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Macrofloristic assemblage of the Paraná Formation (Middle-Upper Miocene) in Entre Ríos (Argentina)

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With 3 figures

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Abstract: The Paraná Formation represents the marine ingression of Middle-Upper Miocene that invaded the Pampean plain and parts of Argentinean Mesopotamia. In its outcroppings, an abundant fossil fauna and flora (palynomorphs, logs, foliar impressions and phytoliths) have been recognized. In Villa Urquiza locality (Entre Ríos Province, Argentina), the outcropping strata are constituted by white sands intermingled with pure clays, gray to grayish-green, with abundant diagonal and flat structures including paleochannels filled with clays. In this study, foliar impressions such as *Myrciophyllum paranaesianum* sp. nov.; *Laurophyllum* sp. (Lauraceae), and *Schinus* aff. *terebinthifolia* (Anacardaicaeae) are described. The assignment of *Laurophyllum* and *Myrciophyllum* and the existence of xerophytic forests are discussed. Taking into account both the habit and habitat of recent plant species related to the fossil material, it is concluded that forests with Podocarpaceae and Araucariaceae existed in higher altitude zones, represented by fossils in the marine environment of the Paraná Formation. It is considered that these species were part of a heterogeneous environment with highlands and flooded lowlands, as part of the Seasonally Dry Neotropical Forest. The climate would have been warm and humid and among the environmental units; there were hydrophylous and mesophylous forests, marshy environments, lentic and lotic aquatic communities. Considering plant leaf impressions and the communities they may represent, vegetation of the Paraná Formation is interpreted to be consistent with the Neotropical Paleophytogeographic Province.

Key words: Macroflora, leaves, Middle Miocene, Paleocommunity, Entre Ríos, Argentina.

1. Introduction

The Paraná Formation, composed of sands, clays and carbonates, represents the marine event that flooded a large part of the Pampean plain and part of the Mesopotamia during the Middle-Upper Miocene (Serravalliano). This unit contains abundant marine vertebrate and invertebrate fossil remains and levels with plant remains (silicified trunks, foliar impressions, palynomorphs, and phytoliths) that represent a continental contribution to beach or shallow water zones. This formation is widely represented in the subsoil, with thickness between 30 and 200 meters, outcropping patchily and with low thickness in relatively few locations (ACEÑOLAZA 2000, 2004).

The presence of these fossils in the Paraná Formation was previously mentioned by D'ORBIGNY (1842), DARWIN (1846), BRAVARD (1858) and FRENGUELLI (1920), but it was not until the decade of 1970 that the palaeobotany was addressed in more detail. Among the studies describing new species, those referred to premineralized logs (LUTZ 1980;

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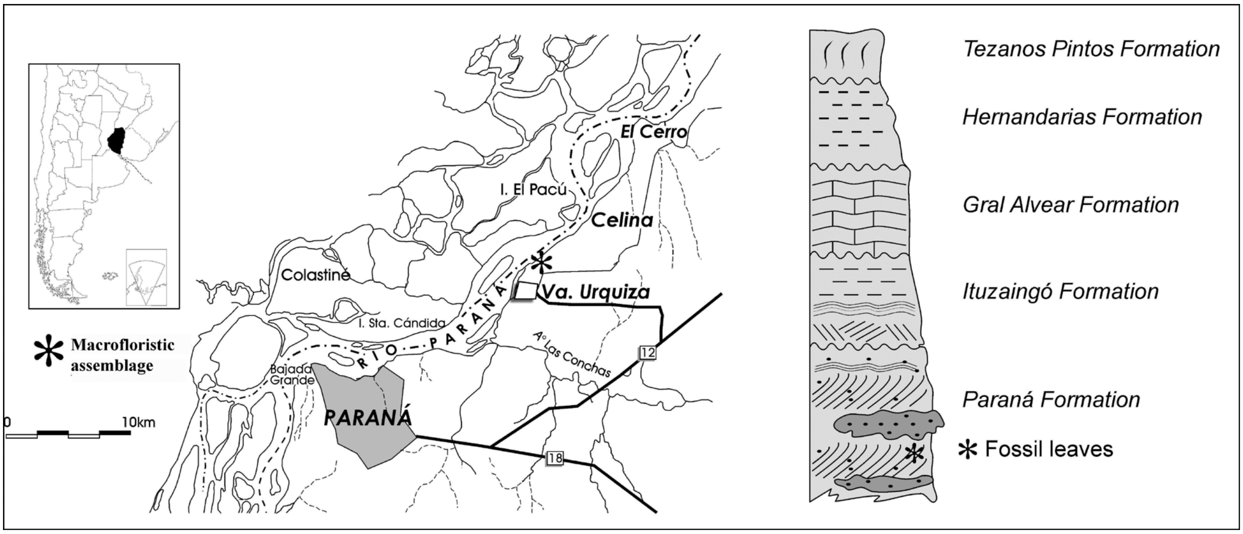

Fig. 1. Outcrop location and its stratigraphy showing the Parana Formation and the positions of leaf imprints.

Brea et al. 2001), palynomorphs (Gamerro 1981; Garralla 1989; Anzótegui 1990), monocot leaves, dicot leaves Aceñolaza & Aceñolaza (1996) and phytoliths (Zucol et al. 2004) are noteworthy.

Geological-paleontological prospecting carried out in different areas of the region, permitted the recognition of new localities with foliar impressions.

Outcroppings located to the south and north of Villa Urquiza port oriented the search to clayish-sandy levels, in which foliar impressions of Lauraceae had been previously found (Aceñolaza & Aceñolaza 1996). New impressions were obtained in this study, some of which, due to their good state of preservation and abundance, permit their assignment to *Laurophyllum* sp. (Lauraceae) and *Myrciophyllum paranaesianum* sp. nov. (Myrtaceae).

It should be noted that leaves studied herein are part of an environment which characteristics have been put in question based on other fossil types by Anzótegui (1990) and Zucol et al. (2004), while Aceñolaza & Aceñolaza (1996) mentioned that that vegetation would have been part of a floristic/environmental context similar to the "Seasonally dry neotropical forest (SDTF)" mentioned later by Pennington et al. (2004). These environments located in the Misiones Nucleus (Pennington et al. 2004), have evergreen species and gallery forests, sharing the landscape with *Araucaria* and *Podocarpus.*

In general, these forests were accompanied by palms, marshes and aquatic communities, which developed under a warm climate, more humid than the present; nevertheless, the existence of a xerophytic paleovegetation mentioned by Anzótegui (1990) must be considered.

2. Study area

Villa Urquiza, Entre Ríos, is situated in the left margin of the Paraná river, about 20 km northwest of the homonymous city (31º37'S; 60º21'W). Material studied herein was collected by the coastal roadside 1 km away from the port (Fig. 1). At this point, a Cenozoic stratigraphic succession about 20 m thick outcrops. Its characteristics, from the uppermost level to the lowermost level are as follows:

• Dusty loess, brown pinkish to brown yellowish, structure massive to prismatic, with carbonate aggregates (tosca) and great internal cohesion, which gives a profile of vertical walls, with a thickness of 2 m. It represents the Lujanense/Holocene = Tezanos Pintos Formation.

erosive discordance

• Brown reddish clay with some gray greenish levels at the base, with carbonate aggregates and black spots of ferric phosphates (Vivianite?). It develops inclined walls, with a thickness of 4 m. This represents the Ensenadense = Hernandarias Formation.

erosive discordance

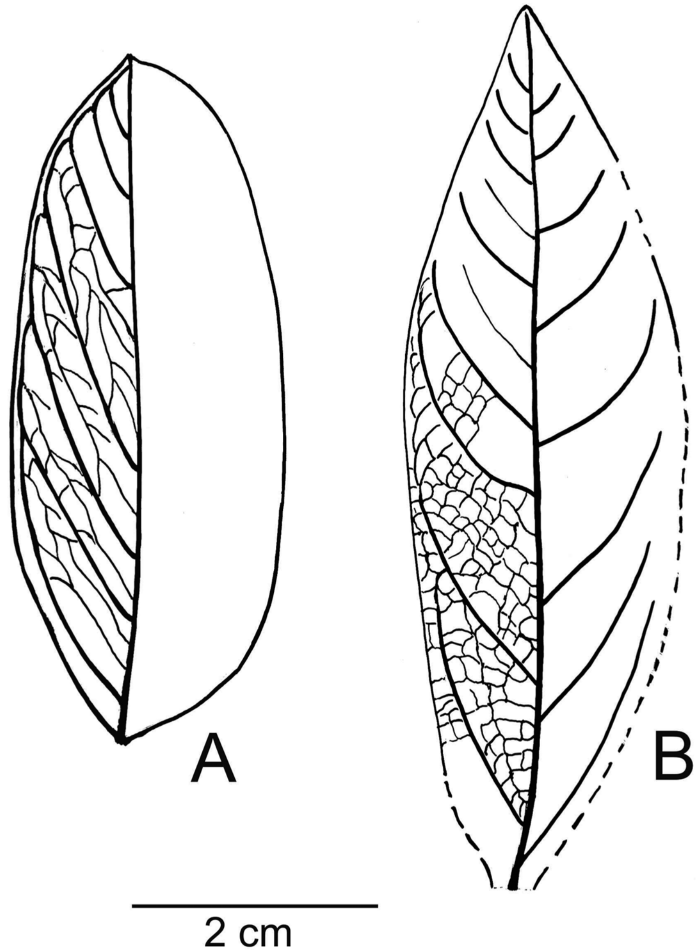

Fig. 2. Leaf shape and venation patterns for:
a – *Myrciophyllum paranaesianum* sp. nov. and
b – *Laurophyllum* sp.

• Volcanic Tosca, massive, with abundant carbonate material and thin layers of vivianita. Carbonate material provides a characteristic partition that makes it recognizable at distance ("calcaire cloissoneé" *sensu* d'Orbigny). Its great cohesion allows the development of nearly vertical walls, with a thickness of 4 m. This represents the Ensenadense = Alvear Formation.

erosive discordance

Greenish clays with intercalations of brownish and whitish sands. These are dominant at the base, displaying a particular well developed diagonal structure. A remarkable abundance of manganesian material is developed in the basal part, which gives a dark color to the level. Also at the base, banks of fine quartz conglomerates are developed, with remains of fishes? And other vertebrates; it has a thickness of 4 m. This represents the Pliocene = Ituzaingó Formation.

erosive discordance

• Whitish yellowish quartz sands, with abundant diagonal and flat structures and intercalations of small banks of pure clays, gray or greenish gray. These clays bear the foliar remains. There also are clay rolling stones and sand banks cemented by silica and log fragments mineralized by opal. The set is apparently 5- m thick, its base being unknown since it is covered by the river. This represents the Middle-Upper Miocene = Paraná Formation.

3. Materials and methods

In some levels, leaves are well preserved and are relatively abundant, although most of specimens are fragmentary; in the case of *Myrciophyllum paranaesianum* sp. nov., basal portions are the most frequently preserved; in the case of *Laurophyllum* sp. only two foliar laminas are quite complete, while the remaining are leaf fragments; in a specimen of *Schinus* aff. *terebinthifolia,* the rock is quite friable. Other levels contain hygroscopic sediments, due to which specimens deteriorate on drying are.

The fossil species have been determined through comparisons with the literature and with Recent specimens of the Herbarium (CTES). Terminology used for descriptions follows Hickey (1974, 1979) and LAWG (1999). Photographs were taken with a digital camera, Sony Cybershot DSC-F717 (2-2,4/ 9,7-48,5).

The material is housed at the Museo Regional de Villa Urquiza (Entre Ríos) under the code MRVU-IF (Museo Regional Villa Urquiza – impresiones foliares).

4. Systematic descriptions

Division Magnoliophyta Cronquist, Takhtajan & Zimmermann 1966
Class Magnoliopsida Cronquist, Takhtajan and Zimmermann 1966
Subclass Hamamelidae Takhtajan 1966
Order Laurales Lindley 1833
Family Lauraceae Jussieu 1789
Genus *Laurophyllum* Goeppert emend. Hill 1986

Type species: Not designated.

Laurophyllum sp.
Figs. 2b, 3b, c, f

Studied material: MRVU-IF 113, 114, 115, 116, 117, 118, 119, 120, 134, 135.

Locality: Villa Urquiza, Entre Ríos Province.

Horizon and age: Paraná Formation, Middle Miocene.

Description: Leaves Ovate-lanceolate, slightly falcate, approximately 4-7 x 0,9-2,6 cm length by width; poorly preserved apex, apparently acute to attenuate; base and petiole not preserved. Eucamptodromous principal venation; middle vein slightly bended in the direction of the leaf blade, with strong relative thickness (2-4 %); 8-10 secondary veins, with thin relative thickness; veins emerge at variable angles, from acute-moderate (45-65º) in basal veins to acute-wide (65-75º) in apical veins. Secondary veins follow a slightly sinuous course, becoming thinner to the apex, and amalgamating superadjacent by veins of minor caliber without forming prominent marginal arches; simple intersecondary veins are present in some of the intercostals spaces. Conspicuous tertiary venation with a reticulate orthogonal model, determining quadrangular or pentagonal areolas, with simple or one-fold ramified veinlets.

Comparisons: These specimens are compared both with fossil and living species having elliptic-narrow, oblong-narrow or ovate-lanceolate leaves, less than 10 cm in length and up to 3 cm width and which principal venation is eucamptodromous.

Fossil leaves having these features, in the north of Argentina, belong to *Nectandra saltensis* Anzótegui, from Palo Pintado Formation, Upper Miocene (Valles Calchaquíes), although they are slightly smaller in size (3.5-5-5 cm in length by 0.7-1.9 cm in width); it is similar to *Laurophyllum* sp. in size, the type of tertiary and quaternary venation, which is reticulate orthogonal conspicuous, but differing in the longer run of the secondary veins and in that their angles of emergence are acute-narrow (20º-35º).

Species from Argentinian Patagonia: *Nectandra prolifica* Berry, *Acrodiclidium flavianum* Hünicken, *Nectandra* sp., *Mespilodaphne longifolia* Engelh., from Middle Eocene (Río Turbio Formation), some of which are published in Berry (1938) and/or Hunicken (1966) and Troncoso (1992), also *Nectandra prolifica* from the Lower Eocene of Quinamávida, show few differences with the species described herein, both in terms of quantity of veins and in the angles of emergence of secondary veins; observed differences can be due, in general, to the variability in leaves. An adequate comparison is precluded by the lack of details in most descriptions.

Among the Argentine species having the features mentioned above, we find *Nectandra megapotamica* (Spreng.) Mez, *Ocotea acutifolia* (Nees) Mez, *O. diospyrifolia* (Meisn.) Mez, *O. lancifolia* (Schott) Mez, *O. puberula* (Rich.) Nees, and *O. pulchella* (Nees.) Mez, which differentiate, in general, in that most of them have elliptic narrow leaves with acuminate base, also *O. pulchella* has only a maximum of 5 secondary veins. They are more similar to *Laurophyllum* sp., the smallest leaves of *Ocotea diospyrifolia* and *O. puberula* in the type of angles of emission of secondary veins, which is moderate in the basal area and acute-wide in the apical zone.

This fossil species remains with open nomenclature until a comprehensive review of fossil species is carried out in order to determine the corresponding combinations between *Laurophyllum* and priority species.

Habit and habitat of modern related species: *Ocotea diospyrifolia* and *O. puberula,* integrate the hygrophilous forests of Argentine NE and NE/ NW respectively.

Subclass Rosidae Takhtajan 1966
Order Myrtales Lindley 1833
Family Myrtaceae Jussieu 1789
Genus *Myrciophyllum* Engelhardt emend. Anzótegui 2002

Type species: *Myrciophyllum ambiguaeoides* Engelhardt 1891

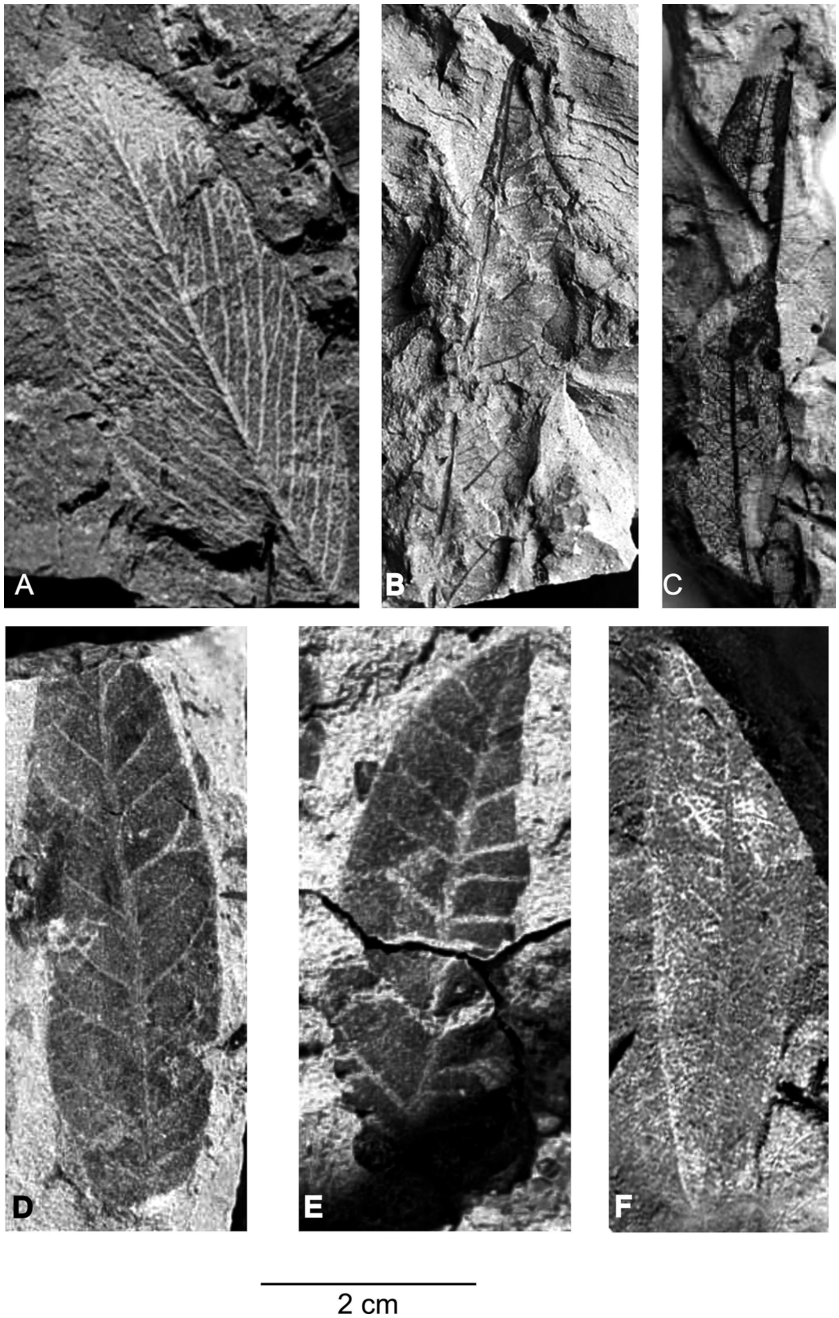

Fig. 3. General view of leaf impressions. **a** – *Myrciophyllum paranaesianum* sp. nov.; **b, c, f** – *Laurophyllum* sp.; **d, e** – *Schinus* aff. *terebinthifolius* Raddi.

Myrciophyllum paranaesianum sp. nov.
Figs. 2a, 3a

Etymology: *paranaesianum* refers to the Paraná Formation, where these leaves have been recovered.

Holotype: MRVU-IF 111.

Other material studied: MRVU-IF 121, 122, 123,124, 125a and b, 126, 132, 133.

Type locality: Villa Urquiza, Entre Ríos Province.

Type horizon and age: Paraná Formation, Middle Miocene.

Diagnosis: Oblong simple leaves; acute slightly mucronate apex, acute to slightly cuneate base, entire margins; scarce and slightly marked trichome bases. Camptodromous principal venation with intramarginal leaves. Straight primary vein with 6-7 subopposed secondary veins, emerging with acute-narrow angles. Composite intersecondary veins with admedial ramification, present in all intercostal spaces, emerging from intramarginal veins with acute-narrow angles. Scarce tertiary veins admedially or exmedially oriented, originating from intersecondary or secondary veins. There is no higher order venation.

Description: Oblong simple leaves, 2,1cm in length by 0,9 cm, in width; acute slightly mucronate apex and acute to slightly cuneate base, entire margins; scarce and slightly marked trichome base. Camptodromous principal venation with intramarginal veins. Straight primary vein with strong relative thickness (2-4%); 6-7 subopposed secondary veins, emerging from the middle vein with acute-narrow angles (15-30º), and directed with a sinuous course to the margin, where they join the intramarginal vein with not marked angles; in the exmedial sector, these angles range 160° to 180°. Composite intersecondary veins with admedial ramification, present in all intercostal spaces, emerging from intramarginal veins with acute-narrow angles (15-30º), the principal branch generally reaches the medial vein. Tertiary veins are scarce and oriented either admedially or exmedially, originating from intersecondary or secondary veins. There is no higher order venation.

Comparisons: It is compared with living and fossil leaves having camptodromous venation with intramarginal veins and secondary veins with acute-narrow angles of emergence (<45º). *Myrciophyllum* sp. 3, from San José Formation, Middle Miocene (Anzótegui & Herbst 2004) shows this type of venation (intramarginal veins and secondary veins that emerge with acute-narrow angles), but differs in the shape, size (lanceolate to loriform, 4 cm in length x 1 cm in width) and in the base, which is slightly more cuneate and the apex, which is more acute to attenuated. *Callistemon* sp., from Navidad Formation (Miocene) of Chile (Troncoso 1992), also differs in the shape and size (oblong narrow, 5 in length x 0.9-1 cm in width) and by having more secondary veins. In the Patagonia flora of Argentina, no single species has secondary veins emerging from such narrow angles. Considering present-day species, according to Kuckling (1988), Mattos (1984), Rotman (1976, 1979, 1982), and Romero & Dibbern (1982), the characteristics of the fossil species are contained in the variability present in the leaves of the following living species of the regional flora: *Psidium cuneatum* Cambess., *P. incanum* (O. Berg) Burret, *P. kennedyanum* Morong, *P. salutare* var. *sericeum* (Cambess.) Landrum, *P. missionum* Legr., *P. luridum* (Spreng.) Burret, and *Paramyrciaria delicatula* (DC) Kausel. With regard to most species of *Psidium*, for this comparison we consider only smallest leaves not exceeding 4 cm in length, which are wider than the rest and have poor secondary veins (6-7); this kind of leaves are generally located at the base of the branch. Differences reside in that, even the smallest leaves, are larger than fossils and have generally elliptic to elliptic-narrow shape (except for the basal leaves of *Psidium cuneatum*), also the angles of emission of secondary veins are more open, oscillating between 30º-40º. In *Psidium luridum*, some secondary veins emerge at 20º but they are more numerous (8-10) in Romero & Dibbern (1982). The fossil species also resembles the slightly ovate leaves of *Paramyrciaria delicatula* in size, number of secondary veins and angle of emission of its secondary veins; however, most leaves of this species are elliptic and very narrow, feature that relates them to *Myrciophyllum* sp. 3 (fossil species already mentioned for San José Formation).

The present new species is erected because of the abundance of fossil specimens found in the Paraná Formation, the uniformity of its characters, all the indicated differences between fossils and living species, and taking into account the morphological variability found in present-day leaves, that reflect the mix of characters described in the fossil species.

Habit and habitat of the related present-day species: *Paramyrciaria delicatula* var. *argentinensis, P. luridum, P. incanum, P. cuneatum, P. kennedyanum, P. missionum*, and *P. cuneatum* are trees or shrubs growing near watercourses, in hygrophilous forests, in small islands or forest remnants interspersed with tall grass prairies in Misiones, Corrientes, and in neighboring countries (Brazil and Uruguay).

Order Sapindales Bentham & Hooker 1862
Family Aanacardiaceae Lindley 1830
Genus *Schinus* Linnaeus 1753

Type species: *Schinus molle* Linnaeus 1753.

Schinus aff. *terebinthifolius* Raddi 1820
Fig. 3d, e

Studied material: MRVU-IF 105 and 106.

Locality: Villa Urquiza, Entre Ríos Province.

Horizon and age: Paraná Formation, Middle Miocene.

Description: Symmetrical foliar blade, oblong, elliptic to elliptic narrow, 2,5 cm in length x 0,9 cm in width; apex and base partially preserved, apparently acute. Entire margin. Glabrous leave surface. Pinnate venation, craspedodromous simple. Straight primary vein of moderate to strong relative thickness. Secondary veins, 7-8 pairs opposite to subopposite straight, bifurcating at least once before reaching the margin; in specimen Nº 105, these minor ramifications join, in some cases, the supra and infradjacent veins. Intersecondary veins are simple and present in some of the intercostal spaces, angles of emergence are equal to those of secondary veins. Tertiary veins are fine and delicate, they are poorly preserved and allow the observation of some dichotomies.

Discussion: *Ocotea* sp., described in ACEÑOLAZA & ACEÑOLAZA (1996) differs from those of group 4 (late phase venation), established by KUCKLING (1987), in size and because none of the species possess craspedodromous simple venation, secondary veins do not reach the margin straightly, they have one or two previous dichotomies, most of them have eucamptodromous-brochidodromous principal venation, only in *Cryptocarya rubra* (MALINA) SKEELS and *Litsea calicaris* (SOL. ex A. CUNN.) BENTH. & HOOK. F. ex KIRK., secondary veins do not describe well defined arches and although they dichotomize once, these branches anastomose in minor arches at the middle part of the leaf blade before reaching the margin; higher order venation (tertiary and quaternary) is conspicuous.

Characteristics regarding venation and shape of the fossil species described herein are within the variability present in *Schinus* aff. *terebinthifolia* from the Chiquimil Formation (ANZÓTEGUI 2004) and in the present-day homonymous species; although in the description, that author indicates that terminal veinlets innervate tooth or crenations of the margins and does not mention the existence of specimens with entire margins, however such specimens were found in the localities of Río Vallecito and Nacimientos de Abajo, Catamarca Province.

Habitat and distribution of modern and fossil species: *Schinus terebinthifolia* RADDI is a woody species with variable appearance, from rhizomic subshrubs of 0.20 m to trees up to 9 m in height. The species is native from southeast Brazil, east Paraguay and northeast Argentina; it grows at the margin of watercourses forming part of forest communities of the Paranaense Province (CABRERA 1994). *Schinus* aff. *terebinthifolia* in ANZÓTEGUI (2006), from the Chiquimil Formation and El Morterito, would have been a shrub member of marsh communities.

5. Taxonomic considerations and general characters of the present-day families

In the families Lauraceae and Myrtaceae, due to their highly variable foliar characteristics (architecture and morphology), the differentiation of genera and species is difficult, both in fossil and living forms. For this reason, we emphasize characters that discriminate them at the family level, and propose the utilization of the morphogenetic denomination for fossil specimens.

In the Lauraceae family, following KUCKLING (1987) and adapting his terminology to HICKEY (1974 and 1978) and LAWG (1999), several categories of leaves are distinguished, based on the principal venation: acrodromous, brochiodromous, eucamptodromous and eucamptodromous-brochiodromous. All of them have entire margins and most have a laminar surface larger than 3 cm both in length and width, corresponding to the categories microphylous, notophylous to mesophylous; acute or cuneate bases and rounded or attenuated apices. In leaves with eucamptodromous or eucamptodromous-brochiodromous venation, secondary veins are generally thin and tertiary venation is strong and conspicuous, with percurrent to reticulate orthogonal patterns.

Despite some differences, HILL (1986), pointed out that WOLFE (1977) had noted that fossil foliage of Lauraceae is difficult to determine to the genus level, even in most favorable circumstances. Consequently, WOLFE (1977) suggested the utilization of organ-genera, that represent morphological types for these leaves, except in the few cases in which the assignment to present-day general can be done with confidence (generally by cuticles). That author adopted and emended the system of KRÄUSEL & WEYLAND (1950) for the following morphogenera: *Laurophyllum,* leaves with secondary veins approximately parallel and of the same thickness and with none or scarce terminal free venation; if venation exists, it is not ramified. *Cinnamomophyllum* leaves with pseudopalmate or triplinervate venation; this is, a pair of secondary veins depart at short distance above the petiole, parallel and of the same thickness of the remaining secondary veins (acrodromous suprabasal venation). Marginal veins and areoles have few or none veinlets. Whenever they have veinlets, these do not ramify.

STURM (1971) showed that leaves of a single living species could fit both morphogenera, and thus he concluded that these genera could not be maintained. In their place, he designed two genera with uncertain affinity to present-day genera of Lauraceae: *Lauraceophylloderma,* for species which preserve cuticle and venation, and *Lauraceophyllum,* for species which only have venation. HILL (1986) states that these genera are invalid, given that *Laurophyllum* and *Cinnamomophyllum* have priority. Even *Laurophyllum* has priority over *Cinnamomophyllum,* because it was published in 1853 by GOEPPERT, while *Cinnamomophyllum* was published in 1950 by KRÄUSEL & WEYLAND. Therefore, HILL (1986) proposed that *Laurophyllum* GOEPPERT emend. HILL has to be used for all fossil leaves of Lauraceae that cannot be assigned to a living genus. The emendation done by this author consists in the inclusion of cuticular characters; he uses the morphogenus for leaves that preserve both venation and cuticle.

CONRAN & CHRISTOPHER (1998) used this morphogenus for triplinervate leaves, but propose to re-establish the genus *Cinnamomophyllum* of KRÄUSEL & WEYLAND (1950) in the future for all triplinervate leaves. However, they also warn that its use could artificially separate many taxa with uni- and triplinervate species.

Berry (1938) founded *Nectandra prolifica* Berry on the basis of a great quantity of specimens varying in shape and size (from delicate falcate leaves to ovate wide, lanceolate or acuminate leaves). Since he was not able to establish lines of separation because of the gradation in specimens, he suggested the use of a morphogenus. He makes similar comments, in the same paper, when describing *Acrodiclidium oligoacenicum* Engl., because he did not find any difference between *Nectandra* Rol. ex Rottb., *Mespilodaphne* Nees & C. Martius ex Nees and *Oreodaphne* Nees & C. Martius ex Nees. In the same way, leaves found in the present study have pinnate eucamptodromous venation and are narrow (less than 3 cm in width). Among modern species illustrated by Kuckling (1987), they are similar to *Cinnamomum tampicense* (Meisn.) Kosterm., *Cryptocarya filicifolia* (Kosterm.) Kosterm., *Lindera angustifolia* Cheng., *L. fragrans* Oliv., *Litsea elongata* (Nees) Benth. & Hook. f., *L. iteodaphne* Ness., *Ocotea microbotrys* (Meisn.) Mez, *Nectandra falcifolia* (Nees.) Cast., and *Nectandra microcarpa* Meisn.

The classification and relationships in present-day Lauraceae has long been considered problematic. In recent years, several aspects have been studied: anatomy of the wood (Richter 1981), cuticles (Nishida & Christophel 1999; Li & Christophel 2000), embryology (Heo et al. 1998), molecular analysis (Rohwer 2000, Chanderbal et al. 2001; Li et al. 2004) and inflorescence morphology (Werff van der & Richter 1996). Nevertheless, Rohwer (1993) pointed out that the use of a particular character applied by different authors would result in several systems. In this way, the delimitation of genera and suprageneric entities is not reliable for many authors.

In the Myrtaceae family, principal venation can be camptodromous with intramarginal veins or brochidodromous; both types of venation generally present intersecondary and tertiary veins admedially ramified (Romero & Arguijo 1981; Christophel & Lys 1986; Pole 1993; Hill & Merrifield 1993). In Anzótegui (2002a) and in Anzótegui & Herbst (2004) it is suggested that the model of camptodromous principal venation with intramarginal veins, should be termed acrodromous; in the present contribution we reconsider the definitions already given by the authors mentioned above and recognize that such name (acrodromous) has to be changed by camptodromous with intramarginal veins. We also observed that when secondary veins, in their course next to the margin, present indentations in the point of contact with superadjacent veins, it is difficult to distinguish whether the type of principal venation is brochidodromous, or camptodromous with intramarginal veins; Anzótegui (2002a) proposed, in order to differentiate both patterns (brochidodromous and camptodromous with intramarginal veins), that the angle of exmedial union between the arches of consecutive secondary veins should be taken into account. When most angles range between 160° and 180°, the type of venation will be interpreted as camptodromous with intramarginal veins, and when the angles are less than the values given above, the type of venation will be considered brochidodromous. On the other hand, Anzótegui (2002a) confirmed what had been pointed out by Berry (1929), Christophel & Lys (1986) and Troncoso (1992) regarding the fact that modern species display great morphological variability in their leaves and that fossil species are generally similar to some of the forms that are part of that variability; it is even possible that fossil species are similar to species of different genera. Consequently, he proposed the use of the morphogenus *Myrciophyllum* Engelhardt emend Anzótegui 2002 to designate fossil leaves of the family Myrtaceae having brochidodromous or camptodromous with intramarginals principal venation, scarce secondary veins (less than 12) and having admedial ramification of the intersecondary and tertiary veins.

In Anacardiaceae, although the shape of the foliar laminas (leaves or leaflets) is quite variable, the pattern of principal venation is more stable. It consists in craspedodromous or craspedodromous-brochidodromous venation, with secondary veins reaching the margin after one or two ramifications, in some cases joining the superadjacent vein with arches of minor diameter. Higher order veins (tertiary or quaternary), are scarce and generally display a ramified exmedial pattern. The margin can either be entire or dentate with simple dentations irregularly distributed.

6. Considerations on flora and environment

The finding of palynomorphs, fossil logs and phytoliths in the Paraná Formation allowed the reconstruction of paleocommunities, such as those mentioned by Zucol et al. (2004), among which, stratified hygrophilous forests, are notable. The arboreal stratum included was Fabaceae Mimosoideas (*Entrerrioxylon victoriensis* LUTZ, *Anadenantheroxylon villaurquicense* BREA, ACEÑOLAZA & ZUCOL, Anacardaiceae (*Astroniumxylon portmanii* BREA, ACEÑOLAZA & ZUCOL, Aquifoliaceae (*Ilexpollenites* sp.), Euphorbiaceae (*Sapium* cf. *haematospermum* MÜLL. ARG. and *Sebastiania* sp.), Myrtaceae (*Myrtipites miocenica* ACEVEDO & ANZÓTEGUI and *Myrtaceidites triangularis* ACEVEDO & ANZÓTEGUI) and Sapindaceae (*Sapindus* cf. *saponaria* L.) in the understory, together with some pteridophytes, such as Dicksoniaceae (*Dicksonia sellowiana* HOOK.), Cyatheaceae (*Alsophila villosa* (HUMB. & BONPL. ex WILLD.) DESV., *A.* cf. *microdonta* (DESV.) DESV., *Cyathea mettenii* KARSTEN and *Cyathidites* cf. *minor* COUPER) *Lycopodium* sp., *Anogramma* sp., *Matonisporites equiexinus* COUPER, among others, and probably Asteraceae. Other inferred communities are: lentic freshwater environments with Azollaceae (*Azolla* sp.), Haloragaceae (*Haloragacidites myriophylloides* COOK. & PIKE), Onagraceae (*Corsinipollenites* sp.), and watercourses with Podostemaceae and Crisostomataceae. Marsh communities and alluvial plains with Polygonaceae (*Polygonum* sp.) and Cyperaceae; there are also assemblages with Arecaceae, Poaceae, Asteraceae, Malvaceae, etc. On the other hand, in the upper levels of the palynological sequence, evidences of marine ingression seem to be given by the finding of 16 species of cysts of dinoflagellates. Another continental community, possibly located away from the sedimentation site, integrated by Podocarpaceae and Araucariaceae, has been also recorded in this region.

The existence of xerophytic forests (Group 3) established through palynomorphs by ANZÓTEGUI (1990) and integrated by *Astronium* sp., *Schinus* sp., *Celtis* sp. and *Janusia* sp., deserves a detailed discussion. This author considered it doubtful when expressing "even when these genera have species that are part of xerophytic forests of the Chacoan Domain, they have other species that are part of the Mixed Forests or their seral communities". In view of the new evidence, the taxa mentioned above will be relocated in other associations. Firstly, the pollen of *Schinus* sp., is assigned to *Striatricolporites gamerroi* ARCHANGELSKI, found by ANZÓTEGUI (2004) in the Chiquimil Formation; secondly, this species accompanies the leaves of *Schinus* aff. *terebinthifolia* RADDI; correspondingly, these leaves are also found in the Paraná Formation, which are mentioned herein; finally, both species of pollen and leaves are related to marshy environments (ANZÓTEGUI 2006). Palynomorphs determined as *Astronium* sp., have been assigned to *Astronium balansae* ENGLER and *Schinopsis balansae* ENGL.; however, following ANZÓTEGUI (2002 b), it was found that they are more similar to the pollinic type *Astronium balansae*. This species is a member of the Misiones Nucleus of the SDTF. In a similar manner, *Janusia* sp. has been considered related to *Janusia guaranitica* (A. ST. HIL.) A. JUSS., following PIRE (2006) it was found that it is more similar to *Callaeum psilophyllum* (A. JUSS.) D. M. JOHNSON, *Heteropterys bicolor* HOOK. & ARN., *H. glabra* HOOK. & ARN., *H. syringifolia* GRISEB. and *Hiraea fagifolia* (DC) A. JUSS., in the absence of 1 equatorial syncolpate, in the presence of rings in pores, in the size of pseudocolps of the pores and grains; the species mentioned belong to the pollinic type *Heteropterys glabra* HOOK. & ARN.; they grow in forests or hygrophilous forests of the Paranaense Province (CABRERA 1994), which are included in the Misiones Nucelus of the SDTF (PENNINGTON et al. 2004).

Palynomorphs of *Celtis* sp. are related, among others, to *Celtis ehrenbergiana* (KLOTZSCH) LIEBM. and *Celtis iguanaea* (JACQ.) SARG. (members of the subtype *Celtis pubescens* SPRENG., in ANZÓTEGUI & MAUTINO 2002), among them, *C. iguanaea* is found both in the Yungas and Paranaense Phytogeographic Provinces (CABRERA 1994); in view of the environment in which the accompanying species are found, it is possible that the fossil species has developed in a humid environment. As a result of this analysis, the xerophytic forests established ANZÓTEGUI (1990), should be replaced, following the designation of PENNINGTON et al. (2004) by "Seasonally dry neotropical forest" (SDTF). These units would have developed in warmer and more humid conditions that at present for that latitude, and would have been accompanied by Arecaceae, Poaceae, Malvaceae (*Sphaeralceae* sp. and *Malvacipollis densiechinata* Anzótegui and Garralla), other Asteraceae, possibly some species of *Acacia* (*Polyadopollenites* sp. 1 and *Polyadopollenites* sp. 2) and Quenopodiaceae. Taking into consideration the habit and habitat of the species studied herein, *Laurophyllum* sp., *Myrciophyllum paranaesianum* sp. nov. would have been part of the STDF constituting part of the arboreal stratum of the riverine forests and *Schinus* aff. *terebinthifolia,* would have been part of its understory stratum or a shrubby physiognomy.

7. Conclusions

The Paraná Formation is integrated by marine sediments containing supratidal sectors intermingled with interspersions from the continental margin, that would correspond to a littoral environment with sandy deposits (Sprechmann & Aceñolaza 1999; Sprechmann et al. 2001; Aceñolaza & Sprechmann 2002), which were surely colonized by vegetation similar to that of the Neotropical Paleophytogeographic Province proposed by Romero (1993) and equivalent to the Subtropical Neogene Paleoflora, proposed by Hinojosa & Villagrán (1997) and Hinojosa (2005).

When interpreting the paleofloristic assemblage, it is considered that the regional landscape was composed by a series of communities, among which the following could be distinguished in the supralittoral area: high forests with Podocarpaceae and Araucariaceae, stratified riverine hygrophilous forests, "Seasonally dry neotropical forest" (SDTF) with Arecaceae and marsh communities. Foliar remains, palynomorphs and silicified logs give evidence in that direction.

Climatic conditions of the region should have been warmer and more humid than those found at present, probably with a marked seasonal character, that allowed the presence of vegetation adapted to those conditions.

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