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Early history of Asteraceae in Patagonia: evidence from fossil pollen grains

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Abstract The Asteraceae are classified into three subfamilies: Barnadesioideae, Cichorioideae, and Asteroideae. It has been suggested that the southern South American subfamily Barnadesioideae is the basal branch of the phylogenetic tree of the family, and Patagonia is the ancestral area of Asteraceae. Here we explore the chronological records of some members of the family, with findings of Mutisiinae (tribe Mutisieae, subfamily Cichorioideae) from the Late Oligocene (28–23 Ma) and of Barnadesioideae and Nassauviinae (Mutisieae) from the Early Miocene (23–20 Ma), all recovered from marine deposits

of Patagonia. Even though the succession of fossil appearances (first Mutisieae) differs from that provided by molecular data (first Barnadesioideae), this new scheme offers additional evidence towards the understanding of the early history of ancestral Asteraceae.

Keywords fossil pollen; Asteraceae; Mutisieae; Barnadesioideae; Oligocene; Miocene; southern South America

INTRODUCTION

The Asteraceae (the sunflowers) are the largest living plant family with about 1600 genera and 23 000 species distributed on all continents except Antarctica (Jeffrey 2007). Daisies, lettuce, artichokes, dandelions, and thistles are just a few examples of the remarkable family Asteraceae, a group of great economic and ecological importance. It constitutes one of the most well-defined families of flowering plants, marked principally by sessile flowers that are grouped into a common receptacle, the head or capitulum.

Phylogenetic analyses within the plant family Asteraceae have revealed that one of its subfamilies, the Barnadesioideae, is the basal branch of the family. However, it was not possible to directly estimate the stratigraphic fit of this branching event since fossils of Barnadesioideae were lacking. Until 1987 the general classification of the family recognised two subfamilies: Cichorioideae (with six tribes) and Asteroideae (with ten tribes). However, a significant change to this classification arose when Jansen & Palmer (1987) in their analysis of restriction site variation found a 22-kilobase inversion in the chloroplast genome in most genera of Asteraceae sampled, but no inversion in all outgroups or in *Barnadesia*, *Chuquiraga*, and *Dasyphyllum* of the South American subtribe Barnadesiinae (9 genera, 88 species), then classified in the tribe Mutisieae (Asteraceae). Barnadesiinae became a major focus of additional molecular analyses (Kim et al. 1992; Kim & Jansen

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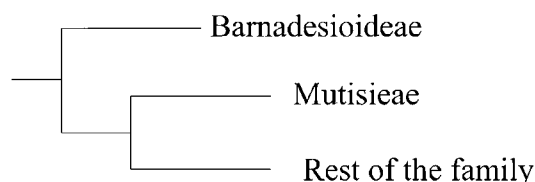


Fig. 1 Simplified, current phylogenetic hypothesis of the relationships among Asteraceae. Some phylogenetic analyses place a few genera of the tribe Mutisieae (sens. lat.) in the rest of the family branch, but all analyses show the Barnadesioideae as the basalmost branch followed by the majority of Mutisieae (sens. lat.).

1995; Kim et al. 2005), which generally supported the initial results. Either Barnadesiinae had the inversion and then lost it, or it never had it in the first place. The latter explanation was widely accepted by most researchers because it represents a more parsimonious hypothesis. As a result, Barnadesiinae was re-classified as the subfamily Barnadesioideae, and placed as the basal branch of the phylogenetic tree of Asteraceae. Although recent analyses have recognised additional subfamilies (Funk et al. 2005), the Barnadesioideae remain as the basal branch in all trees. The tribe Mutisieae (Mutisioideae in some works; 74 genera, c. 865 species) now comprising only the subtribes Mutisiinae and Nassauviinae, follows Barnadesioideae in the phylogenetic sequence (Fig. 1).

The positioning of Barnadesioideae as the sister group of the rest of the family suggested new hypotheses regarding the place and time of origin of the family. Because Barnadesioideae are well represented in Patagonia, southern South America was postulated as the most likely area of origin of Asteraceae (Bremer 1992; Stuessy et al. 1996; Funk et al. 2005). Therefore, it has been pointed out that the finding of fossils in this area is fundamental to tracing the fossil history of Asteraceae (Graham 1996).

Kim et al. (2005) recently proposed a phylogeny for Asteraceae, with the origin of the family at 49–42 Ma, determined using a fossil-calibrated molecular clock. They calibrated the clock with Poaceae (grass family), Oleaceae (olive family), and *Cornus* fossils (dogwood family).

The oldest Asteraceae fossil records (*Tubulifloridites* spp., *Mutisiapollis* spp.), all determined as the subtribe Mutisiinae from the Oligocene (Partridge 1978; Barreda 1993, 1997; Macphail & Hill 1994), are well-preserved pollen grains from accurately dated deposits in the Southern Hemisphere.

The Oligocene age of these fossils agrees with that reported in earlier overviews of the family (Muller 1981; Graham 1996). Some older fossil records exist from Eocene deposits of southern Africa (Zavada & De Villiers 2000), but Scott et al. (2006) pointed out that this dating “requires further confirmation by new research and absolute dating methods”. Those reported from the Late Eocene of the Gulf Coast of Mexico (Elsik & Yancey 2000) might be the oldest ones, but neither description nor illustration was provided. If Barnadesioideae are accepted as the basal branch of Asteraceae, a fossil of this group would be an important element in the calibration of the phylogeny of the family.

Here we present a chronological scheme based on the fossil pollen records of Mutisiinae from the Late Oligocene and Barnadesioideae and Nassauviinae from the Early Miocene of Patagonia (V. Barreda & L. Palazzesi unpubl. data). We also revisit current hypotheses of the origin of the plant family Asteraceae in the light of these findings.

MATERIALS AND METHODS

Both fossil and extant pollen were examined with light microscope and scanning electron microscope. Terminology follows Punt et al. (2007). The grains here analysed were collected by some of us (VB and LP) from sedimentary outcrops in eastern Patagonia (42–52°S), southern Argentina. They come from San Julián, Monte León (Austral basin), Chenque (San Jorge basin), and Puerto Madryn (Valdés basin) formations. The ages of the formations are well constrained based on fossil evidence (e.g., dinoflagellate) and absolute (radiometric) data (Zinsmeister et al. 1981; Feagle et al. 1995; Palamarzuck & Barreda 1998; Scasso et al. 2001; Parras & Casadío 2006). Fossils are housed in MACN: BA PAL. 5701; BA PAL ex CIRGEO 834–959, 994–1007, 1181–1241. For comparison with extant material, we used pollen from the extensive herbarium collection of vouchered Asteraceae at LP. This collection comprises pollen of c. 99 % of the genera of Mutisieae, and 100 % of the genera and species of Barnadesioideae.

RESULTS

The palynology of extant genera of Barnadesioideae and Mutisieae is well characterised (Crisci 1971, 1974; Parra & Marticorena 1972; Urtubey & Tellería

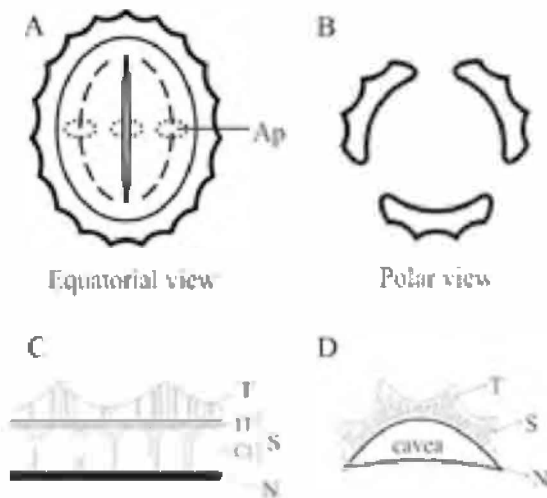


Fig. 2 General view schemes of pollen grains and main exine patterns in Asteraceae. **A**, equatorial view; **B**, polar view; **C**, ecaveate exine (Anthemoid pattern); **D**, caveate exine (Helianthoid pattern). Ap, apertures; S, sexine; T, tectum; Cl, columellae; It, internal tectum; N, nexine.

1998; Tellería & Katinas 2004; Katinas et al. in press); thus, the correspondence in pollen morphology between modern and fossil taxa is well established. Their pollen sculpture and exine structure (Fig. 2) is distinctive enough to distinguish them from other families, and from other tribes of Asteraceae. Pollen with a helianthoid pattern related to the subfamily Asteroideae was also found.

Our fossil data support the following important time intervals (Fig. 3) regarding the appearance and diversification of Asteraceae in southern South America.

28–23 Ma (Late Oligocene, Chattian)

Oldest fossil pollen of the Asteraceae belonging to subtribe Mutisiinae, apparently related to the extant genera *Cnicothamnus*, *Actinoseris*, and *Gochnatia*. Both fossil and extant pollen share the Anthemoid pattern, with the *Mutisia* exine type (Katinas et al. in press) characterised by an echinate surface, ectosexine slightly columellate, and endosexine with stout and ramified columellae (Fig. 4A,B).

23–20 Ma (Early Miocene, Aquitanian)

Diversification of the Anthemoid pattern, and the first records of subtribe Nassauviinae and subfamily Barnadesioideae. Exine in pollen of extant and fossil Nassauviinae is microechinate and the two layers

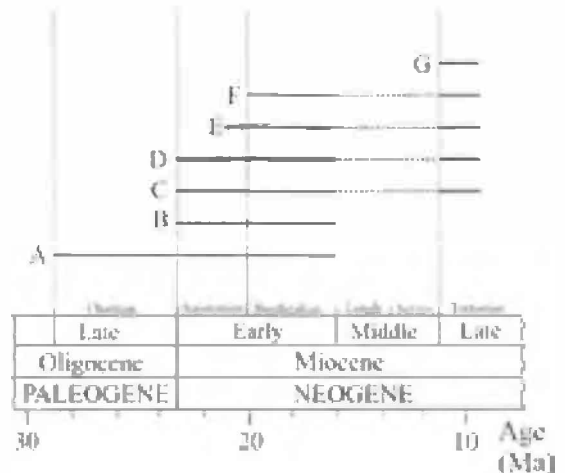


Fig. 3 Stratigraphical distribution of the fossil pollen of Asteraceae in Patagonia. **A**, Mutisiinae type; **B**, *Dasyphyllum* type (Barnadesioideae); **C**, Nassauviinae type (exine *Trixis* type); **D**, *Chuquiraga* type (Barnadesioideae); **E**, Nassauviinae type (exine *Oxyphyllum* type); **F**, Asteraceae type; **G**, *Schlechtendalia* type (Barnadesioideae).

of sexine have delicate columellae (Crisci 1974; Tellería et al. 2003). Differences in the thickness ratio of the two layers of sexine and the internal orientation of the tectum distinguish several exine types (Crisci 1974). The *Trixis* exine type, with the endosexine thicker than the ectosexine (Fig. 4D,E), and the *Oxyphyllum* exine type, with the two layers separated by an internal zig-zag tectum, are found in the fossil pollen of Nassauviinae. The pollen in extant Barnadesioideae has either the Anthemoid or the Helianthoid pattern; it can be psilophate, with a variable number of intercolpal depressions or without them. The exine has a spongy aspect in the psilophate types, while a columellate-granulate structure and a slightly microechinate tectal surface characterises the remaining types (Urtubey & Tellería 1998). The fossil pollen has exine similar to those found in *Chuquiraga* and *Dasyphyllum*, both lacking cavea and with small microspines. In the *Chuquiraga* type the exine is thick (4–6 μm) and has two clearly defined layers in the sexine: a thin ectosexine with columellate-granulate aspect, and a thick endosexine with compact aspect (Fig. 4G,H). In the *Dasyphyllum* type, the exine is thin (c. 3 μm) with a compact aspect.

20–16 Ma (Early Miocene, Burdigalian)

First records of pollen type with Helianthoid pattern in Patagonia. This fossil has a single-layered

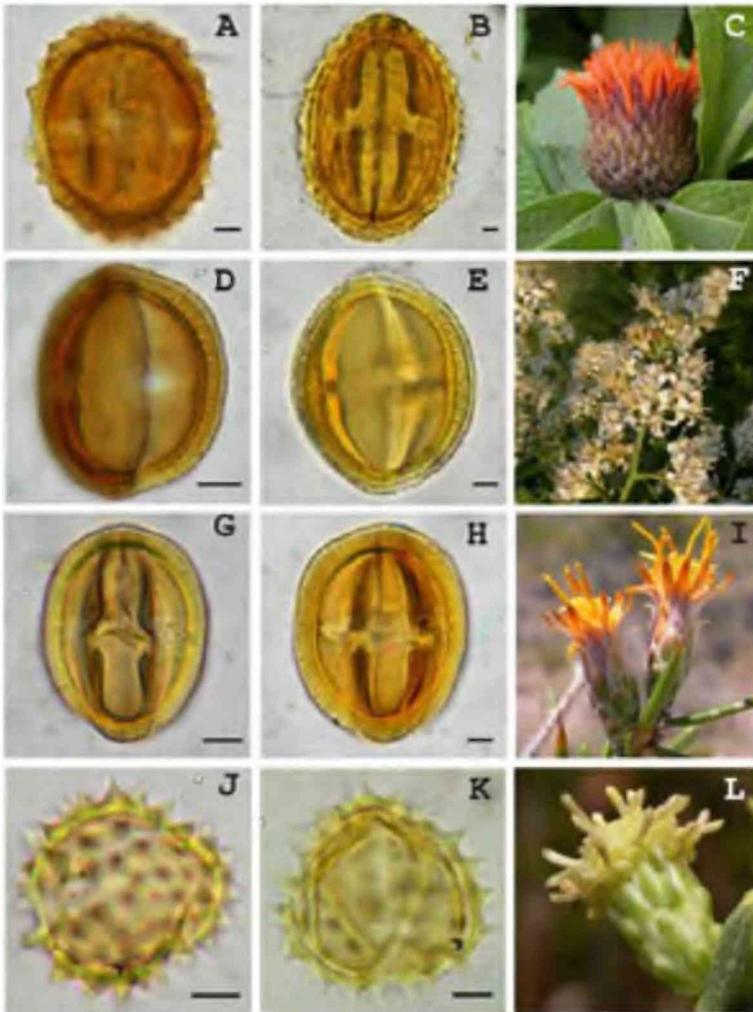


Fig. 4 Fossil pollen of Asteraceae (first column), related extant pollen (second column), and parent plant aspect (third column). **A–C**, Mutisiinae: Fossil pollen, extant pollen, and aspect of the genus *Cnicothamnus*; **D–F**, Nassauviinae: Fossil pollen, extant pollen, and aspect of the genus *Proustia*; **G–I**, Barnadesioideae: Fossil pollen, extant pollen, and aspect of the genus *Chuquiraga*; **J–L**, Astereae: Fossil pollen close to Astereae, extant pollen, and aspect of the genus *Baccharis*. Scale bars = 5 μ m.

exine with intricate columellae and long spines with acute tips. This pattern is found in the extant pollen of most tribes of the subfamily Asteroideae; for comparison we selected pollen of *Baccharis* (tribe Astereae), since it is representative of the pollen types with Helianthoid pattern and long spines (Fig. 4J,K).

11–9 Ma (Late Miocene, Tortonian)

High abundance and diversity of subtribe Nassauviinae, and pollen associated with tribe Astereae. Pollen of a new taxon of subfamily Barnadesioideae assigned to the *Schlechtendalia* type appears, characterised by the lack of cavea, microechinate tectal surface, intercolpal depressions, and a three-layered sexine, the middle one predominant.

DISCUSSION

Oligocene Mutisiinae appears to be the oldest reliable pollen record for the family Asteraceae in Patagonia (Barreda 1993) and world wide (Macphail & Hill 1994; Partridge 1978; Muller 1981; Graham 1996). The earliest pollen of Barnadesioideae and Nassauviinae has been recorded in Patagonia for the Early Miocene (V. Barreda & L. Palazzesi unpubl. data). The importance of these records is enhanced because this is the postulated area of origin of Asteraceae and because Barnadesioideae is considered the basal group of the family (Stuessy et al. 1996; Funk et al. 2005).

Our minimum age of 28–23 Ma for the fossils of Asteraceae (Mutisiinae) and of 23–20 Ma for

Barnadesioideae, with the divergence of lineages in Patagonia, where all three subfamilies are represented, at 20–16 Ma do not match with other estimations (e.g., Kim et al. 2005) of 49–42 Ma for the origin of the family, and major tribal lineages diverging 36–42 Ma, immediately after the basal split between the Barnadesioideae and the rest of the family.

The order of appearance of the different subgroups of Asteraceae in Patagonia (first Mutisieae, second Barnadesioideae) differs from that proposed by the current phylogenies (first Barnadesioideae, second Mutisieae). How might we explain that? It may be that the fossil record in southern South America is still incomplete and new findings will corroborate Barnadesioideae as the basal branch; or that the groups originated elsewhere and migrated to southern South America in the order in which we find them in the fossil record of this area; or that the Mutisieae is the basal branch of the tree since its pollen appeared first and Barnadesioideae appears later, simultaneously with the advanced lineage Nassauviinae (Crisci 1974, 1980; Cabrera 1977). The morphology supports the third possibility. Earlier studies have suggested a close affinity of subfamily Barnadesioideae with tribe Mutisieae. Style and floral similarities supported inclusion of the Barnadesioideae as a subtribe of the tribe Mutisieae (Cabrera 1977). Both groups have styles smooth or with rounded papillae, a character state that distinguishes them from other members of the family (Katinas et al. in press) (style characters are among the most important for delineating tribes and subfamilies of Asteraceae). The main reason for excluding the Barnadesioideae from Mutisieae is the absence of the chloroplast DNA inversion that characterises other Asteraceae; this requires that the morphological evidence be disregarded or re-interpreted. It may also be possible to interpret the molecular evidence to consider the non-parsimonious hypothesis that Barnadesioideae had the inversion (as the rest of Asteraceae) and then lost it. If we consider this hypothesis there would be an agreement of the molecular, fossil, and morphological data.

Much recent research in phylogeny (Felsenstein 2004) and biogeography (Crisci et al. 2003) has relied on phylogenetic trees with node age determined using fossils. Until now, the calibration of the molecular clock of phylogenetic trees involving Asteraceae has used fossils of taxonomically distant groups or of uncertain affinity and/or age. In addition, fossil information on the Barnadesioideae, the basal branch of the tree, was lacking until now.

The sketch of appearances provided by these fossil findings would contribute to a better understanding of the early history of Asteraceae.

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