



## Fossil pollen grains of Asteraceae from the Miocene of Patagonia: Barnadesioideae affinity

Luis Palazzesi<sup>a,\*</sup>, Viviana Barreda<sup>a</sup>, María Cristina Tellería<sup>b,c</sup>

<sup>a</sup> Sección Paleopalynología, División Paleobotánica, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Av. Ángel Gallardo 470, C1405DJR, Buenos Aires, Argentina

<sup>b</sup> Laboratorio de Sistemática y Biología Evolutiva, Museo de La Plata, Paseo del Bosque s/n, 1900 La Plata, Argentina

<sup>c</sup> Laboratorio de Actuopalynología, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Av. Ángel Gallardo 470, C1405DJR, Buenos Aires, Argentina

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### ABSTRACT

New fossil pollen grains were recovered from marine Miocene deposits from eastern Patagonia (southern South America). Sculpture and structure exine features indicate a close relationship with modern Barnadesioideae, a basal lineage within Asteraceae. Barnadesioideae is confined to South America and is represented mainly by shrubs, herbs and some trees occurring in different habitats under a wide range of climatic conditions. It has recently attracted a great deal of attention as it was considered the sister-group to the remaining members of the family based on molecular data. Barnadesioideae has not previously been described in the fossil record. One new genus and three species are erected in *Quillembaypollis gamerroi*, *Q. tayuoides* and *Q. stuessyi* to assemble distinct pollen types clearly similar to those produced today by extant *Chuquiraga*, *Dasyphyllum* and *Schlechtendalia*, respectively. These are the first fossil records of these genera, taking them back 23–20 Ma (*Dasyphyllum* and *Chuquiraga* types) and 11–9 Ma (*Schlechtendalia* type). The new morphotaxon is clearly distinguishable by being microechinate, and by having a thick sexine formed by one (*Q. tayuoides*), two (*Q. gamerroi*) or three (*Q. stuessyi*) layers, as the most prominent features. Their closest living relatives today grow far from the studied site (eastern Patagonia), with the exception of *Chuquiraga* type which is the sole surviving group in the region. Pollen and spore assemblages of Early Miocene age (23–20 Ma) from southern South America indicate that the climate was sub-humid and temperate to warm–temperate. This climatic trend may have allowed *Dasyphyllum* species to radiate in eastern Patagonian forests, while *Chuquiraga* probably occupied more open areas along the coast. Late Miocene (11–9 Ma) palynological assemblages suggest warm but seasonally dry conditions, in which *Schlechtendalia* developed probably in the hinterland vegetation joined with low trees, and halophytic/xerophytic shrubs and herbs.

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### 1. Introduction

The origin and early radiation of Asteraceae may have taken place in South America during Paleogene according to biogeographical, phylogenetical and morphological cladistic studies (DeVore and Stuessy, 1995; Stuessy et al., 1996; Gustafsson et al., 2001). Barnadesioideae is the smallest subfamily of Asteraceae (ca. 90 species) and occurs only in South America, being particularly widespread in the Andean region. It is represented by shrubs (e.g. *Chuquiraga avellanadae* Lorentz., *Doniophyton anomalum* (D. Don) Kurtz), herbs (e.g. *Schlechtendalia luzulaefolia* Less., *Dusenilla patagonica* (O. Hoffmann) Schumann.) and some large trees (*Dasyphyllum* subg. *Archidasyphyllum sensu* Cabrera, 1959). Recent molecular studies indicated that Barnadesioideae is sister to the rest of the family based on the lack of two cpDNA inversions of 22.8 and 3.3 kb, which are present in all the remaining clades of Asteraceae (Kim and Jansen, 1995; Kim et al., 2005). Barnadesioideae has not previously been described in the fossil record although some current evolutionary trees

suggested that their members were present since the Oligocene or Miocene based on morphological cladistic and molecular clock analyses (Stuessy et al., 1996; Kim et al., 2005).

This study is part of a wider and continuing research project about fossil pollen grains related to the Asteraceae and their most closely allied families recovered from the Patagonian late Paleogene–early Neogene interval. In previous studies we analyzed the Asteracean fossil records in Patagonia (Katinas et al., 2007) and presented new morphotaxa to assemble unique fossil pollen grains only found today in the Nassauviinae tribe (Barreda et al., 2008).

In this work the first fossil record of Barnadesioideae is presented on the basis of pollen grains recovered from marine Miocene deposits from eastern Patagonia. Recent systematic and morphological studies on extant pollen grains of the Barnadesioideae will be, joined with new observations, the major source of comparisons.

### 2. Material and methods

Samples containing fossil pollen specimens were collected from the Chenque (23–20 Ma), and Puerto Madryn (11–9 Ma) formations

\* Corresponding author.

E-mail address: [lpalazzesi@macn.gov.ar](mailto:lpalazzesi@macn.gov.ar) (L. Palazzesi).

during field trips in summer 1985 and 1986 by one of us (V.B). The ages of these marine sediments are constrained by paleontological and radiometric data (Zinsmeister et al., 1981; Palamarczuk and Barreda, 1998; Malumián and Nález, 1998; Scasso et al., 2001; Parras et al., 2008). The location of the sampling sites is given in Barreda et al. (2008). Slides containing the fossil specimens analyzed and illustrated in this study are housed at the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” under the numbers 6012, 6013, 6015 of the BA Pal and 842, 894, 901 of the BA Pal ex CIRGEO palynological collection. Pollen grains from extant material were obtained from herbarium specimens (LP) examined and cited by Urtubey and Tellería (1997). Extant pollen grains having the most similar patterns to those of the fossils are described and briefly characterized (Table 1). Pollen terminology follows Punt et al. (2007).

### 3. Pollen of extant Barnadesioideae (Asteraceae): a brief overview

Pollen produced by Barnadesioideae is diverse and has been the focus of much attention for the past decades. The first attempts to understand their morphological patterns (both structural and sculptural) were those undertaken by Wodehouse (1928, 1929) who characterized and illustrated pollen of *Barnadesia*, *Dasyphyllum*, and *Schlechtendalia* species for the first time. Parra and Marticorena (1972) described and illustrated the pollen of some species of *Chuquiraga*, *Dasyphyllum* and *Doniophyton*. Skvarla et al. (1977) analyzed the structure of *Barnadesia*, *Dasyphyllum* and *Schlechtendalia* species under TEM. Gamero (1985) examined the pollen of *Huarpea andina* Cabrera and discussed its taxonomical relationships with *Barnadesia odorata* Griseb. Urtubey and Tellería (1997) studied the pollen morphology of all species of subfamily Barnadesioideae with LM and SEM; they recognized three main pollen types defined by the exomorphology: (1) lophate (*Barnadesia* and *Huarpea*); (2) with intercolpal depressions (*Arnaldoa*, *Dasyphyllum* [subtypes I, II, and III] and *Schlechtendalia*); and (3) without intercolpal depressions (*Chuquiraga*, *Dasyphyllum*, *Doniophyton*, *Duseniella* and *Fulcadea*). Zhao et al. (2000) analyzed, using TEM, the ultrastructure of Barnadesioideae and essentially agreed with the types recognized by Urtubey and Tellería (1997).

### 4. Systematic paleontology

In this study a new genus and three species are erected to accommodate unique fossil pollen grains related to Barnadesioideae on the basis of their aperture features, exomorphology, exine structure-sculpture, and size.

*Quilembaypollis* Palazzesi and Barreda gen. nov. (Plates I and II).  
Type species: *Quilembaypollis gamerroi* Palazzesi and Barreda sp. nov.

*Derivation of name:* with reference to “quilembay”, a native term commonly used to name *Chuquiraga avellanadae*, a woody shrub of Barnadesioideae.

*Diagnosis:* Pollen grains free, isopolar, radiosymmetrical, subprolate, spheroidal to suboblate. Tricolporate, colpi long with smooth membrane, endoaperture lalongate. Exine thick, tectate, microechinate. Sexine thicker than nexine. Sexine formed by one, two or three columellate or columellate–granulate sublayers; the columellae are generally weak and poorly distinguishable.

*Comparisons:* This genus is intended to accommodate fossil dispersed pollen of the *Chuquiraga*, *Dasyphyllum* and *Schlechtendalia* types. It appears to be morphologically close to *Dicrassipollis* defined by Mildenhall and Pocknall (1989) from the Neogene of South Island, New Zealand. However, this last morphotype differs in having a different exine sculpture and structure. *Poluspissusites* defined by Salard-Cheboldaef (1978) and emended by Pocknall (1982) from the Late Oligocene of Southland, New Zealand, is similar in external appearance but differs in having thickened and ramified columellae. Other morphotaxa related to Asteraceae s.l. such as *Tubulifloridites*, *Mutisiapollis* and *Huanilipollis* have a significantly different exine structure and pollen shape.

*Quilembaypollis gamerroi* Palazzesi and Barreda sp. nov. (Plate I, Figs. 1–4)

*Holotype:* Specimen on slide BA Pal. 6015: D42-2 from the Puerto Madryn Formation at Punta Pirámide section on northeastern Chubut Province, Patagonia, Argentina.

*Paratypes:* Specimen on slide BA Pal. ex CIRGEO 842: J32/K32 from the Chenque Formation at Chenque section on southeastern Chubut Province, Patagonia, Argentina. Specimen on slide BA Pal. 6012: A53 from the Puerto Madryn Formation at Punta Pirámide section on northeastern Chubut Province, Patagonia, Argentina.

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

*Distribution:* Eastern Patagonia, Early Miocene to Late Miocene (Chenque and Puerto Madryn Formations).

*Diagnosis:* Pollen grains free, isopolar, radiosymmetrical, subprolate to subspheroidal, medium size. Tricolporate, colpi long, endoaperture lalongate. Exine tectate, microechinate. Sexine 3–4 times thicker than nexine formed by two columellate sublayers, with the endosexine thicker than the ectosexine. Columellae thin, tightly distributed. Nexine thickened towards apertures forming costae.

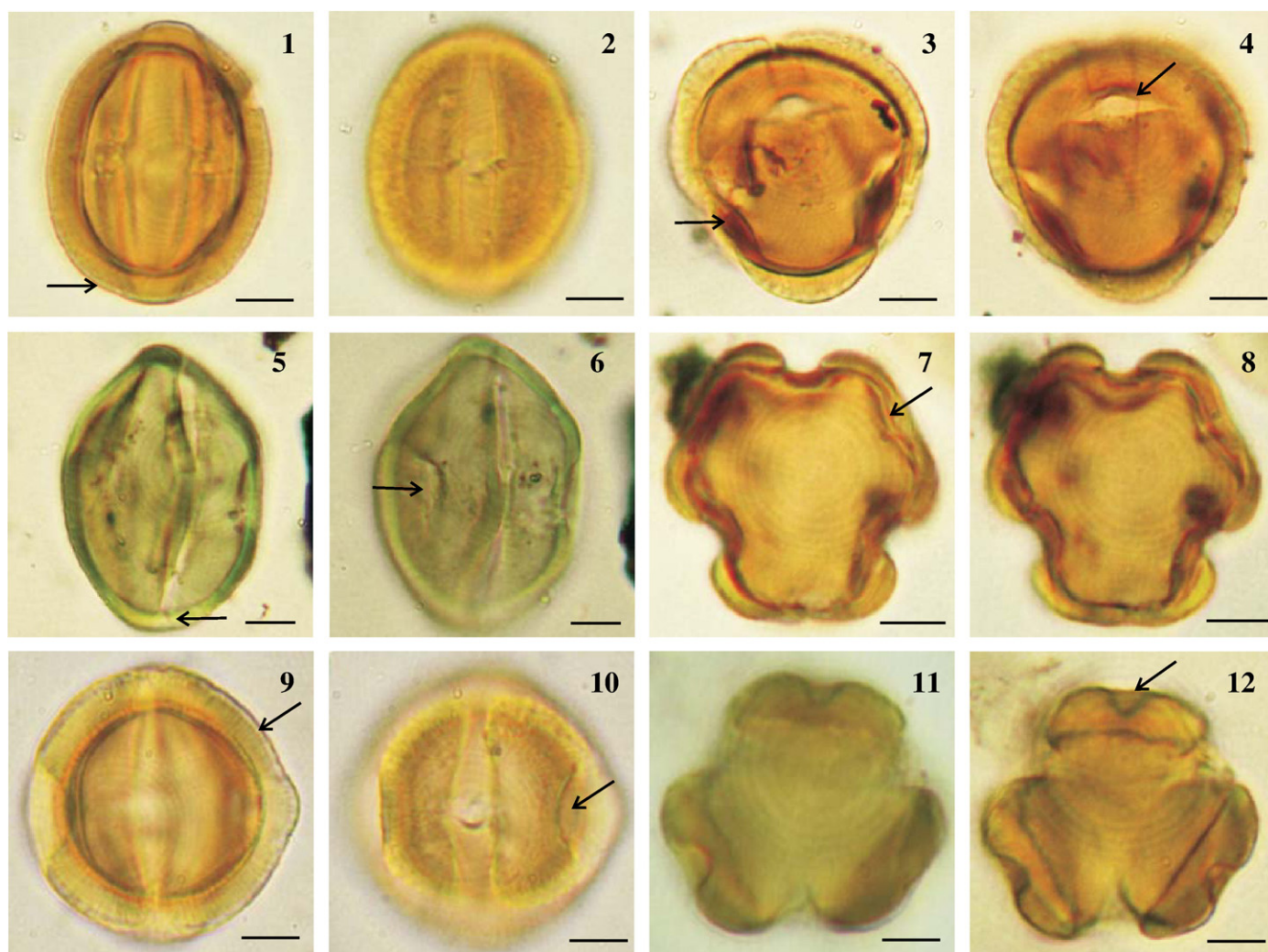
*Derivation of name:* With reference to the Argentinean botanist Juan Carlos Gamero in recognition of his work on extant Asteraceae in South America.

*Description:* Pollen grains of medium size, tricolporate, microechinate, subprolate to subspheroidal in shape; circular to subcircular in polar view. The colpi are long, with acute ends and smooth colpal membrane. The endoaperture is lalongate (5 × 10 μm), with acute equatorial ends. The exine is tectate (ca. 3 μm thick), with the sexine about three to four times thicker than nexine. The sexine is formed by two columellate sublayers, the endosexine (1.5–2 μm) with columellae tightly compacted, and the ectosexine (1–1.2 μm) columellate–granulate. The nexine is thickened towards apertures, forming costae.

**Table 1**

Fossil taxa analyzed: general aspects (number of species, plant habit and geographical distributions) and pollen grain features of their nearest living relatives.

Fossil taxa	Nearest living relative	General aspects	Pollen grain features			
			Number of species, plant habit and geographical distribution	Shape	Dp	De
			(P/E)	(μm)	(μm)	(μm)
<i>Q. gamerroi</i>	<i>Chuquiraga</i> spp.	21 species of small shrubs. Present in the Andes from Colombia to Argentina and Chile	Spheroidal subprolate prolate	27–56	24–50	2.5–5
	<i>Doniophyton</i> spp.	2 species of small shrubs. Present in the Andean and Patagonian region of Chile and Argentina	Subprolate prolate	35–50	28–44	4–7.5
	<i>Duseniella patagonica</i>	Monotypic genus of herbs. Present in the Patagonian region of Argentina	Subprolate–spheroidal	28–36	23–34	3–4
<i>Q. tayuoides</i>	<i>Dasyphyllum</i> spp.	39 species of shrubs and trees. Present in the Andes from Venezuela to northwestern Argentina, central Chile and eastern Brazil	Suboblate spheroidal subprolate	21–46	20–45	ca. 3
<i>Q. stuessyi</i>	<i>Schlechtendalia luzuaefolia</i>	Monotypic genus of herbs. Present in southern Brazil, Uruguay and northeastern Argentina	Subprolate	30–45	28–37	4–5



### Plate I.

- Figs. 1–4. *Quilembaypollis gamerroi* Palazzesi and Barreda sp. nov. 1–2. Specimen on slide BA Pal. BA Pal. 6015: D42-2, Holotype in equatorial view at two focus levels. 1. Optical section showing the thin ectosexine (arrow). 2. High focus showing long colpi with acute ends and smooth colpal membrane. Figs. 3–4. Specimen on slide BA Pal. ex CIRGEO 842: J32/K32. Paratype in polar view at two focus levels. 3. Optical section showing the thickened nexine close to endoapertures (arrow). 4. High focus showing lalongate endoaperture (arrow), and mesoapertural membrane remains.
- Figs. 5–8. *Quilembaypollis tayuoides* Barreda and Palazzesi sp. nov. 5–6. Specimen on slide BA Pal. ex CIRGEO 895: X42-3, Holotype in equatorial view at two focus levels. 5. Optical section showing the exine formed by one layer (arrow). 6. High focus showing an equatorial depression (arrow). Figs. 7–8. Specimen on slide BA Pal. ex CIRGEO 901: E38-2. Paratype in polar view at two focus levels showing the cavea (arrow).
- Figs. 9–12. *Quilembaypollis stuessyi* Palazzesi and Barreda sp. nov. 9–10. Specimen on slide BA Pal. 6013: Y38-3, Holotype in equatorial view at two focus levels. 9. Optical section showing the sexine formed by three layers (arrow). 10. High focus showing an equatorial depression (arrow). Figs. 11–12. Specimen on slide BA Pal. 6013: B46-2. Paratype in polar view at two focus levels showing the thick exine, the apertures and the equatorial depressions. Scale bars 5  $\mu$ m.

**Dimensions:** Polar diameter (10 specimens): 23–30  $\mu$ m. Equatorial diameter (2 specimens): 24–26  $\mu$ m.

**Comparison:** Differs from the remaining members of the morphogenus (*Q. stuessyi* and *Q. tayuoides*) in having the sexine stratified in two layers and in not having equatorial depressions.

**Botanical affinity:** The species agrees in all essential characteristics with pollen of extant *Chuquiraga*, *Dusenella* and *Doniophyton*. These genera are represented mainly by shrubs and are widely distributed in South America from Colombia, to Chile and Argentina (Fig. 1.1).

*Quilembaypollis tayuoides* Barreda and Palazzesi sp. nov. (Plate I, Figs. 5–8; Plate II, Figs. 1–2).

**Holotype:** Specimen on slide BA Pal. ex CIRGEO 895: X42-3 from the Chenque Formation at Punta Delgada section on southeastern Chubut Province, Patagonia, Argentina.

**Paratype:** Specimen on slide BA Pal. ex CIRGEO 901: E38-2 from the Chenque Formation at Playa Las Cuevas section on southeastern Chubut Province, Patagonia, Argentina.

**Type locality and unit:** Punta Delgada section, southeastern Chubut Province, Argentina, Chenque Formation, Early Miocene.

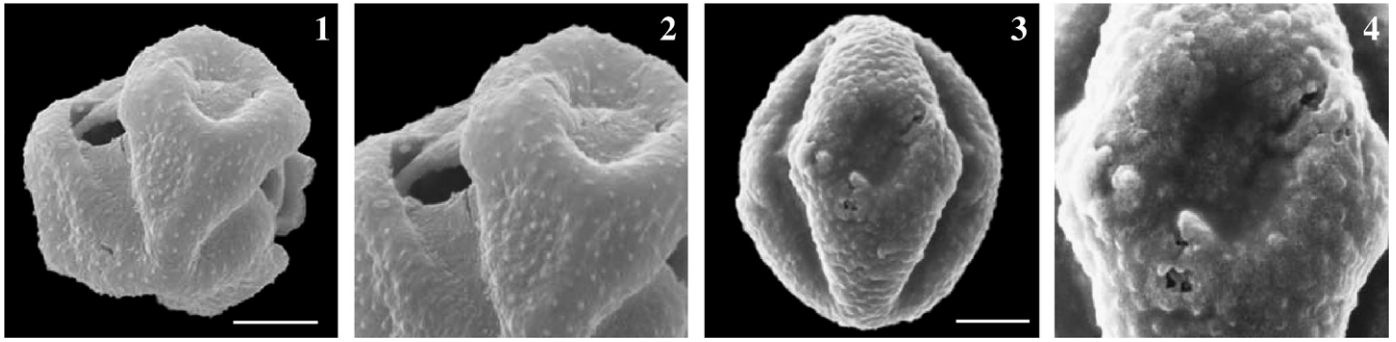
**Derivation of name:** With reference to the common name Tayu, used to name *Dasyphyllum diacanthoides* (Less.) Cabrera, a large tree of Barnadesioideae.

**Distribution:** Eastern Patagonia, Early Miocene (Chenque Formation).

**Diagnosis:** Pollen grains free, isopolar, radiosymmetrical, subprolate, subspheroidal to suboblate, medium size. Tricolporate, colpi long, endoaperture lalongate. Exine tectate, microechinate, with three equatorial depressions, caveate. Sexine two or three times thicker than nexine, reduced in depressions, formed by one layer. Columellae poorly distinguished. Nexine thickened towards apertures forming costae.

**Description:** Pollen grains of medium size, tricolporate, microechinate, subprolate, subspheroidal to suboblate in shape; circular to subangular in polar view. The colpi are long, with acute ends and smooth membrane. The endoaperture is lalongate (3 × 10  $\mu$ m), with





**Plate II.**

Figs. 1–2.  
Figs. 3–4.

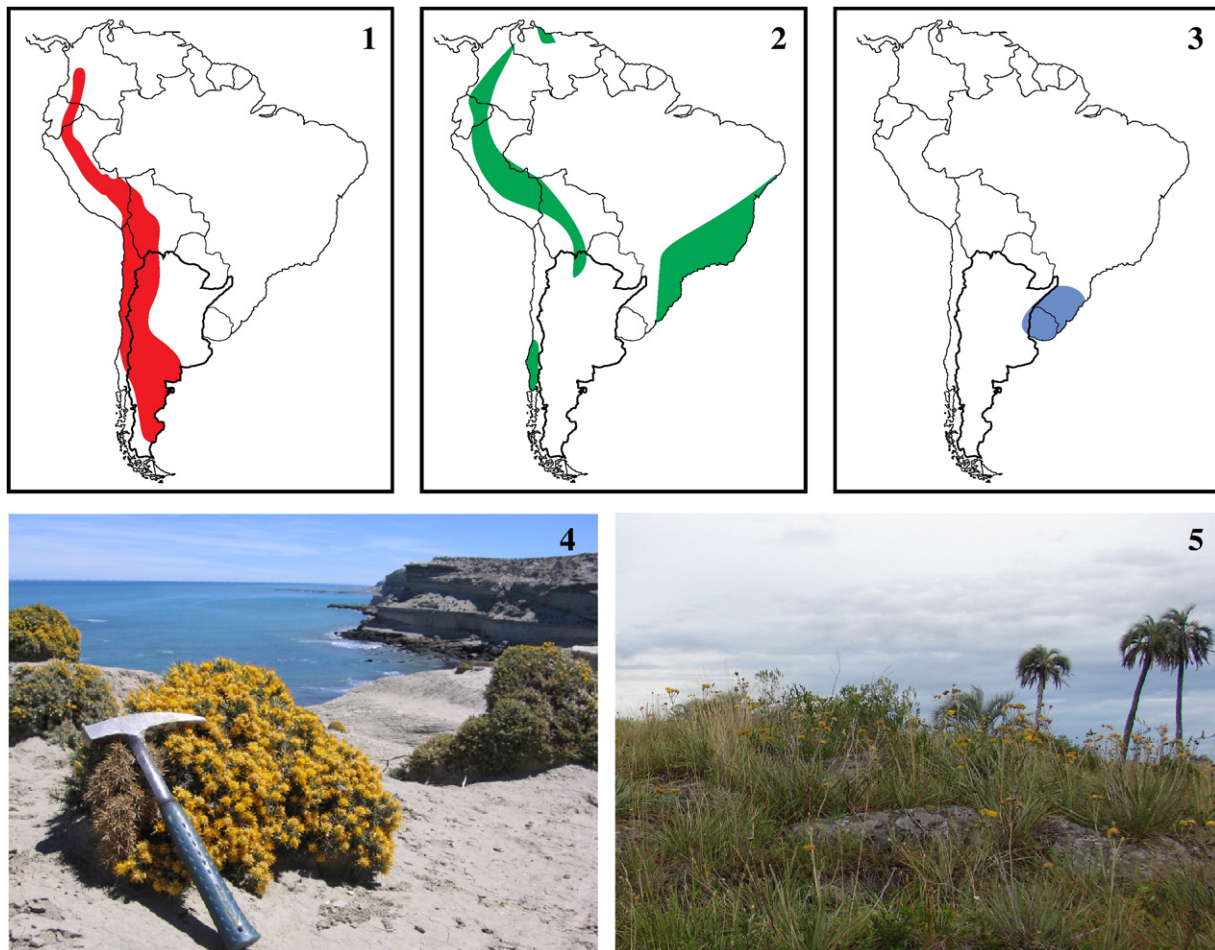
*Quilembaypollis tayuoides* Barreda and Palazzesi sp. nov. SEM photomicrographs. 1. Polar view showing the external features. 2. Detail showing the cavea.  
*Quilembaypollis stuessyi* Palazzesi and Barreda sp. nov. SEM photomicrographs. 3. Equatorial view showing the external features. 4. Detail showing an equatorial depression. Scale bars 5  $\mu\text{m}$ .

acute equatorial ends. The exine is tectate (ca. 1.8–2.5  $\mu\text{m}$  thick), with the sexine two or three times thicker than nexine. The sexine is formed by one layer (1.5–2  $\mu\text{m}$ ), thinning towards equatorial depressions. Columellae poorly distinguished. Cavea present. Three depressions are present at the equatorial region. The nexine is thickened towards apertures, forming costae.

*Dimensions:* Polar diameter (3 specimens): 26–31  $\mu\text{m}$ . Equatorial diameter (2 specimens): 17–21  $\mu\text{m}$ .

*Comparison:* Differs from *Q. gameroi* and *Q. stuessyi* in having one-layered sexine pattern and in being caveate.

*Botanical affinity:* *Q. tayuoides* is similar to species of *Dasyphyllum* type 2, subtype I of Urtubey and Tellería (1997), characterized by



**Fig. 1.** Current geographic distributions of: 1. *Chuquiraga* type 2. 2. *Dasyphyllum* type 2 subtype I of Urtubey and Tellería (1998). 3. *Schlechtendalia luzulaefolia*. 4. Specimens of *Chuquiraga avellanadae* and *Chuquiraga hystrix* at northeastern Patagonia, Península Valdés region. 5. Specimens of *Schlechtendalia luzulaefolia* at Entre Ríos province, El Palmar region, northeastern Argentina. Geographical distributions were taken and modified from Stuessy et al. (1996).

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. 1.2). Pollen of species of *Dasyphyllum* with three equatorial depressions was considered to be related to pollen of *Schlechtendalia luzulaefolia* by Wodehouse (1928). However, they clearly differed from the sexine structure which is commonly one-stratified in *Dasyphyllum* and three-stratified in *Schlechtendalia luzulaefolia* (Urtubey and Tellería, 1997).

*Quilembaypollis stuessyi* Palazzesi and Barreda sp. nov. (Plate I, Figs. 9–12; Plate II Figs. 3–4).

*Holotype*: Specimen on slide BA Pal. 6013: Y38-3 from the Puerto Madryn Formation at Punta Pirámide section on northeastern Chubut Province, Patagonia, Argentina.

*Paratypes*: Specimen on slide BA Pal. 6013: B46-2 from the Puerto Madryn Formation at Punta Pirámide section on northeastern Chubut Province, Patagonia, Argentina. Specimen on slide BA Pal. 6015: X35/Y35 from the Puerto Madryn Formation at Punta Pirámide section on northeastern Chubut Province, Patagonia, Argentina.

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

*Distribution*: Northeastern Patagonia, Late Miocene (Puerto Madryn Formation).

*Diagnosis*: Pollen grains free, isopolar, radiosymmetrical, subprolate, spheroidal to suboblate, medium size. Tricolporate, colpi long, endoaperture lalongate. Exine tectate, microechinate, with three equatorial depressions. Sexine about four times thicker than nexine, formed by three columellate sublayers, with the middle layer always thicker than both endo- and ectosexine. Columellae thin, tightly distributed. Nexine thickened towards apertures forming costae.

*Derivation of name*: With reference to the botanist Tod F. Stuessy in recognition of his work on extant Barnadesioideae.

*Description*: Pollen grains of medium size, tricolporate, microechinate, subprolate, spheroidal to suboblate in shape; circular to subcircular in polar view. The colpi are long, with acute ends and smooth membrane. The endoaperture is lalongate ( $3 \times 5 \mu\text{m}$ ), with acute equatorial ends. The exine is tectate ( $3\text{--}5 \mu\text{m}$  thick), with the sexine about four times thicker than nexine. The sexine is formed by three columellate sublayers, the endosexine ( $0.5 \mu\text{m}$ ) and the ectosexine ( $1 \mu\text{m}$ ) with columellae tightly compacted, and the thicker middle layer ( $2.5 \mu\text{m}$ ) with columellae more sparsely distributed. Three depressions (rarely two) are present at the equatorial region. The nexine is thickened towards apertures, forming costae.

*Dimensions*: Polar diameter (11 specimens):  $23\text{--}27 \mu\text{m}$ . Equatorial diameter (2 specimens):  $24\text{--}26 \mu\text{m}$ .

*Comparison*: Differs from *Q. gamerroi* and *Q. tayuoides* in having a three-layered sexine pattern.

*Botanical affinity*: This species is typical for the *Schlechtendalia* pollen type of the Barnadesioideae. This extant genus is restricted to warm-temperate to warm and grassy areas of southern Brazil, Uruguay and northeastern Argentina (Fig. 1.3).

## 5. Discussion and conclusions

The major evolutionary events in the Barnadesioideae were analyzed by Stuessy et al. (1996) in a phylogenetic and biogeographic context. These approaches have given important insights into the time of origin and diversification of the most important clades of this subfamily, which are in turn fairly similar to those latter proposed by the molecular time estimates (Kim et al., 2005). According to the published information available, the initial differentiation of the Barnadesioideae would have occurred during Oligocene (Kim et al., 2005) or Miocene (Stuessy et al., 1996) times. These ages are in part supported by the fossil record of this subfamily in Patagonia; during the Early Miocene *Dasyphyllum* and *Chuquiraga* types were already

differentiated based on the morphological examination of the fossil pollen grains here reported.

*Chuquiraga* and their most closely allied genera (*Doniophyton* and *Dusenilla*) are widely distributed in South America, especially in arid and semi-arid regions of the Andean Range. In southern South America these are the only surviving genera of Barnadesioideae in the non-Andean regions. In northeastern Patagonia (Península Valdes area) some species of *Chuquiraga* (*Ch. avellanadae* and *Ch. histrix* Don) grow today in small patches and occur even in exposed regions alongside the coast (Fig. 1.4), where only few species survive due to the extreme conditions (e.g. strong winds, sea spray). *Quilembaypollis gamerroi*, which is here related to the *Chuquiraga-Doniophyton-Dusenilla* group (Table 1), is very scarce in the Early Miocene and remained low in abundance even in the Late Miocene. *Chuquiraga* may have evolved during the Miocene near the shoreline, joined with other stress tolerant taxa which are common in this period of time, such as Chenopodiaceae (*Chenopodipollis chenopodiaceoides*), Ephedraceae (*Equisetosporites* spp.) and Convolvulaceae *Cressa* type (*Tricolpites trioblatatus*) (Palazzesi and Barreda, 2004; Barreda and Palazzesi, 2007).

Extant species of *Dasyphyllum* characterized by having pollen grains with three equatorial depressions (Urtubey and Tellería, 1997), as those here identified as *Q. tayuoides*, are today distributed in central Chile, southeastern Brazil and in the Andean region from Venezuela to northwestern Argentina. The fossil species related to this genus is found in trace amounts in eastern Patagonian sediments, and has only been recorded in the Early Miocene so far. During the Early Miocene *Dasyphyllum* coupled with other Gondwanan lineages such as Nothofagaceae, Proteaceae and Winteraceae probably shared similar habitats. It seems likely that the arid and semi-arid conditions that forced all wet-demanding taxa to migrate from the eastern lands of Patagonia during Miocene may have caused dry-tolerant species (including *Chuquiraga*) to radiate from these times onwards.

Today the monotypic *Schlechtendalia* is distributed in southern Brazil, Uruguay and as isolated patches in northeastern Argentina (Fig. 1.5). Fossil pollen grains have been only recorded in Late Miocene deposits so far, according to this study. The lack of this fossil morphotype (*Q. stuessyi*) in Early Miocene sediments implies either: it was not found in pre-Late Miocene records because of the taphonomic or sampling bias in the fossil record; it had not evolved by these times; it was not part of the eastern Patagonian vegetation by these times. *Schlechtendalia luzulaefolia* was postulated to have been part of a specialized flora (or “insular flora”) in southern Brazil during the Late Miocene, the time of the “Entrerriense” high-sea-level event (Rambo, 1954; Mondin and Baptista, 1996). The present finding of the *Schlechtendalia* type in “Entrerriense” deposits of eastern Patagonia (Puerto Madryn Formation) supports the previous assumption. The geographic expansion from the upland to the adjacent lowland areas where this species inhabits today probably occurred during low-sea level stands. *Schlechtendalia* most likely became extinct from Patagonia during the cooling trend of the latest Neogene.

This study establishes a reliable occurrence of Barnadesioideae in the fossil record. Although a more precise time of differentiation of their members must await new evidence, the present findings highlight the importance of studying the fossil record as one of the crucial points in interpreting the time and place of origin of Asteraceae, the most diverse family of living angiosperms on the planet today (Panero and Funk, 2008). The present record of Barnadesioideae together with the relatively large number of fossil sunflower allied taxa being discovered in late Paleogene and early Neogene deposits from Patagonia indicate that southern South America probably had the highest Asteracean diversity of any region. It may be possible to use these fossil records as minimum age calibrations for dating future phylogenetic trees of the family, but care should be taken in doing so until more fossil sunflower remains become discovered in other regions of South America.

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## References

- Barreda, V., Palazzesi, L., 2007. Patagonian vegetation turnovers during the Paleogene–Early Neogene: origin of arid-adapted floras. *The Botanical Review* 73, 3–50. New York Botanical Garden Press.
- Barreda, V., Palazzesi, L., Tellería, M.C., 2008. Fossil pollen grains of Asteraceae from the Miocene of Patagonia: Nassauviinae affinity. *Review of Palaeobotany & Palynology* 151, 51–58.
- Cabrera, A.L., 1959. Revisión del género *Dasyphyllum*. *Revista del Museo de La Plata* 9 (38), 22–99 Argentina.
- DeVore, M.L., Stuessy, T.F., 1995. The place and time of origin of the Asteraceae, with additional comments on the Calyceraceae and Goodeniaceae. In: Hind, D.J.N., Jeffrey, C., Pope, G. (Eds.), *Advances in Compositae Systematics*. Royal Botanic Gardens, Kew, pp. 23–40.
- Gamero, J.C., 1985. Morfología del polen de *Huarpea* y su relación con *Barnadesia* (Mutiseae, Compositae). *Darwiniana* 26, 43–51.
- Gustafsson, M.H.G., Pepper, A.S.R., Albert, V.A., Kallersjö, M., 2001. Molecular phylogeny of the Barnadesioideae (Asteraceae). *Nordic Journal of Botany* 21, 149–160.
- Katinas, L., Crisci, J., Tellería, M.C., Barreda, V., Palazzesi, L., 2007. Early history of Asteraceae in Patagonia: evidence from pollen grains. *New Zealand Journal of Botany* 45, 605–610.
- Kim, K.J., Jansen, R.K., 1995. *NdhF* sequence evolution and the major clades in the sunflower family. *Proceedings of the National Academy of Sciences* 92, 10379–10383.
- Kim, K.J., Choi, K.S., Jansen, R.K., 2005. Two chloroplast DNA inversions originated simultaneously during the early evolution of the sunflower family (Asteraceae). *Molecular Biology and Evolution* 22, 1783–1792.
- Malumián, N., Nález, C., 1998. El género *Transversigerina* y la edad de la transgresión patagónica. 9° Congr. Latinoamer. Geol. y 4°. Congr. Nac. Geol. Econ., vol. 1, pp. 285–290.
- Mildenhall, D.C., Pocknall, D.T., 1989. Miocene–Pleistocene spores and pollen from Central Otago, South Island, New Zealand. *New Zealand Geological Survey. Paleontological Bulletin*, vol. 59, pp. 1–128.
- Mondin, C.A., Baptista, L.R.M., 1996. Relações biogeográficas da tribo Mutiseae Cass. (Asteraceae), sensu Cabrera, no Rio Grande do Sul. *Comun. Mus. Ciênc. Tecnol.*, Pontifícia Universidade Católica do Rio Grande do Sul (PUCRS). Ser. Bot., vol. 2, pp. 49–152.
- Palamarczuk, S., Barreda, V.D., 1998. Bioestratigrafía de dinoflagelados de la Formación Chenque (Mioceno), Provincia del Chubut. *Ameghiniana* 35, 415–426.
- Palazzesi, L., Barreda, V., 2004. Primer registro palinológico de la Formación Puerto Madryn, Mioceno de la provincia del Chubut, Argentina. *Ameghiniana* 41, 355–362.
- Parra, O., Marticorena, C., 1972. Granos de polen de plantas chilenas, II. Compositae–Mutiseae. *Gayana* 21, 9–13.
- Parras, A., Griffin, M., Feldmann, R., Casadío, S., Schweitzer, C., Marenssi, S., 2008. Isotopic ratios and faunal affinities in the correlation of marine beds across the Paleogene/Neogene boundary in southern Patagonia, Argentina. *Journal of South American Earth Sciences* 26, 204–216.
- Panero, J.L., Funk, V.A., 2008. The value of sampling anomalous taxa in phylogenetic studies: major clades of the Asteraceae revealed. *Molecular Phylogenetics and Evolution* 47, 757–782.
- Pocknall, D.T., 1982. Palynology of late Oligocene Pomahaka Estuarine Bed sediments, Waikoiko, Southland, New Zealand. *New Zealand Journal of Botany* 20, 263–287.
- Punt, W., Hoen, P.P., Blacmore, S., Nilsson, S., Le Thomas, A., 2007. Glossary of pollen and spore terminology. *Review of Palaeobotany & Palynology* 143, 1–81.
- Rambo, B., 1954. Análise histórica da flora de Porto Alegre. *Sellowia* 6, 9–112.
- Salard-Cheboldaef, M., 1978. Sur la palynoflore Maestrichtienne et Tertiaire du bassin sédimentaire littoral du Cameroun. *Pollen et Spores* 20, 215–260.
- Scasso, R.A., McArthur, J.M., del Rio, C.J., Martinez, S., Thirlwall, M.F., 2001.  $^{87}\text{Sr}/^{86}\text{Sr}$  Late Miocene age of fossil mollusks in the 'Entrerriense' of the Valdés Peninsula (Chubut, Argentina). *Journal of South American Earth Sciences* 14, 319–329.
- Skvarla, J.J., Turner, B.L., Patel, V.C., Tomb, A.C., 1977. Pollen morphology in the Compositae and in morphologically related families. In: Heywood, V.H., Harborne, J.B., Turner, B.L. (Eds.), *The Biology and Chemistry of the Compositae*, London, pp. 141–265.
- Stuessy, T.F., Sang, T., DeVore, M.L., 1996. Phylogeny and biogeography of the subfamily Barnadesioideae with implications for early evolution of Compositae. In: Hind, D.J.N., Jeffrey, C., Pope, G.V. (Eds.), *Proceedings of the International Compositae Conference, 1994*, Kew. Systematics, vol. 1. Royal Botanic Gardens, Kew, pp. 463–490.
- Urtubey, E., Tellería, M.C., 1997. Pollen morphology of the subfamily Barnadesioideae (Asteraceae) and its phylogenetic and taxonomic implications. *Review of Palaeobotany & Palynology* 104, 19–37.
- Wodehouse, R.P., 1928. Pollen grains in the identification and classification of plants. II. *Barnadesia*. *Bulletin of the Torrey Botanical Club* 55, 449–462.
- Wodehouse, R.P., 1929. Pollen grains in the identification and classification of plants. IV. The Mutiseae. *American Journal of Botany* 16, 297–313.
- Zhao, Z., Skvarla, J.J., Jansen, R.K., DeVore, M.L., 2000. Phylogenetic implications of pollen morphology and ultrastructure in the Barnadesioideae (Asteraceae). *Lundellia* 3, 26–40.
- Zinsmeister, W.J., Marshall, L.G., Drake, R.E., Curtis, G.H., 1981. First radioisotope (potassium–argon) age of marine Neogene Rio Negro beds in Northeastern Patagonia, Argentina. *Science* 212, 440.