

The first record of Lauraceae fossil woods from the Cretaceous Puerto Yeruá Formation of eastern Argentina and palaeobiogeographic implications



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ABSTRACT

In this paper, a new species of fossil wood, *Paraperseoxylon septatum* sp. nov. (Lauraceae), from the Cretaceous of Puerto Yeruá Formation, is described. The fossil wood herein studied has features of the Lauraceae family, and particularly resembles the extant genus *Persea* Mill. The possible climatic conditions of the Puerto Yeruá Formation were inferred using the Vulnerability Index, Mesomorphy ratios and the Taxon Independent Approach of the anatomical features present in the fossil wood described, suggesting a warm and humid to seasonally dry context. This material is the first record known from the Cretaceous of Northeastern Argentina and the earliest occurrence in the Southern Hemisphere of a fossil taxon with feature closest to *Persea*, and clearly establishes the presence of Lauraceae in Northeastern Argentina during the Cretaceous. Nowadays the genus *Persea* has a tropical and subtropical disjunct distribution in the Americas, Asia, and the Canary Islands. The present study provides information pertinent to understanding its phylogenetic context and biogeographic history.

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1. Introduction

The Lauraceae is a large family of woody plants (except for the herbaceous parasite *Cassytha*), with about 50 genera and 2500 to 3000 species distributed throughout tropical to subtropical latitudes (Chanderbali et al., 2001; Taylor et al., 2009). These plants represent an important part of the ecosystem of the tropical and subtropical forest regions in the Old and the New World (Richter, 1981). They are particularly diverse in American and Asian tropics and they also have a large number of species in Australia and Madagascar, but poorly represented in Africa (Cronquist, 1981; Werff and Richter, 1996).

This family is among the most speciose basal angiosperm families (APG III, 2009) and has an extensive fossil record including leaves, woods, pollen, fruits, seeds, and flowers from the Cenozoic,

with some reports as early as the Cretaceous (Herendeen et al., 1994; Taylor et al., 2009; Takahashi et al., 2014).

Wood assignable to the Lauraceae is relatively easy to recognize based on the presence of variable vessel-ray pitting, predominantly solitary small to medium vessels, alternate intervascular pitting, heterocellular rays, mostly one to three cells wide, vasicentric paratracheal parenchyma and oil cells (Metcalf and Chalk, 1950; Scott and Wheeler, 1982; Richter, 1987).

In this contribution, we have erected a new Lauraceae fossil wood species which resembles the extant genus *Persea* Mill., *Paraperseoxylon septatum* sp. nov., recovered in the Puerto Yeruá Formation (Cretaceous), Entre Ríos Province, Argentina and we provided new evidence of the diversity of the Lauraceae family during the Cretaceous. This is the first *Persea*-like wood known from the Cretaceous of Northeastern Argentina.

2. Geological setting

The Puerto Yeruá Formation (De Alba and Serra, 1959) is a Cretaceous succession exposed along the right margin of the

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Uruguay River, between the cities of Concordia and Colón, in the northeast of Entre Ríos Province, Argentina.

It is an intercalated set of fluvial siliciclastic rocks and calcrete horizons with alpha fabric (Tofalo and Pazos, 1999, 2002). These rocks were deposited from tractive-unidirectional currents with high to moderate energy, originated from rivers of sinuosity with lateral channel migration (Tofalo, 1986).

The significant thicknesses of the calcretes present in the Puerto Yeruá Formation is a very important tool for paleoclimate inferences and indicates that the sediments were possibly deposited in intermediate moisture conditions with marked seasonal rains (Tofalo, 1986).

The analyzed locality is near the Puerto Yeruá Village in the Department of Concordia (Fig. 1). Red sedimentary rocks from the Cretaceous unit lie exposed at this locality. This section is approximately two metres thickness, composed of fine to medium, reddish and silicified sands, fine to medium conglomerates and scarce greenish muds. The presence of mud and sand matrix-supported conglomerate is frequent. The top of the sequence is covered by vegetation (Figs. 2 and 3A).

The age of this unit is difficult to determine beyond a Cretaceous age (De Valais et al., 2003). However, this formation was assigned to the Upper Cretaceous based on presence of dinosaur remains *sensu* de Carles pers. com. (in Huene, 1929; pag. 81). Titanosaurid bones were found on the lenticular mud bed of the Uruguay River in Entre Ríos Province (Huene, 1929; Powell, 2003). A few materials analyzed by De Valais et al. (2003), a conical scute probably belonging to an Ankylosauria gen. and sp. indet., a small fragment of tooth from a Theropoda gen. and sp. indet. and a fragment of eggshells, cf. *Sphaerovum erbeni* Mones, do not provide sufficient data to estimate a more accurate age beyond the Cretaceous.

The Puerto Yeruá Formation is correlated with the Guichón Formation (Bossi, 1966) from Uruguay. In the latter, bones belonging to a derived titanosaurian (Eutitanosauria) and eggshells referred to the oogenus? *Sphaerovum* sp. indet. were described (Soto et al., 2009). This material is considered a fine indicator of the Upper Cretaceous for the Campanian–Maastrichtian range

(Casadío et al., 2002). If the presence of *Sphaerovum erbeni* can be confirmed, this would be solid evidence of a Late Cretaceous age (Campanian–Maastrichtian) for the Guichón Formation.

3. Material and methods

The fossil specimen was collected from the Puerto Yeruá fossiliferous Locality, situated in Puerto Yeruá, Entre Ríos Province, Argentina. The outcrop of the Puerto Yeruá Formation is situated at 31° 31' 55.23" S, 58° 1' 34.93" W (Fig. 1).

The material was preserved by siliceous cellular permineralization and has well-preserved secondary xylem. It was thin-sectioned (transversal, radial longitudinal and tangential longitudinal) using standard petrographic techniques. The wood was described and measurements undertaken in accordance with the IAWA recommendations (IAWA Committee, 1989). The quantitative values provided in the anatomical description are averages of 25 measurements. The average is cited first, followed by minimum and maximum values (in parentheses).

The Vulnerability Index (V) and Mesomorphy ratios (M) were calculated using the equations developed by Carlquist (1977). The taxon independent approach (TIA) was used in order to derive clearer insight into the paleoclimate (Martínez-Cabrera et al., 2014). The anatomical characteristics of wood were analyzed in terms of their associated palaeoecological requirements, including: vessel diameter, vessel density, percentage of solitary vessels, vessel arrangement, length of vessel elements, perforation plate types, porosity, axial parenchyma distributions, presence of septate fibers, parenchyma strand and growth rings (Carlquist and Hoekman, 1985; Wheeler and Baas, 1991, 1993; Lindorff, 1994).

The identification of the fossil wood samples was based on reference to wood classical descriptions of extant and fossil plants (Record and Hess, 1942; Metcalfe and Chalk, 1950; Tortorelli, 1956; Richter, 1987; Rancusi et al., 1987; Scott and Wheeler, 1982; Richter and Dallwitz, 2000; León, 2002; Wheeler and Manchester, 2002; InsideWood, 2004-onwards; Dupéron-Laudoueneix and Dupéron, 2005; Wheeler and Dillhoff, 2009).

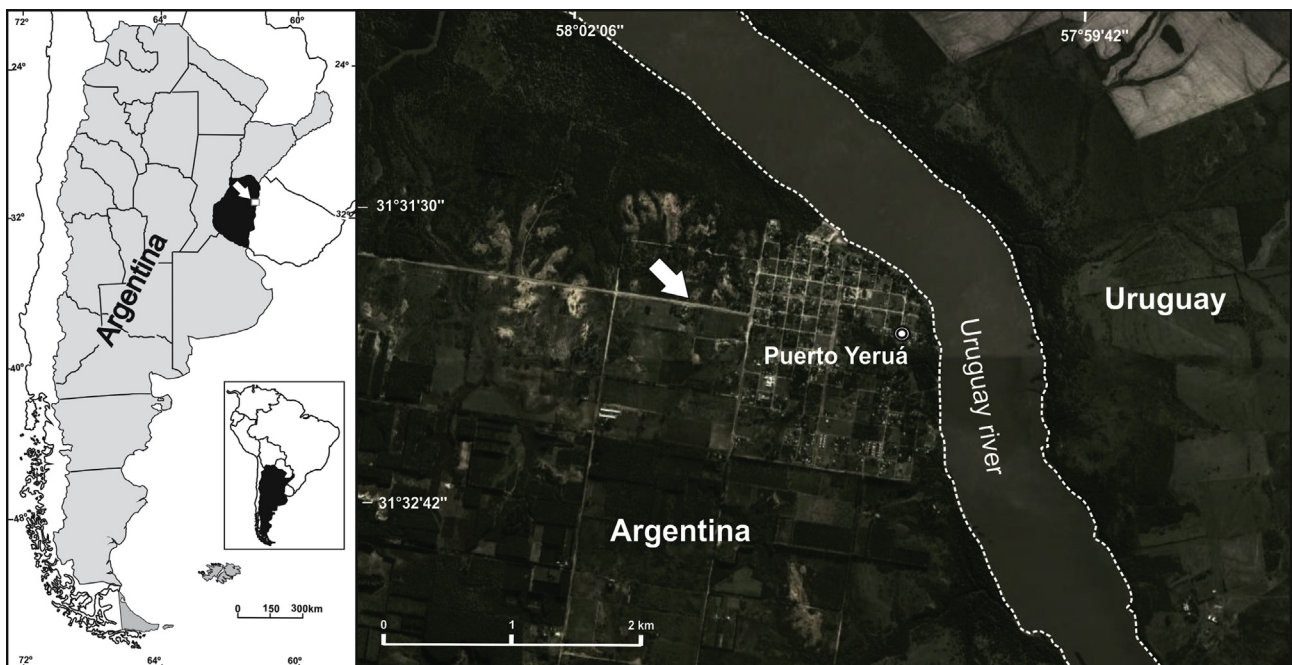


Fig. 1. Location map showing Puerto Yeruá fossiliferous locality, Entre Ríos, Argentina.

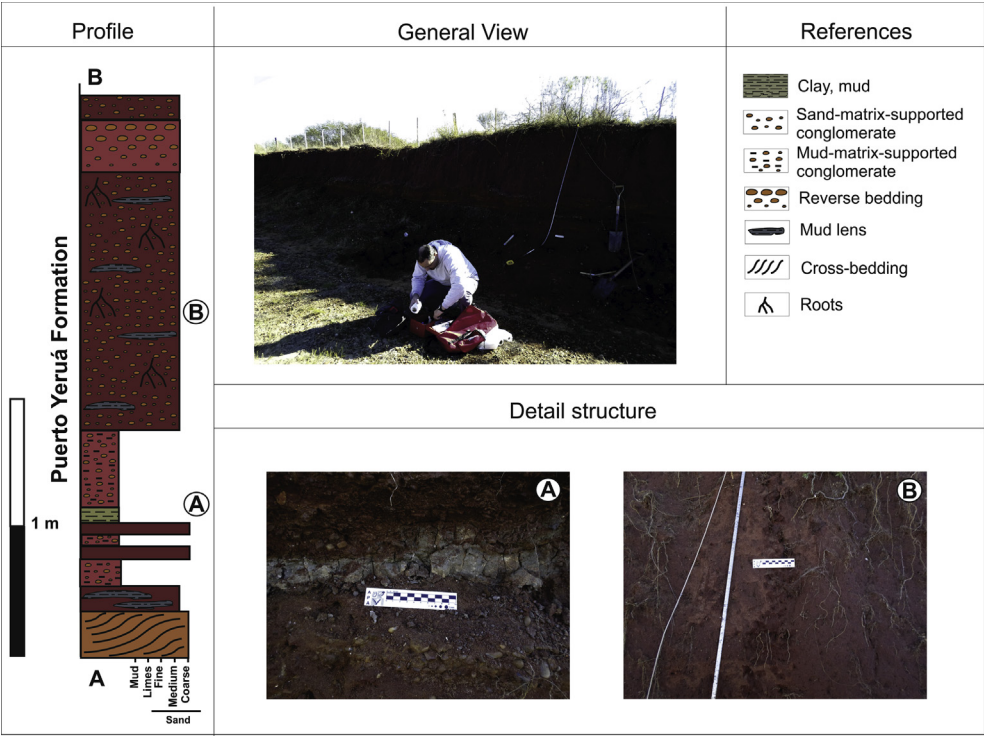


Fig. 2. Schematic profile at the Puerto Yerúa fossiliferous locality, Entre Ríos, Argentina.

The fossil sections were studied with a Nikon Eclipse E200 light microscope (using 40×, 100×, 400× and 1000× magnification levels) and the photomicrographs were taken with a Nikon Coolpix 990 digital camera. In addition, a scanning electron microscope (SEM) was used. The material was prepared for SEM by cutting a 1 cm³ block of wood that was mounted on SEM stubs without coating and then observed in a low vacuum using a SEM LEO

1450VP at the Universidad Nacional de San Luis, San Luis, Argentina and a SEM Jeol JSM-580 OLV at the Universidad Nacional del Nordeste, Corrientes, Argentina.

The macrofossil wood holotype is housed in the Museo de Antropología y Ciencias Naturales de Concordia, Concordia, Entre Ríos Province, Argentina, under the acronym MACNC-Pb 2513, and the isotype and thin-section slides were kept in the repository of

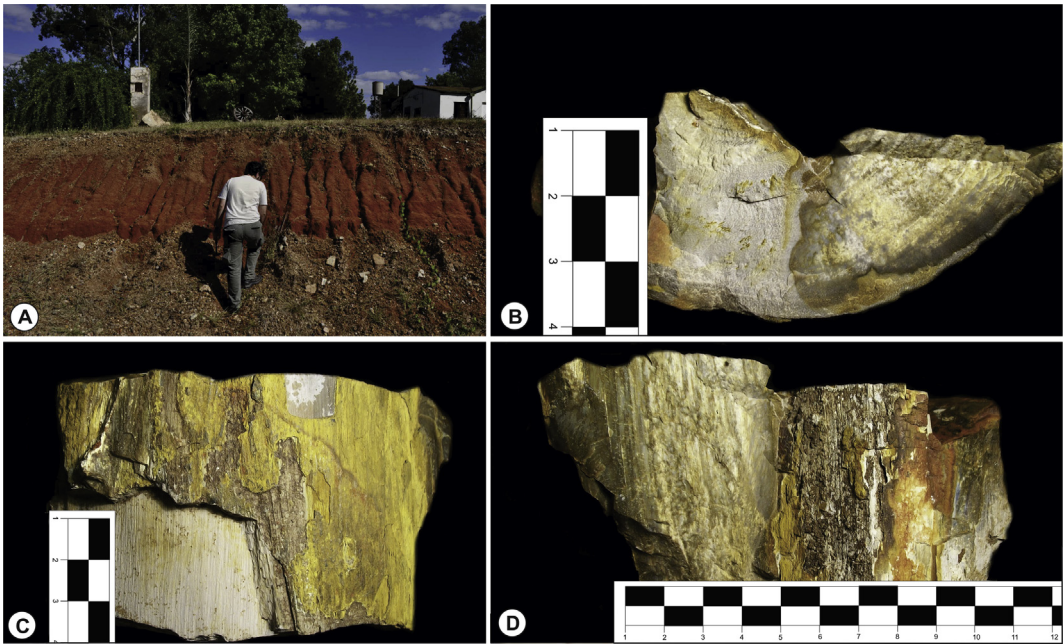


Fig. 3. A. Puerto Yerúa Formation. B–D. *Paraperseoxylon septatum* sp. nov. Holotype: MACNC-Pb 2513.

the Laboratorio de Paleobotánica, CICYTTP-CONICET, Diamante, Entre Ríos Province, Argentina, under the acronyms CIDPALBO-MEG 161 and CIDPALBO-MIC 1739 (a–c).

4. Systematic palaeobotany

Superorder Magnolianae Takht., 1967

Order Laurales Juss. ex Bercht. and J. Presl, 1820

Family Lauraceae Jussieu, 1788

Genus *Paraperseoxylon* Wheeler and Manchester, 2002.

Type species. *Paraperseoxylon scalariforme* Scott and Wheeler, 1982, p. 140, Figs. 23–27, by subsequent designation of Wheeler and Manchester 2002, p. 65, Fig. 16.

Paraperseoxylon septatum sp. nov.

Figs. 3–6.

Derivation of name. The specific epithet refers to the occurrence of septa in fibers and parenchyma.

Holotype. MACNC-Pb 2513.

Isotype. CIDPALBO-MEG 161 and CIDPALBO-MICmic 1739 (a–c).

Type locality. Puerto Yeruá, near Concordia city, in Entre Ríos Province, Eastern Argentina.

Stratigraphic horizon. Puerto Yeruá Formation (Cretaceous).

Diagnosis. Diffuse porous wood; solitary vessels, in radial multiples and rarely in clusters, mean tangential diameter of ≤ 100 μm ; simple and scalariform perforation plates; alternate and sub-opposite intervessel pits; vessel-ray parenchyma pits with distinct borders, similar to intervessel pits; non-septate and septate fibers; vasicentric, aliform to confluent axial parenchyma; 1–2 seriate rays, homocellular to weakly heterocellular, idioblastic secretory cells (“oil or mucilage cells”) common in ray parenchyma and among the fibers.

Description. The fossil specimen consists of an 8 cm long and 15.5 cm wide fragment and is very well preserved (Fig. 3B–D). The species is based on a piece of secondary wood. The pith, primary xylem, cortex and secondary phloem are absent. Growth rings are demarcated by larger radially compressed fiber walls and by terminal parenchyma (Fig. 4A). The wood shows diffuse porosity (Fig. 4A). Vessels are commonly solitary (68%), occasionally in radial multiples of 2–4 (30%) and rarely in clusters (2%) (Fig. 4A and D). The solitary vessels are circular to oval in outline and have thin walls (Fig. 4D). Vessels have a radial diameter of 66 (30–99) μm and a tangential diameter of 59 (20–78) μm . The mean vessel density is 7 (5–12)/ mm^2 . The vessel element length is 173 (110–235) μm , with oblique end walls (Fig. 4B and G). Perforation plates are simple (Figs. 4F and 6E); some are scalariform with 2 or 3 bars (Fig. 4E). Intervessel pits are very small, bordered, rounded, alternate and sub-opposite (Figs. 5E, I and 6E). Their diameters are 7 (6–8) μm .

The fibers are polygonal in outline, abundant, non-septate and sometimes septate, with poor preservation, with a diameter of 12 (10–15) μm and with a wall thickness of 3 (2–5) μm (Figs. 5B, D, H and 6F).

The axial parenchyma is paratracheal, vasicentric, lozenge-aliform to confluent, and has strands of seven to eleven cells (Figs. 4D, 5A, H and 6D).

The rays are commonly uniseriate (72%) and rarely biseriate (28%) (Figs. 4B, G–H, 5A–B and 6C–F). The number of rays per mm linear is 7 (5–9 per mm linear). They are homocellular, composed exclusively of procumbent cells (Figs. 4C, E–F and 6A) and rarely partially heterocellular with one row of upright and/or square cells (Figs. 4I and 5C). The rays' width of is 20 (15–30) μm . The rays' height is 194 (100–370) μm and 12 (3–25) cells high. They are Homogeneous type III of Kribs or Heterogeneous type III of Kribs. There are oil or mucilage cells associated with ray parenchyma (Figs. 4J, L, 6A and F) and among fibers (Figs. 4K and 5G).

Vessel-ray parenchyma pits, with distinct borders, are similar to intervessel pits in size and shape throughout the ray cell (Fig. 5F and J).

5. Discussion

5.1. Comparison with extant species

Oil and mucilage cells are diagnostic character and are limited to very few woody dicotyledons: Annonaceae, Aristolochiaceae, Burseraceae, Canellaceae, Dilleniaceae, Hernandiaceae, Lauraceae, Magnoliaceae, Monimiaceae, Myristicaceae, Piperaceae, Rutaceae, Saurauaceae, Schisandraceae, Winteraceae (Metcalfe and Chalk, 1950). Of these families, only the Lauraceae have growth ring boundaries distinct, simple and scalariform perforation plates, vasicentric axial parenchyma, ray width of 1–3 cells, oil and/or mucilage cells associated with ray parenchyma and present among fibers (InsideWood, 2004 onwards).

Richter (1987) found three classes of vessel-ray parenchyma pits in the Lauraceae, which closely relate to diameter classes of intervessel pits:

Class a: intervessel pits with a diameter of 8 (3–7) μm and vessel-ray parenchyma pits of similar size and shape as intervessel pits, sometimes opening into compound pits which are extended horizontally or vertically or are curved.

Class b: intervessel pits with a diameter of 15 (8–12) μm and vessel-ray parenchyma pits variable in shape, round to oval, to elongated horizontally, vertically or diagonally.

Class c: intervessel pits from 10 to 15 μm with vessel-ray parenchyma pits very large and window-like.

The fossil studied has class a vessel-ray parenchyma pits *sensu* Richter (1987). The extant Lauraceae taxa that have this kind of vessel-ray parenchyma pits are *Actinodaphne* Nees., *Chlorocardium rodiei* (Schomb.) Rohwer, H.G. Richt. & van der Werff, *Laurus* L., *Lindera* Thunb., *Litsea chinensis* Lam., *Neolitsea* (Benth.) Merr., *Persea* Mill. (North American species), *Sassafras* J. Presl and *Umbellularia* (Nees) Nutt. The fossil wood was compared with these genera in Table 1 and it is most closely related with *Persea*.

The wood of *Persea* is similar to most of the other members of the Lauraceae in some characters. However, *Persea* differs from other Lauraceae in having the combination of simple and scalariform perforation plates, homogeneous or heterogeneous rays, vasicentric, lozenge-aliform, confluent and in strand parenchyma, and idioblast present in parenchyma and among the fibers (Record and Hess, 1942; León, 2002).

The extant species of *Persea* are indistinguishable in terms of wood anatomy. Therefore, we cannot assign the Cretaceous fossils to a single extant species.

5.2. Comparison with fossil species

The fossil wood described herein was compared with other fossil genera assigned to Lauraceae (Table 2). *P. septatum* sp. nov. has simple and scalariforms perforation plates. This character is only present in *Cinnamoxylon* Gottwald, *Laurinoxylon* (Felix) emend Duperón, Duperón-Laudoueneix, Sakala and Franceschi, *Paraperseoxylon* Wheeler and Manchester, and *Sassafrasoxylon* Brezinová and Süss (Table 2).

Dupéron-Laudoueneix and Dupéron (2005) reviewed fossil woods assigned to Lauraceae and most of Lauraceae fossil woods have been assigned to the genus *Laurinoxylon* Felix, 1883. The diagnostic characters of this genus are the following: solitary vessels and in radial multiples, simple and scalariform perforation plates, paratracheal parenchyma, 1–5 seriate rays, weakly heterocellular, vessel-ray parenchyma pits very large and elongated, and

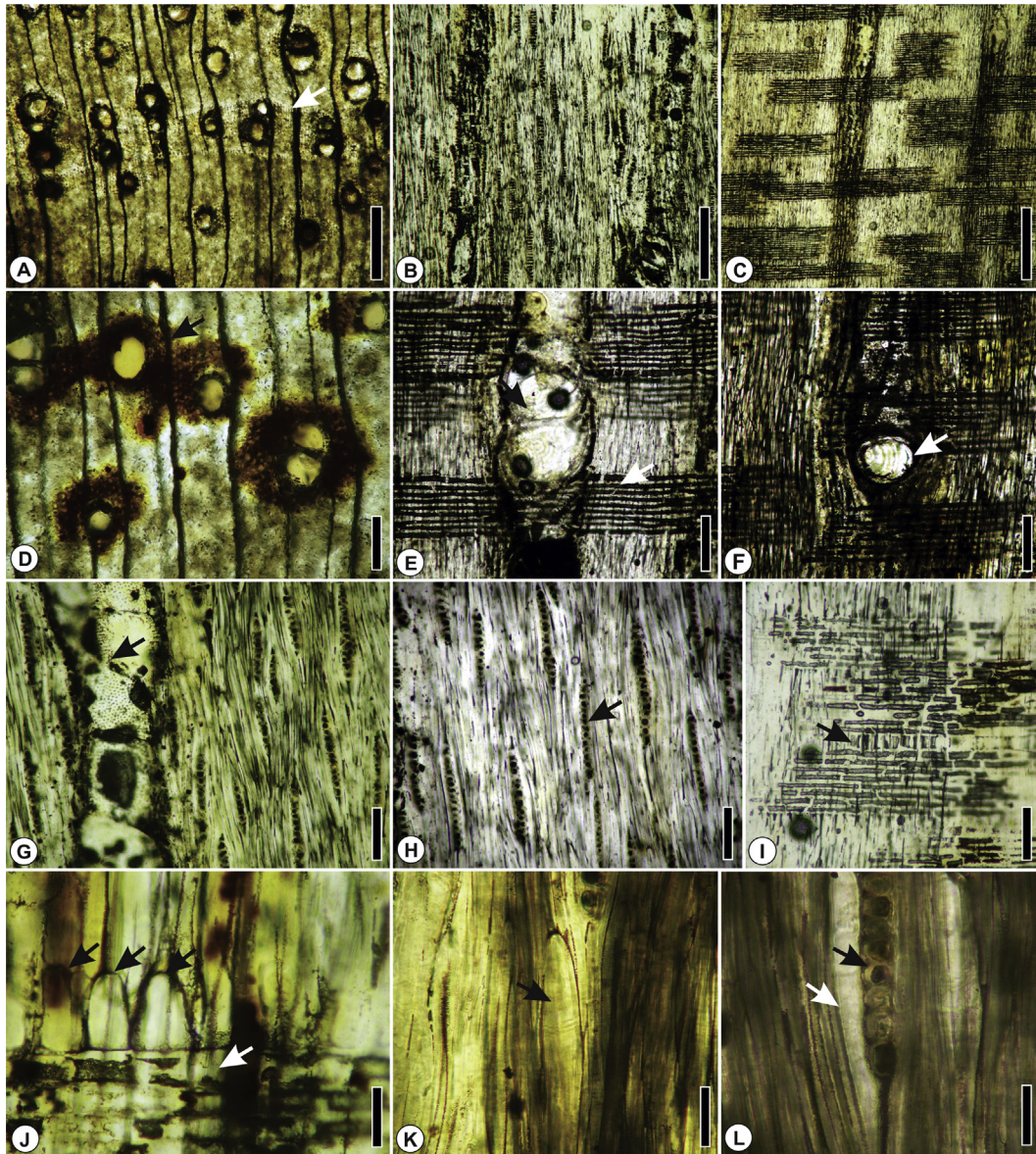


Fig. 4. *Paraperseoxylon septatum* sp. nov. Holotype: MACNC-Pb 2513. A. General view in transverse section (ts), the arrow indicate a growth ring. B. General view in tangential longitudinal section (tls). C. General view in radial longitudinal section (rls). D. Solitary and radial multiples vessels, the arrow indicate confluent parenchyma (ts). E. Homocellular rays (white arrow) and scalariform perforation plate (black arrow; rls). F. Simple perforation plate (white arrow; rls). G. Rays and vessels, the arrow indicates an oblique end wall (tls). H. Uni-biseriate rays (tls). I. Heterocellular ray (rls), the arrow indicates an upright cell. J. Oil or mucilage cells (black arrows) associated with ray parenchyma (white arrow), rls. K. Oil or mucilage cell (black arrow) present among fibers, rls. L. Oil or mucilage cell (white arrow) associated with ray parenchyma (black arrow), tls. Scale bar in A–C = 200 μ m; in D–I = 100 μ m; in J–L = 30 μ m.

oil or mucilage cells (Duperón et al., 2008). *P. septatum* sp. nov. has homocellular and heterocellular narrower rays and the vessel-ray pits are similar to intervessel pits in size and shape (Table 2).

P. septatum sp. nov. differs from *Cinnamomoxylon* Gottwald in the type of ray (Table 2; Dupéron-Laudoueneix and Dupéron, 2005). *Sassafrasoxylon* Brezinová and Süss has ring-porous wood, with multiple rings of earlywood pores; parenchyma sparsely paratracheal; 1–4 seriate rays; vessel-ray pits enlarged, rounded to horizontally elongated and unilaterally bordered which differ from those of the fossil specimen studied herein (Table 2; Poole et al., 2000).

P. septatum sp. nov. is assigned to *Paraperseoxylon* Wheeler and Manchester based on the presence of class a vessel-ray parenchyma pits *sensu* Richter (1987), both simple and scalariform perforation plates and idioblasts scattered among the fibers and occurring in

rays (Wheeler and Manchester, 2002; Wheeler and Dillhoff, 2009). This fossil genus was erected by Wheeler and Manchester (2002) who described a lauraceous fossil, *P. scalariforme* (Scott and Wheeler) Wheeler and Manchester, from the middle Eocene of the Nut Beds Flora of the Clarno Formation, with anatomical characters closest to those of the extant genera *Actinodaphne*, *Laurus*, *Lindera*, *Persea* and *Neolitsea*. This material was originally described as *Ulmium scalariforme* Scott and Wheeler (Scott and Wheeler, 1982). The fossil material described herein is very similar to the type species, but differ from it in the presence of distinct growth ring boundaries, septate and non-septate fibers, homocellular and heterocellular rays, and in the type of axial parenchyma (Wheeler and Manchester, 2002).

In Argentina, a fossil wood, *Laurinoxylon atlanticum* (Romero) Dupéron-Laudoueneix and Dupéron 2005, with closest affinities

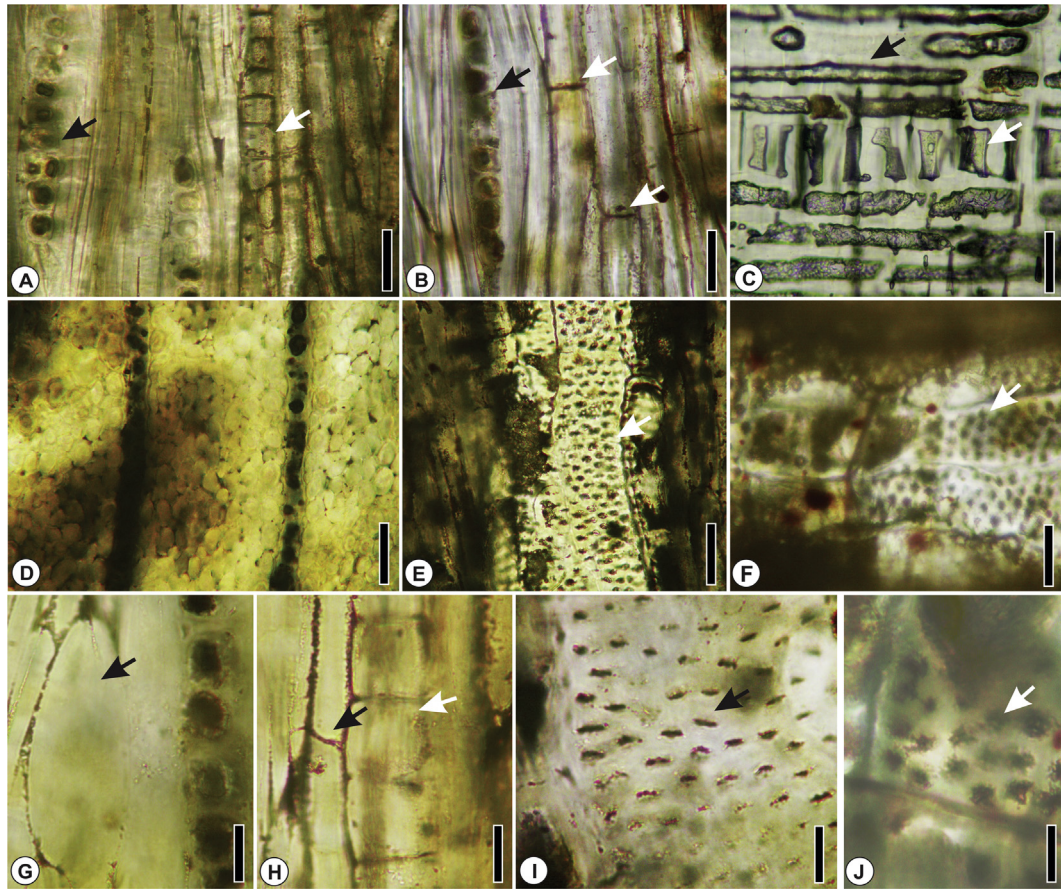


Fig. 5. *Paraperseoxylon septatum* sp. nov. Holotype: MACNC-Pb 2513. A. Biseriate ray (black arrow) and parenchyma strand (white arrow), tls. B. Uniseriate ray (black arrow) and septate fibers (white arrows), tls. C. Detail of a heterocellular rays with procumbent (black arrow) and upright cells (white arrow), rls. D. Detail of the fibers in ts. E. Vessels with alternate intervessel pits (white arrow) in ts. F. Vessel ray pits with distinct borders, similar to intervessel pits (white arrow). G. Detail of oil or mucilage cell (black arrow) present among fibers in tls. H. Detail of a septate fiber (black arrow) next to parenchyma strand (white arrow) in ts. I. Detail of intervessel pits (black arrow). J. Detail of vessel ray pits (white arrow). Scale bar in A–F = 30 μ m; in G–J = 10 μ m.

with the genus *Persea*, specially *P. lingue* (Miers ex Bertero) Nees is reported from the Eocene of Patagonia (Romero, 1970) and upper Oligocene of Neuquén, Argentina (Brea et al., 2015). The material described by Romero (1970) is characterized by diffuse porous wood; solitary vessels, in radial multiples; simple perforation plates; short vessel members with narrow diameters and with mostly alternate intervessel pits; vasicentric parenchyma, sometimes aliform and locally confluent; low rays, 1–2 seriate, heterocellular; narrow fibers with thin walls and few cells with contents, only present in ray cells. The differences between *P. septatum* sp. nov. and *Laurinoxylon atlanticum* are in the type of the perforation plates, ray type and in the absence of oil cells among fibers.

In addition, several fossil woods with Lauraceae affinity in the Cenozoic of Chubut and Entre Ríos in Argentina were studied: *Laurinoxylon chubutense* (Romero) Dupéron-Laudoueneix and Dupéron, *Laurinoxylon artabeae* (Brea) Dupéron-Laudoueneix and Dupéron, *Curtiembreoxylon poledrii* Franco, *Laurinoxylon mucilaginosum* (Brea) Dupéron-Laudoueneix and Dupéron and *Beilschmiedioxylon parataubertiana* Ramos, Brea and Kröhling (Brea, 1995, 1998; Franco, 2012; Ramos et al., 2012). These materials do not have *Persea*-like wood and are different from the new fossil wood studied here.

5.3. Palaeoecology and palaeobiogeographic implications

The *Persea* group sensu Rohwer et al. (2009) consists of seven currently recognized genera: *Alseodaphne* Nees, *Apollonias* Nees,

Dehaasia Blume, *Machilus* Rumphius ex Nees, *Nothaphoebe* Blume, *Persea* Mill. and *Phoebe* Nees, including a total of c. 400 to 450 species. About 80% of these species are distributed in tropical to subtropical Asia, the rest are found in warm-temperate to tropical regions of the New World (Li et al., 2011). These occur mainly in montane forests in Central and South America and range from Mexico to Chile, reaching the Atlantic coastal forests in south-eastern Brazil (Chanderbali et al., 2001). Only two species, *Apollonias barbujaana* (Cav.) Bornm. and *Persea indica* (L.) Spreng., are distributed in the Macaronesian Islands (Li et al., 2011).

The genus *Persea* has a tropical and subtropical disjunct distribution in the Americas, Asia and the Canary Islands (Raven and Axelrod, 1974; Rohwer, 1993). This is due to its extinction in Europe and Africa, with only *P. indica* surviving as endemic in the laurel forests of the northern coast of the Canary Islands (Raven and Axelrod, 1974).

In South America, *Persea* is found chiefly in the montane forests of east central to southern Brazil. There, some species are native. Most of the remaining South American species populate the upper rainforests on the slopes of the Andes. In addition, two endemic species are present in the Guayana Highlands, and *P. lingue* (Nees) reaches into the temperate zones of Chile and Argentina. From the mountain chains of Central America, the genus continues along the Sierra Madre Occidental to the Sierra Madre Oriental of Mexico. Only *P. caerulea* (Ruiz and Pavon) Mez occurs in both South and Central America (Scora and Bergh, 1992). The presence of *P. septatum* sp. nov. in the Argentinian Mesopotamic region implies that

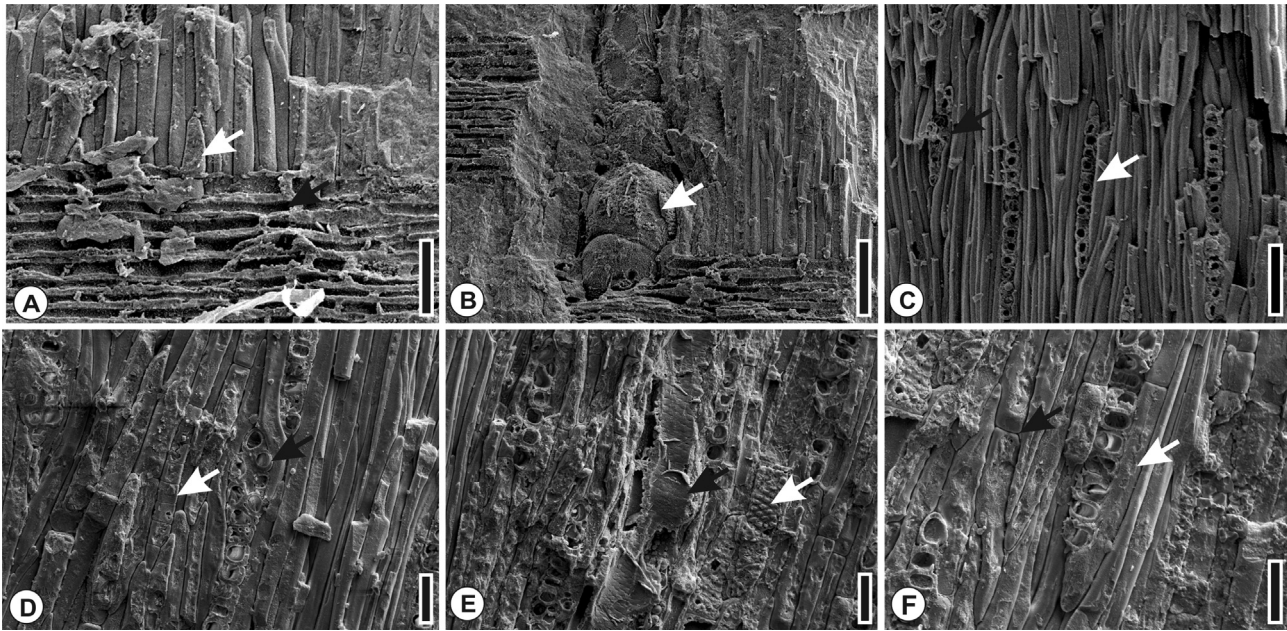


Fig. 6. *Paraperseoxylon septatum* sp. nov. Holotype: MACNC-Pb 2513. A. Oil or mucilage cells (white arrow) associated with ray parenchyma (black arrow) in rls. B. Vessels (white arrow) and homocellular rays in rls. C. Uniseriate (white arrow) and biseriate (black arrow) rays in tls. D. Biseriate ray (black arrow) and parenchyma strand (white arrow) in tls. E. Vessel with a simple perforation plate (black arrow) and intervessel pits (with arrow) in tls. F. Septate fiber (black arrow) and oil or mucilage cell (white arrow) associated with ray parenchyma, tls. Scale bar in A = 15 μ m; in B = 25 μ m; in C = 20 μ m; in D–F = 40 μ m.

this taxon was more widespread in the geological past and has experienced extinction in this region.

Lauraceae fossils are common in Cretaceous and Cenozoic deposits of both the Northern and Southern Hemisphere (Poole et al., 2000 and references therein). *Persea* fossil distribution is different from its present range. It grew in regions that are now temperate and even polar (Scora and Bergh, 1992). Fossil record of *Persea*-like organs is known in North America from the Eocene onwards (Schroeder, 1968; Herendeen et al., 1994; Wheeler and Manchester, 2002), and wood very similar to that of this genus is known from the Eocene of Patagonia (Romero, 1970). This fossil wood from the Cretaceous Puerto Yeruá Formation of the Argentinian Mesopotamic Region is the earliest record of *Persea*-like wood.

The history of the Cretaceous vegetation in the Argentinian Mesopotamic Region is not known. This is the first paleobotanical Cretaceous record for this region. However, the presence of Lauraceae fossils was confirmed in the Cenozoic of this region in several formations by fossil woods, leaf compressions and cuticles: *Ocotea* sp. and *Laurophyllum* sp. (leaves) in the Paraná Formation (upper Miocene); *Nectandra* sp. 1, *Nectandra* sp. 2, *Nectandra* sp.? and *Ocotea* sp.? (leaves), *Laurinoxylon artabaeae* (Brea) Dupéron-Laudoueneix and Dupéron and *C. poledrii* Franco (fossil woods) in the Ituzaingó Formation (upper Cenozoic), *Laurinoxylon mucilaginosum* (Brea) Dupéron-Laudoueneix and Dupéron, *Laurinoxylon artabaeae* (Brea) Dupéron-Laudoueneix and Dupéron and *B. parataubertiana* Ramos, Brea and Kröhlhling (fossil woods) in the El Palmar Formation (Upper Pleistocene) (Anzótegui, 1980; Aceñolaza and Aceñolaza, 1996; Brea, 1998; Anzótegui and Aceñolaza, 2008; Franco, 2012; Ramos et al., 2012).

Many of the anatomical characters observed in *P. septatum* sp. nov. support the idea that the fossil wood studied here possibly lived under warm and humid to seasonally dry environmental conditions. The Vulnerability Index (V) and Mesomorphy ratios (M) in the fossil wood show values of 8.43 and 1458 respectively. These values indicate that *P. septatum* sp. nov. shows mesomorphic features (Carlquist, 1977).

Using TIA method, anatomical features of the fossil wood indicates that the presence of few small vessels, with simple and scalariform (with low bar numbers) perforation plates is common in tropical lowland habitats (Wheeler and Baas, 1991). Distinct growth rings are considered indicators for seasonal climates (Creber and Chaloner, 1984; Wheeler and Baas, 1991, 1993). However, concerning the evolution in wood character, scalariform plates and heterogeneous rays are usually considered primitive characters. *P. septatum* sp. nov. has both primitive and advanced characters, as simple perforation plates and alternate intervessel pits. Most genera of Lauraceae have both scalariform and simple perforation plates, which are considered a transitional position in the Lauraceae. This suggests that Lauraceae are more transitional rather than primitive among the allied families of the Laurales (Heo, 1998). The climate inferred from the wood anatomy of *P. septatum* sp. nov. agrees with sedimentological data (Tofalo, 1986) and suggests a humid to semiarid seasonal climate during this geologic period.

Lauraceae was widespread and diverse by the Early Cretaceous (Renner, 2005). This family radiated when trans-Tethyan migration was relatively easy, and basal lineages were clearly established on the Gondwana or Laurasian terrains by the Late Cretaceous (Renner, 2005). Biogeographic studies suggested that the basal lineages of Lauraceae were sorted into two main geographic groups of Gondwanan or Laurasian origins (Chanderbali et al., 2001; Nie et al., 2007; Li et al., 2011).

Scora and Bergh (1992) proposed the western African Gondwanaland flora, probably by Paleocene time, as the place of origin of *Persea*. For these authors, its ancestral species migrated to Asia, where around 80 species exist today. Other species migrated to southwestern Europe and from there to North America when Eurasia and North America were in direct contact during the Late Cretaceous and islands were scattered along the mid-Atlantic ridge in the Paleogene times. Other species migrated from Africa via Antarctica, which at that time and with its geographic location close to Africa, was covered with tropical rainforests common to

Table 1

Comparison between the selected wood anatomical characters of *Paraperseoxylon septatum* sp. nov. and most related extant genera of Lauraceae. References: Record y Hess 1942; Hwang, 1962; Nazma et al., 1981; Rancusi et al., 1987; Hoadley, 1990; Heo, 1998; Silva Guzmán et al., 1999; León, 2002; InsideWood 2004–onwards.

	Growth rings	Vessels	Perforation plates	Intervessel pits	Fibers	Parénquima	Rays	Idioblast
<i>Paraperseoxylon septatum</i> sp. nov.	Distinct	Small to medium sized (<100 µm). Mostly solitary and radial multiples of 2–4 pores and rarely in clusters.	Simple and scalariform	Small, bordered, rounded, alternate and sub-opposite	Non-septate and sometimes septate	Paratracheal, vasicentric, lozenge-aliform to confluent, and in strands	1–2 seriate, homogeneous	Present in axial and radial parenchyma and among de fibers
<i>Actinodaphne</i> Nees.	Distinct	Moderately small (90–100 µm),	Simple and scalariform	Moderately small (7–10 µm), oppositely	Thick-walled	Apotracheal diffuse	1–2 seriate, rarely triseriate, heterogeneous	Present in axial and radial parenchyma and among de fibers
<i>Chlorocardium rodiei</i> (Schomb.) Rohwer, H.G.Richt. & van der Werff	Absent	115–160 µm of diameter Solitary, radial multiples (2–3) and in clusters	Simple	3.75–5 µm	Non septate, thick walled	Paratracheal, vasicentric, lozenge-aliform, confluent, in strand (3–10 cells)	1–2 seriate, homogeneous, occasionally heterogeneous	Absent
<i>Laurus</i> L.	Distinct	Small (<70 µm). Mostly solitary and radial multiples of 2–4 pores.	Simple and scalariform	Alternate, circular, 7–8 µm	Sometime septate present	Paratracheal and scarce	Predominantly multiseriate with uniseriate tails, heterogeneous and homogeneous	Rarely observed in parenchyma strand
<i>Lindera</i> Thunb.	Distinct	Small (50–65 µm) of diameter. Solitary and in small radial multiples.	In part scalariform with a few coarse bars	Small (5 µm), not crowded	With medium thick gelatinous wall	Sparingly paratracheal	1–3 seriate. Weakly heterogeneous	With much reduced borders to apparently simple
<i>Litsea chinensis</i> Lam.	Distinct or absent	Medium to small, mostly in radial multiples of 2 or 3, rarely 6 and occasionally solitary	Simple and scalariform	Alternate, small to large	Septate and non septate	Paratracheal, vasicentric, scarce	Moderately broad to fine	Present in axial and radial parenchyma and among the fibers
<i>Neolitsea</i> (Benth.) Merr.	Distinct	Medium to small. Solitary vessel outline angular	Simple and scalariform	Alternate, small to medium	Septate and non septate	Paratracheal, vasicentric, in strand	1–3 seriate or multiseriate, heterogeneous,	Present in axial and radial parenchyma
<i>Persea</i> Mill.	Distinct or absent	Mostly medium-sized, occasionally only 70 µm Solitary and radial multiples (2–5), rare in clusters.	Simple and scalariform	Alternate, 9–15 µm	Septate or septate a non septate	Vasicentric, lozenge-aliform, confluent, in strand (2–7 cells)	1–5 seriate, mostly 2–3 seriate; heterogeneous or homogeneous	Present in axial and radial parenchyma and among de fibers
<i>Sassafras</i> J. Presl	Distinct	Circular porosity. Solitary or in small multiples	Simple and scalariform	Medium to large (7–14 µm)	Thin-walled	Fairly abundant, paratracheal and confluent	1–4 seriate, heterogeneous	Present in axial and radial parenchyma and among de fibers
<i>Umbellularia</i> (Nees) Nutt.	Distinct	Small-medium (100–200 µm). Solitary and in multiples of 2 to several	Simple	Alternate, with medium-sized, rounded to angular pits. Small to medium (4–10 µm)	Non septate or septate.	Vasicentric parenchyma	1–4 (mostly 2) seriate, heterogeneous	Present in radial parenchyma

Table 2

Comparison of anatomical characteristics between Lauraceae fossil genera and *Paraperseoxylon septatum* sp. nov. References: [Leisman 1986](#); [Richter, 1987](#); [Wheeler and Manchester 2002](#); [Dupéron-Laudoueneix and Dupéron, 2005](#); [Castañeda-Posadas et al., 2009](#); [Wheeler and Dillhoff, 2009](#); [Franco 2012](#).

	Growth rings	Porosity	Vessels	Perforation plates	Intervessel pits	Fibers	Parénquima	Rays	Vessel ray pits	Idioblast
<i>Paraperseoxylon septatum</i> sp. nov.	Distinct	Diffuse	Solitary, in radial multiples and rarely in clusters	Simple and scalariform	Rounded, alternate and sub-opposite	Non-septate and septate	Paratracheal, vasicentric, lozenge-aliform to confluent, and in strands (7–11 cells)	1–2 seriate, homocellular, and few partially heterocellular	With distinct borders, are similar to intervessel pits in size and shape	In ray parenchyma and among fibers
<i>Argapaloxyton</i> Castañeda-Posadas, Calvillo-Canadell and Cevallos-Ferriz, 2009	Distinct	Diffuse	Solitary, in radial multiples, and few clusters	Simple	Oval and alternate	Septate and non septate	Vasicentric and diffuse	Biseriated mainly homogeneous	Opposite	Present
<i>Beilschmiedioxylon</i> Dupéron-Laudoueneix and Dupéron, 2005	Distinct to indistinct	Diffuse	Solitary and in clusters	Simple	Alternate and large (10–12 µm)		Paratracheal, vasicentric, sometimes in bands	1–6 seriate, heterocellular	Very large and elongated	Present, among fibers
<i>Caryodaphnopsylon</i> Gottwald, 1992				Simple	8–13 µm	Septate	Vasicentric	7–8 (12) cells wide and 1.5–2 (4) mm de long, heterocellular		In parenchyma
<i>Cinnamoxylon</i> Gottwald, 1997				Simple and scalariform			Vasicentric, aliform and confluent	Weakly heterocellular		In rays and parenchyma
<i>Cryptocaryoxylon</i> Leisman, 1986	Distinct		Solitary and in radial multiples of up to four	Simple	Circular, bordered or scalariform pits	Elongate and with pointed ends, pits simple	Sparse, in tangential bands up to 15 cells wide, probably paratracheal	Usually multiseriate, up to 5 cells wide, homocellular		In ray parenchyma and among de fibers
<i>Curtiembrexylon</i> Franco, 2012		Diffuse	Solitary, in radial and tangential series and in clusters	Simple	Very small	Arranged in radial row	Scarce vasicentric	2–3 cells width, homocellular		In ray parenchyma and among the fibers.
<i>Laurinoxylon</i> (Felix) emend Dupéron, Dupéron-Laudoueneix, Sakala and Franceschi, 2008			Solitary and in radial multiples	Simple and scalariform	Alternate and large		Paratracheal	1–5 seriate, weakly heterocellular	Very large and elongated	Present
<i>Mezilaurinoxylon</i> Wheeler and Manchester, 2002		Diffuse	Solitary and in short radial multiples	Simple	Alternate, >10 µm	All septate	Scanty paratracheal to vasicentric	1–5 seriate, heterocellular, usually with one row of marginal square to upright cells	Enlarged and with reduced borders	Occasional in ray margin
<i>Olmosoxylon</i> Estrada-Ruiz, Martinez-Cabrera and Cevallos-Ferriz 2010	Indistinct		Solitary and in radial multiples of 2–4,	Simple	Alternate	Septate and non septate	Scanty paratracheal	Grouped, homocellular and heterocellular	Very large of variable form, class B and C of Richter (1987)	Irregularly distributed in the rays
<i>Paraperseoxylon</i> Wheeler and Manchester, 2002		Diffuse	Solitary and in short radial multiples	Simple and scalariform	Crowded alternate, approximately 5 µm across	Non septate, thin to thick wall	Scanty paratracheal to vasicentric to confluent	1–4 seriate, weakly heterocellular	Richter class a (1987)	Common in ray margins, and scattered among fibers
<i>Richteroxylon</i> Wheeler and Dillhoff, 2009	Distinct to indistinct	Diffuse	Solitary and in short radial multiples	Predominantly simple	Crowded alternate, small to medium	Predominantly non-septate	Scanty paratracheal to vasicentric	1–3 seriate	Similar to intervessel pits in size and shape	Present, associate with rays
<i>Sassafrasoxylon</i> Brezinová and Süß, 1988		Ring		Simple and scalariform	Alternate and bordered		Sparsely paratracheal	Homogeneous to weakly Heterogeneous, 1–4 seriate	Enlarged, rounded to horizontally elongated and unilaterally bordered	Present

South America (Scora and Bergh, 1992). When North and South America joined in the late Neogene, the genus was united again. Mountain building in Central America created new habitats in which speciation could take place (Scora and Bergh, 1992).

Later, Rohwer et al. (2009) considered two possible hypotheses to explain the American–Macaronesian disjunction pattern of the *Persea* group. One is the relict hypothesis: Macaronesian species of Lauraceae may well be interpreted as relicts from the European–Mediterranean Cenozoic laurel forest. An alternative explanation is the long-distance dispersal hypothesis. Rohwer et al. (2009) considered this less likely: the Macaronesian Islands are far too young for a Cretaceous disjunction and a long dispersal in the opposite direction, from America to Macaronesia, seems unlikely too for the present authors because *Persea indica* appears nested among the American species in their analysis. However, this last hypothesis appears to be a possible explanation for the American–Macaronesian disjunction between neotropical *Persea* species and the Macaronesian species for Li et al. (2011).

Li et al. (2011) suggested that the *Persea* group originated from the Perseeae–Lauraeae radiation in early Eocene Laurasia. The tropical and subtropical Amphi-Pacific disjunction pattern of the *Persea* group probably resulted from the disruption of the boreotropical flora by climatic cooling during the mid-to late Eocene. However, the American–Macaronesian disjunction pattern in the *Persea* group is also most likely explained by long-distance dispersal.

The presence of a Cretaceous fossil wood with affinity to *Persea* from the Puerto Yeruá Formation, Eastern Argentina, provides information relevant to understanding the biogeographic history of this genus and its phylogenetic context.

6. Conclusions

A new Cretaceous Lauraceae species, *P. septatum* sp. nov., has been studied from the Puerto Yeruá Formation in Entre Ríos Province, Eastern Argentina. This material, with anatomical characters similar to the extant genus *Persea*, is the first record known from the Cretaceous of Northeastern Argentina.

This is the earliest occurrence in the Southern Hemisphere of a fossil taxon with features closest to *Persea*, now with a tropical and subtropical disjunct distribution in the Americas, Asia, and on the Canary Islands. The modern distribution of *Persea* may represent a relict of a more geographically widespread taxon in the past.

The Vulnerability Index, Mesomorphy ratios and the Taxon Independent Approach indicate that this new fossil wood grew under warm and humid to seasonally dry environmental conditions.

P. septatum sp. nov. clearly establishes the presence of Lauraceae in Northeastern Argentina during the Cretaceous. This material is very important because of the critical role of fossils and because of the morphological considerations of fossils in phylogenetic contexts. The present study provides information pertinent to understanding the phylogenetic context and the biogeographic history of the *Persea*-like group.

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