Southern beech (Nothofagaceae) fossil leaves from the Río Turbio Formation (Eocene–? Oligocene), Santa Cruz Province, Argentina

Carolina PANTI

Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” CONICET, Av. A. Gallardo 470, C1405DJR Buenos Aires, Argentina. E-mail: caropanti@gmail.com.

Abstract: Nothofagus sp. cf. N. obliqua, Nothofagus sp. aff. Nothofagus alessandri and Nothofagus magelhaenica are reported for the first time for the Paleogene Río Turbio Formation along with another five fossil-species: Nothofagus simplicidens, Nothofagus variabilis, Nothofagus lanceolata, Nothofagus subferruginea and Nothofagus dicksonii. Around one hundred specimens of fossil leaves were recorded and analysed throughout the unit, but they are fairly more abundant in the upper member of the Río Turbio Formation where they reach 68% of the overall assemblage. The observed increasing trend in Nothofagus abundance throughout the unit coincides with the beginning of the flora turnover that characterized Patagonian ecosystems from the Late Eocene onwards and it is in agreement with the marked global cooling trend of the terminal Paleogene.

Key words: Nothofagaceae, Nothofagus, Paleogene, Río Turbio, Patagonia.

INTRODUCTION

Nothofagus Blume belongs to the monogeneic family Nothofagaceae and includes 43 extant species of trees (Christenhusz & Byng, 2016) grouped in four monophyletic subgenera (Hill & Read, 1991). The temperate subgenera (Nothofagus, Lophozonia and Fuscospora) are mainly distributed in temperate regions of the Southern Hemisphere (New Zealand, Australia and South America) with some taxa (subgenus Brassospora) extending northward into the tropics (New Guinea and New Caledonia). In South America, Nothofagaceae is represented by 10 species, most of them deciduous, distributed in the Andean Region from 33° to 56° S latitude, with the northern limit determined by the seasonally arid conditions of the Mediterranean climate of central Chile (McQueen, 1976; Donoso, 1996). Below 37° south in both, Chile and Argentina, Nothofagus occurs in two broad types of forests: temperate rainforests on climatically favourable sites, generally associated with Maytenus magellanica, Drimys winteri, Pilgerodendron uviferum and Embobthrium coccineum among others and, a pure or nearly pure Nothofagus forests on less favourable sites referred to as Patagonian or Subantarctic Nothofagus forests (Veblen et al., 1996). In particular, the extant vegetation of the Río Turbio area corresponds to an ecotone between the Patagonian cool temperate rainforest dominated by Nothofagus pumilio (Poeppe. & Endl.) Krasser (Lenga) followed by Nothofagus antarctica (G.Forst.) Oerst. (Nire) (Leon et al., 1998; Cavallaro, 2006) and the steppe dominated by shrubs and herbs.
The oldest fossil records of Nothofagus came from the Upper Cretaceous of Antarctica (Campanian, c. 83 Ma), South America and Australia (Maastrichtian, c. 70 Ma) and correspond to pollen grains (Romero, 1973; Archangelsky & Romero, 1974; Dettmann et al., 1990; Dettmann, 1994; Dutra & Batten, 2000; Moreira Muñoz, 2004). Imprints of leaves related to Nothofagus were recently mentioned by Leppe et al. (2017) from the Lower Maastrichtian of Chile but these fossils remain undescribed in detail. Confident imprints of leaves with Nothofagus affinity were recorded in the Paleogene of Antarctica (Dusén, 1908; Tosolini et al., 2013) and in the Paleocene/Eocene boundary of central Patagonia (Okuda et al., 2006; Hinojosa et al., 2015) but the lineage only became widespread and diverse after the middle Eocene becoming more abundant during the Oligocene (Barreda & Palazzi, 2007; Hinojosa, 2015). Moreover, the middle Eocene–early Oligocene interval was characterized by the invasion of Nothofagus forests in Patagonia in close agreement with a marked cooling trend (Barreda & Palazzi, 2007). Fossil woods of Nothofagaceae were recorded from several regions in Antarctica (Poole, 2002 and references therein) and in Patagonia (Poole, 2002; Pujana, 2009; Brea et al., 2015; Pujana et al., 2015; Egerton et al., 2016; Terada et al., 2006). Records of Nothofagacean leaves from the Paleogene of Patagonia are fairly abundant (eg. Engelhardt, 1891; Dusén, 1899; Fiori 1931, 1939, 1940; Troncoso & Encinas, 2006; Torres et al., 2009; Panti, 2008, 2010, 2011; Vento & Prámparo, 2016, 2018; Cesari et al., 2015). In particular, for the Río Turbio Formation, fossil leaves of Nothofagus only have been mentioned and sometimes described for isolated localities (Tab. 1). This is the first attempt to analyse the record of the family throughout the entire Formation, a unit deposited during the time of expansion of Nothofagus in Patagonia.

In this paper 107 specimens referable to 8 taxonomic units of Nothofagus are described. Some of them are reported for the first time for the Río Turbio Formation. Distribution of fossil Nothofagacean leaves throughout the unit is also analysed with the aim of quantifying the dispersion of the southern beach forests in southern Patagonia during the Eocene/Oligocene.

**Geological Settings**

The Río Turbio Formation (RTF) (Leanza, 1972) crops out in the south western tip of Santa Cruz province, Argentina (Fig. 1) and is mainly composed of mudstones and sandstones deposited in shallow marine and estuarine environments during a period of sea level rise (Malumian et al., 2000). This sequence overlies the Early Paleocene Cerro Dorotea Formation and is separated by an erosional contact from the overlying Río Guillermo Formation (Guerstein et al., 2014). The unit was informally divided into two members: lower and upper (Malumian & Caramés, 1997). Micro and mega-faunistic differences along with the existence of a glauconitic level at the base of the upper member point towards the presence of at least one hiatus of indefinable magnitude between both members (Malumian et al., 2000). The Río Turbio Formation is recognized in literature by its abundant fossil plant content; it includes leaves, woods and palynomorphs (Berry, 1937; Frenguelli, 1941; Hünicken, 1955, 1967, 1995; Archangelsky, 1968, 1969, 1972, Archangelsky & Fasola, 1971; Romero, 1977; Romero & Castro, 1986; Romero & Zamaloa, 1985; Ancibor, 1990; Brea, 1993; Pujana, 2008; Pujana & Ruiz, 2017; Panti, 2010, 2014a, 2018 and Fernández et al., 2012).

Evidence for the age of the RTF comes mainly from two sources. Dinoflagellates suggest an early/middle Eocene and middle/late Eocene ages for the lower and upper members, respectively (Guerstein et al., 2010; González Estebenet et al., 2015). Detrital zircon U/Pb geochronology (Fosdick et al., 2015) restricts the lower member to the Eocene (47–46 Ma) and indicate a significantly younger age for the upper member, Eocene-Oligocene (34–27 Ma).

**MATERIALS AND METHODS**

The leaf imprints described in this paper were collected by the author in different outcrops where both, lower and upper members are exposed (Fig. 2). Because leaves imprints lack organic preservation, comparisons and identification of the fossil impressions were made by use of autapomorphies at species level and then at the generic level by default (Hill, 2001). The specimens with well-preserved venation were studied using modern leaf architectural analysis. Terminology and systematic descriptions follow Ellis et al. (2009) and Hickey & Wolfe (1975). For detailed illustration and detailed analysis, specimens were photographed under unilateral low-angle light with a Nikon DS.F11-U2 digital camera attached to a Nikon SMZ800 stereomicroscope. Draws of the venation patterns and scaling of images were accomplished using Corel Draw X7. Suprageneric nomenclature follows APG IV
Panti: Nothofagaceae fossil leaves from the Río Turbio Formation

RESULTS

Systematic Palaeontology

Order FAGALES Engler, 1892
Family NOTHOFAGACEAE Kuprian, 1962

Table 1. Species of Nothofagus mentioned and/or described for the Río Turbio Formation.

| Nothofagus species                  | Presence at the Río Turbio Formation | References |
|------------------------------------|--------------------------------------|------------|
| Nothofagus australis Dusén         | Upper Member                         | Frenguelli (1941) |
| Nothofagus variabilis Dusén        | Lower and Upper Member               | Berry (1937); Frenguelli (1941); Hünicken (1967) |
| Nothofagus elongata Dusén emend.  | Lower and Upper Member               | Berry (1937); Frenguelli (1941); Hünicken (1967) |
| Romero & Dibbern                   |                                      |            |
| Nothofagus densi-nervosa Dusén     | Lower Member                         | Hünicken (1967) |
| Nothofagus subferruginea (Dusén)   | Lower and Upper Member               | Berry (1937); Frenguelli (1941); Hünicken (1967) |
| Tanai                              |                                      |            |
| Nothofagus simplicidens Dusén      | Upper Member                         | Frenguelli (1941); Vento & Prámparo (2018) |
| Nothofagus dicksonii (Dusén)       | Upper Member                         | Berry (1937); Frenguelli (1941) |
| Tanai                              |                                      |            |
| Nothofagus densinervosa Dusén      | Lower Member                         | Hünicken (1967). |
| Nothofagus serrulata Dusén         | Lower Member                         | Hünicken (1967). |
| Nothofagus lanceolata Dusén        | Upper Member                         | Frenguelli (1941) |
| Nothofagus sp                       | Lower Member                         | Hünicken (1967). |

(2016). Plant fossils are held in the Paleobotanical Collection of the Museo Regional Padre Manuel Jesús Molina (MPM PB) located in Río Gallegos, Santa Cruz province, Argentina.

Genus Nothofagus Blume, 1851

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

The genus Nothofagus is divided into four monophyletic subgenera Brassospora Nothofagus, Lophozonia and Fuscospora, based on pollen, leaf and reproductive morphology (Dettman et al., 1990; Hill & Read, 1991). All recently inferred phylogenies (Hill & Jordan, 1993; Manos, 1997;
Jordan & Hill, 1999; Knapp et al., 2005; Sauquet et al., 2012; Vento & Agraín, 2018) support the monophyly of these four subgenera. Recently, Vento & Agraín (2018) tested the relationships of some South America fossil-species of Nothofagus with the four monophyletic subgenera, supporting their hypothesis that fossils Nothofagus are closely related to the modern species currently distributed in Southern Patagonia.

South American Nothofagus leaves have pinnae venation with simple craspedodromous, curved or recurved secondaries and at least one outer secondary; tertiary veins orthogonal reticulate or percurrent, highest vein order is always fifth, marginal venation is looped with open loops and areoles always small (Romero 1980, Gandelfo & Romero 1992, Premoli 1996). Fossil leaves of Nothofagus vary from very small (less than 1 cm in length) to medium-sized forms (about 9 cm) with rounded to acute marginal teeth, and a few to many secondary veins (Tanai, 1986). All the leaves here described are simple, with variable shape and symmetry. The margin can be serrate or crenate with simple or compound teeth. The venation is pinnate and simple craspedodromous with secondaries veins variable in number (7 to at least 10 pairs) and straight or curved towards the margin. The secondary veins emerge at acute angles from the midvein (40º–60º). Tertiary veins percurrent, straight or sinuous and obtuse to the midvein. Four and fifth order veins are reticular and sometimes have fimbrial and none, one or two agrophic veins.

Following the strict consensus tree obtained by Vento & Agraín (2018) and based on the comparison of the fossil studied with the extant species, the fossils described were grouped according to its possible subgenus categories.

**Subgenus Nothofagus Hill & Read 1991**

* Nothofagus simplicidens Dusén, 1899
  Fig. 3(A-C), Fig. 6 (A-B)

* Nothofagus magellanica (Engelhardt) Dusén; (part). ibid. p. 97, pl. 10, figs. 8, 10-11 (non figs. 2, 7, 9).

* Nothofagus australis Dusén. ibid. p. 100, pl. 8, figs. 9-10.

* Nothofagus cf. lanceolata Dusén; Fiori, p. 49, pl. 1, figs. 19-20.

* Fagus magellanica Engelhardt; p. 648, pl. 2, fig. 19 (non figs. 17-18).

* Fagus cf. dicksoni Dusén; Fiori, p. 112; pl. 1, fig. 13.

**Material.** MPM PB 3132 A-B (Lm24), MPM PB 3152 a/b (Lm29), MPM PB 3160 (Lm24); MPM PB 3001 (Um11), MPM PB 3153 B (Um7)–3154 a/b (Um9), MPM PB 3155–3157 a/b (Um9a), MPM PB 3158 (Um10)–3159 A (Um9a), MPM PB 18309 (Um11).

**Description.** Leaf simple, symmetrical. Laminalar shape oblong to ovate, the apex wide-acute, convex, base rounded to convex. Lamina approximately 2.5 cm long by 1.2 cm wide. Petiole...
marginal. Margin toothed, serrate and crenate. Teeth simple, convex/convex, regular spaced and angular sinuses. Secondary veins ending in the simple teeth, entering along the basal side of the tooth. Venation pinnate and simple craspedodromous, the primary vein moderately thick and nearly straight. At least 7 pairs of secondary veins emerging at acute divergence angle of less than or equal to 41°, straight in course curving up near the margin. Tertiary order venation percurrent, straight to sinuous, with obtuse angle in relation to the midvein. Quaternary veins poorly preserved, seems to be reticulate.

Remarks. The leaf shape along with the venation pattern and the convex/convex simple tooth shape are characters that match the description of Nothofagus simplicidens. This species was formerly described by Dusén (1899) as petiolate leaves of variable size and shape, mainly oblong to oval (sometimes lanceolate) with eight to ten straight secondary veins each supplying the tooth apex. Later, Romero & Dibbern (1985) in their revision of Nothofagus species described by Dusén add the characterization of the leaf margin formed by convex/convex simple tooth. Tanai (1986) revised the species of Nothofagus or Nothofagus-like fossil leaves from South America and West Antarctica. This author considered N. simplicidens distinguishable by its single-serrate margin with obtuse teeth and regularly percurrent tertiary veins with the secondary vein entering straight the main teeth along the basal side of tooth. Vento & Prámparo (2018) mentioned the presence of Nothofagus simplicidens for the Río Turbio Formation. Their specimens are comparable to the ones here described in the leaf size and shape, the simple serrate margin, number of secondary veins and venation pattern.

According to Tanai (1986), five living South American Nothofagus species (Nothofagus alessandri, N. alpina, N. glauca, N. obliqua and N. procera) are characterized by secondary veins that enter the main teeth strait along the basal side of tooth and have percurrent tertiary veins and areoles similar to those described for N. simplicidens. Among all of these, the fossil-species was compared with extant N. obliqua (Mirb.) Oerst. from South America, despite this taxon usually has bi-serrate margin. The Patagonian Nothofagus betuloides (Mirb.) Oerst. is similar to N. simplicidens in the crenulate-serrate margin composed by simple broad teeth but, unlike the fossils, the secondary veins forks near the leaf margin.

Nothofagus variabilis 1899

Description. Leaf simple, symmetrical. Laminar shape ovate, the apex acute, convex, the base convex to rounded. Lamina approximately 2.5 cm long by 1.2 cm wide. Petiole marginal. Margin toothed, serrate, compound teeth irregularly spaced, principal tooth feed by main secondary vein, pointed convex/convex to straight/straight and one to tree secondary teeth irrigated by ramifications of the secondary veins with angular sinuses. Teeth seems to be glandular (Fig. 3D). Venation pinnate and simple craspedodromous, the primary vein moderately thick and nearly straight or slightly sinuous with less 5 to 7 pairs of opposite to sub-opposite secondary veins emerging at narrow divergence angle of less than or equal to 45°, straight in course ending at the main teeth. Tertiary order venation percurrent, with obtuse angle to the midvein, quaternary and quintenary vein both reticulate. Fimbrial vein present.

Remarks. These specimens are characterized by the double serrate margin, well developed fimbrial vein along the margin and the secondary veins entering centrally the principal teeth. These characters match the description of Nothofagus variabilis Dusén (1899, p. 96, pl. IX, figs. 8–13). These leaves are variable in their shape and size reason why Dusén defined three different forms: oblonga, subrotundata and microphylla but according to Tanai (1986) these three forms are difficult to distinguish taxonomically as independent varieties due to gradation of leaf forms that its fossil record possesses. Romero & Dibbern (1985) also abolish these variations and they are no longer considered.

Among the extant species, Tanai (1986) related Nothofagus variabilis with N. fusca (Hook. f.) Oerst. and N. truncata (Colenso) Cockayne mainly due to “the presence of the marginal vein and the secondary veins that enter centrally the main teeth which have glandular tip” but instead, both species have simple teeth. Among the species of South America, N. variabilis shares the
Fig. 3. A–C. *Nothofagus simplicidens*: A. MPM PB 3152; B. MPM PB 3160; C. MPM PB 3158.  
D–F. *Nothofagus variabilis*: D. MPM PB 3002, the arrows show the glandular teeth and siphonostome vein; E. MPM PB 3078; F. MPM PB 3076. G–J. *Nothofagus magellanica*: G. MPM PB 2983; H–J. MPM PB 2979. All scale bars represent 5 mm, except E–F and I–J which is 2.5 mm.
compound serrate margin and the presence of a fimbriate vein with *N. dombeyi* (Mirb.) Oerst. and *N. betuloides* (Mirb.) Oerst., but differs from both in the termination of the secondary veins which forks near the margin and the apical branch reaches the sinus bottom while the basal branch enters the glandular tooth apex centrally.

Subgenus *Lophozonia* (Turcz.) Krasser, 1896. *Nothofagus magelhaenica* (Engelhardt) Dusén, 1899  
Fig. 3 (G-J)

1899 *Nothofagus magellanica* (Engelhardt) Dusén; p. 97, pl. X, figs. 2-7, 11.  
1891 *Fagus magelhaenica* Engelhardt; p. 648, pl. 2, fig. 18 (non figs. 17, 19).  
1937 *Nothofagus elongata* auct. non Dusén; Berry, p. 94, pl. 18, fig. 7.

*Material.* MPM PB 2978 (Lm4); MPM PB 2979 (Um9)–2980 A–B (Um9a), MPM PB 2981 B (Um9a), MPM PB 2982 a/b (Um9a), MPM PB 2983 a/b (Um9a), MPM PB 2984–2985 (Um9a), MPM PB 2987 (Um9a)–2988 (Um10), MPM PB 2990–2998 (Um10), MPM PB 3000 (Um10), MPM PB 3003 A–B (Um11), MPM PB 3073 (Um11)–3074 (Um12), MPM PB 3077 a/b (Um15), MPM PB 3112 F (Um9), MPM PB 18312–18313 (Um11), MPM PB 18314 (Um9).  
*Description.* Leaves simple, symmetrical. Lamina ovate in shape, petiolate with convex base and acute apex, asymmetrical at the base, about 1.2 cm long by 0.6 cm wide (L:W ratio 2:1), nanophyll. Margin serrate with compound teeth, sinus shape angular, primary tooth acute whose sides are convex in the apical side and convex to straight 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. A branch from the secondary vein curves upward and supplies the apex of the subsidiary tooth. Veneration pinnate, primary vein curved, major secondary veins craspedodromous (at least 5 pairs), with regular spacing, emerging at acute angle and decurrent attachment to midvein. Basal secondary with agrophic veins developed on one side only. Intercostal tertiary veins percurrent. Plicate vernation.  
*Remarks.* The two specimens are comparable with the extant species *Nothofagus obliqua* (Mirb.) Oerst. and *N. glauca* (Phill.) Krasser but the last lacks of agrophic veins (Gandolfo & Romero 1992). *Nothofagus obliqua* and the studied specimens show unequal laminae, more than 6 secondary veins, basal secondary veins with outer secondary upon one half of the lamina, tertiary mainly alternate and the principal sinus, which separates two composite teeth, is equidistant from the two adjacent secondary veins (Gandolfo & Romero 1992). *Nothofagus cf. obliqua* was defined by Dusén (1899) upon specimens that show a higher number of secondary veins. Among the fossil-species of *Nothofagus*, the new samples are also comparable to *Nothofagus magelhaenica* in their venation and marginal characters but the specimens described have less number of secondary veins.

Dusén (1899) are single-toothed in margin and not belong to *N. magelhaenica*. Although none of the specimens described by Dusén as *N. magelhaenica* seem to have a complete margin, in some of these it is possible to infer the compound teeth by the bifurcation of the secondary vein near the margin. Both authors, Dusén and Tanai, compare the fossils of *N. magelhaenica* with the extant *N. obliqua* (Mirbel) Oerst. based on the similarities observed in their venation and marginal characters.
**Nothofagus elongata** Dusên, 1899 emend. Romero & Dibbern 1985

*Fig. 4 (E-F), Fig. 6F*

1899 *Nothofagus lanceolata* Dusên; p. 101, pl. VIII, fig. 13.

1899 *Nothofagus cf. obliqua* auct. non. Mirb. Dusên; p. 98, pl. X, fig. 1.

1937 *Nothofagus elongata* Dusên; Berry, p. 94, pl. XVIII, fig. 7.

1941 *Nothofagus lanceolata* Dusên; Frenguelli, p. 182, pl. IV, fig. 1.

1967 *Nothofagus cf. elongata* Dusên; Hünicken, p. 166, pl. 2, fig. 1.

**Material.** MPM PB 3132 C (Lm24); MPM PB 3130 (Um9a)–3131 (Um10), MPM PB 18316 (Um10).

**Description.** Leaf simple. Lamina shape elliptic to ovate, with apex acute and straight and base convex to decurrent. Lamina microphyll, approximately 2 cm long by 0.6 cm wide L:W ratio 3:1. Petiole marginal. Margin serrate, teeth compound. Principal tooth feed by main secondary vein, pointed convex/convex to straight/straight and one to three secondary teeth irrigated by ramifications of the secondary veins with angular sinuses. Venation pinnate and simple craspedodromous, the primary vein moderately thick and slightly sinuous with least 9 pairs of opposite secondary veins emerging at narrow divergence angle of less than or equal to 45º, straight in course ending at the main teeth. Tertiary veins hardly observables, seems to be percurrent, with obtuse angle to the midvein.

**Remarks.** These specimens match the description of *Nothofagus lanceolata* Dusên (1899, p.101, pl. VIII, fig. 13). *Nothofagus lanceolata* and the studied fossil leaves are quite similar in the lamina shape, venation type and toothed margin however, the specimen described by Dusên seems to be slightly asymmetrical towards the base (Fig. 4G).

In their revision of the Fagaceae and Nothofagaceae leaves described by Dusên (1899), Romero & Dibbern (1985) propose that there are no differences between *N. lanceolata* and *N. elongata*. Dusên defined these two species upon the differences in their margin, base shape and number of secondary veins. According to Romero & Dibbern (1985) both fossil-species are composed by leaves with composite teeth and similar number of secondary veins ranging from 9 to 12 representing a single species. Tanai (1986) considered *N. lanceolata* and *N. elongata* as questionable species referable to *Nothofagus* but still recognized as two different taxa which differ mainly by the presence of a compound serrate margin in *N. lanceolata* and a single serrate margin in *N. elongata*.

Among the extant species *N. lanceolata* was compared by Dusên with *Nothofagus dombeyi* but they differ in the number (higher in the fossil-species) and terminations of secondary veins (Tanai, 1986). Romero & Dibbern (1985) mentioned *Nothofagus variabilis* like the most similar species being more comparable in the number of secondary veins and the presence of tertiary teeth occasionally.

**Subgenus Fuscospora** Hill & Read, 1991

*Nothofagus subferruginea* (Dusên) Tanai, 1986

*Fig. 4 (H-K), Fig. 6G*

1899 *Fagus subferruginea* Dusên, p. 94, pl. 8, figs. 1-8.

1937 *Fagus subferruginea* Dusên, Berri, p. 93, pl. 18, fig. 6.

1941 *Fagus subferruginea* Dusên; Frenguelli, p. 180, pl. V, pl. VI, fig. 2.

1967 *Fagus subferruginea* Dusên; Hünicken, p. 163, pl. 1, figs. 12-18.

1999 *Fagus integrifolia* Dusên, p. 95, pl. 8, fig. 12.

1937 *Fagus integrifolia* Dusên; Berri, p. 94.

1941 *Fagus integrifolia* Dusên; Frenguelli, p. 180, pl. V.

1908 *Fagus obscura* Dusên, p. 9, pl. 1, fig. 23.

1967 *Fagus obscura* Dusên; Hünicken, p. 165, pl.1, fig. 19.

1940 *Fagus gortanii* Fiori, p. 14, pl. 5, figs. 5-6.

1940 *Nothofagus cf. engelhardtiana* Fiori, p. 108, pl. 5, fig. 7.

**Material.** MPM PB 3089–3090 a/b (Lm4), MPM PB 3091 a/b (Lm4), MPM PB 3096 (Lm4); MPM PB 2981 (Um9a), MPM PB 3092 (Um9a)–3093 a/b A–B (Um15), MPM PB 3094–3095 (Um16), MPM PB 3097 (Um10), MPM PB 3098–3099 (Um11), MPM PB 3159 B–C (Um9a).

**Description.** Leaf simple. Lamina shape elliptic to ovate, with apex acute to attenuated and base wide acute to obtuse and convex to rounded in shape, slightly asymmetrical. Lamina approximately more than 6 cm long by 2 cm wide, L:W ratio 3:1. Petiole marginal, thick and recurved. Margin double serrated, sometimes simple serrated towards the apex, teeth regularly spaced feed by main secondary vein, pointed concave to straight/convex to concave with rounded sinuses. Venation pinnate the primary vein straight. Secondary veins simple craspedodromous, with at least 11 pairs secondary veins emerging at narrow divergence angle of 42º, 31º–61º, straight in course ending at the main teeth, one branch
Fig. 4. A–D. *Nothofagus* sp. cf. *N. obliqua*: A. MPM PB 3177; B. MPM PB 3176, general view of the fossil leaf; C. MPM PB 3176, detail of the teeth; and D. MPM PB 3176, detail showing the outer secondary veins. E–G. *Nothofagus elongata*: E. MPM PB 3132; F. MPM PB 3131; G. *Nothofagus lanceolata* Dusén, (S165061, Swedish Museum, Stockholm). H–K. *Nothofagus subferruginea*: H. MPM PB 3096; I. MPM PB 3989; J. Detail of the venation of MPM PB 3096; K. MPM PB 3091. Scale bars: A–B=2.5 mm; C–D=1 mm; E–G, J–K=5 mm; H–I=10 mm.
emerging basally, and ending in a subsidiary teeth apex. Secondary veins sub-opposite to alternate. Tertiary veins percurrent, obtuse to mid-vein. Quaternary and quinquevolute veins hardly observable, seems to be reticulate. **Remarks.** Among the fossil-species, the studied specimens match the description of *Nothofagus subferruginea* (Dusén) Tanai in their size, shape, number of secondary veins and margin. According to Tanai (1986) leaves of *N. subferruginea* are sometimes simple toothed on the upper margin of the blade as do in the extant *N. alessandri*. This is in agreement with the specimen illustrated in the Fig. 4K. This fossil-species, formerly described as *Fagus subferruginea*, is a common element found in the fossil associations recovered from the Paleogene of Patagonia (see Tanai, 1986, p. 532) and Antarctica (Barton, 1964, Zastawiak, 1981, Zastawiak et al., 1985, Torres, 1990). It was emended by Tanai (1986) due to the presence of secondary veins directly entering to the teeth with one or three branching veinlets and synonymized with other “*Fagus*” species also described by Dusén (eg. *Fagus obscura* and *Fagus intergigolia*). As noted by Tanai (1986) the fossils described as *N. subferruginea* are closely similar to the extant *Nothofagus alessandri* Espinosa in their lamina shape, venation pattern and tooth. Also, she found resemblances between *N. alessandri* and *Fagus novae-zealandica* Oliver and *F. australis* Oliver from the upper Miocene of New Zealand (Oliver, 1936) and pointed out that *N. subferruginea* and both New Zealand fossils may be closely related.

*Nothofagus dicksonii* (Dusén) Tanai, 1986

Fig. 5 (A-B), Fig. 6H

1899 *Fagus dicksonii* Dusén, p. 95, pl. 8, figs. 14-16.
1908 *Fagus dicksonii* Dusén, p. 9, pl. 1, fig. 12.
1937 *Fagus dicksonii* Dusén; Berry, p. 93, pl. 18, fig. 1.
1941 *Fagus dicksonii* Dusén; Frenguelli, p. 180, pl. IV, fig. 4.

**Material.** MPM PB 2982 A, C (Um9a), MPM PB 3112 (Um9), MPM PB 3113-3115 A-B (Um9a), MPM PB 3116-3117 A-B (Um9a), MPM PB 3118-3120 A-D (Um 9a), MPM PB 3121-3125 (Um9a), MPM PB 3126 a/b (Um10), MPM PB 3127-3129 (Um10), MPM PB 3159 A-I (Um9a).

**Description.** Leaf elliptic to ovate in shape, petiolar with obtuse and convex to rounded base, apex not preserved, at least 3.4 cm long and 2.4 cm wide, microphyll. Margin serrate, with compound teeth, primary teeth acute whose sides are concave in the apical side and concave to flexuous on the basal side. Secondary veins end in the main tooth apex, a branch of the secondary veins seems to feed subsidiary tooth. Venation pinnate,
primary vein straight and stout. Major secondary veins craspedodromous (at least 6 pairs), opposite to sub-opposite, with regular spacing emerging at acute angle (54°, 43°-74°) from mid-vein. Basal secondary with simple agrophic veins developed on one side only. Intercostal tertiary veins opposite percurrent, straight to sinuous, with obtuse angle to the midvein. Quaternary vein fabric reticulate.

Remarks. Nothofagus spp. mentioned by Troncoso & Encinas (2006, fig. 3G) seem to be similar to the specimen here described. Both share the lamina shape, margin type and the general veination pattern. Unfortunately, these specimens were not described in detail, precluding more precise comparisons.

Following the key of leaves of living species of Nothofagus developed by Gandolfo & Romero (1992), among the species that have outer secondary veins the studied specimen seems to be similar to Nothofagus alessandri. They share the composite teeth, the rounded base, the presence of outer secondary veins developed only on one side of the leaf and tertiary veins percurrent. Also, both show a principal sinus, which separates two composite teeth, located just above each secondary.

DISCUSSION AND CONCLUSIONS

One hundred and seven specimens of Nothofagaceae were studied and assigned to two taxonomic units similar to extant species (Nothofagus sp. cf. N. obliqua and Nothofagus sp. aff. N. alessandri), and to six fossil-species. These are: Nothofagus simplicidens, Nothofagus variabilis, Nothofagus lanceolata, Nothofagus subferruginea, Nothofagus dicksonii and Nothofagus...
magelhaenica, being the last species reported for the first time for the unit. With few exceptions (Nothofagus dicksonii and Nothofagus sp. cf. N. obliqua) most of the Nothofagus species are present in both members of the Río Turbio Formation (Tab. 2). However, if we analysed the distribution of the specimens through the entire formation, we observed significant differences in their abundance (Fig. 6). The upper member of the RTF concentrates the 68 % of the Nothofagacean specimens while in the lower member the specimens barely reaches the 17% (Fig. 7). This represents a four-time increase in the Nothofagus abundance toward the upper levels of the Río Turbio Formation.

The deposition of the Río Turbio Formation took place during a particular time-interval characterized by a progressive cooling trend estimated by climate proxy data (Zachos et al., 2001). The associations of leaves recovered from the Río Turbio Formation show a mixture of species with subtropical or tropical affinities (e.g. Lauraceae, Sapindaceae, Malpighiaceae) with others developed in cold temperate climate (see Appendix 1), mainly represented by Nothofagus (Romero, 1978, 1986a; Panti, 2014b).

Even when leaves of Nothofagus were recorded in Patagonia from the Paleocene Ligorio Marquez Formation (Hinojosa et al., 2015), they still remain absent in several associations recovered from the early Eocene (e.g. Río Pichileufú (Berry, 1938), Laguna del Hunco (Berry, 1925, Wilf et al., 2003, 2005), Quinamavida (Troncoso, 1992) and the floras from Arauco, Caleta Cocholgüe and Lota Coronel, (Engelhardt, 1891; Moreno-Chacón, 2000; Moreno-Chacón et al., 2000, 2001; Gayó, 2001)). It is not until the middle Eocene-early Oligocene that the increase in abundance and diversity of Nothofagus occurs (Barreda & Palazzesi, 2007; Hinojosa & Villagrán, 1997; Romero, 1978, 1986b). These ancient Nothofagus forests progressively evolve through the Neogene, and they still survive in the Patagonian Andean Region.

The observed increase in the abundance of cold temperate species such as Nothofagus along
with the decrease in richness and abundance of the megathermal taxa towards the upper member of the Río Turbio Formation (Menéndez, 1971; Panti, 2014b, 2018) would be in line with the global cooling trend. This turnover may have marked the beginning of a new floristic scenario, with a widespread cool-adapted flora across these southern latitudes.

ACKNOWLEDGEMENTS

The author would like to thank S.N. Césari, S. Marenssi, R.R. Pujana and V. Barreda for their assistance in the fieldwork, the reviewers Tania Dutra and Anne-Marie Tosolini for their valuable comments and efforts to improve the manuscript. The funds were provided by the CONICET (Argentina) [grant number PIP 2014-0259].

Appendix 1. Supplementary data to this article can be found online at http://revista.macn.gob.ar/ojs/index.php/RevMus/rt/suppFiles/626/0

REFERENCES

Ancíbor, E. 1990. Determinación xilológica de la made-

Table 2. *Nothofagus* species described and specimens number discriminated by member.

| Nothofagaceae species                  | Specimens number at the Lower member | Specimens number at the Upper member |
|---------------------------------------|--------------------------------------|--------------------------------------|
| *Nothofagus simplicidens*             | 4                                    | 9                                    |
| *Nothofagus variabilis*               | 2                                    | 8                                    |
| *Nothofagus magelhaenica*             | 1                                    | 29                                   |
| *Nothofagus sp. cf. N. obliqua*       | 0                                    | 2                                    |
| *Nothofagus elongata*                 | 1                                    | 3                                    |
| *Nothofagus subferruginea*            | 4                                    | 11                                   |
| *Nothofagus dicksonii*                | 0                                    | 31                                   |
| *Nothofagus sp. aff. N. alessandri*   | 1                                    | 1                                    |

Fig. 7. Number of specimens per species discriminated by member. Dark gray, upper member; light gray, lower member.

Fig. 8. Abundance (%) of the specimens per family recorded at the lower (A) and upper members (B) of the Río Turbio Formation.
Terciario inferior de Río Turbio, Provincia de Santa Cruz. *Ameghiniana* 5(10): 406–416.

Archangelsky, S. 1969. Estudio del paleomicroplancton de la Formación Río Turbio (Eoceno), provincia de Santa Cruz. *Ameghiniana* 6(3): 181–218.

Archangelsky, S. 1972. Especies de la Formación Río Turbio (Eoceno). *Revista del Museo de La Plata* (n.s.) Sección Paleontología 6: 65–100.

Archangelsky, S. & A. Fasola. 1971. Algunos elementos del paleomicroplancton del Terciario inferior de Patagonia (Argentina y Chile). *Revista del Museo de La Plata* (n.s.) Sección Paleontología 6: 1–17.

Archangelsky, S. & E.J. Romero. 1974. Los registros más antiguos del polen de *Nothofagus* (Fagaceae) de Patagonia (Argentina y Chile). *Boletín de la Sociedad Botánica de México* 33: 13–29.

Barreda, V. D. & L. Palazzesi. 2007. Patagonian vegetation turnovers during the Paleogene–early Neogene, 2007, pp. 143–170. Cambridge University Press, Cambridge.

Dettmann, M.E. 1994. Cretaceous vegetation: the microfossil record. In: R.S. Hill (ed.), *History of the Australian Vegetation*, pp. 143–170. Cambridge University Press, Cambridge.

Dettmann, M.E., D.T. Pocknall, E.J. Romero & M.C. Zamulao. 1990. *Nothofagidites* Erdtmann ex Potorie, 1960: a catalogue species with notes on the Paleogeographic distribution of *Nothofagus* Bl. (southern Beech). *New Zealand Geological Survey Palaeontological Bulletin* 60: 79 pp.

Donoso, C. 1996. Ecology of *Nothofagus* Forests in Central Chile. In: T.T. Vehlen, R.S. Hill & J. Read (eds.), The ecology and biogeography of *Nothofagus* forests, pp. 271–292. Yale University Press.

Berry, E.W. 1925. A Miocene flora from Patagonia. *John Hopkins University Studies in Geology* 6: 183–233.

Berry, E.W. 1937. Eocene plants from Río Turbio in the territory of Santa Cruz, Patagonia. *John Hopkins University Studies in Geology* 12: 91–97.

Berry, E.W. 1938. Tertiary Flora from the Río Pichileufu, Argentina. *Geological Society of America, Special Papers* 12: 1–149.

Blume, C.L. 1851. Museum Botanicum Lugduno-Batacum sive stirpium Exoticarum, Novarum vel Minus Cognitarum ex Vivis aut Siccis Brevis Expositio et Descriptio 1: 307.

Brea, M. 1993. Inferencias paleoclimáticas a partir del estudio de los anillos de crecimiento de leños fósiles de la Formación Río Turbio, Santa Cruz, Argentina. I. *Nothofagoxylon paraproceras* Ancibor, 1990. *Ameghiniana* 30(2): 135–141.

Brea, M., A.E. Artabe, J.R. Franzese, A.F. Zucol, L.A. Spalletti, E.M. Morel, G.D. Veiga & D.G. Ganuza. 2015. Reconstrucción de un forest fossil reveals details of the palaeoecology, palaeoenvironments and climatic conditions in the late Oligocene of South America. *Palaeogeography, Palaeoclimatology, Palaeoecology* 418: 19–42. DOI: 10.1016/j.palaeo.2014.11.013

Cavallaro, S. 2006. Vegetación y Fauna. In: D. Rastelli Brea, M., A.E. Artabe, J.R. Franzese, A.F . Zucol, L.A. Brea, M. 1993. Inferencias paleoclimáticas a partir del *Giornale di Geologia* 13: 41–65.

Fiori, A. 1940. Fillite terziare della Patagonia. III. Fillite della rive meridionale del Lago Nahuel Huapi. *Giornale di Geologia* 4: 101–106.

Fiori, A. 1939. Fillite terziare della Patagonia. II. Fillite del Río Nirihau. *Giornale di Geologia* 13: 1–27.

Fiori, A. 1940. Fillite terziare della Patagonia. III. Fillite del Río Chenqueniyeu. *Giornale di Geologia* 14: 94–143.

Fosdick, J.C., J.E. Bostelmann, J. Leonard, R. Ugalde,
J.L. Oyarzún & M. Griffin. 2015. Timing and rates of foreland sedimentation: new detrital zircon U/Pb geochronology of the Cerro Dorotea, Río Turbio, and Río Guillermo formations, Magallanes basin. In: *Proceedings of the XIV Congreso Geológico Chileno*, La Serena, Chile, 763–766.

Frenquelli, J. 1941. Nuevos elementos florísticos del Magallaniano de Patagonia Austral. *Notas del Museo de La Plata, Sección Paleontología* 6(30): 173–202.

Gandolfo, M.A. & E.J. Romero. 1992. Leaf Morphology and a key to species of *Nothofagus* Bl. *Bulletin of the Torrey Botanical Club* 119(2): 152–166. DOI: 10.2307/2997028

Gayó, E. 2001. Estudio taxonómico y fisionómico-climático de la tafoflora Caleta Cochlögque (36° 35’ s y 72° 58’ w), Eoceno inferior, Chile Central. PhD thesis, Universidad de Chile, Chile, 164 pp.

Gómez-Esteban, M.J.; G.R. Guerstein & S. Casadío 2015. Estudio bioestratigráfico y paleoambiental de la Formación Río Turbio (Eoceno Medio–Superior) en el sudoeste de Patagonia (Argentina) basado en quistes de dinoflagelados. *Revista Brasileira de Paleontologia* 18(3): 429–442. DOI: 10.4072/rbpb.2015.3.08

Guerstein, G.R., M.S. Gonzáles Estebenat, M.I. Alperín, S.A. Casadío & S. Archangelsky. 2014. Correlation and paleoenvironments of middle Paleogene marine beds based on dinoflagellate cyst in southwestern Patagonia, Argentina. *Journal of South American Earth Sciences* 52: 166–178. DOI: 10.1016/j.jsam.2014.02.011

Guerstein, G.R., M.R. Rodríguez Raising, S. Casadío, S. Marenssi & O. Cárdenas 2010. Paleontologia del Miembro Inferior de la Formación Río Turbio (Eoceno inferior a medio) en el cañón del río Guillermo, suroeste de Santa Cruz, Argentina. In: *Proceedings of the X Congreso Argentino de Paleontología y Bioestratigrafía*, La Plata, Argentina. Resúmenes: 93.

Hickey, L.J. & J.A. Wolfe 1975. The bases of Angiosperm phylogeny. Vegetative morphology. *Annals of the Missouri Botanical Garden* 62(3): 538–589. DOI: 10.2307/2995267

Hill, R.S. 2001. Biogeography, evolution and paleoecology of *Nothofagus* (Fagaceae): the contribution of the fossil record. *Australian Journal of Botany* 49: 321–332. DOI: 10.1080/03115518808619134.

Hill, R.S. & J. Jordan. 1993. The evolutionary history of *Nothofagus* (Fagaceae). *Australian Systematic Botany* 6: 111–126.

Hill, R.S. & J. Read. 1991. A revised infrageneric classification of *Nothofagus* (Fagaceae). *Biological Journal of the Linnean Society* 40(1): 37–72. DOI: 10.1111/j.1095-8399.1991.tb00199.x

Hinojosa, L.F. & C. Villagrán. 1997. Historia de los bosques del sur de Sudamérica, I: antecedentes paleobotánicos, geológicos y climáticos del Terciario del cono sur de América. *Revista Chilena de Historia Natural* 70: 225–239.

Hinojosa, L.F., A. Gaxiola, M.F. Pérez, F. Carvajal, M.F. Campano, M. Quattrociocchi, H. Nishida, K. Uemura, A. Yabe, R. Bustamante & M.T.K. Arroyo. 2015. Non-congruent fossil and phylogenetic evidence on the evolution of climatic niche in the Gondwana genus *Nothofagus*. *Journal of Biogeography* 43(3): 555–567. DOI: 10.1111/jbi.12650.

Hünicken, M. 1955. Depósitos neocretácicos y terciarios del extremo SSW de Santa Cruz (cueca carbonífera de Río Turbio). *Revista del Instituto Nacional de Ciencias Naturales y Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”*, Ciencias geológicas 4: 1–164.

Hünicken, M. 1967. Flora terciaria de los estratos de Río Turbio, Santa Cruz (niveles plantíferos del arroyo Santa Flavia). *Revista de la Facultad de Ciencias Exactas Físicas y Naturales de la Universidad de Córdoba* 27: 139–227.

Hünicken, M. 1985. Floras cretácicas y terciarias. In: P.N. Stipanicic & M.A. Hünicken (eds.), *Revisión y actualización de los geobotánicos de Kurtz en la República Argentina (I, II, III, IV, V, VI y VII)*, pp. 199–219, Academia Nacional de Ciencias, Córdoba.

Jordan, G.J., & R.S. Hill. 1999. The phylogenetic affinities of *Nothofagus* (Nothofagaceae) leaf fossils based on combined molecular and morphological data. *International Journal of Plant Sciences* 160(6): 1177–1188. DOI: 10.1086/314207.

Knapp, M., K. Stockler, D. Havell, F. Delsuc, F. Sebastiani & P.J. Lockhart. 2005. Relaxed molecular clock provides evidence for long-distance dispersal of *Nothofagus* (southern beech). *PLoS Biology* 3: 3843. DOI: 10.1371/journal.pbio.0030014

Krasser, F. 1896. Bemerkungen zur Systematik der Buchen. *Annalen des Naturhistorischen Hofmuseums Wien* 11: 155–163.

Kuprianova, E.S. 1962. First International Conference of Palynology, Reports Sovietic Palinolinology, 21.

Leanza, A.F. 1972. Andes patagónicos australes. In: A.F. Leanza (ed.), *Geología regional argentina*, 689–706. Academia Nacional de Ciencias, Córdoba.

León, R.J.C., D. Bran, M. Collantes, J.M. Paruelo & A. Soriano. 1998. Grandes unidades de vegetación de la Patagonia extra andina [Main vegetational units of the extra-andean Patagonia]. *Ecología Austral* 8(2): 125–144.

Leppe, M., F. Hinojosa, H. Nishida, T. Dutra, T. Wilberger, C. Trevisan, J.M. Ortuya, J.P. Pino, H. Mansilla & V. Lobos. 2017. Asynchronous oldest record of *Nothofagus* leaves in Antarctica and Patagonia. *Boletín de la Asociación Latinoamericana de Paleobotánica* 15: 1–32.

Malumíán, N. & A. Caramés. 1997. Upper Campanian–Paleogene from the Río Turbio, Provincia de Santa Cruz, 1:250.000. *Boletín del Servicio Geológico Minero* 247: 108 pp.

Manos, P.S. 1997. *Systematics of Nothofagus* (Notho-
Panti, C. 2010. Diversidad florística durante el Paleógeno austral. Revista Chagual (Jardín Botánico de Santiago) 2: 48–56.

Panti, C. 2011. Análisis paleoflorístico de la Formación Austral. Tesis doctoral, Universidad de Buenos Aires, Ciudad Autónoma de Buenos Aires, 209 pp.

Romero, E.J. 1973. Polen fósil de Nothofagus (Nothofagidites) del Cretácico y Paleoceno de Patagonia. Revista del Museo de La Plata (Nueva serie), Sección Paleontología 10.5710/AMGH.05.01.2014.2805.

Romero, E.J. 1978. Paleocología y paleofitogeografía de las tafofloras del Cenofítico de Argentina y áreas vecinas. Ameghiniana 15: 209–227.

Romero, E.J. 1980. Arquitectura foliar de las especies sudamericanas de Nothofagus Bl. Boletín de la Sociedad Argentina de Botánica 19 (1–2): 289–308.

Romero, E.J. 1986a. Paleogeografía y clima de los polenos de angiospermas de la Formación Río Turbio (Eoceno), provincia de Santa Cruz, República Argentina. Ameghiniana 23(1–2): 101–118.

Romero, E.J. 1986b. Polen fósil de Nothofagus (Nothofagidites) del Cretácico y Paleoceno de Patagonia. Revista del Museo de La Plata (Nueva serie), Sección Paleontología 7(47): 291–303.

Romero, E.J. 1986c. Paleogeografía y paleofitogeografía de las tafofloras del Cenofítico de Argentina y áreas vecinas. Ameghiniana 15(1–2): 209–227.

Romero, E.J. 1988. Material fúngico y gramos de polen de angiospermas de la Formación Río Turbio (Eoceno), provincia de Santa Cruz, República Argentina. Ameghiniana 23(1–2): 101–118.

Romero, E.J. & M.C. Zamalloa. 1985. Polen de angiospermas de la Formación Río Turbio (Eoceno), Santa Cruz, Argentina. Ameghiniana 45(4): 677–692.

Poole, I. 2002. Systematics of Cretaceous and Tertiary Nothofagoxylon: implications for southern hemisphere biogeography and evolution of the Nothofagaceae. Australian Systematic Botany 15(2): 247–276. DOI: 10.1071/SB01014.

Prestvik, A. 1996. Leaf architecture of South American Nothofagus (Nothofagaceae) using traditional and new methods in morphometrics. Botanical Journal of the Linnean Society 121: 25–40.

Pujana, R.R. 2008. Estudio paleoxiológico del Paleógeno de Patagonia austral (Formaciones Río Leona, Río Guillermo y Río Turbio) y Antártida (Formación La Meseta). Tesis doctoral, de la Universidad de Buenos Aires, Ciudad Autónoma de Buenos Aires, 182 pp.

Pujana, R.R. 2009. Fossil woods from the Oligocene of southwestern Patagonia (Río Leona Formation), Rosaceae and Nothofagaceae. Ameghiniana 46(4): 621–636.

Pujana, R.R. & D.P. Ruiz. 2017. Podocarpoxylon Gothan reviewed in light of a new species from the Eocene of Patagonia. IAWA Journal 38(2): 220–244. DOI: 10.1163/22941932-20170169.

Pujana, R.R., C. Panti, J.I. Cuitiño, J.L. García Massi ni & S.L. Mirabelli. 2015. A new megaflora (fossil wood, and leaves) from the Miocene of southwestern Patagonia. Ameghiniana 52(3): 350–366. DOI: 10.5710/AMGH.05.01.2014.2805.

Sempere, J., J.M. Sangranú, O. Torrella, C. Panti, A. Cabal & T. Gutiérrez. 2018. Paleofloras of late Miocene age from the Patagonian Province (Argentina). Palaeoecology and paleofitogeography of the tafofloras of the Cenofítica of Argentina and areas vecinas. Ameghiniana 45(4): 677–692.

Sempere, J., J.M. Sangranú, O. Torrella, C. Panti, A. Cabal & T. Gutiérrez. 2018. Paleofloras of late Miocene age from the Patagonian Province (Argentina). Palaeoecology and paleofitogeography of the tafofloras of the Cenofítica of Argentina and areas vecinas. Ameghiniana 45(4): 677–692.

Sempere, J., J.M. Sangranú, O. Torrella, C. Panti, A. Cabal & T. Gutiérrez. 2018. Paleofloras of late Miocene age from the Patagonian Province (Argentina). Palaeoecology and paleofitogeography of the tafofloras of the Cenofítica of Argentina and areas vecinas. Ameghiniana 45(4): 677–692.
