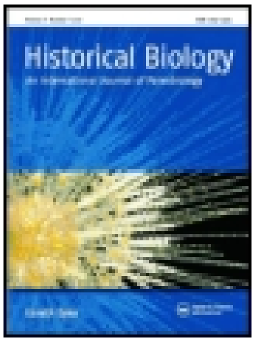

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ARTICLE

Fossil leaves of subtropical lineages in the Eocene–?Oligocene of southern Patagonia

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ABSTRACT
Here I describe and illustrate 19 leaf morphospecies from the Paleogene Río Turbio Formation, Santa Cruz Province, Argentina. They were referred to the extant tropical and subtropical families Lauraceae (9 morphospecies), Malpighiaceae (1 morphospecies), Vitaceae (2 morphospecies), Anacardiaceae (2 morphospecies) and Sapindaceae (5 morphospecies). These taxa were recorded throughout the unit, but they are more abundant in the lower member of the Río Turbio Formation. The observed decreasing trend in megathermal taxa throughout the unit indicates 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.

KEYWORDS
Fossil leaves; angiosperms; cenozoic; patagonia; Argentina

Introduction

Patagonia can be defined as a temperate or cool temperate region (Paruelo et al. 1998)Patagonia is today cold, with cool temperate rainforests on the west and an arid steppe on the east. However, at the beginning of the Cenozoic, higher temperatures allowed the development of significantly diverse floras in southern Patagonia, even more diverse than North American counterparts (Wilf et al. 2003). This climatic scenario, characterized by a low equator to polar temperature gradient (Willis and McElwain 2002), favored plants with tropical affinities to reach middle and high latitudes in both hemispheres (Wilf et al. 2005). In Patagonia, in particular, the abundance of Neotropical taxa characterized several early Paleogene floras (Berry 1938; Wilf et al. 2003; Troncoso et al. 2002; Carpenter et al. 2018), that began to decline towards the Oligocene, being replaced by cool temperate elements (Menendez 1971; Barreda and Palazzesi 2007; Iglesias et al. 2011).

The Río Turbio Formation (RTF) (Leanza 1972) crops out in the south western tip of Santa Cruz Province, Argentina (Figure 1(a)) and is recognized in literature by its abundant fossil plant content; it includes leaves, woods and palynomorphs (Berry (1937a); Frengüelli (1941); Hünicken (1955, 1967, 1995); Archangelsky (1968, 1969, 1972), Archangelsky and Fasola (1971); Romero (1977); Romero and Zamaloa (1985); Romero and Castro (1986); Ancibor (1990); Brea (1993); Pujana (2008), Pujana and Ruiz (2017)); Panti (2010, 2014a, 2014b)) and Fernández et al. (2012)). The RTF is mainly composed of mudstones and sandstones deposited in shallow marine and estuarine environments during a period of sea level rise (Malumián 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 divided into two informal members: lower and upper, on the bases of a major micro and macro faunistic shift, which coincide with a glauconitic horizon representing the beginning of a conspicuous transgressive episode (Malumián and Caramés 1997). Evidence for the age of the RTF comes mainly from two sources, the first, dinoflagellates and the second detrital zircon U/Pb. Dinoflagellate data 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. 2016). Detrital zircon U/Pb geochronology (Fosdick et al. 2015) restrict the lower member to the Early Eocene (47–46 Ma) and indicate a significantly younger age for the upper member, Oligocene (≤ 34–26 Ma).

The RTF flora is of great interest because it bears both, mega (eg. Lauraceae, Sapindaceae and Malpighiaceae) and microthermal (eg. Nothofagaceae and Winteraceae) elements. These types of paleofloras were defined as 'Mixed' by Romero (1986). Previous macrofossil studies involve very few systematic descriptions of specimens recovered from isolated localities, and mainly performed at the beginning of the 20th century (Berry 1937a; Frenguelli 1941; Hünicken 1955, 1967, 1995). The most relevant systematic work was carried by Hünicken (1967) from material collected only from the lower member of the RTF, reporting several species of megathermal affinities. Some of these specimens have been recently revised by Vento and Prámparo (2018). Macrofossil associations from the upper member are broadly characterized by the presence of *Nothofagus* and some other micro and meso–thermal taxa (Berry 1937a; Frenguelli 1941; Hünicken 1995).

In order to achieve a complete systematic knowledge of the RTF macroflora, the RTF was sampled in several localities (Figure 1(b)) to obtain a complete record of the whole unit.

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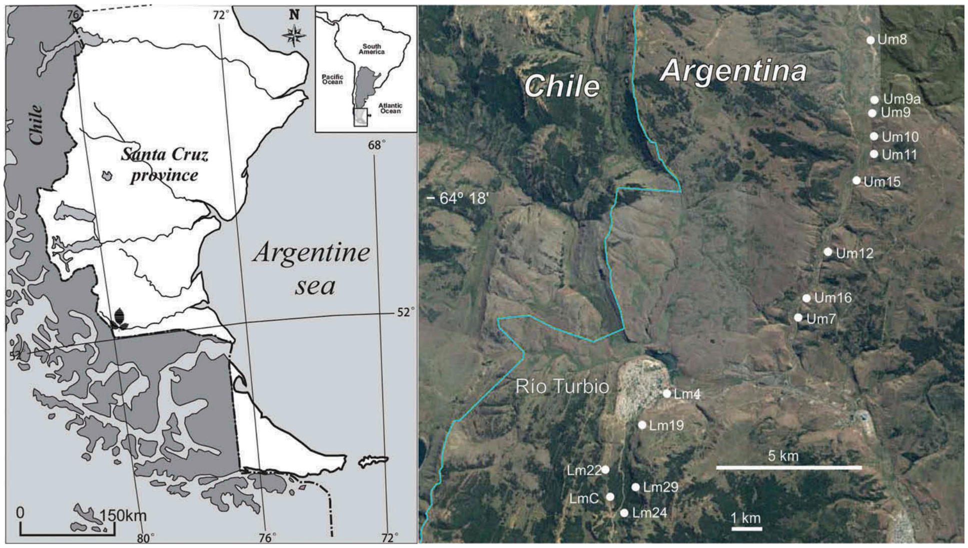

Figure 1. a. Location map. b. Location–bearing samples (Panti 2010).

The purpose of this paper is to continue the systematic study of the macroflora from the Río Turbio Formation, in this opportunity, describing and comparing 71 leaf specimens referred to the megathermal families: Lauraceae, Malpighiaceae, Vitaceae, Anacardiaceae and Sapindaceae. We also aim to analyze the distribution of these megathermal components throughout the unit.

Materials and methods

The leaf imprints described in this paper were collected by the author in a continuous way from different fossil outcrops where both, lower and upper members are exposed (Figure 2). The specimens with well–preserved venation were studied using modern leaf architectural analysis. After their comparison to other southern South American fossils and extant taxa, were referred mainly to known fossil–genera. Exceptions were made for those species defined in the literature for which no fossil–genera are known. In this case where the species is considered valid but the reference to the extant genus is considered tentative; it is indicated with quotation marks.

Here are only described those taxa related to mega and mesothermal families, mostly absent in the area nowadays. The 19 morphospecies are summarized in Table 1 according to its stratigraphic provenance.

Terminology and systematic descriptions follow Ellis et al. (2009) and Hickey and Wolfe (1975). The terms megathermal (> 20°C), mesotherm (> 13°C, < 20°C), and microthermal (< 13°C) proposed by Nix (1982) are used instead of tropical, subtropical, warm temperate, and cool or cold temperate, because the latter terms have geographical connotations as well (Barreda and Palazzesi 2007). The overall of the specimens recovered was plotted according to its stratigraphic distribution and were visualized using bar–plots.

Suprageneric nomenclature follows APG IV (2016). Specimens are housed in the Paleobotanical Collection of the Museo Regional Padre Manuel Jesús Molina (MPM PB) located in Río Gallegos, Santa Cruz Province, Argentina. Those samples which preserve more than one specimen are mentioned as A, B, C, etc., after the accession number.

Paleobotanical content

Order **LAURALES** Juss. ex Bercht. & J.Presl (1820)
Family **LAURACEAE** Juss. (1789)
Genus ***Nectandrophyllum*** Engelhardt 1891
Type species: *Nectandrophyllum* sp. Engelhardt 1891

Nectandrophyllum sp. 1
Figure 3(a)

Material

MPM PB 3149–3150

Location–bearing samples

Lm4, Um16

Description

Laminar size microphyll to notophyll, shape apparently elliptic. Margin untoothed. Primary venation pinnate. Major secondaries simple brochidodromous with regular spacing, decurrent attachment to midvein and angle smoothly increasing proximally. Major secondaries simple brochidodromous, intersecondaries veins span more than 50% of the length of the subjacent secondary and fimbrial vein present. Intercostal tertiary veins percurrent, sinuous and in obtuse angle to primary vein exterior tertiaries looped. Quaternary and quinternary vein fabric, regular reticulate.

Comparisons

These specimens can be compared to *Nectandra prolifica* Berry. According to Berry this species shows great variation in size and shape, ranging from small, slender falcate acuminate forms, intermediate lanceolate acuminate forms and broader ovate acuminate forms. The specimens here described are comparable to the broader ovate acuminate forms that Berry related to 'the suggestive form of the extant

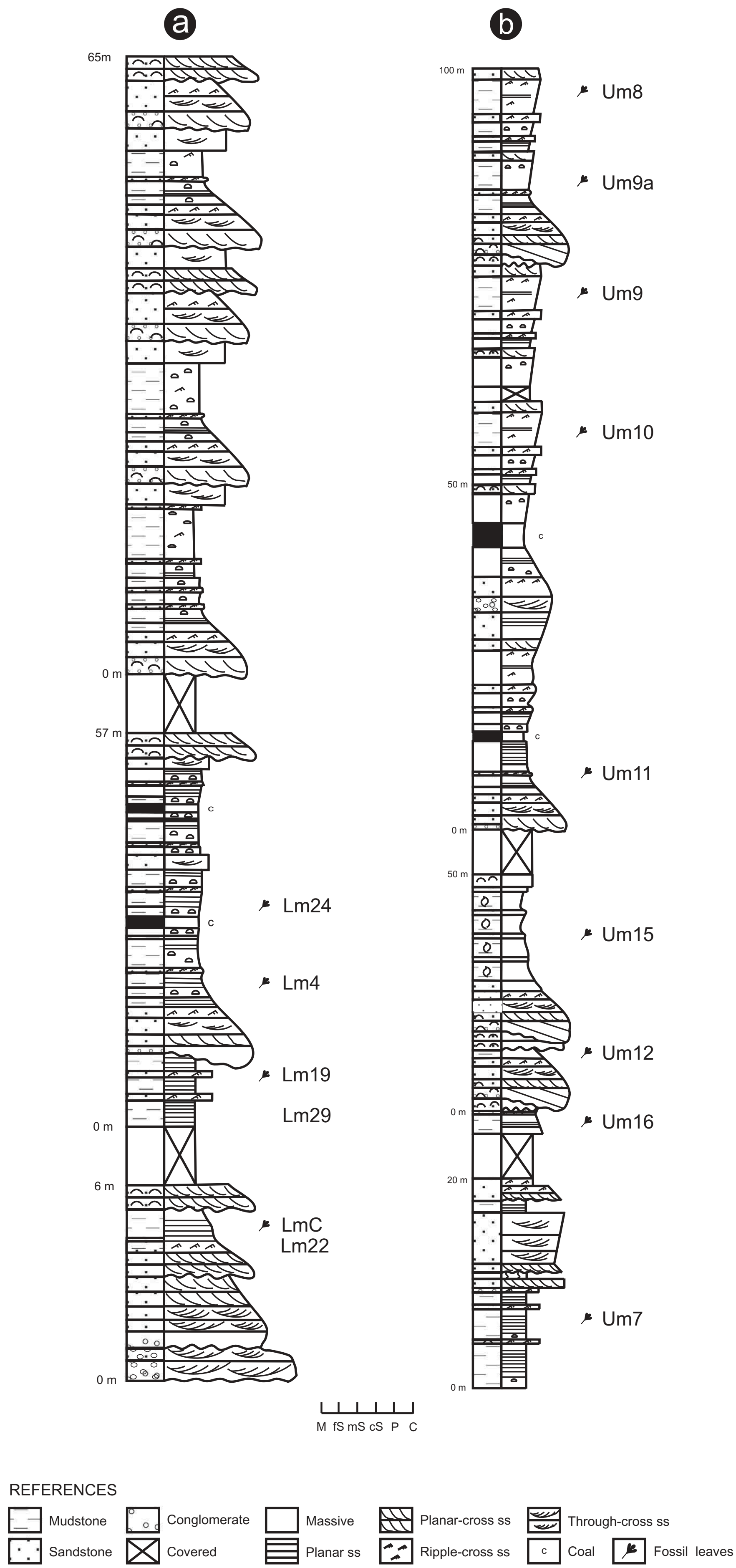

Figure 2. Stratigraphic log of the Río Turbio Formation showing location–bearing samples. Lower member (a); Upper member (b).

Table 1. Morphospecies described and specimens number discriminated by member.

Morphoespecies	Specimens number at the Lower member	Specimens number at the Upper member
Nectandrophyllum sp1	1	1
Nectandrophyllum sp2	9	4
Laurophyllum sp1	4	3
Laurophyllum sp2	1	0
Laurophyllum sp3	0	6
Laurophyllum sp4	2	3
Laurophyllum sp5	1	0
Laurophyllum sp6	1	0
Laurophyllum sp7	1	0
Banisteriophyllum	1	0
Cissites sp1	1	0
Cissites sp2	5	5
Anacardites sp	1	0
*'Schinopsis'*sp	1	0
'Allophylus' graciliformis	3	6
Cupanites sp1	5	0
Cupatines sp2	2	1
Cupanites sp3	2	0
'Paullinia' sp	2	0

Nectandra antillana' (Berry 1938, p. 111). *Nectandra hihua* (Ruiz & Pav.) Rohwer (= *Nectandra antillana* Meisn.) and the fossils described by Berry (1938; p. 111; Pl. 42, fig. 6) shares with our specimens similar leaf form and venation pattern, characterized by pinnate midvein, brochidodromous secondary veins, intersecondaries veins present, tertiary veins percurrently disposed at obtuse angle to the midvein and quaternary and quinternary veins regular reticulate. The main difference seems to be that the basal secondary veins are eucamptodromous. The fragmentary nature of the specimens analyzed does not allow further comparisons.

Botanical affinity

The venation pattern of the studied material matches the one described for several genera of Lauraceae. Similarities in the leaf shape and venation pattern can be observed in some extant species of *Persea, Nectandra* and *Ocotea* among others.

Nectandrophyllum sp. 2
Figure 3(b–c)

Material

MPM PB 2921–2933; 2935

Location–bearing samples: Lm4, LmC, Lm29, Um9a

Description

Blade attachment petiolate, laminar size microphyll to nothophyll, L:W ratio up to 3:1, laminar shape elliptic with medial and basal symmetry symmetrical. Margin untoothed, with acute base angle and cuneate to convex base shape. Primary venation pinnate with no naked basal veins, one basal vein and simple agrophic veins.

Major secondaries eucamptodromous, turning to brochidodromous towards the apex.

Secondary veins with regular spacing, apically projected and excurrent attachment to midvein. Fimbrial vein present. Intercostal tertiary veins alternate percurrent, exterior tertiaries looped. Quaternary and quinternary venation reticulate

Comparisons

These specimens are comparable to the slender forms of *Nectadra prolifica* described by Berry (1938) and Troncoso (1992), (2002)). As both authors mentioned, this species shows great variations in size and form. The Río Turbio specimens are represented by slender forms with basal and middle eucamptodromous secondary veins becoming brochidodromous only towards the apex.

Botanical affinity

There are four *Nectandra* species that inhabit Argentina. Among these, our fossils seem to have a venation pattern and a leaf shape similar to *Nectandra megapotamica* (Spreng.) Mez. and *Nectandra lanceolata* Nees & Mart.

Genus ***Laurophyllum*** Goeppert 1854Type species: *Laurophyllum beilschmiedioides* Goeppert 1854

Laurophyllum sp. 1
Figure 3(d–e)

Material: MPM PB 2940B–2945, 3165

Location–bearing samples

Lm4, LmC, Lm24, Um7, Um16

Description

Blade attachment marginal, laminar size microphyll, L:W ratio 3:1, laminar shape elliptic. Margin untoothed. Primary venation actinodromous, three basal veins and simple agrophic veins. Major secondaries eucamptodromous and sub–opposite, with regular spacing, uniform angles and decurrent attachment to midvein. Minor secondaries simple brochidodromous and marginal secondary vein present. Intercostal tertiary veins opposite percurrent, angle increasing exmedially. Quaternary vein fabric reticulate.

Comparisons

These specimens can be compared to *Notaphoebe ovatifolia* Berry (1938: 114, pl. 41, figs 4–5) and *Notaphoebe neogaea* Berry (1938; p. 114, Pl. 41, fig. 3), both also identified and described by Hünicken for the Río Turbio Formation (1967; p. 175, Pl. III, fig. 5–6). These two species only differ in the lamina width, being wider in *N. ovatifolia* and in the primary pair of basal veins (suprabasal in *N. ovatifolia* and basal in *N. neogaea*). The absence of the leaf base in the material studied precludes an accurate comparison. In the case of the material described by Hünicken as *Notaphoebe neogaea* the primary pair of basal veins are attached to the central vein at different heights, feature not observed in the material described by Berry (1938) and in the specimen here described, which despite having its proximal portion incomplete, it looks like if both veins are attached at the same point. On the other hand, *Laurophyllum* sp. 1 shows similarities in lamina shape

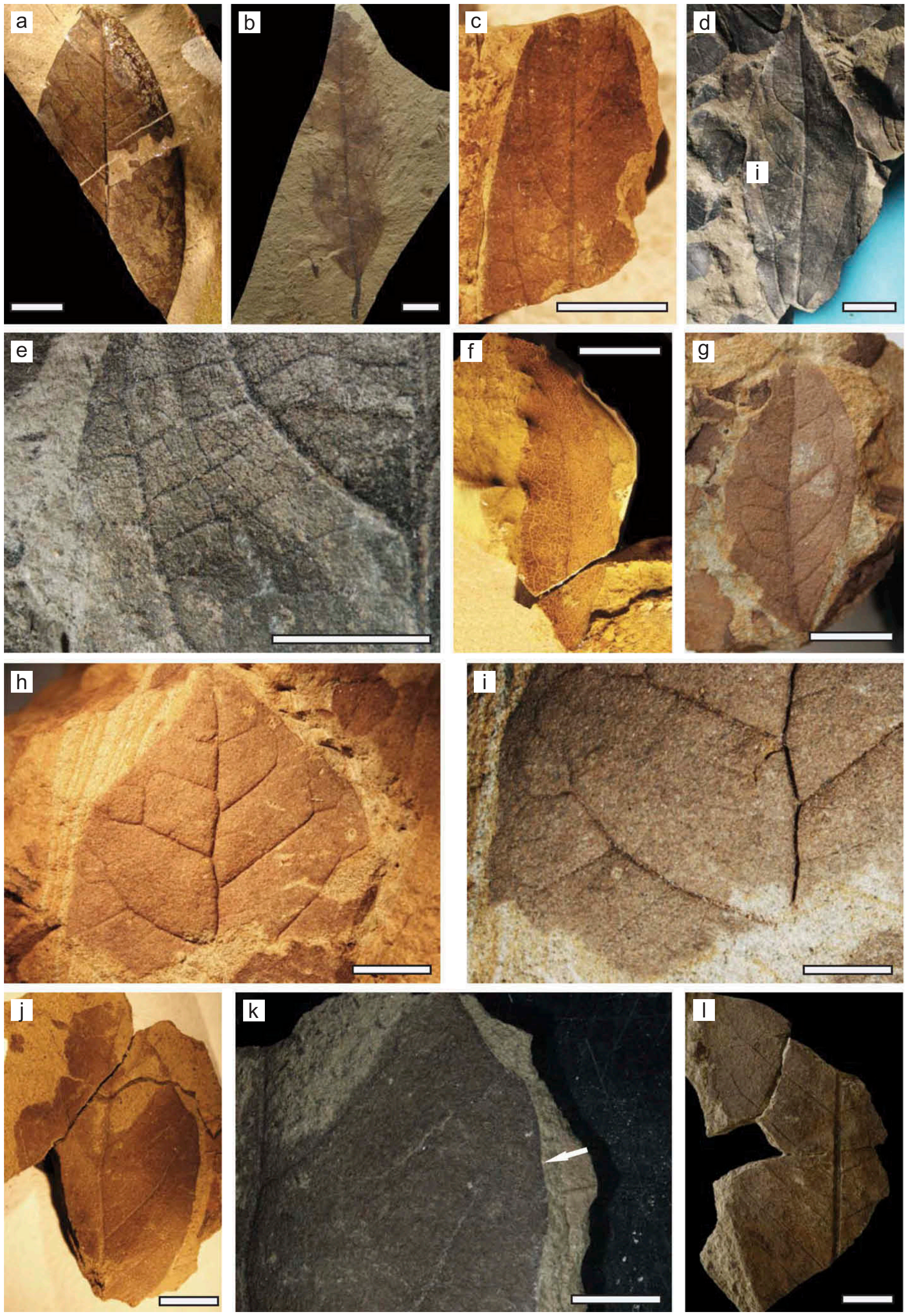

Figure 3. a.Nectandrophyllum sp. 1 (MPM PB 3150) b.Nectandrophyllum sp. 2 (MPM PB 2923) c.Nectandrophyllum sp. 2 (MPM PB 2926) d.Laurophyllum sp. 1 (MPM PB 2940B) e.Laurophyllum sp. 1(MPM PB 2940B) detail of the leaf venation f.Laurophyllum sp. 2 (MPMPB 3172) g.Laurophyllum sp. 3 (MPM PB 3168) h.Laurophyllum sp. 3 (MPM PB 3168) i.Laurophyllum sp. 3 (MPMPB 3167), detail of the leaf venation j.Laurophyllum sp. 4 (MPM 2916) k.Laurophyllum sp. 4 (MPM 2916) detail of the marginal secondary vein l.Laurophyllum sp. 5 (MPM PB 3146)Scale bar e, i, k= 5 mm; a–d, f–h, j, l= 10 mm.

and venation pattern with *Cinnamomum* sp, 2 and *Cinnamomum* sp, 4 described by Troncoso et al. (2002) for the Ligorio Marquez Formation. In particular, the venation in *Cinnamomum* sp, 4 is very similar to that observed in *Laurophyllum* sp. 1, with an opposite first pair of secondary veins and the subsequent ones, sub–opposite to alternate.

Botanical affinity

According to Klucking (1987) the venation pattern that characterized the genus *Notaphoebe* Blume differs from the described for *N. ovatifolia* and *N. neogaea*. Instead, the venation pattern described by Berry is concordant to the venation pattern observed in the extant species of *Cinnamomum* Schaeffer.

Laurophyllum sp. 2
Figure 3(f)

Material

MPM PB 3172.

Location–bearing samples
Lm4

Description
Blade attachment marginal, laminar size microphyll, L:W ratio 3:1, laminar shape elliptic with medial and basal symmetry symmetrical. Margin untoothed. Primary venation pinnate with no naked basal veins, one basal vein and no agrophic veins. Major secondaries simple brochidodromous forming plane arches, with regular spacing, uniform angles and decurrent attachment to midvein. Intramarginal vein present. Intercostal areas irregular. Intercostal tertiary veins opposite reticulate, exterior tertiaries looped. Quaternary veins reticulate. Free veinlets inside the areoles.

Comparisons
Laurophyllum sp. 2 is quite similar to the specimens described as *Acrodiclidium flavianum* by Hünicken (1967, p. 180, Pl. XII, fig. 8), in the overall leaf shape, size and venation pattern. *Acrodiclidium oligocaenicum* Engelhardt another fossil species described from Chile (Engelhardt 1891) and Argentina (Berry 1938), differs from *Laurophyllum* sp. 2 in the lamina shape, being slightly more oblong in *A. oligocaenicum* and in the secondary veins pattern.

Botanical affinity
Hünicken refers previously collected specimens to *Acrodiclidium* Ness. a neotropical Lauraceae genera endemic of Central and South America, based on similarities in the leaf shape, margin and venation pattern with leaves of the extant *Acrodiclidium salicifolium* (Sw.) Griseb. Nowadays *Acrodiclidium* is considered a junior synonym of *Licaria* Aubl. *Licaria salicifolia* (Sw.) Kosterm. (= *Acrodiclidium salicifolium*) have a similar leaf shape and venation pattern. *Umbellularia californica* (Hook. & Arn.) Nutt., another Lauraceae species endemic from the United States, has also very similar venation pattern with secondaries emerging at wide angles from the midvein but seems to differ in the base and apex shape, being both rounded in *U. californica*.

Laurophyllum sp. 3
Figure 3(g–i)

Material
MPM PB 3164D; MPM PB 3166–3169.

Location–bearing samples
Um7, Um10, Um9a

Description
Laminar size microphyll, laminar shape elliptic. Margin untoothed with acute apex angle, attenuate apex; acute base angle and cuneate to decurrent base shape. Primary venation pinnate. Major secondaries festooned brochidodromous with irregular spacing, secondary angle smoothly decreasing proximally and deflected attachment to midvein. Fimbrial vein present. Intersecondaries spam more than 50% of the length of the subjacent secondaries, occur at least one per intercostals area, proximal course parallel to major secondaries, distal course basiflexed. Intercostal tertiary veins reticulate, exterior tertiaries looped.

Comparisons
Among the fossil species *Ocotea menendezi* Hünicken (1967; p.177. Pl. III, fig. 9; Pl. IV, fig. 1) is the most comparable to *Laurophyllum* sp. 3. In both it is possible to observe leaf with the same venation pattern and lamina shape. According to the illustration and diagnosis given by Hünicken, the primary vein in *O. menendezi* is stout and straight whereas in the studied material it follows a zigzag course. However, variations in the course of the primary vein have been observed in extant species of *Ocotea*, making it possible to refer *Laurophyllum* sp. 3 to this genus.

Botanical affinity
Hünicken refers his specimens to this genus due to the similarities observed with *Ocotea caudata* (Ness) Mez. Besides the comparable venation pattern found in *O. menendezi* and *O. caudata* both also present an acuminate apex. Differences can be observed in the leaf margin being sinuous in *O. caudata* and entire in *Ocotea menendezi*. The margin in *Laurophyllum* sp. 3 is not well preserved and the apex is incomplete however, an acuminate tip can be inferred. Among the species that inhabit Argentina, similarities in leaf shape and venation pattern are found with *Ocotea pulchella* (Schott) Mez and *Ocotea lancifolia* (Schott) Mez.

Laurophyllum sp. 4
Figure 3(j–k)

Material
MPM PB 2916–2920.

Location–bearing samples
Lm4, Um9a

Description
Laminar size microphyll. Laminar shape ovate. Margin untoothed. Primary venation pinnate with zig–zag like course. Major secondaries eucamptodromous with irregular spacing, uniform angles and deflected attachment to midvein. Marginal secondary vein present. Intercostal tertiary veins percurrent.

Comparisons
Despite their fragmentary nature, the specimens studied show similarities with *Persea borrelloi* Hünicken (1967; p. 173, Pl. VI, fig. 1), such as the ovate, rhomboidal–like lamina shape, secondary veins that change the angle of divergence towards the leaf margin and percurrent tertiaries.

Botanical affinity
Similarities are found between *Laurophyllum* sp. 4 and *Persea lingue* Nees., an endemic species inhabiting Chubut Province (Argentina) (Pérez Moreau 1984) and Chile (Ezcurra 2010). Both are represented by a rhomboidal–like lamina and secondary veins that curve more sharply near the apical margin.

They are also characterized by the presence of an intramarginal vein and in some cases the primary vein in leaf of *Persea lingue* follows a zigzag course towards the leaf apex.

Laurophyllum sp. 5
Figure 3(l)

Material
MPM PB 3146.

Location–bearing samples
Lm4

Description
Laminar size probably notophyll. Margin untoothed. Primary venation pinnate straight in course. Major secondaries eucamptodromous, thin, with irregular spacing, uniform angles and excurrent attachment to midvein. Fimbrial vein present. Intercostal tertiary veins percurrent. Epimedial tertiary mixed percurrent. Exterior tertiary looped. Quaternary vein percurrent. Quinternary vein reticulate. Aerolation moderate development.

Comparisons
Based on similarities in size and venation, this morphospecies can also be compared to *Persea borrelloi* Hünicken (1967; p. 173, Pl. VI, fig. 1). The species described by Hünicken has smaller divergence angles and more spaced and straight secondary veins. It differs from *Laurophyllum* sp. 4 in the course and gauge of the midvein and in its straighter and more closely spaced secondary veins. Additionally, they can be differentiated by the relative thickness of the secondaries, being notoriously thinner in *Laurophyllum* sp. 5.

Botanical affinity
The material studied can be related to Lauraceae mainly by venation. The noticeable primary vein along with the closely spaced and straighter secondary veins are similar to the ones observed in *Persea venosa* Nees & Mart. ex Nees, an extant species found in the north east of Argentina.

Laurophyllum sp. 6
Figure 4(a)

Material
MPM PB 2939.

Location–bearing samples
Lm4

Description
Leaf very incomplete, laminar size notophyll/microphyll. Primary vein pinnate and stout somewhat curved. Secondary veins curved, maybe eucamptodromous, secondary veins angle approximately 37º to the primary vein; tertiary venation percurrent.

Comparisons
Regardless its fragmentary nature, a large size can be inferred for this specimen, comparable to the largest fossils described by Hünicken, such as cf. *Triumfetta irregulariter–serrata* Engelhardt, *Persea borrelloi* Hünicken and *Goeppertia?* sp. All three have similar proportions and a venation pattern alike the one observed in *Laurophyllum* sp. 6. cf. *Triumfetta irregulariter–serrata* is characterized by a toothed margin and the specimen described and illustrated by Hünicken seems to have a slender primary vein in opposite with the robust vein that is observed in the fossil.

Botanical affinity
Persea Mill. and *Nectandra* Roland ex. Rottb. have similar morphological features such size proportion and a strong primary vein. This allows a relationship between the studied specimens and Lauraceae.

Laurophyllum sp. 7
Figure 4(b)

Material
MPM PB 2961.

Location–bearing samples
Lm4

Description
Lamina size microphyll or nothophyll, shape apparently elliptic. Margin untoothed. Primary venation pinnate. Major secondaries weak brochidodromous with decurrent attachment to midvein. Fimbrial vein present. Intercostal tertiary veins opposite–percurrent; angle to primary obtuse increasing exmedially. Quaternary venation polygonal reticulate.

Comparisons
Among the fossils previously described for the RTF there are similarities with *Nothophoebe ovatifolia* Berry (Hünicken 1967; p. 175, Pl. III, fig. 5). Despite the material described by Hünicken is also fragmentary, the same venation architecture can be observed at the preserved portions: weak brochidodromous secondary veins and opposite–percurrent tertiaries. The same pattern is observable in *Rhamnidium* sp. Hünicken (1967, p. 198, Pl. V; fig. 8), but the secondary veins are more closely spaced and seem to be more numerous than in our specimen.

Botanical affinity
The venation pattern of this fossil can be observed in many genera of Lauraceae, as well as in other families like Rhamnaceae and Melastomataceae. Regardless of the fragmentary state it is possible to observe similarities between the venation pattern of the fossil with some extant *Nectandra* from Argentina such as *N. augusta* Rohwer and *N. lanceolata* Nees. & Mart.

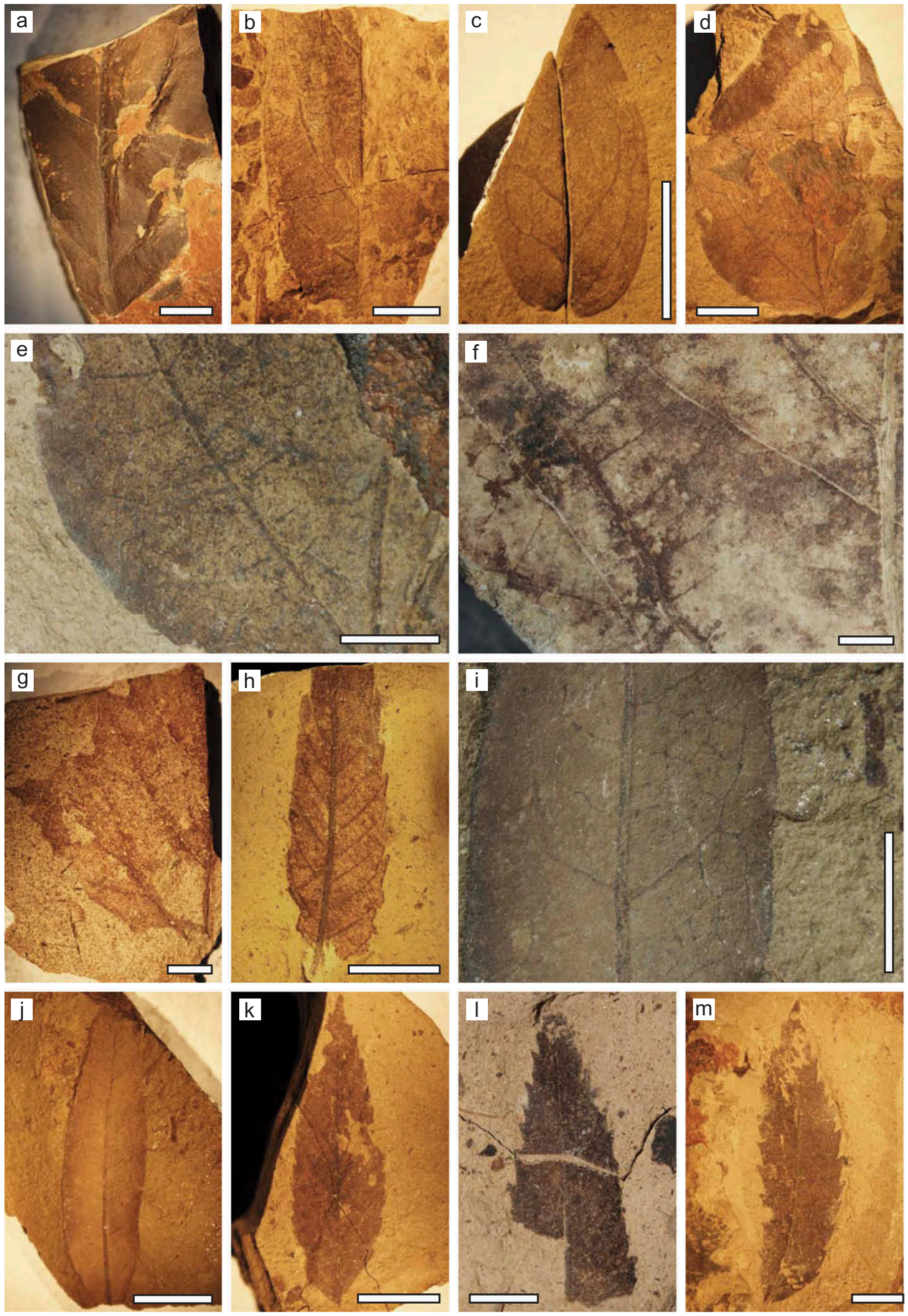

Figure 4. a.Laurophyllum sp. 6 (MPM PB 2939) b.Laurophyllum sp. 7 (MPM PB 2961) c.Banisteriophyllum sp. (MPM PB 2937) d.Cissites sp. 1 (MPM PB 2960) e.Cissites sp. 1, detail of the leaf venation f.Cissites sp. 2 (MPM PB 2953), detail of the leaf venation g.Cissites sp. 2 (MPM PB 2955) h.Anacarditessp (MPM PB 3142) i."Schinopsis" sp. (MPM PB 2972), detail of the leaf venation, j."Schinopsis" sp.(MPM PB 2972) k."Allophylus" graciliformis (Berry) Berry (MPM PB 3080) l."Allophylus" graciliformis (Berry) Berry (MPM PB3086a m.Cupanites sp. 1 (MPM PB 2965)Scale bar e–f, h–i= 5 mm; a–d, g, j–m= 10 mm.

Order **MAGNOLIALES** Juss. ex Berchtold and Presl (1820)
Family **MALPIGHIACEAE** Jussieu (1789)
Genus: ***Banisteriophyllum*** Ettingshausen 1886
Type species: *Banisteriophyllum australiense* Ettingshausen 1886

Banisteriophyllum sp.
Figure 4(c)

Material
MPM PB 2937

Location–bearing samples
Lm4

Description
Blade attachment marginal, laminar size microphyll, L:W ratio 2:1, laminar shape elliptic to obovate, with medial and basal symmetry symmetrical. Margin untoothed, acute base angle and rounded and lightly cordate base shape. Primary venation pinnate with one basal vein. Major secondaries festooned brochidodromous, with irregular spacing, angles more acute on one side of the primary vein and decurrent

attachment to midvein. Marginal secondary vein present. Intercostal tertiary veins percurrent, almost parallel to primary. Exterior tertiaries looped. Quaternary vein reticulate.

Comparisons

This specimen is characterized by a venation pattern and lamina shape that resembles some of the fossil Malpighiaceae described for Patagonia. In particular the specimens assigned to *Banisteria patagonica* Berry (1938; p. 84, Pl. 24, figs.1–2) are quite similar to the fossil here described. Both are represented by elliptic, untoothed leaves, with major secondary veins festooned brochidodromous, sweepingly curved and irregularly spaced, and percurrent tertiary veins arranged in obtuse angle to the midvein. The leaf base in *Banisteria patagonica* is described as rounded instead cordate but nowadays there are few species of Malpighiaceae with cordate base shape.

Botanical affinity

The combination of a broadly rounded cordate base, pinnate venation and entire margin is unusual (Wolfe 1977). However, there are some Malpighiaceae that can be compared to our morphospecies. For example some species of *Aspicarpa* Rich. (eg. *A. hirtella* Rich. and *A. pulchella* (Griseb.) O'Donell & Lourteig.), have rounded leaves with a cordate base. Some species of *Banisteriopsis* C.B.Rob., like *B. adenopoda* (A.Juss.) B.Gates, have a leaf shape and a venation pattern quite alike *Banisteriophyllum* sp. Also it is possible to found similarities in leaf shapes and venation pattern between the fossil studied and other Malpighiaceae belonging to *Tetrapterys* A.Juss. and *Ryssopterys* Blume ex A.Juss., among others.

Order **VITALES** Juss. ex Berchtold and Presl (1820)
Family **VITACEAE** Jussieu (1789)
Genus ***Cissites*** Debey (Capellini and Heer 1866)Type species: *Cissites aceroides* Debey (Capellini and Heer 1866)

Cissites sp. 1
Figure 4(d–e)

Material

MPM PB 2960

Location–bearing samples

Lm4

Description

Leaf partially preserved. Blade attachment marginal, laminar size microphyll, laminar shape triangular. Margin untoothed proximally incomplete, with obtuse base angle and rounded base shape. Primary venation actinodromous with five basal veins. Major secondaries semicraspedodromous, with regular spacing, uniform angles and decurrent attachment to midvein. Minor secondaries brochidodromous. Intercostal tertiary veins alternate percurrent. Exterior tertiaries looped.

Comparisons

The studied specimen resembles *Cissus australe* Hünicken (1967; p. 204, Pl., X, figs 3–5; Pl. XIV, fig. 3). This species is characterized, like the fossils described, by trilobate leaves with a rounded base one central, prominent lobe and two smaller laterals with a pointed–tip. Also between the two the central and the laterals lobes Hünicken mentioned the presence of 3–4 slightly prominent teeth. The poor preservation in the studied material does not allow the observation of this character. Another comparable species is *Cissus rioturbioensis* Hünicken (Hünicken 1967, p. 201, Pl. VII, fig. 8) also represented by trilobate leaves and slightly toothed margin between the lobes but mainly differ in the central lobe shape, being narrower, which gives to the lamina of *Cissites* sp. 1 a more slender shape and a cuneate base instead of rounded. *Bignonia gigantifolia* Engelhardt (1891; p. 660, Pl. X, fig. 6) also has a similar venation pattern and leaf shape, but is much larger than the specimen studied.

Botanical affinity

Several species of *Cissus* L. inhabit today in Argentina. Between these, there exists great variability in leaf shape ranging from rhomboidal–like shape (eg. *Cissus verticillata* (L.) Nicolson & C. E. Jarvis) to lanceolates ones (eg. *Cissus striata* Ruiz & Pavon). The studied specimen shows similarities with *Cissus verticillata* (L.) Nicolson & C.E. Jarvis and also with *Cissus subrhomboidea* (Baker) Planch., from Paraguay.

Cissites sp. 2
Figure 4(f–g)

Material

MPM PB 2950–2959

Location–bearing samples

Lm4, LmC, Lm19, Lm22, UmT7, Um9a, Um8

Description

Blade attachment marginal, laminar size microphyll to notophyll, with medial and basal symmetry. Margin incomplete, with obtuse base angle and cuneate base shape. Primary venation actinodromous, with one basal vein and simple paired agrophic veins. Major secondaries simple semicraspedodromous, with regular spacing, uniform angles and decurrent attachment to midvein. Fimbrial vein present. Intercostal tertiary veins alternate percurrent. Quaternary and quinternary vein fabric reticulate.

Comparisons

Despite any of the specimens were complete, some fragments can be interpreted as trilobate. Both, the lamina and base shape along with the venation pattern, allow comparisons with several Cenozoic leaf records from southern South America as *Cissus rioturbioensis* Hünicken (1967; p. 201, Pl. VIII, figs 1–5, Pl. IX, figs 1–6, Pl. X, figs 1–2 and Pl. XI, figs 3–4), *Mallotus (?) platanoides* Engelhardt (1891; p. 673, Pl. XII, fig. 2), *Cissites patagonica* Berry (1937b; p. 44, Pl. VII, figs 1–3), *Phyllites* sp. 1 Troncoso (1992, p. 168, Pl. 5, fig. 41; Pl. 6, fig. 42) and *Cissus guidoensis* Hünicken (1995; p. 206, Pl. B, figs 9–12, 15–19; Pl. D, figs 5, 11–12; Pl. E, figs 10–11). Although the studied specimens share similarities with all the above mentioned species, *Cissites* sp. 2 is compared to *Cissus rioturbioensis* by the strong resemblance observed in the lamina size, base shape and the venation pattern. This species is characterized by trilobate leaves and differs from *Cissus australe* Hünicken (Hünicken 1967; p. 204, Pl. X, figs. 3–5; Pl. XIV, fig. 3) in the central leaf shape, being trilobate and not romboidal like in *C. australe* and in the course of the basal pair of secondary veins being more eucamptodromous in *C. australe* and more widely divergent in *C. rioturbioensis*.

Botanical affinity

There are several families like Euphorbiaceae Juss., Bignoniaceae Juss., Malvaceae Juss. and Vitaceae Juss. that have similar leaves and can be related mainly by the venation pattern to our morphospecies. The bases of the extant leaves in these families are cordate, instead the largely cuneate base observed in the fossil species. However, great variation in leaf shape even between the leaves of the same plant was observed, finding leaves with cordate base and others with cuneate ones. *Cissites* sp. 2 is very similar to current species of genus *Cissus* L. (Vitaceae) as the Southamerican *Cissus rhombifolia* Vahl.

Order **SAPINDALES** Juss. ex Berchtold and Presl (1820)
Family **ANACARDIACEAE** R. Brown (1818)
Genus ***Anacardites*** Saporta 1861
Type species: *Anacardites spectabilis* Saporta 1861

Anacardites sp.
Figure 4(h)

Material

MPM PB 3142

Location–bearing samples

Lm4

Description

Blade attachment marginal, laminar size nanophyll to microphyll, L:W ratio up to 3:1, laminar shape elliptic with medial symmetry asymmetrical. Margin serrate. Primary venation pinnate. Major secondaries craspedodromous with regular spacing, uniform angles and excurrent attachment to midvein. Marginal secondary vein present. Intercostal tertiary veins percurrent. Tooth spacing irregular, at least 5 to 6 teeth per cm, with a single order of teeth. Sinuses shape angular. Tooth shape concave/retroflexed to straight/retroflexed. Principal vein present, terminating at the tooth apex.

Comparisons

This specimen shares the lamina shape, the irregularly serrated margin and the venation pattern with *Anacardites* sp. Hünicken (1967, p. 188, Pl. IV, figs. 8–9), being especially comparable to the specimen 3104B illustrated in Fig. 9. According to Hünicken this specimen is smaller and quite different in the margin and venation to the others includes in this species. *Anacardites pichileufensis* a leaflet described by Berry (1938: 88, pl. 25, figs 5–7) is also comparable, especially by the fact that our specimen seems to be asymmetrical, feature that commonly occurs in leaflets of a compound leaf.

Botanical affinity

Toothed microphyll leaves with an asymmetrical and cuneate base, craspedodromous secondaries and teeth separated by angular sinuses fed by a main secondary, are characters that can be found in extant Anacardiaceae. Some examples are the genera *Amphipterygium* Schiede ex Standl., *Loxopterygium* Hook. and *Mauria* Kunth. The last two are common in the northwest region of Argentina.

Genus ***Schinopsis*** Engler 1876
Type species: *Schinopsis brasiliensis* Engler 1876
'*Schinopsis*' sp.
Figure 4(i–j)

Material

MPM PB 2972

Location–bearing samples

Lm4

Description

Blade attachment marginal, laminar size microphyll, L:W ratio nearly to 4:1, laminar shape elliptic with medial symmetry symmetrical. Margin untoothed. Primary venation pinnate with no naked basal veins, one basal vein and no agrophic veins. Major secondaries brochidodromous with regular spacing, uniform angles and excurrent to the midvein. Intercostal tertiary veins reticulate, exterior tertiaries looped.

Comparisons

The specimens studied match the description of *Schinopsis* sp. 1 Hünicken (1967; p. 189, Pl., X, fig. 6). It also shares with *Schinopsis patagonica* Berry (1925; p. 206, Pl. 1, fig. 2) the lamina shape, a strong midvein and the divergence angle of the secondary veins. Both, *Schinopsis* sp. 1 and *S. patagonica* have an asymmetrical base and although this feature was not preserved in the studied specimen, it can be inferred by the midvein curvature. Recently, Vento and Prámparo (2018) in their revision of some of the material described by Hünicken for the RTF, suggest that *Schinopsis* sp. 1 and *S. patagonica* maybe correspond to the same species.

Botanical affinity

There are few extant species of *Schinopsis* Engel. that can be found in Argentina. Among these, *Schinopsis lorentzii* (Griseb.) Engl. seems alike to the ones described, having similarities in leaf shape and venation pattern. The other two species present in Argentina, *S. marginata* Engel. and *S. balansae* Engel., have broader leaves.

Family **SAPINDACEAE** Jussieu (1789)
Genus ***Allophylus*** L. (1753)
Type species: *Allophylus zeylanicus* Linnaeus, 1753a

'Allophylus' graciliformis (Berry) Berry
Figure 4(k–l)

Material
MPM PB 3079–3088

Location–bearing samples
Lm4, Um9, Um9a, Um10

Description
Blade attachment marginal, laminar size microphyll, L:W ratio 3:1, laminar shape elliptic with medial symmetry symmetrical and basal width asymmetrical. Margin serrate with acute apex angle, straight apex, acute base angle, and cuneate to convex base shape. Primary venation pinnate with no naked basal veins, one basal vein and no agrophic veins. Major secondaries craspedodromous with regular spacing, uniform angles, decurrent attachment to midvein. Fimbrial vein present. Intercostal tertiary veins percurrent. Cunonioid tooth type. Tooth spacing regular, five to six teeth per cm, with a single order of teeth. Sinus shape angular. Tooth shape concave/convex to concave/straight. Principal vein terminate at the apex tooth. Accessory veins looped. Tooth apex spherulate.

Comparisons
These specimens match with those defined as *Allophylus graciliformis* (Berry) Berry (1938; p.97, Pl. 30, figs. 6–9). Particularly with the fossils described by Hünicken (1967: 192, pl. V, figs 1–6), it is possible to observe a similar base shape between the specimen CPB3149 (Hünicken 1967; Vento and Prámparo 2018) and MPM PB 3080 and an apex shape between the Pl. V, fig. 5 and MPM PB 3086.

Botanical affinity
The fossil species *Allophylus graciliformis* (Berry) Berry is related by the author to the extant *Allophylus edulis* (A. St.–Hil., A. Juss. & Cambess.) Hieron. ex Niederl. present in the north of Argentina. There are three species of *Allophylus* L.

that inhabit today in Argentina. Among these *Allophylus edulis* seems to be alike the specimens described, sharing with them the overall leaf traits and venation pattern.

Genus ***Cupanites*** Schimper, 1874
Type species: *Cupanites miocenicus* (Ettingshausen) Schimper, 1874

Cupanites sp. 1
Figure 4(m); Figure 5(a)

Material
MPM PB 2962–2966

Location–bearing samples
Lm4, Lm24

Description
Blade attachment marginal, laminar size microphyll, L:W ratio 3:1, laminar shape elliptic to oblong with medial symmetry and basal symmetry asymmetrical Margin serrate with acute apex angle, straight apex, acute base angle, and cuneate to convex base shape. Primary venation pinnate with no naked basal veins, one basal vein and no agrophic veins. Major secondaries craspedodromous with regular spacing, uniform angles and decurrent attachment to midvein. Fimbrial vein present. Intercostal tertiary veins percurrent. Quaternary vein fabric reticular, quinternary vein fabric dichotomizing. Cunonioid tooth type, with the principal vein branching at the sinus, the lower branch ends at the apex tooth. Tooth spacing regular, four to five teeth per cm, with a single order of teeth. Sinuses shape angular. Tooth shape straight/convex. Accessory veins looped. Tooth apex spherulate.

Comparisons
Among the fossil species the material matches the description of *Cupania? santacrucencis* Hünicken (1967: 196, pl., VI, figs 5–6). Additionally Hünicken described for the RTF specimens referred to cf. *Cupania patagonica* Berry (1967: 195, pl. VI, fig. 7). Both species only differ in the leaf shape and in the number of secondary veins, being lesser in cf. *C. patagonica. Cupania romeroi* Troncoso (1992: 164, pl. 5, figs 35–40) defined for the Lower Eocene of Chile is comparable to *C.? santacrucensis.* According to Troncoso both represent the same biological species.

Botanical affinity
The cunonioid tooth type may occur in Sapindaceae (among others) and is characterized by a small glandular apex with a principal vein branching below, in or near the sinus tooth (Hickey and Wolfe 1975). The pronounced toothed margin and the overall leaf traits resemble *Athyana weinmannifolia* (Griseb.) Radlk., present nowadays in the Salta and Jujuy provinces of Argentina. *Diatenopterix sorbifolia* Radlk., another species present in Argentina, also has a pronounced toothed margin and comparable leaves, if variable..

Cupanites sp. 2
Figure 5(b–c)

Material
MPM PB 3143–3145B

Location–bearing samples
Lm4, Um7

Description
Blade attachment marginal, laminar size microphyll, L:W ratio 3:1, laminar shape elliptic to oblong with medial and basal symmetry symmetrical. Margin serrate with acute apex

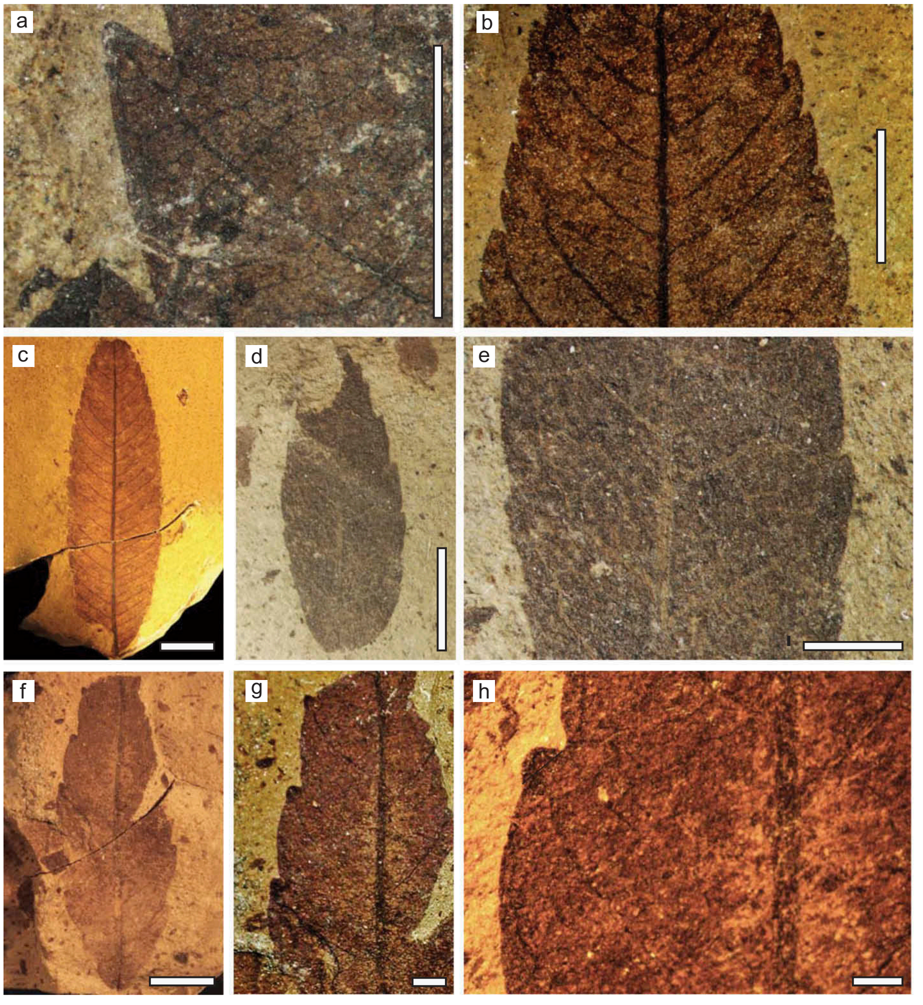

Figure 5. a.Cupanites sp. 1 (MPM PB 2965), detail of the tooth and the leaf venation b.Cupanites sp. 2 (MPM PB 3143), detail of the tooth and the leaf venation c. Cupanites sp. 2 (MPM PB 3143) d.Cupanites sp. 3 (MPM PB 2970) e.Cupanites sp. 3 (MPM PB 2970), detail of the leaf venation f."Paullinia" sp. (MPM PB 3140) g."Paullinia" sp. (MPM PB 3140), detail of the leaf venation h."Paullinia" sp. (MPM PB 3140), detail of the toothScale bar h= 1 mm; d, g= 2.5 mm; a, b, e, f= 5 mm; c= 10 mm

angle, straight apex, acute base angle and cuneate to convex base shape. Primary venation pinnate with no naked basal veins, one basal vein and no agrophic veins. Major secondaries craspedodromous slightly curved with regular spacing, uniform angles, excurrent attachment to midvein. Intercostal tertiary veins percurrent. Cunonioid tooth type. Tooth spacing regular, four teeth per cm, with a single order of teeth. Sinus shape angular. Tooth shape straight/convex or convex/convex. Principal vein terminates on the distal flank. Accessory veins looped. Tooth apex spherulate.

Comparisons

The studied specimens matches the description of *Cupania grosse–serrata* (Engelhardt) Berry (1925: 214, pl. 6, fig. 5), differing only in the more acute divergence angle of the secondary veins. A similar secondary angle to primary vein is observed in the specimens described by Hünicken (1967: 193, pl. VI, figs 8–9), but the midvein seems to be more curved.

Botanical affinity

Cupania grosse–serrata (Engelhardt) Berry is described as 'almost identical' to the extant *Cupania vernalis* Cambess. by Berry (1938), but the teeth in both species seem to be different, being smaller and more acute in the extant species. The specimens studied show similarities in margin and venation pattern with the neotropical species *Cupania latifolia* Kunth despite the leaves being more obovate in the living species.

Cupanites sp. 3
Figure 5(d–e)

Material

MPM PB 2970–2971A

Location–bearing samples

Lm4

Description

Blade attachment marginal, laminar size microphyll, L:W ratio 2.5:1, laminar shape elliptic to oblong with medial symmetry symmetrical and basal symmetry asymmetrical Margin serrate with acute apex angle, straight apex, acute base angle, and cordate base shape. Primary venation pinnate with no naked basal veins, one basal vein and no agrophic veins. Major secondaries simple semicraspedodromous with regular spacing, angle smoothly increasing proximally and decurrent attachment to midvein. Fimbrial vein present. Tooth spacing regular, with a single order of teeth, four to five teeth per cm. Sinus shape angular. Tooth shape straight/flexuous or straight/convex. Principal vein present, terminating at tooth apex. Tooth apex simple.

Comparisons

These specimens show similarities with *Cupania patagonica* Berry (1938: 97 pl. 32, figs 6–7; Hünicken, 1967: 195, pl. VI, fig. 7 as cf. *C. patagonica*). Both are characterized by leaves with basal asymmetry and oblong to elliptic shape, similar teeth and the overall venation pattern. The material here analyzed is smaller than the specimens studied by Berry being more similar in size to the ones described by Hünicken.

Botanical affinity

Nowadays *Cupania* L. is represented in Argentina by a single species: *Cupania vernalis* Cambess. There are similarities between our specimens and the extant species mainly in the toothed margin and leaf shape, despite the differences observed in the size of the lamina.

Genus ***Paullinia*** L. (1753)
Type species: *Paullinia pinnata* L. (1753b)

'*Paullinia*' sp.
Figure 5(f–h)

Material

MPM PB 3139–3140

Location–bearing samples

Lm4

Description

Leaf attachment petiolate. Blade attachment marginal. Laminar size microphyll with L:W ratio of 3.7:1. Laminar shape elliptic to oblong, with medial and basal symmetry symmetrical. Margin serrated. Base angle acute and convex to cuneate base shape. Primary venation pinnate with no naked basal veins, one basal vein and no agrophic veins. Major secondaries craspedodromous with regular spacing, uniform angles and decurrent attachment to midvein. Fimbrial vein present. Intercostal and exterior tertiary veins not clearly observed. Tooth spacing regular, tree teeth per cm, with a single order of teeth. Sinus shape rounded and tooth apex spherulate. Tooth shape concave/retroflexed. Principal vein terminates at the tooth apex.

Comparisons

The specimens were compared to *Cupania patagonica* Berry (1938), but clear differences in teeth arrangement were observed leading its comparison with other Sapindaceae leaves. Among these it was possible to observe similar leaf shape and tooth types with some species of the extant genus *Paullinia* L. There are some fossil species assigned to *Paullinia* (Berry 1938; Hünicken 1967) although, are all represented by bigger specimens. *Paullinia rubiginosifolia* Berry (1938: 92, pl. 28, fig. 1) have a bigger lamina. *Paullinia prerufescens* Berry (1938: 91, pl. 25, figs 10–11) is quite similar to *P. patagonica* Hünicken (1967: 190, pl. XII, fig. 9) and, despite the differences in the lamina size and the teeth shape, some characters are comparable to the studied specimens (e.g. the overall lamina shape, number of secondary veins and the angle of divergence and teeth spacing decreasing to the leaf apex).

Botanical affinity

In his description, Hünicken (1967) mentioned that he refers his specimens to *Paullinia* L. due to the resemblance with the extant *Paullinia elegans* Cambess. despite the differences that he observed in size, venation and teeth. Conversely, the laminar shape, the venation pattern and the leaf margin observed in *Paullinia elegans* are quite similar to the ones observed in the specimens here studied. According to Berry the fossils described by him as *Paullinia prerufescens* show features that would permit their reference equally to either *Serjania* Vell. or *Paullinia* L. The fossils MPM PB 3139 and MPM PB 3140also show characters that can be referred to any of those two genera and both are present today in Argentina, *Paullinia* with three species and *Serjania* with seventeen. Accordingly it is possible to found similarities in the lamina shape, size, venation pattern and teeth with *Paullinia elegans* Cambess., *Paullinia pinnata* L. and *Serjania meridionalis* Cambess., among others.

Previously reported megathermal species

Several species recovered from the Río Turbio Formation were assigned to megathermal families. The first reports came from Berry (1937a), but he mostly describes microthermal elements (except Anacardiaceae) from the upper member. Then, Frenguelli (1941) describes both, megathermal (Lauraceae, Dilleniaceae and Sapindaceae) and other families related to microthermal taxa. Hünicken (1955) mentioned several species, but only few specimens were described and illustrated by the same author in 1967. Among these, he mentioned the presence of Urticaceae, Piperaceae, Dilleniaceae, Malvaceae, Salicaceae, Cucurbitaceae, Sapotaceae and Bignoniaceae in the paleoflora of the Río Turbio Formation, besides the families also mentioned in this study. Some of the species described by Hünicken (1967) are assigned with doubt due to fragmentary fossil material to Moraceae (*Coussapoa*? sp.) Tiliaceae (cf. *Triumfetta irregulariter–serrata* Engelhardt), Cucurbitaceae (*Siolmatra*? *patagonica* Hünicken) and Bignoniaceae (cf. *Bignonia pichileufuana* Berry). Finally, a Malpighiaceae species and 12 species of Myrtaceae have been described by Fernández et al. (2012) and Panti (2014a) respectively.).

Discussion

A total of nineteen leaf taxa were described for the RTF from 71 specimens collected at new sites throughout the unit. These morphospecies were referred to the extant tropical and subtropical families Lauraceae (9 morphospecies), Malpighiaceae (1 morphospecies), Vitaceae (2

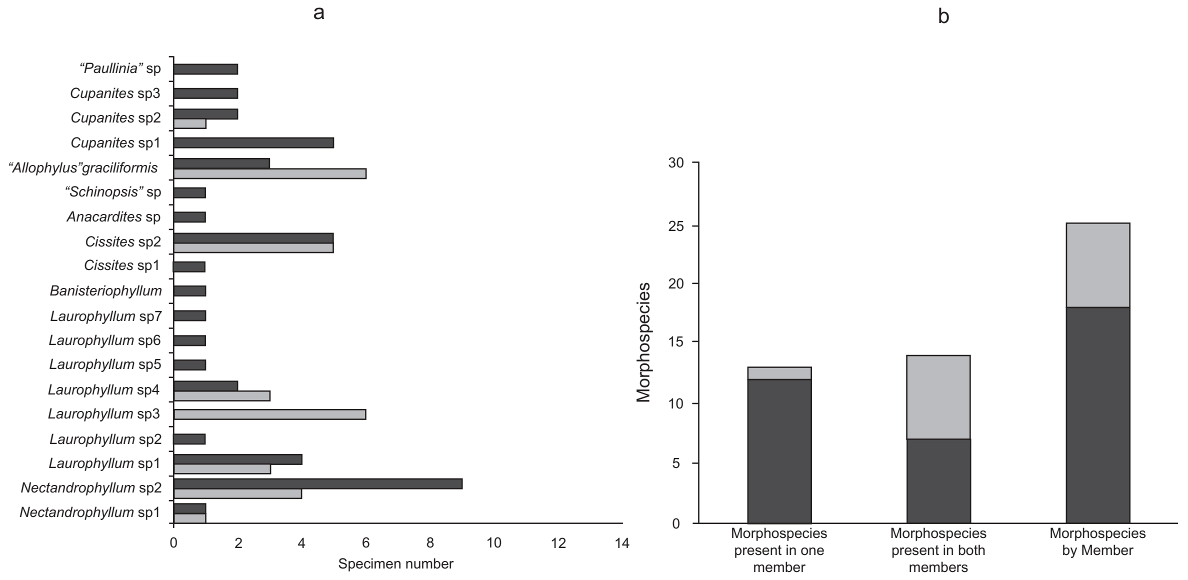

Figure 6. Specimens (a) and morphospecies (b) number discriminate by member. Lower member; Upper member

morphospecies), Anacardiaceae (2 morphospecies) and Sapindaceae (5 morphospecies). Today Lauraceae inhabit warm temperate and tropical regions centered in Southeast Asia and South America. Malpighiaceae are a family of trees shrubs and vines are predominantly distributed in tropical South America, North America, Africa and Southeast Asia. Vitaceae, Sapindaceae and Anacardiaceae, are common in tropical and subtropical regions of the world with few temperate representatives in the case of Anacardiaceae (Heywood 1993). The presence of megathermal taxa in the RTF indicates the existence of warm temperate and humid climates. Nowadays this region can be considered as an ecotone between the steppe dominated by shrubs and herbs and the Patagonian cool temperate rainforest dominated by *Nothofagus pumilio* (Poepp. & Endl.) Krasser (Lenga) followed by *Nothofagus antarctica* (G.Forst.) Oerst. (Ñire) (León et al. 1998; Cavallaro 2006). In both, microthermal taxa dominate the extant vegetation. According to Hünicken (1967) the presence of megathermal elements along the RTF turns scarce towards the upper levels to eventually disappear. Megathermal taxa here reported were recorded throughout the unit however, they are concentrated in the lower member of the Río Turbio Formation. In coincidences with the previously observed by Hünicken we observed a marked decrease in both megathermal species abundance and richness from the lower to the upper member (Figure 6). Among the 19 morphospecies recognized only eight were recorded at the upper member (Table 1; Figure 6(a)). Moreover, there was an almost three–fold decrease in abundance of megathermal taxa towards the upper member (Figure 6(b)). The observed trend indicates the beginning of the floristic turnover that characterized Patagonian ecosystems from the Late Eocene onwards, with megathermal communities being replaced by meso – and microthermal ones; it is also in agreement with the global cooling trend of the terminal Paleogene.

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Disclosure statement

No potential conflict of interest was reported by the author.

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