Fossil pollen indicates an explosive radiation of basal Asteracean lineages and allied families during Oligocene and Miocene times in the Southern Hemisphere

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ABSTRACT

Much of our knowledge of the past distribution and radiation of Asteraceae and allied families depends on the fossil pollen record. In recent years, new discoveries are coming to light from southern Africa, Australia, New Zealand, and southern South America (Patagonia). Unequivocally assigned morphotaxa from accurately dated sediments have permitted for the first time a comprehensive review of the past distribution of the most important core of the sunflower alliance of families (Menyanthaceae, Goodeniaceae, Calyceraceae and Asteraceae). The main goal of this contribution is to explore the major evolutionary radiation of the basal lineages of Asteraceae (Mutisioideae and Barnadesioideae) and allied relatives (Menyanthaceae, Goodeniaceae and Calyceraceae) on the basis of the worldwide fossil pollen records. Several taxa, which today are restricted to isolated geographic regions, were widespread in the Southern Hemisphere during Paleogene times. Menyanthaceae, Goodeniaceae and Mutisioideae (Asteraceae), for example, had a wide distribution over Gondwanan landmasses in the Oligocene and are now drastically reduced in their geographic range. Early Neogene records, in contrast, suggest extinction and diversification events that progressively led to the present day configuration. In broad terms, the distribution of Miocene fossils assigned to this clade (Barnadesioideae, Nassauvieae, and Calyceraceae) agrees with that of their present distribution. The major floristic turnovers coincided with the final isolation of Antarctica, leading to cooler, drier, and more seasonal climates and forced the evolution and distribution of these Gondwanan elements.

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1. Introduction

The evolutionary radiation of the Asteraceae and their closest relatives is one of the most important and yet unresolved questions because unequivocal fossil evidence is scarce for the development of reliable hypotheses. This issue is now becoming resolved thanks to the increasing discovery of fossil Asteraceae, including records of their basal lineages such as Barnadesioideae (Palazzesi et al., 2009), Mutisieae (Partridge, 1978; Graham, 1991, 1996; Macphail and Hill, 1994; Barreda, 1993; Barreda et al., 2009; Zavada and De Villiers, 2000; Scott et al., 2006; Katinas et al., 2007) and Nassauvieae (Barreda et al., 2008b). The picture is complemented by some crucial fossil discoveries of the Menyanthaceae (Mildenhall and Pocknall, 1989; Macphail, 1999; Zetter et al., 1999; Palamarczuk and Barreda, 2000; Barreda et al., 2009), Goodeniaceae (Salard-Cheboldaeff, 1978; Pocknall, 1982; Mildenhall and Pocknall, 1989; Barreda, 1997a,b; Macphail, 1999),

and Calyceraceae (Palazzesi, 2008; Palazzesi et al., 2010). These families comprise the three closest relatives of Asteraceae and they all represent one of the most important cores of the sunflower alliance of families (Lundberg and Bremer, 2003). Notably, fossils assigned to Barnadesioideae, Mutisieae, Nassauvieae (Asteraceae), together with those related to Menyanthaceae, Goodeniaceae and Calyceraceae, have mostly been recorded in Gondwanan areas such as Africa (Cameroon, Angola basin, southern Namibian coast), Australia (northwestern in the Pilbara region, southeastern in the Murray Basin and Tasmania), New Zealand (Southland) and South America (San Jorge, Austral and Valdés basins). The common ancestor of Goodeniaceae, Calyceraceae and Asteraceae may have originated before the final breakup of southern Gondwana (South America–Antarctica–Australia), during early Paleogene times (DeVore and Stuessy, 1995). According to Stuessy et al. (1996) Calyceraceae and Asteraceae probably diverged in southwestern Gondwana (southern South America) and Goodeniaceae in southeastern Gondwana (Australia).

The current study uses the most complete sampling of fossil species within Menyanthaceae, Goodeniaceae, Calyceraceae and basal Asteraceae yet attempt, with the aim of understanding their biogeographic histories in the context of the major palaeoclimatic and

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palaeogeographic events. With corroborated stratigraphic information and unequivocally assigned morphotaxa, it is possible to address the question of when members of this group of families first radiated across the Gondwanan continents.

2. Botanical framework of extant taxa

The sunflower alliance (Bremer and Gustafsson, 1997) consists of 12 families, many of them widely distributed shrubs and herbs. The Menyanthaceae, Goodeniaceae, Calyceraceae and Asteraceae (referenced as MGCA) form a well-supported clade of this alliance based on morphological, palynological, and molecular studies (Skvarla et al., 1977; Gustafsson and Bremer 1995; Gustafsson et al., 1996; Bremer and Gustafsson, 1997; Lundberg and Bremer, 2003). Within the MGCA the cosmopolitan Asteraceae (sunflowers) is the largest family of extant plants. Traditionally, it comprises three major subfamilies (Barnadesioideae, Cichorioideae, and Asteroideae), 17 tribes, and more than 25,000 species of herbs, vines, shrubs and less frequently trees (Bremer, 1994), although molecular phylogenetic analyses (e.g., Panero and Funk, 2002) postulate new tribes and subfamilies. The basal branch of the Asteraceae is the subfamily Barnadesioideae, sister to the rest of the family, with the next clades constituted by members of the subfamily Mutisioideae (Katinas et al., 2008). In turn, Mutisioideae consists of the tribes Mutisieae, Nassauvieae and Stifftieae. The genera of Barnadesioideae are endemic to South America, with an Andean–Patagonian concentration. The genera of Mutisieae are mainly South American (with concentrations in some areas such as the Andes, Patagonia, and the Guayana Highlands) but they are also represented in North and Central America, Asia, Africa; and in Australia by only one species. The tribe Nassauvieae is exclusively Neotropical, with mostly monotypic, endemic, Andean, Chilean, and Patagonian genera, only a few being widespread. Members of Stifftieae are Guayana Highland-centered with some species also represented in northern and eastern Brazil, and the Andes (Katinas et al., 2008).

Menyanthaceae, Goodeniaceae, and Calyceraceae are smaller families of herbs or low shrubs. The sister group to Asteraceae is the small family Calyceraceae; the sister to the Calyceraceae–Asteraceae clade is the medium-sized family Goodeniaceae; and the sister clade to these three families is Menyanthaceae (Lundberg and Bremer, 2003). The Menyanthaceae (5 genera, ca. 70 species) is a family of aquatic and wetland plants scattered throughout the world. The Goodeniaceae (14 genera, ca. 300 species) are generally herbaceous plants with over 95% of the species endemic to arid and semiarid regions of Australia, mainly in the southwest, and in Tasmania. Members of the family can also be found in the shores of southeastern Asia, eastern, southern and western Africa and western South America. The Calyceraceae (6 genera, ca. 55 species) are all herbs common in arid and sandy soils, native to Central and South America. Their highest concentration is in southern South America, where they commonly grow in dry habitats in scrub and steppe vegetation.

3. Methods and geographical setting

In this contribution we analyze the fossil pollen records of Menyanthaceae, Goodeniaceae, Calyceraceae, and the Barnadesiodeae, Mutisieae, and Nassauvieae of the Asteraceae. These records come from published data for Africa (Salard-Cheboldaeff, 1978; Partridge, 1978; Zavada and De Villiers, 2000; Scott et al., 2006), Australia (Macphail and Hill, 1994; Macphail, 1999), New Zealand (Pocknall, 1982; Mildenhall and Pocknall, 1989), and southern South America (Barreda, 1993, 1997a, b; Barreda and Palamarczuk, 2000a,b; Palamarczuk and Barreda, 2000; Barreda et al., 2008a,b, 2009; Palazzesi et al., 2009; Palazzesi et al., 2010).

The geological time scale of Gradstein et al. (2004) is followed. The Eocene Epoch ranges from 55.8 to 33.9 million years ago (Ma) with three stages: Early (55.8–48.6 Ma), Middle (48.6–37.2 Ma) and Late (37.2–33.9 Ma). The Oligocene Epoch ranges from 33.9 to 23.03 Ma with two stages: Early (33.9–28.45 Ma) and Late (28.45–23.03 Ma),

and the Miocene Epoch ranges from 23.03 to 5.33 Ma with three stages: Lower (23.03–15.97 Ma), Middle (15.97–11.61 Ma) and Upper (11.61–5.33).

The material illustrated in this contribution is housed in the following institutional collections: Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (Buenos Aires, Argentina): BA Pal. 5701; BA Pal ex CIRGEO 834–959, 994–1007, 1181–1241; and the Museo Regional Provincial "Padre Manuel Jesús Molina" (Santa Cruz, Argentina): MPM-MP 1922–1930. For comparison with extant material, we used the large reference pollen collections of Urtubey and Tellería (1998), Tellería and Katinas (2004), Katinas et al. (2008) and Tellería (2008).

4. Results

Fossil pollen records of the Menyanthaceae, Goodeniaceae, Calyceraceae and the basal Asteraceae are summarized in the following paragraphs. The oldest supposed fossils are from Africa (Eocene), while unequivocally assigned fossils from accurately dated deposits are from Africa, Australia, New Zealand, and South America (Oligocene, Early Miocene, and Late Miocene). The closest living relatives of each fossil specimen based on pollen are analyzed (when possible) in the context of their habitat and present distribution.

4.1. Eocene (Figs. 1, 2A; Table 1)

Recent surveys indicate southeastern African deposits to bear the oldest (Paleocene–Eocene) pollen records of Asteraceae (Zavada and De Villiers, 2000) (Figs. 1 and 2A; Table 1). The specimens were referred to as *Mutisiapollis viteauensis* (Mutisieae), which was (at that time) the closest fossil species in terms of morphology. However, African specimens have differences in size, structure and sculpture in comparison with the type material of *M. viteauensis* from Patagonia, southern South America (Barreda, 1993). Scott et al. (2006) reassessed the Mutisieae specimens from the same core samples studied by Zavada and De Villiers (2000) and referred the fossils to the *Dicoma* type (sub Mutisieae *sensu* Stix, 1960 and Scott, 1982; and at present referred to Carduoideae); they are characterized by being spheroidal to subprolate, tricolporate, echinate, with prominent columellae. The extant genus *Dicoma* comprises ca. 65 species distributed mainly in South and tropical Africa, Madagascar (Fig. 2B), with a few species in Northeastern Africa and Asia (Bremer, 1994). Scott et al. (2006) constrained the age of these deposits to the Middle Eocene, but pointed out that the temporal assignment requires further confirmation by new research and absolute dating methods. It is worth mentioning that the abundance of Asteraceae in the southeastern African sediments makes up some 25% of the assemblage. Frequencies as high as these are rare before the Pliocene in Australia (see Martin, 1973; Kershaw et al., 1994) and in Patagonia (see Barreda, 1993, 1996; Palazzesi and Barreda, 2004). However, Scott et al. (2006) did not find any typically Neogene specimens such as those widely recognized in Miocene deposits (grass pollen – *Graminidites* spp.– and Astereae type pollen —*Tubulifloridites* spp.). Though we are not yet able to confirm whether this record represents the oldest of the MGCA clade, the accurate study of these specimens might fill important gaps in the evolutionary history of Asteraceae.

Other Paleogene specimens also assigned to *Mutisiapollis* come from southern North America (Elsik and Yancey, 2000; Ramírez Arriaga et al., 2006). Controversy remains as to whether fossils certainly belong to *Mutisiapollis* (specimens were not illustrated or described, in Elsik and Yancey, 2000) or to deposits of the suggested age (unsupported age constrained, in Ramírez Arriaga et al., 2006). Therefore, these two last records are not considered in the present analysis.
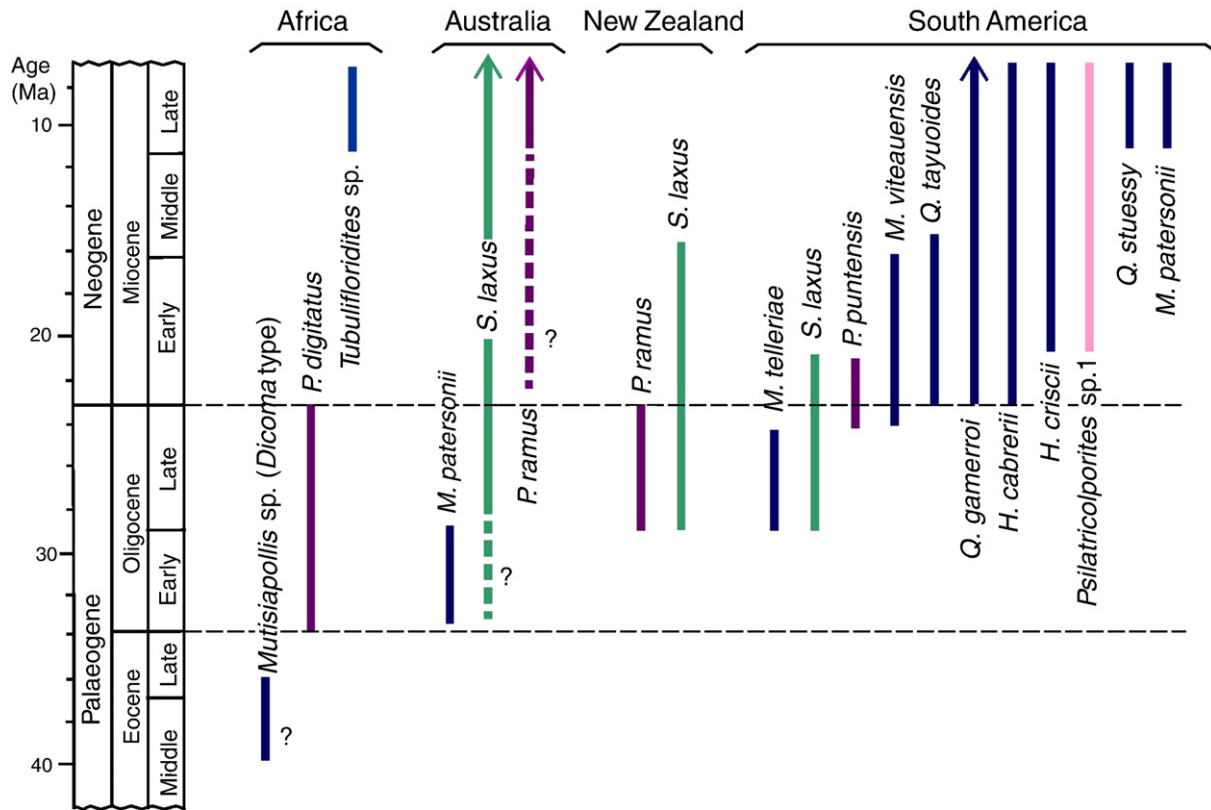
Fig. 1. Time distribution of selected MGCA fossil pollen. References considered are given in Table 1. Menyanthaceae: green line; Goodeniaceae: violet line; Calyceraceae: pink line; Asteraceae: blue line.

4.2. Oligocene (Figs. 1, 2A; Table 1)

To date the oldest confident fossil pollen records of the MGCA occur in the Oligocene and are restricted to three families:

– Menyanthaceae, with *Striasyncolpites laxus* (Plate I, 1): It is characterized by being oblate, tricolporate, parasyncolpate with striate exine. This species occurs in the Oligocene and Miocene of New Zealand, Australia and Patagonia (Mildenhall and Pocknall, 1989; Macphail and Hill, 1994; Macphail, 1999; Palamarczuk and Barreda, 2000; Zetter et al., 1999; Barreda et al., 2009). Based on

comparison with extant forms, a great similarity to the pollen produced by the extant *Villarsia* and *Liparophyllum* can be established. *Villarsia* (ca. 16 species) is a small herb common in swamps, fresh water lagoons, on river flats, or damp soils. It mostly occurs in Australia, with one species in the Cape region of southern Africa and one species in southeastern Asia (Chuang and Ornduff, 1992; Ornduff, 1999). The monotypic *Liparophyllum* is a slender, fleshy, marsh herb that at present grows in New Zealand and Tasmania (Fig. 2B) (Chuang and Ornduff, 1992). In New Zealand, it occurs abundantly in marshy grounds of Stewart Island. In Tasmania

Table 1
Selected fossil pollen of the MGCA and their closest living relatives previously established or herein inferred.

| Morphotaxon	Nearest living relatives	References
Striasyncolpites laxus Mildenhall and Pocknall	Menyanthaceae *Villarsia–Liparophyllum*	Mildenhall and Pocknall, 1989; Macphail and Hill, 1994; Macphail, 1999; Zetter et al., 1999; Palamarczuk and Barreda, 2000; Barreda et al., 2009
Poluspissusites digitatus Salard-Cheboldaeff	Goodeniaceae *Scaevola–Goodenia*	Salard-Cheboldaeff, 1978
Poluspissusites ramus Pocknall	Goodeniaceae *Scaevola–Goodenia*	Pocknall, 1982; Macphail, 1999
Poluspissusites puntensis Barreda	Goodeniaceae *Scaevola–Goodenia*	Barreda, 1997a,b
Psilatricolporites protrudens Palazzesi and Barreda	Calyceraceae *Boopis*	Palazzesi, 2008; Palazzesi et al., 2010
Mutisiapollis sp. (*Dicoma* type)	Asteraceae–Carduoideae–*Dicoma*	Zavada and De Villiers, 2000; Scott et al., 2006
Mutisiapollis patersonii Macphail and Hill	Asteraceae Mutisieae *Mutisia–Chaetanthera*	Macphail and Hill, 1994; Macphail and Stone, 2004; Palazzesi and Barreda, 2004; Palazzesi, 2008
Mutisiapollis telleriae Barreda and Palazzesi	Asteraceae Mutisioideae "Guayana Highland-centered members"	Barreda et al., 2009
Mutisiapollis viteauensis Barreda	Asteraceae Mutisieae *Cnicothamnus–Actinoseris–Gochnatia*	Barreda, 1993; Barreda and Palamarczuk, 2000a b
Tubulifloridites sp.	Asteraceae Mutisioideae/Carduoideae	Partridge, 1978
Quilembaypollis gamerroi Palazzesi and Barreda	Asteraceae Barnadesioideae *Chuquiraga–Duseniella–Doniophyton*	Palazzesi et al., 2009
Quilembaypollis tayuoides Barreda and Palazzesi	Asteraceae Barnadesioideae *Dasyphyllum*	Palazzesi et al., 2009
Quilembaypollis stuessyi Palazzesi and Barreda	Asteraceae Barnadesioideae *Schlechtendalia*	Palazzesi et al., 2009
Huanilipollis cabrerii Barreda and Palazzesi	Asteraceae Nassauvieae *Holocheilus–Proustia–Jungia*	Barreda et al, 2008b
Huanilipollis criscii Barreda and Palazzesi	Asteraceae Nassauvieae *Triptilion*	Barreda et al., 2008b
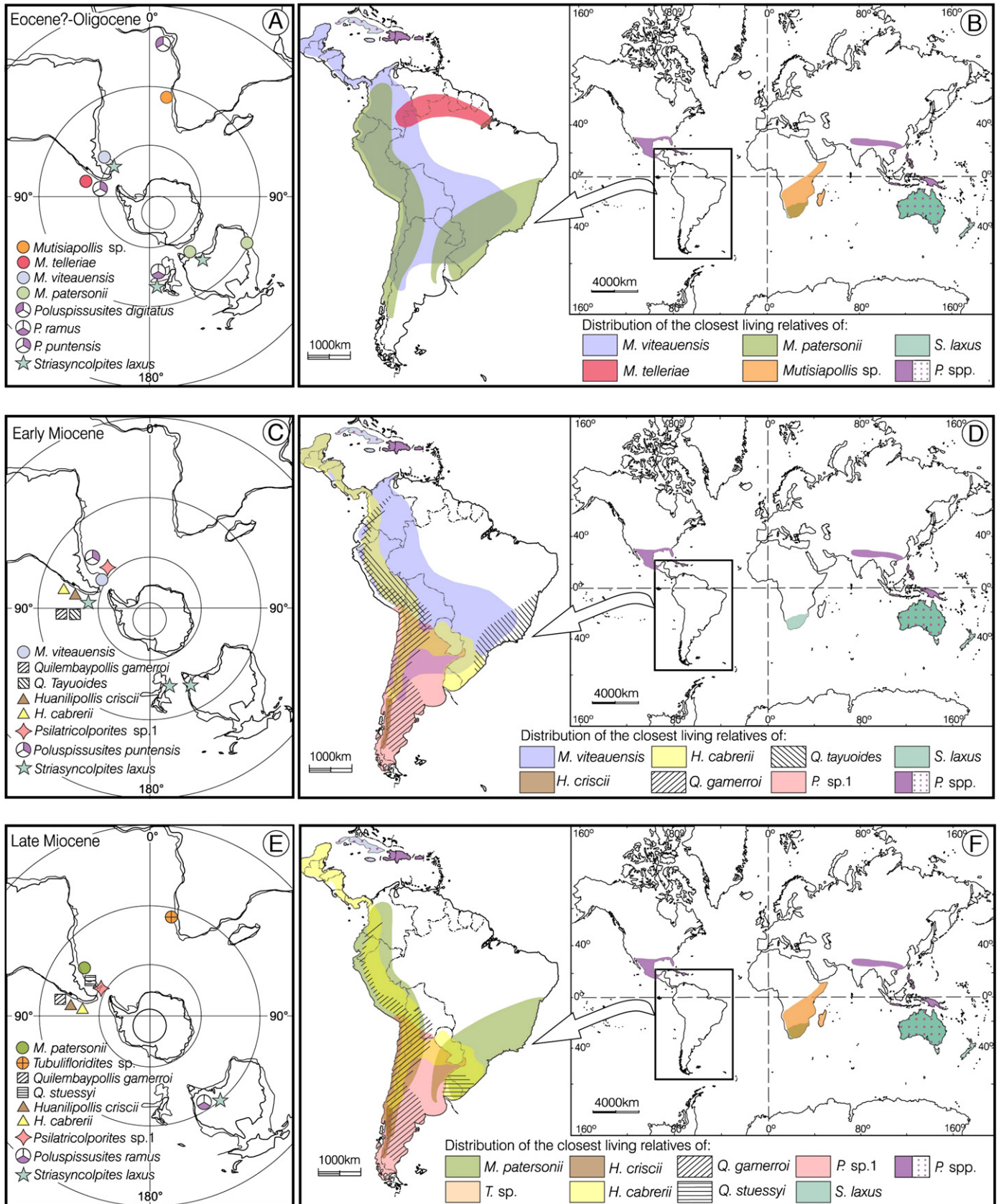
Fig. 2. Palaeogeographic distributions of selected MGCA fossil pollen in the: Eocene?–Oligocene (A), Early Miocene (C) and Late Miocene (E). Main distribution areas of the closest living relatives of the selected MGCA fossils recorded in the: Eocene?–Oligocene (B), Early Miocene (D) and Late Miocene (F). Palaeogeographic maps modified from Smith and Briden (1977). South America possesses the highest diversity of extant taxa related to the fossils selected, and therefore this region is magnified in order to show plant distributions more accurately.

it grows in wet sandy soil on the margin of alpine lakes, and in New Zealand it grows near the shoreline (Petrie, 1879; Kadereit, 2007).

– Goodeniaceae, with *Poluspissusites* spp. (*P. digitatus*, *P. ramus* and *P. puntensis*): They are characterized by being prolate to subprolate, tricolporate, with the exine thicker at poles, clearly stratified and with digitate infratectal columellae. These morphotypes have been reported from the Oligocene of Cameroon (*P. digitatus*) and Late Oligocene and Early Miocene of New Zealand (*P. ramus*) and Patagonia (*P. puntensis*, Plate I, 2), and Late Miocene–Pleistocene of Australia (*P. ramus*) (Salard-Cheboldaeff, 1978; Pocknall, 1982; Barreda, 1997a,b; Macphail, 1999). They have general similarities to the *Scaevola–Goodenia* group (Gustafsson et al., 1997), at present mainly distributed in Australia (Fig. 2B) (Howarth et al., 2003). *Scaevola* (ca. 130 species) is the only genus of Goodeniaceae with a significant number of non-Australian species (ca. 40). They occur throughout the Pacific and Indian Oceans, in the tropical Americas and Africa often as forest trees or shrubs; one species is present in Cuba and one in Socotra (Carolin, 1999a; Rozefelds, 2001; Howarth et al., 2003). Species of *Scaevola* occur principally near the shore, but also in mountains and open woodland savannas. *Goodenia* has more than 180 species, with 178 in Australia, three extending to New Guinea and southern China, and one endemic to Java (Carolin, 2007). Species of *Goodenia* grow mainly on the banks of rivers and near lakes, but they can also be found in open woodlands and heaths on sandy soils, at the foot of mountains, and in forests, grasslands and swamps (Carolin, 1999b).

– Asteraceae–Mutisieae, with *Mutisiapollis* spp. (*M. patersonii, M. telleriae* and *M. viteauensis*): Oligocene fossil records of Asteraceae from Australia and southern South America are always in trace amounts (less than 1%).

M. patersonii is characterized by being prolate, tricolporate, microechinate, with a thick columellate endosexine, and a nexine dumbbell-shaped in outline (Plate I, 6). This species is found from the early Oligocene of Australia (Macphail and Hill, 1994), but it is not recorded until the Miocene in Patagonia (Palazzesi and Barreda, 2004; Palazzesi, 2008). It is similar to pollen of some extant species in both the Andean-centered genera *Chaetanthera* and *Mutisia* (Mutisieae). These species of *Chaetanthera* currently grow in a low dry central valley between the two cordilleras in Chile with extreme summer drought (Tellería and Katinas, 2004). In contrast, species of *Mutisia* with pollen comparable to fossil *M. patersonii* have a broad geographic and environmental distribution (Fig. 2B) (Tellería and Katinas, 2009). It is probable that the Australian and Patagonian specimens referred to as *M. patersonii* represent different extant taxa.

Mutisiapollis telleriae (Plate I, 4) comprises tricolporate–echinate pollen grains with a thick endosexine and robust spines (Barreda et al., 2009). Similar pollen grains were recorded from Miocene deposits at DSDP Site 365 off the west coast of Africa, and referred to *Tubulifloridites* sp. (Partridge, 1978). *Mutisiapollis telleriae* has similarities with genera of the Guayana Highland-centered members of the Mutisioideae of northern Brazil, Colombia, Guyana, and Venezuela (Fig. 2B). They grow on tepuis, a group of isolated sandstone table mountains (Jiménez Rodríguez et al., 2004). It is worth noting that *M. telleriae* is the oldest fossil of Asteraceae to date from Patagonia and has similarities with extant pollen that grows in areas distant from this region.

Mutisiapollis viteauensis (Plate I, 5; Plate II, 1) includes tricolporate, microechinate pollen grains, with stout digitate columellae (Barreda, 1993). It differs from *M. telleriae* in having a thinner endosexine and smaller spines (less than 1 μm high), and from *M. patersonii* in being smaller and having larger spines. *M. viteauensis* is recorded from the Late Oligocene, but it is consistently present by the Miocene. *M. viteauensis* is similar to the extant genera *Cnicothamnus–Actinoseris–Gochnatia* (Mutisieae), mostly confined to South America with the exception of *Gochnatia* that ranges from Mexico to Argentina, with two species in Asia (Fig. 2B). *Cnicothamnus* is a genus of two species from the subtropical forests of Bolivia, and from northwestern Argentina in the Yungas and in the transition forests between the Yungas and Chaco (Cabrera, 1977). *Actinoseris* is a genus of seven species of rocky and grassy places of southeastern Brazil (Minas Gerais, São Paulo, Paraná). *Gochnatia* (70 species) is mainly American with centers of diversity in the Caribbean, southeastern Brazil, Mexico, and the Andes. Species of *Gochnatia* are found in several habitats such as mountain ranges, intermountain valleys, "planalto" of Brazil, dry forests, and grasslands.

4.3. Early Miocene (Figs. 1, 2C; Table 1)

Early Miocene pollen records are characterized by the first reports of Calyceraceae, Barnadesioideae and Nassauvieae. These new records, present always in very low abundances, have only been documented in southern South America. Also, a significant diversification of Asteraceae occurred during this time interval.

Calyceraceae, with *Psilatricolporites protrudens* (Plate I, 3): this pollen is characterized by being tricolporate, and psilate to microgranulate. The sexine is formed by columellae mostly indistinct under light microscopy. The nexine is thickened at equatorial areas near endoapertures resulting in a wall protrusion on the external surface (Palazzesi, 2008; Palazzesi et al., 2010). This species is similar to pollen of extant *Boopis* (ca. 30 species, with some very polymorphic) that grows in Chile, Argentina including Islas Malvinas (Falkland Islands). There are very few in Brazil, Peru, and Bolivia (Fig. 2D) (Hellwig, 2007). They are found mainly in the Andean Range and in Patagonia on rocky and sandy soils, sometimes close to lakes. This is the first fossil record of the family to date (Palazzesi, 2008; Palazzesi et al., 2010). The scarcity in the fossil record of Calyceraceae in eastern Patagonia might be related to the ecological restriction of the family to stress microhabitats (DeVore and Stuessy, 1995).

Asteraceae–Barnadesioideae, with *Quilembaypollis tayuoides* (Plate I, 7; Plate II, 2) and *Q. gamerroi* (Plate I, 8): *Q. tayuoides* and *Q. gamerroi* include distinct pollen types clearly distinguishable by being

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Plate I. Fossil pollen grains here illustrated come from southern South-American outcrops. Scale bar: 10 μm.

Fig. 1.   *Striasyncolpites laxus* Mildenhall and Pocknall (Menyanthaceae), Río Leona Formation, Estancia 25 de Mayo section, MPM-MP 1926e: K39-1.

Fig. 2.   *Poluspissusites puntensis* Barreda (Goodeniaceae), Chenque Formation, Chenque section, Ba Pal ex CIRGEO Palin 881: O50-1.

Fig. 3.   *Psilatricolporites protrudens* Palazzesi and Barreda (Calyceraceae), Puerto Madryn Formation, Punta Pirámides section, Ba Pal 6013: N53-4.

Fig. 4.   *Mutisiapollis telleriae* Barreda and Palazzesi (Mutisieae, Asteraceae), San Julián Formation, Playa La Mina section, Ba Pal ex CIRGEO Palin 995: R52-2.

Fig. 5.   *Mutisiapollis viteauensis* Barreda (Mutisieae, Asteraceae), Chenque Formation, Chenque section, Ba Pal ex CIRGEO Palin 844: H51-2.

Fig. 6.   *Mutisiapollis patersonii* Macphail and Hill (Mutisieae, Asteraceae), Puerto Madryn Formation, Punta Pirámides section, Ba Pal 6015: W42-3.

Fig. 7.   *Quilembaypollis tayuoides* Barreda and Palazzesi (Barnadesioideae, Asteraceae), Chenque Formation, Playa Las Cuevas section, Ba Pal ex CIRGEO Palin 901: C37-3.

Fig. 8.   *Quilembaypollis gamerroi* Palazzesi and Barreda (Barnadesioideae, Asteraceae), Puerto Madryn Formation, Punta Pirámides section, Ba Pal 6015: R40-3.

Fig. 9.   *Quilembaypollis stuessyi* Palazzesi and Barreda (Barnadesioideae, Asteraceae), Puerto Madryn Formation, Punta Pirámides section, Ba Pal 6015: X35-4.

Fig. 10.   *Huanilipollis cabrerii* Barreda and Palazzesi (Nassauvieae, Asteraceae), Chenque Formation, Chenque section, Ba Pal ex CIRGEO Palin 851: D43-2.

Figs. 11–12.   *Huanilipollis criscii* Barreda and Palazzesi (Nassauvieae, Asteraceae), Chenque Formation, Playa Las Cuevas section. 11. Ba Pal ex CIRGEO Palin 901: H43-1. 12. Ba Pal ex CIRGEO Palin 901: F51-1.
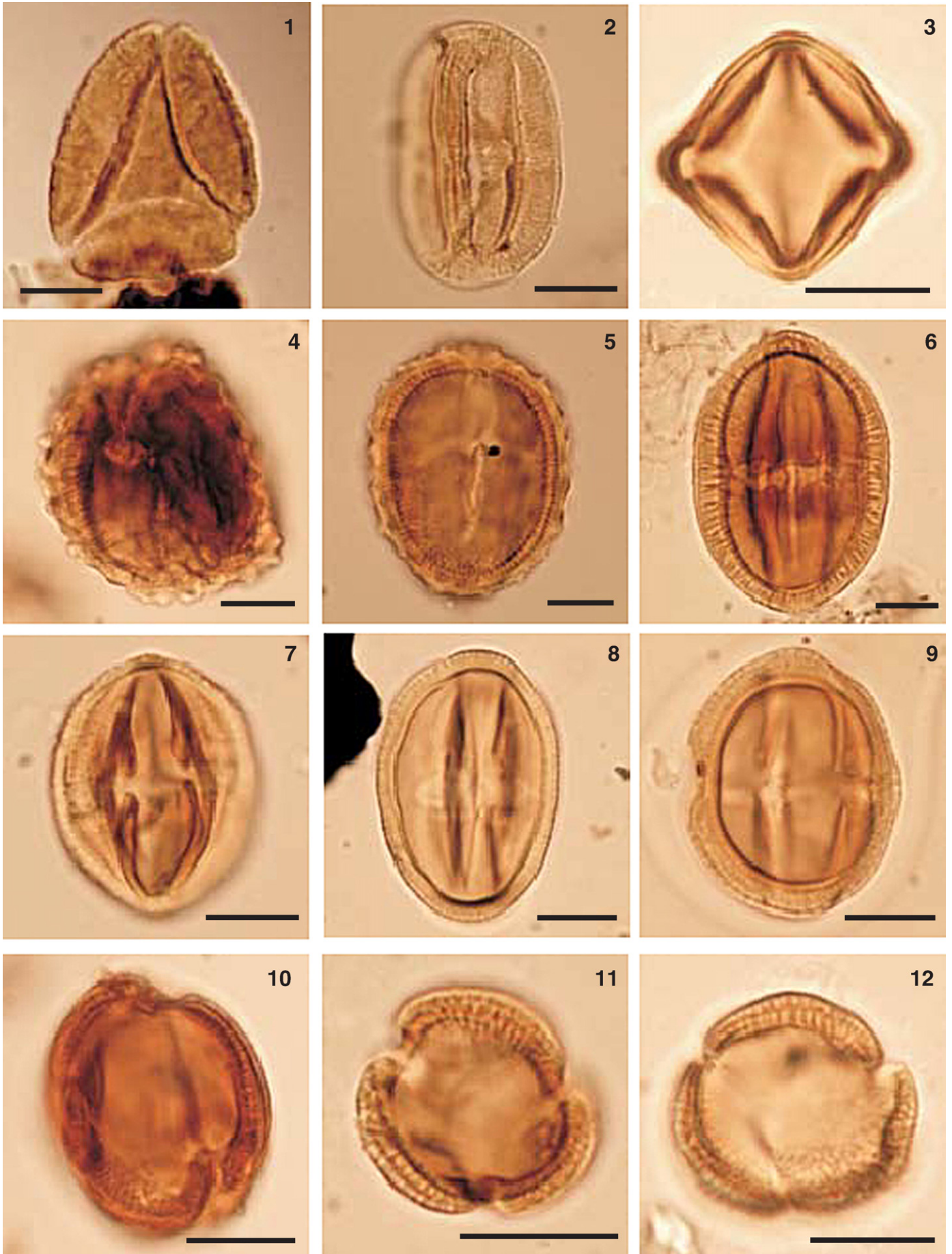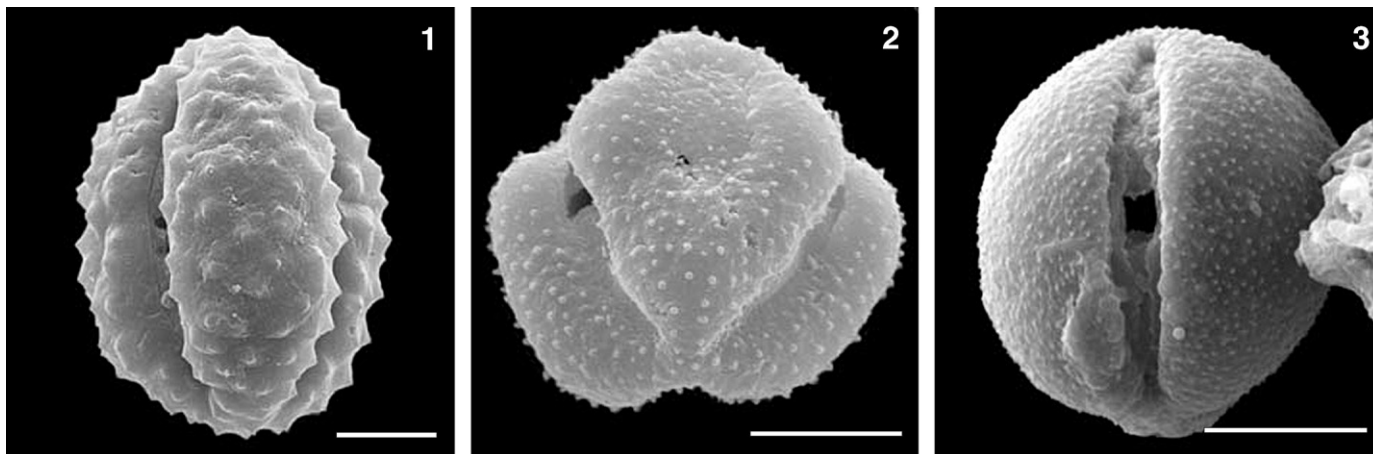
Plate II. SEM photomicrographs of selected fossil Asteracean pollen grains from southern South America. Scale bar: 10 μm.

Fig. 1. Mutisieae (*Mutisiapollis viteauensis* Barreda).
Fig. 2. Barnadesioideae (*Quilembaypollis tayuoides* Barreda and Palazzesi).
Fig. 3. Nassauvieae (*Huanilipollis cabrerii* Barreda and Palazzesi).

microechinate and having a thick sexine formed by one (*Q. tayuoides*) or two (*Q. gamerroi*) layers (Palazzesi et al., 2009). *Q. tayuoides* is similar to pollen of extant *Dasyphyllum*, particularly *Dasyphyllum* type 2, subtype I of Urtubey and Tellería (1998), characterized by being caveate and by having three equatorial depressions. These species are today confined to central Chile, southeastern Brazil and to the Andean region from Venezuela to northwestern Argentina (Fig. 2D). *Q. gamerroi* is similar to pollen of extant *Chuquiraga*, *Duseniella* and *Doniophyton*. *Chuquiraga* (23 species) ranges from the Andes of Colombia south into Argentina and Chile, frequently in xeromorphic habitats of the Andean ranges and Patagonia. The monotypic *Duseniella* is endemic to Patagonian Argentina (Stuessy and Urtubey, 2007). *Doniophyton* (two species) is an Andean–Patagonian genus ranging from northern Chile to southern Argentina (Fig. 2D) (Katinas and Stuessy, 1997).

Asteraceae–Nassauvieae, with *Huanilipollis cabrerii* (Plate I, 10; Plate II, 3) and *H. criscii* (Plate I, 11, 12): *H. cabrerii* is characterized by being subprolate, tricolporate, microechinate and with a complex exine structure. This species is similar to pollen of recent *Holocheilus*, *Jungia*, and *Proustia* (Barreda et al., 2008b). *Holocheilus* has seven species and presently grows in southern Brazil, Paraguay, Uruguay and northern Argentina; *Jungia* has 28 species of herbs, shrubs, subshrubs of Mexico to northern Argentina and Uruguay, and *Proustia* has three species of shrubs and vines of the Andes of Bolivia, Chile and Argentina (Fig. 2D). The pollen of *H. criscii* is similar to *H. cabrerii*, but differs in being smaller, oblate to subspheroidal in shape and having a different exine pattern (Barreda et al., 2008b). This pollen type resembles that of the extant *Triptilion* which comprises seven herbaceous species endemic to central Chile and the subantarctic forests of Chile and Argentina (Fig. 2D) (Katinas et al., 1992, 2008).

4.4. Late Miocene (Figs. 1, 2E; Table 1)

The Late Miocene is characterized by a further diversification of Asteraceae, particularly the tribe Astereae (not considered in the present analysis), and the increase in abundance of Barnadesioideae, Nassauvieae and Calyceraceae.

Asteraceae–Barnadesioideae, with *Quilembaypollis stuessyi* (Plate I, 9): the pollen is characterized by being spheroidal, tricolporate, with three equatorial depressions and the sexine formed by three columellate sublayers (Palazzesi et al., 2009). This pollen type is similar to extant *Schlechtendalia* of the Barnadesioideae, a monotypic genus confined to rocky and sandy soils of warm-temperate to warm and grassy areas of southern Brazil, Uruguay and northeastern Argentina (Fig. 2F) (Stuessy et al., 1996).

Asteraceae–Mutisioideae/Carduoideae with *Tubulifloridites* sp. of Partridge (1978) from the Late Miocene off the west coast of Africa, DSDP Site 365. These specimens show great similarities with both the Guayana Highland-centered members of the Mutisioideae (the closest living relatives of the fossil *M. telleriae*), and some species of Carduoideae.

5. Discussion and conclusions

The evolutionary diversification and radiation of a number of sunflower-related taxa (Menyanthaceae, Goodeniaceae, Calyceraceae and basal Asteraceae) is analyzed for the first time on the basis of the precise chronological position of the fossil bearing deposits. Their major floristic turnovers through space and time are related to the important geologic and palaeoclimatic events that occurred during the Oligocene and Miocene.

Some of the MGCA taxa with a restricted distribution today were once widespread in parts of the Gondwana supercontinent. During Paleogene times, for example, the subfamily Mutisioideae of Asteraceae was distributed in southern South America (Barreda, 1993, 1997b; Katinas et al., 2007; Barreda et al., 2009) and Australia (Macphail and Hill, 1994; Macphail and Stone, 2004), while Carduoideae was confined to Africa (Zavada and De Villiers, 2000; Scott et al., 2006) as shown in Fig. 2. These records indicate that Mutisioideae and Carduoideae diverged as separate subfamilies during Paleogene times. Menyanthaceae and Goodeniaceae, today mainly restricted to the southeastern Pacific region, also had a wider past distribution (Fig. 2). Menyanthaceae was distributed in southern South America, Australia and New Zealand while Goodeniaceae was present in Africa, New Zealand, and southern South America during the Late Oligocene (Fig. 2A). In broad terms, Late Oligocene proxy data suggest warm and humid climates supporting forests with tropical vines, tree ferns and aquatic herbs in the southern Gondwanan continents (Mildenhall and Pocknall, 1989; De Villiers and Cadman, 2001; Martin, 2006; Barreda and Palazzesi, 2007). Open habitat representatives began to radiate at this time (Macphail et al., 1994; Jacobs et al., 1999; Barreda and Palazzesi, 2007). Neighbouring landmasses (mainly South America, Australia and New Zealand) showed a similar floristic composition. However, some differences began to emerge from the Miocene onwards, probably in response to global (drying, cooling and greater seasonality), and regional (uplift of the highest elevation of the Andes) events.

Early Miocene, Calyceraceae and basal members of Asteraceae [Barnadesiodeae (*Chuquiraga–Doniophyton–Duseniella* and *Dasyphyllum*) and Nassauvieae] were already differentiated according to the fossil data (Fig. 2C). The two major groups of Barnadesioideae recorded as fossils, *Chuquiraga* type and *Dasyphyllum* type 2, today grow in different regions under different climatic conditions (Fig. 2D). However, during the Miocene they probably shared a similar geographical distribution, but likely occupied different local microenvironments. In general, most of the dominant groups recorded in the Early Miocene grew in arid or semiarid environments, giving that plant communities a modern appearance. Some sub-humid and warmth-demanding types related to Mutisieae (e.g. *Actinoseris—* species of *Gochnatia*), and Nassauvieae (e.g. *Holocheilus*, *Jungia*) still persisted. In contrast to the Oligocene, the new Early Miocene members of the MGCA clade have only been recorded in southern South America so far (Fig. 2D). This high endemism during Miocene times in South America coincides with a number of important extinctions, including those of *Lagarostrobus*, *Dacrydium*, *Phyllocladus* and Casuarinaceae which are all restricted today to the southeastern Pacific region (Macphail et al., 1994). This floristic change is marked by a divergence in the types of environments that were mainly forced, in turn, by the isolation of Antarctica and the following cooling and rapid expansion of continental ice-sheets.

By the Late Miocene the geographic distribution of the MGCA was roughly similar to that of the present day (Fig. 2E, F). All moisture-demanding Asteraceae became extinct in the non-Andean region of southern South America. The same occurred with Menyanthaceae and Goodeniaceae. On the other hand, records of the seasonally dry adapted Asteraceae with the first *Schlechtendalia* specimens and an important expansion of the *Chuquiraga* type and Calyceraceae occurred. Mutisioideae was no longer recorded in Australia while Mutisioideae or Carduoideae developed in western Africa. In slightly younger deposits (Pliocene) a Mutisieae type specimen was recorded in Central America (Graham, 1991) indicating a more recent northward range expansion of this type.

The timing of origin and diversification of the MGCA members estimated by molecular data (Kim et al., 2005) predates the age of the oldest fossils by several million years. It is highly probable that the age of these fossils represent the time it took for radiation of the MGCA into the palaeoenvironments (coastal locations in the main). No transitional pollen forms have been recorded among these closely related fossils, and hence MGCA members were probably differentiated elsewhere sometime before.

In summary, fossil pollen from Africa, Australia, New Zealand and Patagonia indicate that Menyanthaceae and Goodeniaceae were already differentiated by the Oligocene, as well as Asteraceae with at least two subfamilies. The broad distribution patterns of these families during the Oligocene support previous assumptions of an Eocene origin of the clade. Subsequent extinctions and radiations resulting in their present distribution occurred during Miocene and Pliocene times, well after the major biogeographical isolation of the Gondwanan landmasses. These Southern Hemisphere continents, and particularly Patagonia, are unique in having the highest diversity of sunflower-related fossils of any region known to date. The geographic position of Patagonia in Gondwana during the Cenozoic is crucial to comprehending asterralean distribution models and migration patterns in the Southern Hemisphere.

Acknowledgements

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