

A new early angiosperm leaf from the Anfiteatro de Ticó Formation (Aptian), Santa Cruz Province, Argentina

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Abstract: A new record of angiosperm from Aptian deposits of the Anfiteatro de Ticó Formation (basal unit of the Baqueró Group), in its type locality, north-center of Santa Cruz province, Argentina is reported. This record integrates the fossiliferous level *Williamsonia-Zamites* that contains abundant remains of bennettite leaves and was deposited in floodplain facies. The fossil consists of a single leaf imprint, with entire margin and festooned brochidodromous venation of low rank. It has features that define, in part, the nymphaeaphyll morphological type. This type occurs among the most early assemblages having angiosperms (northeastern Brazil, Portugal, South Australia, eastern North America), and is part of a physiognomic-foliar pool associated to taxa considered to be basal within the group. This foliar morphotype, is found in some members of extant angiosperms of usually herbaceous habit, and perhaps, by analogy, this may have been the original habit of our fossil species. The mega floristic record of eocretaceous angiosperms from Southern Hemisphere is scarce. In spite of them, angiosperm foliar remains from other location (Bajo Tigre) of the Anfiteatro de Ticó Formation are known. They are different to this new record. This incipient diversity suggests an even (pre-Aptian) presence of the angiosperms in the region.

Key words: Angiosperm leaves, Cretaceous, Anfiteatro de Ticó Formation, Argentina.

In 1986 Romero & Archangelsky described the first angiosperm leaf from the lower member of the Baqueró Formation at Bajo Tigre locality (now Anfiteatro de Ticó Formation of the Baqueró Group, see Cladera *et al.*, 2002). This impression is the second record for angiosperms leaves found in the same Formation but from another locality viz. Anfiteatro de Ticó. It should be noted that angiosperms are very rarely found in plant assemblages of the Baqueró Group that is dominated by bennettites and conifers. In fact, they are known to occur so far only in the lower unit of the Group, and are absent in the upper formations (Bajo Tigre and Punta del Barco; Cladera *et al.*, 2002). However, a few angiospermoid foliar imprints were recently reported from a new fossil locality of Punta del Barco Formation (Passalia & Cladera, 2003).

At palynological level, assemblages from this unit are rich in content, dominated by gymnosperms and ferns. The only angiosperm pollen grains were found in anthers as well as dispersed, and they were referred to the genus *Clavatipollenites* (Archangelsky & Taylor, 1993). However, from the top of the Baqueró Group (Punta del Barco Formation) it have been recently reported several angiosperm pollen grains (Llorens, 2003). These in-

clude the genera *Asteropollis*, *Clavatipollenites* and *Monocolpollenites* among others, indicating a major angiosperm representativity although in contrast with the only megascopic record mentioned above.

Evidence is accumulating to prove that primitive angiosperms were present in Patagonia during aptian time, represented by few types of leaves.

MATERIALS AND METHODS

The present material was collected by Georgina del Fueyo and one of the authors (S.A.) during an expedition in 1999. The specimen was found at Anfiteatro de Ticó, western side, Ea. La Magdalena, north-center of Santa Cruz Province, Argentina. The fossiliferous bed belongs to the Anfiteatro de Ticó Formation (basal unit of the Baqueró Group) in its type locality, lower section (Figs. 1-2). Recent isotopic datings were obtained (Ar^{40}/Ar^{39}) that confirm the Aptian age of the Baqueró Group: 118.56 ± 1.4 Ma and 119.7 ± 0.4 Ma (Corbella, 2001).

The fossil is a single foliar imprint that integrates the *Ptilophyllum* Zone (Archangelsky, 2001), fossiliferous level *Williamsonia-Zamites*. This bed

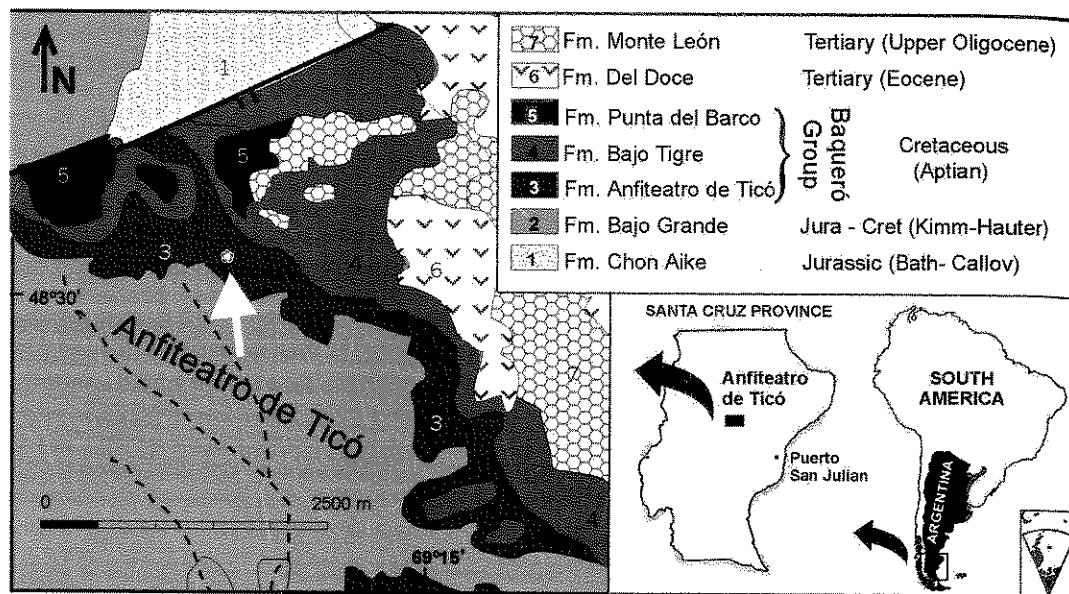


Fig. 1. Geographic location and geologic map of the Anfiteatro de Ticó area showing the site of angiosperm occurrence (white arrow).

contains abundant remains of bennettite leaves included in a friable sandstone lens that was deposited in floodplain facies (Cladera *et al.*, 2002).

The specimen was studied with a LEICA MZ125 microscope. Photographs were taken with a Nikon/Coolpix 990 digital camera. For the description, we follow the terminology of Hickey (1973) and *Manual of leaf architecture* (1999). The specimen is stored in the Paleobotanical Collection of the Museo Argentino de Ciencias Naturales "B. Rivadavia" (BAPb).

SYSTEMATIC

Division Magnoliophyta Cronquist, Takhtajan & Zimmerman, 1966

Class Magnoliopsida Cronquist, Takhtajan & Zimmerman, 1966

Nymphaeaphyll morphotype
(Figs. 3-5)

Main features. Apical fragment of leaf, with obtuse apex, rounded in shape and entire margin (base not preserved). Secondary venation pinnate forming festooned brochidodromous loops. Medial primary vein stout with a straight course at the two basal third of fragment, quickly decreasing in thickness and losing identity toward apex, not reaching it. At the distal third, it branches successively giving rise to a series of loops. Secondary veins arising from midvein, decurrent, alternate,

forming brochidodromous loops of irregular shape and area. Exmedially there are, at least, two or three additional series of loops. Their area, as well as the thickness of veins diminish progressively toward the margin. Veins of tertiary and more higher order forming an irregular polygonal reticulum. Polygonal areoles lack veinlets.

Expanded description. The material consists of a single leaf imprint fragment showing the middle and apical portions. The leaf is 4 cm long and 2.5 cm wide. The apex is obtuse, rounded in shape and its margin is entire (preserved only at the apical and left sides). The lack of the basal part of leaf impedes a description of the primary venation pattern. The secondary venation is pinnate forming festooned brochidodromous loops. The medial primary vein is stout and has a straight course at the two basal third of fragment; it quickly decreases in thickness and loses identity toward apex without reaching it. At the distal third of the leaf, it branches successively and gives rise to a series of loops. It is possible to observe at least four secondary veins arising from the midvein: they are decurrent, alternate with angles of 50-60° and forming brochidodromous loops of irregular shape and area. Relative thickness of secondary veins is thick. Exmedially to secondaries there are, at least, two or three additional series of loops. Their area, as well as the thickness of veins progressively diminish toward the margin. Tertiary and more higher order veins form irregular polygonal reticula (Figs. 3.A-B). Polygonal areoles are about 0.5 mm. and

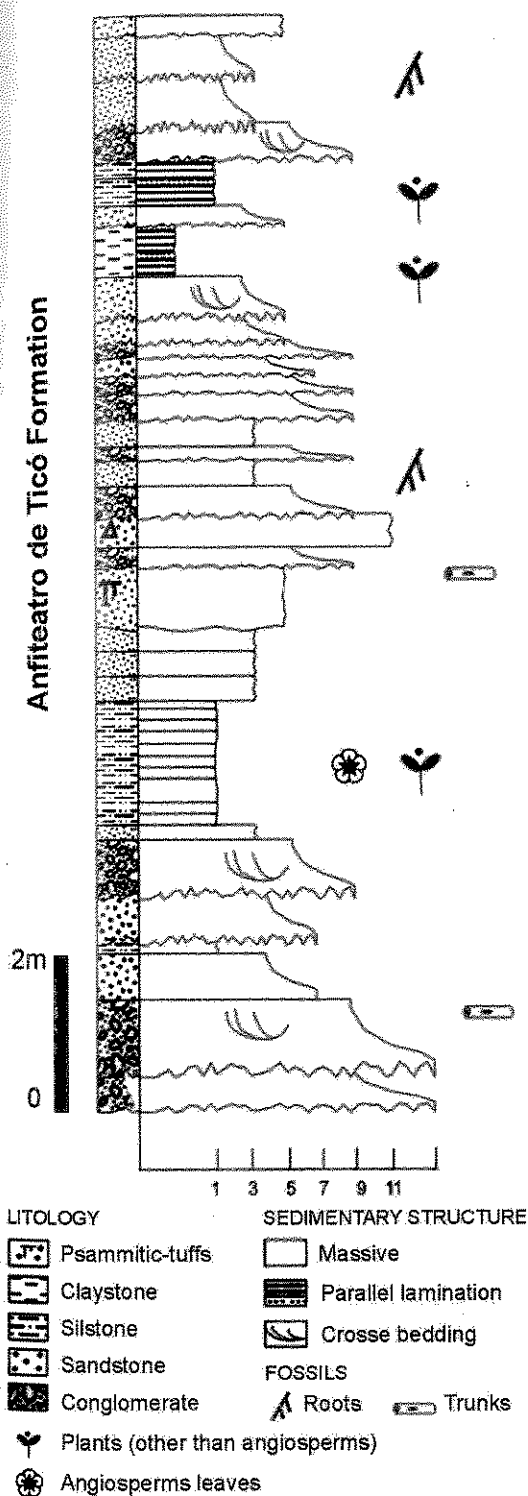


Fig. 2. Lower and middle stratigraphical section of the Anfiteatro de Ticó Formation from their type locality and place of angiosperm occurrence (modified from Cladera et al., 2002).

lack veinlets. The central portion of leaf is vascularized by a midvein and brochidodromous secondaries. The exmedial and apical extremes are innervated by additional series of loops arising from branches of secondaries in the first case, and apical secondaries and midvein in the second case. The leaf imprint surface has numerous little orifices. This porosity may correspond to trichome bases. However, the perforations are often elliptical, and they are absent over veins. Considering the size, these apertures may also correspond to stomatal pores (Figs. 3.C-D). The impression of the opposite face of leaf (Figs. 3.E and 5) showed no perforations, and also polygonal areoles without veinlets.

Remarks. The original foliar organ probably had a very delicate texture. In the same fossiliferous bed there are abundant bennettites. The fragment under study, also shows a segment of *Zamites decurrens* Menéndez with preserved cuticle (fig. 3.A). This fact, and the absence of a cuticle in the angiosperm specimen suggest that the original lamina had a very thin cuticle that may have been easily destroyed during fossilization.

Because of the fragmentary nature of this specimen, lacking its basal part, the possibility also exists that it might correspond to a lobe of a big-lobed leaf. In fact, a lobate leaf has been found at another locality of the same formational unit (Romero & Archangelsky, 1986). However, as far as the authors are aware, the brochidodromous festooned venation pattern appears to be generally associated to unlobed leaves, either peltate or with cordate to truncate base.

Specimen analyzed. BAPb 12280.

Origin. Anfiteatro de Ticó (West Wing), Santa Cruz Province, Argentina.

Stratigraphic horizon. Anfiteatro de Ticó Formation (Baqueró Group), *Ptilophyllum* Biozone, NF *Williamsonia-Zamites*.

Age. Aptian.

DISCUSSION AND COMPARISON

The studied material shares some characters (fundamentally its venation arrangement) with leaves of a nymphaeaphyll morphotype, which was first defined by Krassilov (1977) and redefined later by Crabtree (1987). This type includes several fossil genera: *Castaliites* Hollick, *Hederaephyllum* Fontaine, *Nelumbites* Berry, *Paleonuphar* Hollick, *Populophyllum* Fontaine, *Proteaephyllum* Fontaine (Crabtree, 1987), as well as, *Hydrocotylephyllum* Teixeira, *Menispermities* Lesquereaux (in part), *Nymphaeites* Sternberg (possibly), and *Paranymphaea* Berry, among others.

Considering the few palaeofloras that contain the most early angiosperm records, the

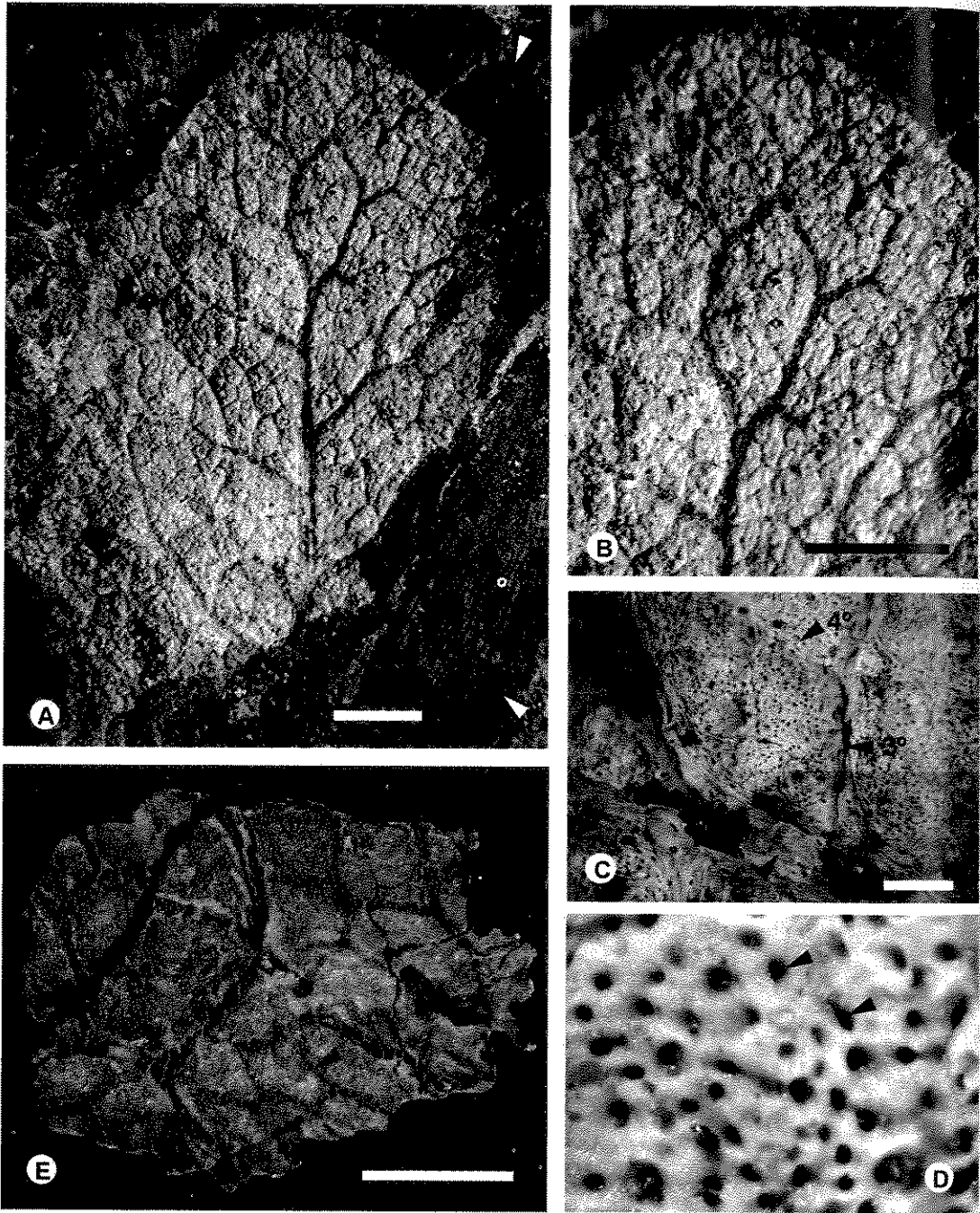


Fig. 3. A-E, Nymphaeaphyll morphotype; A, general aspect (arrows indicate some leaflet of *Zamites decurrens* Menéndez). Scale bar: 0.5 cm; B, detail of apex. Scale bar: 0.5 cm; C, detail from middle leaf imprint zone showing venation of second to fourth order and perforated surface. Scale bar: 0.1 cm. D, detail of perforations (arrows); E, fragment from the opposite face of leaf imprint showing higher venation order. Black arrows indicate an areole (note the absence of veinlets). Scale bar: 0.1 cm (BAPb 12280).

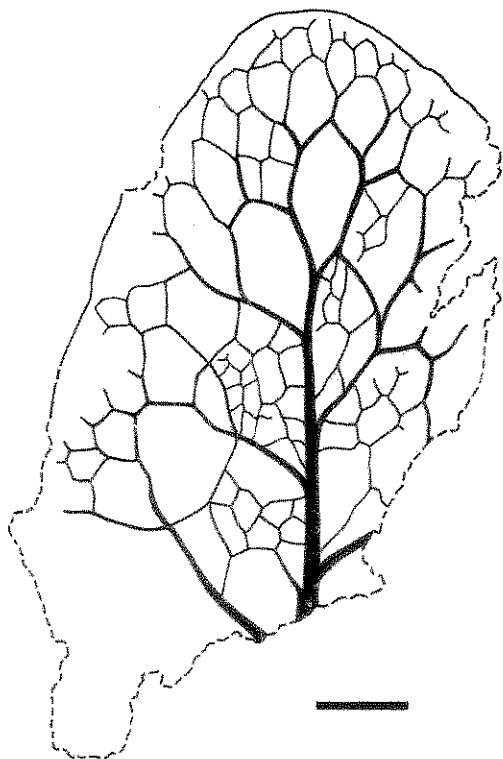


Fig. 4. General aspect. Scale bar: 0,5 cm.

Nymphaeaphyll morphotype occurs so far in three of the four palaeophytogeographic main regions recognized by Vakhrameev (1991) for the Early Cretaceous. According to Hickey's observations (1984), simple leaves with disorganized (low rank *sensu* Hickey, 1971; Hickey *et al.*, 1977) pinnate venation and festooned brochidodromous secondary veins represent the most primitive leaf form known in the angiosperm record. This foliar physiognomy means either an adaptational syndrome to a particular habit or just an "experimental simple shape" (*cf.* Hughes, 1976:142-144). Festooned brochidodromous loops may have provided marginal strengthening for broad, thin leaves (Taylor & Hickey, 1996:254). In the Equatorial Region, there are late Aptian-middle Albian species belonging to the Crato Formation, from northeastern Brazil (Mohr & Friis, 2000; Figs. 4.G and 5.A-E); in the European Province (Euro-Sinian Region), *Hydrocotylephyllum lusitanicum* Teixeira (1948, specially pl. 31, figs. 2-5) was described from the Aptian of Portugal; from the Potomac Province (Euro-Sinian Region), *Proteaphyllum reniforme* Fontaine (zone I, early to middle Aptian), belonging to Potomac Group, eastern North America, has been described (Fontaine, 1889; Berry, 1911; Doyle & Hickey,

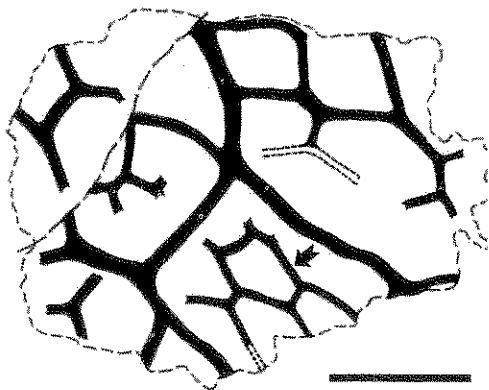


Fig. 5. Fragment from the opposite face of leaf imprint showing higher venation order. Arrow indicate an areole (note the absence of veinlets). Scale bar: 0,1 cm.

1976; Hickey & Doyle, 1977); and in the Australian Province (Austral Region), was found a single specimen from the Aptian of Australia (Taylor & Hickey, 1990). In turn, nymphaeaphyll leaves are also present in slightly younger sequences. Among others: *Populophyllum reniforme* Fontaine, *Nelumbites extenuinervis* Upchurch *et al.* and *N. cf. minimus* Vakhrameev from subzona IIB (early Albian to early late Albian) of Potomac Group (Fontaine, 1889; Upchurch *et al.*, 1994); *N. minimus* Vakhrameev (1952) from the middle Albian of Kazakhstan; *N. aff. minimus* Vakhrameev from the upper Albian of Siberia (Samylina, 1968). All these fossils share the orbicular shape, entire (or crenate) margin and veins forming successive series of festooned brochidodromous loops.

Among fossil nymphaeaphyll leaves, *Nelumbites* is the only genus that has a formal diagnosis. The genus *Nelumbites* was first proposed by Berry (1911) for leaves that had been previously referred to *Menispermites*, but showed a close resemblance to extant *Nelumbo* (Upchurch *et al.*, 1994). Vakhrameev (1952) described formally the genus, later enmended by Upchurch *et al.* (1994) who also designated *M. virginienensis* Fontaine as the type species. Our specimen shares with *Nelumbites* the apex shape, presence of primary and secondaries forming a series of festooned brochidodromous loops, tertiary and more higher venation arrangement and the absence of freely ending veinlets.

In Patagonia, the most comparable record is *Paranymphaea proteaefolia* Berry (1937), from Mata Amarilla Formation, probably Coniacian (Romero, 1978).

Other angiosperm foliar imprints are found in the Anfiteatro de Ticó Formation, although from

another locality (Bajo Tigre). These leaves are basically pinnately or palmately lobed, toothed and with craspedodromous venation (Romero & Archangelsky, 1986). With respect to lamina development and venation arrangement, the new specimen we report here is clearly different. However, both fossils share a similar level of their venation organization (*sensu* Hickey, 1971, 1977). Secondary veins, some of them decurrent, intercostal areas of irregular shape and size, a more or less poor resolution between veins of second and third order, place the Anfiteatro de Ticó specimen in the 'first rank'. On the other hand, the Bajo Tigre specimens have more uniform intercostal areas, belonging to a 'high first rank' (Romero & Archangelsky, 1986).

Among extant plants, the nymphaeaphyll foliar morphotype, is shared by species of several families, usually herbaceous with terrestrial (rhizomatous to scrambling) or aquatic habit: Menyanthaceae (*Nymphoides* Seg.), Polygonaceae (*Antigonon* Endl.), Nelumbonaceae (*Nelumbo* Adans.), Saururaceae (*Gymnotheca* Decne., *Houttuynia* Thunb.), Aristolochiaceae (*Asarum* Linn., *Saruma* Oliver), and Nymphaeaceae (*Nymphaea* Linn.). Some of them (Saururaceae, Aristolochiaceae and Nymphaeaceae), together with Piperaceae, Cabombaceae and monocots (in part), are known as *paleoherbs*. They have been focused, during the last fifteen years, in numerous phylogenetic studies, because of their aggregation as basal angiosperms. Recent genetic studies (Mathews & Donoghue, 1999; Soltis *et al.*, 1999; among others), as well as combined analyses of molecular and morphological data (Doyle & Endress, 2000) revealed the Anita Group (*Amborella* Baill., Nymphaeales, Illiciales, Trimeniaceae and *Austrobaileya* C.T. White) as the basalmost angiosperms. The nymphaeaphyll type is a physiognomic-foliar group that is related to one of these taxa: Nymphaeales.

The increasing palaeontological evidence together with numerous phylogenetic analyses allows to consider, at least, two hypotheses about the nature of the morphology and habit of the most early angiosperms. One, the *Woody Magnoliids Hypothesis*, was analysed by Doyle & Donoghue (1986, 1993). In this, the Magnoliales are placed as a basal sister group of all other angiosperms, following the classical view (e.g., Cronquist, 1981; Takhtajan, 1980), where Magnoliales, Laurales (including Chloranthaceae) and Winterales (known as woody magnoliids) represent an ancestral grade of angiosperm evolution. The alternative view (Paleoherbs Hypothesis), suggests that the ancestral angiosperms were small size herbs, rhizomatous to scrambling, perennial with (at the

most) limited secondary growth, with simple and little flowers. This hypothesis was put forward by Taylor & Hickey (1990, 1992) on the basis of a cladistic analysis, and the discovery of paleoherb-like fossils (leaves with attached inflorescence) from the Aptian of Australia. Further evidences compatible with the herbaceous origin (including fossil records, sedimentological and geochemical data) are summarized and discussed by Taylor & Hickey (1996). In this sense, the fossil here studied appears to be a new piece of evidence compatible with this hypothesis. Both hypotheses propose, from the intrinsic features of the involved taxa (e.g., herbaceous vs. woody), several possibilities about the causality of the gradual angiosperm increase in palaeocomunities, through possible scenarios in which they could irradiate and evolve (for discussion see Doyle & Donoghue, 1993; Wing & Boucher, 1998).

The stratigraphic sequence of fossil angiosperm remains, appear to be more consistent with the Paleoherbs than the Magnoliacean Hypothesis; however, the difference in appearance time of woody vs. herbaceous angiosperm evidences is not so great that it unambiguously favors any of the alternative hypotheses (Doyle & Donoghue, 1993; Wing & Boucher, 1998). Even, the presence of leaves related to Magnoliidae or Hamamelididae (Romero & Archangelsky, 1986) and the new record presented here, that is most probably related to paleoherbs, may constitute a further example of coexistence, at the same time and place of both woody magnoliids and paleoherbs.

CONCLUSIONS

Here we described a new foliar imprint record having features partly defined as belonging to the nymphaeaphyll morphological type. This type occurs among the most early assemblages having angiosperms (northeastern Brazil, Portugal, South Australia, eastern North America), and is part of a physiognomic-foliar pool associated to taxa considered to be basal within the group. This foliar morphotype, is found in some members of extant angiosperms of usually herbaceous habit, and perhaps, by analogy, this may have been the original habit of our fossil species. Hughes (1976:142-144) points out that the nymphaea-phyllan leaf architecture may represent only an "experimental simple shape". However, other authors (Samylina, 1968; Axelrod, 1970; Krassilov, 1977) suggest that this leaf morphology may represent an adaptational syndrome for aquatic habitats. The Anfiteatro de Ticó specimen was perhaps an hydrophyte, associated to the large bodies of calm lentic waters that were developed in Patagonia during the Aptian.

This also suggests, once more, that little herbaceous plants were presents in the early cretaceous associations having angiosperms. However, other type of leaves (Bajo Tigre specimens) suggests that woody angiosperms may have also developed at the same time and place.

In spite of the scarcity of angiosperm leaf records in both hemispheres for this age, the resemblance in both basic aspects: the grade of venation regularity (ranks), and sharing of morphological types should be emphasized. Every new record appears to support this and the fossil we report here is an example.

Finally, the incipient diversity of angiosperms found in Anfiteatro de Ticó Formation, confirms their early development during the Aptian in Patagonia. This suggests an even earlier (pre-Aptian) presence of the group in the region. In this regard, the most accepted theory (based on first occurrences, diversity and relative evidence analyses) considers that angiosperms originally had a low latitudinal distribution, from where they spread toward the poles (Axelrod, 1959; Brenner, 1976; Crane & Lidgard, 1989; Lidgard & Crane, 1990). However (and not discussing the hypothetical angiosperm center of origin), it is becoming evident that its early evolution has been associated to several radiation centers, and some of these may will have been located at higher palaeolatitudes, as that of Patagonia during the Aptian.

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