LEGUME (MIMOSOIDEAE) FOSSIL WOODS FROM THE LATE MIOCENE (SALICAS FORMATION) OF NORTHWESTERN ARGENTINA

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ABSTRACT – Six pieces of fossil wood from the late Miocene of Northwestern Argentina (Salicas Formation) are described. They are all assigned to *Prosopisinoxylon anciborae* Martínez based on the presence of the following diagnostic characters: vessels of two distinct diameter classes, simple perforation plates, vestured pits, abundant axial parenchyma and wide rays. Significant anatomical variation exists among specimens but they are regarded as a single taxonomic unit because usually a gradual transition is observed among most variable characters. A principal component analysis (PCA) was performed and results agree with the taxonomic placement. The analysis also shows discrete clusters of other related Leguminosae fossil-genera. Wood anatomy suggests a warm and dry climate for the zone supporting previous studies.

Key words: Fabaceae, La Rioja, *Prosopisinoxylon anciborae*, PCA.

RESUMO – São descritos seis fragmentos de lenhos fósseis, do Mioceno superior, provenientes da Formação Salicas, Noroeste da Argentina. Todos os fragmentos são identificados como *Prosopinioxylon anciborae* Martinez, com base na presença dos seguintes caracteres diagnósticos: vasos de duas classes distintas, placas de perfuração simples, pontuações ornamentadas, parênquima axial abundante e raios largos. Existe uma variação anatômica significativa entre os espécimes, mas são identificados na mesma unidade taxonômica, porque é observada uma transição gradual nos caracteres mais variáveis. Realizou-se uma análise dos componentes principais (ACP) cujo resultado concorda com a identificação taxonômica. A análise também mostra grupos discretos de outros gêneros fósseis de Leguminosas aparentadas. A anatomia da madeira sugere um clima quente e seco para a região, em concordância com estudos prévios.

Palavras-chave: Fabaceae, La Rioja, *Prosopisinoxylon anciborae*, ACP.

INTRODUCTION

The Leguminosae has an extensive fossil wood record (Gros, 1992; Wheeler & Baas, 1992; Pujana *et al.*, 2011) and fossil woods included in this group are abundant and diversified in South America (Pujana *et al.*, 2011), particularly from the Neogene of northwestern Argentina (Menéndez, 1962; Lutz, 1987; Martínez, 2010; Martínez & Rodriguez Brizuela, 2011). The following fossil-genera have been described from that area: *Paracacioxylon* Menéndez, *Menendoxylon* Lutz, *Mimosoxylon* Müller-Stoll, *Prosopisinoxylon* Martínez and *Gleditsioxylon* Martínez & Rodriguez Brizuela.

The main goals of the present study are: (i) to describe silicified fossil woods assigned to the Leguminosae (Mimosoideae) based on the anatomy of different specimens which have been collected from a single stratigraphical level of the Salicas Formation (late Miocene) in the "Salar de Pipanaco" area; (ii) to perform a Principal Component Analysis (PCA) to evaluate the accuracy of the systematic placement; and to (iii) infer palaeoclimatic data based on wood anatomy.

GEOLOGICAL SETTING

The Salicas Formation crops out in northern and southern La Rioja and Catamarca provinces, respectively, Northwestern Argentina. It was defined by Sosic (1972) and previously known as Schaqui Formation (Turner, 1971). It has an estimated thickness of 600-800 m at the southernmost end of the Salar de Pipanaco. The formation is overlaid by the Las

Cumbres Formation (Pliocene-Pleistocene). It is composed of reddish and yellowish-greyish coarse sands and gravels. It has a late Miocene age, based on fossil mammals studied from a locality called "El Degolladito" (Tauber, 2005; Brandoni *et al.*, 2012). Abundant fossil woods and also leaves and pollen grains (Tauber, 2005) were found in another area "Salar de Pipanaco" (Figure 1), where Tauber & Mazzoni (2003) briefly described borings in fossil woods and Garcia Massini & Pujana (2013) evidence of termite activity. This new locality also bears fossil bones, sloth claws, dermal plates and ichnofossils.

MATERIAL AND METHODS

Six fragments of secondary xylem were collected by one of the authors (OD) from the same stratigraphical horizon of the Salicas Formation in the 90's at 28°33'30.27"S, 66°30'3.51"W. Particular care was taken so that each fragment of wood corresponds originally to different trunks, by collecting pieces that were not in contact or placed very close. However, we cannot assure that the fragments corresponds to different trees. The specimens are silicified and were thin sectioned in transverse, tangential longitudinal and radial longitudinal sections following standard techniques for petrified woods (Hass & Rowe, 1999) and studied using light microscopy. Acetate peels were also made following the technique described by Galtier & Philips (1999). Small fragments of wood were studied by scanning electronic microscopy (**SEM**) after being gold coated. Terminology follows the IAWA recommendations for hardwood identification (IAWA Committee, 1989). Measurements in the description (at least 25 for each character for each specimen) are given as the weighted mean of the six specimens followed by the range in parentheses. When less than 25 measurements were made the character is given as a range preceded by "*ca.*". Minimum estimated diameter is calculated based on growth ring curvature or direct measurements depending on the specimen.

For taxonomic delimitation, the fossil-species-genera criteria of Müller-Stoll & Mädel (1967) and Gros (1992)

were followed. Fossil woods were compared with previously known legume fossil-species found in Gros (1992), InsideWood (2004-onwards), Gregory *et al.* (2009) and Pujana *et al.* (2011).

The six specimens and thin slides are housed in the palaeobotanical collection of the Centro Regional de Investigaciones La Rioja - **CRILAR** (CRILAR Pb 1 to 6) in Anillaco, La Rioja Province, Argentina. Slides bear the specimen numbers followed by a lower case letter usually indicating the sections: **a**, transverse section; **b**, radial longitudinal section; **c**, tangential longitudinal section.

Principal Component Analysis (**PCA**) was performed following the methodology of MacLachlan & Gasson (2010) to corroborate the accuracy of the systematic placement. A correlation matrix (variables were measured in different units) was made based on the characters on Table 1, including some anatomically related legume wood fossil-species from South America and India (with multiseriate rays and presence of axial parenchyma, etc.) and other fossil-species of legume fossil woods from Argentina. Twenty one discrete binomial and continuous characters were included in the same matrix. The analysis was carried out in the PAST programme (Hammer *et al.*, 2001) with missing values set in iterative imputation. For choosing the number of PC suitable for data analysis (PC1 to 3), the scree test (Cattell, 1966) was carried out (not shown).

SYSTEMATIC PALAEOBOTANY

Family LEGUMINOSAE Jussieu, *nom. cons.*
Subfamily MIMOSOIDEAE De Candole

Prosopisinoxylon Martínez, 2010

Type fossil-species. *Prosopisinoxylon anciborae* Martínez, 2010.

Prosopisinoxylon anciborae Martínez, 2010
(Figures 2-3)

Figure 1. Map and satellite image showing fossiliferours locality (black star).

Material. CRILAR Pb 1 to 6.

Repository. CRILAR, La Rioja, Argentina.

New locality. Salar de Pipanaco, «SA1» (28°33'30.27"S, 66°30'3.51"W).

Stratigraphic horizon. Salicas Formation, late Miocene.

Description. Six pieces of secondary xylem, decorticated and with minimum estimated diameters of up to 15 cm are described. Growth rings boundaries indistinct to absent, sometimes marked by the wider vessels being tangentially aligned at the beginning of the ring (Figures 2A-B). Wood mostly diffuse-porous, sometimes with slight tendency to semi-ring-porosity (Figure 2A). Vessels solitary (57%), paired or in radial multiples (21%) or clustered (22%) (Figures 2A,B). Solitary vessels rounded in outline. Perforation plates exclusively simple (Figure 2D). Intervessel pits alternate and vestured; minute to small, *ca.* 3-4 μm in vertical diameter (Figures 2C,H; 3A). Vessel-ray pits similar to intervessel pits in size and shape (Figure 2I). Vessels 112 (25-300) μm in tangential diameter and 121 (20-310) μm in radial diameter. Vessels of two distinct diameter classes. Wider vessels mean 158 μm, narrower clustered vessels mean 54 μm, both in tangential diameter. Vessel density 15 (5-36) vessels per mm². Vessel elements 169 (120-320) μm in length. Tyloses or gums deposits common (Figure 2J). Fibres non-septate and very thick-walled. Axial parenchyma paratracheal, vasicentric, aliform, confluent and in bands more than three cells wide (Figure 2A). Axial parenchyma in strands of up to four cells (Figures 2E-F,H) and occasionally irregularly storied (Figure 2F; 3C). Disjunctive axial parenchyma rare (Figure 3B). Rays 4 (1-7) - seriate and 27 (10-57) cells in height; 61 (23-113) μm in width and 444 (130-1190) μm in height (Figures 2F-G); homocellular and composed of procumbent cells (Figure 2I); with a frequency of 4 (2-7) rays per mm. Prismatic crystals in chambered axial parenchyma cells are present in some specimens in different frequency (Figure 2E).

Comments on the anatomy. Vessel arrangement varies considerably in the same specimen among different growth rings and among specimens. Clusters are less frequently observed in specimens CRILAR Pb 5 and 6 (which are not as nicely preserved as those in most other samples) and in some growth rings of the other specimens. Vessel density also varies significantly, particularly when clusters are present. CRILAR Pb 4 has the highest density, probably because of the high frequency of clusters and long radial multiples. Axial parenchyma is another character that shows great variation. Frequently, aliform to banded axial parenchyma is present in the same specimen, whereas in others only confluent to banded axial parenchyma is observed. CRILAR Pb 4 has narrower rays (mean 2.8 cells wide) than the other fossils, but a gradual transition among specimens is observed up to specimen CRILAR Pb 1 and 5, which have the widest rays (mean 5.2 cells wide). CRILAR Pb 1 has abundant crystals, whereas these were not observed in CRILAR Pb 3, 5 and 6. However, this character is not commonly considered diagnostic, because it is variable on the same species depending on ecological factors. The specimen CRILAR Pb 4 has a spine of 15 mm in length and 3 mm in diameter at the base (Figure 2K).

DISCUSSION

Similarities to extant woods

Diagnostic characters of the fossil woods such as medium to large vessels, abundant axial parenchyma, simple perforation plates, short vessel elements, alternate vestured intervessel pits and homocellular multiseriate rays support assignment of the studied specimens to the Leguminosae. However, the wood of the Leguminosae shares a number of characters with several families of dicots that have the same wood structure with simple perforation plates, alternate intervessel pits, homogeneous rays, etc. (Wheeler & Baas, 1992). The presence of vestured pits is a significant and diagnostic character present in most Leguminosae (Herendeen *et al.*, 1992). Martínez (2010) assigned *Prosopisinoxylon anciborae* to the Leguminosae segregating it from other related families, such as: Apocynaceae, Combretaceae, Dipterocarpaceae, Lythraceae, Melastomataceae, Myrtaceae and Rubiaceae. There are also other families with similar wood anatomy to the Leguminosae: Bignoniaceae, Oleaceae, Moraceae, Sapindaceae, Meliaceae and Thymelaceae. In the Bignoniacae, except in climbers, rays usually do not reach more than four cells wide. The Oleaceae has small and usually solitary vessels and heterogeneous rays. The Moraceae has normally solitary vessels or short radial multiples with oblique or tangential vessel arrangement. The Sapindaceae has small to very small vessels, scarce axial parenchyma and uni to biseriate rays (except in lianas). The Meliaceae has heterogeneous multiseriate rays. Finally, the Thymelaceae has fibres with bordered pits (fibretracheids) and vasicentric tracheids (Metcalfe & Chalk, 1950).

There are three classical subfamilies recognized in the Leguminosae: Mimosoideae, Caesalpinoideae and Papilionoideae, each of which shows different anatomical wood characters (Cozzo, 1951). The wood of the Mimosoideae spp. is very homogeneous and differs from genera of the other two subfamilies in having: diffuse-porous wood without a predominant vessel arrangement, paratracheal parenchyma from scanty to confluent and often banded, homogeneous multiseriate rays composed of procumbent cells and absence of storied elements (Cozzo, 1951; Metcalfe & Chalk, 1950; Baretta-Kuipers, 1981). The fossils studied herein are consistent with those characters. Evans *et al.* (2006), in their revision of mimosoid woods, established four non-natural groups: Mimoseae, Acacieae, Ingeae and Mimozygantheae. The fossil woods studied here were placed in the tribe Mimoseae (Division 4) based on the following features: non-septate fibres, banded parenchyma and presence of uniseriate rays. The Division 4 possesses two groups: Piptadenia group and Prosopis group. The Piptadenia group differs from the fossil collected from the Salicas Formation by the presence of narrower rays (up to three cells wide) and sometimes septate fibres. Prosopis group shares with our material non-septate fibres, axial parenchyma vasicentric to banded and multiseriate (1-7 cells wide) rays. The Prosopis group includes the following genera: *Neptunia* Loureiro, *Piptadeniopsis* Burkart, *Prosopidastrum* Burkart, *Xerocladia*
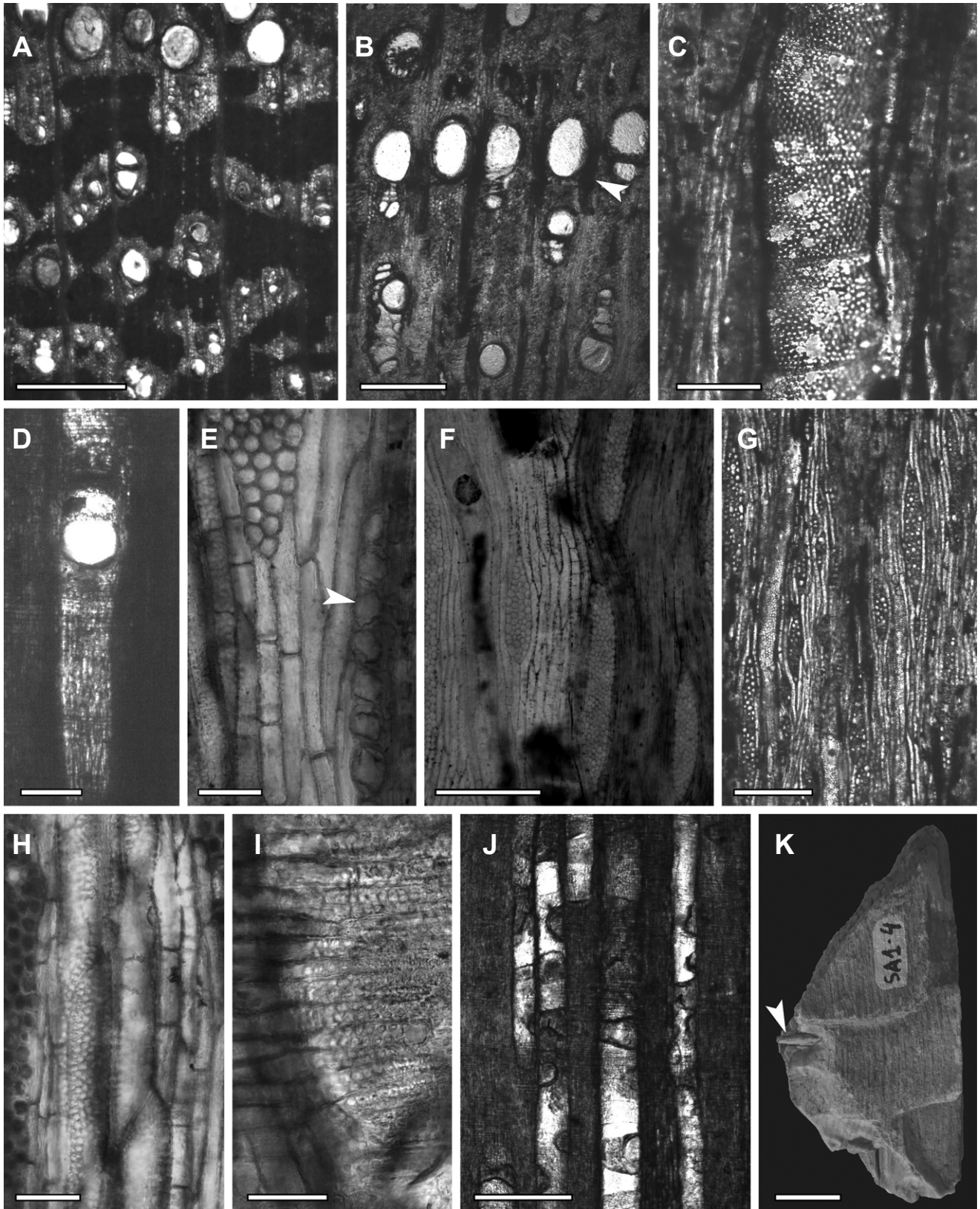
Figure 2. *Prosopisinoxylon anciborae* from the Salicas Formation. **A**, transverse section (TS). CRILAR Pb 4; **B**, growth ring boundary (arrowhead) (TS). CRILAR Pb 3; **C**, short vessel elements and intervessel alternate pits in longitudinal tangential section (LTS). CRILAR Pb 4; **D**, simple perforation plates in longitudinal radial section (LRS). CRILAR Pb 2; **E**, axial parenchyma and crystalliferous parenchyma (arrowhead) (LTS). CRILAR Pb 2; **F**, wide multiseriate rays (LTS). CRILAR Pb 1; **G**, narrower multiseriate rays (LTS). CRILAR Pb 4; **H**, narrow vessels and axial parenchyma (LTS). CRILAR Pb 4; **I**, procumbent ray cells and vessel-ray pitting (LRS). CRILAR Pb 4; **J**, vessels with tyloses or gums (LRS). CRILAR Pb 4; **K**, Hand specimen with spine (arrowhead). CRILAR Pb 4. Scale bars: A,B,J = 500 μm; C = 100 μm; D,F,G = 200 μm; E,H,I = 50 μm; K = 20 mm.
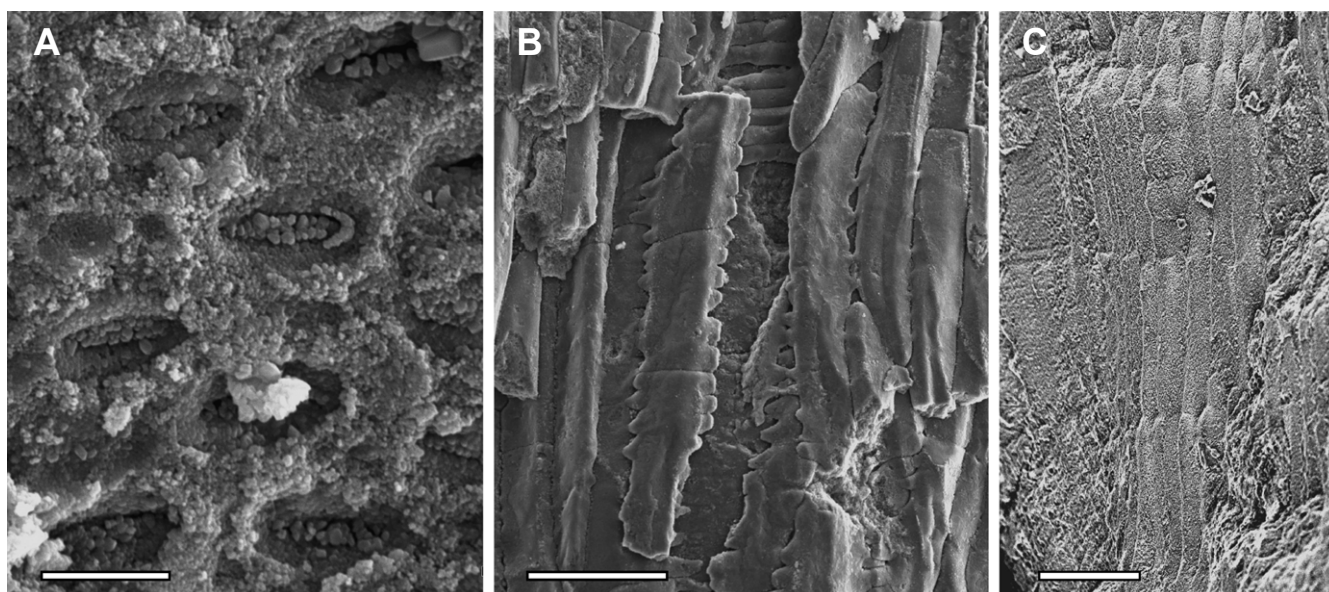
Figure 3. SEM images of *Prosopisinoxylon anciborae*. **A**, Vestured pits. CRILAR Pb 2; **B**, Disjunctive axial parenchyma. CRILAR Pb 1; **C**, storied axial parenchyma. CRILAR Pb 1. Scale bars: A = 5 μm; B,C = 50 μm.

Harvey and *Prosopis* Linné (Evans *et al.*, 2006). *Neptunia* is an herbaceous aquatic or semiaquatic genus, with very scarce secondary growth (Windler, 1966) and detailed wood anatomical descriptions of *Piptadeniopsis*, *Prosopidastrum* and *Xerocladia* have not been done. Only the anatomy of some species of *Prosopis* has been studied in detail (Cozzo, 1951; Tortorelli, 1956; Castro, 1988, 1994). *Prosopis* shows vessels of two distinct diameter classes, with small vessels in clusters, rays 1-7 seriate, the axial parenchyma vasicentric, confluent or banded, and non septate fibres. These anatomical features suggest a close relationship of the fossil wood described herein with living *Prosopis*. For the infrageneric classification, only ultrastructural wood anatomy seems to be useful for delimiting sections (Castro, 1994).

Comparison with fossil woods

The fossil woods described herein differ from other taxa of Mimosoid wood based on simultaneous occurrence of the following characters: vessels of two distinct diameter classes, homogeneous wide rays (1- to 9-seriate), axial parenchyma vasicentric to confluent and banded, and non-septate fibres. Those characters exclude genera with narrow rays (usually 1- to 3-seriate), such as: *Acacioxylon* Schenk (*sensu* Gros, 1992), *Adenantheroxylon* Prakash & Tripathi, 1968, *Anandenantheroxylon* Brea *et al.*, 2001, *Bajacalifornioxylon* Cevallos-Ferriz & Barajas-Morales, 1994, *Holocalyxylon* Brea *et al.*, 2010, *Menendoxylon* Lutz, 1979, *Microlobiusxylon* Franco & Brea 2010, *Mimosoxylon* Müller-Stoll & Mädel, 1967, and *Piptadenioxylon* Suguio & Mussa, 1978. In addition, genera with septate fibres can also be separated: *Albizinium* Prakash, 1975, *Cathormion* Gros, 1994, *Mimosaceoxylon* Lakhanpal & Prakash, 1970, and *Paracacioxylon* Müller-Stoll & Mädel, 1967.

Abundance of axial parenchyma is another important character that allow us to separate the studied fossil woods

from other taxa that show a lower proportion of axial and terminal parenchyma, such as: *Mimosoxylon* Müller-Stoll & Mädel, 1967, and *Dichrostachyoxylon* Müller-Stoll & Mädel, 1967; or terminal parenchyma like in *Tetrapleuroxylon* Müller-Stoll & Mädel, 1967. Vessel grouping is a character of systematic importance that excludes the following taxa: *Euacacioxylon* Müller-Stoll & Mädel, 1967, which has solitary vessels and in radial multiples of 2 or 3, and *Metacacioxylon* Gros and *Paraalbizioxylon* Gros, 1992, which show mostly solitary vessels. *Prosopisinoxylon* shares with the fossil woods described herein the following characters: vessels of two distinct diameter classes, wide (1-9 seriate) rays, non-septate fibres and axial parenchyma confluent and banded. *Prosopisinoxylon* shares many characters with *Paracacioxylon*, but the main difference is that *Paracacioxylon* lacks vessels of two distinct diameter classes. *Prosopisinoxylon castroae* Brea, Zucol & Patterer differs from *P. anciborae* in having wider vessels, lower density of vessels and axial parenchyma arrangement (Brea *et al.*, 2010). The characters present in the new samples described herein allow us to assign it to *Prosopisinoxylon* and among its fossil-species to *P. anciborae* (Table 1). In addition, the holotype of *P. anciborae* was described for a nearby locality and the bearing strata have the same age (Chiquimil Formation, late Miocene) which supports the possibility of finding the same fossil-species.

Principal Component Analysis - PCA

A PCA including related fossil-species and all the new six specimens was carried out. PCA regarding wood anatomy were carried out for extant woods (Wickremasinghe & Herat, 2006; MacLachlan & Gasson, 2010) and they clustered specimens of extant wood into natural groups. The same type of analysis was also used to group fossil specimens (Oakley & Falcon Lang, 2009; Oakley *et al.*, 2009; Pujana *et al.*, 2014).

Table 1. Comparative table of *Prosopisinoxylon anciborae* (including the Salicas Formation fossils) and related species from South America and India. Characters on the table were used in the PCA (1 to 9 continuous, 10 to 21 binomial discrete). Measured values in continuous characters are the mean expressed in μm unless specified between parenthesis. When vessels of two distinct diameter classes are present the mean includes small and large vessels. Discrete characters: growth ring boundaries 1 = indistinct to well marked, 0 = absent; porosity 1 = diffuse 0=semi ring; in the rest of the characters 1 = present, 0 = absent. [a] *sensu* Menéndez (1962) and [b] *sensu* Lutz (1987). * = calculated means and character states based on the original descriptions of the fossil-species.

nº	Specimen / fossil-species	Vessel radial diameter	Vessel tangential diameter	Vessel density (vessels per mm)	Vessel element length	Rays per mm	Ray width (cells)	Ray width	Ray height (cells)	Ray height	Growth ring boundaries	Porosity	Vessels of two dist. diam. classes	Axial parenchyma scanty vasic	Axial parenchyma aliform	Axial parenchyma confluent	Axial parenchyma banded	Axial parenchyma terminal	Crystals	Septate fibres	Helical thickenings	Storied rays
1	CRILAR Pb 1	104	92	15	155	3.7	5.2	66	32	525	1	0	1	0	1	1	1	0	1	0	0	0
2	CRILAR Pb 2	133	111	11	172	3.9	4.2	62	31	482	1	0	1	0	1	1	1	0	1	0	0	0
3	CRILAR Pb 3	123	121	17	158	3.8	4.6	91	27	567	1	0	1	0	0	1	?	0	?	0	0	0
4	CRILAR Pb 4	122	126	23	201	5.6	2.8	35	26	337	1	0	1	0	1	1	1	0	1	0	0	0
5	CRILAR Pb 5	?	?	?	?	3.3	5.2	85	33	422	1	0	1	0	0	1	?	0	?	0	0	0
6	CRILAR Pb 6	?	?	?	159	2.7	4.0	53	21	310	1	0	1	0	0	1	1	0	?	0	0	0
7	*Prosopisinoxylon anciborae*	123	106	12	132	7	4.6*	37	?	240	1	0	1	0	1	1	1	0	1	0	0	0
8	*Prosopisinoxylon castroae*	189	179	8	255	7	3*	57	31	418	1	1	1	0	1	1	0	1	1	0	0	0
9	*Paracacioxylon odonelli* [a]	114*	103*	6	128	7	4*	37	27*	250	1	1	0	1*	1*	1	0	0	1	1	0	0
10	*Paracacioxylon odonelli* [b]	197	159	9	?	?	5	51	40	502	1	1	0	1	0	0	0	0	0	0	0	0
11	*Menendoxylon piptadiensis*	102	83	32	?	?	1	13	10	145	1	1	0	0	0	1	0	0	0	0	0	0
12	*Mimosoxylon santamariensis*	171	132	13	?	?	2	?	16	253	1	0	0	0	0	1	0	0	1	0	0	0
13	*Mimosoxylon caccavariae*	88	101	19	278	7	2.1*	41	23	469	1	0	0	0	1	1	1	1	0	0	0	0
14	*Acacioxylon pseudocavenium*	185*	160*	5*	300*	8.1	2*	25*	14*	255*	1	1	0	0	1	1	1	1	0	0	0	0
15	*Anadenantheroxylon villaurquense*	?	87	7.5	259	8	1.1*	13	11*	175	0	0	0	0	1	0	1	0	0	0	0	0
16	*Microlobiusxylon paranaensis*	96	72	20	164	8	1.2*	13	11	170	1	0	0	0	1	1	0	0	1	0	0	0
17	*Holocalyxylon cozzoi*	65	65	11	235	10	2*	31	11	189	1	0	0	0	1	1	1	1	1	0	0	1
18	*Euacacioxylon bharadwajii*	198*	135*	?	310*	?	5*	52.5*	25*	425*	0	0	0	0	1	1	1	1	0	0	0	0
19	*Euacacioxylon ferrugineum*	?	?	5*	?	7*	3.5*	46*	?	300*	1	0	0	0	1	1	0	1	1	0	0	0
20	*Gleditsioxylon riojana*	222	185	20	171	4	3.7*	50	33	676	1	1	0	0	1	1	0	1	1	0	1	0

The character number of cells per parenchyma strand was not included in the PCA because most of the authors of the fossil-species did not mention that character in their original diagnosis or description and in the rest of the fossil-species there are four cells per parenchyma strand. Other characters (*i.e.* vestured pits, number of crystals per cell, etc.) are uninformative because not all fossil-species have them or at least they were not mentioned in the original description.

Principal component (PC) 1, 2 and 3 explained 26.56%, 19.7% and 12.7% of variance respectively (PC1 to 3 summed 58.9%) and PCs 1 to 10 explained 95.8%. Figure 4 shows a plot of PC 1 with PC 2 (together they explained 46.3% of variance) and PC 1 with PC 3 (39.28% of variance). Cumulative eigenvector values of PC1 to 3 x proportion of variance shown on Table 2, indicate that the three characters responsible for most variance are vessel element length, vessel tangential diameter and ray height (expressed in μm); these are continuous characters. The characters associated to the type of axial parenchyma, vessel density and septate fibres present are all in the bottom of the rank (Table 2), so apparently their diagnostic information is limited for this analysis.
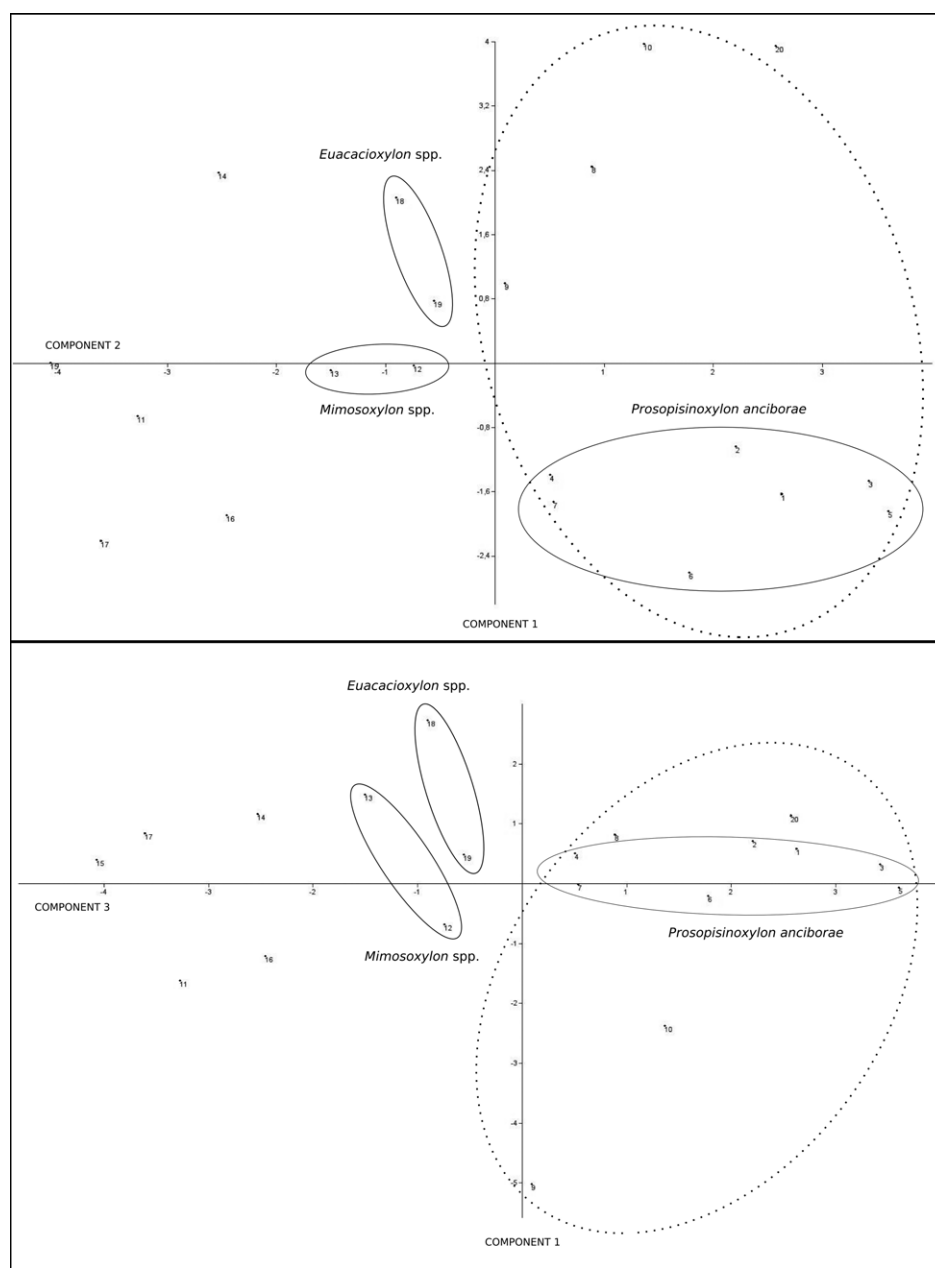

Figure 4. PCA including described specimens and related fossil-species. **A**, PC1 vs PC2. **B**, PC 1 vs PC 3. Numbers correspond to those on Table 1. **7**, *Prosopisinoxylon anciborae*. **8**, *Prosopisinoxylon castroae*. **9**, *Paracacioxylon odonelli* (*sensu* Menéndez, 1962). **10**, *Paracacioxylon odonelli* (*sensu* Lutz, 1987). **11**, *Menendoxylon piptadiensis*. **12**, *Mimosoxylon santamariensis*. **13**, *Mimosoxylon caccavariae*. **14**, *Acacioxylon pseudocavenium*. **15**, *Anadenantheroxylon villaurquense*. **16**, *Microlobiusxylon paranaensis*. **17**, *Holocalyxylon cozzoi*. **18**, *Euacacioxylon bharadwajii*. **19**, *Euacacioxylon ferrugineum*. **20**, *Gleditsioxylon riojana*.

Table 2. Eigenvector values (PC1, 2 & 3 values), summed values x proportion of variance and character ranking for each character.

Variable	PC1	PC2	PC3	Sum PC1-3 x % var.	Rank
Vessel radial diameter	0.099	0.426	0.117	12.50	6
Vessel tangential diameter	0.160	0.403	0.126	13.78	3
Vessel density (vessels per mm)	0.021	0.177	0.004	4.10	21
Vessel element length	0.262	0.234	0.269	14.98	1
Rays per mm	0.387	0.057	0.039	11.90	10
Ray width (cells)	0.351	0.040	0.013	10.29	13
Ray width	0.373	0.024	0.122	11.94	9
Ray height (cells)	0.359	0.182	0.019	13.37	5
Ray height	0.327	0.179	0.195	14.69	2
Growth ring boundaries	0.152	0.085	0.201	8.27	16
Porosity	0.017	0.354	0.248	10.58	12
Vessels of two dist. diam. classes	0.292	0.234	0.104	13.70	4
Axial parenchyma vasicentric	0.045	0.205	0.474	11.25	11
Axial parenchyma aliform	0.124	0.071	0.194	7.15	18
Axial parenchyma confluent	0.083	0.164	0.126	7.04	19
Axial parenchyma banded	0.011	0.230	0.339	9.13	14
Axial parenchyma terminal	0.108	0.242	0.349	12.08	8
Crystals	0.261	0.240	0.064	12.49	7
Septate fibres	0.004	0.057	0.443	6.84	20
Helical thickenings	0.109	0.224	0.100	8.58	15
Storied rays	0.152	0.126	0.074	7.47	17

Positions of the samples assigned to *Prosopisinoxylon anciborae* (CRILAR Pb 1 to 6) are consistent with the proposed systematic treatment. The new specimens and *P. anciborae* holotype can be clustered without overlapping with other fossil-species. As mentioned above, *P. anciborae* shows great intraspecific variability, according to the extensive area that the new samples and the holotype occupy; shown in Figures 4A-B.

Prosopisinoxylon and *Paracacioxylon* together form a discrete cluster, which is shown by a dotted line ellipse on Figures 4A,B. This apparent controversy is probably the result of both fossil-genera sharing the majority of their diagnostic characters, differing only in the presence of vessels of two distinct classes in *Prosopisinoxylon*. *Gleditsioxylon* also shares many characters with these fossil-genera and is included in the same cluster in Figure 4B. *Gleditsioxylon* differs from *Prosopisinoxylon* and *Paracacioxylon* mainly in having helical thickenings. PCA also makes discrete clustering of the two fossil-species of *Euacacioxylon* and the same happens with the two *Mimosoxylon* fossil-species. *Menendoxylon* and *Microlobiusxylon* are closely positioned (Figures 4A,B), and this PCA suggests that their diagnostic characters should be revised.

Climatic inferences

The studied fossil woods are related to extant *Prosopis* which is typical of the driest regions of America (Cabrera, 1971). Furthermore, some peculiar characters of the fossil woods suggest a dry and warm temperature, such as: (i) vessels of two distinct diameter classes (to prevent embolia);

(ii) commonly short vessel elements, which have been usually associated with dry climates (Baas & Schweingruber, 1987; Carlquist, 2001). Medium to large vessel diameter and abundant paratracheal axial parenchyma are usually related to warmer climates (Dickison, 1989; Wiemann *et al.*, 1999). Sometimes marked growth ring boundaries suggest seasonality. In addition, Garcia Massini & Pujana (2013) recently described evidence of Kalotermidae termites, typically of dry environments in fossil woods of these same sediments. The fossil mammals described from the same formation may also suggest a warm and dry climate (Brandoni *et al.*, 2012).

According to the affinity of the fossil woods from the Salicas Formation, the predecessors of extant *Prosopis* would already have been present in dry areas in the late Miocene. Apparently the radiation of most Argentinean *Prosopis* spp. occurred later in the Pliocene (Catalano *et al.*, 2008). This coincides with the amplification of the arid zones of northwestern Argentina (Strecker *et al.*, 1989; Latorre *et al.*, 1997).

CONCLUSIONS

Six fossil wood specimens from the late Miocene Salicas Formation were assigned to the fossil-species *Prosopisinoxylon anciborae* of the Mimosoideae. This fossil-species shows great intraespecific variation in some characters (*e.g.* ray width). They seem to have an affinity to extant *Prosopis*. The PCA supports the systematic placement. Wood anatomy suggests dry and warm conditions in accordance to previous studies.

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