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ARTICLES

A NEW MEGAFLORA (FOSSIL WOOD AND LEAVES) FROM THE MIOCENE OF SOUTHWESTERN PATAGONIA

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Abstract. A new megaflora composed of fossil woods and leaves is described. The bearing sediments overlie the Santa Cruz Formation (early Miocene), making it one of the youngest fossil megafloras described from southern Patagonia. The fossil wood is carbonized and found as clasts within a conglomerate. It includes a few specimens representing Araucariaceae (*Agathoxylon* sp.), Podocarpaceae (*Phyllocladoxylon* sp.), Cupressaceae (*Cupressinoxylon* sp.) and two indeterminable angiosperms with anatomical features consistent with Nothofagaceae. Most leaves are assigned to Nothofagaceae while a few specimens are related to Lauraceae, Typhaceae, Leguminosae, and a conifer. The recovered assemblage suggests a temperate climate similar to that of northern Patagonia today, inhabited by extant relatives of the fossils described herein.

Key words. Fossil woods. Fossil leaves. Arroyo de los Ciervos. Miocene.

Resumen. UNA NUEVA MEGAFLORA (MADERAS Y HOJAS FÓSILES) DEL MIOCENO DEL SUROESTE DE LA PATAGONIA. Una nueva megaflora compuesta por maderas y hojas fósiles es presentada. Los sedimentos portadores sobreyacen a la Formación Santa Cruz (Mioceno inferior), por lo tanto es una de las megafloras más jóvenes del sur patagónico descripta. Las maderas fósiles están carbonizadas y se encuentran como clastos de un conglomerado. Están representadas por unos pocos especímenes de Araucariaceae (*Agathoxylon* sp.), Podocarpaceae (*Phyllocladoxylon* sp.), Cupressaceae (*Cupressinoxylon* sp.) y dos angiospermas no determinadas que poseen una anatomía consistente con la de las Nothofagaceae. Las hojas son en su mayoría asignadas a las Nothofagaceae, acompañadas por Lauraceae, Typhaceae, Leguminosae y una conífera. El conjunto de fósiles sugiere un clima templado similar al actual de la Patagonia norte, donde viven parientes vivos de los fósiles descriptos.

Palabras clave. Maderas fósiles. Hojas fósiles. Arroyo de los Ciervos. Mioceno.

Cenozoic megafloras from southern Patagonia (Argentina) have recently been the subject of numerous studies. The pioneering articles of Dusén (1899), Berry (1922, 1925a, 1925b, 1928, 1935, 1937a, 1937b, 1938), Kräusel (1924), Frenguelli (1941), and Hünicken (1955, 1967) were followed in recent years by a number of papers on fossil wood and leaves from southern Santa Cruz Province in Argentina (Pujana, 2007, 2008, 2009a, b; Pujana *et al.*, 2009; Martínez and Pujana, 2010; Panti, 2010, 2011; Brea *et al.*, 2012; Fernández *et al.*, 2013). Miocene megafloras, mostly fossil leaves, have also been described for Patagonia and adjacent regions (Dusén, 1899; Troncoso, 1991; Hinojosa, 2005; Poole and Cantrill, 2007; Brea *et al.*, 2012). Patagonian megafloras younger than the early Miocene have not been documented.

We describe herein a new wood- and leaf-bearing megaflora from strata younger than “Santacrucense” (early Miocene). In this article some specimens of fossil wood are assigned to fossil-genera while the leaves are assigned to ten morphotypes. Comments about the composition of the fossil forest and comparisons with other megafloras are also included.

STRATIGRAPHIC SETTING

The studied material comes from Neogene strata exposed at Arroyo de los Ciervos(, in the southwestern corner of Santa Cruz Province, Argentina (Fig. 1). The fossil material was collected from a 130 m succession of well-cemented, rounded, clast-supported, medium-sized conglomerates, with minor sandstone and mudstone intercalations (Fig. 2). Below these beds lies a succession of fine to coarse tuffs and tuffaceous sandstones, with some interbedded mudstone layers with preserved root horizons (Fig. 2). The con-

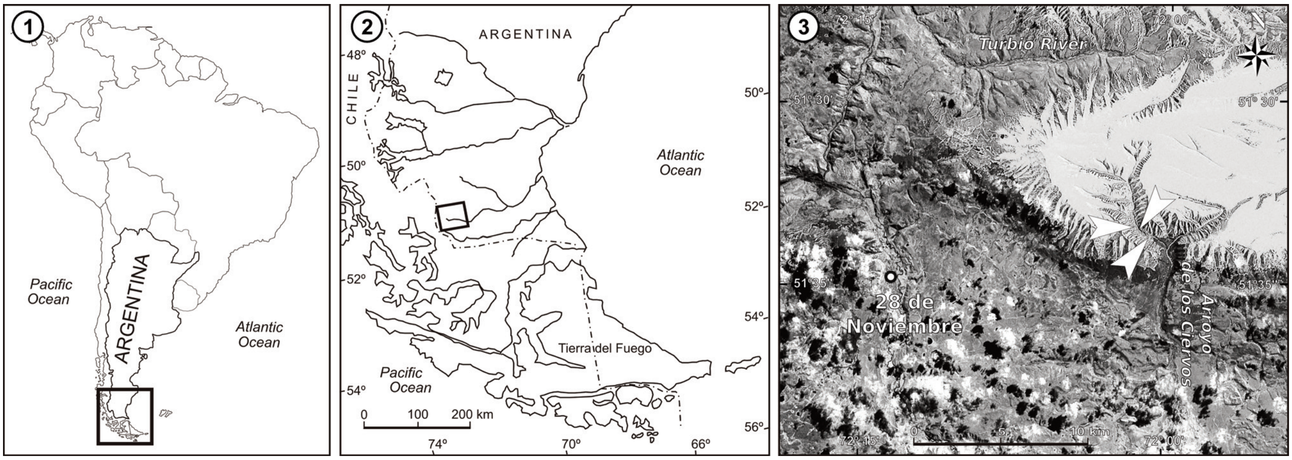

Figure 1. Maps and satellite image of the fossiliferous points. **1,** Map of South America; **2,** Map of southern tip of South America; **3,** Satellite image showing the fossiliferous points (arrowheads).

tact between both sequences is sharp and marks an abrupt change in sedimentation style. The top of the conglomerate strata is marked by a conspicuous bed of up to 25 m of a matrix-supported breccia (Fig. 2). Overlying it is a thick succession of loose, coarse conglomerates of the late Miocene Cordillera Chica Formation (Malumián and Panza, 2000).

These fossil-bearing conglomerates were only mentioned by Brandmayr (1945), who included them within the local, informally named “Santacrucense” stage. Malumián and Panza (2000) included the underlying tuffaceous sediments and the overlying matrix-supported breccia within the Santa Cruz Formation, but they did not mention the 130 m thick conglomeratic beds described here. Formal lithostratigraphic assignment of these beds remains unclear. According to the sedimentological features of these coarse-grained deposits (Fig. 2), they might be a stratigraphic unit different from the Santa Cruz Formation. The age of the conglomeratic strata is restricted by the age of the underlying Santa Cruz Formation, which in the study area was dated as early Miocene (18.1 ± 0.4 Ma) by Fosdick *et al.* (2011). The conglomeratic beds described here overlie the typical beds of the Santa Cruz Formation without transition. This suggests a depositional hiatus and therefore a younger age for the conglomerates. The minimum age for the fossil-bearing conglomerates is restricted by the overlying Cordillera Chica Formation, estimated to be late Miocene (Malumián and Panza, 2000).

The studied carbonized fossil wood and fossil leaf impressions were found within the middle section of the conglomerates (Fig. 2, 3). Fossils were collected at three points along the Arroyo de los Ciervos section and are shown in figure 1: “SC2” (51°33’27.90” S; 72°0’45.40” W) with fossil leaves, “SC3” (51°33’12.85” S; 72°1’14.87” W) with fossil leaves and wood and “SC7” (51°33’10.92” S; 72°1’17.97” W) with fossil wood.

Brandmayr (1945) mentioned abundant silicified fossil wood in the area where our material was collected; the wood mentioned by Brandmayr are large pieces found as clasts lying on the modern bed of a stream; they are of unknown provenance and were not included in our study.

MATERIAL AND METHODS

Carbonized fossil wood (10 samples) was collected from the conglomerates and some of it dried in stoves as it was found under water. Preservation was good enough to observe diagnostic characters for assignment to fossil genera in some samples, whereas only tracheids or vessels and a few additional characters were observed in others. Small fragments of wood were mounted for scanning electron microscopy (SEM) after being gold-coated. In addition, thin sections and acetate peels following standard techniques were obtained (Galtier and Phillips, 1999; Hass and Rowe, 1999), but wood anatomy was only superficially discernible. Whenever possible, descriptions follow the IAWA code for softwood (IAWA committee, 2004) and hardwood (IAWA committee, 1989). The delimitation criteria of Philippe and Bamford (2008) were followed for the gymnosperm fossil-genera. Measurements are given by the average and, in

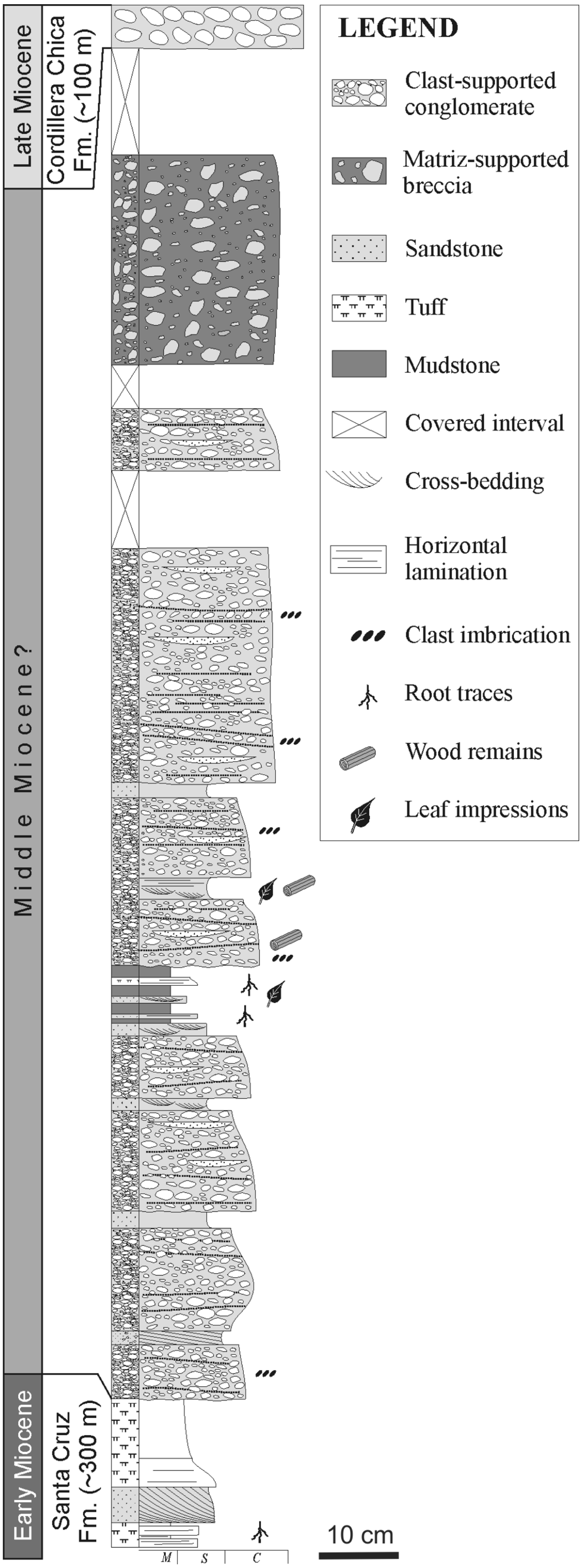

Figure 2. Schematic log of the Arroyo de los Ciervos outcrops.

Figure 3. Carbonized wood embedded in a conglomerate. Scale: 11 cm.

parentheses, the range.

Fossil leaves are preserved as impressions in sandstone (21 samples). Fossil leaves are classified strictly as numerical morphotypes based on morphological affinities, following the procedures of Johnson (1989). Terminology and systematic descriptions follow Ellis *et al.* (2009). Fossil leaves were compared to other southern South American fossils and extant taxa. Suprageneric nomenclature follows Chase and Reveal (2009) and Christenhusz *et al.* (2011) for gymnosperms and APG III (2009) for angiosperms.

The fossils are housed in the palaeobotanical collection of the Museo Padre Molina in Santa Cruz under the accession numbers MPM PB 14470 to 14479 for the fossil wood and MPM PB 14933 to 14953 for the fossil leaves. Samples (*i.e.*, MPM PB 14942) may have one or more leaf imprints, indicated as A, B, C, etc.

SYSTEMATIC PALAEOBOTANY

Fossil wood

Class Equisetopsida C. Agardh, 1825

Subclass Pinidae Cronquist, Takht. and Zimmermann, 1966

Order Araucariales Gorozhankin, 1904

Family Araucariaceae Henkel and W. Hochstetter, 1865 nom. cons.

Genus ***Agathoxylon*** Hartig, 1848

Type species. *Agathoxylon cordaianum* Hartig, 1848. Triassic, Coburg, Freistaat Bayern, Germany.

Agathoxylon sp.
Figure 4.1–3

Material. MPM PB 14472 and 14473.
Geographic occurrence. Arroyo de los Ciervos, Santa Cruz, Argentina.
Stratigraphic occurrence. Arroyo de los Ciervos strata (Miocene).
Description. Radial pitting araucarian, usually biseriate, sometimes triseriate and rarely uniseriate (Fig. 4.1–2). Radial pits 8.2 (7–10) µm in vertical height. Cross-fields with 2 to 5 contiguous cupressoid pits *c.* 7 µm in vertical height

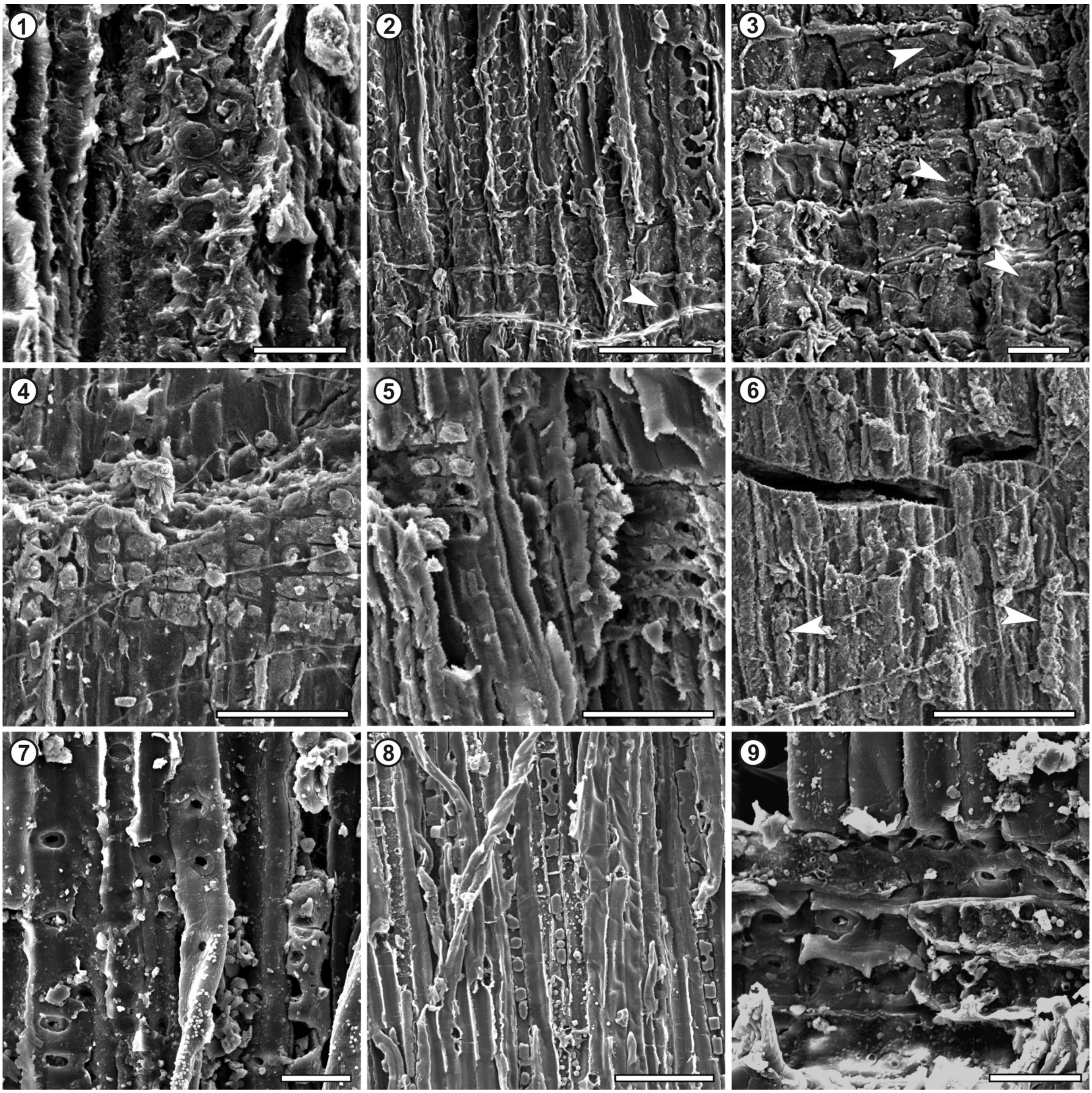

Figure 4. 1–3, ***Agathoxylon*** sp. **1, MPM PB** 14472, alternate triseriate radial pitting; **2, MPM PB** 14473, alternate biseriate radial pitting and cross-fields with cupressoid pits (arrowheads); **3, MPM PB** 14473, cross-fields with contiguous cupressoid pits (arrowheads). **4–6,** ***Cupressinoxylon*** sp. **4, MPM PB** 14479, window-like cross-field pitting; **5, MPM PB** 14479, window-like cross-field pitting; **6, MPM PB** 14479, uniseriate low to medium rays. **7–9,** ***Phyllocladoxylon*** sp. **7,** MPM PB 14478, scattered uniseriate pitting; **8, MPM PB** 14478, axial parenchyma; **9, MPM PB** 14478, cupressoid cross-field pitting, pits arranged in columns ~~(arrowhead)~~. Scale bar= 1, 3, 7, 9 = 20 µm; 2, 4–5 50 µm; 6, 8 = 100 µm.

(Fig. 4.2–3). Rays uniseriate and low, 1–5 cells in height (Fig. 4.3).

Remarks. Araucarian radial pitting and cross-field pitting type allow us to assign these two samples to *Agathoxylon* according to Philippe and Bamford (2008). *Agathoxylon* is a valid name (Philippe and Bamford, 2008) commonly applied to fossil wood with araucarian pitting and cross-field type (Ottone and Medina, 1998; Zamuner and Falaschi, 2005; Crisafulli and Herbst, 2008; Vera and Césari, 2012; Pujana *et al.*, 2014; Rößler *et al.*, 2014). Poor preservation precludes the use of other diagnostic characters (presence of resin plugs, growth ring type, etc.) that would allow assignment to fossil species. The wood anatomy is typical of the living Araucariaceae, which have alternate pitting and contiguous cupressoid pits in the cross-fields (Greguss, 1955). Moreover, the anatomy is consistent with that of *Araucaria araucana* nowadays living in northern Patagonia (Tortorelli, 1956; Rancusi *et al.*, 1987).

Araucariaceae is now almost restricted to the southern hemisphere and comprises about 35 species (Eckenwalder, 2009). Araucariaceae megafossils are common in Patagonia since the Jurassic, but after a peak of abundance in the Early Cretaceous, the family starts to decline (Panti *et al.*, 2012). The Patagonian fossil record of the family includes wood, leaves, reproductive structures and pollen (Panti *et al.*, 2012). The family persists in Patagonia, where it occupies a small area of distribution more than 1200 km north from the fossiliferous locality described here (Enright *et al.*, 1995). Presence of Araucarian wood in the studied area is consistent with a continuous record of the family in southwestern Patagonia until at least the latest Miocene.

Family PODOCARPACEAE Endler, 1847 nom. cons.

Genus ***Phyllocladoxylon*** Gothan, 1905

Type species. *Phyllocladoxylon antarcticum* Gothan, 1908. Paleogene, Marambio (Seymour) Island, Antarctica.

Phyllocladoxylon sp.
Figure 4.4–6

Material. MPM PB 14479.

Geographic occurrence. Arroyo de los Ciervos, Santa Cruz, Argentina.

Stratigraphic occurrence. Arroyo de los Ciervos strata (Miocene).

Description. Radial pitting abietinean, uniseriate. Cross-fields with one large simple pit (oopore), circular to horizontally elongate and with *c.* 8–9 μm in vertical height (Fig. 4.4–5). Rays uniseriate and medium (3–8 cells) in height (Fig. 4.6).

Remarks. Pitting arrangement, absence of tertiary thickenings and cross-field type (large oopores) allows assignment of this sample to *Phyllocladoxylon* (Philippe and Bamford, 2008). Another wood fossil-genus of the Podocarpaceae is *Podocarpoxylon* Gothan, which differs from *Phyllocladoxylon* by having bordered and smaller cross-field pits and frequently more than one pit per cross-field (Philippe and Bamford, 2008; Pujana *et al.*, 2014). *Protophyllocladoxylon* Kräusel differs from *Phyllocladoxylon* by having mixed or araucarian radial pitting, but shares with it the cross-field type (Philippe and Bamford, 2008; Zhang *et al.*, 2010). *Phyllocladoxylon*, particularly abundant in the Eocene of Antarctica (Pujana *et al.*, 2014), was also mentioned for the Cenozoic of Patagonia by Kräusel (1924), Nishida *et al.* (1992) and Terada *et al.* (2006a), indicating that this fossil-genus was a frequent element of the regional flora. In addition, Poole and Cantrill (2007) described a similar carbonized wood (xylotype 5) from the Malvinas (Falkland) Islands.

Phyllocladoxylon is similar to the wood of several living podocarpaceaen genera from the Southern Hemisphere (Pujana *et al.*, 2014). This includes *Phyllocladus* Mirbel from Australasia and *Halocarpus* Quinn from New Zealand (Eckenwalder, 2009). The Podocarpaceae comprises mainly Southern Hemisphere conifers representing about 156 species of evergreen trees and shrubs (Eckenwalder, 2009). Several species of the Podocarpaceae inhabit Patagonia today, but none have *Phyllocladoxylon* wood type.

Order CUPRESSALES Link 1829

Family CUPRESSACEAE Gray 1822 nom. cons.

Genus ***Cupressinoxylon*** Göppert 1850 nom. cons.

Type species. *Cupressinoxylon gothanii* Kräusel 1920 typ. cons. Miocene, Węgliniec, Województwo dolnośląskie, Poland.

Cupressinoxylon sp.
Figure 4.7–9

Material. MPM PB 14478.
Geographic occurrence. Arroyo de los Ciervos, Santa Cruz, Argentina.
Stratigraphic occurrence. Arroyo de los Ciervos strata (Miocene).
Description. Radial pitting abietinean, uniseriate (Fig. 4.6). Radial pits 7–8 µm in vertical height. Cross-fields with frequently 2, sometimes 1 to 4 spaced cupressoid pits *c.* 4–5 µm in vertical height, ordered in rows and columns (Fig. 4.9). Rays uniseriate and very low, 1–3 cells in height (Fig. 4.8). Axial parenchyma present (Fig. 4.8–9).
Remarks. Vaudois and Privé (1971), in a revision of cupressoid fossil wood, state that *Cupressinoxylon* has a wide definition that can include almost all fossil woods of the family. However, scattered uniseriate radial pitting (abietinean) and cupressoid cross-field pits arranged in rows and columns, allow us to assign this sample to *Cupressinoxylon* according to Philippe and Bamford (2008). Although *Cupressinoxylon* can be assigned to the Podocarpaceae with cupressoid cross-field pitting (Pujana *et al.*, 2014), the cross-field pits arranged in rows and columns –as observed in the sample (Fig. 4.9)– and the very low rays, suggest affinities with the Cupressaceae rather than the Podocarpaceae. This fossil-genus has been previously recorded in Patagonia (Kräusel, 1924; Nishida, 1984a, b; Nishida and Nishida, 1988).

Cupressaceae is a conifer family present in both the southern and northern hemispheres and includes about 136 species (Eckenwalder, 2009). The family is present in Patagonia since the Jurassic (Escapa *et al.*, 2008), but during the Cenozoic it was a minor part of the forest vegetation. In modern Patagonia there are three species characterized by having a homogeneous wood anatomy (Roig, 1992). The fossil shares characters with these species, but particularly with *Pilgerodendron uviferum* (D. Don) Florin and *Fitzroya cupressoides* (Molina) I.M. Johnston, which have very short rays (Roig, 1992; Rancusi *et al.*, 1987).

Subclass Magnoliidae Novák ex Takhtajan, 1967

Angiosperm wood 1
Figure 5.1–2

Material. MPM PB 14475.
Geographic occurrence. Arroyo de los Ciervos, Santa Cruz, Argentina.
Stratigraphic occurrence. Arroyo de los Ciervos strata (Miocene).
Description. Vessels solitary or in short (2–3) radial series (Fig. 5.1–2). Perforation plates simple (Fig. 5.2). Vessel radial diameter *c.* 17–22 µm.
Remarks. Only a few diagnostic characters are preserved in this piece of wood. Those present (short radial series, small vessels, simple perforation plates) are consistent with the Nothofagaceae, but the few preserved characters do not preclude other angiosperm families. The Nothofagaceae dominate Patagonian fossil-wood assemblages since at least the Oligocene (Pujana, 2008, 2009a) and numerous fossil wood specimens of this family have been described from this region (Poole, 2002; Terada *et al.*, 2006a, b; Pu-

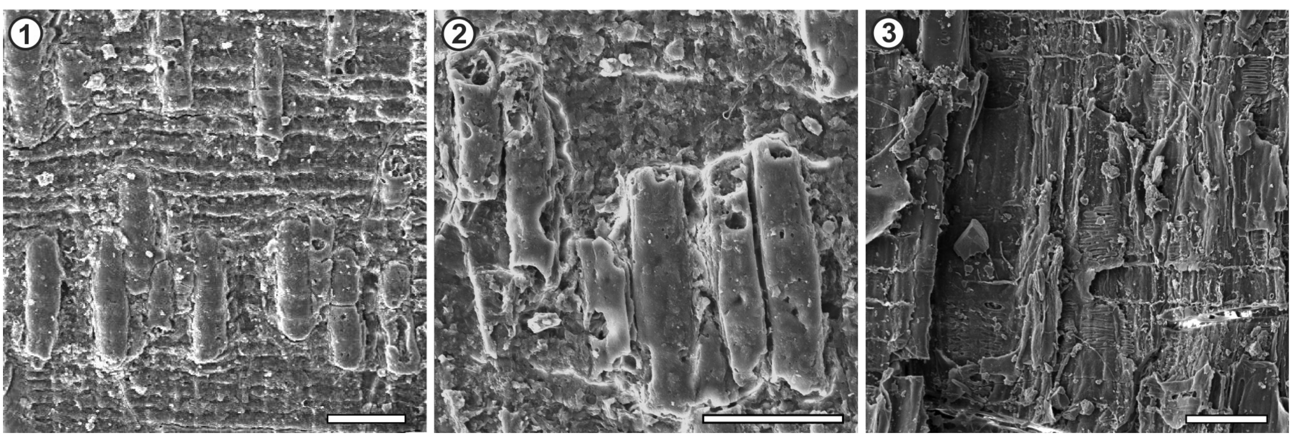

Figure 5. 1–2, “Angiosperm wood 1”, **MPM PB** 14475; **1,** Vessels solitary or in short radial series; **2,** Vessel elements with simple perforation plates. **3,** “Angiosperm wood 2”, **MPM PB** 14477; scalariform intervessel pitting and simple perforation plates (arrowhead). Scale bar= 50 µm.

jana, 2009a; Brea *et al.*, 2012). The abundance of leaves of Nothofagaceae (see below) in the same sediments suggests that this wood probably belongs in this family.

Angiosperm wood 2
Figure 5.3

Material. MPM PB 14476 and 14477.
Geographic occurrence. Arroyo de los Ciervos, Santa Cruz, Argentina.
Stratigraphic occurrence. Arroyo de los Ciervos strata (Miocene).
Description. Vessels with scalariform intervessel pitting (Fig. 5.3). Perforation plates simple. Vessel radial diameter *c.* 40–70 µm.
Remarks. These two samples are consistent with the Nothofagaceae, particularly *Nothofagus pumilio* (Poeppig and Endler) Krasser and *Nothofagus antarctica* (G. Forst.) Oersted of the subgenus *Nothofagus*, which has scalariform intervessel pitting (Rancusi *et al.*, 1987).

Fossil leaves
Class Equisetopsida C. Agardh 1825
Subclass Pinidae Cronquist, Takht. and Zimmermann 1966
? Order Araucariales Gorozhhankin 1904

Morphotype 1
Figure 6.1

Material. MPM PB 14949.
Geographic occurrence. Arroyo de los Ciervos, Santa Cruz, Argentina.
Stratigraphic occurrence. Arroyo de los Ciervos strata (Miocene).
Description. Shoots bearing linear lanceolate leaves up to 20 mm long and 4.7 mm wide. Leaf margins entire. Apex incomplete and base poorly preserved, attachment to the stem may be as wide as the leaf.
Remarks. This leaf resembles the previously described "Type II" of de Laubenfels (1953). All families of living conifers have this type of leaf at some ontogenetic stage (de Laubenfels, 1953). The fossil is similar to *Elatocladus seymourensis* Cantrill, Tosolni & Francis (Cantrill *et al.*, 2001). This conifer, as observed herein, is represented by shoots bearing linear-lanceolate leaves with entire margins. However, leaf attachment to the stem and venation are not preserved in the studied material. Neither preserved are the apex and base of the leaves, precluding closer comparisons.

The presence of wood of the Araucariaceae and Podocarpaceae in the same sediments suggests that this morphotype is probably related to one or the other of these families.

Subclass Magnoliidae Novák ex Takhtajan, 1967
Order Poales Small, 1903
Family Typhaceae Jussieu, 1789 nom. cons.

Morphotype 3
Figure 6.3

Material. MPM PB 14948.
Geographic occurrence. Arroyo de los Ciervos, Santa Cruz, Argentina.
Stratigraphic occurrence. Arroyo de los Ciervos strata (Miocene).
Description. Leaf incomplete, but probably linear and with entire margins. Parallelodromous vein framework, with two orders of veins regularly spaced. More than 15 veins of the first order separated from each other by 0.7 mm. Between these veins there are 9 to 12 minor veins, separated from each other by 0.04 mm, arranged parallel to each other and interconnected by subordinate veins.
Remarks. Linear leaves with several parallel veins running longitudinally are common in many monocotyledonean families. The Poaceae, Cyperaceae, Restionaceae, Potamogetonaceae, Hydrocharitaceae, Arecaceae, and Sparganiaceae/Typhaceae are families with reliable micro and/or macrofossil records in Argentina (Gandolfo *et al.*, 2010). Monocot leaves described from Patagonia usually have been assigned to *Poacites* sp. (Berry, 1925b, 1937b; Fiori, 1939). Other fossil-species are *Chusquea oxyphylla* Frenguelli and Parodi (Frenguelli and Parodi, 1941) and *Thypha kurtzii* Hünicken (Hünicken, 1995). Previous records of *Poacite*s sp. consist of a leaf fragment with longitudinal parallel venation (Berry, 1925b), a fragmentary specimen, which shows three major veins running longitudinally and separated by minor parallel veins (Berry, 1937b), and a small, parallel-veined leaf (Fiori, 1939). *Chusquea oxyphylla* is represented

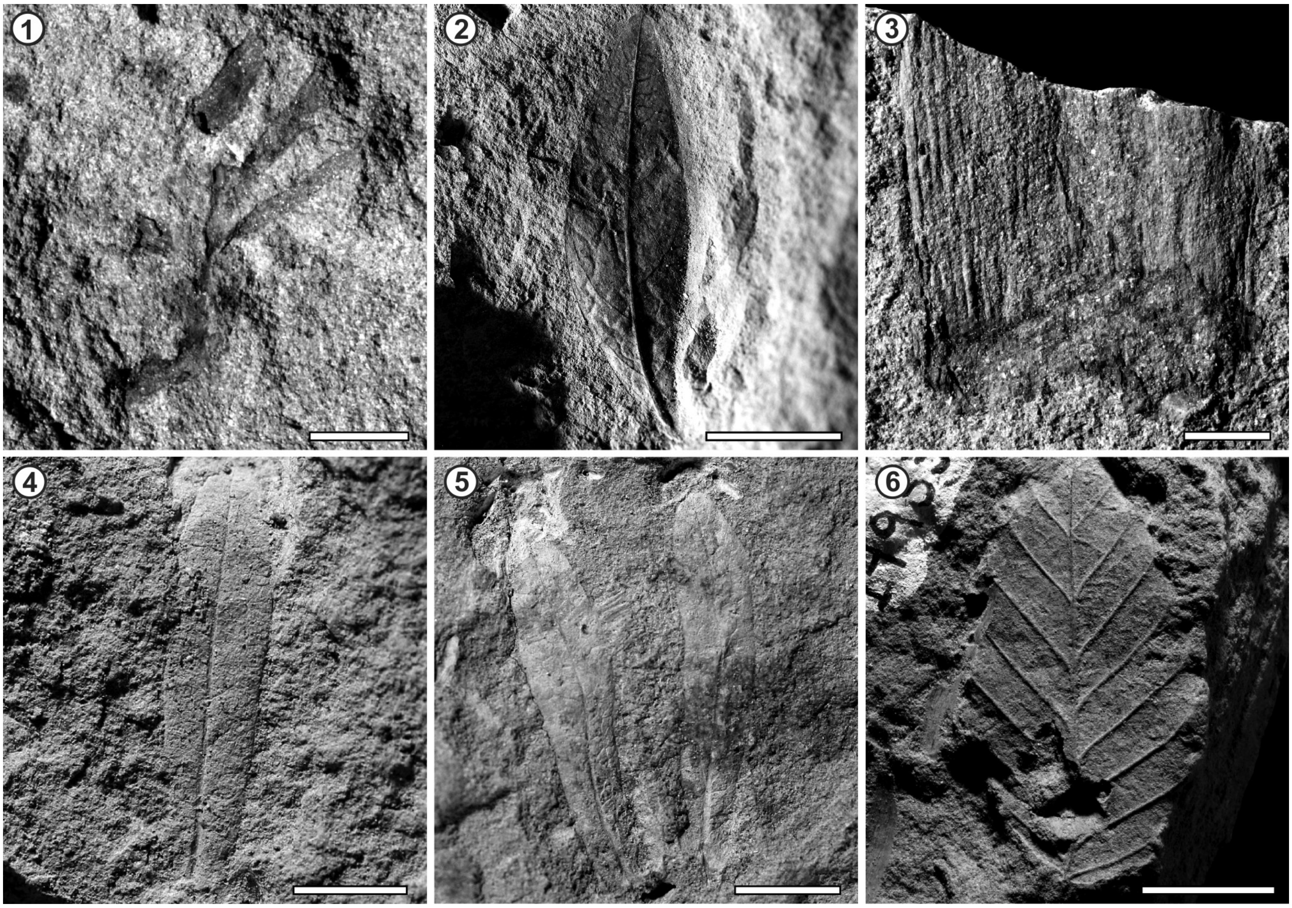

Figure 6. 1, "Morphotype 1", Araucariales, **MPM PB** 14949. **2,** "Morphotype 2", Lauraceae, **MPM PB** 14938. **3,** "Morphotype 3", Typhaceae, **MPM PB** 14948. **4,** "Morphotype 4", Leguminosae, **MPM PB** 14940. **5,** "Morphotype 4", Leguminosae, **MPM PB** 14940. **6,** "Morphotype 5", Nothofagaceae, **MPM PB** 14933. Scale bar= 1–2, 6 = 10 mm. 3–5 = 5 mm.

by stems bearing linear-lanceolate and acuminate leaves that are very small, 15–17 mm long (Frenguelli and Parodi, 1941), unlike the material described herein. The material described here can be positively compared to *Typha kurtzii* Hünicken based on lamina shape, parallel venation and size (Hünicken, 1995). The frequency of the two orders of veins resembles the studied material. According to Hünicken (1995), *Typha kurtzii* differs from the extant *Typha domingensis* Persoon by the number of minor veins that run parallel between the major longitudinal veins. In our specimen these minor veins are not well preserved.

The southernmost distribution of extant Thyphaceae extends to northern Patagonia (Romanutti, 2012), suggesting a wider distribution of this family at least until the latest Miocene. Pollen of Thyphaceae is very similar to that of Sparganiaceae and it is present in Patagonia since the Palaeocene (Archangelsky, 1973).

Order Laurales Jussieu ex Berchtold and J. Presl, 1820

Family Lauraceae Jussieu, 1789 nom. cons.

Morphotype 2

Figure 6.2

Material. MPM PB 14938.

Geographic occurrence. Arroyo de los Ciervos, Santa Cruz, Argentina.

Stratigraphic occurrence. Arroyo de los Ciervos strata (Miocene).

Description. Marginal blade attachment, microphyll laminar size, L:W ratio 3:1, elliptic laminar shape, with medial and basal symmetry. Margin entire, with acute apex angle, straight apex shape, acute base angle, and cuneate base shape. Primary venation pinnate with no naked basal veins, one basal vein and no agrophic veins. Primary vein curved towards the leaf base. Major secondaries simple, brochidodromous, with regular spacing, angles increasing proximally and excurrent attachment to midvein. Interior secondaries, minor secondaries, intersecondaries and intramarginal vein absent. Intercostal tertiary veins reticulate, exterior tertiaries looped.

Remarks. The venation pattern and overall leaf traits are common to many angiosperm families. Among Patagonian fossils, it is similar to *Embothrium precoccineum* Berry (Berry, 1938). The two forms share an acute and cuneate base shape, entire margin, and pinnate primary venation with brochidodromous secondary veins. They differ in tertiary vein order and leaf shape, which in *E. precoccineum* are respectively percurrent and asymmetrical and oblong. Extant *Embothrium coccineum* J.R. Forster and G. Forster has ovate to oblong or lanceolate, rarely linear-lanceolate leaves with entire margin and tertiary veins categorized as random reticulate, characters comparable with the morphotype described here (González *et al.*, 2007). The wide cuneate base and the venation pattern are shared with fossils of the Lauraceae in addition to *E. precoccineum*. Among these, *Nectandra prolifica* Berry seems most similar, sharing the acuminate base and apex, the prominent midvein more or less curved, secondary veins openly spaced and sweepingly curved and ascending, and overall leaf shape. This species shows great variation in size and form, ranging from small, slender, falcate, and acuminate forms to broader, more ovate, and acuminate ones (Berry, 1938). The specimen described here resembles the smaller-ones. A considerable number of extant species belong to *Nectandra* Rol. ex Rottb and have leaves resembling this morphotype.

Fossil leaves assigned to Lauraceae are common in Patagonia (Berry, 1925b, 1938; Hünicken, 1967; Troncoso, 1991, 1992, 2002; Panti, 2010). Lauracean leaves were described from cuticles from early Paleocene rocks of Patagonia (Iglesias *et al.*, 2008). The Lauraceae is a large family distributed mainly in tropical regions, although some genera (*e.g.*, *Persea*) reach temperate areas (Heywood *et al.*, 2007). Today, *Nectandra* spp. inhabit northern Argentina and are absent in Patagonia (Rohwer and Kubitzki, 1993).

Order FABALES Lindler, 1836
Family LEGUMINOSAE Jussieu, 1789 nom. cons.

Morphotype 4
Figure 6.4–5

Material. MPM PB 14940.

Geographic occurrence. Arroyo de los Ciervos, Santa Cruz, Argentina.

Stratigraphic occurrence. Arroyo de los Ciervos strata (Miocene).

Description. Leaves with marginal blade attachment, microphyll laminar size, L:W ratio 4:1, elliptical laminar shape and medial and basal symmetry. Margin entire with acute apex angle, straight and somewhat retuse apex shape, acute base angle, and cuneate base shape. Primary venation pinnate with no naked basal veins, one basal vein and no agrophic veins. Major secondaries simple brochidodromous with regular spacing, angles increasing proximally and excurrent attachment to midvein. Interior secondaries, minor secondaries, intersecondaries absent and intramarginal vein present. Intercostal tertiary veins reticulate, exterior tertiaries looped.

Remarks. These specimens resemble *Prosopis* L. (Leguminosae) as described by Anzótegui *et al.* (2007). They share the acute apex, venation pattern, angle of divergence of the secondary veins and its variations, and overall lamina shape.

The family Leguminosae is documented worldwide in the Cenozoic fossil record. In Patagonia, fossils are represented by pollen, leaf impressions and wood (Anzótegui *et al.*, 2007; Pujana *et al.,* 2011) and the first fossil leaves from Patagonia were described by Berry (1938) from late Paleocene rocks (Anzótegui *et al.*, 2007). The family has several modern representatives in Patagonia, mostly papilionoids of the Patagonian Steppe (Cabrera, 1971).

Order FAGALES Engler, 1892
Family NOTHOFAGACEAE Kuprianova, 1962

Morphotype 5
Figure 6.6

Material. MPM PB 14933, 14935.

Geographic occurrence. Arroyo de los Ciervos, Santa Cruz, Argentina.

Stratigraphic occurrence. Arroyo de los Ciervos strata (Miocene).

Description. Leaves with marginal blade attachment, petiole medium, 4 mm long; microphyll laminar size, L:W ratio 1–2:1, ovate laminar shape with medial and basal symmetry. Serrate margin with acute apex angle, straight apex, acute base angle, and rounded base shape. Primary venation pinnate with no naked basal veins, one basal vein and no agrophic veins. Major secondaries craspedodromous with irregular spacing, uniform angles and decurrent attachment to midvein. Interior secondaries, minor secondaries and intersecondaries absent. Intercostal tertiary veins percurrent. Teeth are inconspicuous.

Remarks. The studied material can be compared to several fossil species of *Nothofagus.* Among these, the fossil morphotype resembles *N. simplicidens* Dusén and *N. variabilis* Dusén in leaf shape and venation (Dusén, 1899).Differences include, for *N. simplicidens*, a leaf margin formed by teeth of two orders and, for *N. variabilis*, a leaf margin formed by simple teeth and the presence of a fimbrial vein (Tanai, 1986). The poor preservation of the leaf margin in the analyzed specimens prevents a closer comparison, but a closer relationship to *N. variabilis* is indicated by the wide-ovate lamina shape, the irregularly spaced secondary veins, and the more widely spaced percurrent tertiaries.

According to Romero and Dibbern (1985) *Nothofagus variabilis* is very similar to leaves of the extant species *Nothofagus obliqua* (Mirbel) Oersted and *Nothofagus glauca* (Philippi) Krasser. These are deciduous trees of the subgenus *Lophozonia* (Turczaninow) Krasser that live in Patagonia today. Differences between these two species include leaf symmetry and the course of the primary and secondary veins.

The Nothofagaceae has a rich fossil record in Patagonia and Antarctica that includes pollen, leaves and wood (Jordan and Hill, 1999; Poole, 2002). The biogeography of the family has been the subject of numerous studies (Hill and Jordan, 1993; Swenson *et al.,* 2001; Heads, 2006). Western forests of Patagonia today are mainly composed of large trees belonging to the Nothofagaceae. The family is also present in New Zealand and Australasia (Heywood *et al.*, 2007).

Morphotype 6

Figure 7.1

Material. MPM PB 14942–14943.

Geographic occurrence. Arroyo de los Ciervos, Santa Cruz, Argentina.

Stratigraphic occurrence. Arroyo de los Ciervos strata (Miocene).

Description. Marginal blade attachment, microphyll laminar size, L:W ratio 1–2:1, laminar shape ovate with medial and basal symmetry. Margin serrate with acute apex angle, straight apex, obtuse base angle, and convex to rounded base shape. Primary venation pinnate with no naked basal veins, one basal vein and no agrophic veins. Primary venation somewhat sinuous in the upper part of the blade. Major secondaries simple, craspedodromous, decurrent attachment to midvein, regularly spaced and emerging at acute angles decreasing towards the base. Interior secondaries, minor secondaries and intersecondaries absent. Intercostal tertiary veins percurrent. Teeth poorly preserved.

Remarks. Venation and laminar shape suggest placing the specimens in the genus *Nothofagus*. Among the fossil species assigned to *Nothofagus*, they are more similar to *N. simplicidens* Dusén, with which the fossil shares a somewhat sinuous midvein and craspedodromous secondaries emerging at increasingly acute angles. A closer comparison with *N. simplicidens* is precluded because certain diagnostic characters (broadly ovate lamina with acute apex and rounded and obtuse shape of base shape; Tanai, 1986) cannot be assessed because of poor preservation. Apparently, *N. simplicidens* lacks a close living relative. It is very similar to another fossil species, *N. australis* Dusén (Romero and Dibbern, 1985), and Tanai (1986) suggests that they are synonyms.

Morphotype 7

Figure 7.2

Material. MPM PB 14950.

Geographic occurrence. Arroyo de los Ciervos, Santa Cruz, Argentina.

Stratigraphic occurrence. Arroyo de los Ciervos strata (Miocene).

Description. Lamina incomplete. Margin serrate with obtuse apex angle, rounded apex, base not preserved. Primary venation pinnate. Primary venation sinuous in the upper part of the blade. Major secondaries simple craspedodromous,

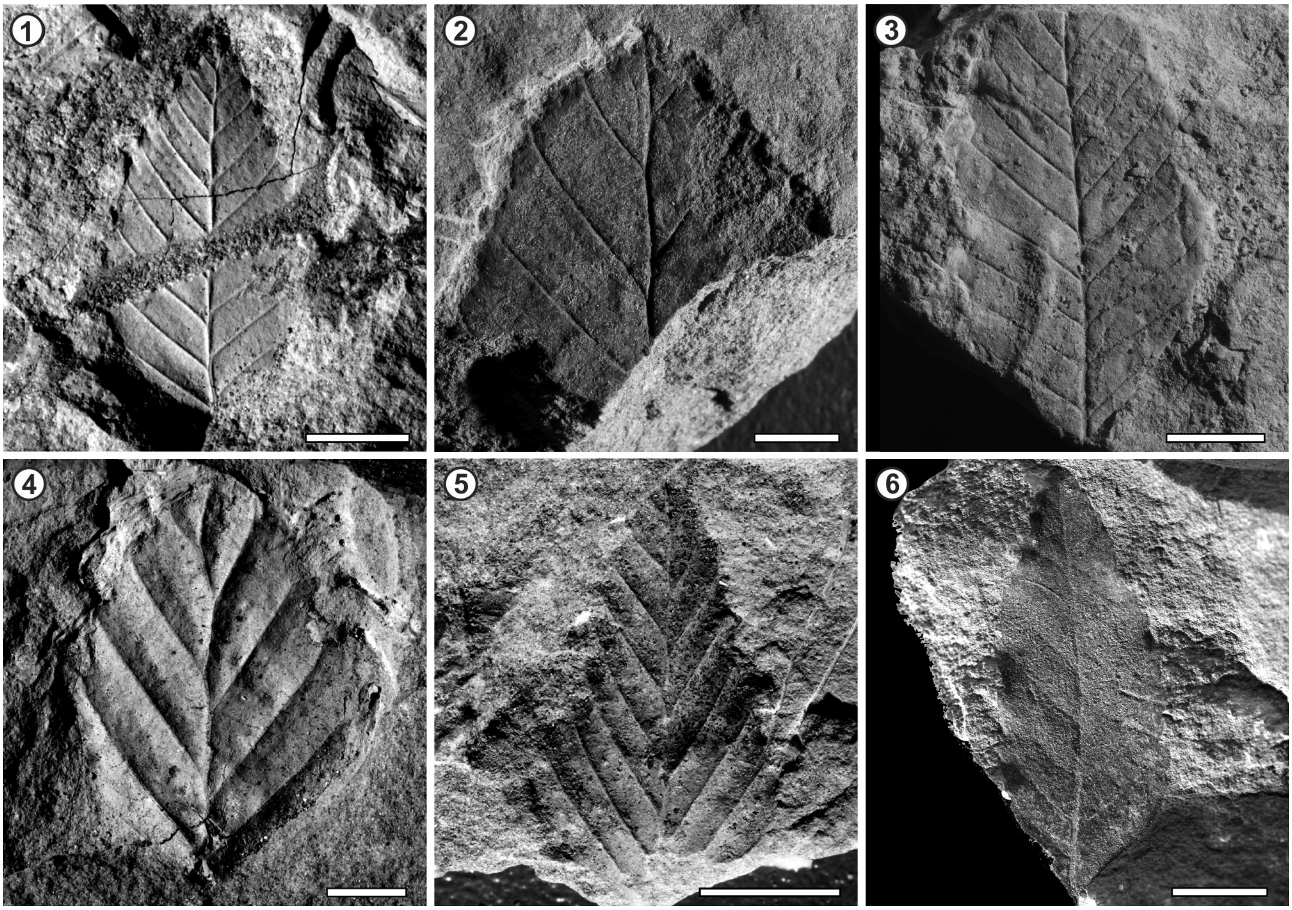

Figure 7. 1, "Morphotype 6", Nothofagaceae, **MPM PB** 14942;. **2,** "Morphotype 7", Nothofagaceae, **MPM PB** 14950; **3,** "Morphotype 8", Nothofagaceae, **MPM PB** 14934; **4,** "Morphotype 9", Nothofagaceae, **MPM PB** 14938; **5,** "Morphotype 9", Nothofagaceae, **MPM PB** 14941; **6,** "Morphotype 10", Rosaceae, **MPM PB** 14946. Scale bar= 1, 3, 5–6 = 10 mm. 2, 4 = 5mm.

regularly spaced and emerging at acute angles. Interior secondaries, minor secondaries and intersecondaries absent. Teeth poorly preserved.

Remarks. This leaf type resembles the fossil species *N. crenulata* Dusén (Dusén, 1908), which is characterized by small leaves with obtuse, blunt apex and a pinnate midvein that is sinuous towards the apex (Tanai, 1986). Our specimen is larger than those described by Dusén, but they share regularly spaced secondary veins. Dusén (1908) compared *N. crenulata* to extant *N. cunninghami*, and Romero and Dibbern (1985) underscored similarities to *N. pumilio*, which differs from *N. crenulata* only in shape, pattern of third veins, and angle of emergence of secondary veins. According to Tanai (1986), *N. crenulata* is remarkably similar to the extant *N. antarctica* (Forst.) Oerst from Patagonia.

Morphotype 8
Figure 7.3

Material. MPM PB 14934.

Geographic occurrence. Arroyo de los Ciervos, Santa Cruz, Argentina.

Stratigraphic occurrence. Arroyo de los Ciervos strata (Miocene).

Description. Marginal blade attachment, microphyll laminar size, L:W ratio 2–3:1, ovate to lanceolate laminar shape. Primary venation pinnate, primary vein nearly straight. Major secondaries simple craspedodromous, decurrent, attached to midvein, regularly spaced and emerging at acute angles from the midvein. Secondary veins straight in course and abruptly curved towards the margin. Interior and minor secondaries and intersecondaries absent. Intercostal tertiary veins percurrent. Teeth poorly preserved.

Remarks. This morphotype shares with *Nothofagus subferruginea* (Dusén) Tanai an ovate-lanceolate lamina shape, a similar number of subopposite craspedodromous secondary veins (10 to 18) and percurrent tertiaries. According to Tosolini *et al*. (2013), *N. subferruginea* has one order of evenly spaced teeth, each having a concave acroscopic and convex to flexous basiscopic side, simple apex and rounded sinus. However, leaf margin of the specimen studied herein are poorly preserved precluding further comparisons of the teeth and secondary-vein development. In *N. subferruginea* the secondaries abruptly arise along the basal side of the tooth (Tanai, 1986). Morphotype 8 is also similar *to Nothofagus glaucifolia* Dutra, but has opposite secondary veins and an asymmetrical leaf base. *Nothofagus subferruginea* and *N. glaucifolia* also differ by the margin; the former has a mostly single-serrated margin, whereas the latter has a double-serrated one. Despite these differences, our specimen shares a greater number of features with *N. subferruginea*. According to Tanai (1986) the fossil leaves of *N. subferruginea* are closely similar to the extant *N. alessandri* Espinosa.

Morphotype 9
Figure 7.4–5

Material. MPM PB 14938–14939, 14941, 14944–14945, 14953

Geographic occurrence. Arroyo de los Ciervos, Santa Cruz, Argentina.

Stratigraphic occurrence. Arroyo de los Ciervos strata (Miocene).

Description. Marginal blade attachment, microphyll laminar size, L:W ratio 1–2:1, ovate to elliptic-oblong laminar shape; venation plicate. Margin serrate with acute apex angle, base cuneate, broadly acute or obtuse. Primary venation pinnate, primary vein nearly straight, somewhat sinuous towards the apex. Secondary veins simple craspedodromous, decurrent attached to midvein, regularly spaced and emerging at acute angles. Secondary veins straight in course; interior and minor secondaries and intersecondaries absent. Tertiary veins percurrent. Teeth poorly preserved.

Remarks. This morphotype groups all the specimens that have plicate venation, which is a reliable indication of deciduousness in the genus *Nothofagus* (Hill and Jordan, 1993). According to Tanai (1986), all species of the section *Nothofagus* are deciduous and lack a fimbrial vein. This morphotype has two forms, one more similar to the fossil *N. densinervosa* (MPM PB 14941, 14953) and another similar to the fossil *N. crenulata* (MPM PB 14938–39, 14944–45). These two fossil-species are included in the section *Nothofagu*s. However, many descriptions of these fossil-species (Dusén, 1899; Tanai, 1986) include illustrations of leaves that are plicate as well as leaves that are not plicate, suggesting that a revision of the fossil-species assigned to the genus *Nothofagus* is necessary. According to Tanai (1986), *N. densinervosa* is closely related to extant *N. pumilio* (Poepp. et Endl.) Oerst. Plicate venation and size in *N. densinervosa* is also comparable to extant deciduous *N. gunnii* (Hook.f.) Oerst. living in Tasmania (Tosolini *et al.,* 2013).

Incertae sedis
Morphotype 10
Figure 7.6

Material. MPM PB 14946.

Geographic occurrence. Arroyo de los Ciervos, Santa Cruz, Argentina.

Stratigraphic occurrence. Arroyo de los Ciervos strata (Miocene).

Description. Marginal blade attachment, microphyll laminar size, L:W ratio 2:1, ovate laminar shape with medial and basal symmetry. Serrate margin with acute apex angle, straight apex, acute base angle, and convex to rounded base shape. Primary venation pinnate with no naked basal veins, one basal vein and no agrophic veins. Major secondaries craspedodromous with regular spacing, uniform angles and decurrent attachment to midvein. Interior and minor secondaries and intersecondaries absent and fimbrial vein present. Intercostal tertiary veins poorly preserved, apparently percurrent. Tooth spacing regular, probably with a single order of teeth. Sinus shape angular. Teeth poorly preserved.

Remarks. Although the fossil is not well preserved, the secondary veins and the teeth resemble some fossil Rosaceae, like *Acaena brandmayri* Frenguelli*,* from the Oligocene of southern Patagonia (Frenguelli, 1941). However, the leaf apex in the specimen described here seems to be more acute and not rounded as in *Acaena*. In addition, there are similarities in venation pattern and leaf margin and shape with the fossil species *Roophyllum serratum* Dusén and *Roophyllum nordenskjoldi* Dusén from southern Patagonia (Dusén, 1899; Panti, 2011).

Fossil wood with similarities to the Rosaceae has been found in older sediments from Patagonia (Nishida *et al*., 1990; Pujana, 2009a). The Rosaceae are distributed worldwide today, with maximum development in northern temperate areas (Heywood *et al*., 2007) and their Cenozoic fossils are abundant and cosmopolitan.

DISCUSSION

Four of the ten carbonized wood samples from Arroyo de los Ciervos could be assigned to a fossil genus, although quantitative features (*e.g*., pit diameter in gymnosperms or vessel diameter in angiosperms) are apparently reduced by the carbonization process, as previously documented (Slocum *et al*., 1978). Three samples (MPM PB 14470, 14471 and 14474) are indeterminate gymnospermous woods (only tracheids devoid of pits were observed). Twenty one of 31 (68%) of the fossil leaf remains were assigned to the Nothofagaceae. Some leaves were not preserved well enough to allow assignment to any family (leaf fragments on MPM PB 14951 and 14952).

The presence of fossil Lauraceae and Leguminosae in Arroyo de los Ciervos suggests a mixed flora dominated by the Nothofagaceae and a significant presence of arboreal conifers. The term mixed flora was defined for associations bearing subantarctic, cool-temperate taxa mixed with subtropical ones (Romero, 1978, 1986). Several mixed floras with Nothofagaceae of middle Eocene or younger ages have been described from the following Patagonian sites (Hinojosa, 2005): Río Turbio (middle Eocene), Ñirihuau (late Eocene/early Oligocene), Las Águilas (late Oligocene) and Goterones/Navidad (early Miocene). The Río Turbio flora has abundant Nothofagacaeae and tropical taxa, such as Sapindaceae and Malpighiaceae (Berry, 1937; Frenguelli, 1941; Hünicken, 1955, 1967; Panti, 2010; Fernández *et al.,* 2012). The Ñirihuau flora described by Fiori (1931, 1939, 1940) is also considered a mixed flora (Hinojosa, 2005). The Las Águilas flora has Nothofagaceae mixed with Lauraceae, Myrtaceae and Leguminosae (Hinojosa and Villagrán, 1997). The Goterones/Navidad flora, from the middle Miocene of central Chile (Troncoso, 1991), is also dominated by Nothofagaceae and it was described as a rainforest mixed flora based on the presence of temperate and some tropical families (*e.g.*, Melastomataceae).

Recently, a flora from the Loreto Formation (late Eocene) was described by Otero *et al*., (2012). It bears some of the fossils mentioned by Dusén (1899) and is dominated by the Nothofagaceae with presence of other temperate families. The megaflora of Carmen Silva in Tierra del Fuego is middle Miocene (Malumián and Olivero, 2006). It displays abundant Nothofagaceae (Dusén, 1899), and is likely coeval to the fossils described herein. The Carmen Silva megaflora is probably the one most closely related to the Arroyo de los Ciervos megaflora based on age and composition. All the families found in Arroyo de los Ciervos, except for the Cupressaceae, are present in the Río Leona Formation (Pujana, 2008, 2009a, b; Barreda *et al*., 2009), an Oligocene unit that crops out in the region, suggesting similar composition of the Miocene forests in southwestern Patagonia. Nothofagaceae, Araucariaceae and Leguminosae wood and Nothofagaceae leaves are also shared with a fossil flora recently described from early Miocene rocks in Patagonia (Santa Cruz Formation) (Brea *et al*., 2012). Poole and Cantrill (2007) described a late Tertiary lignitized wood flora from Malvinas (Falkland) Islands. They found representatives of the families Podocarpaceae, Cupressaceae and probably Cunoniaceae, suggesting a forest composition similar to that described herein.

Most of the fossil plant families found at Arroyo de los Ciervos have living relatives in the subantarctic forests of Argentinean and Chilean Patagonia. The Arroyo de los Ciervos fossils, dominated by Nothofagaceae and conifers and with fewer representatives of the Lauraceae and Leguminosae, suggest a climate similar to that of temperate forests to the north of the studied fossil flora, where comparable taxa occur today. This is consistent with plant geographic range shifts and extinctions influenced by global climate deterioration of the latest Cenozoic (Zachos *et al*., 2001). Unfortunately, the inability to observe growth rings in the carbonized wood precludes assessment of climatic seasonality. However, the palaeolatitude indicates a seasonal climate.

CONCLUSIONS

The fossil flora described herein is one of the younger fossil megafloras from Patagonia. In particular, this paper provides the only data known about forest composition for the southwestern region of Patagonia during the middle or late Miocene. Plant taxa present herein, which represent a mixed flora with Nothofagaceae, are common to other Cenozoic units from Patagonia and represent an assemblage that is also comparable to living plant associations from northern Patagonia. Finally, this record contributes toward filling the gap devoid of fossil plants from southern Patagonia spanning the early Miocene to present.

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