Conifer wood assemblage dominated by Podocarpaceae, early Eocene of Laguna del Hunco, central Argentinean Patagonia

Roberto R. Pujana¹, Peter Wilf², Maria A. Gandolfo³

¹ Museo Argentino de Ciencias Naturales, Ciudad de Buenos Aires 1405, Argentina ² Department of Geosciences and Earth and Environmental Systems Institute, Pennsylvania State University, University Park PA 16802, USA ³ LH Bailey Hortorium, Plant Biology Section, School of Integrative Plant Science, Cornell University, Ithaca, NY 14850, USA

Corresponding author: Roberto R. Pujana (rpujana@gmail.com)

Abstract
During the early Eocene, Patagonia had highly diverse floras that are primarily known from compression and pollen fossils. Fossil wood studies from this epoch are scarce in the region and largely absent from the Laguna del Hunco flora, which has a highly diverse and excellently preserved compression assemblage. A collection of 26 conifer woods from the Laguna del Hunco fossil-lake beds (early Eocene, ca. 52 Ma) from central-western Patagonia was studied, of which 12 could be identified to genus. The dominant species is Phyllocladoxylon antarcticum, which has affinity with early-diverging Podocarpaceae such as Phyllocladus and Prumnopitys. A single specimen of Protophyllocladoxylon francisae probably represents an extinct group of Podocarpaceae. In addition, two taxonomic units of cf. Cupressinoxylon with putative affinity to Podocarpaceae were found. Diverse Podocarpaceae taxa consistent with the affinities of these woods were previously reported from vegetative and reproductive macrofossils as well as pollen grains from the same source unit. Some of the woods have galleries filled with frass. Distinct growth ring boundaries indicate seasonality, inferred to represent seasonal light availability. Growth ring widths suggest that the woods came from mature trees, whereas the widths and types of some rings denote near-uniform temperature and water availability conditions.

Keywords
fossil forests, Huitrera Formation, Paleogene, Podocarpaceae, South America, wood anatomy
Introduction

The early Eocene Earth had warm climates worldwide (e.g., Zachos et al. 2001). In Patagonia, the southernmost region of South America, early Eocene ecosystems had highly diverse floras from mesothermal rainforest environments (Wilf et al. 2003, 2005, 2009; Barreda and Palazzesi 2007).

The volcanic-lacustrine strata of the Tufolitas Laguna del Hunco of the Eocene Huitrera Formation exposed at Laguna del Hunco in northwestern Chubut, central Patagonia, have long been known for their diverse and superbly preserved plant fossils (e.g., Berry 1925). According to previous paleobotanical studies, an extremely diverse mesothermal flora dominated by angiosperms, coupled with a significant presence of ferns and conifers, was present in the area (e.g., Wilf et al. 2003, 2005; Barreda et al. 2020). Among the conifers, Podocarpaceae (Wilf 2012, 2020; Wilf et al. 2017; Andruchow-Colombo et al. 2019), Cupressaceae (Wilf et al. 2009), and Araucariaceae (Wilf et al. 2014; Barreda et al. 2020; Rossetto-Harris et al. 2020) are well-represented in the flora. The modern biogeographic affinities of the Laguna del Hunco flora are diverse, and especially large concentrations of survivor genera are found in the tropical West Pacific region (e.g., Wilf et al. 2013).

Although fossil leaves, reproductive structures, and pollen are well documented, a comprehensive study of the woods from Laguna del Hunco is lacking. Petersen (1946) reported fossil trunks exposed in the upper portion of the fossil lake beds, but so far, the only described silicified specimen is a stem of the osmundaceous fern Todea from the southern exposures of the Tufolitas (Bippus et al. 2019; Bomfleur and Escapa 2019). In general, studies of Patagonian Eocene woods are scarce. From Argentinean Patagonia, Brea et al. (2009) described a conifer collected from the Koluel-Kaike Formation, and recently Pujana and Ruiz (2019) described an assemblage from the Río Turbio Formation with woods of Araucariaceae, several Podocarpaceae, Proteaceae, Cunoniaceae, and Nothofagaceae. From the Ligorio Márquez Formation in central-south Chilean Patagonia, Terada et al. (2006a) described a few woods of Araucariaceae, Podocarpaceae, and Cunoniaceae, and Terada et al. (2006b) described another small assemblage with Araucariaceae, Podocarpaceae, and Nothofagaceae from the Loreto Formation in southern Chilean Patagonia.

During a recent field season, we collected a large sample of fossil woods from the Tufolitas Laguna del Hunco, including both angiosperms and conifers. In this contribution, we treat the conifer woods from Laguna del Hunco for the first time. This work comprises the largest study to date of the Laguna del Hunco flora from per-mineralized wood specimens, otherwise known almost entirely from compression and palynomorph remains.

Materials and methods

Fossil-wood samples were collected 3–5 December 2016 from 10 localities in the exposures of the Tufolitas Laguna del Hunco, Huitrera Formation, at Laguna del
Hunco (Fig. 1; Table 1). The TufoLitas Laguna del Hunco are tuffaceous caldera-lake sediments that belong to the volcaniclastic-pyroclastic complex of the middle Chubut River (Aragón and Mazzoni 1997). The age of the TufoLitas Laguna del Hunco at Laguna del Hunco is constrained to the early Eocene (Ypresian) by the combination of a $52.22 \pm 0.22$ Ma $^{40}$Ar-$^{39}$Ar age analyzed from sanidines in a tuff from the middle of the 170 m section, additional $^{40}$Ar-$^{39}$Ar ages from the lake beds as well as associated units, and paleomagnetic data (Wilf et al. 2003, 2005; Wilf 2012; Gosses et al. 2020). The studied fossil woods were found on strata throughout the local TufoLitas section.
of Wilf et al. (2003; Fig. 1), including the upper third of the section that contains few compression fossils, and even the uppermost lake beds below the hill-capping Andesitas Huancache (per Aragón and Mazzoni 1997). Most specimens were found exposed on slopes, clean of attached sediment and with abraded surfaces, indicating that they were reworked downslope to an unknown extent from various possible source levels within the Tufoitas.

The 26 conifer fossil woods studied here (Table 2) are part of a larger collection of 87 wood samples. All studied specimens are decorticated and consist of permineralized (mostly by silica) secondary xylem, and their preservation is quite variable; only 12 of the 26 specimens could be assigned to generic level. Of the remaining specimens, 56 are identified as angiosperms (under separate study) and five, due to very poor preservation, could not be determined to any taxonomic group.

All specimens are housed at the Museo Paleontológico Egidio Feruglio, Trelew, Chubut Province, Argentina, repository acronym MPEF-Pb (Table 2). Thin sections of each sample bear the specimen number followed by a lower case series letter. We prepared thin sections (transverse, TS; tangential longitudinal, TLS; radial longitudinal, RLS) following standard techniques and studied them using light microscopy. Small fragments (radial views) of the samples were gold-coated and observed with scanning electron microscopy (SEM, Philips XL30 located in the Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina). Microscopic images were taken with a Leica DM500 microscope with a Leica DFC420 camera. Images were processed with GIMP 2.8.22 software, and measurements from the images were taken with IMAGEJ 1.52 software.

We followed the terminology of the IAWA Softwood Committee (2004) and the Si and Cp indices of Pujana et al. (2016) for describing wood anatomy. These two indices quantify the intertracheary pitting; e.g., Si = 1.00 indicates that all the intertracheary pits are uniseriate, S > 1.00 indicates that there are two- or more-seriate pits, Cp = 0% that pits are non-contiguous, and Cp = 100% that all pits are contiguous (Pujana et al. 2016). We also followed the definitions of Philippe and Bamford (2008) for classifying intertracheary pitting into the categories abietinean, mixed, and araucarian. In abietinean intertracheary pitting, most (ca. > 90%) of the pits in the radial walls are non-contiguous, are rounded in outline, and when in rows are opposite. In araucarian

### Table 1. Geographical coordinates of the localities where the fossils were collected.

| Sampling locality | Geographical coordinates (DDM) | n° of conifer woods studied (identified to genus) |
|-------------------|-------------------------------|-----------------------------------------------|
| LU2               | 42°27.53'S, 70°02.26'W        | 1 (1)                                         |
| LU4               | 42°27.51'S, 70°02.43'W        | 2 (1)                                         |
| LU6               | 42°27.54'S, 70°02.48'W        | 4 (2)                                         |
| LU8               | 42°27.68'S, 70°02.56'W        | 1 (1)                                         |
| LU9               | 42°27.60'S, 70°02.52'W        | 2 (0)                                         |
| LU12              | 42°27.67'S, 70°02.28'W        | 1 (0)                                         |
| LU15              | 42°28.28'S, 70°02.92'W        | 1 (1)                                         |
| LU16              | 42°28.23'S, 70°02.76'W        | 6 (1)                                         |
| LU22              | 42°27.42'S, 70°02.09'W        | 7 (4)                                         |
| LU23              | 42°27.63'S, 70°02.25'W        | 1 (1)                                         |
pitting, most (ca. > 90%) of the pits are contiguous and commonly alternate and angular in outline. Mixed pitting is when the pitting arrangement is between araucarian and abietinean. When possible, at least 15 measurements or observations of each character were made per specimen. Measurements are expressed as the mean followed by the range and mean standard deviation (SD) in parentheses. Measurements reported from species with more than one specimen were taken from all samples. Taxonomic determination was implemented using the criteria of Philippe and Bamford (2008) for delimiting conifer fossil-genera, while Bengston (1988) was followed for open nomenclature names.

For growth ring classification, we followed the scheme of Creber and Chaloner (1984). Minimum estimated diameters (MED) of the trunks/stems were measured directly on the sample or roughly calculated based on the curvature of the growth rings; when they had virtually straight growth ring boundaries, a 50 cm diameter was assigned.

**Systematic Paleontology**

**Genus Protophylocladoxylon Kräusel**

*Protophylocladoxylon francisiae* Pujana, Santillana & Marenssi

Figure 2A–F

**Studied material.** MPEF-Pb 10694.

**Locality.** LU2 at Laguna del Hunco (Fig. 1, Table 1), Chubut Province, Argentina.

**Stratigraphic provenance.** Tufolitas Laguna del Hunco, Huitrera Formation (Ypresian, early Eocene).

**Description.** Growth ring boundaries are distinct (Fig. 2A, B), latewood with 1–3 rows of tracheids (Fig. 2B). Tracheids are roundish to polygonal as seen in transverse section (Fig. 2B). Intertracheary pitting in radial walls is mixed, uni- to biseriate, predominantly uniseriate (Si = 1.25), contiguous (Cp = 88.1%), and mostly alternate, rarely opposite, when biseriate (Fig. 2C, D). Intertracheary pits are hexagonal to rounded in outline; 19.2 (13.8–24.6, SD = 1.9) μm in vertical diameter (Fig. 2C, D). Tracheid tangential diameter is 44.5 (30.3–61.2, SD = 7.0) μm. Cross-fields have 1–4, mean 1.9, pits per cross-field (Fig. 2E, F). Cross-field pits are circular with simple borders (rarely with narrow borders; 14.8 (11.8–18.4, SD = 1.8) μm in vertical diameter (Figs 2E, F, 6A). Horizontal walls of ray parenchyma cells are smooth (Fig. 2E). Wall alteration (not helical thickening) of the secondary walls of tracheids is observed (Fig. 2G). Average ray height is medium, 5.6 (1–13, SD = 3.2) cells high, rays are exclusively uniseriate (Fig. 2H, I) and with a frequency of 3.5 (2–5, SD = 0.9) rays per mm.

**Remarks.** This specimen is characterized by its distinct growth ring boundaries, uni- to biseriate mixed intertracheary radial pitting, cross-fields usually with one or two mostly simple pits, relatively wide tracheids, uniseriate rays, and absence of resin-plugs and axial parenchyma. These characters indicate that this wood belongs to the fossil-genus *Protophylocladoxylon*, because of the mixed radial pitting, simple large pits in the
cross-fields, uniseriate rays, and smooth ray cell walls (Philippe and Bamford 2008). Conservation of the name *Protophylocladoxylon* was recently proposed by Zijlstra and Philippe (2020). Among the more than 20 species of the genus, *P. francisiae* is distinguished by its distinct growth ring boundaries, uni- to biseriate and mixed radial pitting, and absence of axial parenchyma and resin plugs (Zhang et al. 2010; Pujana et al. 2014).

*Protophylocladoxylon francisiae* was first described by Pujana et al. (2014) from material collected from the Eocene La Meseta Formation, Seymour/Marambio Island, Antarctica, and it was later reported from the Paleocene Cross Valley and Sobral formations.
that crop out on the same island (Pujana et al. 2015; Mirabelli et al. 2018). It is also present in the Eocene-Oligocene Río Turbio Formation, Santa Cruz Province, southern Patagonia (Pujana and Ruiz 2019). Interestingly, as is the case at Laguna del Hunco, this species is always a minor component of its floras and never dominates the assemblages.

The fossil-genus Protophyllocladoxylon is quite controversial. Vajda et al. (2016) suggested that Protophyllocladoxylon represents various unrelated botanical groups, principally because of its long temporal range from the Paleozoic to the Cenozoic (Zhang et al. 2010; see also Andruchow-Colombo et al. 2019). Pujana and Ruiz (2019) suggested that P. francisiae, in particular, could represent an extinct member of the Podocarpaceae because it has the general wood anatomy of the family but does not conform to any of the extant genera.

Genus Phyllocladoxylon Gothan

Phyllocladoxylon antarcticum Gothan

Figure 3A–L

**Studied material.** MPEF-Pb 10707, 10710, 10747, 10765, 10767, 10773 and 10776.

**Localities.** LU6, LU15 and LU22 at Laguna del Hunco (Fig. 1, Table 1), Chubut Province, Argentina.

**Stratigraphic provenance.** Tufolitas Laguna del Hunco, Huitrera Formation (Ypresian, early Eocene).

**Description.** Growth ring boundaries are distinct (Fig. 3A, B), latewood with ca. 3–10 rows of tracheids (Fig. 3B). Tracheids are roundish to polygonal as seen in transverse section (Fig. 3B, C). Intertracheary pitting in radial walls is abietinean, mostly uniseriate, rarely biseriate (Si= 1.03), mostly non contiguous (Cp= 11.9%), and opposite when biseriate (Fig. 3D–F). Intertracheary pits are rounded in outline; 18.3 (12.5–26.4, SD = 1.9) μm in vertical diameter (Fig. 3D–F). Tracheid tangential diameter is 33.2 (16.3–56.6, SD = 4.7) μm. Cross-fields have mostly 1, very rarely 2, mean 1.04, pits per cross-field (Fig. 3G–I). Cross-field pits are ellipsoidal with simple borders (rarely with narrow borders) and sometimes pointed; 13.0 (7.8–17.6, SD = 1.6) μm in vertical diameter (Fig. 3G–I, 6C). Wall alteration (not helical thickening) of the secondary walls of tracheids is observed (Fig. 3J). Horizontal walls of ray parenchyma cells are smooth (Fig. 3G, H). Average ray height is medium, 8.2 (1–34, SD = 5.0) cells high, rays are exclusively uniseriate (Fig. 3K, L) and with a frequency of 6.5 (3–11, SD = 0.2) rays per mm.

**Remarks.** Abietinean intertracheary radial pitting and cross-fields with usually one large simple pit (Philippe and Bamford 2008) are the observed key characters, allowing confident placement of these Patagonian woods within Phyllocladoxylon. Distinct growth ring boundaries, absence of axial parenchyma and resin plugs, and predominantly uniseriate radial pitting are characteristics of the species Phyllocladoxylon antarcticum (Gothan 1908; Pujana et al. 2014).
Figure 3. *Phyllocladoxylon antarcticum*: A Growth rings of type D (TS), MPEF-Pb 10747 B detail of a growth ring of type D boundary (TS), MPEF-Pb 10776 C detail of roundish tracheids (TS), MPEF-Pb 10765 D opposite contiguous biseriate intertracheary radial pits (arrowheads) (RLS), MPEF-Pb 10767 E uniseriate non contiguous intertracheary radial pits (scanning electron microscope, SEM), MPEF-Pb 10776 F uniseriate contiguous (arrowheads) and non contiguous intertracheary radial pits (SEM), MPEF-Pb 10776 G cross-fields with large simple pits (RLS), MPEF-Pb 10707 H cross-fields with large pointed and narrow-bordered pits (RLS), MPEF-Pb 10765 I cross-fields with large simple pits (SEM), MPEF-Pb 10710 J wall alteration of the secondary walls of tracheids (RLS), MPEF-Pb 10767 K uniseriate rays (TLS), MPEF-Pb 10767 L uniseriate rays (TLS), MPEF-Pb 10747. Scale bars: 5 mm (A); 200 μm (B, K); 100 μm (C, L); 50 μm (D, F, G, H, I, J); 20 μm (E).
Specimen MPEF-Pb 10767 frequently has biseriate opposite pits (Fig. 3D), and wider (in tangential section) tracheids, similar to *Protophyllocladoxylon*. However, most of its pits are non-contiguous (Cp= 23.1%), the growth rings are wider, and it has one pit per cross-field, all of which are features of the species *Phyllocladoxylon antarcticum*. Two other specimens, MPEF-Pb 10733 and 10778, are not very well preserved and are assigned to cf. *P. antarcticum* because two of the main characters (intertracheary radial pitting and cross-fields) are poorly preserved and therefore barely discernible (Table 2).

*Phyllocladoxylon antarcticum* is the most common species in our sample of conifer woods from Laguna del Hunco. In Patagonia, it was previously recorded in the Cretaceous (Nishida et al. 1990), Eocene (Pujana and Ruiz 2019), and in sediments of unknown ages (Kräusel 1924). On the Antarctic Peninsula, the fossil-species is the dominant component of the Eocene of Seymour/Marambio Island wood flora (Torres et al. 1994; Pujana et al. 2014) and a common component of wood floras from the Late Cretaceous of James Ross Island (Pujana et al. 2017), the Paleocene of Seymour/Marambio Island (Pujana et al. 2015; Mirabelli et al. 2018), and the Eocene of the Fildes Peninsula of King George/25 de Mayo Island (Torres and Lemoigne 1988; Oh et al. 2020).

Torres and Lemoigne (1988) suggested a possible relationship of *P. antarcticum* with the extant genera *Phyllocladus* Rich., *Dacrydium* Sol. ex G.Forst., *Microcachrys* Hook. *Prumnopitys* Phil., and *Podocarpus* Labill. Pujana et al. (2014) suggested affinities with several basal extant Podocarpaceae: the prumnopityoid clade (including *Phyllocladus* and *Prumnopitys*), *Microstrobos* Garden and LAS Johnson, and *Microcachrys* (Knopf et al. 2012); all of those taxa share with the fossils similar wood anatomy, abietinean radial pitting, and, predominantly, one large simple pit per cross-field (Pujana et al. 2014).

Recently, a compressed branch bearing phylloclades from Laguna del Hunco was assigned to the newly described fossil-genus *Huncocladus* Andruchow-Colombo et al., a stem relative of *Phyllocladus* (Andruchow-Colombo et al. 2019), and pollen having affinity with *Microcachrys* (Barreda et al. 2020) was also reported from Laguna del Hunco. These fossils could be related to *Phyllocladoxylon antarcticum*, although more evidence is necessary to confirm this hypothesis. *Prumnopitys andina* (Poepp. ex Endl.) de Laub., the only extant species of its genus from Patagonia, and *Phyllocladoxylon antarcticum* share similar wood anatomy (Pujana et al. 2017), and it is possible that the fossil-species could be related to the extant *P. andina*.

**Genus Cupressinoxylon Göppert**

**cf. Cupressinoxylon sp. 1**

Figure 4A–I

**Studied material.** MPEF-Pb 10733.

**Locality.** LU8 at Laguna del Hunco (Fig. 1, Table 1), Chubut Province, Argentina.

**Stratigraphic provenance.** Tufolitas Laguna del Hunco, Huitrera Formation (Ypresian, early Eocene).
**Description.** Growth ring boundaries are distinct (Fig. 4A, B), with a gradual transition from earlywood to latewood (Fig. 2B). Tracheids are roundish to polygonal as seen in transverse section (Fig. 4C). Intertracheary pitting in radial walls is abietinean, predominantly uniseriate (Si = 1.01), very rarely biseriate, non-contiguous (Cp = 7.2%), and opposite when biseriate (Fig. 4D). Intertracheary pits are rounded in outline; 13.9 (10.4–15.8, SD = 1.1) μm in vertical diameter (Fig. 4D). Tracheid tangential diameter is 24.2 (18.8–32.4, SD = 3.3) μm. Axial parenchyma is present, scarce, and apparently with a tendency to be tangentially zonate (Fig. 4C, G, I). Cross-fields have 1–2, mostly one, mean 1.2, pits per cross-field (Fig. 4D–G). Cross-field pits are

**Figure 4.** *cf. Cupressinoxylon* sp. 1, MPEF-Pb 10733: **A** Growth rings (TS) **B** detail of a growth ring boundary (TS) **C** Detail of roundish tracheids and axial parenchyma (arrowheads) (TS) **D** uniseriate non-contiguous intertracheary radial pits and cross-field pit (arrowhead) (SEM) **E** and **F** cross-fields with bordered pits (SEM) **G** axial parenchyma (arrowhead) and cross-fields with bordered pits (RLS) **H** uniseriate rays (TLS) **I** uniseriate rays (TLS). Scale bars: 5 mm (**A**); 500 μm (**B**); 100 μm (**C, I**); 20 μm (**D, E, F, G**); 200 μm (**H**).
Conifer woods from Eocene of Patagonia

circular and bordered, apparently the border is usually wider than the aperture, and the aperture is rounded; 7.4 (5.2–9.6, SD = 1.2) μm in vertical diameter (Figs 4D–G, 6B). Horizontal walls of ray parenchyma cells are smooth (Fig. 4E–G). Average ray height is medium, 4.0 (1–11, SD = 1.9) cells high, rays are exclusively uniseriate (Fig. 4H–I) and with a frequency of 6.7 (4–8, SD = 1.2) rays per mm.

Remarks. Abietinean intertracheary radial pitting and apparently cupressoid pits in the cross-fields (bordered pits with the border wider than the aperture) indicate that this specimen belongs to the genus *Cupressinoxylon*, following Philippe and Bamford (2008). *Cupressinoxylon* includes wood with affinity to Cupressaceae and Podocarpaceae, with cupressoid cross-field pits (Pujana et al. 2014).

Cross-field pit border width is a key character of *Cupressinoxylon*. The poor preservation of this specimen prevents clear observation of the cross-field pits and also of the axial parenchyma walls; consequently, this specimen cannot be assigned with confidence to this fossil-genus and it is left as cf. *Cupressinoxylon*. Philippe and Bamford (2008) suggested that specimens in which the pit border is thinner than the aperture can also assigned to *Podocarpoxylon* Gothan.

The particular specimen studied here seems to be more similar to Podocarpaceae than to Cupressaceae because of the number of pits per cross-field. One, rarely two, pits per cross-field is common in the Podocarpaceae, whereas it is rarely observed in Cupressaceae (Tainter 1968; Greguss 1972; Meylan and Butterfield 1978; Roig 1992; Vidaurre Echeverría et al. 1987; Woltz et al. 1998; Vásquez Correa et al. 2010). Nevertheless, at this point we are not able to determine with certainty its affinity.

cf. *Cupressinoxylon* sp. 2
Figure 5A–I

**Studied material.** MPEF-Pb 10778.

**Locality.** LU23 at Laguna del Hunco (Fig. 1, Table 1), Chubut Province, Argentina.

**Stratigraphic provenance.** Tufolitas Laguna del Hunco, Huintrera Formation (Ypresian, early Eocene).

**Description.** Growth ring boundaries are distinct (Fig. 5A, B), with a gradual transition from earlywood to latewood (Fig. 5B). Tracheids are mostly polygonal as seen in transverse section (Fig. 5B). Intertracheary pitting in radial walls is abietinean, uni- to biseriate, predominantly uniseriate (Si = 1.06), non-contiguous (Cp = 6.3%), and opposite when biseriate (Fig. 5C–E). Intertracheary pits are mostly rounded in outline; 18.4 (14.9–23.9, SD = 2.2) μm in vertical diameter (Fig. 5C–E). Tracheid tangential diameter is 32.7 (18.7–46.1, SD = 7.1) μm. Cross-fields have 1–2, mostly one, mean 1.1, pits per cross-field (Fig. 5F–H). Cross-field pits are circular and bordered, apparently the border is usually wider than the aperture, and the aperture is rounded; 11.7 (7.7–13.7, SD = 1.8) μm in vertical diameter (Fig. 4F–H, 6D). Horizontal walls of ray parenchyma cells are smooth (Fig. 4F–H). Average ray height is medium, 5.9 (2–15, SD= 3.1) cells high, rays are exclusively uniseriate (Fig. 5I) and with a frequency of 6.6 (4–9, SD = 1.4) rays per mm.
Remarks. This specimen shares with cf. *Cupressinoxylon* sp. 1 the abietinean intertracheary radial pitting and bordered cross-field pits, and it also conforms to *Cupressinoxylon* according to Philippe and Bamford (2008). Unfortunately, it is also poorly preserved and could not be assigned with confidence to *Cupressinoxylon*. It differs from cf. *Cupressinoxylon* sp. 1 because sp. 2 has larger pits and lacks axial parenchyma. It also seems to be more similar to the Podocarpaceae than to Cupressaceae because they share the number of pits per cross-field (one, rarely two). In addition, in this specimen the mean diameter of the cross-field pits exceeds 10 μm, a feature present in
Conifer woods from Eocene of Patagonia

South American species of *Prumnopitys* (Woltz et al. 1998; Vásquez Correa et al. 2010) and in other Podocarpaceae genera (Greguss 1955) but mostly absent in Cupressaceae, which usually have smaller pits (Greguss 1955, 1972; Roig 1992).

**Growth rings**

Due to preservation, complete growth rings were only observed in a few specimens. Nonetheless, all the samples have distinct, well-defined growth ring boundaries (e.g., Figs 2A, 3A, 4A, 5A). Growth ring widths were measured where possible (Table 3). Growth rings are of types B and D (Table 3) of Creber and Chaloner (1984). The majority are type D, with abrupt transition from earlywood to latewood (Figs 2A, B, 3A), and only one specimen is type B, with a gradual transition from earlywood to latewood (Fig. 5A, B; Table 3). The mean ring width can reach 2.8 mm (Table 3). The minimum estimated age of the trees was grossly calculated to be 54 to 110 years, based on the curvature of the rings and the mean ring width (Table 3).

**Galleries**

Two samples of indeterminate conifers (Fig. 7; Table 2) have frass-filled galleries inside. Specimen MPEF-Pb 10736 has a gallery ca. 1.2 mm in diameter, horizontally oriented and parallel to the growth rings, filled with apparently spherical, sometimes slightly ellipsoidal, coprolites of ca. 200–300 μm in diameter (Fig. 7A). Unfortunately, this sample is not well preserved, and the content may have been modified during the fossilization process. On the other hand, sample MPEF-Pb 10725 has a gallery of ca. 1.3 mm diameter that abruptly narrows and bifurcates (Fig. 7B), also horizontally oriented and parallel to the rays. The fill of this gallery has better preservation, and

---

**Figure 6.** Schematic drawing of the cross-fields: A *Protophyllocladoxylon francisiae* B cf. *Cupressinoxylon* sp. 1 C *Phyllocladoxylon antarcticum* D cf. *Cupressinoxylon* sp. 2. Scale bar: 50 μm.
the content (frass) is clearly seen. The frass is compact, powdery, and made up of fragments of tracheids of ca. 100–300 μm in length, sometimes solitary and sometimes still united to adjacent tracheids (Fig. 7C).

**Figure 7.** Galleries in two indeterminate conifer woods: A gallery filled with apparently spherical coprolites (TS), MPEF-Pb 10736 B gallery filled with compact frass (RLS), MPEF-Pb 10725 C detail of the frass (RLS), MPEF-Pb 10725. Scale bars: 500 μm (A, B); 200 μm (C).

**Table 2.** Wood anatomy of studied conifer samples. Locality (LU); Seriation index (Si); Contiguity percentage (Cp) [%]; Mean vertical diameter of radial pits (VDRP) [μm]; Mean tracheid tangential diameter (TTD) [μm]; Mean pits per cross-field (PxCF); Mean vertical diameter of cross-field pits (VDCP) [μm]; Mean ray height (RH) [cells]; Mean rays per mm (RxM). * indicates fewer than 15 measurements.

| MPEF-Pb | Taxonomic unit                  | LU | Si   | Cp   | VDRP | TTD | PxCF | VDCP | RH  | RxM |
|---------|-------------------------------|----|------|------|------|-----|------|------|-----|-----|
| 10694   | *Protophyllocladoxylon francisci* | 2  | 1.25 | 88.1 | 19.2 | 44.5| 1.97 | 14.8 | 5.6 | 3.5 |
| 10697   | cf. *Phyllocladoxylon*         | 4  | 1.00*| 5.6* | 15.6 | ?   | 1.00*| 11.4*| ?   | ?   |
| 10700   | Indeterminate conifer          | 4  | 1.00*| 7.1* | 14.6 | ?   | ?    | ?    | ?   | ?   |
| 10707   | *Phyllocladoxylon antarcticum* | 6  | 1.00 | 12.5 | 19.3 | 33.1| 1.07 | 10.8 | 10.1| 8.2 |
| 10710   | *Phyllocladoxylon antarcticum* | 6  | 1.03 | 8.5  | 20.9 | 29.5| 1.11 | 12.0 | 7.9 | 8.4 |
| 10724   | Indeterminate conifer          | 6  | ?    | ?    | ?    | ?   | ?    | ?    | ?   | ?   |
| 10725   | Indeterminate conifer          | 6  | ?    | ?    | ?    | ?   | ?    | ?    | ?   | ?   |
| 10733   | cf. *Cupressinoxylon* sp. 1    | 8  | 1.01 | 7.2  | 13.9 | 24.2| 1.15 | 7.4  | 4.0 | 6.7 |
| 10736   | Indeterminate conifer          | 9  | ?    | ?    | ?    | ?   | ?    | ?    | ?   | ?   |
| 10739   | Indeterminate conifer          | 9  | ?    | ?    | ?    | ?   | ?    | ?    | ?   | ?   |
| 10742   | Indeterminate conifer          | 12 | ?    | ?    | ?    | ?   | ?    | ?    | ?   | ?   |
| 10747   | *Phyllocladoxylon antarcticum* | 15 | 1.00 | 9.6  | 17.5 | 32.1| 1.03 | 14.0 | 5.9 | 5.7 |
| 10748   | Indeterminate conifer          | 16 | ?    | ?    | ?    | 1.00*| ?    | ?    | ?   | ?   |
| 10749   | cf. *Phyllocladoxylon*         | 16 | 1.00*| 9.5* | 16.8*| ?   | 1.00*| 13.7*| 9.5 | 9.6*|
| 10750   | Indeterminate conifer          | 16 | 1.00*| 12.5*| ?   | ?    | ?    | ?    | ?   | ?   |
| 10751   | Indeterminate conifer          | 16 | ?    | ?    | ?    | 1.00*| ?    | ?    | ?   | ?   |
| 10753   | Indeterminate conifer          | 16 | ?    | ?    | ?    | ?   | ?    | ?    | ?   | ?   |
| 10754   | Indeterminate conifer          | 16 | ?    | ?    | 30.7 | ?   | ?    | 5.8  | 5.8*| ?   |
| 10765   | *Phyllocladoxylon antarcticum* | 22 | 1.00 | 13.4 | 16.4 | 31.7| 1.00 | 13.6 | 5.6 | 4.0 |
| 10766   | Indeterminate conifer          | 22 | ?    | ?    | ?    | ?   | ?    | ?    | ?   | ?   |
| 10767   | *Phyllocladoxylon antarcticum* | 22 | 1.17 | 23.1 | 19.1 | 42.1| 1.00 | 14.6 | 11.6| 5.1 |
| 10771   | Indeterminate conifer          | 22 | ?    | ?    | ?    | ?   | ?    | ?    | ?   | ?   |
| 10773   | *Phyllocladoxylon antarcticum* | 22 | 1.00*| 5.3* | 17.1*| 31.2| 1.00 | 12.9 | 6.2 | 8.1*|
| 10775   | Indeterminate conifer          | 22 | 1.00*| 16.3*| 15.1 | ?   | 1.00*| ?    | ?   | ?   |
| 10776   | *Phyllocladoxylon antarcticum* | 22 | 1.00 | 10.6 | 17.5 | 32.5| 1.06 | 13.2 | 9.9 | 6.3 |
| 10778   | cf. *Cupressinoxylon* sp. 2    | 23 | 1.06 | 6.3  | 18.4 | 32.7| 1.09 | 11.7 | 5.9 | 6.6 |


The conifers represent about 30% of the total collected wood assemblage, indicating an important presence of this clade within the forest canopy. Even though not all the conifer woods could be identified, two taxa belong undoubtedly to Podocarpaceae, *Protophyllocladoxylon francisiae* and *Phyllocladoxylon antarcticum*, while the other two, *cf. Cupressinoxylon* sp. 1 and *cf. Cupressinoxylon* sp. 2, are putative Podocarpaceae. Consequently, we found a significant species richness (four types of woods) from only twelve samples that could be identified to genus.

The family Podocarpaceae was apparently the dominant conifer component within the Laguna del Hunco wood flora, with the caveat of small sample size. The family is also abundant and strikingly diverse at generic level in the intensively collected compression flora (>7,000 specimens), including remains of *Acmopyle* Pilg., *Dacrycarpus* (Endl.) de Laub., *Podocarpus*, and *Retrophyllum* CN Page as well as the extinct phyllocladoid genus *Huncocladus* (Wilf 2012, 2020; Wilf et al. 2005, 2017; Andruachow-Colombo et al. 2019). Moreover, the pollen grains of the Podocarpaceae are the most abundant among all gymnosperms so far recorded at Laguna del Hunco; they are represented by seven species within five fossil-genera (*Gamerroites* Archangelsky, *Dacrycarpites* Cookson and Pike, *Lygistepollenites* Harris, *Microcachryidites* Cookson, and *Podocarpidites* Cookson; Barreda et al. 2020).

Nevertheless, Araucariaceae, which are not yet known in the wood flora, are the most abundant conifer compression fossils at Laguna del Hunco, where *Agathis* Salisb. (formerly “Zamia”) and *Araucaria* Juss. compressions are each more common than any podocarp genus (Wilf et al. 2005, 2014; Rossetto-Harris et al. 2020). *Papuacedrus prechilensis* (Berry) Wilf et al. (Cupressaceae) is also well-represented in the compression flora (Wilf et al. 2005, 2009) but does not correspond exactly to any of the wood fossils because the living genus usually has one to five pits per cross-field (Greguss 1972).

This discrepancy in the family proportional abundances between the woods and compression macrofossils could result from many factors, most likely including the number of fossils studied, local variations of the source flora in time and space, and well-known differences in the taphonomic pathways for wood vs. other plant parts (e.g., Behrensmeyer et al. 2000). For example, many wood specimens were found in the upper part of the section at Laguna del Hunco (Fig. 1), and thus they must be younger than and possibly represent a slightly different source composition from

| MPEF-Pb | Taxonomic unit                     | GRT | MW     | Min.–Max. | SD  | n  | MED  | MA  |
|---------|-----------------------------------|-----|--------|-----------|-----|----|------|-----|
| 10694   | *Protophyllocladoxylon francisiae*| D   | 681    | 262–1314  | 327 | 21 | 15   | 110 |
| 10707   | *Phyllocladoxylon antarcticum*    | D   | 816    | 300–1324  | 307 | 19 | 12   | 73  |
| 10747   | *Phyllocladoxylon antarcticum*    | D   | 1400   | 371–3056  | 678 | 15 | 15   | 54  |
| 10778   | *cf. Cupressinoxylon* sp. 2        | B   | 2786   | 2258–3742 | 517 | 7  | 50   | 90  |
the great majority of the compression samples, which are much more abundant in the middle part of the section (e.g., Wilf et al. 2003). The upper part of the section is more tuffaceous than the middle, probably reflecting rapid volcanic fill during the late phases of the caldera lake and a more frequently disturbed paleoenvironment (e.g., Aragón and Mazzoni 1997). We were only able to identify with certainty 12 specimens, and it is probable that with a larger wood sample, the occurrence of other conifer families from the compression flora, such as Araucariaceae and Cupressaceae, could be confirmed in the future. Nevertheless, the dominant status of the Podocarpaceae in fossil wood assemblages is a pattern observed for Patagonian and Antarctic woods during the Eocene (Pujana et al. 2014; Pujana and Ruiz 2017, 2019), whereas Cupressaceae and Araucariaceae, if present, were usually uncommon in all the wood floras of this epoch.

Podocarpaceae are today distributed mainly in the Southern Hemisphere and Malesia and are almost entirely restricted to rainforest or wet montane environments (de Laubenfels 1969; Hill and Brodribb 1999; Brodribb 2011; Cernusak et al. 2011). The family is ancient, with potential fossils from the Middle Triassic of Antarctica (e.g., Axsmith et al. 1998), and its fossil record from the Mesozoic through most of the Cenozoic is restricted to Southern Hemisphere land masses (Hill and Brodribb 1999). Interestingly, Podocarpaceae are often the most abundant gymnosperm group in living angiosperm-dominated rainforests (Brodribb 2011), as is the case for the Laguna del Hunco wood flora.

Growth ring boundaries of all samples are usually distinct (although some boundaries are not very well-defined), which indicates seasonality. The growth rings (type D; e.g., Figs 2A, B, 3A) are associated with the retardation of cambial activity, while the presence of type B (e.g., Fig. 5A, B) indicates a long growing season with an adequate water supply (Creber and Chaloner 1984). However, some Podocarpaceae with type D growth rings have wood that is not significantly affected by environmental factors, and can only be used in analyses of ring widths (Creber and Chaloner 1984). These types (B and D) of growth rings are consistent with the light regime at the paleolatitude of the sediments (about 47°S) and with previous paleotemperature and paleoprecipitation estimates based on leaf physiognomy and inferred drought-intolerance of many of the conifer taxa. The Laguna del Hunco compression assemblage, especially the conifer fraction, indicates no significant rainfall seasonality and very mild temperature seasonality (Wilf et al. 2003, 2005, 2009; Wilf 2012; Merkhofer et al. 2015).

The estimated minimum ages based on growth ring widths suggests that the specimens were mature trees at the time of deposition. We infer that the remains of *Protophyllocladoxylon francisiae* came from a tree older than 100 years (Table 3). In one sample, the type of growth ring (type B according to Creber and Chaloner 1984) and width of the growth rings reveal a significant and uniform growth of more than 5 mm in diameter annually (mean ring width 2.8 mm, widest ring of 3.7 mm, Table 3) which is similar to those of Podocarpaceae growing in wet Patagonian forests today (e.g., Rozas et al. 2016). Interestingly, the plant would have grown more than the global mean ring width of ca. 1.1 mm of extant conifers (Falcon-Lang 2005).
Galleries found in the woods were apparently produced by arthropod borers. They are filled with coprolites and particulate frass. This type of fill is produced by many types of arthropods (e.g., Platypodidae beetles, Tarno et al. 2011). The frass found is insufficient for its identification, mainly because the literature on wood debris produced by modern arthropods is scarce (Nuorteva & Kinnunen 2008) and mostly focused on northern hemisphere taxa (e.g., Hay 1968; Solomon 1977; Tarno et al. 2011). However, arthropod galleries are often found in Patagonian fossil woods (e.g., Genise 1995; Pujana et al. 2020), and mite coprolites were found in the permineralized Todea stem from southern exposures of the Tufolitas Laguna del Hunco (Bippus et al. 2019).

Conclusions

Herein, we report the first taxonomic study of conifer fossil woods from the highly fossiliferous Laguna del Hunco exposures. The proportion of conifers in this fossil wood assemblage (ca. 30%) indicates a significant presence of this group within the paleoflora. We document the family Podocarpaceae with confidence as the dominant component of the Laguna del Hunco wood paleoflora. The family is represented by two fossil species, Protophyllocladoxylon francisi and Phyllocladoxylon antarcticum. Additionally, two species assigned to the genus Cupressinoxylon (cf. Cupressinoxylon sp.1 and sp.2) are probably representatives of the family as well. Although sample size is small compared with the compression flora, these data strongly indicate that Podocarpaceae were important components of the Laguna del Hunco flora.

Podocarpaceae dominance in the fossil woods is consistent with diverse, abundant podocarpaceous macrofossil compressions and pollen grains previously described from the same section, including vegetative and reproductive structures related to several extant podocarp genera. However, in the Laguna del Hunco compressions, Araucariaceae are the dominant conifers, Cupressaceae are also well represented, and both families are found in the palynoflora. Neither family is yet known from the wood flora, presumably a result of lower sample size available for the woods by two orders of magnitude (10s of wood fossils vs. 1000s of compression fossils) or unknown taphonomic factors.

Growth rings indicate seasonality, probably because of the seasonal light regime at paleolatitude ca. 47°S, and mature tree development. The galleries found in two woods indicate arthropod interactions.

Acknowledgments

We thank the MEF staff, including P. Puerta, M. Caffa, M. Krause, L. Reiner, and E. Ruigomez, for logistical support on the 2016 field trip, stratigraphic discussions, and collections support; H. Padula and C. Greppi for field assistance; S. Mirabelli for preparing the thin sections; and Secretaría de Cultura del Chubut for access permits.
This research was supported by National Science Foundation grants DEB-1556666, DEB-1556136, EAR-1925755, and EAR-1925481; CONICET grant PIP 2014-0259; and ANPCyT grant PICT 2017-0671.

References

Andruchow-Colombo A, Wilf P, Escapa IH (2019) A South American fossil relative of Phyllocladus: Huncocladus laubenfelsii gen. et sp. nov. (Podocarpaceae), from the early Eocene of Laguna del Hunco, Patagonia, Argentina. Australian Systematic Botany 32: 290–309. https://doi.org/10.1071/SB18043

Aragón E, Mazzoni MM (1997) Geología y estratigrafía del complejo volcánico piroclástico del río Chubut medio (Eoceno), Chubut, Argentina. Revista de la Asociación Geológica Argentina 53: 243–256.

Axsmith BJ, Taylor TN, Taylor EL (1998) Anatomically preserved leaves of the conifer Nothophyllum krauselii (Podocarpaceae) from the Triassic of Antarctica. American Journal of Botany 85(5): 704–713. https://doi.org/10.2307/2446541

Barreda VD, Palazzesi L (2007) Patagonian vegetation turnovers during the Paleogene-early Neogene: Origin of arid-adapted floras. Botanical Review 73(1): 31–50. https://doi.org/10.1663/0006-8101(2007)73[31:PVTDTP]2.0.CO;2

Barreda VD, Zamaloa MC, Gandolfo MA, Jaramillo C, Wilf P (2020) Early Eocene spore and pollen assemblages from the Laguna del Hunco fossil-lake beds, Patagonia, Argentina. International Journal of Plant Sciences 181(6): 594–615. https://doi.org/10.1086/708386

Behrensmeyer AK, Kidwell SM, Gastaldo RA (2000) Taphonomy and paleobiology. Paleobiology 26(sp4): 103–147. https://doi.org/10.1666/0094-8373(2000)26[103:TAP]2.0.CO;2

Bengston P (1988) Open nomenclature. Palaeontology 31: 223–227.

Berry EW (1925) A Miocene flora from Patagonia. Johns Hopkins University Studies in Geology 6: 183–251.

Bippus AC, Escapa IH, Wilf P, Tomescu AMF (2019) Fossil fern rhizomes as a model system for exploring epiphyte community structure across geologic time: Evidence from Patagonia. PeerJ 7: e8244. https://doi.org/10.7717/peerj.8244

Bomfleur B, Escapa IH (2019) A silicified Todea trunk (Osmundaceae) from the Eocene of Patagonia. Paläontologische Zeitschrift 93(3): 543–548. https://doi.org/10.1007/s12542-019-00479-6

Brea M, Bellosi ES, Krause M (2009) Taxaceoxylon katuatenkum sp. nov. en la Formación Koluel-Kaike (Eoceno inferior-medio), Chubut, Argentina: Un componente de los bosques subtropicales paleógenos de Patagonia. Ameghiniana 46: 127–140.

Brodribb TJ (2011) A functional analysis of podocarp ecology. In: Turner BL, Cernusak LA (Eds) Ecology of the Podocarpaceae in Tropical Forests. Smithsonian Institution Scholarly Press, Washington, 165–173. https://doi.org/10.5479/si.0081024X.95.165

Cernusak LA, Adie H, Bellingham PJ, Biffin E, Brodribb TJ, Coomes DA, Dalling JW, Dickie IA, Enright NJ, Kitayama K, Ladd PG, Lambers H, Lawes MJ, Lusk CH, Morley RJ, Turner BL (2011) Podocarpaceae in tropical forests: A synthesis. In: Turner BL, Cernusak
Conifer woods from Eocene of Patagonia

LA (Eds) Ecology of the Podocarpaceae in Tropical Forests. Smithsonian Institution Scholarly Press, Washington, 189–195. https://doi.org/10.5479/si.0081024X.95.189

Creber GT, Chaloner WG (1984) Influence of environmental factors on the wood structure of living and fossil trees. Botanical Review 50(4): 357–448. https://doi.org/10.1007/BF02862630

de Laubenfels DJ (1969) A revision of the Malesian and Pacific rainforest conifers, I. Podocarpaceae, in part. Journal of the Arnold Arboretum 50: 274–369. https://doi.org/10.5962/bhl.part.24691

Falcon-Lang HJ (2005) Global climate analysis of growth rings in woods, and its implications for deep-time paleoclimate studies. Paleobiology 31(3): 434–444. https://doi.org/10.1666/0094-8373(2005)031[0434:GCAOGR]2.0.CO;2

Genise JF (1995) Upper Cretaceous trace fossils in permineralized plant remains from Patagonia, Argentina. Ichnos 3(4): 287–299. https://doi.org/10.1080/1042094950386399

Gosses J, Carroll AR, Bruck BT, Singer BS, Jicha BR, Aragón E, Walters AP, Wilf P (2020) Facies interpretation and geochronology of diverse Eocene floras and faunas, northwest Chubut Province, Patagonia, Argentina. Geological Society of America Bulletin 132. [In Press]

Gothan W (1908) Die fossilen Hölzer von der Seymour und Snow Hill insel. Wissenschaftliche Ergebnisse der Schwedischen Südpolar Expedition 1901-1903(3): 1–33.

Greguss P (1955) Identification of living gymnosperms on the basis of xylotomy. Akadémiai Kiadó, 1–613.

Greguss P (1972) Xylotomy of the living conifers. Akadémiai Kiadó, 1–329.

Hay CJ (1968) Frass of some wood-boring insects in living oak (Coleoptera: Cerambycidae; Lepidoptera: Cossidae and Aegeriidae). Annals of the Entomological Society of America 61(2): 255–258. https://doi.org/10.1093/aesa/61.2.255

Hill RS, Brodribb TJ (1999) Southern conifers in time and space. Australian Journal of Botany 47(5): 639–696. https://doi.org/10.1071/BT98093

IAWA Softwood Committee (2004) IAWA list of microscopic features for softwood identification. IAWA Journal 25(1): 1–70. https://doi.org/10.1163/22941932-90000349

Knopf P, Schulz C, Little DP, Stu T, Dennis W (2012) Relationships within Podocarpaceae based on DNA sequence, anatomical, morphological, and biogeographical data. Cladistics 28(3): 271–299. https://doi.org/10.1111/j.1096-0031.2011.00381.x

Kräusel R (1924) Beiträge zur Kenntnis der fossilen Flora Südamerikas 1. Fossile Hölzer aus Patagonien und benachbarten Gebieten. Arkiv för Botanik 19: 1–36.

Merkhofer L, Wilf P, Haas MT, Kooymann RM, Sack L, Scoffoni C, Cúneo NR (2015) Resolving Australian analogs for an Eocene Patagonian paleorainforest using leaf size and floristics. American Journal of Botany 102(7): 1160–1173. https://doi.org/10.3732/ajb.1500159

Meylan BA, Butterfield BG (1978) The structure of New Zealand woods. New Zealand Department of Scientific and Industrial Research, Wellington, 1–250.

Mirabelli SL, Pujana RR, Marenssi SA, Santillana SN (2018) Conifer fossil woods from the Sobral Formation (lower Paleocene, Western Antarctica). Ameghiniana 55(1): 91–108. https://doi.org/10.5710/AMGH.27.07.2017.3095

Nishida M, Ohsawa T, Rancusi MH (1990) Miscellaneous notes on the petrified coniferous woods from central Chilean Patagonia, XI Region, Chile. In: Nishida M (Ed.) A report of
the paleobotanical survey to Patagonia, Chile (1989). Faculty of Science, Chiba University, Chiba, 21–29.

Nuorteva M, Kinnunen KA (2008) Insect frass in Baltic amber. Bulletin of the Geological Society of Finland 80(2): 105–124. https://doi.org/10.17741/bgsfl/80.2.003

Oh C, Philippe M, McLoughlin S, Woo J, Lepe M, Torres T, Park TYS, Choi HG (2020) New fossil woods from lower Cenozoic volcano-sedimentary rocks of the Fildes Peninsula, King George Island, and the implications for the trans-Antarctic Peninsula Eocene climatic gradient. Papers in Palaeontology 6(1): 1–29. https://doi.org/10.1002/spp2.1256

Petersen CS (1946) Estudios geológicos en la región del río Chubut medio. Boletín de la Dirección de Minas y Geología 59: 1–137.

Philippe M, Bamford MK (2008) A key to morphogenera used for Mesozoic conifer-like woods. Review of Palaeobotany and Palynology 148(2-4): 184–207. https://doi.org/10.1016/j.revpalbo.2007.09.004

Pujana RR, Ruiz DP (2017) *Podocarvoxylon* Gothan reviewed in the light of a new species from the Eocene of Patagonia. IAWA Journal 38(2): 220–244. https://doi.org/10.1163/22941932-20170169

Pujana RR, Ruiz DP (2019) Fossil woods from the Eocene-Oligocene (Río Turbio Formation) of southwestern Patagonia (Santa Cruz Province, Argentina). IAWA Journal 40(3): 596–626. https://doi.org/10.1163/22941932-40190253

Pujana RR, Santillana SN, Marenssi SA (2014) Conifer fossil woods from the La Meseta Formation (Eocene of Western Antarctica): Evidence of Podocarpaceae-dominated forests. Review of Palaeobotany and Palynology 200: 122–137. https://doi.org/10.1016/j.revpalbo.2013.09.001

Pujana RR, Marenssi SA, Santillana SN (2015) Fossil woods from the Cross Valley Formation (Paleocene of Western Antarctica): Araucariaceae-dominated forests. Review of Palaeobotany and Palynology 222: 56–66. https://doi.org/10.1016/j.revpalbo.2015.07.010

Pujana RR, Ruiz DP, Martínez LCA, Zhang Y (2016) Proposals for quantifying two characteristics of tracheid pit arrangement in gymnosperm woods. Revista del Museo Argentino de Ciencias Naturales 18: 117–124. https://doi.org/10.22179/REVMACN.18.455

Pujana RR, Raffi ME, Olivero EB (2017) Conifer fossil woods from the Santa Marta Formation (Upper Cretaceous), Brandy Bay, James Ross Island, Antarctica. Cretaceous Research 77: 28–38. https://doi.org/10.1016/j.cretres.2017.04.016

Pujana RR, Aramendía I, Cuitiño JJ (2020) Fossil woods from the middle Miocene (Río Correntoso Formation) of Patagonia (northern Santa Cruz Province, Argentina). Ameghina. https://doi.org/10.5710/AMGH.25.02.2020.3284 [In press]

Roig FA (1992) Comparative wood anatomy of southern South America Cupressaceae. IAWA Bulletin 13(2): 151–162. https://doi.org/10.1163/22941932-90001263

Rossetto-Harris G, Wilf P, Escapa IH, Andruchow-Colombo A (2020) Eocene Araucaria sect. *Eutacta* from Patagonia and floristic turnover during the initial isolation of South America. American Journal of Botany 107(5): 806–832. https://doi.org/10.1002/ajb2.1467

Rozas V, Le Quesne C, Muñoz A, Puchi P (2016) Climate and growth of *Podocarpus salignus* in Valdivia, Chile. Dendrobiology (Poznan) 76: 3–11. https://doi.org/10.12657/denbio.076.001
Conifer woods from Eocene of Patagonia

Solomon JD (1977) Frass characteristics for identifying insect borers (Lepidoptera: Cossidae and SesIIDa; Coleoptera: Cerambycidae) in living hardwoods. Canadian Entomologist 109(2): 295–303. https://doi.org/10.4039/Ent109295-2

Tainter FH (1968) Microscopic identification of commercial Chilean woods. La identificación microscópica de las maderas comerciales chilenas. Special Publication Three. School of Forestry, University of Montana, Missoula, 27 pp.

Tarno H, Qi H, Endoh R, Kobayashi M, Goto H, Futai K (2011) Types of frass produced by the ambrosia beetle *Platypus quercivor us* during gallery construction, and host suitability of five tree species for the beetle. Journal of Forest Research 16(1): 68–75. https://doi.org/10.1007/s10310-010-0211-z

Terada K, Asakawa TO, Nishida H (2006a) Fossil woods from Arroyo Cardenio, Chile Chico Province, Aisen (XI) Region, Chile. In: Nishida H (Ed) Post-Cretaceous floristic changes in southern Patagonia, Chile. Faculty of Science and Engineering, Chuo University, Tokyo, 57–65. http://c-faculty.chuo-u.ac.jp/~helecho/57-65.pdf

Terada K, Asakawa TO, Nishida H (2006b) Fossil woods from the Loreto Formation of Las Minas, Magallanes (XII) region, Chile. In: Nishida H (Ed) Post-Cretaceous floristic changes in southern Patagonia, Chile. Faculty of Science and Engineering, Chuo University, Tokyo, 91–101.

Torres T, Lemoigne Y (1988) Maderas fósiles terciarias de la Formación Caleta Arctowski, isla Rey Jorge, Antártica. Serie Científica Instituto Antártico Chileno 37: 69–107.

Torres T, Marenssi SA, Santillana SN (1994) Maderas fósiles de la isla Seymour, Formación La Meseta, Antártica. Serie Científica Instituto Antártico Chileno 44: 17–38.

Vajda V, Linderson H, McLoughlin S (2016) Disrupted vegetation as a response to Jurassic volcanism in southern Sweden. In: Kear BP, Lindgren J, Hurum JH, Milan J, Vajda V (Eds) Mesozoic biotas of Scandinavia and its Arctic territories. Geological Society, London, Special Publications 434. The Geological Society of London, London, 127–147. https://doi.org/10.1144/SP434.17

Vásquez Correa ÁM, Alcántara Vara E, Herrera Machuca MÁ (2010) Wood anatomy of Colombian Podocarpaceae (*Podocarpus, Prumnopitys* and *Retrophyllum*). Botanical Journal of the Linnean Society 164(3): 293–302. https://doi.org/10.1111/j.1095-8339.2010.01087.x

Vidaurre Echeverría SF, Rallo de la Barra M, Ulloa Alvarez I, Rosende Beytía R (1987) Anatomía de Chilean conifers [Anatomía de las coníferas chilenas]. In: Proceedings of VI Reunión sobre Investigación y Desarrollo en Productos Forestales. Universidad de Concepción, Concepción, 1–15.

Wilf P (2012) Rainforest conifers of Eocene Patagonia: Attached cones and foliage of the extant Southeast Asian and Australasian genus *Dacrycarpus* (Podocarpaceae). American Journal of Botany 99(3): 562–584. https://doi.org/10.3732/ajb.1100367

Wilf P (2020) Eocene “*Chusquea*” fossil from Patagonia is a conifer, not a bamboo. PhytoKeys 139: 77–89. https://doi.org/10.3897/phytokeys.139.48717

Wilf P, Cúneo NR, Johnson KR, Hicks JF, Wing SL, Obradovich JD (2003) High plant diversity in Eocene South America: Evidence from Patagonia. Science 300(5616): 122–125. https://doi.org/10.1126/science.1080475
Wilf P, Johnson KR, Cúneo NR, Smith ME, Singer BS, Gandolfo MA (2005) Eocene plant diversity at Laguna del Hunco and Río Pichileufú, Patagonia, Argentina. American Naturalist 165(6): 634–650. https://doi.org/10.1086/430055

Wilf P, Little S, Iglesias A, Zamaloa MDC, Gandolfo MA, Cúneo NR, Johnson KR (2009) 
Papuacedrus
(Cupressaceae) in Eocene Patagonia: A new fossil link to Australasian rainforests. American Journal of Botany 96(11): 2031–2047. https://doi.org/10.3732/ajb.0900085

Wilf P, Cúneo NR, Escapa IH, Pol D, Woodburne MO (2013) Splendid and seldom isolated: The paleobiogeography of Patagonia. Annual Review of Earth and Planetary Sciences 41(1): 561–603. https://doi.org/10.1146/annurev-earth-050212-124217

Wilf P, Escapa IH, Cúneo NR, Kooyman RM, Johnson KR, Iglesias A (2014) First South American 
Agathis
(Araucariaceae), Eocene of Patagonia. American Journal of Botany 101(1): 156–179. https://doi.org/10.3732/ajb.1300327

Wilf P, Donovan MP, Cúneo NR, Gandolfo MA (2017) The fossil flip-leaves (Retrophyllum, Podocarpaceae) of southern South America. American Journal of Botany 104(9): 1344–1369. https://doi.org/10.3732/ajb.1700158

Woltz P, Gondran M, Marguerier J, Gajardo R (1998) Xylologie des conifères endémiques des Andes meridionales au MEB. III. Podocarpaceae. Revue de Cytologie et de Biologie Végétales - Le Botaniste 21: 3–14.

Zachos JC, Pagani M, Sloan L, Thomas E, Billups K (2001) Trends, rhythms, and aberrations in global climate 65 Ma to present. Science 292(5517): 686–693. https://doi.org/10.1126/science.1059412

Zhang Y, Wang J, Liu LJ, Li N (2010) 
Protophyllocladoxylon jingyuanense
sp. nov., a gymnospermous wood of the Serpukhovian (Late Mississippian) from Gansu, Northwest China. Acta Geologica Sinica 84(2): 257–268. https://doi.org/10.1111/j.1755-6724.2010.00160.x

Zijlstra G, Philippe M (2020) (2741) Proposal to conserve the name Protophyllocladoxylon (fossil Coniferophyta: Coniferales) with a conserved type. Taxon 69(2): 412–413. https://doi.org/10.1002/tax.12227