

Revision of the Proteaceae Macrofossil Record from Patagonia, Argentina

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Abstract

Proteaceae are restricted to the Southern Hemisphere, and of the seven tribes of the subfamily Grevilleoideae, only three (Macadamieae, Oriteae, and Embothrieae) have living members in Argentina. Megafossil genera of Proteaceae recorded from Patagonia include *Lomatia*, *Embothrium*, *Orites*, and *Roupala*. In this report, we evaluate and revise fossil Argentine Proteaceae on the basis of type material and new specimens. The new collections come from the Tufolitas Laguna del Hunco (early Eocene, Chubut Province), the Ventana (middle Eocene, Río Negro Province), and the Río Ñirihuau (late Oligocene-early

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Miocene, Río Negro Province) formations, Patagonia, Argentina. We confirm the presence of *Lomatia preferruginea* Berry, *L. occidentalis* (Berry) Frenguelli, *L. patagonica* Frenguelli, *Roupala patagonica* Durango de Cabrera et Romero, and *Orites bivascularis* Romero, Dibbern et Gandolfo. Fossils assigned to *Embothrium precoccineum* Berry and *E. pregrandiflorum* Berry are doubtful, and new material is necessary to confirm the presence of this genus in the fossil record of Patagonia. A putative new fossil species of Proteaceae is presented as Proteaceae gen. et sp. indet. Fossil Proteaceae are compared with modern genera, and an identification key for the fossil leaf species is presented. Doubtful historical records of Proteaceae fossils for the Antarctic Peninsula region and Patagonia are also discussed. Based on this revision, the three tribes of Proteaceae found today in Argentina were already present in Patagonia by the early Eocene, where they probably arrived via the Australia-Antarctica-South America connection.

Resumen

La familia Proteaceae está restringida al Hemisferio Sur, y en Argentina sólo tres (Macadamieae, Oriteae y Embothrieae) de las siete tribus de la subfamilia Grevilleoideae están representadas. En Patagonia, megafósiles asignados a Proteaceae incluyen los géneros *Lomatia*, *Embothrium*, *Orites* y *Roupala*. En este trabajo, se evalúan y revisan todos los registros fósiles de Proteaceae para Argentina basados en el material tipo y en nuevos especímenes. Las nuevas colecciones fueron realizadas en las formaciones Tufolitas Laguna del Hunco (Eoceno Temprano, Provincia del Chubut), Ventana (Eoceno Medio, Provincia de Río Negro) y Río Ñirihuau (Oligoceno Tardío- Mioceno Temprano, Provincia de Río Negro), Patagonia, Argentina. Se confirma la presencia de *Lomatia preferruginea* Berry, *L. occidentalis* (Berry) Frenguelli, *L. patagonica* Frenguelli, *Roupala patagonica* Durango de Cabrera et Romero, and *Orites bivascularis* Romero, Dibbern et Gandolfo. Los fósiles asignados a *Embothrium precoccineum* Berry and *E. pregrandiflorum* Berry son dudosos, y nuevo material es necesario para confirmar la presencia de este género en el registro fósil de Patagonia. Una posible nueva especie fósil es presentada como Proteaceae gen. et sp. indet. Los fósiles asignados a Proteaceae son comparados con géneros modernos, y se proporciona una clave para la identificación de las especies fósiles. Los registros fósiles históricos dudosos de Proteaceae para la región de la Península Antártica y Patagonia son también discutidos. Basados en esta revisión, las tres tribus de Proteaceae que se hallan hoy en Argentina se encontraban ya presentes en Patagonia durante el Eoceno temprano, donde probablemente arribaron vía la conexión Australia- Antártida- Sudamérica.

Introduction

Proteaceae, with approximately 70 genera and over 1700 species, is one of the most diverse families of the Southern Hemisphere; it is restricted to tropical and subtropical regions and to sclerophyll heaths and woodlands on oligotrophic soils (Johnson & Briggs, 1975, 1981; Cronquist, 1981). The family is considered to be a relict group from Gondwana because of its disjunct modern distribution (Johnson & Briggs, 1963, 1975, 1981; Weston & Crisp, 1994) in Australia, Africa, Central and South America, and in limited places in Asia and the Pacific Islands (Johnson & Briggs, 1975, 1981; Harden, 1990). The family has a significant fossil record of pollen, leaves, fruits, and wood found in Australia, New Zealand, Antarctica, and Argentina (Frenguelli, 1943; Orlando, 1964; McNamara & Scott, 1983; Christophel, 1984; Troncoso, 1986; Christophel &

Greenwood, 1987; Carpenter & Hill, 1988; Durango de Cabrera & Romero, 1988; Hill & Christophel, 1988; Romero et al., 1988; Ancibor, 1989; Dettmann & Jarzen, 1991, 1996, 1998; Christophel et al., 1992; Carpenter et al., 1994; Jordan, 1995; Askin & Baldoni, 1998; Jordan et al., 1998; Vadala & Greenwood, 2001).

Living Proteaceae are trees or shrubs characterized by variable leaf morphology (leaves can be simple, compound, highly divided, etc.), diverse inflorescence types (some of which can bear more than 1000 flowers, Johnson & Briggs, 1981), and their specialized, seasonal "proteoid roots" (McCarthy, 1995). Johnson and Briggs (1975) provided a classification based on morphological characters, in which the family is divided into five subfamilies: Persoonioideae, Proteoideae, Sphalmioideae, Carnarvonioideae, and Grevilleoideae. A later treatment by Douglas (1995), also based on morphology, slightly modified Johnson and Briggs classification and divided the family into seven subfamilies; Douglas recognized the five subfamilies as presented by Johnson and Briggs and added the subfamilies Bellendenoideae and Eidotheoideae, each one comprising one genus. In a more recent paper, Hoot and Douglas (1998) proposed, on the basis of molecular data (*atpB* and *atpB-rbcL* intergenic spacer region sequences), the same seven subfamilies. However, one problem with this analysis is the limited number of species sampled, only 46 of approximately 1700 known. A new suprageneric classification of the Proteaceae was proposed by Weston and Barker (2006), based on supertree analysis of molecular data using matrix representation and parsimony.

Grevilleoideae, the only subfamily found in Argentina, is characterized by paired flowers that are subtended by a common bract (Douglas 1995), and its monophyly is supported by its auriculate cotyledons, and its follicular fruits (Weston & Barker, 2006). This widely distributed subfamily contains seven, six, or four tribes depending on what classification is adopted. Johnson and Briggs (1975), on the basis of morphology, proposed seven tribes: Embothrieae, Macadamieae, Oriteae, Knightieae, Helicieae, Grevilleae, and Banksieae. Hoot and Douglas (1998), using molecular data, proposed the same tribes, except for Grevilleae, which is included within Macadamieae. Weston and Barker (2006) suggest four tribes for the subfamily, based on morphology and molecular data: Roupaleae (including Oriteae, Knightieae, and Helicieae), Embothrieae (including Grevilleae), Macadamieae, and Banksieae. However, Weston and Barker point out that more studies are necessary to confirm the monophyly of Roupaleae. Therefore, for the purpose of this paper, we accept the taxonomic treatment of Johnson and Briggs (1975) and Hoot and Douglas (1998), at least until the monophyly of Roupaleae is confirmed and the necessary taxonomic changes are published and accepted.

According to the taxonomic treatments here adopted, only three tribes within Grevilleoideae (Embothrieae, Macadamieae, and Oriteae) are currently found in Argentina. The Embothrieae have two genera, the monospecific *Embothrium*, endemic to South America, and *Lomatia*, which is found in Australia and South America. The Macadamieae are represented by two genera, the South American endemic *Gevuina* and the South and Central American endemic *Roupala*. Oriteae contain the genus *Orites*, which is restricted to temperate regions of Australia and southern South America (Prance & Plana, 1998; Torres, 1998; Xifreda & Sanso, 2001). In Argentina, *Lomatia*, *Embothrium*, and *Gevuina* are confined to the Andean-Patagonian forests (Sleumer, 1954, 1984; Xifreda & Sanso, 2001); *Roupala* inhabits the rainforests of Misiones, Jujuy, and Salta Provinces (Dimitri, 1974; Legname, 1982; Xifreda & Sanso, 2001), and *Orites* is disjunct between Neuquén, Río Negro, and Chubut Provinces in Patagonia and northern Salta Province.

All extant Argentine genera, except *Gevuina*, have purported fossil representatives

from the Patagonian region of Argentina. Assignments include *Embothrium pregrandiflorum* and *Embothrium precoccineum* (Berry, 1938), *Lomatia occidentalis*, *L. patagonica*, and *L. preferruginea* (Berry, 1925, 1938; Frenguelli, 1943; Gunckel Luer, 1957), *Orites bivascularis* (Berry, 1925; Frenguelli, 1943; Romero et al., 1988), and *Roupala patagonica* (Durango de Cabrera & Romero, 1988). With the exception of *O. bivascularis* infructescences, all of the fossil species are based on compression-impression leaves. Ancibor (1989) described a petrified root from the Lower-Middle Eocene Río Turbio Formation (Hünicken, 1966) in Santa Cruz Province, southern Patagonia. This material was assigned to the genus *Lomatia*, based on the presence of xylological characters comparable to the extant species *L. hirsuta*.

Most of the Argentine Proteaceae fossil species were described during the first half of the twentieth century by Dusén (1907, 1916), Berry (1925, 1932, 1938), Frenguelli (1943), and Gunckel Luer (1957), and these studies typically included a high proportion of misidentified fossil taxa (Christophel, 1980; Romero et al., 1988; Wilf et al., 2005) and lack of proper diagnosis.

The goal of this paper is to revise the fossil Argentine Proteaceae making use of recent collections to provide proper and emended descriptions, to revise type designations, and to make comparisons with living relatives. Fossils of uncertain position within Proteaceae, coming from several Patagonian and Antarctic Peninsula region basins, are also discussed.

Materials and Methods

GEOLOGICAL BACKGROUND AND AGE

The fossil material studied here comes from three different geological units in northwestern Patagonia (Fig. 1). The oldest one is known as the Tufolitas Laguna del Hunco (Aragón & Mazzoni, 1997; included in the Huitrera Formation in older literature). This unit is derived from tuffaceous caldera-lake deposits that belong to the middle Chubut River volcanic-pyroclastic complex (Aragón & Mazzoni, 1997). The age of the fossiliferous horizons was originally thought to be Miocene (Berry, 1925), and later, Paleocene to middle Eocene (Archangelsky, 1974; Arguijo & Romero, 1981; Mazzoni et al., 1991). Recent $^{40}\text{Ar}/^{39}\text{Ar}$ analyses from three airfall tuffs found interbedded with the fossils, coupled with the detection of six paleomagnetic reversals in the 170-m lake sequence, indicate an early Eocene age near 52 Ma, including an age of 51.91 ± 0.22 Ma from a tuff containing sanidine (Wilf et al., 2003, 2005). The main fossiliferous exposures are found at 42.5°S , 70°W (see Wilf et al., 2003, 2005, for detailed information).

The second unit is Río Pichileufú, within the Ventana Formation, where a tuffaceous lacustrine sequence broadly similar in lithology to Laguna del Hunco, but more poorly exposed, crops out (Berry, 1938; Aragón & Romero, 1984). Traditionally, this sequence, located at 41.2°S , 70.8°W , has been correlated with the Tufolitas Laguna del Hunco, primarily on the basis of shared plant species. Romero (1978) initially suggested a Paleocene-early Eocene age; however, González Díaz (1979) indicated a middle Eocene age based on K/Ar radioisotopic analyses of Ventana exposures with uncertain relationship to the floras. Recent $^{40}\text{Ar}/^{39}\text{Ar}$ analyses of three tuffs, one found immediately above the fossil plants, give a high-precision middle Eocene age of 47.46 ± 0.05 Ma (Wilf et al., 2005), 4.5 my younger than the Laguna del Hunco floras.

The Ñirihuau Formation contains fine-grained sediments and coal beds deposited in

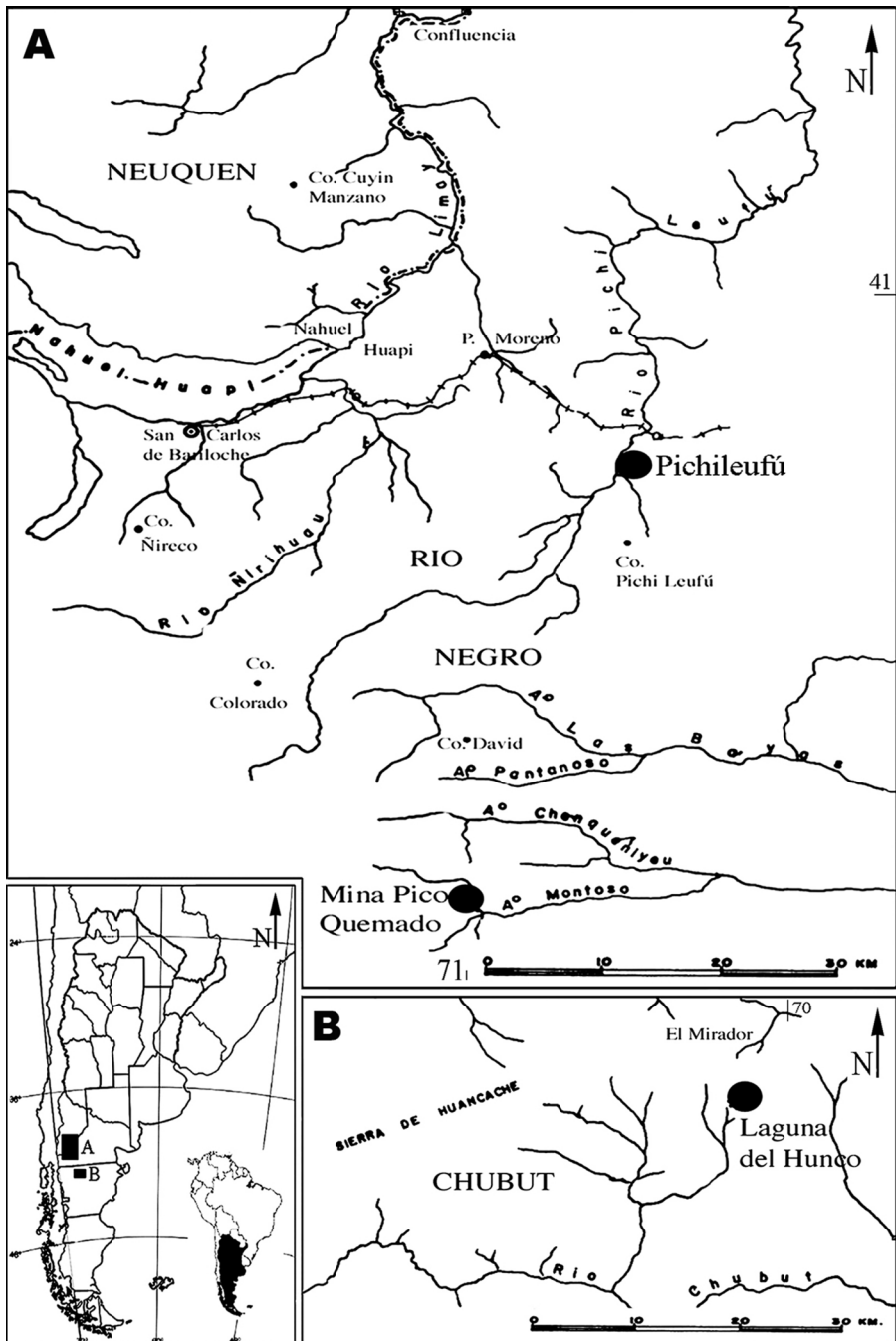


Fig. 1. Map of Argentina showing areas of study. **A.** Localities of Pichileufú and Mina Pico Quemado, Río Negro Province. **B.** Close-up showing the geographic position of the Laguna del Hunco localities, northwest Chubut Province. Redrawn from Aragón and Romero (1984).

pond and swamp environments. At the Pico Quemads locality, the plant material occurs interbedded with and immediately above the coal beds (Aragón & Romero, 1984). Malumíán (1999) interpreted this unit as being late Oligocene-early Miocene in age on the basis of palynological content and stratigraphic relationships.

MATERIAL PROCEDURE, PREPARATION, AND EXAMINATION

Fossils are preserved as impressions and were prepared according to standard methods (dégagement and small pneumatic hammer). Studied material comes from collections at the Museo Paleontológico Egidio Feruglio, Chubut, Argentina (MPEF-Pb); National Museum of Natural History, Smithsonian Institution, USA (USNM); Museo de Ciencias Naturales de La Plata, Buenos Aires, Argentina (LPPb); Fundación Miguel Lillo, Tucumán, Argentina (LilPb), and Departamento de Ecología, Genética y Evolución, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Argentina (FCENCBPB).

For comparison, leaves of modern species were cleared using the technique developed by Foster (1953) and modified by Dizeo de Strittmatter (1973). Two modifications were introduced: methylene blue was used for staining instead of safranin O, and semi-transparent polyester resin 3% was used for mounting rather than Canada balsam.

Fossil and modern leaves are described using the terminology of Dilcher (1974), Hickey (1974), Hickey and Wolfe (1975), and the Leaf Architecture Working Group (1999), and they were examined using a Zeiss MC80DX stereoscopic microscope with a camera lucida attachment.

Systematics

Family: Proteaceae A. L. de Jussieu

Subfamily: Grevilleoideae Engler

Tribe: Embothriace Meisner

Subtribe: Lomatinae Johnson & Briggs

Genus: *Lomatia* R. Brown 1810

Lomatia occidentalis (Berry) Frenguelli 1943.

Figures: Figs. 2 A–G

Synonyms: *Lomatites occidentalis* Berry 1925 (p. 200, Pl. IX, Figs. 1–3)

Lectotype: USNM 219076 (Berry 1925, Pl. IX, Fig. 3, here designated and illustrated in Fig. 2A)

Paratypes: USNM 219074 and 219075.

Type locality: Historic locality at Laguna del Hunco, 42°20'S, 70°W (Berry, 1925), Chubut Province, Argentina.

Age and stratigraphy: Early Eocene, Tufolitas Laguna del Hunco.

Additional studied material: MPEF-Pb 988, 1035, and 1037 (Laguna del Hunco, Locality 2 of Wilf et al., 2003); MPEF-Pb 987, 995, 997, 1031, 1032, 1033, 1036, 1038, 1039, and 1043 (Locality 4); MPEF-Pb 1030 (Locality 13), and MPEF-Pb 1034 (Locality 15) (precise geographic coordinates for each locality are given by Wilf et al., 2003). MPEF-Pb 178, 974, 989, 996, 998, and 999 (float specimens, see Wilf et al., 2003). LPPb 960, 2465–2468, 2530–2533, 11363–11370, 20424–20426, 20428–20433, and

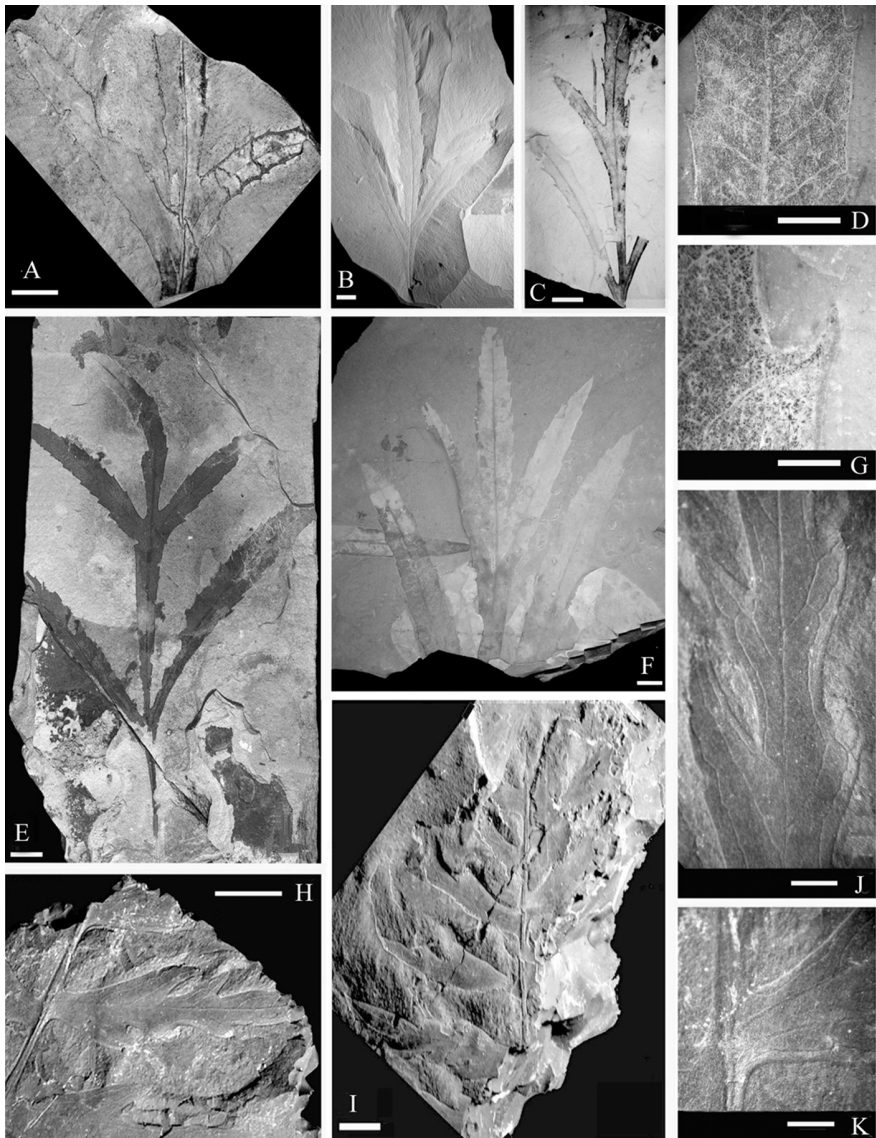


Fig. 2. A–G. *Lomatia occidentalis* (Berry) Frenguelli 1943. **A.** Lectotype, USNM 219076. **B.** LPPb 20437, general aspect showing the winged midvein. **C.** MPEF-Pb 178, imparipinnately lobed leaf with subalternate lobes. **D.** MPEF-Pb 998, showing detail of the venation of a tooth. The medial vein is the direct continuation of a secondary vein. **E.** MPEF-Pb 974, imparipinnately lobed leaf showing the winged midvein, the wing expanded toward the bases of lobes and increasing in width toward the insertion of the superjacent leaflet. **F.** MPEF-Pb 1031, showing the acute apex of lobes. **G.** MPEF-Pb 998 showing detail of the simple teeth separated by angular sinuses. **H–K.** *Lomatia patagonica* Frenguelli 1943; LPPb 335. **H.** A fragment of the holotype showing detail of the asymmetric, sessile, and deeply incised leaflets. **I.** Larger fragment of the holotype showing bipinnatisect leaf with pairs of lobed leaflets. **J.** Detail of the venation of the leaflets. Note the margin entire, and the lobules culminating in an acute, spinose apex. **K.** Detail of point of insertion of the leaflet at its base. **A, B, C, E, F, H, and I,** scale bar = 1 cm; **D,** scale bar = 0.25 cm; **G,** scale bar = 0.125 cm; **J and K,** scale bar = 0.25 cm.

20437; FCENCBPB 171, 172, 173, 174, 175, 176, 177, 178, 179, 182, and 183 (these specimens come from the historic locality at Laguna del Hunco).

Revised description: Imparipinnate or pinnatisect leaf, mesophyll, up to 19 cm long and 10 cm wide, with one apical and at least two pairs of lateral leaflets/lobes incised nearly to midvein (Figs. 2A–C, E, and F). Leaflets/lobes alternate to subalternate, symmetric, linear-lanceolate to oblong, base decurrent and apex acute, 6–10 cm long and 1–2 cm wide. Midvein winged, wing expanded toward the bases of lobes and increasing in width toward the insertion of the superjacent leaflet (Fig. 2E). Margin serrate, one tooth per secondary vein. Teeth simple, concave on the apical and convex (CC/CV) or straight (CC/ST) on the basal with acute apex, separated by angular sinuses and spaced regularly (1–3 teeth per cm). Teeth vascularized by medial veins that are the direct continuations of the secondary veins, or by tertiary veins emerging from secondary veins (Fig. 2D and G). Primary vein category pinnate, without agrophic veins. Secondary vein category semicraspedodromous or craspedodromous, secondary veins in 6–18 pairs, regularly spaced, emerging at a uniform, acute angle, with slightly curved course. When the secondary veins are craspedodromous, they bifurcate, and one of the ramifications is fused to the superjacent secondary vein at an acute angle (Fig. 2D). Intercostal areas well developed, with one or two intersecondary veins in each intercostal area. Some intersecondary veins reach the bifurcation of the secondary vein and are fused to it at a right angle (Fig. 2D). Tertiary vein category alternate, random reticulate, with sinuous course, emerging at inconsistent obtuse angles. Fourth-order vein category random reticulate. Fifth-order vein category poorly developed. Areoles moderately well or well developed, 3–5-sided. Ultimate marginal venation looped and forming a fimbrial or intramarginal vein. Freely ending veinlets are two or more-branched.

Lomatia patagonica Frenguelli 1943.

Figures: Figs. 2H–K

Holotype: LPPb 335 (Frenguelli, 1943, Fig. 2A, Pl. IV, here designated and illustrated in Figs. 2 H–K).

Type locality: Historic locality of Morro Revancha, close to Pico Quemado, between Norquínco and Las Bayas, Río Negro Province, Argentina.

Age and stratigraphy: Late Oligocene-early Miocene, Ñirihuau Formation.

Revised description: Bipinnatisect leaf, mesophyll, at least 13 cm long and 7.8 cm wide, with seven pairs of lobed leaflets. Leaflets asymmetric, sessile, subopposite, ovate-lanceolate microphylls; base asymmetric, acute, and decurrent (Fig. 2H); apex acute; 3.2–5.5 cm long and 0.9–1.25 cm wide. Leaflets deeply incised and of variable shape, size, and position on the rachis (median leaflets larger and more deeply lobed than distal and proximal leaflets). Margin entire, including lobules, each lobule culminating in an acute, spinose apex. Rachis 1 mm wide, grooved, and slightly winged. Primary vein category of leaflets pinnate, simple, straight in course, and reaching the apex of the apical lobule, without agrophic veins. Secondary vein category camptodromous or craspedodromous, 8–10 pairs emerging irregularly at a uniform acute angle (Fig. 2J). Intercostal areas well developed, with one intersecondary vein, simple or compound. At the base there are two lateral veins that emerge from the rachis, of smaller gauge than the rest of the secondary veins (Fig. 2K). Tertiary vein category random reticulate, emerging at straight-acute angle on the superior side, and at obtuse-straight angle on the inferior side. Ultimate marginal venation complete, looped.

Lomatia preferruginea Berry 1938.

Figures: Figs. 3A–J

Lectotype: USNM 219145 (Berry, 1938, Pl. 14, Fig. 6, here designated and illustrated in Fig. 3A).

Paratype: USNM 219144 (Berry, 1938, Pl. 14, Figs. 5 and 7, here illustrated in Fig. 3E and H).

Type locality: Historic locality of Río Pichileufú, Río Negro Province, Argentina (Berry, 1938, precise location not given).

Age and stratigraphy: Middle Eocene, Ventana Formation.

Additional studied material: MPEF-Pb 972 (Laguna del Hunco, Locality 15 of Wilf et al., 2003), MPEF-Pb 1040 and 1041 (Locality 13). FCENCBPB 184 and 185 A, B (historic locality at Laguna del Hunco).

Revised description: Imparipinnately compound leaf, up to 15 cm long and 16 cm wide, with one apical and at least five pairs of leaflets (Figs. 3A, B, F, and G). Leaflets asymmetric, with opposite or subopposite insertion on rachis, usually sessile, ovate or elliptic, apex acute, base decurrent, up to 9–11 cm long and 2–2.5 cm wide (Figs. 3H and J). Leaflet margin serrate and often lobed; teeth compound, 2–3 per secondary vein and 1–2 per cm of margin, the number of teeth diminishing toward the leaflet apex to one per secondary vein; teeth irregularly spaced and separated by rounded sinuses; first- and second-order teeth concave on the apical flank and convex on the basal (CC/CV; Figs. 3C, D, and H). The principal vein of the first-order tooth is the direct continuation of a secondary vein that enters the tooth medially (Fig. 3E); the venation of the second-order tooth is a bifurcation of the secondary vein, which enters the tooth medially (Fig. 3E). At the base of several leaflets, there is a small tooth irrigated by a secondary vein of less gauge than the other ones (Fig. 3I). Primary vein category of leaflets pinnate, simple, with straight course, without agrophic veins. Secondary vein category craspedodromous, 7–8 pairs, curved course, emerging at regular, acute angles and spaced regularly, forming well-developed intercostal areas (Figs. 3E and H). Simple intersecondary veins present, bifurcating close to the margin at both sides of the sinus, one branch fusing with the ramification of the secondary vein that irrigates the tooth. Tertiary vein category random reticulate, emerging at obtuse angle, with sinuous course and nonuniform variability. Fourth-order vein category reticulate. Fifth-order vein category poorly preserved. Ultimate marginal venation looped. Areoles poorly preserved.

Comments: Of the 12 extant species of *Lomatia*, seven have imparipinnately compound leaves, and only *L. ferruginea* (Cav.) R. Br. 1810 is restricted to southern South America (Prance & Plana, 1998), while the remaining species are found in Australia (Carpenter & Hill, 1988; Harden, 1990). *Lomatia ferruginea* leaves are bipinnate, and the leaflet lobes are deeply incised with entire margins and acuminate apices; the apical lobe is falcate, and the leaflets lack basal veins (Gonzalez et al., 2004). The basic leaf architecture of *L. ferruginea* and fossil Argentine species of *Lomatia* is quite similar. They all present the same pattern for the primary, secondary, tertiary, and quaternary vein categories; agrophic veins are lacking, and the marginal ultimate venation is looped.

Berry (1925) erected the species *Lomatites occidentalis* without designating a holotype. His description was based on three fossils collected by Clark in 1922 at the “Mirhoja” locality, of unknown stratigraphic position in the Laguna del Hunco sequence, but most likely Locality 4 of Wilf et al. (2003). The three specimens are housed at the USNM. Although Berry placed the fossils within the fossil genus *Lomatites* Saporta,

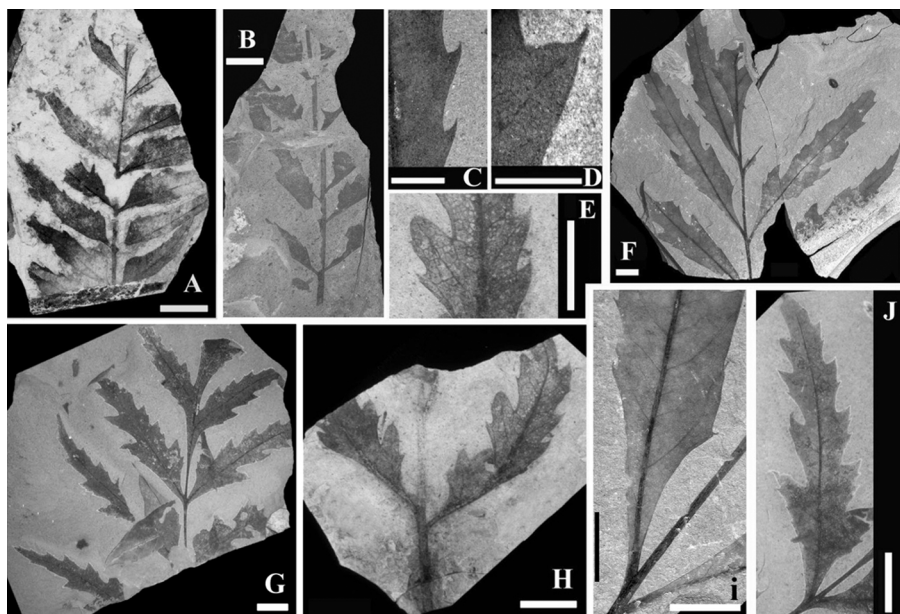


Fig. 3. *Lomatia preferruginea* Berry 1938. **A.** Lectotype, USNM 219145, showing the asymmetric leaflets, with opposite or subopposite insertion on rachis. **B.** FCENCBPB 185, imparipinnately compound leaf, with at least five pairs of leaflets. **C** and **D.** MPEF-Pb 972. **C.** Detail of the teeth. **D.** Detail of tooth venation. The principal vein is the direct continuation of a secondary vein that enters the tooth medially. **E.** Paratype, USNM 219144, showing detail of the accessory tooth venation. **F.** MPEF-Pb 972, in general aspect. **G.** FCENCBPB 184, showing the acute apex and decurrent base of the leaflets. **H.** Paratype, USNM 219144, detail of the leaflets with serrate margin, the teeth irregularly spaced and separated by rounded sinuses. **I.** MPEF-Pb 972, detail of tooth venation and leaflet insertion on the rachis. **J.** FCENCBPB 184, detail of a leaflet. Note the number of teeth diminishing toward the leaflet apex to one per secondary vein. **A, B, F–J,** scale bar = 1 cm; **C–E,** scale bar = 0.5 cm.

Frenguelli (1943), who collected numerous additional fossils (housed at LPPB) probably at the same locality, emended Berry's description on the basis of the additional collection and transferred *Lomatites occidentalis* to the modern genus *Lomatia*, though he did not designate types. The 1999 and 2002 expeditions to Laguna del Hunco have yielded more than 45 fossils assignable to *Lomatia occidentalis*, including much more complete material (Figs. 2E and F), thus adding new characters to the previous description.

Lomatia occidentalis is characterized by the symmetric, deeply incised, narrow, sharp-pointed pinnate lobes; the winged midvein with the wing expanded toward the bases of lobes and increasing in width toward the insertion of the superjacent leaflet, the margin serrate with one tooth per secondary vein, the secondary vein pattern semicraspedodromous or craspedodromous, including the fusion of the bifurcation of the secondary vein with the superjacent secondary vein and the intersecondary vein, the fourth-order vein category random reticulate, and the ultimate marginal venation looped and forming a fimbrial or intramarginal vein. The secondary vein category and its semicraspedodromous or craspedodromous patterns are clearly visible in some of the new specimens (Fig. 2D), in which undoubtedly the bifurcation of the secondary vein is reached by the inter-

secondary vein at a right angle, and its bifurcation is fused to the superjacent secondary vein. Apparently, the three distal leaflets are of the same size, except in one specimen (MPEF-Pb 988) in which the apical leaflet is larger than the remaining ones.

Another fossil species of *Lomatia*, *L. patagonica*, was erected by Frenguelli (1943) based on only one specimen (LPPb 335). So far, this is the only fossil known for this species. While revising the material, it was noticed that the specimen is broken into three fragments; for that reason, the specimen illustrated in this report (Fig. 2H–K) differs from the original photograph. Nevertheless, the fragments have definitely preserved *Lomatia* characters, allowing the maintenance of the taxonomic placement of this fossil within the genus.

Lomatia patagonica is unquestionably different from the other *Lomatia* fossil species. The leaves are bipinnatisect, with seven pairs of lobed asymmetric sessile leaflets (Fig. 2I), deeply incised and of variable shape, size, and position on the rachis (median leaflets larger and more deeply lobed than distal and proximal leaflets); the leaflet margins are entire, and each lobule culminates in an acute, spinose apex; their rachises are grooved, and slightly winged.

Lomatia preferruginea was described by Berry (1938) from the Río Pichileufú flora, based on two specimens: USNM 219144 (Fig. 3H) and USNM 219145 (Fig. 3A). These fossils are incomplete leaves that were described as mainly imparipinnate with 4–5 lateral pairs of leaflets in addition to the apical one; the leaflets are asymmetric and almost falcate, deeply lobed with serrate margins, acute apices, and cuneate to decurrent bases. Even though Berry (1938) described the venation as camptodromous and/or craspedodromous with the teeth irrigated by a tertiary vein, he mentioned that the venation is poorly preserved as well. In addition, he also asserted that the available fossil material is “not sufficient to elucidate certain features which one might wish to know” (Berry, 1938). The new specimens from recent collections at Laguna del Hunco (Fig. 3F) are better preserved than those described by Berry, and besides the presence of some of the previously described characters as diagnostic of *L. preferruginea*, they also provide new characters that allow a more complete description of the species. Berry (1938) described the leaflet margins as lobed, because the specimens he studied show marginal indentations incised more than a quarter of the distance to the leaflet midvein. However, the new specimens reveal that the margins are actually deeply serrate with compound teeth, and also that the sinuses separating the teeth are very deep. Therefore, the correct interpretation is that the leaflets are both lobed and toothed (Figs. 3E, H–J). The venation of the tooth arises from the bifurcation of a secondary vein (Figs. 3C–E) and not a tertiary vein as suggested by Berry (1938). The finding of *L. preferruginea* at the Laguna del Hunco locality extends the geographical and temporal distribution of this species and confirms its presence in Patagonia by the early Eocene.

Subtribe: *Embothriinae* Endlicher

Genus *Embothrium* J. R. Forst. & G. Forst. 1775

?*Embothrium pregrandiflorum* Berry 1938.

Figures: Figs. 4A–D.

Holotype: USNM 40399 (Berry, 1938, Pl. 16, Fig. 7, here designated and illustrated in Fig. 4D).

Type locality: Historic locality of Río Pichileufú, Río Negro Province, Argentina (Berry, 1938, precise location not given).

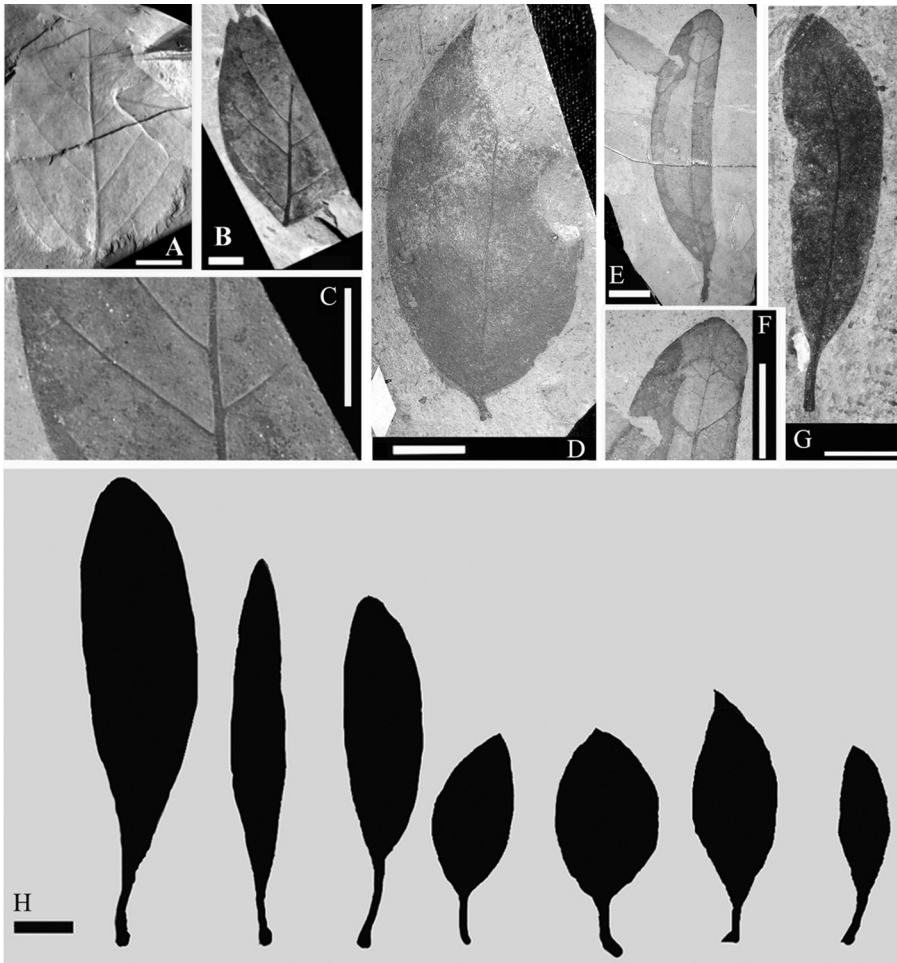


Fig. 4 A–D. *?Embothrium pregrandiflorum* Berry 1938. **A.** LPPb 2381. Leaf with entire margin and first-order venation pinnate simple, and straight. **B–C.** LilPb 5787. **B.** Symmetric, ovate to elliptic leaf. **C.** Detail of the brochidodromous venation. **D.** Holotype, USNM 40399. **E–G.** *?Embothrium precoccineum* Berry 1938. **E.** Holotype, USNM 40398 B. **F.** USNM 40398 B, detail of the rounded apex. **G.** Paratype, USNM 40398 A. **H.** *Embothrium coccineum* J.R. Forst. & G. Forst. 1776. Silhouettes of extant leaves showing intraspecific shape variability. **A–H,** scale bar = 1 cm.

Age and stratigraphy: Middle Eocene, Ventana Formation.

Additional material studied: LPPb 2381 and LilPb 5787 (both specimens come from the historic locality at Laguna del Hunco, Chubut Province, Argentina).

Revised description: Symmetric, ovate to elliptic notophylls, with probably acute apex and wide acute base (Figs. 4A, B, and D), 6.5 cm long and 3.2 cm wide. Petiole marginal without notable broadening (Fig. 4D), slightly curved, 0.4 cm long. Margin entire. Primary vein category pinnate simple, straight (Figs. 4A and B). Secondary vein cate-

gory brochidodromous, with at least five pairs of veins emerging at acute angles (Fig. 4C), course slightly curved, joining the superjacent veins at acute angles. Intercostal areas of medium size, well developed, lacking intersecondary veins. Tertiary vein category percurrent. Fourth- and fifth-order vein categories orthogonal reticulate, forming well-developed, oriented, polygonal areoles, 3–5-sided. Ultimate marginal venation looped.

?*Embothrium precoccineum* Berry 1938

Figures: Figs. 4E–G.

Lectotype: USNM 40398 B (Berry, 1938, Pl. 16, Figs. 5 and 6, here designated and illustrated in Figs. 4E and F).

Paratype: USNM 40398 A (Berry, 1938, Pl. 16, Figs. 3 and 4, here illustrated in Fig. 4G).

Type locality: Historic locality of Río Pichileufú, Río Negro Province, Argentina (Berry, 1938, precise location not given).

Age and stratigraphy: Middle Eocene, Ventana Formation.

Revised description: Lamina asymmetric, oblong, simple microphyll (Figs. 4E and G), rounded apex (Fig. 4F), and acute-cuneate base (Figs. 4E and G), 4.5–7.5 cm long and 1–2 cm wide. Petiole normal and marginal, slightly curved, 0.7–1.1 cm long. Margin entire. Primary vein category simple pinnate, curved course (Fig. 4E). Secondary vein category brochidodromous, with at least seven pairs of veins that emerge at moderate acute angles (45°–55°), slightly curved course joining the superjacent veins at moderate acute angles. Intercostal areas wide, well developed, some with simple intersecondary veins that reach only to the middle of the areas. Tertiary vein category percurrent. Fourth- and fifth-order vein categories orthogonal reticulate. Quadrangular areoles well developed. Ultimate marginal venation seems to be looped.

Comments: Berry (1938) described two fossil species within the extant genus *Embothrium*, *E. pregrandiflorum* and *E. precoccineum*, both from Río Pichileufú, Río Negro Province. *Embothrium pregrandiflorum* is based on only one specimen, which is here designated as the holotype. The additional fossils studied here were collected at the historic Laguna del Hunco locality in Chubut Province (Figs. 4A–C). They have the diagnostic characters of the fossil species and also provide information on the higher order venation patterns, the areoles, and the ultimate marginal venation, which were unknown until now.

Embothrium precoccineum is based on two specimens, now housed at the Smithsonian Institution. Although they are two different specimens, both are cataloged under the same collection number (USNM 40398A and B). Unfortunately, no other collection has yielded any additional specimens of this species; therefore, the description provided here is the result of restudying the specimens described by Berry in 1938. The new study provides a better understanding of this fossil by adding information on the higher order venation, areoles, and ultimate marginal venation, which Berry did not describe in his original work.

The extant species *Embothrium coccineum* J. R. Forst. & G. Forst. 1775 is the only Argentine member of the subtribe Embothriinae, and it is restricted to the Andean Patagonian forests (Xifreda & Sanso, 2001). It is characterized by leaves of variable size and form, ovate to oblong or lanceolate, rarely linear-lanceolate (Fig. 4H), with entire margin, tertiary vein category random reticulate, and fourth- and fifth-order vein categories regularly polygonal (Gonzalez et al., 2004).

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. Nevertheless, they differ in size, number of secondary veins, tertiary and fourth-order venation, and the ultimate marginal venation. The leaves of ?*E. pregrandiflorum* are symmetric and ovate to elliptic, have five pairs of secondary veins, and 3–5-sided areoles, while ?*E. precoccineum* has asymmetric oblong microphylls, seven pairs of secondary veins, and the four-sided areoles. ?*Embothrium pregrandiflorum* apparently lacks intersecondary veins, while the other two species have simple intersecondary veins. Also, both fossil species have third vein category percurrent, fourth vein category reticulate orthogonal, and marginal ultimate venation looped, while the modern species has third and fourth vein categories random reticulate and regular polygonal reticulate, respectively, and incomplete marginal ultimate venation with the veinlets reaching the margin freely.

In summary, the fossils have several characters in common with the modern genus *Embothrium*. Nevertheless, the limited number of specimens available and the fact that they are not well preserved make the taxonomic assignment uncertain. Perhaps these two doubtful species, ?*E. precoccineum* and ?*E. pregrandiflorum*, represent a single natural species. *Embothrium coccineum* (Fig. 4H) shows high foliar intraspecific variability, which is also observable within individuals. Nevertheless, until additional material is collected and studied this cannot be confirmed for the fossil species. Owing to these concerns, we prefer to consider the assignment of the fossils to *Embothrium* as doubtful, and therefore we consider these specimens as ?*Embothrium*.

Tribe: Macadamieae Venkata Rao

Subtribe: Roupalinae Johnson & Briggs

Genus: *Roupala* Aublet 1775

Roupala patagonica Durango de Cabrera & Romero 1988.

Figures: Figs. 5A–G.

Holotype: YPF pb 2147, housed at the Fundación Miguel Lillo, Tucumán, Argentina.

Type locality: Historic locality at Laguna del Hunco, Chubut Province, Argentina (Durango de Cabrera & Romero, 1988, precise location not given).

Age and stratigraphy: Early Eocene, Tufolitas Laguna del Hunco.

Additional studied material: MPEF-Pb 992 (Laguna del Hunco, Locality 25 of Wilf et al., 2003), LilPb 5799 (Laguna del Hunco, historic locality).

Revised description: Imparipinnately compound leaves, up to 8–20 cm long and 4.5–10 cm wide, with one apical and 3–5 pairs of asymmetric ovate leaflets (Figs. 5A–D). Leaflets opposite to alternate with apex acute, base acute decurrent (Fig. 5E), up to 4–9 cm long and 1.5–4 cm wide, petiolule normal and marginal. Leaflets margin serrate, teeth simple and/or compound, of variable shape, concave on the apical and convex on the basal side (CC/CV type mainly toward the apex of the leaflets), and straight on the apical and convex on the basal side (ST/CV type mainly at the base of the leaflets), 1–2 teeth per secondary vein, the number of teeth decreasing toward the apex of the leaflet to one per secondary vein, irregularly spaced, and separated by rounded sinuses. The venation of the simple tooth and of the principal tooth of the compound teeth is the direct continuation of a secondary vein that enters the tooth medially; the venation of the second-order tooth is a bifurcation of the secondary vein entering the tooth medially as well (Figs. 5F–G). Primary vein category of leaflets pinnate and simple with straight course. Secondary vein category

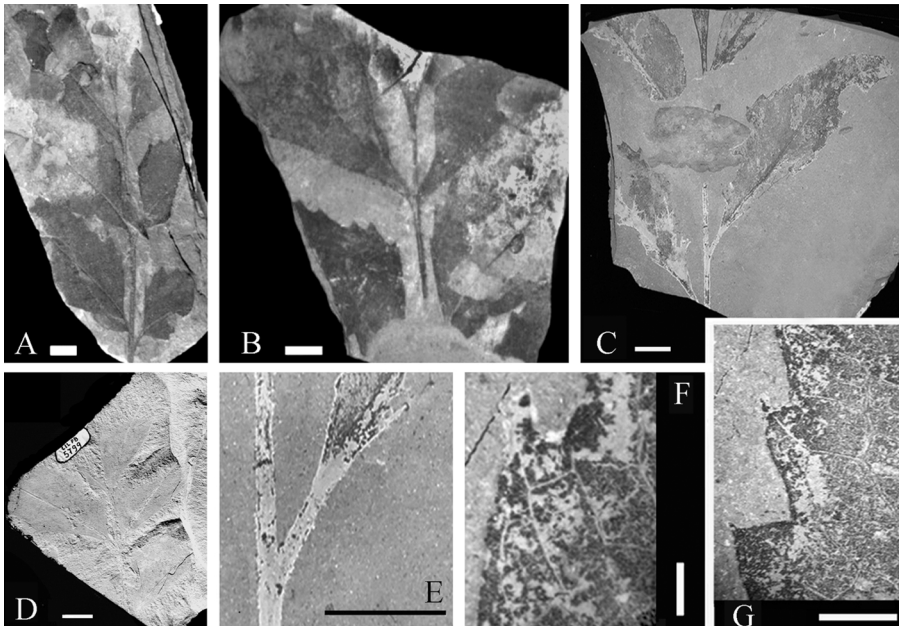


Fig. 5. *Roupala patagonica* Durango de Cabrera & Romero 1988. **A.** Holotype, YPF pb 2147, imparipinnately compound leaf, with a single apical and three pairs of asymmetric ovate leaflets. **B.** Holotype, YPF pb 2147, counterpart. **C.** MPEF-Pb 992, showing the entire margin at the base of the leaflets. **D.** LilPb 5799. General aspect of the compound leaf. **E–G.** MPEF-Pb 992. **E.** Detail of leaflet insertion on the rachis. **F.** Detail of tooth venation. **G.** Detail of the tooth main vein, which is the direct continuation of a secondary vein that enters the tooth medially. **A–E,** scale bar = 1 cm; **F,** scale bar = 0.1 cm; **G,** scale bar = 0.25 cm.

semicraspedodromous, 5–7 pairs of secondary veins, curved and regularly spaced, emerging at uniform acute angles. Tertiary vein category random reticulate, with acute-straight superior angle and obtuse inferior angle. Fourth- and fifth-order vein categories reticulate. Areoles well developed, 4–5-sided. Ultimate marginal venation looped.

Comments: *Roupala patagonica* is based on three specimens; all were collected from localities at Laguna del Hunco. Troncoso and Romero (1998) recorded *Roupala* sp. at the Bullileo locality (? late Eocene-Early Miocene) in central Chile. Unfortunately, they did not provide a description or an illustration of the fossil.

Living *Roupala* are exclusively from tropical, mostly montane areas of Central and South America. In Argentina, there are two extant species, *R. meisneri* Sleumer 1954 and *R. brasiliensis* Klotzsch 1841; both produce simple leaves (from the apical reproductive branches) and compound, imparipinnate ones (from the basal young branches). The leaves are highly variable in size, and can have entire or serrate margins, with marginal teeth concave on the apical and convex on the basal side; the two can be differentiated using leaf architecture as shown by Gonzalez et al. (2004). Extant and fossil Argentine *Roupala* have compound, imparipinnate leaves, asymmetric ovate microphyll leaflets with serrate margin, teeth of concave/convex type, primary vein category pinnate, simple and straight, higher vein categories reticulate, areoles well developed and

4–5-sided, and the ultimate marginal venation looped. Also, all of the species lack agrophic veins. The extant species differ from the fossil species in size, the secondary vein category pattern, and number of secondary veins.

Roupala patagonica, like *Lomatia occidentalis* and *L. preferruginea*, possesses imparipinnate leaves but differs from the fossil *Lomatia* species in the shape of the leaflets and the combination of tooth and sinus types. The differences between *R. patagonica* and the fossil species of *Lomatia* are clear: *L. occidentalis* is distinguished by its deeply incised pinnate lobation (Fig. 2E), *L. preferruginea* has lobed leaflets with serrate margins, having irregularly spaced simple or compound teeth (Figs. 3F–H), and *L. patagonica* has bipinnate leaves with deep lobes and entire margins and two basal lateral veins; also, the leaflets are sessile (Figs. 2H–K). *Roupala patagonica* has asymmetric ovate leaflets and simple or compound teeth of variable shape, as described above.

Indeterminate genus and species

Proteaceae gen. et sp. indet.

Figures: Figs. 6A–H; 7A, B.

Reference specimen: MPEF-Pb 991 (Figs. 6C–H).

Referred specimens: MPEF-Pb 986 (Fig. 6A), 990 (Fig. 6B), and 1042.

Type locality: Locality 13 of Wilf et al., 2003, Laguna del Hunco, Chubut Province, Argentina.

Age and stratigraphy: Early Eocene, Tufolitas Laguna del Hunco.

Description: Imparipinnate leaves, mesophylls, at least 17 cm long and 14 cm wide, with at least five pairs of ovate microphyll leaflets, rachis smooth or rough (Figs. 6A–C; Fig. 7A). Leaflets opposite, with acute to acuminate apex and asymmetric base, with one side acute and decurrent, while the other side is truncate (Fig. 6H); 7 cm long and 1–1.5 cm wide, petiolule normal and marginal. Leaflets margin serrate, simple, or compound teeth, concave/convex (CC/CV type, Fig. 6F), spaced regularly, and separated by rounded sinuses, one or two teeth per secondary vein and three teeth per centimeter. Teeth are irrigated by a bifurcation of a secondary vein that enters the tooth medially and/or dorsally (Figs. 6E–F). When the teeth are compound, the secondary vein goes toward the main tooth's sinus, and it bifurcates before reaching the margin; the basal bifurcation reaches the secondary tooth and enters it medially, while the remaining bifurcation reaches the main tooth and enters it dorsally, or this bifurcation fuses to an intersecondary vein (Figs. 6D–G; Fig. 7B). Petiolule short, normal, and marginal. Primary vein category pinnate, simple with straight course, and reaching the apex of the leaflet. Agrophic veins absent. Secondary vein category craspedodromous-semicraspedodromous, although some of the basal leaflets show the secondary veins mostly at their base as reticulate (Fig. 7B), 8–12 pairs of secondary veins emerging regularly at acute angle; the veins that bifurcate emerge at an acute uniform angle, and they are uniformly spaced. Intercostal areas well developed, intersecondary veins present, simple or compound, only one per intercostal area. Third vein category reticulate, emerging at straight-acute angle at the superior side and obtuse-straight angle at the inferior side. Fourth and fifth vein category reticulate. Areoles well developed, 4–5-sided. Ultimate marginal venation complete, looped. Some leaflets show a pair of lateral veins that emerge from the petiolule and are less wide than the secondary veins.

Comments: This putative new Proteaceae fossil species is based on four specimens, all collected from localities at Laguna del Hunco. It is characterized by its compound

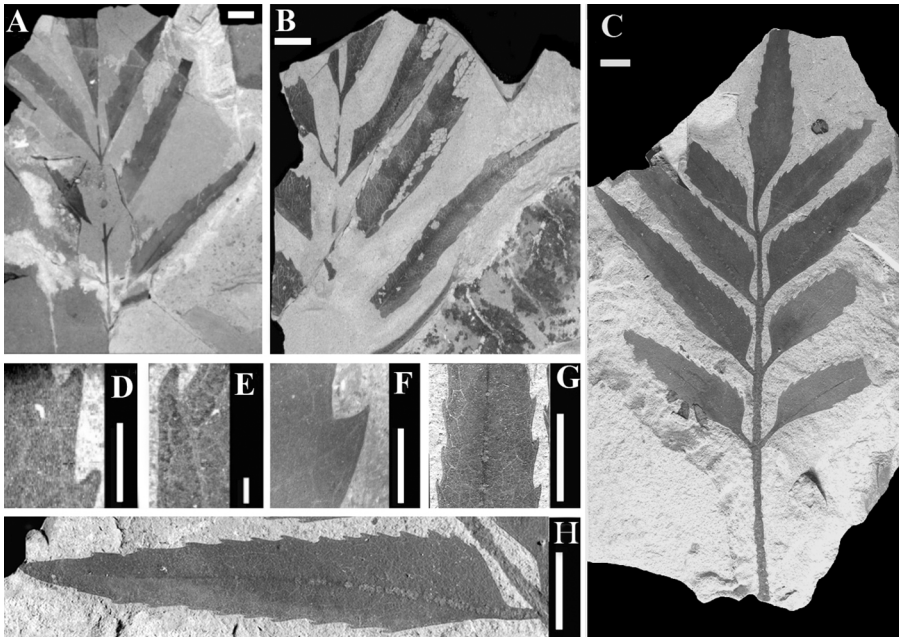


Fig. 6. Proteaceae gen. et sp. indet. **A.** MPEF-Pb 986, imparipinnately compound leaf with three lateral pairs of leaflets. **B.** MPEF-Pb 990. **C–H.** MPEF-Pb 991. **C.** General view of the leaf showing the four pairs of leaflets plus the apical leaflet. **D.** Detail of the compound teeth, showing the main and secondary teeth. **E** and **F.** Detail of tooth venation. Teeth are irrigated by a bifurcation of a secondary vein that enters the tooth medially and/or dorsally. **G.** Detail of the craspedodromous-semicraspedodromous venation. **H.** Detail of a leaflet showing the acuminate apex, asymmetric base, and serrate margin. **A–C, G, H,** scale bar = 1cm; **D** and **F,** scale bar = 0.25 cm; **E,** scale bar = 0.1 cm.

leaves (Figs. 6A–C; Figs. 7A, B), its leaflets with asymmetrical base and serrate margin (Fig. 6H), and its higher order venation pattern.

Although it has imparipinnate leaves like extant and fossil species of *Lomatia* and *Roupala*, it differs from all of them. This putative new species and *Lomatia patagonica* differ in the way that the lamina is attached to the rachis, the number of basal veins, the absence/presence of lobes, and the shape of the leaflets. *Lomatia preferruginea* and this Proteaceae fossil species differ in tooth type and venation, number of teeth per secondary vein, and teeth distribution along the margin. It also can be distinguished from *L. occidentalis* by the leaflet shape, rachis type, distribution of the teeth along the margin, and tooth venation.

Differences are noticeable between this Proteaceae species and *R. patagonica*, since they vary in the size, shape and base of the leaflets, placement of the teeth along the margin, teeth venation, secondary vein category, and number of secondary vein pairs. This putative new Proteaceae fossil species corresponds to neither Patagonian fossils previously described nor to any modern species of *Lomatia* or *Roupala*. Nevertheless, until more comparisons can be established with other extant members of the family, we consider that placement within a Proteaceae modern genus is not advisable at this point.



Fig. 7. Proteaceae gen. et sp. indet. **A.** Reconstruction of a leaf. **B.** Detail of leaflet base venation. Scale bar = 1 cm.

Tribe: Oriteae Johnson & Briggs

Genus *Orites* R. Brown 1810

Orites bivascularis (Berry) Romero, Dibbern & Gandolfo 1988.

Figures: Figs. 8A–H.

Synonyms: *Carpolithus bivascularis* Berry 1925 (p. 232, Pl. IV, Figs. 2, 3).

Lomatia occidentalis (Berry) Frenguelli 1943 (p. 205, Pl. II, Figs. 1, 2).

Holotype: USNM 219113; counterpart LPPB 236 (Fig. 8B).

Type Locality: Historic locality Laguna del Hunco, Chubut Province, Argentina.

Additional studied material: MPEF-Pb 159, 993, and 994 (Laguna del Hunco, float specimens of Wilf et al., 2003); LPPb 20434 and 20435 (Laguna del Hunco, historic locality); FCENCBPB 4, 5, 6, and 181 (Laguna del Hunco, historic locality).

Age and stratigraphy: Early Eocene, Tufolitas Laguna del Hunco.

Revised description: Infructescence with elliptic sessile foliicles spirally attached on a main axis (Figs. 8A, B, D, F) by stout peduncles (Fig. 8H). Follicles emerging from the axis at acute (approximately 30°) or straight angles. Distance between fruits approximately 0.25–1 cm. Main axis of the infructescence is 1.5–2 mm wide, and it has rhombic vascular scars spirally arranged and separated by approximately 2–3 mm (Figs. 8B, D, and F). Follicles with a longitudinal (dorsal?) dehiscence facing the main axis (Figs. 8D, E), 18.5–23 mm long and 7–8 mm wide; the peduncles are 1.5–2.5 mm long. Most of the fruits have an obliquely striate surface (Figs. 8C, G, and H). Follicles have an

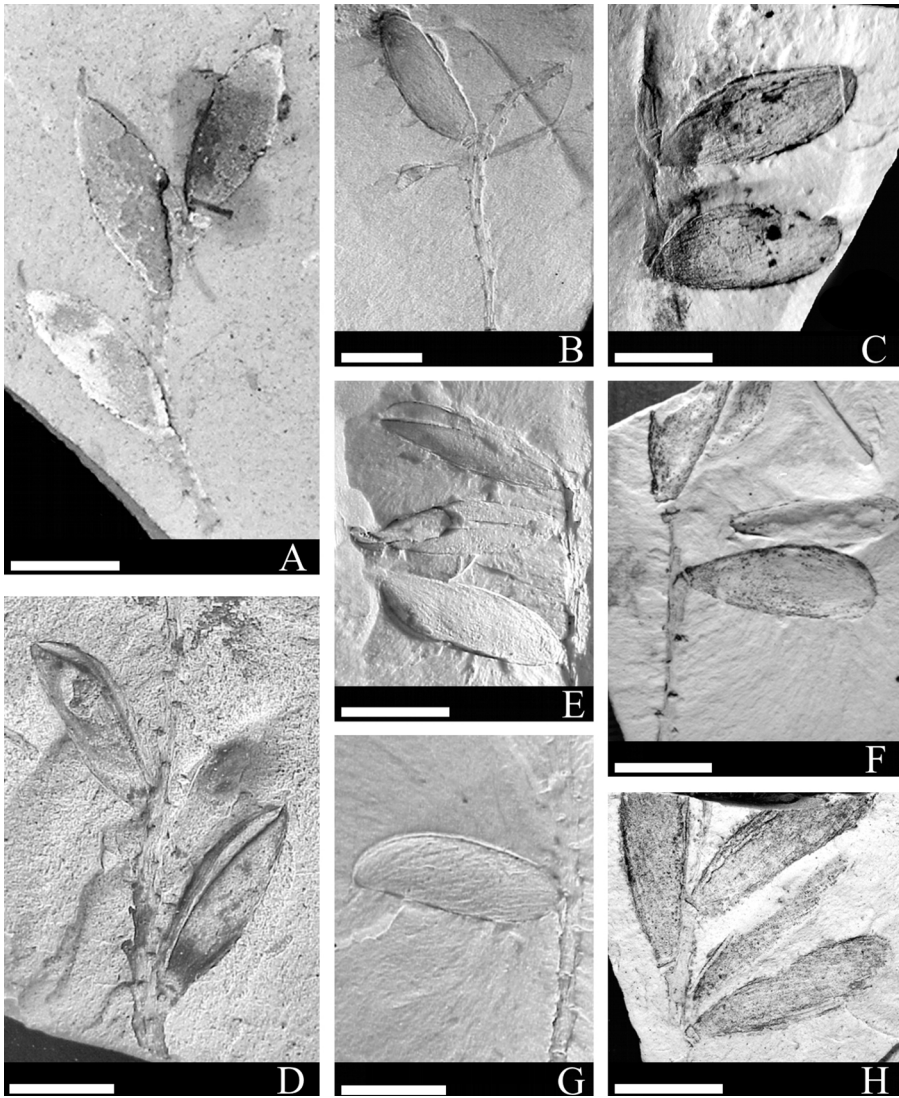


Fig. 8. *Orites bivascularis* (Berry) Romero, Dibbern & Gandolfo 1988. **A.** LPPb 20435. Infructescence, with three elliptic follicles spirally arranged on a main axis. Note the apical "rostrum." **B.** Holotype, LPPb 236. **C.** MPEF-Pb 159. Two follicles with striate surface. **D.** FCENCBPB 4. Two follicles with a longitudinal ventral suture. Main axis with rhombic scars. **E.** FCENCBPB 5. Three slightly opened follicles. **F.** MPEF-Pb 994. Axis with attached follicles. **G.** FCENCBPB 6. **H.** MPEF-Pb 993. Four striate follicles. Scale bar = 1 cm.

elongated apical “rostrum” that is curved and conical, 1.5–3.3 mm long and 0.5–0.7 mm wide (Fig. 8A).

Comments: Berry (1925; Pl. IV, Fig. 2) described the specimen now housed at the Smithsonian Institution as an axis with woody fruits that are subsessile, elongated, and elliptical in lateral profile. Although he said “it is impossible to reach a definitive conclusion regarding the botanical affinities . . .”, he compared the fruit with several extant genera such as *Picramnia* (Simaroubaceae), *Paullinia* (Sapindaceae), and *Connarus* (Connaraceae) and designated the fossil as *Carpolithus bivascularis*. Frenguelli (1943) described specimens similar to *C. bivascularis* that he collected at the “same stratigraphic levels” as *Lomatia occidentalis* leaves from Laguna del Hunco. He discussed Berry’s generic affiliation of the fossil fruits and considered that, because the fruits came from the same level as the leaves, the fossil infructescences could belong to *Lomatia*. Consequently, he described and illustrated the fossil fruits as *Lomatia occidentalis* (Berry) Frenguelli. Romero et al. (1988) revised the material housed at the Smithsonian Institution and at the Museo de La Plata, and they studied additional fossils housed at the Universidad de Buenos Aires. These authors concluded that the fossils share similarities with the modern genus *Orites*, and transferred the fossil species to the extant genus, establishing the fossil species *Orites bivascularis* (Berry) Romero et al. In their paper, Romero et al. (1988) provided a complete description of the fossils and emended the original determination of the species. In addition to the new fossils, we reviewed the materials studied by Romero et al. (1988). After careful comparisons between fossils and extant specimens, we arrived at the conclusion that the fossils can be placed without reservations within the modern genus *Orites*, as they were previously assigned by Romero et al. (1988).

Orites leaves are symmetric, simple, elliptic or oblong lanceolate, sometimes lobed, with entire margin and pinnate brochidodromous venation. As of yet, there are no reports of fossil *Orites* leaves in Argentina. This lack may be due to the fact that *Orites* leaves lack distinctive diagnostic features, making their recognition among other angiosperms difficult. However, as discussed by Romero et al. (1988), the combination of characters preserved in the infructescences from Laguna del Hunco secure their placement as members of the genus. The placement within Grevilleoideae is based on the type of fruit (dehiscent follicles), which is a characteristic of the subfamily (Johnson & Briggs, 1963; Stevens, 2001; Weston & Barker, 2006); the assignment to *Orites* is supported by the fact that the fossil follicles are subsessile with a short peduncle that left a pair of vascular scars on the infructescence axis, and have an acuminate apex or a rostrum at their apices.

Although there are nine extant species of the genus *Orites* (Wrigley & Fagg, 1991; George & Hyland, 1995), only *Orites myrtoidea* (Poepp. & Endl.) Engl. 1889 lives in Argentina. This species is of particular interest because of its disjunct distribution within Argentina, since it is found in Neuquén, Río Negro, and Chubut provinces, Patagonia, and in the northern Salta Province (Xifreda & Sanso, 2001).

Discussion

PATAGONIAN SPECIES

The present study confirms the presence of three Proteaceae genera in Patagonia during the Paleogene, *Lomatia* with three species, and *Roupala* with one, a putative new

Proteaceae, all represent fossil leaf species, and *Orites* with one fossil species represented by fruits. The presence of ?*Embothrium* is questionable, since the identification of the fossils is doubtful. The corroboration of these species is based on leaf architecture characters preserved (leaf architectural characters of the Patagonian fossil species are summarized in Table I) and comparisons established with extant species. We note that no comprehensive leaf architecture survey has been done for the Proteaceae, which has enormous foliar diversity (Johnson & Briggs, 1975; Douglas, 1995). Therefore, while we have established numerous similarities between the fossil taxa and their likely extant representatives, it is not possible at this time to categorically exclude all other conceivable assignments for the fossils (e.g., *Neorites* can have leaves similar to *Roupala*). Given these constraints, and the lack of preserved cuticle, we prefer not to further adjust the generic assignments. Nevertheless, the fossils show distinctive combinations of leaf architecture characters (size and shape of leaves and leaflets, margin type including teeth and sinuses, and venation pattern) that strongly associate them with Proteaceae genera.

We also mention the argument that taxonomic placement of fossils within Proteaceae based only on leaf characters is not possible or at least questionable (see for example Carpenter & Hill, 1988; Carpenter & Jordan, 1997; Jordan et al., 1998). However, the three cuticular apomorphies (brachyparacytic stomata, trichomes leaving a round scar on the epidermis, and at least some trichome bases overlying more than one basal epidermal cell) used to define Proteaceae are not found in all Proteaceae species (Jordan et al., 1998). These authors remark on the fact that, for example, *Bellendena montana* R. Br. 1810 lacks brachyparacytic stomata and that many members of the Tribe Proteoideae do not have the "typical" trichomes; yet these species are considered to be members of Proteaceae. Jordan et al. (1998, p. 467) also state that there are "other distinctive features which can be used to assign some fossils to extant groups," and one of these characters is the unusual leaf forms. This statement agrees with Carpenter and Jordan's (1997), who accepted that "some forms are immediately recognizable as likely Proteaceae." This is also supported by Pole et al. (1993), who placed specimens within Proteaceae on the basis of few characters of leaf architecture and cuticle, although the cuticle features preserved on those fossils are not the apomorphies for Proteaceae. Pole (1998) pointed out that, in the case of the Family Proteaceae, in absence of cuticular features the gross morphology can be characteristic enough to identify remains to family and in some cases to generic level as well. Consequently, the lack of cuticle could not preclude the assignment of the Patagonian fossils within the Proteaceae genera.

SPECIES OF UNCERTAIN POSITION

A few additional fossil species from Patagonia (Argentina and Chile) and Seymour (Vicomodoro Marambio in Argentine literature) Island, Antarctic Peninsula region, have been attributed to the Proteaceae (Dusén 1907, 1916; Berry, 1932; Gunckel Luer, 1957; Orlando, 1964). These records are summarized in Table II. These fossils include leaves (the majority of the fossils), fruits, and wood. However, most of these species are based on one or few poorly preserved specimens, and, consequently, their taxonomic placements are doubtful. Although we did not have access to these fossils, we provide below a short discussion based on the literature available and on our analysis of extant species.

Embothriophyllum: Dusén (1907) described *Embothriophyllum dubium* on the basis of several leaf impressions exhumed from Oligocene sediments at the Río de las Minas

Table I
Leaf architectural summary of the fossil Patagonian Proteaceae
Key: CC = concave; CV = convex; ST = straight; apical/base.

	<i>Lomatia occidentalis</i>	<i>Lomatia patagonica</i>	<i>Lomatia preferruginea</i>	<i>?Embohrhium pregrandiflorum</i>	<i>Roupala patagonica</i>	Proteaceae gen. et sp. indet.
Organization	Imparipinnate lobed	Bipinnatisect	Imparipinnate	Simple	Imparipinnate	Imparipinnate
Size	Mesophyll	Mesophyll	Mesophyll	Microphyll	Noto- to mesophyll	Mesophyll
Length	19 cm	>13 cm	>15 cm	4.5–7.5 cm	8–20 cm	17 cm
Width	10 cm	7.8 cm	16 cm	1–2 cm	4.5–10 cm	14 cm
Shape	Ovate	Ovate	Ovate	Oblong	Ovate to elliptic	Ovate
Symmetry	Symmetric	Symmetric	Symmetric	Asymmetric	Symmetric	Symmetric
Petiole or rachis	Midvein winged	Midvein grooved and slightly winged	Petiole short, normal and marginal	Petiole marginal, slightly curved	Petiole normal and marginal	Petiole normal and marginal
Leaflets or lobes						
Arrangement	Alternate-subalternate	Subopposite	Opposite-subopposite	—	Opposite-alternate	Opposite
Number	2 pairs of lateral lobes + one apical	7 pairs of leaflets	At least 5 pairs of leaflets	—	3–5 pairs of leaflets	5 pairs of leaflets
Size (cm)	6–10 × 1–2	3–6 × 0.9–1.3	9–11 × 2–2.5	6.5 × 3.2	4–9 × 1.5–4	7 × 1–1.5
Shape	Linear-lanceolate to oblong	Ovate-lanceolate	Ovate or elliptic	—	Ovate	Ovate
Symmetry	Symmetric	Asymmetric	Asymmetric	—	Asymmetric	Asymmetric
Base shape	Decurrent	Acute-decurrent	Decurrent	—	Acute-decurrent	Decurrent
Apex shape	Acute	Acute	Acute	—	Acute	Acute-acuminate
Margin	Serrate	Entire, lobed	Serrate, often lobed	—	Serrate	Serrate
Tooth type/shape	Simple, CC/CV or CC/ST	Each lobule cuneates in an acute apex with a small spine	Compound, CC/CV	—	Simple and/or compound, CC/CV (apex), ST/CV (base)	Simple or compound, CC/CV
Sinus shape	Angular	—	Rounded	—	Rounded	Rounded
Teeth/cm	1–3	—	1–2	—	1–2	3
Tooth spacing	Regular	—	Irregular	—	Irregular	Regular
Teeth/2nd vein	1	—	1–3	—	1–2	1–2
Tooth venation	Medially by V2 or V3	—	Main tooth medially by V2; accessory tooth medially by branches of V2	—	Main tooth medially by V2; accessory tooth medially by bifurcation of V2	Medially and/or dorsally by a bifurcation of V2

Primary vein	Pinnate, simple and straight	Pinnate, simple and straight	Pinnate, simple and straight	Pinnate, simple and straight	Pinnate, simple and curved	Pinnate, simple and straight	Pinnate, simple and straight
Secondary veins	Craspedodromous or semicraspedodromous	Craspedodromous	Craspedodromous	Craspedodromous	Brochidodromous	Semicraspedodromous	Craspedodromous to semicraspedodromous
Intersecondary veins	6–18 pairs	7–8 pairs	7–8 pairs	7–8 pairs	At least 7 pairs	5–7 pairs	8–12 pairs
Third veins	Regularly spaced	Regularly spaced	Regularly spaced	Regularly spaced	1, simple	Regularly spaced	Regularly spaced
Fourth veins	1–2, simple	1–2, simple	1–2, simple	1–2, simple	1, simple	—	1, simple or compound
Fifth veins	Alternate, random reticulate	Random reticulate	Random reticulate	Random reticulate	Percurrent	Random reticulate	Compound Reticulate
Areolation	Poorly developed	—	—	—	Orthogonal reticulate	Reticulate	Reticulate
Marginal ultimate venation	Moderate or well developed	—	—	—	Orthogonal reticulate	Reticulate	Reticulate
Comments	3–5-sided	—	—	—	Well developed	Well developed	Well developed
	Looped, fimbrial vein	Looped	Looped	Looped	4-sided	4–5-sided	4–5-sided
	Midvein wing increasing in width toward the insertion of the superjacent leaflet	Base of leaflets with 2 lateral veins that emerge from the rachis	—	—	Looped	Looped	Looped
					—	—	Basal leaflets with reticulate V2

Table II
Records of Proteaceae megafossils in Patagonia and the Antarctic Peninsula region
Key: L = leaf; S = seed; F = fruit; W = wood; * = species of uncertain position.

Locality	Formation	S. Lat.	Age	Fossil	Fossil taxa	Reference
Patagonia (Chile and Argentina)						
Laguna del Hunco, Chubut Province	Tufolitas Laguna del Hunco	42°28'	Early Eocene	L	<i>Lomatites occidentalis</i>	Berry, 1925
				L	<i>Lomatia occidentalis</i>	Frenguelli, 1943
				L	<i>Lomatia occidentalis</i>	This paper
				L	<i>Lomatia preferruginea</i>	This paper
				L	? <i>Embothrium</i> <i>precoccineum</i> *	This paper
Río Turbio, Santa Cruz Province Pichileufú, Río Negro Province	Río Turbio Ventana	51°33' 41°07'	Eocene Middle Eocene	L	<i>Roupala patagonica</i>	Durango de Cabrera & Romero, 1988
				L	<i>Roupala patagonica</i>	This paper
				L	Proteaceae gen. et sp. indet.	This paper
				F	<i>Orites bivascularis</i>	Romero et al., 1988
				F	<i>Orites bivascularis</i>	This paper
Río de las Minas, Punta Arenas Morro Revancha, Río Negro Province Cañadón Hondo, Chubut Province Bullileo, Central Chile	Loreto Ñirihua Not indicated Not indicated	53°10' 41° 45°-46° 36°14'	Oligocene Late Oligocene - Early Miocene ?Late Oligocene - Early Miocene ? late Eocene - Early Miocene	W (root?)	<i>Lomatia</i> sp.	Ancibor, 1989
				L	? <i>Embothrium</i> <i>precoccineum</i> *	Berry, 1938
				L	? <i>Embothrium</i> <i>pregrandiflorum</i> *	Berry, 1938
				L	<i>Lomatia</i> <i>preferruginea</i>	Berry, 1938
				L	<i>Embothriophyllum</i> <i>dubium</i> *	Dusén, 1907
Morro Revancha, Río Negro Province Cañadón Hondo, Chubut Province Bullileo, Central Chile	Ñirihua Not indicated Not indicated Not indicated	41° 45°-46° 36°14'	Late Oligocene - Early Miocene ?Late Oligocene - Early Miocene ? late Eocene - Early Miocene	L	<i>Lomatia</i> <i>patagonica</i>	Frenguelli, 1943
				S	<i>Embothrites simpsoni</i> *	Berry, 1932
				L	<i>Roupala</i> sp.*	Troncoso & Romero, 1998

Seymour Island	Cross Valley and La Meseta	64°15'	Paleocene, Eocene	L	<i>Lomatia angustiloba</i> *	Dusén, 1916
				L	<i>Lomatia brevipinna</i> *	Dusén, 1916
				L	<i>Lomatia serrulata</i> *	Dusén, 1916
				L	<i>Lomatia seymourensis</i> *	Dusén, 1916
				L	<i>Knighthia andreae</i> *	Dusén, 1916
King George Island	Fossil Hill	62°	Paleocene - Eocene	L	<i>Lomatia antarctica</i> *	Orlando, 1964
				L	<i>Lomatia mirabilis</i> *	Li, 1994

locality in southern Chile. Dusén related the fossil material with extant *Embothrium*. The fossil leaves are lanceolate, with entire margins and probably short petioles. The fossils preserve only the gross morphology, and there is no indication of their venation pattern; therefore, the assignation to *Embothrium*, and to Proteaceae, is difficult to sustain.

Embothrites: Berry (1932) described a fossil seed (impression and counterpart) from the Cañadón Hondo locality (probably Late Oligocene-Early Miocene in age), Chubut Province, Argentina, and assigned them to the fossil species *Embothrites simpsoni* Berry. The fossil seed is compressed, bifacial, and winged. Berry compared it with seeds of extant "South American genus *Embothrium*, since the seed is associated with *Embothrium*-like leaves referred to *Embothriophyllum dubium* Dusén." Nevertheless, the seeds do not have any diagnostic character preserved that allows their placement within the family Proteaceae.

Lomatia: Dusén (1916) described four fossil species within the genus *Lomatia*, *L. angustiloba*, *L. brevipinna*, *L. serrulata*, and *L. seymourensis*. All of these materials come from Paleogene sediments of Seymour Island, Antarctica. *Lomatia angustiloba* and *L. brevipinna* are characterized by having imparipinnate lobed leaves, but the fossils are so poorly preserved that they completely lack venation characters. Dusén (1916) believed that these two fossil species were related to the extant *Lomatia ferruginea*, which is today restricted to the Patagonian Andes. *Lomatia serrulata* and *L. seymourensis* have simple, ovate leaves, with decurrent bases; their margin is serrate at the apex, while the rest is entire. The fossils lack details of venation. Dusén (1916) related these two species to the extant *L. dentata* (Ruiz & Pav.) R. Br. 1810, which is found today in the Patagonian rainforests of Argentina and Chile. Gunckel Luer (1957) suggests that these four species can be clustered into two groups: *L. angustiloba*-*L. brevipinna* and *L. serrulata*-*L. seymourensis*, because they cannot be separated on the basis of the preserved characters. Nonetheless, he did not make any taxonomic changes for these species, and until now, the four of them have been treated as suggested by Dusén (1916).

Dusén (1916) also described the species *Caldcluvia mirabilis*; however, after comparing the fossils with extant *Caldcluvia* (Cunoniaceae) and *Lomatia ferruginea*,

Li (1994) concluded that the fossils have more resemblance to *Lomatia* than to *Caldcluvia*, and therefore he placed the fossils within the genus *Lomatia*. Li pointed out that the leaflets are isolated and that no higher order venation is preserved.

At this point, we consider that new specimens with better preservation are required to confirm the affinities of the Antarctic taxa described by Dusén with extant *Lomatia* and also with Proteaceae.

Orlando (1964) described *Lomatia antarctica*, a fossil leaf, collected at the Paleocene-Eocene sandstones of the Ardley Peninsula, King George Island (25 de Mayo Island in Argentine literature), South Shetland Islands, Antarctica. This single specimen is an impression of a compound leaf (imparipinnate), described as probably coriaceous, ovoid in shape with a winged rachis and entire margin. The leaf is composed of an apical leaflet and two lateral ones (both lateral leaflets are shorter than the apical one). Although these are characters found in extant and fossil *Lomatia* species, the lack of venation precludes the taxonomic placement within the genus *Lomatia* at this point. New specimens with better preservation are required to confirm the assignment.

Knightia: Dusén (1916) also described fossils as belonging to the modern genus *Knightia* R. Br. 1810, and erected the fossil species *K. andreae*. These fossils were collected at the same fossil locality as the *Lomatia* fossils from Seymour Island. *Knightia andreae* has large linear leaves, at least 12 cm long and 4 cm wide and with serrate margins. Details of venation are not preserved, and hence comparisons with the extant genus *Knightia* are not of much value. Doktor et al. (1996), on the basis of additional fossils collected at the same formation, arrived at the conclusion that it is impossible to assign these fossils to Proteaceae, and they created a new artificial genus *Knightiophyllum* to accommodate them.

BIOGEOGRAPHICAL IMPLICATIONS

Proteaceae is considered to be a relict group of Gondwana, disjunctly distributed among the Southern Hemisphere's continents and having Australia and Southern Africa as its centers of high diversity. The family is widespread and highly diverse in Australia, where the five subfamilies and all tribes except for Proteae are represented (Johnson & Briggs, 1981). The Proteae are restricted to Africa and Madagascar, where they are accompanied by members of the tribes Conospermeae within the subfamily Proteoideae and Macadamieae within the subfamily Grevilleoideae (Johnson & Briggs, 1981; Werberling, 1999). In South and Central America, only members of the subfamily Grevilleoideae are found, and only three, Oriteae, Embothrieae, and Macadamieae, of the seven tribes are represented (Johnson & Briggs, 1981). Remarkably, only members of the tribe Macadamieae are established on the three continents (Africa, South America, and Australia), in each case showing high generic endemism.

Johnson and Briggs (1963, 1975), on the basis of their comprehensive studies of the family, hypothesized that the family originated in northern Gondwana and that the initial radiation took place in a temperate to warm and humid climate. Afterward, Johnson and Briggs (1981) suggested that the ancestors of the subfamilies must have evolved in Gondwana before the separation of its constituent landmasses. They also suggested that the majority of the tribes and subtribes must have evolved by the beginning of the Late Cretaceous, and that the most likely place of subsequent divergence was Australia, where all the subfamilies are found. Palynological data support these ideas (Dettmann, 1989; Dettmann & Jarzen, 1991). The pollen fossil record indicates that the family in-

deed originated in northern Gondwana during the Late Cenomanian, radiated during the Turonian via an unknown route to the southern high latitudes, and underwent major diversification at least in Australia during the Santonian-Maastrichtian, in which at least four of the seven subfamilies were already present, among them the Grevilleoideae (Dettmann & Jarzen, 1991). Weberling (1999) suggested that at the beginning of the Paleogene (65.5 Ma), long after the break-up of Gondwana, the sclerophyllous forms probably evolved in regions already separated by oceans, independently from the forms adapted to humid-hot or drier climates. Although the route taken by Proteaceae progenitors into the southern high latitudes is still unknown (Askin & Baldoni, 1998), Prance and Plana (1998) suggested that American Proteaceae are indeed "outliers" from the centers of diversity (Australia and South Africa) and that they arrived to South America via two possible routes: (1) the Gondwana route, before the separation of South America and (2) the Australia-Antarctica-South America connection.

In southern South America, the genera *Embothrium*, *Lomatia*, and *Orites* could have arrived through the Australia-Antarctica-South America pathway. These three genera have a well-known fossil record in Australia (Hill & Christophel, 1988; Carpenter & Hill, 1988; Jordan et al., 1991; Jordan, 1995; Carpenter & Jordan, 1997; Pole, 1993, 1994, 1997; Jordan et al., 1998; Vadala & Greenwood, 2001) and South America (Berry, 1932; Frenguelli, 1943; Romero et al., 1988; Ancibor, 1989; this paper). According to Raven and Axelrod (1974), this is evidence of the existence of an Australia-Antarctic-South America terrestrial connection. Therefore, a terrestrial interchange of elements including Proteaceae could have been established (Hill et al., 1995). Evidence of the Gondwana route is supported by pollen grains obtained from the Maastrichtian Arnot Pipe, which is part of the Gamoep cluster of volcanic pipes in the Namaqualand region, South Africa (Scholtz, 1985). Scholtz described two species, *Propylipollis meyeri* Scholtz, with affinities to genera within Grevilleoideae and Persoonioideae, and *Triporopollenites namaquensis* Scholtz, probably also related to members of Grevilleoideae.

The genus *Roupala*, together with *Euplassa* and *Panopsis*, all endemics to tropical South America, probably reached South America from Australia before the complete break-up of Gondwana. The presence of these tropical elements of montane forests supports the existence of advantageous environmental conditions in Patagonia during the early-middle Eocene, permitting the evolution of forms that are today restricted to tropical areas. This coincides with previous paleofloristic interpretations (i.e., Menendez, 1971; Romero, 1978, 1986) and the more recent paleoclimatic analyses (Wilf et al., 2003, 2005) regarding the existence in the early to middle Eocene Patagonic floras of genera whose closest living relatives inhabit tropical or subtropical regions.

Raven and Axelrod (1974) suggested that *Roupala* might be descended from an extinct African ancestor that migrated to South America through northern South America during the Miocene. In one view, the occurrence of *Roupala* in the early Eocene Laguna del Hunco flora suggests a different dispersal route, from the south to the north (Durrango de Cabrera & Romero, 1988). The results of the present study support a possible northward migration for *Roupala*, as suggested by Prance and Plana (1998), where the changing paleoenvironmental conditions were more favorable, and possibly in response to the general climate cooling following the Eocene climatic optimum. Alternatively, it is quite possible that *Roupala* was more widespread in the past and has become restricted to the north, where the climatic conditions are more favorable. To date, there are no fossils in Australia and Antarctica assignable to *Roupala*.

Concluding Remarks

The family Proteaceae is represented in Argentina by fossil and extant species that belong to the tribes Embothrieae, Macadamieae, and Oriteae, within the subfamily Grevilleoideae. Based on this revision, these three tribes were well established in Patagonia by the Eocene. The confirmation of *Roupala* as a component of the paleoflora suggests that the genus had a widespread South American distribution in the past. Several fossil species historically assigned to Proteaceae from the Antarctic Peninsula region and from southern Patagonia need to be restudied to confirm their taxonomic position and refine the biogeographic hypothesis, but this requires additional collections.

Key Based on Leaf Characters of Fossil Proteaceae from Patagonia

- A- Simple leaves, with entire margin.
 - B- Asymmetric, elongate microphylls, rounded apex and acute-cuneate base *Embothrium precoccineum*
 - BB- Symmetric, ovate to elliptic microphylls, acute apex and acute wide base *Embothrium pregrandiflorum*
- AA- Compound pinnate or pinnatisect leaves, leaflets with entire or serrate margins C
 - C- Leaflets with entire margin and lobules, lobules with entire margin *Lomatia patagonica*
 - CC- Leaflets with serrate margin with or without lobules D
 - D- Rachis winged, symmetric leaflets, margin with simple teeth regularly spaced *Lomatia occidentalis*
 - DD- Rachis not winged, asymmetric leaflets, margin with simple and compound teeth E
 - E- Leaflets with lobules *Lomatia preferruginea*
 - EE- Leaflets without lobules F
 - F- Asymmetric base with both sides acute decurrent. Secondary veins semi-craspedodromous. Teeth irregularly spaced *Roupala patagonica*
 - F- Asymmetric base with one side acute decurrent and the other truncate. Secondary veins craspedodromous or semicraspedodromous, reticulate at some basal leaflets. Teeth regularly spaced *Proteaceae gen. et sp. indet.*

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