



Early angiosperm diversification: evidence from southern South America

Sergio Archangelsky^a, Viviana Barreda^{a,*}, Mauro G. Passalia^b, Maria Gandolfo^c, Mercedes Prámparo^d, Edgardo Romero^a, Rubén Cúneo^e, Alba Zamuner^f, Ari Iglesias^f, Magdalena Llorens^g, Gabriela G. Puebla^d, Mirta Quattrocchio^h, Wolfgang Volkheimer^d

^a División Paleobotánica, Museo Argentino de Ciencias Naturales B. Rivadavia, CONICET, Av. Angel Gallardo 470, C1405DJR, Buenos Aires, Argentina

^b Instituto de Investigaciones en Biodiversidad y Medioambiente, CONICET-UNCo, Quintral 1250 (8400), San Carlos de Bariloche, Argentina

^c L.H. Bailey Hortorium, Department of Plant Biology, Cornell University, Ithaca, NY 14853, USA

^d IANIGLA-CCT CONICET, Adrián Ruiz Leal s/n, Casilla Correo 131, C5500, Mendoza, Argentina

^e Museo Paleontológico Egidio Feruglio, Av. Fontana 140, C9100, Trelew, Chubut, Argentina

^f División de Paleobotánica, Facultad de Ciencias Naturales y Museo de La Plata, Paseo del Bosque s/n, C1900, La Plata, Argentina

^g CNEA Regional Patagonia, 26 de Noviembre s/n CC 178 (9100), Trelew, Argentina

^h Departamento de Geología, Universidad del Sur, San Juan 670, C8000, Bahía Blanca, Argentina

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ABSTRACT

In this report, we analyze the angiosperm fossil record (micro- and megafossil) from the central and southern basins of Argentina, southern South America, deposited between the late Barremian (128.3 Ma) to the end of the Coniacian (85.8 Ma). Based on this analysis, three major stages in the evolution of the angiosperms in the southernmost region of South America are established as follows: the late Barremian–Aptian, the latest Aptian–earliest Albian, and the middle Albian–Coniacian. The comparison between our fossil data set and those from Australia, North America, Asia and Europe suggest that the evolution and diversification of the angiosperms at mid and high latitudes in both hemispheres occurred roughly synchronously.

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1. Introduction

Today, with approximately 300,000 species distributed worldwide, the angiosperms are the dominant group of vascular plants in terrestrial ecosystems. Even though they constitute the most diverse and economically important group of plants, many uncertainties still exist concerning their origin, evolution and diversification. Paleobotanists and neobotanists have recognized that the fossil record provides vital evidence for elucidating the origin and early evolution of the flowering plants; likewise, they agree that a sound study of the angiosperm fossil record with emphasis on those fossils exhumed from Lower to mid-Cretaceous sediments is imperative to fully comprehend their appearance, rise, diversification and dominance (Hughes, 1973; Retallack and Dilcher, 1986).

Fossil angiosperms, both mega and microfossils, were recorded throughout the world close to the Barremian/Aptian boundary (Friis et al., 2006). However, the oldest records, represented by pollen grains in eastern Israel (Brenner and Bickoff, 1992) and by pollen grains, leaves and inflorescences in northeastern China (Sun

and Dilcher, 2002), appeared slightly earlier during the late Valangian–early Hauterivian (Neocomian). Paleobotanical data, gathered so far primarily from North America and Europe indicate that angiosperms underwent major diversification during the mid-Cretaceous (Vakhrameev, 1991; Crane, 1987; Crane and Lidgard, 1989; Lidgard and Crane, 1990; Crane et al., 1995; Crepet et al., 2004; Heimhofer et al., 2005, 2007, and citations therein) and probably achieved dominance in some habitats during the Turoonian (Hughes, 1976). However, it was not until the Cenozoic when the angiosperms attained an ecological prominence comparable to the level that they have today (Friis et al., 2006). Nevertheless, this pattern has mainly been established for the Northern Hemisphere. In the Southern Hemisphere Cretaceous angiosperm fossil data are not so abundant, but in addition to the evidence from Argentina presented herein (see references below), there are records from Brazil, Africa, Australia and Antarctica (Dettmann, 1973; Doyle et al., 1977; Dettmann and Thomson, 1987; Regali and Viana, 1989; Burger, 1990; Taylor and Hickey, 1990; Cantrill and Nichols, 1996; Pole, 2000; Mohr and Friis, 2000). Although the available data are still scanty for southern South America, in recent years a wealth of information concerning the early fossil record of angiosperms has been gathered from the central and southern basins of Argentina (e.g. Prámparo, 1999; Palamarczuk et al., 2000; Passalia et al., 2001;

* Corresponding author.

E-mail address: vbarreda@macn.gov.ar (V. Barreda).

Llorens, 2003; Puebla, 2004; Cúneo and Gandolfo, 2005; Barreda and Archangelsky, 2006; Quattrocchio et al., 2006; Vallati, 2001a,b, 2006; Iglesias et al., 2007; Passalia, 2007; Archangelsky et al., 2008; Medina et al., 2008) adding new evidence to the previously known (e.g. Berry, 1937; Menéndez, 1959; Volkheimer and Salas, 1975a,b; Romero and Archangelsky, 1986; Archangelsky and Taylor, 1993; Archangelsky et al., 1994). The data presented herein are critical because they increase our understanding of the evolution and radiation of early angiosperms in the Southern Hemisphere, including early forms of differentiating angiosperm lineages, and most importantly because the geological age is accurately known for each one of the formations where these fossils were collected. In this regard, the age of several dated angiosperm bearing strata are now confirmed by ammonites, dinoflagellate cysts and radiometric techniques. This gives a strong support for the sequence postulated here. The geographic position of Argentina in Gondwana and the history of its sedimentary basins during the Cretaceous are crucial to comprehending angiosperm distribution models and migration patterns in the Southern Hemisphere, particularly for South America. The basins' history and geographic position are correlated with several major geological events that changed paleoenvironmental conditions, and consequently correspond with the disappearances and appearances of taxa. These key events started with the beginning of the breakup of Gondwana during the Late Jurassic, the opening of the South Atlantic during the earliest Cretaceous (as a consequence of the formation of continental extensional rift basins in central western Argentina, like the San Luis Basin), the initial uplift of the Cordillera Principal in the Barremian–Cenomanian (at the same time that a volcanic cordillera developed during the Aptian–Albian), and culminated in the deformation and final uplift of the Andean Cordillera during the Cenozoic. In Barremian–Albian times, the Neuquén and the Austral basins developed differently. The Neuquén Basin records the presence of progressively shallower sedimentation that ended with the deposition of evaporites and continental red beds (Huitrin–Rayoso Group) followed by the continental sedimentation of the Neuquén Group during the Cenomanian–Campanian, controlled by the initial uplift of the Andes, which provided an important western source of sediments (Macellari, 1988). The Austral Basin registered marine sedimentation throughout the Cretaceous with two “transgressive peaks” represented by two transgressions caused by increases in sea level, the first probably during the Cenomanian–Turonian and the second during the Coniacian–Santonian (Riccardi, 1988).

In this report, we analyze data collected in Argentina (between 32° S and 52° S) during the critical period of time between the late Barremian and Coniacian, as a first attempt to comprehend the timing of appearance and evolutionary changes of ancestral angiosperms in southern South America.

The angiosperm fossil record (see Appendix) was compiled from five Cretaceous Argentinean basins, the central-western San Luis and Neuquén basins and the southern Deseado Massif, San Jorge Gulf and Austral basins (Fig. 1).

2. Material and methods

In this study, all the available information concerning ancestral angiosperms of south western Argentina, between the late Barremian (128 Ma) and the Coniacian (85.8 Ma), was evaluated. The Cretaceous angiosperm record from Patagonia is largely based on pollen grains and leaf impressions. Here we consider as angiospermous characters the presence of a tectate–columellate sexine in the case of pollen grains, and a hierarchical network of successively thinner veins for the leaves.

The chronostratigraphic assignment of the units that bear the micro- and megaflores were based on: radiometric dating (RD),

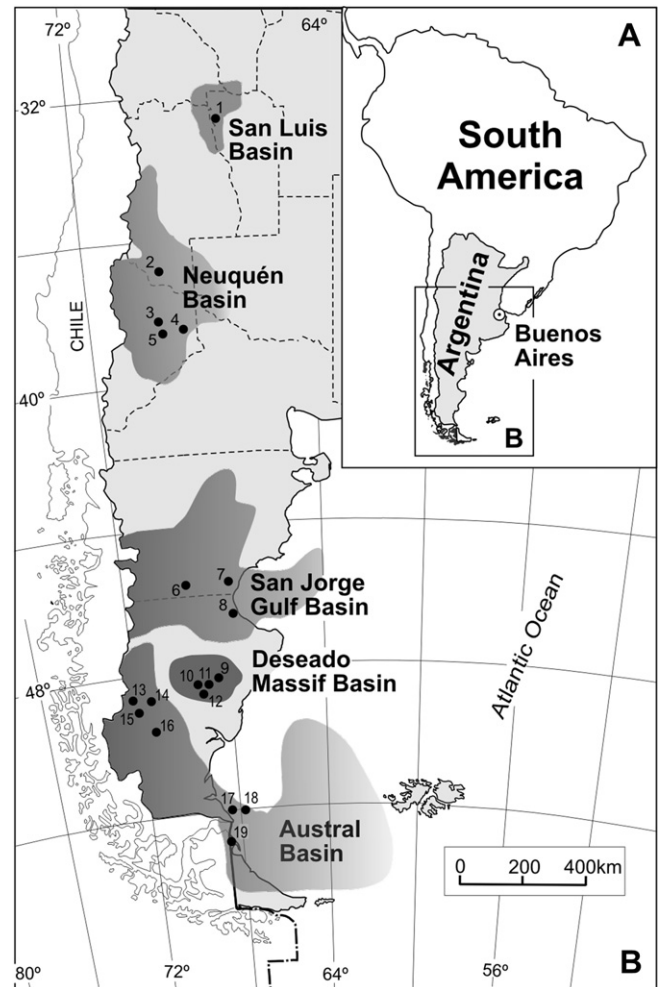


Fig. 1. A. Location map. B. Detail of Central and Southern Argentina showing Cretaceous basins (grey areas) and location of the geological units carrying the angiosperms (points 1–19). 1, La Cantera Formation. 2, El Zampal section (Huincul Formation). 3, Cerro Lisandro Formation. 4, Portezuelo Formation. 5, Quili Malal Member (Rayoso Formation). 6, Castillo Formation. 7, Pozo D-129 Formation. 8, Cañadon Seco Formation. 9, Bajo de los Corrales area (un-named Formation). 10, Anfiteatro de Ticó area (Anfiteatro de Ticó Formation). 11, Bajo Tigre area (Anfiteatro de Ticó Formation). 12, Meseta Baqueró area (Punta del Barco Formation). 13, Bajo Comisión section (Kachaiké Formation). 14, La Horqueta section (Río Mayer and Piedra Clavada formations). 15, Arroyo Caballo Muerto section (Kachaiké Formation). 16, Quebrada Don Nielsen and Tres Lagos sections (Piedra Clavada Formation); María Elena and Mata Amarilla sections (Mata Amarilla Formation). 17, *Inoceramus* Inferior Formation. 18, Margas Verdes Formation. 19, Springhill Formation.

biostratigraphy (ammonites, dinoflagellate cysts and palynomorphs) (BS) and stratigraphic correlation (SC). The units considered are: Springhill Formation (BS), *Inoceramus* Inferior and Margas Verdes Formations (offshore) (BS) and Río Mayer (BS), Kachaiké (BS), Piedra Clavada (BS) and Mata Amarilla (BS) Formations (continental) of the Austral Basin; the Anfiteatro de Ticó (RD), Punta del Barco (RD) and Bajo de los Corrales, Un-named Formation of the Deseado Massif Basin; the Pozo D-129 (BS), Castillo (RD) and Bajo Barreal (Cañadón Seco) Formations (RD) of the San Jorge Gulf Basin; the Quili Malal Member of the Rayoso Formation (BS) and Huincul, Cerro Lisandro and Portezuelo Formations (belonging to Neuquén Group known as “Strata with Dinosaurs”) (SC) of the Neuquén Basin; and, finally, the La Cantera Formation of the San Luis Basin (SC) (Fig. 2). In the Appendix 1 the stratigraphic distribution and ages of the pollen and leaf morphotypes are presented in detail.

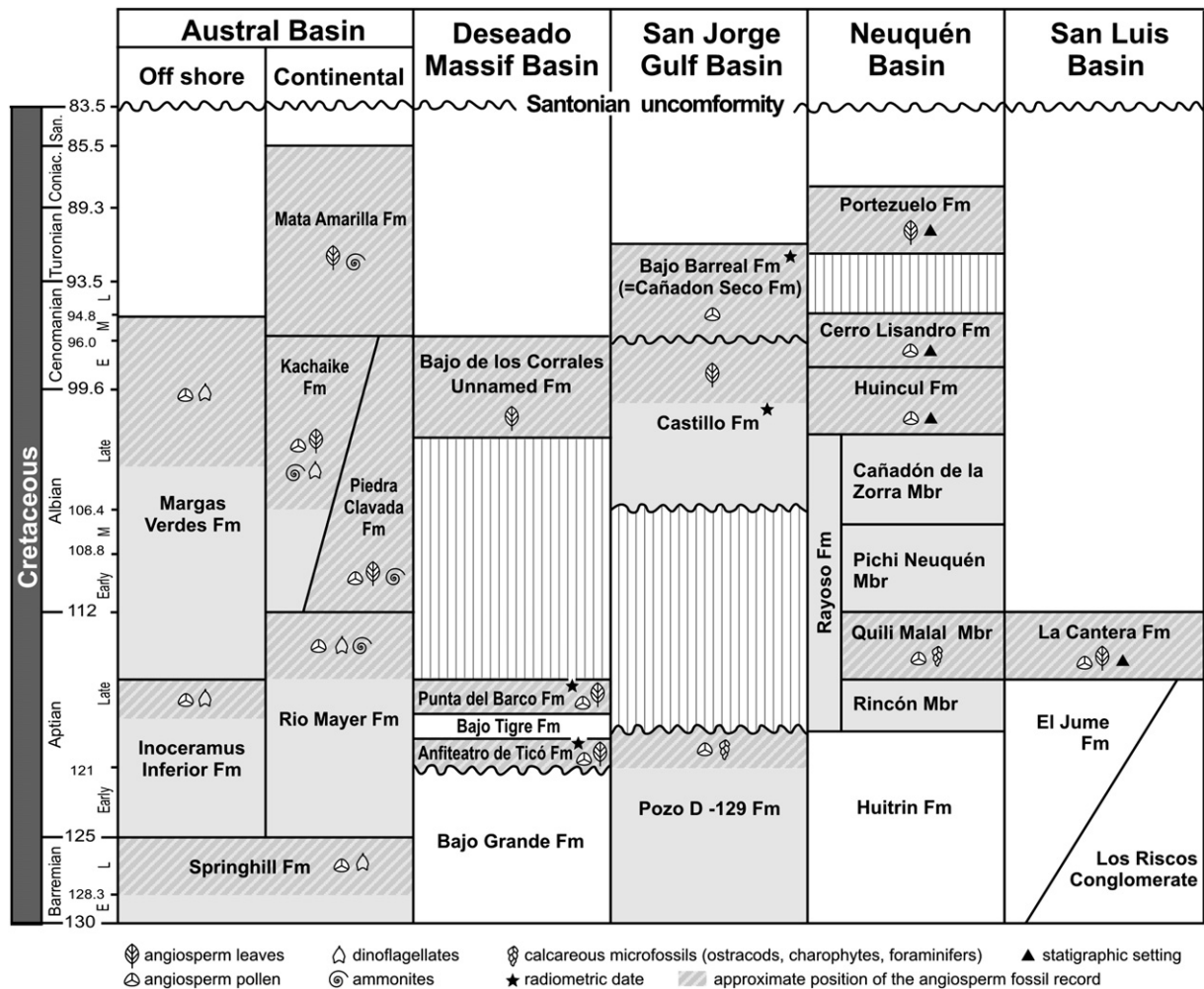


Fig. 2. Stratigraphic chart of selected Cretaceous formations of Central and Southern basins of Argentina carrying pollen and/or leaf angiosperm records (grey areas). Banded area indicates an approximate position of the angiosperm fossil record within each formation. Independent age controls (dinoflagellates; ammonites; calcareous microfossils and radiometric dates) are also included. Cretaceous boundaries from the geological time scale of Gradstein et al. (2004).

The geological time scale of Gradstein et al. (2004) was followed in assigning ages to the floras. The Cretaceous Period, the youngest of the Mesozoic Era, ranges from 145.5 ± 4.0 to 65.5 ± 0.3 Ma with two epochs: Early (145.5 ± 4.0 – 99.6 ± 0.9 Ma) and Late (99.6 ± 0.9 – 65.5 ± 0.3 Ma) (Ogg et al., 2004).

3. Results and discussion

Based on the taxonomic composition of the floras, including the chronological distribution and relative abundance of angiosperms, three major stages of angiosperm evolution can be recognized for the Cretaceous of southernmost South America (Fig. 3): Stage I, or the late Barremian–Aptian phase, is characterized by the appearance of the first angiosperms within gymnosperm–fern dominated floras; Stage II or the latest Aptian–earliest Albian phase, includes the first definitive occurrences of eudicots among gymnosperm–fern dominated floras; Stage III, or the middle Albian–Coniacian phase, is clearly characterized by a progressive angiosperm diversification as indicated by several leaf and pollen morphotypes; and their increasing participation in plant communities to the end of this phase.

Stage I occurs during the late Barremian–Aptian, when the first angiosperm pollen and leaf remains appear. During this stage, the angiosperms are marginally represented and constitute the

subordinate component of floras dominated by gymnosperms, pteridophytes and bryophytes (Archangelsky, 2001, 2003; Quattrocchio et al., 2006). Leaf remains correspond to three basal morphotypes, while pollen grains have a delicate exine with microreticulate sculpture and a variable number of poorly-defined to well-developed apertures. Leaves (119.65 ± 0.45 Ma) correspond to the nymphaeaphyll (1mf) (Passalia et al., 2003) and micro-mesophyll lobate serrate leaf (2mf) (Romero and Archangelsky, 1986) morphotypes. As like many early angiosperm leaves, both of these morphotypes have decurrent multistranded veins, a character considered a symplesiomorphy within the angiosperms (Taylor and Hickey, 1996). Leaves with festooned brochidodromous secondary veins, that characterize the nymphaeaphyll morphotype, have also been recognized in Aptian beds from North America (*Proteaphyllum reniforme* Fontaine; Doyle and Hickey, 1976) and Australia (Taylor and Hickey, 1990). Pollen has been referred to the *Clavatipollenites* complex (1p) (Archangelsky and Gamarro, 1966; Archangelsky and Taylor, 1993; Vallati, 1996; Archangelsky and Archangelsky, 2002, 2004; Quattrocchio et al., 2006). These pollen types are documented at several outcrops and first appear nearly synchronously worldwide (Kemp, 1968; Heimhofer et al., 2005).

Later within Stage I, a new foliar type, the crenate lobate morphotype (3mf), appears in slightly younger deposits ca. 118.56 ± 1.4 Ma. These leaves are similar to those described by

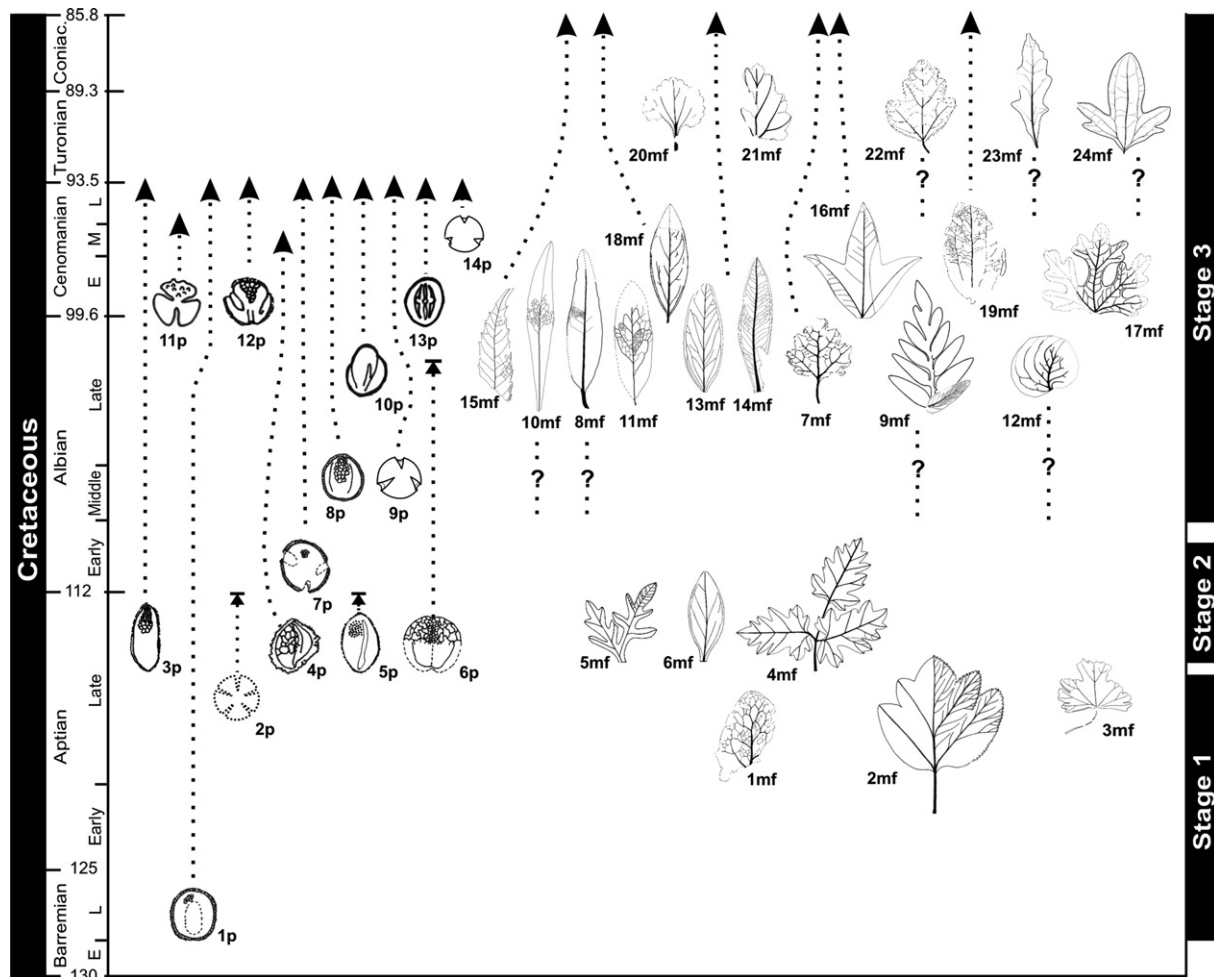


Fig. 3. Summary of pollen (p) and megafossil leaf (mf) morphotypes records from Cretaceous basins of Argentina considered in this study. **Stages I–III** represent major events in the development of the angiosperms in the southernmost region of South America established in this study. *Clavatiipollenites* complex (1p), *Asteropollis asteroides* (2p), *Liliacidites* sp. (3p), *Pennipollis peroreticulatus* (4p), *Stellatopollis* sp. (5p), *Afropollis* spp./*Schrankipollis* spp. (6p), *Tricolpites* sp. (7p), *Rousea* sp. (8p), *Tricolporoidites* sp. (9p), *Psilatricolpites* sp. (10p), *Verrutricolpites* sp. (11p), *Dryadipollis* sp. (12p), *Nyssapollenites* sp. (13p), tricolporate with reduction of the colpi (14p), nymphaeaphyll morphotype (1mf), lobate serrate morphotype (2mf); crenate lobate morphotype (3mf), trifoliolate morphotype (4mf), pinnatilobate nanophyll morphotype (5mf), pinnate brochidodromous morphotype (6mf), *Thorrhalla dentata* (7mf), *Thorphyllum patagonica* (8mf), *Kachaikenia compuesta* (9mf), *Rogersia australis* (10mf), festooned brochidodromous morphotype (11mf), eucamptodromophyll morphotype (12mf), *Myrtoidea* sp. (13mf), *Myrtoidea patagonica* (14mf), elongated serrate morphotype (15mf), palmatilobate brochidodromous morphotype (16mf), multilobate morphotype (17mf), elongated eucamptodromous to weak brochidodromous morphotype (18mf), acrodromophyll morphotype (19mf), crenate unlobed morphotype (20mf), crenate (large teeth) morphotype (21mf), pinnatilobed ovate morphotype (22mf), pinnatilobed elliptical morphotype (23mf), palmatilobed eucamptodromous morphotype (24mf). Cretaceous boundaries from the geological time scale of Gradstein et al. (2004).

Teixeira (1948) from Cretaceous sediments of Portugal as *Hydrocotylophyllum*, a morphotype previously recognized in the late Albian of Antarctica (Cantrill and Nichols, 1996). Pollen records, represented by *Retimonocolpites* sp. A, *R.* sp. B, *Retiacolpites* sp., *Clavatiipollenites hughesii*, *Asteropollis asteroides* (2p) and *Monocolpopollenites* sp., indicate an incipient increase in angiosperm diversity by the end of this phase (Llorens, 2003).

Stage II includes latest Aptian–earliest Albian floras. It is characterized by the presence of the first definitive fossils with affinities to the eudicots. Fossil leaves are distinctive from those of the previous stage. Two morphotypes represent the earliest record of compound leaves in South America (Puebla, 2004). These are the trifoliolate morphotype (4mf) and the pinnatilobate nanophyll (5mf). A third morphotype, the pinnate brochidodromous (6mf) (Puebla, 2004) shows a well-defined intramarginal vein. The initial increase in angiosperm pollen diversity observed at the end of Stage I is well documented during Stage II. Several species of *Clavatiipollenites* and *Asteropollis asteroides* are well-represented, in addition to new forms such as *Liliacidites* (3p), *Pennipollis peroreticulatus* (4p),

Stellatopollis (5p) and several species of *Afropollis* spp. (6p) (Prámparo, 1990, 1994, 1999; Vallati, 1995, 2006; Medina et al., 2008). While its systematic affinities remain unresolved, *Afropollis* is here considered to be angiospermous due to the presence of reticulate sculpture supported by low columellae and the aperture type as suggested by Hesse and Zetter (2005).

Microreticulate tricolpate pollen grains related to the ancestral eudicots make their first appearance at the end of this stage in the earliest Albian (Volkheimer and Salas, 1975a,b; Medina et al., 2008), as it has been observed in other mid and high latitude Cretaceous associations of North America (Doyle and Hickey, 1976), Europe (Heimhofer et al., 2005, 2007) and Australia (Dettmann, 1973; Burger, 1990). In equatorial suites, however, the first appearance of eudicots occurred earlier by the early Aptian (Brenner and Bickoff, 1992), and in Brazil this event coincides with a peak of abundance of *Afropollis* (Regali and Viana, 1989).

Pollen types of these first eudicots have been referred to *Tricolpites* (7p) and *Retitricolpites* (Volkheimer and Salas, 1975a,b; Medina et al., 2008). The presence of three apertures would have

provided a selective advantage to the eudicots because of the increase in the number of available sites for germination. This fact, joined with the shift in the aperture position from poles to the equator, would have had a great influence in the success and radiation of this group (Furness and Rudall, 2004).

Several pollen species (*Asteropollis asteroides* and *Stellatopollis* spp.) become extinct during this phase.

Angiosperms are represented at Stage II by few taxa (Vallati, 2006; Prámparo, 1990, 1999; Medina et al., 2008) growing within a gymnosperm/fern dominated landscape.

Stage III includes sediments of middle Albian-Coniacian age and is characterized by a progressive increase in both angiosperm diversity and relative abundance. Younger records of the *Afropollis*?/*Schrankipollis* group have been reported from the middle-late Albian of Patagonia (Barreda and Archangelsky, 2006; Archangelsky et al., 2008), associated with the first findings of ulcerate pollen grains of winteraceous affinity (*Walkeripollis*). New tricolpate reticulate forms with variable lumens (*Rousea*, 8p), tricolpate psilate forms (10p) and tricolporoid ones (9p) appear, indicating that these pollen morphotypes evolved during the Albian. These palynological assemblages are associated with leaf remains belonging to *Thorhallenia dentata* characterized by elliptic to ovate laminae, toothed margin and craspedodromous to actino/palinactinodromous venation (Passalia, 2007), and several leaf morphotypes. These morphotypes are represented by elliptic leaves with entire margins and pinnate brochidodromous venation (*Thorphyllum patagonica*, 8mf), leaflets with a strong fimbrial vein (*Kachaikenia compuesta*, 9mf), festooned leaves with brochidodromous venation (*Rogersia australis*, 10mf), and, finally, a morphotype represented by a rounded lamina and eucamptodromous venation (12mf) (Cúneo and Gandolfo, 2005). Two new morphotypes are also found that are considered variants of the previously mentioned pinnate brochidodromous form (6mf). Both morphotypes are characterized by secondary veins admedially or exmedially ramified, one of them with a single intramarginal vein (13mf) while the other, *Myrtoidea patagonica* (Passalia et al., 2001), has a double intramarginal vein (14mf). In addition, leaf remains with elongated lamina and small teeth (15mf) appear for the first time. Towards the end of the Albian and the beginning of the Cenomanian, there is an increment in the number of leaf morphotypes. They are represented by higher numbers of palmatilobed leaves (16mf and 17mf), elongated leaves with entire margins and both, pinnate eucamptodromous (18mf) and brochidodromous venation (possibly related to *Myrtoidea* type), and finally, acrodromophyll leaves (19mf). Coincident with this change in the megafloora, there is an increase in angiosperm pollen diversity. Tricolpate forms with variable sculpture, such as gemmate or verrucose (*Verrutricolpites*, 11p), other tricolporoid and clearly tricolporoid forms (*Dryadopollis*, 12p), and forms with developed colpi costae related to *Nyssapollenites* (13p) are present. The presence of endoapertures is another feature of strong adaptive significance in the evolution of eudicots. Recent studies on extant pollen grains indicate that endoapertures may have harmomegathic functions (Furness et al., 2007), being a crucial advantage for early eudicots to colonize drier niches.

Within the Cenomanian, pollen grains with a remarkable reduction of the polar axis and shortening of the colpi (14p) appear, suggesting the probable emergence of the triplicate forms.

A very diverse angiosperm assemblage of fossil leaves can be identified in the Cenomanian?–Coniacian strata. In comparison with the oldest angiosperm records, this angiospermous assemblage shows a great increase in diversity as well as in relative abundance within the whole represented taphocenosis. Although with variations, some previously identified morphotypes are present (1mf, 13mf, 14mf, 16mf, 18mf, 19mf) (Berry, 1928, 1937; Iglesias et al., 2007) in conjunction with new ones, such as

pinnatilobed leaves with ovate (22mf) or elliptical (23mf) shape, and palmatilobed forms with secondary veins eucamptodromous (24mf). A variety of serrate, unlobed forms are also well represented, including leaves with craspedodromous and semi-craspedodromous venation (Berry, 1928; Iglesias et al., 2007). Finally, from late Turonian – early Coniacian levels, leaves with crenate (21mf and 22mf) and serrate margin (similar to 15mf type) occur (Passalia et al., 2008). Currently, no palynological records are available for the Turonian–Coniacian interval, although certain pollen forms (3p, 7p, 8p, 11p, 12p, and 13p) have been recuperated from younger sediments not included in this study, suggesting its continuity.

The progressive increase in angiosperm diversity and relative abundance observed during the late Barremian–Coniacian interval in southern South America can be compared with those previously reported from the Southern (e.g. Australian basins) and Northern Hemispheres (e.g. Potomac Group sequence, Western Portuguese and Algarve basins, Northeast China and Siberian basins). In addition to the data presented here, the angiosperm history in southern latitudes during the Cretaceous has been reconstructed on the basis of pollen and leaf records mainly from Australian beds (e.g. Dettmann, 1973; Pole, 2000). In the Northern Hemisphere, while the Potomac Group sequence is one of the classic paleofloristic succession from North America (Doyle and Hickey, 1976), the Western Portuguese and Algarve basins from Europe are well known by their megafossil, mesofossil and pollen diversity (e.g. Friis et al., 1994; Heimhofer et al., 2005, 2007). Equally important are the angiosperm records from Northeastern China (Sun and Dilcher, 2002; Sun et al., 2000, 2008), as well as those from the Siberian region (see Krassilov, 1997). It is worth noting that, although with some differences in the time of the first angiosperm appearances, a similar pattern of angiosperm diversification has been observed worldwide. The major successions of events that have been identified in both northern and southern hemispheres can be synthesized as following:

The late Neocomian–early Aptian is characterized by the first angiosperm records with pollen grains having delicate exines and poorly defined apertures and leaf morphotypes characterized by decurrent multistranded veins drawing an incipient disorganized hierarchical network pattern. The Aptian/Albian is marked by an early phase of angiosperm radiation and the appearance of the first eudicot lineages in almost all continents (3-aperturate pollen grains and eudicot-related leaves). The late Albian–Coniacian shows a great increase in both angiosperm diversity and abundance. The pollen types include an important variability of sculpture and apertures and many types of leaf display a well-defined venation patterns.

This comparison suggests that the first events in the evolution and diversification of the angiosperms in both hemispheres, at mid and high latitudes, occurred roughly synchronously.

4. Final remarks

The data presented in this report suggest the presence of three stages in the evolution of the angiosperms at the southern tip of South America. Although these data do not contradict the idea that the angiosperms did not achieve dominance in nearly all environments of the Southern Hemisphere until the Maastrichtian as suggested by Hughes (1976), studies including sediments of Coniacian to Maastrichtian age are necessary to confirm this. It would be unsurprising that the angiosperms became dominant in some habitats before the end of the Cretaceous in the southernmost tip of South America. However, more field work and research is necessary to confirm this fact. Further field work and laboratory research is currently being undertaken with the goal of providing information

in hopes that the Southern Hemisphere angiosperms can continue to be considered in a more global perspective.

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Appendix 1

Stratigraphic distributions and ages of pollen (1–14p) and leaf (1–24mf) morphotypes, with short descriptions of the leaves.

Pollen morphotypes

1p) *Clavatipollenites* complex

Stratigraphic position and age:

1. Anfiteatro de Ticó Fm, Deseado Massif Basin, (Archangelsky and Gamero, 1966; Archangelsky and Taylor, 1993); late Aptian (118.56–119.7 Ma) (Corbella, 2001).
2. Punta del Barco Fm, Deseado Massif Basin (Llorens, 2003); late Aptian (118.56–119.7 Ma) (Corbella, 2001).
3. Pozo D-129 Fm, San Jorge Basin; Aptian (Vallati, 1996).
4. Inoceramus Inferior Fm (off shore) Austral Basin; Aptian (Palamarczuk et al., 2000).
5. Ranquiles Fm = Quili Malal Member, Rayoso Fm (Leanza, 2003), Neuquén Basin; Aptian (Vallati, 1995).
6. La Cantera Fm, San Luis Basin; Neocomian (Yrigoyen, 1975); late Aptian (Prámparo, 1990, 1994, 1999).
7. Río Mayer and Piedra Clavada Fms, La Horqueta section, Austral Basin; latest Aptian-early Albian (Medina et al., 2008)
8. Springhill Fm, Austral Basin; late Barremian (Quattrocchio et al., 2006)

2p) *Asteropollis asteroides*

Stratigraphic position and age:

1. Punta del Barco Fm, Deseado Massif Basin (Llorens, 2003); late Aptian (118.56–119.7 Ma) (Corbella, 2001).
2. Inoceramus Inferior Fm (off shore) Austral Basin; Aptian (Palamarczuk et al., 2000).
3. Ranquiles Fm = Quili Malal Member, Rayoso Fm (Leanza, 2003), Neuquén Basin; Aptian (Vallati, 1995).
4. Huitrín Fm = Quili Malal Member, Rayoso Fm (Leanza, 2003), Neuquén Basin; Earliest Albian (Volkheimer and Salas, 1975a,b).
5. La Cantera Fm, San Luis Basin; Neocomian (Yrigoyen, 1975); late Aptian (Prámparo, 1990, 1994, 1999).

3p) *Liliacidites* sp.

Stratigraphic position and age:

1. Ranquiles Fm = Quili Malal Member, Rayoso Fm (Leanza, 2003), Neuquén Basin; Aptian (Vallati, 1995).
2. Bajo Barreal Fm = Cañadón Seco Fm (Archangelsky et al., 1994); Cenomanian- (91–95.8 Ma) (Bridge et al., 2000).
3. Piedra Clavada Fm, Quebrada Don Nielsen and Tres Lagos sections, Austral Basin; middle-late Albian (Archangelsky et al., 2008).
4. Río Mayer and Piedra Clavada Fms, La Horqueta section, Austral Basin; latest Aptian-early Albian (Medina et al., 2008)

4p) *Pennipollis peroreticulatus* (Brenner) Friis, Pedersen and Crane

Stratigraphic position and age:

1. La Cantera Fm, San Luis Basin; Neocomian (Yrigoyen, 1975); late Aptian (Prámparo, 1990, 1994, 1999).
2. Huincul and Cerro Lisandro Fms, Neuquén Basin; Albian?-Cenomanian (Vallati, 1995).
3. Kachaiké Fm, Bajo Comisión section, Austral Basin (Barreda and Archangelsky, 2006); late Albian-early Cenomanian (Aguirre-Urreta, 2002; Guler and Archangelsky, 2006).
4. Kachaiké Fm, Caballo Muerto Creek section, Austral Basin (Llorens, 2005); late Albian-early Cenomanian (Aguirre-Urreta, 2002; Guler and Archangelsky, 2006).
5. Piedra Clavada Fm, Quebrada Don Nielsen and Tres Lagos sections, Austral Basin; middle-late Albian (Archangelsky et al., 2008).

5p) *Stellatopollis* sp.

Stratigraphic position and age:

1. La Cantera Fm, San Luis Basin; Neocomian (Yrigoyen, 1975); late Aptian (Prámparo, 1990, 1994, 1999).

6p) *Afropollis* spp./*Schrankipollis* spp.

Stratigraphic position and age:

1. La Cantera Fm, San Luis Basin; Neocomian (Yrigoyen, 1975); late Aptian (Prámparo, 1990, 1994, 1999).

- Ranquiles Fm = Quili Malal Member, Rayoso Fm (Leanza, 2003), Neuquén Basin; Aptian (Vallati, 1995).
- Bajo Comisión section, Kachaïke Fm, Austral Basin (Barreda and Archangelsky, 2006); late Albian–early Cenomanian (Aguirre-Urreta, 2002; Guler and Archangelsky, 2006).
- Piedra Clavada Fm, Quebrada Don Nielsen and Tres Lagos sections, Austral Basin; middle-late Albian (Archangelsky et al., 2008).
- Piedra Clavada Fm, La Horqueta section, Austral Basin; early Albian (Medina et al., 2008)

7p) *Tricolpites* sp

Stratigraphic position and age:

- Huitrin Fm = Quili Malal Member, Rayoso Fm (Leanza, 2003), Neuquén Basin; Earliest Albian (Volkheimer and Salas, 1975a,b).
- Bajo Barreal Fm = Cañadón Seco Fm (Archangelsky et al., 1994); Cenomanian (91–95.8 Ma) (Bridge et al., 2000).
- Caballo Muerto Creek section, Kachaïke Fm, Austral Basin (Llorens, 2005); late Albian–early Cenomanian (Aguirre-Urreta, 2002; Guler and Archangelsky, 2006).
- Piedra Clavada Fm, Quebrada Don Nielsen and Tres Lagos sections, Austral Basin; middle-late Albian (Archangelsky et al., 2008).
- Piedra Clavada Fm, La Horqueta section, Austral Basin; early Albian (Medina et al., 2008).

8p) *Rousea* sp.

Stratigraphic position and age:

- Huincul Fm, Neuquén Basin; Albian?–Cenomanian (Vallati, 2001a).
- Bajo Barreal Fm = Cañadón Seco Fm (Archangelsky et al., 1994); Cenomanian (91–95.8 Ma) (Bridge et al., 2000).
- Piedra Clavada Fm, Quebrada Don Nielsen and Tres Lagos sections, Austral Basin; middle-late Albian (Archangelsky et al., 2008).

9p) *Tricolporoidites* sp.

Stratigraphic position and age:

- Margas Verdes Fm (off shore) Austral Basin; late Albian–Cenomanian (Palmarczuk et al., 2000).
- Huincul Fm, Neuquén Basin; Albian?–Cenomanian (Vallati, 2001a)
- Bajo Comisión section, Kachaïke Fm, Austral Basin (Barreda and Archangelsky, 2006); late Albian–early Cenomanian (Aguirre-Urreta, 2002; Guler and Archangelsky, 2006)
- Caballo Muerto Creek section, Kachaïke Fm, Austral Basin (Llorens, 2005); late Albian–early Cenomanian (Aguirre-Urreta, 2002; Guler and Archangelsky, 2006)
- Piedra Clavada Fm, Quebrada Don Nielsen and Tres Lagos sections, Austral Basin; middle-late Albian (Archangelsky et al., 2008).

10p) *Psilatricolpites* sp.

Stratigraphic position and age:

- Huincul Fm, Neuquén Basin; Albian?–Cenomanian (Vallati, 2001a).
- Bajo Comisión section, Kachaïke Fm, Austral Basin (Barreda and Archangelsky, 2006); late Albian–early Cenomanian (Aguirre-Urreta, 2002; Guler and Archangelsky, 2006).

11p) *Verrutricolpites* sp.

Stratigraphic position and age:

- Bajo Barreal Fm = Cañadón Seco Fm (Archangelsky et al., 1994); Cenomanian (91–95.8 Ma) (Bridge et al., 2000).
- Margas Verdes Fm (off shore) Austral Basin; late Albian–Cenomanian (Palmarczuk et al., 2000).
- Huincul and Cerro Lisandro Fms, Neuquén Basin; Albian?–Cenomanian (Vallati, 2001a, 2001b, 2006).

12p) *Dryadopolis* sp.

Stratigraphic position and age:

- Huincul and Cerro Lisandro Fms, Neuquén Basin; Albian?–Cenomanian (Vallati, 2001a, 2001b).
- Margas Verdes Fm (off shore) Austral Basin; late Albian–Cenomanian (Palmarczuk et al., 2000).

13p) *Nyssapollenites* sp.

Stratigraphic position and age:

- Bajo Barreal Fm = Cañadón Seco Fm (Archangelsky et al., 1994); Cenomanian (91–95.8 Ma) (Bridge et al., 2000).
- Margas Verdes Fm (off shore) Austral Basin; late Albian–Cenomanian (Palmarczuk et al., 2000).
- Huincul Fm, Neuquén Basin; Albian?–Cenomanian (Vallati, 2001a).

14p) *Tricolporate* with reduction of the colpi

Stratigraphic position and age:

- Margas Verdes Fm (off shore) Austral Basin; Cenomanian (Palmarczuk et al., 2000).

Leaf morphotypes1mf) *Nymphaeaphyll* morphotype

Description: Leaf simple, probably rounded, base unknown, apex obtuse. Margin entire. Venation actinodromous or pinnate. Primary and secondary veins branching more or less equally, forming festooned brochidodromous loops of irregular size and shape. Third and higher order veins random polygonal reticulate. Areoles lack veinlets. Marginal veins form weak brochidodromous loops (Passalia et al., 2003).

Stratigraphic position: Anfiteatro de Ticó Fm, Deseado Massif Basin.

Age: late Aptian (118.56–119.7 Ma) (Corbella, 2001).

2mf) *Lobate serrate* morphotype

Description: Leaf simple, micro-mesophyll, pinnately- and/or palmately-lobed, base truncate to obtuse, apex of each lobe obtuse. Margin serrate, teeth simple with glandular-like tips. Venation pinnate and craspedodromous. Intersecondary veins present. Tertiary veins exmedially ramified (Romero and Archangelsky, 1986).

Stratigraphic position: Anfiteatro de Ticó Fm, Deseado Massif Basin.

Age: late Aptian (118.56–119.7 Ma) (Corbella, 2001).

3mf) *Crenate lobate* morphotype

Description: Leaf flabellate, lamina incised with three rounded lobes, petiole marginal. Margin crenate. Venation actinodromous to palinactinodromous.

Stratigraphic position: Punta del Barco Fm, Deseado Massif Basin.

Age: late Aptian (118.56–119.7 Ma) (Corbella, 2001).

4mf) *Trifoliolate* morphotype

Description: Leaf ternate (trifoliolate). Leaflets with 3–5 small lobes or teeth with glandular-like tips. Venation pinnate and craspedodromous; intramarginal vein present (Puebla, 2004).

Stratigraphic position: La Cantera Fm, San Luis Basin.

Age: late Aptian (Yrigoyen, 1975; Prámparo, 1994).

5mf) *Pinnatilobate nanophyll* morphotype

Description: Leaf compound, leaflets pinnatilobed, nanophyll. Leaflet lobes of variable shape and development, separated by deep sinuses, and innervated by a midvein and an intramarginal vein connected by transverse veins of irregular course and lower caliber (Puebla, 2004)

Stratigraphic position: La Cantera Fm, San Luis Basin.

Age: late Aptian (Yrigoyen, 1975; Prámparo, 1994).

6mf) *Pinnate brochidodromous* morphotype

Description: Leaf simple, elliptic, apex acute, base cuneate. Margin entire. Venation pinnate brochidodromous; secondary veins give rise to an intramarginal vein (Puebla, 2004).

Stratigraphic position: La Cantera Fm, San Luis Basin.

Age: late Aptian (Yrigoyen, 1975; Prámparo, 1994).

7mf) *Thorhallenia dentata* Passalia

Description: Leaf simple, lamina slightly incised, sometimes giving the appearance of being lobate. Petiole marginal. Margin dentate, teeth simple or compound. Venation pinnate craspedodromous or actinodromous to palinactinodromous; secondary veins opposite to subopposite; tertiary veins alternate percurrent and reticulate (Passalia, 2007).

Stratigraphic position: Bajo Comisión section, Kachaike Fm, Austral Basin (continental).

Age: late Albian-early Cenomanian (Aguirre-Urreta, 2002; Guler and Archangelsky, 2006).

8mf) *Thorphyllum patagonica* Cúneo et Gandolfo

Description: Leaf simple, ovate, and symmetrical, base acute decurrent, apex acute. Petiole marginal. Margin entire. Venation pinnate brochidodromous; tertiary veins random reticulate, fourth-order veins reticulate and polygonal (Cúneo and Gandolfo, 2005).

Stratigraphic position: Caballo Muerto section, Kachaike Fm, Austral Basin (continental).

Age: late Albian-early Cenomanian (Aguirre-Urreta, 2002; Guler and Archangelsky, 2006).

9mf) *Kachaikenia compuesta* Cúneo et Gandolfo

Description: Leaf pinnately compound; leaflets alternate; each leaflet ovate, base acute, apex acute to obtuse rounded. Margin of basal leaflets entire, but pinnately lobed on apical leaflets. Venation pinnate craspedodromous; secondary veins irregularly spaced; tertiary venation random reticulate; areoles well developed. Fimbrial ultimate marginal venation (Cúneo and Gandolfo, 2005).

Stratigraphic position: Caballo Muerto Creek section, Kachaike Fm, Austral Basin (continental).

Age: late Albian-early Cenomanian (Aguirre-Urreta, 2002; Guler and Archangelsky, 2006).

10mf) *Rogersia australis* Cúneo et Gandolfo

Description: Leaf simple, elliptic, symmetrical, base acute cuneate, apex acute straight. Margin entire. Venation pinnate brochidodromous; secondary veins irregularly spaced and forming loops; tertiary veins alternate and ramified; fourth-order veins polygonal reticulate; areoles well developed (Cúneo and Gandolfo, 2005).

Stratigraphic position: Caballo Muerto Creek section, Kachaike Fm, Austral Basin (continental).

Age: late Albian-early Cenomanian (Aguirre-Urreta, 2002; Guler and Archangelsky, 2006).

11mf) Festooned brochidodromous morphotype

Description: Leaf simple, probably elliptic, base acute, apex unknown, petiole marginal. Margin entire. Venation pinnate brochidodromous; secondary veins festooned, irregularly spaced; tertiary veins regular polygonal; fourth-order veins regular reticulate; areoles well developed (Morphotype 1 from Cúneo and Gandolfo, 2005).

Stratigraphic position: Caballo Muerto Creek section, Kachaike Fm, Austral Basin (continental).

Age: late Albian-early Cenomanian (Aguirre-Urreta, 2002; Guler and Archangelsky, 2006).

12mf) Rounded eucamptodromous morphotype

Description: Leaf simple, rounded, base wide obtuse, slightly cordate; apex rounded; petiole marginal. Margin entire. Venation pinnate eucamptodromous, secondary veins becoming more crowded towards the base; intersecondary veins present and weak; tertiary veins probably random reticulate; ultimate marginal venation looped (Morphotype 4 from Cúneo and Gandolfo, 2005).

Stratigraphic position: Caballo Muerto Creek section, Kachaike Fm, Austral Basin (continental) (Cúneo and Gandolfo, 2005).

Age: late Albian-early Cenomanian (Aguirre-Urreta, 2002; Guler and Archangelsky, 2006).

13mf) *Myrtoidea* sp.

Description: Leaf simple, elliptic, symmetrical, base acute, apex obtuse acute. Margin entire. Venation pinnate brochidodromous. Secondary veins numerous, unbranched as well as admedially or exmedially ramified. Intramarginal vein well-developed (Passalia et al., 2001).

Stratigraphic position: Bajo de los Corrales Un-named Formation, Deseado Massif Basin.

Age: possibly Albian to Cenomanian (Passalia et al., 2001).

14mf) *Myrtoidea patagonica* Passalia, Romero et Panza

Description: Leaf simple, narrow elliptic, base acute cuneate, apex acute. Margin entire. Venation pinnate brochidodromous with numerous pairs of secondary veins unbranched as well as admedially or exmedially ramified. Intersecondary veins

sometimes present; double intramarginal vein present; tertiary veins with irregular pattern (Passalia et al., 2001).

Stratigraphic position: Bajo de los Corrales, Un-named Formation, Deseado Massif Basin.

Age: possibly Albian to Cenomanian (Passalia et al., 2001).

15mf) *Elongated serrate morphotype*

Description: Leaf or leaflet elliptic or ovate; apex acute, base unknown. Margin serrate, small teeth, regularly spaced. Venation pinnate craspedodromous to semi-craspedodromous; secondary veins numerous. (Magnoliidae *incertae sedis* from Passalia et al., 2001).

Stratigraphic position: Bajo de los Corrales, Unnamed Formation, Deseado Massif Basin.

Age: possibly Albian to Cenomanian (Passalia et al., 2001).

16mf) Palmitilobate brochidodromous morphotype

Description: Leaf simple. Orbicular or elliptical. Margin entire, palmitilobate (3-lobed). Primary venation actinodromous; secondary veins brochidodromous.

Stratigraphic position: upper section of Castillo Fm, San Jorge Gulf Basin.

Age: Lower Cenomanian (97.9 Ma) (Bridge et al., 2000).

17mf) Multilobate morphotype

Description: Leaf profusely lobed. Margin entire. Venation actinodromous; secondary veins brochidodromous (*Cissites parvifolius* (Font.) Berry var. *argentina* Menéndez from Menéndez, 1959).

Stratigraphic position: upper section of Castillo Fm San Jorge Gulf Basin.

Age: Lower Cenomanian (97.9 Ma) (Bridge et al., 2000).

18mf) Elongated eucamptodromous to weak brochidodromous morphotype

Description: Leaf simple, elliptic, base acute, apex acute, petiole marginal. Margin entire. Venation pinnate eucamptodromous to weak brochidodromous. (*Laurophyllum proteaeifolium* Berry from Menéndez, 1959).

Stratigraphic position: upper section of Castillo Fm San Jorge Gulf Basin.

Age: Lower Cenomanian (97.9 Ma) (Bridge et al., 2000).

19mf) Acrodromophyll morphotype

Description: Leaf simple, probably elliptic, base and apex rounded; petiole probably marginal. Margin entire. Venation acrodromous, secondary veins ending in an intramarginal vein.

Stratigraphic position: upper section of Castillo Fm, San Jorge Gulf Basin.

Age: Lower Cenomanian (97.9 Ma) (Bridge et al., 2000).

20mf) Crenate unlobed morphotype

Description: Leaf simple, elliptic to ovate, base obtuse, apex obtuse. Margin crenate. Venation pinnate with decurrent secondary veins crowded toward the base. (Passalia et al., 2008)

Stratigraphic position: Portezuelo Fm, Neuquén Basin.

Age: late Turonian–early Coniacian (Leanza and Hugo, 2001).

21mf) Crenate (large teeth) morphotype

Description: Leaf simple, elliptic to ovate, base obtuse, rounded to cordate; apex acute to obtuse. Margin crenate. Teeth large, double-convex with rounded and nonglandular apex. Venation pinnate craspedodromous. Secondary veins running near to the basal side of the tooth and reaching their apex. (Passalia et al., 2008)

Stratigraphic position: Portezuelo Fm, Neuquén Basin.

Age: late Turonian–early Coniacian (Leanza and Hugo, 2001).

22mf) Pinnatilobed ovate morphotype

Description: Leaf simple, shape ovate, base obtuse, apex obtuse. Margin entire, pinnatilobate, lobes simple or compound. Venation pinnate craspedodromous, secondary veins reaching the margin to innervate the lobes. Subopposite and percurrent tertiary venation. Tertiary veins are brochidodromous close to margin forming a weak intramarginal vein (Morphotype MA107 from Iglesias et al., 2007).

Stratigraphic position: María Elena and Mata Amarilla sections, Mata Amarilla Fm, Austral Basin (continental).

Age: Cenomanian-Coniacian (Riccardi and Rolleri, 1980; Nullo et al., 1999).

23mf) Pinnatilobed elliptical morphotype

Description: Leaf simple, shape elliptical, base acute, decurrent in shape. Apex acute, convex in shape. Margin entire, pinnatilobate, lobes simple. Venation pinnate semicraspedodromous, more than one secondary vein per lobe (Morphotype MA108 from Iglesias et al., 2007).

Stratigraphic position: Mata Amarilla section, Mata Amarilla Fm, Austral Basin (continental).

Age: Cenomanian-Coniacian (Riccardi and Rolleri, 1980; Nullo et al., 1999).

24mf) Palmatilobed eucamptodromous morphotype

Description: Leaf simple, orbicular or elliptical; base obtuse, apex odd-lobed. Margin entire, palmatilobate (3–5 lobed, rarely seven or more). Primary venation palinactinodromous; secondary veins eucamptodromous, weakly developed. Weak tertiary veins compound percurrent pattern (Morphotype MA106 from Iglesias et al., 2007).

Stratigraphic position: María Elena and Mata Amarilla sections, Mata Amarilla Fm, Austral Basin (continental).

Age: Cenomanian-Coniacian (Riccardi and Rolleri, 1980; Nullo et al., 1999).