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## Redescription and reassignment of the fossil wood *Menendoxylon piptadiensis* from the Pliocene Andalhuala Formation, South America

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A restudy of the holotype of the fossil wood *Menendoxylon piptadiensis* Lutz, 1987 has revealed that this taxon possesses several diagnostic anatomical features not associated with Leguminosae-Mimosoideae to which it was originally referred. The combined presence of laticiferous tubes, axial parenchyma apotracheal diffuse and paratracheal vasicentric, strands of 2–7 cells, homocellular rays, simple perforation plates, vested intervessel pits, and non-septate fibres with distinctly bordered pits are diagnostic characteristics that support its transfer to the family Apocynaceae and a particular resemblance with species of the tribe Willughbeieae within the subfamily Rauvolfioideae. The fossil is closest to *Parahancornia fasciculata*, *Parahancornia peruviana* and *Couma guianensis*, with anatomical characteristics especially similar those of *Parahancornia fasciculata*. The extant *Parahancornia* is most closely related to the fossil, supporting the hypothesis that this genus was more widespread in the past. Currently, it is distributed in the Neotropics, temperate Brazil and tropical South America (northern Bolivia, north-eastern Perú, Colombia and Guayana). The material studied here is the first fossil wood from South America with an affinity to Apocynaceae and a new combination is erected, *Parahancornioxylon piptadiensis* (Lutz) Moya & Brea gen. et comb. nov. Eco-anatomical characteristics, Carlquist's index and the nearest living relatives (NLRs) indicate a warmer and more humid climate in north-west Argentina during the Pliocene, probably associated with tropical forests.

**Keywords:** systematics; Apocynaceae; *Menendoxylon*; *Parahancornia*; fossil wood; Argentina

### Introduction

In 1979, one of us (AIL) described the new fossil genus *Menendoxylon* with three new species: *M. vasallensis*, *M. areniensis* and *M. mesopotamiensis*. These three fossil wood species were found in the late Pleistocene El Palmar Formation and late Miocene Ituzaingó Formation (lower Member) in Entre Ríos Province, north-western Argentina (Lutz 1979; Brea & Zucol 2011; Brunetto *et al.* 2013; Franco & Brea 2013). All are closely related to the Piptadenia Group of plants. Subsequently, Lutz (1987) erected a new species, *M. piptadiensis*, from the Pliocene Andalhuala Formation of north-west Argentina. *Menendoxylon piptadiensis* was also assigned to the subfamily Mimosoideae, with resemblance to the extant *Piptadenia rigida* Benth.

The Andalhuala Formation contains a very diverse and important fauna of vertebrate fossils, including abundant

mammals, birds and reptiles (Ameghino 1889; Frenguelli 1936; Marshall & Patterson 1981; Bossi *et al.* 1998; Powell 1998). In addition, leaf impressions of Fabaceae, Anacardiaceae, Cyperaceae and Equisetales, stems and petrified woods have been described (Menéndez 1962; Fernández & Bravo 1985; Lutz 1987; Durango de Cabrera *et al.* 1997; Anzótegui *et al.* 2007b). The fossil plants recovered in the Andalhuala Formation indicate a warm climate, with xerophyte vegetation and riparian forests (Anzótegui *et al.* 2007b). The general depositional environment indicates high- and low-sinuosity rivers, with small shallow lakes in the floodplains (Bossi & Palma 1982; Bossi *et al.* 1998; Georgieff 1999).

In this paper, the holotype of *Menendoxylon piptadiensis* is reviewed, redescribed and illustrated in detail, and its systematic position discussed. The use of modern methods has allowed a more detailed and accurate characterization of the anatomy of the wood. The main goal is to

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reassign this fossil wood to the family Apocynaceae and the subfamily Rauvolfioideae. We propose a new genus of fossil wood, which resembles the extant *Parahancornia*, and name it *Parahancornioxylon piptadiensis* (Lutz) Moya & Brea gen. et comb. nov.

In South America, the fossil record of the family Apocynaceae ranges from the Paleocene to the Pliocene (c. 61.7–1.8 Ma), and includes leaf impressions (Berry 1917) and palynomorphs (Regali *et al.* 1974; Quattrochio & Volkheimer 1990; Hoorn 1994a, b; Jaramillo & Dilcher 2001; Mautino & Anzótegui 2002). However, there are no reports of fossil apocynaceous woods from Argentina. On the other hand, fossil woods of Apocynaceae are common in North America and Europe (Kruse 1954; Gazeau-Koeniguer 1976; Gottwald 1966; Privé-Gill 1982; Wheeler *et al.* 1987; Crawley 2001; Gregory *et al.* 2009).

## Geological setting

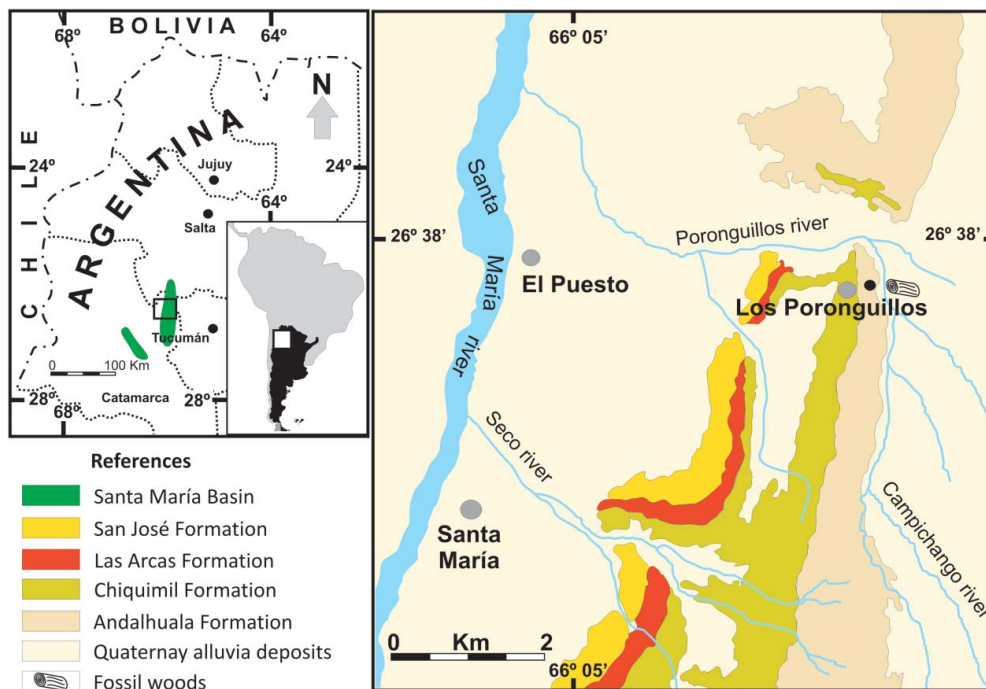
The Miocene–Pliocene Santa María Group is located in north-west Argentina at the eastern Andean margin, between the Cumbres Calchaquies and Sierras del Aconquija to the east and the Sierras de Quilmes to the west. The sequence is exposed in Catamarca, Tucumán and Salta provinces (Kleinert & Strecker 2001; Martínez 2010) (Fig. 1). The Santa María Group is represented by six formations; from the base upwards these are: San José, Las Arcas, Chiquimil, Andalhuala, Corral Quemado and Yasyamayo formations (Bossi & Palma 1982). The fossil

material studied here was recovered from the Andalhuala Formation at the locality Los Poronguillos in Catamarca Province (Fig. 1).

The Andalhuala Formation (c. 900–1300 m thick) overlies the Chiquimil Formation and consists of grey medium- to coarse-grained sandstone (see Bossi & Palma 1982; Grier & Dallmeyer 1990). In the Santa María Valley, a tuff in the lower part of the section is dated at c. 6 Ma (Marshall & Patterson 1981), and the unit is capped regionally by a dacitic tuff dated at c. 3.4 Ma (Strecker *et al.* 1987). The Andalhuala Formation is well known for its rich plant fossils (Menéndez 1962; Lutz 1987; Durango de Cabrera *et al.* 1997; Anzótegui *et al.* 2007b). As a result of considerable fieldwork since the 1980s in the Miocene–Pliocene of the Santa María Group in the north-west region of the Catamarca–Tucumán, petrified woods, leaf impressions and palynomorphs have been discovered in the San José, Chiquimil and Andalhuala formations (Lutz 1987; Mautino & Anzótegui 1998, 2002; Anzótegui 2004; Anzótegui & Herbst 2004; Anzótegui *et al.* 2007a, b; Martínez 2010, 2014, among others).

## Material and methods

**Repository.** The holotype fossil specimen and microscope slides are housed in the Colección Paleontológica de la UNNE ‘Dr Rafael Herbst’, Facultad de Ciencias Exactas y Naturales y Agrimensura, Universidad Nacional del Nordeste, Corrientes, Argentina, under the acronyms



**Figure 1.** Location map of the Los Poronguillos fossil locality in the Santa María Valley, Catamarca Province, Argentina (modified from Martínez 2010).

**CTES-PB** for the wood specimen and **CTES-PMP** for the slides.

The fossil wood studied here was permineralized by silica and has well-preserved anatomical features of the secondary xylem. The holotype (CTES-PB 6141) was thin-sectioned to make the three standard sections (cross, tangential and radial sections). The material was studied with a Nikon eclipse E200 light microscope and the photomicrographs were taken with a Nikon Coolpix S4 digital camera.

Material was prepared for scanning electron microscopy (SEM) by cutting a 2 cm<sup>3</sup> block of the wood that was mounted on SEM stubs without coating, and observed in low-vacuum conditions using a Phenom Pro Desktop SEM at the Laboratorio de Microscopía Electrónica (EMLAB), CICYTTP-CONICET, Diamante, Entre Ríos, Argentina.

Recommendations of the International Association of Wood Anatomists (IAWA) List of Microscopic Features for Hardwood Identification (IAWA Committee 1989) were used. Terminology proposed by Tortorelli (1956) and Carlquist (2001) was also considered. Systematic assignment follows the Angiosperm Phylogeny Group (APG IV 2016). Quantitative values provided in the anatomical descriptions are of 25 measurements, with the average cited first, followed by the minimum and maximum values which are given in parentheses. The UTHSCSA Image Tool Program version 3.0 (2002) was used to measure the elements in the photomicrographs.

For identification of the fossil wood and comparison with extant and fossil species, we used the InsideWood website (InsideWood 2004–ongoing; Wheeler 2011), and descriptions by Metcalfe & Chalk (1950), Cronquist (1981), Miller & Détienne (2001), Baas *et al.* (2007), Simões *et al.* (2007), Lens *et al.* (2008) and Williams (2011). The compendia of fossil wood names by Gregory (1994) and Gregory *et al.* (2009) were used for reference.

Principal Component Analysis (PCA) was performed to corroborate the accuracy of systematic placement, and to test the delimitation of the taxon. A correlation matrix was made based on 21 anatomical features (all discrete characters) and standardized mean values of all characters (Supplemental material). This descriptive technique was used with the objective of establishing the limits and the diagnostic characters of the fossil woods. PCA with wood anatomy characters has been tested previously for its appropriateness in taxon delimitation (Wickremasinge & Herat 2006; Oakley & Falcon-Lang 2009; Oakley *et al.* 2009; MacLachlan & Gasson 2010; Henderson & Falcon-Lang 2011; Pujana *et al.* 2014). Some characters (porosity, type of perforation plates, type of intervessel pits, presence of vested pits, vasicentric axial parenchyma) were not included in the PCA because they were the same in all specimens and are thus uninformative. However, many characters not present in the IAWA code (IAWA

Committee 1989) were used for the PCA: mostly solitary vessels; mostly in radial multiple vessels; solitary, short radial multiples and clusters; solitary, short radial multiples, long radial multiples and in clusters; solitary and short radial multiples (see Supplemental material). Also, cluster analysis was used to make a classification of the groups. For the intra population Euclidean<sup>2</sup> distance was used. The analysis was performed using InfoStat version 2015 (Di Rienzo *et al.* 2015).

The vulnerability index ( $V = \text{mean vessel diameter} / \text{mean vessel frequency}$ ) and mesomorphy ratio ( $M = V$  multiplied by mean vessel member length) were calculated using the equations developed by Carlquist (1977). The method based on the climatic tolerance of the nearest living relatives (NLRs) was used. The NLR approach has been applied widely to interpret past climate and environments (Mosbrugger 2009).

## Systematic palaeontology

Order **Gentianales** Jussieu ex Berchtold  
& J. Presl, 1820

Family **Apocynaceae** Jussieu, 1789

Subfamily **Rauvolfioideae** Kostel, 1834

Tribe **Willughbeieae** A. DC., 1844

Genus ***Parahancornioxylon*** gen. nov.

**Basionym.** *Menendoxylon piptadiensis* Lutz, 1987: 128–129, pl. 1, figs 1–5.

**Diagnosis.** Vessels mostly solitary, radial multiples of 2–5 cells, and in clusters; perforation plate exclusively simple; intervessel pits alternate, bordered and vested; axial parenchyma apotracheal diffuse-in-aggregates and paratracheal vasicentric; homocellular rays composed exclusively of procumbent cells; 1–3-seriate; vessel-ray pits similar to intervessel pits in shape and size; non-septate fibres, fibre pits bordered; prismatic crystals in short chains in chambered axial parenchyma; laticiferous tubes.

**Etymology.** The name *Parahancornioxylon* refers to the affinity with the extant genus *Parahancornia*.

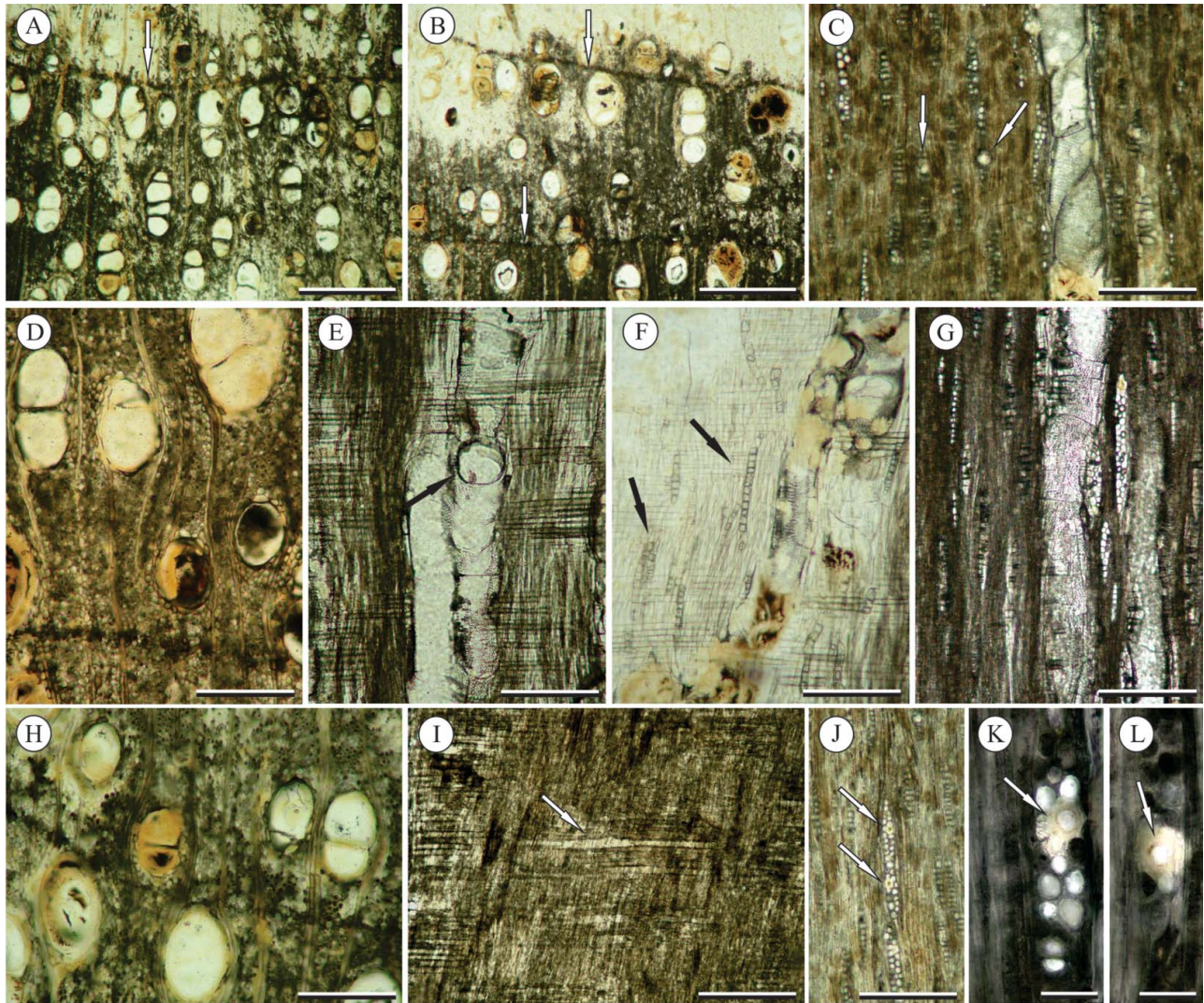
*Parahancornioxylon piptadiensis* (Lutz) Moya &  
Brea gen. et comb. nov.  
(Figs 2–4)

**Diagnosis.** As for the genus.

**Holotype.** CTES-PB 6141 (wood specimen) and CTES-PMP 3494, 3495 and 3496 (three slides).

**Occurrence.** Los Poronguillos, Catamarca Province, Argentina; Pliocene, Andalhuala Formation.

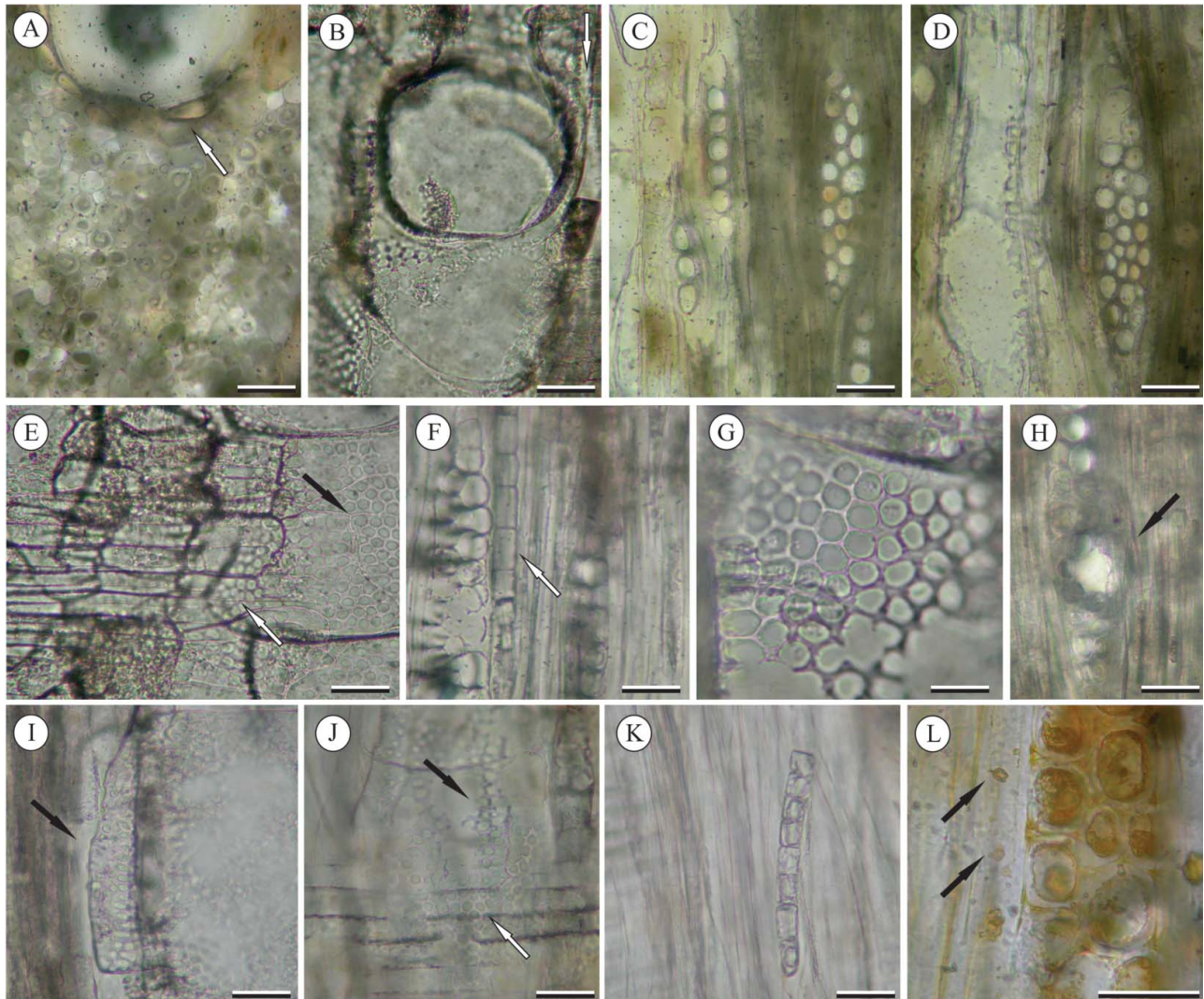
**Description.** Growth rings are distinct, demarcated by a band of compressed fibres (Fig. 1A). The wood is diffuse-



**Figure 2.** *Parahancornioxylon piptadiensis* (Lutz). **A, B**, transverse section showing distinct growth rings (white arrows), diffuse porous wood, solitary vessels and multiple vessels in radial. **C**, longitudinal tangential section showing rays with laticiferous tubes (white arrows). **D**, transverse section showing details of axial parenchyma vasicentric and apotracheal diffuse-in-aggregates. **E**, longitudinal radial section showing homocellular rays and simple perforation plates (black arrow) with straight to oblique end walls. **F**, longitudinal radial section showing prismatic crystals in chambered axial parenchyma (black arrows). **G**, longitudinal tangential section showing uni-seriate, biseriate and triseriate rays. **H**, transverse section showing axial parenchyma that is vasicentric and confluent. **I**, longitudinal radial section showing radial details of laticiferous tubes (white arrow). **J–L**, longitudinal tangential section showing details of laticiferous tubes (white arrows). Scale bars: A, B = 500  $\mu\text{m}$ ; C–J = 200  $\mu\text{m}$ ; K–L = 30  $\mu\text{m}$ .

porous. Vessels are mostly solitary (44%) and usually in radial multiples of two elements (39%), occasionally in radial multiples of three, four and five elements (11, 2 and 1%, respectively), and rarely in clusters (3%) (Fig. 1A). Vessels are circular to oval in outline, with thin to thick walls 9 (5–13)  $\mu\text{m}$  thick. Mean tangential vessel diameter is 83 (28–134)  $\mu\text{m}$ , and mean radial vessel diameter is 120 (26–202)  $\mu\text{m}$  (Figs 2A, 3A, 4C). Mean vessel element length is 65 (26–133)  $\mu\text{m}$  (Fig. 2B, C). Mean vessel density is 11 (9–13) vessels/ $\text{mm}^2$ . Perforation plates are exclusively simple (Figs 2B, 4I). Intervessel pits are alternate, small, 5.5 (4–6.5)  $\mu\text{m}$  in diameter, bordered with elongated apertures and vested (Figs 2F, 3D, 4D, E, F,

G, H, J). Vessel-ray pits are similar to intervessel pits in shape and size (Figs 3B, 4J). Fibres are rounded to hexagonal in outline in cross section with a tendency towards radial arrangement. They are very thin walled, 1.7 (1.5–2.5)  $\mu\text{m}$  thick, with a mean diameter of 5 (3–7.5)  $\mu\text{m}$ , and non-septate. Fibres have distinctly bordered pits (Figs 3C, 4M). Axial parenchyma is scanty paratracheal vasicentric, confluent, and apotracheal diffuse-in-aggregates (Figs 2A, 3A, 4C); there are 4–7 cells per parenchyma strand. Parenchyma cells have simple pits (Fig. 4K, L). Rays are homocellular, composed exclusively of procumbent cells, 10 per linear mm (7–13 per linear mm) (Figs 2B, E, 4I), frequently 1–3-seriate (Fig. 4A, B); 12 cells (4–23 cells)

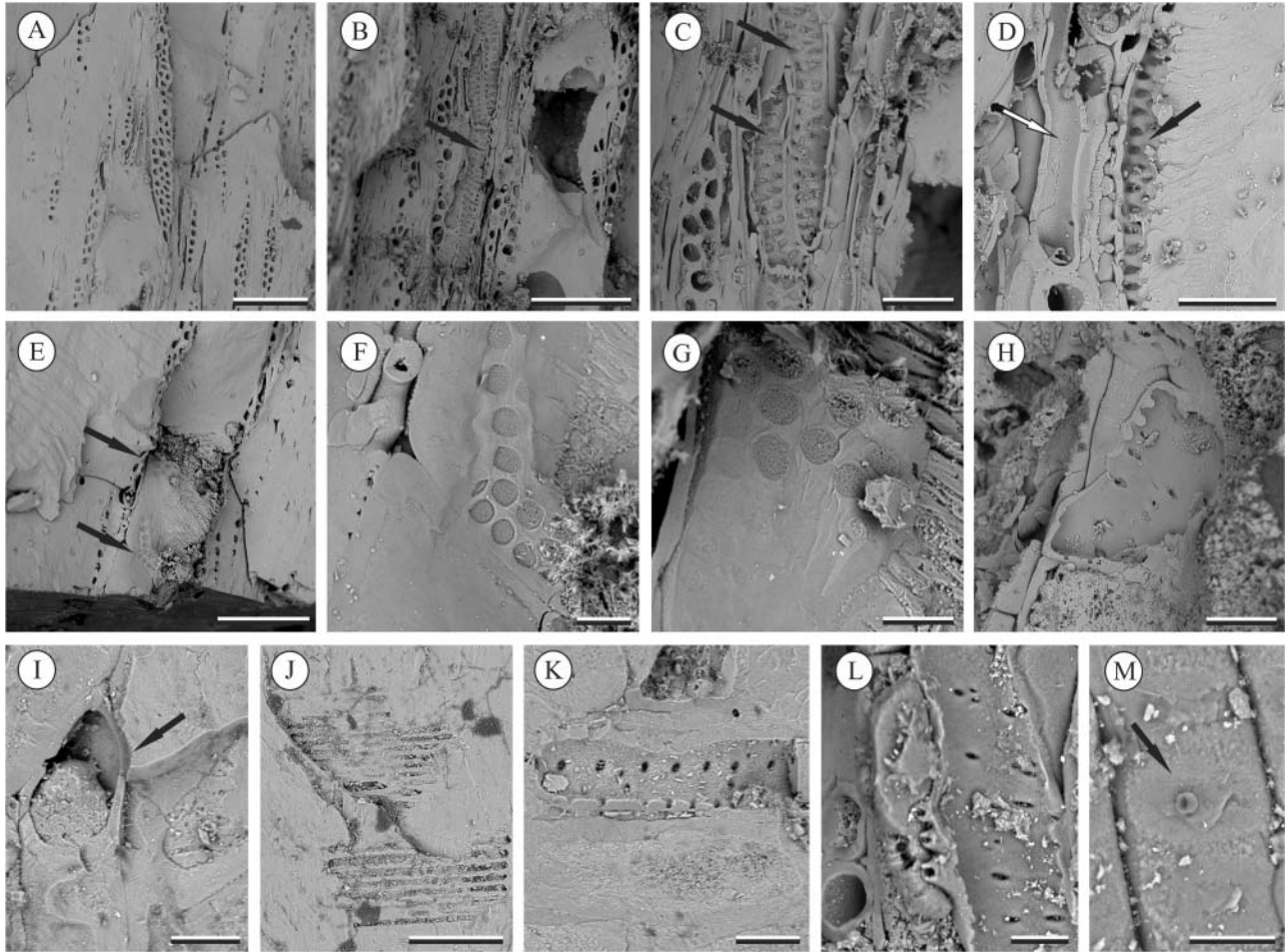


**Figure 3.** *Parahancornioxylon ptiadiensis* (Lutz). **A**, transverse section showing details of vessel, axial parenchyma vasicentric (white arrow) and fibres. **B**, longitudinal radial section showing details of simple perforation plate. **C**, longitudinal tangential section showing details of uniseriate and biseriate rays. **D**, longitudinal radial section with details of triseriate ray. **E**, longitudinal radial section showing details of vessel-ray pits (white arrow) and intervessel pits. **F**, longitudinal radial section with seven cells per parenchyma strand. **G**, longitudinal radial section showing details of alternate intervessel pits. **H**, longitudinal radial section with details of laticiferous tubes (black arrow). **I**, longitudinal radial section showing details of narrow vessel. **J**, longitudinal radial section with details of intervessel pits (black arrow) and vessel-ray pits (white arrow). **K**, longitudinal radial section showing details of prismatic crystals in long chains of crystalliferous chambered axial parenchyma. **L**, longitudinal radial section with details of bordered fibre pits (black arrows). Scale bars: A–K = 30  $\mu\text{m}$ ; L = 20  $\mu\text{m}$ .

or 150  $\mu\text{m}$  (70–279  $\mu\text{m}$ ) high, 17  $\mu\text{m}$  (9–34  $\mu\text{m}$ ) in width. Procumbent cells have simple pits (Fig. 2C, D). Laticiferous tubes are present in rays (Fig. 2C–E). Prismatic crystals are in short (3–14) chains in chambered axial parenchyma, one crystal per cell or chamber (Fig. 3C).

**Comparisons with extant taxa.** Apocynaceae is a family of flowering plants of very diverse habit, including trees, shrubs, lianes, stem succulents and a few herbs. Members of the family possess a global distribution, with the highest diversity in the tropics and subtropics, and are native

to Europe, Asia, Africa, Australia and America, with some temperate members (Metcalf & Chalk 1950; Endress & Bruyns 2000; Stevens 2001; Morales 2005; Endress *et al.* 2007, 2014). Apocynaceae *sensu lato* belongs to the Gentianales, an order of (eu)Asteridae with five families – Apocynaceae, Gelseminaceae, Gentianeaceae, Loganiaceae and Rubiaceae (APG IV 2016) – and can be distinguished by the presence of latex (Middleton 2007). Nonetheless, the exact taxonomic position of Apocynaceae within the order is disputed (Struwe *et al.* 1994; Endress *et al.* 1996; Potgieter 1999; Backlund *et al.* 2000; Potgieter & Albert 2001; Bremer *et al.* 2002). It is



**Figure 4.** *Parahancornioxylon piptadiensis* (Lutz). **A**, longitudinal tangential section showing uni-triseriate rays. **B**, longitudinal tangential section showing rays and narrow vessel. **C**, longitudinal tangential section with details of narrow vessels (black arrows). **D**, longitudinal tangential section showing details of parenchyma cell (white arrow) and inner intervessel pits (black arrow). **E**, longitudinal tangential section showing vessel with bordered and vested intervessel pits (black arrows). **F**, **G**, longitudinal tangential section with detail of vested pits viewed in outer wall of the vessel. **H**, longitudinal tangential section showing details of vested pits viewed from the lumen side of the vessel. **I**, longitudinal radial section with details of simple perforation plate (black arrow). **J**, longitudinal radial section showing homocellular rays. **K**, longitudinal radial section with details of simple pits in parenchyma cell. **L**, longitudinal tangential section showing details of simple pits in axial parenchyma cell. **M**, longitudinal radial section with details of bordered fibre pits. Scale bars: A, B, J = 100  $\mu\text{m}$ ; C, D = 30  $\mu\text{m}$ ; E = 80  $\mu\text{m}$ ; F, G, I, K–M = 10  $\mu\text{m}$ ; H = 20  $\mu\text{m}$ .

one of the 10 largest families of angiosperms, with about 5000 species in 366 genera (Zarucchi *et al.* 1995; Stevens 2001; Endress *et al.* 2007, 2014; Williams 2011; Rapini 2012; Morokawa 2014). The subfamily Rauvolfioideae was formerly placed with Apocynoideae in a narrowly defined Apocynaceae *sensu stricto*, closely related to the former Asclepiadaceae (including Asclepiadoideae, Periplocoideae and Secamonoideae) (Lens *et al.* 2008).

Rauvolfioideae *sensu* Simões *et al.* (2007) comprises about 980 species distributed among 84 genera and 10 tribes, representing about one-quarter to one-fifth of the species diversity within the family (Stevens 2001; Lens *et al.* 2008). In the APG IV (2016), Rauvolfioideae comprises 11 tribes and is paraphyletic, believed to be a 'primitive' group (Endress & Bruyns 2000). Molecular

phylogenetic analyses provided new insights into higher level relationships: the traditional Rauvolfioideae as well as Apocynoideae (Apocynaceae *sensu stricto*) are now proven to be paraphyletic, while the former Asclepiadaceae is considered to be polyphyletic with its separate components all nested in Apocynoideae (Livshultz *et al.* 2007; Simões *et al.* 2007). Consequently, contemporary systematists favour the recognition of one broadly defined Apocynaceae *sensu lato* family (Judd *et al.* 1994; Endress *et al.* 1996; Sennblad & Bremer 1996, 2002; Endress & Bruyns 2000; Potgieter & Albert 2001; Morales 2005; Livshultz *et al.* 2007; Simões *et al.* 2007).

The combination of diagnostic anatomical features indicates that the fossil wood described in this paper has a great affinity with Apocynaceae-Rauvolfioideae (Metcalf

& Chalk 1950; Miller & Détienne 2001; InsideWood 2004; Lens *et al.* 2008; Williams 2011). Using the InsideWood database (see coding in IAWA Committee 1989), the combination of the diffuse-porous wood (5p), vested pits (29p), non-septate fibres (66p), ray width 1–3 cells (97r), all ray cells procumbent (104r), laticiferous or tanniferous tubes (132r), prismatic crystals present (136p) with zero allowable mismatches, retrieved three species of Apocynaceae: *Parahancornia fasciculata* Lam. (Benoit), *Parahancornia peruviana* Aubl. and *Couma guianensis* Aubl. (Table 1). *Parahancornia fasciculata* and *Parahancornioxylon piptadiensis* have in common more characteristics, including 7–13 rays per linear mm, very thin-walled to thin-walled fibres, 4–8 cells per axial parenchyma strand, laticiferous tubes (see CTFTW 8044 in the InsideWood database) and prismatic crystals in chambered axial parenchyma cells (Table 1). Currently, this genus is distributed in the Neotropics, temperate Brazil and tropical South America (northern Bolivia, north-eastern Perú, Colombia and Guyana) (Miller & Détienne 2001; InsideWood 2004; Altamirano Azurduy & Ramos de Sousa 2009; Cornejo & Janovec 2010). *Parahancornia peruviana* and *Couma guianensis* have vessels mostly in radial multiples and rays that are commonly biseriate; also *C. guianensis* lacks laticiferous tubes in rays (Table 1). *Parahancornioxylon piptadiensis* is distinguished from the most closely related species by the presence of distinct growth rings.

**Comparisons with fossil species.** Eight fossil woods assigned to the Apocynaceae were compared with *Parahancornioxylon piptadiensis*. *Aspidospermoxylon uniseriatum* (Kruse 1954; Eocene of North America) and *Apocynoxylon silvestris* (Gazeau-Koeniguer 1976; Eocene of Europe), two taxa assigned with certainty to Apocynaceae, differ from the fossil material studied here because they have heterocellular rays. In addition, *A. silvestris* lacks canals in the rays.

*Apocynoxylon? oldhavenense* (Crawley 2001; Palaeogene of Europe), also possibly assigned to Lecythidaceae?, has heterocellular rays, large rays commonly 4- to 10-seriate, lacks canals in the rays, and has axial parenchyma in narrow bands. *Apocynoxylon sapotaceoides* (Crawley 2001; Palaeogene of Europe), showing affinities with Sapotaceae?, has vessels in diagonal and/or radial patterns, vessels mainly in radial multiples of four or more elements, and heterocellular and uniseriate rays features not observed in *Parahancornioxylon piptadiensis*. *Paraapocynaceoxylon barghoorni* (Wheeler, Lee & Matten 1987; Upper Cretaceous of North America) differs from the Argentinian specimen described here because it has a low density of vessels, axial parenchyma scanty paratracheal and apotracheal in narrow (1–2 cells wide) bands, and strands of 8–10 cells.

*Grangeonixylon apocynorubioides* (Privé-Gill 1982; Oligocene? of Europe) and *Grangeonixylon dangouense* (Sakala *et al.* 1999; Eocene of Europe), two taxa of uncertain family (possibly Rubiaceae or Apocynaceae), differ from the Argentinian fossil in the presence of heterocellular rays, occasional 4- to 10-seriate rays, and the absence of laticiferous tubes.

*Coumoxylon hartigii* (Gottwald 1966; Eocene of Europe), of uncertain family (possibly Moraceae or Apocynaceae), differs from *Parahancornioxylon piptadiensis* in the presence of radial canals, exclusively uniseriate rays, and possibly vascular or vasicentric tracheids.

## Principal component analysis

Principal component analysis is an important tool to estimate the combined contribution of all studied variables. PCA was carried out here using all species assigned to the genus *Menendoxylon*: *M. vasallensis* Lutz, 1979, *M. arenensis* Lutz, 1979, *M. mesopotamiensis* Lutz, 1979 and *M. piptadiensis* Lutz, 1987. Anatomical descriptions of these woods were corroborated. Principal components 1, 2 and 3 explained 43.5, 19.2 and 16.9% of the variance, respectively. PC1 and PC2 summed explained 62.7% (Fig. 5A), PC 1 to 3 summed explained 79.6% (Fig. 5B), and cumulative PCs 1 to 4 explained 94.0% of the total variation.

Figure 5A shows a plot of PC 1 against PC 2 in which specimen CTES-PB 6141 is clearly distinguished from the group composed of *Menendoxylon* species. The solitary vessels, the radial multiple short, gums and dark contents in the vessels, diffuse apotracheal parenchyma, biseriate rays, triseriate rays, and laticiferous tubes contribute to the separation of *Parahancornioxylon piptadiensis* and *Parahancornia fasciculata* from the other taxa.

Several characters dominate the loadings of PC1: growth rings, combination of vessels solitary-radial multiple short, vested intervessel pits, gums or dark contents, septate fibres, vasicentric and confluent axial parenchyma, diffuse apotracheal parenchyma, crystals in parenchyma, and laticiferous tubes are highly correlated (Table 1).

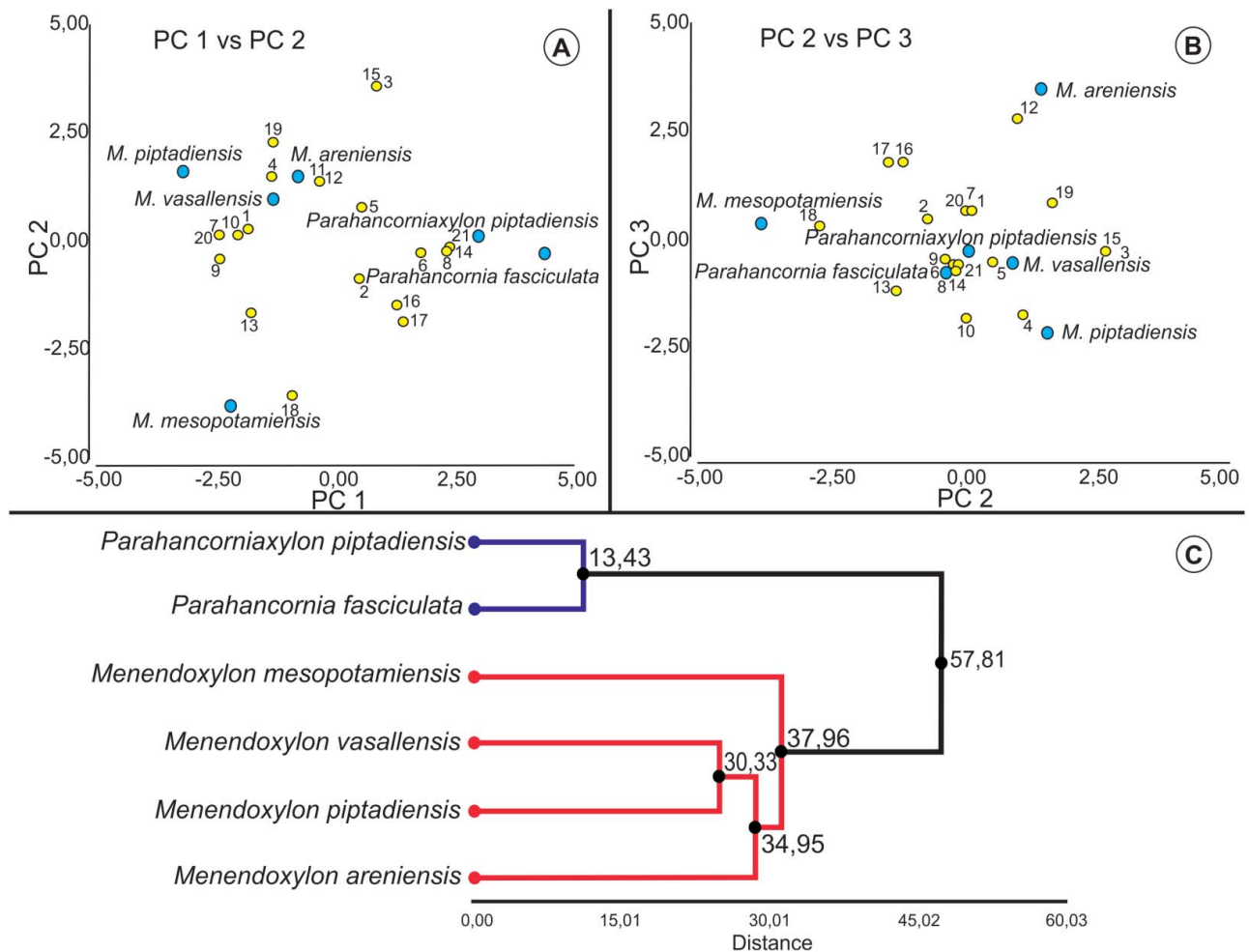
PC2 is dominated mostly by the solitary vessels, usually in radial multiple vessels, the combination of solitary vessels-short radial multiples-long radial multiples in clusters, uniseriate rays, tetraseriate rays, and type of ray cells (Table 1). The characters that contribute less to explaining the variability are: mostly solitary vessels and the combination of solitary vessels-short radial multiples-long radial multiples-clusters.

Six characters dominate PC3: combination of solitary vessels-short radial multiples-clusters, with fibrous, banded or marginal axial parenchyma, vasicentric and aliform axial parenchyma, biseriate rays, and triseriate rays.



**Table 1.** Comparison between *Parahancornioxylon piptadiensis* and the related extant species *Parahancornia fasciculata*, *Parahancornia peruviana* and *Couma guianensis* (Miller & D tienne 2001; InsideWood 2004-ongoing; Lens *et al.* 2008).

	<i>Parahancornia fasciculata</i>	<i>Parahancornia peruviana</i>	<i>Couma guianensis</i>	<i>Parahancornioxylon piptadiensis</i>
<b>Vessels</b>				
Growth rings	Indistinct or absent	Indistinct or absent	Indistinct or absent	Distinct
Porosity	Diffuse-porous	Diffuse-porous	Diffuse-porous	Diffuse-porous
Vessel groupings	Vessels mostly solitary and in short (2–3) radial multiples	Vessels mostly in radial multiples	Vessels mostly in radial multiples	Vessels mostly solitary and in short (2–3) radial multiples
Tangential diameter ( $\mu\text{m}$ )	110 (40–150)	100 (40–160)	60 (120–230)	83 (28–134)
Density ( $\text{mm}^2$ )	11 (6–15)	8 (6–13)	6 (8–13)	11 (9–13)
Perforation plates	Simple	Simple	Simple	Simple
Intervessel pits	Alternate and vested, circular or oval, 4–5 $\mu\text{m}$	Alternate and vested	Alternate and vested	Bordered and vested, polygonal, (5.5) 4–6.5 $\mu\text{m}$ in diameter
<b>Fibres</b>				
Type	Non-septate	Non-septate	Non-septate	Non-septate
Wall thickness	Very thin- to thick-walled	Thin- to thick-walled	Thin- to thick-walled	Very thin-walled to thin-walled
Pits	Distinctly bordered	Distinctly bordered	Distinctly bordered	Distinctly bordered
<b>Rays</b>				
Type	Homoellular, procumbent cells, but less elongated	Homoellular, procumbent cells	Homoellular, procumbent cells	Homoellular, procumbent cells
Number per mm linear	7–9	4–12	4–12	7–13
Width	(1–) 2 cells wide	2 (3) cells wide. Rays with multiseriate portion(s) as wide as uniseriate portions	2 cells wide	1–3 cells wide
Height ( $\mu\text{m}$ )	560 (400–1000)	480 (300–700)	360 (200–500)	150 (70–279)
<b>Axial parenchyma</b>				
Type	Apotracheal diffuse-in-aggregates	Apotracheal diffuse-in-aggregates. In narrow bands or lines, and reticulate	Apotracheal diffuse-in-aggregates. In narrow bands or lines, and reticulate	Apotracheal diffuse-in-aggregate
Strand (cells)	5–8	4–8	6–8	4–7
<b>Crystals</b>				
Parenchyma axial	When present, crystals in short (4–12) chains in chambered axial parenchyma, one crystal per cell or chamber	Prismatic crystals	Prismatic crystals	Prismatic crystal in short (3–14) chains in chambered axial parenchyma, one crystal per cell or chamber
Ray cells	Absent	Absent	Absent	Absent
<b>Tubes</b>				
	Laticiferous tubes present (slightly larger in diameter than ray cells, occasionally two in the same ray)	Laticiferous tubes present	Laticiferous tubes absent	Laticiferous tubes present



**Figure 5.** Principal component analysis (PCA) and cluster analyses. **A**, plot of PC 1 vs PC 2 showing two groups: the group composed of species of *Menendoxylon* and a group comprising *Parahancornioxylon piptadiensis* (Lutz) and *Parahancornia fasciculata*. **B**, plot of PC 2 vs PC 3. **C**, cluster analysis distinguishing two groups.

*Parahancornioxylon piptadiensis* forms a group with *Parahancornia fasciculata*, separate from the *Menendoxylon* group, in the PC1 vs PC2 plot (Fig. 5A). However, in the PC2 vs PC3 plot (Fig. 5B), the *Parahancornia* group is adjacent to *M. vasallensis* whereas *M. piptadiensis*, *M. mesopotamiensis* and *M. areniensis* are isolated. As mentioned above, the presence of diffuse apotracheal axial parenchyma, crystals in parenchyma, and laticiferous tubes especially separates the *Parahancornia* group from the *Menendoxylon* group. Most of the taxa are clearly distinguished, particularly in the PC1 vs PC2 plot. Therefore, the analysis is consistent with the proposed taxonomic treatment. The genus *Menendoxylon* erected by Lutz (1979), with four species included (Lutz 1979, 1987), is currently under review by one of us (EM).

A dendrogram was generated on the basis of the similarity index, classifying all six species into two major clusters at 25.65 dissimilarity coefficient. Figure 5C shows results of the cluster analysis: the *Parahancornia*

and *Menendoxylon* groups are separated by a Euclidean distance of 49.68.

## Discussion

The wood anatomy of Apocynaceae, according to Cronquist (1981), is characterized by the presence of stems that occasionally develop anomalous structures, vessels with simple perforation plates or scalariform with occasional bars, vested intervessel pits, septate fibres with simple pits or non-septate fibres with bordered pits, and heterocellular to homocellular rays of 1–5 cells in width. An anomalous structure of the axis occurs in the lianes, taking the form of furrows lined with phloem or of interxylary phloem. The outstanding anatomical characters are the occurrence of laticiferous canals and crystals of various types, which are sometimes useful for the identification of species (Metcalf & Chalk 1950). In addition to

these diagnostic features, more variable characters can sometimes be used to distinguish between tribes. Examples are the occurrence and location of prismatic crystals (four main types: in rays, in axial parenchyma, a combination of these, or absent). Moreover, when calcium oxalate crystals are present, different types (prismatic, elongate and/or microcrystals) can be observed in the marginal ray cells and sometimes in the septate fibres (Lens *et al.* 2008).

A phylogenetic trend is found towards shorter vessel elements, more pronounced vessel grouping, higher tracheid abundance, more paratracheal parenchyma, and fewer cells per axial parenchyma strand in the more diverging clades. The mean number of cells per axial parenchyma strand has a clear evolutionary trend in Apocynaceae *sensu lato*. The major evolutionary lines within the tribes Tabernaemontaneae *sensu lato*, Vinceae and Willughbeieae can be defined through the two major vessel grouping patterns – exclusively solitary vessels vs abundant radial vessel multiples – that prove to be phylogenetically useful (Lens *et al.* 2008).

Some characters stand out in the wood anatomy of Rauvolfioideae when compared with the rest of the Apocynaceae *sensu lato* – for example, decreasing vessel element length, more pronounced vessel grouping, tracheid abundance, and high frequency of paratracheal parenchyma. In addition, the number of cells per axial parenchyma strand steadily decreases towards the more derived Apocynaceae (Lens *et al.* 2008).

Rauvolfioideae is characterized by the following: growth ring boundaries usually indistinct; wood diffuse-porous in most genera, but with a tendency to (semi)ring-porosity in the climbing genera; vessel predominantly solitary, with vessel grouping typically in radial multiples of 2–4 (–6) vessels in the non-climbing tribe Alstonieae and in the non-climbing genera of Willughbeieae; vessel outline generally rounded to elliptical; perforation plates exclusively simple; intervessel pits alternate, pits 3–8  $\mu\text{m}$  in horizontal diameter, vested. Vessel-ray pits are similar to intervessel pits in size and shape. Tracheids are usually absent, confined to just a few tribes of Rauvolfioideae. Non-septate fibres with distinctly bordered pits in the radial and tangential walls (= fibre tracheids) are common in all tribes; septate fibres with simple to minutely bordered pits concentrated in radial walls (= libriform fibres) are typically present in most genera of Tabernaemontaneae; fibres are mainly thin walled or thin- to thick walled. Within the subfamily Rauvolfioideae some wood features remain constant, such as simple perforation plates, alternate vested intervessel pits and vessel-ray pits that are similar in shape and size to the intervessel pits, while many wood features vary conspicuously throughout the subfamily. In addition, these variable features are more or less uniform at the tribal level (Lens *et al.* 2008).

The wood anatomy of climbers and non-climbers in Apocynaceae deserves comment. Baas *et al.* (2007) proposed a divergence in vessel grouping between the erect species (vessels in multiples common) and climbers (predominantly solitary vessels). Within the tribe Willughbeieae (subfamily Rauvolfioideae), this distinction in vessel grouping is fully supported, but at the subfamily level it suggests the relationship is more complex. Frequent radial vessel multiples are also observed in the genera *Parahancornia* and *Couma*. Two well-supported major clades are present: a New World clade consisting of erect trees (*Couma*, *Lacmellea*, *Hancornia* and *Parahancornia*) and an Old World clade consisting of lianas (*Saba* and *Willughbeia*). The two clades can be easily recognized by their vessel grouping (abundant radial vessel multiples vs exclusively solitary, respectively). Prismatic crystals are typically present in chambered axial parenchyma cells in some species of Willughbeieae. Laticiferous tubes are common in all climbing genera of Willughbeieae plus the non-climbing *Parahancornia* (Simões *et al.* 2007; Lens *et al.* 2008).

The presence of homocellular rays, abundant radial vessel multiples, crystals in axial parenchyma and/or laticiferous tubes are the distinctive features between climbing and non-climbing Willughbeieae (Baas *et al.* 2007; Lens *et al.* 2008). These features are observed in the fossil material studied here. However, no combination of distinctive wood characters could be elucidated for the tribe (Lens *et al.* 2008, table 1, p. 1202). This, added to the limited information on the wood anatomy of these speciose groups, limits the comparisons that can be made with fossil material. However, the presence of laticiferous tubes, prismatic crystals in chambered axial parenchyma cells, vested pits, homocellular rays and 1–3-seriate rays establishes a close relationship with the modern *Parahancornia*.

The vulnerability index (V) and mesomorphy ratio (M) in the fossil wood show values of 7.54 and 490, respectively. Such values indicate mesomorphic features (Carlquist 1977). The diffuse-porous wood, wide vessel diameter, low vessel density, and simple perforation plate are indicators of warm and humid climates, while the short vessel elements could suggest seasonality in temperature or in rainfall (E. A. Wheeler & Baas 1991). Using the NLR method, Carlquist's index and eco-anatomical features observed in *Parahancornioxylon piptadiensis* support the idea that this taxon could have lived under warm and humid climatic conditions.

## Conclusions

Restudy of *Menendoxylon piptadiensis* has allowed observation of anatomical features not previously identified.

Hence, *M. piptadiensis* is excluded from the genus *Menendoxylon*, and placed in the new genus *Parahancornioxylon*, representing the first fossil wood with affinities to Apocynaceae from South America.

The specimen described here increases our knowledge of the fossil flora of the Andalhuala Formation, and reinforces the idea of a warm climate for the region during the Early Pliocene. *Parahancornioxylon piptadiensis* lived together with a plant association (trees, shrubs, herbs in xerophyte and riparian vegetation) mainly related to the families Anacardiaceae and Fabaceae, under a warm subtropical climate (Anzótegui *et al.* 2007b). Moreover, the presence of this fossil wood adds new information for future research regarding the historical biogeography of the family.

The presence of *Parahancornioxylon piptadiensis* in the fossil record supports the hypothesis that *Parahancornia* was more widespread in the past, with subsequent retraction to its current relict distribution probably by the last glacial advance of the Pleistocene.

Restudy of the remaining species within the *Menendoxylon* group is necessary to establish their affinities to one another and to Leguminosae.

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## Supplemental data

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