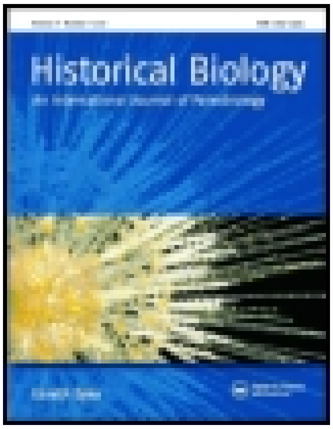

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Myrtaceae fossil leaves from the Río Turbio Formation (Middle Eocene), Santa Cruz Province, Argentina

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Myrtaceae, the gum tree family, is a large angiosperm clade of 5671 species mostly distributed in tropical and subtropical regions of the world. In the southernmost tip of South America (Santa Cruz province) where the fossils analysed in this study come from (Río Turbio Formation), this family is virtually absent and the extant vegetation is largely dominated by deciduous *Nothofagus pumilio* and *Nothofagus antarctica*. During the early Paleogene, however, the Myrtaceae were an important element in southern Patagonian floras. Here, we report and describe ten taxa related to the extant genera *Eugenia*, *Myrcia*, *Psidium*, *Myrcianthes* and possible *Eucalyptus* and *Campomanesia*. The presence of a high diversity of Myrtaceae during the Eocene in one of the southernmost regions of the world could be thought as unusual. However, during this period of time (45 Ma), a number of other tropical lineages also reached these high latitudes probably as a consequence a warming climatic trend. In fact, through the Paleocene–Early Eocene interval, climatic conditions were the warmest of the Cenozoic. After this period of time, a progressive decline in temperature forced the migration of megathermal elements towards lower latitudes and, at the same time, led to the expansion of forest dominated by *Nothofagus* which predominate the region today.

Keywords: Myrtaceae; fossil; Río Turbio; Argentina

1. Introduction

Myrtaceae comprises 5671 species and 132 genera (Govaerts et al. 2008) of small shrubs and trees (Heywood 1993; Simpson 2006) distributed in tropical and subtropical regions of the world, particularly in America and eastern and south-western Australia (Heywood 1993), being more diverse at the southern hemisphere (Heywood et al. 2007). In Argentina, there are 62 species belonging to the tribe Metrosidereae (Benth.) Wilson and Myrteae DC. Most of them are found in subtropical regions but seven species are restricted to cold temperate areas in Patagonia (Rotman 2000). Leaf morphologies that allow to differentiate the Myrtaceae from other families are based on the presence of a prominent paramarginal and one or two intramarginal veins, secondary veins parallel among each other and tertiary veins almost parallel to the midvein. All of these characters are considered synapomorphies for the group (Pole 1993; Soares-Silva 2000).

The Myrtaceae has a rich megafossil record in the Cenozoic of Patagonia that includes woods, leaves, fruits and seeds (Engelhardt 1891; Dusén 1908; Berry 1922, 1925, 1928, 1937a, 1938; Fiori 1938, 1939–1940; Traverso 1951; Frenguelli 1953; Hünicken 1955, 1967, 1995; Ragonese 1980; Romero and Arguijo 1981; Nishida 1984; Nishida et al. 1988; Troncoso et al. 1992; Poole et al. 2001; Troncoso 2002; Panti et al. 2008; González 2009; Pujana 2009; Gandolfo et al. 2011; Panti 2011; Hermsen et al. 2012). The oldest known record belongs to *Myrtoidea patagonica* (Passalía et al. 2001), an imprint of leaf recovered from the Aptian of the Santa Cruz province, Argentina. In particular, for the Río Turbio Formation fossil Myrtaceae are represented by pollen (Romero and Zamaloa 1985), leaf imprints (Hünicken 1967) and wood (Pujana 2008) (Table 1).

The main aim of this article is to perform a complete analysis of the fossil leaf impressions of the family Myrtaceae recovered from the Río Turbio Formation. We describe the new fossil taxa and re-evaluate those previously reported for this unit. Finally, a dichotomous key based on foliar characters (Table 2) was performed to identify the Myrtaceae species described for the Río Turbio Formation.

2. Geological setting

The Río Turbio Formation crops out in the south-western tip of Santa Cruz province (Figure 1) and is well known in the literature for its rich fossil content (Berry 1937b; Frenguelli 1941; Hünicken 1955, 1967, 1995; Archangelsky 1968, 1969, 1972; Archangelsky and Fasola 1971; Romero 1977; Romero and Zamaloa 1985; Romero and Castro 1986; Ancíbor 1990; Brea 1993; Pujana 2008). It is represented by thick sedimentary sequences deposited in shallow marine and estuarine environments. It overlies the lower Paleocene deposits of the Cerro Dorotea Formation and is separated by an erosional contact from the overlying

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Table 1. Fossil Myrtaceae described for the Río Turbio Formation.

Eugenia rioturbioensis Hünicken	Leaf	Hünicken (1967)
Psidium licciardoi Hünicken	Leaf	Hünicken (1967)
Myrcia chubutensis Berry	Leaf	Hünicken (1967)
Myrcia reticulato-venosa Engelhardt	Leaf	Hünicken (1967)
Myrcia sp. Hünicken	Leaf	Hünicken (1967)
Myrtaceidites verrucosus	Pollen	Romero and Zamaloa (1985)
Xylotipo 2	Wood	Pujana (2008)

Río Guillermo Formation (Guerstein et al. 2014). Malumián and Caramés (1997) divided it into two members due to the presence of highly glauconitic horizon which coincides with a major micro- and macrofaunistic change, and is interpreted as the base of a conspicuous transgressive episode (Figure 2). The Lower Member is considered to be late Early to early Middle Eocene in age based on dinoflagellate data (Guerstein et al. 2010) and the Upper Member, according to paleontological record, was deposited during the late Middle Eocene (Guerstein et al. 2014).

3. Materials and methods

Fossil leaf imprints from the Río Turbio Formation were collected by the author from different localities within both Lower and Upper Members (Figure 2). Using morphological affinities, the material was initially sorted into morphotypes. For naming the samples, the criteria of Peppe et al. (2008) were followed. The terminology and systematic descriptions follow the formats of Hickey (1973), Carr et al. (1986) and Ellis et al. (2009). The work of González (2011a, 2011b, 2011c) which has clarified the foliar architecture of the extant Myrtaceae genera of Argentina, and how their leaves can be distinguished was critical for this study. To assign a morphotype to a particular taxon, fossil specimens were compared with others previously reported from southern South America and, in some cases; the imprints were also compared with extant representatives. Finally a dichotomous key was conducted to clarify how all the Myrtaceae of the Río Turbio Formation are distinguished. 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.

Table 2. Dichotomous key for the Myrtaceae described for the Río Turbio Formation.

1.1 Elliptic leaf shape	2
1.2 Elliptic to ovate leaf shape	4
2.1 Leaf falcate	*Eucalyptus* sp.
2.2 Leaf no falcate	3
3.1 Base convex	*Myrcia bagualensis*
3.2 Base decurrent	*Myrcia deltoidea*
4.1 Secondary veins joint forming a V towards the leaf margin	5
4.2 Other secondary vein joint	7
5.1 Leaf surface with undulations	*Eugenia rioturbioensis*
5.2 Leaf surface smooth	6
6.1 Third venation order random reticulate	*Eugenia* sp. 1
6.2 Third venation order admedially ramified	*Eugenia* sp. 2
7.1 Base convex to subrounded	8
7.2 Base rounded	*Myrcianthes* sp.
8.1 Secondary veins bifurcate towards the margin	*Psidium* sp.
8.2 Secondary veins brochidodromous	*Psidium licciardoi*

4. Paleobotanical content

Order **MYRTALES** Juss. exBercht. & J. Presl (1820)

Family **MYRTACEAE** Juss. (1789)

Genus ***Eucalyptus*** L'Héritier, 1788

'Eucalyptus' sp

Figure 3(a–c)

Material studied: MPMPB 2905; 2907–2909

Description. Blade attachment marginal, laminar size microphyll to notophyll, L:W ratio 3:1, laminar shape elliptic and falcate, with medial symmetry and basal asymmetry. Margin entire with acute apex angle, straight apex shape, acute base angle and cuneate base shape. Primary venation pinnate, with no naked basal veins, one basal vein and no agrophic veins. Major secondaries simple camptodromous, with regular spacing, angles that smoothly increase proximally and decurrent attachment to midvein. Interior secondaries absent, minor secondaries absent, intersecondaries sometimes present and paramarginal and intramarginal vein present. Intercostal tertiary veins admedially ramified. Areoles moderately developed, 4–5 sided shows little dots barely preserved within that are interpreted as leaf glands.

Comparisons. The specimens described can be compared with the fossil species *Myrcia chubutensis* described by Berry (1925, p. 223, pl. 2, fig. 6; 1935, p. 119, pl. 44, figs. 5–6) and Hünicken (1967, p. 214, pl. XII, figs. 1–3). Both are characterised by an elliptic to somewhat falcate lamina shape, acute apex and cuneate base shape and similar venation pattern characterised by numerous camptodromous broquidodromous secondary veins that run parallel among each other and a paramarginal vein formed by the joint of the secondaries and an intramarginal vein towards the leaf margin.

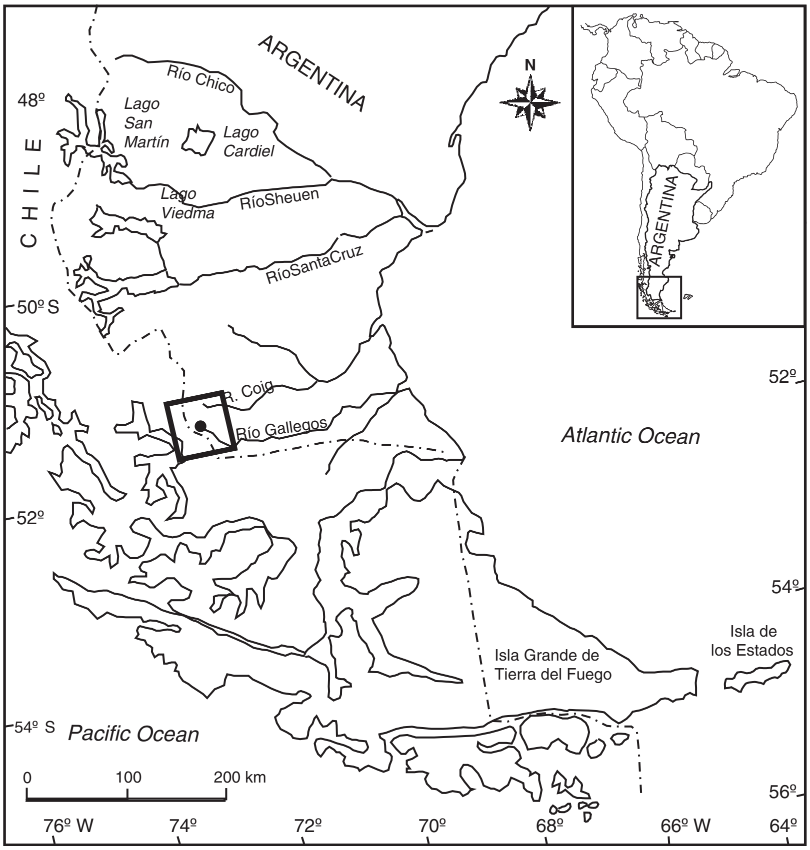

Figure 1. Location map.

In her dissertation, González (2009) mentioned that the fossils described by Berry (1925, 1938) as *Myrcia chubutensis* do not belong to *Myrcia*. According to González (2009), this genus is characterised by elliptic leaves, without laminar glands and with one paramarginal and one or two intramarginal veins. However, the fossils assigned to *Myrcia chubutensis* have elliptic to lanceolate, somewhat falcate leaves, laminar glands and one paramarginal and one intramarginal vein. In her analysis of the extant Myrtaceae of Argentina (González 2011a, 2011b, 2011c), she does not find any species with this combination of characters but noted that it is present in some extant *Eucalyptus.*

Because of this, she concluded that those specimens assigned as *Myrcia chubutensis* actually must be assigned to *Eucalyptus* L'Hér. Gandolfo et al. (2011) reject the possibility of including in *Eucalyptus* the leaves described as *Myrcia chubutensis* supporting Johnson and Briggs's (1984) argument that, according to the venation pattern observed, these specimens show affinities to subgenus *Symphyomyrtus*, although they did not detail this observation. Hermsen et al. (2012) argue that the *Myrcia chubutensis* material is represented by very poorly preserved specimens, and the original drawings by Berry (see pl. 2, fig. 6 in Berry, 1925; pl. 44, figs. 5, 6 in Berry, 1938) also suggest poor preservation of the vein architecture of these leaves and because of this they decided not to transfer the *Myrcia chubutensis* material to *Eucalyptus*.

Botanical affinity. Sensu Pole (1993) a falcate leaf shape, a paramarginal vein that runs parallel to the leaf margin, a single intramarginal vein and the presence of laminar glands is a combination that is unique to *Eucalyptus* s.l. Although the leaf glands are barely observed due to preservation, the material studied meets all the characteristics mentioned by Pole and because of this, it is considered to be closely related to *Eucalyptus*.

Genus ***Eugenia*** L. 1753

Eugenia rioturbioensis Hünicken

Figure 3(d)

Material examined: MPMPB 3173B

Diagnosis enlarged. Leaf microphyll, elliptic to ovate with medial and basal symmetry. Leaf surface with undulations. Acute base angle and cuneate to decurrent base shape. Apex unknown. Margin entire. Petiole strong and marginal, 0.5 cm long. Primary venation pinnate, midvein strong and straight. More than seven pairs of thin, alternate

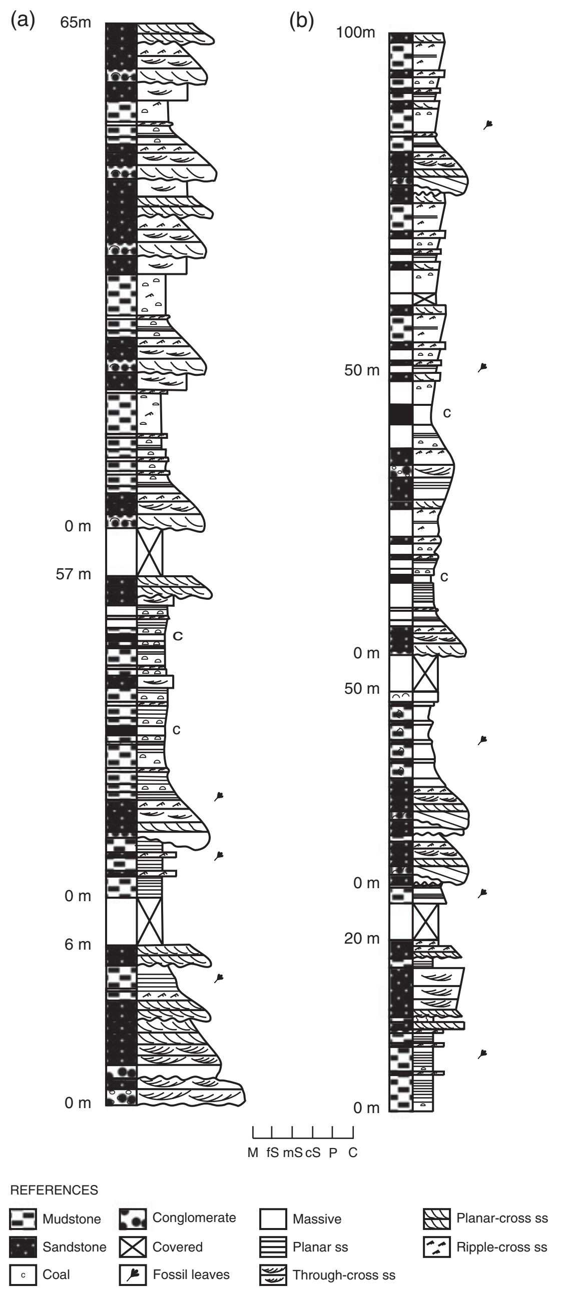

Figure 2. Stratigraphic log of the Río Turbio Formation showing location of Myrtaceae-bearing samples. (a) Lower Member and (b) Upper Member.

and straight, camptodromous broquidodromous secondary veins which diverge from the midvein at wide acute angles (70°). Basal pair emerges at acutest angle (35°–40°). One paramarginal vein formed by the secondary veins and one intramarginal vein formed by tertiary loops. Intersecondary veins present. Tertiary and fourth veins randomly reticulate.

Description. Leaf attachment petiolated, blade attachment marginal. Laminar size microphyll, laminar shape elliptic to ovate with medial and basal symmetry. Margin entire with acute base angle, and slightly decurrent base shape. Primary venation pinnate with no naked basal veins, one basal vein and no agrophic veins. Major secondaries simple camptodromous brochidodromous with irregular spacing, emerging at acute angles (basal angle more acute than the others) and excurrent attachment to midvein. Interior secondaries absent, minor secondaries absent and paramarginal and intramarginal vein present. One or two intersecondaries veins per intercostal area, span more than 50% of the length of the subjacent secondary, proximal and distal course parallel to major secondaries. Intercostal tertiary veins irregular reticulate. Fourth order venation randomly reticulate.

Remarks and comparisons. A new specimen highly similar to the type material of *Eugenia rioturbioensis* defined by Hünicken (1967) allows the enlargement of the original diagnosis. The presence of diagnostic morphological characters such as the leaf surface undulations that differentiate this species from other fossil *Eugenia* (Hünicken 1967) are clearly recognised in the studied material. González (2009) supported that *Eugenia rioturbioensis* was based on an incomplete and unique specimen and the description given by Hünicken is not enough for the placement of this taxon in *Eugenia*. Here, we added a well-preserved specimen. Although our description is based on a single exemplar, its preservation allows to observe several characters that relate it to *Eugenia* and which were absent in the diagnoses proposed by Hünicken.

Botanical affinity. Several morphological characters support the placement within *Eugenia* Mitch. ex L. The venation pattern is characterised by paramarginal vein which run from the base towards leaf apex, with secondary veins forming a 'V' or indentation that points towards the midvein (Klucking 1988) and one intramarginal vein formed by the tertiary loops. According to González (2009, 2011c), this genus is characterised by the presence of one paramarginal vein and one or two intramarginal ones. In the case of one intramarginal vein, this is formed by the loops of the tertiary veins such as in the fossil studied. Also *Eugenia*, like the material described, shares simple and symmetrical leaves, 8–17 pairs of secondary veins which emerge at acuter angles at the leaf base, one paramarginal and one intramarginal vein and tertiary and fourth order venation randomly reticulate.

Eugenia sp. 1

Figure 3(e, f)

Material examined: MPMPB 2912–2914

Description. Laminar size microphyll, laminar shape ovate to elliptic, with medial and basal symmetry. Margin entire with base acute and cuneate. Primary venation pinnate with no naked basal veins, one basal vein and no agrophic veins. Major secondaries simple camptodromous brochidodromous, emerging at acute angles (basal angle more acute than the others) and decurrent attached to midvein.

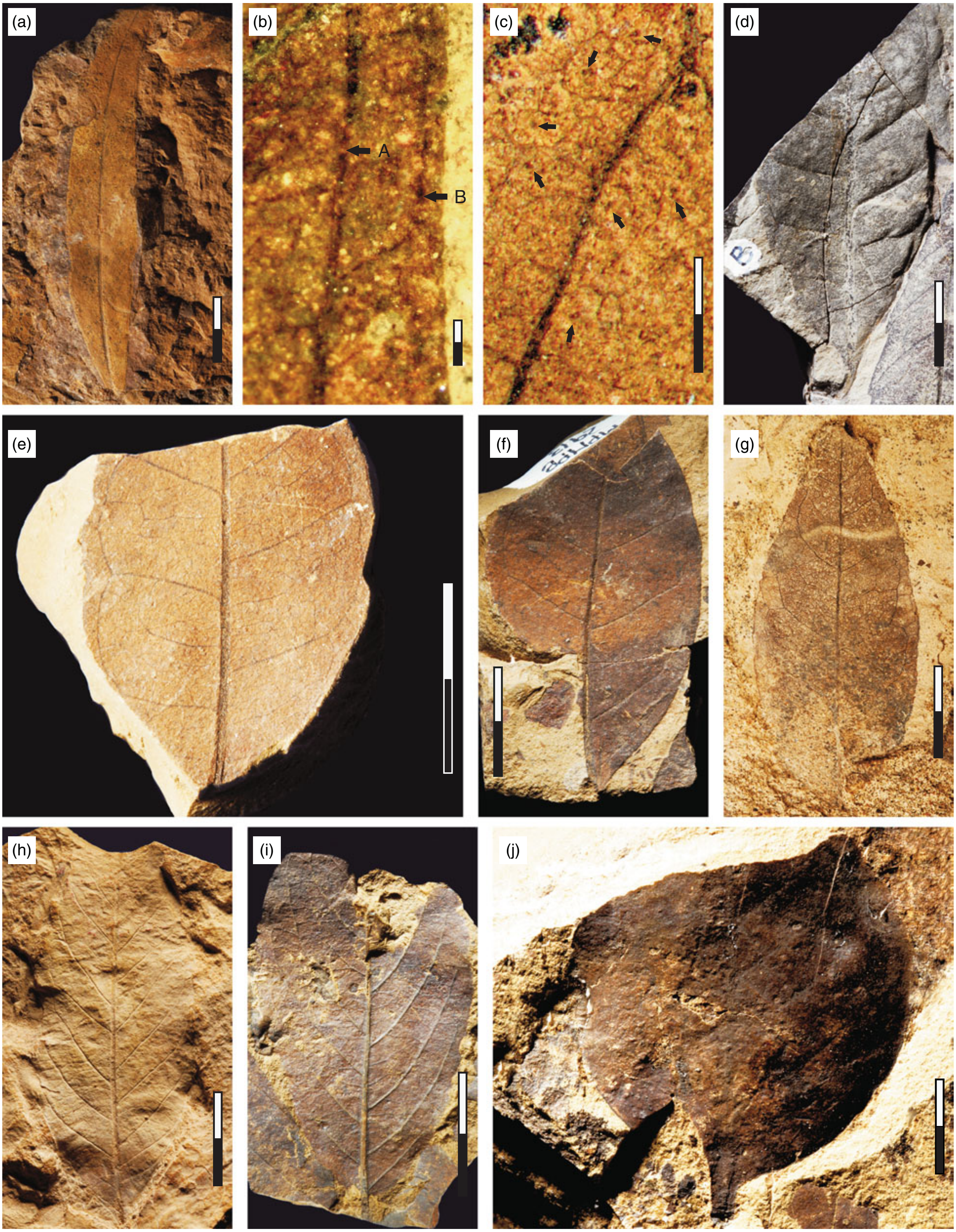

Figure 3. (Colour online) (a–c) ‘*Eucalyptus*’ sp. MPM PB 2908; (b) detail of the venation pattern: (A) paramarginal vein and (B) intramarginal vein; (c) leaf glands; (d) *Eugenia rioturbioensis* MPM PB 3173; (e and f) *Eugenia* sp. 1 MPM PB 2912 and 2913; (g) *Eugenia* sp. 2 MPM PB 3161; (h and i) *Psidium* sp. MPM PB 3147 and 3148; (j) *Myrcianthes* sp. MPM PB 2938. Bar a and d–j = 10 mm; bar b and c = 1 mm.

Interior secondaries absent, minor secondaries absent and paramarginal vein present. One intramarginal vein formed by the loops of the tertiary veins. Intersecondaries present, span more than 50% of the length of the subjacent secondary, proximal course is parallel to major secondaries and distal course ramifying or parallel to major secondary. Intercostal tertiary veins randomly reticulate, exterior tertiaries looped. Quaternary vein fabric reticulate, quinternary vein fabric dichotomous.

Comparisons. The material described differs from *Eugenia rioturbioensis* in its smaller size and in the smooth leaf surface. There are three fossil species described as *Eugenia* for Patagonia: *Eugenia comparabilis* Hollick (Berry 1939, p. 151, pl. XIX, fig. 3; Fiori 1939, p. 105, pl. V, figs. 1–3) has a greater number of secondary veins and they are more closely spaced than in the fossil studied. *Eugenia rioturbioensis* Hünicken (1967, p. 212, pl. XII, figs. 1–3) is bigger and is characterised by leaf surface undulations. Finally, *Eugenia* sp. (González 2009), unlike the specimen described, has two intramarginals veins.

Botanical affinity. According to González (2011c), *Eugenia* is characterised by simple, symmetric leaves with margin entire, pinnate primary venation without agrophic veins, one paramarginal vein and one or two intramarginal ones and camptodromous brochidodromous secondary veins irregularly disposed with angle of divergence smaller at the basal pair. All these characters are observable in the material studied and that is why is related to this genus.

Eugenia sp. 2

Figure 3(g)

Material examined. MPMPB 3161

Description. Leaf microphyll, laminar shape elliptic to ovate with medial and basal symmetry. Margin entire with acute base angle, and cuneate base shape. Primary venation pinnate with no naked basal veins, one basal vein and no agrophic veins. Major secondaries simple brochidodromous with irregular spacing, uniform angles and decurrent attachment to midvein. Interior secondaries absent, minor secondaries absent and paramarginal and intramarginal vein present. Intersecondaries present, span more than 50% of the length of the subjacent secondary, occurs at least one per intercostals area, proximal and distal course is parallel to major secondaries. Intercostal tertiary veins admedially ramified, exterior tertiaries looped. Fourth order venation reticulate.

Comparisons. It differs from *Eugenia* sp. 1 in its more pronounced, scalloped paramarginal vein as well in the divergence angle of the secondary veins, being more open in *Eugenia* sp. 1. Among the fossil species, it is more similar to *Eugenia comparabilis* although this seems to have more regularly spaced and disposed secondary veins than the fossil studied.

Botanical affinity. As was discussed earlier, the simple and symmetric leaves with entire margin, pinnate primary venation without agrophic veins, the presence of paramarginal vein and one intramarginal veins along with the camptodromous broquidodromous secondary veins irregularly disposed allow to relate this specimen to *Eugenia*. Among the extant species of *Eugenia* that inhabit Argentina, it is possible to observe great similarities with *Eugenia mansoni* O. Berg. Both are characterised by simple leaves, petiolated, nanophyll to microphyll, elliptic or obovate with acute and cuneate base and somewhat acuminate or convex apex. Margin entire, a paramarginal vein formed by the joint of the secondary veins and an intramarginal vein formed by the tertiary loops. Secondary veins irregularly spaced, intersecondary veins present and third and fourth venation order randomly reticulate.

Genus ***Psidium*** L. 1753

Psidium sp

Figure 3(h, i)

Material examined. MPMPB 3147–3148

Description. Blade attachment marginal, laminar size microphyll, laminar shape elliptic to ovate with medial and basal symmetry. Margin entire with acute base angle and convex or subrounded base shape. Primary venation pinnate with no naked basal veins, one basal vein and no agrophic veins. Major secondaries camptodromous brochidodromous distally, with regular spacing, uniform angles and excurrent attachment to midvein. Interior secondaries absent, minor secondaries absent and fimbrial vein present. One (sometimes two) intersecondaries veins originating near the superjacent secondary, proximal course perpendicular to midvein and distal course reticulating or ramifying. Intercostal tertiary veins mixed percurrent with obtuse angle to primary vein that increase admedially, to the apex is randomly reticulate. Exterior tertiaries looped. Quaternary and quinternary vein fabric reticulate.

Comparisons. There are few fossil species described from Patagonia, and assigned to *Psidium* L., *Psidium membranaceum* Engelhardt (1891, p. 678, pl. XI, fig. 1), *Psidium araciforme* Berry (1938, p. 120, pl. 44, fig. 10) and *Psidium licciardoi* Hünicken (1967, p. 213, pl. XIII, fig. 1); all described for the Paleogene of Patagonia. The three show secondary bifurcate towards the margin and percurrent tertiaries at the base but are larger than the material studied. *Psidium licciardoi* Hünicken (1967, p. 213, pl. XIII, fig. 1) described for the same Formation, shows wider angles of divergence for the secondary veins instead the studied specimens which secondary veins diverge at angles that are more comparable to the ones observed in *Psidium araciforme* and *Psidium membranaceum*.

Botanical affinity. Morphological characters, such as the elliptic to ovate lamina shape and the eucamptodro-

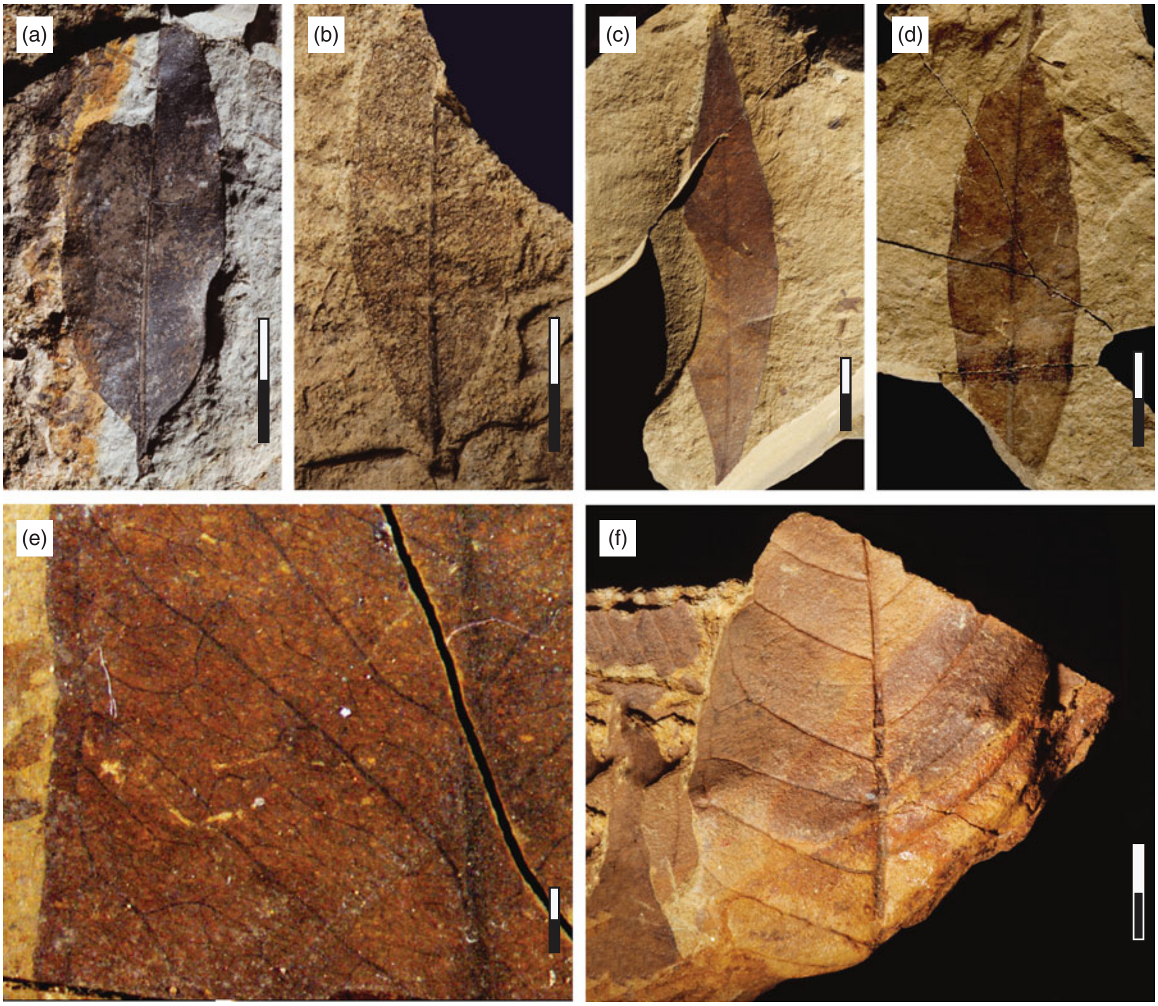

Figure 4. (Colour online) (a and b) *Myrcia bagualensis* MPM PB2947 and 2948; (c and d) *Myrcia deltoidea* MPM PB 2906, (e) detail of the venation pattern; (f) Morphotype RTF 1 MPM PB 3170. Bar a–d = 10 mm; bar e = 1 mm.

mous venation pattern, support the placement of this species within *Psidium* L. According to González (2009, 2011b), *Psidium* attributes are based on the combination of several characters such as the presence of one paramarginal vein which is sometimes observable only in the leaf apex, secondary veins that bifurcate near the leaf margin and tertiary that mix two venation patterns: one percurrent at the leaf base and one randomly reticulate towards the apex. In the studied specimens, it is possible to observe these character combinations, except the paramarginal vein due to the apex incompleteness.

Genus ***Myrcianthes*** O. Berg. 1856

Myrcianthes sp

Figure 3(j)

Material studied. MPMPB 2938

Description. Leaf microphyll to notophyll. Blade attachment marginal, petiole marginal and robust. Laminar shape probably elliptic with medial and basal symmetry. Margin entire with obtuse base angle, and rounded base shape. Primary venation pinnate with no naked basal veins, one basal vein and no agrophic veins. Major secondaries camptodromous brochidodromous with irregular spacing and decurrent attachment to midvein, paramarginal vein present, intramarginal vein barely observed and tertiary veins randomly reticulate. The leaf surface seems to be covered with several small dots.

Comparisons. Among the fossils described from Patagonia, none of these share the combination of a pronounced rounded base shape and the leaf venation observed in the fossil studied. Comparable venation pattern along with leaf glands are observed in *Myrcianthes* sp. González (2009) described from Laguna del Hunco but the leaf base in this species is acute and cuneate.

Botanical affinity. Although the venation pattern in the material is hard to observe, it is still possible to find similarities with *Myrcianthes* Berg. This genus is characterised by intersecondary veins that emerge from the paramarginal vein (González 2009, 2011c). Although it is not possible to observe the intersecondary veins in the studied material, the base shape, the simple leaf, the camptodromous broquidodromous secondary veins and the form and size of the petiole are characters that are comparable to the extant *Myrcianthes callicoma* McVaugh and *Myrcianthes coquimbensis* (Barnéoud) Landrum and Grifo. The former is a tree species of the mountain forest of Bolivia and Argentina (Ayarde 2000) and *Myrcianthes coquimbensis* is the only species of this genus that inhabit Chile (García-Guzman et al. 2012) and is restricted to the Coquimbo area (Landrum and Griffo 1988). Both are characterised by simple, thick and coriaceous leaves, with rounded base shape and venation composed by a pinnate primary vein more prominent at the leaf base and faintly secondaries disposed in up to six pairs. These characters can be observed in the studied material as well. Also, *Myrcianthes coquimbensis* is defined by Landrum and Griffo (1988) as strongly glandular which is comparable with the glandular–punctate leaf that is shown in the fossil.

Genus ***Myrcia*** DC. Ex Guill. 1827

Myrcia bagualensis (Dusén) Hünicken

Figure 4(a, b)

1899. Myrtiphyllum bagualense Dusén 1899: Plate III, figs. 1–4

1928. Myrcia nitens Berry non Engelhardt 1891: 23, pl. III, figs. 1–9

Material examined. MPMPB 2946–2949

Description. Blade attachment marginal, laminar size microphyll, laminar shape elliptic to oval, with medial and basal symmetry. Margin entire with acute base angle and convex base shape. Primary venation pinnate with no naked basal veins, one basal vein and no agrophic veins. Major secondaries simple brochidodromous with regular spacing, uniform angles and decurrent attachment to midvein. Interior secondaries absent, minor secondaries absent, intersecondaries hardly observed and intramarginal vein present. Intercostal tertiary veins admedially ramified. Exterior tertiaries looped.

Comparisons. There are several fossils described as *Myrcia* for the Paleogene of Patagonia. Among these, the studied material matches with the description given for *Myrcia bagualensis* (Dusén) Hünicken. Both are characterised by ovate to elliptic small leaves with regularly spaced camptodromous brochidodromous secondary veins. In particular, the morphotype is especially similar to the specimens of the figs. 7 and 9 described by Berry (1928).

Botanical affinity. The elliptic leaves without glands, the presence of one paramarginal and one intramarginal vein and secondary veins that emerge at wide acute angles allow a comparison with *Myrcia* DC ex Guill.

Myrcia deltoidea (Engelhardt) González

Figure 4(c–e)

1891. Myrcia reticulato-venosa Engelhardt: 679, pl. V, fig. 10

1938. Myrcia deltoidea forma *ovata* Berry: 118, pl. 44. fig. 1

Material examined. MPM PB2903 a/b–2904; 2906 a/b

Description. Blade attachment marginal, laminar size microphyll, laminar shape elliptic to oval, with medial and basal symmetry, sometimes with basal asymmetry. Margin entire with acute base angle and decurrent to cuneate base shape, apex acuten and atenuate. Primary venation pinnate with no naked basal veins, one basal vein and no agrophic veins. Major secondaries numerous, camptodromous brochidodromous, regularly spaced, with uniform angles and decurrent attached to midvein. Interior secondaries absent, minor secondaries absent, intersecondaries hardly observed and one intramarginal vein present. Intercostal tertiary veins and quaternary veins random reticulate. Exterior tertiaries looped. Quinquenary venation dichotomising.

Comparisons. Among the fossils described for Patagonia, these specimens are comparable with *Myrcia deltoidea* Engelhardt. Both share the elliptic lamina shape, the number and divergence angle of the camptodromous brochidodromous secondary veins, the tertiary and quaternary random reticulate venation orders and the presence of one paramarginal vein formed by the secondary and one intramarginal vein formed by the tertiary ones. According to González (2009), the species described by Berry (1938) as *Myrcia reticulato-venosa* and *Myrcia deltoidea* forma *ovata* represents the same taxa and is synonymised to *Myrcia deltoidea*. This species was already mentioned and described by Hünicken for the Río Turbio Formation. Despite its poor description and illustration, the specimens described here support the presence of this taxon for the association.

Botanical affinity. The assignment of the studied material to *Myrcia* seems to be adequate. Like the fossil analysed, this genus is characterised by elliptic leaves with 10–20 camptodromous broquidodromous secondary veins which emerge at acute angles from the midvein, third and fourth venation order random reticulate and one prominent paramarginal vein and one (or two) intramarginal vein (González 2011a). Among the living species, it shares at least 18 characters with *Myrcia multiflora* (González 2009), such as the leaf shape, the number and arrangement of secondary veins, the angle of divergence and the random reticulate tertiary vein among others.

Morphotype RTF 1

Figure 4(f)

Material examined. MPMPB 3170–3171

Description. Blade attachment marginal, laminar size microphyll, laminar shape elliptic with medial and basal symmetry. Margin entire with acute base angle, and convex to rounded base shape. Primary venation pinnate with no naked basal veins, one basal vein and no agrophic veins. Major secondaries simple camptodromous brochidodromous with irregular spacing and decurrent attached to midvein, one intramarginal vein. Interior secondaries absent, minor secondaries absent, intersecondaries present. Tertiary veins barely observed seem to be percurrent. Exterior tertiaries looped.

Comparisons. The preservation of the material studied makes the comparison difficult. Among the fossil Myrtaceae described from Patagonia, the specimen resembles those related to *Psidium*; however, *Psidium membranaceum* Engelhardt, *Psidium araciforme* Berry, *Psidium licciardoi* Hünicken and *Psidium* sp., described earlier, are characterised by more 'like eucamptodromous' closely spaced secondary veins.

Botanical affinity. Similarities with *Psidium* L. and *Campomanesia* Ruiz & Pav can be found. As was mentioned earlier, the paramarginal vein in *Psidium* L. is sometimes observable only at the leaf apex, and the specimens analysed lack this portion of the leaf which can explain why it was not observed. Also, it shares with the studied material the camptodromous brochidodromous venation pattern along with the lamina shape, the irregular distribution of the secondary veins, the presence of intersecondary veins and looped ultimate marginal venation. These latter characters are also found in *Campomanesia* Ruiz & Pav. which is also characterised by the absence of paramarginal vein. Among the extant Myrtaceae that inhabit Argentina, the specimen described is closely comparable to *Campomanesia xanthocarpa* Berg. Both share comparable lamina shape; similar number of camptodromous broquidodromous secondary veins irregularly spaced which emerges, from the pinnate and straight midvein, at acute angles. Although the preservation of the studied material avoids a closer comparison to any of these two genera, there are no fossil leaves described for Patagonia and assigned or compared with *Campomanesia* Ruiz & Pav.

5. Comments on previously reported species

Hünicken (1967) described two species, *Psidium licciardoi* Hünicken and *Myrcia* sp., that were not found in the present collection. *Psidium licciardoi* was defined upon a single specimen and the material illustrated by Hünicken is very scarce avoiding the observation of those characters that can relate it to Myrtaceae. For example, *Psidium licciardoi* shows some characters such as venation pattern and a lamina shape that are comparable to those species belonging to this genus but in the illustration, the secondary veins seem to end in arches and do not bifurcate as is expected in *Psidium*. Similar issues occur with *Myrcia* sp. The elliptic shape of the leaf, along with the secondaries that form one paramarginal vein is consistent with *Myrcia*, but according to the illustration given by Hünicken, it seems to have a highest number of secondary veins than that expected for the genus. In order to justify these assignments properly, it is necessary to incorporate more specimens.

6. Discussion

The family Myrtaceae is well represented in the Río Turbio paleoflora by 12 taxas that can be related to the extant genera *Eugenia*, *Myrcia*, *Myrcianthes*, *Psidium* and possible *Eucalyptus* and *Campomanesia*. Interestingly, any one of these are present today in the study area. They are mainly growing in tropical areas of America and eastern and south-western Australia. In Argentina, in particular, the Myrtaceae are frequent in the Mesopotamia (Misiones, Corrientes and Entre Ríos) and throughout the north-western (Salta, Jujuy and Tucumán), with the genus *Eugenia* reaching the southernmost distribution, extending to the Buenos Aires province (Rotman 2000). Although some genera inhabit Patagonia (*Ugni*, *Amomyrtus*, *Tepualia*, *Luma*, *Myrceugenia* and *Myrteola*) even today, none of these are found in the area of Río Turbio. Nowadays this region can be considered as an ecotone between the steppe and the Patagonian rain forest (Burkart et al. 1999). The steppe is dominated by shrubs and herbs (León et al. 1998) and the Patagonian rain forest, in Río Turbio, is dominated by *Nothofagus pumilio* (Lenga) followed by *Nothofagus antarctica* (Ñire) (Cabarallo 2006). The high diversity of Myrtaceae found in the Río Turbio Formation along with the presence of other megathermal components such as those of the Lauraceae, Malpighiaceae, Sapindaceae, Myricaceae, Ulmaceae, Rubiaceae and Bombacaceae (Hünicken 1955; Troncoso and Romero 1998; Panti 2010) support the presence of a warm temperate biome in the southern tip of Patagonia. This is in agreement with the mean annual temperature estimates based on leaf physiognomic analysis that prevail at the fossil locality at its deposition (Panti 2010). During the Paleocene–Early Eocene interval, climatic conditions were warm enough to allow the expansion of megathermal angiosperms towards middle and high latitudes (Barreda and Palazzesi 2007). After this interval, a progressive decline in temperature led to the replacement of this flora by a new flora adapted to cooler climates (Troncoso and Romero 1998) with the development of *Nothofagus* forests which still dominates this region today.

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