



First record of *Styracoxylon* (Styracaceae) from Southern Hemisphere: Arroyo Feliciano Formation (Upper Pleistocene), Entre Ríos, Argentina



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ABSTRACT

A new species, *Styracoxylon thyllosum* sp. nov., is described from the Upper Pleistocene Arroyo Feliciano Formation of the Gualeguay Basin in eastern Argentina. It is the first unequivocal record of the *Styracoxylon van der Burgh* (1978) in South America and was previously known only from the Pliocene of the Rhine area, Netherlands. This fossil specimen was recovered in the Consorcio Paso Sociedad Locality (Federal, Entre Ríos, Argentina). The new fossil species is characterized by growth ring boundaries distinct, with diffuse-porous wood. Vessels are mostly in radial multiples of 2–6 elements, occasionally solitary and rarely in clusters. Tylosis is abundant. Perforation plates are usually scalariform (5–20 bars) and rarely simple. Intervessel pits are small, bordered, and alternate to opposite. Rays are frequently 2–4 (6) seriate and rarely uniseriate, heterocellular, and of two distinct ray sizes. Fibers are non-septate, with distinctly bordered pits, and rounded to hexagonal in outline.

The axial parenchyma is apotracheal diffuse and diffuse-in-aggregates, and in strands of 8–12 cells. Vascular tracheids possibly present. Wood anatomical features suggest a relationship with Styracaceae, and the fossil specimen shows affinity with the extant genus *Styrax* Linnaeus.

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1. Introduction

The Styracaceae is a dicotyledonous family of woods or shrubs, usually evergreen, containing 11 genera and approximately 160 species (Fritsch et al., 2001; Fritsch, 2004). These taxa are distributed in eastern Asia, western Malaysia, and South America, where they are distributed throughout the Neotropics (Fritsch, 1999, 2001) and the southeast of the United States (Fig. 1). The family is widespread but with a disjunct distribution, occurring from warm-temperate to tropical areas (Fritsch et al., 2001). Traditionally, the Styracaceae were included within the Ebenales (Tortorelli and Castiglioni, 1948; Metcalfe and Chalk, 1950; Gonsoulin, 1974; Dickson and Phend, 1985; Cronquist, 1988; Takhtajan, 1997), but molecular data suggest affinities to the Ericales (Fritsch, 1999, 2001; Fritsch et al., 2001; Anderberg et al., 2002; APG III, 2009). There are no obvious synapomorphies diagnosing the Ericales as a monophyletic group, but the only ubiquitous embryological character state is the presence of tenuinucellate ovules (Schönenberger et al., 2005). The wood anatomical features also give the impression that Ericales are heterogeneous (Anderberg et al., 2002). However, there are some patterns of variation, e.g., most families have scalariform perforation plates, and exclusively simple perforations

are being restricted to a few families (Baas et al., 2000; Anderberg et al., 2002). Ericales is an order characterized by mainly solitary vessels, scalariform, or mixed simple and scalariform perforation plates, distinctly bordered fiber pits, apotracheal parenchyma, and heterocellular rays, usually of two distinct sizes (Baas et al., 2000). Based on the morphology of vessels, fibers, and the distribution of axial parenchyma, two major wood types can be distinguished within Ericales: (1) a primitive type with solitary vessels, scalariform perforation plates, mainly opposite to scalariform vessel pitting, fibers with distinctly bordered pits and diffuse or diffuse-in-aggregates axial parenchyma (this is nearly identical to the wood structure in the more basal outgroup Cornales) and (2) a “derived” type with in radial multiple vessels and the tendency to alternate intervessel pitting, which must have evolved in at least two separate evolutionary lines. The members of the “primitive” wood type grow in tropical montane or more temperate to arctic regions while the tropical lowland species possess a “derived” wood type (Lens et al., 2007).

The main goal of this paper is to describe a fossil wood that has the diagnostic features of the Styracaceae. This fossil specimen was found in sediments of the Arroyo Feliciano Formation (Upper Pleistocene) in the fossiliferous locality of Consorcio Paso Sociedad, Entre Ríos, Argentina (approximately 31° 03' S, 58° 38' W) (Fig. 2A), and is the first fossil wood record from this formation.

The fossil wood was compared with extant genera of the Styracaceae, and the genus *Styrax* L. is the most closely related to it. Styracaceae are

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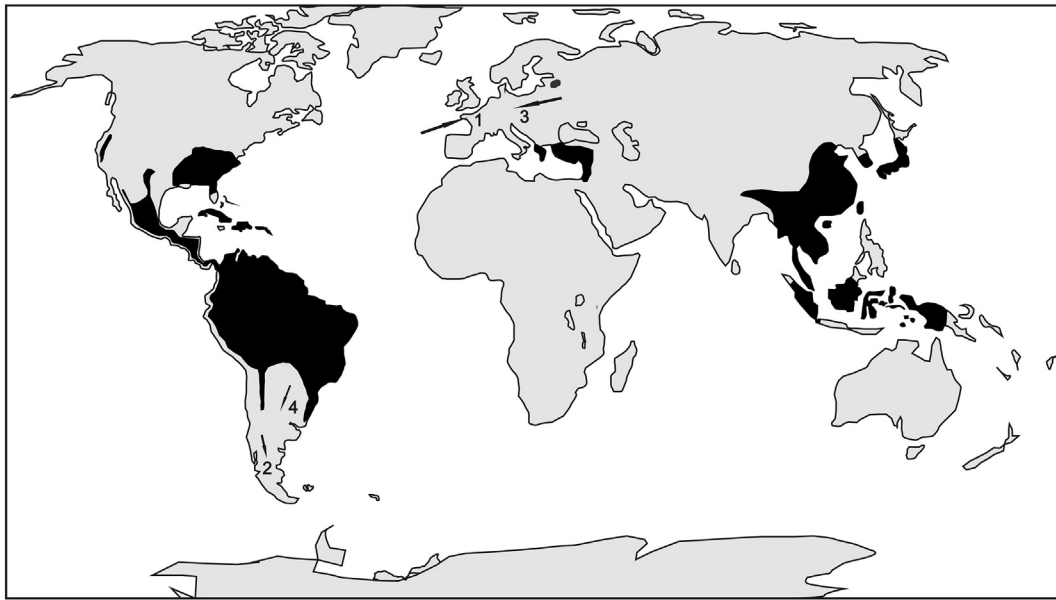


Fig. 1. Biogeography distribution of extant genera from Styracaceae Family (dark grey shading), taken from Fritsch (1999) and Tropics, Missouri Botanical Garden, 20 July 2013 [<http://www.tropics.org>], and the fossiliferous localities of fossil woods: (1) *Styracoxylon rhenanum* (van der Burgh, 1978) of the Lower Pliocene, Rhine Basin, The Netherlands; (2) uncertain genus of Styracaceae of the Palaeocene-Eocene, Patagonia, Argentina (Raigemborn et al., 2009); (3) *Coryloxylon nemejci* and *C. tertiarum* (Prakash et al., 1971; Sakala et al., 2010) of the Oligocene-Lower Miocene, the Czech Republic; (4) *Styracoxylon thyllosum* sp. nov. (this paper) of the Upper Pleistocene, Entre Ríos Province, Argentina.

represented in the American continent by the genera *Halesia* J. Ellis ex Land *Styrax sensu lato* according to Wallnöfer (1997), where the genus *Pamphilia* Mart. ex A. DC. was transferred to *Styrax* as a section (Wallnöfer, 1997; Fritsch and Lucas, 2000; Zuloaga et al., 2008) or *Pamphilia* as a synonym of *Styrax* series *Valvatae sensu* Frisch (1999). *Styrax* has approximately 100 species and is distributed mainly in tropical areas but also in subtropical and temperate zones, extending from the south of the United States to northern Argentina (Tortorelli, 1956; Fritsch, 1999, 2001; Fritsch et al., 2001; APG III, 2009; Missouri Botanical Garden [<http://www.tropics.org>]).

In Argentina, the Styracaceae fossil record is very sparse; only one wood specimen was assigned to this family (Fig. 1). This fossil was found in the Peñas Coloradas Formation (Upper Palaeocene-Eocene) from Patagonia, Argentina (Raigemborn et al., 2009). This wood specimen was considered in an uncertain generic position because some diagnostic anatomical features are not well preserved. Additionally, Berry (1925, 1938) studied fossil leaves with *Styrax* affinity from the Tertiary of Río Pichileufú and Mirhoja, Mirador Mesa, Patagonia, Argentina: *Styrax glandulifera* Berry and *Styrax acuminatififormis* Berry. This last species was also found in the Laguna del Hunco (early Eocene) north-

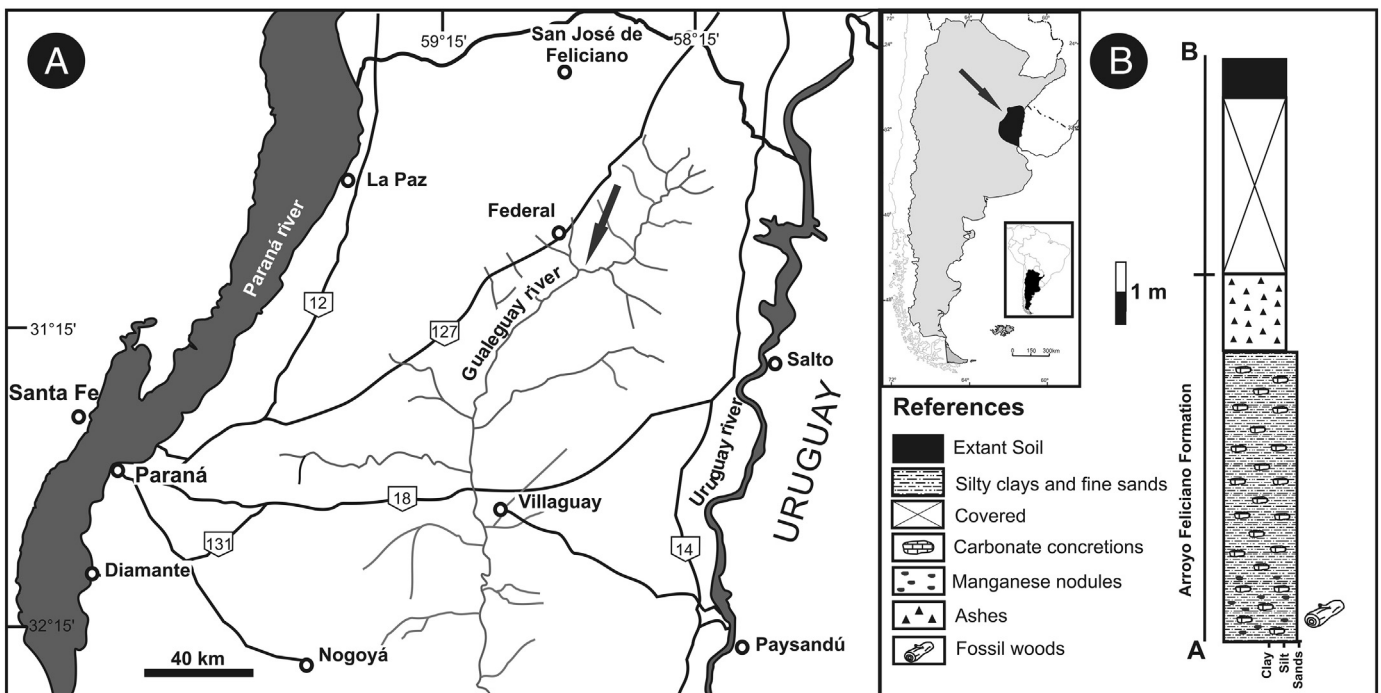


Fig. 2. Geographic map location (A), the arrow indicates the locality fossil and lithological profile (B) in which the fossil wood was collected.

western Chubut Province, Argentina [<http://bhort.bh.cornell.edu/histology/taxalH.html>]. In eastern Argentina, only one leaf impression affinity of *Styrax* was reported from the Miocene in the Paraná Formation and was related to humid forest (Anzótegui and Aceñolaza, 2006).

The fossil wood reported herein presents a combination of diagnostic anatomical features that allow the recognition of a new species of *Styracoxylon* van der Burgh (1978), *Styracoxylon thyllosum* sp. nov., from the Upper Pleistocene of Argentina. It is the first reliable record of the *Styracoxylon* in the Southern Hemisphere and was only previously known from the Pliocene of the Rhine area, within the Netherlands (van der Burgh, 1978).

2. Geological and paleontological setting

The fossil wood specimen was found in the Arroyo Feliciano Formation. This continental deposit was defined by Iriondo et al. (1985) and represents an alluvial and fluvial unit deposited in the tributary valleys of the Parana and Uruguay Rivers (Entre Ríos, Argentina). The Arroyo Feliciano Formation, 2–5 m thick, was probably deposited during the Upper Pleistocene known in the geological literature of Argentina as the Lujanian Stage/Age (Iriondo and Kröhling, 2008).

The Arroyo Feliciano Formation in Entre Ríos Province has outcrops mainly along on both margins of the Gualeguay River and the major rivers and streams and constitutes the highest terrace (Iriondo et al., 1985; Iriondo and Kröhling, 2008). It is mainly composed of well-graded fine sands and whitish to light green silts. The formation consists of massive and rarely very thin and poorly defined lamination. In the lowest part of the sequence, there are abundant manganese nodules, and carbonate concretions are very common through the sequence.

During the Upper Pleistocene, more humid conditions prevailed than at present, and the mean annual precipitation (MAP) was estimated to have been 10 times greater than the present-day (Iriondo et al., 1985; Iriondo and Kröhling, 2008).

The presence of *Toxodon platensis*, *Myiodon darwini*, and *Lestodon* sp. correlated tentatively the Arroyo Feliciano Formation with the Bonaerian-Lujanian State/Age of the Buenos Aires Province, Argentina (Brunetto et al., 2012).

3. Material and methods

The fossil material described in this paper was recovered from the basal levels of the Upper Pleistocene Arroyo Feliciano Formation (Fig. 2B) at the Consorcio Paso Sociedad Locality, near the City of Federal in Entre Ríos Province, Argentina. The sedimentary deposits are well exposed being approximately 6 m thick without exposed base and are mainly composed of light grey-to-white silty clays and fine sands with carbonate concretions. Also, manganese nodules in the lowest parts of the profile are observed. The stratification is very thin and poorly defined. At the top of the profile, a volcanic ash lens (approximately 1 m thick) with marked laminar stratification is present (Fig. 2B).

The fossil specimen consists of permineralized wood with well-preserved anatomical features where only secondary xylem tissue is preserved. Transverse, tangential, and radial thin sections of the woods were prepared for study using standard lapidary techniques.

The description and anatomical terminology used in this paper generally follow the recommendations of the International Association of Wood Anatomists lists of microscopic features for hardwood identification (IAWA Committee, 1989), with some terms also taken from Chattaway (1932), Kribs (1935), Tortorelli (1956) and Carlquist (2001). The bibliographic lists provided by Gregory (1994) and Gregory et al. (2009) were used. The assignment, the descriptions, and the comparisons with fossil and extant woods were performed following the InsideWood web site (InsideWood, 2004–onwards) and descriptions made by Tortorelli and Castiglioni (1948), Metcalfe and Chalk (1950), Tortorelli (1956), van der Burgh (1978), Dickison and Phend (1985), ter Welle and Dickison in Wallnöfer (1997), and Sakala

et al. (2010). Systematic assignment follows the Angiosperm Phylogeny Group (APG III, 2009). Names used are as found in the International Plant Names Index (The Plant List, 2010).

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

The material was studied with a Nikon Eclipse E200 light microscope and the photomicrographs were taken with a Nikon Coolpix S4 digital camera. The holotype fossil specimen and microscope slides are kept in the Laboratorio de Paleobotánica (CICYTTP-CONICET), Diamante, Argentina, under the acronym CIDPALBO-MEG 64 and CIDPALBO-MIC 714. The isotype was deposited in the Colección Paleontología, Museo de Antropología y Ciencias Naturales “Conscripto Bernardi”, Conscripto Bernardi, Argentina, under the acronym M05.

4. Results

4.1. Systematic palaeobotany

Order: Ericales Dumortier 1829

Family: Styracaceae Candolle and Sprengel, 1821, nom. cons.

Genus: *Styracoxylon* van der Burgh, 1978

Species: *Styracoxylon rhenanum* van der Burgh, 1978; Rhine Basin, The Netherlands, Lower Pliocene, pp. 245–246, taf. 10, Figs. 1–7.

S. thyllosum sp. nov. Moya, Brea et Franco (Plates I, II)

Derivation of name: The specific epithet, *thyllosum*, refers to the presence of abundant tyloses in vessel elements.

Holotype: CIDPALBO-MEG 64, CIDPALBO-MIC 714 (three slides) (Plates I, II).

Isotype: M05.

Repository: Colección Paleobotánica, Centro de Investigaciones Científicas y Transferencia de Tecnología a la Producción (CICYTTP-CONICET), Diamante, Entre Ríos, Argentina and Colección Paleontología, Museo de Antropología y Ciencias Naturales “Conscripto Bernardi”, Conscripto Bernardi, Entre Ríos, Argentina.

Type locality: Consorcio Paso Sociedad Locality, Federal, Entre Ríos, Argentina.

Type horizon: Arroyo Feliciano Formation, Upper Pleistocene (31° 03' S–58° 38' W).

Species diagnosis: Diffuse-porous wood, vessels mostly in radial multiples of 2–6 elements, also solitary and in clusters; tyloses; scalariform (5–20 bars) and rarely simple perforation plates; small, bordered, alternate to opposite intervessel pits; heterocellular, (1) 2–4 (6) seriate rays; non-septate fibers with distinctly bordered pits; diffuse and diffuse-in-aggregate apotracheal axial parenchyma, axial parenchyma 8–12 cells per strand; crystals in rays cells and in chambered axial parenchyma cells; vascular tracheids probably present.

Description: In transverse section, the growth rings are demarcated by radial compressions of fibers. The wood is semi-ring porous to diffuse porous, and the vessels are mostly in radial multiples of 2–4 elements (27%, 36%, and 12%, respectively) and >4 elements (15%), occasionally solitary and rarely in clusters (10%) (Plate I, 1, 4, 5, 12). Vessels are circular in outline, with thick walls of 10 (7–14) μm thick (Plate II, 4). The mean tangential diameter of the vessels is 100 (43–152) μm , and the mean radial diameter is 80 (20–170) μm . The mean vessel density is 22 (14–31)/ mm^2 . The presence of tyloses is observed mainly in greater vessels (Plates I, 5; II, 4). The apotracheal axial parenchyma is diffuse and diffuse-in-aggregate (Plate I, 1, 4). The fibers are rounded to hexagonal in outline, with radial rows arrangement, abundant and non-septate (Plate II, 10) with a mean diameter of 12 (7–17) μm , very thin to thick-walled, 4 (2–6) μm in thickness.

In tangential section, the vessels are very short, with a mean length of 155 (55–675) μm . The perforation plates are mostly scalariform with 5–20 bars (Plate II, 2, 11) and rarely simple (Plate 4C) with straight to

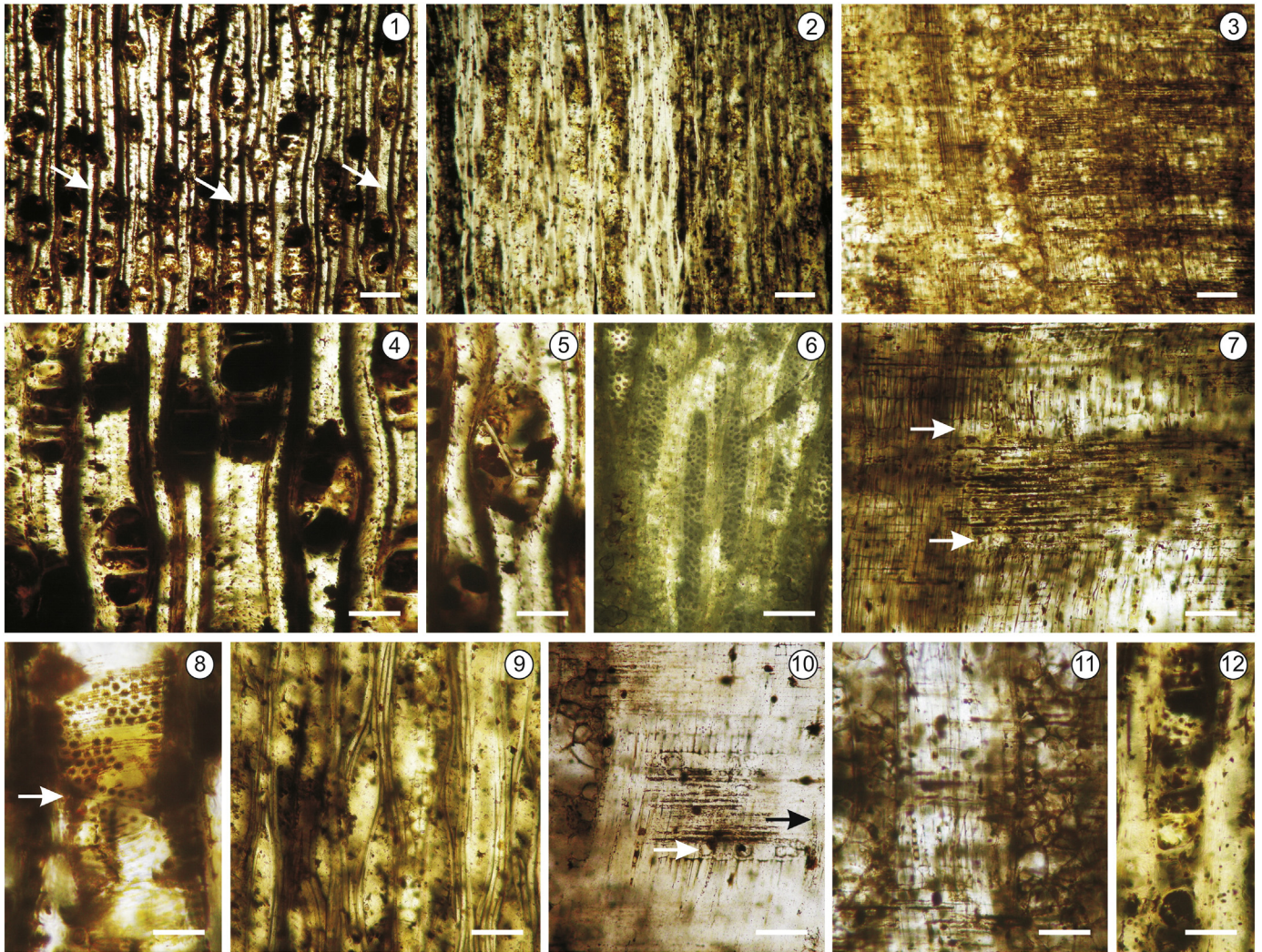


Plate I. *Styracoxylon thyllosum* sp. nov. Moya, Brea et Franco. Holotype CIDPALBO-MEG 64.

- (1) Transverse section; the arrow indicates growth ring demarcated by radial compression of fibers.
- (2) Tangential longitudinal section, general view. Multiseriate rays.
- (3) Radial longitudinal section, general view. Heterocellular rays.
- (4) Transverse section, detail of transverse section showing solitary and radial multiple vessels and diffuse and diffuse-in-aggregate apotracheal axial parenchyma.
- (5) Transverse section, vessel in cluster with tyloses.
- (6) Tangential longitudinal section, detail of the multiseriate rays.
- (7) Radial longitudinal section, detail of heterocellular rays composed of procumbent cells with 1–2 rows of upright and/or square marginal cells (arrows).
- (8) Tangential longitudinal section, intervessel pits; the arrow indicates an oblique end wall.
- (9) Tangential longitudinal section, detail of multiseriate rays.
- (10) Radial longitudinal section, showing parenchyma in strands (black arrow) and crystal in square or upright ray cells (white arrow).
- (11) Radial longitudinal section, vessel with tyloses.
- (12) Transverse section, showing vessels in radial multiples of more than 4. (Scale bar in 1–12 = 200 μ m).

oblique end walls (Plate I, 8). The intervessel pits are very small, alternate to opposite, oval to hexagonal in outline (Plates I, 8; II, 6, 9, 13, 14) with a mean diameter of 6 (5–8) μ m, with elongated apertures (Plate II, 14). There are scalariform pits in some small vessels. The rays are of two distinct sizes (Plates I, 6, II, 7), multiseriate with uniseriate terminal portions, moderately numerous to numerous. The mean number of rays is 7 (4–10) per linear mm, and the uniseriate rays are scarce (Plates I, 2, 6, 9; II, 5, 7, 8). The mean height of the multiseriate rays is 379 (187–587) μ m with 21 (9–34) cells high. The mean height of the uniseriate rays is 164 (87–325) μ m with 7 (4–13) cells high. The multiseriate and uniseriate rays are extremely low. The mean width of the multiseriate rays is 54 (32–75) μ m, moderately wide, 2–6 seriate. The uniseriate rays are very thin with a mean width of 19 (15–25) μ m. The prismatic crystals are present in upright and/or square ray cells

(Plate II, 16). The axial parenchyma has strands of 8–12 cells (Plates I, 10, II, 5), with dark deposits and crystals in chambered axial parenchyma, one crystal per chamber (Plate II, 5). The fibers have 1–2 rows of bordered pits with oval apertures (Plate II, 12). The vascular tracheids have very small, alternate, and bordered pits, with probably double helical thickenings (Plate II, 1).

In radial section, the multiseriate and uniseriate rays are heterocellular with procumbent body cells and 1–2 rows of upright and/or square marginal cells (Plate I, 3, 7, 10). There are dark deposits and probably silica bodies in ray cells (Plate I, 7). The prismatic crystals are present in axial parenchyma and rays cells, mainly in square or upright cells (Plate I, 10). The vessels-ray pits have distinct borders and are similar to intervessel pits (Plate II, 15). The tylosis is common in vessels (Plate I, 11).

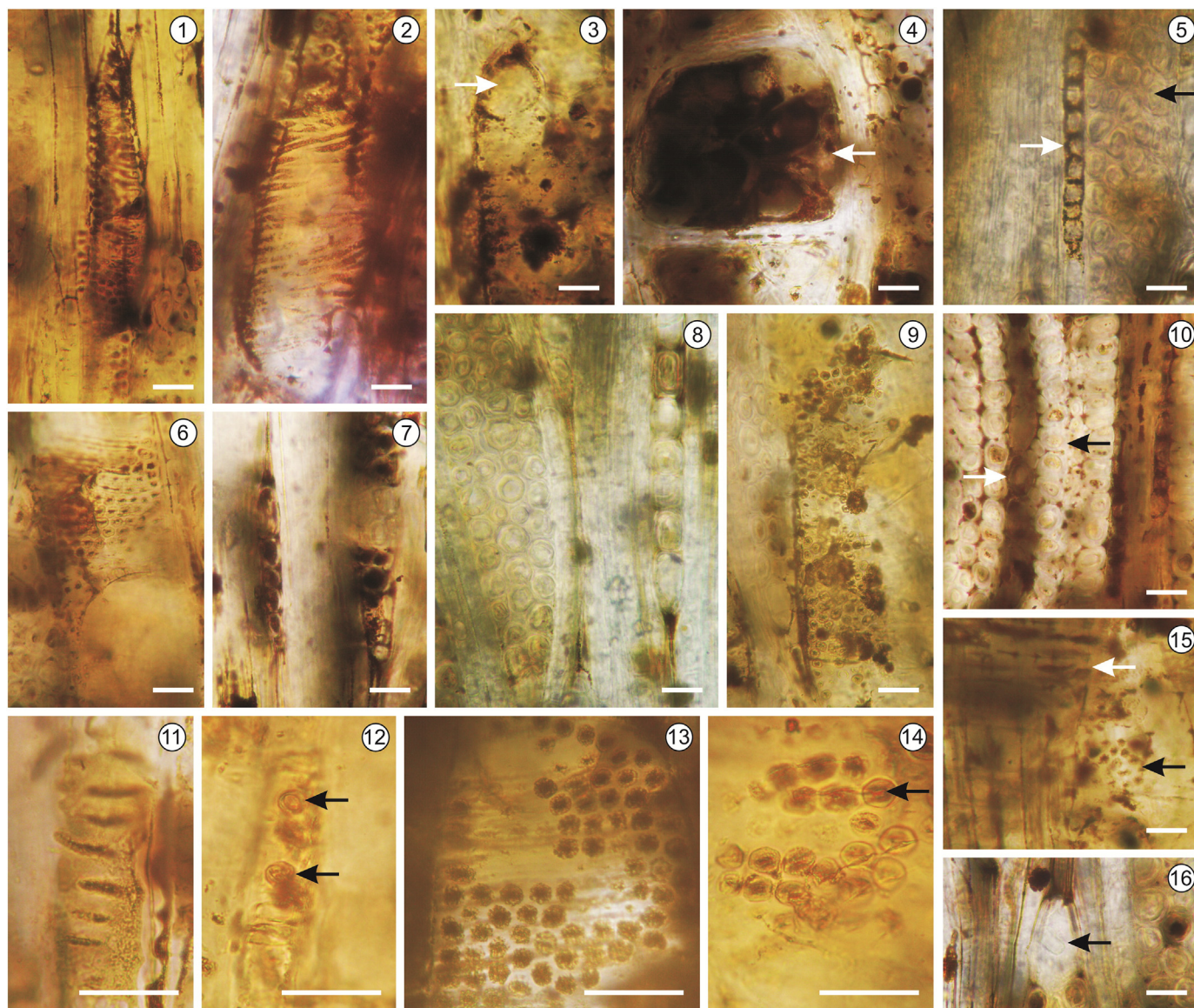


Plate II. *Styracoxylon thyllosum* sp. nov. Moya, Brea et Franco. Holotype CIDPALBO-MEG 64.

- (1) Tangential longitudinal section, possibly vascular tracheids with alternate, very small, bordered pits, and helical thickenings.
- (2) Tangential longitudinal section, scalariform perforation plate.
- (3) Tangential longitudinal section, simple perforation plate (arrow).
- (4) Transverse section, vessel with tyloses (arrow).
- (5) Tangential longitudinal section, axial parenchyma in strands with one crystal per chamber (white arrow), and multiseriate ray (black arrow).
- (6) Tangential longitudinal section, vessel with intervessel pits.
- (7, 8) Tangential longitudinal section, uniseriate, and multiseriate rays.
- (9) Tangential longitudinal section, vessel with intervessel pits.
- (10) Transverse section, fibers rounded to hexagonal in outline, with radial rows arrangement (black arrow) and rays (white arrow).
- (11) Tangential longitudinal section, detail of the scalariform perforation plate.
- (12) Tangential longitudinal section, fibers with one row of bordered pits.
- (13, 14) Tangential longitudinal section, detail of vessel with intervessel pits; the arrow indicates elongated pit apertures.
- (15) Radial longitudinal section; black arrow indicates vessels-ray pits with distinct borders and white arrow show ray cells.
- (16) Tangential longitudinal section, prismatic crystal in ray cells (arrow). (Scale bar in 1–10, 15–16 = 20 μ m; in 11–14 = 10 μ m).

5. Discussion

5.1. Comparisons with extant species

The key anatomical features of the studied material (diffuse to ring-porous wood, small vessels with straight to oblique end walls, mainly scalariform and rarely simple perforation plates, usually scalariform to opposite and alternate intervessel pits, diffuse and diffuse-in-aggregates apotracheal axial parenchyma, usually 2–4 seriate and

sometimes up to 6 seriate rays, rays of two distinct sizes and markedly heterogeneous) are common features in Styracaceae (Metcalf and Chalk, 1950; Gonsoulin, 1974; Miller, 1976; Dickison and Phend, 1985; ter Welle and Dickison in Wallnöfer, 1997; Carlquist, 1980; Baas et al., 2000; Machado et al., 2007; Schweingruber et al., 2013). Some of the above-mentioned characters also occur in the Sapotaceae, Symplocaceae, and Ebenaceae (Table 1). All these families are within the Order Ericales *sensu* APG III (2009). However, Ebenaceae differs by the presence of exclusively simple perforation plates and the absence

Table 1
Wood anatomical characteristics of the families in the order Ericales references: Tortorelli and Castiglioni (1948), Metcalfe and Chalk (1950), Tortorelli (1956), Dickison and Phend (1985), ter Welle and Dickison in Wallnöfer (1997), and Schweingruber et al. (2013).

Order Ericales						
Families		Styracaceae	Sapotaceae	Ebenaceae	Symplocaceae	
VESSELS	Porosity	Ring porous	Semi-ring porous?	Ring porous	–	
	Arrangement	Diagonal and/or radial pattern	Diagonal and/or radial pattern	Diagonal and/or radial pattern	–	
	Perforation plates	Scalariform and simple	Scalariform and simple	Simple	Scalariform	
	Groupings	Solitary and in radial multiples of 4 or more	In radial multiples of 4 or more	Solitary and in radial multiples of 2–4 or more	Exclusively solitary	
	Tangential diameter	50 µm	100–200 µm	25–100 µm	100 µm	
	Tyloses and deposits	Present	Present	Present	–	
	Intervessel pits	Alternate, opposite, scalariform	Alternate	Alternate	Scalariform, opposite	
	Vessels per square millimeter	10–20	5–20	2–4, and 15	15–100	
	Prismatic crystals	Present	Present	–	–	
	Helical thickenings	Absent	Present	–	Present	
RAYS	Width	Uniseriate and multiseriate of 2–4 (5–6)	Uniseriate and multiseriate of 2–3 (1–6)	Uniseriate and multiseriate of 1–2 (3–4)	Uniseriate and multiseriate of 2–5 (9–12)	
	Cellular composition	Heterocellular (procumbent body cells and 2–4 rows of upright and/or square marginal cells)	Heterocellular (procumbent body cells and 2–4 rows of upright and/or square marginal cells)	Heterocellular (procumbent body cells and 2–4 rows of upright and/or square marginal cells) and homocellular	Heterocellular, (procumbent body cells and 2–4 rows of upright and/or square marginal cells). and homocellular	
	Deposits	Present	Present	Present	–	
	Rays per mm	9–15	9–15	10–17	10–15	
	Crystals	Present	Present	Present	–	
	Axial parenchyma	Paratracheal	Absent or scarce	–	Scarce	–
		Apotracheal	Present	Present	Present	Present
		Prismatic crystals	Present	Present	Present	–
	Tracheids and fibers	Vascular/vasicentric tracheids	Present	Present	–	–
		Helical thickenings	Present	–	–	Present
Prismatic crystals		Present	Present	Present	–	
Secretory elements	Intercellular canals and tubes	Rare	Laticifers tubes	–	–	

of vessels in clusters. The presence of exclusively solitary vessels, vessels with angular outline in transverse section and exclusively uniseriate rays is characteristic of the Symplocaceae. These features were not observed in the fossil wood described in this paper. The characters such as laticiferous tubes, axial parenchyma in bands, and exclusively solitary vessels present in Sapotaceae differ from the fossil specimen (Metcalfe and Chalk, 1950; Tortorelli, 1956) (Table 1).

In North and South America, the Styracaceae are represented by the genera *Halesia* and *Styrax sensu lato* (including *Pamphilia sensu* Wallnöfer, 1997). The anatomical characters of the fossil material are closely resemble the genus *Styrax*. A clear distinction between *Halesia* and *Styrax* is not possible based only on wood according to Dickison and Phend (1985). Nevertheless, *Halesia* has vessels with angular to circular in outline, mostly opposite intervessel pits and absent tylosis, with some species lacking crystals (Dickison and Phend, 1985; Sakala et al., 2010). *Styrax* Section *Pamphilia* (= genus *Pamphilia sensu* Perkins, 1907) *sensu* Wallnöfer (1997) or *Pamphilia* as a synonym of *Styrax* series *Valvatae sensu* Frisch (1999), differs from the fossil wood by presenting multiseriate rays of 2–3 cells, scalariform perforation plate with ≥ 14 bars, mainly apotracheal parenchyma uniformly distributed in tangential bands, and by lacking crystals in ray cells (ter Welle and Dickison in Wallnöfer, 1997). *Styrax* is characterized by indistinct to distinct growth rings boundaries, which, when present, are represented by narrow to wide bands of compressed fibers, diffuse to semi-ring-porous or ring-porous wood, latewood usually without vessels, solitary vessels and in radial multiples of 2–7 (8), mainly scalariform perforation plates with 3 to 13 (26) bars and rare simple perforation plates, opposite to alternate or exclusively alternate intervessel pits; amorphous solid deposits occur in vessels of some species, abundant diffuse and diffuse-in-aggregate apotracheal axial parenchyma and scarce paratracheal axial parenchyma, fibers with distinctly bordered pits; the rays are heterogeneous, uniseriate to multiseriate; uniseriate rays composed by upright,

square or procumbent cells, and the multiseriate rays with procumbent body cells and with upright and/or square marginal cells. Calcium oxalate crystals are usually observed in most species. Prismatic crystals are almost restricted to the chambers of axial parenchyma. The silica is not always present in all species (Dickison and Phend, 1985; Machado et al., 2007).

According to these premises, the comparisons of the fossil wood were made with selected and more akin species: *Styrax leprosus*, *Styrax camporum*, *Styrax subargenteus*, *Styrax officinalis*, and *Styrax benzoin*. *S. thyllosum* sp. nov. differs from *S. leprosus* because this extant species present vessels in radial multiple with ≥ 4 elements and solitary and alternate intervessel pits. The differences between *S. camporum* and *S. thyllosum* lay in the presence of scalariform and foraminate perforation plates, and perforated ray cells. *S. subargenteus* differs from the fossil specimen by the absence of simple perforation plates. *S. officinalis* has groups of sieve tubes, and *S. benzoin* is not akin to the new fossil wood because it has intercellular canals of traumatic origin (Table 2).

The tropical species of the genus *Styrax* have more crystals than temperate species. The crystals are observed in only three genera of Styracaceae: *Styrax*, *Halesia*, and *Bruinsmia* (Sakala et al., 2010). The presence of tyloses, vascular tracheids, and mixed scalariform and simple perforation plates, observed in the fossil material, were also observed in extant species of *S. benzoin*, *S. officinalis*, *S. platanifolius*, and *S. texanus* (Carlquist, 1980; Dickison and Phend, 1985; Damayanti et al., 2012; Schweingruber et al., 2013). The presence of a combination of scalariform and simple perforation plates may be correlated to the semi-ring porous wood as reported by Dickison and Phend (1985). These features were observed in species that inhabit seasonally dry regions of the southwest and west of North America and suggest an adaptation to dry environments (Dickison and Phend, 1985; Machado et al., 1997). The predominance of fibers with distinctly bordered pits in the

Table 2
Comparisons between closely related species of the genus *Styrax* and the fossil wood. References: Tortorelli (1956), Carlquist (1980), Dickinson and Phend (1985), Machado et al. (1997, 2007), Sakala et al. (2010), Damayanti et al. (2012), Schweingruber et al. (2013).

Species	Vessels		Rays				Fibers		Tracheids	Intercellular canals	Parenchyma strand length (cells)	Prismatic crystals		
	Porosity	Perforation plates	Tangential diameter (µm)	Tyloses and deposits	Intervessel pits	Width (cells)	Type	Perforated ray cells					Rays per mm	Pits
<i>Styracoxylon thyllosum</i> nov. sp.	D–S	Sc–Si	45–150	Tyloses	Alternate and opposite	1–5	He	A	26	B	P	P	A	Upright ray cells, axial parenchyma cells
<i>Styrax leprosus</i>	D	Sc	100	A	Alternate	1–4	He	A	11–14	B	P	P	A	Axial parenchyma cells
<i>Styrax officinalis</i>	S	Sc, Si, Re, Fo	100–200	Tyloses	Alternate	1–3	He	A	4–12	B	P	P	A	Axial parenchyma cells
<i>Styrax camporum</i>	D	Sc, Fo	50–106	Gum deposits	Circular to oval	1–3	He	P	11–20	B	P	P	A	Upright ray cells, axial parenchyma cells
<i>Styrax subargenteus</i>	D	Sc	35–90	A	Alternate	1–4	He	A	11–15	B	P	P	A	Axial parenchyma cells
<i>Styrax benzoin</i>	D	Sc	160	With deposit and tyloses common	Alternate	1–4	He	A	3–7	B	P and septate	P	A	Fibers, axial parenchyma cells, upright ray cells

Key to abbreviations used:

A = absent; P = present.

Growth ring: D = diffuse-porous; S = semi-ring porous.

Perforation plates: Si = simpler; Sc = scalariform; Fo = foraminiferate; Re = reticulate.

Rays type: He = heterocellular.

Pits: B = bordered.

wood of the *Styrax* species studied agrees with previous descriptions of the wood of Styracaceae (Carlquist, 1980; Machado et al., 2007).

5.2. Comparison with fossil species

Two fossil genera of Styracaceae are known in the world (Fig. 1): *Styracoxylon* (van der Burgh, 1978), with affinity to *Styrax*, and *Coryloxylon* (Prakash et al., 1971; Sakala et al., 2010), which was created for fossil wood related to *Corylus* sp. and assigned within the family Betulaceae by Prakash et al. (1971). This last fossil genus was recently reviewed by Sakala et al. (2010), who redescribed the species of this genus: *Coryloxylon nemejcii* and *C. tertiarum*, and included them within Styracaceae. These authors propose that the affinity with *Corylus* sp. is questionable and that the difference in vessel arrangement between *Coryloxylon nemejcii* and *C. tertiarum* do not seem to be systematically significant and can be explained by intraspecific or individual variability (Sakala et al., 2010). Furthermore, they did not observe the aggregate rays described by Prakash et al. (1971). Both species of *Coryloxylon* have anatomical characters closely related to Styracaceae by the presence of exclusively scalariform perforation plates, solitary vessels, or in radial multiples, uniseriate, and multiseriate heterocellular rays, diffuse, and diffuse-in-aggregates apotracheal axial parenchyma and prismatic crystals or silica. The fossil wood described in this paper differs from *Coryloxylon* (Prakash et al., 1971; Sakala et al., 2010) by the presence of diffuse-porous wood, mostly multiseriate rays of 3–4 cells wide, the absence of prismatic crystals in ray cells, and the absence of tyloses in vessel elements.

The fossil wood shows a vessel diameter of 100 to 200 µm, scalariform perforation plates, alternate to opposite intervessel pits, diffuse, and diffuse-in-aggregates apotracheal axial parenchyma and occasionally paratracheal axial parenchyma, rays of two distinct sizes, heterocellular, uniseriate, and multiseriate, body ray cells procumbent with 2–4 upright or square marginal cells, indicating placement in within *Styracoxylon* (van der Burgh, 1978). *Styracoxylon rhenanum* differs from *S. thyllosum* sp. nov. by the presence of vessels in radial multiples of 2–4 elements, scalariform perforation plates with ≤ 14 bars, and the absence of tylosis. The fossil wood shares anatomical features with Styracaceae fossil species already known. However, its combination of diagnostic features allows the recognition of a new species from the Upper Pleistocene of Argentina: *S. thyllosum* sp. nov.

The combination of diagnostic anatomical features indicates that the fossil wood described in this paper has a great affinity with Styracaceae (Metcalfe and Chalk, 1950; Gonsoulin, 1974; Miller, 1976; Dickinson and Phend, 1985; Wallnöfer, 1997; Machado et al., 2007; Schweingruber et al., 2013) and is the first unequivocal fossil wood with affinity to this family from Argentina.

5.3. Historical biogeography of the Styracaceae

The dicotyledonous family Styracaceae is distributed among all the major Tertiary mixed-mesophytic forest refugia of the Northern Hemisphere. Dispersal-vicariance analysis and Fitch parsimony optimization support a Eurasian origin for the Styracaceae, with subsequent dispersion to the Americas (Fritsch et al., 2001). The European origin is supported by the fossil record (see Manchester et al., 1999; Fritsch et al., 2001 and references herein), and the presence of *Styrax* in South America is the result of migration from southern North America at some time in the Neogene (Fritsch, 1999). The migration between the Americas and Eurasia via either the Bering land bridge or, more likely, the North Atlantic land bridge during the warm interval of the Eocene along with other evergreen boreotropical elements has presented phylogenetic evidence against a pantropical dispersion of evergreen elements in *Styrax*. Also, several vegetative characters in the Styracaceae are potentially

significant biogeographically in relation to adaptations to temperate or tropical climates (Fritsch et al., 2001).

The woody angiosperm genus *Styrax* is widespread but presents a disjunct distribution, occurring in the Americas, eastern Asia, and the Mediterranean region. The genus is the largest and most widespread of the all genera in the Styracaceae. In South America, it is distributed among a wide array of habitats, including lowland rain forest, montane rain forest, subparamo, tepui scrub, cerrado, and restingia vegetation (Fritsch, 2001).

The monophyly of the group of species of *Styrax* from western North America and western Eurasia provides qualified support for the Madrean–Tethyan hypothesis, which proposes a Cenozoic floristic connection among the semi-arid regions (Fritsch, 2001).

The phylogenetic data and the presence of seeds and fruits fossils from Eocene of Europe suggest, for the first time, that *Styrax* is a boreotropical element. This hypothesis was suggested by Fritsch (2001). The period and the means by which *Styrax* migrated to South America are not inferable from the available data. Fruits of neotropical *Styrax* species were suggested to have been bird-dispersed (Fritsch, 1999), providing a viable scenario for at least a limited long-distance dispersal across such a barrier (Fritsch, 2001).

The absolute time of migration of members of the *Styrax* to South America cannot be directly estimated because the fossil record from the neotropics is still insufficient (Fritsch, 1999). However, the complete absence of *Styrax* in Africa suggests that migration took place subsequent to the breakup of West Gondwana. The fossil record of the genus extends back to at least the Oligocene and possibly the Eocene in North America and Eurasia (Palamarev, 1987; Mai, 1995). If the origin of the genus can be dated from the earliest fossil evidence, then the migration must have taken place sometime after the Eocene or the Oligocene, which would be consistent with Raven and Axelrod's (1974) earliest time of migration to South America (Fritsch, 1999).

6. Conclusions

S. thyllosum sp. nov., recovered in the Arroyo Feliciano Formation (Upper Pleistocene), constitutes the first record of fossil wood for this unit and a reliable record of the Styracaceae in South America. In addition, it is the fourth record of Styracaceae fossil wood in the world.

The fossil record studied in this paper and the *Styrax* sp. fossil leaf found in the Paraná Formation by Anzótegui and Aceñolaza (2006) support the idea that the Styracaceae was present in the east of Argentina since at least the Miocene, corroborate its presence to latitudes approximately 30°S, and provide evidence that this family was more widespread in the past in South America.

If the Patagonia Styracaceae fossil reports (Berry, 1925, 1938; Raigemborn et al., 2009; [<http://bhort.bh.cornell.edu/histology/taxaLH.html>]) are reliable, the first occurrence of the family in South America would be from at least the Upper Palaeocene. Alternatively, the above-mentioned fossils would suggest a different dispersal route, from the south to the north, across the Antarctica route (Pennington and Dick, 2004). Thus, it is quite possible that Styracaceae were more widespread in the past and then became restricted to the north. This route, the Australia–Antarctica–South America connection, was previously proposed by González et al. (2007) for the historical biogeography reconstruction of Proteaceae.

The specimen described herein increases our knowledge on the wood fossil of Styracaceae in the Southern Hemisphere. Moreover, the presence of this fossil wood adds new information for future research regarding the historical biogeography of the family Styracaceae. New material from Patagonia is necessary to confirm the presence of Styracaceae in the fossil record in the southernmost part of South America during the Palaeogene.

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