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Fossil woods from the Oligocene of southwestern Patagonia (Río Leona Formation). Rosaceae and Nothofagaceae

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Abstract. Systematic studies of angiosperm fossil woods from sediments of the Río Leona Formation were continued. A new morphospecies of *Maloidoxylon* with affinity to Rosaceae was described and constitutes, together with the fossil pollen from the same strata, the oldest South American fossil with this familial affinity. Nothofagaceae fossil woods are represented by the morphospecies *Nothofagoxylon scalariforme* Gothan, *Nothofagoxylon kraeuseli* Boureau et Salard, *Nothofagoxylon triseriatum* Torres et Lemoigne, *Nothofagoxylon ruei* Salard and a new morphospecies of *Nothofagoxylon*. Three of the four subgenera of *Nothofagus* were recognized in the fossil woods and a new infrageneric affinity for *Nothofagoxylon ruei* was proposed. The described woods have affinity to extant genera and species that inhabit Patagonia, except for the Rosaceae wood where the generic affinity is not well-established.

Resumen. Maderas fósiles del Oligoceno del sudoeste de la Patagonia (Formación Río Leona). Rosaceae y Nothofagaceae. Se continuaron los estudios sistemáticos de maderas fósiles de angiospermas de la Formación Río Leona. Se describió una nueva morfoespecie de *Maloidoxylon* afín a las Rosaceae que constituye, junto al polen fósil de los mismos estratos, el fósil más antiguo de Sudamérica con afinidad a esa familia. Las maderas afines a las Nothofagaceae están representadas por las morfoespecies *Nothofagoxylon scalariforme* Gothan, *Nothofagoxylon kraeuseli* Boureau et Salard, *Nothofagoxylon triseriatum* Torres et Lemoigne, *Nothofagoxylon ruei* Salard y una nueva morfoespecie de *Nothofagoxylon*. Se reconocen en las maderas fósiles tres de los cuatro subgéneros de *Nothofagus* y una nueva afinidad infragenérica es propuesta para *Nothofagoxylon ruei*. Las maderas descriptas poseen afinidad a especies y géneros actuales que habitan Patagonia, excepto por la madera de Rosaceae cuya afinidad genérica no está bien establecida.

Key words. Wood anatomy. Patagonia. Oligocene. Secondary xylem. Rosaceae. Nothofagaceae.

Palabras clave. Anatomía de maderas. Patagonia. Oligoceno. Xilema secundario. Rosaceae. Nothofagaceae.

Introduction

The Río Leona Formation outcrops in southwestern Patagonia and represents continental depositions during the Oligocene in southern Patagonia. Sediments of the formation contain abundant fossil woods with excellent preservation. The fossil wood assemblage is dominated by Nothofagaceae along with frequently encounters Proteaceae, Atherospermataceae, Myrtaceae, Anacardiaceae, Leguminosae, Rosaceae, Araucariaceae and Podocarpaceae (Pujana, 2007; 2008; in press). Although the fossil leaves are not abundant, Nothofagaceae also dominates these assemblages along with leaves belonging to the Myrtaceae and possibly Grossulariaceae (César*i et al*., 2006). Pollen from shrub and tree taxa identified from this formation have been assigned to the Nothofagaceae, Onagraceae, Rosaceae, Proteaceae, Leguminosae, Chlorantaceae, Compositae, Myrtaceae, Euphorbiaceae, Symplocaceae, Anacardiaceae, Araucariaceae and Podocarpacaeae (Barreda *et al*., 2009).

The palaeoenvironment of the Río Leona Formation was interpreted as a fluvial system by Marenssi *et al*. (2005). The age of this formation is constrained by the overlying Centinela Formation referred to the Late Oligocene to Early Miocene on the basis of Sr and Ar isotopes dating techniques (Parras *et al*., 2008) and the unconformably underlying Man Aike Formation referred to the Middle to Late Eocene of dating records obtained for marine invertebrates (Camacho *et al*., 2000).

This paper continues systematic studies of angiosperm fossil woods from the Río Leona Formation (see Pujana 2007; 2008; 2009) with the detailed wood

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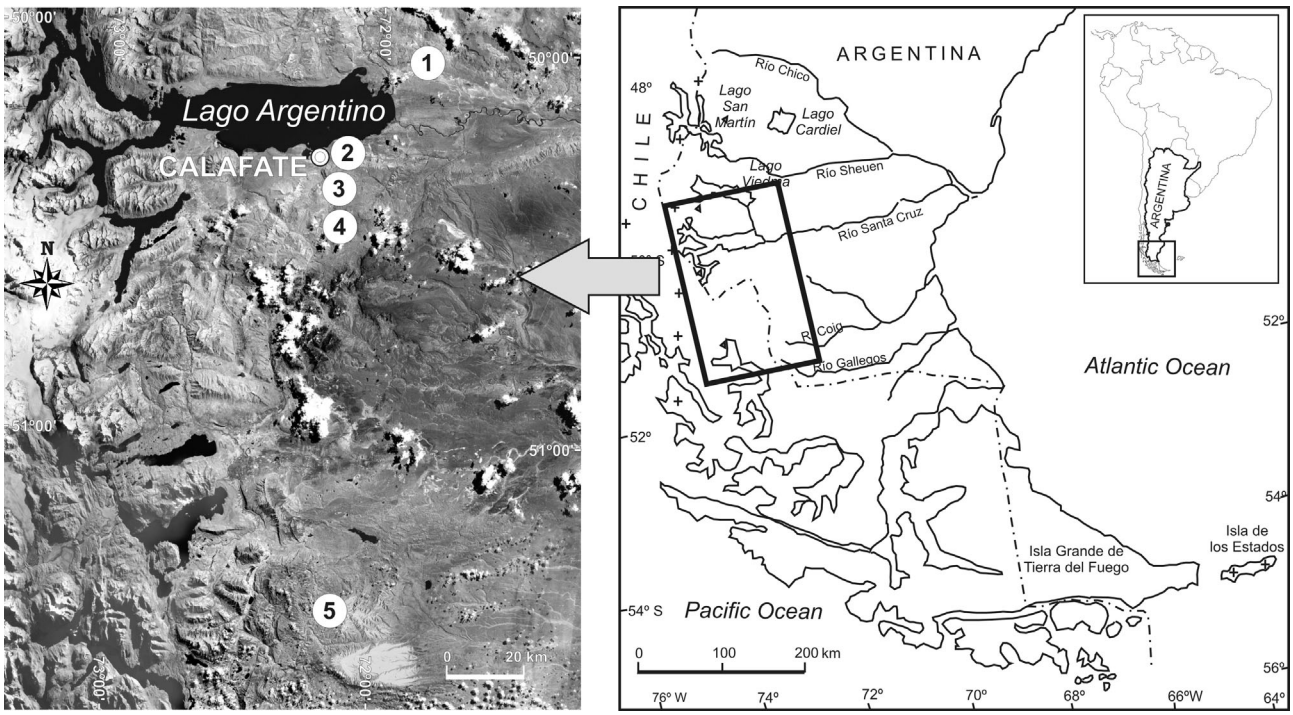

Figure 1. Map and satellite image showing the fossiliferous localities / *mapa e imagen satelital con las localidaes fosilíferas*. **1,** Estancia La Laurita. **2,** Cerro Calafate. **3,** Arroyo de los Guanaquitos. **4,** Arroyo de las Bandurrias. **5,** Arroyo Oro.

anatomy description and discussion of five morphospecies with affinity to the Nothofagaceae and one with Rosaceae. Descriptions of known species are made with particular comments on the specimens from Rio Leona, and a new morphospecies of Nothofagaceae and one of Rosaceae are described.

Materials and methods

Woods were collected from five localities in southwestern Patagonia were the Río Leona Formation outcrops. The fossiliferous localities are: Estancia La Laurita (50º 06′ 32′′ S 71º 49′ 49′′ W), Cerro Calafate (50º 21′ 18′′ S 72º 10′ 12′′ W), Arroyo de los Guanaquitos (50º 27′ 15′′ S 72º 14′ 12′′ W), Arroyo de las Bandurrias (50º 31′ 24′′ S 72º 15′ 33′′ W) and Arroyo Oro (51º 24′ 37′′ S 72º 11′ 29′′ W) (figure 1). All samples were geographically and stratigraphically (figure 2) located.

The specimens are silicified and were thin sectioned in transverse, tangential longitudinal and radial longitudinal sections following standard techniques for petrified woods (i.e. Hass and Rowe, 1999) and studied using light microscopy. To complement the thinsectioned material acetate peels were also made following the recommendations of Galtier and Phillips (1999), but those never show better anatomy detail than thin cuts. Terminology follows the IAWA recommendations for hardwood identification (IAWA Committee, 1989), measurements (at least 25 for each character) are given as the mean followed by the range in parentheses, and descriptions are based on the best preserved specimens (holotypes and paratypes in new taxa). Minimum estimated diameter is calculated based on growth ring curvature or direct measurements depending on the specimen. Systematic placement at the familial and suprafamilial level follows the APG II (2003) classification. For fossil woods with affinity to Nothofagaceae the morphospecies criteria of Poole (2002) were followed.

Specimens and thin slides are housed in the palaeobotanical collection of the Museo Regional Provincial Padre Manuel Jesús Molina (MPMPB) located in Río Gallegos, Santa Cruz Province, Argentina. Slides bear the specimen numbers followed by a lower case letter usually indicating the sections: a, transverse section, b, radial longitudinal section, and c, tangential longitudinal section.

Systematic palaeontology

Genus ***Maloidoxylon*** Grambast-Fessard, 1966

Type species. *Maloidoxylon castellanense* Grambast-Fessard, 1966.

Maloidoxylon cesariae sp. nov.
Figure 3

Holotype. MPMPB 2160.
Paratype. MPMPB 2158.
Other specimens. MPMPB 1969, 1970, 2157, 2159, 2163, 2164, 2173, 2176, 2181 and 2192.
Type locality. Arroyo de los Guanaquitos.

Derivatio nominis. *Cesariae*, after Argentine palaeobotanist Silvia N. Césari for her numerous works in this discipline.

Affinity. Angiospermae, Rosales, Rosaceae.

Diagnosis. Secondary xylem with distinct growth rings. Diffuse porosity. Vessels very narrow, solitary and very crowded (> 300 vessels per mm²). Perforation plates simple. Intervessel pits circular with alternate to opposite arrangement. Fibres with bordered pits on radial and tangential walls. Diffuse axial parenchyma. Rays heterocellular, uniseriate or biseriate, rarely triseriate and very abundant, normally 10-20 rays per mm. Disjunctive ray parenchyma.

Description. Specimens assigned to this morphospecies do not reach more than 6 cm in diameter. Preservation is good, and many anatomical characters were difficult to observe in most of the specimens. Specimens were found inside concretions (figure 3.1) and in life position. Some of them have the pith preserved composed of circular to oval parenchymatic cells with a diameter of 37 (22-48) µm (figure 3.5). Tension wood was observed in some specimens (figure 3.4). Growth ring boundaries are weakly marked by the reduction of the radial diameter of the last one or two rows of latewood fibres (figure 3.2). Growth rings have a width of *ca*. 0.25-0.5 mm near the pith and *ca*. 0.5-1 mm distant from the pith. Porosity is diffuse with some growth rings vessels having a tendency to align at the beginning of the ring (figure 3.2). Vessels are solitary, rarely in contact, and have a circular to angular outline (figure 3.3). They are extremely small, with a tangential diameter of 16 (10-22) µm and a density of 436 (325-520) vessels per mm². Vessel element length is *ca*. 150 µm. Perforation plates are simple. Intervessel pitting is opposite to alternate, with pits of *ca*. 2 µm in diameter and scarce, due to the normal solitary arrangement of vessels (figure 3.6). Vessel-ray pitting was not observed. Fibres are non-septate, very thick walled, have a width of *ca.* 8 µm and bordered pits (fibretracheids) on radial and tangential walls of *ca*. 2 µm in diameter (figure 3.8). Diffuse axial parenchyma is common, in strands of commonly more than 8 cells; each parenchymatic cell has a length of 20 (13-31) µm (figure 3.7). Rays are heterocellular and uniseriate or biseriate, rarely triseriate. They are composed of procumbent cells in biseriate and triseriate portions and upright to square cells in uniseriate rays and uniseriate portions of biseriate and triseriate rays (figure 3.9). Ray parenchyma cells have one or two circular dark bodies. Disjunctive ray parenchyma

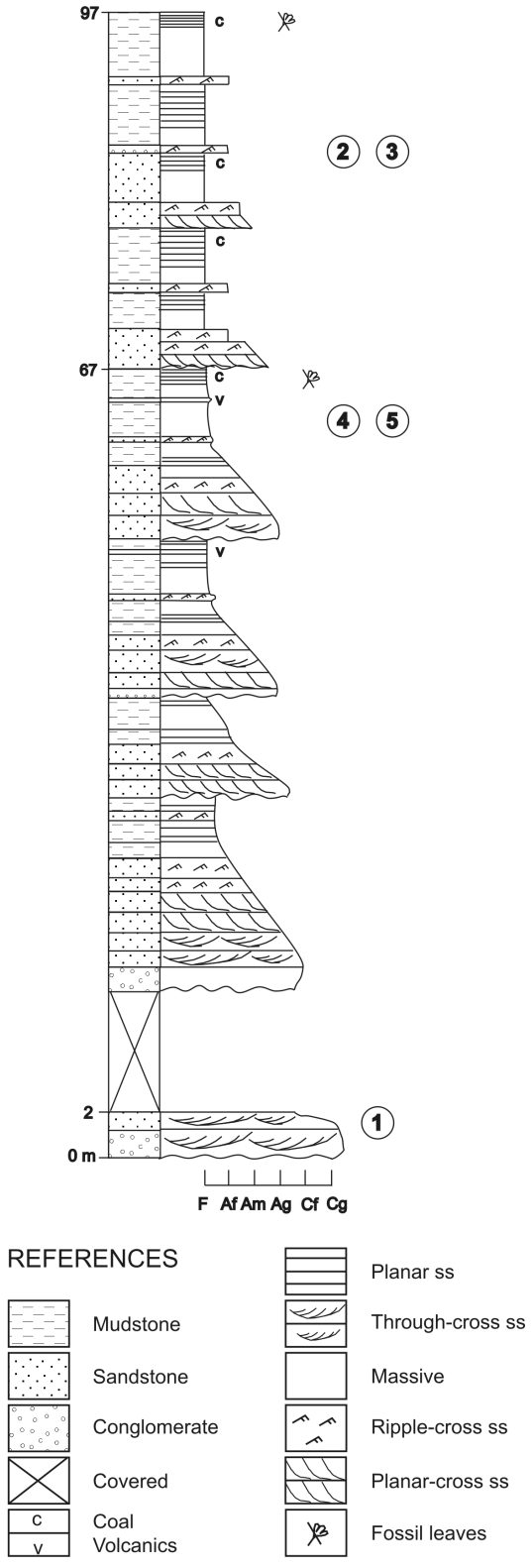

Figure 2. Stratigraphic log with the fossil bearing strata approximately located in the "Estancia 25 de Mayo" section from Marenssi *et al*. (2005) / *perfil esquemático con la ubicación aproximada de los estratos fosilíferos ubicados en la sección "Estancia 25 de Mayo" de Marenssi* et al. *(2005).* **1,** Estancia La Laurita. **2,** Cerro Calafate. **3,** Arroyo de los Guanaquitos. **4,** Arroyo de las Bandurrias. **5,** Arroyo Oro.

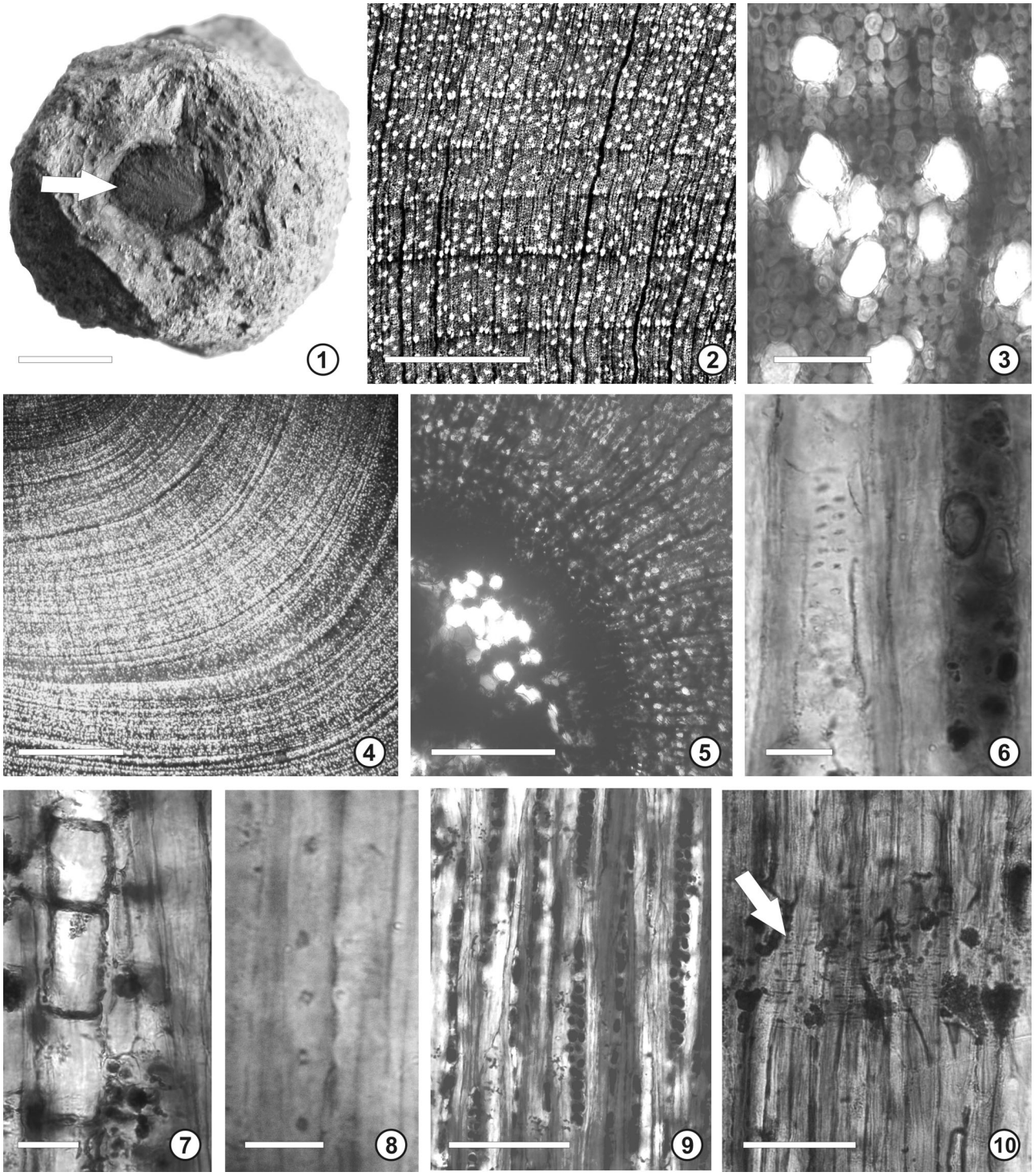

Figure 3. ***Maloidoxylon cesariae*** sp. nov. **1,** concretion containing the fossil sample (arrow) / *concreción conteniendo el ejemplar fósil (flecha)*. Scale bar / *escala gráfica*: 1 cm. (MPMPB 2158, paratype). **2,** general view of a transverse section (TS) / *aspecto general de sección transversal (ST)*. Scale bar / *escala gráfica*: 500 µm. (MPMPB 2160, holotype / *holotipo*. **3,** detail of TS / *detalle de ST*. Scale bar / *escala gráfica*: 50 µm. (MPMPB 2158, paratype). **4,** tension wood (TS) / *leño de tensión (ST)*. Scale bar / *escala gráfica*: 1 mm. (MPMPB 2160, holotype). **5,** pith with parenchymatic cells (TS) / *médula con células parenquimáticas (ST)*. Scale bar / *escala gráfica*: 200 µm. (MPMPB 2160, holotype). **6,** opposite to alternate intervessel pitting in tangential longitudinal section (TLS) / *puntuaciones intervasculares opuestas a alternas en sección longitudinal tangencial (SLT)*. Scale bar / *escala gráfica*: 10 µm. (MPMPB 2160, holotype). **7,** diffuse axial parenchyma (TLS) / *parénquima axial difuso (SLT)*. Scale bar / *escala gráfica*: 20 µm. (MPMPB 2160, holotype). **8,** fibres with bordered pits (TLS) / *fibras con puntuaciones areoladas (SLT)*. Scale bar / *escala gráfica*: 10 µm. (MPMPB 2160, holotype). **9,** uniseriate and biseriate rays (TLS) / *radios uniseriados y biseriados (SLT)*. Scale bar / *escala gráfica*: 100 µm. (MPMPB 2160, holotype). **10,** disjunctive ray parenchyma in radial longitudinal section (RLS) / *parénquima radial disyunto en sección longitudinal radial (SLR)*. Scale bar / *escala gráfica*: 50 µm. (MPMPB 2160, holotype).

parenchyma is present (figure 3.10). Ray frequency is *ca*. 10-20 rays per mm.

Discussion. All the specimens came from the same locality where they are abundant and do not show significant anatomical variation. The small stem diameter indicates that they were part of small trees or shrubs, while the tension wood indicates an oblique position of the stems, probably suggesting a shrub habit.

Rosaceae woods are comparable with the fossils, they have small vessels that are generally solitary, simple perforation plates, alternate intervessel pitting and commonly more or less distinct growth rings boundaries (Zhang, 1992). However in many species rays are multiseriate (normally uniseriate or biseriate in the fossils) and in some species they are homocellular (heterocellular in the fossils) (see Rancusi *et al*., 1987). Nevertheless an affinity to this family is proposed. Unfortunately, there are no detailed wood anatomical descriptions for many extant Patagonian shrubs. (i.e., *Tetraglochin* Kunze ex Poepp. or *Margyricarpus* Ruiz and Pav.), limiting the number of comparisons to extant Rosaceae woods of the region. Fossil pollen with affinity to *Polylepis* Ruiz *et* Pav. and other rosaceous pollen were found in sediments of Río Leona Formation (Barreda *et al*., 2009). Today the genus *Polylepis* does not occur in Patagonia. Wood of *Polylepis tomentella* Wedd. from more northerly regions of Argentina and from southern Bolivia is anatomically similar in most characters and has disjunctive parenchyma and pitted fibres, but it has wider rays (Ancibor, 1984). Presence of rosaceous pollen in the sediments of Río Leona Formation (Barreda *et al*., 2009) suggests that the wood could be related to other Rosaceae, like the shrubs *Tetraglochin*, with close affinity to *Polylepis* (Eriksson *et al*., 2003) which its wood anatomy and pollen morphology are unknown. The extant Rosaceae species *Quillaja saponaria* Mol. and *Kageneckia oblonga* Ruiz *et* Pav. from Chile are also similar, they have small, usually solitary vessels, but they have wider rays and disjunctive parenchyma has not been reported in them (Rancusi *et al*., 1987). Rubiaceae also has similar wood anatomy, although extant Patagonian plants of this family are all herbaceous (Bacigalupo, 1999). Characters shared between the Rubiaceae and the fossils just described are: solitary vessels, bi-triseriate rays and disjunctive parenchyma (Jensen *et al*., 2002). Disjunctive parenchyma seems to be a useful diagnostic character to assign the fossils to Rosaceae (or Rubiaceae) affinity and is also supposed to be a primitive character (León H. and Espinoza, 1999).

Chilechicoxylon microporosum Nishida *et al*. (1990) is a unique fossil wood taxon from Patagonia that was assigned to the Rosaceae. It differs from the Río Leona specimens as it has wider vessels and rays and scalariform intervessel pitting. The morphogenus *Maloidoxylon* was described by Grambast-Fessard (1966) for a Rosaceae fossil wood from Europe and was characterized by having narrow vessels, diffuse porosity, heterocellular rays, alternate intervessel pitting and fibres with bordered pits. She described one morphospecies for that morphogenus, *Maloidoxylon castellanense* Grambast-Fessard. Wheeler and Matten (1977) subsequently described many specimens from North America and assigned them to *Maloidoxylon galbreathii* Wheeler *et* Matten and *Maloidoxylon coloradense* Wheeler *et* Matten. Privé-Gill (1981) added another morphospecies, *Maloidoxylon lutetianum* Privé-Gill. Recently, Wheeler *et* Manchester (2003) described *Maloidoxylon annae* Wheeler and Manchester, also very similar to the material described here. However this latter morphospecies has helical thickenings in vessels and lacks disjunctive parenchyma. *Maloidoxylon cesariae* differs from the five morphospecies of *Maloidoxylon* principally in having disjunctive ray parenchyma and narrower and denser vessels, and also in lacking scalariform perforation plates which are present in *M. lutetianum* and *M. castellanense*. Based on these differences the specimens of Río Leona Formation are placed in a new morphospecies of *Maloidoxylon* with affinity to Rosaceae.

The Rosaceae in Patagonia are now represented mostly by herbaceous plants, although several shrubs live there such as *Tetraglochin* (Grondona, 1984). Rosaceae is believed to have radiated from North America during the Eocene (DeVore and Pigg, 2007), consequently the arrival of this family to South America should be later. This record constitutes, together with the fossil pollen from the same strata, the oldest fossil Rosaceae from South America.

Genus ***Nothofagoxylon*** Gothan, 1908

Type species. *Nothofagoxylon scalariforme* Gothan, 1908.

Nothofagoxylon scalariforme Gothan, 1908
Figure 4

Synonyms. 1984. *Nothofagoxylon antarcticus* Torres: 39-52; fig. 3. 1908. *Laurinoxylon uniseriatum* Gothan: 16-19; plate 2 fig. 3-11. 1924. *Laurinoxylon uniradiatum* (Gothan) Kräusel: 25-28; plate 4 fig.1-4.
Lectotype. Specimen nº 14 (S004067). Swedish Museum of Natural History, Stockholm, Sweden.
Syntypes. Specimens nº 13 (S004053) and nº 18 (S004068). Swedish Museum of Natural History, Stockholm, Sweden.
Type locality. Marambio (Seymour) Island, Antarctica.
New specimens. MPMPB 1950, 1956, 1962, 2124, 2142, 2146, 2149, 2152, 2155, 2170, 2171, 2200, 2201, 2204 and 2218.
New localities. Cerro Calafate, Arroyo de las Bandurrias, Arroyo de los Guanaquitos and Arroyo Oro.

Affinity. Angiospermae, Fagales, Nothofagaceae, *Nothofagus* (*Nothofagus*).

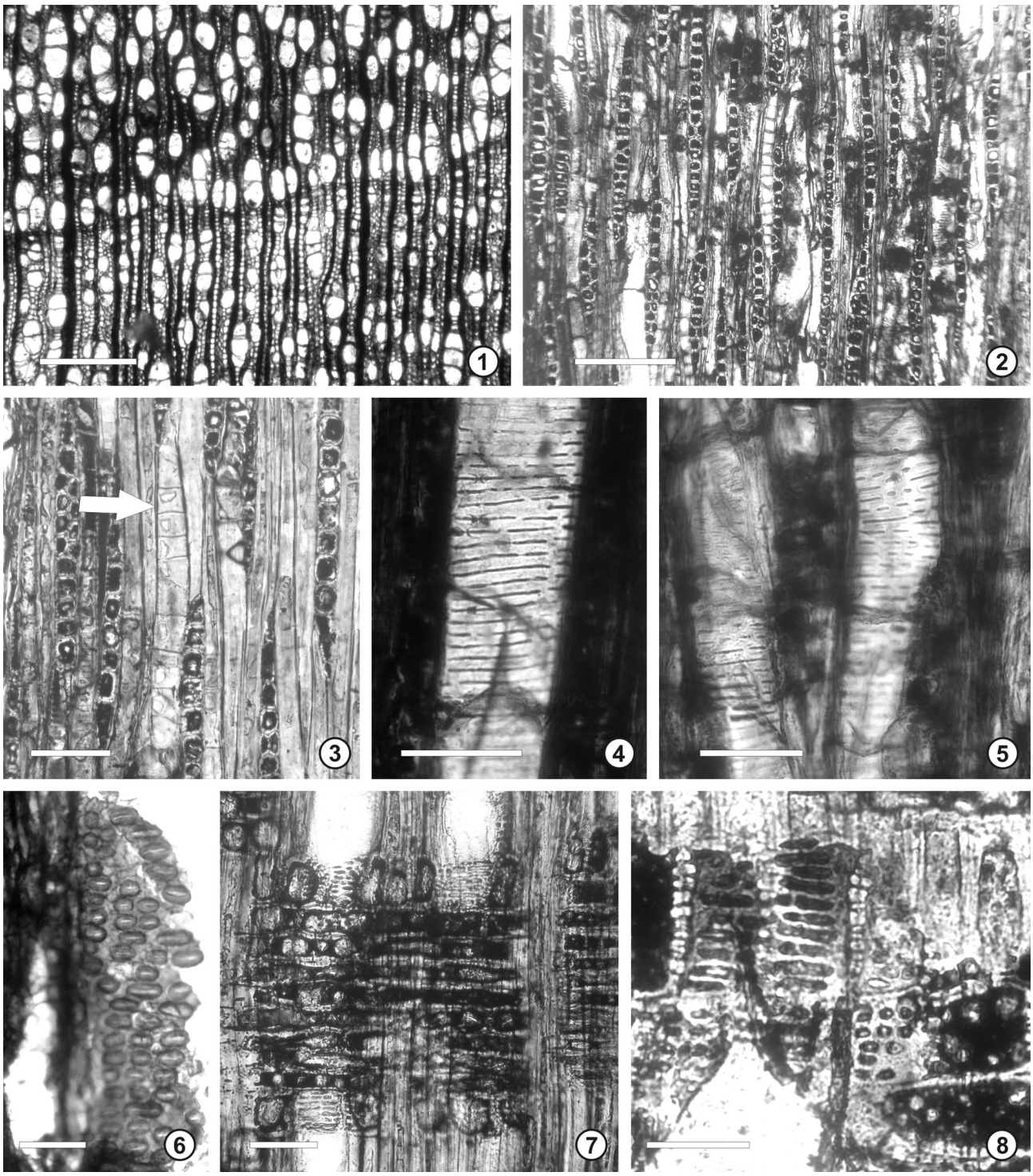

Figure 4. ***Nothofagoxylon scalariforme*** Gothan, 1908. **1,** general view of a transverse section (TS) / *aspecto general de sección transversal (ST)*. Scale bar / *escala gráfica*: 500 µm. (MPMPB 2204). **2,** uniseriate rays (TLS) / *radios uniseriados (SLT)*. Scale bar / *escala gráfica*: 200 µm. (MPMPB 2124). **3,** axial parenchyma (arrow) (TLS) / *parénquima axial (flecha) (SLT)*. Scale bar / *escala gráfica*: 50 µm. (MPMPB 2218). **4,** scalariform intervessel pitting (RLS) / *puntuaciones intervasculares escalariformes (SLR)*. Scale bar / *escala gráfica*: 50 µm. (MPMPB 2149). **5,** scalariform to opposite intervessel pitting (RLS) / *puntuaciones intervasculares escalariformes a opuestas (SLR)*. Scale bar / *escala gráfica*: 50 µm. (MPMPB 2171). **6,** opposite intervessel pitting (RLS) / *puntuaciones intervasculares opuestas (SLR)*. Scale bar / *escala gráfica*: 20 µm. (MPMPB 2212). **7,** radial cells (RLS) / *células radiales (SLR)*. Scale bar / *escala gráfica*: 100 µm. (MPMPB 2152). **8,** circular to horizontally elongated vessel-ray pits (RLS) / *puntuaciones radio-vasculares circulares a alargadas horizontalmente (SLR)*. Scale bar / *escala gráfica*: 20 µm. (MPMPB 2152).

Description. The specimens have a minimum estimated diameter of up to 25 cm. Growth ring boundaries are marked by the reduction of vessel size and radial diameter of the last one to three latewood fibres (figure 4.1). Porosity is diffuse to semi-ring porous and the vessels are solitary or frequently in radial multiples of up to four vessels (figure 4.1). Vessels have a tangential diameter of 53 (13-118) μm and have a density of 178 (73-398) vessels per mm^2. Vessel elements are 143 (55-338) μm in length. Perforation plates are simple, rarely scalariform perforation plates with few bars are present in the latewood vessels. Intervessel pitting arrangement is scalariform to opposite, very rarely alternate (figure 4.4-6). Vessel-ray pits are circular to horizontally elongated with an opposite to scalariform arrangement (figure 4.8). Diffuse axial chambered crystalliferous parenchyma, with one crystal per cell, is present usually in strands of more than 8 cells (figure 4.3). Axial parenchyma abundance varies among samples. Rays are uniseriate or uniseriate partially biseriate (figure 4.2-3) and 10-18 rays per mm. They are composed of procumbent body cells with normally one row of upright to square marginal cells (figure 4.7).

Discussion. Some anatomical variability occurs among the specimens. Growth ring width has significant variation, can reach up to *ca*. 6 mm in some specimens (MPMPB 2204), while are very narrow in others, *ca*. 0.21 mm in MPMPB 2171. Axial parenchyma was not found in all of the specimens and in others it is relatively frequent (i.e. MPMPB 1956, 2124 and 2152). Uniseriate rays with biseriate portions were found in some specimens (i.e. MPMPB 2218), while others have exclusively uniseriate rays. Specimen MPMPB 2204 has the lowest mean vessel density, 89 vessels per mm^2, while in other specimens can reach up to 398 vessels per mm^2 (MPMPB 2171). Almost certainly these anatomical variations indicate different specimen ages or organs more than intraspecific variation and are not significant enough to place these specimens in different morphospecies according to the *Nothofagoxylon* species criteria of Poole (2002).

Some specimens (MPMPB 2152, 2218 and 2149) show signs of biodeterioration, they have tunnels, some of them filled with pellets, similar to those produced by oribatid mites (Labandeira *et al*., 1997; Kellog and Taylor, 2004).

Uniseriate or uniseriate partially biseriate rays and opposite to scalariform intervessel pitting occur in the extant species *Nothofagus pumilio* (Poepp. and Endl.) Krasser, *Nothofagus betuloides* (Mirb.) Oerst., *Nothofagus dombeyi* (Mirb.) Oerst. and *Nothofagus nitida* (Phil.) Krasser, all of them placed in *Nothofagus* subgenus *Nothofagus*, whose wood is characterized by uniseriate rays and opposite intervessel pitting. The specimens have an affinity to the subgenus rather than a particular species of it.

Nothofagoxylon scalariforme was described by Gothan (1908) based on specimens of Marambio (Seymour) Island. Uniseriate or partially biseriate rays are the main character to distinguish it from other morphospecies such as *Nothofagoxylon kraeuseli* Boureau and Salard (1960) or *Nothofagoxylon triseriatum* Torres and Lemoigne (1988). *Nothofagoxylon ruei* Salard (1961) also normally has uniseriate rays, but its intervessel pitting is predominantly alternate, while *N. scalariforme* intervessel pitting is opposite to scalariform. Fossil woods assigned to *N. scalariforme* are abundant in the Río Leona Formation, indicating an important presence of woods with affinity to *Nothofagus* subgenus *Nothofagus*.

Nothofagoxylon triseriatum Torres *et* Lemoigne, 1988
Figure 5

Synonym. 1988. *Nothofagoxylon paleoglauca* Torres et Lemoigne: 85-90; plate VI and VII.
Holotype. A-PF-51, Colección Paleoxilológica Torres, Instituto Antártico Chileno, Santiago, Chile.
Paratype. A-PF-53, Colección Paleoxilológica Torres, Instituto Antártico Chileno, Santiago, Chile.
Type locality. Cerro Bosque Petrificado, 25 de Mayo (King George) Island, Antarctica.
New specimens. MPMPB 1966 and 1967.
New locality. Arroyo de los Guanaquitos.

Affinity. Fagales, Nothofagaceae, *Nothofagus* (*Lophozonia*).

Description. Both specimens have a minimum estimated diameter of *ca*. 20 cm. Growth ring boundaries are marked by the reduction of the vessel size and radial diameter of the last 15 to 20 latewood fibres (figure 5.1-2). The wood is semi-ring porous (figure 5.1-2). Growth rings are *ca*. 5 mm in width. Vessels are solitary or in radial multiples of two or three vessels, latewood radial multiples can be up to six vessels (figure 5.1-2). Vessel density is 40 (30-54) vessels per mm^2 and tangential diameter is 80 (45-115) μm. Vessel elements are *ca*. 650 μm in length. Perforation plates are simple and horizontal, rarely scalariform with few bars and oblique perforation plates are present in the latewood vessels (figure 5.3). Intervessel pits are circular to polygonal with an alternate to opposite arrangement (figure 5.6-7). Vessel-ray pits are circular (figure 5.8). Fibres are thin walled. Rays are triseriate or biseriate (figure 5.5), rarely reach more than 1 mm in height and they are in a frequency of 7 to 12 per mm, normally 8 or 9, and are composed of procumbent cells in the body and one row of square to upright marginal cells (figure 5.4).

Discussion. The two specimens assigned to *N. triseriatum* are similar except for minor differences such as frequency of rays per mm.

Anatomy of this morphospecies is similar to ex-

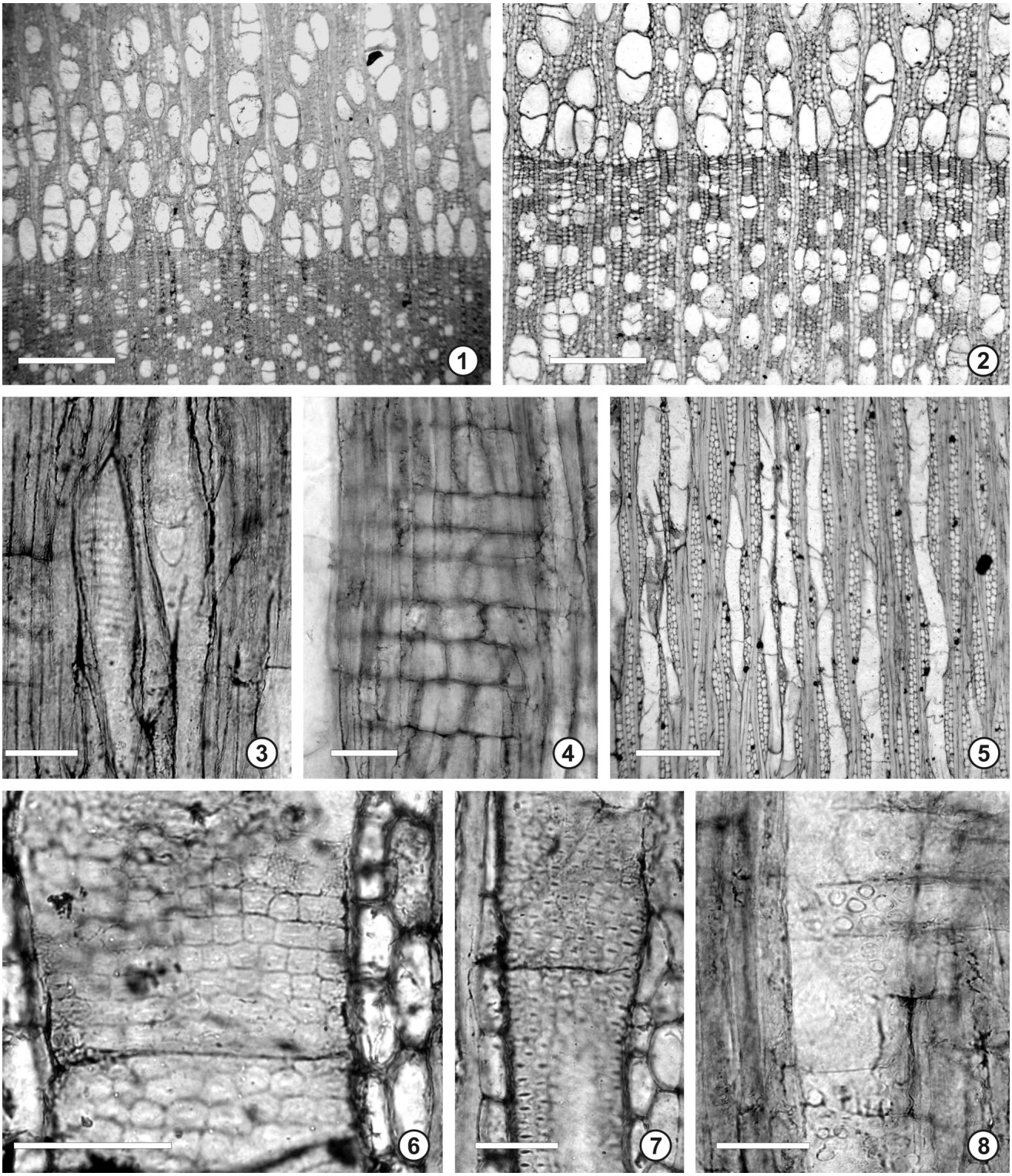

Figure 5. ***Nothofagoxylon triseriatum*** Torres *et* Lemoigne, 1988. **1,** general view of a transverse section (TS) / *aspecto general de sección transversal (ST).* Scale bar / *escala gráfica*: 500 µm. (MPMPB 1967). **2,** general view of a transverse section (TS) / *aspecto general de sección transversal (ST).* Scale bar / *escala gráfica:* 500 µm. (MPMPB 1966). **3,** scalariform perforation plates (RLS) / *placas de perforación escalariforme (SLR).* Scale bar / *escala gráfica*: 50 µm. (MPMPB 1966). **4,** radial cells (RLS) / *células radiales (SLR).* Scale bar / *escala gráfica*: 50 µm. (MPMPB 1966). **5,** Biseriate and triseriate rays (TLS) / *radios biseriados y triseriados (SLT).* Scale bar / *escala gráfica*: 500 µm. (MPMPB 1966). **6,** opposite intervessel pitting (RLS) / *puntuaciones intervasculares opuestas (SLR).* Scale bar / *escala gráfica*: 50 µm. (MPMPB 1967). **7,** opposite intervessel pitting (RLS) / *puntuaciones intervasculares opuestas (SLR).* Scale bar / *escala gráfica*: 50 µm. (MPMPB 1966). **8,** circular vessel-ray pits (RLS) / *puntuaciones radio-vasculares circulares (SLR).* Scale bar / *escala gráfica*: 50 µm. (MPMPB 1966).

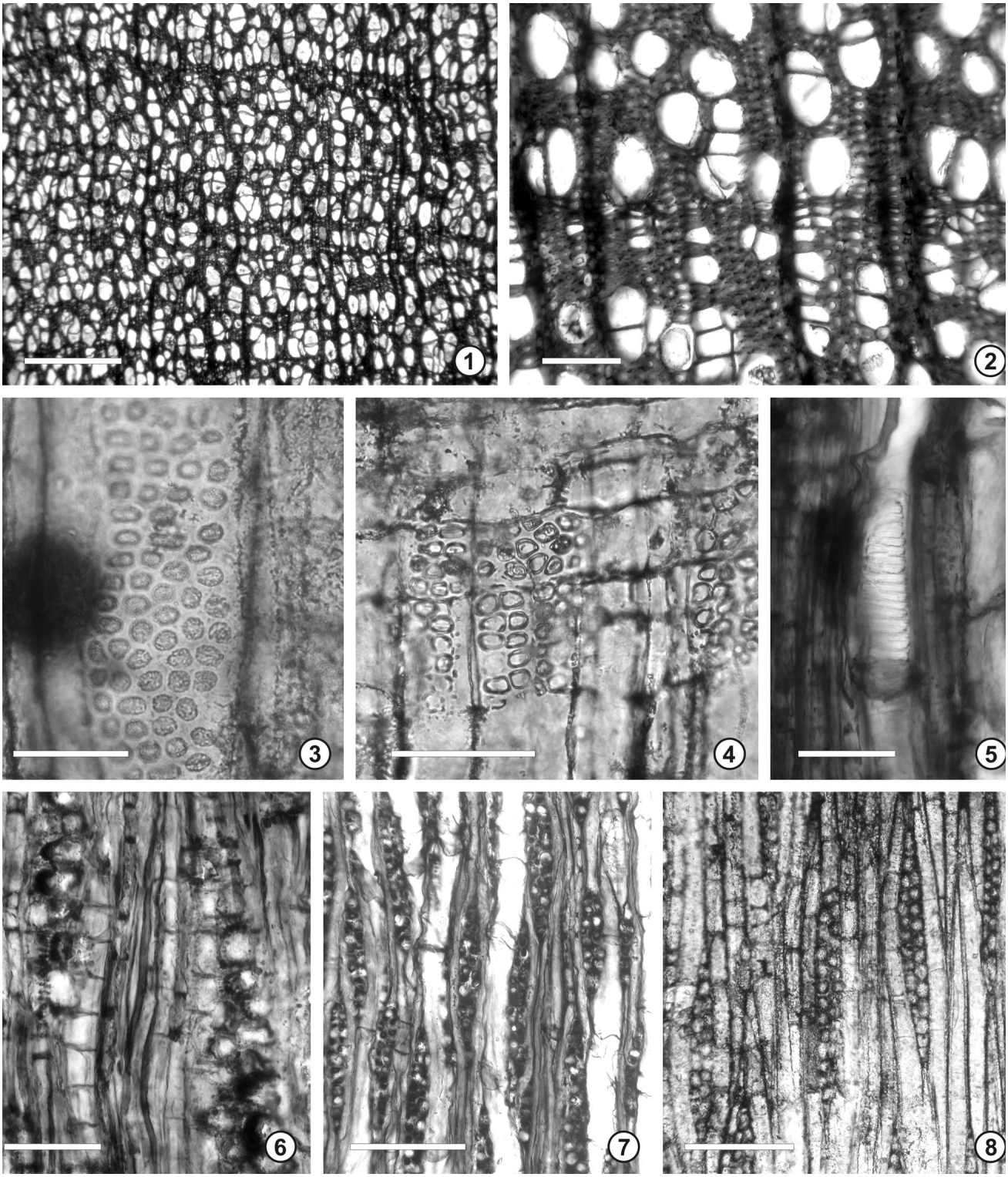

Figure 6. ***Nothofagoxylon kraeuseli*** Boureau *et* Salard, 1960. **1,** general view of a transverse section (TS) / *aspecto general de sección transversal (ST)*. Scale bar / *escala gráfica*: 500 µm. (MPMPB 2106). **2,** detail of TS showing growth ring boundary / *detalle de ST con límite de anillo*. Scale bar / *escala gráfica*: 100 µm. (MPMPB 2116). **3,** opposite to alternate intervessel pitting (RLS) / *puntuaciones intervasculares opuestas a alternas (SLR)*. Scale bar / *escala gráfica*: 50 µm. (MPMPB 2138). **4,** circular vessel-ray pits (RLS) / *puntuaciones radio-vasculares circulares (SLR)*. Scale bar / *escala gráfica*: 50 µm. (MPMPB 1994). **5,** scalariform perforation plate (RLS) / *placa de perforación escalariforme (SLR)*. Scale bar / *escala gráfica*: 50 µm. (MPMPB 2106). **6,** axial parenchyma (TLS) / *parénquima axial (SLT)*. Scale bar / *escala gráfica*: 50 µm. (MPMPB 2106). **7,** biseriate rays (TLS) / *radios biseriados (SLT)*. Scale bar / *escala gráfica*: 200 µm. (MPMPB 2182). **8,** biseriate rays (TLS) / *radios biseriados (SLT)*. Scale bar / *escala gráfica*: 200 µm. (MPMPB 1994).

tant woods of the *Nothofagus* subgenus *Lophozonia* Turcz., particularly *Nothofagus alpina* (Poepp. and Endl.) Oerst. Biseriate or triseriate rays and tangential diameter of vessels suggest affinity to the subgenus *Lophozonia*. In Patagonia also inhabit *Nothofagus obliqua* (Mirb.) Oerst. and *Nothofagus glauca* (R. Phil) Krasser, but they have narrower vessels and are diffuse porous while in *N. triseriatum* and *N. alpina* are semi-ring porous. However, vessel density of *N. triseriatum* is more similar to *N. obliqua* according to Rivera (1988), but Rancusi *et al.* (1987) observed a lower vessel density for that species. Apparently vessel density has a considerable intraspecific variation.

Poole (2002) included *N. paleoglauca* Torres *et* Lemoigne (1988) in *N. triseriatum* because they only differ in presence of septated fibres, helical thickenings (characters dependent on the preservation) and in the predominance of biseriate rays (character dependent on the age of the ring). The Río Leona Formation woods just described differ from the holotype of *N. triseriatum* as they have slightly narrower vessels and the frequency of triseriate rays does not reach 50%. *Nothofagoxylon menendezii* Ragonese (1977) is also similar, but its rays are normally biseriate, intervessel pitting alternate to scalariform and there are abundant crystals in the rays, all these characters are absent from the Río Leona Formation fossils.

Nothofagoxylon kraeuseli Boureau *et* Salard, 1960
Figure 6

Synonym. 1986. *Nothofagoxylon ohzuanum* Nishida, Nishida, H. *et* Nasa: 28-31; fig. 2-5.
Holotype. Specimen nº 1410B, Collection de Paléobotanique de l' Université Pierre et Marie Curie, Paris, France.
Type locality. Cerro Dorotea.
New material. MPMPB 1982, 1992, 1994, 2106, 2116, 2138, 2177, 2182, 2202 and 2324.
New localities. Cerro Calafate, Estancia La Laurita, Arroyo de los Guanaquitos and Arroyo Oro.

Affinity. Angiospermae, Fagales, Nothofagaceae, *Nothofagus* (*Lophozonia*).
Description. Specimens have minimum estimated diameters between 11 and 24 cm.

Growth ring boundaries are marked by the reduction of radial diameter of the last three to eight latewood fibres (figure 6.2). Wood is diffuse to semiring porous (figure 6.1-2). Vessels are solitary or in radial multiples of up to five vessels, their tangential diameter is 56 (25-100) μm and there are 137 (53-254) vessels per mm². Vessel element length is 207 (117-294) μm. Perforation plates are simple and sometimes scalariform with few bars in latewood small vessels (figure 6.5). Intervessel pits are circular to horizontally elongated with usually opposite to alternate arrangement (figure 6.3), rarely scalariform. Vessel-ray pitting is similar to intervessel pitting (figure 6.4). Diffuse axial parenchyma is present (figure 6.6). Rays are typically biseriate (figure 6.7-8), but there are uniseriate rays with biseriate portions. They are in a frequency of normally 5 to 11 rays per mm.
Discussion. Among the specimens of Río Leona Formation, variable characters are: ray height, presence of axial parenchyma and scalariform perforation plates, although these two latter characters are difficult to observe and they are never abundant in the specimens that have it. Tangential vessel diameter is another variable character, from a mean of 43 μm in specimen MPMPB 2106 to a mean of 71 μm in MPMPB 1982. Vessel density is also variable in specimens assigned to *N. kraeuseli*, the mean is lower than 100 vessels per mm² in some specimens (i.e. MPMPB 1992 and 2202) and bigger than 200 in others (i.e. MPMPB 2106). Growth ring width is normally *ca.* 3-4 mm in most specimens, except in specimen MPMPB 2106 that has a mean width of *ca.* 0.6 mm. The latter specimen has fungi hyphae and spores inside some vessels.

Biseriate rays suggest an affinity to the *Nothofagus* subgenus *Lophozonia*, which includes the South American species *Nothofagus glauca*, *Nothofagus alpina* and *Nothofagus obliqua*, all of them with normally biseriate rays and anatomical characters comparable with this morphospecies.

The studied woods have the main characters described by Boureau and Salard (1960) when naming *N. kraeuseli* based on specimens from Cerro Dorotea locality: biseriate rays, diffuse axial parenchyma and rare scalariform perforation plates in narrow latewood vessels. Later, Terada *et al.* (2006) described more samples from the same locality and assigned them to the same morphospecies. *N. scalariforme* has normally uniseriate or partially biseriate rays, which differs from *N. kraeuseli*. In addition, intervessel pitting is normally scalariform to opposite in *N. scalariforme* while normally alternate to opposite in *N. kraeuseli*. *Nothofagoxylon menendezii* is also similar, but it has mostly alternate intervessel pitting and frequent triseriate rays (18 %), which *N. kraeuseli* lacks. *Nothofagoxylon triseriatum* has normally triseriate rays and larger vessels than *N. kraeuseli*..

The presence of many samples with affinity to the *Nothofagus* subgenus *Lophozonia*, confirms the abundance of this subgenus in sediments from the Rio Leona Formation. Moreover, pollen grains comparable to the subgenus ("*menziesii*" type) are also present (Barreda *et al*., 2009).

Nothofagoxylon ruei Salard, 1961
Figure 7

Synonyms. 1988. *Laurinoxylon ruei* (Salard) Nishida, Nishida, H. *et* Rancusi: 9-12. 1961. *Nothofagoxylon boureaui* Salard: 250-260; plates 32-35. 1950. *Nothofagoxylon neuquense* Cozzo: 3-10; figs. 1-3, 5-7. 1990. *Nothofagoxylon paraprocera* Ancibor: 179-184; figs. 1-2.

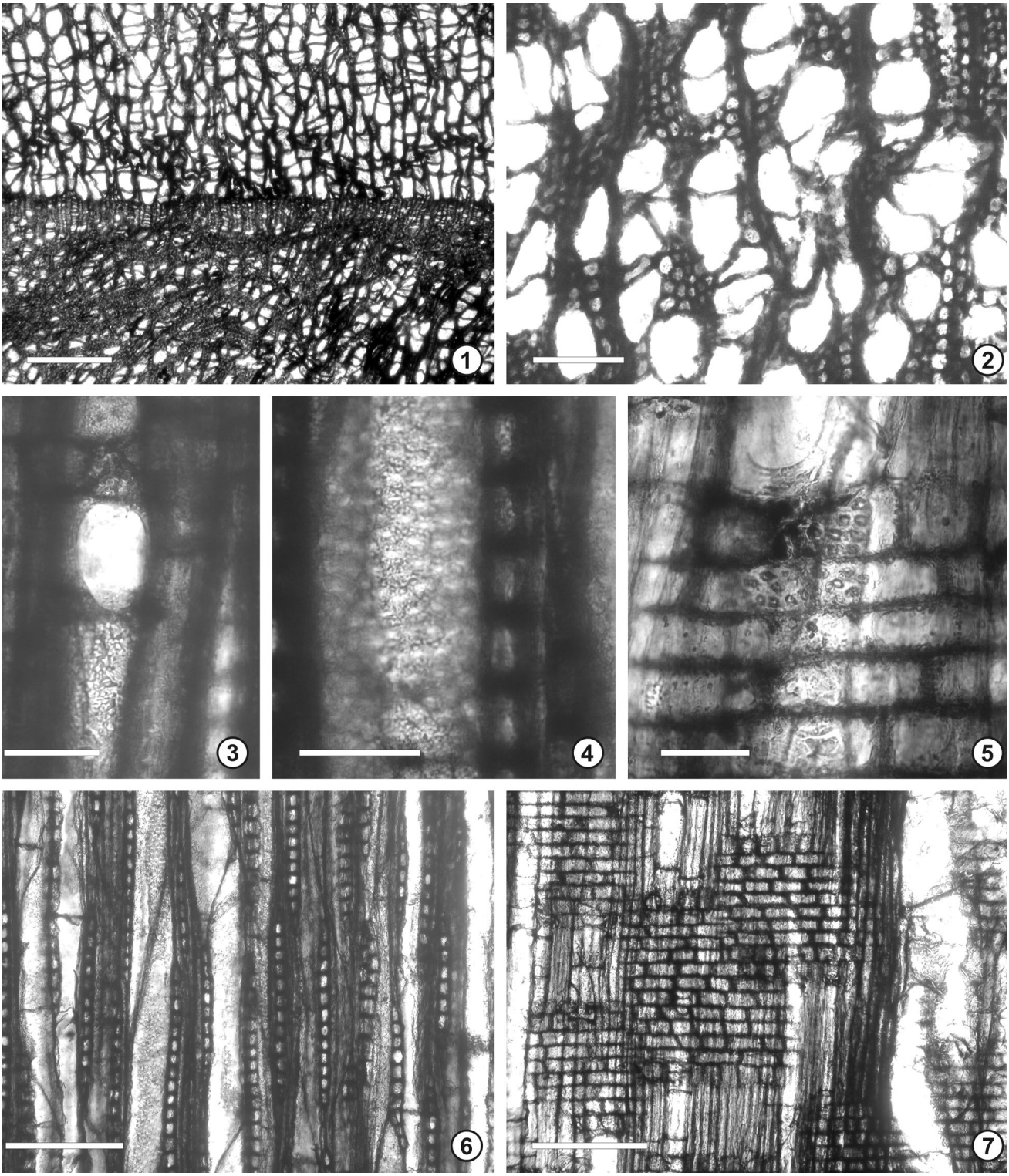

Figure 7. ***Nothofagoxylon ruei*** Salard, 1961. (MPMPB 2193). **1,** general view of a transverse section (TS) / *aspecto general de sección transversal (ST)*. Scale bar / *escala gráfica*: 500 µm. **2,** detail of TS / *detalle de ST*. Scale bar / *escala gráfica*: 100 µm. **3,** simple perforation plate (RLS) / *placa de perforación simple (SLR)*. Scale bar / *escala gráfica*: 50 µm. **4,** alternate intervessel pitting (RLS) / *puntuaciones intervasculares alternas (SLR)*. Scale bar / *escala gráfica*: 50 µm. **5,** circular vessel-ray pits (RLS) / *puntuaciones radio-vasculares circulares (SLR)*. Scale bar / *escala gráfica*: 50 µm. **6,** uniseriate rays (TLS) / *radios uniseriados (SLT)*. Scale bar / *escala gráfica*: 200 µm. **7,** radial cells (RLS) / *células radiales (SLR)*. Scale bar / *escala gráfica*: 200 µm.

Holotype. Specimen nº 1410A, Collection de Paléobotanique de l' Université Pierre et Marie Curie, Paris, France.
Type locality. Cerro Dorotea.
New material. MPMPB 2193.
New locality. Arroyo de los Guanaquitos.

Affinity. Angiospermae, Fagales, Nothofagaceae, *Nothofagus* (*Fuscospora*).
Description. The sample is a secondary xylem fragment that has a minimum estimated diameter of 7 cm. Growth ring boundaries are marked by the reduction of the radial diameter of the last five to ten latewood fibres and reduction in the latewood vessel diameter. Growth rings are *ca*. 2.8 mm in width. Wood is semi-ring porous. Vessels are solitary or frequently in radial multiples of up to 4 vessels, rarely more or in clusters. Vessel tangential diameter is 45 (22-78) µm, vessel elements are *ca*. 550 µm in length and vessel density is 235 (204-292) vessels per mm^2. Perforation plates are simple and very oblique. Intervessel pits are horizontally elongated *ca*. 5x7 µm in size, and with alternate to rarely opposite arrangement. Vessel-ray pits are circular with a diameter of *ca.* 6 µm. Fibres are thin walled. Rays are uniseriate, very rarely locally biseriate, can reach up to 26 cells in height and composed of parenchymatic procumbent cells with normally one row of upright marginal cells. They are in a frequency of 9 to 13 rays per mm.
Discussion. This specimen resembles the wood of *Nothofagus alessandri* Espinosa, of *Nothofagus* subgenus *Fuscospora* Hill *et* Read from Patagonian forests. Its wood has rays up to 22 cells in height and mainly uniseriate, opposite to alternate intervessel pitting and very oblique perforation plates (Rancusi *et al*., 1987). *Nothofagus solandri* (Hook. f.) Oerst. from New Zealand also has these characters and resembles *N. ruei* (Patel, 1986).

Poole (2002) gave this morphospecies a *Nothofagus* subgenus *Lophozonia* affinity based on the absence of undulating growth rings and aggregate rays. However, *Nothofagus alessandri* molecular analysis places it in *Nothofagus* subgenus *Fuscospora* (Manos, 1997). This species also lacks undulating growth rings and aggregated rays and is the most similar extant species to *N. ruei*. Consequently, a *Nothofagus* subgenus *Fuscospora* affinity is proposed for this morphospecies.

Uniseriate rays and opposite to alternate intervessel pitting allowed assigning the specimen to the morphospecies *N. ruei* described by Salard (1961) for a specimen of the nearby Cerro Dorotea locality. Poole (2002) includes *Nothofagoxylon boureaui*, which has exclusively uniseriate rays and is also from that locality and *Nothofagoxylon paraprocera* from Río Turbio Formation in *N. ruei*. According to Poole (2002) the specimens assigned by Terada *et al*. (2006) to *Laurinoxylon uniseriatum* should be placed in *N. ruei*, because of the alternate intervessel pitting and high uniseriate rays and not in *Nothofagoxylon scalariforme* (=*L. uniseriatum sensu* Poole (2002)). Consequently, even though the specimen described here is particularly similar to those specimens of Cerro Dorotea locality described by Terada *et al*. (2006), it is placed in *N. ruei*.

This specimen of *Nothofagoxylon ruei* confirms the presence of wood of *Nothofagus* subgenus *Fuscospora* in the Oligocene of Patagonia, although it is less common than the other two subgenera of *Nothofagus*.

Nothofagoxylon aggregatum sp. nov.
Figure 8

Holotype. MPMPB 1997.
Type locality. Estancia La Laurita.

Derivatio nominis. *aggregatum*, Latin, for the frequent vessel clusters and radial multiples.
Affinity. Angiospermae, Fagales, Nothofagaceae, *Nothofagus* (*Lophozonia*).
Diagnosis. Secondary xylem with distinct growth rings. Semiring porosity. Vessels small in radial multiples of up to *ca*. 9 vessels and in clusters in the latewood. Perforation plates simple. Intervessel pitting usually alternate sometimes opposite or scalariform. Vessel-ray pitting scalariform to opposite. Tyloses present. Axial parenchyma diffuse. Rays heterocellular and normally triseriate, sometimes uni-biseriate or 4-seriate.
Description. The specimen has a minimum estimated diameter of 13 cm. Growth ring boundaries are marked by the reduction of the radial diameter of the last three to five rows of latewood fibres and reduction in the latewood vessel diameter. Growth rings are *ca*. 2.7 mm in width. Wood is semi-ring porous. Vessels are in radial multiples of up to 9 vessels and sometimes are in clusters of 6-10 vessels in the latewood. Vessels have a tendency to diagonal arrangement in the latewood. Vessel tangential diameter is 51 (27-88) µm, density is 116 (81-168) vessels per mm^2. Vessel element length was difficult to determine, but seems to be *ca*. 250-300 µm in length. Tyloses are abundant. Perforation plates are simple and horizontal or slightly oblique. Intervessel pits are polygonal to horizontally elongated with usually an alternate pitting, but also rarely opposite to scalariform in vessel element endings. Vessel-ray pits are horizontally elongated with opposite to scalariform arrangement. Fibres are thin walled. Axial parenchyma is diffuse and composed of usually 4-7 cells per parenchyma strand. Rays are usually triseriate, rarely uni-biseriate or partially 4-seriate. There are 4 to 8, normally 5 or 6, rays per mm. Rays are hetero-

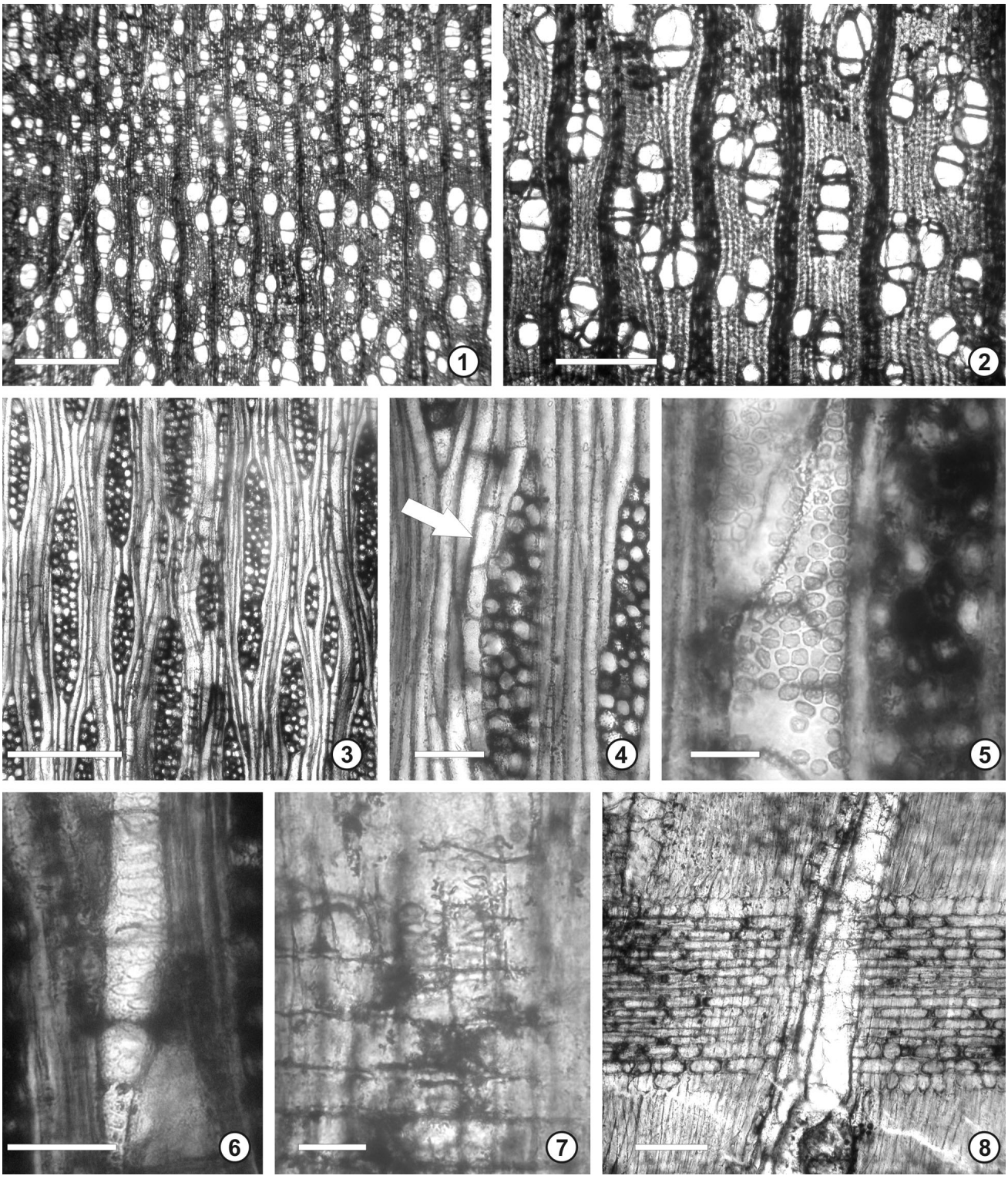

Figure 8. ***Nothofagoxylon aggregatum*** sp. nov. (MPMPB 1997, holotype). **1,** general view of a transverse section (TS) / *aspecto general de sección transversal (ST)*. Scale bar / *escala gráfica*: 500 µm. **2,** detail of TS / *detalle de ST*. Scale bar / *escala gráfic*a: 200 µm. **3,** triseriate rays (TLS) / *radios triseriados (SLT)*. Scale bar / *escala gráfica*: 200 µm. **4,** axial parenchyma (arrow) (TLS) / *parénquima axial (flecha) (SLT)*. Scale bar / *escala gráfica*: 50 µm. **5,** alternate to opposite intervessel pitting (TLS) / *puntuaciones intervasculares alternas a opuestas (SLT)*. Scale bar / *escala gráfica*: 20 µm. **6,** opposite to scalariform intervessel pitting (TLS) / *puntuaciones intervasculares opuestas a escalariformes (SLT)*. Scale bar / *escala gráfica*: 50 µm. **7,** opposite to scalariform vessel-ray pitting (RLS) / *puntuaciones radio-vasculares opuestas a escalariformes (SLR)*. Scale bar / *escala gráfica*: 20 µm. **8,** radial cells (RLS) / *células radiales (SLR)*. Scale bar / *escala gráfica*: 200 µm.

cellular, composed of parenchymatic procumbent body cells with one row of square to upright marginal cells.

Discussion. Triseriate rays suggest an affinity to *Nothofagus* subgenus *Lophozonia*, represented in Patagonia by three extant species (*Nothofagus alpina*, *Nothofagus obliqua* and *Nothofagus glauca*) and one hybrid (*Nothofagus leoni* Espinosa). However, all of these species differ from this fossil. *Nothofagus obliqua* and *Nothofagus alpina* have usually biseriate, very rarely triseriate rays (Diaz Vaz, 1987; Rancusi *et al*., 1987; Rivera, 1988). *Nothofagus glauca* is very similar, although rays are commonly biseriate and sometimes triseriate (Rancusi *et al*., 1987). *Nothofagus leoni*, a hybrid between *Nothofagus glauca* and *Nothofagus obliqua* (Donoso and Landrum, 1979), has frequent clusters of vessels and usually triseriate rays as does the specimen just described (Rancusi *et al*., 1987) and is the most similar to the Río Leona specimen.

Morphospecies *N. triseriatum* is similar to the proposed new morphospecies *N. aggregatum* but its rays are commonly biseriate and vessel-ray pits are always circular. *Nothofagoxylon aggregatum* has predominantly triseriate rays, opposite to scalariform vessel-ray pitting and also significantly narrower vessels. Moreover, in *N. triseriatum* vessels are rarely in radial multiples and clusters. *Nothofagoxylon aconcaguense* Pons *et* Vicente (1985) also rarely has radial multiples or clusters, vessels are wider and it has vertically fused rays, a character absent from *N. aggregatum*. *Nothofagoxylon menendezii* Ragonese (1977) has significant lower vessel density, normally biseriate rays and circular or elliptical vessel-ray pits. The new species commonly has clusters or radial multiples of vessels, with a tendency to form diagonal bands in the latewood, opposite to scalariform vessel-ray pitting and normally triseriate rays. These characters allow assigning the fossil to a new morphospecies of *Nothofagoxylon*.

Nothofagoxylon aggregatum is not a common morphospecies, only one specimen was found in Río Leona Formation sediments. *Nothofagoxylon aggregatum* constitutes the third morphospecies of Río Leona Formation fossil woods assigned to *Nothofagus* subgenus *Lophozonia*.

Comments on *Nothofagoxylon* wood

Extant species of *Nothofagus* are divided into four subgenera supported by molecular analysis (Martin and Dowd, 1993; Manos, 1997). Fossil woods with affinity to three of them, *Lophozonia* (*N. triseriatum*, *N. kraeuseli* and *N. aggregatum*), *Nothofagus* (*N. scalariforme*) and *Fuscospora* (*N. ruei*) were found. Only subgenus *Brassospora* was not found, although apparently pollen with this affinity (type "brasii") was found in the sediments (Barreda *et al*., 2009). Poole (2002) also noted and commented the worldwide absence of fossil woods referable to subgenus *Brassospora*.

Fossil woods were classified using Poole's (2002) criteria. She reduced the number of morphospecies, and recognized significant intraspecific anatomical variability. Except for subgenus *Lophozonia*, where five morphospecies considered comparable to extant species were maintained, she suggested affinity to extant subgenera levels, rather than to extant species levels. For example, according to Poole's (2002) criteria for fossil wood morphospecies, wood of extant species *N. pumilio*, *N. antarctica* and *N. betuloides* would be placed in the same morphospecies (*Nothofagoxylon scalariforme*). In addition, variable characters are found in many morphospecies; i.e. intervessel pitting in *N. kraeuseli* can be alternate to scalariform, confirming the intraspecific variability in each morphospecies.

Nothofagaceae fossil woods show a clear dominance in the fossil woods from the Río Leona Formation representing about 70 % of the total samples studied including angiosperms and gymnosperms (Pujana, 2008). The same type of dominance characterizes the fossil woods of the Cerro Dorotea locality (Terada *et al*., 2006), with presumed Oligocene-Miocene age, and Caleta Arctowski fossil forest (Torres and Lemoigne, 1988) from the Eocene-Oligocene of Antarctica. Nothofagaceous fossil wood dominates among the angiosperms from the upper Cretaceous to the Eocene (Cantrill and Poole, 2005). However, Nothofagaceous fossil wood represents less than 50 % of the total woods from the Eocene of Antarctica (Cantrill and Poole, 2005), suggesting that the overall dominance (including angiosperms and gymnosperms) of these trees was posterior. The abundance of Nothofagaceous wood from Patagonia (Terada *et al*., 2006; Pujana, 2008) and from Antarctica (Torres and Lemoigne, 1988) indicates that this group was the dominant element in the arboreal strata of past forests of Antarctica and Patagonia since the Oligocene.

Conclusions

A new morphospecies, *Maloidoxylon cesariae*, with Rosaceae affinity was described and becomes the oldest Rosaceae fossil of South America.

New infrageneric affinity for *Nothofagoxylon ruei* was proposed and a new morphospecies *Nothofagoxylon aggregatum* with Nothofagaceae affinity was described.

Fossil woods with affinity to all the extant *Nothofagus* subgenera, except subgenus *Brassospora*, were found.

Fossil pollen of Nothofagaceae and Rosaceae affinity and fossil leaves of Nothofagaceae affinity were also found in the formation corroborating the presence of the taxa here described.

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