



The late Oligocene flora from the Río Leona Formation, Argentinian Patagonia



Silvia N. Césari^{a,*}, Carolina Panti^a, Roberto R. Pujana^a, Jane E. Francis^b, Sergio A. Marensi^c

^a Museo Argentino de Ciencias Naturales, “B. Rivadavia”, Av. Ángel Gallardo 470, C1405DJR Buenos Aires, Argentina

^b British Antarctic Survey High Cross, Madingley Road, Cambridge CB3 0ET, United Kingdom

^c IGEBA, Departamento de Geología, Universidad de Buenos Aires (1428), Argentina

ARTICLE INFO

Article history:

Received 24 July 2014

Received in revised form 9 January 2015

Accepted 12 January 2015

Available online 28 January 2015

Keywords:

Oligocene

Fossil leaves

Fern

Conifer

Angiosperms

Patagonia

ABSTRACT

A late Oligocene plant macrofossil assemblage is described from the Río Leona Formation, Argentinian Patagonia. This includes a fern, “*Blechnum*” *turbioense* Frenguelli, one species of conifer, and sixteen angiosperm taxa. Rosaceae, Myrtaceae, Proteaceae, Lauraceae, Anacardiaceae and Typhaceae are represented by one species in each family. Five species are considered to be members of the Fabales. Three leaf taxa together with *Carpolithus* seeds are placed in the Nothofagaceae. Palynomorphs and permineralized woods complete the floral record of the Río Leona Formation, which is considered early late Oligocene based on radiometric dating and palynofloras.

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1. Introduction

Vegetation changes through the Cenozoic in the Southern Hemisphere are well-documented in fossil record of Argentina, where leaves and wood as well as spores and pollen, provide useful evidence for reconstructions of the floras (e.g., Wilf et al., 2005; Palazzesi and Barreda, 2007; Barreda et al., 2010). Patagonia is the most important region where continuous sedimentary sequences provide abundant fossil assemblages which have been described since the end of 19th century (Conwentz, 1885).

The Río Leona Formation (Furque, 1973) contains abundant fossil plant assemblages including wood, leaves and palynomorphs in the El Calafate and Río Turbio areas (Frenguelli, 1941; Barreda et al., 2004; Césari et al., 2006; Pujana, 2007, 2008, 2009a, 2009b; Barreda et al., 2009). In the El Calafate area, this unit unconformably rests on the middle–late Eocene Man Aike Formation (Marensi et al., 2002) and is overlain by the late Oligocene–early Miocene Centinela Formation (Marensi et al., 2003; Guerin et al., 2004; Parras et al., 2008) later referred by Cuitiño and Scasso (2010) as Estancia 25 de Mayo Formation. A Burdigalian age was obtained from U–Pb ratios of zircon grains (20.05 Ma at the lower part and 19.1 Ma for the upper portion) from the Estancia 25 de Mayo Formation (Cuitiño et al., 2012). These stratigraphical relationships were used to constrain the age of the Río

Leona Formation to the Oligocene. Palynological studies allowed the refinement of the age to early late Oligocene (Barreda et al., 2009).

The deposits of the Río Leona Formation represent a progressive transition from fluvial systems of high to low energy (Marensi et al., 2005). The basal conglomerates contain abundant transported fossil logs, and the upper section preserves some stumps in growth position. The foliage is preserved in the same shales containing palynomorphs. The first mention of plant fossils from the Río Leona Formation were made by Frenguelli (1941) who pointed out the presence of *Nothofagus* in outcrops located 1 km the east of the Estancia Dorotea.

The analysis of the fossil leaves shows the presence of at least one species of fern, scarce conifer remains and 16 morphotypes of angiosperms. Temperate and humid conditions were inferred for the deposition of the Río Leona Formation by Barreda et al. (2009) based on spore–pollen assemblages dominated by floristic groups today growing under cool–temperate climates (Podocarpaceae, Nothofagaceae, Proteaceae). The aim of this paper is to describe the fossil leaves and analyze the affinities of the flora with coeval assemblages.

2. Material and methods

A collection of 772 fossil impressions of leaves from the Río Leona Formation were recovered in two localities (Fig. 1) at the south western tip of Santa Cruz Province, a few kilometers south of the El Calafate city. Together with this collection, some collections documented by Frenguelli (1941) from the same area were revised. The specimens with well-preserved

* Corresponding author.

E-mail address: scsari@macn.gov.ar (S.N. Césari).

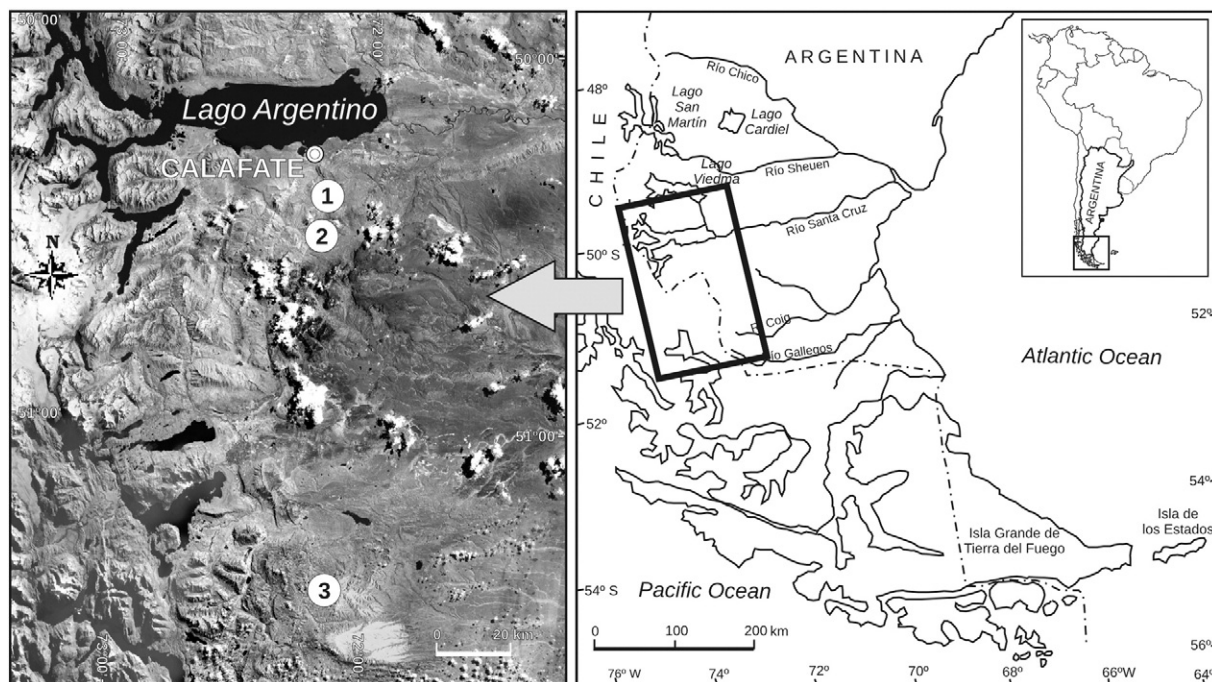


Fig. 1. Map and satellite image showing the fossiliferous localities.

venation were studied using modern leaf architectural analysis and referred mainly to known fossil-genera. Exceptions were made with leaves usually referred to natural taxa (e.g., *Nothofagus* Bl.) and the species defined by Frenguelli (1941) for which no fossil-genera are known. This last case, where the species is considered valid but the reference to the extant genus is considered tentative; it is indicated with quotation marks. Descriptions follow the methodology of Ellis et al. (2009) and taxonomy follows the proposals of Angiosperm Phylogeny Group (APG III, 2009), Chase and Reveal (2009) and Christenhusz et al. (2011). Plant fossils figured in this paper are held in the Padre Manuel Jesus Molina Museum (Río Gallegos, Argentina) under catalog numbers MPM PB 14480–14714 and 16366–16490.

3. Geological setting

Fossils described in this paper were collected from two separated outcrops (Arroyo de los Guanaquitos and Arroyo de las Bandurrias) of the upper part of the Río Leona Formation within the Estancia 25 de Mayo (Figs. 1, 1–2) and a southern outcrop in Arroyo Oro (Fig. 1, 3). In this area the Río Leona Formation is up to 100 m thick and consist of a fining-upward succession of conglomerates to carbonaceous shales (Fig. 2) previously described by Marensi et al. (2005). The succession is interpreted as being deposited in fluvial settings that range from high-energy braided systems at the base to low-energy meandering and anastomosed systems towards the top (Marensi et al., 2005).

The fossiliferous interval occurs in the upper 30 m of the unit (Fig. 2) which is composed of mudstones (40%), sandstones (30%), carbonaceous shales (25%), tuffs (5%), and very scarce fine-grained conglomerates (5%). The distinctive character of this interval is the abundance of fine-grained rocks with greenish mudstones presenting a homogeneous and distinctive orange weathering color, typical of Río Leona Formation outcrops. These fine-grained rocks form tabular beds of mainly massive or laminated sandy mudstones and include thin levels of very fine-grained massive or rippled laminated sandstones. Decimeter-thick, white tuff beds with normal grading are preserved within the mudstones. Some tree stumps are preserved in living positions at the top of sandstone intercalations penetrated by roots. Carbonaceous shales forming black tabular beds, 10–100 cm thick, contain abundant though

very poorly preserved plant remains. Coarser clastics form fining-upward cycles, 2–4 m thick, from very fine-grained, massive conglomerates to fine-grained, massive, tabular cross-bedded or ripple laminated sandstones with some plant remains. Laterally continuous, low-angle internal surfaces are interpreted as lateral accretion surfaces.

Channels are represented by low relief erosional bases and coarse lag deposits, followed by fining-upward sandstone successions with low-angle lateral accretion surfaces that correspond to fine-grained point bars. Floodplains are represented by fine grained sediments formed by suspension settling, or more energetic, instantaneous floods, interpreted as crevasse splay deposits. The predominance of floodplain deposits with dark carbonaceous deposits characterizes the two localities and indicates poorly drained interchannel areas. The crudely defined fining upward cycles, high proportion of fines, and the relatively low width-to-depth ratio of the channels suggest a fluvial system with small channels and oversized plains. A network of fluvial channels within a coastal plain environment is envisaged for this period (Marensi et al., 2005).

4. Systematics

Class Equisetopsida

Subclass Filicopsida

Order Polypodiales

Family Blechnaceae

Genus *Blechnum* Linnaeus, 1753

Type species: *Blechnum occidentale* Linnaeus, 1753

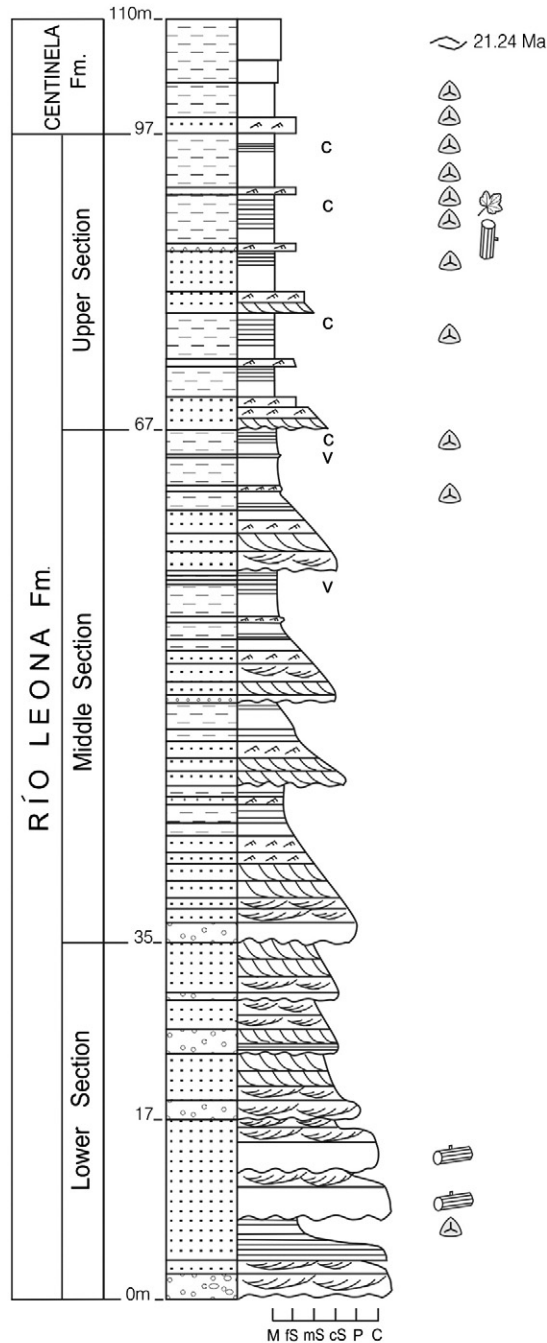
"Blechnum" turbioense Frenguelli, 1941

Plate I, 1–7

Syntypes: LPPB 4113 and 4114, Museo de La Plata, Paleobotany Collection.

Original diagnosis: "L. fronde anguste lineari-lanceolata, pinnata; pins sessilibus; frondium sterilium pins alternis vel suboppositis, linearibus, vertice rotundatis, rectis aut leviter falcatis, margine integerrimis, frondium apicem versus angustioribus, ad basin brevioribus, semiorbiculatis; fertilium oppositis, linearibus, valde angustioribus longioribusque, acuminatis vel subacutis, indusio margine integro".

"Estancia 25 de Mayo-Cerro Piramides" composite section



REFERENCES

	mudstone		massive		pollen-spores
	sandstone		ripple-cross ss		wood
	conglomerate		planar-cross ss		leaves
	planar ss		trough-cross ss		Marine invertebrates
	coal		tuff		

Fig. 2. Composite section showing the stratigraphic location of the samples.

Description: The overall shape of the imparipinnate dimorphic frond is unknown. The largest pinna fragment is 31.4 mm long by 16.5 mm wide with a rachis 2–3 mm in width. Pinnules are sub-opposite to alternate (Plate I, 2–3) and adjacent pinnules rarely overlap. The pinnules reduce towards the base of the pinna forming laminae of subtriangular to rounded outline and wide base (Plate I, 4–5). All pinnules have entire margins and are inserted by a wide base. Rounded pinnules are 3.5–4 mm wide (Plate I, 1, 7) and the lanceolate pinnules, in some cases slightly falcate, are 5–7 mm wide and 7–10 mm long (Plate I, 2). Apical pinnule is lanceolate (Plate I, 6). The pinnule midvein departs the rachis at 70°–86°. Secondary veins are subopposite or alternate, with six to seven secondary veins along one side of the pinnule midvein. Secondary veins are prominent and arise at 38–45° to the midvein. Secondary veins arch immediately adjacent to the midvein, once forked in the basal third and pass straight to and intersect the pinnule margin.

5. Comparisons

Although fertile pinnules are absent in the material studied here, Frenguelli (1941) described indusia and noted the close similarity with *Blechnum penna-marina* (Poir.) Kuhn. Rolleri and Prada (2006) coincided in this affinity and proposed that *Blechnum turbioense* Frenguelli may be assigned to *B. penna-marina* (de la Sota, 1970). The reduced pinnules described here at the base of the pinnae of *B. turbioense* are not recognized in the extant species, but are present in other species of the *B. penna-marina* group (Rolleri and Prada, 2006). *Blechnum penna-marina* and allied species are common component of the Andean Patagonian flora and some have a wide distribution in South America, Australia, Tasmania, New Zealand, South Africa, islands of the Atlantic, Indian and southern Pacific oceans. Rolleri and Prada (2006) argued that recent studies in plants of *B. penna-marina* in Argentina and Chile of different sizes (from 20 to 45–50 cm in height) that coexist in the same environment showed morphologic similarities supporting the proposal of de la Sota (1970), Duran (1997) and Oliveira Dittrich (2005) on the unnecessary definition of infraspecific categories.

Blechnum L. has been cited in New Zealand and South America for Miocene and Eocene assemblages (Pole, 1992; Anzótégui and Horn, 2011). Other Argentinian Paleogene macrofloristic remains of this family were recognized in the Oligocene Rancahué Formation (Neuquén Province). Several permineralized fern remains from the Rancahué Formation were considered of probable Blechnacean affinity by Vera (2010).

Specimens illustrated: MPM PB 14540, 14552, 14554, 14560, 14562, 14565, 14568 (See Appendix for remainder material)

Subclass Pinidae

Order Araucariales

Family Podocarpaceae

Genus *Elatocladus* Halle, 1913

Type species: *Elatocladus heterophyllus* Halle, 1913

Elatocladus sp.

Plate I, 8–10

Description: Axes of 19 mm long and 16 mm wide that bear leaves of 10.6 mm in length and 1.6 mm wide (Plate I, 8) helically inserted but flattened bifacially. Apex acute, straight to convex in shape. Leaves inserted by the whole base without petiole, lanceolate in shape and not imbricate. Leaves emerge opposite to subopposite at acute angles from the axes (40°–53°) and appear to have a twist at the leaf base (Plate I, 8, 10). Leaves traversed by a single midvein (Plate I, 9).

Comparisons: Leaves seem to have a twist at the leaf base as it is observed in the Podocarpaceae; the endemic Chilean extant species *Podocarpus nubigenus* Lindl. is similar in the size and shape of the leaves. However, without cuticle remains it is not possible to place the fossils into an extant genus. *Podocarpus*-like fossil leaves lacking cuticular information are referred to the fossil-genus *Elatocladus* Halle. Axes bearing similar leaves, with a prominent midvein and twisted base were



Plate I. 1–7. *Blechnum turbioense* Frenguelli. 1. rounded pinnules, MPM PB 14560. 2. falcate pinnules, MPM PB 14565; 3. falcate pinnules, MPM PB 14552; 4. Basal furcated axes bearing subtriangular laminae, MPM PB 14568. 5. Basal pinnules, MPM PB 14454. 6. Apical segment MPM PB 14562. 7. Basal segment with rounded pinnules MPM PB 14540. 8–10. *Elatocladus* sp., 8. Subopposite leaves, MPM PB 14496. 9. Leaves with a single midvein, MPM PB 14495. 10. Detail of leaves showing subcircular scars, MPM PB 14497. Scale = 5 mm.

reported as “Morphotype 11” from the Sloggett Formation, Argentina (Panti et al., 2008) and *Elatocladus seymouriensis* Cantrill et al. from the Seymour Island (Cantrill et al., 2011).

Some leaves have subcircular scars (plate I, 10) on the laminar surface that probably represent insect-mediated damage and resemble piercing-and-sucking activities of terrestrial arthropods.

Specimens illustrated: MPM PB 14495–14497 (See Appendix for remainder material).

Subclass Magnoliidae

Order Rosales

Family Rosaceae

Genus *Rubus* Linnaeus, 1753

Type species: *Rubus fruticosus* Linnaeus, 1753

“*Rubus*” *primaverae* Frenguelli, 1941

Plate II, 1–9

Syntypes: LPPB 4098 (Plate II, 1) and 4100 (Plate II, 2), Museo de La Plata, Paleobotany Collection.

Diagnosis enlarged: Leaf pinnately compound, petiolate, with two types of leaflets: entire and trilobate. Trifoliolate leaves with petiolulate ovate leaflets of acute apex. Terminal leaflet slightly longer than the lateral leaflets; lateral leaflets, with incipient trilobation. Primary venation pinnate, secondary veins craspedodromous. Leaflets palmately 3-lobed, petiolulate, ovate, base rounded to truncate, lobe apices acute. Primary venation palinactinodromous, costal secondary venation craspedodromous. In both types of leaflets the course of lateral secondary veins is straight to slightly curved concave toward the apex and then straightening. Tertiary venation opposite to alternate percurrent, highest order venation regular polygonal reticulate. Margin serrate, teeth convex/convex, compound, sinus angular, 1 subsidiary tooth per compound tooth. Principal vein present with termination at apex of tooth.

Description: Leaves compound, microphyll, with two types of leaflets. Trifoliolate fragments are odd-pinnately compound, petiolulate, with ovate leaflets of acute apex and serrate margin (Plate II, 3, 5, 8). The terminal leaflet (Plate II, 6), 24–28 mm in length and 18–19 mm in width, is longer than the laterals (14–21 mm long and 9–15 mm wide). Lateral leaflets have a basal shortly incised projection or incipient lobe. The three leaflets have secondary veins craspedodromous. Lamina trilobate (Plate II, 3), petiolulate, petiolule 0.80 mm in width. Lamina 20–45 mm in length (from the tip of the medial lobe to the distal end of the petiole) by 18–33 mm in width with L: W ratio of 1–2:1. Base rounded to truncate, lobes ovate with apices acute to round. Basal margin of the blade shows a vestigial lobulation (Plate II, 7). Primary veins palinactinodromous, with 5 basal veins, the middle vein runs directly to the leaf apex, lateral veins straight to slightly concave. Both types of leaflets, entire and trilobate, have costal and minor secondary venation craspedodromous, arising at acute angles (35°) from the midvein, course straight or concave toward the apex, at least 4 diverging from the medial primary vein. Interior secondaries present in the trilobulate leaves. Intercostal tertiary veins alternate percurrent to opposite and convex to forming a chevron; epimedial tertiary veins opposite to alternate percurrent (Plate II, 9). Fourth-order venation polygonal reticulate; fifth-order venation apparently dichotomizing; areolation well-developed; freely-ending ultimate venation one-or-more-branched. Tooth spacing regular, shape convex-convex to flexuous/straight, angular sinus, apex rounded or mammillate, teeth usually compound with one subsidiary tooth, principal veins terminate at the tooth apex, looped accessory veins (Plate II, 4).

Comparisons: *Rubus primaverae* was originally described as having trifoliolate and trilobate leaves with margins serrate-dentate, venation distinctive, secondary veins alternate pinnate. Examination of the original specimens (reillustrated in Plate II, 1–2) shows that they share all the architectural characters with the leaves here described. Frenguelli (1941) compared the trifoliolate leaves (Plate II, 2) with the mature leaves of primocanes and floricanes in many extant species of *Rubus*. He considered that the trilobulate leaves would be characteristic of the flowering floricanes. *Rubus* is a biennial plant, in the first year an actively growing vegetative shoot (primocane) is produced; in the second year the same shoot produces lateral branches, flowers and fruits (floricane) before dying. However, there is no evidence of this condition in the fossil material, except the close association of both types of leaves.

Fiori (1931) described several specimens referred to *Alnus barilochensis* Fiori, which Frenguelli (1941) considered very similar to *Rubus primaverae*. If a revision of the original specimens studied by Fiori (1931) confirms that both species are equivalent, Fiori's species would have priority. Fragmentary leaves referred to *Rubus primaverae* are found in West Antarctica (King George Island) to the end of Eocene–Early Oligocene (Zastawniak, 1981; Dutra, 2001). Incomplete leaves from the Río Guillermo Formation in Arroyo Oro locality (Fig. 1, 3) were described as *Rubus?* sp. and compared with *R. primaverae* by Panti (2011).

Rubus is known from the Eocene (Chandler, 1962, 1963) and some extant species of *Rubus*, such as *Rubus saxatilis* L. is very similar to *R. primaverae* in having trifoliolate and lobate leaves. Among the extant species of Rosaceae native from the Patagonian region, *Rubus geoides* J. E. Sm., *R. ulmifolius* Schott and *Geum magellanicum* Comm. ex Pers. are the only taxa comparable with the specimens from the Río Leona Formation.

The trilobate leaves here described also bear a close resemblance to those of extant *Ribes* L. Leaves of this saxifrage are similar in being lobed and petiolate with secondary venation craspedodromous, tertiary venation opposite percurrent, fourth-order venation regular polygonal reticulate and freely-ending ultimate venation. Also share the teeth, simple and/or compound, usually CV/CV with primary venation rosoid. However, three primary veins exit the distal end of the petiole in *Ribes*, the medial divides the lamina in half lengthwise, and each of the laterals divides into three or more primary veins. *Ribes* is today distributed widely in the Northern Hemisphere and into the Andes of South America.

Wolfe and Schorn (1990) suggested that the main difference between *Ribes* and similar leaves of other Rosaceae is the venation of the teeth that is more weakly developed, with subsidiary veins that do not reach the apical foramen in the latter. Leaves of *Physocarpus* (Cambess.) Raf. are also similar to our specimens but differ in having the central lobe larger than the lateral lobes and have three basal primary veins emerging from the same point. These leaves were mentioned by Oh and Potter (2005) in a molecular phylogenetic study of Neillieae (the tribe of Rosaceae to which *Physocarpus* belongs); they noted and agreed with the transfer of the leaves from *Physocarpus* to *Ribes*, though did not enumerate their reasons for agreeing with the transfer.

White (2005) proposed that *Rubus* and *Ribes* genera show a gradation of forms, where the pinnatifid and three lobed leaves have basal flares or splays. These basal splays may be a precondition for the development of the palmate leaf form by an accentuation of the basal flares (i.e. *Rubus*).

The leaves studied here are the only component in a stratigraphic level just above the permineralized stems found in life position and related to Rosaceae by Pujana (2009b), thereby strengthening their relationship with that family.

Specimens illustrated: LPPB 4098, 4100; MPM PB 14689, 14692, 14702, 14703, 14710, 14714 (See Appendix for remainder material).

Order Fabales

Family Fabaceae

Fossil Fabaceae are well-documented from the Cenozoic across the world. Leaves of this family are similar and placement in subfamilies is very difficult based only on this organ. Therefore, it seems more useful to refer the fossil leaves to fossil-genera and indicate the possible relationship with an extant species. Recently, Wang (2012) proposed to abandon the use of *Leguminosites* Bowerbank for legume isolated remains of more than one organ type. *Parvileguminophyllum* Herend. and Dilcher and *Leguminophyllum* Escalup-Bassi can be used for fossil legume leaves and, although they may be taxonomically synonymous, *Leguminophyllum* has priority (Wang, 2012).

Genus *Leguminophyllum* Escalup-Bassi, 1971

Type species: *Leguminophyllum emarginatum* Escalup-Bassi, 1971

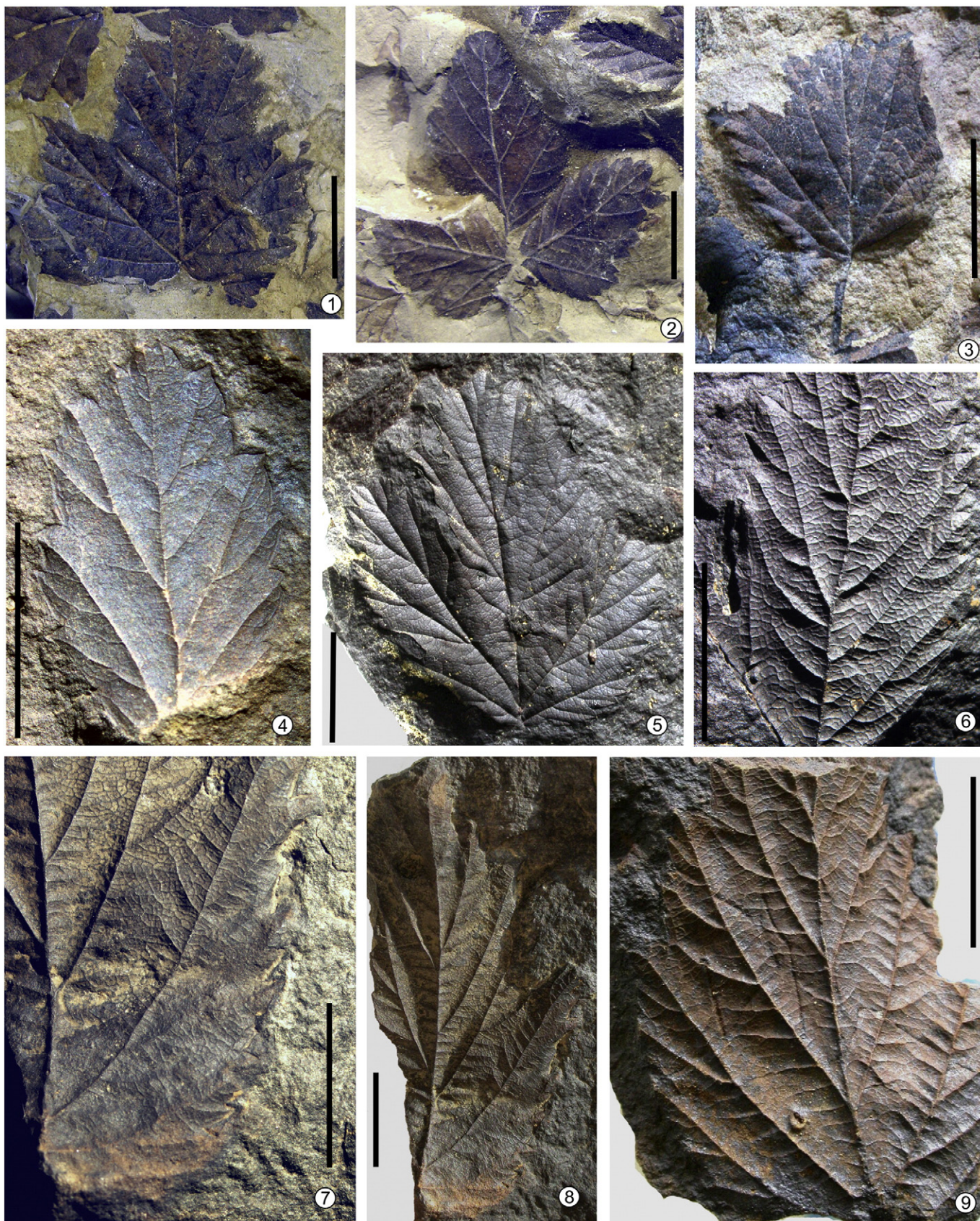


Plate II. 1–9. *Rubus primaverae* Frenguelli. 1. Leaf trilobate, Syntype, LPPB 4098; 2. Trifoliate leaf, Syntype, LPPB 4100; 3. Leaf trilobate with petiolule preserved, MPM PB 14689; 4. Detail of the tooth, MPM PB 14692; 5. Leaf trilobate showing the primary venation palinactinodromous and the secondary venation craspedodromous MPM PB 14702; 6. Detail of the venation of the medial lobe of a trilobate leaf, MPM PB 14703; 7. Detail of Fig. 8 showing the basal margin of the leaf, MPM PB 14710; 8. Leaf trilobate, MPM PB 14698; 9. Leaf with distinctive alternate to opposite percurrent tertiary veins forming a chevron, MPM PB 14714. Scale = 10 mm.

Leguminophyllum sp. 1

Plate III, 1–3

Description: Leaflets about 13 mm long and 5.7 mm wide, elliptic in shape (Plate III, 1, 3). Apex slightly emarginated, base slightly asymmetric and somewhat rounded in shape. Primary venation pinnate, midvein prominent. Secondary venation brochidodromous, secondaries irregularly spaced (Plate III, 2). The course of secondary veins is straight. Secondary vein angle acute (40°–80°) to primary vein, decreasing proximally. Tertiary venation reticulate and forming loops outside secondaries.

Comparisons: The material described can be compared to some genera of Leguminosae and has greatest similarities with *Sophora* L. Our specimens are very similar to the extant *Sophora cassioides* (Phil.) Sparre from Patagonia in having leaflets with an emarginated apex, asymmetric base and venation pattern. The presence in the Río Leona Formation of fossil wood of the Leguminosae (Pujana, 2008, 2009b), and pollen grains consistent with *Sophora* L. (Barreda et al., 2009), reinforces the possible affinity of the leaflets here described.

Specimens illustrated: MPM PB 14502, 14503 (See Appendix for remainder material).

Leguminophyllum sp. 2

Plate III, 4, 5, 9, 12

Description: Leaflets about 8–26 mm long and 4–12 mm wide, elliptic in shape (Plate III, 4, 12). Apex convex, base slightly asymmetric, convex in shape. Primary venation pinnate, midvein straight in course, slightly curved toward the base. Secondary venation brochidodromous, irregular spaced (Plate III, 4–5, 9). The course of secondary veins is straight and strongly curved towards the margin. Secondary vein angle acute (35°–90°) to primary vein. Secondary angle decreasing proximally. Tertiary venation reticulated.

Comparisons: The small leaf size along with the slightly asymmetric base and venation pattern allow placement within Fabaceae. The venation pattern described in the fossil seems to be more similar to those seen in *Caesalpinia* L. However the specimens differ from those described here as *Caesalpinites* sp. in the irregular spacing and divergence angle of the secondary veins, being widely spaced and diverging acutely in the apex in *Leguminophyllum* sp. 2. The shape of the specimens resemble the leaflets of the extant *Sophora macrocarpa* J.E. Sm., another native legume from Chile. Berry (1938) described *Cassia argentinensis* Berry having slightly larger leaves, similar in shape but with a more constant angle of divergence of the secondary veins.

Specimens illustrated: MPM PB 14500, 14511, 14514, (See Appendix for remainder material).

Leguminophyllum sp. 3

Plate III, 11

Description: Leaflet rounded, about 10 mm long and 11 mm wide (Plate III, 11). Apex rounded, base slightly asymmetric, rounded in shape, petiolate. Primary venation pinnate, midvein straight in course. Secondary venation brochidodromous, secondaries regularly spaced. The course of secondary veins is straight and strongly curved towards the margin. Secondary vein angle acute (55°–61°) to primary vein. Tertiary venation reticulated poorly defined.

Comparisons: The leaf size and the rounded lamina along with the asymmetrical base shape and the venation pattern are most similar to that seen in *Chamaecrista* Moench. and *Desmodium* Desv. Among the extant species the fossil is most similar to *Chamaecrista celiae* (Irwin and Berneby) Irwin and Berneby differing only in the larger laminar size of the extant species, native from central Brazil. *Desmodium adscendens* D.C., a worldwide distributed species, present also in Brazil, possesses a comparable laminar size.

The single leaf examined has a circular scar that is interpreted to be the result of insect damage and represents a feeding hole following the criteria of Labandeira et al. (2007). These authors described this type of

scar as a ring of excised tissue with a central disk of tissue loosely attached representing a hole feeding.

Material: MPM PB 14513.

Genus *Prosopis* Linnaeus, 1767

Type species: *Prosopis spicigera* Linnaeus, 1767.

cf. "*Prosopis*" sp.

Plate III, 8

Description: Leaf nanophyll, about 11 mm long and 2.5 mm wide, oblong to elliptic in shape (Plate III, 8). Apex incomplete, base slightly asymmetric, cuneate in shape. Petiolule short and displaced to one side. Primary venation pinnate, midvein straight in course, slightly curved proximally. Secondary venation brochidodromous, secondaries irregularly spaced. The course of secondary veins is slightly sinuous and strongly curved towards the margin. Secondary vein angle acute (50°–80°) to primary vein. Proximally, the secondary angles became wide acute. Tertiary venation reticulated but poorly preserved.

Comparisons: The small size, along with the slightly asymmetric base, suggests a relation with Fabaceae. Among the fossil species described it seems to be similar to those related to *Prosopis* described from the Pliocene by Anzótegui et al. (2007). Both share the asymmetrical base and acute apex, the venation pattern, the angle of divergence of the secondary veins and form. The presence of Mimosoideae in the Río Leona Formation is supported by the presence of pollen grains related to this subfamily by Barreda et al. (2009).

Material: MPM PB 14500.

Genus *Caesalpinites* Saporta, 1862

Type species: *Caesalpinites dispersus* Saporta, 1862.

Caesalpinites sp.

Plate III, 6–7

Description: Leaflets about 9.8–16 mm long and 5.4–10 mm wide, elliptic in shape. Apex not preserved, base slightly asymmetric, rounded to convex in shape with short petiolule (Plate III, 6). Primary venation pinnate, midvein prominent, strongly curved (Plate III, 7). Secondary venation brochidodromous, secondaries regularly spaced. The course of secondary veins is straight and strongly curved towards the margin. Secondary vein angle acute (52°–82°) to primary vein, decreasing proximally. Tertiary venation hardly observed.

Comparisons: The size, asymmetric base and venation pattern of the studied material, allow a comparison with some extant species belonging to *Caesalpinia*. Some fossils species related to *Caesalpinia* have been described by Berry (1939). *Caesalpinia prebahamensis* Berry (Berry, 1939, p. 115, pl. XV. figs. 4–5) described from the Miocene of Cuba is characterized by small and asymmetrical leaflets (17.5 mm long and 7.5 mm wide) with entire margin and a strong midvein usually curved and brochidodromous secondaries.

Tosolini et al. (2013) described *Leguminosites* sp. from the Seymour Island, and remarks its similarities in venation, small L:W ratio, entire-margin, thick texture and convex apex with extant Leguminosae (e.g., *Sophora* sp.) differing only on its broader base. The species was considered similar to *Leguminosites patagonicus* Berry from Argentina (Berry, 1925). However the specimen described by Berry (1925) is a larger leaf of 8 cm in length with camptodromous venation. The leaves from Seymour Island are broadly similar to the described here.

Material: MPM PB 14484, 14505.

Order Fagales

Family Nothofagaceae

Genus *Nothofagus* Blume, 1851

Type species: *Nothofagus antarctica* (G. Forster) Oersted, 1871

Nothofagus simplicidens Dusén, 1899

Plate IV, 3–5

Description: Leaves oblong-ovate, petiolate (Plate IV, 5), with rounded to convex base and acute apex, symmetrical, about 2 cm long and 1.1 cm wide. Margin single-serrate (Plate IV, 4). Venation pinnate,



Plate III. 1–3. *Leguminophyllum* sp. 1, 1. Complete leaf with emarginated apex, MPM PB 14502, 2. Detail of venation, MPM PB 14502, 3. Leaf with emarginated apex, MPM PB 14503, 4–5, 9, 12. *Leguminophyllum* sp. 2, 4–5. Leaves with base slightly asymmetric, MPM PB 14511, 9. Detail of venation, MPM PB 14514, 12. Complete leaf, MPM PB 14500, 6–7. *Caesalpinites* sp., 6. Leaf showing petiolule, MPM PB 14484, 7. Leaf with curved midvein, MPM PB 14505. 8. cf. *Prosopis* sp. MPM PB 14500, 11. *Leguminophyllum* sp. 3, rounded leaf with subcircular scar, MPM PB 14513. Scale = 5 mm.

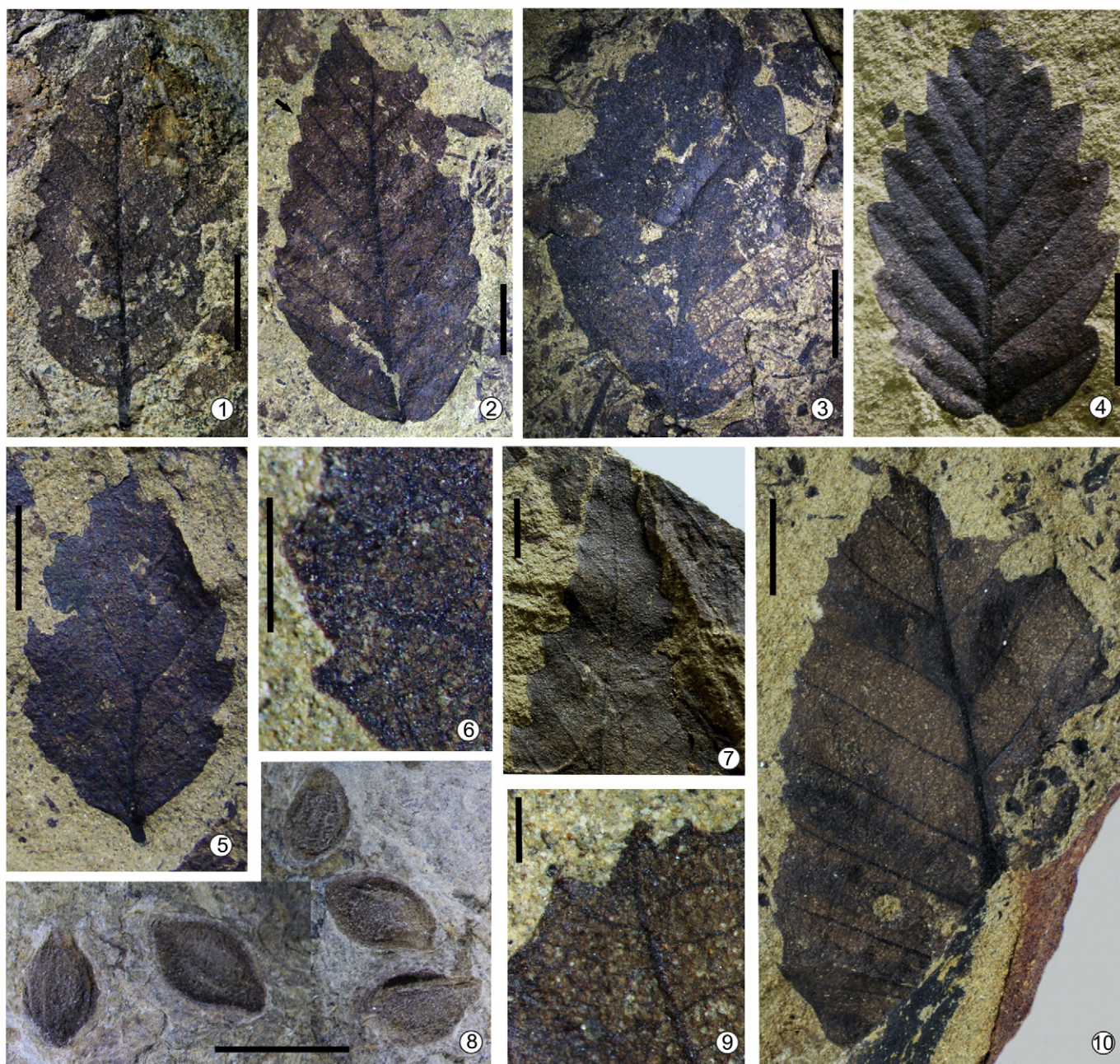


Plate IV. 1–2. 6. *Nothofagus magelhaenica* (Engelhardt) Dusén, 1. Leaf with petiole, MPM PB 14625, 2. Leaf with margin double serrate (arrow in 2); 3–5. *Nothofagus simplicidens* Dusén, 3. Leaf showing detail of venation, MPM PB 14638, 4. Leaf showing simple tooth, MPM PB 14664, 5. Leaf with petiole, MPM PB 14668; 7, 9, 10. *Nothofagus subferruginea* (Dusén) Tanai, 7. Apex of leaf, MPM PB 14657, 9. Detail of serrate margin, MPMPB 15648, 10. Incomplete leaf MPM PB 14648, 7; 8. *Carpolithus* sp., MPMPB 14597. Scale = 5 mm in 1–8, 10; = 1 mm in 9.

primary vein straight, secondary veins craspedodromous, with regular spacing, emerging at acute angle from the midvein, straight course. Tertiary veins opposite percurrent, straight to sinuous, with obtuse angle to the midvein (Plate IV, 3). Quaternary veins percurrent, quinary veins reticulate. Tooth simple convex/convex, regularly spaced, sinus angular.

Comparisons: Dusén (1899) described this species from southern Patagonia as small leaves with short petiole, of variable shape and size, usually oblong to oval, sometimes lanceolate with eight to ten straight secondary veins each supplying the tooth apex. Later, Romero and Dibbern (1985) characterized the original specimens of *N. simplicidens* as ovate-oblong leaves, primary venation pinnate, secondary veins craspedodromous (seven to ten pairs), vein course straight, and margin with convex/convex simple tooth.

Tanai (1986) revised the species of *Nothofagus* or *Nothofagus*-like leaf fossils from South America and West Antarctica. This author considered *N. simplicidens* distinguishable by its single-serrate margin and regularly percurrent tertiary veins with the secondary vein straightly entering the main teeth along the basal side of tooth. It was compared with extant *N. obliqua* (Mirb.) Oerst. from South America, although this taxon usually has bi-serrate margin. The endemic Andean Patagonian species *Nothofagus betuloides* (Mirb.) Oerst. is similar to *N. simplicidens* in its margin crenulate-serrate with broad teeth. **Specimens illustrated:** MPM PB 14638, 14664, 14668 (See Appendix for remainder material).

Nothofagus magelhaenica (Engelhardt) Dusén, 1899
Plate IV, 1, 2, 6

Description: Leaves elliptic in shape, petiolate (Plate IV, 1), with rounded to convex base and acute apex, symmetrical, about 3 cm long and 1.5 cm wide; serrate with compound teeth, primary teeth, acute whose sides are convex in the apical side and convex to slightly concave in the basal side. The secondary veins end in the main tooth apex which is accompanied with a small subsidiary tooth in their basal side (Plate IV, 2). A branch from the secondary vein curves upward and supplies the apex of the subsidiary tooth (Plate IV, 6). Venation pinnate, primary vein straight or slightly arcuate, secondary veins craspedodromous, with regular spacing, emerging at acute angle from the midvein, straight course. Tertiary veins opposite percurrent, straight to sinuous, with obtuse angle to the midvein. Quaternary veins percurrent.

Comparisons: This specimen fits the description given by Tanai (1986) for *N. magelhaenica*, represented by elliptic leaves with acute to obtuse base, craspedodromous secondary veins diverging from the pinnate midvein at acute angles and margin serrate with two orders of teeth. This species was originally described by Engelhardt (1891) as *Fagus magelhaenica* from Southern Chile and later was transferred to *Nothofagus* by Dusén (1899). This combination was accepted by Tanai (1986) even though she considered that all the specimens illustrated by Dusén (1899) are single-toothed in margin and not belong to *magelhaenica*. Tosolini et al. (2013) misinterpreted the synonymy proposed by Dutra and Batten (2000) in considering that all the specimens assigned by Tanai (1986) to *N. magelhaenica* were reassigned to *N. glaucifolia* Dutra and Batten.

This species occurs in Eocene–Oligocene deposits from the high latitudes of South America and the Cretaceous of Antarctica (Dusén, 1899; Tanai, 1986).

Specimens illustrated: MPM PB 14625, 14659 (See Appendix for remainder material).

Nothofagus subferruginea (Dusén) Tanai, 1986

Plate IV, 7, 9, 10

Description: Fragments of leaves probably ovate, with acute apex (Plate IV, 7). Primary venation pinnate, primary vein straight. At least eight pairs of craspedodromous, opposite to subopposite secondaries veins, with regular spacing, straight in course and emerging at acute angles from the midvein (Plate IV, 10). Secondary veins straightly entering teeth; one branch emerging basally, and ending in a subsidiary teeth apex (Plate IV, 9). Tertiary veins alternate percurrent, with obtuse angle to the midvein. Quaternary and quaternary venation reticulate.

Comparisons: The specimens are closely similar to the extant leaves of *Nothofagus alessandri* Espinosa in their lamina shape, venation pattern and tooth. Among the fossil species, *Nothofagus subferruginea* (Dusén) Tanai, described from the Paleogene of Patagonia and Antarctica (Tanai, 1986; Dutra, 2001; Cantrill et al., 2013), is the fossil species that shows more similarities to the extant species (Tanai, 1986).

Specimens illustrated: MPM PB 14648, 14657 (See Appendix for remainder material).

Genus *Carpolithus* Brongniart 1822

Type species: *Carpolithus thalictroides* Brongniart 1822.

Carpolithus sp.

Plate IV, 8

Description: Two types of isolated seeds are recognized closely associated in the same sample, two-flanged and three-flanged. The three-flanged seeds are the most common and are 3–4 mm in length and 2 mm in width. They are preserved almost as tridimensional casts in the sediment, suggesting a coriaceous texture (Plate IV, 8).

Comparisons: The fossil-genus *Carpolithus* has been used for fossil fruits and seeds (e.g., Schneider, 2007; Wang, 2011; Wang et al., 2013). The small structures from the Río Leona Formation are very similar to *Nothofagus* seeds in shape and size; the smaller seeds between the Patagonian species are produced by *N. dombeyi*, *N. betuloides*, *N. nitida* and *N. antarctica*. *Nothofagus alessandri* produces seeds similar to the described here. The small seeds are produced inside a woody cupule of

four valves. The bi-flanged central seed is plane with two lateral triflanged seeds (Navarro-Cerrillo et al., 2013).

Specimens illustrated: MPM PB 14597.

Order Myrtales

Family Myrtaceae

Genus *Myrtiphyllum* Dusén, 1899

Type species: *Myrtiphyllum bagualense* Dusén, 1899

Myrtiphyllum bagualense Dusén, 1899

Plate V, 3–4, 7–8

1899 *Myrtiphyllum bagualense* Dusén, 1899, p. 103, pl. XI, 7–9

1928 *Myrcia nitens* Berry non Engelhardt 1891, p. 23, pl. III, 1–9.

1995 *Myrcia bagualensis* (Dusen) Hünicken, p. 314; pl. E: 10–17; 19–20.

Lectotype (here designated): Dusén, 1899, Plate XI, fig. 7.

Description: Leaves elliptic to ovate (Plate V, 3), petiolate (Plate V, 7), with acute apex (Plate V, 3–4) and rounded to convex base, symmetrical, about 20.5 mm long and 6.8 mm wide. Margin entire. Primary venation pinnate, midvein prominent and straight (Plate V, 3). Numerous pairs of simple brochidodromous secondaries with regular spacing, emerging from the midvein at acute angles (74°). They terminate in a paramarginal vein and an intramarginal vein that closely parallels the leaf margin (Plate V, 8). Tertiary veins admedially ramified. Exterior tertiaries looped.

Comparisons: Myrtaceae leaves are distinguished by a prominent paramarginal vein, an intramarginal vein, parallel venation of secondary category and third category veins almost parallel to the medial vein (González, 2011). Leaf bases are decurrent with a prominent petiole. The material examined in this study can be compared with the original specimens of *Myrtiphyllum bagualense* (Dusén, 1899) and *Myrcia bagualensis* (Dusén) Hünicken, the last described by Hünicken (1995). These taxa are characterized by ovate to lanceolate leaves, with a strong midvein and numerous secondary veins that usually emerge from the midvein at acute angles but in some specimens can reach 80°–85°. Original specimens described by Dusén (1899) as *Myrtiphyllum bagualense* were later included by Berry (1938) into *Myrcia nitens* Berry. We prefer to place the species in the fossil-genus because there is no enough evidence supporting the belonging of the leaves to the extant genus. Nevertheless, *Myrcia* DC. ex Guillemín is the more similar extant genus with its elliptic leaves without glands, one paramarginal vein, one or two intramarginal veins and secondary venation emerging at 65°–85° (González, 2011).

Specimens illustrated: MPM PB 14499, 14500, 14507 (See Appendix for remainder material).

Myrtiphyllum sp.

Plate V, 10

Description: Leaves incomplete, nanophylls, about 12 mm long and 7 mm wide, elliptic to ovate in shape (Plate V, 10). Apex acute and attenuate, base slightly asymmetric, rounded to convex in shape. Primary venation pinnate, midvein prominent, strongly curved towards the leaf base. Secondary venation brochidodromous, at least 6 pairs of secondary veins irregularly spaced. The course of secondary veins is straight and strongly curved towards the margin. Secondary vein angle 52°–82° to primary vein, decreasing proximally. Tertiary and fourth venation order random reticulate. One intramarginal vein, paramarginal vein present and formed by the exmedial tertiaries. Leaf glands can be observed on the leaf surface.

Comparisons: Despite the description is based upon two specimens, some characters like the venation pattern along with the presence of one intramarginal and one paramarginal vein together with the observation of leaf glands, allow a comparison to Myrtaceae. Similar leaf shape, size, number of secondary veins and venation pattern can be found in some of the extant species of *Luma* A. Gray, *Eugenia* L. and *Myrcogenia* O. Berg (see González, 2011).

Material: 14494, 14509.



Plate V. 1–2. *Anacardites pichileufensis* Berry, MPM PB 14543. 1. Detail of teeth, 3–4, 7–8. *Myrtillophyllum bagualense* Dusén, 3. Complete leaf, MPM PB 14500, 4. Incomplete leaf, MPM PB 14499, 7. Base of leaf with petiole, MPM PB 14507, 8. Detail of venation showing paramarginal and intramarginal veins (arrows), MPM PB 14499, 5, 9. *Embotriophyllum* sp. MPM PB 14610, 9. Detail of venation, 10. *Mirtiphyllum* sp., leaf with glands, MPM PB 14509, 6. *Laurophyllum* sp., MPM PB 14510, 11–12. “*Typha*” sp., 11. detail of venation showing transverse veins (arrows in 12), MPM PB 146153. Scale = 10 mm in 2, 3, 4, 5, 6, 7, 12; Scale = 5 mm in 8, 10, 11; Scale = 1 mm in 1, 9.

Order Sapindales

Family Anacardiaceae

Genus *Anacardites* Saporta in Heer, 1861

Type species: *Anacardites spectabilis* Saporta in Heer, 1861.

Anacardites pichileufensis Berry, 1938

Plate V, 1–2

Description: Trifoliate fragment odd-pinnately compound, with elliptic leaflets of serrate margin, 9.5 mm in length and 4 mm in width (Plate V, 2). Lateral leaflets sessile, opposite, base asymmetric, rounded on the proximal side and straight on the distal side. Primary venation pinnate, midvein prominent. Secondary venation craspedodromous, with regular spacing. Course of secondary veins is straight to slightly

curved concave toward the apex. Secondary veins arising at 54°. Tooth simple, concave/convex (Plate V, 1). Principal veins terminate at the tooth apex.

Comparisons: *Anacardites* sp., described by Hünicken (1967) from the Río Turbio Formation, is similar to the specimen here described. Both are characterized by small leaves or leaflets, up to 30 mm long, lanceolate with margin serrate and secondary veins arising at 45–50°. Hünicken compared his specimens with *A. pichileufensis* Berry, described by Berry (1938) from Patagonia which, like in the fossil described herein, the terminal leaflet seems to be more equilateral while the lateral ones are characterized by inequilateral bases.

Material: MPM PB 14543.

Order Proteales

Family Proteaceae

Genus *Embothriophyllum* Dusén, 1899

Type species: *Embothriophyllum dubium* Dusén, 1899

Embothriophyllum sp.

Plate V, 5, 9

Description: Leaf ovate to elliptic, microphyll, with acute apex and symmetrical, acute to decurrent base, about 49 mm long and 22 mm wide (Plate V, 5). Margin poorly preserved but entire when visible. Primary venation pinnate, simple and straight. At least seven pairs of brochidodromous secondaries irregularly spaced, emerging from the midvein at acute angles (50°), secondary veins course regularly curved. Intersecondary veins present. Third venation order random reticulate, fourth and fifth vein categories regular polygonal reticulate (Plate V, 9). Marginal ultimate venation hardly observed.

Comparisons: The material here described is very similar to the leaves of the extant *Embothrium coccineum* Forst. and Forst.; both species show entire, simple and symmetrical leaves, ovate to elliptic in shape and also comparable sizes. The pinnate primary venation along with the brochidodromous secondaries and the reticulate tertiaries, along with the fourth and fifth polygonal venation categories are similar to the venation pattern described by González et al. (2004) for the extant species. There are few fossil records of Proteaceae in Argentina. Berry (1938) described two species belonging to the extant *Embothrium* Forst. and Forst., *E. pregrandiflorum* Berry and *E. precoccineum* Berry, both from Río Pichileufú. The specimen here described is more comparable to *E. pregrandiflorum*. Both species share a symmetrical, ovate to elliptic leaf with acute apex and acute base; pinnate primary venation order and brochidodromous secondary veins, but differ in the number of secondaries and in the tertiary venation pattern which is percurrent in *E. pregrandiflorum*. Also the species described by Berry (1938) apparently lack intersecondary veins. On the other hand, *E. precoccineum*, despite the pinnate primary venation and the secondary brochidodromous venation with seven pairs of secondaries, has an asymmetrical leaf with a percurrent tertiary venation pattern.

In the revision of the fossil Proteaceae from South America by González et al. (2007) both fossil species, *E. pregrandiflorum* and *E. precoccineum*, and the modern *E. coccineum* have simple leaves with entire margins, with the secondary vein category always brochidodromous, and the areoles well-developed but they differ in size, number of secondary veins, tertiary and fourth-order venation, and the ultimate marginal venation. The specimens analyzed here have several characters in common with the modern genus *Embothrium*; nevertheless the limited number of specimens and poor preservation make the generic assignment uncertain.

The specimen illustrated by Torres et al. (2013) as *Persea* sp. from equivalent strata in Chile, is very similar to the leaves described here especially the attenuate base that is similar to extant *Embothrium*.

Material studied: MPM PB 14610.

Order Laureales

Family Lauraceae

Genus *Laurophyllum* Goeppert, 1857

Type species: *Laurophyllum beilschmiedoides* Goeppert, 1857

Laurophyllum sp.

Plate V, 6

Description: Leaf incomplete, ovate to elliptic, microphyll, with acute apex (Plate V, 6) and the base not preserved. Margin entire. Primary venation pinnate, simple and straight. At least seven pairs of brochidodromous secondaries irregularly spaced, emerging from the midvein at acute angles (52°), secondary veins course regularly curved. Intersecondary veins not observable. Third venation order percurrent. Marginal ultimate venation hardly observed.

Comparisons: Despite its poor preservation the specimen can be compared to Lauraceae. The lamina shape along with the venation pattern, are comparable with those found in *Nectandra* Roland ex. Rottb. and *Nothaphoebe* Bl. The leaves in both genera are characterized by elliptic laminae with decurrent base and acuminate apex. The venation differs in the number of secondary veins pairs, which is greater in *Nothaphoebe*. Also this genus is characterized by the presence of intersecondary veins in the basal portion of the leaf that are absent in *Nectandra*. The incompleteness of the basal portion of the leaf studied material prevents a closer comparison to any these genera.

Material: MPM PB 14510.

Order Poales

Family Typhaceae

Genus *Typha* Linnaeus, 1753

Type species: *Typha latifolia* Linnaeus, 1753.

Typha sp.

Plate V, 11–12

Description: Leaves simple linear in shape, with parallel margins (Plate V, 12). Leaf blade at least 15 cm long and 2 cm wide. Thirteen to fifteen veins extending longitudinally through the lamina lie more or less parallel to each other and regularly spaced at 1.5 mm. The longitudinal veins are interconnected by small transverse ones (Plate V, 11). Between the principal veins it is possible to observe few narrower veins also parallelly disposed.

Comparisons: This type of leaf is commonly related to monocotyledonean families like Poaceae, Cyperaceae, Restionaceae, Potamogetonaceae, Hydrocharitaceae, Arecaceae, and Sparganiaceae/Typhaceae. All of these families have micro and/or macrofossil records in Argentina (Gandolfo et al., 2010). Mostly of the monocot leaves described from Patagonia were assigned to *Poacites* sp. (Berry, 1925, 1937; Fiori, 1939) and are represented by small and fragmentary leaves with veins that run longitudinally and minor parallel veins between these. *Chusquea oxyphylla* Frenguelli and Parodi (Frenguelli and Parodi, 1941) is other fossil monocot described for Patagonia but it is quite different to our specimen.

Specimens referred as *Typha* have been mentioned for the Río Turbio and Río Guillermo formations and for the Última Esperanza locality in Chile (Hünicken, 1995). According to Hünicken (1995) the specimens belonging to the Hauthal collection have strong similarities with the current species *Typha domingensis* Pers. sharing 13 to 15 longitudinal veins. However, the specimens collected at the Río Guillermo Formation have a higher vein number between the principal longitudinal veins, and it was considered to be a different taxon named *Typha kurtzii* Hünicken (Hünicken, 1995). The preservation of the specimens studied here makes it difficult to observe the number of narrower veins, and so a closer comparison is not possible.

Specimen illustrated: MPM PB 14615 (See Appendix for remainder material).

6. Composition of the flora

Based on palynology Barreda et al. (2009) recognized the presence of the angiosperm families Anacardiaceae, Asteraceae, Casuarinaceae, Chloranthaceae, Euphorbiaceae, Fabaceae, Gunneraceae, Loranaceae,

Menyanthaceae, Myrtaceae, Misodendraceae, Nothofagaceae, Onagraceae, Poaceae, Proteaceae, Restionaceae and Rosaceae (Table 1) in the Río Leona Formation. Nothofagaceae (*Nothofagidites* spp.) is the most abundant with the *fusca* type dominant. Proteaceae and Myrtaceae are infrequent and the fern spores are dominated by the Polypodiaceae (*Polypodiisporites* sp.) although Blechnaceae spores are consistently present. Barreda et al. (2009) also mentioned the record of Rosaceae, represented by the pollen *Psilatricolporites quenua* Barreda and Palazzesi and *Psilatricolporites* sp. Pujana (2009a) described a new wood fossil-species of *Maloidoxylon* with affinity to the Rosaceae; its small stem diameter and presence of tension wood suggest a shrub habit. It constitutes, together with the fossil pollen from the same strata, the oldest confident South American fossils with this affinity. The Rosaceae in Patagonia are now represented mostly by herbaceous plants, although several shrubs live there such as *Tetraglochin* Poepp. (Grondona, 1984). The abundant leaves of *Rubus primaverae* here described came from the same stratigraphic levels where specimens of *Maloidoxylon* Grambast-Fressard are preserved in life position, and complete the fossil record of the family in the Río Leona Formation. 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.

Other fossil woods described by Pujana (2007, 2008, 2009a, b) include representatives of Nothofagaceae along with frequently encountered Proteaceae, Atherospermataceae, Myrtaceae, Anacardiaceae, Leguminosae, Araucariaceae and Podocarpaceae.

Several palynological taxa are not represented by macrofossils e.g. *Ischyosporites areapunctatis* (Stuchlik) Barreda and *Matonisporites ornamentalis* (Cookson) Partridge, spores which can be ascribed to Dicksonaceae. This fern family is a common component of humid tropical forests around the world although can be found in temperate and cool temperate environments in New Zealand and Australia. In addition to these ferns, *Lophosoria*-like spores (*Cyatheidites annulatus* Cookson) were also encountered in the unit but not in the leaf bed. Araucariaceae is only represented in the palynological and wood records whereas Podocarpaceae is represented by more species in the pollen assemblage than in the macrofossil record.

Some of the pollen, e.g. *Mutisiapollis telleriae* Barreda et al. (Asteraceae), *Tricolpites reticulatus* Cookson (Gunneraceae), *Diporites aspis* Pocknall and Mildenhall (Onagraceae) derives from mainly herbaceous plants, rarely preserved as macrofossils and not represented in the studied fossil horizons. Other angiosperms pollen such as *Myrtacidites verrucosus* Partridge (Myrtaceae), *Psilatricolporites operculatus* van der Ham. and Wijmstra (Euphorbiaceae), *Nothofagidites*

Table 1
Species of palynomorphs, woods and imprints of foliage identified in the Río Leona Formation.

	Family	Pollen	Woods	Leaves
Bryophyte	Ricciaceae	<i>Reboulisporites fuegiensis</i>		
Ferns	Blechnaceae	<i>Peromonolites vellosus</i>		"Blechnum" <i>turbioense</i>
	Dicksoniaceae	<i>Ischyosporites areapunctatis</i>		
		<i>Matonisporites ornamentalis</i>		
	Polypodiaceae	<i>Polypodiisporites</i> sp.		
Conifers	Pteridaceae	<i>Murincingulisporis chenquensis</i>		
	Araucariaceae	<i>Araucariacites australis</i>	<i>Agathoxylon</i> <i>Podocarpxylon</i>	<i>Elatocladus</i> sp.
	Podocarpaceae	<i>Gameroites</i> cf. <i>psilasaccus</i> , <i>Lygistipollenites florinii</i>		
		<i>Microcachrydites antarcticus</i>		
		<i>Phyllocladites mawsonii</i> , <i>Podocarpidites elegans</i>		
		<i>P. rugulosus</i>		
Angiosperms	Anacardiaceae	<i>Striatricolporites</i> cf. <i>gameroi</i>	<i>Resinaxylon schinusoides</i>	<i>Anacardites pichileufensis</i>
	Asteraceae	<i>Mutisiapollis telleriae</i>		
	Atherospermataceae		<i>Laurelites doroteaensis</i>	<i>Laurophyllum</i> sp.
	Casuarinaceae	<i>Haloragacidites harrisii</i>		
	Chloranthaceae	<i>Clavatipollenites</i> sp.		
	Euphorbiaceae	<i>Psilatricolporites operculatus</i>		
	Fabaceae	<i>Margocolporites</i> sp. <i>M. tenuireticulatus</i>	<i>Doroteoxylon vicente-perezii</i> "xilotipo 3"	<i>Leguminophyllum</i> sp. 1 <i>Leguminophyllum</i> sp. 2 <i>Leguminophyllum</i> sp. 3 <i>Caesalpinites</i> sp. cf. <i>Prosopis</i> sp.
	Gunneraceae	<i>Tricolpites reticulatus</i>		
	Loranthaceae	<i>Gothanipollis</i> sp. 1		
	Lophosoriaceae	<i>Cyatheidites annulatus</i>		
	Menyanthaceae	<i>Striasyncolpites laxus</i>		
	Myrtaceae	<i>Myrtacidites verrucosus</i> <i>M.</i> sp.	<i>Myrceugenellites oligocenum</i>	<i>Myrtiphyllum bagualense</i> <i>Myrtiphyllum</i> sp.
	Myzodendraceae	<i>Compositoipollenites</i> cf. <i>tarragoensis</i>		
	Nothofagaceae	<i>Nothofagidites americanus</i>	<i>Nothofagoxylon scalariforme</i> <i>N. triseriatum</i> <i>N. kraeuseli</i> <i>N. rui</i> <i>N. aggregatum</i>	<i>Nothofagus magelhaenica</i> , <i>Nothofagus simplicidens</i> <i>Nothofagus subferruginea</i> <i>Carpolithus</i> sp.
		<i>N. acromegacanthus</i>		
		<i>N. dorotensis</i>		
		<i>N. flemingii</i>		
		<i>N. saraensis</i>		
		<i>N. tehuelchesii</i>		
	Onagraceae	<i>Corsinipollenites</i> sp.		
	Proteaceae	<i>Diporites aspis</i>	<i>Scalarixylon grandiradiatum</i> <i>Scalarixylon patagonicum</i>	<i>Embothriophyllum</i> sp.
		<i>Granodiporites nebulosus</i>		
		<i>Triporopollenites minor</i>		
		<i>Proteacidites</i> sp. 1		
	Restionaceae	<i>P.</i> sp. B		
	Rosaceae	<i>Milfordia</i> sp.		
	Thyphaceae	<i>Psilatricolporites quenua</i> , <i>Psilatricolporites</i> sp.	<i>Maloidoxylon cesariae</i>	"Rubus" <i>primaverae</i> "Thypa" sp.
		<i>Graminidites</i> sp. <i>Sparganiaceapollenites barungensis</i>		

spp. (Nothofagaceae) represent shrubby or tree vegetation that, without or minor transport have a macroscopic record in the studied deposits. Proteaceae are represented by several pollen species related to extant *Embothrium* (*Granodiporites nebulosus* Partridge) and leaves described as *Embothriophyllum* sp. Fabaceae pollen related to *Sophora* (*Margocolporites* sp.) is locally abundant as well as leaves of *Leguminophyllum* closely related to native species of the extant genus.

The fossil evidence suggests a moderately low diversity of the forest vegetation, with southern taxa like Araucariaceae, Nothofagaceae, Podocarpaceae. Arborescent ferns (Cyatheaceae) and herbaceous angiosperms (Gunneraceae and Onagraceae) comprised the understory. Probably the conifers, with low representation, were subordinate components or grew further from of the depositional site. Surrounding the forests would have developed sclerophyllous vegetation with Myrtaceae, Proteaceae and Anacardiaceae (Barreda et al., 2011).

An increasing trend from low to high temperature values through early to late Oligocene was proposed by Zachos et al. (2001) based on isotopic data. Romero (1993) suggested a cold-temperate climate during the Oligocene in Patagonia whereas Barreda (1997) and Barreda and Palamarczuk (2000) proposed a warm climate with high frequency of tropical taxa during the latest Oligocene. The Río Leona Formation contains one of the few late Oligocene paleofloristic records that provide information to infer the climatic conditions in the region. According to Barreda et al. (2009), the environmental conditions were humid and temperate considering the requirements of the extant Podocarpaceae, Araucariaceae, Nothofagaceae and ferns. The composition of the paleoflora indicates that it consists of a number of elements still present in the Andean Patagonian flora (e.g., *Blechnum*, *Nothofagus*, *Rubus*, *Embothrium*) that grow under cool-temperate and humid conditions. Fabaceae leaves analogous to *Sophora cassioides*, a tree native of Chile, also suggest humid conditions.

7. Comparisons and discussion

Recently, Torres et al. (2013) described the occurrence of a well-preserved flora in fluvial deposits correlated with the Río Leona Formation outcropping in the Sierra Baguales, Magallanes, Chile. Torres et al. (2013) recognized a slightly higher diversity with at least 19 morphotypes of leaves, with *Nothofagus* as the dominant species represented by *N. simplicidens*, *N. densinervosa*, *N. variabilis*, *N. paleoalexandri*, *N. subferruginea*, *N. serrulata*, and *N. crenulata*. The subordinate elements include representatives of Myrtaceae, Lauraceae, Asteraceae, and less frequently species from the Berberidaceae and Rosaceae. Rare specimens such as *Berberis* L. thorns, unidentified inflorescences, impressions of a conifer assigned to cf. *Lepidothamum fonkii* Phil., *Eucalyptus chubutensis*, *Araucaria* sp. and fern leaf impressions were also recovered. These last species were not still recognized in the Argentinian outcrops. Torres et al. (2013) proposed an early Miocene age for the Chilean paleoflora based on the age of 20 to 19 Ma of the overlying Estancia 25 de Mayo Formation (Cuitiño et al., 2012).

The Patagonian upper Oligocene–middle Miocene Ñirihau Formation contains a paleoflora studied by Fiori (1939, 1940), Frenguelli (1943), Romero and Arguijo (1981), Menéndez and Caccavari (1966), Falaschi et al. (2013) and Caviglia and Zamalao (2014). The lower section of this unit is characterized by a “mixed flora” with *Nothofagus* (Romero, 1978) while the upper section represents an association of the subantarctic type similar to the flora described by Dusén (1899) for the Loreto Formation (Oligocene) dominated by *Nothofagus* species. The term “mixed flora” was defined by Romero (1978, 1986) for Palaeogene associations which bear sub-Antarctic cool temperate taxa mixed with subtropical ones.

Caviglia and Zamalao (2014) described from the Ñirihau Formation, in the Pico Quemado locality, an assemblage including the Nothofagaceae, Myrtaceae, Rosaceae, Myricaceae, Malvaceae and Fabaceae where the genus *Nothofagus* was found to be the dominant. *Nothofagus magelhaenica* and *N. simplicidens* are the only species shared with the Río Leona paleoflora.

The late Oligocene Abanico Formation in Cerro Las Aguilas (Chile) also contains a “mixed flora” with *Nothofagus serrulata*, *Persea* Mill., *Phoebe* Nees, *Laurophyllum* spp., *Myrcia* D.C., Myrtaceae spp., *Cassia* L., *Berberis*, *Blechnum* and *Austrocedrus* Florin and Boutleje (Sellés and Hinojosa, 1997). This flora includes tropical- subtropical taxa and subantarctic species.

8. Conclusions

The early late Oligocene Río Leona Formation preserves in Patagonia one of the few records of well-dated floras. Leaf impressions of ferns, conifers and angiosperms allow the recognition of 18 fossil taxa which provide information about the possible climatic conditions during the deposition of the unit. Two species originally described by Frenguelli (1941), “*Rubus*” *primaverae* and “*Blechnum*” *turbioense* are for the first time rediscovered in the region. Other species have a wide distribution in the Paleogene of Patagonia like *Myrtiphyllum bagualense*, *Nothofagus simplicidens*, *Nothofagus magelhaenica* and *Nothofagus subferruginea*. The probable record of *Prosopis* is mentioned for the first time in Patagonia and the Leguminosae are represented by four morphotaxa. Many of the plant families represented in the palynological assemblages are also in the macrofloristic record. The apparent moderate diversity of the macrofloristic assemblage is also present in the palynological record and fossil wood recovered from the formation. The presence of Podocarpaceae, Nothofagaceae, Myrtaceae, Anacardiaceae families and genera of Rosaceae, Proteaceae and ferns at present growing in the Andean Patagonia suggests similar environmental conditions, temperate and humid, during the development of the vegetation.

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.revpalbo.2015.01.002>.

Acknowledgments

We thank two anonymous reviewers for their helpful comments. J. Francis is grateful for funding from the University of Leeds to support the fieldwork in Argentina. The research was financed by the Argentinian Agencia Nacional de Promoción Científica y Tecnológica.

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