vessels; vessel lengths of 60–(180)–360 µm.

Fibers are thick-walled with diameters of 11–(17)–26 µm (Fig. 5K). Paratracheal vasicentric axial parenchyma are complete and in some cases confluent (Fig. 5E, F).

Rays are very difficult to observe owing to the poor preservation of the material. Only uni- and biseriate with 11–14 cells high (Fig. 5H) are preserved. Heterocellular rays are composed of procumbent and upright or square cells in radial section.

Comparisons with extant species. The key anatomical features of the studied material (large and wide vessels, many narrow vessel elements in addition to wide vessel elements, wide vessels with solitary distribution and narrow vessels grouped in clusters, and helical thickenings in vessels) are common features in dicotyledonous lianas or small shrubs.

In particular, the secondary xylem in the lianas, vines and small shrubs includes large and wide vessels, large rays and abundant axial parenchyma, increasing climbing strategies, water conductivity and storage performance (Carlquist 1985, Wheeler & LaPasha 1994, Angyalossy *et al.* 2012, Masrahi 2014). Vasicentric tracheids, fibriform vessel elements, helical thickenings in vessels, starch-rich parenchyma adjacent to vessels and other parenchyma distributions are also present in plants with these growth habits. Many vines and lianas have narrow vessels grouped in clusters in addition to

Fossil species	Rays						
	Porosity	Growth rings	Vessels	Type	Width	Axial parenchyma	Fibers
<i>Rhaphithamnoxylon artabae</i> gen. et sp. nov.	Diffuse	Distinct	Mostly solitary, also in radial multiple of 2-4 and in clusters. Tangential diameters 17-(35)-60 µm. 2-(5)-11 per mm ² . Perforation simple. Intervessel pits alternate.	Heterocellular multiseriolate rays and homocellular uniseriate rays	1-3 cells	Vasicentric and scarce	Arranged in radial rows, thick walls.
<i>Gmelina hubetensis</i> Yang, 1997	Semi-ring to ring porous	Distinct	Mostly solitary, also in radial multiples 2-4. Tangential diameter: 90-140 µm. 4-8 vessels per mm ² . Simple perforation plates. Alternate intervessel pits.	Heterogeneous Type III	2-6 cells	Vasicentric and scarce	Thin-walled. Septate fibers present.
<i>Gmelina tertiara</i> Bande, 1986	Diffuse	Distinct	Solitary, in multiple radials of 2-3 elements and in clusters. Tangential diameter: 50-180 µm. Radial diameter: 80-250 µm. Simple perforation plates. Alternate intervessel pits.	Weakly heterogeneous	1-3 cells	Paratracheal, vasicentric, aliform and confluent	Septate
<i>Gmelina wahanensis</i> Yang, 1993	Semi-ring to ring porous	Distinct	Vessels mostly solitary. Simple perforation plates. Alternate intervessel pits. Abundant tyloses.	Heterogeneous Type III	Multiseriate	Vasicentric, scarce, paratracheal and aliform	Thin-walled. Septate fibers present.
<i>Tectonoxylon prambachense</i> Hofmann, 1944	Distinct	Distinct	Solitary, in multiple radials of 2-3 elements and in clusters. Simple perforation plates. Tyloses present.	Homocellular	1-3 cells	Diffuse and paratracheal	Thick-walled

(Continued)

Table 2. (Continued).

Fossil species	Porosity	Growth rings	Rays			Fibers	
			Vessels	Type	Width		Axial parenchyma
<i>Vitexoxylon aethiopicum</i> Lemoigne, 1978	Diffuse		Solitary, in multiple radials of 2–5 elements, small. 2–5 vessels per mm ² . Simple perforation plates. Bordered intervessel pits. Abundant tyloses.	Heterogeneous	1–3 cells	Diffuse and vascentric	Non-septate
<i>Vitexoxylon africanum</i> Prakash, Awasthi & Legmoigne, 1981	Diffuse	Distinct	Solitary and multiple radial elements of 2–5 elements. Tangential diameter: 120–360 µm. Radial diameter: 60–400 µm. Vessels 5–7 per mm ² . Simple perforation plates. Alternate intervessel pits. Tyloses present. Mostly solitary or in radial groups of 2–3 elements. Tangential diameter: 90–153 µm. Radial diameter: 99–153 µm. 8–20 vessels per mm ² . Simple perforation plates. Very small bordered intervessel pits.	Homocellular to heterocellular	1–3 seriate, mostly biseriata.	Paratracheal vascentric in complete. Apotracheal in bands of 2–3 cells at the beginning of the growth ring	Arranged in radial rows. Septate.
<i>Vitexoxylon indicum</i> Ingle, 1972	Diffuse	Distinct		Homocellular	1–3 cells	Paratracheal and metatracheal	Arranged in radial rows Septate.
<i>Vitexoxylon miocenicum</i> Prakash & Tripathi, 1972	Diffuse	Distinct	Tangential diameter: 100–200 µm. Simple perforation plates. Alternate intervessel pits.	Homocellular to heterocellular	4–10 seriate	Scanty paratracheal, vascentric	Septate
<i>Vitex</i> sp. cf. <i>simplicifolia</i> Oliver, 1875	Diffuse	Indistinct	Mostly solitary, in some cases in radial multiples of 2 or 3. Tangential diameter: 31–194 µm. 9–14 vessels per mm ² . Simple perforation plates. Alternate intervessel pits.	Heterocellular multiseriata rays and homocellular uniseriate rays	1–5 cells	Paratracheal, vascentric, probably confluent	Septate

Table 2. Comparison of anatomical characteristics between Verbenaceae fossil genera and *Rhaphithamnoxydon artabaeae* gen. nov. and sp. nov.

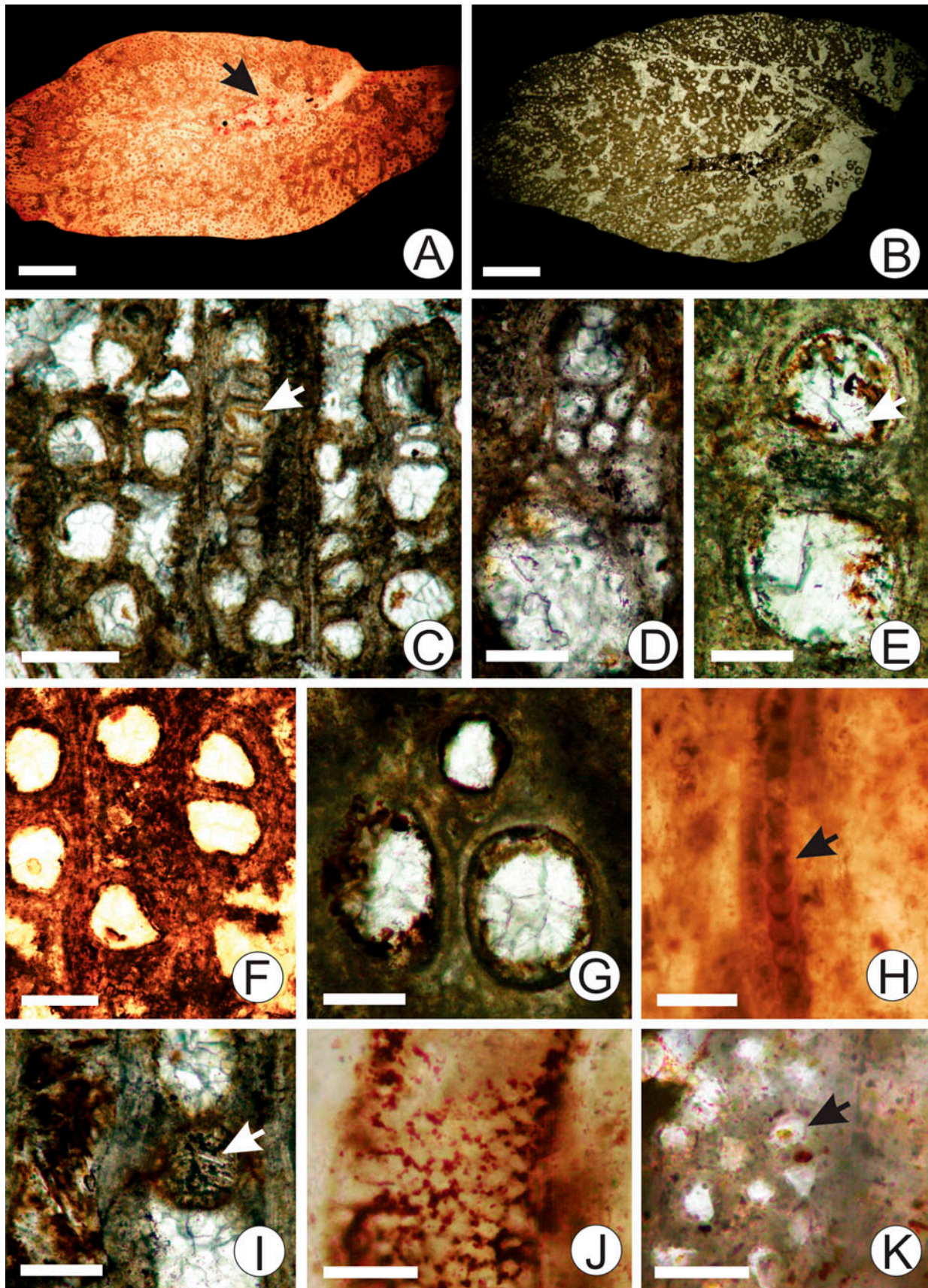


Fig. 5. Mariño unknown dictio 1 (MCNAM-PB 1395 and MCNAM-PB 1397). **A**, Transverse section showing indistinct growth rings and diffuse porous secondary xylem of MCNAM-PB 1395; the arrow indicates poorly preserved pith. **B**, Transverse section showing indistinct growth rings and diffuse porous secondary xylem of MCNAM-PB 1397; **C**, Transverse section showing solitary and radial multiple vessels of four or more vessels (arrow) of MCNAM-PB 1397. **D**, Narrow and wide vessel elements of MCNAM-PB 1397. **E**, Radial multiple vessels of MCNAM-PB 1397. **F**, Transverse section showing solitary and radial multiple vessels of MCNAM-PB 1397. **G**, Vessels in clusters of MCNAM-PB 1395. **H**, Uniseriate ray (arrow) of MCNAM-PB 1397. **I**, Vessel with simple perforation plate (arrow) of MCNAM-PB 1397. **J**, Alternate invessel pits of MCNAM-PB 1395. **K**, Detail of fibers (arrow) of MCNAM-PB 1395. Scale bars: A, B = 1000 μ m, C = 300 μ m, D, E, G, I = 100 μ m, F = 200 μ m, H = 50 μ m, J, K = 30 μ m.

wide vessel elements as in the case of analysed wood (see Fig. 5D). These narrow vessels may take the form of fusiform cells, slightly wider than imperforate tracheary elements, and they may function as mechanical support, water storage cells and contribute to hydraulic stability (Gutiérrez *et al.* 2009). Lianas, vines and small shrub plants have solitary broad vessels, whereas narrow vessels are commonly distributed in clusters (Gutiérrez *et al.* 2009).

The presence of helical thickenings in vessels is common in woody temperate plants, chiefly those of dry habitats and cold areas. Vines and lianas tend not to occur in extremely cold or dry climates, although they may occur where low temperatures and drought are episodic and moderate (Carlquist 1985). The presence of thickening of xylem walls provides strength and reduces the risk of cell collapse and ensuing embolism in the advent of high tension created by severe water deficit and high evapotranspiration (Masrahi 2014). Perforation plates in vessels of vines and lianas are predominantly simple; this accords with the idea that simple plates offer the least impediment to water flow, and thereby promote efficient conductivity. With respect to wall pitting in longitudinal sections of vessels, alternate pits may have greater selective value in self-supporting growth forms than in vines or lianas (Carlquist 1991). The presence of simple perforation plates in these fossil specimens should enhance the conductivity of water and reduce resistance to water flow, whereas the thickening of xylem walls provides strength against collapse under increased tension (Carlquist 1991, Masrahi 2014).

Fabaceae, Sapindaceae and Bignoniaceae include many vines with diffuse-porous wood or having indistinct growth rings, vessels in radial multiples of four or more and commonly arranged in clusters, with simple perforation plates, alternate intervessel pits and paratracheal parenchyma (InsideWood, 2004–onwards). Bignoniaceae and Leguminosae are two of the most liana-rich families (Angyalossy *et al.* 2012).

Comparisons with fossil species. Just two fossil vines or liana species have been recorded from Argentina. *Lardizabaloxylon lardizabaloides* Schönfeld, 1954 from either Upper Cretaceous or Palaeogene strata of Patagonia was closely related to *Lardizabala* Ruiz & Pav. of the Lardizabalaceae (Schönfeld 1954). This liana species differs from the fossil studied herein because it has primary and secondary xylem, and most importantly incorporates widely spaced vascular wedges separated by broad medullary rays (Schönfeld 1954, Tidwell *et al.* 2010).

Lutz & Martínez (2007) described *Ranunculodendron anzoteguiiae*, a fossil vine from the upper Miocene of the Palo Pintado Formation, northwestern Argentina. *Ranunculodendron anzoteguiiae* has eccentric pith, with four protoxylem vessels and secondary xylem divided into wedges by parenchymatous rays, all surrounded by

cambium, phloem and cortex (Lutz & Martínez 2007). The Mariño fossil differs from it in the great vessel diameters and the presence of vessels in clusters and radial multiples of four or more.

Unfortunately, the preservation of this type of fossil wood is fairly poor, and it could not be assigned to any known taxon. It is difficult to distinguish between intervessel pits, vessel-ray parenchyma pits and ray cells. Fibers are poorly preserved, and so their lumens are difficult to observe.

Discussion

Palaeoenvironmental setting

The Miocene vegetation history of Patagonia and the mid-west of Argentina is poorly known. Fossil woods and phytolith assemblages from the Miocene are scarce (Schönfeld 1954, Hünicken 1995, Schönning & Bandel 2004, Zucol *et al.* 2007, Brea *et al.* 2012) but palynological evidence from the middle–late Miocene of northeastern Patagonia (Guler *et al.* 2001, 2002, Guler 2003, Palazzesi & Barreda 2004, Barreda & Palazzesi 2007) documents a flora characterized by an increasing diversity and abundance of xerophytic taxa, including Asteraceae, Amaranthaceae and Convolvulaceae. Expansion of these xerophytic taxa, coupled with extinctions of megathermal/non-seasonal vegetation, would have been associated with both tectonic and climatic forcing factors that promoted the development of aridity and extreme seasonality. These arid-adapted late Miocene floras are very similar to the modern Patagonia vegetation characterized by widespread steppe in extra-Andean Patagonia and with forest restricted to the western humid upland regions of the Patagonian cordillera (Barreda & Palazzesi 2007).

The Mariño Formation sedimentary succession was deposited in a complex low-gradient fluvial system where arid or semi-arid conditions prevailed. Evidence for this includes the occurrence of oxidized floodplain deposits, incipient calcrete bands and fluvial sandstone lithofacies that suggest deposition under ephemeral flow regimes, and a thick succession of eolian deposits.

Verbenaceae biogeography

Verbenaceae includes about 36 genera and *ca* 1035 species of trees, shrubs, and some lianas and herbs (Schweingruber *et al.* 2013). They are particularly important components of arid to semi-arid communities in North and South America where they are locally dominant in some communities, but they are also present in wet and dry tropical forests, high Andean grasslands and cloud forests (Marx *et al.* 2010, Olmstead 2013). A secondary centre of distribution is found in Africa (Olmstead 2013).

Distributions within the New World extend from Patagonia in southern South America to Canada, although very few species distributions extend north of the arid southwestern United States. Generic diversity is at its greatest in southern South America, presumably because the Andean uplift contributed to arid environments in what is now Argentina, where several clades have diversified, and to more mesic ecosystems nearby in northern Argentina that host representatives of many of the more wet-tropical groups (Marx *et al.* 2010). The distribution pattern described for Verbenaceae is similar to that of Bignoniaceae and Solanaceae, which originated and diversified initially in the New World. Bignoniaceae and Verbenaceae have unequivocally South American ancestral areas and diversified throughout the New World, including North America, but also established toeholds on other continents, primarily in the Southern Hemisphere (Olmstead *et al.* 2009, Marx *et al.* 2010, Olmstead 2013).

Divergence time estimates for the crown of the family are inferred to date to the Late Cretaceous or Paleogene, after the separation of South America from Africa (Olmstead 2013).

Rhaphithamnus species are spinescent shrubs. This genus consists of two species restricted to southern South America, in a longitudinal range of 45–30°S. *Rhaphithamnus spinosus* (Juss.) Moldenke occurs in mainland Chile and adjacent Argentina (Moldenke 1937); *R. venustus* (Philippi) Robinson, 1916 is endemic to the two islands (Masatierra and Masafuera) of the Juan Fernández Archipiélago (Sun *et al.* 1996, Marx *et al.* 2010, Olmstead, 2013).

The close distributional and morphological affinities of the *Rhaphithamnus spinosus* and *R. venustus* suggest that at one time, they might have formed a single generic complex throughout southern South America. Progressive drying probably developed as a result of the southern Andean orogeny and subsequent Pleistocene glaciation. These events gave rise to the vast, arid Atacama Desert in northern Chile, which may have isolated the populations and led to generic differentiation (Sun *et al.* 1996).

Conclusions

Rhaphithamnoxylon artabeae gen. et sp. nov. (Verbenaceae) has been erected based on a single sample of well-preserved fossil from Miocene strata of Argentina. It is very similar to extant *Rhaphithamnus* anatomically. The other fossil twigs found at the same stratigraphic level and described under open nomenclature are similar to the woods of dicotyledonous vines, lianas and small shrubs. These are the first palaeobotanical records from the Miocene Mariño Formation.

The occurrence of Verbenaceae wood with affinity to *Rhaphithamnus* in the Mariño Formation is not surprising given the modern distribution of the latter is

restricted to 45–30°S. This fossil wood is affiliated with Verbenaceae and adds to the sparse fossil record of this family.

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