



## Research papers

## Fossil woods from late Pleistocene sediments from El Palmar Formation, Uruguay Basin, Eastern Argentina

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## ABSTRACT

The Santa Ana fossiliferous locality (Entre Ríos, Argentina) of the El Palmar Formation is located in the southernmost part of the Uruguay Basin, in eastern Argentina. It contains evidence of a late Pleistocene paleoflora, consisting mainly of fossil woods. These remains were studied and are described based on anatomically preserved secondary xylem. Two new morphospecies of *Mimosoxylon* Müller-Stoll et Mädler 1967 and *Prosopisoxylon* Martínez 2010 are described, as well as two new morphogenera, related to *Holocalyx* Micheli, 1883 and *Amburana* Schwacke et Taub. 1894. These two new morphogenera represent the first recorded fossil wood with affinity to Faboideae from the Uruguay Basin. *Schinopsixylon heckii* Lutz 1979, (Anacardiaceae) was also recognized. These fossil woods are discussed here in terms of floristic composition and palaeoclimatic requirements. The morphotypes described here, as well as previously recorded ones from the Uruguay Basin, increases our understanding of floral diversity during the late Pleistocene in this region.

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## 1. Introduction

The Uruguay Basin is located in the southeastern region of South America, covers an area of around 365,000 km<sup>2</sup> (Fig. 1), corresponds with parts of Brazil, Uruguay and Argentina with the largest area occurring in the southern Brazil states of Santa Catarina and Rio Grande do Sul. The rest of the basin occurs in the western half of Uruguay with a small part in Eastern Argentina as well (García et al., 2000; Iriondo and Kröhling, 2008).

The Uruguay River formed during the Pliocene over basalts from the Upper Cretaceous known as the Serra Geral Formation (Iriondo, 1996). Climatic conditions appear to have been primarily responsible for the geologic evolution of sediments in Argentina's Entre Ríos province during the Quaternary. Many geological formations have been defined for the Argentinean littoral region (known locally as "Mesopotamia"), associated with time periods from the Lower Pleistocene to the Upper Holocene (Iriondo, 1980, 1996; Iriondo and Kröhling, 1997, 2007, 2008).

This paper describes fossil wood remains from the El Palmar Formation (late Pleistocene). This unit is often regarded as belonging

to one of the warmest interval during the Last Interglacial (Iriondo, 1996, 1998; Iriondo and Kröhling, 2001, 2008). These deposits outcrop in the Santa Ana locality (Fig. 2), and comprise the upper terrace on the western bank of the Uruguay River (Iriondo, 1980; Iriondo and Kröhling, 2001, 2007, 2008).

Palaeontological studies of the El Palmar Formation have revealed abundant and diverse floral and faunal remains (Tonni, 1987; Zucol et al., 2004; Ferrero et al., 2007). The paleofloral record from the El Palmar Formation is rich in petrified woods and phytolith assemblages (Lutz, 1979, 1980, 1984, 1986; Brea, 1998, 1999; Brea and Zucol, 2001; 2007; Brea et al., 2001a; Zucol et al., 2005). These paleofloral assemblages are characterized by the occurrence of arboreal, shrub and herbaceous elements belonging to the Lauraceae, Combretaceae, Myrtaceae, Fabaceae, Anacardiaceae, Arecaceae, Podostemaceae, Poaceae and Cyperaceae families.

Prado (2000) and Pennington et al. (2000) propose that during the Pleistocene, Seasonally Dry Tropical Forests (SDTFs), were more widespread and continuous in South America, with rainforest and montane taxa largely confined to gallery forests. For this reason, the composition of these fossil wood assemblages will be important for understanding Pleistocene vegetation distribution in South America, and will provide a good opportunity to corroborate the hypothesis previously elaborated by these authors. The palaeogeographic and palaeoecological implications of these taxa's distribution were analyzed by taking into account ecological and distributional characteristics of their nearest living relatives.

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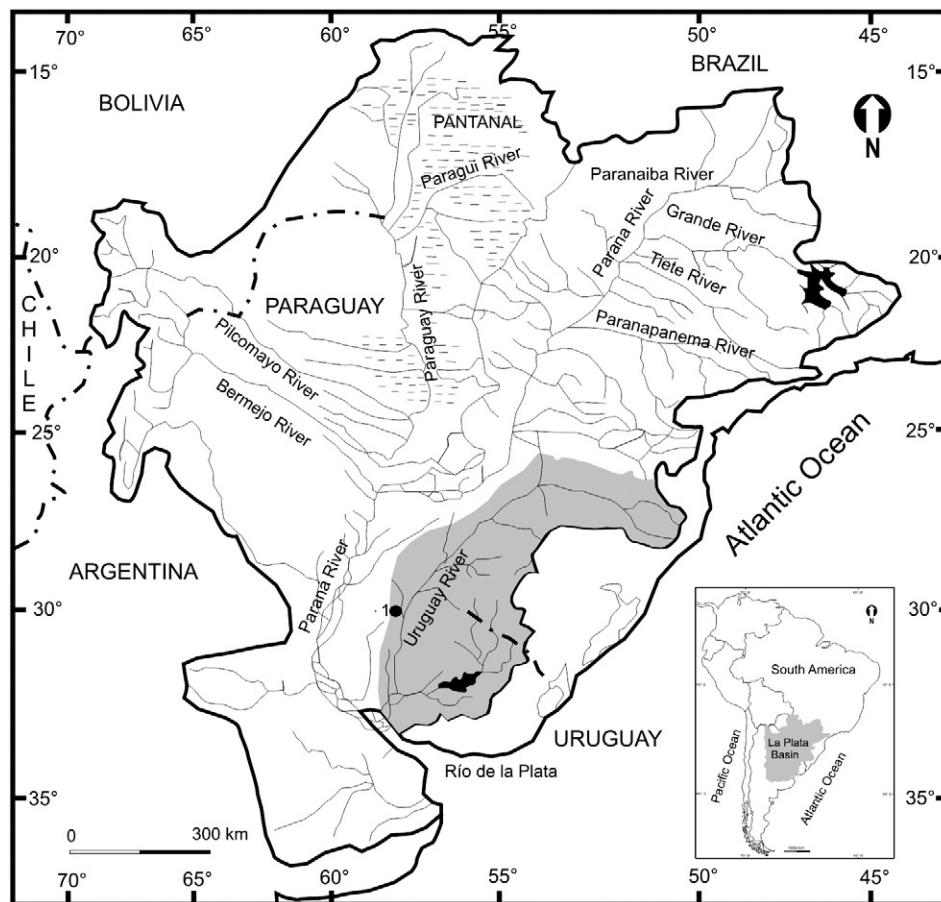


Fig. 1. Geographic map of the Uruguay Basin (in grey). Black outline: La Plata Basin 1. Santa Ana fossiliferous locality (Entre Ríos, Argentina). (modified from García et al., 2000).

## 2. Geological and palaeontological setting

The El Palmar Formation defined by Iriondo (1980), who described an ancient, late Pleistocene, flood plain of the Uruguay River deposited. This flood plain was probably developed during the Oxygen Isotopic State 5a, which corresponds to the Last Interglacial (Iriondo, 1996, 1998; Iriondo and Kröhling, 2001). OIS 5a is considered to have been the warmest interval of the late Pleistocene. In the geological literature, the El Palmar Formation has also been called the Salto Chico Formation (Rimoldi, 1962), the Ubajay Formation (Gentili and Rimoldi, 1979; Aceñolaza, 2007) in Argentina and the Salto Formation in Uruguay (Bossi, 1969; Veroslavsky and Montañó, 2004; Montañó, 2004).

The El Palmar Formation is found along a 4–15 km wide strip, in outcrops along the 200 km western margin of the Uruguay River, between the Mocoretá River (Corrientes province, Argentina) and the city of Concepción del Uruguay (Entre Ríos province, Argentina) (Fig. 2). It is mainly composed of medium, reddish and yellowish ochre sands. Lenses of gravel and pebbles up to 90 m long and up to 2 m thick are interspersed in quartzose sand masses. The coarse fractions are composed of chalcedony. In areas adjacent to these conglomerate lenses, medium-to-thick sandstones layers with planar stratification, rich in fossil wood remains, are very commonly present (Iriondo, 1980; Iriondo and Kröhling, 2008). Sand strata and gravel lenses represent channel facies, while fine sediments represent floodplain facies. This formation, which is 3 to 12 m thick, is found at the modern surface and has not been buried since its deposition (Iriondo and Kröhling, 2001).

Studies carried out on the El Palmar Formation, including sedimentological characterization and mineralogical and absolute dating analyses, are extensively documented in Iriondo and Kröhling (2008).

The type stratigraphic locality (Iriondo, 1980) for this formation, which contains abundant fossil remains, is found in El Palmar National Park (Zucol et al., 2005). Relatively close to the city of Federación in Argentina, this formation was dated to  $80,670 \pm 13,420$  years BP by TL (thermoluminescence dating) (Iriondo and Kröhling, 2001), while near to the city of Salto in Uruguay, an age of  $88,370 \pm 35,680$  years BP was also obtained by TL (Iriondo and Kröhling, 2008).

The presence of *Stegomastodon platensis* Ameghino, a fossil vertebrate of the Lujanian stage/age found in the locality of Colón, characterizes the El Palmar Formation (Tonni, 1987). For years it was the only vertebrate fossil record, but more recently a diverse vertebrate assemblage (*Megatherium* Cuvier, *Mylodon* Owen, *Macrauchenia* Owen, *Toxodon* Owen, *Tapirus* Brännich, *Equus* Linnaeus, *Morenelaphus* Carette, *Stegomastodon* Pohlig, and *Antifer* Ameghino) was described from El Boyero locality ( $31^{\circ} 25' S$ ,  $58^{\circ} 58' W$ ), near the city of Concordia (Fig. 2). Discovery of these eight new taxa has substantially increased knowledge of the palaeovertebrate biodiversity of the El Palmar Formation, while the presences of *Equus* (A.) cf. *neogeus* Lund. implies a Lujanian age (late Pleistocene–early Holocene) (Ferrero et al., 2007).

## 3. Materials and methods

Fossil wood remains described in this paper were recovered from the middle levels of the late Pleistocene El Palmar Formation at the Santa Ana locality, near the city of Concordia in the Eastern Argentinean province of Entre Ríos ( $30^{\circ} 54' 16.1'' S$ ,  $57^{\circ} 55' 45.9'' W$ , Figs. 2 and 3; Iriondo and Kröhling, 2001, 2008).

The deposits are well exposed at the Santa Ana locality (Federación Department, Entre Ríos province, Argentina), where one vertical section was examined and measured in detail with bed-by-bed description (Figs. 2 and 3). At this locality, the El Palmar Formation

outcrops extensively and comprises the upper terrace of the Uruguay River. The sequence is a continental clastic unit composed of successions of conglomerate, thick sand, sandstone, clay, and mud beds (Fig. 3). The measured vertical profile at the Santa Ana exposure is about 4.2 m thick. The lowest part consists of olive clay in one layer, while the next lowest part is characterized by red sandstone with planar cross-stratification. The middle part of the profile is composed of thick reddish-to-yellowish sands and conglomerates with fossil wood remains. The upper part is characterized by thick red sands and green muds. Finally, at the top of the profile lies a thin layer of conglomerate (Fig. 3). The sedimentary sequence in which this fossil wood assemblage is preserved consists of a continental unit that resulted from deposition by a complex fluvial system, with sandstone and/or conglomerate channels and floodplain facies (Iriando and Kröhling, 2008).

The fossil specimens are permineralized wood with well-preserved anatomical features. They were thin-sectioned in three characteristic sections (cross, tangential and radial section). The terminology for the wood descriptions follows the IAWA Lists of Features Suitable for Hardwood Identification wherever possible (IAWA Committee, 1989), but some terms were taken from Carlquist (2001). The identification of fossil woods was performed by using the wood atlases and descriptions of Metcalfe and Chalk (1950), Cozzo (1950, 1951), Tortorelli (1956), Castro (1991, 1994), Roth and Giménez (1997, 2006), Evans et al. (2006), Richter and Dallwitz (2000 onwards), as well as the InsideWood database [2004-onwards]).

The Vulnerability Index (V) and Mesomorphy ratios (M) were calculated following the equations developed by Carlquist (1977). The Vulnerability Index is used as an indicator of hydric conductivity. A low value indicates greater capacity for withstanding water stress or freezing. High values for the Mesomorphic ratios denote mesomor-

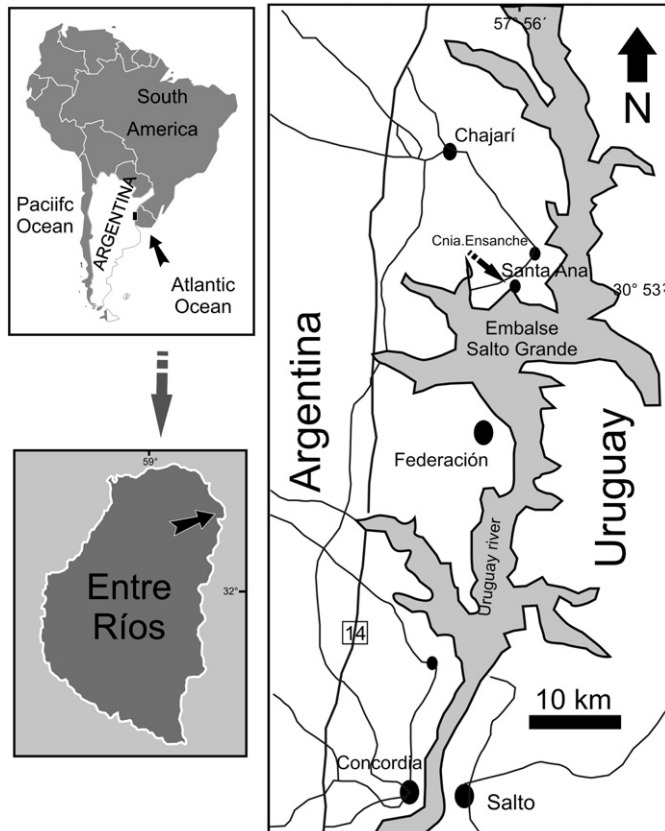


Fig. 2. Location map showing the Santa Ana fossiliferous locality, Entre Ríos province, Argentina.

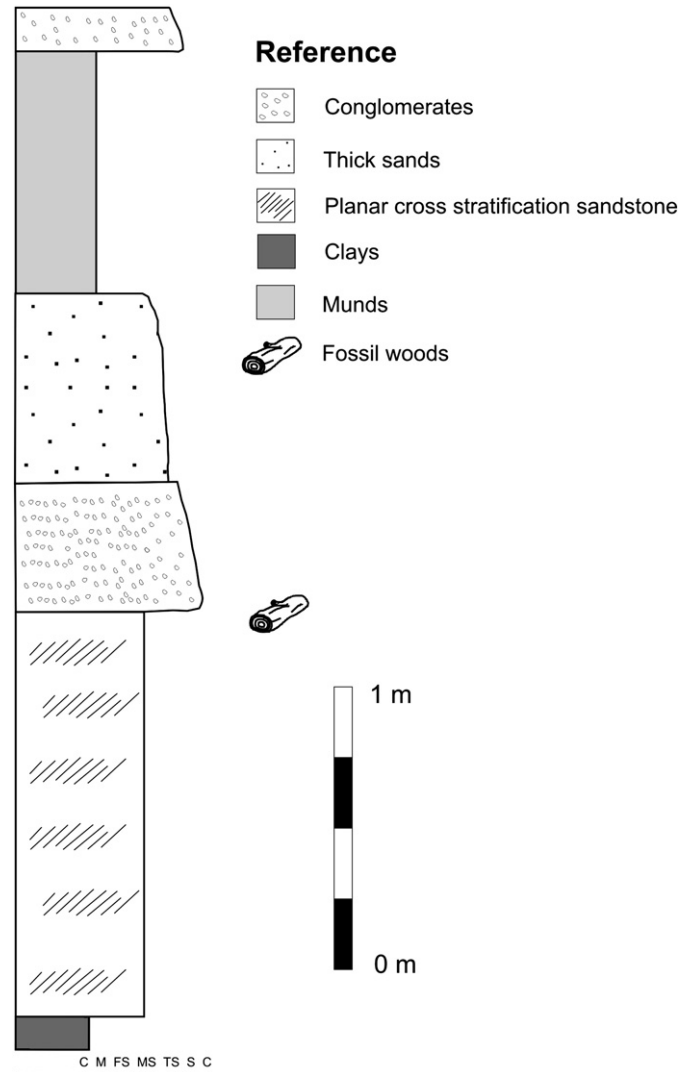


Fig. 3. Schematic profile of the late Pleistocene in the riverside cliffs by the Uruguay River, in the region of Santa Ana, Entre Ríos province, Argentina.

phic wood structure (Carlquist, 1977). Diameter of vessels, number of vessels per  $\text{mm}^2$ , degree of vessels grouping, length of vessel elements, perforation plate, porosity, and growth rings were also analyzed in terms of palaeoecological requirements (Carlquist and Hoekman, 1985; Wheeler and Baas, 1991, 1993; Lindorft, 1994; Woodcock, 1994; Moglia and Giménez, 1998).

Systematic assignment follows the APG (2009), which is based primarily on molecular (mostly DNA sequence) data and the strict recognition of “monophyletic” groupings. The International Plant Names Index was used for the names of extant species (IPNI, 2004). The quantitative values provided in the anatomical descriptions are averages of 25 measurements. The average is cited first, followed by the minimum and maximum values, which are given in parentheses.

In this contribution we follow Avise and Johns (1999) proposal for the use of fossil generic names. However, several paleobotanists agree that fossils from the Pliocene onwards should be assigned to an extant genus if possible (Collinson, 1986). In our case, this is impossible because our fossil materials have preserved only the secondary xylem.

The material was studied with a Nikon Eclipse E200 light microscope and the photomicrographs were taken with a Nikon Coolpix S4 digital camera. Fossil Materials and microscope slides are kept in the Laboratorio de Paleobotánica (CICYTTP-CONICET), Diamante, Argentina, under the acronyms CID-PALBO and CID-PALBO mic.



## 4. Results

### 4.1. Systematic palaeobotany

Family FABACEAE Lindley, 1836

Subfamily MIMOSOIDEAE Candolle, 1825

Genus *Mimosoxylon* Müller-Stoll Mädél, 1967

Type species: *Mimosoxylon tenax* (Felix) Müller-Stoll Mädél, 1967.

*Mimosoxylon caccavariae* nov. sp. Brea, Zucol et Patterer (Plate I)

*Derivatio nominis*: The specific name, *caccavariae*, is dedicated to the memory of Marta Alicia Caccavari, who has studied extant and fossil Argentinean Mimosoideae.

*Holotype*: CID-PALBO 15, CID-PALBO mic. 491 (three microscopic slides).

*Repository*: Laboratorio de Paleobotánica, CICYTTP-CONICET, Diamante. *Stratigraphic horizon*: El Palmar Formation, late Pleistocene (30° 54' 16.1" S, 57° 55' 45.9" W).

*Locality*: Santa Ana Locality, Uruguay Basin, Argentina

*Species diagnosis*: Diffuse porous, local tendency for dendritic patterning of vessels; vessels mostly solitary, radial multiples of 2–4, clusters; small vessels, moderately numerous (<30 per mm<sup>2</sup>); perforation plate simple; intervessel pits small, bordered, alternate, oval, more widely spaced; rays homocellular and composed of procumbent cells, rarely weakly heterocellular composed of procumbent and square cells; uniseriate, rarely biseriate and sporadically multiseriate rays 3–4 cells wide; smaller and narrow rays; <60 cells high; <9 rays/mm; axial parenchyma abundant, vasicentric, in some cases banded and marginal; fibers non-septate and hexagonal in outline.

*Description*: Indistinct to distinct growth rings, marked by radially flattened and slightly thick-walled fibers. Diffuse porous, locally with a tendency towards dendritic patterning of vessels (Plate I, 1). Vessels solitary (48%), in radial multiples of 2–4 (5–7) (18%, 11%, 8%, 6%, 3% and 2% respectively) and in clusters (4%) (Plate I, 1, 3). The vessels are circular to oval in outline, small with a mean tangential diameter of 101 (65–145) µm and a mean radial diameter of 88 (41–148) µm. The mean vessel density is 19 (11–32)/mm<sup>2</sup>. The mean vessel element length is 278 (177–457) µm. Perforation plates are exclusively simple (Plate I, 4), with oblique end walls (Plate I, 4, 5). Intervessel pits are small, probably bordered, alternate, oval, vested and widely spaced (Plate I, 5, 6). Their diameter is 7 (0.7–10) µm. The apertures are oval or linear and commonly coalesce. Fibers are thick-walled (4 µm) with a mean diameter of 14 (5–19) µm. They are abundant, non-septate and hexagonal in outline (Plate I, 7). Pits were not observed.

The paratracheal axial parenchyma is abundant, vasicentric, in some cases banded and marginal (Plate I, 1, 3). Rays are homocellular and composed of procumbent cells (Plate I, 8), rarely weakly heterocellular composed of procumbent and square cells, with 7 per linear mm (4–9 per linear mm). Rays are uniseriate (37%), rarely biseriate (31%) and sporadically multiseriate rays 3–4 cells wide (16%, 16% respectively) with a mean width of 41 (17–82) µm (Plate I, 2, 4). The mean height of rays is 469 (27–1630) µm and 23 (3–61) cells high. Prismatic crystals in chambered axial parenchyma cells were not observed.

*Comparison*: The presence of vested pits and vessel elements with simple perforation plate (Judd et al., 1999) are the synapomorphies that allow placement of this specimen in the Fabales. The combination of solitary vessels and vessels in radial multiples; simple perforation plates; axial parenchyma that is abundant and confluent or banded; uniseriate or rarely biseriate rays, homocellular rays composed of procumbent cells, and non-septate fibres (Baretta-Kuipers, 1981; Wheeler and Baas, 1992; Evans et al., 2006) occur in the Mimosoideae. These characters also occur in the Bignoniaceae, Sapindaceae, Moraceae and Meliaceae but the presence of vested pits is diagnostic of Fabaceae (Wheeler and Baas, 1992).

Although it would be difficult to identify a mimosoid plant to genus level based solely on its wood anatomy, the fossil wood has diagnostic characters, which allow comparing with *Mimosa* L. Although *Mimosa* is a complex genus, this fossil specimen is anatomically similar to it. *Mimosa* is comprised of more than 500 pan-tropical and pan-subtropical species that are quite variable in their features. There is a high degree of variation between individual species of the same genus, even for the key characters, which is quite atypical of the Mimosoideae (Cozzo, 1951; InsideWood, 2004-onwards; Evans, et al., 2006). However, recent phylogenetic analysis based on the chloroplast nucleotide sequences of the *trnL* intro and the *trnL-trnF* have revealed that the genus *Mimosa* is monophyletic and that *Piptadenia viridiflora* (Kunth) Benth. is the species most closely related to *Mimosa* (Bessega et al., 2008).

Nine fossil genera (Table 1) and seventeen fossil wood species of Mimosoideae are known from South America: *Acacioxylon* (1 species, late Eocene, Chile; Nishida, 1981, 1984); *Anadenantheroxylon* (1 species, middle-late Miocene, Argentina; Brea et al., 2001b); *Menendoxylon* (4 species, Pliocene, Argentina; Lutz, 1979, 1987); *Mimosoxylon* (4 species, Oligocene, Colombia; age unknown, Brazil; late Miocene and Pliocene, Argentina and probable late Cretaceous, Mexico; Felix, 1899; Silva Curvello, 1955; Pons, 1983; Lutz, 1987, 1991); *Paraalbizioxylon* (1 species, Cenozoic, Uruguay; Schuster, 1910; Gros, 1992); *Tetrapleuroxylon* (2 species, Cenozoic, Peru; age unknown, Brazil; Felix, 1882; Boureau, 1953); *Paracacioxylon* (2 species, Pliocene, Argentina and Paleocene, Argentina; Menéndez, 1962; Lutz, 1987; Brea et al., 2008); *Piptadenioxylon* (2 species, late Pleistocene, Brazil and Miocene, Argentina; Suguio and Mussa, 1978; Franco and Brea, 2008) and *Prosopisioxylon* (1 species, Miocene, Argentina; Martínez, 2010).

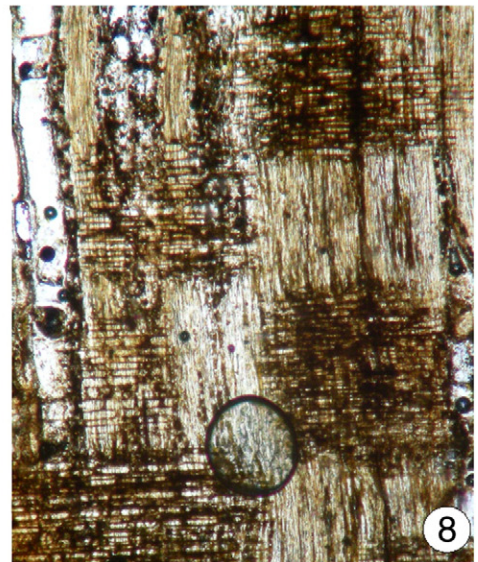
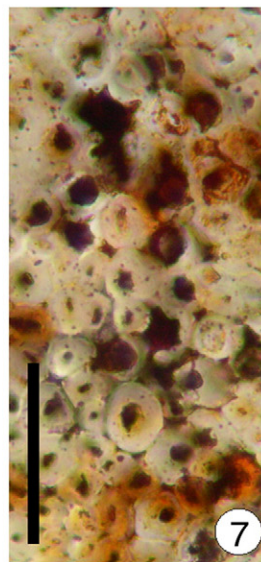
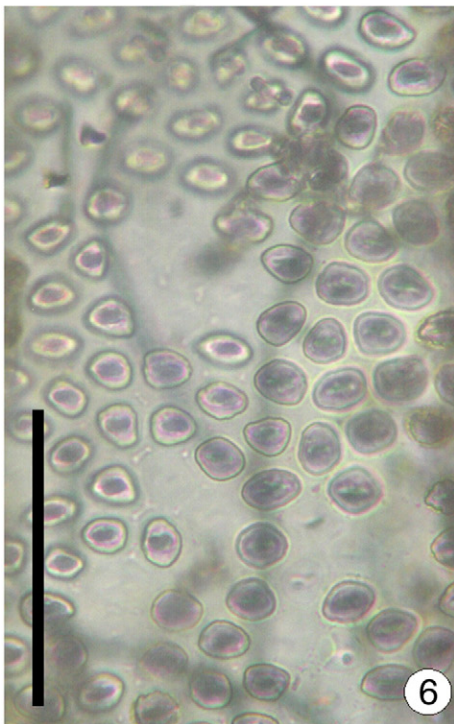
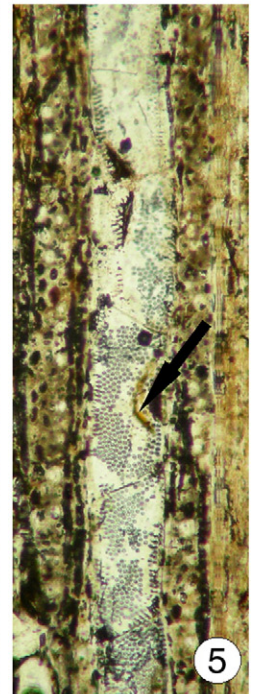
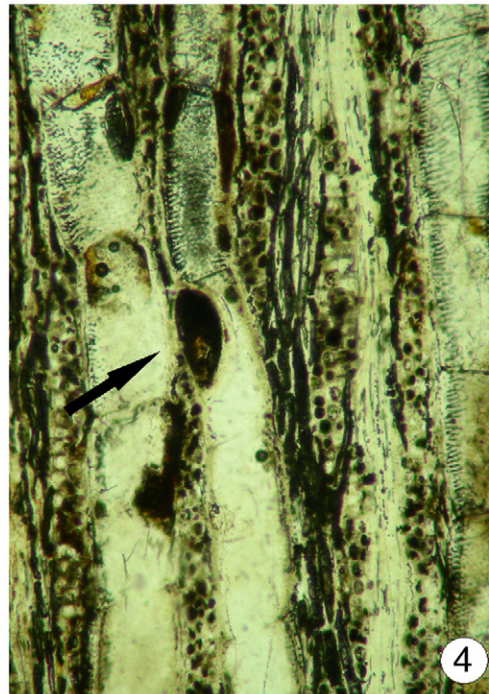
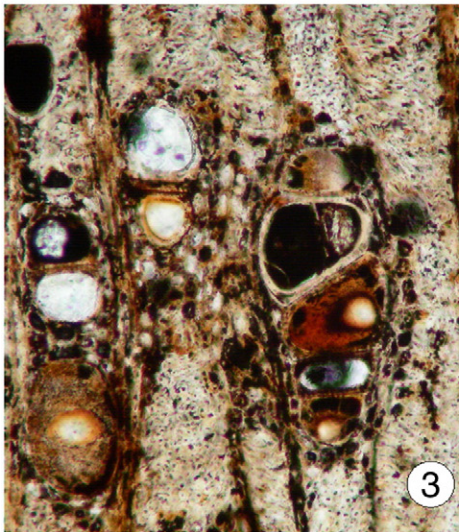
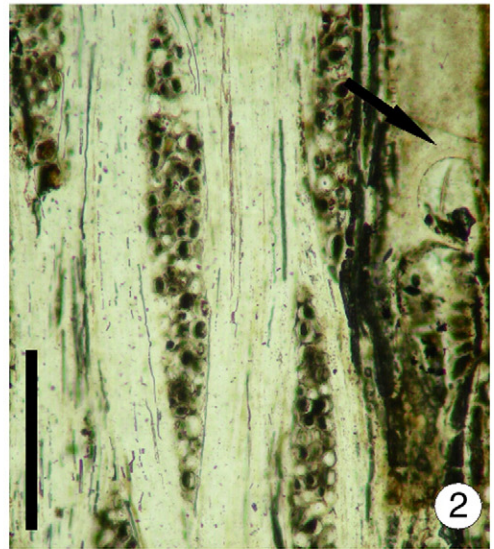
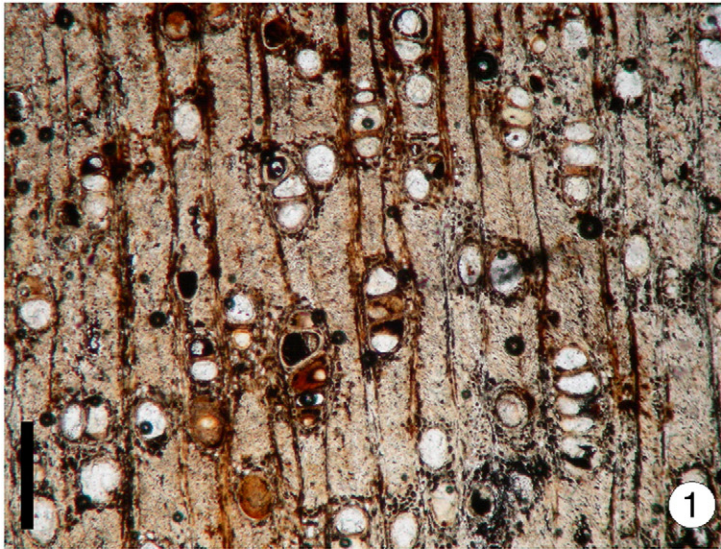
The structure of this fossil wood allows it to be assigned to the genus *Mimosoxylon* (Müller-Stoll and Mädél, 1967; Lutz, 1987, 1991; Gros, 1992; Cevallos-Ferriz and Barajas-Morales, 1994; InsideWood, 2004-onwards), which is characterized by vessels that are solitary or in radial multiples, small-to-medium alternate intervascular pits, homogeneous and rarely weakly heterogeneous, 1–3 seriate, rays, axial parenchyma that is narrow vasicentric, partly weakly aliform rare confluent, terminal or initial, and non-septate fibers. According to the comparison made among the described 5 species of *Mimosoxylon* (Table 2), the specimen studied differs in various characteristics (vessel grouping, vessels/mm<sup>2</sup>, ray type), and therefore it is assigned to a new species, *Mimosoxylon caccavariae* Brea, Zucol et Patterer nov. sp.

The fossil wood from Santa Ana site described previously differs from all other morphospecies: *Mimosoxylon acacioides* Kramer

**Plate I.** *Mimosoxylon caccavariae* sp. nov. Brea, Zucol et Patterer. Holotype CID-PALBO 15.

1. Transverse section, general view. Wood diffuse porous. Axial parenchyma vasicentric and banded and abundant fibers.
2. Tangential longitudinal section, detail of multiseriate rays and simple perforation plate (arrow).
3. Transverse section, detail of disposition of vessels, fibers and vasicentric and banded axial parenchyma.
4. Tangential longitudinal section, general view. Disposition of vessels and rays in longitudinal section. Multiseriate rays and vessels with oblique end walls and simple perforation plate (arrow).
5. Tangential longitudinal section, general view. Vessel wall with small alternate vested pits.
6. Tangential longitudinal section, detail of small, bordered, alternate, oval, vested and more widely spaced Intervessel pits.
7. Transverse section, detail of thick-walled, non-septate and hexagonal fibers.
8. Radial longitudinal section, detail of homocellular rays composed of procumbent cells. (Scale bar in 1 = 750 µm; in 2, 3, 4, 5 and 8 = 200 µm; in 7 = 12 µm; in 6 = 3 µm).







**Table 1**  
Comparison of the characters of the fossil genera of Mimosoideae records in South America.

Morphogenus	Vessels	Intervascular pitting, type	Intervascular pitting, size	Ray type	Ray width	Axial parenchyma type	Fiber type
<i>Acacioxylon</i>	Predominantly solitary	–	Not indicated	Homogeneous	1–3 seriate	Paratracheal, uniseriate apotracheal in bands	Libriform
<i>Anadenantheroxylon</i>	Solitary, radial multiples of 2–4 and clusters	–	–	Homogeneous	1–2 seriate	Paratracheal vasicentric and confluent	Non-septate
<i>Menendoxylon</i>	Predominantly solitary, radial multiples of 2–3	Alternate	Small to medium	Homogeneous to heterogeneous	1–3 seriate	Vasicentric aliform, shorts bands	Non septate, sporadically septate
<i>Mimosoxylon</i>	Solitary, radial multiples	Alternate	Small to medium	Homogeneous, rarely weakly heterogeneous	1–3 seriate	Narrow vasicentric, partly weakly aliform, rare confluent, terminal or initial	Non-septate
<i>Paraalbizioxylon</i>	Solitary and radial multiple	–	Small to medium	Homogeneous	1–6 seriate never only uniseriate	Paratracheal, in some cases apotracheal, diffuse, terminal	Septate and non-septate
<i>Tetrapleuroxylon</i>	Solitary and radial multiples	Alternate	Medium	Homogeneous to weakly heterogeneous	1–5 seriate	Vasicentric aliform, partly confluent, terminal or initial	Non-septate
<i>Paracacioxylon</i>	Solitary, radial multiples of 2–4 and clusters	Alternate, compressed and vested	Small to medium	Homogeneous	1–6 seriate	Paratracheal vasicentric, aliform, confluent. Apotracheal diffuse	Septate and non-septate
<i>Piptadenioxylon</i>	Solitary, rarely radial multiple	Alternate	Small	Homogeneous	2–3 seriate	Vasicentric	Non-septate
<i>Prosopisinoxylon</i>	Vessels of two distinct diameter classes; solitary, radial multiples and clusters	Alternate	Small to medium	Homogeneous	1–9 seriate	Paratracheal vasicentric, aliform and confluent to banded. Apotracheal diffuse	Non-septate

(1974) has 80% solitary vessels and tangential diameter vessels of  $< \mu\text{m}=200 \mu\text{m}$ . *Mimosoxylon calpocalycoides* Lemoigne (1978) differs in the tangential diameter of vessels and the arrangement of axial parenchyma. *Mimosoxylon krameri* Lemoigne (1978) has storied structure, a feature not observed in *M. caccavariae*. *Mimosoxylon santamariensis* Lutz (1987) has 80% solitary vessels, rarely radial multiple vessels, exclusively homocellular rays and exclusively vasicentric axial parenchyma. This new species is more closely comparable to *Mimosoxylon tenax* (Müller-Stoll and Mädler, 1967; Cevallos-Ferriz and Barajas-Morales, 1994) from the Cretaceous and Oligocene–Miocene of Mexico, but this species differs in the number of vessels per  $\text{mm}^2$ , vessel grouping, axial parenchyma type and number of ray per linear mm (Table 2).

#### Genus *Prosopisinoxylon* Martínez 2010

Type species: *Prosopisinoxylon anciborae* Martínez 2010

*Prosopisinoxylon castroae* sp. nov. Brea, Zucol et Patterer (Plate II)

*Derivatio nominis*: The specific name, *castroae*, in honour of Dr. María Agueda Castro in recognition to her significant and extensive work on the wood anatomy of the genus *Prosopis* in Argentina.

*Holotype*: CID-PALBO 17, CID-PALBO mic. 493 (three microscopic slides).

*Additional material*: CID-PALBO 20, CID-PALBO mic. 496 (three microscopic slides).

*Repository*: Laboratorio de Paleobotánica, CICYTTP-CONICET, Diamante.

*Stratigraphic horizon*: El Palmar Formation, late Pleistocene (30° 54' 16.1" S, 57° 55' 45.9" W).

*Locality*: Santa Ana Locality, Uruguay Basin, Argentina.

*Species diagnosis*: Semi-ring to diffuse porous; vessels predominantly solitary, radial multiples of 2–4, clusters; vessels of two different sizes, small-to-medium; vessels moderately few ( $<10$  per  $\text{mm}^2$ ); perforation plate simple; intervessel pits small, bordered and alternate; rays homocellular, composed of procumbent cells; 2–5 seriate and rarely uniseriate; small and narrow;  $<30$  cells high; 6–10 rays/mm; axial parenchyma paratracheal vasicentric, confluent, marginal and rarely aliform; fibers thick and very-thick walled, non-septate and hexagonal in outline; crystals in chambered axial parenchyma cells with a single prismatic crystal per chamber.

*Description*: Growth rings distinct, marked by marginal parenchyma. Semi-ring to diffuse porous (Plate II, 1). Vessels solitary (52%), in radial multiples of 2–4 (23%, 17% and 3% respectively) and in clusters (8%) (Plate II, 1). Vessels are circular in outline, some with dark deposits, and of two different sizes, with an overall mean tangential diameter of 179  $\mu\text{m}$  and a mean radial diameter of 189  $\mu\text{m}$ . The two distinct vessel sizes are: (a) small- to medium-sized, with a mean radial diameter of 135 (101–177)  $\mu\text{m}$  and a mean tangential diameter of 127 (89–177)  $\mu\text{m}$ ; and (b) moderately large-to large, with a mean radial diameter of 243 (202–304)  $\mu\text{m}$  and a mean tangential diameter of 232 (203–278)  $\mu\text{m}$ . The mean vessel density is 8 (5–10)/ $\text{mm}^2$ . The mean vessel element length is 255 (143–375)  $\mu\text{m}$ . Perforation plates are exclusively simple (Plate II, 3), with oblique or straight end walls (Plate II, 2,3). Intervessel pits are small, bordered, alternate, and vested (Plate II, 6,8). Their diameters are 5 (3–7)  $\mu\text{m}$ . The apertures are circular and they coalesce. Tyloses are abundant and present in many vessels (Plate II, 1,2).

Fibers are hexagonal in outline, non-septate, thick and very-thick walled (Plate II, 9), with a mean thickness of 4 (3–5)  $\mu\text{m}$  and a mean diameter of 12 (7–15)  $\mu\text{m}$ . Pits were not observed. The axial parenchyma is vasicentric and confluent, rarely aliform (Plate II, 1). Marginal parenchyma is also present (Plate II, 1). The rays are multiseriate, 2–5 cells wide (5%, 67%, 14%, and 5% respectively) and uniseriate (9%) (Plate II, 4). The mean number of rays per linear mm is 7 (6–10 per linear mm). They are homocellular, composed exclusively of procumbent cells (Plate II, 7). The mean width of rays is 57 (34–75)  $\mu\text{m}$ . The mean height of rays is 418 (129–852)  $\mu\text{m}$  and 31 (12–60) cells high. Prismatic crystals are present in chambered axial parenchyma cells with one crystal per chamber (Plate II, 5).

*Comparison*: The wood characters of the Fabaceae are vessel elements of medium to short length, solitary, multiple series to clusters, perforation plates are always simple, intervessel pits vested, low rays, mainly homogeneous and the parenchyma is usually abundant and paratracheal. The fossil wood is better placed within of the subfamily Mimosoideae because of the presence of diffuse-porous wood without a predominant vessel pattern, vasicentric, aliform to confluent, often banded paratracheal parenchyma, crystals in chambered parenchyma axial cells and homogeneous rays (Baretta-Kuipers, 1981; Wheeler and Baas, 1992). The diagnostic features present in this fossil wood suggest affinities with this subfamily, and

the most closely-related genus is *Prosopis* L. The fossil wood has a combination of anatomical features related to those present in the Algarobia Section, Serie Chilenses, including semi-ring to diffuse porous; vessels that are solitary, in radial multiples of 2–4, and in clusters; simple perforation plate; axial parenchyma that is vasicentric, confluent, marginal, and rarely aliform; vested inter-vessel pits; homocellular rays; and prismatic crystals (Castro, 1991, 1994).

The combination of features in the Pleistocene fossil wood is diagnostic for *Prosopisinoxylon* (Martínez, 2010) morphogenus (Table 1), with affinity to the extant genus *Prosopis*. The anatomical characters used to separate *Prosopisinoxylon* from the rest of Mimosoideae fossil genera are vessels of two different sizes, short and wide rays [4–7 (1–9)] seriate, non-septate fibres, and parenchyma that is vasicentric, from confluent to aliform, and banded (see Table 1).

*Prosopis* has almost 45 species, which are important elements of arid and semiarid environments, with only a few members of the genus partially distributed in sub-humid tropical or subtropical regions (for more detail see Catalano et al., 2008).

Molecular analysis suggests that *Prosopis* is not a natural group, and that the divergence between Section Strombocarpa and Section Algarobia plus Section Monilicarpa occurred in the Oligocene. Furthermore, the diversification of the group formed by species of Serie Chilensis, Pallidae and Ruscifoliae is thought to have begun in the Pliocene (Catalano et al., 2008). These authors propose that the major diversification within the lineages of American species of *Prosopis* is coincident with the expansion of American arid areas, suggesting a climatic control for diversification of the group.

*Prosopisinoxylon castroae* Brea, Zucol et Patterer nov. sp. differs from the type species, *P. anciborae*, by the presence of diffuse porosity and differences in the number of vessels per mm<sup>2</sup>, width of rays, and arrangement of axial parenchyma (Table 3). Several anatomical characters presents in both species of *Prosopisinoxylon* such as short vessel elements and vessels of two distinct diameter classes would indicate xeric conditions (Martínez, 2010).

#### Subfamily FABOIDEAE Rudd, 1972

Genus ***Holocalyxylon*** gen. nov. Brea, Zucol et Patterer

Type species: *Holocalyxylon cozzoi* gen. nov. et sp. nov. Brea, Zucol et Patterer

*Holocalyxylon cozzoi* gen. nov. et sp. nov. Brea, Zucol et Patterer (Plate III)

*Derivatio nominis*: The generic name, *Holocalyxylon*, refers to the affinity with the genus *Holocalyx*. The specific name, *cozzoi*, is dedicated to the memory of Domingo Cozzo, who has studied many Argentinean woody species of legumes.

*Holotype*: CID-PALBO 16, CID-PALBO mic. 492 (three microscopic slides).

*Additional material*: CID-PALBO 18, CID-PALBO mic. 494 (three microscopic slides).

*Repository*: Laboratorio de Paleobotánica, CICYTTP-CONICET, Diamante.

*Stratigraphic horizon*: El Palmar Formation, late Pleistocene (30° 54' 16.1" S, 57° 55' 45.9" W).

*Locality*: Santa Ana Locality, Uruguay Basin, Argentina.

*Generic diagnosis*: Diffuse porous; vessels mostly solitary, occasionally in radial multiples and rarely in clusters; small and moderately numerous; intervessel pits small-to-medium, bordered and alternate; rays homocellular, composed of procumbent cells; mostly biseriate, occasionally uniseriate; rays storied; axial parenchyma apotracheal in marginal bands, aliform to confluent, to predominantly banded; fibers non-septate; prismatic crystals in chambered axial parenchyma cells with one crystal per chamber, but with no crystals in the ray cells.

*Species diagnosis*: Diffuse porous; vessels mostly solitary, occasionally in radial multiples and rarely in clusters; small vessels; moderately numerous (<17 per mm<sup>2</sup>); perforation plate simple; intervessel pits small-to-medium, bordered, alternate, circular; rays homocellular, composed of procumbent cells; mostly biseriate, occasionally uniseriate; short and narrow rays; <12 rays/mm; rays storied; axial parenchyma apotracheal in marginal bands 1–3 cells wide, also aliform to confluent, to predominantly banded; fibers thick and very-thick walled, non-septate and hexagonal in outline; prismatic crystals present in chambered axial parenchyma cells with one crystal per chamber.

*Description*: Growth rings indistinct to distinct, demarcated by marginal parenchyma bands 2–4 cells wide when present (Plate III, 1). Diffuse porous. Vessels solitary (47%), in radial multiples of 2–5 (34%, 8%, 3%, and 2% respectively) and in clusters (5%) (Plate III, 1,4). The vessels are circular in outline with a mean tangential diameter of 65 (72–110) µm and a mean radial diameter of 65 (41–151) µm. The mean vessel density is 11 (7–17)/mm<sup>2</sup>. The mean vessel element length is 235 (136–300) µm. Perforation plates are simple (Plate III, 6), with straight to lightly oblique end walls (Plate III, 3). Intervessel pits are small-to-medium, bordered, alternate, circular, and probably vested (Plate III, 3,5). Their diameter is 7 (5–10) µm. Fibers are hexagonal in outline, non-septate, mostly thick and very-thick walled, with a mean thickness of 5 (4–6) µm and a mean diameter of 14 (9–17) µm. Pits were not observed. The apotracheal axial parenchyma is present in marginal bands 1–3 cells wide (Plate III, 1). The paratracheal parenchyma varies from aliform to confluent, to predominantly banded (Plate III, 1,4). The bands are variable in width from narrow to wide (2–7 cells). The rays are mostly biseriate (78%) or triseriate (13%), although some uniseriate rays are also present (9%) (Plate III, 2,3,7). The mean number of rays per linear mm is 10 (8–12) per linear mm. Rays are homocellular, and composed exclusively of procumbent cells (Plate III, 8). The mean width of rays is 31 (14–41) µm. The mean height of rays is 189 (102–286) µm and 11 (4–20) cells high. Storied rays are observed (Plate III, 2). Prismatic crystals are present in chambered axial parenchyma cells with one crystal per chamber (Plate III, 9).

*Comparison*: Angyalossy-Alfonso and Miller (2002) establish that characters for all species of Swartzieae vary as follows: intervessel pits are from small to large (4–10 µm); rays are homocellular to heterocellular with 1–2 rows of upright cells, ray width is from exclusively uniseriate to mostly 2–3 cells wide; ray height has a range of means from 160 to 617 µm; vessel diameters have a range of means from 48 to 274 µm; number of vessels per mm<sup>2</sup> has a range of means from 1 to 61; number of rays per linear mm is usually 6 to 16; rays are either storied or non-storied; number of rays per mm linear ranges from 2 to 6 (for storied rays); axial parenchyma ranges from aliform with marginal or irregularly banded apotracheal parenchyma to predominantly banded; axial parenchyma band width ranges from 1 to 2 cells to more than 5 cells; and number of cells per parenchyma strand ranges from 2 to 4. Features with the greatest diagnostic value for this tribe are intervessel pit size, ray width and frequency, storied structure, axial parenchyma strand length, parenchyma band width, and vessel diameter Angyalossy-Alfonso and Miller (2002). Within the Swartzieae tribe, the fossil specimen is closely related to *Holocalyx Micheli*.

The presence of crystals in ray cells is relatively uncommon in Faboideae wood, although prismatic crystals in chambered axial parenchyma cells are almost ubiquitous. This is therefore a potentially useful taxonomic feature at the genus or species level (Gasson and Webley, 1999). According to Gasson and Webley (1999) *Holocalyx* is highly similarity in wood anatomy to six genera present in Swartzieae and Sophoreae Tribes: *Exostyles*, *Harleyodendron*, *Lecointea*, *Zollernia*, *Acosmium* and *Aldina*. However, *Holocalyx* differs from all these in having only homocellular rays, which are more regularly storied, and in lacking crystals in the ray cells (Gasson, 1994; Gasson and Webley, 1999).

**Table 2**  
Comparison of anatomical features among *Mimosoxylon caccavariae* and morphospecies of *Mimosoxylon* morphogenus (partially adapted from Lutz, 1987, 1991; Cevallos-Ferriz and Barajas-Morales, 1994; InsideWood, 2004-onwards).

	Region	Age	Vessel grouping	Vessels/ mm <sup>2</sup>	Tangential vessel diameter (µm)	Ray type	Ray width in cell number	Ray per linear mm	Storied structure	Axial parenchyma type	Fiber type	Crystals
<i>Mimosoxylon caccavarii</i> nov. sp. Brea, Zucol et Patterer	NEA	Pe	S, VRM [2 to 4 (5–7)], VC	11–32	65–145	Ho, few He	1–4	4–9	A	V, B, M	NS	N
<i>Mimosoxylon</i> <i>acacioides</i> Kramer	West-Borneo	M-P	S	<= 5	>= 200	Ho	1–3	4–12	A	V, A, M	?	C
<i>Mimosoxylon calpocalycoides</i> Lemoigne	Omo Valley, Ethiopia	P	?	5–20	100–200	Ho	1–3	4–12	A	A, C, M	?	N
<i>Mimosoxylon krameri</i> Lemoigne	Omo Valley, Ethiopia	M	?	5–20	100–200	Ho	1, few 2–3	>= 12	P, R, AP, VE	D, V	?	N
<i>Mimosoxylon tenax</i> (Felix) Müller-Stoll et Mädél *	Oaxaca, Mexico	C	VC	8–24	50–100	Ho, He	1–3	8–14	A	V	?	N
<i>Mimosoxylon tenax</i> (Felix) Müller-Stoll et Mädél **	Baja California Sur, Mexico	O-M	S, VRM (2 to 4)	4–12	88–198	Ho	2–4	5–10	A	V, A, C, M	NS	A
<i>Mimosoxylon</i> sp. Gottwald	Europe	E	?	?	100–200	Ho	1–3	?	A	V, A, C	S	A, C
<i>Mimosoxylon santamariensis</i> Lutz	NOA	M	S, few VRM	12–17	75–175	Ho	1–3	?	A	V	NS	A
<i>Mimosoxylon</i> sp. Lutz	NEA	P	S, VRM	10–20	47–244	Ho	3–5	?	A	V	NS	A

Key to abbreviations used:

- \* Müller-Stoll and Mädél (1967), \*\* Cevallos-Ferriz and Barajas-Morales (1994).
- Region: NOA = northwestern Argentina, NEA = northeastern Argentina
- Age: C = Cretaceous, E = Eocene, O–M = Oligocene–Miocene, M = Miocene, M–P = Miocene–Pliocene, P = Pliocene, Pe = Pleistocene
- Vessel grouping: S = solitary (80% or more), VRM = vessels in radial multiples of 4 or more VC = vessel clusters
- Ray type: Ho = homocellular, He = heterocellular
- Storied structure: A = absent, P = present, R = in ray, AP = in axial parenchyma, VE = in vessel elements
- Axial parenchyma type: D = diffuse, A = aliform, V = vasicentric, B = banded, C = confluent, M = marginal
- Fiber types: S = septate, NS = non-septate
- Crystals: N = not seen, R = in ray cells, F = in fibres, A = in axial parenchyma, C = prismatic crystals in chambered axial parenchyma cells. All are prismatic crystals.

*Holocalyx* occurs in the southern of Brazil, Paraguay and north of Argentina (20° 50' S to 28° S). This species is frequently found in gallery forest of the humid Chaco region, in areas with annual average temperatures of 18 to 22 °C, and a mean annual precipitation of 1200–2200 mm (Tortorelli, 1956; Prado, 2000).

Genus **Amburanaxylon** gen. nov. Brea, Zucol et Patterer  
Type species: *Amburanaxylon tortorellii* gen. nov. et sp. nov. Brea, Zucol et Patterer

*Amburanaxylon tortorellii* gen. nov et sp. nov. Brea, Zucol et Patterer (Plate IV)

*Derivatio nominis*: The specific name, *tortorellii*, is dedicated to the memory of Lucas Tortorelli, pioneer of Argentinean xylogy.

*Holotype*: CID-PALBO 13, CID-PALBO mic. 489 (three microscopic slides).

*Repository*: Laboratorio de Paleobotánica, CICYTTP-CONICET, Diamante.

*Stratigraphic horizon*: El Palmar Formation, late Pleistocene (30° 54' 16.1" S, 57° 55' 45.9" W).

*Locality*: Santa Ana Locality, Uruguay Basin, Argentina.

*Generic diagnosis*: Diffuse porous; vessels mostly solitary, radial multiples of 2–5, clusters; medium-sized; few (<5 per mm<sup>2</sup>);

perforation plate simple; intervessel pits medium, bordered, and alternate; rays homocellular; uniseriate, sporadically 2–3 seriate or rarely 4-seriate; axial parenchyma vasicentric and confluent; fibers thick and very-thick walled, and non-septate.

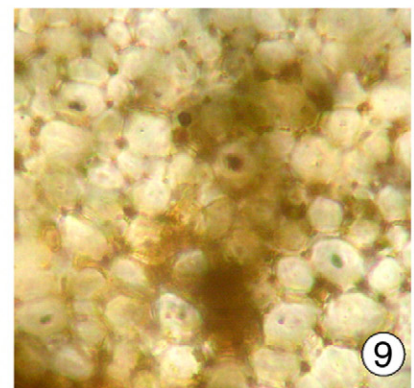
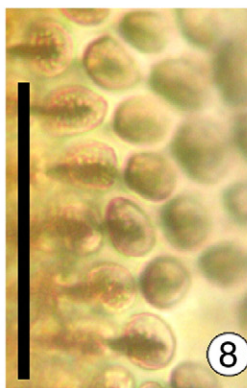
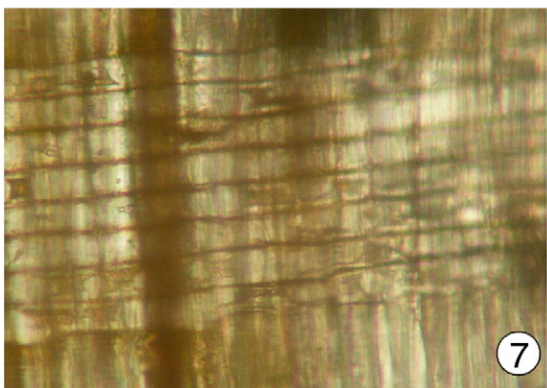
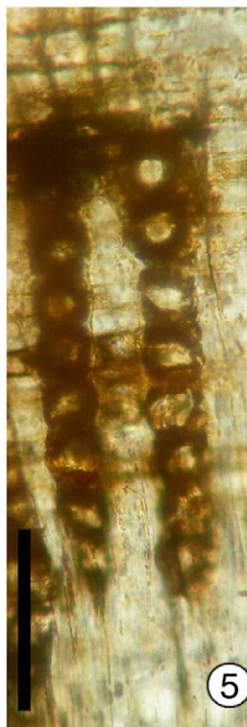
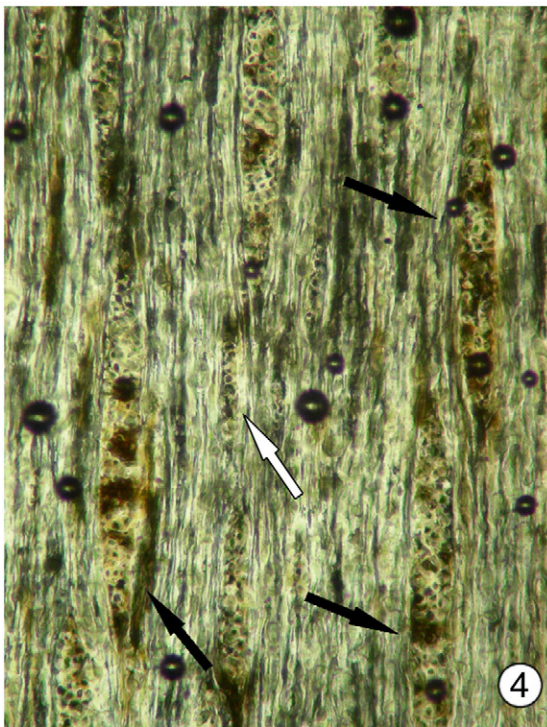
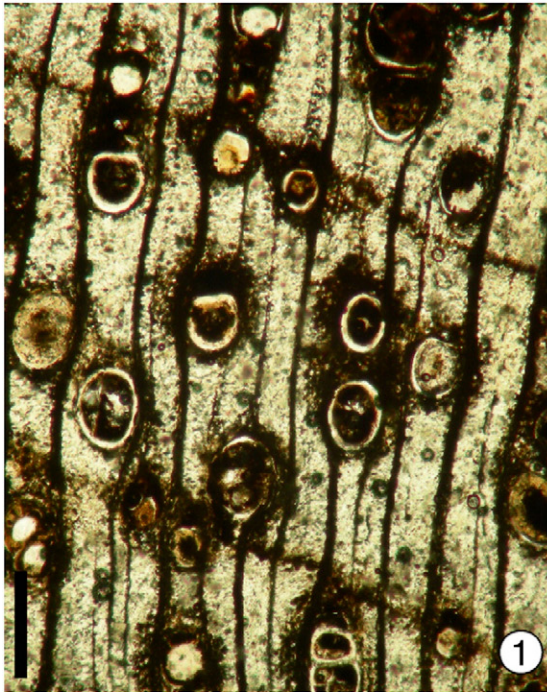
*Species diagnosis*: Diffuse porous; vessels mostly solitary, radial multiples of 2–5; clusters; medium-sized;; few (<5 per mm<sup>2</sup>); perforation plate simple; intervessel pits medium, bordered, alternate and polygonal; rays homocellular and composed of procumbent cells; mainly uniseriate, sporadically biseriate or triseriate, and rarely tetraseriate; smaller and narrow rays; <–9 rays/mm; axial parenchyma vasicentric and confluent; fibers mostly thick and very-thick walled, abundant and non-septate.

*Description*: Growth rings indistinct or absent. Diffuse porous (Plate IV, 1). Vessels predominantly solitary (64%) (Plate IV, 1,2), in radial multiples of 2–5 (15%, 10%, 3%, and 3% respectively) (Plate IV, 1,2,3) and rarely in clusters (5%) (Plate IV, 3). No contents were observed in the vessels (Plate IV, 1,2,3). The vessels are circular in outline, medium-sized, with a mean tangential diameter of 198 (150–244) µm and a mean radial diameter of 199 (92–288) µm. The mean vessel density is 3 (2–5)/mm<sup>2</sup>. The mean vessel element length is 471 (289–808) µm. Perforation plates are simple (Plate IV, 5,12). Intervessel pits are medium,

**Plate II.** *Prosopisinoxylon castroae* sp. nov. Brea, Zucol et Patterer. Holotype CID-PALBO 17.

1. Transverse section, general view showing vessels distribution, axial parenchyma and growth rings.
2. Tangential longitudinal section, general view showing short vessels with oblique or straight end walls.
3. Tangential longitudinal section, details of simple perforation plates and disposition of rays.
4. Tangential longitudinal section, general view showing uniseriate ray (white arrow) and multiseriate rays (black arrows).
5. Radial longitudinal section, detail of prismatic crystals in chambered axial parenchyma.
6. Tangential longitudinal section, detail of vessels showing arranged intervessel pits and rays.
7. Radial longitudinal section, detail of homocellular rays showing procumbent cells.
8. Radial longitudinal section, detail of bordered, alternate, vested and small intervessel pits.
9. Transverse section, detail of thick and very-thick walled, non-septate and hexagonal in outline fibers. (Scale bar in 1 and 2 = 750 µm; in 3, 4 and 6 = 200 µm; in 5, 7 and 9 = 12 µm; in 8 = 3 µm).







**Table 3**Comparison of anatomical features among *Prosopisinoxylon anciborae* (Martínez, 2010) and *Prosopisinoxylon castroae* nov. sp. Brea, Zucol et Patterer.

	Region	Age	Porosity	Vessel grouping	Vessels/mm <sup>2</sup>	Tangential vessel diameter (µm)	Ray type	Ray width in cell number	Ray per linear mm	Axial parenchyma type
<i>Prosopisinoxylon castroae</i> nov. sp. Brea, Zucol et Patterer	NEA	Pe	SRP to D	S, VRM, VC	5–10	Vessels of two different sizes 179 (89–278)	Ho	1–5	7 (6–10)	V, C, Al, M
<i>Prosopisinoxylon anciborae</i> Martínez	NOA	M	D	S, VRM, VC	9–19	Vessels of two different sizes 106 (28–213)	Ho	4–7 (1–9)	7 (5–11)	V, C, Al, B, Ap

Key to abbreviations used:

- Region: NOA = northwestern Argentina, NEA = northeastern Argentina
- Age: M = Miocene, Pe = Pleistocene
- Porosity: D = diffuse, SRP = semi-ring porous
- Vessel grouping: S = solitary, VRM = vessels in radial multiples of 4 or more VC = vessel clusters
- Ray type: Ho = homocellular
- Axial parenchyma type: Ap = apotracheal diffuse, Al = aliform, V = vasicentric, B = banded, C = confluent, M = marginal

bordered, alternate, polygonal and probably vested (Plate IV, 9,10). Their diameter is 6 (3–10) µm. Fibers are mostly thick and very-thick walled, abundant and non-septate (Plate IV, 11). Pits were not observed. The paratracheal axial parenchyma is vasicentric and confluent (Plate IV, 1,2,3). The rays are frequently uniseriate (60%), although biseriate (16%), triseriate (16%) and tetraseriate rays (8%) are also present (Plate IV, 7,8). The mean number of rays per linear mm is 6 (4–9) per linear mm. They are homocellular and composed exclusively of procumbent cells (Plate IV, 4,6,12). The mean width of rays is 48 (23–81) µm, while the mean height of rays is 387 (150–774) µm and 14 (6–24) cells high.

**Comparison:** The Sophoreae tribe is characterized by diffuse porous, frequently uni-triseriate and sporadically multiseriate rays, paratracheal axial parenchyma, and completely or incompletely storied structure (Cozzo, 1950; Tortorelli, 1956; Fujii et al., 1994; Gasson and Wray, 2001). The fossil specimen is similar to the genus *Amburana* Schwacke et Taub, especially to *A. cearensis* (Tortorelli, 1956; Roque et al., 2007). *Amburana* is typical of open and deciduous tropical forest, and is found mostly in the Caatinga and Cerrado vegetation areas of Brazil. There are also reports of this genus presence in northern Argentina, Paraguay, Bolivia and southeastern Peru (Leite, 2005). The genus *Amburana* currently is considered to contain two species, *A. cearensis* (Fr. Allem.) A.C. Smith and *A. acreana* (Ducke) A.C. Smith. (Leite, 2005).

**Plate III.** *Holocalyxylon cozzoi* sp. nov. Brea, Zucol et Patterer. Holotype CID-PALBO 16.

1. Transverse section, general view showing vessels and fibers distribution, apotracheal axial parenchyma in marginal bands with 1–3 cells width (white arrow) and paratracheal axial parenchyma aliform to confluent, to predominantly banded.
2. Tangential longitudinal section, general view showing rays storied.
3. Tangential longitudinal section, general view, vessel elements showing arranged intervessel pits and uniseriate ray (white arrow) and 2–3 seriate rays (black arrows).
4. Transverse section, detail of vessels and aliform axial parenchyma.
5. Radial longitudinal section, detail of small to medium, bordered, alternate, circular and probably vested intervessel pits.
6. Tangential longitudinal section, general view showing vessel with simple perforation plate.
7. Tangential longitudinal section, detail of 2–3 seriate rays.
8. Radial longitudinal section, general view showing homocellular rays.
9. Tangential longitudinal section, detail of prismatic crystals in chambered axial parenchyma cells with one crystal per cell. (Scale bar in 1 and 2 = 750 µm; in 4, 5, 6, 7 and 8 = 200 µm; in 9 = 12 µm).

**Plate IV.** *Amburanoxylon tortorellii* sp. nov. Brea, Zucol et Patterer. Holotype CID-PALBO 13 (see on page 46).

1. Transverse section, general view showing vessels distribution, vasicentric and confluent axial parenchyma and abundant fibers.
2. Transverse section, showing solitary and radial multiples of 5 elements and vasicentric axial parenchyma.
3. Transverse section, showing cluster and radial multiples of 2 elements.
4. Radial longitudinal section, general view showing rays.
5. Tangential longitudinal section, showing simple perforation plate and arranged intervessel pits (arrow).
6. Radial longitudinal section, general view showing homocellular rays composed by procumbent cells.
7. Tangential longitudinal section, showing disposition of rays.
8. Tangential longitudinal section, detail showing of uniseriate and multiseriate rays.
9. Tangential longitudinal section, showing intervessel pits (arrow) and short vessels with oblique or straight end walls.
10. Tangential longitudinal section, detail showing medium, bordered, alternate and polygonal intervessel pits.
11. Transverse section, detail showing mostly thick and very-thick walled, non-septate and narrow lumen (arrows) fibers.
12. Radial longitudinal section, detail of vessels showing simple perforation plate and disposition of rays. (Scale bar in 1, 2, 3 and 4 = 750 µm; in 5, 6, 7, 8, 9, and 12 = 200 µm; in 10 and 11 = 12 µm).

**Plate V.** *Schinopsixylon heckii* Lutz, 1979. Material CID-PALBO 12 (see on page 47).

1. Transverse section, general view showing solitary, in radial multiple and in long radial multiple (arrow) vessels and vasicentric, lozenge-aliform and confluent paratracheal axial parenchyma.
2. Transverse longitudinal section, general view showing solitary, in radial multiples and in cluster vessels and vasicentric, lozenge-aliform and confluent paratracheal axial parenchyma.
3. Tangential longitudinal section, general view showing multiseriate rays with secretory canal and uniseriate rays (arrow).
4. Transverse section, detail of hexagonal in outline, non-septate and very thick-walled fibers.
5. Transverse section, detail showing tyloses and gums? in vessel.
6. Tangential longitudinal section, detail of multiseriate rays with two secretory canals and uniseriate ray.
7. Tangential longitudinal section, detail of multiseriate rays with one secretory canal.
8. Tangential longitudinal section, detail of multiseriate and uniseriate (arrow) rays and vessel with tyloses. (Scale bar in 1 and 2 = 750 µm; in 3 and 8 = 200 µm; in 4, 5, 6 and 7 = 12 µm).



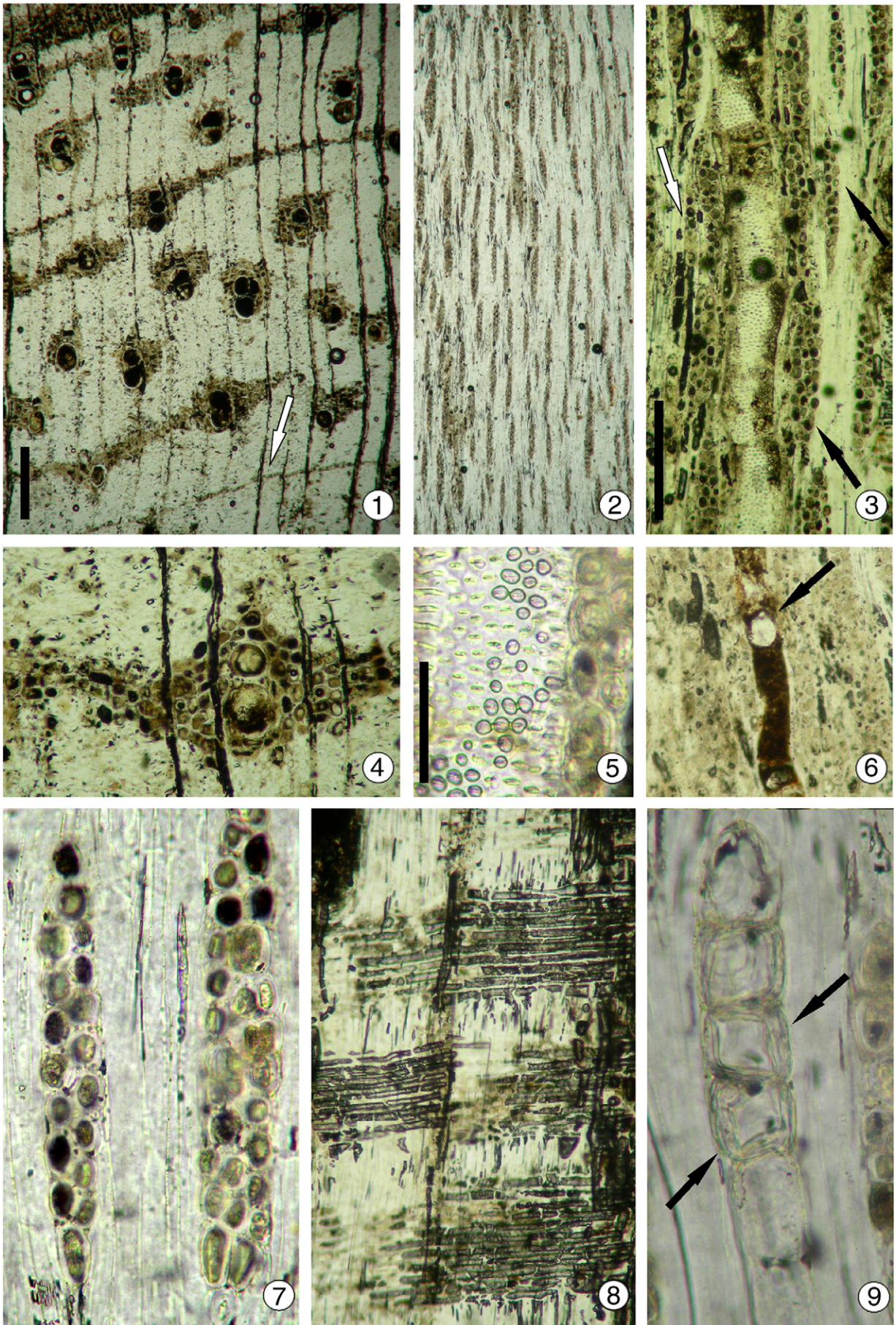


Plate III .



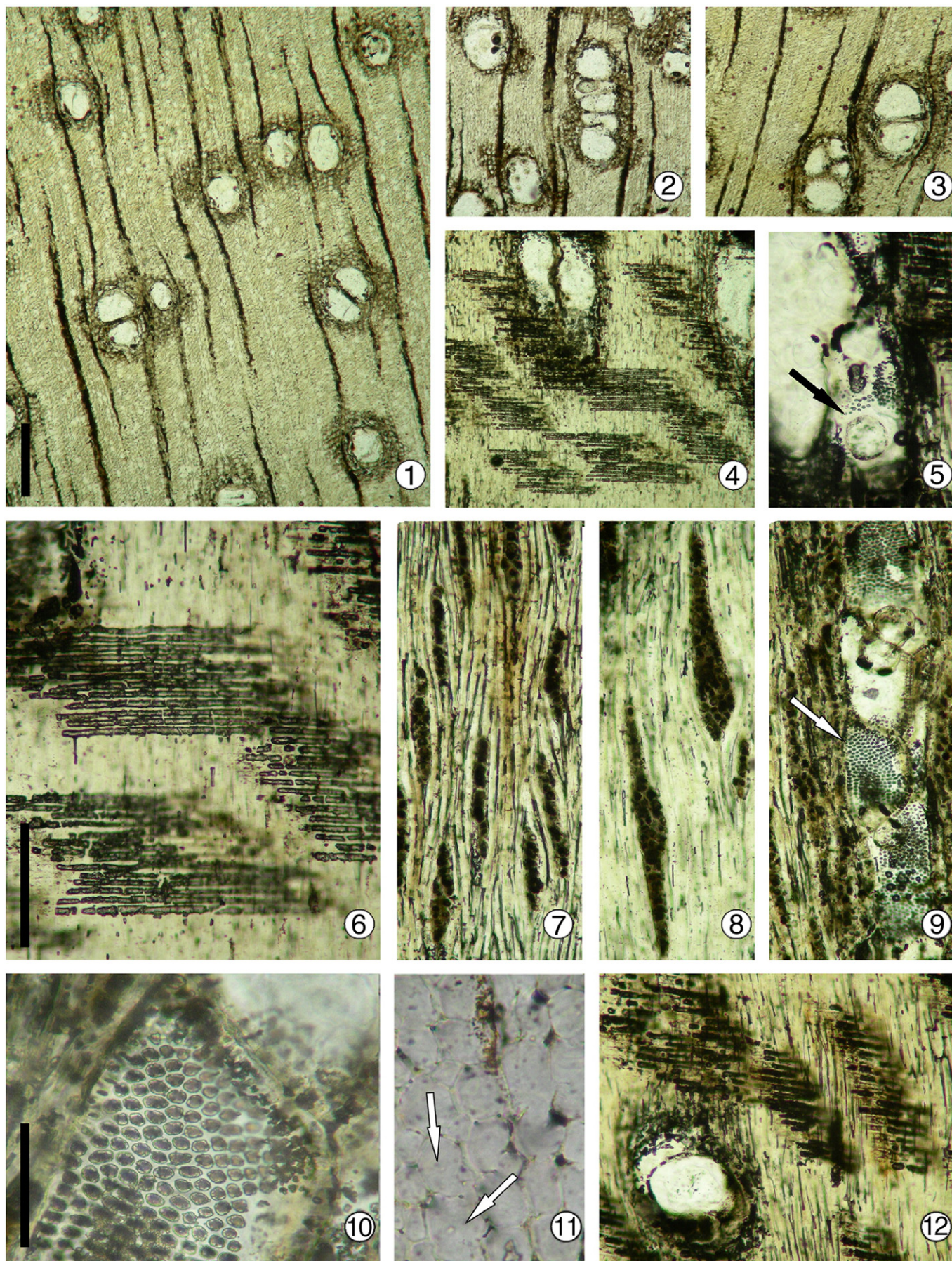


Plate IV (caption on page 44).



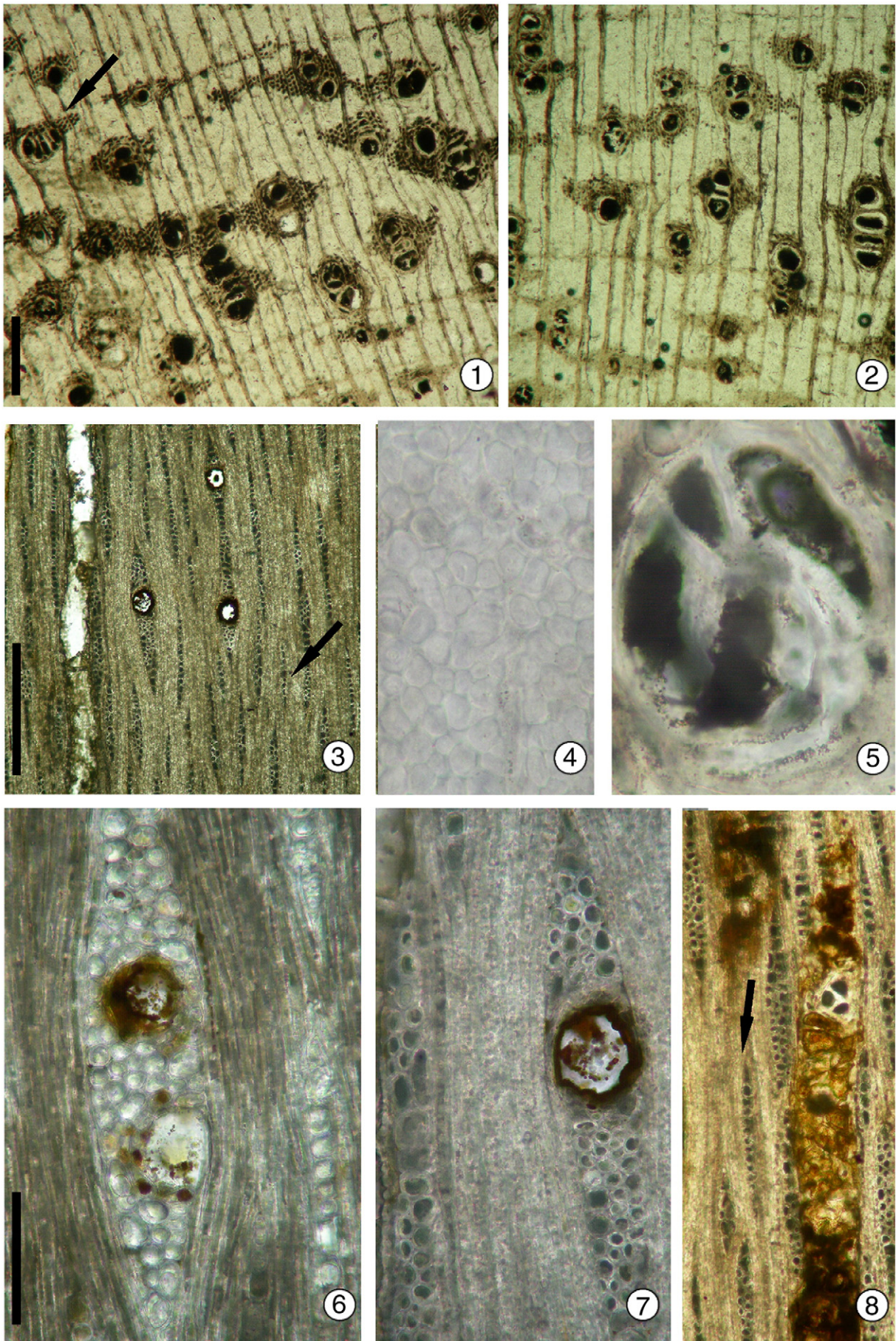


Plate V (caption on page 44).



**Table 4**  
Habitat preference, phenology, habit and extant distribution of the nearest living relatives of the fossil woods from the El Palmar Formation.

Family	Fossil genus	Living relative	Habitat preference	Phenology	Habit	Extant distribution of the nearest living relatives
Lauraceae	<i>Laurinoxylon</i>	<i>Ocotea</i> , <sup>a</sup> <i>Nectandra</i> and <i>Phoebe</i>	HF	D	T (20–25 m)	Tropical and subtropical regions of the world, the main centers are in Southeast Asia and tropical America
Cambretaceae	<i>Terminalioxylon</i>	<i>Terminalia</i> <sup>a</sup>	HF	D	T or S (7–18 m)	Paraguay, Brazil and Argentina
Myrtaceae	<i>Eugenia</i>	<i>Eugenia</i>	HF	E	T or Sh	Paraguay, Brazil, Uruguay and Argentina
Fabaceae (Mimosoideae)	<i>Menendoxylon</i>	?	?	?	?	?
Fabaceae (Mimosoideae)	<i>Mimosoxylon</i>	<i>Mimosa</i>	DF, HF	D <sup>b</sup>	T, Sh, C, L (1, 4–8 m) <sup>b</sup>	Pantropical and subpantropical American continent <sup>c</sup>
Fabaceae (Mimosoideae)	<i>Prosopisinoxylon</i>	<i>Prosopis</i> <sup>a</sup>	DF	E, D	T (3–16 m)	Arid and semiarid environments around the world <sup>d</sup>
Fabaceae (Faboideae)	<i>Holocalyxylon</i>	<i>Holocalyx</i> <sup>e</sup>	HF	E	T (20–30 m)	Brazil, Paraguay and nonwestern Argentina
Fabaceae (Faboideae)	<i>Amburanaxylon</i>	<i>Amburana</i> <sup>e</sup>	DF, HF <sup>f</sup>	D <sup>f</sup>	T (15–25 m) <sup>f</sup>	Mostly Brazil, notably in the Caatinga and Cerrado regions. Also, Peru, Bolivia and Argentina <sup>g</sup>
Anacardiaceae	<i>Schinopsixylon</i>	<i>Schinopsis</i> <sup>a</sup>	DF, HF	E	T (20–30 m)	Bolivia, Paraguay, Brazil and Argentina
Arecaceae	<i>Palmoxylon</i>	<i>Butia</i>	S <sup>g</sup>	E <sup>g</sup>	Sp (> 14 m) <sup>g</sup>	Temperate-humid savannas of southern South America <sup>g</sup>

Key to abbreviations used:  
Habitat preference: DF = dry forests, HF = humid forests, S = savannas with palm forests.  
Phenology: E = evergreen, D = deciduous.  
Habit: T = trees, Sp = stipite, Sh = shrubs, C = woody climbers, L = lianas.

- <sup>a</sup> Roth and Giménez (2006).  
<sup>b</sup> Martínez-Cabrera et al. (2006).  
<sup>c</sup> Bessega et al. (2008).  
<sup>d</sup> Catalano et al. (2008).  
<sup>e</sup> Tortorelli (1956).  
<sup>f</sup> Leite (2005).  
<sup>g</sup> Zucol et al. (2005).

**Table 5**  
Anatomical wood data used to calculate the Vulnerability Index (V) and Mesomorphy ratios (M). Percentage of grouping vessels; Perforation plates: SI, simple perforation plate; Porosity: S, wood semi-ring-porous; D, wood diffuse-porous.

Taxa	Family	Vessel tangential diameter (μm)	Vessels per. mm <sup>2</sup>	Vessel element length (μm)	Percentage of grouping vessels	Perforation plates	Porosity	Vulnerability Index (V)	Mesomorphy Index (M)
<i>Mimosoxylon</i>	Fabaceae (Mimosoideae)	101 (65–145)	19 (11–32)	278 (177–457)	52%	SI	D	5.31	1478
<i>Prosopisinoxylon</i>	Fabaceae (Mimosoideae)	179 (89–278)	8 (5–10)	255 (143–375)	51%	SI	D to S	22.37	5706
<i>Holocalyxylon</i>	Fabaceae (Faboideae)	65 (72–110)	11 (7–17)	235 (136–300)	52%	SI	D	5.91	1389
<i>Amburanaxylon</i>	Fabaceae (Faboideae)	198 (150–244)	3 (2–5)	471 (289–808)	36%	SI	D	66	31,086
<i>Schinopsixylon</i>	Anacardiaceae	65 (21–103)	17 (9–24)	216 (61–368)	47%	SI	D	3.82	826

Family ANACARDIACEAE R. Br. 1818  
Genus *Schinopsixylon* Lutz 1979  
Type species *Schinopsixylon herbstii* Lutz 1979

*Schinopsixylon heckii* Lutz 1979 (Plate V)  
*Holotype*: PB-CTES 4826 (slides PMP-CTES 1202 a–d).  
*Syntypes*: PB-CTES 4906, PMPCTES 1203 (Lutz, 1979).  
*Material examined*: CID-PALBO 12, CID-PALBO mic. 488 (three microscopic slides).  
*Repository*: Laboratorio de Paleobotánica, CICYTTP-CONICET, Diamante.  
*Stratigraphic horizon*: El Palmar Formation, late Pleistocene (30° 54' 16.1" S, 57° 55' 45.9" W).  
*Locality*: Santa Ana Locality, Uruguay Basin, Argentina.  
*Other materials*: LPPB 12418 (slides pmlPPB 1281–1303) (Brea, 1999).  
*Description*: Growth rings made distinct by a small band of fibers. Diffuse porous. Vessels are solitary (52%), or in radial multiples of 2–3 (4–5) (13%, 12%, 5%, and 1% respectively) (Plate V, 1,2). They are also present in clusters and in long radial multiples (16%) (Plate V, 1). The vessels are circular to oval in outline, many with dark deposits. They have a mean tangential diameter of 65 (21–103) μm and a mean radial diameter of 66 (31–106) μm. The mean vessel density is 17 (9–24)/mm<sup>2</sup>. The mean vessel element length is 216 (61–368) μm. Perforation plates are exclusively simple. Intervessels pitting are bordered and alternate. Tyloses and gums or resins? are present in many vessels and abundant (Plate V, 1,2,3). Fibers are hexagonal in outline, abundant, non-septate and very thick-walled (Plate V, 4), with a mean thickness of 3 (2–3) μm and a mean diameter of 8 (5–10) μm.

The apotracheal axial parenchyma is diffuse-in-aggregates and the paratracheal axial parenchyma is vasicentric, lozenge-aliform and commonly confluent (Plate V, 1,2). The rays are mostly uniseriate (25%), biseriate (35%), and tetraseriate (25%), with some triseriate rays (15%) also present (Plate V, 3,8). The mean number of rays per linear mm is 9 (6–13) per linear mm. Rays are heterocellular and composed of procumbent and upright cells. The mean width of rays is 42 (10–75) μm. The mean height of rays is 344 (170–807) μm and 16 (7–25) cells high. In some cases, multiseriate rays present one or two secretory canals containing tannins? (Plate V, 3,6,7). Crystals were not observed in axial parenchyma, in vessels or in rays.  
*Comparison*: The combination of diffuse porosity; vessels that are solitary or in radial multiples; simple perforation plate; diffuse-in-aggregates apotracheal axial parenchyma, vasicentric, lozenge-aliform and commonly confluent paratracheal axial parenchyma; tyloses in vessels; uniseriate and multiseriate rays; multiseriate rays with secretory canals and non-septate fibers, occur in *Schinopsixylon heckii* Lutz, 1979 in the Anacardiaceae. The fossil wood especially resembles that of the two extant species *Schinopsis balansae* Engl. and *Schinopsis lorentzi* (Gris.) Engl. The *Schinopsixylon heckii* wood type is common in Quaternary sediments in Argentina (see Zucol et al., 2004).

## 5. Discussion

The El Palmar Formation has yielded well-preserved deposits of permineralized wood. A total of 14 morphotypes have been recorded, with 10 of these reported in previous papers. These taxa include two lauraceous woods (*Laurinoxylon mucilaginosum* [Brea] Dupéron-



Laudoueneix and Dupéron, 2005; *Laurinoxylon artabeae* [Brea] Dupéron-Laudoueneix and Dupéron, 2005), one combretaceous wood (*Terminalioxylon concordiensis* Brea and Zucol, 2001), one myrtaceous wood (*Eugenia* sp. Brea et al., 2001a), several legumes woods (*Menendoxylon mesopotamiensis* Lutz, 1979, *Menendoxylon areniensis* Lutz, 1979, *Menendoxylon piptadiensis* Lutz, 1987), one anacardiaceous wood (*Schinopsisxylon heckii* Lutz, 1979) and two palm stipites (*Palmoxylon concordiensis* Lutz, 1980, and *Palmoxylon yuqueriensis* Lutz, 1984).

The previous palaeobotanical data and distributions of the nearest living relatives (Table 4) demonstrated the existence of mixed humid forests, semi-arid forests and palm paleocommunities during the late Pleistocene in the southernmost areas of the Uruguay Basin. These are characteristic elements of subtropical to tropical flora, and indicate a temperate-warm and humid-subhumid to semi-arid climate (Zucol et al., 2004, and references therein; Brea and Zucol, in press).

Characteristic elements such as Lauraceae, Combretaceae and Myrtaceae (Brea, 1998; Brea and Zucol, 2001, 2007, in press; Brea et al., 2001a; Zucol et al., 2004, 2005) may have grown in gallery forests, while the Anacardiaceae and Leguminosae–Mimosoideae (Lutz, 1979; Brea, 1999) indicate the presence of dry forests. The predilection of legumes for semi-arid to arid habitats is related to a nitrogen-demanding metabolism (McKey, 1994).

The abundance of members of Arecaceae (Lutz, 1980, 1984, 1986; Zucol et al., 2004, 2005), which are characteristic elements of subtropical–tropical flora, supports arguments for the existence of extensive areas of palms during this time interval. This abundance also indicates a temperate-warm and humid climate.

This contribution adds two new morphospecies and two new morphogenera for the El Palmar Formation, *Mimosoxylon caccavariae*, *Prosopisinoxylon castroae*, *Holocalyxylon cozzoi* and *Amburanoxylon tortorellii*. These taxa have close relatives in present ecosystems (see Table 4).

The majority of the fossil woods have distinct growth rings, indicating that these trees were growing where there was seasonal variation in water availability, and that they were mainly deciduous. The presence of diffuse porosity, or diffuse with a tendency towards semi-ring porosity, as was observed in *Mimosoxylon caccavariae*, might be related to semi-arid and arid climatic conditions (Moglia and Giménez, 1998). *Prosopisinoxylon castroae* has short vessel elements and vessels of two distinct diameter classes, which would indicate xeric conditions. This taxon probably would have grown in a seasonally dry climate (Martínez, 2010). The presence of vested pits, which are associated with prevention of embolism, have been related to dry zone plants (Lindorf, 1994), and were present in *Mimosoxylon caccavariae* and *Prosopisinoxylon castroae*.

Many of the anatomical characters observed in the fossil woods from El Palmar Formation, such as diffuse porosity, small diameter vessels (<200 µm), grouped or multiple vessels, short vessel elements, and simple perforation plates (Table 5), are likely to have contributed to hydraulic safety (Wheeler and Baas, 1991, 1993). The low vessels frequencies observed in *Amburanoxylon tortorellii* (vessels density <5 mm<sup>2</sup>) could be used as an indicator of wet tropical conditions, whereas simple perforation plates are often considered to have been an adaptation for more efficient water transport (Table 5) (Wheeler and Baas, 1993; Woodcock et al., 2000).

Vulnerability Index (V) and Mesomorphy ratios (M) (Table 5) show values ranging from 3.82 to 66 and 826 to 31,086 respectively. *Amburanoxylon tortorellii* present the most mesomorphic features, whereas *Schinopsisxylon heckii* has a Vulnerability Index of 3.82. This demonstrates that these woods show evidence of well-developed xeromorphic features. When the value of this index differs from that which is expected, for example, when mesomorphic wood anatomy is found in xeric species, a mitigating effect based on other plant features can be assumed (Carlquist, 1977; Lindorf, 1994). In our case, *Prosopisinoxylon castroae* shows very high Vulnerability

Index values (Table 5). The information is supported by extant species of *Prosopis* and *Acacia* from the Chaco region of Argentina, two genera with special adaptations to a semi-arid to arid climate. They have high Vulnerability Index values (3–5), and their alternative means of survival in times of water stress is the development of deep rooting to access the water table (Moglia and Giménez, 1998).

## 6. Conclusions

New information about paleobotanical record has been added for the southernmost areas of the Uruguay Basin, increasing the palaeobiodiversity knowledge during the late Pleistocene. Four new members of the Mimosoideae and Faboideae subfamilies have been recorded for the El Palmar Formation. *Holocalyxylon* and *Amburanaxylon* are also the first fossil woods recorded from the Uruguay Basin with affinity to the Faboideae.

The presence of *Holocalyxylon* and *Amburanaxylon*, two morphogenera linked to the extant genera *Holocalyx* and *Amburana*, supports the hypothesis proposed by Prado (2000) and Pennington et al. (2000), which suggests that Seasonally Dry Tropical Forests (SDTFs) were more widespread during the Pleistocene, and in fact represented a continuous extension in South America. These data are supported by the existence of other fossil records for taxa such as, *Astroniumxylon parabalansae* (Franco and Brea, 2008; Franco, 2009); *Astroniumxylon bonplandianum* (Franco, 2009); *Astroniumxylon portmannii* (Brea et al., 2001b); *Solanumxylon paranensis*, *Piptadenioxylon paraexcelsa* (Franco and Brea, 2008); *Anadenantheroxylon villaurquicense* (Brea et al., 2001b); *Laurophyllum* sp., *Myrciophyllum paranaesianum* and *Schinus* aff. *terebinthifolius* (Anzótegui and Aceñolaza, 2008).

The evidence presented here also supports the argument that these morphospecies were part of a heterogeneous environment. Two fossil forest types can be distinguished by their species composition: a tropical–subtropical humid gallery forest type with *Holocalyxylon cozzoi* and *Amburanoxylon tortorellii*, and a semi-arid forests type with the presence of *Mimosoxylon caccavariae*, *Prosopisinoxylon castroae*, and *Schinopsisxylon heckii*. These forests were developed during the Oxygen Isotopic State 5a (late Pleistocene), which corresponds to the Last Interglacial. In agreement with the wood anatomy of the flora from the El Palmar Formation, sedimentological data (Iriondo and Kröhling, 2008) and phytolith assemblages (Zucol et al., 2005) have suggested a temperate-warm, humid-semiarid climate during this geologic time period.

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## References

- Aceñolaza, F.G., 2007. Geología y Recursos Geológicos de la Mesopotamia Argentina. Serie de Correlación Geológica 22, 1–149.
- Angyalossy-Alfonso, V., Miller, R.B., 2002. Wood anatomy of the Brazilian species of *Swartzia* and considerations within the tribe Swartzieae. IAWA Journal 23, 359–390.
- Anzótegui, L.M., Aceñolaza, P.G., 2008. Macrofloristic assemblage of the Paraná Formation (Middle–Upper Miocene) in Entre Ríos (Argentina). Neues Jahrbuch für Geologie und Paläontologie 248, 159–170.
- APG, I.I.I., 2009. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. Botanical Journal of the Linnean Society 161, 105–121.

- Avisé, J.C., Johns, G.C., 1999. Proposal for a standardized temporal scheme of biological classification for extant species. *Proceedings of the National Academy of Science* 96, 7358–7363.
- Baretta-Kuipers, T., 1981. Wood Anatomy of Leguminosae: its relevance to taxonomy. In: Polhill, R.M., Raven, P.H. (Eds.), *Advances in Legume Systematic 2*. The Royal Botanical Gardens, Kew, pp. 677–705.
- Bessegga, C., Hopp, H.E., Fortunato, R.H., 2008. Toward a phylogeny of *Mimosa* (Leguminosae: Mimosoideae): a preliminary analysis of southern South American species based on chloroplast DNA sequence. *Annals of the Missouri Botanical Garden* 95, 563–575.
- Bossi, J., 1969. Geología del Uruguay. Universidad de la República, Departamento de Publicaciones. Colección Ciencias 12. 2ª Edición, Montevideo. 464 pp.
- Boureau, E., 1953. Etude paléoxylologique du Sahara. XIX. Leguminosylon ersanense n. sp., bois fossile des collines d'Ersane (Sahara soudanais). *Bulletin du Muséum d'Histoire Naturelle, Paris* 2, 353–359.
- Brea, M., 1998. *Ulmium muclaginosum* n.sp. y *Ulmium artabeae* n.sp., Dos leños fósiles de Lauraceae en la Formación El Palmar, provincia de Entre Ríos, Argentina. *Ameghiniana* 35, 193–204.
- Brea, M., 1999. Leños fósiles de Anacardiaceae y Mimosaceae de la Formación El Palmar (Pleistoceno superior), departamento de Concordia, provincia de Entre Ríos, Argentina. *Ameghiniana* 36, 63–69.
- Brea, M., Zucol, A.F., 2001. Maderas fósiles de Combretaceae de la Formación El Palmar (Pleistoceno), provincia de Entre Ríos, Argentina. *Ameghiniana* 38, 499–517.
- Brea, M., Zucol, A.F., 2007. New fossils record from Uruguay basin related to El Palmar Formation floristic composition. *Ameghiniana* 44 (4-suplemento), 78R.
- Brea, M., Zucol, A.F., in press (2011). The Paraná-Paraguay Basin: a review of the geological and paleoenvironmental records. In: Albert, J.S., Reis, R.R. (Eds.), *Historical Biogeography of Neotropical Freshwater Fishes*. University of California.
- Brea, M., Zucol, A.F., Scopel, A., 2001a. Estudios paleobotánicos del Parque Nacional El Palmar (Argentina): I. Inclusiones minerales en leños fósiles de Myrtaceae. *Natura Neotropicalis* 32, 33–40.
- Brea, M., Aceñolaza, P.G., Zucol, A.F., 2001b. Estudio paleoxilológico en la Formación Paraná, Entre Ríos, Argentina. XI Simposio Argentino de Paleobotánica y Palinología. Asociación Paleontológica Argentina, Publicación Especial, 8, pp. 7–17.
- Brea, M., Zamuner, A.B., Matheos, S.D., Iglesias, A., Zucol, A.F., 2008. Fossil Wood of the Mimosoideae from the early Paleocene of Patagonia, Argentina. *Alcheringa* 32, 427–441.
- Candolle, A.P.de., 1825. *Leguminosae. Prodromus systematis naturalis regni vegetabilis* 2. Treuttel and Würtz, Paris, pp. 93–524.
- Carlquist, S., 1977. Ecological factors in wood evolution: a floristic approach. *American Journal of Botany* 64, 887–896.
- Carlquist, S., 2001. Comparative wood anatomy. Systematic, ecological, and evolutionary aspects of dicotyledon wood. Springer Series in Wood Science. Springer. 448 pp.
- Carlquist, S., Hoekman, D.A., 1985. Ecological wood anatomy of the woody southern Californian flora. *IAWA Bulletin* n.s. 6, 319–347.
- Castro, M.A., 1991. Ultrastructure of vestures on the vessel wall in some species of *Prosopis* (Leguminosae–Mimosoideae). *IAWA Bulletin* n.s., 12, 425–430.
- Castro, M.A., 1994. Maderas argentinas de *Prosopis*. Atlas anatómico. Ed. Secretaría General de la Presidencia de la Nación. 101 pp.
- Catalano, S.A., Vilardi, J.C., Tosto, D., Saidman, B.O., 2008. Molecular phylogeny and diversification history of *Prosopis* (Fabaceae: Mimosoideae). *Biological Journal of the Linnean Society* 93, 621–640.
- Cevallos-Ferriz, S.R.S., Barajas-Morales, J., 1994. Fossil woods from the El Cien formation in Baja California Sur: Leguminosae. *IAWA Journal* 15, 229–245.
- Collinson, M.E., 1986. Use of modern generic names for plant fossils. In: Spicer, R.A., Thomas, B.A. (Eds.), *Systematic and Taxonomic Approaches in Palaeobotany: Systematics Association Special*, vol. 31, pp. 91–104.
- Cozzo, D., 1950. Anatomía del leño secundario de las leguminosas Papilionoideas Argentinas silvestres y cultivadas. Instituto Nacional de Investigaciones de las Ciencias Naturales y Museo Argentino Bernardino Rivadavia: Ciencias Botánicas, 1, pp. 223–361.
- Cozzo, D., 1951. Anatomía del leño secundario de las leguminosas Mimosoideas y Cesalpinoideas Argentinas silvestres y cultivadas. Instituto Nacional de Investigaciones de las Ciencias Naturales y Museo Argentino Bernardino Rivadavia: Ciencias Botánicas, 2, pp. 63–146.
- Dupéron-Laudoueneix, M., Dupéron, J., 2005. Bois fossils de Lauraceae: nouvelle découverte au Cameroun, inventaire et discussion. *Annals de Paléontologie* 91, 127–151.
- Evans, J.A., Gasson, P.E., Lewis, G.P., 2006. Wood anatomy of the Mimosoideae (Leguminosae). *IAWA Journal Supplement* 5 117 pp.
- Felix, J., 1882. Stüden übre Fossile Hölzer. Druck von Pöschel und Trepte, Leipzig. 84 pp.
- Felix, J., 1899. Fossile Hölzer Von Tlacolula, pp. 46–51. In *Versteinerungen aus dem Mexikanischen Staat Oaxaca*, Felix, J. & Nathorst, A., In Beiträge zur Geologie und Paläontologie der Republik Mexico 2, J. Felix and H. Lenk, eds., A. Felix, Leipzig, 39–54.
- Ferrero, B., Brandoni, D., Noriega, J.I., Carlini, A.A., 2007. Mamíferos de la Formación El Palmar (Pleistoceno tardío) de la provincia de Entre Ríos, Argentina. *Revista del Museo Argentino de Ciencias Naturales* n.s. 9, 109–117.
- Franco, M.J., 2009. Leños fósiles de Anacardiaceae en la Formación Ituzingó (Plioceno–Pleistoceno), Toma Vieja, Paraná, Entre Ríos, Argentina. *Ameghiniana* 46, 587–604.
- Franco, M.J., Brea, M., 2008. Leños fósiles de la Formación Paraná (Mioceno Medio), Toma vieja, Paraná, Entre Ríos, Argentina: registro de bosques estacionales mixtos. *Ameghiniana* 45, 699–717.
- Fujii, T.P., Baas, P., Gasson, P., Ridder-Numan, J.W.A., 1994. Wood anatomy of the *Sophora* group. Pp 205–249. In: Ferguson, I.K., Tucker, S. (Eds.), *Advances in Legume Systematics 6, Structural Botany*. The Royal Botanic Gardens, Kew, pp. 205–249.
- García, N.O., Ghiotto, M.A., Silber, M.L., 2000. About the relations between ENSO and rainfalls in the southeast of South America. 15th Conference on Hydrology, Abstract. 4 pp.
- Gasson, P., 1994. Wood anatomy of the tribe Sophoreae and related Caesalpinoideae and Papilionoideae. In: Ferguson, I.K., Tucker, S. (Eds.), *Advances in Legume Systematics 6, Structural Botany*. The Royal Botanic Gardens, Kew, pp. 165–203.
- Gasson, P., Webley, P., 1999. Wood anatomy of exostyles venusta (Swartziaeeae, Papilionoideae, Leguminosae). *IAWA Journal* 20, 59–66.
- Gasson, P., Wray, E.J., 2001. Wood anatomy of *Cyathostegia mathewsii* (Swartziaeeae, Papilionoideae, leguminosae). *IAWA Journal* 22, 193–199.
- Gentili, C., Rimoldi, H., 1979. Mesopotamia. Academia Nacional de Ciencias, Segundo Simposio Geología Regional Argentina: Academia Nacional de Ciencias, Córdoba, 1, pp. 185–223.
- Gros, J.P., 1992. A synopsis of the fossil record of mimosoid legume Wood. In: Herendeen, P.S., Dilcher, D.L. (Eds.), *Advances in Legume Systematics*, 4, The Fossil Record. The Royal Botanic Gardens, Kew, pp. 69–84.
- IAWA Committee, 1989. IAWA list of microscopic feature for hardwood identification. International Association of Wood Anatomists. *Bulletin* 10, 219–332.
- InsideWood, 2004-onwards. Published on the Internet. <http://www.insidewood.lib.ncsu.edu/search> [June 2009].
- IPNI, 2004. The International Plant Name Index. <http://www.ipni.org> [Accessed 19 december 2009].
- Iriondo, M.H., 1980. El Cuaternario de Entre Ríos. Asociación de Ciencias Naturales del Litoral. *Revista* 11, 125–141.
- Iriondo, M.H., 1996. Estratigrafía del Cuaternario de la Cuenca del río Uruguay. 13º Congreso Geológico Argentino y 3º Congreso de Exploración de Hidrocarburos (Buenos Aires). *Actas* 4, 15–25.
- Iriondo, M., 1998. Excursion guide N° 3, Loess in Argentina: temperate and tropical. Province of Entre Ríos. International Association for Quaternary Research, International Joint Field Meeting, pp. 1–27.
- Iriondo, M.H., Kröhlhling, D., 1997. The tropical loess. In: Zhisheng, A., Weijian, Z. (Eds.), *Quaternary Geology. Proc. 30th International Geological Congress*. VSP International Sciences Publishing, Beijing, pp. 61–77.
- Iriondo, M.H., Kröhlhling, D., 2001. A neofossil kaolinitic mineral in the Upper Pleistocene of NE Argentina. International Clay Conference 12 (Bahía Blanca), Abstract, 6.
- Iriondo, M.H., Kröhlhling, D., 2007. La Formación El Palmar (informalmente Fm Salto Chico) y el acuífero San Salvador. Entre Ríos. 5º Congreso Argentino de Hidrogeología (Paraná). *Resúmenes*, pp. 433–441.
- Iriondo, M.H., Kröhlhling, D., 2008. Cambios ambientales en la cuenca del Uruguay (desde el Presente hasta dos millones de años atrás). Colección Ciencia y Técnica. Universidad Nacional del Litoral, Santa Fe. 360 pp.
- Judd, W., Campbell, C., Kellogg, E., Stevens, P., 1999. *Plant Systematics*. Sinauer Associates, Inc, Sunderland, Massachusetts, USA. 464 pp.
- Kramer, K., 1974. Die Tertiären Hölzer Südost-Asiens (Under Ausschluss der Dipterocarpaceae). 1. Teil. The Tertiary woods of Southeast-Asia (Dipterocarpaceae excluded). Par 1. *Palaeontographica* Abt. B 144, 45–181.
- Leite, E.J., 2005. State-of-knowledge on *Amburana cearensis* (Fr. Allen.) A.C. Smith (Leguminosae: Papilionoideae) for genetic conservation in Brazil. *Journal of Nature Conservation* 13, 49–65.
- Lemoigne, Y., 1978. Flores Tertiares de la Haute Vallée de l'Omo (Ethiopie). *Palaeontographica* 165B, 80–157.
- Lindley, J., 1836. *Genera and species of Orchidaceous plants*. Londres, 553 pp.
- Lindorff, H., 1994. Eco-anatomical wood features of species from a very dry tropical forest. *IAWA Journal* 15, 361–376.
- Lutz, A.I., 1979. Maderas de angiospermas (Anacardiaceae y Leguminosae) del Plioceno de la provincia de Entre Ríos, Argentina. *Facena* 3, 39–63.
- Lutz, A.I., 1980. *Palmoxydon concordiense* n. sp. del Plioceno de la Provincia de Entre Ríos, República Argentina. 2º Congreso Argentino de Paleontología y Bioestratigrafía y 1º Congreso latinoamericano de Paleontología (Buenos Aires). *Actas* 3, 129–140.
- Lutz, A.I., 1984. *Palmoxydon yuqueriense* n. sp. del Plioceno de la Provincia de Entre Ríos, Argentina. 3º Congreso Argentino de Paleontología y Bioestratigrafía (Corrientes). *Actas* 197–207.
- Lutz, A.I., 1986. Descripción morfo-anatómica del estípide de *Palmoxydon concordiense* Lutz del Plioceno de la provincia de Entre Ríos, Argentina. *Facena* 6, 17–32.
- Lutz, A.I., 1987. Estudio anatómico de maderas terciarias del Valle de Santa María (Catamarca-Tucumán), Argentina. *Facena* 7, 125–143.
- Lutz, A.I., 1991. Descripción anatómica de *Mimosoxylon* sp. Del Plioceno (Formación Ituzingó) de la provincia de Corrientes, Argentina. *Revista de la Asociación de Ciencias Naturales del Litoral* 22, 3–10.
- Martínez, L.A.C., 2010. *Prosopisoxylon anciborae* nov. gen. et sp. (Leguminosae, Mimosoideae) from the Late Miocene Chiquimil Formation (Santa María Group), Catamarca, Argentina. *Review of Palaeobotany and Palynology* 158, 262–271.
- Martínez-Cabrera, H.I., Cevallos-Ferriz, S.R.S., Poole, I., 2006. Fossil Woods from early Miocene sediments of the El Cien Formation, Baja California Sur, Mexico. *Review of Palaeobotany and Palynology* 138, 141–163.
- McKey, D., 1994. Legumes and nitrogen: the evolutionary ecology of a nitrogen-demanding lifestyle. In: Sprent, J.I., McKey, D. (Eds.), *Advances in Legume Systematic 5, The Nitrogen Factor*. The Royal Botanic Gardens, Kew, pp. 211–228.
- Menéndez, C.A., 1962. Leño petrificado de una leguminosa del terciario de Tiopunco, provincia de Tucumán. *Ameghiniana* 2, 121–126.
- Metcalf, C.R., Chalk, L., 1950. *Anatomy of the Dicotyledons* 2 Vol. Clarendon Press, Oxford. 724pp.



- Micheli, M., 1883. Mémoires de la Société de Physique et d'Histoire Naturelle de Genève 28, 41.
- Moglia, G., Giménez, A.M., 1998. Rasgos anatómicos característicos del hidrosistema de las principales especies arbóreas de la región Chaqueña argentina. Investigaciones Agrarias: Sistemas de Recursos Forestales 7, 53–71.
- Montaño, J., 2004. El acuífero Salto: Un recurso hídrico cenozoico. In: Veroslavsky, G., Ubilla, M., Martínez, S. (Eds.), Cuencas sedimentarias de Uruguay. Geología, Paleontología y Recursos Naturales. Cenozoico. DIRAC-FC. Montevideo, Uruguay, pp. 315–322.
- Müller-Stoll, W.R., Mädler, E., 1967. Die Fossilen Hölzer Eine Revision der mit Leguminosen verglichenen fossilen Hölzer und beschreibungen älter und neue Arten. Paleontographica B119, 95–174.
- Nishida, M., 1981. Petrified woods from the Tertiary of Mocha Island (a preliminary report). In: Nishida, M. (Ed.), A Report of the Paleobotanical Survey of Southern Chile by Grant-in-Aid for Overseas Scientific Survey. Chiba University, Yayoicho, Japan, pp. 31–33.
- Nishida, M., 1984. The anatomy and affinities of the petrified plants from the Tertiary of Chile. III. Petrified woods from Mocha Island, Central Chile. In: Nishida, M. (Ed.), Contributions to the Botany of the Andes. Tokyo, Academia Scientific Book, pp. 96–110.
- Pennington, R.T., Prado, D.E., Pendry, C.A., 2000. Neotropical seasonally dry forest and Quaternary vegetation changes. Journal of Biogeography 27, 261–273.
- Pons, D., 1983. Contribution à l'étude paléobotanique du Mésozoïque et du Cénozoïque de Colombie, Thèse Dr. Etat, Université Pierre et Marie Curie, Paris, 655 pp.
- Prado, D.E., 2000. Seasonally dry forest of tropical South America: from forgotten ecosystems to a new phytogeographic unit. Edinburgh Journal of Botany 57, 437–461.
- Richter, H.G., Dallwitz, M.J., 2000 onwardss. Commercial timbers: descriptions, illustrations, identification and information retrieval. <http://www.biodiversity.uno.edu/delta/> (18 October).
- Rimoldi, H.V., 1962. Aprovechamiento del río Uruguay en la zona de Salto Grande. Estudio geotectónico-geológico para la presa de compensación proyectada en Paso Hervidero (provincia de Entre Ríos). Primeras Jornadas de Geología Argentina (San Juan), Anales 2, 287–310.
- Roque, R.M., Cortés, M.G., Moreno, J.R., 2007. Clave de identificación de macroscópica para 22 especies maderables de Bolivia. Revista Forestal Venezolana 51, 179–193.
- Roth, I., Giménez, A.M., 1997. Argentine Chaco forests. Dendrology, tree structure, and economic use. 1. The semi-arid Chaco. Encyclopedia of Plant Anatomy. 180 pp.
- Roth, I., Giménez, A.M., 2006. Argentine Chaco Forests. Dendrology, tree structure, and economic use. 2. The humid Chaco. Encyclopedia of Plant Anatomy. 204 pp.
- Rudd, V.E., 1972. Leguminosae-Faboideae-Sophoreae. North American Flora 7, 1–53.
- Schuster, J., 1910. Ueber Nicolien und Nicolienähnliche Hölzer. Kongliga Svenska Vetenskapsakademiens Årsbok 45, 1–18.
- Schwacke, C.A.W., Taubert, P.H.W., 1894. Nat. Pflanzenfram. 3, 387.
- Silva Curvello, W., 1955. Sobre um vegetal do linho de Fonseca, Minas Gerais. Anais da Academia Brasileira de Ciências 27, 293–296.
- Suguio, K., Mussa, D., 1978. Madeiras fósseis dos aluviões antigos do Rio Tietê, São Paulo. Boletim IG. Instituto de Geociências da Universidade de São Paulo, 9, pp. 25–45.
- Tonni, E.P., 1987. *Stegomastodon platensis* y la antigüedad de la Formación El Palmar, en el Departamento Colón, Entre Ríos. Ameghiniana 24, 323–324.
- Tortorelli, L.A., 1956. Maderas y Bosques Argentinos. Editorial ACME, S.A.C.I., Buenos Aires. 910 pp.
- Veroslavsky, G., Montaño, J., 2004. Sedimentología y estratigrafía de la Formación Salto (Pleistoceno). In: Veroslavsky, G., Ubilla, M., Martínez, S. (Eds.), DIRAC-FC. Montevideo, Uruguay, pp. 147–166.
- Wheeler, E., Baas, P., 1991. A survey of the fossil record for dicotyledonous wood and its significance for evolutionary and ecological wood anatomy. IAWA Bulletin n.s. 12, 275–332.
- Wheeler, E., Baas, P., 1992. Fossil wood of the Leguminosae: a case study in xylem evolution and ecological anatomy. In: Herendeen, P.S., Dilcher, D.L. (Eds.), Advances in Legume Systematics, 4. The fossil Record. The Royal Botanic Gardens, Kew, pp. 207–223.
- Wheeler, E., Baas, P., 1993. The potentials and limitations of dicotyledonous wood anatomy for climatic reconstructions. Paleobiology 19, 487–498.
- Woodcock, D.W., 1994. Occurrence of woods with a gradation in vessel diameter across the ring. IAWA Journal 15, 377–385.
- Woodcock, D.W., Dos Santos, G., Reynel, C., 2000. Wood characteristics of Amazon forest types. IAWA Journal 21, 277–292.
- Zucol, A.F., Brea, M., Lutz, A., Anzótégui, L., 2004. Aportes al conocimiento de la paleobiodiversidad del Cenozoico superior del Litoral argentino: Estudios Paleoflorísticos. In: Aceñolaza, F.G. (Ed.), Temas de la Biodiversidad del Litoral Fluvial Argentino. Miscelánea, 12. INSUGEO, Tucumán, pp. 91–102.
- Zucol, A.F., Brea, M., Scopel, A., 2005. First record of fossil wood and phytolith assemblages of the Late Pleistocene in El Palmar National Park (Argentina). Journal of South American Earth Sciences 20, 33–43.