

A NEW RECORD OF FOSSIL WOOD OF VOCHYSIACEAE FROM THE LATE PLEISTOCENE (ARROYO FELICIANO FORMATION), ARGENTINA, SOUTH AMERICA

ELIANA MOYA & MARIANA BREA

Facultad de Ciencia y Tecnología, Universidad Autónoma de Entre Ríos, Laboratorio de Paleobotánica, Centro de Investigaciones Científicas y Transferencia de Tecnología a la Producción (CICyTTP-CONICET), Dr. Matteri y España sn, E3105BWA, Diamante, Entre Ríos, Argentina.
li.196@hotmail.com, cidmbrea@gmail.com

ABSTRACT—A new species of *Qualeoxylon* Suguio & Mussa is described from the Late Pleistocene Arroyo Feliciano Formation of the Gualeguay Basin on eastern Argentina. It is the second record of this genus in South America and was previously only known from Late Eocene to Early Miocene (late Pleistocene for some authors) on the Itaquaquecetuba Formation, São Paulo, Brazil. This new fossil species was recovered in the Consorcio Paso Sociedad fossil locality (Federal, Entre Ríos, Argentina). Wood anatomical features suggest a close relationship with Vochysiaceae and is an affinity with the extant genus *Qualea*. This fossil wood is consistent with the warm and humid climate inferred for this region during the upper Pleistocene. The discovery of *Qualeoxylon* in Arroyo Feliciano Formation supports the hypothesis that the Vochysiaceae was more widespread in the past than today.

Key words: wood anatomy, Vochysiaceae, *Qualeoxylon*, *Qualea*, late Pleistocene, Arroyo Feliciano Formation.

RESUMO—Uma nova espécie de *Qualeoxylon* Suguio & Mussa é descrita para a Formação Arroyo Feliciano Bacia Gualeguay, Pleistoceno final no leste da Argentina. É o segundo registro desse gênero na América do Sul, até agora só conhecido para o Eoceno Superior a Mioceno Inferior (Pleistoceno Superior para alguns autores) da Formação Itaquaquecetuba, São Paulo, Brasil. O espécime aqui estudado foi coletado na localidade fossilífera Consorcio Paso Sociedad (Federal, Entre Ríos, Argentina). As características anatômicas da madeira sugerem uma relação com a família Vochysiaceae e uma afinidade com o atual gênero *Qualea*. Esta madeira fóssil condiz com o clima quente e úmido inferido para esta região durante o Pleistoceno final. A descoberta de *Qualeoxylon* na Formação Arroyo Feliciano apoia a ideia de que a família Vochysiaceae foi mais amplamente distribuída no passado que nos dias atuais.

Palavras-chave: anatomia da madeira, Vochysiaceae, *Qualeoxylon*, *Qualea*, Pleistoceno final, Formação Arroyo Feliciano.

INTRODUCTION

Vochysiaceae A.St.-Hil. is a Neotropical family belonging to the Order of Myrtales, composed of trees and shrubs, includes eight genera and *ca.* 200 species. The components are commonly distributed in lowland tropical America, Mexico to the south of Brazil and, are well represented in the savanna areas in the Cerrado, Central Brazil. Most species occur in tropical America and only two are distributed in West Africa (Huber, 1909; Quirk, 1980; Heywood, 1985; Litt & Cheek, 2002; Sajo & Rudall, 2002; Carmo-Oliveira & Lange de Morretes, 2009). This family has been divided into two tribes: Vochysieae Dumortier, 1829 with five genera: *Callisthene* Martius, 1826 (11 spp.), *Qualea* Aublet, 1775 (*ca.* 60 spp.), *Ruizterania* Marcano-Berti, 1969 (15 spp.), *Salvertia* Saint-Hilaire, 1820 (1 sp.) and *Vochysia* Aublet, 1775 (*ca.* 140 spp.) and Erismeeae Dumortier, 1829 with three genera: *Erisma* Rudge, 1805 (16 spp.), *Erismadelphus* Mildbraed, 1913 (2 spp.) and *Korupodendron* Litt & Cheek, 2002 (1 sp.) (León, 2003; Hiroaki Shimizu, 2009). The two latter are distributed

in tropical Africa (Metcalf & Chalk, 1950; León, 2003; Kawasaki, 2007; Carmo-Oliveira & Lange de Morretes, 2009; Hiroaki Shimizu, 2009; Rissi & Cavassan, 2013).

Traditionally, the Vochysiaceae were included inside the Polygalales (Hutchinson, 1967; Cronquist, 1968; Takhtajan, 1969; Quirk, 1980; Kawasaki, 2007) but other studies do not agree with such affinity (see more in Conti *et al.*, 1996, 1997).

All families included in the Myrtales are characterized by a combination of two anatomical features: bordered vested intervessel pits of the secondary xylem and bicollateral bundles in the primary stem, resulting in the presence of intraxylary or internal phloem in woody stems (Van Vliet & Baas, 1984). These wood anatomical features combined with other characters, anatomical (Quirk, 1980; Van Vliet & Baas, 1984; Baas *et al.*, 2000), embryological (Tobe & Raven, 1983; Boesewinkel & Venturelli, 1987; Hiroaki Shimizu, 2009), and DNA analysis (Conti *et al.*, 1996, 1997) suggested that Vochysiaceae would fit better inside the Myrtales (Van Vliet & Baas, 1984; Carlquist, 2001; Kawasaki, 2007).

The Vochysiaceae is included inside of a group of families who have Anfi-Atlantic distribution (Figure 1), which supports the argument of both long-distance dispersal across the Atlantic as vicariance of western Gondwana biota by diffusion through the bottom of the Atlantic ocean (Sytsma *et al.*, 2004).

The present paper describes a new permineralized wood that has diagnostic characters of the Vochysiaceae. This Argentinean fossil wood, found in the Late Pleistocene Arroyo Feliciano Formation of Argentina, is more related with the extant *Qualea*. The combination of diagnostic anatomical features allows their assignment to a new species of the genus *Qualeoxylon* Suguio & Mussa, 1978.

STUDY AREA

The fossil wood was recovered from the basal levels of the Arroyo Feliciano Formation in the fossil locality Consorcio Paso Sociedad that outcrop near the city of Federal in Entre Ríos Province, Argentina (Figure 2).

This lithological unit was defined by Iriando *et al.* (1985) and represents alluvial and fluvial deposits distributed in the tributaries valleys of the Parana and Uruguay rivers (Entre Ríos, Argentina). The sedimentation was probably developed during the late Pleistocene (Iriando & Kröhling, 2008). During the late Pleistocene more humid conditions prevailed that at present, and it was estimated that the mean annual precipitation (MAP), was ten times larger than the extant rivers (Iriando *et al.*, 1985; Iriando & Kröhling, 2008).

This Formation (2-6 m thick) outcrops mainly along the margins of the Gualeguay River and the major rivers and streams, and constituted the highest terrace in the Entre Ríos Province (Iriando *et al.*, 1985; Iriando & Kröhling, 2008). The sequence is mainly composed of well selected fine sands and whitish to light green silts. It is massive and rarely presents very thin and poorly defined lamination or stratification. At the top of the profile occurs an ash lens (*ca.* 1 m thickness) with marked laminar stratification. At the lowest of the sequence

are abundant manganese nodules and carbonate concretions are very common along the sequence (Figure 3).

This unit is known by the presence of abundant vertebrate fossils: *Toxodon platensis*, *Myiodon darwini* and *Lestodon* sp. have been reported by Brunetto *et al.* (2012) and tentatively correlated the Arroyo Feliciano Formation with the Bonaerian-Lujanian State/Age of the Buenos Aires Province, Argentina (Brunetto *et al.*, 2012).

MATERIAL AND METHODS

The fossil wood is permineralized by silica and has 44 cm long and 9.5 cm in diameter. Thin sections were made using standard petrographic techniques. The material was thin-sectioned in the three characteristic sections (transverse, tangential longitudinal and radial longitudinal section). The recommendations of the IAWA Lists of Microscopic Features for Hardwood Identification (IAWA Committee, 1989) were used. Terminology proposed by Tortorelli (1956) and Carlquist (2001) was also considered. The bibliographic lists made by Gregory (1994) and Gregory *et al.* (2009) were used.

The identification of the fossil wood and comparison of the specimen to extant and fossil species were done using the InsideWood web site (InsideWood 2004-onwards) and descriptions by Metcalfe & Chalk (1950), Tortorelli (1956), Quirk (1980), Kawasaki (2007). Systematic assignment follows the APG III (2009).

The quantitative values provided in the anatomical descriptions are averages of 25 measurements. The average is cited first, followed by the minimum and maximum values, which are given in parentheses. The UTHSCSA Image Tool program Version 3.0 was used to measure the elements through photomicrographs.

The material was studied with a Nikon Eclipse E200 light microscope and the photomicrographs were taken with a Nikon Coolpix S4 digital camera.

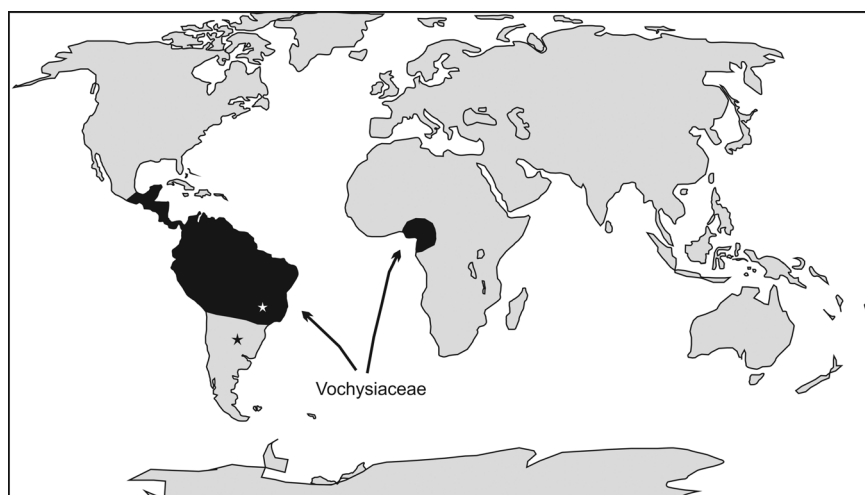


Figure 1. Distribution of extant genera from Vochysiaceae, in Africa and the fossiliferous localities of fossil woods. **Symbols:** ☆, *Qualeoxylon itaquaquecetubense* (Suguio & Mussa, 1978 - Late Eocene to Early Miocene) from River Tietê, Itaquaquecetuba Formation, São Paulo, Brazil; ★, *Qualeoxylon felicianensis* sp. nov. of the late Pleistocene, Gualeguay River, Entre Ríos Province, Argentina (modified from Heywood, 1993; Sytsma *et al.*, 2004; Hiroaki Shimisu, 2009).

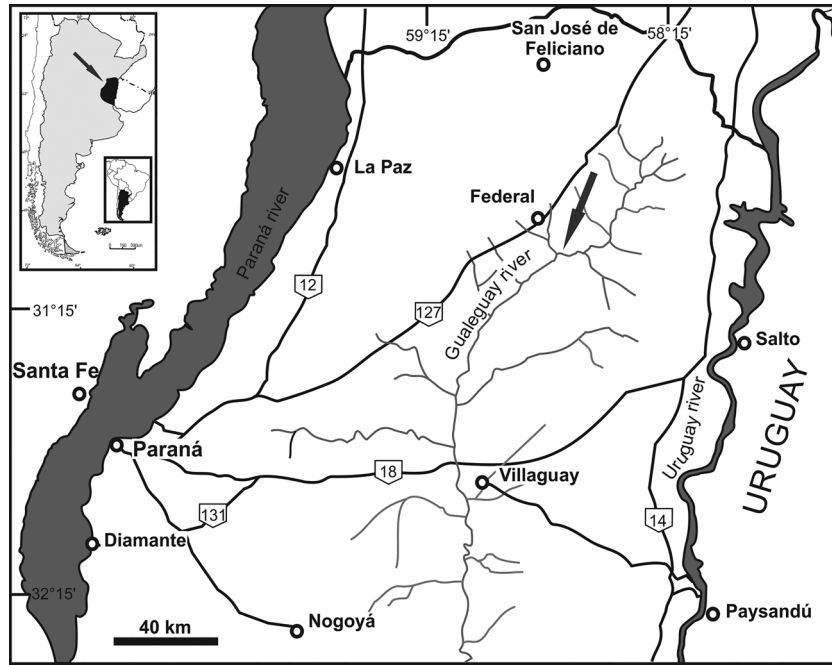


Figure 2. Geographic map location showing the Consorcio Paso Sociedad locality, Entre Ríos, Argentina (black arrow).

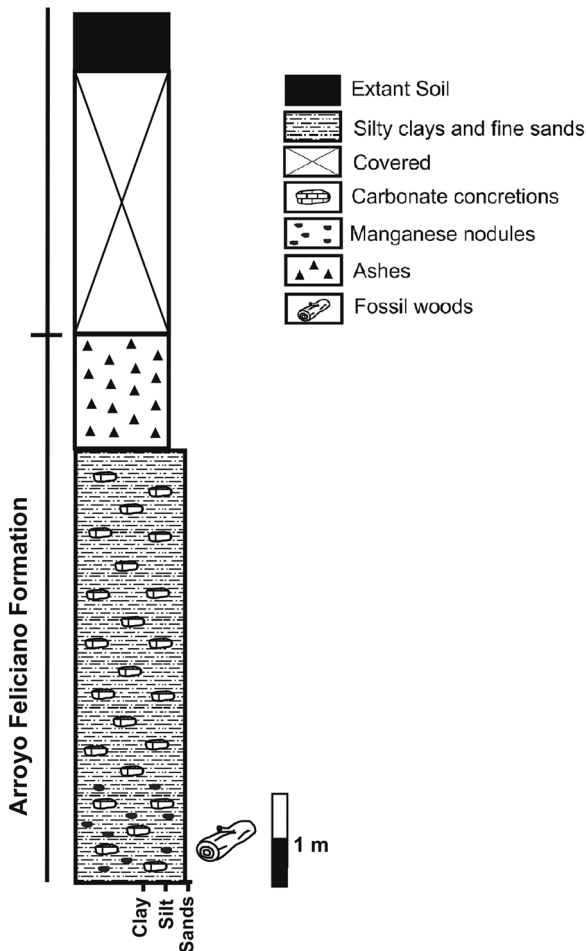


Figure 3. Schematic profile at the Consorcio Paso Sociedad locality where, the fossil wood was collected.

The holotype fossil specimen and microscope slides are kept in Colección Paleobotánica, Centro de Investigaciones Científicas y Transferencia de Tecnología a la Producción (CICyTTP-CONICET), Diamante, Entre Ríos, Argentina, under the acronym **CIDPALBO-MEG 65** and **CIDPALBO-MIC 715**. The isotype was deposited in the Colección Paleontología, Museo de Antropología y Ciencias Naturales “Conscripto Bernardi”, Conscripto Bernardi, Argentina, under the acronym M06.

SYSTEMATIC PALEONTOLOGY

Order MYRTALES Juss. ex Bercht. & J. Presl. 1820
 Family VOCHYSIACEAE A.St-Hil. 1820
 Tribe VOCHISIEAE Dumort., 1829

Qualeoxylon Suguio & Mussa, 1978

Type species. *Qualeoxylon itaquaquecetubense* Suguio & Mussa, 1978.

Qualeoxylon felicianensis sp. nov.
 (Figures 4-5)

Holotype. CIDPALBO-MEG 65, CIDPALBO-MIC 715 (three slides).

Isotype. M06.

Stratigraphic provenance. Arroyo Feliciano Formation.

Age. Late Pleistocene.

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

Etymology. The specific epithet, *felicianensis*, refers to the name of geological formation where this fossil was recovered.

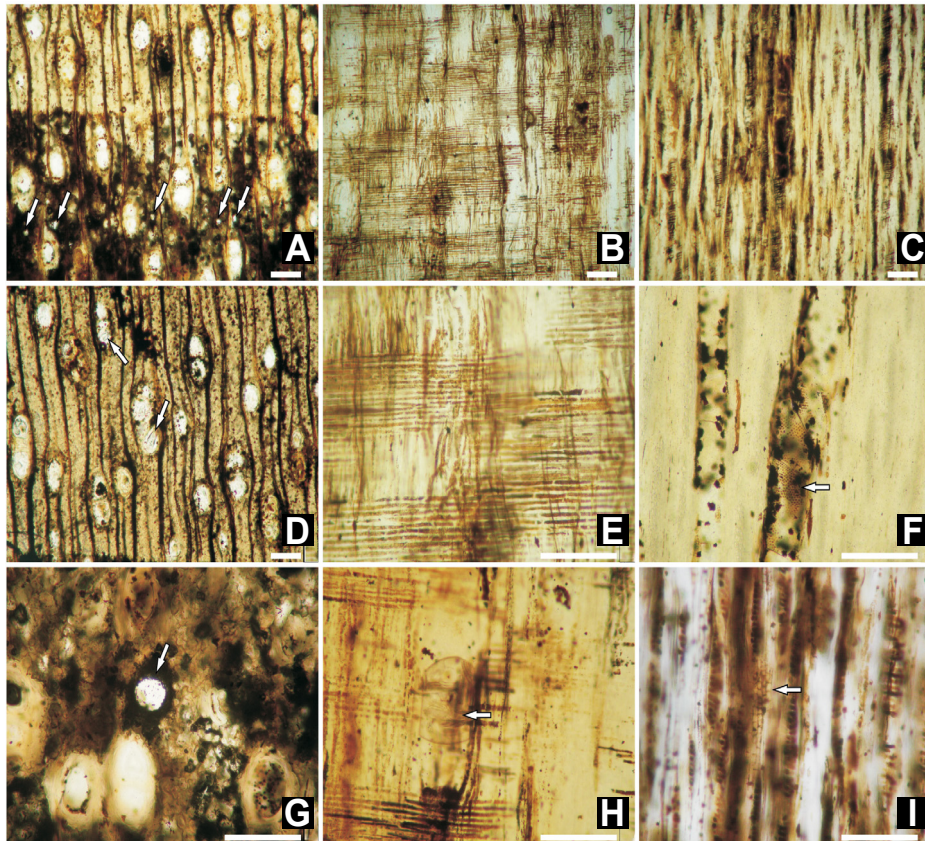


Figure 4. *Qualeoxylon felianensis*, sp. nov. **A**, transverse section, general view. Wood diffuse porous, axial parenchyma vascentric scarce and confluent, and traumatic diffuse axial canals (arrows); **B**, radial longitudinal section, general view. Rays homocellular; **C**, tangential longitudinal section, general view. Rays uniseriate and multiseriate; **D**, transverse section, detail of disposition of vessels and prismatic crystals in vessels (arrows); **E**, radial longitudinal section, detail of homocellular rays; **F**, tangential longitudinal section, detail of intervessel pits bordered (arrow); **G**, transverse section, detail of traumatic diffuse axial canals (arrow), axial parenchyma paratracheal vascentric, confluent; **H**, radial longitudinal section, detail of simple perforation plates (arrow); **I**, tangential longitudinal section, detail of axial parenchyma apotracheal diffuse-in- aggregated (arrow). Scale bars = 200 μm .

Diagnosis. Wood rings boundaries distinct; diffuse porous; vessels solitary, radial multiples of 2-4 cells and some in clusters; exclusively simple perforation plates; intervessels pitting bordered, alternate and vested; homocellular rays, composed of exclusively procumbent cells; 1-3 cells wide; vessel-ray pitting similar to intervessel pitting; axial parenchyma strands 7-16 cells; axial parenchyma paratracheal scanty, vascentric, confluent, aliform and apotracheal diffuse and diffuse-in-aggregated; non-septate and libriform fibers; traumatic diffuse axial canals; crystals in chambered axial parenchyma cells.

Description. In transverse section, growth rings boundaries distinct by fibers compression (Figure 4A). Diffuse porosity. Vessels mostly solitary (42.93%), in radial multiples of 2-4 elements (54.57%) and in clusters (2.52%). Vessel circular in outline in transverse section, with thick walls of 9 (7-11) μm in thickness. Mean tangential diameter of 130 (55-177) μm and mean radial diameter of 94 (62-137) μm . Mean vessel density of 12 (6-21)/ mm^2 (Figures 4A,D,G; 5A). Axial parenchyma paratracheal vascentric scarce, confluent, with very short bands, aliform (Figures 4A,G) and apotracheal diffuse, diffuse-in-aggregated. Fibers rounded to hexagonal

in outline, disorderly and abundant, non-septate, mean diameter of 9 (5-11) μm , with very thin to thick-walled, 3 (2-5) μm in thickness. Prismatic crystals in vessels (Figure 4D). Traumatic diffuse axial canals (Figures 4A,G; 5B). In tangential section, mean vessel elements length of 155 (55-675) μm (Figures 4B,F). Perforation plates exclusively simple with straight to oblique end walls (Figures 4H; 5D). Intervessel pits large, bordered, alternate to opposite, vested, oval to hexagonal in outline with mean diameter of 13 (10-16) μm (Figures 4F; 5E,F,O,P). Rays uniseriate and multiseriate (2-3). Mean height of 267 (122-485) μm and 20 (10-36) cells high. Mean width rays of 27 (12-45) μm . Rays few, 3 (2-5) per linear mm (Figures 4C; 5K). Axial parenchyma apotracheal diffuse and diffuse-in-aggregated (Figures 4I; 5G,H). Axial parenchyma in strands of 11 (7-16) cells. Prismatic crystals in chambered axial parenchyma cells, one crystal per chamber (Figures 5I-L,Q). Possibly gums and dark deposits present. Traumatic axial canals with epithelial cells of axial canals (Figures 5C,M).

In radial section, rays homocellular, composed exclusively of procumbent cells, vessel-ray pits similar to intervessel pits, bordered, alternate and polygonal (Figures 4B,E; 5N).

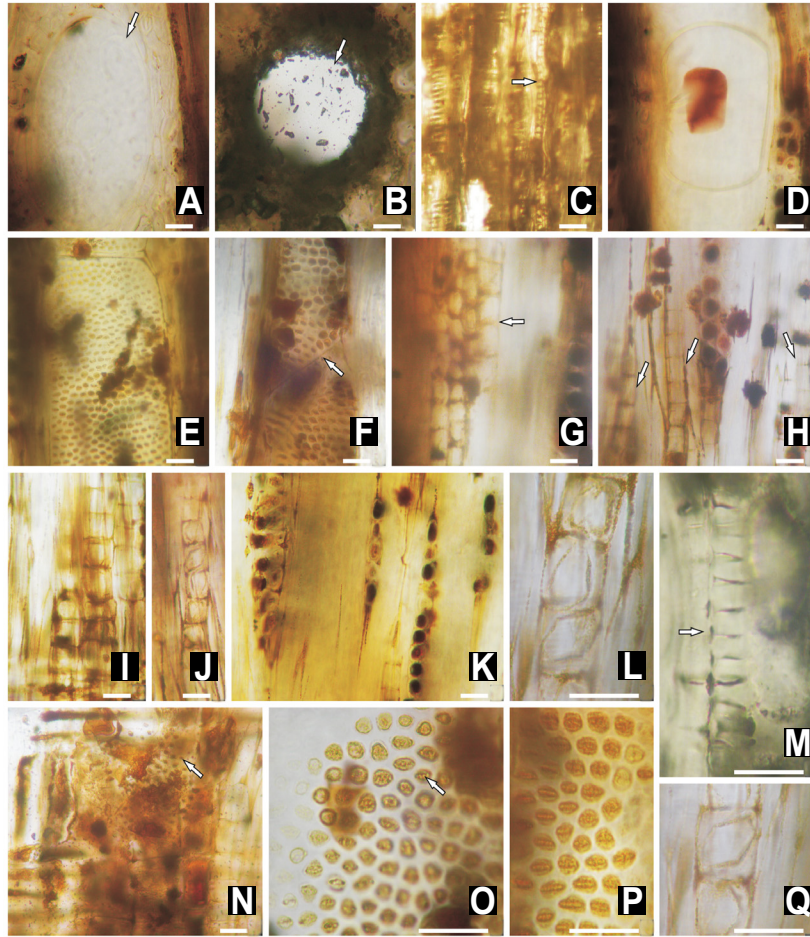


Figure 5. *Qualeoxylon felianensis* sp. nov. **A**, transverse section, detail of solitary vessel; **B**, transverse section, view of traumatic axial canal show epithelial cells (arrow); **C**, tangential longitudinal section, detail of traumatic axial canal (arrow); **D**, radial longitudinal section, simple perforation plates; **E**, tangential longitudinal section, detail of intervessel pits alternate to opposite; **F**, tangential longitudinal section, detail of intervessel pits with straight to oblique end walls (arrow); **G**, tangential longitudinal section, detail of axial parenchyma apotracheal diffuse-in-aggregated (arrow); **H**, tangential longitudinal section, detail of axial parenchyma apotracheal diffuse (arrows); **I-J**, radial longitudinal section, detail of prismatic crystals in chambered axial parenchyma cells, one crystal per chamber; **K**, tangential longitudinal section, detail of rays uniseriate and multiseriate (2-3); **L, Q**, tangential longitudinal section, detail of prismatic crystals in chambered axial parenchyma cells; **M**, tangential longitudinal section, detail of traumatic axial canals showing epithelial cells of axial canals (arrow); **N**, radial tangential section, detail of vessel-ray pits similar to intervessel pits (arrow); **O-P**, tangential longitudinal section, detail of intervessel pits bordered and vested (arrow). Scale bars = 20 μ m.

DISCUSSION

Comparisons with extant species

The combination of diagnostic anatomical features indicate that the fossil wood described here have a great affinity with Vochysiaceae (Metcalf & Chalk, 1950; Quirk, 1980; Kawasaki, 2007). This specimen is the first fossil wood with affinity to this family from Argentina.

Vochysiaceae is characterized by the presence of diffuse porous growth rings usually absent or indistinct, intervessel pits vested, only libriform fibers, banded axial parenchyma (apotracheal in *Callisthene*, *Erisma*, *Erismadelphus*, paratracheal in *Qualea*, *Salvertia*, *Vochysia*) and intercellular canals. Rays homocellular (*Qualea* and *Salvertia*) or heterocellular (*Callisthene*, *Erisma*, *Erismadelphus*, *Vochysia*); all uniseriate in *Erismadelphus*, predominantly multiseriate in *Callisthene* and *Qualea*, and often predominantly uniseriate

in *Salvertia*, *Vochysia*, and *Erisma* (Quirk, 1980). Included phloem is present only in *Erisma* and *Erismadelphus* (Kawasaki, 2007). The most diagnostic characters for the family are: intervessel pits vested, exclusively libriform fibers, banded axial parenchyma and traumatic intercellular canals (Metcalf & Chalk, 1950; Quirk, 1980). *Qualea* differs from the other six genera of the Vochysiaceae family in anatomical characters as: diffuse porous, growth rings absent to distinct, vessels mostly solitary, some in radial multiples of 2-3 elements, largest vessel diameters, 220 (100-350) μ m; length vessels, 490 \pm 76 (140-1,175) μ m; intervessel pits, 6 (3-12) μ m; vessel-ray pitting similar to intervessel pits; fibers some septate, with a diameters of 16.3 (11-22) μ m; rays multiseriate (70%) and uniseriate (30%), typically homocellular and heterocellular composed by procumbent cells and one or two rows of square or upright cells in some rays of *Q. albiflora*, *Q. dinizii*, and *Q. acuminata* only; uniseriates with some procumbent, mostly

square and upright cells; height of tallest rays, 678 (300-1,860) μm and 14 (10-90) cells tall; ray width, 45 (20-110) μm and 3 [2 to 4 (rare)] cells wide; parenchyma paratracheal vascentric to aliform and strongly confluent in some species, apotracheal parenchyma diffuse to diffuse-in-aggregates or with some very short bands (*Q. acuminata*, *Q. dinizii*, *Q. homosepala*, *Q. grandiflora*, *Q. impexa*, *Q. paraensis*, *Q. rosea*, *Q. retusa*, *Q. sellowii*); crystals common in the axial parenchyma, few in the rays; silica and traumatic axial gum ducts fairly common (Quirk, 1980).

León (2003) postulated that the wood anatomy of *Qualea* and *Ruizterania* is very similar and suggests that it is not possible to differentiate both genus using anatomical features. This study is consistent with statements by Sajo & Rudall (2002) about their study foliar anatomy and molecular data according to Litt (1996).

In his paper, Kawasaki (2007) includes in *Qualea* but does not formalize the synonymy. So far there is no synonymy of species names *Ruizterania* under *Qualea*, so both genera are considered separately (Hiroaki Shimizu, 2009). Most studies about Vochysiaceae are directed to the genus *Erisma* and *Vochysia* and there is few information of the xylem anatomy of *Qualea* and *Ruizterania*. *Ruizterania* differs from *Qualea* by the presence of silica in radial cells and absence of prismatic crystals, but the studies of León (2003), show that these are not good features for separation. According to the present discussion, the fossil wood on study is more similar to *Qualea* by anatomical affinity and also by the extant geographical distribution (Table 1).

Qualea has ca. 60 species distributed from Central America to South America (Sajo & Rudall, 2002; Kawasaki, 2007), which, according to Stafleu (1953), were included in two

subgenera: subg. *Qualea* with four sections (*Trichanthera*, *Qualea*, *Costatifolium*, *Polytrias*) and subg. *Amphilochia* (Mart.) Stafleu. Section *Trichanthera* was recognized as a separate genus, *Ruizterania* Marcano-Berti (1969). These sections present different pattern in the foliar anatomy (Sajo & Rudall, 2002). *Qualea* today is present in the Misiones Province from Argentina (Flora Argentina, 2012; Grandtner & Chevrette, 2013).

Comparisons with fossil species

Only one fossil wood of Vochysiaceae is known in the world: *Qualeoxylon itaquaquecetubense* described by Suguio & Mussa (1978) and recovered in the alluvial deposits of the Tietê River, Itaquaquecetuba Formation, São Paulo Basin, São Paulo, Brazil. These deposits were assigned to the Late Pleistocene (Suguio & Mussa, 1978) but the age is very controversial in the literature. Studies based on palynology have assigned this unit from the Late Eocene to Early Miocene (Lima *et al.*, 1991; Yamamoto, 1995; Santos *et al.*, 2010).

The anatomical characteristics of the fossil wood agree with the features described for the genus *Qualeoxylon* (Suguio & Mussa, 1978). The features of *Qualeoxylon* are: diffuse porous; vessels solitary and in radial multiples of 2-4 elements; medium to large-sized in cross section; 3-4 vessels/ mm^2 ; perforation plates exclusively simple; intervessel pits alternate and vested; axial parenchyma paratracheal vascentric and confluent; prismatic crystals in chambered axial parenchyma cells; rays homocellular; mostly triseriate, occasionally uniseriate and biseriate; ray height 12-15 cells; 8-9 rays per mm^2 ; fibers non-septate with simple pits. The fossil wood described herein differs from *Qualeoxylon itaquaquecetubense* (Table 1) by presence of 6-21 vessels/ mm^2 , axial parenchyma paratracheal aliform and apotracheal

Table 1. Comparison between extant and fossil species with affinity to *Qualeoxylon felicianensis* sp. nov. **Abbreviations:** **A**, absent; **Al**, aliform; **At**, alternate; **ACD**, axial canals diffuse; **C**, confluent; **D**, diffuse; **D-A**, diffuse-in-aggregates; **I/A**, indistinct or absent; **ICTO**, Inter-cellular canals of traumatic origin; **L-Al**, lozenge-aliform; **P**, present; **Pc**, all ray cells procumbent; **Pc-US**, procumbent with one row of upright and/or square marginal cells; **S**, simple; **SIP**, similar to intervessel pits; **V**, vascentric; **W-Al**, winged-aliform.

Species	Growth ring	Porosity	Perforation plates	Intervessel pits	Vestured pits	Vessel-ray pitting	Tangential diameter	Vessel mm^2	Tyloses and deposits	Apotracheal parenchyma	Paratracheal parenchyma	Width, rays	Cellular composition, rays	Intercellular canals	Prismatic crystals
<i>Qualea dinizii</i>	I/A	D	S	At	P	SIP	100-200 μm	5-20	-	A	V, Al, C, L-Al, W-Al	-	Pc	A	P
<i>Qualea rosea</i>	I/A	D	S	At	P	SIP	$\geq 200 \mu\text{m}$	≤ 5 , 5-20	Gums and other	D/D-A	V, Al, C, L-Al, W-Al (?)	1 to 3 cells	Pc/Pc-US (V)	ACD, ICTO	P
<i>Qualea coerulea</i>	I/A	D	S	At	P	-	100-200 μm	≤ 5 , 5-20	-	A	V, Al, C, L-Al (?), W-Al (?)	1 to 3 cells	Pc	ICTO	P
<i>Qualea cordata</i>	I/A	D	S	At	-	-	-	-	-	D	V, Al, C, L-Al, W-Al	1 to 3 cells	Pc	-	-
<i>Qualeoxylon itaquaquecetubense</i>	I/A	D	S	At	P	-	100-200 μm	3-4	-	A	V, C	1 to 3 cells	Pc	A	P
<i>Qualeoxylon felicianensis</i> sp. nov.	P	D	S	At	P	SIP	55-177 μm	6-21	A	D/D-A	V, Al, C	1 to 3 cells	Pc	ACD, ICTO	P

diffuse and diffuse-in-aggregates; rays height 10-20 cells and diffuse axial canals of traumatic origin; and so assigned to a new species, *Qualeoxylon felicianensis* sp. nov.

Biogeography of the Vochysiaceae

Myrtales includes four families (Psiloxylaceae, Heteropyxidaceae, Myrtaceae and Vochysiaceae). Based on the fossil record and on their extant distribution in the tropical, subtropical, and warm-temperate regions of the Southern Hemisphere it was proposed that the Myrtales probably originated in the Middle Cretaceous of West Gondwanaland or Australasia (Muller, 1981; Johnson & Briggs, 1984; Raven, 1988; Conti *et al.*, 1997). Their disjunct patterns in the southern hemisphere are explained by vicariance, including migration and long-distance dispersal (Sytsma *et al.*, 2004).

Vochysiaceae are clearly neotropical (Figure 1); the African representatives of the family are nested within a South American clade and may have reached Africa (Keay & Stafleu, 1953) by long-distance dispersal in the Neogene, when the Atlantic had already rifted *ca.* 80 million years ago in the equatorial region (Sytsma *et al.*, 2004; Kubitzki, 2007). The molecular phylogenetic relationships and clock calibration analyzed by Sytsma *et al.* (2004) includes African *Erismadelphus* within a South American clade but the second African genus *Korupodendron* was not available for DNA analysis (see fig. 5 in Sytsma *et al.*, 2004). The phylogenetic tree argues that South America is the plesiomorphic geographic area for Vochysiaceae (Litt, 1999; Sytsma *et al.*, 2004).

On the American continent, Vochysiaceae is distributed in Mexico, Central America, Colombia, Venezuela, Guyana, Suriname, French Guiana, Ecuador, Peru, Brazil, Bolivia, Paraguay and Argentina (Marcano-Berti, 2005). Vochysiaceae inhabits in tropical forests and savannas, especially in Brazil (Kawasaki, 1998). The ampho-Atlantic distribution is of great phytogeographical interest (Axelrod, 1970; Thorne, 1972).

The biogeographical shift within the Vochysiaceae between South America and Africa, whether due to dispersal or vicariance, occurs after the crown group node in Vochysiaceae has already diversified in South America. Biogeographical shifts to South America (and to the Mediterranean and Africa) are more recent (Sytsma *et al.*, 2004).

CONCLUSIONS

Qualeoxylon felicianensis sp. nov., recovered from the Arroyo Feliciano Formation (late Pleistocene) constitutes the second record of this fossil wood type in South America and the first record of the *Qualeoxylon* in Argentina. In addition, it is the second record of Vochysiaceae fossil wood in the world.

Qualeoxylon felicianensis sp. nov. indicates a warmer and more humid climate in the region during the Late Pleistocene, probably associated with tropical and subtropical forests that developed during the deposition of the Arroyo Feliciano Formation. The present data agreed with the geological and sedimentological data previously established by Iriondo *et al.* (1985) and Iriondo & Kröhling (2008).

The presence of this fossil record supports the hypothesis that *Qualea* was more widespread in the past and that is present in this region since, at least, the late Pleistocene.

The specimen described herein increases our knowledge of the wood fossil record of Vochysiaceae, will contribute to the characterization of the biogeographical patterns of plants in the Neotropics during the Pleistocene, will be also useful in phylogenetic analyses.

ACKNOWLEDGEMENTS

The authors express are to P. Pérez Lindo who found this valuable fossil wood and for field assistance access to collections and generously arranged the loan of the fossil material. This papers was supported financially by the Agencia Nacional de Promoción Científica y Tecnológica (ANPCyT), Project PICT 2008 n° 0176 and Universidad Autónoma de Entre Ríos, PIDP Res. 1423/09 UADER. The authors also would like to express their thanks to the two anonymous reviewers and the editor for their valuable help in providing critical and constructive comments. We are also grateful to A. Kloster for her help and assistance.

REFERENCES

- APG III. 2009. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *Botanical Journal of the Linnean Society*, **161**:105-121. doi:10.1111/j.1095-8339.2009.00996.x
- Aublet, J.B.C.F. 1775. *Histoire des Plantes de la Guiane Française*. Pierre-François DIDOT. 206 p. London & Paris.
- Axelrod, D.I. 1970. Mesozoic paleogeography and early angiosperm history. *Botanical Review*, **36**:277-319. doi:10.1007/bf02858880
- Baas, P.; Wheeler, E. & Chase, M.W. 2000. Dicotyledonous wood anatomy and the APG system of angiosperm classification. *Botanical Journal of the Linnean Society*, **134**:3-17. doi:10.1111/j.1095-8339.2000.tb02343.x
- Boesewinkel, F.D & Venturelli, M. 1987. Ovule and seed structure in Vochysiaceae. *Botanische Jahrbücher für Systematic Pflanzengeschichte und Pflanzengeographie*, **108**:547-566.
- Brunetto, E.; Ferrero, B.S.; Marino, J.; Tentor, F.; Sturtz, M.; Zamboni, L. & Casanave, L. 2012. Evolución geológica del Pleistoceno del centro de Entre Ríos: In: CONGRESO ARGENTINO DE CUATERNARIO Y GEOMORFOLOGÍA, 5, 2012. Resúmenes, Río Cuarto, p. 1-5.
- Carmo-Oliveira, R. & Lange de Morretes, B. 2009. Stigmatic surface in the Vochysiaceae: reproductive and taxonomic implications. *Acta Botanica Brasileira*, **23**:780-785. doi: 10.1590/S0102-33062009000300018
- Carquist, S. 2001. *Comparative wood anatomy. Systematic, Ecological and evolutionary Aspects of Dicotyledons Wood*. New York, Springer, 448 p.
- Conti, E.; Litt, A. & Sytsma, K.J. 1996. Circumscription of Myrtales and their relationships to other Rosids: evidence from rbcL sequence data. *American Journal of Botany*, **83**:221-233.
- Conti, E.; Litt, A.; Wilson, P.G.; Graham, S.A.; Briggs, B.G.; Johnson, L.A.S. & Sytsma, K.J. 1997. Interfamilial relationships in Myrtales: molecular phylogeny and patterns of morphological evolution. *Systematic Botany*, **22**:629-647. doi:10.2307/2419432
- Cronquist, A. 1968. *The evolution and classification of flowering plants*. Boston. Houghton Mifflin Co., 396 p.

- Dumortier, B.C. 1829. Vochysiaceae. In: B.C. Dumortier (ed.) *Analyse des familles des plantes avec l'indication des principaux genres qui s'y rattachent*. J. Casterman, Tournay, 41 p.
- Flora Argentina, 2012. Plantas vasculares de la República Argentina. <http://www.floraargentina.edu.ar/>; accessed on 22/04/2015.
- Grandtner, M.M. & Chevrette, J. 2013. *Dictionary of Trees, South America: nomenclature, taxonomy and ecology*. 1st ed. New York, Elsevier, 1176 p.
- Gregory, M. 1994. Bibliography of systematic wood anatomy of dicotyledons. *IAWA Journal*, **1**:1-265.
- Gregory, M.; Poole, I. & Wheeler, E. A. 2009. Fossil dicot wood names and annotated list with full bibliography. *IAWA Journal*, **6**:1-128.
- Heywood, V.H. 1985. *Las Plantas con Flores*. Editorial Barcelona, Reverté S.A., 332 p.
- Heywood, V.H. 1993. *Flowering plants of the world*. New York, Oxford University Press, 336 p.
- Hiroaki Shimizu, G. 2009. *Vochysiaceae na Serra do Cipó, Minas Gerais, Brasil*. Programa de Pós-Graduação em Biologia Vegetal, Universidade Estadual de Campinas, M.Sc. thesis, 149 p.
- Huber, J. 1909. Mattas e madeiras amazônicas. *Boletim Museu Goeldi*, **6**:91-225.
- Hutchinson, J. 1967. *The genera of flowering plants. II. Dicotyledons*. Oxford, Clarendon Press. 659 p.
- IAWA Committe. 1989. IAWA list of microscopic feature for hardwood identification. *IAWA Bulletin*, **10**:219-332.
- InsideWood. 2004-onwards. Available at <http://insidewood.lib.ncsu.edu/search/>; accessed on 22/04/2015.
- Iriondo, M.; Tardivo, R.N. & Ceruti, C.N. 1985. Geomorfología y cuaternario del tramo inferior del arroyo Feliciano (Entre Ríos, Argentina). *Revista de la Asociación de Ciencias Naturales del Litoral*, **16**:149-156.
- Iriondo, M. & Kröhling, D. 2008. *Cambios ambientales en la cuenca del Uruguay (desde el Presente hasta dos millones de años atrás)*. Colección Ciencia y Técnica, Universidad Nacional del Litoral, 360 p.
- Johnson, L.A.S. & Briggs, B.G. 1984. Myrtales and Myrtaceae: a phylogenetic analysis. *Annals of the Missouri Botanical Garden*, **71**:700-756.
- Kawasaki, M.L. 1998. Systematics of *Erisma* (Vochysiaceae). *Memoirs of the New York Botanical Garden*, **81**:1-40.
- Kawasaki, M.L. 2007. Vochysiaceae. In: Kubitzki, K. (ed.) *The families and genera of vascular plants. Flowering plants eudicots*, Springer, p. 480-487. doi:10.1007/978-3-540-32219-1_55
- Keay, R.W. & Stafleu, F.A. 1953. *Erismanadelphus*. *Acta Botanica Neerlandica*, **1**:595-597.
- Kubitzki, K. 2007. *The families and genera of vascular plants*. Hamburg, Springer Press, 509 p.
- León, W.L. 2003. Anatomía xilemática comparativa de los géneros *Qualea* y *Ruizterania* (Vochysiaceae). *Pittieria*, **32**:69-81.
- Lima, M.R.; Melo, M.S. & Coimbra, A.M. 1991. Palinología de sedimentos da Bacia de São Paulo, Terciário do Estado de São Paulo, Brasil. *Revista do Instituto Geológico*, **12**:7-20. doi:10.5935/0100-929x.19910001
- Litt, A. 1996. Phylogeny of the Vochysiaceae: implications of molecular data for floral evolution. *American Journal of Botany*, **83**:175.
- Litt, A. 1999. *Floral morphology and phylogeny of Vochysiaceae*. University of New York, Ph.D. Thesis, 528 p.
- Litt, A. & Cheek, M. 2002. *Korupodendron songweanum*, a new genus and species of Vochysiaceae from West-Central Africa. *Brittonia*, **54**:13-17. doi:10.1663/0007-196X(2002)054[0013:KSANGA]2.0.CO;2
- Marcano-Berti, L. 1969. Un nuevo género de las Vochysiaceae. *Pittieria*, **2**:3-27.
- Marcano-Berti, L. 2005. Vochysiaceae. In: P.E. Berry; K. Yatskievych & B.K. Holst (eds.) *Flora of the Venezuelan Guayana*. Rutaceae-Zygophyllaceae, Missouri Botanical Garden Press, p.500-524.
- Martius, C.F.P. von. 1826. *Nova genera et species plantarum*. Vol. 1, 123 p.
- Metcalfe, C.R. & Chalk, L. 1950. *Anatomy of the Dicotyledons*. Oxford, Clarendon Press, p. 871-893.
- Mildbraed, G.W.J. 1913. Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie, **49**:549.
- Muller, J. 1981. Fossil pollen records of extant angiosperms. *Botanical Review*, **47**:1-142. doi:10.1007/bf02860537
- Quirk, J.T. 1980. Wood anatomy of the Vochysiaceae. *IAWA Bulletin*, **1**:172-179.
- Raven, P.H. 1988. Onagraceae as a model of plant evolution. In: L. Gottlieb & S. Jain (eds) *Plant evolutionary biology*. London, Chapman and Hall, p.85-107.
- Rissi, M.N. & Cavassan, O. 2013. Uma proposta de material didático baseado nas espécies de Vochysiaceae existentes em uma trilha no cerrado de Bauru – SP. *Biota Neotropica*, **13**:27-41. doi.org/10.1590/S1676-06032013000100003
- Rudge, E. 1805. *Plantarum Guianae Rariorum Icones et Descriptiones*. Richard Taylor, 32 p.
- Saint-Hilaire, A.F.C.P. von. 1820. Mémoires du Muséum d'Histoire Naturelle. vol. 6, 6:259 p.
- Sajo, M.G. & Rudall, P.J. 2002. Leaf and stem anatomy of Vochysiaceae in relation to subfamilial and suprafamilial systematics. *Botanical Journal of the Linnean Society*, **138**:339-364. doi:10.1046/j.1095-8339.2002.00025.x
- Santos, D.B.; Garcia, M.J.; Saad, A.R. & Bistrichi, C.L. 2010. Palinostratigrafia da Formação Itaquaquacetuba, Bacia de São Paulo, Brasil. *Revista Brasileira de Paleontologia*, **13**: 205-220. doi:10.4072/rbp.2010.3.05
- Stafleu, F.A. 1953. A monograph of the Vochysiaceae. III. *Qualea*. *Acta Botanica Neerlandica*, **2**:144-217.
- Suguió, K. & Mussa, D. 1978. Madeiras fósseis dos aluviões antigos do Rio Tietê, São Paulo. *Boletim IG USP*, **9**:5-45. doi:10.11606/issn.2316-8978.v9i0p25-45.
- Sytsma, K.J.; Litt, A.; Zjhra, M.L.; Pires, J.C.; Nepokroeff, M.; Conti, E.; Walker, J. & Wilson, P.G. 2004. Clades, clocks, and continents: historical and biogeographical analysis of Myrtaceae, Vochysiaceae, and relatives in the southern hemisphere. *International Journal of Plant Sciences*, **165**: S85-S105. doi:1058-5893/2004/1650S4-0007
- Takhtajan, A. 1969. *Flowering plants and dispersal*. Smithsonian Institution Press, City of Washington, 310 p.
- Thorne, R.F. 1972. Major disjunctions in the geographic ranges of seed plants. *Quarterly Review of Biology*, **47**:365-411.
- Tobe, H. & Raven, P.H. 1983. An embryological analysis of Myrtales: its definition and characteristics. *Annals of the Missouri Botanical Garden*, **70**:71-94.
- Tortorelli, L.A. 1956. *Maderas y bosques argentinos*. Buenos Aires, Editorial ACME, 910 p.
- UTHSCSA ImageTool Version 3.0 Final. World Wide Web: <http://ddsdx.uthscsa.edu/dig/download.html>; accessed on 22/04/2015.
- Van Vliet, G.J.C.M. & Baas, P. 1984. Wood Anatomy and Classification of the Myrtales. *Annals of the Missouri Botanical Garden*, **71**:783-800.
- Yamamoto, I. 1995. *Palinología das Bacias Tafrogênicas do Sudeste (Bacias de Taubaté, São Paulo e Resende): Análise Bioestratigráfica Integrada e Interpretação Paleoambiental*. Curso de Pós-Graduação em Geociências, Universidade Estadual Paulista, Rio Claro, M.Sc. thesis, 217 p.