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Combretaceous fossil wood from Ituzaingó Formation (Late Miocene?), Argentina, indicate a coastal marine environment

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ABSTRACT

A new anatomical study of the fossil material assigned to *Menendoxylon areniensis* Lutz, 1979 (family Fabaceae) was performed. In this study, new wood anatomical characteristics were observed. These are diagnostic characters present in the family, Combretaceae. Also, its presence suggests an adaptation to environmental variability: numerous vessels (mean 14–52 vessels/mm^2), small vessel diameter (mean 26–103 µm), and low vessel height (mean 76–329 µm). The fossil is closest to the genera, *Conocarpus* and *Laguncularia*, with anatomical characteristics that are particularly similar to those of *Conocarpus erectus*. *C. erectus* is a species associated with mangroves and is classified as pseudo mangrove or peripheral species. *Mangroveoxylon areniensis* gen. et comb. nov., recovered in the Late Miocene? of Ituzaingó Formation is the first record of fossil wood that indicates a coastal marine environment, which is further south of the tropics. This could resemble a tropical environment with species developing at different levels of the land.

Keywords: ***Conocarpus*, *Laguncularia*, wood anatomy, *Menendoxylon*, Combretaceae.**

1. Introduction

The genus *Menendoxylon* was created by Lutz (Lutz, 1979) when she described the new species: *Menendoxylon areniensis, M. vasallensis,* and *M. mesopotamiensis,* all wood species closely related to the Piptadenia Group (Leguminosae), from the Late Miocene? Ituzaingó Formation (Lower Member *sensu* Brunetto et al., 2013) and Late Pleistocene El Palmar Formation in Paraná and Uruguay Basins, respectively. Both basins are located in north-eastern Argentina (Lutz, 1979; Brea, 1999; Brea and Zucol, 2011; Brunetto et al., 2013; Franco and Brea, 2013; Moya et al., 2017). Later, Lutz (1987) described a fourth species, *M. piptadiensis* which also resembles *Piptadenia rigida* Benth. This taxon was recovered from the Pliocene Andalhuala Formation of northwest Argentina. Recently, a reviewed, redescription, and reassignment of the holotype (CTES–PB 6141) of *M. piptadiensis* has revealed that this taxon possesses many anatomical features associated to the family Apocynaceae (Moya et al., 2017). Other material assigned to *M. piptadiensis* (Brea, 1999), recovered in Punta Viracho fossil locality (Concordia, Entre Ríos province), is currently under review by one of us (E.M.).

The family Combretaceae belongs to the order Myrtales, comprising *ca*. 13 genera and 500 species (Heywood et al., 2007; APG IV, 2016). This family has two subfamilies:

Combretoideae and Strephonematoideae (van Vliet and Baas, 1984), distributed throughout the tropics, with some extensions to subtropical and warm temperate regions (Exell and Stace, 1966; Heywood et al., 2007; Stace, 2007), and they include trees, shrubs, subshrubs, or lianes, sometimes mangroves, and are rarely spiny. Combretaceae can be important constituents of forest, savannah, and mangrove swamp, and can occur from sea level (in Southeast Asia) to over 3,000 m altitude.

Currently, the Combretaceae occur throughout the tropics, with short extensions into warm temperate zones, e.g., 37°15’S in Argentina (Stace, 2007). The two largest genera, *Combretum* and *Terminalia*, occur in all continents. One mangrove, *Laguncularia*, occurs in America (east and west coasts) and West Africa, and the other, *Lumnitzera*, from East Africa to Australia (Stace, 2007).

The mangrove associate, *Conocarpus*, has a similar distribution to *Laguncularia*, but there is also a second non-mangrove species (*Conocarpus lancifolius*) in northeast Africa and Arabia. *Anogeissus* occurs in both Africa and Asia, but the other seven genera are confined to one continent. There are only three amphi-Atlantic species: *Laguncularia racemosa*, *Conocarpus erectus*, and *Terminalia lucida* (Stace, 2007). In Mexico and Cuba, *C. erectus* generally occupies the last strip of mangrove in areas with less flood and salinity (see Fig. 1), so it can grow under conditions of permanent or seasonal flooding in sites with strong and moderate salinity (Menéndez and Guzmán, 2002; Basañez Muñoz et al., 2008).

In this paper, we restudy two specimens of *M. areniensis* (CTES–PB 2932-1 and CTES–PB 2932-2) that is based on four specimens: the holotype (PB–CTES 4824 and PMP–CTES 1206) and three additional material (CTES–PB 2931-1, CTES–PB 2931-2, and CTES–PB 2931-3). The reviewed, re-described, and illustrated material allowed to discuss its systematic position.

The main aim of the present paper is to redescribe and reassign one fossil taxon to the Combretaceae, subfamily Combretoideae. We have erected a new fossil wood species, which resembles the extant mangrove genera, *Conocarpus* and *Laguncularia*. *Mangroveoxylon areniensis* gen. *et* comb. nov., recovered in the Late Miocene of Ituzaingó Formation and is the first record of fossil wood that indicates coastal marine environment.

2. Geological and paleontological setting

The fossil material was found in Hernandarias locality, Entre Ríos (bank of the Paraná River), and comes from sandy, reddish, brown, sometimes yellowish sediments, and even whitish, generally friable although hardened locally (Fig. 2). This unit corresponds to Ituzaingó Formation (Herbst, 1971; Iriondo and Rodriguez, 1973; Brunetto, 2015).

The Ituzaingó Formation outcrops from the left bank of the Paraná River in the Corrientes and Entre Ríos provinces (Argentina), as well as along several rivers and tributary streams. The fossil records are not frequent in sections of Corrientes, only plant debris, freshwater invertebrates and palynomorphs. Nevertheless, in the Entre Ríos province, the fossil record of vertebrates is extensive. Brunetto et al. (2013) recognize the existence of a lower member of the Ituzaingó Formation in the Toma Vieja locality (Entre Ríos province), formed by lower members that include well-established levels of stratified fine gravel, selected and stratified sands, as well as clay stratum, principally where the fossil record is concentrated. The age of lower members is assigned to Late Miocene by Brunetto et al. (2013). This hypothesis is based on biochronological evidence (fossil mammals) and the stratigraphic position of the new recognized unit, which exceeds radiometric levels of Paraná Formation.

The formation presents rich and diverse paleoflora, mostly found in Entre Ríos (Late Miocene?, according to Brunetto et al., 2013) and Corrientes provinces (Pliocene, see Contreras et al., 2019). The leaves, palynomorphs, and woods record are characterized by ferns (Cyatheaceae, Lycopodiaceae, Polypodiaceae, Azollaceae, Pteridaceae, Hymenophyllaceae), the conifer Podocarpaceae, and several; flowering plants families (Winteraceae, Lauraceae, Amaranthaceae, Chenopodiaceae, Polygonaceae, Ulmaceae, Moraceae, Sapotaceae, Euphorbiaceae, Fabaceae, Myrtaceae, Proteaceae, Celastraceae, Aquifoliaceae, Anacardiaceae, Meliaceae, Rutaceae, Malpighiaceae, Compositae, Poaceae, Cyperaceae, and Arecaceae) (Anzótegui and Lutz, 1987; Franco, 2012; Franco and Brea, 2013; Franco et al., 2013). The phytolith assemblages reported in Ituzaingó Formation of the Corrientes province are characterized by herbaceous and herb/arboreal dicot, megathermal/mesothermal grasses (Panicoideae, Chloridoideae, and Danthonoideae), and Panicoideae and Erthroideae that suggest a subtropical climate with marked seasonality (Contreras et al., 2019).

3. 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. The reference lists by Gregory (1994) and Gregory et al. (2009) were used. Terminology proposed by Tortorelli (1956) and Carlquist (2001) was also considered.

For the identification of fossil wood samples and comparison of fossil materials with extant and fossil species, the InsideWood web site (InsideWood, 2004 onward; Wheeler,

2011) and descriptions by Metcalfe and Chalk (1950), van Vliet (1978, 1979), Silva and Espinoza (1995), León (2001), and Jantsch et al. (2018) were consulted.

The material was studied with a Nikon eclipse E200 light microscope and Nikon eclipse E200POL, and photomicrographs were taken with a Nikon Coolpix S4 and DS-3M digital camera. Systematic assignment follows the APG IV (2016). The quantitative values provided in 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 elements through photomicrographs.

The material was prepared for scanning electron microscopy (SEM) by cutting a 2 cm^3 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 "Dr. Domingo Liotta," CICYTTP (CONICET-Prov. E.R.-UADER), Diamante, Entre Ríos, Argentina.

The holotype fossil specimen and microscope slides are housed at the Colección Paleontológica de la UNNE "Dr. Rafael Herbst," Facultad de Ciencias Exactas y Naturales y Agrimensura, Universidad Nacional del Nordeste, Corrientes, under acronyms CTES-PB for wood specimen and CTES-PMP for slides.

4. Results

4.1. Systematic paleontology

Orden Myrtales Reichenbach

Familia Combretaceae R. Brown, nom. cons.

Genus *Mangroveoxylon* Moya *et* Brea gen. nov.

Species *M. areniensis* (Lutz) Moya *et* Brea gen. nov. et. comb. nov.

Basionym. *M. areniensis* Lutz, 1979: 49–51, figs. 13–15.

Generic diagnosis: Diffuse-porous wood. Vessels mostly solitary and radial multiples. Simple perforation plates. Intervessel pits alternate, bordered, and vestured. Rays heterocellular with cells mixed throughout the ray; uniseriate and biseriate rays. Axial parenchyma apotracheal diffuse and axial paratracheal vasicentric. Fibers minute, simple bordered pits, and nonseptate and septate. Prismatic crystal presents. Radial vessels presents.

Etymology: The generic epithet is derived from the mangrove word, chosen for the affinity of the fossil wood with mangrove species.

Mangroveoxylon areniensis (Lutz) Moya and Brea gen. nov. et comb. nov.

(Figs. 3, A–H; 4, A–N)

Specific diagnosis: Growth rings are distinct, demarcated by marginal parenchyma, and sometimes by compressed fibers. Vessels mostly solitary, radial multiples of 3–7 cells, also tangential multiples, and in clusters. Rays heterocellular with procumbent, square, and upright cells mixed throughout the ray, commonly uniseriate, rarely biseriate. Fibers minute, simple-bordered pits, nonseptate, and septate. Axial parenchyma apotracheal diffuse and axial paratracheal vasicentric, and confluent. Disjunctive ray parenchyma cell walls. Prismatic crystals in square and upright ray cells.

Holotype: CTES–PB 2932-1 (wood specimen) and CTES-PMP N° 3645 al 3647 (three slides).

Isotype: CTES–PB 2932-2 (wood specimen) and CTES-PMP N° 3648 al 3650 (three slides).

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.

Type locality: Hernandarias city, Entre Ríos province, Argentina

Stratigraphic horizon: Ituzaingó Formation

Age: Late Miocene?

4.2. Taxonomic comments on the Menendoxylon areniensis species

Menendoxylon areniensis had been assigned by Lutz (1979) to Leguminoseae-Mimosoideae with close relations to Piptadenia group. *M. areniensis* was described based on four specimens (CTES–PB 4824 with one specimen and CTES–PB 2932 as additional material with three specimens; see Lutz 1987; p. 128). In this paper, we always refer to the study of CTES–PB 2932 specimen. The new description is based on new thin section slides. The specimens, CTES–PB 2932-1 and CTES–PB 2932-2, are reviewed and redescribed, with a new affiliation proposed to species of the family Combretaceae.

4.3. Description

Growth rings are distinct, slightly defined by marginal parenchyma and sometimes by compressed fibers (Fig. 3, A–D). Diffuse-porous wood (Fig. 3, A). Vessels are mostly solitary (50%), in radial multiples of 2 elements (31%), in radial multiples of 3 and 4–7 elements (10, 5% and 6, 5%, respectively), few clusters (1%) and tangential multiples (1%). Perforation plates are exclusively simple (Fig. 4, A–B). Intervessel pits are alternate, bordered, and vestured (Fig. 4, C–E) with branched terminations forming a network that covers the opening of the pit (=branched vestures, see Fig. 5), 6 (4–7) µm in diameter. Vessels are circular to oval in outline, with thin to thick walls, and 7 (5–12) µm in diameter. Mean tangential vessel diameter is 69 (26–103) µm and mean radial vessel diameter is 72 (22–123) µm. Mean vessel density is 33 (14–52) vessels/mm^2. Mean vessel element length is 150 (76–329). Tyloses and gums occur (Fig. 4, F). Fibers are somewhat circular to oval, sometimes angular, tangentially flattened, particularly when at the end of the growth ring (Fig. 3, A–D). The fibers are thick walled, 9 (6–13) mm thick, minute with a mean diameter of 3 (1, 5–4) µm, are septate and nonseptate with simple bordered pits (Fig. 4, G). Axial parenchyma apotracheal diffuse. Axial paratracheal vasicentric is scarce, in a row of 1–2 cells round vessels, and confluent. The vasicentric parenchyma cells are flattened to conform to the vessels' wall; the remaining are variable in shape but often the widest radially (Fig. 3, C–D). Axial paratracheal vasicentric septate of 4–7 cells per axial parenchyma strand (Fig. 4, H–I). Scalariform bordered pits in axial parenchyma cells (Fig. 4, I–J). Disjunctive ray parenchyma cell walls (Fig. 4, A). Rays heterocellular with procumbent, square, and upright cells mixed throughout the ray are fairly numerous 9 (5–13) per mm, and linear (Fig. 4, K–M). Rays are exclusively uniseriate and some are with biseriate portions (Fig. 4, K). The mean height of rays is 181 (94– 378) µm with 14 (6–27) cells high and are very thin with a mean width of 18 (13–35) µm. The cells of rays are radially elongated, occasionally compressed near vessels (Fig. 3, F). Prismatic crystals in square and upright ray cells, some in procumbent cells (Fig. 3, F), and in axial parenchyma cells are scarce (Fig. 3, G–H). "Radial vessels" occur (*sensu* van Vliet 1979; Fig. 4, N).

5. Discussion

Samples, CTES-PB 2932-1 and 2932-2, previously assigned with affinity to the genus *Piptadenia* by Lutz (1979) were redescribed, and a new affiliation with affinity to mangrove species of the family Combretaceae is proposed, *Mangroveoxylon areniensis* (Lutz) Moya and Brea gen. nov. et comb. nov. The characteristic of heterocellular rays with procumbent, square, and upright cells mixed throughout the ray is a diagnostic characteristic of fossil species. Although extant species, *Piptadenia excelsa*, present heterocellular rays, the square and upright cells are found to be marginal to the body of the ray of procumbent cells.

5.1. Comparison with extant taxa

The wood anatomy of family, Combretaceae, is characterized by diffuse-porous to ring-porous wood; diameter of vessels is between 50–280 µm; vessels are mostly solitary with radial multiples of 4 to several cells; mostly 5–20 vessels/mm^2, simple perforation plates, intervessel pits alternate and vestured, tyloses and gums occur, and a height of vessels from 300 to 500 µm. Fibers are septate in some genera (*Conocarpus*) and have medium to very thick walls. Axial parenchyma is paratracheal predominantly, aliform to confluent. Rays are uniseriate, some with biseriate portions in most genera; mostly 8–12 rays per mm. Rays are homocellular and heterocellular. Crystals present in axial parenchyma and cells of rays (Metcalfe and Chalk, 1950; León, 2001).

Materials under study have a close relationship with Combretoideae, and are anatomically related by the presence of: diffuse-porous wood, vessels solitary, and/or in radial multiples, generally uniseriate rays, sometimes 2–3 seriate rays, heterocellular to homocellular, axial parenchyma paratracheal scarce, confluent, marginal, and diffuse rare, presence of fibers: septate and nonseptate, and crystals with variable forms in cells of rays and axial parenchyma cells.

The intervessel pits of *Mangroveoxylon areniensis* (Lutz) Moya and Brea gen. nov. et comb. nov. correspond to Type B according to van Vliet (1978) with an intermediate shape between 2 and 3 (see Fig. 5 modified of van Vliet, 1978). Type B is a pit type, in which ornaments ("Trunk-like") are united and branch dichotomically into several extensions or finer branches. From the inside of vessels, a compact branch can be seen loosely placed or highly separated with ornaments of roughly equal thickness. In Type B ornamentation with Form 2, most ornaments (trunks) are thick and elaborately branched. In Form 3, ornaments barely branch. The ornament of Type A with Form 1 is only in the genus *Strephonema*, and the remaining genera of family Combretaceae presents vestured pits of Type B with Form 2 and/or 3 (van Vliet, 1978).

Van Vliet (1979) defines terminal cells of the rays (Fig. 4, N) as special elements of the rays, which appear in some genera of Combretaceae, and are of diagnostic value for the genera within subtribe Combretinae. These cells are connected to a very narrow axial vessel or with vascular tracheids through a perforation. They are called "radial vessels" and are found exclusively in uniseriate rays or in uniseriate tails of multiseriate rays. They are not different from a normal ray cell, but also have some typical vessel characteristics such as bordered, vestured, and alternate pits besides parenchyma cells.

The presence or absence of growth rings is not a diagnostic character to define the genera of family Combretaceae. In some genera, such as *Lumnitzera*, growth rings have only been found in some parts of the studied samples. According to van Vliet (1979) and Silva and Espinoza (1995), *Conocarpus erectus* presents growth rings demarcated by parenchyma cells and compressed fibers. Other studies demonstrated the presence of growth rings in mangrove species (Duke et al., 1981; Sousa et al., 1982; Carreras, 1988) and the formation of annual rings, but only in species of the genus *Rhizophora* (*R. mangle* and *R. mucronata*) (Menezes et al., 2003; Verheyden et al., 2004a, b, 2005). Sousa et al. (1982) and Carreras (1988) describe the presence of distinct growth rings in *L. racemosa* trees from the northeast of Brazil and Cuba. Tomlinson and Craighead (1972) concluded that *Laguncularia racemosa* does not form growth rings in mangroves of South Florida. According to Duque Estrada et al. (2008), the growth rings in *L. racemosa* were scarcely distinct on microscopic examination, but they were highly distinguishable macroscopically. Consequently, the presence or absence of growth rings would not be a diagnostic value to differentiate other mangrove species (Duque Estrada et al., 2008).

5.2. Mangrove fossil species

There is an extensive paleobotanical record for the family Combretaceae that includes wood, leaves, flowers, fruits, and pollen from the Middle Cretaceous onward (c.100 Ma.). All these are attributed to current or fossil genera based on extant genera (Stace, 2007; Gregory et al., 2009).

Regarding the fossil record of mangrove species, it includes leaves, flowers, wood, and fruits, but nevertheless, it is not very extensive. According to Plaziat (1995), precise records of ancient mangroves mainly rely on pollen grains, fruits, and logs transported. In addition, decaying wood in this environment produces acidic peats or sediments rich in organic matter in which the diagnostic remains may be scarce or absent. This generates an incomplete and generally inaccurate knowledge of fossil mangroves (Plaziat, 1995).

The mangrove genera present in the American continent, *Laguncularia*, *Conocarpus*, and *Pelliciera*, may have had a western Gondwanan origin (Exell and Stace, 1972; Raven and Axelrod, 1974). *Laguncularia* and *Pelliciera* are monotypic, and there is no fossil record of these genera outside of America and West Africa. *Conocarpus erecta* L. is distributed in the mangroves on both sides of the Atlantic, and there are no fossil records outside its area of current distribution (Graham, 1964). One other species of *Conocarpus*, *C. lancifolius* Engl. is distributed in the fluvial valleys of the highest areas of northern Somalia, East Africa (Graham, 1964). Leaves of *Laguncularia* and *Conocarpus* are reported from the Eocene of southeastern North America (Berry, 1924, 1930), and fossil *Laguncularia* pollen is reported from the Miocene of the Mexican Gulf Coast (Graham, 1976). In addition, for the Cuban Pleistocene, Berry (1934) mentions the presence of *Conocarpus* sp.

5.3. The paleoecological and paleogeographic significance of Mangroveoxylon

The set of wood anatomical characteristics in *Mangroveoxylon areniensis* (Lutz) Moya and Brea gen. nov. et comb. nov., suggests an adaptation to environmental variability: numerous vessels (mean, 33 vessels/mm^2), small vessel diameter (mean, 69 µm), and low vessel length (mean, 150 µm). Furthermore, *M. areniensis* (Lutz) Moya and Brea gen. nov. et comb. nov. have a low vulnerability index (VI = 2), which corresponds to the adaptation of these species that are subject to high water stresses and strong negative pressures typical of a brackish environment. To withstand the salinity levels, these species are characterized by high vessel frequencies, small vessel diameter, and low vessel length, which allow water to pass efficiently (Yáñez-Espinosa et al., 2004; Schmitz et al., 2006; Yáñez-Espinosa and Flores, 2011).

The mangrove species are characterized by the vessel density increases from low- to high-salinity areas, from high to low flooding level in most of them, and from a temporal to prolonged flooding period (Schmitz et al., 2006). The water stress effect causes the reduction of cell size in these species, characterized by the short length of vessel element (Tyree and Jarvis, 1982).

The Nearest Living Relative, *C. erectus* is a species associated with the mangroves and classified as pseudo mangrove or peripheral species (Menéndez and Guzmán, 2002; Basañez Muñoz et al., 2008). *C. erectus* is located further inland in areas that are within the limits of the highest tides with less flood and salinity, so it can grow under conditions of permanent or seasonal flooding in sites with strong and moderate salinity (Tomlinson, 1986; Menéndez and Guzmán, 2002; Basañez Muñoz et al., 2008, see Fig. 1). This adaptation would explain the presence of mangrove species during the Late Miocene even after complete marine regression.

Similar to other plants that are adapted to coastal environments, ocean currents can carry out the dispersion of mangroves (Rico Gray, 1993). The route of migration of mangroves to America through the Tethys Sea is supported by paleobotanical evidence. The fossil records in Europe and in the region where the Tethys Sea was found suggest that this area was a very important dispersion passage in the distribution of flora (see Rico Gray, 1993 and cited herein). The mangrove species had to advance and develop along the coasts of the Tethys Sea, crossing the Atlantic Ocean between Spain and the United States, or between Africa and South America. This hypothesis is reinforced by the distribution of the same species in America and West Africa. The mangroves of America had a wider geographical distribution in the past, but their reduction seems to be related to the influence of climate on soil salinity between the Miocene and Pliocene (Jiménez, 1984; Addicot, 1966).

Crassostrea rhizophorae Guilding, 1828 is a species of oysters of the Ostreidae family and they live fixed to the roots of *Rhizophora mangle* (Nikolic, Bosh, and Alfonso, 1976) on the Atlantic coast where temperatures vary between 19°C and 32°C (Nikolic, 1969; Rodríguez Romero and Tello Cetina, 2011). This fossil species of oyster was registered for the Late Miocene (9.47 Ma, Pérez, 2013a; 7.50–6.00 Ma, del Río et al., 2018) in the Parana Formation from northeastern Argentina (Muravchik et al., 2004; Pérez et al., 2013). This record probably indicates the presence of mangrove species or trees adapted to marine conditions during the last marine transgression when temperature conditions allowed the development of these environments.

This leads us to think that if favorable conditions, such as high temperatures, remained during the Miocene, it is possible that it allowed mangrove species to colonize the coasts of what was then the "Paranaense Sea." In addition, it assumes that seawater temperatures were much higher than the current at the same latitude.

6. Conclusions

This is the first complete anatomical description of a fossil wood related to mangrove species. Anatomical characteristics of *Mangroveoxylon areniensis* gen. nov. et. comb. nov. and the affinity give us the idea that the fossil like its near living relative (*Conocarpus erectus*) supports low levels of salinity, so the species could survive a long period of time until its extinction even after a complete retreat from the Paranaense Sea. *M. areniensis* gen. nov. et. comb. nov. would have developed near salty water on account of the marine transgression in the coasts of the Paranaense Sea or at least in coastal lagoons together with estuary marshes and freshwater wetlands.

It is the only mangrove record more widespread to the south, and the only one that could have existed in Argentina. The environment could resemble a tropical environment with its own tropical species and associated with coastal environments developing at different levels of the land.

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Figure Captions

Fig. 1. The general illustration of mangrove zonation depicts a pattern that extends from the shore to usually higher in elevation. *Conocarpus erectus*, considered as a pseudo-mangle, is usually found in areas seldom inundated by tidal waters.

Fig. 2. Map of Hernandarias locality, Entre Ríos province (bank of the Paraná River, Argentina) showing the location of the fossil wood.

Fig. 3. A–H, ***Mangroveoxylon areniensis*** gen. nov. and comb. nov. **A–B=** optical microscope images and **E–I=** petrographic microscope images. **A–C:** Transverse section of diffuse-porous wood, and narrow growth rings slightly defined by marginal parenchyma and sometimes by compressed fibers (white arrows); paratracheal and marginal parenchyma cells (black arrows). **D:** Transverse section and detail of axial parenchyma confluent (black arrow and white border line). **E:** Radial longitudinal section and detail of fibers with simple bordered pits. **F:** Transverse section and detail of septate fibers (arrow) **G:** Radial longitudinal section and prismatic crystals in square and upright ray cells. **H–I:** Radial longitudinal section and prismatic crystals in axial parenchyma cells.

Fig. 4. **A–N**, ***Mangroveoxylon areniensis*** gen. nov. and comb. nov. **A–N**, scanning electron microscopy images. **A:** Radial longitudinal section and detail of disjunctive parenchyma cell walls (black arrow) and simple perforation plate (white arrow). **B:** detail of simple perforation plate. **C:** Radial longitudinal section and intervessel pits alternate, bordered, and vestured (white arrows). **D–E:** Radial longitudinal section and intervessel pit pair showing vesturing pits (white arrows). **F**: Tangential longitudinal section and a general view showing tyloses (white arrow) in vessel and heterocellular rays. **G:** Tangential

longitudinal section and fibers with simple bordered pits (white arrows). **H:** Tangential longitudinal section and detail of cells per axial parenchyma strand. **I:** Tangential longitudinal section and scalariform-bordered pits in axial parenchyma cells (white arrow). **J:** Tangential longitudinal section and detail of pits in axial parenchyma cells. **K:** Tangential longitudinal section and detail of uniseriate heterocellular ray with procumbent (black arrow) and square and upright cells (white arrows) mixed throughout the ray. **L:** Radial longitudinal section and detail of heterocellular ray with procumbent (black arrows) and square and upright cells (white arrows) mixed throughout the ray. **M:** Radial longitudinal section and detail of pits in square and upright cells in the ray (black arrow). **N**: Tangential longitudinal section and a general view showing the "Radial vessels" with pits (white arrow).

Fig. 5. Illustration of two types of intervessel pit pairs, showing vesturing pits present mostly in the genera of *Combretaceae* according to van Viet (1978, 1979). **A:** Vestured pit Type B with Form 2 and most ornaments (trunks and white arrows) are thick and elaborately branched (black arrows). **B**, Vestured pit Type B with Form 3 and ornaments (trunks and white arrows) rarely branch (black arrows).

Declaration of Interest

The authors declare that there are no conflicts of interest regarding the publication of this paper.

Declarations of interest: none

Highlights

- Combretaceae fossil Wood (Late Miocene?)
- Ituzaingó Formation: coastal marine environment.
- Redescription of *Menendoxylon areniensis* (Ituzaingó Formation)