



First fossil record of Calyceraceae (Asterales): Pollen evidence from southern South America

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ABSTRACT

A new fossil pollen species (*Psilatricolporites protrudens* sp. nov) is described from Miocene sedimentary sections of the Chenque and Puerto Madryn formations (Chubut province, Argentina). The fossil pollen grains are characterized by being small, tricolporate, subspheroidal to suboblate in shape; rhombic outline in equatorial view and subtriangular in polar view. The exine is tectate and columellate; the nexine is thickened toward endoapertures resulting in a typical wall protrusion on the external surface. These morphological features point to a possible relationship with *Gamocarpha* type of the Calyceraceae. Most species of this type grow in high-altitude arid habitats or in coastal locations under extreme climatic condition. The gradual spread of the stress-adapted Calyceraceae as well as other phylogenetically related taxa (e.g. Barnadesioideae, Mutisioideae) during the Miocene in southern South America may have been triggered by the increasing aridity and seasonality caused by Andean uplift. This fossil record represents the first finding of Calyceraceae, the most closely related family of Asteraceae, and provides evidence for the timing of their geographic radiation.

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1. Introduction

The timing of the evolutionary radiation of an important clade in the sunflower alliance of families (Menyanthaceae–Goodeniaceae–Calyceraceae–Asteraceae) has been virtually impossible to infer because of the scarcity of fossil data. Among these, Asteraceae has been the most represented family in the fossil record, with several morphotaxa documented from Paleogene times and onwards (Graham, 1996). Menyanthaceae and Goodeniaceae, in contrast, have been poorly documented so far. This first fossil record of Calyceraceae adds a significant component to the sunflower alliance from which Menyanthaceae, Goodeniaceae and Asteraceae–Barnadesioideae and Mutisioideae have recently been published based on specimens from Patagonia (Barreda et al., 2008, 2009; Palazzesi et al., 2009).

Calyceraceae consist of four genera and ca. 60 species, all endemic to southern South America, except one species confined to the Falkland (Malvinas) Islands (Hellwig, 2007). The family is represented by herbaceous species usually found as isolated populations in specialized microhabitats (DeVore and Stuessy, 1995). Asteraceae is very likely to be the closest relative of Calyceraceae based on molecular and morphological data (DeVore and Stuessy, 1995; Carlquist and DeVore, 1998; Lundberg and Bremer, 2003). Both families were postulated to have diverged from an ancestral lineage in

southeastern Gondwana (South America) during Paleogene times (Stuessy et al., 1996). In this study we present pollen grains of the Calyceraceae collected from Miocene deposits of eastern Patagonia and analyze this first finding in the context of the most important floristic events in the early Neogene of southern South America, particularly considering their most closely related taxa.

2. Material and methods

Fossil pollen grains come from a number of sedimentary strata exposed in eastern Patagonia assigned to the Chenque (Early Miocene) and Puerto Madryn (Late Miocene) formations. Location sites are given in Barreda et al. (2008). Samples were collected in field summer trips to Patagonia in 1986 by VB. Age constraints are based on indirect (fossils) and direct (isotopic) evidence (Zinsmeister et al., 1981; Palamarczuk and Barreda, 1998; Malumián and Nañez, 1998; Barreda and Palamarczuk, 2000; Scasso et al., 2001). Slides containing the specimens illustrated are housed in the palynological collection of the Museo de Ciencias Naturales “Bernardino Rivadavia” BA Pal ex CIRGEO 901” and “BA Pal 6011”. Specimen location of the slides is according to the England finder coordinates. Fossil pollen grains have been compared with extant specimens illustrated by Gustafsson et al. (1997) and DeVore et al. (2007). In some cases, recent pollen grains were re-analyzed to observe specific features of the nearest living forms. Pollen terminology follows Punt et al. (2007). The generic circumscription given by Hellwig (2007) is followed in this study,

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who recognized four genera (*Acicarpha*, *Boopis*, *Calycera* and *Gamocarpha*) and treated *Nastanthus* and *Moschopsis* as junior synonyms of *Boopis*.

3. Results

3.1. Extant pollen

The pollen morphology of Calyceraceae was examined by Skvarla et al. (1977), Avetisjan (1980), Hansen (1992) and DeVore et al. (2007). The pollen grains are ecaeate, tectate, microperforate and microechinate. Two major groups are distinguished: (1) the *Calycera* type (*Acicarpha* and *Calycera*) and (2) the *Gamocarpha* type (*Boopis* and *Gamocarpha*). These two groups are mainly characterized by having (*Calycera* type) or lacking (*Gamocarpha* type) intercolpal concavities (depressions between colpi). The *Calycera* type is further distinguished by having angulaperturate apertures and colpal ledges (ridges of exine that line the inner margin of the colpi) according to DeVore et al. (2007). The exine has short, thin and unbranched columellae, similar to those found in some Barnadesioideae genera such as *Dasyphyllum*. The external morphology of the *Dasyphyllum* type 2 (pollen with intercolpal depression *sensu* Urtubey and Tellería, 1997) and the *Calycera* type is virtually identical and they can only be distinguished based on the outline. In equatorial view, the pollen of *Dasyphyllum* type 2 is elliptic and in the polar view is circular. In contrast, the pollen of *Calycera* type has rhombic outline in equatorial view and is angulaperturate in polar view. On the other hand, pollen of the *Gamocarpha* type is recognized by being planaperturate rather than angulaperturate and by lacking colpal ledges. The exine shows an Anthemoid-like pattern, similar to that recognized in some Asteracean groups (e.g. Mutisioideae) characterized by the absence of cavus. *Calycera* and *Gamocarpha* types are not sharply defined because some *Boopis* species show morphological patterns of the *Calycera* type (e.g. *Boopis gracilis* Phil.) and some *Calycera* species show patterns of the *Gamocarpha* type (e.g. *Calycera pulvinata* J. Rémy). Molecular phylogenetic studies would probably assist in understanding such discrepancy. The *Gamocarpha* type, without intercolpal depressions, is usually regarded as basal while the *Calycera* type, with intercolpal depressions, as derived (Hellwig, 2007).

3.2. Fossil pollen

3.2.1. Systematic paleontology

Psilatricolporites Van der Hammen, 1956 ex Van der Hammen and Wijmstra, 1964

Type species: *Psilatricolporites operculatus* Van der Hammen and Wijmstra, 1964

Psilatricolporites protrudens Palazzesi and Barreda sp. nov (Plate I, figs 1–4; Plate II fig. 2)

Holotype: Specimen on slide BA Pal. 6011 from the Puerto Madryn Formation at Punta Pirámide section in northeastern Chubut Province, Patagonia, Argentina.

Paratypes: Specimen on slide BA Pal. ex CIRGEO 901 from the Chenque Formation in southeastern Chubut Province, Patagonia, Argentina.

Type locality and unit: Punta Pirámide section, northeastern Chubut, Argentina, Puerto Madryn Formation, Late Miocene.

Distribution: Eastern Patagonia, Early Miocene (Chenque Fm) to Late Miocene (Puerto Madryn Fm). The ages of the fossil bearing deposits were constrained based on palaeontological data, and independently supported by radiometric information (Barreda and Palamarczuk, 2000; Scasso et al., 2001; Parras et al., 2008).

Diagnosis: Pollen grains free, isopolar, radiosymmetrical, subspheroidal to suboblate, small. Tricolporate, colpi short, ora lalongate. Exine tectate and psilate (under light microscopy). Sexine thicker than nexine, formed by thin and tightly distributed columellae; tectum scarcely perforate. Nexine thickened towards endoapertures forming a distinct protrusion on the external surface.

Derivation of name: In reference to the robust wall protrusion on the external surface, near endoapertures.

Description: Pollen grains small, tricolporate, psilate (LM), appearing faintly microechinate under SEM, subspheroidal to suboblate; rhombic outline in equatorial view and subtriangular with flat to concave intercolpal regions in polar view. Colpi relatively short, with rounded ends and psilate colpal membrane. Endoaperture lalongate (ca. 2–2.5 µm), with acute equatorial ends. Exine tectate (1.2–1.5 µm thick), with the sexine about 3 times thicker than the nexine. Nexine thickened at the equatorial areas near endoapertures resulting in a wall protrusion on the external surface. Sexine formed by columellae and mostly indistinct under LM.

Dimensions: Equatorial diameter (11 specimens): 15–22 µm. Polar diameter (2 specimens): 17–19 µm.

Comparison: The new species differs from other *Psilatricolporites* taxa in having a robust wall protrusion on the external surface near the endoapertures.

Remarks: *P. protrudens* is very scarce in Early Miocene sediments and is usually found poorly preserved (Plate I, figs 1–2). We have only been able to illustrate this species under SEM from the Late Miocene assemblage where it is more commonly found (Plate II, fig. 2).

Botanical affinity: Miocene specimens are morphologically identical to those of the *Gamocarpha* type (Plate III, figs 1–2). The intercolpal concavities and colpal ledges, unique to the *Calycera* type, are lacking in the fossil forms. The Anthemoid-like exine pattern of the *Gamocarpha* type could not be observed under LM, except in the

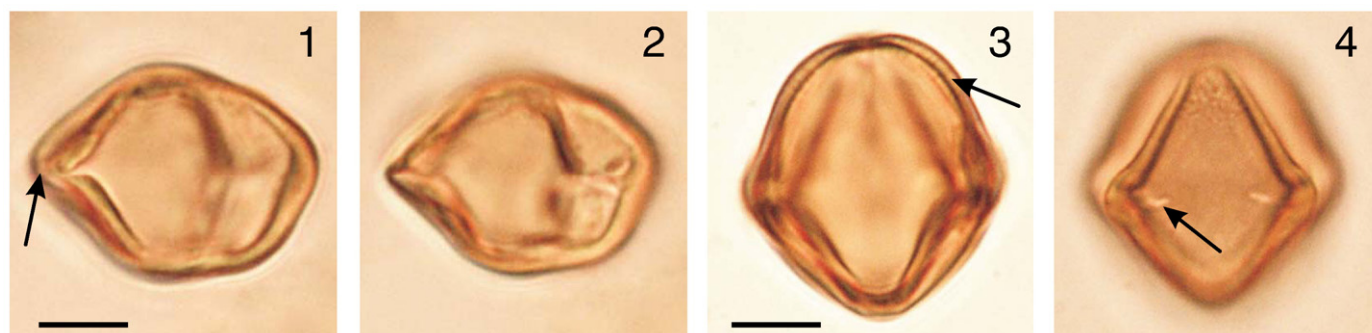


Plate I. 1–4. *Psilatricolporites protrudens* Palazzesi and Barreda sp. nov. LM photos.

- 1–2. Paratype BA Pal. ex CIRGEO 901: E37–4 from Early Miocene deposits. Arrow indicates wall protrusion;
- 3–4. Holotype BA Pal. 6011: N43 from Late Miocene deposits.
3. Arrow indicates columellate exine layer.
4. Arrow indicates lalongate apertures; bar: 5 µm.

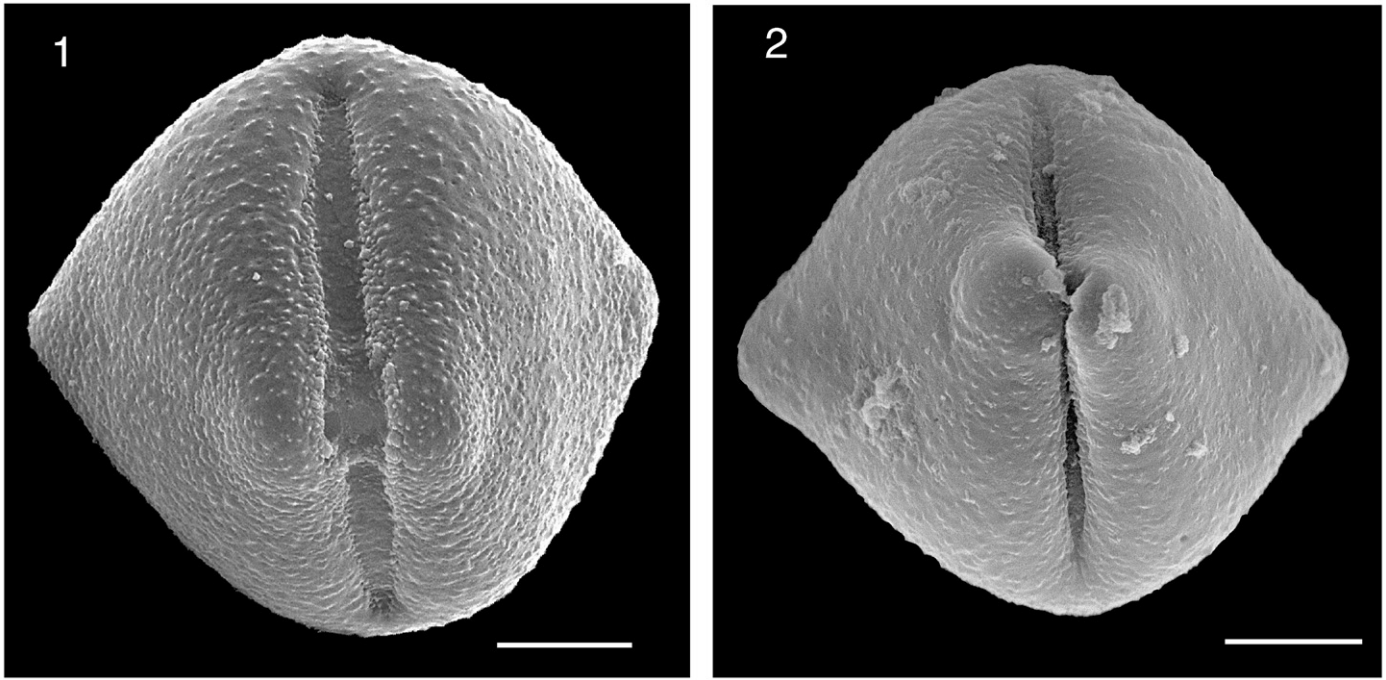


Plate II.

1. Extant (*Boopis anthemoides* Juss.) and
2. fossil (*Psilatricolporites protrudens* Palazzesi and Barreda sp. nov) pollen photomicrographs using SEM; bar: 5 μ m. Note the lack of suprategal elements on the fossil specimen probably due to poor preservation conditions.

absence of the cavus. The only apparent difference between *Psilatricolporites protrudens* and living forms of the *Gamocarpha* type is the virtual absence of microspines and perforations on the former according to SEM observations (Plate II, figs 1–2). These minor differences may be due to poor preservation rather than being diagnostic features.

4. Discussion and conclusions

Calyceraceae has been present in southern South America since at least the Early Miocene. In the fossil record it is commonly found associated with other stress-tolerant angiosperms more widely distributed such as Chenopodiaceae (*Chenopodipollis chenopodiaceoides*) and Convolvulaceae (*Cressa/Wilsonia*; *Tricolpites trioblatus*). These two families are rare in Late Oligocene deposits becoming frequent in the Early Miocene and rising to prominence in Late Miocene sediments from Patagonia, Australia and New Zealand (Barreda and Palazzesi, 2007; Martin, 2006). Most members of these families, including some Calyceraceae, are found today in saline or alkaline coastal locations (Plate III, fig. 3), growing on margins of ephemeral lakes, salt marshes, and flood plains of streams. In southern South America by the Miocene these families probably radiated in such stress environments where extremely few other angiosperms survived. Other important groups, also documented for the first time in the Early Miocene were *Chuquiraga*, and *Dasyphyllum* type 2 (pollen with intercolpal depression *sensu* Urtubey and Tellería, 1997) of the Barnadesioideae (Palazzesi et al., 2009). Calyceraceae and Barnadesioideae are closely related, and may have diverged in southern South America sometime before the Early Miocene (Stuessy et al., 1996). We have not found transitional fossil forms in sediments older than Miocene from Patagonia. The poor preservation conditions of the pre-Late Miocene pollen grains of Calyceraceae may easily lead to overlooking them, or to misidentification. If we assume that Calyceraceae originated in southern South America, as postulated by Stuessy et al. (1996), and that the nearest living relative of the fossils found in Patagonia (*Gamocarpha* type) had in the past similar

ecological niches, then it is likely that the early evolution of this family occurred in stress regions such as coastal swamp environments during the Eocene or the Oligocene when these types of settings were widespread in central and southern Patagonia (Romero, 1977; Barreda, 1997; Barreda et al., 2009). It may well be that *Gamocarpha* and other related genera are derived from radiations that took place during Early Miocene when a number of distinct episodes of aridification occurred. It is uncertain whether adaptations for extreme xeromorphy in the Calyceraceae existed during Miocene, before extreme widespread aridity had developed. The lack of megafossils prevent detailed analyses, but it is likely that xeromorphism arose later, after uplift of the southern Patagonian Andes which led to considerable aridification in the eastern lands from the Late Miocene onwards (Blisniuk et al., 2005).

Calyceraceae fossils have not been recorded in other continents to date. Other phylogenetically allied groups with a restricted distribution today (e.g. Menyanthaceae mainly in south Pacific regions and Mutisioideae Asteraceae mainly in South America) are known to have had a wider distribution in the past as they have been found in Oligocene sediments of Africa, Australia, and South America (Barreda et al., unpublished results). The lineages probably dispersed across these continents stimulated by the warm conditions prevailing before the final isolation of Antarctica, which is thought to have occurred about 30My before present (Lawver and Gahagan, 2003). The biogeographical timing of continental isolation most likely occurred from the Miocene onwards, when an effective dispersal barrier was established among southern Gondwanan land-masses. However, it may differ for lineages with different dispersal capabilities. Calyceraceae may have radiated in South America—as postulated in this study—during Miocene times, as well as other basal Asteraceae (e.g. Mutisioideae and Barnadesioideae). Only the more derived Asteracean groups (Asteroideae tribes) first documented from the Early Miocene in many distantly separated sites colonized virtually all continents in a relatively short period of time (Wang, 2004). The particularly good dispersal capability of Asteraceae seems to

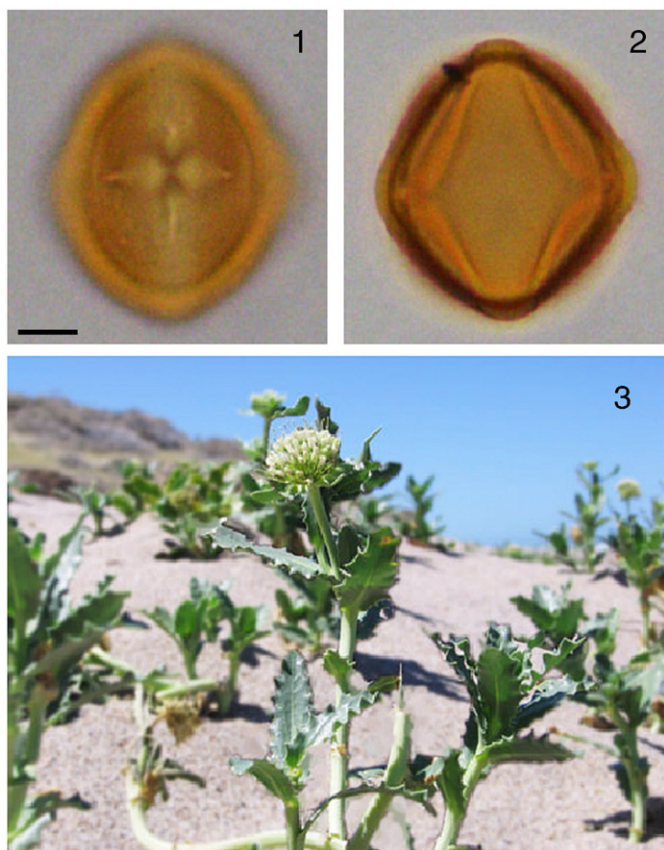


Plate III.

- 1–2. Extant pollen grains of the *Calycera pulvinata* J. Rémy (*Gamocarpha* type); bar: 5 μ m.
 3. Pioneer species of the Calyceraceae growing on coastal dunes under the extreme climatic conditions in eastern Patagonia (Chubut province).

contradict the fact that most of its basal members and its sister Calyceraceae are confined to some regions of South America. One possible explanation is that, in Calyceraceae and probably in Barnadesioideae, fruit dispersal may be the greatest barrier to ecological settlement. A persistent modified calyx, termed “pappus” in Asteraceae, plays a major role in seed dispersal in most members of this family. However in some ancestral groups, like in some Nassauviinae (e.g. *Polyachyrus* and *Moscharia*), the pappus, when present, is completely deciduous and probably does not assist in fruit in dispersal (Katinas and Crisci, 2000). In Calyceraceae the pappus-like calyx is persistent, and sometimes is lignified and spiny (Hellwig, 2007). The early pappus, as stated by Stuessy and Garver (1996), may have played a defensive role probably protecting the head. The notable morphology of Calyceraceae is usually explained as an adaptation to extreme conditions (Carlquist and DeVore, 1998) and almost certainly without any advantages for fruit dispersal.

The Calyceraceae fossils establish the presence of *Gamocarpha*-related species in the Miocene of southern South America. The first major radiation of this family occurred during a period of significant shift to more arid conditions that caused extinction of numerous Gondwanan elements but had little effect on the Calyceraceae.

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