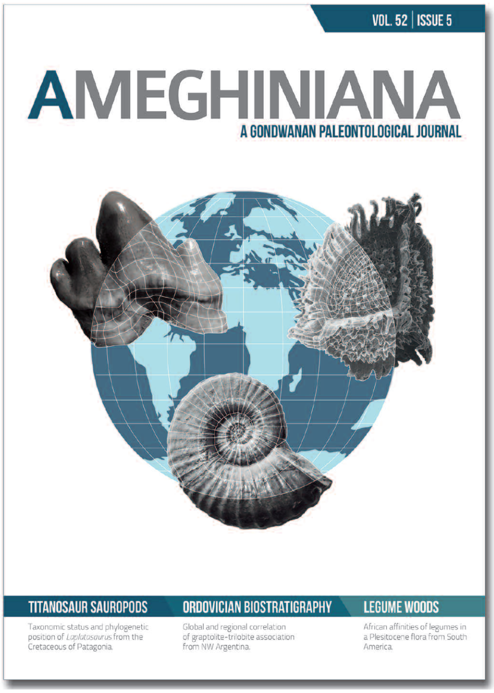
AMEGHINIANA
A GONDWANAN PALEONTOLOGICAL JOURNAL

LEGUME FOSSIL WOODS FROM THE ARROYO FELICIANO FORMATION (LATE PLEISTOCENE, NORTHEASTERN ARGENTINA): PALEOBIOGEOGRAPHIC IMPLICATIONS

ELIANA MOYA[1,2]
MARIANA BREA[1,2]



[1]Laboratorio de Paleobotánica, Centro de Investigaciones Científicas y Transferencia de Tecnología a la Producción, Consejo Nacional de Investigaciones Científicas y Técnicas (CICyTTP-CONICET), Dr. Materi y España s/n, E3105BWA Diamante, Entre Ríos, Argentina.
[2]Facultad de Ciencia y Tecnología, Universidad Autónoma de Entre Ríos, Sede Oro Verde-Diamante, Ruta Nacional 11 km 10,5 (3100) Oro Vede, Entre Ríos, Argentina.

Submitted: Decemeber 16th, 2014 - **Accepted:** June 24th, 2015

To cite this article: Eliana Moya and Mariana Brea (2015). Legume fossil woods from the arroyo Feliciano Formation (late Pleistocene, northeastern Argentina): paleobiogeographic implications. *Ameghiniana* 52: 558–573.

To link to this article: http://dx.doi.org/10.5710/AMGH.24.06.2015.2875

ARTICLES
AMEGHINIANA - 2015 - Volume 52 (5): 558 – 573
ISSN 0002-7014

LEGUME FOSSIL WOODS FROM THE ARROYO FELICIANO FORMATION (LATE PLEISTOCENE, NORTHEASTERN ARGENTINA): PALEOBIOGEOGRAPHIC IMPLICATIONS

ELIANA MOYA[1,2] AND MARIANA BREA[1,2]

[1]Laboratorio de Paleobotánica, Centro de Investigaciones Científicas y Transferencia de Tecnología a la Producción, Consejo Nacional de Investigaciones Científicas y Técnicas (CICyTTP-CONICET), Dr. Materi y España s/n, E3105BWA Diamante, Entre Ríos, Argentina. *li.196@hotmail.com*; *cidmbrea@gmail.com*

[2]Facultad de Ciencia y Tecnología, Universidad Autónoma de Entre Ríos, Sede Oro Verde-Diamante, Ruta Nacional 11 km 10,5 (3100) Oro Vede, Entre Ríos, Argentina.

Abstract. Two new genera of late Pleistocene Mimosoideae from Argentina are described. The fossils were recovered from the Arroyo Feliciano Formation in the upper Río Gualeguay Basin, eastern Argentina. The anatomical features suggest a relationship with *Cylicodiscus* Harms for the first one and *Abarema* Pittier and *Hydrochorea* Barneby and J.W. Grimes for the second. *Cylicodiscuxylon paragabunensis* gen. nov. and sp. nov. is characterised by diffuse-porous wood, solitary vessels, in radial multiples and in clusters; alternate and vestured intervessel pits; vasicentric, aliform, lozenge-aliform and confluent axial parenchyma, strands of 5–11 cells, prismatic crystals in chains in chambered axial parenchyma cells; 1–3 (4) seriate rays and homocellular, vessel-ray parenchyma pits similar in size and shape to intervessel pits, and non-septate fibres. *Abaremaxylon hydrochorea* gen. nov. and sp. nov. has the following diagnostic features: diffuse-porous wood, solitary vessels, in radial multiples and in clusters; alternate and vestured intervessel pits; vasicentric, aliform and unilateral aliform, confluent axial parenchyma, strands of 4–16 cells; prismatic crystals in chains in chambered axial parenchyma cells; exclusively uniseriate and homocellular rays, and non-septate fibres. The fossils described herein represent the first report of legume woods from the Río Gualeguay Basin. The record of *Cylicodiscuxylon* in southern South America supports the existence of an old relationship with the African flora and *Abaremaxylon* reinforces the idea that Neotropical flora was widespread in the past. The analysis of fossil plants suggests that they grew under warm and humid to semi-arid climatic conditions.

Key words. Wood anatomy. Fabaceae: Mimosoideae. *Abaremaxylon. Cylicodiscuxylon.* Arroyo Feliciano Formation. Late Pleistocene.

Resumen. LEÑOS FÓSILES DE LEGUMINOSAS EN LA FORMACIÓN ARROYO FELICIANO (PLEISTOCENO SUPERIOR, NORESTE DE ARGENTINA): IMPLICANCIAS PALEOBIOGEOGRÁFICAS. Dos nuevos géneros de Mimosoideae del Pleistoceno tardío de Argentina son descriptos. Los fósiles fueron hallados en la Formación Arroyo Feliciano, cuenca superior del Río Gualeguay, este de Argentina. Los caracteres anatómicos sugieren una relación con *Cylicodiscus* Harms para el primer ejemplar y *Abarema* Pittier y *Hydrochorea* Barneby y J.W. Grimes para el segundo. *Cylicodiscuxylon paragabunensis* gen. nov. y sp. nov. está caracterizado por porosidad difusa, vasos solitarios, múltiples radiales y agrupados; punteaduras intervasculares alternas y ornadas; parénquima axial vasicéntrico, aliforme, aliforme de alas cortas y confluente, parénquima septado de 5–11 células, cristales prismáticos en células del parénquima axial; radios 1–3 (4) seriados, homocelulares, punteaduras radio-vasculares similares en tamaño y forma a las punteaduras intervasculares y fibras no septadas. *Abaremaxylon hydrochorea* gen. nov. y sp. nov. tiene los siguientes caracteres diagnósticos: porosidad difusa, vasos solitarios, múltiples radiales y agrupados; punteaduras intervasculares alternas y ornadas; parénquima axial vasicéntrico, aliforme, aliforme unilateral y confluente, parénquima septado de 4–16 células; cristales prismáticos en células del parénquima axial; radios exclusivamente uniseriados y homocelulares y fibras no septadas. Estos fósiles representan el primer registro de leguminosas para la Cuenca del Río Gualeguay. El registro de *Cylicodiscuxylon* en el sur de América del Sur apoya la existencia de una vieja relación con la flora Africana y *Abaremaxylon* refuerza la idea que la flora Neotropical estaba más distribuida hacia el sur en el pasado. El análisis de las plantas fósiles sugiere que crecieron bajo condiciones climáticas cálidas y húmedas a semi-áridas.

Palabras clave. Anatomía de madera. Fabaceae: Mimosoideae. *Abaremaxylon. Cylicodiscuxylon.* Formación Arroyo Feliciano. Pleistoceno tardío.

FABACEAE or Leguminosae is a very large family and includes approximately 730 genera and 19,400 species of trees, shrubs, herbs and vines with a worldwide range (Lewis *et al.*, 2005). The Fabaceae are traditionally classified into three subfamilies Caesalpinoideae, Mimosoideae and Papilionoideae (Polhill, 1981; Silva *et al.*, 1989; Mabberley, 1990; Lewis *et al.*, 2005; Simpson, 2006; APG III, 2009). Mimosoideae comprises 78 genera and 3,270 species (Lewis *et al.*, 2005) and it is mostly tropical to subtropical in distribution. This subfamily includes four tribes: Mimosae, Ingeae, Acacieae and Mimozygantheae (Evans *et al.*, 2006), and inhabits arid and semiarid regions throughout the world

(Luckow *et al*., 2003; Schrire *et al*., 2005a, b).

The fossil record of wood, leaves, flowers, fruits, and pollen of Fabaceae is extensive, and the oldest fossil legumes are petrified woods from the Upper Cretaceous of Sudan assigned to *Cassinium dongolense* Giraud and Lejal-Nicol, which suggests a relationship with the extant *Cassia* L. (Caesalpinoideae; Giraud and Lejal-Nicol, 1989). A review of the diverse and abundant Cenozoic fossils was made by Herendeen (1992) and multiple subsequent contributions have significantly increased the worldwide fossil record of legumes (Calvillo-Canadell and Cevallos-Ferriz, 2005; Lavin *et al*., 2005; Taylor *et al*. 2009; Wing *et al*., 2009; Pujana *et al*., 2011).

Lavin *et al*. (2005) inferred the diversification of the Fabaceae crown-group at 59 Ma. This age, based on molecular clock estimates of phylogenetic analyses, is younger than South American fossils belonging to Mimosoideae (Iglesias *et al*., 2007; Brea *et al*., 2008) colected in rocks dated at 64.7–63.5 Ma (Wilf and Escapa, 2015). These Paleocene mimosoid fossils might support the previous estimates proposed by Wikström *et al*. (2001) who estimated a Campanian age for the diversification of Fabaceae (74–79 Ma).

Currently, the oldest known Mimosoideae records are from the Paleocene (Salamanca Formation) of Patagonia, Argentina (Iglesias *et al*., 2007; Brea *et al*., 2008) and the Paleocene–Eocene boundary (Wilcox Formation) of USA (Crepet and Taylor, 1985, 1986). The first includes legume leaflets (Iglesias *et al*., 2007) and the fossil wood *Paracacioxylon frenguellii* Brea, Zamuner, Matheos, Iglesias and Zucol, which significantly resemble modern elements of *Acacia* s.l. (Brea *et al*., 2008). The second consists of the compressed flowers *Protomimosoidea buchananensis* Crepet and Taylor, whose diagnostic characters suggest a close relationship (ancestral or sister group) between the subfamiliy Mimosoideae and the Dimorphandra group of the tribe Caesalpinieae of the subfamily Caesalpinioideae (Crepet and Taylor, 1986).

In South America, the family Fabaceae has an extensive record of fossil wood (Pujana *et al*., 2011). Legume fossil woods are very diverse and have a long record from the Paleocene to the Pleistocene (Gregory *et al*., 2009), and a broad geographical range from the southernmost part of Patagonia to northern Colombia. Mimosoideae is better represented (61%) than Caesalpinioideae and Papilionoideae (39%) in the fossil record of South America. In Argentina, the records of legume wood are mainly from three areas, *i.e*., Northwest (Neogene), Northeast (Neogene) and Patagonia (Paleogene and Neogene), with all three subfamilies represented (Pujana *et al*., 2011).

The fossil wood record of the Arroyo Feliciano Formation is poorly known (Moya, 2012, 2013; Moya *et al*., 2013; Moya and Brea, 2015) but here we describe two new genera and species of Mimosoideae. They represent the first report of fossil wood with affinities to *Cylicodiscus* Harms for one specimen and *Abarema* Pittier and *Hydrochorea* Barneby and J.W. Grimes for the other. The combination of diagnostic anatomical features allow their assignment to two new genera, *i.e*., *Cylicodiscuxylon* gen. nov. and *Abaremaxylon* gen. nov.

Cylicodiscus is included in the tribe Mimosae. It is monotypic and lives from Sierra Leone to the Ivory Coast, Ghana, Nigeria, Cameroon and Gabon in West Africa, in tropical rain forests and seasonally dry forests (Lewis *et al*., 2005; Ayarkwa and Owusu, 2008).

Abarema and *Hydrochorea* are included in the tribe Ingeae, and these taxa have many anatomical features in common (Lewis *et al*., 2005). Today, *Abarema* includes 46 endemic species of trees with a Neotropical distribution. It is typical of tropical lowland or "*terra firme*", montane humid forests, coastal woodlands, and coastal bushlands. *Hydrochorea* ssp. are usually trees or arborescent shrubs and the genus is widely distributed over the Amazon-Guayana forests (Barneby and Grimes, 1996; Díaz and Rosales, 2006).

The new fossil woods described here increase our understanding of legume diversity during the late Pleistocene and add new records to the list of Fabaceae in northeastern of Argentina.

GEOLOGICAL AND PALEONTOLOGICAL SETTING

The studied fossil woods were collected from the basal beds of the Arroyo Feliciano Formation exposed at Consorcio Paso Sociedad (31° 03′ S, 58° 38′ W), near the city of Federal in Entre Ríos Province, Argentina (Fig. 1).

The Arroyo Feliciano Formation, which is 2–6 m thick, outcrops mainly along both banks of the Río Gualeguay and the major rivers and streams in central and northern Entre Ríos Province (Iriondo *et al*., 1985; Iriondo and Kröhling, 2008; Brunetto *et al.*, 2012, 2015). This continental deposit was defined by Iriondo *et al.* (1985) and represents alluvial and fluvial deposits distributed in the tributary valleys of the Paraná and Uruguay Rivers (Entre Ríos Province, Argentina). The Arroyo Feliciano Formation is mainly composed of well-selected fine sands and whitish to light-green silts. It is massive and only rarely presents lamination or stratification, which are very thin and poorly defined whenever present. In the lowest part of the section there are abundant manganese nodules and carbonate concretions which are also very common along the entire section.

Sedimentological data from the Arroyo Feliciano Formation suggest more humid conditions than those currently prevailing in the area (Iriondo *et al.*, 1985). At Consorcio Paso Sociedad, the *c.* 6 m thick sedimentary deposits of the Arroyo Feliciano Formation are well exposed. The base is not exposed and the unit is mainly composed of light grey-to-white silty clays and fine sands with carbonatic concretions. Manganese nodules occur in the lowest parts of the section. The stratification is very thin and poorly defined. At the top of the section lies a volcanic ash lens (*c.* 1 m thick) with marked laminar stratification (Figs. 2, 3).

The Arroyo Feliciano Formation was deposited during the late Pleistocene (Iriondo and Kröhling, 2008). The presence of *Toxodon platensis*, *Mylodon darwini* and *Lestodon* sp. (Brunetto *et al.*, 2012) and *Hippocamelus* sp. (Alcaraz and Ferrero, 2013) has been reported. The Arroyo Feliciano Formation has been tentatively correlated with the Bonaerian–Lujanian Stage/Age in Buenos Aires Province, Argentina (Brunetto *et al.*, 2012). The rich vertebrate content originally attributed to the Arroyo Feliciano and Tezanos Pintos formations (Ferrero, 2009; Brunetto *et al.*, 2015 and references therein) is now considered as belonging to the Salto Ander Egg Formation. Recently, detailed stratigraphic and sedimentological analyses allowed discriminating the Salto Ander Egg Formation as a different geological unit (Brunetto *et al.*, 2012, 2015).

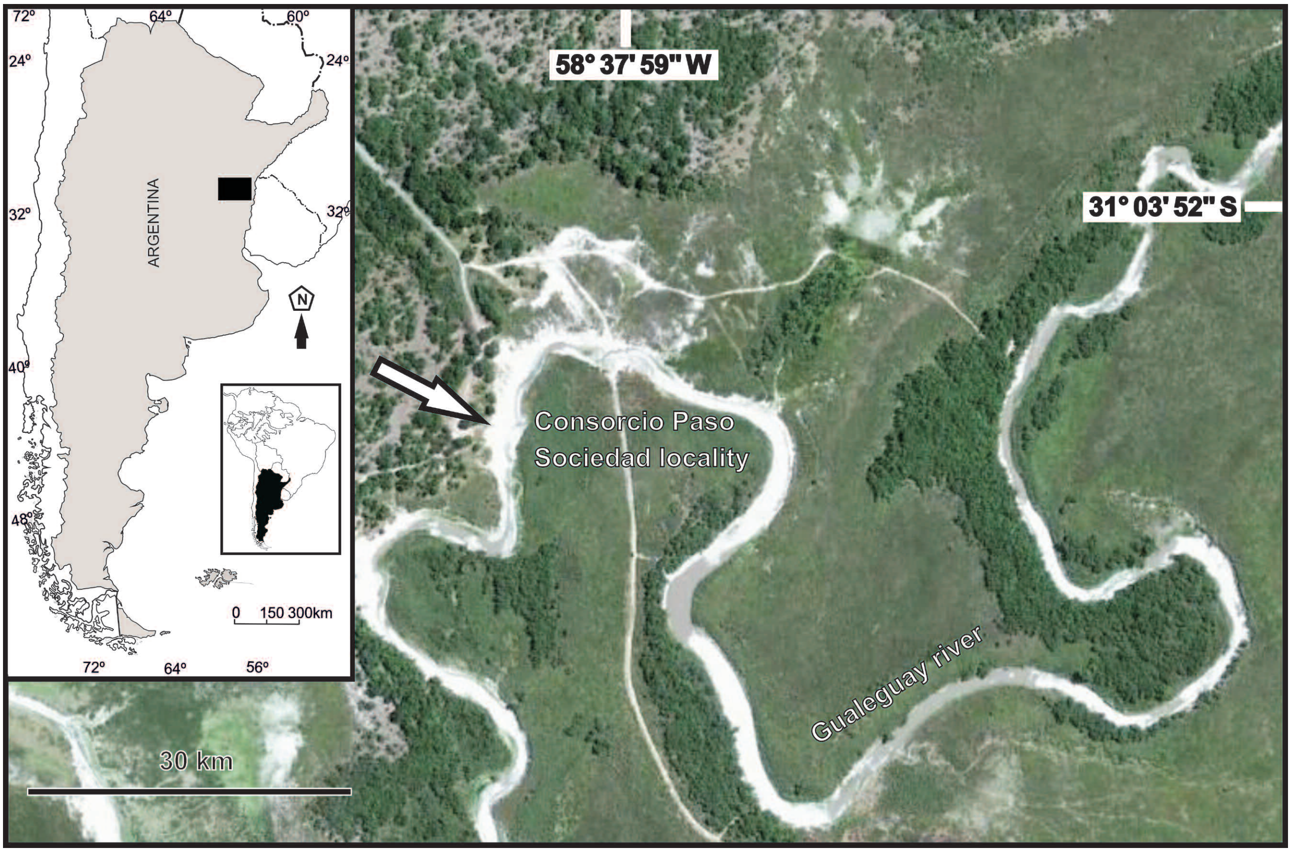


Figure 1. Location map showing the fossil locality Consorcio Paso Sociedad, Entre Ríos, Argentina.

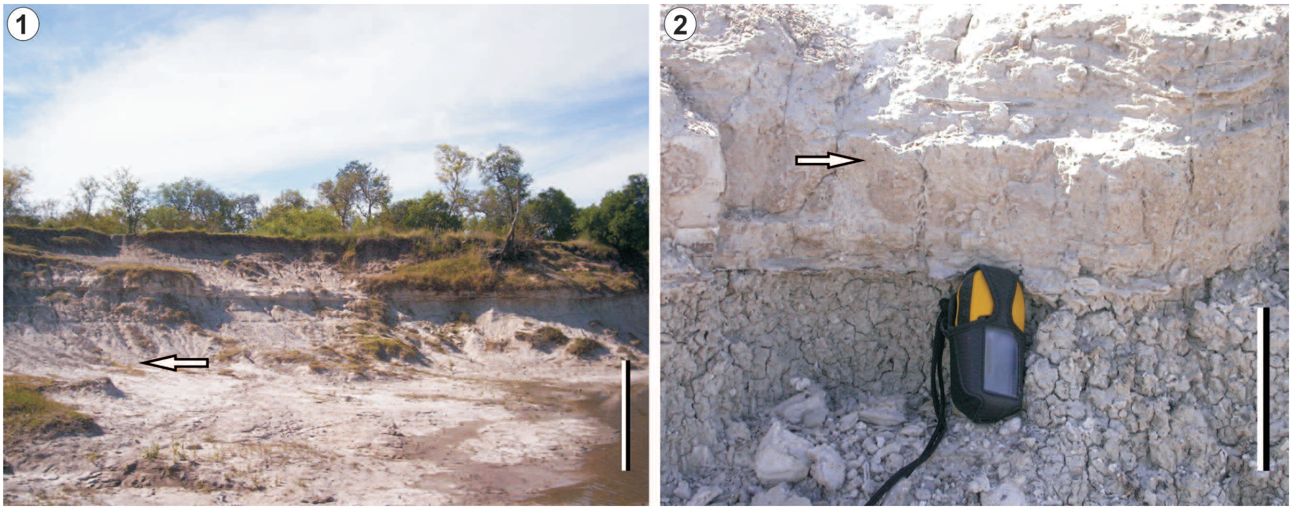


Figure 2. 1, general view of the fossil locality Consorcio Paso Sociedad, where the fossil woods were found (arrow). **2,** detail of the section of the Arroyo Feliciano Formation. The arrow indicates the volcanic ashes. Scale bars: 1= 1, 88 m; 2= 0, 12 m.

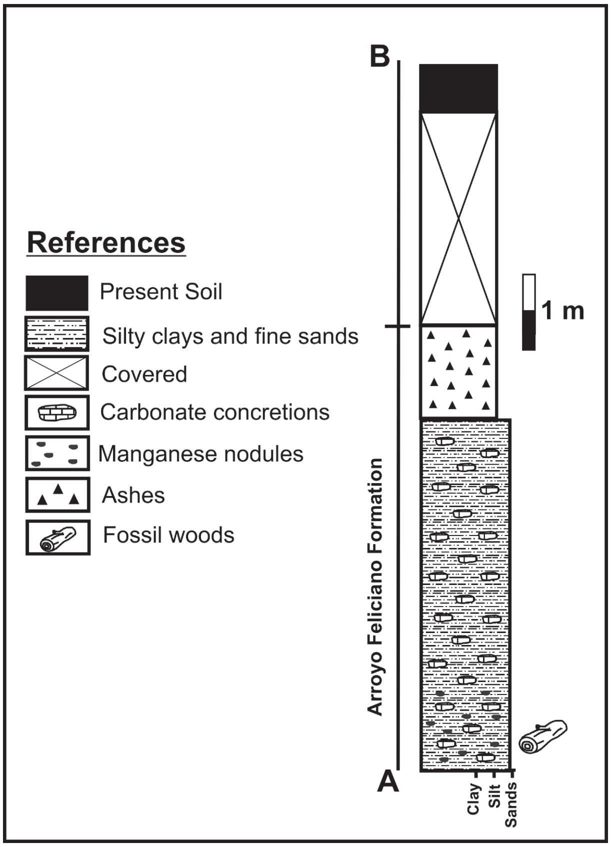


Figure 3. Schematic section at the Consorcio Paso Sociedad.

MATERIAL AND METHODS

The fossil specimens were permineralized by silica and bear well-preserved anatomical features of the secondary xylem. They were thin-sectioned in three standard sections (cross, tangential and radial sections). The recommendations of the IAWA List of Microscopic Features for Hardwood Identification (IAWA Committee, 1989) were used. Terminology proposed by Tortorelli (1956) and Carlquist (2001) was also considered. The reference lists by Gregory (1994) and Gregory *et al*. (2009) were used.

For identification of the fossil wood samples and comparison of the fossil materials with extant and fossil species we used the InsideWood web site (InsideWood, 2004–onwards; Wheeler, 2011), Commercial timbers web site (Richter and Dallwitz 2000–onwards) and descriptions by Metcalfe and Chalk (1950), Cozzo (1951), Tortorelli (1956), Ayensu and Bentum (1974), Baretta-Kuipers (1981), Cassens and Miller (1981), Wheeler and Baas (1992), Barros and Callado (1997), Judd *et al*. (1999), Espinosa de Pernía and Melandri Pírela (2000), Evans *et al*. (2006) and León (2008). Systematic assignment follows the APG III (2009).

The Vulnerability Index (**V**) and Mesomorphy ratios (**M**) were calculated using the equations developed by Carlquist (1977). 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. The UTHSCSA Image Tool program Version 3.0 was used to measure the elements through photomicrographs.

The material was studied with a Nikon Eclipse E200 light microscope and the photomicrographs were taken with a Nikon Coolpix S4 digital camera. The holotype fossil specimen and microscope slides are housed in the Laboratorio de Paleobotánica, Centro de Investigaciones Científicas y Transferencia de Tecnología a la Producción, Consejo Nacional de Investigaciones Científicas y Técnicas (**CICyTTP-CONICET**), Diamante, Argentina, under the acronyms **CIDPALBO-MEG** 62 (**CIDPALBO-MIC** 712) and **CIDPALBO-MEG** 66 (**CIDPALBO-MIC** 716). The isotypes were deposited in the Colección Paleontología, Museo de Antropología y Ciencias Naturales "Conscripto Bernardi", Conscripto Bernardi, Argentina, under the acronyms M01 and B.

SYSTEMATIC PALEONTOLOGY

Family Fabaceae Lindley, 1836
Subfamily Mimosoideae de Candolle, 1825
Tribe Mimoseae Bronn, 1822

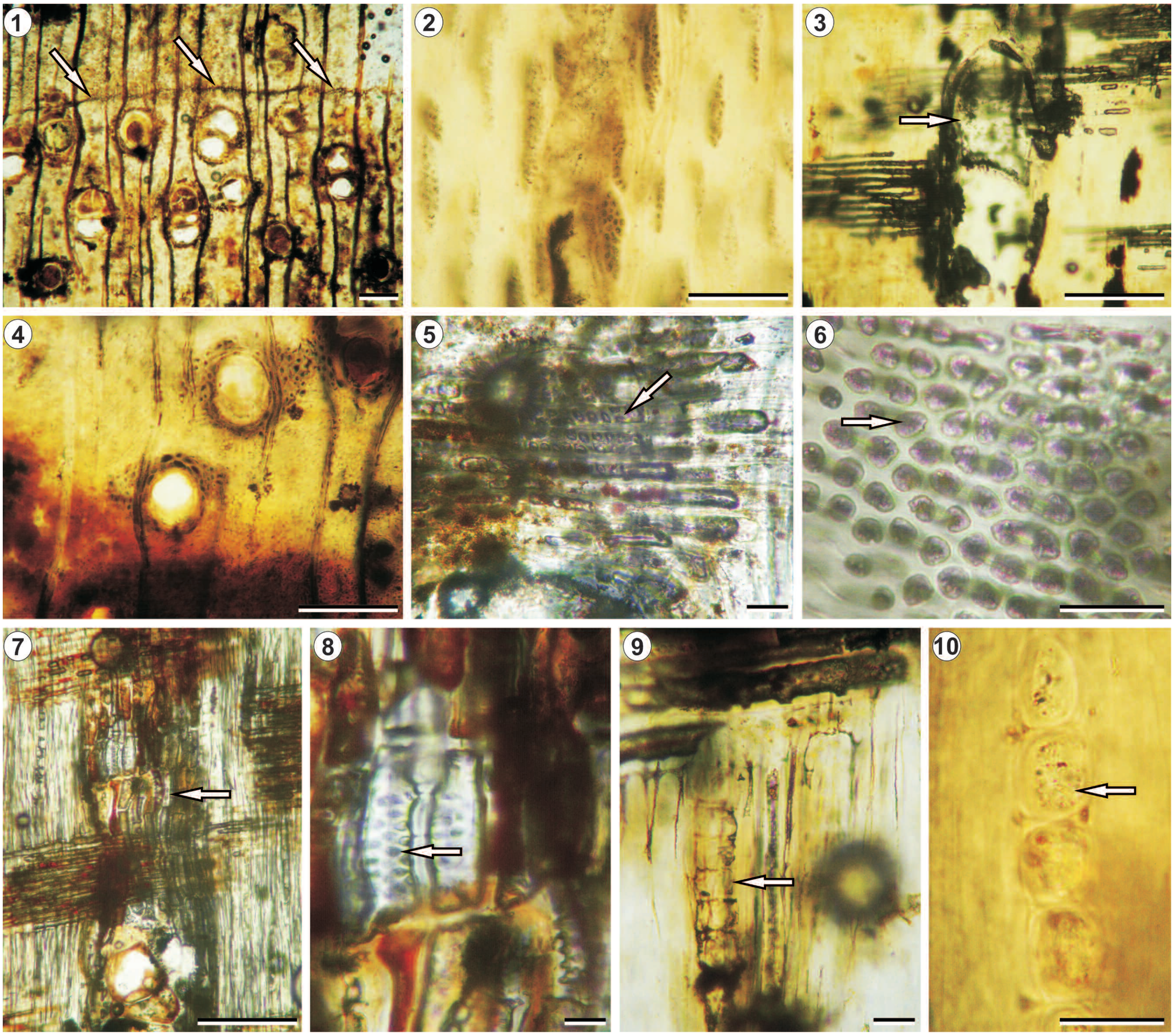


Figure 4. 1–13, ***Cylicodiscuxylon paragabunensis*** gen. nov. et sp. nov., **CIDPALBO-MEG** 66, **CIDPALBO-MIC** 716.**1,** cross section, general view showing growth rings (arrows), diffuse porous wood and vasicentric, aliform, lozenge-aliform and confluent axial parenchyma; **2,** tangential section, general view showing uniseriate and multiseriate rays; **3,** radial section, showing simple perforation plates (arrow) and homocellular rays; **4,** cross section, detail of vessels and axial parenchyma; **5,** radial section, detail of ray pits (arrow); **6,** tangential section, detail of intervessel pits, alternate and vestured (arrow); **7,** radial section, detail of vasicentric axial parenchyma, parenchyma strand (arrow) and homocellular rays; **8,** radial section, detail of simple pits in parenchyma cells (arrow); **9,** radial section, detail of prismatic crystals in chambered axial parenchyma cells (arrow); **10,** tangential section, detail of ray cells (arrow)**.** Scale bars**:** 1–4, 7= 200 µm; 5–6, 8–10= 20 µm.

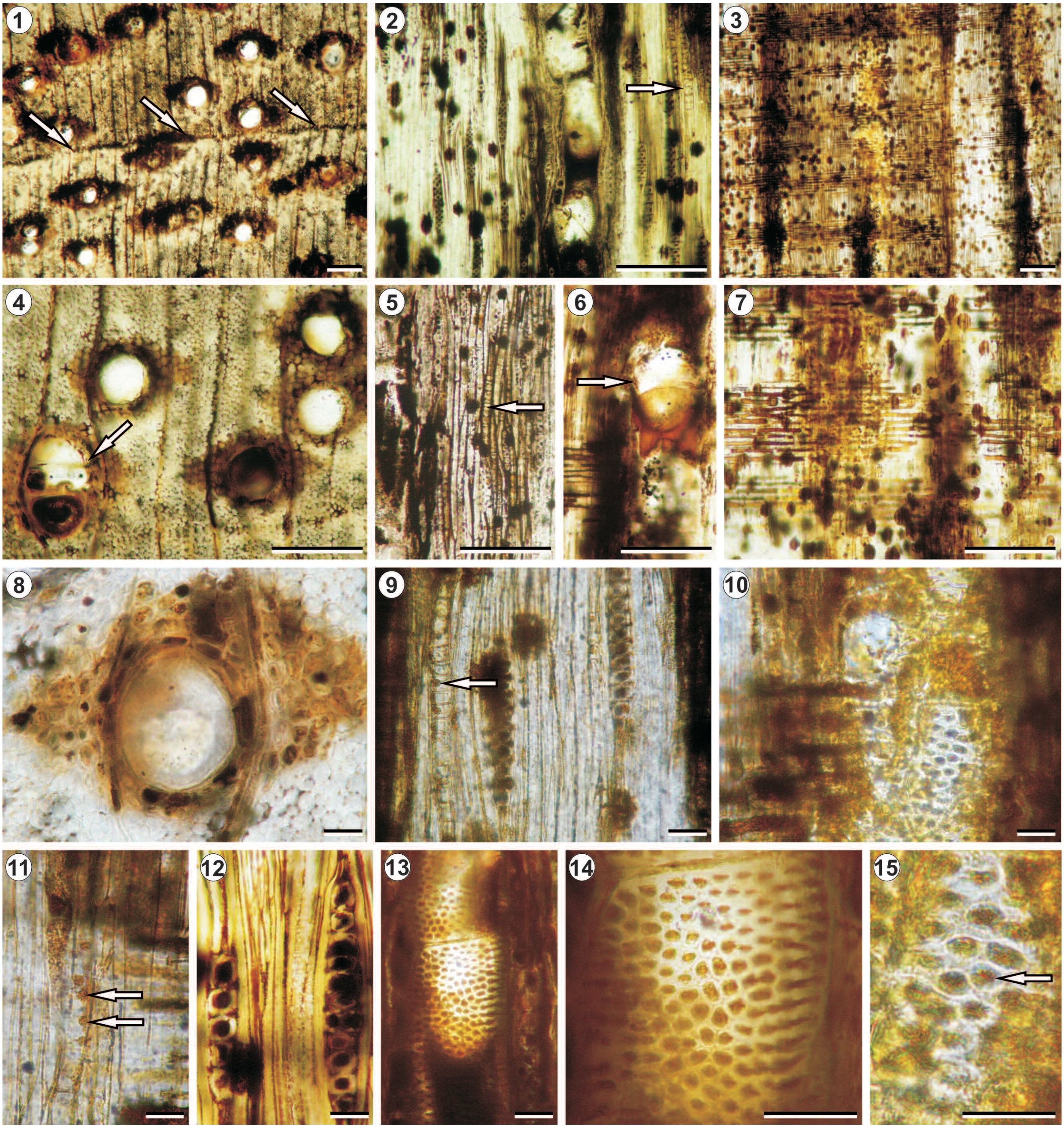


Figure 5. 1–15, ***Abaremaxylon hydrochorea*** gen. nov. et sp. nov. (**CIDPALBO-MEG** 62, **CIDPALBO-MIC** 712). **1,** cross section, general view showing growth rings (arrows), diffuse porous wood and vasicentric, aliform, unilateral aliform, confluent axial parenchyma; **2,** tangential section, general view showing exclusively uniseriate rays and rarely with biseriate portions and parenchyma strand (arrow); **3,** radial section, general view showing homocellular rays; **4,** cross section, detail of vessels solitary and in radial multiples of 3 (arrow), and axial parenchyma; **5,** tangential section, detail of rays and prismatic crystals in fibres (arrow); **6,** radial section, simple perforation plate; **7,** Radial section, detail of homocellular rays; **8,** cross section, detail of vessel with pit walls, vasicentric axial parenchyma, and fibres; **9,** tangential section, detail of prismatic crystals in long chains of chambered axial parenchyma crystalliferous cells (arrow) and uniseriate rays; **10,** radial section, vessel-ray pits; **11,** radial section, detail of simple to minutely bordered pits in fibres (arrows); **12,** tangential section, detail of rays; **13,** tangential section, intervessel pits; **14,** tangential section, detail of intervessel pits; **15,** radial section, detail of vessel-ray pits (arrow). Scale bars: 1–7= 200 µm; 8–15= 20 µm.

Genus *Cylicodiscuxylon* gen. nov.

Cylicodiscuxylon paragabunensis gen. nov. et sp. nov.

Figure 4.1–10

Derivation of name. The generic name, *Cylicodiscuxylon*, refers to its affinity with *Cylicodiscus*. The specific name, *paragabunensis*, refers to its resemblance to the extant species *C. gabunensis*.

Diagnosis. Distinct growth rings, diffuse-porous wood, mostly solitary vessels, in radial multiples of 2–5, occasionally in clusters; simple perforation plates; bordered, alternate, vestured and small to medium intervessel pits; vessel-ray parenchyma pits similar in size and shape to intervessel pits; gums or other deposits present; vasicentric, aliform, lozenge-aliform and confluent axial parenchyma, strands of 5–11 cells; prismatic crystals in chains in chambered axial parenchyma cells; frequently 1–3 (4) seriate rays, mostly biseriate, homocellular composed exclusively by procumbent cells; non-septate fibres.

Holotype. CIDPALBO-MEG 66, CIDPALBO-MIC 716 (three slides).

Isotype. B.

Geographic occurrence. Consorcio Paso Sociedad, Federal, Entre Ríos, Argentina (31° 03′ S, 58° 38′ W).

Stratigraphic occurrence. Arroyo Feliciano Formation, late Pleistocene.

Description. In cross section, growth rings are demarcated by radial compression of fibres (Fig. 4.1). Diffuse porous wood. Vessels are mostly solitary (53%), in radial multiples of 2–5 (29%, 12%, 2% and 1% respectively) and in clusters (3%) (Fig. 4.1, 4.4). Vessels are circular in outline, well demarcated, with thick walls, 11 (6–16) µm thick (Fig. 4. 4). Average tangential diameter of 124 (74–170) µm and average radial diameter of 133 (56–198) µm. The average vessel density is 6 (5–7)/ mm^2. Dark deposits are observed, brown and amber, attributed to “gums” (Fig. 4.1, 4.4). The paratracheal axial parenchyma is vasicentric, aliform, lozenge-aliform and confluent. Fibres are rounded to hexagonal in outline, non-septate, disorderly and abundant, with very thin to thick-walls 4 (2–5) µm thick, and with a mean diameter of 10 (6–16) µm (Fig. 4.1, 4.4).

In tangential section, the vessel element average length is 219 (81–431) µm. Perforation plates are exclusively simple; intervessel pits are alternate, bordered and vestured, oval to hexagonal in outline, small to medium (Fig. 4.6). Their average diameter is 7 (5– 8) µm. Rays are frequently 1–3 (4) seriate, mostly biseriate. The average height is 186 (110–300) µm and 11 (6–19) cells high. The mean width of the rays is 29 (15–42) µm, fine to very fine, with 2.4 (2–3) per linear mm (Fig. 4.2, 4.10). Axial parenchyma strands are composed of 8 (5–11) cells (Fig. 4.7–8).

In radial section, rays are homocellular, composed exclusively of procumbent cells (Fig. 4.3, 4.5, 4.7–9), vessel-ray parenchyma pits similar in size and shape to intervessel pits (Fig. 4.5). Perforation plates are exclusively simple with straight to oblique end walls (Fig. 4.3). Fibres are non-septate (Fig. 4.7). Parenchyma cells have simple pits (Fig. 4.7–8). Many ray cells carry a dark content (Fig. 4.3, 4.5, 4.7–9). Prismatic crystals are present in chambered axial parenchyma cells with one crystal per chamber (Fig. 4.9).

Tribe INGEAE Bentham and Hooker, 1865

Genus *Abaremaxylon* gen. nov.

Abaremaxylon hydrochorea gen. nov. et sp. nov.

Figure 5.1–15

Derivation of name. The generic and specific names refer to the alliance between *Abarema* and *Hydrocorea* whose differences in anatomical features are not explicit enough for distinction.

Diagnosis. Distinct growth rings, diffuse porous wood, mostly solitary vessels, in radial multiples of 2–4, rarely in clusters; simple perforation plates; bordered, alternate, vestured and small to medium intervessel pits; vessel-ray pits similar in size and shape to intervessel pits, gums or dark deposits probably present; vasicentric, aliform, unilateral aliform, confluent axial parenchyma, strands of 4–16 cells; prismatic crystals in chains in chambered axial parenchyma cells; rays uniseriate or less commonly with biseriate portions, homocellular composed exclusively by procumbent cells; non-septate fibres.

Holotype. CIDPALBO-MEG 62, CIDPALBO-MIC 712 (three slides).

Isotype. M01.

Geographic occurrence. Consorcio Paso Sociedad, Federal, Entre Ríos, Argentina (31° 03′ S, 58° 38′ W).

Stratigraphic occurrence. Arroyo Feliciano Formation, late Pleistocene.

Description. In cross section, growth rings are demarcated by radial compression of fibres (Fig. 5.1). Wood is diffuse porous, locally with a tendency to dendritic distribution of vessels. Vessels are mostly solitary (84%), in radial multiples of 2–3 (10% and 5% respectively) and rarely tangential multiples or in clusters (1%) (Fig. 5.1, 5.4). Vessels are circular in outline, well demarcated and with thick walls, 10 (6–17) µm thick. Pit walls are clearly visible in cross section (Fig. 5.8).

Table 1. Comparison of anatomical characteristics of* Cylicudiscus gabunensis *based on different bibliographic data and* Cylicodiscuxylon paragabunensis *gen. nov. et sp. nov.

		*InsideWood database**	*Commercial timbers***	*Ayensu and Bentum (1974)*	**Cylicodiscuxylon paragabunensis** *gen. nov. and sp. nov.* ***
Vessels	***Porosity*** ***Perforation plates***	*diffuse-porous* *simple*	*diffuse-porous* *simple*	*diffuse-porous* *simple*	*diffuse-porous* *simple*
	Groupings	–	*solitary, radial multiple (2–3 vessels), occasionally clusters*	*mostly solitary, occasionally in multiples of 2 or 3*	*mostly solitary, radial multiple (1–4 vessels), occasionally clusters*
	Tangential diameter	*100–200 µm*	*130–330 µm*	*168–322 µm*	*74–170 µm*
	Tyloses and deposits	*gums and other deposits in heartwood vessels*	*deposits present*	*deposits presents in some vessels and rays*	*deposits present*
	Intervessel pits	*alternate, vestured pits*	*alternate, vestured pits*	*alternate pits*	*alternate, bordered and vestured pits*
	Vessels per square millimetre	*≤5*	*1–4; very few*	–	*5–7*
Rays	***Width***	*1–3 cells*	*3–5 cells*	*1–2 cells*	*1–3 cells*
	High	*4–10-cells*	–	*biseriate rays 8 to 55 cells, uniseriate rays 5 to 15 cells*	*6–19 cells*
	Cellular composition	*all procumbent*	*all procumbent*	*all procumbent*	*all procumbent*
	Rays per mm	*4–12 rays*	*5–7 rays*	–	*2–3 rays*
Axial Parenchyma	***Paratracheal***	*vasicentric, aliform, lozenge-aliform, confluent*	*vasicentric, aliform, lozenge-aliform, confluent , 2–6 cells per parenchyma strand*	*sometimes vasicentric, conspicuously banded*	*vasicentric, aliform, lozenge-aliform, confluent , 5–11 cells per parenchyma strand*
	Prismatic crystals	*present*	*present, one cristal per cell*	–	*present, one cristal per cell*
Fibres	***Pits***	*simple to minutely bordered pits*	*simple to minutely bordered pits*	–	–
	Non-septate or septate	*non-septate*	*non-septate*	–	*non-septate*
	Walled	*thin-to thick-walled*	*thin-to thick-walled*	–	*thin-to thick-walled*

** InsideWood. 2004-onwards.*
*** Richter, Dallwitz, 2000–onwardss.*
**** this paper.*

The average tangential diameter is 108 (60–160) µm and the average radial diameter is 107 (70–150) µm. Average vessel density is 10 (5–21)/ mm^2. Dark deposits are observed, brown and amber, attributed to "gums" (Fig. 5.1, 5.4). The paratracheal axial parenchyma is vasicentric, aliform, unilateral aliform and confluent. Fibres are rounded to hexagonal in outline, non-septate, disorderly and abundant, with very thin to thick-walls 2 (1–3.5) µm thick and with a mean diameter of 14 (8–20) µm (Fig. 5.1, 5.4, 5.8).

In tangential section, the vessel element average length is 601 (320–1125) µm (Fig. 5.2). Perforation plates are exclusively simple with straight to oblique end walls (Fig. 5.2); intervessel pits are alternate, bordered and vestured, oval to hexagonal in outline, small. Their average diameter is 6 (5–7) µm (Fig. 5.13–14). Rays are exclusively uniseriate (98%), and some are uniseriate with biseriate portions. The average height is 125 (71–193) µm and 8 (4–13) cells high. The average width of the rays is 17 (13–23) µm. Rays are few to moderately numerous, 5 (3–6) per linear mm (Fig. 5.2, 5.5, 5.9, 5.12). Vasicentric axial parenchyma strands are composed of 2–4 cells. Prismatic crystals are present in long chains of chambered axial parenchyma crystalliferous cells, 8 (4–16) cells, with a single prismatic crystal per chamber (Fig. 5.2, 5.9). Non-septate fibres are present (Fig. 5.9). Prismatic crystals were also observed in fibres (Fig. 5.5).

In radial section, the rays are homocellular, composed exclusively of procumbent cells (Fig. 5.3, 5.7), the vessel-ray pits are similar to intervessel pits, bordered, alternate and polygonal (Fig. 5.10, 5.15). Perforation plates are exclusively simple (Fig. 5.6). In most cells, dark content was observed (Fig. 5.2–3, 5.5–7, 5.10–12). Fibres have simple to minutely bordered pits (Fig. 5.11).

DISCUSSION

Comparison with extant species

The presence of vestured pits, vessel elements with simple perforation plates and homocellular rays are the features that allow placing these specimens in the Fabales. In addition, the combination of diffuse porous wood, solitary vessels and vessels in radial multiples, simple perforation plates, alternate and vestured intervessel pits, vessel-ray parenchyma pits similar to intervessel pits, axial parenchyma that is abundant and vasicentric, aliform, confluent or banded, commonly 2–4 cells per strand, uniseriate or rarely biseriate rays, homocellular rays composed of procumbent cells, and non-septate fibres occur in the Mimosoideae (Metcalfe and Chalk, 1950; Cozzo, 1951; Tortorelli, 1956; Baretta-Kuipers, 1981; Wheeler and Baas, 1992; Barros and Callado, 1997; Judd *et al.*, 1999; Espinosa de Pernía and Melandri Pírela, 2000; Evans *et al.*, 2006; León 2008). The diagnostic features present in these fossil woods suggest affinities with Mimoseae and Ingeae tribes, respectively (Evans *et al.*, 2006).

Molecular data have shown the tribe Mimoseae to be polyphyletic (Luckow *et al.*, 2000, 2003; Miller *et al.*, 2003, 2013). Evans *et al.* (2006) proposed that the wood anatomy appears to support the 14 informal Mimoseae groups (*sensu* Luckow, 2005) due to similarities between the constituent genera. On the basis of wood anatomy, the suprageneric groups can be divided into five divisions, and the first fossil wood described here falls within the Mimoseae Division 5 (Evans *et al.*, 2006). The *Cylicodiscus* group is monospecific (Ayarkwa and Owusu, 2008) and characterised by wide and few vessels per mm^2, aliform and confluent, not banded axial parenchyma, 2–3 seriate rays and non-septate fibres. All these features were used to place this group within Mimoseae Division 5 (Evans *et al.,* 2006). Table 1 shows anatomical characteristics shared between *Cylicodiscus gabunensis* and *Cylicodiscuxylon paragabunensis* gen. nov. et sp. nov.

The second fossil wood described here is related to tribe Ingeae. Phylogenetic analyses concur that Ingeae and Acaciae are derived from the Mimoseae (Doyle *et al.*, 2000; Luckow *et al.*, 2000). On the basis of anatomical features (septate or non-septate fibres, presence or absence of banded parenchyma and rays width) the Ingeae tribe is divided into four divisions. The second fossil wood described from the Arroyo Feliciano Formation can be placed in the Ingeae Division 4, characterized by non-septate fibres, not banded parenchyma and uniseriate rays (Evans *et al.*, 2006). Division 4 also includes the genera *Abarema*, *Chloroleucon* (Benth.) Britton and Rose, *Enterolobium* Mart., *Falcataria* (I.C. Nielsen) Barneby and J.W. Grimes, *Hydrochorea*, *Leucochloron* Barneby and J.W. Grimes, *Pithecellobium* Mart., *Samanea* (Benth.) Merr., *Serianthes* Benth. and *Wallaceodendron* Koord. *Abarema* and *Hydrochorea* share many characteristics and are the genera most closely related to *Abaremaxylon hydrochorea* gen. nov. et sp. nov. The ana-tomical features of this fossil wood and the species of the *Abarema* alliance (Evans *et al.*, 2006) are shown in Table 2.

TABLE 2. Comparison of **Abaremaxylon hydrochorea** *gen. nov. et sp. nov. with extant species of Abarema Alliance - Tribe Ingeae (data taken from Evans* **et al.**, *2006).*

Species	*Growth rings*	*Average tangential vessel diameter (µm)*	*Vessels/mm²*	*Radial multiple vessels*	*N° of vessels/RM*	*IVP diameter (µm)*	*Cluster*	*Fibre wall thickness thin/ med/ thick*	*Septate fibres*	*Axial parenchyma*	*confluent parenchyma*	*banded parenchyma*	*N° of cells/strand*	*Ray/mm*	*Rays width (cell)*	*Homocellular rays*	*Crystals*	*Gum*
Abaremaxylon hydrochorea *Moya and Brea*	*D*	*108*	*10*	*O*	*2–4*	*5–7*	*R*	*med*	*N*	*A/ V/C*	*F*	*N*	*1–4*	*5*	*1*	*Y*	*F, A*	*R, V, AP*
A. alexandri *(Urban) Barneby and Grimes*	*I*	*150*	*11*	*F*	*2–4*	*3–6*	*R*	*med*	*N*	*A*	*F*	*N*	*2–4*	*7*	*1(2)*	*Y*	*F, A*	*R, V*
A. glauca *(Urban) Barneby and Grimes*	*A/I*	*173*	*17*	*F*	*2–7*	*3–6*	*O*	*med*	*N*	*A/C*	*C/ VC*	*CO*	*1–4*	*7*	*1(2)*	*Y*	*F, A*	*R, AP*
A. jupunba *(Willd.) Britton and killip*	*A*	*153*	*8*	*O*	*2*	*c. 6*	*N*	*med*	*N*	*V/A*	*O*	*N*	*2–4*	*9*	*1(2)*	*Y*	*F, A*	*AP*
A. langsdorfii *(Pittier) Barneby and Grimes*	*A*	*128*	*13*	*F*	*2–4*	*3–6*	*O*	*Med/ thick*	*N*	*(V)A*	*O*	*N*	*2–4*	*8*	*1*	*Y*	*F, A*	*V*
A. macradenia *(Pittier) Barneby and Grimes*	*I*	*178*	*9*	*F/C*	*2 (3)*	*c. 6*	*R*	*med*	*N*	*A*	*C*	*N*	*2–4*	*7*	*1(3)*	*Y*	*F, A*	*R, AP*
Hydrocorea corymbosa *(Rich) Barneby and Grimes*	*D/I*	*153*	*9*	*F*	*2–6 (10)*	*6–9*	*R/ O*	*Thin*	*N*	*A*	*R/ O*	*N*	*1–4*	*8*	*1*	*Y*	*F, A*	*R/F*
Hydrocorea gongrijpii *(Kleinhoonte) Barneby and Grimes*	*I*	*178*	*10*	*F*	*2–6 (8)*	*6–9*	*R*	*Med*	*N*	*V/A*	*O*	*N*	*1–4*	*7*	*1(2)*	*Y*	*F, A*	*R*

Abbreviations: growth rings: **A,** absent, **I,** indistinct, **D,** distinct; Radial multiples, clusters and axial parenchyma confluent (occurrence): **R,** rare (<10%), **O,** occasional (10– 30 %), **F,** frequent (30– 60%), **C,** common (60– 80%), **VC,** very common (>80%); **RM:** radial multiple; **IVP:** intervessel pitting measured horizontally in µm; septate fibres: **Y,** yes, **N,** not seen; axial parenchyma: **A,** aliform, **V,** vasicentric, **S,** scanty, **W,** winged aliform, **U,** unilateral, **C,** confluent, **B,** banded; axial parenchyma banded: **Y/N,** yes/no, **MB,** marginal bands only, **CO,** banding through confluence only, **reg,** regular, **irr,** irregular, **dis,** discontinuous, **cnt,** continuous; rays: **Y,** homocellular, **N,** heterocellular; crystals (location of): **N,** not seen, **F,** chambered fibres, **A,** chambered axial parenchyma, **R,** chambered ray cell. All are prismatic crystal; gum (location of): **N,** not seen, **R,** ray cell, **AP,** axial parenchyma cells; **V,** vessels, **F,** fibres.

Comparisons with fossil species

Nine fossil genera of the Mimosoideae are currently known from South America, *i.e.*, *Mimosoxylon*, Müller-Stoll and Mädel 1967, *Tetrapleuroxylon* (Felix) Müller-Stoll and

Mädel 1967, *Paracacioxylon* (Menéndez) Müller-Stoll and Mädel 1967, *Piptadenioxylon* Suguio and Mussa 1978, *Menendoxylon* Lutz 1979, *Anadenantheroxylon* Brea, Aceñolaza and Zucol 2001 emend. Franco and Brea 2013, *Prosopisinoxylon* Martínez 2010, *Microlobiusxylon* Franco and Brea 2010, and *Paraalbizioxylon* (Gross) Martínez 2014

Table 3. Comparison the characters of the fossil genera of Mimosoideae *records in South America.*

Fossil genus	*Vessels*	*Intervascular pitting, type*	*Intervascular pitting, size*	*Ray type*	*Ray width*	*Axial parenchyma type*	*Fibre type*
Mimosoxylon *Müller-Stoll and Mädel 1967*	*solitary, radial multiples*	*alternate*	*small to medium*	*Ho, rarely weakly He*	*1–3 seriate*	*narrow vasicentric, partly weakly aliform, rare confluent, terminal or initial*	*non-septate*
Tetrapleuroxylon *(Felix) Müller-Stoll and Mädel 1967*	*solitary and radial multiples*	*alternate*	*medium*	*Ho to weakly He*	*1–5 seriate*	*vasicentric aliform, partly confluent, terminal or initial*	*non-septate*
Paracacioxylon *(Menéndez) Müller-Stoll and Mädel 1967*	*solitary, radial multiples of 2–4 and clusters*	*alternate, compressed and vestured*	*small to medium*	*Ho*	*1–6 seriate*	*paratracheal vasicentric, aliform, confluent. Apotracheal diffuse*	*septate and non-septate*
Piptadenioxylon *Suguio and Mussa 1978*	*solitary, rarely radial multiple*	*alternate*	*small*	*Ho*	*2–3 seriate*	*vasicentric*	*non-septate*
Menendoxylon *Lutz 1979*	*predominantly solitary, radial multiples of 2–3*	*alternate*	*small to medium*	*Ho to He*	*1–3 seriate*	*vasicentric aliform, shorts bands*	*Septate, sporadically non-septate*
Anadenantheroxylon *Brea, Aceñolaza and Zucol 2001*	*solitary, radial multiples of 2–4 and clusters*	–	–	*Ho*	*1–2 seriate*	*paratracheal vasicentric and confluent*	*non-septate*
Prosopisinoxylon *Martínez 2010*	*vessels of two distinct diameter classes; solitary, radial multiples and clusters*	*alternate*	*small to medium*	*Ho*	*1–9 seriate*	*paratracheal vasicentric, aliform and confluent to banded. Apotracheal diffuse*	*non-septate*
Microlobiusxylon *Franco and Brea 2010*	*solitary , radial multiples of 2–3 and clusters*	*alternate and vestured*	*minute to small*	*Ho*	*1–2 seriate*	*paratracheal vasicentric, aliform and confluent*	*non-septate*
Paraalbizioxylon *(Gross) Martínez 2014*	*solitary and radial multiple*	–	*small to medium*	*Ho*	*1–6 seriate never only uniseriate*	*paratracheal, in some cases apotracheal, diffuse, terminal*	*septate and non-septate*
Cylicodiscuxylon *gen. nov.*	*solitary, radial multiples of 2–5 and clusters*	*alternate and vestured*	*small to medium*	*Ho*	*1–3 seriate*	*paratracheal vasicentric, aliform and confluent*	*non-septate*
Abaremaxylon *gen. nov.*	*solitary, radial multiples of 2–4 and clusters*	*alternated and vestured*	*small to medium*	*Ho*	*1–seriate*	*paratracheal vasicentric, aliform, unilateral aliform and confluent*	*non-septate*

Abbreviations: Ho, *Homogeneous,* ***He,*** *Heterogeneous.*

(Tab. 3). *Tetrapleuroxylon*, *Paracacioxylon*, *Prosopisinoxylon* and *Paraalbizioxylon* differ from the fossil woods described here by the presence of multiseriate rays (≤9 cells). *Mimosoxylon*, *Tetrapleuroxylon* and *Menendoxylon* present both homocellular and heterocellular rays. Non-septate and septate fibres are present in *Paracacioxylon*, *Menendoxylon* and *Anadenantheroxylon*. *Piptadenioxylon* has scarce vasicentric parenchyma and absence of uniseriate rays, and *Microlobiusxylon* differs from both of the new genera studied here by the vessel grouping and size of intervessel pits. *Cylicodiscuxylon* gen. nov. differs from *Abaremaxylon* gen. nov. by the type of rays and axial parenchyma. *Abaremaxylon* gen. nov. has only uniseriate rays and vasicentric, aliform, unilateral aliform and confluent axial parenchyma (Tab. 3).

African–South American flora connections and paleobiogeographic implications

The extant monotypic genus *Cylicodiscus* has a restricted distribution in West and West-Central Africa (Ayarkwa and Owusu, 2008). *Cylicodiscus gabunensis* Harms is found in deciduous and/or evergreen tropical rain forests and seasonally dry forests. The young trees can be found in small gaps in the forest and have winged flat seeds, which are dispersed by wind currents. Scattering of seed by explosive dehiscence of the pod also occurs. Additionally, the seeds are eaten by several primate species (Ayarkwa and Owusu, 2008).

The phylogenetic analyses proposed by Luckow *et al*. (2003), Luckow (2005) and Bouchenak-Khelladi *et al*. (2010) place the genus *Cylicodiscus* in an isolated position within the Mimosoideae, more closely related to the *Leucaena*, *Prosopis*, *Dichrostachys* and *Piptadenia* groups. The Bayesian matK analyses by Lavin *et al*. (2005) estimated the Mimosoideae crown clade to be 42.4 ± 2.6 Ma, 38.4 ± 3.8 Ma (Lewis *et al*., 2005) while Bouchenak-Khelladi *et al*. (2010), using a relaxed Bayesian clock, estimates for the Mimosoideae ages ranging from 61.8 to 58.0 Ma.

The two proposals about origin and dispersion for legumes are the Gondwanan and the Boreotropics hypotheses. A moist equatorial megathermal origin of legumes during the mid to Late Cretaceous supported the long-held West Gondwanan hypothesis for the origin of the family. The earliest branching lineages would have occurred in South America and Africa, and North American taxa would be relatively recent offshoots from South American ancestors (Raven and Axelrod, 1974; Doyle and Luckow, 2003).

The Boreotropics origin holds the hypothesis that the origin and diversification of Fabaceae occurred along the margin of the Tethys Seaway during the early Cenozoic, where the early radiation of the family took place in the Northern Hemisphere, and that South American taxa are recent offshoots from North American ancestors (Doyle and Luckow, 2003). This hypothesis is supported by the likelihood that legumes originated in seasonally dry environments (Schrire *et al*., 2005a,b).

Transatlantic disjunctions at the genus level can be explained by long-distance oceanic dispersal or rafting events and may have been aided by island hopping and oceanic or wind currents (Renner, 2004). Family-level disjunctions may have an old Gondwanan origin (c. 80 Ma) involving biogeographic isolation after the split of West Gondwana (Pennington and Dick, 2004; Renner, 2004).

The transatlantic dispersion and colonization of landmasses by plants could have occurred via long-distance dispersal by ocean currents, wind currents, and transport on birds/primates/rodents (Renner, 2004). The paleogeographic reconstructions proposed by Bandoni de Oliveira *et al*. (2009) suggested the existence of a series of islands in the South Atlantic 40–50 Ma ago.

These disjunct distributions and dispersal paths have been proposed for Platyrrhine monkeys and Caviomorph rodents. If monkeys and rodents arrived on a unique successful floating island, that same island is likely to have brought lots of seeds, insects and other organisms (Renner, 2004; Bandoni de Oliveira *et al*., 2009).

The review by Renner (2004) analyzes *c.* 110 genera containing species on both sides of the tropical Atlantic and infers that transatlantic dispersal by water (in both directions) appears more common than dispersal by wind or on birds. Dispersal of seeds across the tropical Atlantic has been confirmed for the Arecaceae, Bromeliaceae, Burseraceae, Cluisiaceae, Lemnaceae, Malvaceae, Melastomataceae, Rapataceae and Rhizophoraceae families.

The existence of an old relationship with the African flora and close links with Central America and tropical South America was previously proposed by Brea *et al*. (2012) for the historical biogeographic reconstruction of *Entrerrioxylon victoriensis* Lutz 1981 emend. Brea, Franco and Lutz (Brea *et al.*, 2012), a caesalpinoid fossil wood resembling the tribe Detarieae *s.l.* collected in the Late Miocene Paraná Formation.

Four global legume biomes were identified by Schrire *et al.* (2005a, b), *i.e.*, Suculent (S), Grass (G), Rainforest (R) and Temperate (T). Lineages confined to the S biome gave rise to sub-lineages occupying all other biomes and the R biome taxa are primarily derived from dry S and G biome taxa. The Nearest Living Relatives (NLRs) of the fossil woods are *Cylicodiscus* and *Abarema* occupying G and R biomes. These biomes have been less persistent as a result of the predictable water requirement affected by climatic fluctuations (Schrire *et al.*, 2005a,b).

CONCLUSION

Two new genera of fossil Mimosoideae have been recorded from the late Pleistocene in the Río Gualeguay Basin, *Cylicodiscuxylon* gen. nov. and *Abaremaxylon* gen. nov. These fossil woods represent the first report of fossil legume woods from the Arroyo Feliciano Formation.

Many of the anatomical features observed in *Cylicodiscuxylon paragabunensis* gen. nov. et sp. nov. and *Abaremaxylon hydrochorea* gen. nov. et sp. nov. support the idea that the fossil woods studied herein probably lived under warm and humid environmental conditions, including diffuse porosity, vasicentric to confluent axial parenchyma, mostly solitary vessels and low-density.

C. paragabunensis has a Vulnerability Index (**V**) of 21 and Mesomorphy ratios (**M**) of 4599, and *A. hydrochorea* show values of 11 and 6611 respectively. Such values indicate that these woods show evidence of mesomorphic features.

Abaremaxylon hydrochorea gen. nov. et sp. nov., related to *Abarema* and *Hydrocorea*, reinforces the idea that the Neotropical flora was widespread in the past. The presence of *Cylicodiscuxylon paragabunensis* gen. nov. et sp. nov., close to *C. gabunensis*, supports the existence of an old relationship with the West-Central Africa flora and is the first extra-African fossil record resembling this extant genus.

The puzzling appearance of mimosoids closely related to African forms in the late Pleistocene fossil record from South American challenges ideas on their origin and dispersion, as South America was an isolated continent during most of the Cenozoic. The transatlantic disjunct distributions of several extant plant and animal groups are interpreted as the result of plate tectonics, phylogeny and vicariance, or long-distance dispersal events. The scarce data on the fossil *Cylicodiscus* group (Jacobs *et al.*, 2010; Pan *et al.*, 2012) do not suggest rejecting any biogeographic hypothesis. Nonetheless, the Boreotropics origin and subsequent dispersal, across the Thetys seaway-North America-South America route may be less likely because of the absence of *Cylicodiscus* in North America.

Recent molecular phylogenetic analyses of the Mimosoideae estimated the divergence of *Cylicodiscus* in the Eocene (*c.* 40 Ma) (Bouchenak-Khelladi, *et al.*, 2010). Accordingly, we inferred that the modes of dispersal could have been via floating on rafting islands or/and jumping along stepping-stone volcanic islands facilitated by favorable westward paleocurrents and paleowinds from Africa to America. The development of entirely winged flat seeds in *Cylicodiscus*, which are dispersed by wind and/or primate seed dispersal probably favored the dispersion from West Africa to South America.

The occurrence of *C. paragabunensis* gen. nov. et sp. nov in South America during the Pleistocene implies that this taxon was more widespread in the past and has become extinct at some time during the Pleistocene.

Climatic information of every known Nearest Living Relatives (NLRs) of the fossil wood taxa identified in the Arroyo Feliciano Formation and the assumption that the climatic requirements of Cenozoic plant taxa were similar to those of their NLRs indicates that the fossil plants could have grown under warm and humid to semi-arid conditions.

The fossil woods described here increase our knowledge on the fossil record of the Fabaceae-Mimosoideae in South America and the paleobiodiversity data from northeastern Argentina during the late Pleistocene. New fossil specimens from South America are necessary to confirm the presence of the *Cylicodiscus* group during the Cenozoic.

ACKNOWLEDGMENTS

We are grateful to P. Perez Lindo who found this valuable fossil wood and for the field assistance and access to the collections under his care, as well as for generously arranging the loan of the fossil material. The authors would like to express their thanks to E. Brunetto, two anonymous reviewers and the Editor for their valuable help in providing critical and constructive comments. This paper was financially supported by the Agencia Nacional de Promoción Científica y Tecnológica (ANPCyT), Project PICT 2008 N°0176 and Universidad Autónoma de Entre Ríos, PIDP Res. 1423/09 UADER.

REFERENCES

Alcaraz, M.A., and Ferrero, B.S. 2013. *Hippocamelus* Leuckart (Artiodactyla, Cervidae) en el Pleistoceno de la provincia de Entre Ríos, Argentina. *Ameghiniana* 50 Suplemento: 5R.

APG III. 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.

Ayarkwa, J., and Owusu, F.W. 2008. *Cylicodiscus gabunensis* Harms. Record from PROTA4U. In: D. Louppe, A.A. Oteng-Amoako, and M. Brink (Eds.), *PROTA* (Plant Resources of Tropical Africa / Ressources végétales de l'Afrique tropicale), Wageningen, Netherlands. World Wide Web <http://www.prota4u.org/search.asp>

Ayensu, E.S., and Bentum, A. 1974. Commercial timbers of West Africa. *Smithsonian Contributions to Botany* 14: 1–69.

Bandoni de Oliveira F., Cassola Molina E., and Marroig G. 2009. Paleogegraphy of the South Atlantic: a route for primates and rodents into the New World? In: P.A. Garber, A. Estrada, C.J. Bicca-Marques, E.W. Heymann and K.B. Strier (Eds.), *South American primates, developments in primatology: progress and prospects*. New York, Springer Science, p. 55–68.

Baretta-Kuipers, T. 1981. Wood Anatomy of Leguminosae: its relevance to taxonomy. In: R.M. Polhill and P.H. Raven (Eds.), *Advances in legume systematic, Part 2.* Royal Botanical Gardens, Kew, p. 677–705.

Barneby, R.C., and Grimes, J.W. 1996. Silk Tree, Guanacaste, Monkey's Earing. A generic System for the *Synandrous* Mimosaceae of the Americas. Part. I, *Abarema*, *Albizia* and Allies. *Memoirs of the New York Botanical Garden* 74: 1–292.

Barros, C.F., and Callado, C.H. 1997. *Madeiras da Mata Atlântica. Anatomia do lenho de espécies ocorrentes nos remanescentes florestais do Estado do Rio de Janeiro– Brasil*. 5. 1. Instituto de Pesquisas Jardim Botânico do Rio de Janeiro, Rio de Janeiro, 86 p.

Benthan, G., and Hooker, J.D. 1865. Genera plantarum. Vol. 1. pp. 434–600. Reeve and Co. London.

Bouchenak-Khelladi, Y., Maurin, O., Hurter, J., and van der Bank, M. 2010. The evolutionary history and biogeography of Mimosoideae (Leguminosae): An emphasis on African acacias. *Molecular Phylogenetics and Evolution* 57: 495–508.

Brea, M., Aceñolaza, P.G., and Zucol, A.F. 2001. Estudio paleoxilológico en la Formación Paraná, Entre Ríos, Argentina. *11° Simposio Argentino de Paleobotánica y Palinología* (Tucumán), Publicación Especial no. 8, Asociación Paleontológica Argentina: 7–17.

Brea, M., Zamuner, A.B., Matheos, S.D., Iglesias, A., and Zucol, A.F. 2008. Fossil wood of the Mimosoideae from the early Paleocene of Patagonia, Argentina. *Alcheringa* 32: 427–441.

Brea, M., Franco, M.J., and Lutz, A.I. 2012. Redescription and reassignment of *Entrerrioxylon victoriensis* from the Upper Miocene, Paraná Formation, South America. *Review of Palaeobotany and Palynology* 185: 13–25.

Bronn, H. 1822. De formis plantarun Leguminosarum. Sumtibus caroli Groos. Bibliop. Ac adem. Heidelberg.

Brunetto, E., Ferrero, B.S., Marino, J., Tentor, F., Sturtz, M., Zamboni, L., and Casanave, L. 2012. Evolución geológica del Pleistoceno del centro de Entre Ríos. *Congreso Argentino de Cuaternario y Geomorfología* (Río Cuarto) *Actas* 5: 1–5.

Brunetto, E., Ferrero, B.S., and Noriega, J.I. 2015. Late Pleistocene lithostratigraphy and sequences in the Southwestern Mesopotamia (Argentina): evidences of the Last Interglacial Stage. *Journal of South American Earth Sciences* 58: 111–128.

Calvillo-Canadell, L. and Cevallos-Ferriz , S.R.S. 2005. Diverse assemblage of Eocene and Oligocene Leguminosae from Mexico. *International Journal of Plant Sciences* 166: 671– 692.

Carlquist, S. 1977. Ecological factors in wood evolution: a floristic approach. *American Journal of Botany* 64: 887–896.

Carquist, S. 2001. *Comparative wood anatomy*. Systematic, Ecological and evolutionary Aspects of Dicotyledons Wood. Springer Series in Wood Science, Springer, Berlin 448 p.

Cassens, D.L., and Miller, R.B. 1981. Wood anatomy of the New World *Pithecellobium* (*sensu lato*). *Journal of the Arnold Arboretum* 62: 1–44.

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: 63–146.

Crepet, W.L., and Taylor, D.W. 1985. The diversification of the Leguminosae: first fossil evidence of the Mimosoideae and Papilionoideae. *Science* 228: 1087–1089.

Crepet, W.L., and Taylor, D.W. 1986. Primitive mimosoid flowers from the Paleocene-Eocene and their systematic and evolutionary implications. *American Journal of Botany* 73: 548–563.

De Candolle, A.P. 1825. Leguminosae. Pp. 93–524 in Prodromus systematis naturalis regni vegetabilis, vol 2. Paris: Treuttel and Wurtz.

Díaz, W., and Rosales, J. 2006. Análisis florístico y descripción de la vegetación inundable de várzeas Orinoquenses en el Bajo Río Orinoco, Venezuela. *Acta Botánica Venezuelica* 29: 39–68.

Doyle, J.J., Chappill, J.A., Bailey, C.D., and Kajita, T. 2000.Towards a comprehensive phylogeny of legumes: evidence from *rbcL* sequences and non-molecular data. In: P. Herendeen and A. Bruneau (Eds.), *Advances in legume systematic, Part 2.* Royal Botanical Gardens, Kew, London, p. 1–20.

Doyle, J.J., and Luckow, M.A. 2003.The rest of the iceberg. Legume diversity and evolution in a phylogenetic context. *Plant Physiology* 131: 900–910.

Espinosa de Pernía, N., and Melandri Pírela, J.L. 2000. Estudio anatómico del leño de cinco especies comerciales de la Subfamilia Mimosoideae en Venezuela. *Pittieria* 1: 75–88.

Evans, J.A., Gasson, P.E., and Lewis, G.P. 2006. Wood anatomy of the Mimosoideae (Leguminosae). *IAWA Journal* Supplement 5: p. 1–117.

Ferrero, B.S. 2009. [*Diversidad y evolución de los Mamíferos del Cuaternario de la provincia de Entre Ríos Argentina. Aspectos bioestratigráficos y paleozoogeográficos de una fauna particular.* Tesis doctoral, Facultad de Ciencas Naturales y Museo, Universidad Nacional de La Plata, La Plata, 425 p. Unpublished.].

Franco, M.J., and Brea, M. 2010. *Microlobiusxylon paranaensis* gen. nov. et sp. nov. (Fabaceae-Mimosoideae) from the Pliocene-Pleistocene of Ituzaingó Formation, Paraná Basin, Argentina. *Revista Brasileira de Paleontología* 13: 103–114.

Franco, M.J., and Brea, M. 2013. Leños fósiles de leguminosas de la Formación Ituzaingó, Entre Ríos, Argentina: implicancias paleoecológicas y paleobiogeográficas. *Ameghiniana* 50: 167–191.

Giraud, B., and Lejal-Nicol, A. 1989. *Cassinium dongolense* n. sp. bois fossile de Caesalpiniaceae du Nubien du Soudan septentrional. *Review of Palaeobotany and Palynology* 59: 37–50.

Gregory, M. 1994. Bibliography of systematic wood anatomy of dicotyledons. *IAWA Journal* 1: 1–265.

Gregory, M., Poole, I., and Wheeler, E.A. 2009. Fossil dicot wood names and annotated list with full bibliography. *IAWA journal*, Supplement 6: 1–128.

Herendeen, P.S. 1992. The fossil history of the leguminosae from the Eocene of southeastern North America. In: P.S. Herendeen and D.L. Dilcher (Eds.), *Advances in Legume Systematics. Part 4. The fossil Record*, The Royal Botanic Gardens, Kew, London, p. 85–160.

IAWA Committee. 1989. IAWA List of Microscopic Features for Hardwood Identification. *IAWA Bulletin* 10: 219–332.

Iglesias, A., Wilf, P., Johnson, K.R., Zamuner, A.B., Cúneo, N.R., Matheos, S.D., and Singer, B.S. 2007. A Paleocene lowland macroflora from Patagonia reveals significantly greater richness than North American analogs. *Geology* 35: 947–50.

InsideWood. 2004-onwards. Worl Wide Web: http://insidewood.lib.ncsu.edu/search

Iriondo, M., Tardivo, R.N., and Ceruti, C.N. 1985. Geomorfología y Cuaternario del tramo inferior del Arroyo Feliciano (Entre Ríos, Argentina). *Revista de la Asociación de Ciencias Naturales del Litoral* 16: 149–156.

Iriondo, M., and Kröhling, 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 p.

Judd, W., Campbell, C., Kellogg, E., and Stevens, P. 1999. *Plant Systematics*. Sinauer Associates, Inc, Sunderland, Massachusetts, 464 p.

Lavin, M., Herendeen, P.S., and Wojciechowski, M.F. 2005. Evolutionary rates analysis of Leguminosae implicates a rapid diversification of lineages during the Tertiary. *Systematic Biology* 54: 530–549.

León, W.J. 2008. Anatomía de madera en 31 especies de la Subfamilia Mimosoideae (Leguminosae) en Venezuela. *Revista Colombia Forestal* 11: 13–135.

Lewis, G.P., Schrire, B.D., Mackinder, B.A., and Lock, M. 2005. *Legumes of the world*. Royal Botanic Gardens, Kew, London, 577 p.

Lindley, J. 1830. An Introduction to the natural system of botany. Longman, Rees, Orme, Brown and Green. Londres, 393 p.

Luckow, M. 2005. Tribe Mimoseae. In: G. Lewis, B. Schrire, B. Msckinder, and M. Lock (Eds.), *Legumes of the world*. Royal Botanic Gardens, Kew, p. 163–183.

Luckow, M., White, P.W., and Bruneau, A. 2000. Relationships among the basal genera of mimosoid legumes. In: P. Herendeen and A. Bruneau (Eds.), *Advances in Legume Systematics, Part 9*, Royal Botanic Gardens, Kew, London, p. 165–180.

Luckow, M., Miller, J.T., Murphy, D.J., and Livshultz, T. 2003. A phylogenetic analysis of Mimosoideae (Leguminoseae) based on chloroplast DNA sequence data. In: B.B. Klitgaard and A. Bruneau (Eds.), *Advances in legumes systematics*, *Part 10*: Higler Level Systematic, Royal Botanic Gardens, Kew, London, p. 197–220.

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. 1981. *Entrerrioxylon victoriensis* nov. gen. et sp. (Leguminosae) del Mioceno superior (Fm. Paraná) de la provincia de Entre Ríos, Argentina. *Facena* 4: 21–29.

Mabberley, D. 1990. *The Plant Book*. Cambridge University Press. New York. 707 p.

Martínez, L. 2010. *Prosopisinoxylon 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, L. 2014. Fossil legume woods from the Late Miocene, Chiquimil Formation (Santa María Basin), Argentina. *Review of Palaeobotany and Palynology* 201: 1–11.

Metcalfe, C.R., and Chalk, L. 1950. *Anatomy of the Dicotyledons*. Vol. 2 Claredon Press, Oxford, p. 871–893

Miller, J.T., Grimes, J.W., Murphy, D.J., Bayer, R.J., and Ladiges, P.Y. 2003. A phylogenetic Analysis of the Acacieae and Ingeae (Mimosoideae: Fabaceae) based on *trnK, matK, psbA-trnH,* and *trnL/trnF* Sequence Data. *Systematic Botany* 28: 558–566.

Miller, J.T., Murphy, D.J., Ho, S.Y.W., Cantrill, D.J., and Seigler, D. 2013. Comparative dating of *Acacia*: combining fossils and multiple phylogenies to infer ages of clades with poor fossil records. *Australian Journal of Botany* 61: 436–445.

Moya, E. 2012. Estudio preliminar sobre leños fósiles del Pleistoceno Superior en la provincia de Entre Ríos, Argentina. *Primera Reunión argentina de Estudiantes de Paleontología*, *RAdEP*. (La Plata), *Libro de resúmenes*, p. 32.

Moya, E. 2013. Primer registro de Vochysiaceae en el noreste argentino: un leño fosil del Plistoceno Superior de la Formación Arroyo Feliciano. *Ameghiniana Suplemento Resúmenes* 50: 61R.

Moya, E., Brea, M., and Franco, M.J. 2013. Styracaceae en el Pleistoceno Superior en el noreste de Argentina. *Ameghiniana Suplemento Resúmenes* 50: 16R.

Moya, E., and Brea, M. 2015. A new record of fossil wood of Vochysiaceae from the Upper Pleistocene (Arroyo Feliciano Formation), Argentina, South America. *Revista Brasileira de Paleontologia* 18: 83–90.

Müller-Stoll, W.R., and Mädel, E. 1967. Die fossilen Leguminosen-Hölzer. Eine Revision der mit Leguminosen verglichenen fossilen Hölzer und Beschreibugen älterer und neuer Arten. *Palaeontographica* B 119: 95–174.

Pan, A.D., Currano, E.D., Jacobs, B.F., Feseha, M., Tabor, N., and Herendeen, P.S. 2012. Fossil *Newtonia* (Fabaceae: Mimoseae) seeds from the Early Miocene (22–21 Ma) Mush Valley in Ethiopia. *International Journal of Plant Sciences* 173: 290–296.

Pennington, R.T., and Dick, C.W. 2004. The role of immigrants in the assembly of the South American rainforest tree flora. *Philosophical Transactions of the Royal Society B* 359: 1611–1622.

Polhill, R.M. 1981. Abreae. In: R.M. Polhill, and P.H. Raven (Eds.), *Advances in legume systematics*, *Part 1*. Royal Botanic Gardens, Kew, London p. 243–244.

Pujana, R.P., Martínez, L.C.A., and Brea, M. 2011. El registro de maderas fósiles de Leguminosae de Sudamérica. *Revista del Museo Argentino de Ciencias Naturales*, s.n. 13: 183–194.

Raven, P.H., and D.I. Axelrod. 1974. Angiosperm biogeography and past continental movements. *Annals of the Missouri Botanical Garden* 61: 39–637.

Renner, S. 2004. Plant dispersal across the Tropical Atlantic by wind and sea currents. *International Journal of Plant Sciences* 165 (S4), Tropical Intercontinental Disjunctions: S23–S33.

Richter, H.G., and Dallwitz, M.J. 2000–onwardss. *Commercial timbers: descriptions, illustrations, identifications, and information retrieval*. English, French, German, Portuguese, and Spanish. Worl Wide Web: http://delta-intkey.com

Schrire, B.D., Lavin, M., and Lewis, G.P., 2005a. Global distribution patterns of the Leguminosae: insights from recent phylogenies. In: I. Friis, and H. Balslev (Eds.), *Plant Diversity and Complexity Patterns – Local, Regional and Global Dimensions*: Biologiske Skrifter 55, Copenhague, p. 375–422.

Schrire, B.D., Lewis, G.P., and Lavin, M. 2005b. Biogeography of the Leguminosae. In: G. Lewis, B. Schrire, B. Mackinder, M. Lock (Eds.), *Legumes of the world*. Royal Botanic Gardens, Kew, London, p. 21–54.

Silva, A., Blanco, C., and Lindorf, H. 1989. Anatomía de la madera de nueve leguminosas de Venezuela. *Acta Botanica Brasilica* 2: 115–134.

Simpson, M.G. 2006. *Plant Systematics*. Elsevier Academic Press, Londres, 590 p.

Suguio, K., and Mussa, D. 1978. Madeiras fósseis dos aluviões antigos do Rio Tietê, São Paulo. Boletim IG. *Instituto de Geociências da Universidade de Sao Paulo* 9: 25–45.

Taylor, T.N., Taylor, E.L., and Krings, M. 2009. *Paleobotany. The biology and evolution of fossil plants*. Second Edition, Elsevier Academic Press, Amsterdam, Burlington, 1230 p.

Tortorelli, L.A. 1956. *Maderas y bosques Argentinos*. Ed. ACME, S.A.C.I. Buenos Aires, 910 p.

UTHSCSA ImageTool Version 3.0 Final. World Wide Web: http://ddsdx.uthscsa.edu/dig/download.html.

Wheeler, E.A. 2011. Inside Wood – A Web resource for hardwood anatomy. *IAWA Journal*: 32: 199–211.

Wheeler, E.A., and Bass, P. 1992. Fossil wood of the Leguminosae: a case study in xylem evolution and ecological anatomy. In: P. Herendeen, and D.L. Dilcher (Eds.), *Advances in legume systematics*, *Part 4. The fossil record*. Royal Botanic Gardens, Kew, London, p. 281–301.

Wikström, N., Savolainen, V., and Chase, M.W. 2001. Evolution of angiosperms: calibrating the family tree. *Proceedings of the Royal Society of London Series B* 268: 2211–2220.

Wilf, P., and Escapa, I.H. 2015. Green Web or megabiased clock? Plant fossils from Gondwanan Patagonia speak on evolutionary radiations. *New Phytologist* 207: 283–290.

Wing, S.L., Herrera, F., Jaramillo, C.A., Gómez-Navarro, C., Wilf, P., and Labandeira, C.C. 2009. Late Paleocene fossils from the Cerrejón Formation, Colombia, are the earliest record of Neotropical rainforest. *Proceedings of the National Academy of Sciences* 106: 1827–18632.

doi: 10.5710/AMGH.24.06.2015.2875

Submitted: Decemeber 16th, 2014

Accepted: June 24th, 2015