



Research paper

Fossil legume woods from the Late Miocene, Chiquimil Formation (Santa María Basin), Argentina



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ABSTRACT

The legume fossil record is varied and abundant in the Cenozoic strata, especially throughout the Neogene. In northwestern Argentina there are outcrops of the Santa María Group, including the Miocene and Pliocene continental formations of the Santa María valley. These cenozoic formations contain a great variety of fossil remains (plants, invertebrates and vertebrates). In this paper, a new species of fossil wood, *Paraalbizioxylon caccavariae* Martínez (Leguminosae, Mimosoideae) nov. sp., from Upper Miocene Argentina, is described. The fossil wood herein described has features of the Mimosoideae subfamily, and particularly of the extant genus *Albizia* Durazzini and *Acacia* Miller. The diagnostic features present in the new fossil are: semi-ring to diffuse porous, medium to large diameter vessels, simple perforation plates, alternate and vested intervessel pits, homogenous rays (generally 2-seriate), scanty paratracheal parenchyma, and diffuse and cristiferous apotracheal parenchyma. The possible climatic conditions of the Chiquimil Formation were inferred from the xylological features present in the fossil wood described, suggesting a humid forest with a marked season in the localities studied.

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1. Introduction

The Leguminosae *nom. cons. et nom. alt.*, or Fabaceae Lindley, *nom. cons.*, is a diverse family of flowering plants and holds the third place as regards the number of species among the Magnoliophytes, containing c. 9.4% of eudicots, and occupying the 16% of all the woody species in the neotropical rainforest (Burnham and Johnson, 2004).

Traditionally, the Leguminosae was divided into three classical subfamilies: Mimosoideae, Caesalpinoideae and Papilionoideae (Cozzo, 1951); however, both molecular and morphological analyses have shown that this is a monophyletic group which is divided into six or seven groups: Cercideae, Detarieae, *Duparquetia*, Dialiineae, Umtizia, Caesalpinoideae s.s, Mimosoideae and Faboideae (Stevens, 2001).

The Mimosoideae Candolle subfamily is composed of herbs, shrubs or trees with a pantropical distribution that comprises 78 genera with 3270 living species (Lewis et al., 2005). In Argentina, there are 19 genera with 140 species which inhabit almost every phytogeographic areas (Cabrera, 1971; Zuloaga and Morrone, 1999).

The Mimosoideae fossil wood is well represented in the fossil record, from the Cretaceous to the Pliocene, with 21 genera distributed in almost every continents (Gros, 1994; Martínez, 2010), with 26 records in South America (Pujana et al., 2011; Franco and Brea, 2013), seven of which have been recorded in Argentina: *Anadenantheroxylon* Brea, Aceñolaza and Zucol, 2001, *Paracacioxylon* Müller-Stoll et Mädel (Lutz, 1987), *Menendoxylon* Lutz, 1979, *Mimosoxylon* Müller-Stoll et Mädel (Lutz, 1987), *Piptadenioxylon* Suguio et Mussa (Franco and Brea, 2008),

Microlobiusxylon Franco and Brea, 2010 and *Prosopisnoxylon* Martínez, 2010 (Herbst et al., 2007; Franco and Brea, 2008, 2010).

In this research, a new species of fossil wood from Chiquimil Formation (upper Miocene – Santa María Group) in northwestern Argentina is described. This fossil, which has close affinities to the mimosoid, has been compared with extant and fossil woods; the descriptions and comparisons permit to erect it in a new species of Leguminosae fossil wood: *Paraalbizioxylon caccavariae* Martínez nov. sp.

2. Geological setting

The permineralized wood samples were collected from three different localities in the Santa María Valley (Sierras Pampeanas, Argentina): Tiopunco (Tucumán province), Puerta del Corral Quemado, and Río Agua Verde (Catamarca province) (Fig. 1).

The Sierras Pampeanas are reverse fault-bounded mountain blocks of Precambrian to Palaeozoic basement rocks in the foreland of the central Andes (Strecker et al., 1989).

The Andes and piedmont landforms are geologically quite young (with their initial uplift beginning less than 11 Ma ago) and appear to have been a regional phenomenon contemporary with the onset of tectonism in the rest of the Sierras Pampeanas. The uplift in the northern most Sierras Pampeanas fault blocks of Sierra de Quilmes, Sierras Calchaquies, and Sierras del Aconquija began about 7 Ma ago and became pronounced about 3.4 to 4 Ma ago (Kleinert and Strecker, 2001). The movements ended 2.9 Ma afterwards, when the conformable Miocene–Pliocene Santa María Group was overthrust, faulted, and folded in the course of the main basement uplift (Strecker et al., 1989).

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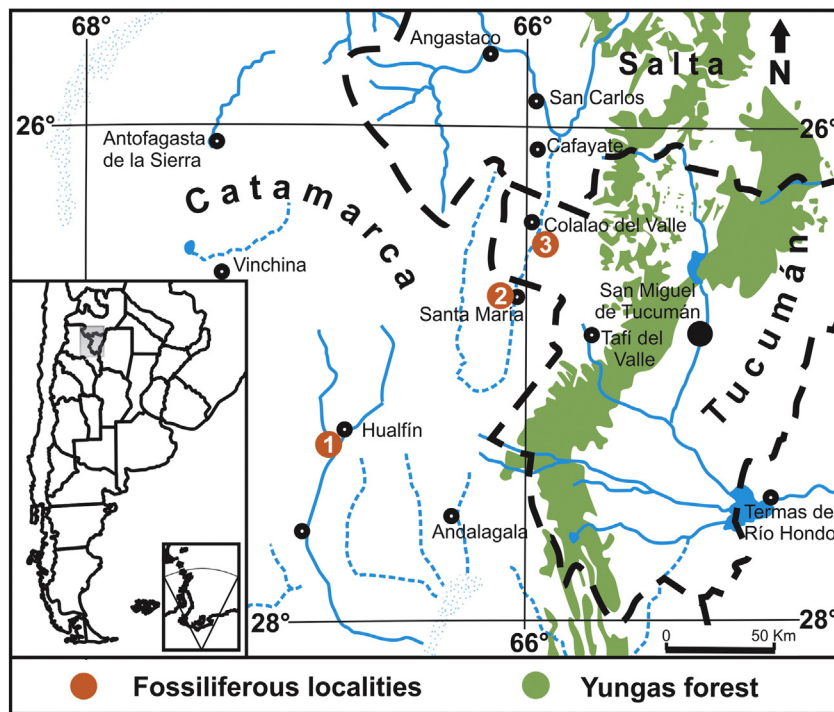


Fig. 1. Location map of the fossiliferous localities and current distribution of Yungas Forest. 1. Puerta del Corral Quemado. 2. Río Agua Verde. 3. Tiopunco.

In the Santa María Valley there are Cenozoic units overlying the crystalline basement. In this area, the Santa María Group is exposed (Galván and Ruiz Huidobro, 1965), including Miocene to Pliocene continental formations. The group is divided into six formations, from the base to the top: the San José, Las Arcas, Chiquimil, Andalhuala, Corral Quemado and Yasyamayo formations (Bossi and Palma, 1982). The fossil woods studied in this paper come from the Chiquimil Formation.

The Chiquimil Formation is a Miocene sequence of yellow-grey, green and brown volcanoclastic sandstone, siltstone and minor mudstone deposited in fine-grained sediments, with a thickness of 750–900 m (Marshall and Patterson, 1981; Bossi and Palma, 1982; Bossi et al., 1987). This Formation has an age of between 6.02 Ma and 6.68 Ma (late Miocene), dated with K–Ar (Marshall and Patterson, 1981).

The deposits of Chiquimil Formation has a diverse fossil record of invertebrates (Herbst et al., 2000; Morton and Herbst, 2001), vertebrates (Marshall and Patterson, 1981; Powell, 1998; Herbst et al., 2000) and plants (Lutz, 1987; Mautino and Anzotegui, 1998, 2002a,b; Herbst et al., 2000; Anzotegui, 2004; Martínez and Lutz, 2004, 2006).

The geological and fossil records suggest the existence of fluvial channels or shallow lakes with flood plains, wetlands and woods on river banks in a humid subtropical and seasonally dry climate (Mautino and Anzotegui, 2002a, 2002b; Anzotegui, 2004; Martínez, 2010).

3. Materials and methods

In order to study the wood anatomy, thin sections were made using traditional techniques to describe the fossils. Microscopic slides of the transverse (TS), radial (RLS) and tangential (TLS) wood sections were made in order for them to be observed with a Leica Diaplan Microscope. The woods were examined with JEOL JSM 6360 LV scanning electron microscopy (SEM), the fossil woods were fractured and adhered to aluminium stubs using nail polish, and coated with a gold layer.

The terminology for the description of woods follows the IAWA list of microscopic features (IAWA Committee, 1989). The vestrated pits are classified and described following the criteria of Othani and Ishida (1976). The cell dimensions are based on at least 25 measurements; the numbers between parentheses indicate the minimum and maximum

values. The tree rings were measured in order to obtain the mean sensitivity (Creber and Francis, 1999).

The fossil woods were classified by consulting classical descriptions of extant and fossil plants such as Cozzo (1950, 1951); Evans et al. (2006); Gros (1994), Müller-Stoll and Mädel (1967); Metcalfe and Chalk (1950), and Tortorelli (1956). The digital collection of InsideWood database (2004-onwards) has also been consulted.

The systematic classification of the superfamily follows the APG (1998, 2009), as regards the Leguminosae in the subfamilies of Elias (1981).

The fossil wood and thin sections (-PMP and -Pm) are deposited in the Paleontological Collection of the Facultad de Ciencias Exactas y Naturales y Agrimensura, Universidad Nacional del Nordeste, Corrientes, Argentina (CTES-) and in the Paleobotanical Collection of the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina (BAPb-).

Systematic Palaeobotany

Eudicots *sensu* APG III

Core Eudicots *sensu* APG III

Fabids *sensu* APG III

Fabales Bromhead

Family Leguminosae Jussieu, *nom. cons. et nom. alt.*/Fabaceae Lindley, *nom. cons.*

Subfamily Mimosoideae De Candolle

Genus *Paraalbizioxylon* Gros (1992)¹ *emend.* Martínez

Type. *Paraalbizioxylon bavaricum* (Selmeier) Gros (1992) *emended* Martínez

Emended generic diagnosis. Diffuse porous to semi-ring porous. Vessels: solitary, in radial multiples, and/or in clusters. Perforation plates: simple. Intervessel pits: vestrated and alternate, small to medium. Rays: homogeneous, uni- to hexaseriate (never exclusively uniseriate). Axial parenchyma paratracheal scanty to confluent. Apotracheal parenchyma: present or absent. Terminal parenchyma: present or absent. Fibres: septate or non-septate.

¹ The genera *Paraalbizioxylon* was erected by Gros (1992) in order to group two species of *Ingoxylon* which required new combinations (*sensu* Gros, 1990).

Note: The specific diagnosis was emended to include semi-ring porous; vessels in radial multiple, and/or in clusters; vested pits; axial parenchyma paratracheal scanty to confluent; apotracheal parenchyma present or absent; terminal parenchyma present or absent. Species. *Paraalbizioxylon caccavariae* Martínez sp. nov.

Diagnosis. Secondary wood. Wood semi-ring to diffuse-porous. Vessels circular to oval in outline; solitary and in radial multiples. Vessel elements short. Perforation plates simple. Intervessel pits small, oval to circular, alternate and vested. Rays: homogeneous, procumbent cells, uni- to triseriate, Kribs Homogeneous type II. Axial parenchyma paratracheal scanty to vasicentric. Apotracheal parenchyma diffuse, with prismatic crystals in chambered cells and with a single rhomboid crystal per chamber. Fibres non-septate, with simple pits and thick-walled.

Holotype: CTES-PB 12363, CTES-PMP 3434, CTES-PMP 3435 and CTES-PMP 3436 (Plates I–III). All slides (CTES-PMP 3434, 3435 and 3436) were made from a single specimen (CTES-PB 12363).

Paratypes: CTES-PB 12360, CTES-PMP 3437, CTES-PMP 3438 and CTES-PMP 3439. CTES-PB 14137, CTES-PMP 3440, CTES-PMP 3441 and CTES-PMP 3442.

BAPb 9285, BAPb-Pm 644, BAPb-Pm 645, BAPb-Pm 646 and BAPb-Pm 647.

Repository: Facultad de Ciencias Exactas y Naturales y Agrimensura, Universidad Nacional del Nordeste, Corrientes, Argentina (CTES-PB and CTES-PMP); and Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina (BAPb).

Holotype locality: CTES-PB 12363, Puerta del Corral Quemado, Belén Department, Catamarca Province, Argentina.

Paratype localities: CTES-PB 12360, Tiopunco, Tucumán province, Argentina. CTES-PB 14137 and BAPb-9285, Río Agua Verde, Catamarca province, Argentina.

Stratigraphic horizon: Santa María Group, Chiquimil Formation, Upper Miocene.

Etymology: The specific name is dedicated to the memory of Prof. Marta Caccavari for her important contributions and extensive studies on the Mimosoids.

4. Description

The fossil specimens consist of many pieces of permineralized logs with a preserved secondary xylem. The wood, in transverse sections, shows distinct growth rings, marked by thick-walled and radially flattened fibres and a lower diameter of the vessels in the latewood; and it is a semi-ring to diffuse porous wood, with vessels arranged in a diagonal pattern (Plate I, 1).

Vessels: In cross-section, they are solitary or in radial multiples of 2–3 in the early wood, and in radial multiples of 2–3, 4 or more in the late wood, and almost circular to oval in outline (Plate I, 1–4).

The vessels have a mean radial diameter of 184 (128–246) μm and a tangential diameter of 145 (85–181) μm . There is an average of 17 (10–23) vessels per mm^2 . Some vessel lumina are completely filled with what appears to be gums or resins (Plate I, 1, 2). In longitudinal section, the vessels are straight to slightly sinuous (Plate I, 5); the cells are short with a mean length of 220 (160–288) μm . The end walls of vessels are horizontal or oblique without tails (Plate I, 5, 6). The vessels show simple perforation plates (Plate I, 6). The intervessel pits are oval to circular, and small, with a mean vertical diameter of 4 (4–6) μm . The pits are alternate and vested (Plate I, 7); they are present only in the outer wall of vessel elements. The ornaments are conspicuous, consisting of very small to small, unbranched vested (Type 1 and Type 2 *sensu* Othani and Ishida, 1976) (Plate III, 1, 2). The vested is placed around the pit inner aperture, partially or totally covering the pit chamber (Plate III, 1, 2). The inner wall of vessels is completely smooth (Plate III, 3). The vessel-ray pits are similar to intervessel pits in size and shape throughout the ray cell (Plate I, 8 and Plate III, 4).

Parenchyma: The axial paratracheal parenchyma is scanty to vasicentric in cross section (Plate I, 2–4). The paratracheal parenchyma cells have a mean radial diameter of 12 (6–24) μm and tangential diameter of 14 (8–24) μm (Plate I, 4). In longitudinal section, the parenchyma cells are in strand with 3–4 cells; these cells have a mean length of 36 (15–49) μm (Plate II, 2). Some parenchyma cells are disjunctive (Plate II, 3; Plate III, 5).

The apotracheal parenchyma is diffuse; its cells have a mean radial diameter of 12 (6–24) μm and a mean tangential diameter of 14 (8–24) μm . In longitudinal section, the apotracheal parenchyma shows chambered cells with a single rhomboid crystal per chamber (Plate II, 4; Plate III, 7). On average, each parenchyma cell has 12 chambers (6–25). The chambers have a mean length of 13 (8–20) μm (Plate II, 4).

Rays: In transverse section, the rays have from straight to sinuous disposition (Plate I, 1–4). In tangential section, there are 8 rays (5–11) per mm, with 20 (6–42) cells high with an average height of 300 (96–567) μm , and a mean width of 18 (8–26) μm . The rays are uni- to triseriate, generally biseriate (Kribs Homogeneous type II). Radial cells have a mean height of 9 (6–14) μm and a mean width of 8 (4–16) μm (Plate II, 5, 6). In radial section, the rays are homocellular of procumbent cells, and regularly with contents, which are probably gums (Plate I, 8; Plate III, 4).

Fibres: The fibres have thick walls, small lumen, pitted and non-septate; with a mean radial diameter of 9 (4–16) μm and a mean tangential diameter of 8 (4–12) μm . In the radial walls of fibres there are simple pits (Plate III, 6).

Storied structure: Absent in all elements.

Fungal remains: The hyphae are observed in the lumina of vessel elements. These hyphae are septate, and have a mean diameter of 4 μm (Plate IV, 1, 2). The hyphae are ramified, and mostly have both terminal and intercalary chlamydospores, with a diameter of 12 μm (Plate IV, 2, 3).

4.1. Discussion

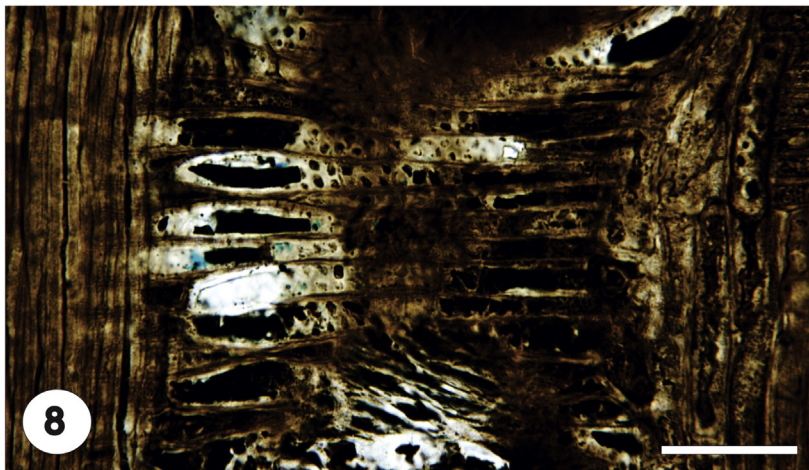
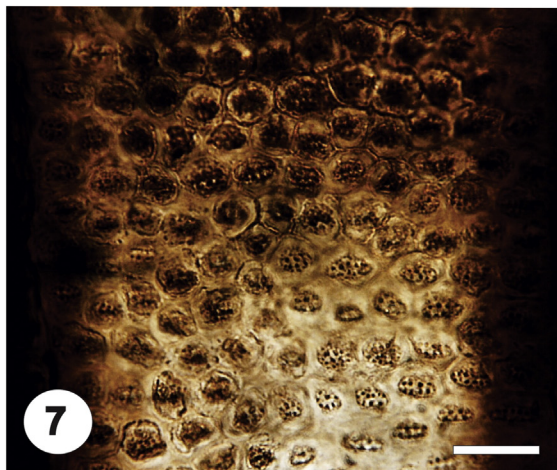
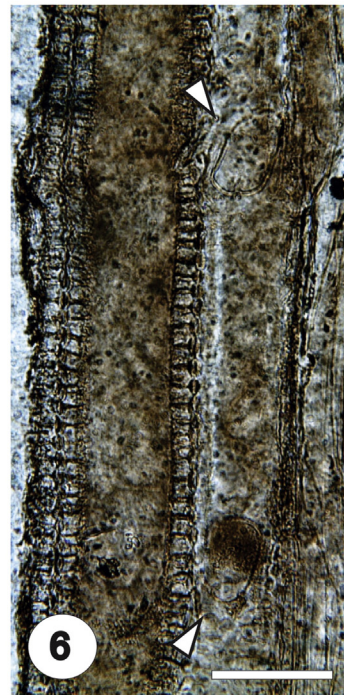
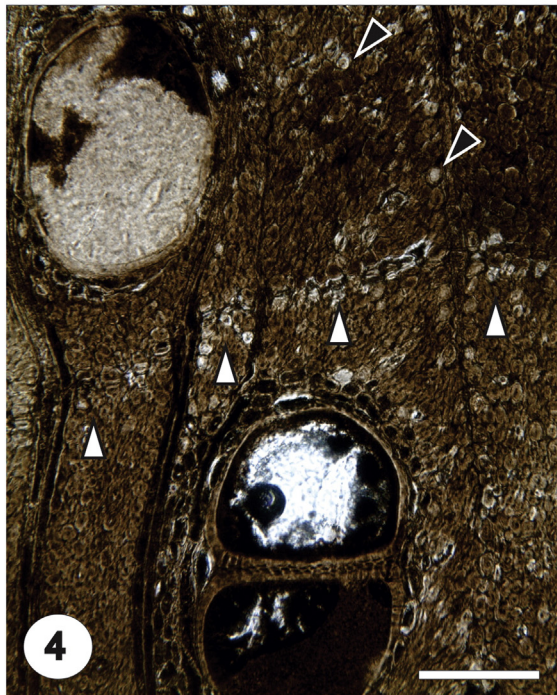
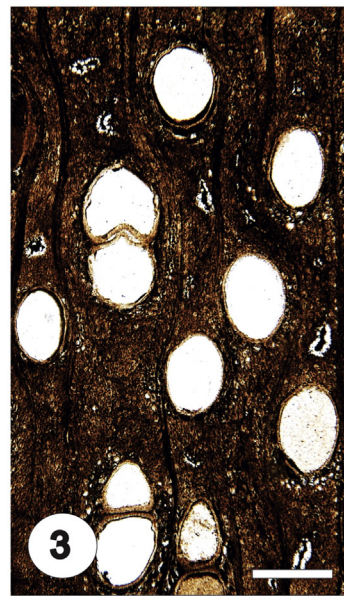
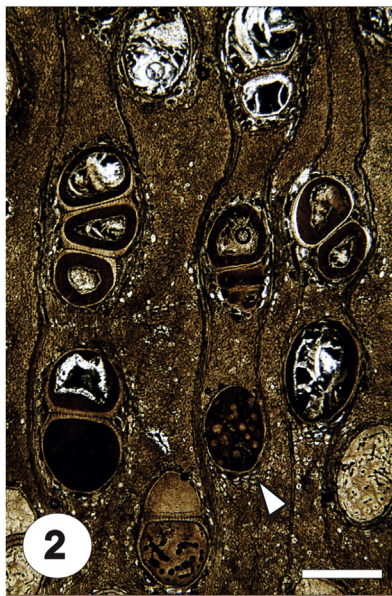
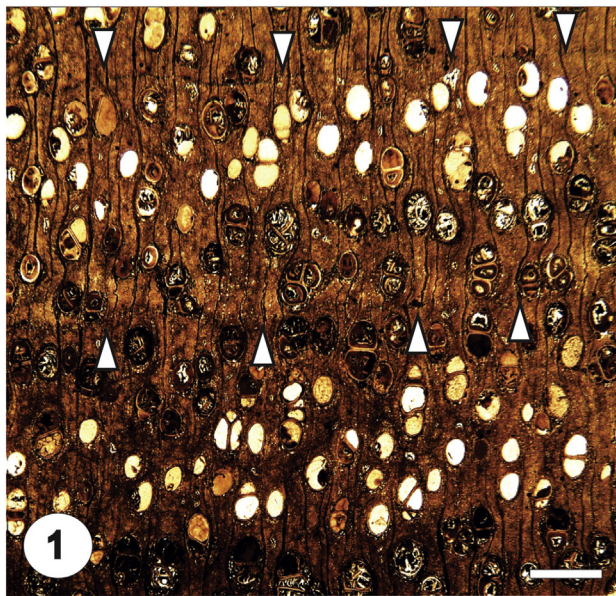
The features described in the fossil woods, such as vessel elements of short length, simple perforation plates, vested pits (except in some caesalpinoid species), generally homogeneous rays, the paratracheal parenchyma, which is usually abundant, and the apotracheal parenchyma, which is often chambered and crystalliferous (Baretta-Kuipers, 1981), are distinctive of the Leguminosae family.

Although the molecular and morphological analyses of the data strongly support the monophyly of the Leguminosae, the relationships at the base of the Fabaceae are still uncertain. In addition, these analyses show that the classical Caesalpinoideae are paraphyletic, and that the Mimosoideae, together with the Faboideae, are monophyletic (Wojciechowski et al., 2004).

According to Cozzo (1951), the Mimosoideae subfamily has a set of particular wood anatomical features. Most of them are present in the fossil wood described, namely: vested pits; vessel-ray pitting similar to intervessel pitting in shape and size paratracheal parenchyma from scanty to vasicentric, aliform to confluent and often banded, axial parenchyma in strands with crystals in chambered parenchyma axial cells; homogeneous multiseriate rays with procumbent cells and storied elements absent (Cozzo, 1950, 1951; Metcalfe and Chalk, 1950; Baretta-Kuipers, 1981). All these features are present in the fossil woods described herein.

4.2. Comparison with living mimosoid woods

The Mimosoideae subfamily has five conventional Tribes: Parkieae, Mimozyantheae, Mimoseae, Acacieae and Ingeae (Elias, 1981). Nevertheless, molecular data show that those relationships are non-natural, e.g. the Mimoseae are polyphyletic and the Acacieae and Ingeae Tribes seem to be derived from within Mimoseae (Grimes, 1995; Luckow et al., 2000, 2003; Miller et al., 2003).



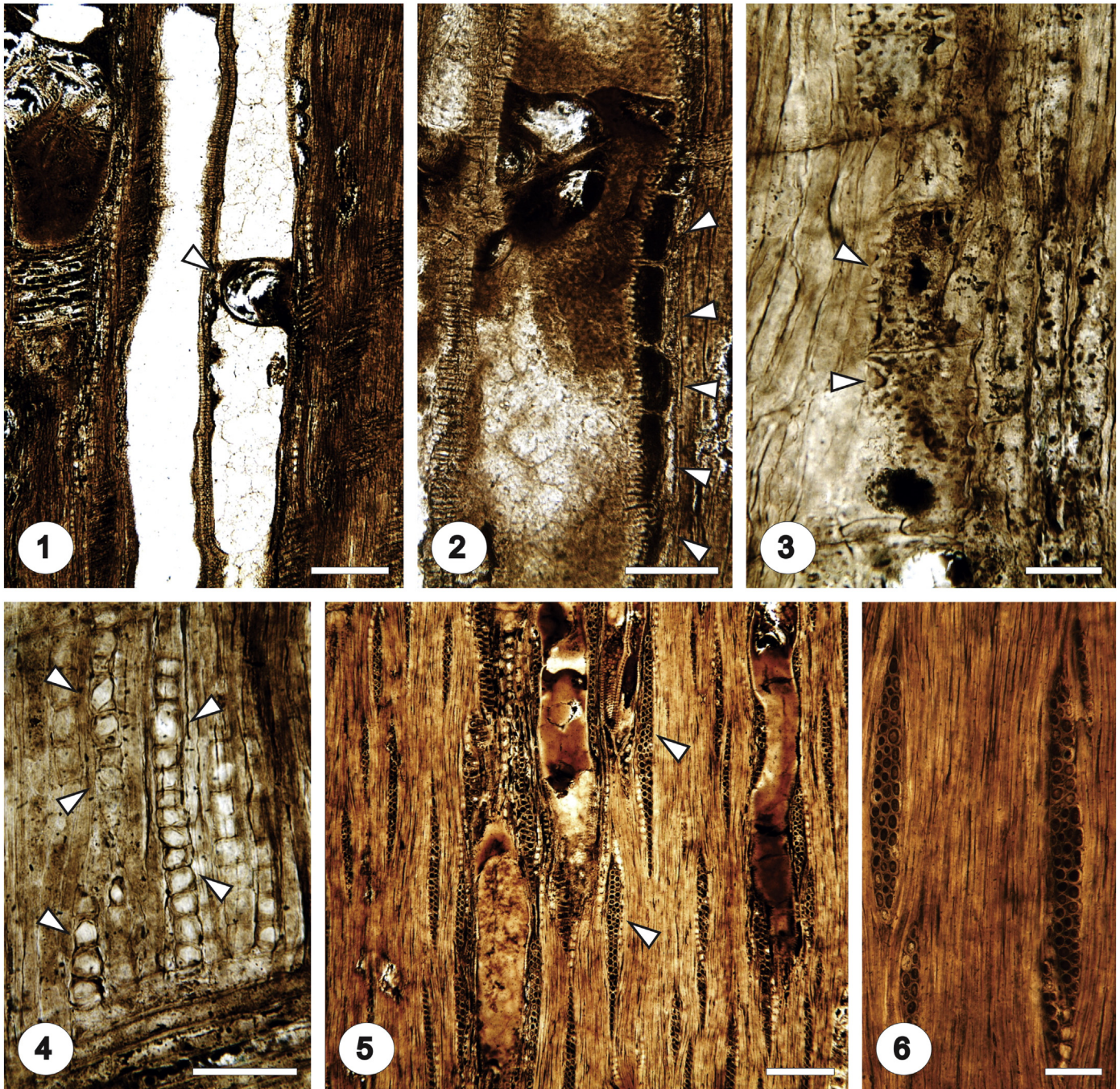


Plate II. *Paraalbizioxylon caccavariae* Martínez nov. sp. All LM (holotype).

1. RLS. Tylosis or gum deposit (arrow). CTES-PMP 3436. Scale bar = 200 μ m.
2. RLS. Paratracheal parenchyma (arrows). CTES-PMP 3436. Scale bar = 100 μ m.
3. TLS. Disjunctive paratracheal parenchyma (arrows). CTES-PMP 3435. Scale bar = 50 μ m.
4. RLS. Prismatic crystals in chambered axial parenchyma cells (arrows). CTES-PMP 3436. Scale bar = 50 μ m.
5. TLS. Rays disposition. Uni- to triseriate rays (arrows). CTES-PMP 3435. Scale bar = 200 μ m.
6. TLS. Rays (detail). CTES-PMP 3435. Scale bar = 100 μ m.

Plate I. *Paraalbizioxylon caccavariae* Martínez nov. sp. All LM (holotype).

1. TS. General view. Distinct growth rings (arrows). Wood ring to semi-porous. CTES-PMP 3434. Scale bar = 500 μ m.
2. and 3. TS. General view of vessels. Vessels with probable gums (arrow) and axial paratracheal parenchyma from scanty to vasicentric. CTES-PMP 3434. Scale bar = 200 μ m.
4. TS. Scanty axial paratracheal parenchyma, diffuse apotracheal parenchyma (black arrows) and growth ring marked (white arrow). CTES-PMP 3434. Scale bar = 100 μ m.
5. TLS. General view. Disposition of vessels and rays in longitudinal section. CTES-PMP 3435. Scale bar = 200 μ m.
6. TLS. Details of simple perforation plates (arrows). CTES-PMP 3435. Scale bar = 100 μ m.
7. RLS. Vessel wall with alternate vested pits. CTES-PMP 3436. Scale bar = 20 μ m.
8. RLS. Rays structure. Procumbent ray cells with vessel-ray pits (arrows). CTES-PMP 3436. Scale bar = 50 μ m.

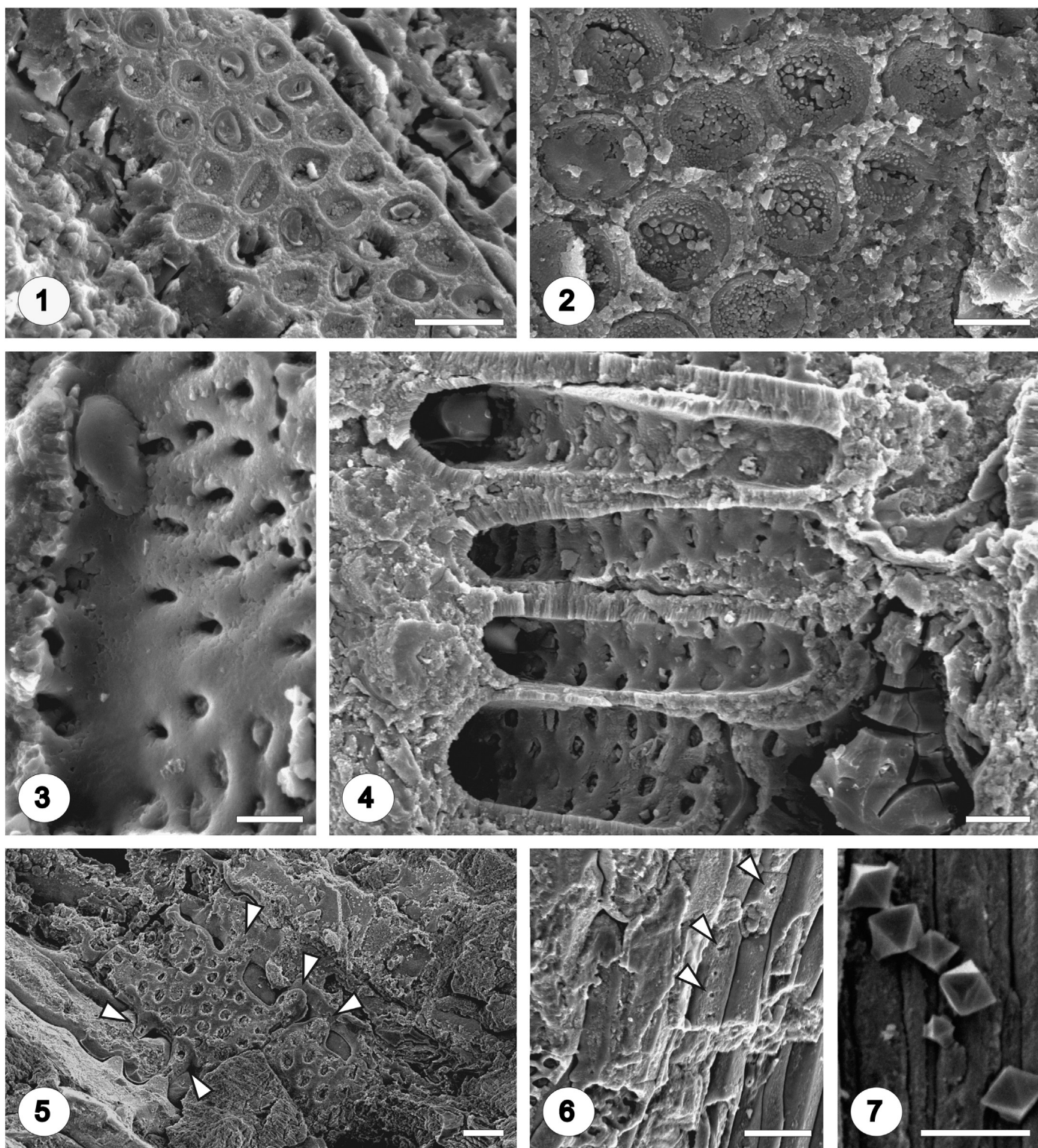


Plate III. *Paraalbizioxylon caccavariae* Martínez nov. sp. CTES PB-12.363. All SEM (holotype).

1. and 2. TLS. Exterior surfaces of vessel elements. 1. Ultrastructure of vessel wall with alternate vestured pits (general view). Scale bar = 10 μ m. 2. Exterior surfaces of vessel elements. Vestured pits (detail). Scale bar = 5 μ m.
3. Internal surfaces of vessel elements. Scale bar = 5 μ m.
4. RLS. Rays structure. Procumbent ray cells with vessel-ray pits. Scale bar = 10 μ m.
5. TLS. Disjunctive paratracheal parenchyma (arrows). Scale bar = 10 μ m.
6. RLS. Fibres with simple pits (arrows). Scale bar = 20 μ m.
7. TLS. Prismatic crystals of axial parenchyma cells. Scale bar = 20 μ m.

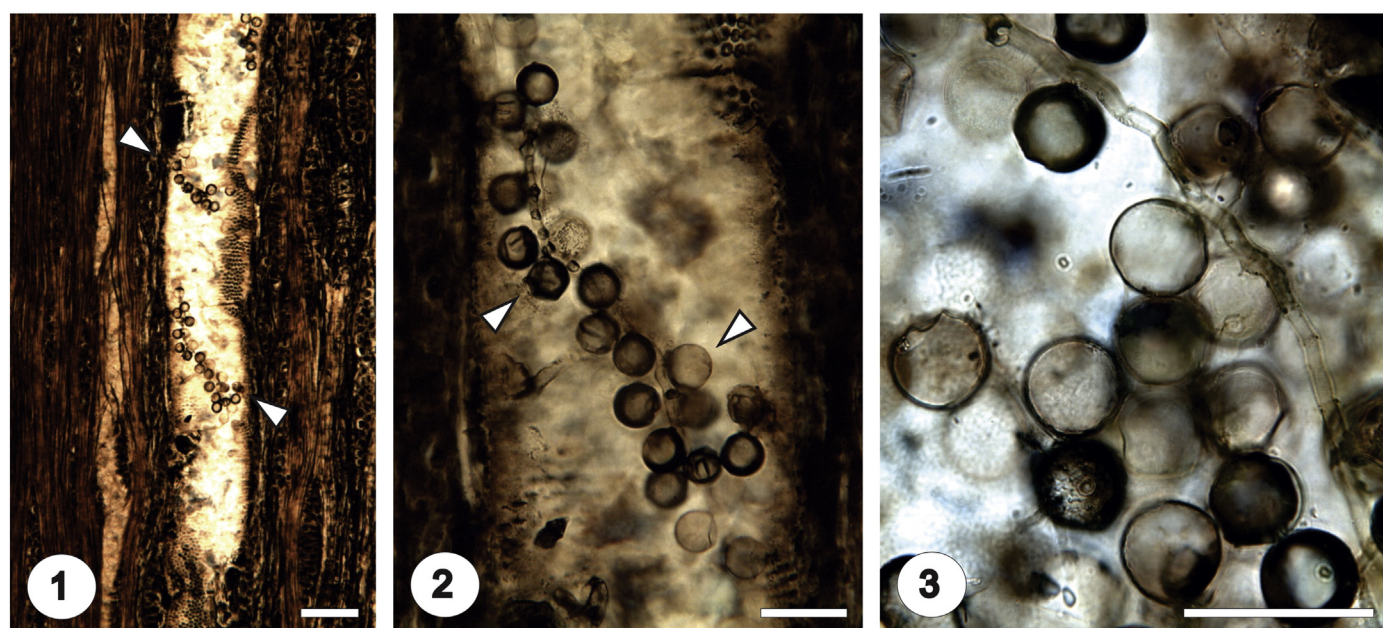


Plate IV. *Paraalbizioxylon caccavariae* Martínez nov. sp. BAPb-Pm 645. All LM (paratype).

1. and 2. TLS. Vessels with hyphae and chlamydospores (arrow). Scale bar = 100 µm.
3. TLS. Hyphae and chlamydospores (detail). Scale bar = 25 µm.

Table 1

Taxonomical key for fossil mimosoid woods.

1.1.	1- to 2-seriate rays	Microlobiusxylon Franco et Brea
1.2.	1- to 3-seriate rays	2
1.3.	1- to multiseriate rays	3
2.1.	Vessels: mostly solitary	Acacioxylon Schenk
2.2.	Vessels: solitary and short radial groups of 2–3	Menendoxylon Lutz
2.3.	Vessels: solitary, radial and in clusters	4
3.1.	1- to 6-seriate rays	5
3.2.	More than 6-seriate rays	6
4.1.	Only vasicentric paratracheal parenchyma	Piptadenioxylon Suguio et Mussa
4.2.	Diffuse, vasicentric aliform, confluent parenchyma	Adenantheroxylon Prakash et Tripathi
4.3.	Vasicentric, complete, lozenge-aliform and confluent parenchyma	Anadenantheroxylon Brea, Aceñolaza et Zucol <i>emended</i> Franco et Brea
4.4.	Parenchyma narrow vasicentric, partly slightly aliform, rare confluent and terminal	Mimosoxylon Müller-Stoll et Mädél
5.1.	Vessels: mostly solitary	7
5.2.	Vessels: solitary, radial multiples and/or clusters	8
6.1.	1- to 10-seriate rays	9
6.2.	More than 10-seriate rays	Metacacioxylon Gros
7.1.	Terminal parenchyma	Albizinium Prakash
7.2.	Terminal parenchyma absent	Cathormion fo Gros
8.1.	Aliform to confluent parenchyma	Tetrapleuroxylon Müller-Stoll et Mädél
8.2.	From scanty, aliform, confluent or banded and diffuse parenchyma	Paraalbizioxylon Gros <i>emended</i> Martínez
9.1.	Vessels of 2 different diameters	Prosopisinoxylon Martínez
9.2.	Without vessels of 2 different diameters	10
10.1.	Terminal parenchyma present	Dichrostachyoxydon Müller-Stoll et Mädél
10.2.	Terminal parenchyma absent	11
11.1.	Fibres non-septate	Euacacioxylon Müller-Stoll et Mädél
11.2.	Fibres usually septate	12
12.1.	Parenchyma paratracheal and diffuse strands	Mimosaceoxylon Lakhanpal et Prakash
12.2.	Parenchyma vasicentric, often confluent forming irregular bands	Paracacioxylon Müller-Stoll et Mädél

In order to study the extant Mimosoideae woods, [Evans et al. \(2006\)](#) grouped this subfamily in four non-natural categories: Mimoseae, Acaciae, Ingeae and Mimosygantheae.

According to [Evans et al. \(2006\)](#), the fossil woods studied were classified into three tribes Mimoseae, Acaciae and Ingeae, considering the following features: non-septate fibres, non-banded parenchyma and uni- to triseriate rays.

In the Mimoseae Tribe there are five divisions, of them the Division 5 has a set of features comparable to the fossils studied here (non-septate fibres, non-banded, uniseriate rays present). However, the genera included in this division generally have a great development of axial parenchyma (from vasicentric to confluent), and the rays are typically uniseriate (two- and triseriate occur in some species).

The Ingeae Tribe has four divisions: the Divisions 1 and 2 have septate fibres, and the Division 3 has banded parenchyma, features which are not present in fossil woods described. Most of the features of the wood studied here are related to Division 4 (non-septate fibres, non-banded and uniseriate rays present). There are 10 genera comprised in the Division 4: *Abarema* Pittier, *Chloroleucon* (Benth) Record, *Enterolobium* Martius, *Falcataria* (Nielsen) Barneby et Grimes, *Hydrochorea* Barneby et Grimes, *Leucochloron* Barneby et Grimes, *Pithecellobium* Martius, *Samanea* (Benth) Merrill, *Serianthes* Benth and *Wallaceodendron* Koorders ([Evans et al., 2006](#)). The genera *Abarema*, *Chloroleucon*, *Enterolobium*, *Falcataria*, *Hydrochorea*, *Leucochloron*, *Serianthes* and *Wallaceodendron* differ in having axial parenchyma from aliform to confluent, while all the species of *Pithecellobium* have patches of apotracheal parenchyma, and radial multiple vessels are frequent in the genus *Samanea* ([Evans et al., 2006](#)). On the other hand, the genus *Albizia* Durazzini is put in an “Unplaced” category. This genus has a variable anatomy, but this occurs because most of the species of this taxon have had many taxonomic rearrangements. It is interesting to note that the type species *Albizia julibrissin* Durazzini shares most of the wood features with *Paraalbizioxylon caccavariae*, such as: larger vessels, fibres non-septate with simple pits, 3–4 cells per parenchyma strand, and a diffuse and crystalliferous apotracheal parenchyma. However, they differ in the abundance and disposition of the axial parenchyma, which is from paratracheal to confluent ([InsideWood, 2004](#)).

Table 2
Comparison among the species of *Paraalbizioxylon*.

	<i>Paraalbizioxylon bavaricum</i> (Selmeier) gross	<i>Paraalbizioxylon hungaricum</i> (Greguss) gross	<i>Paraalbizioxylon nathorstii</i> (Schuster) gross	<i>Paraalbizioxylon cienense</i> (Cevallos-Ferriz and Barajas-Morales) Martínez nov. comb.	<i>Paraalbizioxylon caccavariae</i> Martínez nov. sp.
Porosity	Diffuse to semi-ring porous	Diffuse porous	Diffuse porous	Diffuse porous	Diffuse to semi-ring porous
Vessel grouping	Solitary, short radial multiples and some in multiples of 3 or more	Solitary, short radial multiples and some in multiples of 3 or more	Solitary and short radial multiples	Solitary, short radial multiples and some in multiples of 3 or more	Solitary and in short radial multiples
Paratracheal parenchyma	Vasicentric to confluent	Vasicentric to aliform and banded	Vasicentric to aliform	Vasicentric	Scanty to vasicentric
Terminal parenchyma	Present	Absent?	Absent	Absent	Absent
Rays width (cells)	1- to 3 seriate	1- to 4-seriate	1- to 2 seriate	1-seriate (2–4)	2-seriate (1–3)
Fibres	Septate	Septate?	Septate	Non-septate	Non-septate

The members of the Acacieae Tribe are numerous (c. 1450 species of *Acacia* Miller) and the genus *Acacia* is not monophyletic (Luckow et al., 2000, 2003; Robinson and Harris, 2000). This fact makes it difficult to establish accurate features that should allow us to distinguish this genus from others. Among the South American species, *Acacia visco* Lorentz ex Grisebach shows more similarities to *Paraalbizioxylon caccavariae*, only differing in its having occasionally septate fibres and two- to tetraseriate rays (Cozzo, 1951; Tortorelli, 1956).

Therefore, the variation in the anatomical characters of the wood present in the Mimosoideae, the paucity of the studies of some genera (e.g. *Acacia*, *Albizia*, *Mimosa*) and the set of features observed in *Paraalbizioxylon caccavariae*, possibly place it in an unclear systematic status.

However, the “unclear position” of this fossil wood is in accordance to Luckow et al. (2003) who have proved that the recognized tribes of Mimosoideae are not monophyletic. In their analysis, the Mimoseae form a basal grade, with the Ingeae and the Acacieae nested within it. Furthermore, the relationships among some species of *Acacia* and other genera such as: *Albizia*, *Calliandra*, *Chloroleucon*, *Enterolobium*, *Inga* and *Samanea* are still unsolved. The genus *Acacia* (and thus the Acacieae tribe) is mostly paraphyletic; *Acacia* subg. *Acacia* is monophyletic and is part of a polytomy that contains some species from *Piptadenia* group of the Mimoseae, the *Parkia*, and a clade of all other “acacias” and the Ingeae. Moreover, in that analysis, the genus *Albizia* is polyphyletic as well (Luckow et al., 2003). In addition, it is interesting to note that the *Acacia visco* is a sister to the Ingeae clade. Therefore, the relationships that have been stated are congruent with the “uncertain position” of *Paraalbizioxylon caccavariae* and its mix of anatomical characters, which resemble those of the extant members of the Acacieae and Ingeae tribes.

4.3. Comparison with fossil mimosoid woods

There are 17 genera of Mimosoideae fossil woods erected and described, of them: *Eucacioxylon* Müller-Stoll and Mädél, 1967, *Dichrostachyoxylon* Müller-Stoll and Mädél, 1967, *Metacacioxylon* Gros, 1988, *Mimosaceoxylon* Lakhanpal and Prakash, 1970, *Paracacioxylon* Müller-Stoll and Mädél, 1967 and *Prosopisinoxylon* Martínez, 2010 differ from the fossil studied by the presence of large rays (uni to 18-seriate).

The abundance and arrangement of the parenchyma is a useful character to allow us to distinguish among different types of mimosoid wood. The following genera differ from the fossil studied here in the distribution and abundance of the paratracheal parenchyma: *Acacioxylon* Schenk (in Gros (1994)), *Adenantheroxylon* Prakash and Tripathi, 1968, *Albizinium* Prakash, 1975, *Anadenantheroxylon* Brea,

Aceñolaza and Zucol, 2001, *Cathormion* fo² Gros, 1994, *Menendoxylon* Lutz, 1979, *Metacacioxylon* Gros, *Microlobiusxylon* Franco and Brea, 2010, *Mimosoxylon* Müller-Stoll and Mädél, 1967, *Piptadenioxylon* Suguio and Mussa, 1978, *Paracacioxylon*, *Prosopisinoxylon* and *Tetrapleuroxylon* Müller-Stoll and Mädél, 1967.

Finally, there are two genera, which are close to the fossil wood of the Chiquimil Formation: *Bajacalifornioxylon* Cevallos-Ferriz and Barajas-Morales, 1994 and *Paraalbizioxylon* Gros, 1992. However, the diagnosis of the *Bajacalifornioxylon* genus, which was established by Cevallos-Ferriz and Barajas-Morales (1994), is too similar to that of *Paraalbizioxylon*.

The diagnosis of *Bajacalifornioxylon* and *Paraalbizioxylon* is too similar (e.g., diffuse-porous wood, perforation plate simple, vessels solitary or in clusters, fibres septate or nonseptate, parenchyma paratracheal vasicentric, parenchyma apotracheal diffuse, rays 1 and multiseriate). Although, the diagnosis of *Bajacalifornioxylon* is very detailed; it differs from *Paraalbizioxylon* in some minor details. Besides, the genus *Paraalbizioxylon* Gros was before published (ICBN, Division I. Principle III). Therefore, this work suggests the transference of the *Bajacalifornioxylon cienense* to *Paraalbizioxylon cienense* (Cevallos-Ferriz et Barajas-Morales) Martínez nov. comb., thus invalidating the *Bajacalifornioxylon* genus.

The newly emended generic diagnosis of *Paraalbizioxylon* emended is applied to fossil members of the Mimosoideae, making them close to some extant species of *Acacia* and *Albizia*.

The comparison can also be made using the taxonomical key for fossil mimosoid woods in Table 1.

To summarize this section, the fossils of the Chiquimil Formation studied here have been included into the *Paraalbizioxylon* genus and thus belong to a new species: *Paraalbizioxylon caccavariae* Martínez nov. sp.

There are five species of *Paraalbizioxylon*: *Paraalbizioxylon bavaricum* (Selmeier, 1973); Gros (1992), *Paraalbizioxylon hungaricum* (Greguss, 1969); Gros (1992), *Paraalbizioxylon nathorstii* (Schuster, 1910); Gros (1992), *Paraalbizioxylon cienense* (Cevallos-Ferriz and Barajas-Morales, 1994) Martínez nov. comb., and *Paraalbizioxylon caccavariae* Martínez nov. sp. (this paper).

The presence of non-septate fibres in *Paraalbizioxylon caccavariae* is a useful character to separate this taxon from all those fossil species with septate fibres such: *Paraalbizioxylon bavaricum* and *Paraalbizioxylon nathorstii*. The scanty development of wood parenchyma present in *P. caccavariae* contrasts with that observed in *P. bavaricum*, *Paraalbizioxylon hungaricum* and *P. nathorstii*. Finally, *P. caccavariae* differs from *Paraalbizioxylon cienense* in having the combination of diffuse

² The designation “*Cathormion* fo” were constructed to indicate fossil wood that is very close to the extant genus *Cathormion*. The acronym “fo” indicates fossil wood with a diagnosis based on wood anatomical characters (*sensu* Gros, 1992).

Table 3

Mean sensibility (MS), Vulnerability index (VI) and Mesomorphy index (MI) of *Paraalbizioxylon caccavariae* woods from Chiquimil Formation.

Fossil specimens	Locality	MS	VI	MI
CTES-PB12363	Puerta del Corral Quemado	0.360	8.37	1842.23
CTES-PB 12360	Tiopunco	0.836	5.70	1191.30
CTES-PB 14137	Río Agua Verde	0.307	8.31	1601.64
BAPB 9285	Río Agua Verde	0.642	6.79	1329.12

to semi-ring porous woods, solitary vessels and in short radial multiples, scanty to vasicentric parenchyma and rays commonly biseriate. The differences among them are seen in Table 2.

4.4. Palaeoecological inferences

Several techniques are used to determine the palaeoclimate from fossil plants. One of them is referred to as the nearest-living-relative method (NLR) (Mosbrugger, 1999). This technique compares fossil plants to the modern plants to which they are most closely related and assumes that the climatic tolerance of both has remained the same through geologic time. In this sense, *Paraalbizioxylon caccavariae* shows a combination of anatomical wood features, which are quite similar to those present in *Acacia visco*. This living species is a tree of low-to-medium stature (3 to 25 m tall); it inhabits seasonal forests, coastal areas and riversides; among 1000–2000 (3500) m, in South America (Argentina, Bolivia and Chile) (Rico-Arce, 2007). At present, *A. visco* grow close to the studied area in the Yungas forest (Brown, 2009).

The Yungas is a biogeographic province that extends along the tropical Andes, reaching its southern limit in northern Argentina (Cabrera and Willink, 1980). The precipitation in the area is characterized by a monsoonal regime, with rainfall concentrated in the summer and early autumn months (November–April), with a water deficit from the end of autumn until mid-spring (Grau and Veblen, 2000). However, forest composition, diversity, and disturbance regime vary along the elevational range from 400 to 3000 m (Brown et al., 2001). In addition to rainfall, fog interception adds substantial moisture to vegetation and soil, particularly during the dry months (Hunzinger, 1997).

The qualitative features of the wood (i.e. growth rings, anatomy) were used to obtain the palaeoenvironmental conditions under which *Paraalbizioxylon caccavariae* developed.

In addition, the presence of growth rings can indicate a great variety of environmental factors, supported by dendrochronological studies. The change in the wood structure, which produces growth rings, is a physiological process (regulated by hormones) which is influenced by ecological factors (e.g. water supply, temperature, photoperiod, etc.). Therefore, the presence of distinct growth rings indicates a rate of growth determined by seasonal changes (Creber, 1977; Carlquist, 2001; Francis and Poole, 2002).

The presence of well-marked growth rings in the fossil woods studied shows that their growth environment was characterized by well-defined seasons.

The ring series of fossil woods were measured in all samples, ranging in length from 6 to 14 rings; and the mean sensibility (MS) was calculated as well (Table 3). The MS is the mean variability in ring width over a series of rings (Douglass, 1928). The MS between 0 and 0.3 is termed “complacent” while those above are “sensitive” (Creber and Francis, 1999).

The MS range in the samples varies from 0.307 to 0.836, having a MS of more than 0.3 (sensitive). The trees with sensitive rings indicate that there were significant episodes of erratic climate and that the environment was not relatively uniform and constant from year to year. The sensitive rings are present in trees that grew with a water supply restricted in average or in mountainous areas on thin soils often (Creber, 1977).

On the other hand, several anatomical features present in the dicotyledonous woods are influenced by environmental conditions (e.g. vested pits, parenchyma type, length, diameter and number of vessels per mm²) and could allow the interpretation of past climatic regimes (Carlquist, 1975, 2001; Wheeler and Baas, 1993). Nevertheless, some of these features are very conservative (e.g. vesturing, short vessels and simple perforation plates), and help characterize whole families. The features such as vesturing and short vessels would have originated in response to dry habitats (Carlquist, 2001); these characters were not considered here, because they probably are related to the origin of the Leguminosae family in moist and dry forests of tropical lands (Raven and Polhill, 1981).

Individually, the wide vessel-elements could be considered an adaptation to rapid flow rates (Carlquist, 1975); and the low vessel density is typical of the lowland tropical species (Wheeler and Baas, 1991, 1993).

Those features allow constructs indices of ecological significance, such as vulnerability and mesomorphy (Carlquist, 1977). The “Vulnerability” is the mean vessel diameter divided by the mean number of vessels per mm² of transection. The low value for vulnerability can be constructed as a high degree of “safety” under water stress conditions and, therefore, xeromorphy. The values below 1.0 of “Vulnerability index” would indicate a high degree of xeromorphy (Carlquist, 1977).

The “Mesomorphy” is another useful index, which is obtained by multiplying the “Vulnerability index” by mean vessel element length (Carlquist, 1977). This index allows know the xeromorphy (values below of 30.0) or the mesomorphy (with values higher than 1000 in the species of humid subequatorial forests) (Carlquist, 1977, 1982).

The fossil woods of the Chiquimil Formation have vulnerability values on a scale of 5.70 to 8.37 and a mesomorphy of 1191.30 and 1842.23, which suggests that those trees would have grown under mesic conditions in a humid subtropical forest (Table 3).

These data are congruent with those reported by Mautino and Anzótegui (2002a, 2002b) and Anzótegui (2004), who suggest the existence of a humid subtropical and seasonally dry climate. However, in other localities, some pollen assemblages and fossil woods in Chiquimil Formation indicate less humid or xeric conditions (Mautino and Anzótegui, 2002a, 2002b; Martínez, 2010). These assemblages probably suggest the presence of an ecotone in some areas of the Chiquimil Formation, between the humid subtropical region (Yungas forest) and seasonally dry subtropical region (Chaco) comparable to the present day.

5. Conclusions

Paraalbizioxylon caccavariae is a new species of fossil wood from the Chiquimil Formation. The anatomical characters of the fossil studied and the ecological indices are related to the existence of a seasonal subtropical climate during the deposition of the Chiquimil Formation in all localities studied. It is remarkable that, regardless of ring width, the MS values for the whole assemblage are highly consistent.

Furthermore, the anatomical features of *Paraalbizioxylon caccavariae* are very similar to those of living tropical and sub-tropical species of *Acacia*, particularly *Acacia visco*. The South American species of *Acacia* grow from arid to humid regions. However, *A. visco* inhabits seasonal forests, coastal areas and riversides; among 1000–2000 m, such as the Yungas forest (Fig. 1).

The presence of fossil woods with close affinities to *Acacia visco* strongly corroborates the hypothesis of a humid forest (comparable to Yungas with a subtropical monsoonal climate) with a marked season in the localities studied. In this period, probably the forest had a great distribution before the uplift of the Andes. Then, the progressive uplift of the Andes formed a barrier that stopped the humid winds and rains from the Pacific Ocean, and produced arid conditions in this area, thus reducing the current extension of forest (Yungas).

Finally, this research suggests the existence of a seasonal regime (monsoonal) to the studied area, similar to present day, at least during the late Miocene.

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