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Paleocene Las Violetas Fossil Forest: wood anatomy and paleoclimatology

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Abstract

Las Violetas Fossil Forest of the Salamanca Formation was a mixed forest of Paleocene age located in the Golfo San Jorge Basin, central Patagonia of Argentina, which includes conifers (previously studied), dicots and palms. In the present work, the dicot fossil woods outcropping in one of the fossiliferous levels (L3) of the Salamanca Formation are described, taxonomically assigned, and their affinities are discussed. They are three new species, including a new genus related to the Myrtaceae and Laurales. The complete fossiliferous assemblage is used to infer the climate and environment of the fossil forest. This assemblage represents a parautochtonous fossil plant association that lived either on the margins of channels or exposed bars in well-drained soils, probably tropical red-soils, close to their depositional setting (tidal channels and bars of an estuary). Warm and humid conditions and porous host-rocks favored the silicification of woods and pigmentation with Fe, resulting in yellow-orange and green fossil woods. We apply growth ring analysis to the conifer woods. For the dicots, wood anatomical characters influenced by the environment were analyzed, and the Vulnerability and Mesomorphy indices were used. These methods, comparisons with extant forests and the sedimentology, suggest that the Las Violetas Fossil Forest was an evergreen forest that developed under uniform growing seasons that ended abruptly, with an abundant water supply and high mean annual temperatures.

Key words. Salamanca Formation; Golfo San Jorge Basin; dicot woods; Myrtaceae; Laurales; growth rings.

1. Introduction

The early Cenozoic was a period of globally warm temperatures and high concentrations of greenhouse gases. Paleocene climate reconstructions indicate that during this time, the Earth experienced extreme variability (e.g., Zachos et al., 2001). Most global models of early Paleogene climatic conditions come from the Northern Hemisphere (Pagani et al., 2006; Sluijs et al., 2006; Zachos et al., 2006, among others). In contrast, there are few data for Paleocene climates in the Southern Hemisphere (Woodburne et al., 2013). Early Paleocene climatic considerations with focus on Patagonia come from plant remains (Petriella, 1972; Petriella and Archangelsky, 1975; Brea et al., 2005a, 2005b, 2008, 2011; Barreda and Palazzesi, 2007; Iglesias et al., 2007; Raigemborn et al., 2009, 2018a; Scafati et al., 2009), paleofauna (Pascual and Ortiz-Jaureguizar, 1990; Pascual et al., 1996; Gelfo et al., 2009; Bona et al., 2018), and sedimentological evidences (Andreis et al., 1975; Andreis, 1977). Biotic proxies indicate humid and warm conditions, which are consistent with the warm off-shore seawater temperatures inferred from abiotic proxies.

The Salamanca Formation, an early–middle Danian (early Paleocene; ca. 65.7–63.5 Ma; following Clyde et al., 2014) shallow marine unit of the Golfo San Jorge Basin (GSJB) of central Patagonia, Argentina (Fig. 1A) (Feruglio, 1949; Andreis et al., 1975; Martínez, 1992; Somoza et al., 1995; Matheos et al., 2001; Iglesias, 2007; Foix et al., 2015; Comer et al., 2015; among others), records a high richness of fossil remains. It includes microfossils (Camacho, 1967; Méndez, 1966; Chebli and Serraiotto, 1974), bivalves and brachiopods (Chebli and Serraiotto, 1974), echinoids (Parma and Casadío, 2005), turtles and alligators (Staesche, 1929; Simpson, 1937; Bona, 2005, 2007; Bona and De La Fuente, 2005; Bona et al., 2018), and mammals (Bonaparte et al., 1993; Bonaparte and Morales, 1997; Pascual et al., 1992, 2002; Forasiepi and Martinelli, 2003; Gelfo and Pascual, 2001; Gelfo, 2007; Gelfo et al., 2007, 2009). Plant remains are also abundant, with leaves (Martínez, 1992; Iglesias, 2007; Iglesias et al., 2007; Jud et al., 2017), flowers (Jud et al., 2017; Jud et al., 2018a, 2018b), palm stipes (Romero, 1968), palm fruits (Futey et al., 2012), and palynomorphs (Archangelsky, 1973, 1976; Romero, 1973; Archangelsky and Romero, 1974; Archangelsky and Zamaloa, 1986; Clyde et al., 2014). Fossil woods are also abundant in the Salamanca Formation (Berry, 1932; Ragonese, 1980; Brea et al., 2005a, 2005b, 2007, 2008, 2011; Ruiz et al., 2017). Paleoclimatic inferences from all these fossils arrive at the same conclusion inferred by other proxies that suggest that the Paleocene flora from the Salamanca Formation developed under humid and warm-temperate conditions, and without limiting factors. The presence of thermophilic groups such as palms (Romero, 1968; Futey et al., 2012; Ruiz et al., 2017), alligators (Bona, 2007; Bona et al., 2018), and podocarps that grow in nearly exclusively high rainfall environments (Iglesias et al., 2007) suggest a warm and humid climate during the deposition of the Salamanca Formation. Mean annual temperature of 14.1 ± 2.6 °C and mean annual precipitation of at least 115 cm (+50/–35 cm) were estimated based on standard techniques of leaf-margin analyses (Iglesias et al., 2007). Fossil wood growth rings from the Víctor Szlápelis and Ormaechea Petrified Forests (also Salamanca Formation, south of the study area) and the Ameghino Petrified Forest (north of the study area) were analyzed (Brea et al., 2005a, 2005b, 2011), and also conclude that the forests lived under humid and warm conditions.

Las Violetas Fossil Forest (Estancia Las Violetas; North Flank of the GSJB, Fig. 1A–C) is the most recently known fossil forest mentioned for the Salamanca Formation. At this locality, four fossiliferous levels (L1, L2, L3, and L4; Fig. 2) were defined throughout the outcrops of the unit. These levels include conifer and dicot permineralized trunks, branches and twigs, palm stipes, palm fruits and seeds, and leaf impressions (Somoza et al., 1995; Futey et al., 2012; Ruiz et al., 2017), and are evidence of forested coastal settings that developed during the early Paleocene at middle–high paleolatitudes of South America. This fossil forest provides an excellent opportunity to (1) expand the knowledge of Paleocene dicot wood anatomy by describing and taxonomically assigning new dicot fossil woods recovered in the fossiliferous level L3 from the Salamanca Formation, and (2) increase paleoclimate information from South America by incorporating climatic inferences based on fossil wood anatomy of the assemblage cropping out in fossiliferous levels L2 and L3 from the Las Violetas Fossil Forest.

2. Materials and methods

The samples come from the Estancia Las Violetas locality (Salamanca Formation), Chubut Province, Argentina (45° 04’ S, 66° 59’ W) (Fig. 1). The stratigraphic position of the fossiliferous levels included in this study (L2 and L3) were referred to the sedimentological section published by Ruiz et al. (2017, see Fig. 2), and consequently, sedimentological inferences are the same. Colors of the paleobotanical materials, including petrified woods and fruits, were described using the Geological Rock-Color Chart (2009). Colored wood-samples from L2 and L3 were selected to characterize the mineralogy of fossil woods using X-Ray Diffraction (XRD) following the methodology described in Raigemborn et al. (2014). Diffractograms were run on X PANalytical model X'Pert PRO diffractometer, using Cu/Ni radiation and generation settings of 40 KV and 40 mA (Centro de Investigaciones Geológicas, La Plata, Argentina).

Four fossiliferous levels were identified (L1–L4) (Fig. 2) (see also Ruiz et al., 2017) comprising gymnosperm and dicot woods, palm stipes and palm fruit remains. Anatomy and systematics of the gymnosperm woods from L2 were previously studied (Ruiz et al., 2017), and work is in progress on the fossil woods from L4 and palm remains from all the fossiliferous levels. In the present contribution, we focused on the anatomy and systematic affinities of 10 dicot fossil woods from L3, and the paleoclimatic inferences from the fossil assemblage of the fossiliferous levels L2 and L3.

For the study of the fossil woods, we obtain thin sections of all the samples in the three standard sections used in the study of wood anatomy: transverse section (TS), tangential longitudinal section (TLS), and radial longitudinal section (RLS).

Descriptions and comparisons follow the anatomical terminology recommended by the IAWA list of the microscopic features for hardwood identification (IAWA Hardwood Committee, 1989). An extensive bibliography was consulted for assignments and comparisons (InsideWood, 2004-onwards; Wheeler, 2011; Gregory et al., 2009, among others). The characters used for InsideWood database searches are followed with their numerical code between parentheses (all searches with 0 allowed mismatching).

The specimens were observed using a Nikon Eclipse E200 and a Leica DM2500 - light microscopes, and the pictures were taken with a Nikon Coolpix S4 digital Camera and Leica DFC290 digital camera. An average of at least 25 measurements is given for each value, followed by the minimum and maximum in parentheses. The percentage of vessels per square mm were counted individually, truly counted all the vessels per square mm (i.e. including all the vessels in radial multiples or groups); the percentage of solitary vessels and radial multiples were calculated counting groups as a unit (i.e., a radial multiple of three was counted as, 1 not as 3). The studied material is deposited in the paleobotanical collection at the Museo Paleontológico Egidio Feruglio, Trelew, Chubut Province, Argentina (labelled as MPEF-Pb 8385–8390, 8392–8401).

Fossil woods were analyzed with different methods to get paleoclimatic information. Growth ring analysis included: the presence or absence of growth ring boundaries (indicative of seasonal or non-seasonal climates respectively), detection of false rings (caused by drought, fire and/or insect attack) and detection of frost rings (caused by freezing temperatures during the growth season) (Fritts, 1976; Schweingruber, 1988). Measurements like mean ring width, mean maximum ring width, mean minimum ring width, narrowest ring, and widest ring were calculated in all the specimens with distinct growth ring boundaries as an indicator of growth conditions. Annual Sensitivity (AS) and Mean Sensitivity (MS) were calculated in those samples with ten or more measurable growth-rings. The former indicates the variability in growth ring width from year to year, and the latter is an indicator of the variability in growth rate over the lifespan of the tree (Fritts, 1976; Creber and Francis, 1999). A value of 0.3 is taken to distinguish between “complacent” trees that grew under a favorable and uniform climate ($MS < 0.3$) from those that are “sensitive” to fluctuating climate parameters ($MS > 0.3$).

The growth rings were analyzed using the classification scheme of Creber and Chaloner (1984) to categorize different earlywood/latewood relationships, and the method described by Falcon-Lang (2000a, 2000b) to analyze the relationship between leaf longevity and the distinctiveness of the growth ring boundary. A minimum of 30 cells of width per ring was required. The cumulative algebraic sum of each cell’s deviation from the mean of the radial diameters was calculated for each growth ring increment and plotted as a zero-trending curve (CSDM curve) (Creber and Chaloner, 1984). For each ring increment, the percentage skew of the zenith of CSDM curves from the center of the plot was calculated. Deciduous conifers give CSDM curves that are dominantly left-skewed or symmetrical, whereas evergreen conifers have right-skewed CSDM curves (Falcon-Lang, 2000a, 2000b) dominantly. Growth rings can be wider in the younger parts of the tree near the piths, and that could affect tree ring analyze. In this case, the estimated trunk diameter, grossly based on the ring curvature and the divergence of the rays, indicates all the samples were from matures parts of the trees, far from the pith.

Carlquist (1977) discussed the correlations between xylem anatomy and habitat. Herein we apply the two formulae he devised as indicators of the plants' adaptation to the available water in their habitat. They are the Vulnerability index (V= mean vessel diameter divided by the mean vessel frequency) and the Mesomorphy index (M= V multiplied by the mean vessel member length). V is an indicator of hydraulic conductivity and risk of suffering embolisms, with high V values typical of efficient water conductors. M indicates if the wood structure is adapted to a mesomorphic environment (ca. M>200) or to a xeric condition (ca. M<75).

Besides the characters employed by Carlquist (1977), there are other anatomical characters of dicotyledonous woods which are related to the climate (i.e. porosity, vessel diameter, presence of vessels with helical thickenings, distribution of axial parenchyma, presence of septate fibres and others) (Wheeler and Baas, 1991, 1993, 2019; Wheeler et al., 2007; Baas and Wheeler, 2011; Carlquist, 2012). Besides, anatomical characters are also used to estimate temperature and precipitation values (Wiemann et al., 1998, 1999). Although we could not apply the Wiemann et al. (1998, 1999) equations due to the limited number of samples, dicotyledonous woods from L3 were analyzed, taking into account those characters of paleoecological importance and their correlation with climatic variables to obtain some general paleoclimatic inferences.

3. Geological and sedimentological framework

Las Violetas Fossil Forest is located in the eastern part of the north flank of the Golfo San Jorge Basin (hereafter GSJB), towards the north of Comodoro Rivadavia City (Fig. 1A and B). The GSJB is a mainly extensional basin in central Argentinean Patagonia related to the Gondwana break-up during the Late Jurassic and Early Cretaceous (Fitzgerald et al., 1990). The shallow marine Salamanca Formation (early–mid Danian; Clyde et al., 2014) represents the first Atlantic transgressive event in the GSJB (e.g., Malumián and Nañez, 2011). Its deposition exceeded the north Cretaceous limit of the GSJB, and towards the northeast of the study area the limestones of the lower part of the Salamanca Formation, the Bustamante Member (following Andreis et al., 1975), took place directly over the Jurassic volcanic rocks of the Marifil Complex. However, in the study area, the outcrops of the Salamanca Formation are characterized by the siliciclastic deposits of the middle–upper Hansen Member (sensu Andreis et al., 1975), which are known as the *Banco Verde* and the *Banco Negro Inferior* (following Feruglio, 1949). The former unit is followed by the "*Niveles Transicionales*", as was defined by Raigemborn et al. (2010), and by the continental deposits of the Río Chico Group (lower Paleocene–middle Eocene; Krause et al., 2017) which are overlying by the marine Chenque Formation (lower Miocene; Cuitiño et al., 2015), and the glaciofluvial "*Rodados Patagónicos*" (Fig. 1B).

In the Las Violetas Fossil Forest, the regionally extended *Banco Verde* consists of greenish conglomerates, sandstones, and siltstones arranged in a fine-grained upward succession of ~16 m-thick that correspond to an estuarine setting dominated by tidal currents (Ruiz et al., 2017) (Fig. 2). In the deposits corresponding to sub-environments of tidal flat, tidal channels, and tidal bars Ruiz et al. (2017) identified four fossiliferous levels (L1 to L4) (see Fig. 2 for reference). Sandy tidal flat deposits of the central estuary bear twigs, stipes and palm fruits of the L1. High-energy tidal bar and tidal channel deposits of the central–inner estuary bear the plant levels L2 to L4. The L2, previously studied by Ruiz et al. (2017), preserves a parautochtonous association of vegetative parts (trunks, branches, twigs) and reproductive structures (palm fruits). Petrified woods at this level range in colors from dark yellowish-orange (10YR 6/6) through moderate brown (5YR 4/4) to dusky brown (5YR 2/2), and from pale greenish yellow (10Y 8/2) through grayish yellow-green (5GY 7/2) to light green (5G 7/4). Palm fruits are grayish yellow-green (5GY 7/2) or grayish green (10GY 5/2) in color. The L3 preserves dicot trunks and branches (whose anatomy and systematic affinities are discussed in the present work), and palm stipites and fruits. Fossil remains at this level are characterized by the presence of large trunks (up to ca. 1.5 m), unrounded branches, and twigs with colors that range from very pale orange (10YR 8/2) through moderate yellow-green (5GY 7/4) to brownish-black (5YR 2/1). Palm fruits are rounded and have the same color as fruits from L2. X-ray diffraction analysis of woods of both L2 and L3 indicates that the dominant mineral in the fossil wood samples is silica. Finally, the fossiliferous level L4 bears still undescribed trunks, branches, twigs, stipes, and palm fruits that will be studied. Deposits of sand flat areas of the outer part of the central estuary overlie beds bearing the mentioned fossil plants. The estuarine succession of the Salamanca Formation ends with blackish pedogenically modified coastal plain deposits (i.e., swamp deposits) of the *Banco Negro Inferior* (e.g., Raigemborn et al., 2010; Ruiz et al., 2017) (Fig. 2). Sedimentological and biological (fossil plants, fossil traces) features of this succession of the Salamanca Formation was interpreted by Ruiz et al. (2017) as a tidal-influence littoral environment, located very close to the coastline, that grades upward to coastal swamp settings.

4. Systematic paleontology

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

Family Myrtaceae Juss., 1789

Fossil-genus *Myrceugenellites* Nishida, Nishida and Nasa, 1988

Type species. *Myrceugenellites maytenoides* Nishida, Nishida and Nasa, 1988

Synonymy.

2001. *Myrceugenelloxylon maytenoides* (Nishida, Nishida and Nasa) Poole, Hunt and Cantrill: 44, figs. 39–46.

Myrceugenellites grandiporosum sp. nov. Ruiz, Brea and Pujana

Fig. 3

Diagnosis. Secondary xylem with indistinct growth ring boundaries. Vessel diameters medium (-wide), exclusively solitary (90% or more). Less than 50 vessels per mm^2. Vessel elements length >800 μm. Perforation plates scalariform with numerous bars (>20). Intervessel pits scalariform to opposite. Vessel-ray pits bordered, circular and opposite. Diffuse and scanty paratracheal axial parenchyma. Nonseptate fibres with distinctly bordered pits. Rays uniseriate or uniseriate with bi-triseriate portions almost the same width than the uniseriate parts.

Derivation nominis. The specific name, *grandiporosum,* refers to the relatively wide diameters of the vessel elements compare with the other species of the same genus.

Holotype. MPEF-Pb 8393.

Paratype. MPEF-Pb 8392.

Other material. MPEF-Pb 8394, 8395, 8396, 8397 and 8398.

Type locality. Estancia Las Violetas, Chubut, Argentina.

Type stratigraphic horizon. L3 fossiliferous level, Hansen Member (*Banco Verde*), Salamanca Formation.

Age. Early Paleocene, Chron 28n, Danian.

Description. Dicot wood. Growth ring boundaries are indistinct, marked by the reduction of the radial diameter of the last rows of latewood fibers (Fig. 3A). Wood is diffuse-porous, with 14 (9–20) vessels per mm^2. Vessels are solitary (96%), rarely in tangential pairs (2%), in clusters (1%), or in radial multiples of two (1%) (Fig. 3A–C). Vessels are circular in outline; 145 (62–194) µm in tangential diameter, 134 (43–189) µm in radial diameter; 1728 (1133–2384) µm in length. Vessel elements have tails; end walls are steeply inclined; perforation plates are scalariform with 34 (24–44) bars (Fig. 3E–G). Some perforation plates have forked bars (Fig. 3G). Intervessel pits are scalariform to opposite (circular or transitional) (Fig. 3H, I), with a vertical diameter of 5.5 (4.0–6.7) µm and a horizontal diameter of 10.2 (6–35.7) µm.

Axial parenchyma is scanty paratracheal and diffuse. Parenchyma cells have small, circular, and opposite pits (Fig. 3 D, O–Q).

Nonseptate fibers are 28.2 (15.3–42.3) μm in tangential diameter. They have distinctly bordered pits on radial and tangential walls, 8.1 (6.5–9.7) μm in vertical diameter, and elongate cross apertures (Fig. 3O–Q). Fiber walls seem to be thick, but we could not observe them accurately because they have some degradation or collapse.

Rays are mostly uniseriate (ca. 90%) (Fig. 3N), homocellular with all upright cells. There are also heterocellular rays (ca. 10%) with long uniseriate portions composed of upright cells similar to the uniseriate rays (Fig. 3N–P), and bi- or triseriate portions as wide as the uniseriate portions composed of procumbent cells (Fig. 3N–P). There are 11 (8–14) rays per mm, 2.8 (0.6–5.7) mm, and 18 (4–18) cell high. Rays are 32.3 (14.5–59.3) μm wide. Vessel-ray pits are circular and opposite, similar to the circular intervessel pits (Fig. 3J–M), and with a diameter of 6.1 (3.9–8.3) μm. Ray cells have dark contents (Fig. 3P).

Remarks. MPEF-Pb 8392 and 8393 have excellent preservation; the other five samples assigned to this fossil-species are not well preserved. All measurements are from the holotype. The seven specimens do not exhibit any significant variation among them other than a slight variation in the quantitative characters like vessel tangential diameter.

4.1. *Affinity and comparisons*

The combination of characters of diffuse-porous wood, commonly solitary vessels, circular or elliptical in outline, vessels bearing steeply inclined end walls, exclusively scalariform perforation plates with numerous bars (sometimes forked bars), intervessel pits circular or elliptical, opposite and scalariform, axial parenchyma scarcely visible, rays 1- to 3-seriate, vessel-ray pits circular to elliptical opposite or scattered are present in *Myrceugenellites* Nishida, Nishida and Nasa (Nishida et al., 1988). There are two species of

Myrceugenellites, *Myrceugenellites maytenoides* Nishida, Nishida and Nasa and *Myrceugenellites oligocenum* Pujana, and both are different from *Myrceugenellites grandiporosum* in the number of vessels per mm^2, vessel tangential diameter and type of axial parenchyma (Nishida et al., 1988; Pujana, 2009; Table 1). *Myrceugenellites maytenoides* can also be differentiated by its sometimes scalariform vessel-ray pits (Nishida et al., 1988) and *M. oligocenum* by having exclusively opposite intervessel pits and the absence of triseriate rays (Pujana, 2009) (Table 1). Because of these differences, the fossil woods from the Salamanca Formation are assigned to a new species of *Myrceugenellites*.

There are other nine fossil-genera with diffuse-porous wood (5r), solitary vessels (9r), exclusively scalariform perforation plates with numerous bars (14r, 17r) and 1- to 3-seriate rays (97r), but they differ from *Myrceugenellites* in the following characters:

1- *Aextoxicoxylon* Nishida, Nishida and Nasa has scalariform perforation plates with numerous up to 110 bars, intervessel pits most frequently scalariform, vessel-ray pits horizontally elongated and fibers without distinctly bordered pits (Nishida et al., 1988).

2- *Cercidiphylloxylon* Prakash, Březinová and Bůžek has small vessels and diffuse axial parenchyma commonly associated with the growth rings (Prakash et al., 1971).

3- *Cornoxylon* Conwentz has tangentially zonate axial parenchyma (Conwentz, 1882; Vater, 1884).

4- *Ericaceoxylon* Van del Burgh has both simple and scalariform perforation plates, helical thickenings in vessels, banded axial parenchyma, wider rays (up to seven cells wide) and intervessel pits are not observed (Van del Burgh, 1964).

5- *Hamamelidoxylon* Lignier has vessel-ray pits horizontally elongated (Grambast-Fessard, 1969; Van der Burgh, 1973; Gottwald, 1992; Wheeler and Manchester, 2002; Takahashi and Suzuki, 2003).

6- *Illicioxylon* Gottwald has wider rays (up to six cells wide), vessel-ray pits horizontally elongate, possible helical thickenings, and sclerotic cells included in the wood with rhomboidal crystals and druses (Gottwald, 1992).

7- *Mastixioxylon* Gottwald has wider rays (up to 12 cells wide), vessel-ray pits horizontally elongate to scalariform and resin canals (Gottwald, 1992).

8- *Weinmannioxylon* Petriella has wider rays (up to six cells wide) and more abundant apotracheal axial parenchyma (Petriella, 1972; Pujana et al., 2018).

9- *Schimoxylon* Kramer has vessel-ray pits horizontally elongate to scalariform (Kramer, 1974).

Nishida et al. (1988) related *Myrceugenellites maytenoides* with the Myrtaceae based on the diffuse-porous wood, the solitary vessels, the diffuse axial parenchyma, the scalariform perforation plates, the multiseriate rays with uniseriate margins and the fused rays (two or three rays fused at their uniseriate margins). Pujana (2009) also related the genus with the Myrtaceae, and discarded other families from Patagonia with similar wood anatomy (Cunoniaceae, Monimiaceae, Atherospermataceae, and Lauraceae) mainly by the presence of horizontally elongated vessel-ray pits with opposite to scalariform arrangement. However, no comparisons with woods outside the Patagonian region were carried out, making this affinity doubtful.

Extant woods from different families appear when looking for extant species with the main characters of *Myrceugenellites*: diffuse-porous wood (5r), solitary vessels (9r), scalariform perforation plates (14r) with numerous bars (17p), fibers with bordered pits (62r), scanty paratracheal axial parenchyma (78p) and rays 1- to 3-seriate (97r). However, these families also present other characters that make them unsuitable to include *Myrceugenellites*. Buxaceae woods have very small vessels, and markedly heterocellular rays and only *Buxus* L. has paratracheal parenchyma (Metcalfe and Chalk, 1950; InsideWood, 2004-onwards). Within the Ctenolophonaceae, only *Ctenolophon englerianus* Mildbr. shares the mentioned features, and has alternate intervessel pits, more abundant axial parenchyma (including vasicentric, aliform, confluent and diffuse-in-aggregates), occasionally rays 4–10 cells wide, disjunctive parenchyma and prismatic crystals in chambered axial parenchyma cells (Metcalfe and Chalk, 1950; InsideWood, 2004-onwards). *Weigela* Thunb. from the Caprifoliaceae is also very similar to *Myrceugenellites* but, like most of the members of this family, is a shrub with small or very small vessels (Metcalfe and Chalk, 1950; InsideWood, 2004-onwards). Hamamelidaceae woods have small vessels, large and horizontally elongate vessel-ray pits, apotracheal axial parenchyma, and exclusively heterocellular rays (Metcalfe and Chalk, 1950; InsideWood, 2004-onwards). Illiciaceae woods have very to moderately small vessels, scalariform perforation plates with very numerous bars (up to 150), vessel-ray pits horizontally elongate, and heterocellular rays (Metcalfe and Chalk, 1950; InsideWood, 2004-onwards). Olacaceae also has large and simple vessel-ray pits (Metcalfe and Chalk, 1950; InsideWood, 2004-onwards). Pentaphylacaceae members are shrubs or small trees commonly from Asia, and *Adinandra* Jack is similar to the fossil but has large and horizontally elongate vessel-ray pits (Metcalfe and Chalk, 1950; InsideWood, 2004-

onwards). Symplocaceae woods have small and angular vessels, often with spiral thickenings, only apotracheal axial parenchyma and fibers commonly with spiral thickenings (Metcalfe and Chalk, 1950; InsideWood, 2004-onwards). Humiriaceae and Icacinaceae have exclusively heterocellular rays (Metcalfe and Chalk, 1950; InsideWood, 2004-onwards).

Consequently, Myrtaceae is the most suitable family for including *Myrceugenellites grandiporosum*. Myrtaceae species have both small and large vessels, solitary vessels, both exclusively simple or scalariform perforation plates (in *Myrceugenia* O. Berg and *Myrtus* L.) with a large number of bars, intervessel pits typically alternate but also opposite (in *Myrceugenia* and *Myrtus*), vessel-ray pits small, axial parenchyma can be both apotracheal or paratracheal, rays typically up to 2–3 cells wide, exclusively uniseriate or with only occasional biseriate parts, both homogeneous and heterogeneous rays, fibers typically with bordered pits both in tangential and in radial walls, that can be septate or nonseptate. Besides, there are fossil leaves of Myrtaceae in the Salamanca Formation (Iglesias, 2007) and it is recorded since the cretaceous to the present in Patagonia (Passalia et al., 2001; Prámparo et al., 2007; Gandolfo et al., 2007; Iglesias et al., 2007).

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

Fossil-genus *Patagonoxylon* gen. nov. Ruiz, Brea and Pujana

Diagnosis. Diffuse-porous wood. Vessels solitary and in radial multiples. Scalariform perforation plates. Opposite intervessel pits. Scanty paratracheal and diffuse axial parenchyma. Fibers with distinctly bordered pits. Homocellular and heterocellular rays, multiseriate. Scalariform vessel-ray pits. Idioblasts in rays.

Derivation nominis. Patagonoxylon refers to the geographical (Patagonia) provenance of the specimen.

Type species. *Patagonoxylon scalariforme* sp. nov. Ruiz, Brea and Pujana

Fig. 4

Diagnosis. Growth rings boundaries absent. Vessels solitary or in radial multiples mostly of two. Perforation plates scalariform with less than 20 bars.

Derivation nominis. The specific name, *scalariforme*, refers to the type of perforation plates.

Holotype. MPEF-Pb 8399.

Type locality. Estancia Las Violetas, Chubut, Argentina.

Type stratigraphic horizon. L3 fossiliferous level, Hansen Member (*Banco Verde*), Salamanca Formation.

Age. Early Paleocene, Chron 28n, Danian.

Description. Dicot wood. Growth ring boundaries are absent. Wood is diffuse-porous with 29 (16–51) vessels per mm^2. Vessels solitary (66.6%), in radial multiples of two or three vessels (27.0%), in radial multiples of four or more (4.4%), clusters (1.5%), and in tangential pairs (0.5%) (Fig. 4A–C). Vessels are circular to oval in outline, with a tangential diameter of 60 (18–104) μm, and a radial diameter of 86 (44–137) μm. Vessel elements are 771 (506–1158) μm long, and they usually have tails. Perforation plates are deeply inclined and scalariform with 9 (4–16) bars (Fig. 4E, F, J). Intervessel pits are scalariform to opposite (Fig. 4G, H) and opposite to alternate (Fig. 4I), with a vertical diameter of 6.3 (4.6–8.0) μm. Tyloses are common (Fig. 4P).

Axial parenchyma is scanty paratracheal and diffuse (Fig. 4O, P).

Fibers have some decay, and therefore measurements of the lumen diameter and wall thickness could not be taken. They have bordered pits of 5.3 (4.2–6.2) μm in vertical diameter with elliptic apertures (Fig. 4R, S).

Rays are fusiform in shape, mostly homocellular, composed exclusively of procumbent cells, although some are heterocellular with body ray cells procumbent and one or two rows of upright marginal cells (Fig. 4J, M). There are 7 (6–8) rays per mm. Rays are multiseriate, 4 (3–7) cells, and 78 (44–139) μm wide; 28 (9–78) cells and 1.2 (0.3–2.7) mm in height. Rays have large oil cells (idioblasts) in the body or in their margins (Fig. 4N, Q, R). Vessel-ray pits are scalariform, with reduced borders and a vertical diameter of 9.0 (3.8–14.0) μm (Fig. 4K, L).

4.2. *Affinity and comparisons*

Patagonoxylon is characterized by the diffuse-porous wood (5r), scalariform perforation plates (14r), larger rays commonly 4–10 seriate (98p), and the presence of oil cells (304r). There are other fossil-genera with these characteristics but easily distinguishable from *Patagonoxylon*. *Cinnamomoxylon* Gottwald is a Lauraceae wood that differs from *Patagonoxylon* by its simple perforation plates (in addition to the scalariform ones) and alternate intervessel pits (Gottwald, 1997). *Laurinium* Unger was originally included in the Lauraceae, with a vague description, and many of the fossil-species were later transferred to *Laurinoxylon* (see Dupéron-Laudoueneix and Dupéron, 2005). Nevertheless, apart from its taxonomic problems, this fossil-genus has a majority of simple perforation plates and alternate intervessel pits (Unger, 1845; Dupéron-Laudoueneix and Dupéron, 2005). Another Lauraceae wood similar to *Patagonoxylon* is *Laurinoxylon* Felix emend Dupéron, Sakala and Dupéron-Laudoueneix, but it has simple or simple and scalariform perforation plates (never exclusively scalariform) and alternate intervessel pits. *Laurinoxylon intermedium* Huard and *L. aniboides* Süss and Mädel have exclusively scalariform perforation plates and scalariform intervessel pits, but they are different from *Patagonoxylon* because of their apotracheal axial parenchyma in tangential bands. Besides, due to their exclusively scalariform perforation plates, these two species should not be placed in *Laurinoxylon* (Felix, 1883; Süss and Mädel, 1958; Huard, 1967; Dupéron et al., 2008). The Monimiaceae genera *Atherospermoxylon* (Kräusel) Mädel and *Protoatherospermoxylon* Mädel, also resemble *Patagonoxylon,* but they have exclusively apotracheal axial parenchyma (Mädel, 1960; Poole and Gottwald, 2001).

The combination of features present in *Patagonoxylon* makes it difficult to include it in an extant family. Canellaceae and Dilleniaceae are characterized by having exclusively scalariform perforation plates and large oil cells (idioblasts), but they have exclusively solitary vessels and different type of rays than *Patagonoxylon* (Metcalfe and Chalk, 1950). Other families with scalariform perforation plates and large oil cells (idioblasts) are Magnoliaceae and Monimiaceae, but they have predominantly apotracheal axial parenchyma, occasionally in tangential bands (Metcalfe and Chalk, 1950). Lauraceae have oil cells commonly, but they have alternate intervessel pits and do not have exclusively scalariform perforation plates, although they can be both simple and scalariform in some extant and fossil species (Metcalfe and Chalk, 1950; Dupéron-Laudoueneix and Dupéron, 2005). The combination of characters of *Patagonoxylon* is not present in any extant wood and can not be associated precisely with any family (Metcalfe and Chalk, 1950; InsideWood, 2004-onwards). Since *Patagonoxylon* has many characters in common with Monimiaceae and Lauraceae, most of the similar fossil genera are from these families, and both families are Laurales (APG IV, 2016), we include *Patagonoxylon* into this order without a definitive family.

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

Family Lauraceae Juss., 1789

Fossil-genus *Mezilaurinoxylon* Wheeler and Manchester, 2002

Type species. *Mezilaurinoxylon eiporosum* Wheeler and Manchester, 2002

Mezilaurinoxylon oleiferum sp. nov. Ruiz, Brea and Pujana

Fig. 5

Diagnosis. Vessels solitary and in radial multiples mostly of two. Vessel mean tangential diameter >100 μm, perforation plates simple, intervessel pits transitional and alternate. Vessel-ray parenchyma pits mostly enlarged, also scalariform and opposite. Axial parenchyma scanty paratracheal. Rays multiseriate, heterocellular, up to 6 cells wide, some with uniseriate margins of upright cells. Oil cells in rays or occasionally among fibers.

Derivation nominis. The specific name, *oleiferum*, refers to the presence of the oil cells.

Holotype. MPEF-Pb 8400.

Paratype. MPEF-Pb 8401.

Type locality. Estancia Las Violetas, Chubut, Argentina.

Type stratigraphic horizon. L3 fossiliferous level, Hansen Member (*Banco Verde*), Salamanca Formation.

Age. Early Paleocene, Chron 28n, Danian.

Description. Growth ring boundaries are absent. Wood is diffuse-porous with 16 (8–26) vessels per mm^2. Vessels are solitary (59.0%), in short, radial multiples of two or three cells (34.0%), long radial multiples of four or more cells (4.7 %), and in clusters (2.3%) (Fig. 5A–C). Solitary vessel elements are circular to oval in outline and are 137 (76–183) μm in tangential diameter, 121 (67–192) in radial diameter, and 575 (387–803) μm in length. Perforation plates are simple (Fig. 5E). Intervessel pits are circular in outline, alternate to occasionally opposite (Fig. 5 F–I), with a tangential diameter of 9.9 (7.0–12.7) μm. Tyloses are common (Fig. 5 J, O, Q).

Fibers are septate (Fig. 5P, Q), with a tangential diameter of 18.7 (7.7–26.4) μm and a wall thickness of 3.0 (1.7–5.0) μm.

Axial parenchyma is scanty paratracheal (Fig. 5D, G, Q).

Rays are mostly heterocellular (Fig. 5J) and in tangential section, sometimes fusiform in shape (Fig. 5O, P); 956 (160–2800) μm high. Most rays are multiseriate (88%), 4 (2–8) cells, and 88.2 (26.3–157.0) μm wide. Some of them have uniseriate margins with one to seven upright cells. There are also multiseriate rays connected by uniseriate portions or by thinner multiseriate portions. In a smaller proportion (12 %), there are exclusively uniseriate rays, 1–6 cells high, similar to the uniseriate portions of the multiseriate rays. Most of the ray-vessel pits are enlarged or fenestriform [window-like] (Fig 5K, L) with a vertical diameter of 24.6 (10.8–29.2) µm, some are smaller, circular and bordered (Fig. 5K) and some are horizontally elongate with slightly reduced borders (Fig. 5M).

Large oil cells (idioblasts) with orange contents that fill almost all the cell occur in the margins of multiseriate rays or as one of the cells of the uniseriate portion between two multiseriate portions of rays. They are also very rarely isolated between fibers (Fig. 5N–Q). Also, some parenchyma ray cells have dark drops (Fig. 5L, N).

Remarks. Measurements were taken from the holotype. The two specimens do not exhibit any significant variation among them other than a slight variation in the quantitative characters like vessel tangential diameter. Some of the intervessel pits seem to be vestured (Fig. 5H, I), but this could be an artifact result of later permineralization , or accumulation of extractives around pit apertures. Both samples have fungal hyphae and probable conidia inside the fibers and the vessels (Fig. 5R–T).

4.3. *Affinity and comparisons*

The main characters of the fossils, i.e., diffuse-porous wood (5r), simple perforation plates (13r), alternate intervessel pits (22r), multiseriate rays more than 4 cells wide (98p) and oil cells (304r), are found in in at least 10 fossil-genera (sensu InsideWood, 2004-onwards) from which *Mezilaurinoxylon* is the one with more characters in common (Table 2). *Duguetiaxylon* Soares, Kloster, Gnaedinger, Riker, Lima and Motta, *Polyalthioxylon* Estrada-Ruiz, Upchurch, Wheeler and Mack and *Pygmaeoxylon* Bande are three Monimiaceae easily distinguish from *Mezilaurinoxylon*. They have different type of vessel-ray pits, different types of axial parenchyma distribution, and exclusively homocellular rays (except *Duguetiaxylon*) (Bande, 1973; Estrada-Ruiz, Upchurch, Wheeler and Mack, 2012; Soares et al., 2017). Besides, oil cells are not mentioned in the original diagnosis/descriptions of *Duguetiaxylon* and *Polyalthioxylon* (Bande, 1973; Soares et al., 2017). The rest of the comparable fossil woods (Table 2) are related to the Lauraceae, and they are *Beilschmiedioxylon* Dupéron-Laudoueneix and Dupéron, *Caryodaphnopsoxylon* Gottwald and *Cryptocaryoxylon* Leisman with scalariform vessel-ray pits, different type of axial parenchyma and different oil cell distribution (Leisman, 1986; Gottwald, 1992; Dupéron-Laudoueneix and Dupéron, 2005). *Cinnamomoxylon* Gottwald has both simple and scalariform perforation plates, and oil cells in rays and axial parenchyma (Wheeler and Manchester, 2002; Dupéron-Laudoueneix and Dupéron, 2005). *Ulminium* Unger also has similar characters (sensu InsideWood, 2004-onwards), but it is a synonym of *Laurinoxylon*, which is a nomen conservadum (sensu Dupéron et al., 2008). *Laurinoxylon* Felix emend Dupéron, Sakala and Dupéron-Laudoueneix has fibers with bordered pits, and the description is not clear about the type of vessel-ray pits, the septation of the fibers and the position of the oil cells (Dupéron et al., 2008).

According to the original diagnosis of *Mezilaurinoxylon*, it has alternate intervessel pits and enlarged vessel ray pits. *Mezilaurinoxylon oleiferum* has alternate to transitional intervessel pits and not only enlarged but also small and scalariform vessel-ray pits. We do not consider those differences significant enough to establish a new fossil-genus. Consequently, the fossils are described as a new species of *Mezilaurinoxylon*.

The characteristics of *Mezilaurinoxylon* are commonly found in lauraceous woods: vessels solitary and in short radial multiples, simple perforation plates, large vessel-ray pits, paratracheal parenchyma, septate fiber, and oil cells.

5. Results

5.1. *Growth rings analysis*

Growth ring analysis was carried out only in the conifer woods from the L2 because they all have distinct growth ring boundaries. In the dicot woods from L3, growth rings boundaries can be observed only in *Myrceugenellites grandiporosum*, and they are indistinct and difficult to observe; therefore, these woods were set aside from this analysis.

A total of 70 ring series were measured, most of them short (8–21 rings), because growth rings are very wide, 2.20 (0.26–5.20) mm (Table 3 and Fig. 6). The minimum required of ten rings per sequence to calculate the Annual Sensitivity (AS) and the Mean Sensitivity (MS) indices were counted only in three samples (Table 3 and Figs. 6 and 7). MPEF-Pb 8388 and MPEF-Pb 8390 (both *Cupressinoxylon*) showed to be complacent but, although both MS values are very similar (0.26 and 0.20), AS values are not (Table 3 and Fig. 7). This indicates that the sample MPEF-Pb 8388 (with SA values up to 1) could be affected by extreme climatic events (Table 3 and Fig. 7). The sample MPEF-Pb 8385 (*Podocarpoxylon multiparenchymatosum*) shows AS and MS values typical of a sensitive wood (Table 3 and Fig. 7).

Except for the sample MPEF-Pb 8388 (*Cupressinoxylon artabeae*) all the conifers have growth rings with 30 or more cells of width and the CSDM curves from Creber and Chaloner (1984) could be calculated (Fig. 8). The percentage of latewood is low, with a maximum of 23.39% (Table 4). The rings are type D and E following Creber and Chaloner (1984) classification. These two types are essentially similar, and both indicate growing seasons that are relatively uniform, but each has a terminal event representing a cessation or retardation of cambial activity. In type D, the ring boundary is more marked, while in type E, it is so faint that it almost escapes notice (Creber and Chaloner, 1984).

Skew values are all higher than 12 (Table 4), indicating that all the trees were evergreen (Falcon-Lang, 2000a). Ring marked index (RMI) values are all low, most of them lower than 20 (Table 4) except for MPEF-Pb 8387 with a RMI of 23.69. The lower values would indicate a foliar retention between 3 and 15 years like the extant *Araucaria araucana* (Molina) K. Koch and a RMI of 23.69 would indicate a foliar retention of 3–6 years like *Cedrus libani* A. Rich., or 3–5 years like *Picea abies* (L.) H. Karst. The low percentage of latewood with a maximum of 23.39% (Table 4) is also in agreement with those results. On the other hand, the percentage of diminution has high values (Table 4), which corresponds to species from deciduous to six years of foliar retention. Making consensus of the obtained results, the conifer trees from Las Violetas Fossil Forest would have been evergreen with a foliar retention of about 3–6 years.

False rings are present in *Cupressinoxylon artabeae* and cf. *Cupressinoxylon* (Table 3). They are marked by the gradual decrease of tracheid radial diameter and a later gradual increase of it. This suggests a new water supply before the stop of the growing season.

5.2. *Vulnerability and Mesomorphy indices*

The Vulnerability (V) and Mesomorphy (M) indices of the dicot fossil wood from L3 are shown in table 5. The three species have very high values of both indexes (V=2.07–10.36 and M=4923.44–17897.14), suggesting a markedly mesomorphic environment, with an abundant water supply and free from frost and/or droughts.

5.3. *Wood characters influenced by the environment*

Anatomical characters of paleoecological significance in dicot fossil woods from L3 were analyzed to obtain some general paleoclimatic inferences. The relatively wide tangential diameter of vessels (in *Myrceugenellites grandiporosum* and *Mezilaurinoxylon oleiferum*) and the low density of vessel per mm^2 (in the three taxa) are common in present-day tropical regions (Van der Graaff and Baas, 1974; Baas and Xinying, 1986; Schweingruber, 1988; Wheeler and Baas, 1991, 1993; Carlquist, 2001; Baas and Wheeler, 2011). Two of the three taxa (*Myrceugenellites grandiporosum* and *Patagonoxylon scalariforme*) have scalariform perforation plates, a character typical of woods from cool-temperate to polar climates, or environments with stable humidity (Baas and Schweingruber, 1987; Wheeler and Baas, 1991, 1993, 2019; Baas, 1982; Wheeler et al., 2007; Carlquist, 2012). Helical thickenings are absent in the three taxa, and this would be consistent with tropical and humid environments. However, this character does not appear until the Eocene in the Southern Hemisphere (Van der Graaff and Baas, 1974; Baas and Xinying, 1986; Baas and Schweingruber, 1987; Wheeler and Baas, 1991, 1993; Wheeler et al., 2007; Carlquist, 2001, 2012), and hence it was not included in the paleoclimatic study. *Myrceugenellites grandipororum* and *Mezilaurinoxylon oleiferum* have septate fibers, a character more common in tropical floras than in temperate floras (Schweingruber, 1988; Baas and Schweingruber, 1987; Wheeler and Baas, 1991; Wheeler et al., 2007). The three taxa have scanty paratracheal axial parenchyma, which is commonly found (although not exclusively) in places with low temperatures (Morris et al., 2016; Plavcová et al., 2016). However, more elaborate patterns of paratracheal axial parenchyma are not common until the Eocene (Wheeler and Baas, 1991, 1993).

Because we only studied three different dicot woods, the presence or absence of these indicative characters only allow us to make some suggestions about the past climate and compare them with the rest of the results.

6. Discussion

6.1. *Paleoclimatic inferences from fossil woods*

Growth rings boundaries are well marked in all the conifer woods from Las Violetas Fossil Forest but not in the dicot woods. At present, this situation is common in tropical regions without a marked seasonality (Wheeler and Bass, 1993). It is notable the average ring width of ca. 2 mm and the maximum of 5 mm, indicating great periods of growth, with an abundant water supply and high temperatures (Brea et al., 2005a). These values are similar than those obtained for other Paleocene forests of the same basin (Table 6). The percentage of latewood is low, and this could be related to a decrease in the amount of water availability at the end of the season. AS and MS values are consistent with that; although they were complacent woods living in an environment without major climatic disturbances, extreme events could happen eventually such as extreme precipitation or floods, or on the other hand, prolonged droughts and fires. Growth rings types D and E (Creber and Chaloner, 1984) reinforce this assumption because they indicate relatively uniform growing seasons but with a terminal event representing a cessation or retardation of cambial activity (Creber and Chaloner, 1984).

The high values obtained, both of Vulnerability and Mesomorphy indices (V=2.07–10.36 and M=4923.44–17897.14) suggest that the early Paleocene in the Golfo San Jorge

Basin was a period of abundant water availability and the dicots were mesophytes or hydrophytes. The environment was free of frost and/or drought. This suggestion is also supported by the presence of wood characters influenced by the environment like scalariform perforation plates (Baas, 1982; Baas and Schweingruber, 1987; Wheeler and Baas, 1991, 1993; Wheeler et al., 2007; Carlquist, 2012). False rings are in agreement with a favorable hydric environment too. They suggest water supply fluctuation, which can be related to additional rains at the end of the growing season.

The most reliable wood characters influenced by the environment to take into account in this case are the wide tangential diameter of the vessels, the low frequency of vessels per mm^2, the presence of septate fibers, and the absence of helical thickenings. Those characters are all expected in environments with warm temperatures (Van der Graaff and Baas, 1974; Baas and Xinying, 1986; Baas and Schweingruber, 1987; Schweingruber, 1988; Wheeler and Baas, 1991; Carlquist, 2001, 2012; Wheeler et al., 2007). On the other hand, axial parenchyma is scarce in all the samples and in recent floras that could be considered indicative of low temperatures (Morris et al., 2016; Plavcová et al., 2016; Wheeler and Baas, 2019). However, during the Paleocene abundant axial parenchyma in elaborated patterns was not common in the Southern Hemisphere (Wheeler and Baas, 1991, 1993), making this feature unsuitable to use as a paleoclimate indicator in this case. The same case would be the ring porosity, another feature common in warm environments (and absent in Las Violetas Fossil Forest) but with a scarce record in the Southern Hemisphere (Wheeler and Baas, 1991, 1993, 2019; Wheeler et al., 2007; Baas and Wheeler, 2011). Finally, the scalariform perforation plates are indicative of both cold temperature and montane tropical climate where water supply is abundant (Baas, 1982; Baas and

Schweingruber, 1987; Wheeler and Baas, 1991, 1993; Wheeler et al., 2007; Carlquist, 2012). Nevertheless, we also have to be cautious with this feature because it is a plesiomorphic one, and its abundance could be related to age and not with the environmental conditions. It is important to notice that in all cases, there are only three different dicots recorded, and the low number of taxa could bias the real proportions of these anatomical characters in the forest.

6.2. *Comparisons with other Paleocene fossil forests*

Forests were widely distributed in Patagonia during the Paleocene. Those fossil forests have also been studied from a paleoenvironmental and paleoclimatic point of view (Brea et al., 2005a, 2005b, 2011) (Table 6).

Three other fossil forests are known from the Salamanca Formation: 1) Víctor Szlápelis Petrified Forests (45° 57’ 31’’ S - 69° 18’ 49’’ W), 2) Ormaechea Petrified Forests (45° 48’ 53’’ S - 69° 04’ 01’’ W), and 3) Ameghino Petrified Forest (43° 33’ 12’’ S and 66° 15’ 58’’ W). Gymnosperms dominated these three fossil forests. The woods described from Víctor Szlápelis Petrified Forest (Brea et al., 2005a) have mean growth ring widths of 1.31–6.03 mm, with a mean width of 2.66 mm. The maximum ring width is 11.30 mm. The Mean Sensitivity (MS) ranges from 0.39 to 1.42, with an average of 0.68 (Table 6). The woods from the Ormaechea Petrified Forest, also known as the Sarmiento Petrified Forest (Brea et al., 2005b), have a mean growth ring width of 2.10 (0.28–6.59) mm. The MS values range from 0.34 to 0.95, with an average of 0.59 (Table 6). False rings were observed in many wood specimens from both of these two fossiliferous localities (Table 6).

All samples have very narrow regions of latewood, indicating a very rapid cessation of growth. The well-developed earlywood indicates that the trees grew fast in a very favorable environment during the growing season or may be attributable to the inherent genetic characteristics of the tree. The presence of false rings and high MS values might reflect that these trees grew near the forest borders as well as near the climatically-determined limits of their distribution. Tree rings analysis suggests that these trees grew under warm-temperate and humid climatic conditions, with dry summers and rainy springs (Brea et al., 2005a). The high MS (Mean Sensitivity) and AS (Annual Sensitivity) values in these forests indicate that there was a marked seasonality with extensive favorable growth periods and restricted unfavorable ones. Las Violetas Fossil Forest is very similar to these two forests, and the same conditions can be assumed. The only notable difference is the MS mean value, which is lower in Las Violetas, being in the limit between sensitive and complacent, and not markedly sensitive like in Víctor Szlápelis and Ormaechea Petrified Forests (Table 6). Nevertheless, this might be either due to the lower number of samples or to that the trees were not in the borders of the forests. Finally, fossil woods from Ameghino Petrified Forest (Brea et al., 2011), have mean ring widths of 1.23 (1.11–2.69) mm, and this is the only one that is markedly complacent (MS=0.19), and false rings are not recorded. The uniform width of the rings is a signal of stable environments where no single limiting factor existed. This type of growth is correlated with trees that grow in forest interiors (Fritts et al., 1965; Francis, 1986) and is also a feature of extensive and dense forests (Taylor et al., 1990).

The Bororó Fossil Forest is located 200 km west of the Ameghino Petrified Forest (Cerro Bororó Formation, Paleocene). This forest, like the Las Violetas Fossil Forest, has not only conifers but also dicot trunks and palm stipes (Petriella, 1972). This forest was probably humid, with abundant water supply along the entire growing season and had warm mean annual temperatures higher than 20°C and without frosts (Ruiz, 2018).

Another important plant association from the Salamanca Formation is that of Palacio de Los Loros, where 36 angiosperm leaf species were described, including some related with the Myrtaceae and Lauraceae (Iglesias, 2007; Iglesias et al., 2007). Moreover, using standard techniques of leaf-margin and leaf-area analyses from 33 dicot leaves, Iglesias et al. (2007) estimated a mean annual temperature of 14.1 ± 2.6 °C and mean annual precipitation of at least 115 cm (+50/–35 cm).

The Antarctic Peninsula also has records of Paleocene forests. One of them is from the Sobral Formation (Lower Paleocene) in Seymour (Marambio) Island, where Araucariaceae dominates the assemblage, but also with dicots (Mirabelli et al., 2017). Growth rings had a width of 1.29 (2.0–4.6) mm and a MS of 0.17 (Francis, 1986). Overlying the Sobral Formation is the Cross Valley Formation of late Paleocene age, where there is a virtual absence of angiosperm woods and conifers are dominant, especially the Araucariaceae (Pujana et al., 2015). Growth rings of Cross Valley Formation are 1.29 (0.67–2.8) mm, narrower than those of the Sobral Formation (Table 6). MS is 0.26, being complacent like most of the Paleocene forests (Table 6).

Australia has an abundant paleobotanical record, but there are only a few Paleocene localities like the late Paleocene macroflora from Lake Bungarby that contains at least 40 taxa including *Eucryphia*, Proteaceae, Lauraceae, Cunoniaceae, Podocarpaceae, Cupressaceae and putative *Nothofagus* (Hill, 1994).

6.3. *Comparisons with extant forests*

As mentioned before, conifers and palms are present in L2 and dicots and palms in L3. Even though those fossiliferous levels could be separated by an undefined period of time, they probably constituted the same type of fossil forest with continuous development, free from important environmental changes. Reasons to make this assumption are the continuous record of palms and the same type of sediments (see also section 6.4). The record of only conifers in L2 and only dicots in L3 could be due to sampling size or due to their spatial distribution among the forest. Nowadays, conifers of the Southern Hemisphere usually occur in patches among angiosperms in mixed forests. This is the case of Andean Patagonian forests, where stands dominated by *Austrocedrus chilensis* (D. Don) Pic. Serm. and Bizzarriare is inserted within other forest types, usually with Nothofagaceae, depending on the latitude (Armesto et al., 1996). Sometimes it is also common an altitudinal zonation, like in Malaysia, where conifers are dominant at high altitudes near the treeline (3000–3900 m) (Johns, 1982).

Thus, as previously proposed (Ruiz et al., 2017), considering only the conifers, the closest modern ecological equivalent of the Las Violetas Fossil Forest would be the rainforests in the coastal areas of New Zealand, New Caledonia, southeastern Australia (Hill, 1994; Jaffré, 1995), Atlantic forests (Hueck, 1978) and temperate Andean Patagonian forests (Donoso, 1993; Armesto et al., 1996; Garndner and Lara, 2003). In New Caledonia, conifers are mostly found in very wet conditions (in dense rainforests, at higher altitudes and the margins of watercourses) and are adapted to extreme habitat conditions (except for aridity) (Jaffré, 1995; Farjon, 2007). They also grow along stream-sides and appear perfectly adjusted to temporary inundation.

Taking into account the dicot woods, these extant forests scenarios also fit well with the probable environment of Las Violetas Fossil Forest, where the Myrtaceae and Laurales are the most common dicots in the fossil assemblage until the date. In the north of New Caledonia, the swampy forests and some degraded coastal sites are dominated by Myrtaceae species, and only two species of conifers are strictly confined to river margins and marshes. These are *Dacrydium guillatiminii* limited to just four localities scattered along several kilometers on the margins of rivers and *Retrophyllum minor*, which grows at the margins of several watercourses and more rarely on lateritic duricrust in shallow depressions, flooded from time to time (Jaffré, 1995). The New Caledonia forests are also rich in palms and tree-ferns such as *Cyathea* Sm. and *Dicksonia* L'Hér. (Jaffré, 1995). Forests with Proteaceae, Myrtaceae, and Lauraceae occur in at least six of the extant Australian rainforest types (Webb, 1959; Hill, 1994), and a similar scenario is common in New Guinea. Extant Australian species of Myrtaceae grow as canopy dominants of subtropical-warm temperate rainforest of the east coast (Hill, 1994).

The Atlantic Forests of South America comprise a dense ombrophilous forest that encompasses the mixed coastal rainforest with mainly *Araucaria* and *Podocarpus* and dominated by Lauraceae in the south of its distribution, including mangroves, sandy-soil forests, shrubs and grasslands (Galindo-Leal and Gusmão Câmara, 2003). In Misiones (northeastern Argentina), there are evergreen trees, including species of the Lauraceae, Fabaceae, Myrtaceae, and Meliaceae, among others, and also palms. No species is dominant because many species share space in densities that vary as a result of small soil or microclimatic differences. This area counts with clear water rivers, stone-filled channels, rapids and falls, and deep alluvial soils on their banks (Galindo-Leal and Gusmão Câmara, 2003).

Mediterranean region of central Chile has a mesophytic vegetation, with precipitation of 20–100 cm/year and mean annual temperatures between 15–20° C. The flora is characterized by a Chilean endemic palm, *Jubaea chilensis* (Molina) Baill, restricted to some humid valleys and piedmonts of the Relict Coastal Cordillera in the Maule Region (32–34°S). It coexists with Rosaceae, Lauraceae, Cunoniaceae, Winteraceae, Myrtaceae. and Nothofagaceae. In these forests, there are also Cupressaceae in pure stands and confined to the margins of rivers (Donoso, 1993; Armesto et al., 1996; Garndner and Lara, 2003).

The presence of palm remains in Las Violetas Fossil Forest is an important component of the fossil association from the environmental point of view. Palms occur nowadays in the forests mentioned before, with a distribution mostly limited by the 18° C mean annual temperature isotherm. The only exceptions are New Zealand with an isotherm of 12° C (Volkheimer, 1971) and El Maule in Chile with a 15° C isotherm (Flores et al., 2016). Although the detailed anatomy descriptions of the palm stipes and fruits from Las Violetas Fossil Forest is still in preparation, it is relevant for this paleoenvironmental study to mention and highlight that some of the fossil stipes present aerenchyma (Fig. 9). This type of parenchyma is present in plants that grow in anoxic soils and could indicate hypoxic or temporarily flooded soils, where air spaces or channels in the stipes allows exchanges of gases in the submerged tissues.

6.4. *Paleoenvironmental reconstruction*

As was interpreted in previous works (Clyde et al., 2014; Comer et al., 2015; Ruiz et al., 2017), the flora of the Salamanca Formation grew in coastal lowland forests associated with a tidal estuarine environment. Similarly to the previously analyzed L2 (Ruiz et al., 2017), fossil plants of the currently analyzed L3 appear to have been deposited not far from where they grew (i.e., the association of diverse big trunks with different preservation, together with unrounded branches and twigs, and rounded fruits). Consequently, we consider plant fossil assemblages of the L3 as a parautochtonous association (following Gastaldo, 2001) that was not transported out of their habitat (i.e., was preserved in their growth environment, although not in life position) to the burial sites. In estuarine settings as those of the Salamanca Formation, intertidal flat areas (i.e., tidal flat, tidal sand flats, coastal marshes), the margins of tidal channels, and terrestrial freshwater settings (i.e., stream banks and exposed bar forms) can develop soils that support marginal or riparian vegetation (e.g., Allen and Gastaldo, 2006).

Considering that L2 and L3 are parautochtonous assemblages, it is possible that these plants were living close to their depositional setting (tidal channels and tidal bars), possibly on the margins of the channels and/or on exposed bars between channel belts, where well-drained soils can develop. Channel erosion during high-velocity floods or tidal cycles would have undercut channel bank margins, incorporating the plants into the adjacent channel. Nevertheless, we do not discard the possibility that some plants (e.g., palms) were living in environments with greater moisture availability, impeded drainage, and lower elevation than between channel belts, subjected to periodic floods or tidal cycles. Although there are no preserved paleosol levels or rooting bases in L2 and L3 that would represent the substratum where plants grew and can provide paleoclimatic information, plant macrofossils suggest that Las Violetas Fossil Forest was a rainforest. Modern and ancient soils that support tropical and warm-humid forests, like those of the Las Violetas Fossil Forest, are Oxisols (tropical deeply weathered soils) and Ultisols (base-poor forest soils) (Retallack, 2001). Paleo-Ultisols and -Oxisols can include Fe-rich indurated horizons (duricrusts and plinthites) (Retallack, 2001; Krause et al., 2010; Raigemborn et al., 2018b). For example, modern-day analogs for the hypothesized paleosols of the Salamanca Formation occur in Misiones (northeastern Argentina; ~27° SL) where the native forest develops over red Fe-rich and well-drained Oxisols and Ultisols (e.g., Panigatti, 2010).

Using the mineralization and coloring of fossilized woods (i.e., presence of chemical elements), we can speculate about their preservational environment (e.g., Williams et al., 2010; Mustoe and Acosta, 2016). According to Buurman (1972), the silicification of woods, as in the L2 and L3, is favored by warm and humid climates and porous host-rocks that allow percolating of silica-rich groundwater (Buurman, 1972). In both L2 and L3, there are specimens with yellow-orange- and green-hues. These colors could be attributed mainly to the occurrence of trace amounts of Fe in the structure of silica (e.g., Mustoe and Acosta, 2016). The source of colorant phases, in this case the Fe, could be derived from matrix enclosing the buried woods and/or derived from elements transported from a more distant source by groundwater (Mustoe and Acosta, 2016). In both study cases, plants of L2 and L3 are preserved in greenish coarse facies (conglomerates and sandstones) containing glauconite (see Ruiz et al., 2017), a Fe-rich green mineral, which could be a source for Fe in these woods. However, we do not dismiss the possibility that groundwater transported Fe from the hypothesized Fe-rich soils (i.e., Ultisols and Oxisols) where the plants grew. These types of soils are rich in Fe-minerals such as hematite (red) and goethite (yellow-brown), which would source the pigment for coloring silicified woods of the Las Violetas Fossil Forest.

7. Conclusions

Las Violetas Fossil Forest developed during the early Paleocene in the north of the Golfo San Jorge Basin. In the early stages, the forest comprised a variety of conifers and also palms (L2), and later woody angiosperms appear (L3).

The fossil assemblage of L2 and L3 represents a parautochtonous fossil plant association that lived either on the margins of channels or along exposed bars in well-drained soils, probably tropical red-soils like Ultisols and/or Oxisols, developed close to their depositional setting (tidal channels and bars of an estuary). Warm and humid conditions, together with the porous nature of the channels and bars that host the fossils, favored the silicification of woods and its pigmentation with Fe, resulting in yellow-orange and green fossil woods.

All the wood samples of the L3 are angiosperms. They include a new species of Myrtaceae (*Myrceugenellites grandiporosum*), a new species of Lauraceae (*Mezilaurinoxylon oleiferum*), and a new genus related to the Laurales (*Patagonoxylon scalariforme*).

Fossil tree ring analysis, Vulnerability and Mesomorphy indices, and the analysis of wood characters influenced by the environment suggest that this was an evergreen forest that developed under relatively uniform growing seasons, abundant water supply, and high mean annual temperatures, where frosts and droughts were uncommon or absent. Eventual excesses of water, including flooding, could have occurred.

These paleoenvironmental and paleoclimatological conclusions are in agreement with the ones observed in other fossil forests of similar ages in Patagonia, Antarctica, and Australasia.

The systematic composition of the fossil forest also agrees with the paleoclimatic and paleoenvironmental inferences. The same association of families, including Cupressaceae and/or Podocarpaceae, Lauraceae, Myrtaceae, and palms, are found nowadays in warm-temperate and humid evergreen forests. Their extant equivalents of Las Violetas Fossil Forest would be forests like those found in Australasia, the Maule Region (in Chile), and the Atlantic Forest (Southern Brazil and Misiones Province in Argentina).

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References

Allen, J.P., Gastaldo, R.A., 2006, Sedimentology and taphonomy of the Early to Middle Devonian plant-bearing beds of the Trout Valley Formation, Maine. In: Greb, S.F., DiMichele, W.A. (Eds.), Wetlands through time: Geological Society of America Special Paper, 399, 57–78. DOI: 10.1130/2006.2399(03).

Andreis, R.R., 1977. Geología del área de Cañadón Hondo, Departamento Escalante, Provincia del Chubut, República Argentina. Obra del Centenario del Museo de La Plata, 4, 77–102.

Andreis, R.R., Mazzoni, M.M., Spalletti, L.A., 1975. Estudio estratigráfico y paleoambiental de las sedimentitas terciarias entre Pico Salamanca y Bahía Bustamante, Provincia de Chubut, República Argentina. Revista de la Asociación Geológica Argentina, 30, 85–103.

APG IV., 2016. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants. Botanical Journal of the Linnean Society, 181, 1–20.

Archangelsky, S., 1973. Palinología del Paleoceno de Chubut. I: descripciones sistemáticas. Ameghiniana, 10, 339–199.

Archangelsky S., 1976. Palinología del Paleoceno de Chubut. II. Diagramas polínicos. Ameghiniana, 13, 43–55.

Archangelsky, S., Romero, E., 1974. Polen de Gimnospermas (Coníferas) del Cretácico Superior y Paleoceno de Patagonia. Ameghiniana, 11, 217–236.

Archangelsky, S., Zamaloa, M.C., 1986. Nuevas descripciones palinológicas de las Formaciones Salamanca y Bororó, Paleoceno de Chubut (República Argentina). Ameghiniana, 23, 35–46.

Armesto, J.J., Villagrán, C., Arroyo, M.K., 1996. Ecología de los bosques nativos de Chile. Editorial Universitaria, Santiago de Chile, Chile, 470 pp.

Bande, M.B., 1973. A petrified dicotyledonous wood from the Deccan Intertrappean beds of Mandla District, Madhya Pradesh. Botanique, Nagpur, 4, 41–47.

Barreda, V., Palazzesi, L., 2007. Patagonian vegetation turnovers during Paleogene–Early Neogene: Origin of arid-adapted floras. The Botanical Review, 73, 31–50. https://doi.org/10.1663/0006-8101(2007)73%5b31:PVTDTP%5d2.0.CO;2

Baas, P., 1982. Systematic, phylogenetic, and ecological wood anatomy. History and perspectives. In: Baas, P. (Ed.), New Perspectives in Wood Anatomy. Forestry Sciences 1, Springer, DordrechtIn, 23–58.

Baas, P., Schweingruber, F.H., 1987. Ecological trends in the wood anatomy of trees, shrubs and climbers from Europe. IAWA Journal, 8, 245–274.

Baas, P., Wheeler, E.A., 2011. Wood anatomy and climate change. In: Hodkinson, T.R., Jones, M.B. (Eds.), Climate Change, Ecology and Systematic, Cambridge University Press, Cambridge, United Kingdom, 141–155.

Baas, P., Xinying, Z. 1986. Wood anatomy of trees and shrubs from China. I. Oleaceae. IAWA Bulletin, 7, 195–220.

Berry, E.W., 1932. Fossil plants from Chubut territory collected by The Scarritt Patagonian Expedition. American Museum Novitates, American Museum of Natural History, New York, 536, 1–10.

Bona, P., 2005. Sistemática y biogeografía de las tortugas y los cocodrilos paleocenos de la Formación Salamanca, provincia de Chubut, Argentina. Ph.D thesis, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Argentina.

Bona, P., 2007. Una nueva especie de *Eocaiman* Simpson (Crocodylia, Alligatoridae) del Paleoceno Inferior de Patagonia. Ameghiniana, 44, 435–445.

Bona, P., De La Fuente, M.S., 2005. Phylogenetic and paleobiogeographic implications of *Yaminuechelys maior* (Staesche, 1929) new comb., a large long-necked chelid turtle from the early Paleocene of Patagonia, Argentina. Journal of Vertebrate Paleontology, 25, 569–582. https://doi.org/10.1671/0272-4634(2005)025[0569:PAPIOY]2.0.CO;2.

Bona, P., Ezcurra, M.D., Barrios, F., Fernández Blanco, V., 2018. A new Palaeocene crocodylian from southern Argentina sheds light on the early history of caimanines. Procceedings Royal Society B 285: 20180843. http://dx.doi.org/10.1098/rspb.2018.0843.

Bonaparte, J.F., Morales, J., 1997. Un primitivo Notonychopidae (Litopterna) del Paleoceno Inferior de Punta Peligro, Chubut, Argentina. Estudios Geológicos, 53, 263–274.

Bonaparte, J.F., Van Valen, L.M., Kramartz A., 1993. La fauna local de Punta Peligro, Paleoceno inferior, de la provincia del Chubut, Patagonia, Argentina. Evolutionary monographs, 14, 1–61.

Brea, M., Matheos, S., Zamuner, A., Ganuza, D., 2005a. Análisis de los anillos de crecimiento del bosque fósil de Víctor Szlápelis, Terciario inferior del Chubut, Argentina. Ameghiniana, 42, 407–418.

Brea, M., Zucol, A.F., Matheos, S., Raingemborn, M.S., 2005b. Growth-ring analysis of Lower Paleocene gymnosperm woods from the central Patagonia, Argentina. Ameghiniana, 42 Suplemento, 17R–18R.

Brea, M., Matheos, S.D., Raigemborn, M.S., Iglesias, A., Zucol, A.F., Prámparo, M., 2007. Aspectos paleoecológicos y paleoambientales del Bosque Petrificado Ameghino (Daniano), Chubut, Argentina. 4th European Meeting on the Palaeontology and Stratigraphy of Latin America. Cuadernos del Museo Geominero, 8, 45–50.

Brea, M., Zamuner, A.B., Matheos, S.D., Iglesias, A., Zucol, A.F., 2008. Fossil wood of the Mimosoideae from the early Paleocene of Patagonia, Argentina. Alcheringa, 32, 427–441.

Brea, M., Matheos., S.D., Raigemborn, M.S., Iglesias, A., Zucol, A.F., Prámparo, M., 2011. Paleoecology and paleoenvironments of Podocarp trees in the Ameghino Forest (Golfo San Jorge Basin, Patagonia, Argentina): Constraints for Early Paleogene paleoclimate. Geological Acta, 9, 13–28.

Buurman, P., 1972. Mineralization of fossil wood. Scripta Geologica, 12, 1–43.

Camacho, H.H., 1967. Las transgresiones del Cretácico superior y Terciario de la Argentina. Revista de la Asociación Geológica Argentina, 22, 253–280.

Carlquist, S., 1977. Ecological factors in wood evolution: a floristic approach. American Journal of Botany, 64, 887–896.

Carlquist, S., 2001. Comparative Wood Anatomy. Systematic, Ecological, and Evolutionary Aspects of Dicotyledon Wood. Springer-Verlag, Berlin, 436 pp.

Carlquist, S., 2012. How wood evolves: a new synthesis. Botany, 90, 901–940. https://doi.org/10.1139/b2012-048.

Chebli, G., Serraiotto, A., 1974. Nuevas localidades del Paleoceno marino en la región central de la provincia del Chubut. Revista de la Asociación Geológica Argentina, 29, 311–318.

Clyde, W.C., Wilf, P., Iglesias, A., Slingerland, R.L., Barnum, T., Bijl, P.K., Bralower, T.J., Brinkhuis, H., Comer, E.E., Huber, B.T., Ibañez-Mejia, M., Jicha, B.R., Krause, M., Schueth, J.D., Singer, B.S., Raigemborn, M.S., Schmitz, M.D., Sluijs, A., Zamaloa, M.C., 2014. New age constraints for the Salamanca Formation and lower Río Chico Group in the western San Jorge Basin, Patagonia, Argentina: implications for K/Pg extinction recovery and land mammal age correlations. Geological Society of America Bulletin, 126, 289–306. DOI: 10.1130/B30915.1.

Comer, E.E., Slingerland, R.L., Krause, J.M., Iglesias, A., Clyde, W.C., Raigemborn, M.S., Wilf, P., 2015. Sedimentary facies and depositional environments of diverse Early Paleocene Floras, north-central San Jorge Basin, Patagonia, Argentina. Palaios, 30, 553–573. DOI: 10.2110/palo.2014.064.

Conwentz. H.,1882. Fossile Hölzer aus der Sammlung der königlichen geologischen Landesanstalt zu Berlin. Jahrbuch der Königlich Preussischen Geologischen Landesanstalt, 1881, 144–171.

Creber, G.T., Chaloner, W.G., 1984. Influence of environmental factors on the wood structure of living and fossil trees. The Botanical Review, 50, 357–448.

Creber, G.T., Francis, J.E., 1999. Fossil tree-ring analysis: palaeodendrology. Fossil Plants and Spores: Modern Techniques. Geological Society, London, 1999, 245–250.

Cuitiño, J.I., Scasso, R.A., Ventura Santos, R., Mancini, L.H., 2015. Sr ages for the Chenque Formation in the Comodoro Rivadavia region (Golfo San Jorge Basin, Argentina): stratigraphic implications. Latin America Journal of Sedimentology and Basin Analysis, 22, 3–12.

Donoso, C., 1993. Bosques templados de Chile y Argentina. Variación, Estructura y Dinámica. Editorial Universitaria, Santiago de Chile, Chile, 484 pp.

Dupéron-Laudoueneix, M., Dupéron, J., 2005. Bois fossiles de Lauraceae: nouvelle découverte au Cameroun, inventaire et discussion. Annales de Paléontologie, 91, 127–151. https://doi.org/10.1016/j.annpal.2005.03.002.

Dupéron, Jean., Sakala, J., Dupéron-Laudoueneix, M., De Franceschi, D., 2008. Ulminium diluviale Unger: historique de la découverte et nouvelle étude. Annales de Paléontologie, 94, 1–12. https://doi.org/10.1016/j.annpal.2007.12.003.

Estrada-Ruiz, E., Upchurch Jr., G.R., Wheeler, E.A., Mack, G.H., 2012. Late Cretaceous Angiosperm woods from the Crevasse Canyon and Mcrae Formations, South-central New Mexico, USA: Part 1. International Journal of Plant Sciences, 173, 412–428. DOI: 10.1086/664714.

Falcon-Lang, H.J., 2000a. The relationship between leaf longevity and growth ring markedness in modern conifer woods and its implications for paleoclimatic studies. Paleography, Palaeoclimatology, Palaecology, 160, 317–328. https://doi.org/10.1016/S0031-0182(00)00079-1

Falcon-Lang, H.J., 2000b. A method to distinguish between woods produced by evergreen and deciduous coniferopsids on the basis of growth ring anatomy: a new palaeoecological tool. Palaeontology, 43, 785–793. https://doi.org/10.1111/1475-4983.00149.

Farjon, A., 2007. A Handbook of the World's Conifers. Volume I. Brill Press. Leiden, Boston, 1111 pp.

Felix, J., 1883. Untersuchungen über fossile Hölzer. I. Zeitschrift der Deutschen Geologischen Gesellschaft, 35, 59–92.

Feruglio, E., 1949. Descripción geológica de la Patagonia I, II, III. Dirección General de Yacimientos Petrolíferos Fiscales. Buenos Aires, Argentina, 750 pp.

Figari, E.G., Strelkov, E., Laffitte, G., Cid de La Paz, M.S., Courtade, S.F., Celaya, J., Vottero, A., Lafourcade, P., Martinez, R., Villar, H.J., 1999. Los sistemas petroleros de la Cuenca del Golfo San Jorge: Síntesis estructural, estratigráfica y geoquímica. IV Congreso de Exploración y Desarrollo de Hidrocarburos, 197–237. Buenos Aires.

Fitzgerald, M.G., Mitchum Jr, R.M., Uliana, M.A., Biddle, K.T., 1990. Evolution of the San Jorge Basin, Argentina. AAPG Bulletin, 74, 879–920.

Flores, S, Promis, A., Faúndez, L., 2016. Caracterización florística y estructural de la población natural de *Jubaea chilensis* (Molina) Baill. más austral de Chile. Phyton, 85, 324–332.

Foix, N., Paredes, J.M., Giacosa, R.E., Allard, J.O., 2015. Arquitectura estratigráfica del Paleoceno en el flanco norte de la Cuenca Del Golfo San Jorge, Patagonia Central. Revista de la Asociación Geológica Argentina, 72, 96–106.

Forasiepi, A.M., Martinelli, A., 2003. Femur of a monotreme (Mammalia, Monotremata) from the Early Paleocene Salamanca Formation of Patagonia, Argentina. Ameghiniana, 40, 625–630.

Francis, J.E., 1986. Growth rings in Cretaceous and Tertiary wood from Antarctica and their palaeoclimatic implications. Palaeontology, 29, 665–684.

Fritts, H.C., 1976. Tree-rings and Climate. Academic Press New York, New York, 567 pp.

Fritts, H.C., Smith, D.G., Cardis, J.W., Budelsky, C.A., 1965. Tree-ring characteristics along a vegetation gradient in northern Arizona. Ecology, 46, 393–401.

Futey, M.K., Gandolfo, M.A., Zamaloa, M.C., Cúneo, R., Cladera, G., 2012. Arecaceae fossil fruits from the Paleocene of Patagonia, Argentina. Botanical Review, 78, 205–234. DOI: 10.1007/s12229-012-9100-9.

Galindo-Leal, C., Gusmão Câmara, I., 2003. The Atlantic Forest of South America: Biodiversity Status, Threats, and Outlook (State of the Hotspots, Vol. 1), Island Press, 408 pp.

Gandolfo, M.A., Gonzalez, C.C., Zamaloa, M.C., Cúneo, N.R., Wilf, P., Johnson, K., 2007. Eucalyptus (Myrtaceae) macrofossils from the early Eocene of Patagonia, Argentina. 5° Southern Connection Conference, Adelaide, Australia, Abstract, p. 32.

Garndner, M.F., Lara, A., 2003. The conifers of Chile: an overview of their distribution and ecology. Acta Horticulturae, 615, 165–170.

Gastaldo, R.A., 2001, Plant taphonomy, in Briggs, D.E.G., and Crowther, P.R. (Eds.), Palaeobiology II: Oxford, Blackwell Scientific, 314–317.

Gelfo, J.N., 2007. The “Condylarth” *Raulvaccia peligrensis* (Mammalia: Didolodontidae) from the Paleocene of Patagonia, Argentina. Journal of Vertebrate Paleontology 27, 651–660. https://doi.org/10.1671/0272-4634(2007)27[651:TCRPMD]2.0.CO;2.

Gelfo, J.N., Pascual, R., 2001. *Peligrotherium tropicalis* (Mammalia, Dryolestida) from the early Paleocene of Patagonia, a survival from a Mesozoic Gondwanan radiation. Geodiversitas, 23, 369–379.

Gelfo, J.N., Ortiz-Jaureguizar, E., Rougier, G.W., 2007. New remains and species of the “condylarth” genus *Escribania* (Mammalia: Didolodontidae) from the Palaeocene of Patagonia, Argentina. Earth and Environmental Science Transactions of the Royal Society of Edinburgh, 98, 127–138. https://doi.org/10.1017/S1755691007006081.

Gelfo, J.N., Goin, F.J., Woodburne, M.O., Muizon, C.D., 2009, Biochronological relationships of the earliest South American Paleogene mammalian faunas: Palaeontology, 52, 251–269. DOI: 10.1111 /j.1475 -4983 .2008 .00835.x.

Geological Rock Color Chart, 2009. Production: Munsell Color X-rite 4300 44th Street S.E., Grand Rapids, MI 49512, USA.

Gottwald, H., 1992. Hölzer aus marinen sanden des oberen Eozän Von Helmstedt (Niedersachsen). Palaeontographica B, 225, 27–103.

Gottwald, H., 1997. Alttertiäre Kieselhölzer aus miozänen Schottern der ostbayerischen Molasse bei Ortenburg. Documentae Naturae, 109, 1–83.

Grambast-Fessard, N., 1969. Contribution a l’étude des flores Tertiaires des régions provençales et alpines: V Deux bois de dicotyledones a caracteres primitifs du Miocene superieur de Castellane. Naturalia Monspeliensia. Serie botanique, 20, 105–118.

Gregory, M., Poole, I., Wheeler, E.A., 2009. Fossil dicot wood names: an annotated list with full bibliography. IAWA Supplement, 6, 220 pp.

Hill, R.S., 1994. History of Australian Vegetation. Cretaceous to Recent. Cambridge University Press, Cambridge, 443 pp.

Huard, J., 1967. Etude de trois bois de Lauracées fossiles des formations à lignite néogènes d’Arjuzanx (Landes). Revue Générale de Botanique,74, 81–105.

Hueck, K., 1978. Los bosques de Sudamérica. Sociedad Alemana de Cooperación Técnica, Eschborn, Alemania, 476 pp.

IAWA Hardwood Committee, 1989. IAWA List of Microscopic Features for Hardwood Identification. IAWA Bulletin n.s., 10, 219–332.

Iglesias, A., 2007. Estudio Paleobotánico, paleoecológico y paleoambiental en secuencias de la Formación Salamanca, del Paleoceno Inferior en el sur de la Provincia de Chubut, Patagonia, Argentina, Ph.D. thesis, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Argentina, 244 pp.

Iglesias, A., Wilf, P., Zamuner, A.B., Johnson K., Cúneo, R., Singer, B., 2007. A Paleocene lowland macroflora from Patagonia reveals significantly greater richness than North American analogs. Geology 35, 947–950. DOI: 10.1130/G23889A.1.

InsideWood, 2004-onwards. Published on the Internet http://insidewood.lib.ncsu.edu/search.

Jaffré, T., 1995. Distribution and ecology of the conifers of New Caledonia. In: Enright, N.J., Hill, R.S. (Eds.), Ecology of the Southern Conifers. Melbourne University Press., 171–196.

Johns, R.J., 1982. Plant Zonation. In: Gressitt, J.L. (Ed.), Biogeography and Ecology of New Guinea. Monographiae Biologicae, 42. W. Junk, The Hague, Netherlands, 309–330.

Jud, N.A., Gandolfo, M.A., Iglesias, A., Wilf, P., 2017. Flowering after disaster: Early Danian buckthorn (Rhamnaceae) flowers and leaves from Patagonia. Plos One, 12, e0176164.

Jud N.A., Gandolfo, M.A., Iglesias, A., Wilf, P., 2018a. Fossil flowers from the early Palaeocene of Patagonia, Argentina, with affinity to Schizomerieae (Cunoniaceae). Annals of Botany, 121, 431-442. DOI: 10.1093/aob/mcx173.

Jud, N.A., Iglesias, A., Wilf, P., Gandolfo, M. A., 2018b. Fossil moonseeds from the Paleogene of West Gondwana (Patagonia, Argentina). American Journal of Botany, 105, 1–16. DOI:10.1002/ajb2.1092

Kramer, K., 1974. Die Tertiären Hölzer Südost-Asiens (Unter Ausschluss Der Dipterocarpaceae). I. Teil. Palaeontographica Abteilung B, 144, 45–181.

Krause, J.M., Bellosi, E., Raigemborn, M.S., 2010. Lateritized tephric palaeosols from Central Patagonia, Argentina: a southern high-latitude archive of Palaeogene global greenhouse conditions. Sedimentology, 57, 1721–1749. https://doi.org/10.1111/j.1365-3091.2010.01161.x.

Krause, J.M., Clyde, W.C., Ibañez-Mejía, M., Schmitz, M.D., Barnum, T., Bellosi, E., Wilf, P., 2017. New age constraints for early Paleogene strata of central Patagonia, Argentina: implications for the timing of south American land mammal ages. Geological Society of America Bulletin. https://doi.org/10.1130/B31561.1.

Kräusel, R., 1939. Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. IV. Die fossilen Floren Ägyptens. Abhandlungen / Bayerische Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse., 47, 140 pp.

Leisman, G.A., 1986. *Cryptocaryoxylon gippslandicum* gen. et sp. nov., from the Tertiary of eastern Victoria. Alcheringa, 10, 225–234.

Mädel, E., 1960. Monimiaceen-Hölzer aus den oberkretazischen Umzamba-Schichten von Ost-Pondoland (S-Afrika). Senckenberg. Lethaea, 41, 331–391.

Malumián, N., Nañez, C., 2011. The Late Cretaceous–Cenozoic transgressions in Patagonia and the Fuegian Andes: foraminifera, palaeoecology, and palaeogeography. Biological Journal of the Linnean Society, 103, 269–288. https://doi.org/10.1111/j.1095-8312.2011.01649.x.

Martínez, G.A., 1992. Paleoambiente de la Formación Salamanca en La Pampa María Santísima, Departamento Sarmiento, Provincia de Chubut. Revista de la Asociación Geológica Argentina, 47, 293–303.

Matheos, S.D., Brea, M., Ganuza, D., Zamuner, A., 2001. Sedimentología y paleoecología del Terciario Inferior en el sur de la Provincia del Chubut, República Argentina. Revista de la Asociación Argentina de Sedimentología, 8, 93–104.

Méndez, I., 1966. Foraminíferos, edad y correlación estratigráfica del Salamanquense de Punta Peligro (45°30´S; 67°11´W), Provincia del Chubut. Revista de la Asociación Geológica Argentina, 21, 127–157.

Metcalfe, C.R., Chalk, L., 1950. Anatomy of the dicotyledons. Clarendon Press. Oxford, 1500 pp.

Mirabelli, S.L., Pujana, R.R., Marenssi, S.A., Santillana, S.N., 2017. Conifer Fossil Woods from the Sobral Formation (Lower Paleocene, Western Antarctica). Ameghiniana 55, 91–108. https://doi.org/10.5710/AMGH.27.07.2017.3095.

Morris, H., Plavcová, L., Cvecko, P., Fichetler, E., Gillingham, M.A.F., Martínez-Cabrera, H.I., McGlinn, D.J., Wheeler, E.A., Zheng, J., Zieminska, K., Jansen, S., 2016. A global analysis of parenchyma tissue fractions in secondary xylem of seed plants. New Phytologist, 209, 1553–1565. DOI: 10.1111/nph.13737.

Mustoe, G., Acosta, M., 2016. Origin of petrified wood color. Geosciences, 6, 25. DOI:10.3390/geosciences6020025.

Nishida, M., Nishida H., Nasa, T., 1988. Anatomy and affinities of the petrified plants from the Tertiary of Chile (V). Botanical Magazine, Tokyo, 101, 293–309.

Pagani, M., Pedentchouk, N., Huber, M., Sluijs, A., Schouten, S., Brinkhuis, H., Sinninghe Damste, J.S., Dickens, G.R., the Expedition 302 Scientists, 2006. Arctic hydrology during global warming at the Palaeocene/Eocene thermal maximum. Nature, 442, 671–675. DOI: 10.1038/nature05043.

Panigatti, JL., 2010. Argentina 200 años, 200 suelos. Ed. INTA Buenos Aires. 345 pp.

Parma, S.G., Casadío, S., 2005. Upper Cretaceous–Paleocene Equinoids from Northern Patagonia, Argentina. Journal of Paleontology, 79, 1072–1087. https://doi.org/10.1666/0022-3360(2005)079%5B1072:UCEFNP%5D2.0.CO;2

Pascual, R., Ortiz-Jaureguizar, E., 1990. Evolving climates and mammal faunas in Cenozoic South America. Journal of Human Evolution, 19, 23–60. https://doi.org/10.1016/B978-0-12-260345-7.50006-0.

Pascual, R., Archer, M., Ortiz Jaureguizar, E., Prado, J.L., Godthelp, H., Hand, S.J., 1992. First discovery of monotremes in South America. Nature, 356, 704–706.

Pascual, R., Ortiz-Jaureguizar, E., Prado, J.L., 1996. Land mammals: paradigm of Cenozoic South American geobiotic evolution. In: Arratia G. (Ed.), Contribution of Southern South America to Vertebrate Paleontology, Müncher Geowissenschaftliche Abhandlungen (A), 30, 265–319.

Pascual, R., Goin, F., Balarino, L., Udrizar, D.E., 2002. New data on the Paleocene monotreme *Monotrematum sudamericanum*, and the convergent evolution of triangulate molars. Acta Palaeontologica Polonica, 47,487–492.

Passalia, M.G., Romero, E.J., Panza, J.L., 2001. Improntas foliares del Cretácico de la provincia de Santa Cruz, Argentina. Ameghiniana, 38, 73–84.

Petriella, B., 1972. Estudio de maderas petrificadas del Terciario inferior del área central de Chubut (Cerro Bororó). Revista del Museo de La Plata n. s., 6, 159–254.

Petriella, B., Archangelsky, S., 1975. Vegetación y Ambiente en el Paleoceno de Chubut. Actas del Primer Congreso Argentino de Paleontología y Bioestratigrafía, 1, 257–270.

Plavcová, L., Hoch, G., Morris, H., Ghiasi, S., Jansen, S., 2016. The amount of parenchyma and living fibres affects storage of nonstructural carbohydrates in young stems and roots of temperate trees. American Journal of Botany, 103, 603–612. DOI:10.3732/ajb.1500489.

Poole, I., Gottwald, H., 2001. Monimiaceae sensu lato, an element of Gondwanan polar forests: evidence from the Late Cretaceous–Early Tertiary wood flora of Antarctica. Australian Systematic Botany, 14, 207–230. https://doi.org/10.1071/SB00022.

Prakash, U., Březinová, D., Bůžek, C., 1971. Fossil Woods from Doupovské hory and Ceské stredohorí. Northern Bohemia. Palaeontographica Abt. B, 133, 1–6.

Prámparo, M.B., 2007. Historia evolutiva de las angiospermas (Cretácico–Paleógeno) en Argentina a través de los registros. Publicación Especial de la Asociación Paleontológica Argentina, 11, 157–172.

Pujana, R.R., 2009. Fossil woods from the Oligocene of southwestern Patagonia (Río Leona Formation). Atherospermataceae, Myrtaceae, Leguminosae and Anacardiaceae. Ameghiniana, 46, 523–535.

Pujana, R.R., Panti, C., Cuitiño, J.I., García Massini, J.L., Mirabelli, S.L., 2015. A new megaflora (fossil woods and leaves) from the Miocene of southwestern Patagonia. Ameghiniana, 52, 350–366. DOI: 10.5710/AMGH.05.01.2014.2805.

Pujana, R.R., Iglesias, A., Raffi, M.E., Olivero, E.B., 2018. Angiosperm fossil woods from the Upper Cretaceous of Western Antarctica (Santa Marta Formation). Cretaceous Research, 90, 349–362. DOI: 10.1016/j.cretres.2018.06.009.

Ragonese, A.M., 1980. Leños fósiles de dicotiledóneas del Paleoceno de Patagonia, Argentina. I. *Myrceugenia chubutense* n. sp. (Myrtaceae). Ameghiniana, 17, 297–311.

Raigemborn, M., Brea, M., Zucol, A., Matheos, S., 2009. Early Paleogene climatic conditions at mid latitude Southern Hemisphere: Mineralogical and paleobotanical proxies from continental sequences in Golfo San Jorge basin (Chubut, Patagonia, Argentina). Geologica Acta, Climate and Biota of the Early Paleogene Special Volume, 7, 125–145. DOI: 10.1344/105.000000269.

Raigemborn, M.S., Krause, J.M., Bellosi, E., Matheos, S.D., 2010. Redefinición estratigráfica del Grupo Río Chico (Paleógeno inferior), en el norte de la cuenca del Golfo San Jorge, Chubut, Argentina. Revista de la Asociación Geológica Argentina, 67, 239–256.

Raigemborn, M.S., Gómez-Peral, L., Krause, J.M., Matheos, S.D., 2014. Controls on clay mineral assemblages in an Early Paleogene nonmarine succession: implications for the volcanic and paleoclimatic record of extra-Andean Patagonia, Argentina. Journal of South American Earth Sciences, 52, 1–23. https://doi.org/10.1016/j.jsames.2014.02.001.

Raigemborn, M.S., Iglesias, A., Gómez Peral, L., Brea, M., Arrouy, J., Stromberg, C., Beilinson, E., Pérez, L., Matheos, S., 2018a. Una mirada multidisciplinaria para estimar el paleoclima del Paleógeno inferior de Patagonia (Argentina). XVI Reunión Argentina de Sedimentología. General Roca, Actas, 167.

Raigemborn, M.S., Beilinson, E., Krause, J.M., Varela, A.N., Bellosi, E., Matheos, S., Sosa, N., 2018b. Paleolandscape reconstruction and interplay of controlling factors of an Eocene pedogenically-modified distal volcaniclastic succession in Patagonia. Journal of South American Earth Sciences, 86, 475-496. https://doi.org/10.1016/j.jsames.2018.07.001.

Retallack, G.J., 2001. Soils of the Past, second ed. Blackwell Science Ltd., Oxford, 404 pp.

Romero, E.J., 1968. *Palmoxylon patagonicum* n. sp. del Terciario Inferior de la Provincia del Chubut, Argentina. Ameghiniana, 5, 417–432.

Romero, E.J., 1973. Polen fósil de “*Nothofagus*” (“*Nothofagidites*”) de Cretácico y Paleoceno de Patagonia. Revista del Museo de La Plata (NS), Paleontología, 7, 291–303.

Ruiz, D.P., 2018. Estudios paleoclimáticos del Paleógeno y Mioceno inferior del centro y sur de la Patagonia argentina en base a la anatomía de maderas fósiles. Ph.D. thesis, Facultad de Ciencias Naturales y Museo, La Plata, Argentina, 237 pp.

Ruiz, D.P., Brea, M., Raigemborn, M.S., Matheos, S.D., 2017. Conifer woods from the Salamanca Formation (early Paleocene), Central Patagonia, Argentina: Paleoenvironmental implications. Journal of South American Earth Sciences, 76, 427–445. https://doi.org/10.1016/j.jsames.2017.04.006.

Scafati, L., Melendi, D.L., Volkheimer, W., 2009. A Danian subtropical lacustrine palynobiota from South America (Bororó Formation, San Jorge Basin, Patagonia - Argentina). Geologica Acta, 7, 35–61.

Schweingruber, F. H., 1988. Tree rings. Basics and Applications of dendrochronology. Kluwer Academic Publishers, Dordrecht, Holland, 279 pp.

Simpson, G.G., 1937. An ancient eusuchian crocodile from Patagonia. American Museum Novitates, 965, 1–20.

Sluijs, A., Schouten, S., Pagani, M., Woltering, M., Brinkhuis, H., Sinninghe Damste, J.S, Dickens, G.R., Huber, M., Reichart, G., Stein, R., Matthiessen, J., Lourens, L.J., Pedentchouk, N., Backman, J., Moran, K., the Expedition 302 Scientists, 2006. Subtropical Arctic Ocean temperatures during the Palaeocene/Eocene thermal maximum. Nature, 441, 610–613. DOI:10.1038/nature04668.

Soares, E.A.A., Riker, S.R., Kloster, A.C., Gnaedinger, S.C, Lima, F.J.L., Motta, M.B., 2017. First record of Annonaceae wood for the Neogene of South America, Amazon Basin, Brazil. Brazilian Journal of Geology, 47, 95–108. DOI: 10.1590/2317-4889201720160085.

Somoza, R., Cladera, G., Archangelsky, S., 1995. Una nueva tafoflora paleocena de Chubut, Patagonia. Su edad y ambiente de depositación. VI Congreso Argentino de Paleontología y Biostratigrafía, Actas, 265–269. Trelew.

Staesche, K., 1929. Schildrkrötenreste aus der oberen Kreide Patagoniens. Paläeontographica, 72, 103–112.

Süss, H., Mädel, E., 1958. Über Lorbeerhölzer aus miozänen Schichten von Randeck (Schwäbische Alb) und Ipolytarnóc (Ungarn). Geologie, 7, 80–99.

Takahashi, K.I., Suzuki, M., 2003. Dicotyledonous fossil wood flora and early evolution of wood characters in the Cretaceous of Hokkaido, Japan. IAWA Journal, 24, 269–309. DOI: https://doi.org/10.1163/22941932-90001597.

Taylor, G., Truswell, E.M., McQueen, K.G., Brown, M.C., 1990. Early Tertiary palaeogeography, landform evolution and palaeoclimates of the Southern Monaro, N.S.W. Australia. Palaeogeography, Palaeoclimatology, Palaeoecology, 78, 109–134.

Unger, F., 1845. Synopsis plantarum fossilium. Leipzig, 330 pp.

Van Der Burgh, J., 1973. Hölzer der niederrheinischen braunkohlenformation, II. Hölzer der braunkohlengruben “Maria Theresia” zu herzogenrath,“Zukunft West” zu eschweiler und “Victor”(Zülpich mitte) zu Zülpich. Nebst einer systematisch-anatomischen bearbeitung der gattung Pinus L. Review of Palaeobotany and Palynology, 15, 73–275. https://doi.org/10.1016/0034-6667(73)90001-8.

Van der Graaff, N.A., Baas, P., 1974. Wood anatomical variation in relation to latitude and altitude. Blumea, 22, 101–121.

Vater, H., 1884. Die fossilen Hölzer der Phosphoritlager des Herzogsthums Braunschweig. Zeitschrift der Deutschen Gesellschaft, 36, 783–853.

Volkheimer, W., 1971. Aspectos paleoclimáticos del Terciario argentino. Revista del Museo Argentino de Ciencias Naturales. Paleontología, 1, 243–264.

Webb, L.J., 1959. A physiognomic classification of Australian rainforests. Journal of Ecology, 47, 551–70.

Wheeler E.A., 2011. InsideWood - A web resource for hardwood anatomy. International Journal of Wood Anatomists Journal, 32, 199–211.

Wheeler, E.A., Baas, P., 1991. A survey of the fossil record for Dicotiledonous rood and its significance for evolutionary and ecological Wood Anatomy. IAWA Journal, 12, 275–332.

Wheeler, E.A., Baas, P., 1993. The potentials and limitations of dicotyledonous wood anatomy for climatic reconstructions. Paleobiology, 19, 487–498.

Wheeler, E.A., Baas, P., 2019. Wood evolution: Baileyan trends and Functional traits in the fossil record. IAWA Journal, 40, 2–42. https://doi.org/10.1163/22941932-40190230.

Wheeler, E.A., Manchester, S.R., 2002. Woods of the Middle Eocene Nut Beds Flora, Clarno Formation, Oregon, USA. IAWA Journal, Supplement 3, 188 pp.

Wheeler, E.A., Baas, P., Rodgers, S., 2007. Variations in dicot wood anatomy: global analysis based on the InsideWood database. IAWA Journal, 28, 229–258. https://doi.org/10.1163/22941932-90001638.

Wiemann, M.C., Wheeler, E.A., Manchester, S.R., Portier, K.M., 1998. Dicotyledonous wood anatomical characters as predictors of climate. Palaeogeography, Palaeoclimatology, Palaeoecology, 139, 83–100.

Wiemann, M.C., Manchester, S.R., Wheeler, E.A., 1999. Paleotemperature estimation from dicotyledonous wood anatomical characters. Palaios, 14, 459–474.

Williams, C.J., Trostle, K.D., Sunderlin, D., 2010. Fossil wood in coal-forming environments of the late Paleocene–early Eocene Chickaloon Formation. Palaeogeography, Palaeoclimatology, Palaeoecology, 295, 363–375. https://doi.org/10.1016/j.palaeo.2010.02.027.

Woodburne, M.O., Goin, F.J., Bond, M., Carlini, A.A., Gelfo, J.N., López, G.M., Iglesias, A., Zimicz, A.N., 2013. Paleogene land mammal faunas of South America: a response to global climatic changes and indigenous floral diversity. Journal of Mammalian Evolution. http://dx.doi.org/10.1007/s10914-012-9222-1.

Zachos, J., Pagani, M., Sloan, L., Thomas, E., Billups, K., 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. Science, 292, 686–693. DOI: 10.1126/science.1059412.

Zachos, J.C., Schouten, S., Bohaty, S., Quattlebaum, T., Sluijs, A., Brinkhuis, H., Gibbs S.J., Bralower, T.J., 2006. Extreme warming of mid-latitude coastal ocean during the Paleocene-Eocene Thermal Maximum: Inferences from TEX86 and isotope data. Geology, 34, 737–740. https://doi.org/10.1130/G22522.1.

FIGURES

Fig. 1. Location of the study area. A- Map showing position and boundaries of the Cretaceous Golfo San Jorge Basin (long-dash line) and limits of the North Flank (short-dash line) following Figari et al. (1999), and the position of the study area. B- Geological map of the Estancia Las Violetas area, showing the position of the Las Violetas forest (modified from Raigemborn et al., 2010 and Ruiz et al., 2017). C- General appearance of

the Cenozoic outcrops at the study area (SF: Salamanca Formation; RCG: Río Chico Group; CF: Chenque Formation). [2-column]

Fig. 2. Sedimentary profile, at Estancia Las Violetas locality showing the position of the fossiliferous plant levels (L1 to L4). FA1 to FA4 corresponds to the facies associations described and interpreted in Ruiz et al. (2017). [2-column]

Fig. 3. *Myrceugenellites grandiporosum* MPEF-Pb 8393. A–B- TS: a general view and indistinct growth ring boundaries (arrowheads). C–D- TS: diffuse axial parenchyma (white arrowheads) and scanty paratracheal axial parenchyma (black arrowheads). E–F- RLS: scalariform perforation plates. G- TLS: scalariform perforation plate with some forked bars (white arrowhead). H- TLS: scalariform to opposite intervessel pits (black arrowhead) and opposite intervessel pits (white arrowhead). I- TLS: opposite intervessel pits. J- RLS: general view of a heterocellular ray and ray-vessel pits (arrowhead). K–M- RLS: circular, bordered, and opposite ray-vessel pits (white arrowheads). N- TLS: general view with uniseriate rays and partly biseriate rays (arrowhead). O- TLS: scanty paratracheal axial parenchyma (white arrowhead) and fibers with bordered pits (black arrowhead). P- TLS: diffuse axial parenchyma (white arrowhead) and parenchyma ray cells with dark contents (black arrowhead). Q- TLS: detail of fiber pits (white arrowhead) and axial parenchyma pits (black arrowhead). Bars: A: 1 mm, B,N: 500 μm; C,J,O: 200 μm; E–G,P: 100 μm; D,H,I,K–M,Q: 50 μm. [2-column]

Fig. 4- *Patagonoxylon scalariforme* MPEF-Pb 8399. A–B- TS: general view. C- TS: axial parenchyma (black arrowheads) and oil cell (white arrowhead). D- TS: axial parenchyma

(arrowhead). E–F- RLS: scalariform perforation plates. G–H- TLS: scalariform to opposite intervessel pits. I- TLS: opposite intervessel pits. J- RLS: general view with homocellular rays and scalariform perforation plates (arrowhead). K–L- RLS: vessel-ray pits (arrowheads). M- TLS: general view of multiseriate rays. N- TLS: multiseriate rays with oil cells (arrowhead). O- TLS: diffuse axial parenchyma (arrowhead). P- LTS: scanty paratracheal axial parenchyma (arrowhead) and tyloses (black arrowhead). Q- TLS: oil cells detail (arrowhead). R–S- TLS: fibers with bordered pits (arrowheads). Bars: A,B,M: 500 μm; C,J,N: 200 μm; O,P: 100 μm; D–I,K,L,Q–S: 50 μm. [2-column]

Fig. 5- ***Mezilaurinoxylon oleiferum*** **MPEF-Pb 8400**. A- TS: general view. B–C - TS: tyloses (white arrowheads) and oil cells (black arrowheads). D - TS: paratracheal axial parenchyma (arrowheads). E- RLS: simple perforation plates (white arrowheads). F- TLS: opposite to alternate intervessel (white arrowhead) and oil cell detail (black arrowhead). G- TLS: transitional and alternate intervessel pits and scanty paratracheal axial parenchyma (white arrowheads). H–I- RLS: transitional and alternate intervessel pits probably vestured (white arrowheads). J- RLS: general view of heterocellular rays and oil cells (white arrowheads). K- RLS: enlarged vessel-ray pits (white arrowhead) and small opposite vessel-ray pits (black arrowhead). L–G- RLS: enlarged vessel-ray pits detail (white arrowhead) and ray parenchyma cell with dark contents (black arrowhead). M- RLS: scalariform vessel-ray pits N- RLS: detail of oil cells. O- TLS: tyloses (black arrowheads) and oil cell in a ray (white arrowheads). P- TLS: septate fibers (white arrowheads) and oil cells (black arrowhead). Q- TLS: oil cell among fibers (white arrowhead) and scanty paratracheal axial parenchyma (black arrowhead). R- TS: fungal hyphae (white arrowhead). S- TLS: fungal conidia (black arrowhead). **MPEF-Pb 8401.** T- TLS: fungal hyphae (white

arrowhead). Bars: A,J,O: 500 µm; B,E,P,Q: 200 µm; C,K: 100 µm; D,F,G,H,L–N,T: 50 µm; I,R,S: 25 µm. [2-column]

Fig. 6- Graphics showing variation in growth-ring sequences of the samples with more than ten rings. Ring width in mm. [Single column]

Fig. 7- Histograms of annual sensitivities (AS). The pointed lines indicate the position of the Mean Sensitivity (MS). [Single column]

Fig. 8- Mean tracheid radial diameters of one cell increment (continuous line) and CSDM curves (pointed line) both in µm. The vertical lines mark the zenith of the curve, and their position at the right side respect the center of the CSDM curve indicates the trees were evergreen. [2-column]

Fig. 9- ***Palmoxylon sp.*** **MPEF-Pb 8401.** A–B- TS: aerenchyma (arrowheads). Bars: A: 500 µm; B: 200 µm. [Single column]

Table 1

Comparison of anatomical wood features among *Myrceugenellites* species. GR (growth rings): P= presents, I= indistinct, D= distinct; Po (Porosity): D= difusse-porous wood; VA (vessel arrangement): S= solitary, R= in radial multiples, P= pairs, G= in groups; PP (perforation plates): S= scalariform, number of bars in parentheses; VETD (vessel elements mean tangential diameter) in µm; IP (intervessel pits): E= scalariform, O= opposite; AP (axial parenchyma): SP= scanty paratracheal, D= difusse, A= absent; R (rays): He= heterocellular, Ho= homocellulars; RS (rays seriation); RVP (ray vessels pits); F (fibers with bordered pits): P= present, A= absent; OC (oil cells): A= absent, P= present. In bold are the characters sharing by *Myrceugenellites grandiporosum* and the other fossil species.

Fossil-species	Formation and age	GR	Po	VA	Vessels per mm^2	PP	VETD	IP	AP	R	RS	Rays per mm^2	RVP	F	OC
Myrceugenellites grandiporosum sp. nov. Ruiz, Brea and Pujana, this paper	Salamanca Fm. (Paleocene), Chubut, Argentina	**I**	**D**	**S (R, A)**	**14 (9–20)**	**S (24–44)**	**145**	**E to O**	**SP, D**	**He, Ho**	**1s and 2-3s with 1s extremes**	**10–15**	**Bordered, circular and opposite**	**P**	**A**
Myrceugenellites maytenoides Nishida, Nishida and Nasa, 1988	Mina Chilena Fm. (Late Oligocene–Early Miocene) and/or The Filaret Fm. (Late Miocene), Cerro Dorotea, Chile	**D**	**D**	**S (R, G)**	430 (200–590)	**S (14–60)**	42.5	**E to O**	D	**He**	2(3)s with 1s extremes, rarely 1s	?	Scalariform to circular and opposite	?	**A**
Myrceugenellites oligocenum Pujana, 2009	Río Leona Fm. (Miocene), Santa Cruz, Argentina	**D**	**D**	**S, P**	250 (102–380)	**S (25–45)**	29	O	?	?	1s and 2s with 1s extremes	**10–16**	**Bordered, circular and opposite**	**P**	**A**

Table 2

Comparative features of fossil-genera with diffuse porous wood, rays with 4 or more cells wide and presence of oil cells. VA (vessel arrangement): So= solitary, R= in radial multiples, C= in clusters; PP (perforation plates): Sca= Scalariform, Si= simple; IP (intervessel pits): O= opposite, Alt= alternate, Sca= scalarifom; VRP (vessel-ray pits); AP (axial parenchyma): SP= scanty paratracheal, Pa= paratracheal, VC= vasicentric, Al= Aliform, Co= confluent, B= banded, R= reticular, T=terminal, Di= diffuse; SF (septate fibers): A=absent, P= present; FB (fibers with bordered pits): A= absent, P= present; Rays: He= heterocellular, Ho= homocellular; RW (ray width) in cells. DOC (distribution of oil cells). In bold are the characters sharing by *Patagonoxylon* and other fossil genera.

Fossil-genera	**VA**	**PP**	**IP**	**VRP**	**AP**	**SF**	**FB**	**Rays**	**RW**	**DOC**	**Comments and other characters**
Patagoxylon gen. nov. Ruiz, Brea and Pujana, this paper	**So, R**	**Sca**	**Sca to O**	**Scalariform**	**SP, D**	**A**	**P**	**He, Ho**	**4 (3–7)**	**In rays**	
Beilschmiedioxylon Dupéron-Laudoueneix and Dupéron, 2005	So, C	Si	Alt	**Scalariform**	Pa, B, T	?	A	He	?	Among fibers	
Caryodaphnopsoxylon Gottwald, 1992	**So, R**	Si	Alt	**Scalariform**	VC	?	A	He	7–8 (12)	Among axial parenchyma	
Cinnamomoxylon Gottwald, 1997	**So, R**	Si and Sca	Alt	**Oval to scalariform**	VC, Al, SP	**A**	A	He	1–5	In rays and axial aprenchyma	
Cryptocaryoxylon Leisman, 1986	**So, R**	Si	Alt	**Scalariform**	B	?	A	Ho	1–5	Occasionally in groups, in rays	
Laurinoxylon Felix, 1883 emend Dupéron, Sakala and Dupéron-Laudoueneix, 2008	**So, R**	Si, Si and Sca	Alt	?	Pa	?	P	He	1–5	?	Rays>1mm high
Mezilaurinoxylon Wheeler and Manchester, 2002	**So, R**	Si	Alt	Oval to windows like	**SP**, VC	P	A	He	1–5	**In rays**	
Atherospermoxylon (Kräusel, 1939) Mädel, 1960	**So, R**	**Sca**	Sca to O	**Oval to scalariform**	Di	P	**P**	He	**1–10**	Absent or in rays	Rays commonly <1mm high
Protoatherospermoxylon Mädel, 1960	**So, R**	**Sca**	Sca to O	**Oval to scalariform**	Di	P	**P**	He	1–6 (12 or more)	**In rays**	Rays commonly >1mm high
Duguetiaxylon Amaral Soares, Cabral Kloster, Gnaedinger, Riker, da Cruz Lima and Motta, 2017	**So, R**	Si	Alt	Alternate	B	**A**	A	**Ho, He**	?	**In rays**	Oil cells not mentioned in the generic diagnosis but present in Present in *D. amazonicum*
Pygmaeoxylon Estrada-Ruiz, Upchurch, Wheeler and Mack, 2012	**So, R**	Si	Alt	**Scalariform**	**SP**	**A**	A	**Ho**	**3–10**	**In rays**	Vessels <100 µm in diameter
Polyalthioxylon Bande, 1973	**So, R**, C	Si	Alt	?	VC, B, R	**A**	A	Ho	**3–6 (1–9)**	**In rays**	Oil cells are not mention in the original description

Table 3

Summary of the growth-ring data of Paleocene conifer wood from the fossiliferous level L2. MRW: mean ring width, MaW: maximal ring width, MiW: minimal ring width, SD: standard deviation, AS: Annual Sensitivity, MS: Mean Sensitivity. Width values in mm.

Sample number	No. of growth ring	False rings	Frost rings	MRW	MaW	MiW	SD	AS	MS
MPEF-Pb 8385	14	0	0	1.59	3.00	0.26	0.79	0.00–1.54	0.41
MPEF-Pb 8386	7	0	0	2.25	3.55	1.32	0.87	---	---
MPEF-Pb 8387	8	0	0	3.75	5.20	0.86	1.51	---	---
MPEF-Pb 8388	21	3	0	0.80	1.42	0.27	0.33	0.01–1.01	0.26
MPEF-Pb 8389	9	1	0	2.16	2.91	0.87	0.76	---	---
MPEF-Pb 8390	11	0	0	2.67	4.17	1.57	0.81	0.01–0.46	0.20
Mean	---	---	0	2.20	3.75	0.86	0.84	0.01–1.00	0.29

Table 4

Results of the quantification of growth-rings markedness parameters of Paleocene conifer woods from the fossiliferous level L2. RMI: Ring Markness Index.

Sample number	Percentage of earlywood	Percentage of latewood	Skew percentage	Percentage of diminution	RMI
MPEF-Pb 8385	93.15%	6.85%	67.12%	71.44%	4.89
MPEF-Pb 8386	78.43%	21.57%	13.72%	70.61%	15.23
MPEF-Pb 8387	76.61%	23.39%	47,22%	89.78%	23.69
MPEF-Pb 8389	86.00 %	14.00%	22.00%	69.60%	11.13
MPEF-Pb 8390	86.36%	13.64%	36.36%	71.94%	9.80

Table 5

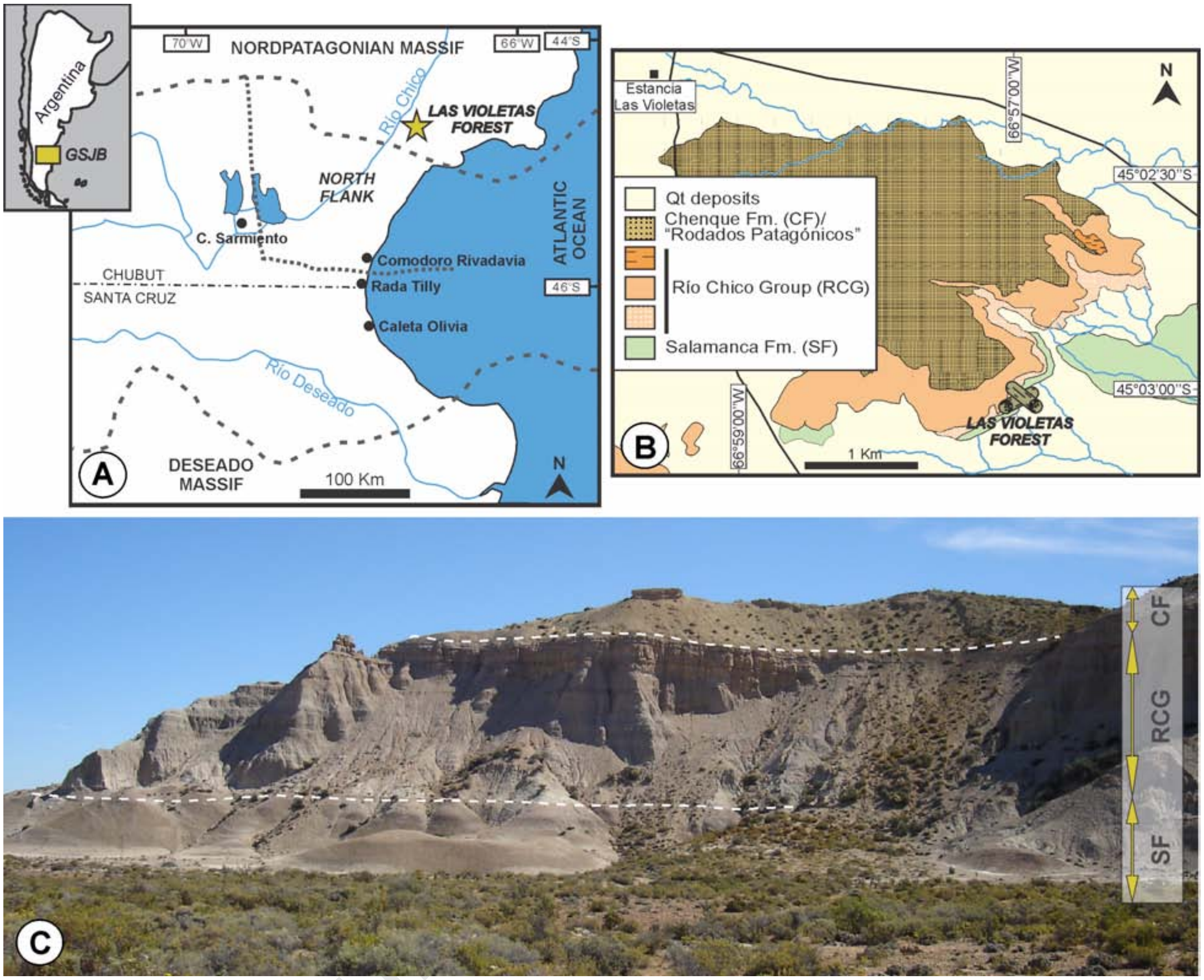
Anatomical wood data of Paleocene dicot woods from the fossiliferous level L3 used to calculate the Vulnerability Index (V) and the Mesomorphy Index (M).

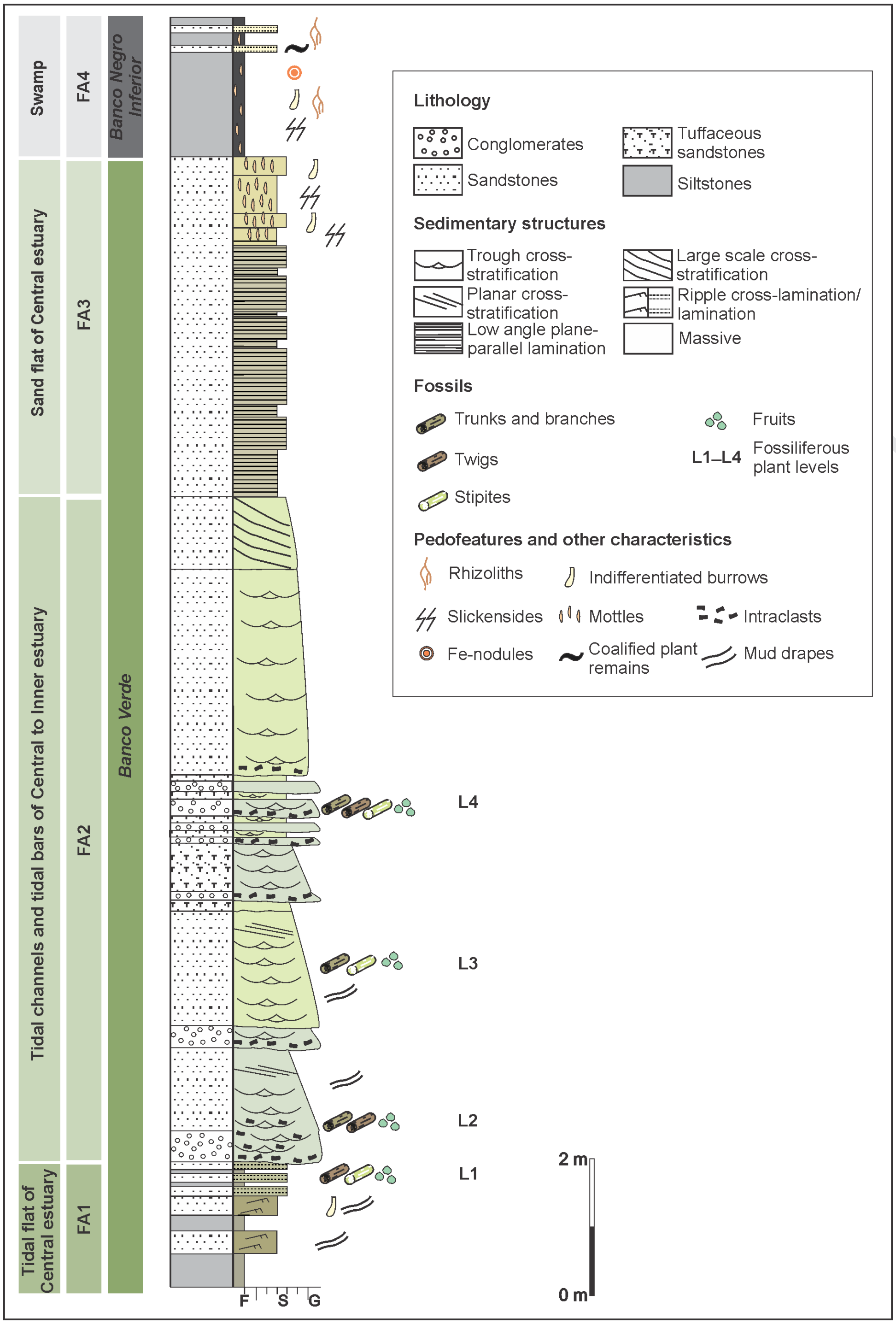
	Vessel tangential diameter	**Vessels per square mm^2**	**Vessel elements lenght**	**V**	**M**
Myrceugenellites grandiporosum	145	14	1728	10.36	17897.14
Patagonoxylon scalariforme	60	29	771	2.07	1595.17
Mezilaurinoxylon oleiferum	137	16	575	8.56	4923.44

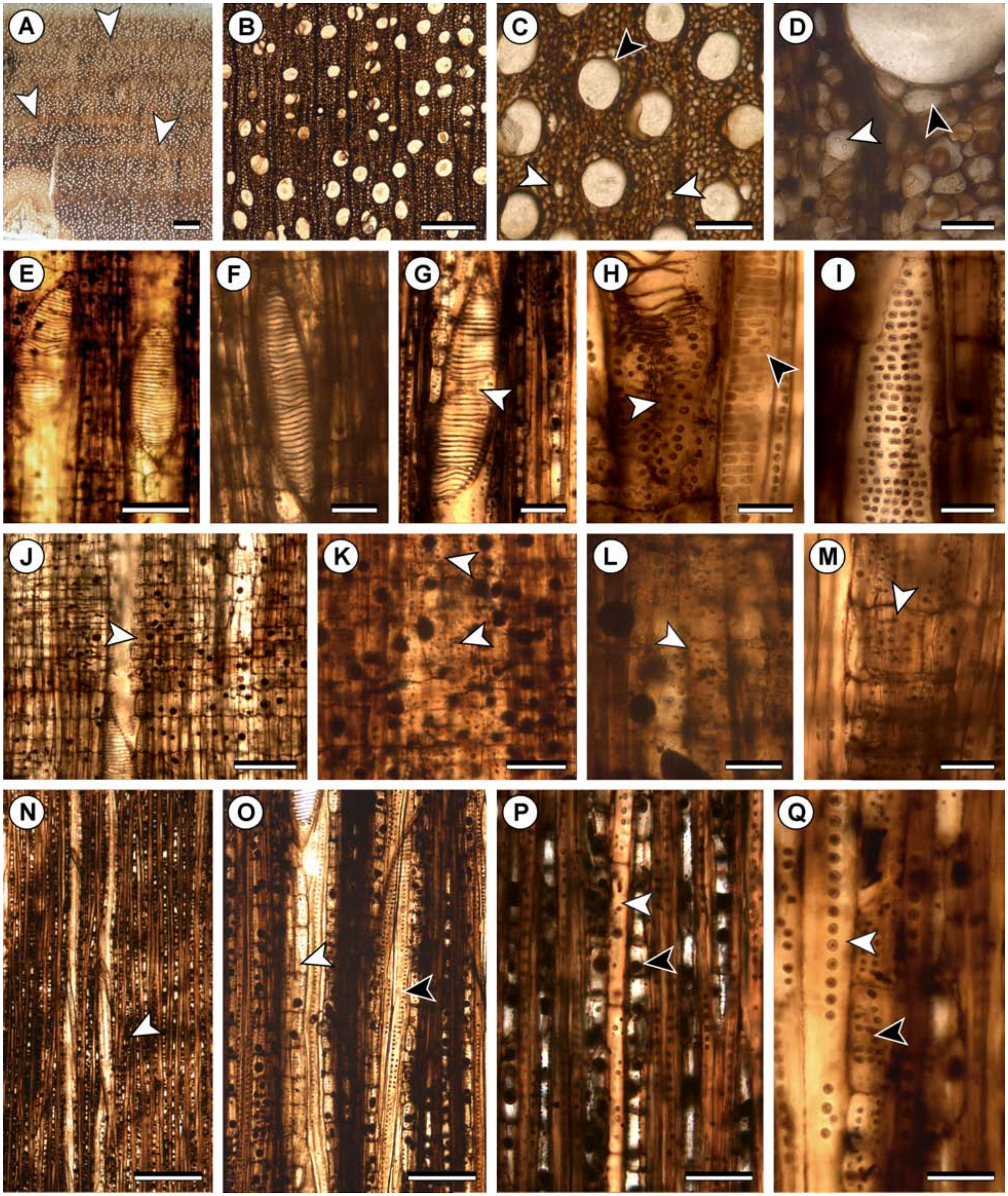
Table 6

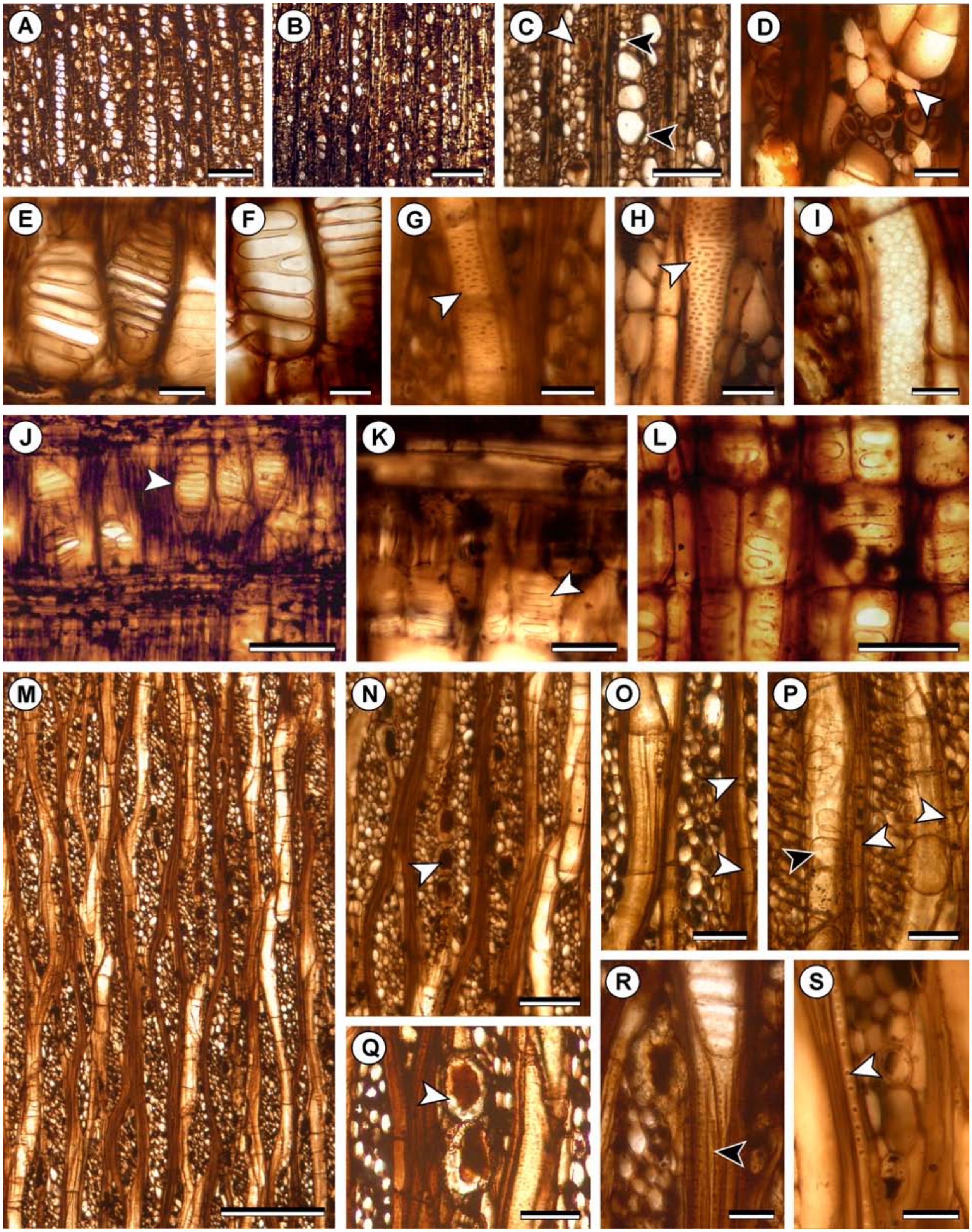
Comparison of results in growth rings analysis of Paleocene forests in Patagonia and Antarctica. AS: Annual Sensivity, MS: Mean Sensivity, S: sensitive, C: complacent, P: present, A: absent.

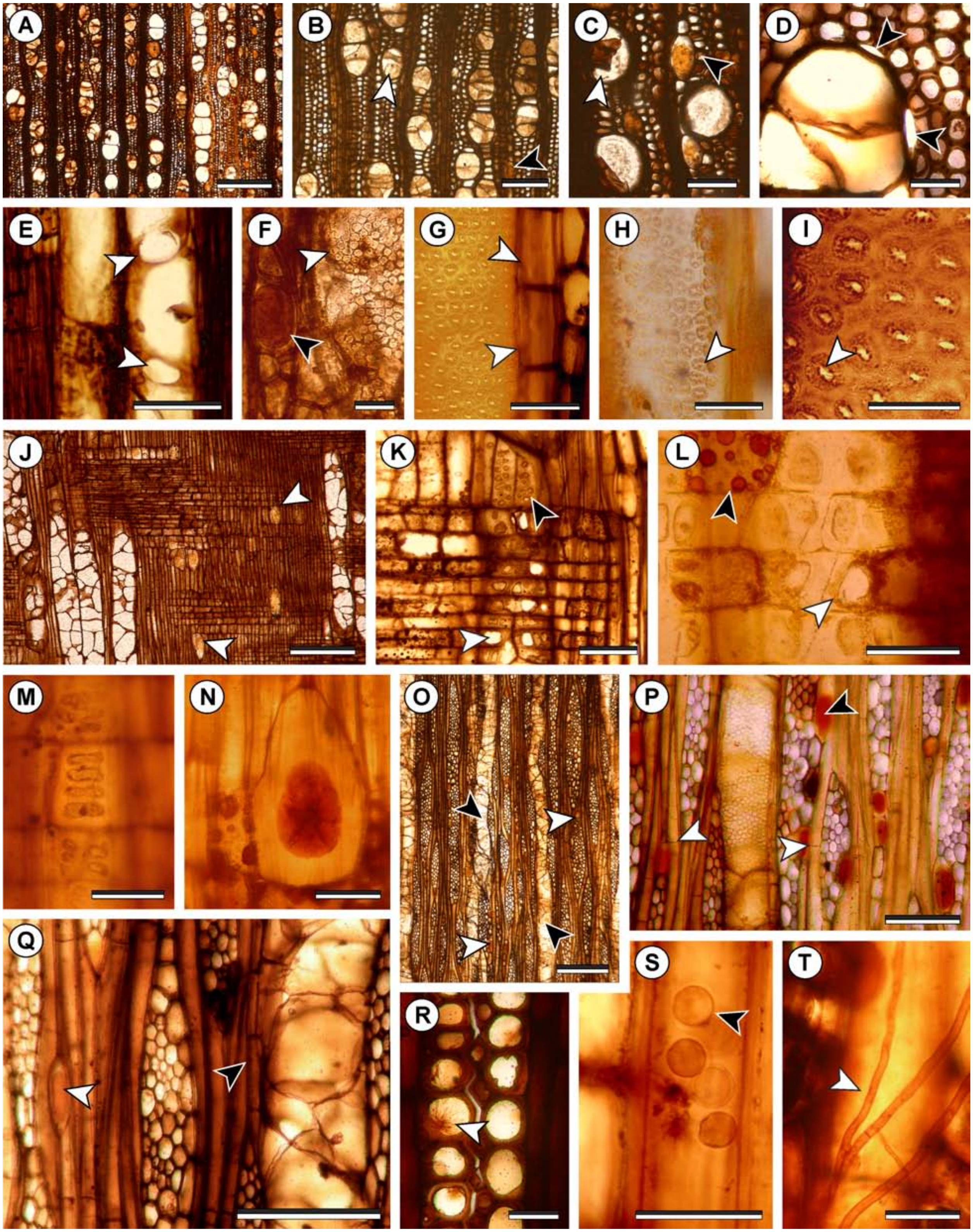
Fossil forest	**Formation**	**N° of analyzed rings**	**Mean ring width**	**Mean interval of ring widths**	**Minimum ring width**	**Maximum ring width**	**Interval of AS values**	**Mean MS**	**Interval of MS values**	**False rings**
Víctor Szlápelis, Chubut, Argentina (Brea et al., 2005a)	Salamanca Fm. (Paleocene)	236	2.66	1.31–6.03	0.17	11.30	0–1.70	0.68 (S)	0.39–1.42	P
Ormachaea, Chubut , Argentina (Brea et al., 2005b)	Salamanca Fm. (Paleocene)	---	2.10	---	0.28	6.59	---	0.59 (S)	0.34 –0.95	P
Ameghino, Chubut, Argentina (Brea et al., 2011)	Salamanca Fm. (Paleocene)	169	1.23	1.11–2.69	0.63	3.62	0.05–0.72	0.19 (C)	0.09–0.29	---
Las Violetas, Chubut, Argentina (this paper)	Salamanca Fm. (Paleocene)	70	2.20	0.86–3.75	0.26	5.20	0.01–1.00	0.29 (C)	0.20–0.40	P
Seymour Island (Francis, 1986)	Sobral Fm. (Paleocene)	27	2.58	---	2.00	4.60	---	0.17 (C)	---	A
Seymour Island (Francis, 1986)	Cross Valley Fm. (Paleocene)	56	1.29	---	0.67	2.80	---	0.26 (C)	---	A

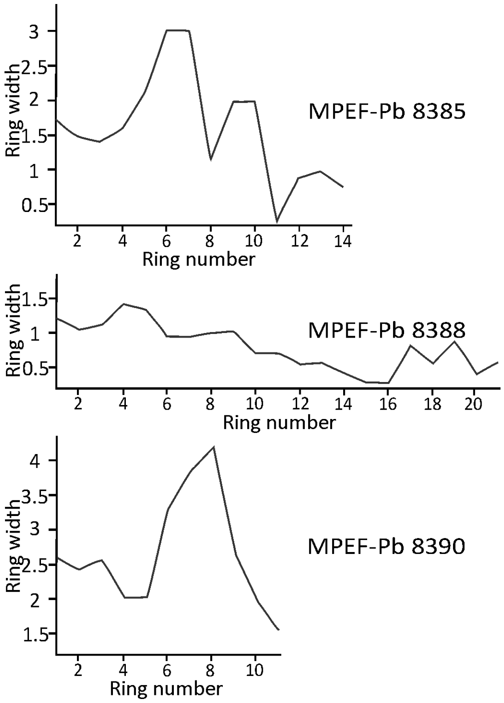

Argentina
GSJB
70°W
66°W
44°S
46°S
NORDPATAGONIAN MASSIF
Río Chico
LAS VIOLETAS FOREST
NORTH FLANK
C. Sarmiento
Comodoro Rivadavia
Rada Tilly
Caleta Olivia
ATLANTIC OCEAN
CHUBUT
SANTA CRUZ
Río Deseado
DESEADO MASSIF
100 Km
N
A
Estancia Las Violetas
66°57'00"W
45°02'30"S
45°03'00"S
66°59'00"W
Qt deposits
Chenque Fm. (CF)/ "Rodados Patagónicos"
Río Chico Group (RCG)
Salamanca Fm. (SF)
LAS VIOLETAS FOREST
1 Km
N
B
CF
RCG
SF
C

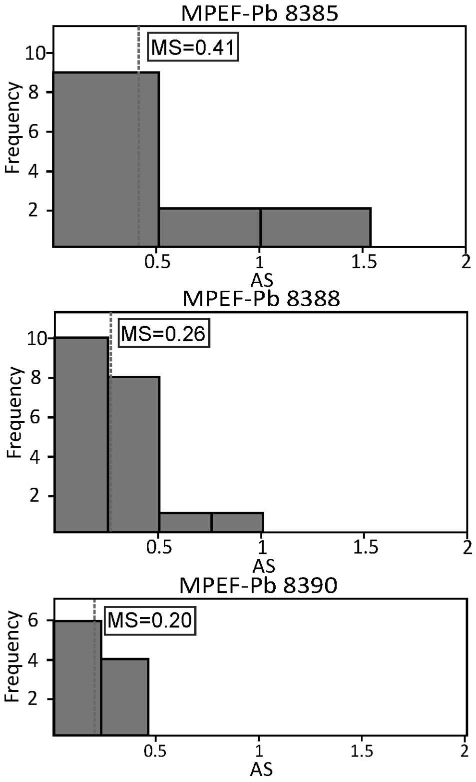

Swamp
FA4
Banco Negro Inferior
Sand flat of Central estuary
FA3
Tidal channels and tidal bars of Central to Inner estuary
FA2
Banco Verde
Tidal flat of Central estuary
FA1
L4
L3
L2
L1
2 m
0 m
F
S
G
Lithology
Conglomerates
Sandstones
Tuffaceous sandstones
Siltstones
Sedimentary structures
Trough cross-stratification
Planar cross-stratification
Low angle plane-parallel lamination
Large scale cross-stratification
Ripple cross-lamination/ lamination
Massive
Fossils
Trunks and branches
Twigs
Stipites
Fruits
L1–L4 Fossiliferous plant levels
Pedofeatures and other characteristics
Rhizoliths
Indifferentiated burrows
Slickensides
Mottles
Intraclasts
Fe-nodules
Coalified plant remains
Mud drapes

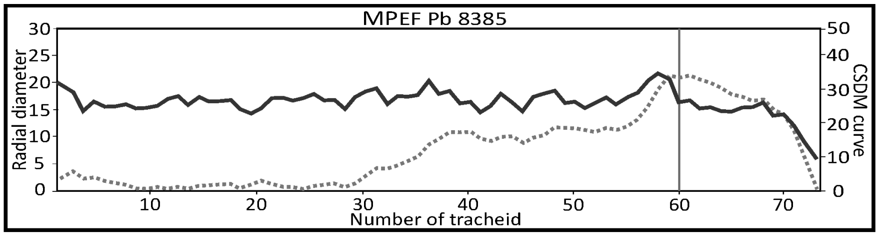

A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
P
Q

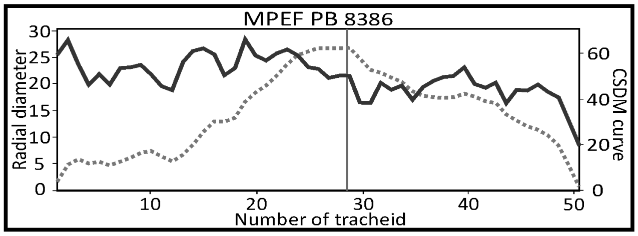

A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
P
Q
R
S

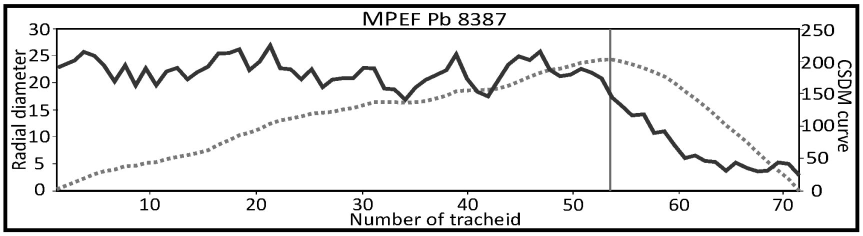

A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
P
Q
R
S
T

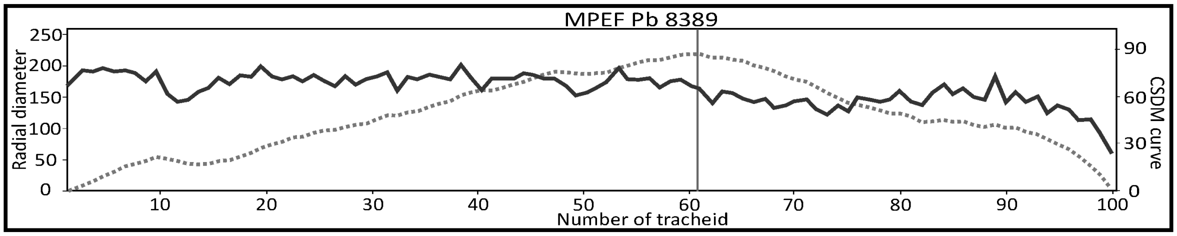

Ring width
3
2.5
2
1.5
1
0.5
2 4 6 8 10 12 14
Ring number
MPEF-Pb 8385
Ring width
1.5
1
0.5
2 4 6 8 10 12 14 16 18 20
Ring number
MPEF-Pb 8388
Ring width
4
3.5
3
2.5
2
1.5
2 4 6 8 10
Ring number
MPEF-Pb 8390

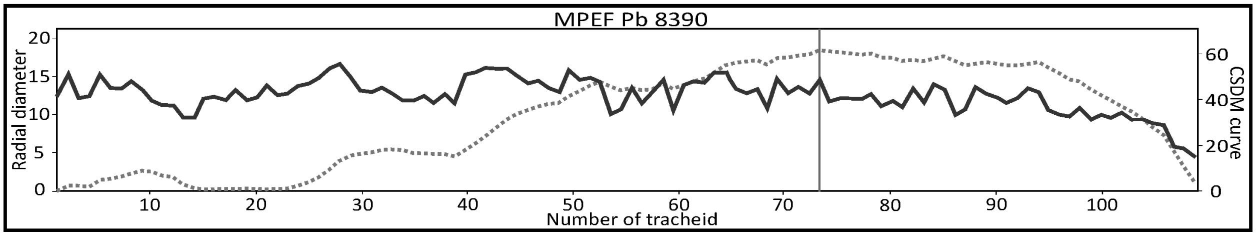

MPEF-Pb 8385
MS=0.41
Frequency
10
8
6
4
2
0.5
1
1.5
2
AS
MPEF-Pb 8388
MS=0.26
Frequency
10
8
6
4
2
0.5
1
1.5
2
AS
MPEF-Pb 8390
MS=0.20
Frequency
6
4
2
0.5
1
1.5
2
AS

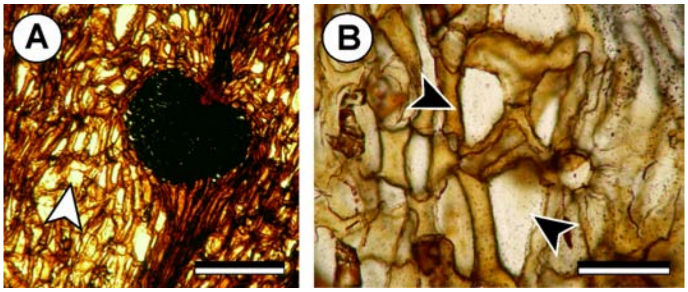

MPEF Pb 8385
Radial diameter
0
5
10
15
20
25
30
CSDM curve
0
10
20
30
40
50
10
20
30
40
50
60
70
Number of tracheid


MPEF PB 8386
Radial diameter
0
5
10
15
20
25
30
CSDM curve
0
20
40
60
10
20
30
40
50
Number of tracheid


MPEF Pb 8387
Radial diameter
0
5
10
15
20
25
30
CSDM curve
0
50
100
150
200
250
10
20
30
40
50
60
70
Number of tracheid


MPEF Pb 8389
Radial diameter
0
50
100
150
200
250
CSDM curve
0
30
60
90
10
20
30
40
50
60
70
80
90
100
Number of tracheid


MPEF Pb 8390
Radial diameter
0
5
10
15
20
CSDM curve
0
20
40
60
10
20
30
40
50
60
70
80
90
100
Number of tracheid


A
B

Highlights

The mixed forest Las Violetas developed in Central Patagonia during the Paleocene.

Dicots of the fossil forest were represented by Myrtaceae and Lauraceae.

The forest represents a parautochtonous association of plants living on an estuary.

Fossil woods analysis suggest a warm-temperate and humid evergreen forest.

Conflict of Interest and Authorship Conformation Form

- All authors have participated in (a) conception and design, or analysis and interpretation of the data; (b) drafting the article or revising it critically for important intellectual content; and (c) approval of the final version.

- This manuscript has not been submitted to, nor is under review at, another journal or other publishing venue.

- The authors have no affiliation with any organization with a direct or indirect financial interest in the subject matter discussed in the manuscript

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