Lauraceous fossil woods from the early Eocene of Laguna del Hunco, Argentine Patagonia

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Two silicified fossil woods from the Huitrera Formation at Laguna del Hunco, Chubut Province, Argentina, are identified as a new species of *Laurinoxylon*. The supporting characters include the absence of growth ring boundaries, vessels solitary or in short radial multiples, simple and scalariform perforation plates, alternate intervessel pitting, scalariform vessel-ray pits, scarce axial parenchyma, septate fibres, rays usually one to four cells wide, and idioblasts commonly associated with rays and rarely with the axial parenchyma. The fossil woods resemble members of the Perseae-Cinnamomeae-Laureae clade but do not closely match any extant genus; therefore, they probably represent an extinct lineage. Although lauraceous woods are known from other Paleocene and Eocene floras of Patagonia, the presence of the family at Laguna del Hunco was previously based only on leaf compressions without preserved cuticular details. The new record confirms the occurrence of Lauraceae in the diverse Laguna del Hunco flora, which contains many genera that associate with the family in extant rainforests.

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THE DIVERSITY, composition, and geological context of the flora of the Tufolitas Laguna del Hunco in the Huitrera Formation, northwestern Patagonia, indicate an everwet, mid-latitude late-Gondwanan rainforest surrounded a caldera lake during the early Eocene Climate Optimum (Wilf *et al.* 2005, 2013, Barreda *et al.* 2020, Rossetto-Harris *et al.* 2020, Gosses *et al.* 2021, Andruchow-Colombo *et al.* 2023). Previous work, based primarily on quantitative counts of compression fossils (Wilf *et al.* 2005), showed that the angiosperms largely dominated the canopy, but conifers belonging to Podocarpaceae (Wilf 2012, 2020, Wilf *et al.* 2017, Andruchow-Colombo *et al.* 2019, Pujana *et al.* 2020), Cupressaceae (Wilf *et al.* 2009) and Araucariaceae (Wilf *et al.* 2014, Barreda *et al.* 2020, Rossetto-Harris *et al.* 2020), were also common. Overall, the fossil flora has a well-established Gondwanan signal based on the presence of numerous genera that are extant in Australasian and Southeast Asian rainforests (e.g., Wilf *et al.* 2009, 2014, 2017, 2019, 2023, Wilf 2012, Rossetto-Harris *et al.* 2020, Zamaloa *et al.* 2020).

In addition to adpressions of leaves (Berry 1925, Wilf *et al.* 2005, Knight & Wilf 2013), reproductive structures (Hermsen & Gandolfo 2016, Jud *et al*. 2018, Deanna *et al.* 2020, Zamaloa *et al.* 2020, Matel *et al.* 2022, Wilf *et al.* 2023) and pollen (Barreda *et al.* 2020) indicating extreme floral diversity, silicified woods are abundant at Laguna del Hunco (Petersen 1946). Descriptions of fossil woods and other silicified materials contribute to a more complete understanding of floral diversity and composition (Bomfleur & Escapa 2019, Pujana *et al.* 2020, Brea *et al.* 2021).

Lauraceous woods are readily identified by the combination of vessels that are solitary and in short radial multiples with alternate intervessel pits, vasicentric axial parenchyma, narrow heterocellular rays, and idioblasts (Tupper 1927, Record & Hess 1942, Stern 1954, Richter 1981). Fossil Lauraceae woods are abundant worldwide, and many fossil-genera comprising hundreds of fossil-species have been described from deposits ranging in age from the Cretaceous to the Pliocene (Süss 1958, InsideWood 2004-onwards, Dupéron-Laudoueneix & Dupéron 2005, Gregory *et al.* 2008). In Patagonia, there are a few records of the family from Paleocene to Miocene deposits (Nishida *et al.* 1990, Pujana 2022).

Lauraceous pollen is notorious for poor preservation (Kubitzki 1981, Truswell *et al.* 1987) and is absent at Laguna del Hunco (Barreda *et al.* 2020). In contrast, leaves with lauraceous affinity are abundant, suggesting that the family was an important component of the forest canopy and understory (Wilf *et al.* 2005, 2019). However, because the leaves lack cuticular preservation necessary to confidently diagnose lauraceous foliage (e.g., Carpenter *et al.* 2018), uncertainty remains regarding the presence of the family. Their preservation in association with abundant leaves of castaneoid Fagaceae and rare *Castanopsis* (D. Don) Spach infructescences (later corroborated with castaneoid pollen grains, Barreda *et al.* 2020) led Wilf *et al.* (2019) to suggest the presence of an ancient oak-laurel forest comparable to those found at lower montane elevations over large areas of Southeast Asia. Also, Knight and Wilf (2013) described leaves of the closely related lauralean families Atherospermataceae and Monimiaceae in the flora.

Among a large wood assemblage collected in December 2016 from the well-studied Laguna del Hunco exposures (Fig. 1), two specimens preserved lauraceous characteristics. Here, we describe the anatomy of these fossil woods and discuss their palaeoecological and biogeographic importance.

Materials and methods

The Tufolitas Laguna del Hunco are tuffaceous caldera-lake sediments that belong to the volcaniclastic-pyroclastic complex of the middle Chubut River (Aragón & Mazzoni 1997). Their age at the Laguna del Hunco site is well constrained to the early Eocene (Ypresian) by a 52.22 ± 0.22 Ma ^{40}Ar-^{39}Ar age analysed from sanidines from the middle of the fossiliferous 170 m section and additional ^{40}Ar-^{39}Ar ages from the lake beds and associated units, including the underlying Barda Colorada Ignimbrite (Wilf *et al.* 2003, 2005, Wilf 2012, Gosses *et al.* 2021).

Fossil woods at Laguna del Hunco, like the specimens described previously by Brea *et al.* (2021) and Pujana *et al.* (2020), were found ex situ on exposed strata throughout the local Tufolitas section of Wilf *et al.* (2003; Fig. 1), including the upper third of the section that contains few compression fossils and up to the uppermost lake beds below the hill-capping Andesitas Huancache (per Aragón & Mazzoni 1997). They consist of decorticated permineralized secondary xylem and were found exposed on slopes, clean of attached sediment, and with abraded surfaces, indicating that they were reworked downslope to an unknown extent from various possible source levels within the Tufolitas, including the uppermost strata as indicated by Petersen (1946). The two studied specimens were found at wood site LU20 (42° 27' 49.90" S, 70° 2' 23.90" W) as part of a larger collection of 87 wood specimens (Pujana *et al.* 2020). The specimens are housed in the Paleobotanical Collection of the Museo Paleontólogico Egidio Feruglio, Trelew, Chubut Province, Argentina, under accession numbers MPEF-Pb 10759 (a–e) and 10760 (a–f). The thin sections of each specimen bear the specimen number followed by a lowercase series letter.

Thin sections (transverse, TS; tangential longitudinal, TLS; radial longitudinal, RLS) were prepared following standard techniques (Haas & Rowe 1999) and studied using light microscopy. Small fragments were gold-coated and observed using a scanning electron microscope (Zeiss Gemini SEM 360) located in the Museo Argentino de Ciencias Naturales, Buenos Aires City, Argentina. Transmitted light micrographs were taken with a Leica (https://www.leica-microsystems.com) DM750 microscope with a RisingCam (Chloe Rising Tech Limited, China) C3CMOS camera. Images were taken with RisingView (Chloe Rising Tech Limited, China) 20230723 and processed using GIMP (https://www.gimp.org) 2.10.34 free software. Measurements were acquired from the images using ImageJ (https://imagej.net/ij) 1.53 free software.

When possible, at least 25 measurements or observations of every character were made for each specimen. The measurements are reported as the weighted mean of the values of the two specimens, followed by the range and mean standard deviation (SD) in parentheses. We followed the IAWA Committee (1989) recommendations for angiosperm wood anatomy descriptions, with the following modifications. The vessel lumen diameter was replaced by the vessel diameter including the vessel wall, to simplify comparisons with older wood anatomy descriptions (e.g., Poole & Gottwald 2001, Wheeler & Manchester 2014, Pujana *et al.* 2018). We calculated the number of vessels per group, herein abbreviated as Ci (Carlquist's index), following Carlquist (1984), who considered a group to be present when vessels are in contact, not merely close. We consulted diverse sources for systematic character information, including InsideWood (2004-onwards [accessed during 2023–2024]), "*Fossil Dicot Wood Names*" (Gregory *et al.* 2009), and extensive literature searches. For suprageneric classification, we followed APG IV (2016). Authorities for extant taxa were taken from the IPNI (2024) database.

Systematic paleontology

Order LAURALES Juss. ex Bercht. & J.Presl

Family LAURACEAE Juss. nom. cons.

Laurinoxylon Felix emend. Dupéron *et al.,* 2008

Type species

Laurinoxylon diluviale (Unger) Felix emend. Dupéron *et al.,* 2008

Laurinoxylon patagonicum Pujana, Jud, Wilf & Gandolfo sp. nov.

(Figs 2, 3)

Diagnosis

Growth ring boundaries absent. Vessels solitary or in short radial multiples. Perforation plates scalariform with few bars (more common) or simple. Vessel-ray parenchyma pits mostly scalariform. Axial parenchyma scarce. Fibres septate and non-septate. Heterocellular rays mostly 2–4 cells wide. Idioblasts common in rays and rare in axial parenchyma.

Etymology

The specific epithet denotes the Patagonian region, where the fossils were found.

Holotype

MPEF-Pb 10760 (Figs 2C, D, G, I, K–M, 3B, D–F, H, J–L).

Paratype

MPEF-Pb 10759 (Figs 2A, B, E, F, H, J, 3A, C, G, I).

Type locality, unit and age

LU20 (42º 27’ 49.9’’ S 70º 2’ 23.9’’ W, Fig. 1), Laguna del Hunco, Chubut Province, Argentina. Huitrera Formation, early Eocene (Ypresian).

Description

Growth ring boundaries are absent (Fig. 2A). Wood is diffuse-porous (Fig. 2A–C). Vessels are solitary (51%), in tangential pairs (7%), or in short radial multiples of two (32%), three or more (9%), or grouped (1%), Ci = 1.66 (Fig. 2A–C). Vessel tangential diameter is 73 (23–134, SD = 19) µm; vessel wall thickness is *ca* 1–2 µm; there are 23 (13–35, SD = 4) vessels per mm^2. Vessel element length is difficult to observe because of the abundant tyloses. Perforation plates are simple (difficult to observe) or scalariform and very oblique (> 45º to the horizontal plane), with 3.1 (2–6, SD = 1.2) bars per plate and 3.2 (2–4) bars per 100 µm; bars are *ca* 3–6 µm thick (Fig. 2D–G). Scalariform perforation plates are apparently more abundant than simple perforation plates. Intervessel pits are alternate, circular, 8.3 (6.3–10.2, SD = 0.8) µm in vertical diameter (Fig. 2H, I). Vessel-ray parenchyma pits are horizontal (scalariform) to rarely opposite with much-reduced borders, *ca* 12.5 (9.8–16.4) µm in vertical diameter (Fig. 2J–L); Type II of Richter (1981) is the most similar. Tyloses are common (Figs 2B, 3C). Axial parenchyma is scarce, diffuse, and scanty paratracheal (Figs 2M, 3C, I–K). Fibres are thin-walled, some are septate, appearing similar to parenchyma strands, and may be pitted (bordered and *ca* 6 µm in diameter) in radial walls (Fig. 3A–E). Rays are 3.2 (1–6, SD = 0.9) cells wide; 11.9 (4–22, SD = 4.3) cells high (Fig. 3C–E), and heterocellular, composed of procumbent cells in the body of the ray 29 (13–54, SD = 7) µm high and usually one row of upright cells 66 (50–99, SD = 12) µm high; in some cases there is a gradual transition between the two types (Fig. 3F–K); ratio upright/procumbent cells 2.27:1. Ray frequency is 5.9 (4–9, SD = 1.1) rays per mm. Idioblasts are common, associated with ray parenchyma and rarely with axial parenchyma (3E–L). In rays, idioblasts are locally adjacent (Fig. 3H), mostly marginal but also mixed through the ray, and were observed in all rays. Idioblasts are slightly larger or more inflated than adjacent ray or axial parenchyma cells (Fig. 3G–K).

Remarks

Some characters could only be observed in a few thin sections because of the variable quality of preservation. These include the simple perforation plates in both specimens, the vessel-ray pits in the holotype, and the axial parenchyma in the paratype. The differences between the holotype and paratype are shown in Table 1. Axial parenchyma and idioblasts are more common in the holotype. Although some differences between the specimens can be considered significant (i.e., vessel frequency or ray width), they are consistent with normal intraspecific variation. Süss (1958) noted that the frequency of vessels varies significantly even within single samples of some *Laurinoxylon* fossil woods, suggesting that this heterogeneity is common in the fossil-genus.

In both specimens, there is no noticeable curvature of the growth rings as observed in TS, and the rays are approximately parallel (Fig. 2A). This suggests that the specimens are fragments of mature wood derived from large trees.

To facilitate comparisons of the anatomical diversity within the large fossil-genus *Laurinoxylon,* Mantzouka *et al.* (2016) distinguished several informal *Laurinoxylon* types based on the distribution of idioblasts in the wood. The distribution of idioblasts associated with the rays and axial parenchyma in *Laurinoxylon patagonicum* matches their Type 2a. We note that the Mantzouka *et al.* (2016) classification does not correspond to monophyletic groups.

Comparisons with fossil woods

Several fossil-genera have been circumscribed to organise the diversity of lauraceous woods in the fossil record, including *Laurinoxylon* (Table 2). Our comparative survey focused on species of *Laurinoxylon* (Table 3), as emended by Dupéron *et al.* (2008). This includes several fossil-species that were assigned to other fossil-genera, but later synonymized by Dupéron-Laudoueneix & Dupéron (2005). *Laurinoxylon* is characterised by having vessels solitary or in short radial multiples, simple and scalariform perforation plates with few bars, alternate intervessel pitting, tyloses, scanty paratracheal axial parenchyma, heterocellular rays, pitted fibres, and the presence of idioblasts associated with ray parenchyma and axial parenchyma (Table 3). It is a large fossil-genus with more than one hundred species, many of which do not have detailed published descriptions. The validity of many of these poorly known taxa has been discussed for many years (e.g., Süss 1958, Mantzouka *et al.* 2016). For example, Süss (1958) recognized only 15 of 44 species as properly described and assigned to *Laurinoxylon*. More recently, Dupéron-Laudoueneix & Dupéron (2005) revised *Laurinoxylon* and synonymized some other fossil-genera.

To facilitate comparisons when describing new fossil lauraceous woods, the fossil-genera *Cinnamomoxylon* Gottwald, 1997 and *Mezilaurinoxylon* Wheeler & Manchester, 2002 were segregated from *Laurinoxylon* with narrower circumscriptions (Gottwald 1997, Wheeler & Manchester 2002). The diagnosis of *Cinnamomoxylon* shares many characteristics with that of *Laurinoxylon* as emended by Dupéron *et al.* (2008); *Mezilaurinoxylon,* has exclusively simple perforation plates and idioblasts confined to rays (Wheeler & Manchester 2002). The specimens from Patagonia do not conform to *Cinnamomoxylon* because they have some scalariform perforation plates and idioblasts associated with axial parenchyma, and they do not have vasicentric to confluent axial parenchyma.

The combination of characteristics that differentiates *Laurinoxylon patagonicum* from other *Laurinoxylon* species is the absence of growth ring boundaries, the common scalariform perforation plates, and the scanty paratracheal axial parenchyma (Table 3). *Laurinoxylon dabieshanense* Yang, 1993 from the Cenozoic of China is very similar to *L. patagonicum* in most of the described characters but differs in its distinct growth ring boundaries (Yang *et al.* 1993). The description of *L. dabieshanense* is not detailed and lacks illustrations; therefore, a more comprehensive comparison cannot be made. *Laurinoxylon weylandii* Berger, 1953 from the Upper Cretaceous of Europe has similar anatomy to the Patagonian species, but the distribution and frequency of its idioblasts are unclear (Berger 1953). If *L. weylandii* lacks idioblasts, it should be excluded from *Laurinoxylon* following Dupéron *et al.* (2008).

In Patagonia, there are six prior reports of fossil Lauraceae wood: *Laurinoxylon atlanticum* (Romero) Dupéron-Laudouoeneix & Dupéron, 2005 (Romero 1970), *Laurinoxylon chubutense* (Brea) Duperón-Laudoueneix & Duperón, 2005 (Brea 1995), and *Mezilaurinoxylon oleiferum* Ruiz *et al., 2020* (Ruiz *et al.* 2020) from the Paleocene; *Paraperseoxylon* sp. (Brea *et al.* 2015) from the Oligocene; *Laurinoxylon atlanticum* Brea *et al.*, 2012 (Brea *et al.* 2012) from the Miocene; and *Laurinium beilschmiedioides* Nishida *et al., 1990* from a locality of uncertain age in Chilean Patagonia (Nishida *et al.* 1990). All these taxa have exclusively simple perforation plates differing from *L. patagonicum* (Romero 1970, Brea 1995, Brea *et al.* 2012, 2015, Ruiz *et al.* 2020). *Laurinoxylon atlanticum* further differs from *L. patagonicum* because it has more abundant axial parenchyma, and its idioblasts are unclear (Romero 1970). *Laurinoxylon chubutense* is different from *L. patagonicum* because, in addition to having more abundant axial parenchyma, it is characterized by narrower rays, and its idioblasts occur only in rays (Brea 1995). *Laurinoxylon beilschmiedioides* lacks tyloses, and its vessel-ray parenchyma pits are highly variable, including circular and oval forms, scalariform to vertically elongated orientations, and alternate or opposite arrangements (Nishida *et al*. 1990). *Mezilaurinoxylon oleiferum* has larger vessel-ray pits than *L. patagonicum* and idioblasts among fibers (Ruiz *et al.* 2020).

In Antarctica, the only lauraceous wood described is *Sassafroxylon gottwaldii* Poole et al., 2000 from the Cretaceous of Seymour Island (Poole *et al.* 2000). This species is distinguished from *Laurinoxylon* spp. by its ring-porous wood (Table 1). In addition, Gothan (1908) described *Laurinoxylon uniseriatum* Gothan, 1908 and originally hypothesised an affinity with the Lauraceae, but Poole (2002) later transferred this species to *Nothofagoxylon* Gothan, 1908.

Similarities to extant woods

The presence of idioblasts in fossil woods is a useful character when making comparisons with modern taxa because it occurs in only a handful of extant families and is usually absent from eudicots. Idioblasts are found among Magnoliales (Annonaceae and Magnoliacaeae) and Laurales (Lauraceae and in the monotypic family Gomortegaceae). We can rule out an affinity for the new fossils with Annonaceae, whose woods are characterised by banded axial parenchyma and wide multiseriate rays not present in the fossils (Metcalfe & Chalk 1950, InsideWood 2004-onwards). *Laurinoxylon patagonicum* cannot be placed within Magnoliaceae, which have scalariform or opposite intervessel pitting (Liang *et al.* 1993, InsideWood 2004-onwards). *Gomortega keule* (Molina) Baill., 1869, the only extant species of Gomortegaceae, has exclusively solitary vessels (Stern 1954, Rancusi *et al.* 1987). Although idioblasts have been reported in other families, they are very rare, or the families have markedly different anatomical characteristics from Lauraceae (e.g., Hernandiaceae Monimiaceae, Winteraceae; Carlquist 2001). In contrast, diffuse porosity, vessels solitary or in short radial multiples, alternate intervessel pits, common tyloses, paratracheal axial parenchyma, heterocellular rays, and idioblasts, all present in the *L. patagonicum* fossils, are the wood anatomical characteristics of most Lauraceae (Tupper 1927, Record & Hess 1942, Stern 1954, Richter 1981).

Lauraceae represents a large, predominantly tropical, family comprising about 50 genera and 2500–3000 species (Rohwer 1993). The tribal and generic divisions and phylogenetic relationships within Lauraceae have long been controversial (Tian *et al.* 2021). Recent investigations based on plastid genomes have supported the recognition of nine monophyletic groups (Song *et al.* 2020, Liu *et al.* 2021). Here, we follow the classification and nomenclature of Liu *et al.* (2021), in which the tribe Perseae of Van der Werff & Richter (1996) was split into Perseae and Cinnamomeae. Four of the nine groups of Lauraceae, *Hypodaphnis* (Richter 1981)*,* Neocinnamomeae (Richter 1981), Caryodaphnopsidae (Richter 1981, Gonzales Casimiro 2008), and the *Mezilaurus*-group (Dechamps 1979, Nardi Berti & Edlmann Abbate 1992, Santini Junior *et al.* 2021) have exclusively simple perforation plates, unlike the fossils. Cryptocaryeae have well-distinguished wood anatomy, with terminal axial parenchyma and an absence of septate fibres (except *Dahlgrenodendron* J.J.M.Van der Merwe & A.E. Van Wyk, 1988 see Richter & Van Wyk 1990) among other characteristics that differ from the fossils (Dechamps 1979, Richter 1981, Rancusi *et al.* 1987, Barros & Callado 1997). Cassytheae are parasites that do not develop secondary xylem (Weber 1981). A combination of commonly simple and rarely scalariform perforation plates, as expressed in the fossils, is present in some species of Perseae, Cinnamomeae and Laureae (the other three groups, e.g., Richter 1981, Sonsin *et al.* 2014, León 2017), which together form a monophyletic group (hereinafter called the PCL clade). Some species with this combination of perforation plates include *Aniba ovalifolia* Mez, 1889, *Cinnamomum oliveri* F.M. Bailey, 1892, *Nectandra angustifolia* (Schrad.) Nees & Mart., 1883 and *Ocotea pulchella* Mart., 1830 (Dadswell & Eckersley 1940, Tortorelli 1956, León & Espinoza de Pernía 2000, Marchiori *et al.* 2009, Sonsin *et al.* 2014). The high frequency of scalariform perforation plates in *L.*

patagonicum suggests that it belongs to the PCL clade, although this feature is unusual in Lauraceae.

Although idioblasts are present in most species of Lauraceae, they are absent or rare in some extant species (e.g., *Caryodaphnopsis fosteri* Van der Werff*,* 1986, *Nectandra rigida* (Kunth) Nees, 1836, *Nectandra leucantha* Nees, 1848, *Nectandra puberula* Nees*, 1836* and *Ocotea pulchella*; Barros & Callado 1997, Barros *et al.* 2001, Gonzales Casimiro 2008, Sonsin *et al.* 2014, Heerdt *et al.* 2016). Among those with idioblasts, relatively few species (e.g., *Ocotea aciphylla* (Nees & Mart.) Mez, 1889, *Ocotea indecora* (Schott) Mez, 1889, *C. fosteri and N. puberula*) have idioblasts associated with both the rays and the axial parenchyma (Barros *et al.* 2001, Gonzales Casimiro 2008) as expressed in the new fossil-species.

The combination of abundant scalariform perforation plates, the large number of idioblasts associated with the ray and axial parenchyma, and the absence of terminal parenchyma supports the conclusion that *Laurinoxylon patagonicum* is related to the PCL clade. However, *L. patagonicum* can be distinguished from extant PCL species, which typically have more abundant axial parenchyma, and their frequency of scalariform perforation plates is generally lower.

In Patagonia, the extant species most similar to *Laurinoxylon patagonicum* is *Persea lingue* (Miers ex Bertero) Nees, 1836 of the Perseae. However, *P. lingue* was described as having simple perforation plates (Wagemann 1947, Rancusi *et al.* 1987) or mostly simple with rare scalariform perforation plates (Nardi Berti & Edlmann Abbate 1992). It also has distinct growth ring boundaries and helical thickenings (Rancusi *et al.* 1987), unlike *L. patagonicum*.

Unfortunately, it is difficult to distinguish many genera of Lauraceae based only on wood anatomy because of overlapping anatomical variation (Stern 1954, Prakash *et al.* 1971, Richter 1981). Some exceptions are Cryptocaryeae, the members of which have terminal parenchyma and other distinctive characteristics (see above), and some other genera, such as *Sassafras* J. Presl, *1825,* which has ring-porous wood. For example, in some genera (e.g., *Ocotea Aubl., 1775*) some species have simple perforation plates and others both simple and scalariform perforation plates (Dadswelll & Eckersley 1940, Richter 1981, León 2017). In other genera (e.g., *Aniba Aubl., 1775*) idioblasts are present in some species but not others (León & Espinoza de Pernía 2000). Overall, *L. patagonicum* shares the largest number of characters with the PCL clade.

Discussion

Lauraceae record at Laguna del Hunco

Patagonia has a considerable record of leaves and woods of Lauraceae, but pollen is not usually reported because the thin exine of the pollen preserves poorly (Truswell *et al.* 1987). In the Laguna del Hunco flora, based on a badly preserved leaf fragment Berry (1925) described *"Nectandra" patagonica* Berry, 1925, as a Lauraceae fossil, but this assignment is doubtful. However, Wilf *et al.* (2005) reported several abundant, well-preserved leaf morphotypes with leaf architecture typical of Lauraceae from much larger recent collections, but cuticles are not yet reported. Thus, *Laurinoxylon patagonicum* is the first reliable species of fossil wood of Lauraceae and the most definite record of the family within the Laguna del Hunco flora.

Comments on Lauraceae

Lauraceae is a large family distributed primarily throughout tropical and subtropical regions of the world (Rohwer 1993, Chanderbali *et al.* 2001) and its species are common in lowland and premontane tropical forests and evergreen oak-laurel forests worldwide (Tagawa 1997). Even the PCL clade, the group to which *Laurinoxylon patagonicum* likely belongs, is pantropical. Because the Laguna del Hunco flora has strong floristic affinities to modern Australasian-Southeast Asia forests, we focused our effort on comparisons with South American and Australasian Lauraceae. The floras of South America, Australia, New Guinea, and adjacent lands include many Lauraceae trees. Most of these taxa belong to Cryptocaryeae, but there are also many species of the PCL clade, even though Laureae is absent from South America (Le Cussan *et al.* 2007, Grandtner & Chevrette 2014, Barstow *et al.* 2022).

The presence of woods in the Eocene of Laguna del Hunco related to the PCL clade sensu Liu *et al.* (2021) strongly suggests that this clade was present in South America at least in the early Eocene. According to Chanderbali *et al.* (2001), the lauraceous fossil record suggests a Laurasian origin for the family, but the Cryptocaryeae and the *Mezilaurus*-group are supposed to have a Gondwanan origin.

Liu *et al.* (2021) suggested that Perseae (=*Perseae* group) originated in Laurasia during the Eocene, and some members later arrived in South America. Similarly, Chanderbali *et al.* (2001) proposed that the *Ocotea* complex (which includes most Cinnamomeae of Liu *et al.* 2021) arrived in South America from Laurasia during the Eocene. The *L. patagonicum* fossils, if they belong to either of these two groups, do not contradict these hypotheses (Chanderbali *et al.* 2001, Liu *et al.* 2021) but also do not support them without corroboration from well-dated Laurasian fossils. Finally, Laureae, the third PCL tribe that could be related to the new fossils, is widespread in Australia and Southeast Asia (Van der Werff 2001, Le Cussan *et al.* 2007) like many other extant relatives of constituents of the floral assemblage, but there is no other evidence of fossils or extant species of Laureae in South America.

As discussed earlier, it is not possible to establish a close affinity of *L. patagonicum* to a particular extant genus or species based on the wood anatomy, but there are many similarities to the species of the PCL clade *sensu* Liu *et al.* (2021). Considering the significant differences in the anatomy with any extant member of the PCL clade from South America, including *Persea lingue*, we hypothesise that *L. patagonicum* comes from a lineage of Lauraceae that became extinct. Nonetheless, we note that wood anatomical data is poorly known for many lauraceous species distributed in the areas that contain the most survivor genera from Laguna del Hunco, such as Australia (e.g., Dadswell & Eckersley 1940).

Conclusions

Laurinoxylon patagonicum, a new species of fossil wood, with typical characteristics of the Lauraceae (common scalariform perforation plates, scarce axial parenchyma and abundant idioblasts in rays) is described and represents the first definitive occurrence of the family in the highly diverse early Eocene Laguna del Hunco flora. Although this new Patagonian species is similar to some genera of the PCL clade *sensu* Liu *et al.* (2021), a more precise affinity to extant species could not be established. Therefore, the new fossils most likely represent an extinct lineage of Lauraceae. This record adds to the substantial record of megafossils of Lauraceae from Patagonia.

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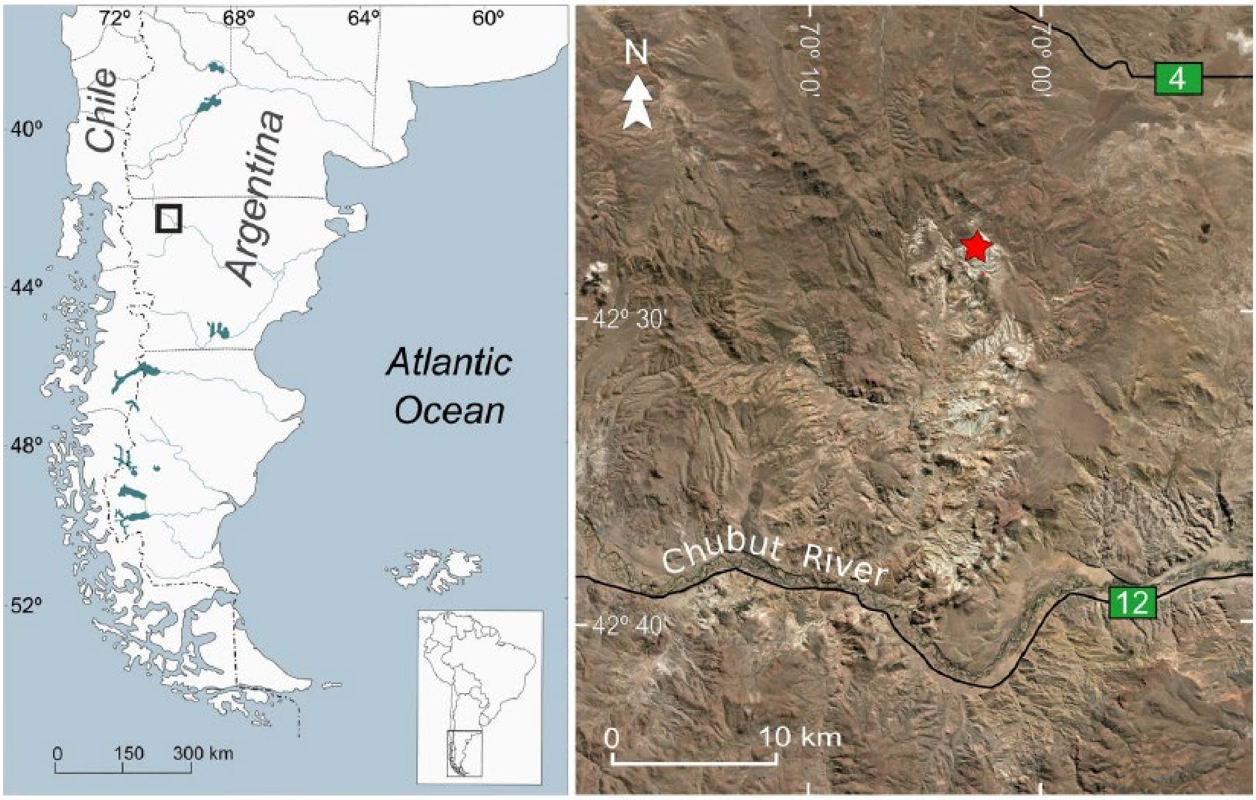


Figure 1. Map and satellite image (Google, CNES / Airbus) showing the sampling location (red star) of the fossils described.

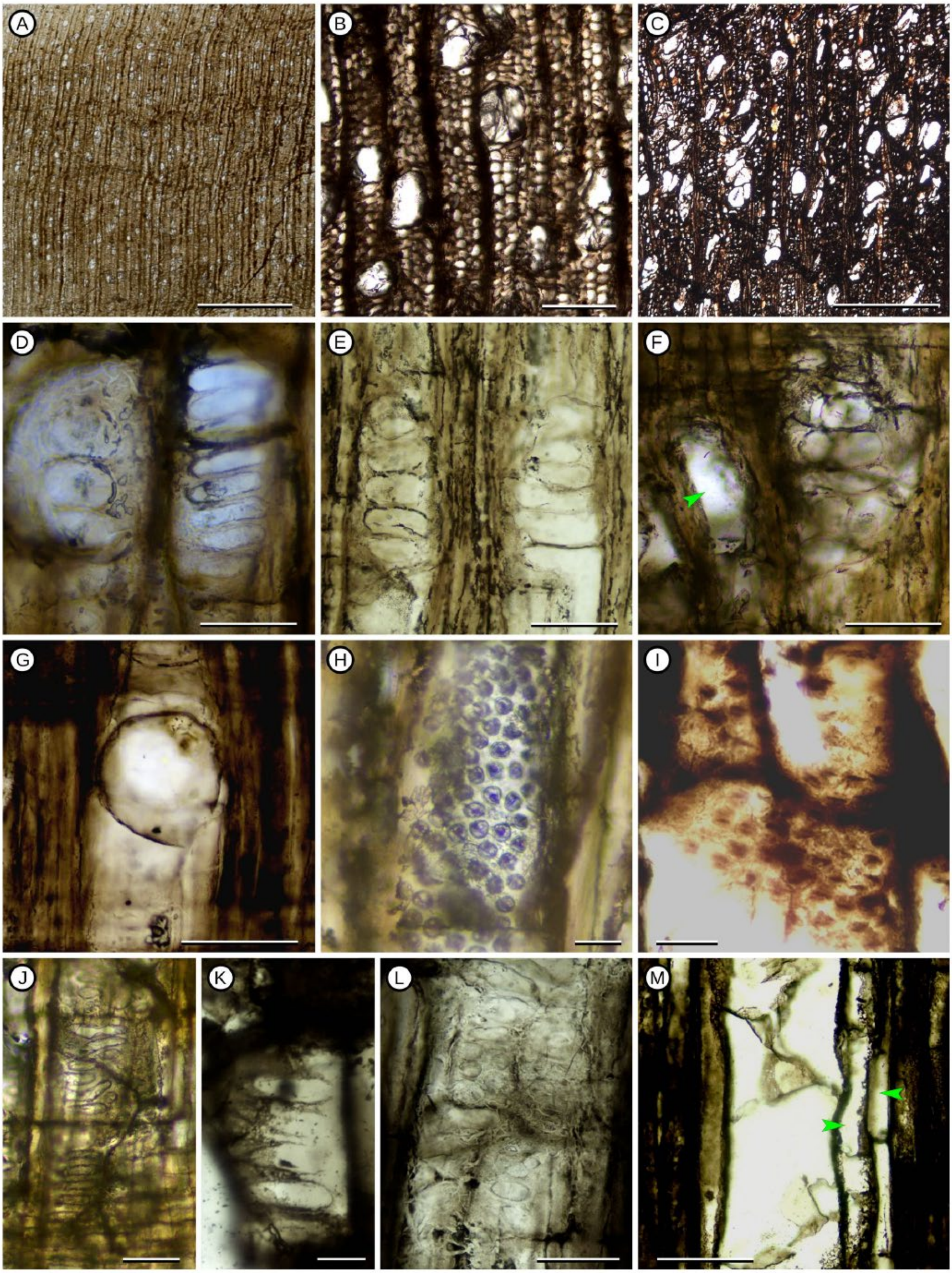


Figure 2. Wood anatomy of *Laurinoxylon patagonicum*. MPEF-Pb 10759 (Paratype) & 10760 (Holotype). **A–B,** Vessels solitary or in short radial multiples (TS). MPEF-Pb 10759. **C,** Vessels solitary or in short radial multiples (TS). MPEF-Pb 10760. **D,** Two scalariform perforation plates (RLS). MPEF-Pb 10760. **E,** Two scalariform perforation plates (RLS). MPEF-Pb 10759. **F,** A scalariform perforation plate and a seemingly

simple perforation plate (arrowhead) (RLS). MPEF-Pb 10759. **G,** A simple perforation plate (RLS). MPEF-Pb 10760. **H,** Circular and alternate intervessel pits (RLS). MPEF-Pb 10759. **I,** Circular and alternate intervessel pits (RLS). MPEF-Pb 10760. **J,** Scalariform vessel-ray pits (RLS). MPEF-Pb 10759. **K,** Scalariform vessel-ray pits (RLS). MPEF-Pb 10760. **L,** Scalariform to transitional vessel-ray pits (RLS). MPEF-Pb 10760. **M,** Paratracheal axial parenchyma (arrowheads) (RLS). MPEF-Pb 10760. Scale bars: **A** = 2 mm, **B** = 200 μm, **C** = 500 μm, **D, J, L** = 50 μm, **E, F, G, M** = 100 μm, **H, I, K** = 20 μm.

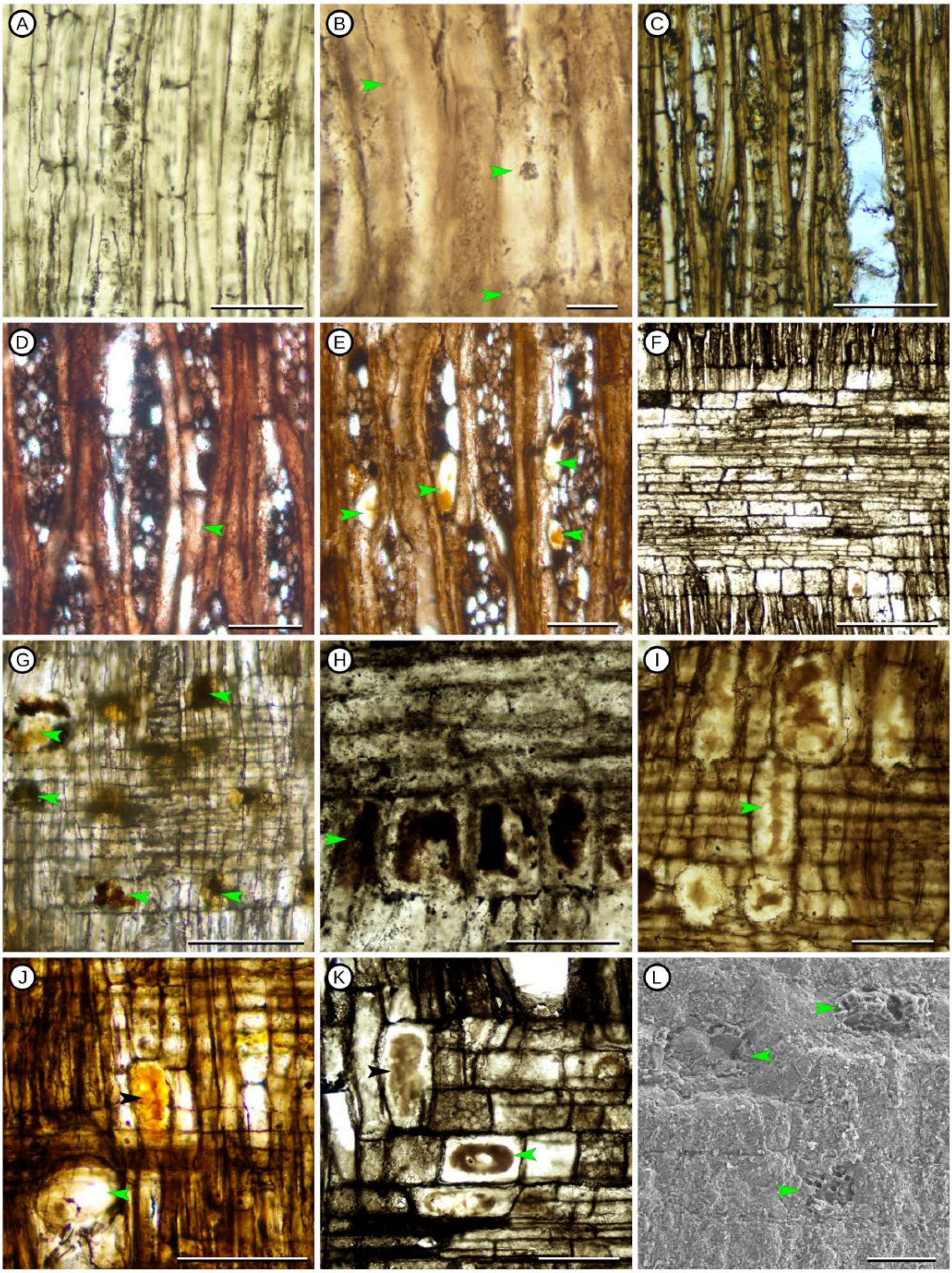
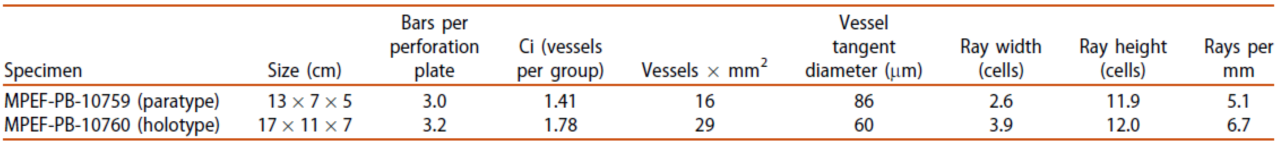


Figure 3. Wood anatomy of *Laurinoxylon patagonicum*. MPEF-Pb 10759 (Paratype) & 10760 (Holotype). **A,** Septate fibers (RLS). MPEF-Pb 10759. **B**, Fiber pits seemingly bordered (RLS). MPEF-Pb 10760. **C,** Uni- to biseriate rays (TLS). MPEF-Pb 10759. **D,** Multiseriate rays and axial parenchyma (arrowhead) (TLS). MPEF-Pb 10760. **E,** Rays with idioblasts (arrowheads) (TLS). MPEF-Pb 10760. **F,** Heterocellular ray (RLS). MPEF-

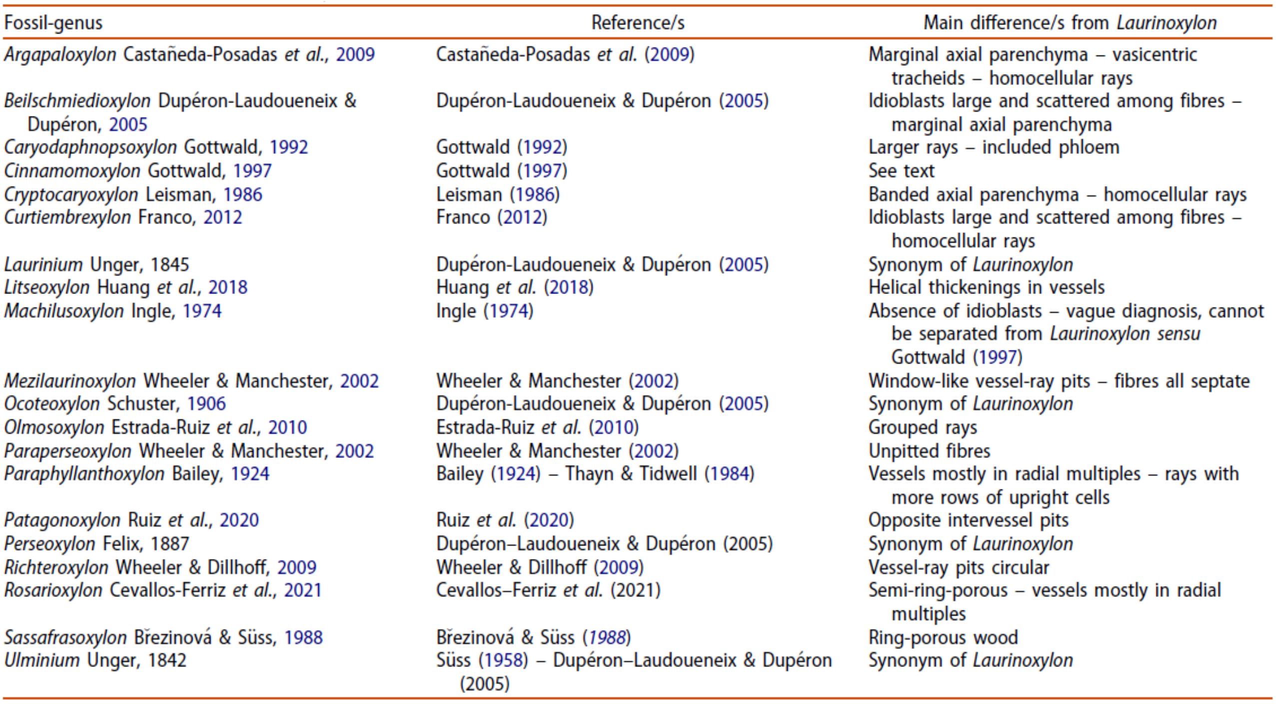
Pb 10760. **G,** Ray with associated idioblasts (arrowheads) (RLS). MPEF-Pb 10759. **H,** A row (arrowhead) of idioblasts associated with rays (RLS). MPEF-Pb 10760. **I,** Idioblasts associated with rays and with axial parenchyma (arrowhead) (RLS). MPEF-Pb 10759. **J,** Idioblasts associated with axial parenchyma (black arrowhead) and a simple perforation plate (green arrowhead) (RLS). MPEF-Pb 10760. **K,** Idioblasts associated with rays (procumbent cell, green arrowhead) and with axial parenchyma (black arrowhead) (RLS). MPEF-Pb 10760. **L,** Idioblasts associated with rays in SEM. MPEF-Pb 10760. Scale bars: **A, D, E, H, I, K** = 100 μm, **B** = 20 μm, **F, G, J** = 200 μm, **L** = 50 μm.

Table 1. Comparison of the holotype (MPEF-Pb 10760) and paratype (MPEF-Pb 10759) of *Laurinoxylon patagonicum*. Values are given as means.



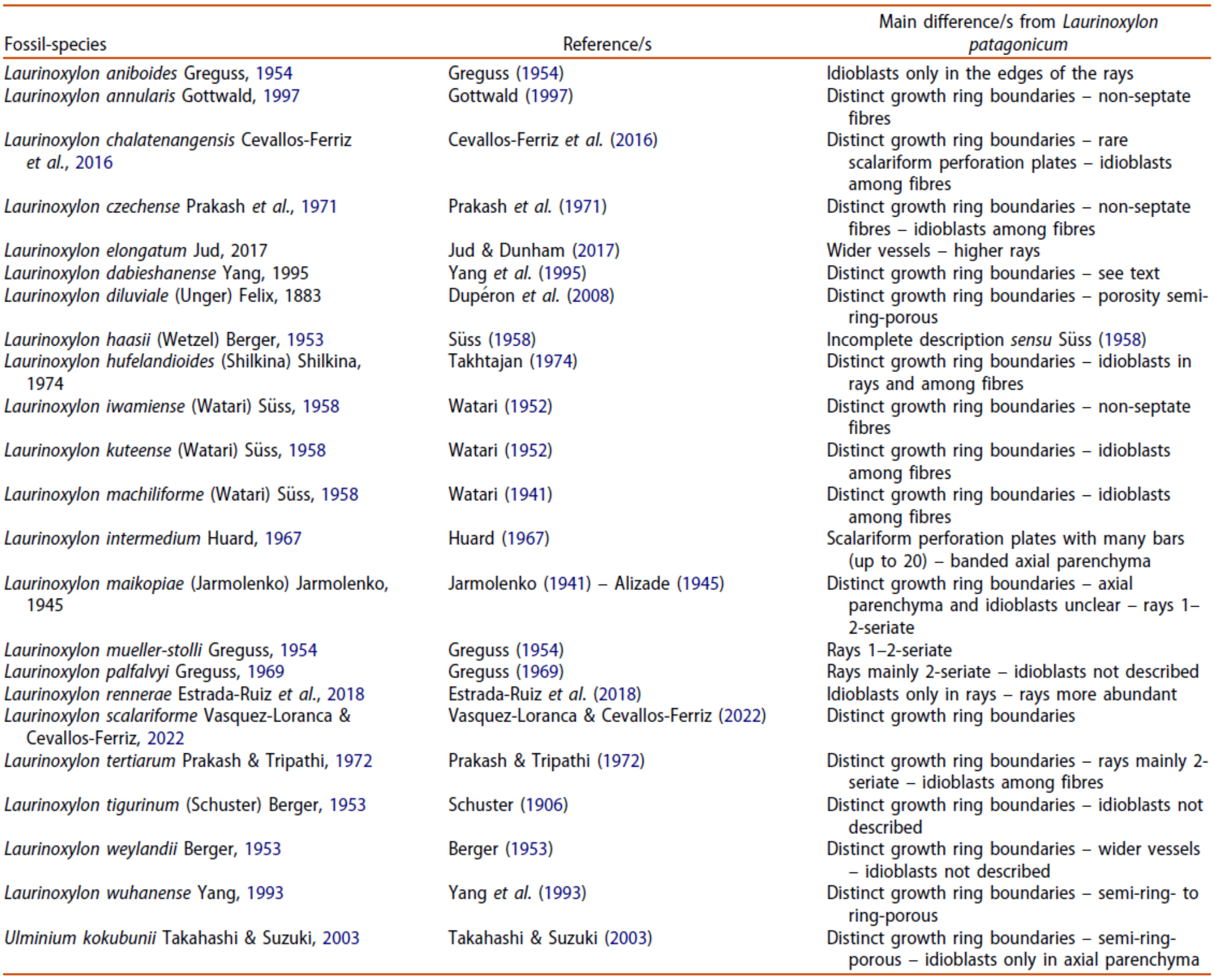
Specimen	Size (cm)	Bars per perforation plate	Ci (vessels per group)	Vessels × mm^2	Vessel tangent diameter (μm)	Ray width (cells)	Ray height (cells)	Rays per mm
MPEF-PB-10759 (paratype)	13 × 7 × 5	3.0	1.41	16	86	2.6	11.9	5.1
MPEF-PB-10760 (holotype)	17 × 11 × 7	3.2	1.78	29	60	3.9	12.0	6.7

Table 2. Comparison of *Laurinoxylon* with lauraceous fossil-genera.



Fossil-genus	Reference/s	Main difference/s from *Laurinoxylon*
Argapaloxylon Castañeda-Posadas *et al.*, 2009	Castañeda-Posadas *et al.* (2009)	Marginal axial parenchyma – vasicentric tracheids – homocellular rays
Beilschmiedioxylon Dupéron-Laudoueneix & Dupéron, 2005	Dupéron-Laudoueneix & Dupéron (2005)	Idioblasts large and scattered among fibres – marginal axial parenchyma
Caryodaphnopsoxylon Gottwald, 1992	Gottwald (1992)	Larger rays – included phloem
Cinnamomoxylon Gottwald, 1997	Gottwald (1997)	See text
Cryptocaryoxylon Leisman, 1986	Leisman (1986)	Banded axial parenchyma – homocellular rays
Curtiembrexylon Franco, 2012	Franco (2012)	Idioblasts large and scattered among fibres – homocellular rays
Laurinium Unger, 1845	Dupéron-Laudoueneix & Dupéron (2005)	Synonym of *Laurinoxylon*
Litseoxylon Huang *et al.*, 2018	Huang *et al.* (2018)	Helical thickenings in vessels
Machilusoxylon Ingle, 1974	Ingle (1974)	Absence of idioblasts – vague diagnosis, cannot be separated from *Laurinoxylon sensu* Gottwald (1997)
Mezilaurinoxylon Wheeler & Manchester, 2002	Wheeler & Manchester (2002)	Window-like vessel-ray pits – fibres all septate
Ocoteoxylon Schuster, 1906	Dupéron-Laudoueneix & Dupéron (2005)	Synonym of *Laurinoxylon*
Olmosoxylon Estrada-Ruiz *et al.*, 2010	Estrada-Ruiz *et al.* (2010)	Grouped rays
Paraperseoxylon Wheeler & Manchester, 2002	Wheeler & Manchester (2002)	Unpitted fibres
Paraphyllanthoxylon Bailey, 1924	Bailey (1924) – Thayn & Tidwell (1984)	Vessels mostly in radial multiples – rays with more rows of upright cells
Patagonoxylon Ruiz *et al.*, 2020	Ruiz *et al.* (2020)	Opposite intervessel pits
Perseoxylon Felix, 1887	Dupéron–Laudoueneix & Dupéron (2005)	Synonym of *Laurinoxylon*
Richteroxylon Wheeler & Dillhoff, 2009	Wheeler & Dillhoff (2009)	Vessel-ray pits circular
Rosarioxylon Cevallos-Ferriz *et al.*, 2021	Cevallos–Ferriz *et al.* (2021)	Semi-ring-porous – vessels mostly in radial multiples
Sassafrasoxylon Březinová & Süss, 1988	Březinová & Süss (*1988*)	Ring-porous wood
Ulminium Unger, 1842	Süss (1958) – Dupéron–Laudoueneix & Dupéron (2005)	Synonym of *Laurinoxylon*

Table 3. Comparison of *Laurinoxylon patagonicum* with *Laurinoxylon* spp. that have scalariform perforation plates (and *Ulminium kokubunii*).



Fossil-species	Reference/s	Main difference/s from *Laurinoxylon patagonicum*
Laurinoxylon aniboides Greguss, 1954	Greguss (1954)	Idioblasts only in the edges of the rays
Laurinoxylon annularis Gottwald, 1997	Gottwald (1997)	Distinct growth ring boundaries – non-septate fibres
Laurinoxylon chalatenangensis Cevallos-Ferriz *et al*., 2016	Cevallos-Ferriz *et al.* (2016)	Distinct growth ring boundaries – rare scalariform perforation plates – idioblasts among fibres
Laurinoxylon czechense Prakash *et al*., 1971	Prakash *et al.* (1971)	Distinct growth ring boundaries – non-septate fibres – idioblasts among fibres
Laurinoxylon elongatum Jud, 2017	Jud & Dunham (2017)	Wider vessels – higher rays
Laurinoxylon dabieshanense Yang, 1995	Yang *et al.* (1995)	Distinct growth ring boundaries – see text
Laurinoxylon diluviale (Unger) Felix, 1883	Dupéron *et al.* (2008)	Distinct growth ring boundaries – porosity semi-ring-porous
Laurinoxylon haasii (Wetzel) Berger, 1953	Süss (1958)	Incomplete description *sensu* Süss (1958)
Laurinoxylon hufelandioides (Shilkina) Shilkina, 1974	Takhtajan (1974)	Distinct growth ring boundaries – idioblasts in rays and among fibres
Laurinoxylon iwamiense (Watari) Süss, 1958	Watari (1952)	Distinct growth ring boundaries – non-septate fibres
Laurinoxylon kuteense (Watari) Süss, 1958	Watari (1952)	Distinct growth ring boundaries – idioblasts among fibres
Laurinoxylon machiliforme (Watari) Süss, 1958	Watari (1941)	Distinct growth ring boundaries – idioblasts among fibres
Laurinoxylon intermedium Huard, 1967	Huard (1967)	Scalariform perforation plates with many bars (up to 20) – banded axial parenchyma
Laurinoxylon maikopiae (Jarmolenko) Jarmolenko, 1945	Jarmolenko (1941) – Alizade (1945)	Distinct growth ring boundaries – axial parenchyma and idioblasts unclear – rays 1–2-seriate
Laurinoxylon mueller-stolli Greguss, 1954	Greguss (1954)	Rays 1–2-seriate
Laurinoxylon palfalvyi Greguss, 1969	Greguss (1969)	Rays mainly 2-seriate – idioblasts not described
Laurinoxylon rennerae Estrada-Ruiz *et al*., 2018	Estrada-Ruiz *et al.* (2018)	Idioblasts only in rays – rays more abundant
Laurinoxylon scalariforme Vasquez-Loranca & Cevallos-Ferriz, 2022	Vasquez-Loranca & Cevallos-Ferriz (2022)	Distinct growth ring boundaries
Laurinoxylon tertiarum Prakash & Tripathi, 1972	Prakash & Tripathi (1972)	Distinct growth ring boundaries – rays mainly 2-seriate – idioblasts among fibres
Laurinoxylon tigurinum (Schuster) Berger, 1953	Schuster (1906)	Distinct growth ring boundaries – idioblasts not described
Laurinoxylon weylandii Berger, 1953	Berger (1953)	Distinct growth ring boundaries – wider vessels – idioblasts not described
Laurinoxylon wuhanense Yang, 1993	Yang *et al.* (1993)	Distinct growth ring boundaries – semi-ring- to ring-porous
Ulminium kokubunii Takahashi & Suzuki, 2003	Takahashi & Suzuki (2003)	Distinct growth ring boundaries – semi-ring-porous – idioblasts only in axial parenchyma