



Research paper

Conifer fossil woods from the La Meseta Formation (Eocene of Western Antarctica): Evidence of Podocarpaceae-dominated forests



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ABSTRACT

A new collection of 120 fossil wood samples from early Eocene sediments of the La Meseta Formation is studied. Conifers represent 68% of the total amount of wood samples. The specimens show significant conifer diversity and were placed in seven fossil-species. Samples are assigned to the Podocarpaceae, probably Cupressaceae and Araucariaceae. New fossil-species of *Protophyllocladoxylon* and *Phyllocladoxylon* (Podocarpaceae) and two new nomenclatural combinations are proposed. Comments about the systematic position of each genus and species represented are made. The systematic is based on anatomical data and supported by statistical analysis. A PCA of 78 woods and 12 characters was performed to confirm the taxon delimitation and discrete clusters are represented in the plots for most of each species. *Phyllocladoxylon antarcticum* is the most common wood type followed by *Cupressinoxylon*, *Agathoxylon* and other Podocarpaceae. In accordance with previous studies, our samples suggest that during the early Eocene forests of the northeastern part of the Antarctic Peninsula were dominated by conifers, particularly Podocarpaceae.

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1. Introduction

Fossil woods from Antarctica are abundant and their presence was first mentioned by Eight (1833). Göppert (1881) described briefly some woods from the Kerguelen Islands; Beust (1884) described in some detail *Cupressinoxylon antarcticum* Beust and later Crié (1889) *Cupressoxylon kerguelense* Crié. Sharman and Newton (1894, 1898) briefly mentioned the anatomy of some coniferous fossil woods from Seymour (Marambio) Island collected by Larsen and Donald in two expeditions in 1893 (Sharman and Newton, 1898). Later, systematic studies of fossil woods continued when Gothan (1908) described in more detail samples from Seymour (Marambio) and Snow Hill Islands collected by Larsen and Donald in 1893 and by the Swedish South Polar Expedition of Nordenskjöld in 1901–1903.

Palaeobotanical research in the La Meseta Formation includes studies on leaves (Dusén, 1908; Case, 1988; Doktor et al., 1996; Gandolfo et al., 1998a), a flower (Gandolfo et al., 1998b), pollen (Cranwell, 1959; Askin and Fleming, 1982; Zamalao et al., 1987; Askin, 1991) and also woods (Torres et al., 1994a; Poole and Gottwald, 2001; Poole, 2002; Poole et al., 2003; Cantrill and Poole, 2005a). Furthermore, Francis (1986), Brea (1998) and Francis and Poole (2002) studied growth rings of some fossil woods from this formation. In this article an extensive new

collection of fossil woods were anatomically studied in detail. Woods were collected from different stratigraphic units (allomembers) of the formation. Multivariate analysis (PCA) was used in order to test the delimitation of fossil-species.

2. Geological setting

The La Meseta Formation (Elliot and Trauman, 1982) represents an Eocene incised valley fill (estuarine system) developed in the northern part of the James Ross Basin, at the NE of the Antarctic Peninsula. Marensi et al. (1998) divided the formation into six allomembers and described shallow marine and deltaic palaeoenvironments. Initially, a middle to late Eocene age was assigned to the La Meseta Formation based on invertebrate and vertebrate fossil records (Zinsmeister, 1984; Woodburne and Case, 1996). However, it was later extended to the early Eocene based on dinoflagellate cysts (Cocozza and Clarke, 1992). Strontium-derived ages support this age (Dingle et al., 1998; Dutton et al., 2002; Ivany et al., 2006, 2008) (Fig. 1) and suggest that the deposition of the La Meseta Formation took place during the Eocene. Most recent studies (Montes et al., 2010), although still in progress, indicate that the lower and middle parts of the La Meseta Formation (Valle de las Focas, Acantilados, Campamento, Cucullaea I and the lower part of Cucullaea II allomembers) were deposited during the early Eocene and sedimentation may have begun as early as late Paleocene.

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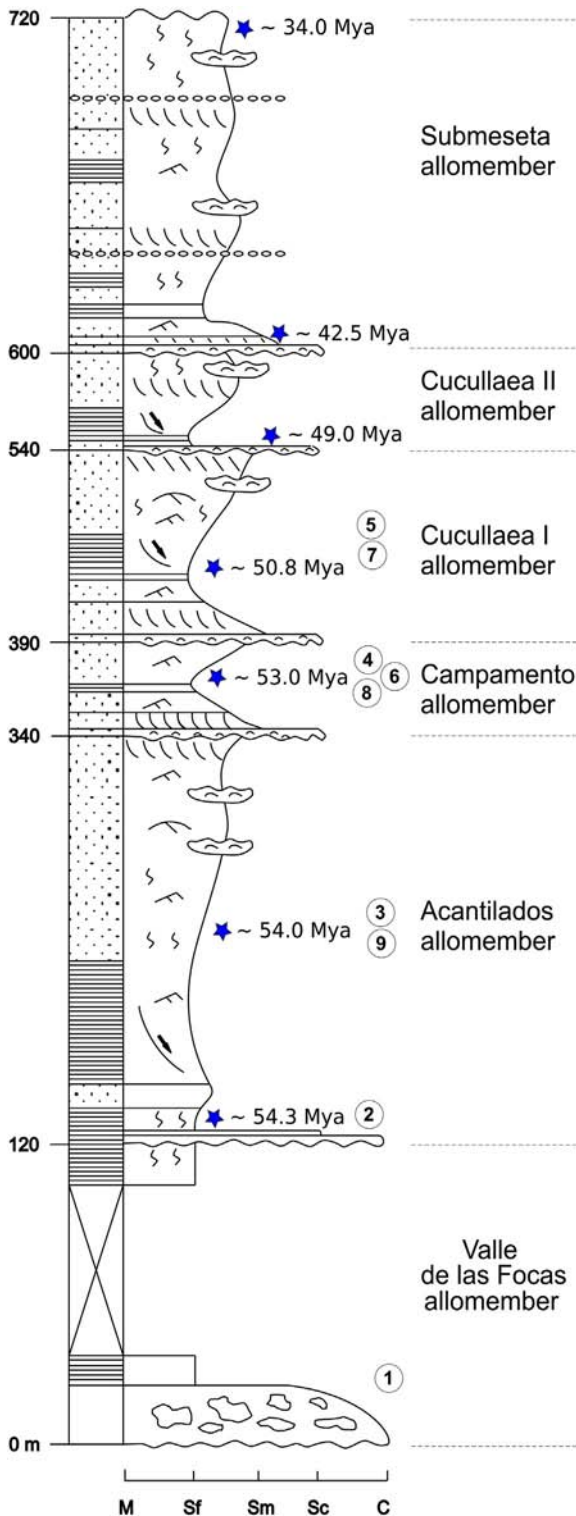


Fig. 1. Simplified log of the La Meseta formation showing its allomembers, datings correspond to Dingle et al. (1998), Dutton et al. (2002) and Ivany et al. (2006, 2008). Numbers correspond to the fossiliferous localities. (1 = Valle de las Focas allomember, 2 = Acantilados allomember [I], 3 = Acantilados allomember [II], 4 = Campamentos allomember [I], 5 = Cucullaea I allomember [I], 6 = Campamentos allomember [II], 7 = Cucullaea I allomember [II], 8 = Campamentos allomember [III], 9 = Acantilados allomember [III]).

Adapted from Marensi et al. (1998) and Montes et al. (2010).

All but two samples (BA Pb 14502 and 14503) presented in this paper were collected from early Eocene sediments. Locality 1 (Valle de las Focas allomember) is regarded as possibly late Paleocene based on

new magnetostratigraphic studies (Montes et al., 2010) but it may correspond to reworked material from the underlying Sobral Formation.

3. Material and methods

Fossil woods were collected by the authors in sediments of the La Meseta Formation in Seymour (Marambio) Island in February 2005. They come from nine different localities that correspond to the lower and middle parts of the formation (Figs. 1, 2). Fossil wood specimens are decorticated secondary xylem permineralized by carbonates. Stratigraphical and geographical notes were taken for all of the specimens, and particular care was taken to try to assure that each fragment of wood corresponds originally to different trees.

The material studied herein is a collection of 82 conifer woods, out of 120 wood samples (the other 38 samples are angiosperms). They are housed at the Palaeobotanical Collection of the Museo Argentino de Ciencias Naturales, under accession numbers BA Pb 1400 to 14519 (Appendix A). Slides bear the specimen number followed by a lower case letter.

The specimens were thin sectioned in transverse, tangential longitudinal and radial longitudinal sections following standard techniques for petrified woods (Hass and Rowe, 1999) and studied using light microscopy. In addition, acetate peels were also made following the recommendations of Galtier and Phillips (1999). Small fragments of most of the woods were observed at SEM. Most of the 82 observed conifers (78 specimens) were well preserved enough for the observation of diagnostic characters and for assigning them to a fossil-species (Appendix A).

At least 25 measurements or observations of each character for each specimen of types were made and at least 15 for most of the rest of the specimens. In the previously named species descriptions, measurements are expressed as the weighted mean followed by the range of all the specimens assigned to that species.

The terminology of Richter et al. (2004) was followed for describing conifer wood anatomy. For fossil-genera delimitation, the criteria of Philippe and Bamford (2008) were followed. Other fossil gymnosperm wood anatomy reviews like those of Stopes (1914), Kräusel (1949) and Vaudois and Privé (1971) were consulted. Wood anatomy was compared with that of extant plants, predominantly from southern hemisphere (i.e. Greguss, 1955; Patel, 1968b; Rancusi et al., 1987; Roig, 1992).

Principal Component Analysis (PCA) was performed following the methodology of Möller et al. (2007) and MacLachlan and Gasson (2010) to examine the taxon discrimination. Twelve characters (six discrete and six continuous) and 76 specimens (four poorly preserved samples and two branches were excluded) were used to make the matrix (Appendix A). Three discrete characters (numbers four, seven and twelve of the Appendix A) are binary and the other three discrete are ordinal (numbers one, two and six of the Appendix A). The three discrete ordinal characters could have been presented as means with decimals as we did with the other continuous data. Instead, we wrote the mean in fractions (i.e. 1.25, 2, 2.5) as if they were discrete characters, but theoretically they can be treated as continuous. We write the means in fractions in those three characters because in some specimens the number of measurements or observations is not significant. Jolliffe (2002) considers that if PCA is performed as a descriptive technique, the analysis can be run regardless of the nature of the original variables. PCA with discrete and continuous wood anatomy characters were previously probed to be appropriate for taxon delimitation (Wickremasinghe and Herat, 2006; Oakley and Falcon-Lang, 2009; Oakley et al., 2009; MacLachlan and Gasson, 2010; Henderson and Falcon-Lang, 2011). A correlation matrix (variables were measured in different units) was made based on those characters. Some characters were not included in the PCA (i.e.: ray width, distinct/absent growth ring boundaries and helical thickenings) because they were the same in all the specimens (thus they are uninformative). However, many characters not present in the IAWA code (Richter et al., 2004) were used for the PCA, i.e.: tangential diameter of tracheids, radial and cross-field pit sizes and vertical

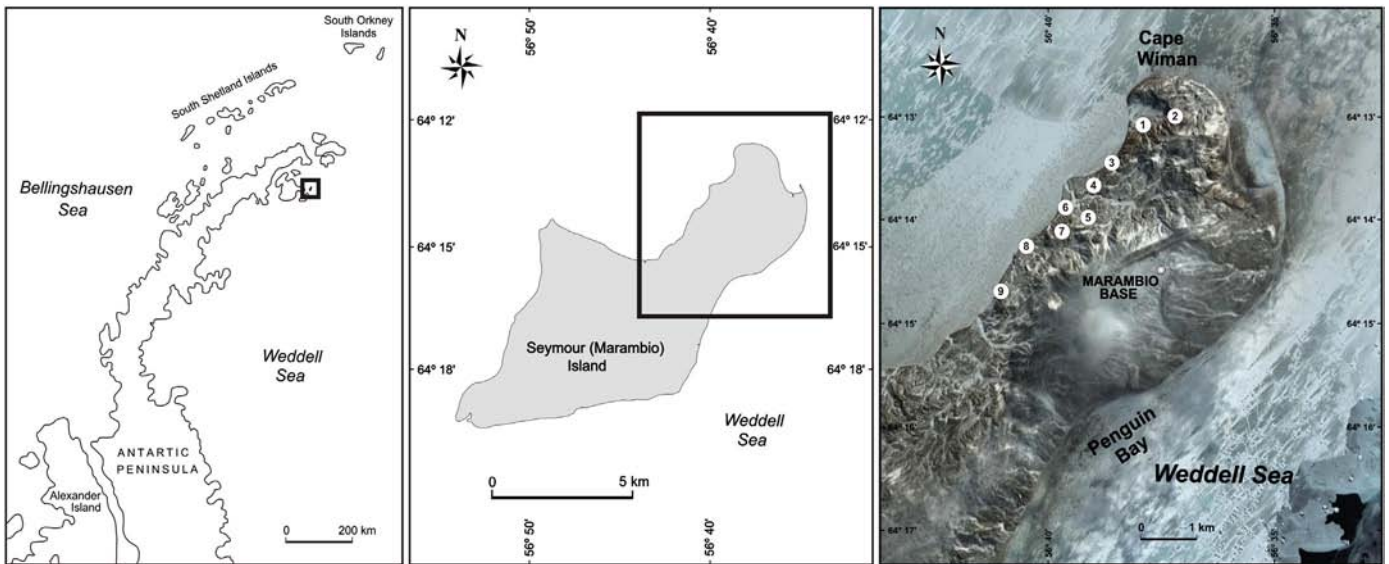


Fig. 2. Map and satellite image showing fossiliferous localities. Numbers are the same than those of Fig. 1.

diameter of ray parenchyma cells. The analysis was performed using PAST programme version 2.15 (Hammer et al., 2001) with missing values set in iterative imputation. For choosing the number of PC suitable for data analysis, the scree test (Cattell, 1966) was used (not shown).

4. Systematic palaeontology

Family Podocarpaceae

Protophyllocladoxylon Kräusel

Type species *Protophyllocladoxylon leuschii* Kräusel

Protophyllocladoxylon francisiae nov. sp. (Plate I, 1–8)

Holotype: BA Pb 14416 (Plate I, 1–4, 7, 8).

Paratype: BA Pb 14418 (Plate I, 5).

Other specimen: BA Pb 14438.

Repository: Colección de Paleobotánica, Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina.

Type locality: Locality 5 (see Figs. 1, 2), Seymour (Marambio) Island, Western Antarctica.

Other locality: Locality 7 (see Figs. 1, 2), Seymour (Marambio) Island, Western Antarctica.

Stratigraphic horizon: Cucullaea I allomember, La Meseta Formation.

Etymology: after Prof. Jane Francis for her extensive research on polar palaeobotany and geology.

Diagnosis: Growth ring boundaries distinct. Tracheid radial pitting mixed, predominantly alternate and contiguous (araucarian), uni and biseriolate, rarely triseriate. Cross-fields with one or two oopores, horizontally elongated and contiguous in a row when two are present. Rays uniseriate, medium. Axial parenchyma absent.

Description: Growth ring boundaries distinct (Plate I, 1). Latewood consists of two to five tracheids with reduced radial diameter (Plate I, 1). Transition from early- to latewood abrupt (Plate I, 1–4). Tracheid radial pitting uni to biseriolate, scattered to contiguous, opposite to alternate (mixed type) (Plate I, 2, 3, 6). Radial pits circular to hexagonal, 16.4 (11.1–20.5) μm in vertical diameter. Tracheid tangential diameter 37.9 (25.0–47.5) μm . Bordered pits with ca. 14 μm in vertical diameter on tangential walls, less abundant than in radial walls (Plate I, 7). Axial parenchyma absent. Cross-field pitting “window-like” (fenestriform) with one or two large simple pits (oopores) per cross-field (Plate I, 3–5). Cross-field pits horizontally elongated and 14.1 (10.8–19.1) μm in vertical diameter (Plate I, 3–5). When two pits are present in the cross-fields,

contiguous and arranged in one row (Plate I, 3–5). Horizontal end walls of ray parenchyma cells smooth (Plate I, 3–5). Parenchymatic ray cells 14.1 (15.0–22.5) μm in vertical diameter (Plate I, 3–6). Rays medium, 7.6 (1–21) cells high, exclusively uniseriate (Plate I, 7–8) and with a frequency of 3.7 (2–5) rays per mm.

4.1. Comparisons with fossil woods

According to Philippe and Bamford (2008), mixed type of pitting on the tracheid radial walls and large simple pits (oopores) in the cross-fields allow us to assign the specimens to *Protophyllocladoxylon*. However, *Protophyllocladoxylon* includes significant anatomical variation among its constituent taxa. Most of them have exclusively araucarian radial pitting, but there are also mixed type of radial pitting in some species (Philippe and Bamford, 2008; Zhang et al., 2010).

Species of *Protophyllocladoxylon* with distinct growth ring boundaries and absence of axial parenchyma that has almost exclusively one pit per cross-field are: *Protophyllocladoxylon dolianitii* Mussa, *Protophyllocladoxylon derbyi* (Oliveira) Maheshwari and *Protophyllocladoxylon natalense* (Warren) Schultze Motel (Mussa, 1958; Schultze Motel, 1961; Maheshwari, 1972). *Protophyllocladoxylon indicum* Pant and Singh has up to quadriseriate radial pits and significantly higher rays (Pant and Singh, 1987). *Protophyllocladoxylon lechangense* Wang and *Protophyllocladoxylon cortaderitaense* Menéndez have always alternate and contiguous (araucarian) radial pitting (Menéndez, 1956; Wang, 1993). *Protophyllocladoxylon quedlinburgense* Schultze Motel, *Protophyllocladoxylon franconium* Vogellehner and *Protophyllocladoxylon oolithicum* Vogellehner have predominantly or exclusively uniseriate pitting and normally only one pit per cross-field (Schultze Motel, 1961; Vogellehner, 1966).

Microcachryxylon gothani Torres et al. was described from the Cretaceous of James Ross Island (Torres et al., 1994b). According to the ICBN (McNeill et al., 2012), Philippe and Bamford (2008) considered it a validly published name for woods with abietinean radial pitting and oopores in the cross-fields. It has similar cross-field pits (one or two oopores) to *Protophyllocladoxylon francisiae* but has axial parenchyma. According to the original description, tracheid pitting is uni to biseriolate (opposite), but also a tendency to alternate and triseriate pitting is illustrated in the original figures (Plate I, 5). If a mixed type of pitting is present in *M. gothani*, this fossil-species should be transferred to *Protophyllocladoxylon* following Philippe and Bamford's (2008) criteria.

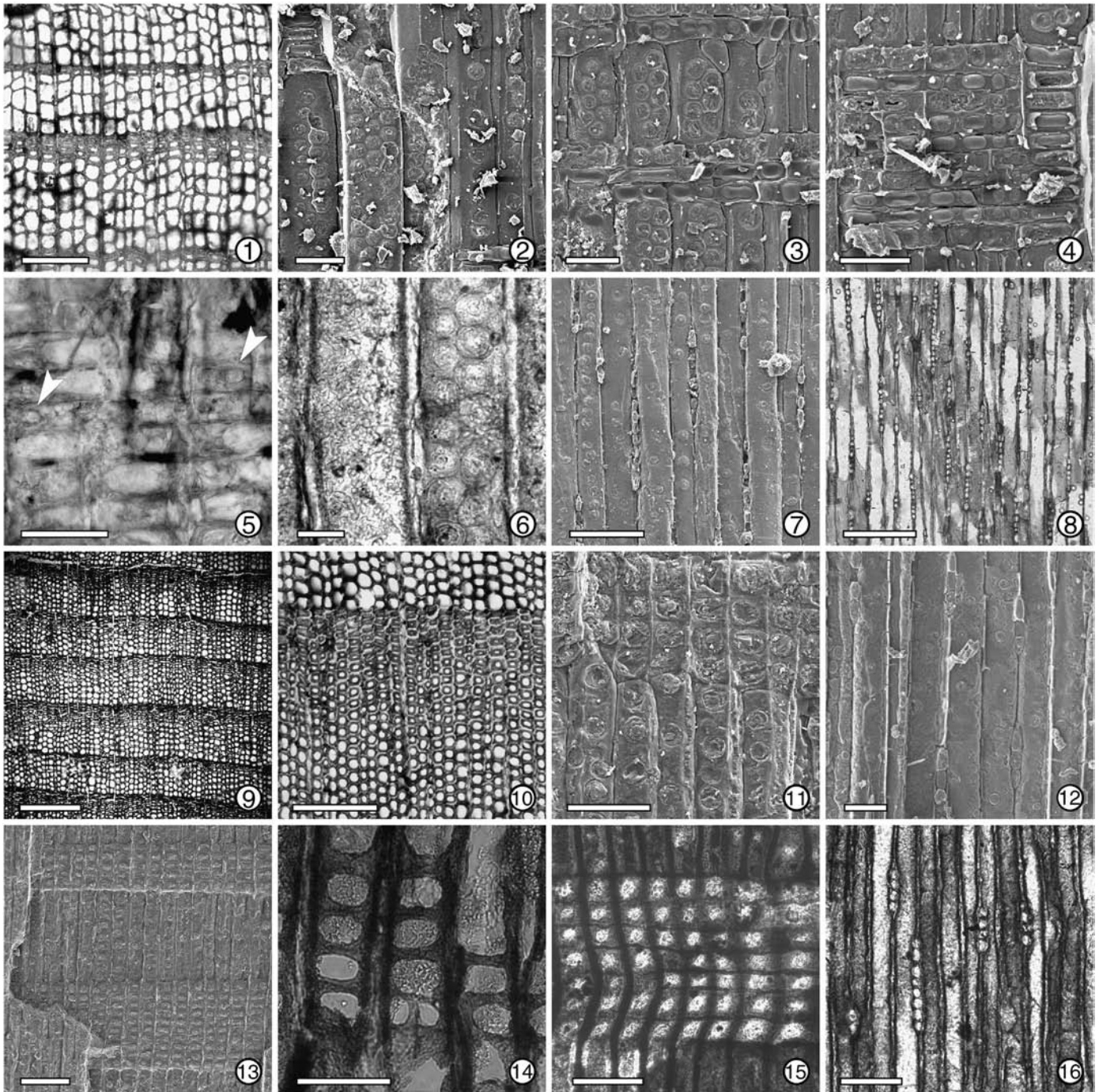


Plate I. Wood anatomy of *Protophyllocladoxylon francisiae* (1–8) and *Phyllocladoxylon antarcticum* (9–16). 1. Growth rings (TS). Bar: 200 μm . BA Pb 14416 holotype. 2. SEM image of alternate and scattered pitting on tracheid radial walls. Bar: 50 μm . BA Pb 14416 holotype. 3. SEM image of alternate pitting on tracheid radial walls and one or two pits per cross-field. Bar: 50 μm . BA Pb 14416 holotype. 4. SEM image of cross-field pits. Bar: 50 μm . BA Pb 14416 holotype. 5. Cross-field pits (LRS). Bar: 100 μm . BA Pb 14418 paratype. 6. Alternate radial pitting. Bar: 20 μm . BA Pb 14438. 7. SEM image of rays and tangential pits. Bar: 100 μm . BA Pb 14416 holotype. 8. Ray height (LTS). Bar: 200 μm . BA Pb 14416 holotype. 9. Growth rings (TS). Bar: 500 μm . BA Pb 14435. 10. Growth ring boundary (TS). Bar: 200 μm . BA Pb 14446. 11. SEM image of cross-field pits and radial pitting. Bar: 50 μm . BA Pb 14462. 12. SEM image of tangential pits and rays. Bar: 20 μm . BA Pb 14462. 13. SEM image of cross-field pits and radial pitting. Bar: 100 μm . BA Pb 14440. 14. Cross-field pits (LRS). Bar: 50 μm . BA Pb 14473. 15. Cross-field pits (LRS). Bar: 50 μm . BA Pb 14503. 16. Rays (LTS). Bar: 100 μm . BA Pb 14408.

Protophyllocladoxylon, which according to Zhang et al. (2010) includes 28 species, occurs from the Carboniferous to the Cretaceous. The described fossils are the youngest record of this fossil-genus.

4.2. Similarities to extant woods

Cross-field pits suggest a relationship to the Podocarpaceae (see also below the discussion about *Phyllocladoxylon* similarities to extant

woods). Although alternate (araucarian) pitting is usually associated to the Araucariaceae, some Podocarpaceae have mixed radial pitting. This type of radial pitting is present in the Podocarpaceae of the following genera: *Lepidothamnus* Philippi, *Manoao* Molloy, *Dacrydium* Lambert, *Podocarpus* Persoon, *Dacrycarpus* (Endlicher) de Laubenfels, *Pruennopitys* Philippi and *Phyllocladus* Mirbel (Patel, 1967a, 1967b, 1968a; Meylan and Butterfield, 1978). However, most *Dacrydium*, *Dacrycarpus*, *Lepidothamnus* and *Podocarpus* cross-field pits are smaller

and more numerous than in *Phyllocladoxylon francisiae*. *Phyllocladus*, *Prumnopitys* and *Manaoa* are grouped in the Prumnopytidioid clade, to which *P. francisiae* could be related.

Family Podocarpaceae

Phyllocladoxylon Gothan

Type species: *Phyllocladoxylon muelleri* (Schenk) Gothan

Phyllocladoxylon antarcticum Gothan (Plate I, 9–16)

Synonymy:

Mesembrioxylon antarcticum Seward, 1919, Fossil Plants IV, 210

Podocarpoxyylon sp. “A” Brea, 1998, Anál. leños fósiles coníf. Fm. La Meseta, Isla Seymour, p. 167–168, fig. 4

Syntypes: S004054, S004055, S004056, S004058, S004059, S004062, S004076, S004102 and S004115 (nos. 5, 9, 19–22 and 38 of Gothan, 1908), Swedish Museum of Natural History, Stockholm, Sweden.

New specimens: BA Pb 14404, 14406, 14408, 14417, 14423, 14425, 14427, 14428, 14433, 14435, 14437, 14440, 14441, 14446, 14450, 14454, 14457, 14459, 14462, 14464, 14465, 14466, 14468, 14471, 14472, 14473, 14475, 14476, 14478, 14479, 14485, 14487, 14488, 14491, 14492, 14494, 14500, 14501, 14502, 14503, 14505, 14509, 14515, 14516 and 14519.

New localities: Localities 1, 2, 3, 4, 5, 6 and 7 (see Figs. 1, 2), Seymour (Marambio) Island, Western Antarctica.

New stratigraphic horizon: Valle de las Focas, Acantilados, Campamento and Cucullaeae I allomembers, La Meseta Formation, early Eocene.

Description: Growth ring boundaries distinct (Plate I, 9–10). Latewood consists of 2–9 tracheids with reduced radial diameter (Plate I, 9–10). Transition from early- to latewood gradual to abrupt (Plate I, 9–10). Tracheid radial pitting uniseriate, rarely biseriate (Plate I, 11, 13). Radial pits circular, 15.4 (11.2–22.2) μm in vertical diameter and mostly scattered (Plate I, 11). Tracheid tangential diameter 30.9 (17.5–50) μm . Rare bordered pits with ca. 11 μm in vertical diameter on tangential walls (Plate I, 12). Axial parenchyma absent. Cross-field pitting “window-like” (fenestriform) with one, rarely two, large rounded to pointed simple pits (oopores) per cross-field (Plate I, 11, 13–15). When two pits are present, normally in the latewood, contiguous and arranged in one row or very rarely in one column. Cross-field pits horizontally elongated and 13.8 (8.4–21.0) μm in vertical diameter (Plate I, 14). Horizontal and end walls of ray parenchyma cells smooth (Plate I, 13–15). Rays very low to medium, 5.2 (1–16, rarely more) cells high, exclusively uniseriate (Plate I, 12, 16) and with a frequency of 4.0 (1–8) rays per mm. Parenchymatic ray cells 17.8 (12.9–27.5) μm in vertical diameter.

4.3. Comparisons with fossil woods

Phyllocladoxylon was created by Gothan (1905) to include *Phyllocladus muelleri* Schenk. Later Seward (1919) created *Mesembrioxylon* Seward to group *Phyllocladoxylon* and *Podocarpoxyylon* Gothan, but is considered illegitimate (Philippe and Bamford, 2008). According to Philippe and Bamford (2008), *Phyllocladoxylon* is a fossil-genus characterized by large simple cross-field pits (“window-like”) subpointed to pointed, and abietinean pitting on the tracheid radial walls. *Podocarpoxyylon* differs from *Phyllocladoxylon* in its cross-field pit type; oculipores in *Podocarpoxyylon* and oopores in *Phyllocladoxylon* (Philippe and Bamford, 2008). Gothan (1908) suggested when he described *Phyllocladoxylon antarcticum*, that this fossil-species is easily distinguishable by its cross-field pits.

Phyllocladoxylon antarcticum specimens described by Gothan (1908) were collected from the same island where the fossils presented here come, but presumably from older sediments where Cross Valley and Sobral formations outcrop (Zinsmeister, 1988). A variation in the cross-field type, that was observed in *P. antarcticum* by Torres and Lemoigne (1988), from pointed oculipores (in the latewood) to “window-like” (fenestriform) oopores (“phyllocladoid”) was also

observed in the specimens described herein, but the pits in the new material are always simple or finely bordered. Kräusel (1949) considered *P. antarcticum* as a synonym of *Cupressinoxylon latiporosum* Conwentz from northern Patagonia and transferred the latter to *Phyllocladoxylon*, creating the new combination *Phyllocladoxylon latiporosum* (Conwentz) Kräusel. However, according to Conwentz (1885), *C. latiporosum* has axial parenchyma and sometimes biseriate rays. Therefore, we consider *P. antarcticum* to be a separate fossil-species, different from that described by Conwentz (1885). *Phyllocladoxylon antarcticum* was also mentioned by Kräusel (1924) and Nishida et al. (1992) from Patagonia, and Torres and Lemoigne (1988) described it from King George (25 de Mayo) Island, Antarctica. Brea (1998) described two specimens with large simple cross-field pits (oopores) from the La Meseta Formation and assigned them to *Podocarpoxyylon* sp. “A”, which according to the illustrations of the cross-field pits (Brea, 1998, Fig. 4C), are similar to those of *P. antarcticum*.

Of the *Phyllocladoxylon* species lacking axial parenchyma, Kräusel (1949) separated *Phyllocladoxylon eboracense* (originally described by Holden, 1913 as *Paraphyllocladoxylon eboracense*) with tangential pits from the other fossil-species lacking tangential wall pits. Tangential wall pits are smaller and less numerous than those on the radial walls. This character is difficult to observe light-microscopically in specimens with this type of preservation. On the studied specimens, it was only observed by SEM, so we consider that this diagnostic character could be easily overlooked. We suggest that *P. eboracense* is probably a synonym of *Phyllocladoxylon antarcticum* according to the description of Holden (1913): scattered pits on radial walls, large pits on the cross-fields and presence of tangential wall pits. Kräusel (1949) considered *P. eboracense* a different fossil-species because Gothan (1908) did not describe tangential pits and also because he synonymised *P. antarcticum* with *Cupressinoxylon latiporosum* that has axial parenchyma, criteria we do not agree with, as it was stated before. However, the type specimens should be re-examined. *Phyllocladoxylon muelleri* was briefly described and has always oblique cross-field pits. *Phyllocladoxylon fusiforme* (Sahni) Kräusel and *Phyllocladoxylon fluviale* (Sahni) Kräusel have always oblique pointed smaller pits in the cross-fields and according to the authors the preservation of the samples is not good enough to make detailed description of them (Sahni, 1920). *Phyllocladoxylon xinqiuensis* Cui et Liu was described from the Lower Cretaceous of China (Cui and Liu, 1992). According to the diagnosis the only difference with *P. antarcticum* is the ray height (1–5, frequently 2, cells high). However, *P. xinqiuensis* also has growth ring boundaries not well marked and cross-field pits seem to be smaller (Cui and Liu, 1992). Finally, *Phyllocladoxylon annulatus* Patton has only bordered pits (oculipores) on the cross-fields (Patton, 1958) so according to Philippe and Bamford (2008) it does not fit in *Phyllocladoxylon* and should be transferred to another fossil-genus, probably to *Podocarpoxyylon*.

4.4. Similarities to extant woods

Phyllocladoxylon is characterized by having one, rarely two, large subpointed to pointed pits (oopore) per cross-fields, or “phyllocladoid” pits sensu Kräusel (1917) and abietinean radial pitting. This character is only found, among the extant Podocarpaceae, in most of the species of the Prumnopytidioid clade sensu Knopf et al. (2012) plus *Microstrobos* Garden and Johnson and *Microcachrys tetragona* Hooker (Greguss, 1955; Patel, 1967a, 1967b, 1968a; Meylan and Butterfield, 1978). Although this cross-field pit type is shared by most of the species of the mentioned group (*Lagarostrobos* Quinn, *Manaoa*, *Halocarpus* Quinn and *Phyllocladus*, *Prumnopitys*), *Lepidothamnus* and some *Prumnopitys* seems to have simple but smaller pits in its cross-fields (Meylan and Butterfield, 1978). Cross-field pits and the scattered pits on the tracheid radial walls (abietinean) allow us to consider *Phyllocladoxylon antarcticum* related to the taxa previously mentioned. Apparently, this type of cross-field pits evolved early in the family if we consider recent phylogenetic classification (Knopf et al., 2012).

Lagarostrobus, *Microstrobus* and *Microcachrys* have axial parenchyma (Greguss, 1955; Tegnér, 1966) while *Manoao*, *Halocarpus* and *Phyllocladus* lack axial parenchyma (Greguss, 1955; Patel, 1967a, 1968a). The wood of *Phyllocladus* spp. resembles *Phyllocladoxylon antarcticum* in having distinct growth ring boundaries, large cross-field pits, the presence of tangential pits and lack of axial parenchyma (Patel, 1968a). *Prumnopitys taxifolia* (Solander ex D. Don) de Laubenfels

is very similar to *P. antarcticum*, it has the same cross field type, and lacks axial parenchyma, but growth rings are indistinct (Patel, 1967b), while they are distinct in *P. antarcticum*.

Phyllocladoxylon pooleae nov. sp. (Plate II, 1–8)

Holotype: BA Pb 14400 (Plate II, 1, 3, 5, 8).

Paratypes: BA Pb 14403 (Plate II, 7) and 14481 (Plate II, 2, 4, 6).

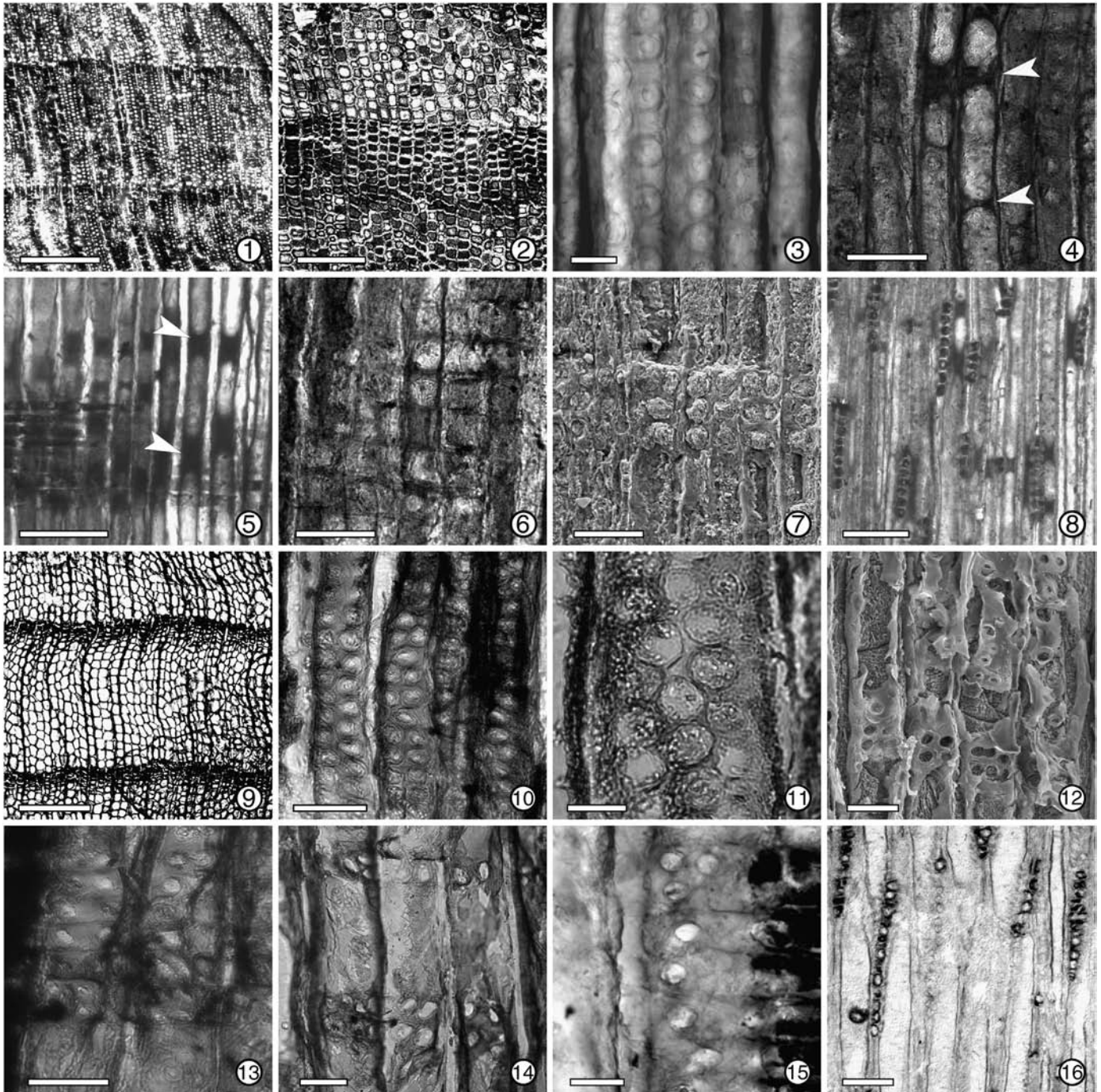


Plate II. Wood anatomy of *Phyllocladoxylon pooleae* (1–8) and *Podocarpoxylon aparenchymatosum* (9–10). 1. Growth rings (TS). Bar: 500 μ m. BA Pb 14400 holotype. 2. Growth ring boundary (TS). Bar: 200 μ m. BA Pb 1481 paratype. 3. Scattered uniseriate radial pitting (LRS). Bar: 20 μ m. BA Pb 14400 holotype. 4. Resin plugs (arrows) (LRS). Bar: 50 μ m. BA Pb 14481 paratype. 5. Resin plugs (arrows) and ray (LRS). Bar: 100 μ m. BA Pb 14400 holotype. 6. Cross-field pits (LRS). Bar: 50 μ m. BA Pb 14481 paratype. 7. SEM image of cross-field pits. Bar: 50 μ m. BA Pb 14403 paratype. 8. Rays (LTS). Bar: 100 μ m. BA Pb 14400 holotype. 9. Growth ring (TS). Bar: 500 μ m. BA Pb 14495. 10. Opposite to alternate pitting (LRS). Bar: 50 μ m. BA Pb 14486. 11. Opposite to alternate pitting (LRS). Bar: 20 μ m. BA Pb 14496. 12. SEM image of Two pits per cross-field. Bar: 50 μ m. BA Pb 14489. 13. Cross-field pits. Bar: 50 μ m. BA Pb 14486. 14. Two pits per cross-field (LRS). Bar: 50 μ m. BA Pb 14489. 15. Cross-field pits (LRS). Bar: 50 μ m. BA Pb 14484. 16. Rays (LTS). Bar: 200 μ m. BA Pb 14484.

Type locality: Locality 5 (see Figs. 1, 2), Seymour (Marambio) Island, Western Antarctica.

Other locality: Locality 6 (see Figs. 1, 2), Seymour (Marambio) Island, Western Antarctica.

Stratigraphic horizon: Campamento and Cucullaeae I allomembers, La Meseta Formation, early Eocene.

Etymology: after Dr. Imogen Poole for her research on Antarctic fossil wood anatomy.

Diagnosis: Growth ring boundaries distinct. Tracheid radial pitting abietinean and predominantly uniseriate. Cross-fields with one, rarely two, large simple pits (oopores) horizontally elongated. Rays uniseriate low to medium height. Resin plugs common. Axial parenchyma absent.

Description: Growth ring boundaries distinct (Plate II, 1–2). Latewood consists of 2–8 tracheids with reduced radial diameter (Plate II, 1–2). Transition from early- to latewood gradual to abrupt (Plate II, 1–2). Tracheid radial pitting uniseriate and scattered (Plate II, 3–4), sometimes contiguous and very rarely biseriate and opposite to subopposite. Radial pits circular, 14.3 (11.1–17.5) μm in vertical diameter and mostly scattered (Plate I, 11). Tracheid tangential diameter 34.9 (27.5–42.5) μm . Rare bordered pits with ca. 9 μm in vertical diameter on tangential walls. Axial parenchyma is absent. Dark resin plugs are common and with variable height, always associated to the rays (Plate II, 4–5, 8). Cross-field pitting “window-like” (fenestriform) with one, rarely two, large rounded to pointed simple pits (oopores), sometimes finely bordered, per cross-field (Plate II, 6–7). When two pits are present, usually in the latewood, contiguous and arranged in one row. Cross-field pits horizontally elongated and 13.9 (8.6–15.5) μm in vertical diameter (Plate II, 6–7). Horizontal end walls of ray parenchyma cells smooth (Plate II, 6). Rays very low to medium, 4.9 (1–11) cells high, exclusively uniseriate (Plate II, 8) and with a frequency of 3.1 (2–5) rays per mm. Parenchymatic ray cells 16.3 (12.5–18.7) μm in vertical diameter.

4.5. Comparisons with fossil woods

This new fossil-species is very similar to *Phyllocladoxylon antarcticum* except for the presence of resin plugs. Very rare biseriate subopposite to alternate pitting was observed in the three specimens assigned to *Phyllocladoxylon pooleae*, but not sufficient enough to assign them to *Protophyllocladoxylon* that has araucarian or mixed radial pitting. The presence of resin plugs was already used to separate among wood fossil-species. Since *Dadoxylon pseudoparenchymatosum* Gothan was separated by Gothan (1908) from previously known Araucariaceae fossil woods, many authors consider this character useful for separating fossil-species (i.e. Nishida et al., 1990; Gnaedinger, 2007). This character was already present in Podocarpaceae woods since the Jurassic (Gnaedinger, 2007).

4.6. Similarities to extant woods

This fossil-species can be related to the same group as *Phyllocladoxylon antarcticum* (see above). As far as we know no resin plugs similar to those described herein were previously reported for Podocarpaceae wood. Trabeculae that resemble resin plugs have been described for the Podocarpaceae *Retrophyllum* Page and *Podocarpus* (Grosser, 1986; Vásquez Correa et al., 2010).

Family Podocarpaceae

Podocarpoxydon Gothan

Type species: *Podocarpoxydon juniperoides* Gothan

Podocarpoxydon aparenchymatosum Gothan (Plate II, 9–16)

Holotype: S004109 (no. 17 of Gothan, 1908), Swedish Museum of Natural History, Stockholm, Sweden.

New specimens: BA Pb 14484, 14486, 14489, 14495 and 14496.

New locality: Locality 4 (see Figs. 1, 2), Seymour (Marambio) Island, Western Antarctica.

New stratigraphic horizon: Campamento allomember, La Meseta Formation.

Description: Growth ring boundaries distinct (Plate II, 9). Latewood consists of 1–7 tracheids with reduced radial diameter (Plate II, 9). Transition from early- to latewood gradual to abrupt (Plate II, 9). Tracheid radial pitting uni to triseriate, scattered or contiguous, opposite to subopposite (abietinean) and rarely alternate (Plate II, 10–12). Radial pits circular, 15.3 (11.1–19.1) μm in vertical diameter. Tracheid tangential diameter 45.3 (32.5–62.5) μm , pits on tangential walls not observed. Axial parenchyma absent. Cross-field pitting taxodioid, with usually two, sometimes one or rarely three, four or up to five pits per cross-field, (Plate II, 12–15). Cross-field pits usually not contiguous and ordered in one row (Plate II, 12–15); circular to vertically elongated and 10.7 (6.5–19.0) μm in vertical diameter, with reduced borders (oculipores) and diagonal aperture, mostly near vertical but sometimes near horizontal (Plate II, 12–15). Horizontal and end walls of ray parenchyma cells smooth (Plate II, 12–15). Rays medium, 9.2 (1–17) cells high, exclusively uniseriate (Plate II, 16) and with a frequency of 4.9 (2–8) rays per mm. Parenchymatic ray cells 19.3 (13.7–27.5) μm in vertical diameter.

Note. Preservation of some specimens assigned to this fossil-species is poor, in BA Pb 14484 and 14496 some characters could not be observed (Appendix A), but were assigned based on the PCA (see below).

4.7. Comparisons with fossil woods

Podocarpoxydon is characterized by wood lacking resin canals and spiral thickenings, with abietinean radial pitting and usually not more than four oculipores per cross-fields (Philippe and Bamford, 2008). In the original description of *Podocarpoxydon aparenchymatosum*, Gothan (1908) did not describe the radial pitting arrangement in detail. The fossils described herein, that are very similar to the material described by Gothan (1908, plate 1, Figs. 9–11), have many of the radial pits contiguous, opposite to rarely alternate but never hexagonal in shape. If we consider a mixed radial pitting for this samples, they should be placed in another genus according to the key of Philippe and Bamford (2008). However, until the holotype is re-examined we choose to keep the samples in *Podocarpoxydon*.

Kräusel (1924) separated *Podocarpoxydon dusenii* Kräusel from *Podocarpoxydon aparenchymatosum* because the former has usually resin bodies in the ray cells. In addition, rays are taller and sometimes biseriate, it has frequently one or sometimes two (in spring wood) cross-field pits and has scarce axial parenchyma (Kräusel, 1924). *Podocarpoxydon paleosalignum* Nishida from Mocha Island, Chile differs from *P. aparenchymatosum* in having axial parenchyma (Nishida, 1984a). *Podocarpoxydon paleoandinum* Nishida, also from Mocha Island has usually one large, apparently simple, pit per cross-field (Nishida, 1984a), suggesting that is probable a *Phyllocladoxylon* with axial parenchyma. *Podocarpoxydon fildense* Zhang et Wang is very similar, but the authors separate it from *P. aparenchymatosum* because it has sometimes more than two pits in the cross-fields pits and radial pitting is apparently not always uniseriate (Zhang and Wang, 1994), but its similarities to *P. aparenchymatosum* suggest it probable synonymous.

Podocarpoxydon aparenchymatosum can be distinguished from the previously described Podocarpaceae (*Protophyllocladoxylon francisiae* and *Phyllocladoxylon* spp.) not only by its radial and cross-field pitting, but also by its higher rays and tangentially wider tracheids (Appendix A).

4.8. Similarities to extant woods

The type of cross-field present in *Podocarpoxydon aparenchymatosum* is frequent, but not exclusively, in the Podocarpaceae. Some southern hemisphere *Podocarpus* such as *Podocarpus hallii* Kirk from New Zealand or *Podocarpus hallii nubigenus* Lindley from Patagonia have taxodioid

(pit aperture wider than the borders) cross-field pitting similar to *P. aparenchymatosum*, but they have abundant axial parenchyma (Patel, 1967b; Rancusi et al., 1987). However, according to Greguss (1955) only *Phyllocladus* (of the Podocarpaceae) lacks axial parenchyma, so a close affinity to any extant Podocarpaceae is not possible to determine.

Family Araucariaceae

Agathoxylon Hartig

Type species: *Agathoxylon cordaianum* Hartig

Agathoxylon pseudoparenchymatosum (Gothan) nov. comb. (Plate III, 1–5)

Basionym: *Dadoxylon pseudoparenchymatosum* Gothan, 1908, Die fossilen Hölzer von der Seymour und Snow Hill Insel, (10–11), (Plate I, 1–3, 12–16)

Synonymy:

Araucarioxylon novaezeelandii Stopes, 1914, Ann. Bot. 27, 348, pl. XX

Araucarioxylon kerguelense Seward, 1919, Fossil Plants IV, 185–186, fig. 714

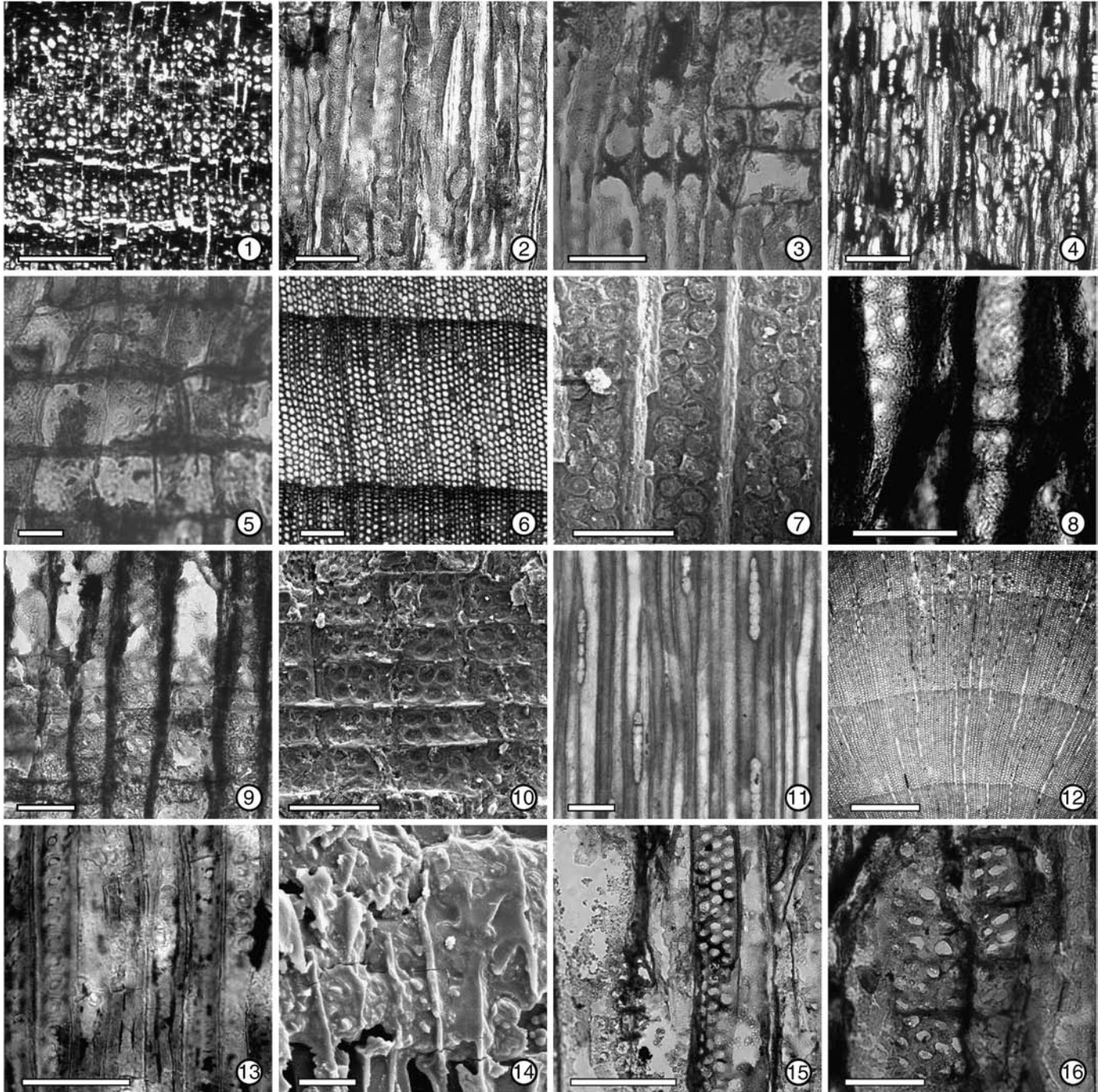


Plate III. Wood anatomy of *Agathoxylon pseudoparenchymatosum* (1–5), *Agathoxylon antarcticus* (6–11) and Araucariaceae branches (12–16). 1. Growth rings (TS). Bar: 500 μ m. BA Pb 14412. 2. Uniseriate radial pitting (LRS). Bar: 0 μ m. BA Pb 14412. 3. Resin plugs (LRS). Bar: 50 μ m. BA Pb 14412. 4. Rays (LTS). Bar: 200 μ m. BA Pb 14412. 5. Cross-field pits (LRS). Bar: 20 μ m. BA Pb 14412. 6. Growth ring (TS). Bar: 500 μ m. BA Pb 14445. 7. SEM image of alternate pitting on tracheid radial walls. Bar: 50 μ m. BA Pb 14436. 8. Radial pitting and cross-field pits (LRS). Bar: 50 μ m. BA Pb 14432. 9. Radial pitting and cross-field pits (LRS). Bar: 50 μ m. BA Pb 14436. 10. SEM image of cross-field pits. Bar: 50 μ m. BA Pb 14445. 11. Rays (LTS). Bar: 200 μ m. BA Pb 14445. 12. Growth rings (TS). Bar: 500 μ m. BA Pb 14506. 13. Contiguous uniseriate radial pitting (LRS). Bar: 50 μ m. BA Pb 14506. 14. SEM image of cross-field pits. Bar: 20 μ m. BA Pb 14506. 15. Radial pitting (LRS). Bar: 100 μ m. BA Pb 14497. 16. Cross-field pits (LRS). Bar: 50 μ m. BA Pb 14497.

Dadoxylon kerguelense Edwards, 1921, Ann. Bot. 35, 614–615, pl. XXIII
Dadoxylon kauparaense Edwards, 1926, Trans. Proc. New Zealand Inst. 56, 127, fig. 11–13

Araucarioxylon chilense Nishida, 1970, Ann. Rep. Foreign Stud. Coll. Chiba Univ. 5, 14–15, fig. 4, pl. II)

Araucarioxylon pseudoparenchymatosum Nishida, 1984, Anatomy Affinities Petrified Plants Tertiary Chile II, 89–90, pl. LXXXI

Syntypes: S004052, S004060, S004061, S004104, S004107 and S004112 (nos. 2, 3, 8, 10, 12 and 25 of Gothan, 1908), Swedish Museum of Natural History, Stockholm, Sweden.

New specimen: BA Pb 14412.

New locality: Locality 5 (see Figs. 1, 2), Seymour (Marambio) Island, Western Antarctica.

New stratigraphic horizon: Cucullaea I allomember, La Meseta Formation.

Description: Growth ring boundaries distinct (Plate III, 1). Latewood consists of four to six tracheids with reduced radial diameter (Plate III, 1). Transition from early- to latewood abrupt (Plate III, 1). Tracheid radial pitting uniseriate, rarely biseriate, and alternate (araucarian) (Plate III, 2). Radial pits hexagonal, 12.5 (11.1–14.3) μm in vertical diameter. Tracheid tangential diameter 35.8 (30.0–45.0) μm . Tangential pits and axial parenchyma not observed. Dark resin plugs with different height abundant and associated to the rays (Plate III, 3–4). Cross-field pitting araucarioid with 2–6 contiguous bordered pits (oculipores) per cross-field (Plate III, 5). Cross-field pits are circular and 6.5 (5.0–7.9) μm in vertical diameter (Plate III, 5). Horizontal end walls of ray parenchyma cells smooth (Plate II, 3, 5). Rays medium, 4.9 (2–10) cells high, exclusively uniseriate (Plate III, 4) and with a frequency of 3.7 (2–5) rays per mm. Parenchymatic ray cells 27.3 (25.0–32.5) μm in vertical diameter.

4.9. Comparisons to fossil woods

Agathoxylon is a validly published name and the use of which is legitimate (Philippe and Bamford, 2008). It is the prevailing view to use it for Araucariaceae-like fossil woods (Röbner et al., in press). *Agathoxylon* is characterized by alternate pitting (araucarian) on tracheid radial walls, absence of helical thickenings and araucarioid cross-field type (Philippe and Bamford, 2008). In recent years, this fossil-genus has been used by some authors for new South American fossil woods (Torres and Philippe, 2002; Zamuner and Falaschi, 2005; Pujana et al., 2007). In addition, *Dadoxylon* spp. and *Araucarioxylon* spp. with araucarioid cross-field pitting have been recently re-accommodated in *Agathoxylon* (i.e. Crisafulli and Herbst, 2010).

Agathoxylon pseudoparenchymatosum was described by Gothan (1908) and is characterized by having uni- or biseriate araucarian pitting, low rays, and several pits per cross-field and septa-like structure. Nishida (1984b) transferred it to *Araucarioxylon*. Edwards (1921) suggested that the structures described by Gothan (1908) could be thin resin plugs (instead of trabeculae). Moreover, the presence of resin tracheids in the material of Gothan (1908) also suggests that tracheids are filled with different amounts of resin, from thin resin plugs (septa-like structures) to thicker resin fillings in other part of the tracheids. In the fossil described herein, resin plugs were observed (Plate III, 3–4) and all the other features coincide with those of *A. pseudoparenchymatosum*.

Araucarioxylon novaezeelandii, *Araucarioxylon kerguelense* and *Dadoxylon kauparaense* all have resin plugs and were previously considered synonymous of *Agathoxylon pseudoparenchymatosum* (Kräusel, 1924; Florin, 1940). *Araucarioxylon chilense* was considered as a synonym of *Agathoxylon pseudoparenchymatosum* by Nishida (1984b). *Araucarioxylon chapmanae* Poole and Cantrill is very similar and has resin plugs but frequently bi- to triseriate radial pitting (Poole and Cantrill, 2001), while on *A. pseudoparenchymatosum* only uni- or biseriate pitting is observed.

Therefore we suggest using *Agathoxylon pseudoparenchymatosum* for fossil woods with the following characters: growth ring boundaries distinct, araucarian radial pitting, uni to biseriate, resin plugs and resiniferous tracheids, lack of axial parenchyma, cross-fields with usually 4–6 pits and rays uniseriate low to medium.

4.10. Similarities to extant woods

Araucariaceae woods are homogeneous and therefore it is difficult to assign the fossil-species to a particular living species or even to a subgenus. Extant Araucariaceae from South America, *Araucaria angustifolia* (Bertoloni) Kuntze and *Araucaria araucana* (Molina) K. Koch, rarely have resiniferous tracheids (Tortorelli, 1956) and other Araucariaceae from Australia show also resin plugs (Greguss, 1955; Bamber, 1979). Thomson (1914) mentioned that trabeculae (transverse walls) are present in the Araucariaceae but these look different to resin plugs and also that the amount of resin (that determines the resin plug height) varies significantly in different tracheids of the same wood.

Agathoxylon antarcticus (Poole et Cantrill) nov. comb. (Plate III, 6–14)
 Basionym: *Araucariopitys antarcticus* Poole et Cantrill, 2001, Palaeontology 44, 1086, pl. I, 2–10

Synonymy:

Agathoxylon matildense Zamuner and Falaschi, 2005, Ameghiniana 42, 340, fig. 2

Agathoxylon sp. Pujana et al., 2007, Rev. Mus. Argent. Cienc. Nat. 9, 163–164, fig. 3

Holotype: P. 1806.9 British Antarctic Survey, Cambridge, United Kingdom.

New specimens: BA Pb 14424, 14432, 14434, 14436 and 14445.

Emended diagnosis: Secondary wood with predominantly uniseriate pitting. Biseriate pitting, alternate, close-packed, pits circular to hexagonal and confined to the ends of tracheids. Cross-fields characterized by 1–9 pits, usually 2–6. Rays very low to medium, uniseriate.

New localities: Localities 5 and 7 (see Figs. 1, 2), Seymour (Marambio) Island, Western Antarctica.

New stratigraphic horizon: Cucullaea I allomember, La Meseta Formation.

Description: Growth ring boundaries distinct (Plate III, 6). Latewood consists of 2–4 tracheids with reduced radial diameter (Plate III, 6). Transition from early- to latewood gradual to abrupt (Plate III, 6). Tracheid pitting on radial walls uni- to biseriate (predominantly uniseriate) and alternate (araucarian) (Plate III, 7–9). Radial pits hexagonal, 12.6 (9.5–17.5) μm in vertical diameter. Tracheid tangential diameter 32.3 (22.5–45.0) μm . Tangential pits and axial parenchyma not observed. Cross-field pitting araucarioid with 1–8, usually 2–5, contiguous bordered pits (oculipores) per cross-field (Plate III, 8–10). Cross-field pits circular 8.5 (5.7–12.0) μm in vertical diameter (Plate III, 8–10). Horizontal end walls of ray parenchyma cells smooth (Plate III, 8–10). Parenchymatic ray cells 22.4 (15.9–27.5) μm in vertical diameter. Rays medium, 5.5 (2–10, rarely up to 19) cells high, exclusively uniseriate (Plate III, 11) and with a frequency of 3.3 (1–5) rays per mm.

4.11. Comparisons with fossil woods

Araucarian radial pitting, araucarioid cross-field pitting and uniseriate rays allow us to assign the samples to *Agathoxylon*. According to Philippe and Bamford (2008) *Araucariopitys* Hollick and Jeffrey has terminal wall of ray cell pitted to nodular and mixed type of radial pitting. Poole and Cantrill (2001) assigned their material to *Araucariopitys* based on the uniseriate pitting of the radial walls and araucarioid cross-field pitting. However, considering the original description and diagnosis of Poole and Cantrill (2001) and according to the criteria of Philippe and Bamford (2008) the fossil-species can be assigned to *Agathoxylon*, and a new combination is proposed. *Agathoxylon antarcticus* can be defined by having distinct growth ring boundaries, uni- to biseriate araucarian

radial pitting, usually 2–6 araucarioid cross-field pits, the lack of axial parenchyma and resin plugs and very low to medium uniseriate rays. Poole and Cantrill (2001) also mention that there is a tendency of pitting concentrated at the end of the tracheids. This tendency is found in extant Araucariaceae (Tortorelli, 1956) and we do not consider this character significant enough to justify the creation of a new fossil-genus. *Agathoxylon matildense* is very similar to *A. antarcticus*; it only has slightly lower rays (Zamuner and Falaschi, 2005), therefore we consider it a synonym. An emendation of the original diagnosis is proposed in order to exclude the mode and mean values, because a diagnosis refers to a taxon and not to a sample, Art. 38.2 ICBN (McNeill et al., 2012) and also to include cross-field pits with one pit per cross-field. In addition, the terminology of the ray height was changed according to the IAWA code (Richter et al., 2004) for softwoods (“rays short” to “rays very low to medium”).

4.12. Similarities to extant wood

The anatomy of *Agathoxylon antarcticus* is similar to that of *Araucaria araucana* from Patagonia (Greguss, 1955; Tortorelli, 1956; Rancusi et al., 1987). However, it is also similar to other Araucariaceae (Greguss, 1955), because, as was mentioned before, the wood is homogeneous in this family. Most of the variability of the wood anatomy in the family is in the growth ring type, quantitative features of cross-fields and radial pitting (uni- to tri- or multiseriate) and the presence of axial parenchyma and resin plugs.

Family Araucariaceae

Branches (two samples BA Pb 14497 and 14506)

Comments: These two samples seem to be fragments of small branches according to their narrow diameter (<2 cm). Apparently they can be referred to different fossil-species. BA Pb 14506 has uniseriate contiguous (hexagonal) pitting, and 3–5 pits per cross-field and distinct growth ring boundaries. These characters resemble *Agathoxylon antarcticus* (see above). On the other hand, BA Pb 14497 has up to pentaeriate pits, up to six pits per cross field and indistinct growth ring boundaries. This specimen can be related to *Dadoxylon kellerense*, that has usually triseriate radial pitting and many pits (oculipores) per cross-field (Lucas and Lacey, 1981).

Family Cupressaceae or Podocarpaceae

Cupressinoxylon Göppert nom. cons.

Type species: *Cupressinoxylon subaequale* Göppert

Cupressinoxylon hallei Kräusel, 1924 (Plate IV, 1–9)

Synonymy:

Cupressinoxylon sp. (cf. *gothani*) Kräusel, 1924, Arkiv f. Bot. 19, 16, pl. II, 8–10

Cupressinoxylon parenchymatosum Torres et al., 1985, Mem. III Congr. Latinoamericano Paleont. 568, pl. I, 1–6

Cupressinoxylon magellanicum Nishida and Nishida, 1988, Preliminary stud. petrified plants Cretotertiary Chile p. 26, pl. XIV

Cupressinoxylon seymourense Torres et al., 1994, Ser. Científica INACH 44, 30, pl. IV

Cupressinoxylon sp. Poole et al., 2001, Ann. Bot. 88, 36, fig. 2–4, 6.

Holotype: no. 20 of Kräusel (1924), Swedish Museum of Natural History, Stockholm, Sweden.

New specimens: BA Pb 14419, 14429, 14439, 14444, 14463, 14467, 14474, 14477, 14480, 14482, 14483, 14493, 14507 and 14513.

New localities: Localities 4, 5, 6 and 7 (see Figs. 1, 2), Seymour (Marambio) Island, Western Antarctica.

New stratigraphic horizon: Campamento and Cucullaea I allomembers, La Meseta Formation.

Description: Growth rings boundaries distinct (Plate IV, 1–3). Latewood consists of 3–12 tracheids with reduced radial diameter (Plate IV, 1–3).

Transition from early- to latewood gradual to abrupt (Plate I, 1–3). Tracheid pitting in radial wall uniseriate rarely biseriate and opposite, scattered, and rarely contiguous (abietinean) (Plate IV, 4–5). Radial pits circular, 14.3 (9.5–19.1) μm in vertical diameter. Tracheid tangential diameter 32.1 (17.5–60.0) μm . Bordered pits with ca. 13 μm in vertical diameter on tangential walls, very scattered. Striations in tracheid walls present. Axial parenchyma scarce to abundant, and more frequent in the latewood. Cross-field pitting cupressoid with usually one or two, rarely up to seven bordered pits with included oblique aperture (oculipores) per cross-field (Plate IV, 8–10). Cross-field pits circular and 6.7 (4.5–9) μm in vertical diameter (Plate IV, 8–10) and usually ordered in rows and/or columns. Horizontal end walls of ray parenchyma cells smooth (Plate IV, 7–10). Rays very low to medium, 3.5 (1–19) cells high, exclusively uniseriate (Plate IV, 11–12) and with a frequency of 3.4 (0–7) rays per mm. Parenchymatic ray cells 21.1 (13.7–27.5) μm in vertical diameter.

4.13. Comparisons with fossil woods

Although some variation was observed in the mean ray height among specimens, we did not separate them as different taxonomic units because the ray height is a variable character frequently depending on the age of the rings or the organ (Richter et al., 2004; Falcon-Lang, 2005), and the variation is not very significant (i.e. mean ray height from 4.0 to 7.8 cells).

In their revision of Cupressaceae fossil woods, Vaudois and Privé (1971) assigned the following features to *Cupressinoxylon*: cross-field pits with oblique pore, ray cell walls smooth and abundant axial parenchyma. They also comment that *Cupressinoxylon* has a wide definition that can include almost all Cupressaceae fossil woods. Philippe and Bamford (2008) redefine the fossil-genus for woods with abietinean radial pitting and oculipores usually ordered in rows and columns. These cross-field pits are usually not contiguous and small. The here studied fossils share all characters with the latter definition.

Cupressinoxylon hallei Kräusel was created by Kräusel (1949) based on the description of one sample from Patagonia that he described previously (Kräusel, 1924) without assigning it to a specific level (*Cupressinoxylon* sp. cf. *gothani*). The fossil-species was considered by Vaudois and Privé (1971) in their revision of the Cupressaceae fossil woods. It is characterized by having distinct growth ring boundaries, very low to medium rays, presence of axial parenchyma, smooth vertical and horizontal ray cell walls and frequently two, but sometimes one or more than two cupressoid pits arranged in rows and columns in the cross-fields. All of these characters are found in the samples from the La Meseta Formation and therefore assigned to *C. hallei*.

Cupressinoxylon jurassica Lutz from North America and *Cupressinoxylon mochaense* Nishida from Chile differ from *Cupressinoxylon hallei* in usually having biseriate portions in the rays (Lutz, 1930; Nishida, 1984a). *Cupressinoxylon hookeri* Arber from Australia has usually one pit per cross-field (Arber, 1904). Seward (1919) transferred the latter fossil-species to *Mesembrioxylon*, an invalid fossil-genus; it should probably be placed in *Podocarpoxyton*. According to their original descriptions, *Cupressinoxylon parenchymatosum* and *Cupressinoxylon seymourense* show no significant differences with *C. hallei*, hence we consider them as synonyms (Torres et al., 1985, 1994a; Brea, 1998). *Cupressinoxylon chilensis* Torres, from the Tertiary of Chile (Torres, 1981), was considered not validly published by Nishida et al. (1988). *Cupressinoxylon krauseli* Eckhold described by Eckhold (1922) was considered as an incompletely described and doubtful species by Kräusel (1949) and Vaudois and Privé (1971). *Cupressinoxylon magellanicum* was separated from *C. parenchymatosum* because of the different amounts of axial parenchyma (Nishida and Nishida, 1988). The amount of axial parenchyma (not the presence or absence of it) is a variable character on the same wood that we consider not different enough in these two latter fossil-species for treating them as separate species; we consider both names to be synonyms of *C. hallei*.

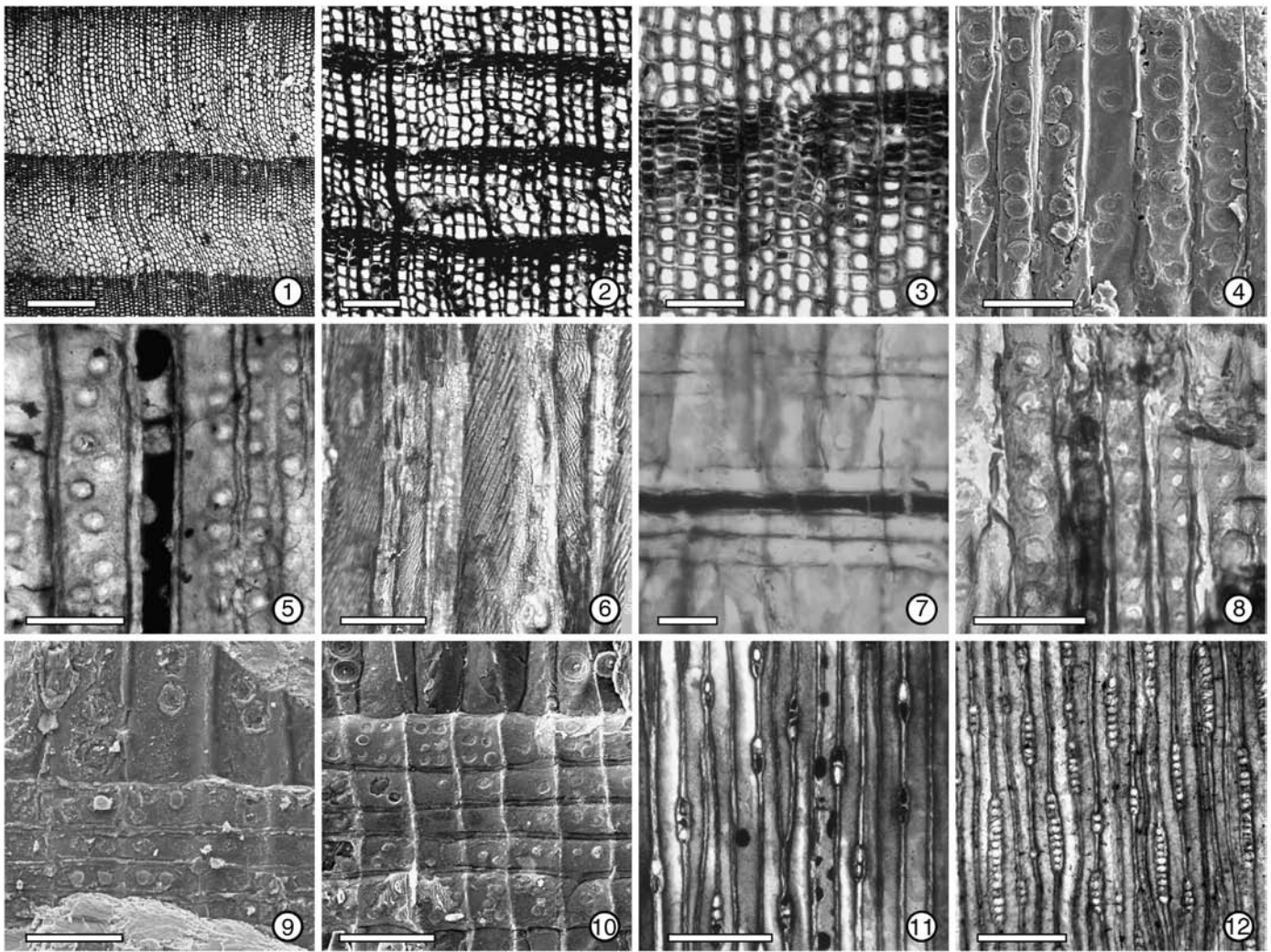


Plate IV. Wood anatomy of *Cupressinoxylon hallei*. 1. Growth rings (TS). Bar: 500 μm . 14480. 2. Growth rings (TS). Bar: 200 μm . 14474. 3. Growth ring boundary. Bar: 200 μm . BA Pb 14513. 4. SEM image of scattered uniseriate radial pitting. Bar: 50 μm . BA Pb 14429. 5. Axial parenchyma (LRS). Bar: 50 μm . BA Pb 14513. 6. Striations on tracheid walls. Bar: 50 μm . BA Pb 14477. 7. Parenchymatic ray cells with dark contents (LRS). Bar: 50 μm . BA Pb 14483. 8. Radial pitting and cross-field pits (LRS). Bar: 50 μm . BA Pb 14463. 9. SEM image of radial pitting and cross-field pits. Bar: 50 μm . BA Pb 14480. 10. SEM image of cross-field pits. Bar: 50 μm . BA Pb 14439. 11. Rays (LTS). Bar: 200 μm . BA Pb 14439. 12. Rays (LTS). Bar: 200 μm . BA Pb 14513.

4.14. Similarities to extant woods

Cupressoid cross-field pitting (the cross-field type that defines *Cupressinoxylon*) is found not only in living members of the Cupressaceae, but also in living Podocarpaceae (Richter et al., 2004; Vásquez Correa et al., 2010). Therefore, *Cupressinoxylon* may not represent only the Cupressaceae. In addition, some Podocarpaceae with cupressoid cross-field pitting like *Dacrydium cupressinum* Solander ex Lambert, have also low rays and axial parenchyma (Patel, 1967a). Living Cupressaceae from southern Patagonia, Australia and New Zealand have homogeneous woods, which do not exhibit significant anatomical variation, and they resemble *Cupressinoxylon hallei*. *Cupressinoxylon hallei* may not represent a single species; many living Cupressaceae species may be indistinguishable in their wood anatomy.

The living Cupressaceae from Patagonia have distinct growth ring boundaries, similar cross-field pits (cupressoid with few pits), axial parenchyma and a very low to medium ray height (Philips, 1941; Boutelje, 1955; Greguss, 1955; Roig, 1992). These characters are shared with *Cupressinoxylon hallei*. *Fitzroya cupressoides* Johnston can be separated from the other two Cupressaceae from South America, *Austrocedrus chilensis* (D. Don) Pichi Sermolli et Bizzand and *Pilgerodendron uviferum* Florin, by their nodular parenchymatic walls (Philips, 1941; Boutelje, 1955; Roig, 1992). The most similar Cupressaceae from New Zealand

is *Libocedrus plumosa* Druce, because it has fewer pits per cross-field than the other species from there, *Libocedrus bidwillii* Hooker f. (Patel, 1968b). All the other characters are shared between *L. plumosa* and *C. hallei*. Australian Cupressaceae can be distinguished from *C. hallei*: *Callitris* Ventenat have indistinct to absent growth ring boundaries, resiniferous ray cells and callitroid thickenings, *Cupressus* L. have frequently biseriate rays and nodular thickenings on ray cells, *Diselma archeri* Hooker f. is a shrub that has normally “arrow shape” radial cells and *Actinostrobus* are shrubs that have callitroid thickenings and axial parenchyma tangentially zonate (Patton, 1927; Philips, 1941; Heady and Evans, 2005). The most similar taxa (*A. chilensis*, *P. uviferum* and *L. plumosa*) are members of the Callitroideae subfamily sensu Yang et al. (2012) to which *C. hallei* seems to be related.

5. PCA

PCA was previously used to group angiosperm fossil wood specimens (Oakley and Falcon-Lang, 2009; Oakley et al., 2009) and is here used to analyse a large dataset of conifer fossil woods.

Principal components (PC) 1, 2 and 3 explained 33.9%, 22.6% and 11.6% of variance respectively (PC 1 to 3 summed 68.1%) and cumulative PCs 1 to 8 explained 96.0%. The obtained results are in accordance with previous studies that have similar proportions (i.e. MacLachlan and

Gasson, 2010). Fig. 3 shows a plot of PC 1 with PC 2 (together they explain 56.5% of variance) and PC 1 with PC 3 (34.3% of variance). Cumulative eigenvector values of PC1 to 3 × proportion of variance are shown in Table 1. The high ranked characters are pitting arrangement,

diameter and type of cross-field pits, ray height and presence of axial parenchyma. Pitting arrangement and cross-field pitting are crucial to determine higher taxonomic range as the family and fossil-genera. Ray height contributes to separate *Podocarpoxyylon aparenchymatosum*

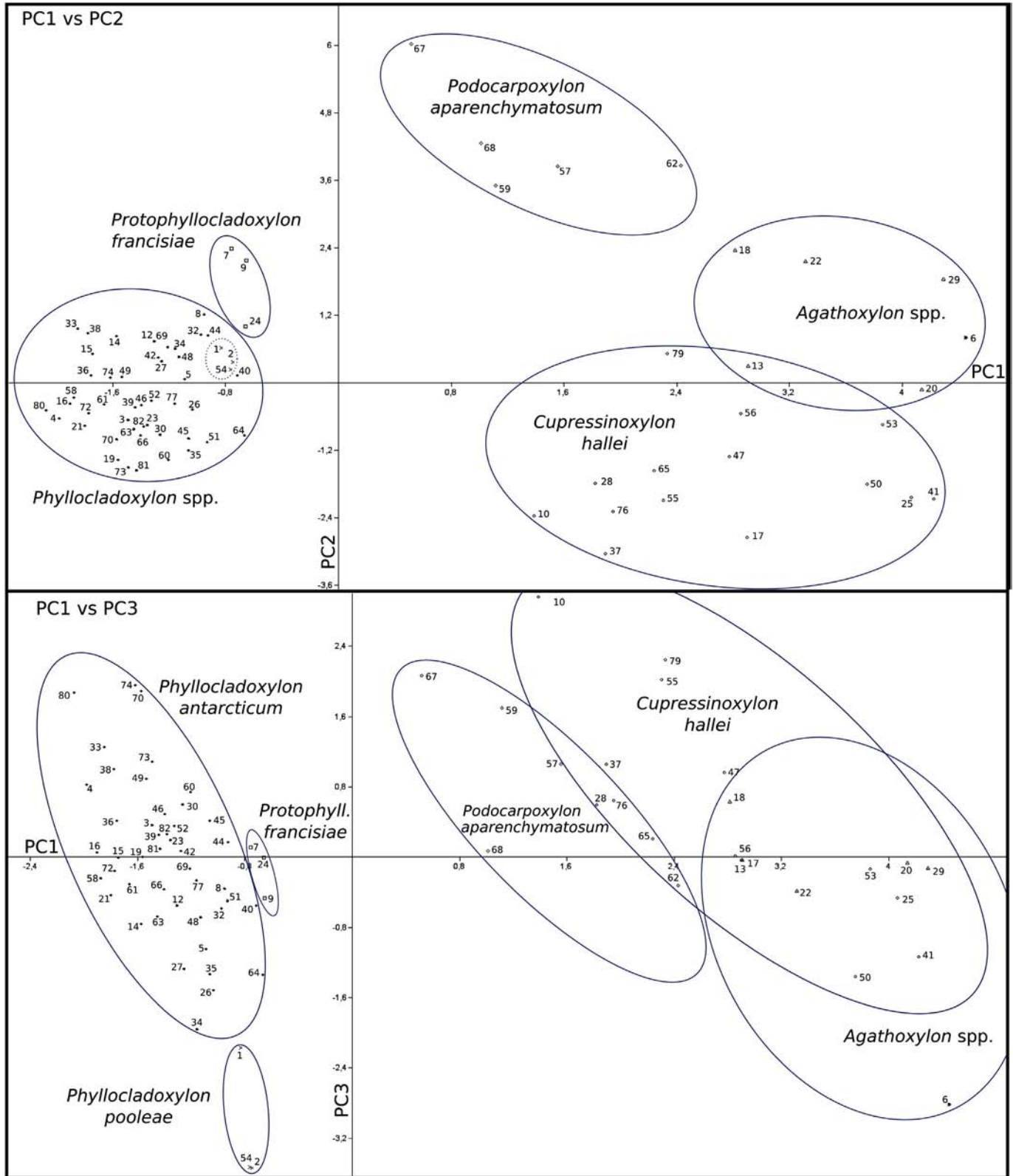


Fig. 3. PCA of 78 fossil woods. PC 1 versus PC2 and PC2 versus PC3. Ellipses are not statistically significant. Symbols: *Phyllocladoxyylon antarcticum*, dots; *Phyllocladoxyylon pooleae*, crosses; *Protophylladoxyylon francisiae*, squares; *Podocarpoxyylon aparenchymatosum*, diamonds; *Agathoxyylon antarcticus*, triangles; *Agathoxyylon pseudoparenchymatosum*, star; *Cupressinoxyylon hallei*, circles.

Table 1

Eigenvector values (PC1, 2 and 3 values), summed values \times proportion of variance and character ranking for each character.

Character	PC1	PC2	PC3	Sum PC1–3 \times % var.	Rank
Tracheid pitting	0.127	0.510	0.098	16.972	7
Pitting arrangement	0.240	0.435	0.130	19.493	1
Vertical diameter of radial pits	0.218	0.169	0.150	12.953	11
Axial parenchyma	0.317	0.262	0.130	18.192	5
Tangential diameter of tracheids	0.157	0.440	0.248	18.167	6
Number of pits per cross-field	0.452	0.044	0.027	16.629	8
Cross-field pits type	0.468	0.028	0.170	18.458	3
Vertical diameter cross-field pits	0.404	0.102	0.293	19.416	2
Ray height	0.118	0.478	0.304	18.367	4
Ray cell height	0.351	0.023	0.196	14.686	10
Rays per mm	0.167	0.125	0.642	15.967	9
Resin plugs	0.031	0.046	0.462	7.478	12

(that has higher rays) from the others, and the absence of axial parenchyma contributes to separate the Podocarpaceae from the other two genera. Several characters dominate the loadings of PC1, and as expected, type, diameter and number of cross-field pits are highly correlated (Table 1). PC2 is dominated by radial pitting type and arrangement, tracheid diameter and ray height (Table 1). The characters at the bottom of the rank that contribute less to explain the variability are: presence of resin plugs, ray cell height and diameter of radial pits. Rays per mm and presence of resin plugs dominate in PC3, but the variation of this component is limited (11.6%).

Fig. 3 shows discrete clusters for most of the fossil-genera in the PC1 versus PC2 plot. *Phyllocladoxylon pooleae* (dotted line) is included in *Phyllocladoxylon antarcticum*. However, in the PC2 versus PC3 plot *Phyllocladoxylon* spp. are separated in two discrete clusters. As mentioned above, the presence of resin plugs separates these two fossil-species. Only one sample drop in the conjunction of the ellipses of *Agathoxylon* spp. and *Cupressinoxylon hallei* in PC1 versus PC2 plot (BA Pb 14424). However, according to the alternate radial pitting this sample is clearly more related to *Agathoxylon*. Some overlapping is observed in PC2 versus PC3 plot, particularly in *Cupressinoxylon* and *Agathoxylon*, although radial pitting allows separating this two fossil-genera.

In conclusion, most of the taxa are clearly distinguished, particularly in PC1 versus PC2, allowing to form discrete clusters for most of them in the plots showed (Fig. 3). Therefore, the analysis is consistent with the proposed taxonomic treatment. Moreover, PCA also contributes to assure the taxonomic placement to specimens where some characters could not be observed because they were not sufficiently preserved (Appendix A).

6. Comments on systematics

Large dataset studies always provide more anatomical variability than studies based on a few samples. In this study, the collection of 82 conifer woods shows that intraspecific variability is significant and should be considered when defining fossil-species, as was previously noted for fossil angiosperm woods (Oakley et al., 2009). Fossil-species are frequently named based on a singly sample only and the narrow diagnosis with quantitative values prevents to assign further specimens to it. Therefore, they may be emended to include specimens with slight anatomical variations, as it was the case here with *Agathoxylon antarcticum*. The same occurs on descriptions of extant woods, where they are usually based in a fragment of mature woods at the height of the chest, and anatomical variability is not considered and is probed to be high, particularly among different organs (Falcon-Lang, 2005). Thus finding a close affinity to an extant species is problematic even for Cenozoic fossil woods.

On the samples assigned to *Cupressinoxylon hallei*, BA Pb 14513 has a mean ray height of 7.6 while the other samples do not reach a mean higher than 4. As stated before we did not consider this difference enough to separate them into two fossil-species, as all the other

characters are shared with the other samples (Appendix A). Even in extant species, for example for *Fitzroya cupressoides*, Rancusi et al. (1987) observed ray heights of one to seven cells while Greguss (1955) recorded the rays as one to 19 cells high, so intraspecific variation is not infrequent. When a gradual transition exists between the anatomy of the specimens they should be regarded as a single taxonomic unit, and consider this variability intraspecific. For this reason, numerous synonyms were proposed herein for some fossil-species, particularly *C. hallei*.

SEM observations are illustrated for the first time on fossil woods from the La Meseta Formation and demonstrate to be indispensable for the observation of several characters. Cross-field pits are easily recognized and thus the woods can be assigned to a particular fossil taxon. The presence of tangential pits is a character usually considered diagnostic (Vaudois and Privé, 1971), but it was usually only observed using SEM in this type of preservation (permineralized by carbonates). Tangential pits are easily observed under SEM (Plate I, 7), but in thin sections and acetate peels from the same specimen it is extremely difficult to observe these tangential pits light-microscopically (Plate I, 8). This character remains apparently usually unnoticed (see for example discussion of Patel, 1968b regarding *Libocedrus bidwillii*).

Finally, cross-field pit size (vertical diameter) resulted in a significant character for delimiting fossil-species and is also a high ranked character in the PCA (Table 1). *Protophyllocladoxylon francisiae* and *Phyllocladoxylon* spp. have ca. 14 μ m in vertical diameter, while *Podocarpoxydon aparenchymatosum* ca. 12 μ m and *Cupressinoxylon hallei* and *Agathoxylon* spp. ca. 7–8 μ m (Appendix A). In addition, as expected, cross-field type, size and number are highly correlated in the PCA (Table 1).

7. Forest composition

Evidence from fossil plants, sediments and isotopes indicates that the late Palaeocene and early Eocene experienced warm climates at high latitudes, at least on the margins of the Antarctic Peninsula (Francis et al., 2009). Climatic deterioration around Seymour (Marambio) Island seems to have begun during the middle Eocene (Dingle et al., 1998) and further cooling took place during the late Eocene (Ivany et al., 2008). Elsewhere in Antarctica the higher diversity and thermophilous plant assemblages of the early Eocene were replaced by vegetation dominated by the Nothofagaceae (Francis et al., 2009).

The studied fossil forests appear to be dominated by conifers, particularly *Phyllocladoxylon antarcticum* frequently with *Agathoxylon*, *Protophyllocladoxylon*, *Podocarpoxydon* and *Cupressinoxylon* (Appendix A). Conifer woods represent 68% of the total amount of woods from the formation. Most of them are Podocarpaceae, which includes 72% of the conifers (not counting *Cupressinoxylon* that may represent the Podocarpaceae). Conifer woods are more abundant than the angiosperm woods in most of the allomembers: in Cucullaea I 60% of conifers (on 67 samples), Campamento 86% (on 43 samples), Acantilados 38% (on 8 samples) and Valle de las Focas 100% (on 2 samples).

According to previous fossil wood studies of large datasets, Cantrill and Poole (2005b) indicate a conifer dominance (ca. 60%), particularly Podocarpaceae, on the wood flora of the Eocene of several localities of the Antarctic Peninsula. These results agree with the fossils studied herein although some differences are observed on the proportion of the fossil-genera. Dominance of Nothofagaceae was observed by Torres and Lemoigne (1988) for the Eocene/Oligocene boundary of Western Antarctica based on 100 samples, where they obtained 90% of Nothofagaceae. Poole et al. (2001) described 25 fossil wood samples from King George (25 de Mayo) Island finding 24% of conifers and 48% of Nothofagaceae. These differences in composition with more or less coeval fossil woods from Antarctica, like the ones studied herein, was explained by Poole et al. (2001) as a volcanic arc that separated the floras. Moreover, that assemblage is slightly younger ca. 49–42 Ma than the flora studied herein. For the Oligocene and Oligocene–lower

Miocene of Patagonia, similar proportions were observed by Pujana (2008) and Terada et al. (2006), with approximately 70% Nothofagaceae. According to these fossil woods studies, the Nothofagaceae-dominated forests were well established by the Oligocene in Antarctica as well as in Patagonia, while in the late Paleocene–early Eocene the conifers, particularly Podocarpaceae, still dominated the Antarctic assemblages. Unfortunately no fossil wood was found in the upper allomembers, Cucullaea II and Submeseta where the sediments extend up to the middle and late Eocene (Fig. 1). This interval and up to the Eocene/Oligocene boundary, when climatic deterioration seems to have started (Dingle et al., 1998; Francis et al., 2009), coincides with the rising dominance of the Nothofagaceae.

Although fossil leaf studies from the La Meseta Formation are not abundant, they show the presence of conifers (Podocarpaceae and Araucariaceae) and angiosperms dominated by Nothofagaceae leaves (Case, 1988; Doktor et al., 1996; Gandolfo et al., 1998a). Pollen analyses also have an abundance of Nothofagaceae and Podocarpaceae but indicate the presence of Araucariaceae and other angiosperms (Cranwell, 1959; Askin and Fleming, 1982; Zamaloa et al., 1987; Askin, 1991). Therefore, the taxa found on the fossil woods are consistent with previous palynological and fossil leaf studies.

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Appendix A

List of studied specimens. MED = minimum estimated diameter [cm]. 1. Tracheid radial pitting: uniseriate = 1 to biseriate = 2 and fractions. 2. Pitting arrangement (bordered pits on radial tracheid walls): contiguous = 0 to scattered = 1 and fractions. 3. Vertical diameter of bordered pits on tracheid radial walls [μm]. 4. Axial parenchyma: present = 1 or absent = 0. 5. Tangential diameter of tracheids [μm]. 6. Number of pits per cross-field in fractions. 7. Cross-field pits type: oculipores = 1 and oopores = 0. 8. Vertical diameter of cross-field pits [μm]. 9. Ray height [cells]. 10. Ray cell height [μm]. 11. Rays per mm. 12. Resin plugs: present = 1 or absent = 0. Unknown values denoted by “?”.

Appendix B. Supplementary data

Supplementary data associated with this article can be found in the online version, at <http://dx.doi.org/10.1016/j.revpalbo.2013.09.001>. These data include Google maps of the most important areas described in this article.

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