

# Eocene Patagonia Fossils of the Daisy Family

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**A**steraceae, the family of daisies, sunflowers, and dandelions, is the most diverse family of flowering plants on Earth in terms of numbers of genera and species and widespread distribution. Its most prominent feature is the capitulum, a cluster of sessile flowers crowded onto a receptacle and an efficient reproductive unit that might have provided a larger pollinator target.

Asteraceae and their most closely related families (Goodeniaceae and Calyceraceae in Asterales) have a meager fossil record (1). Although plant megascopic preservation is uncommon (2), fossil pollen grains are widely recorded, particularly during the Neogene (1, 3). The oldest pollen records are assigned to subfamilies Carduoideae and Mutisioideae from the Paleogene of Africa, Australia, and southern South America (4–7).

We describe here a fossil capitulum unequivocally assignable to Asteraceae associated with dispersed pollen grains in Middle Eocene [47.5 × 10<sup>6</sup> years ago (Ma)] rocks from northwestern Patagonia, southern South America.

The fossil (Fig. 1) consists of a loosely cymose capitulescence with long pedunculate capitula. At least the central capitulum appears to be fully mature. It possesses several series of protective bracts (phyllaries), the basal-most decurrent onto the long peduncle. Intermediate bracts are widely oblong, with an apparent rounded apex. Flowers (~80) are relatively large, with a developed ligule or lip. Slender projections like hairs (pappus) are present among flowers. Pollen grains are tricolporate, echinate, with well-developed spines and a bilayered acaveate exine. These morphological features fit well with fossil *Mutisiapollis telleriae* from the Oligocene of Patagonia and in part with *Mutisiapollis viteauensis* from Africa (4, 5, 7).

Several features indicate a close relationship with extant Asteraceae (table S1). The particular arrangement of the capitula in a cymose capitulescence, the many-flowered capitula with multiseriate-imbricate involucre bracts, the pappus-like structures, and the pollen morphology represent a unique combination of features of Asteraceae. The acaveate exine and the conspicuous spines with uneven arrangement characterize pollen of most members of Stiffitiae and Wunderlichioideae centered in the Guayana Highland, some

Gochnatieae (Mutisioideae *sensu lato*), and some Dicomae and Oldenburiaceae (Carduoideae) (8–10) and exclude the subfamily Barnadesioideae.

The Eocene paleoclimatic scenario inferred for the fossil-bearing locality suggests warm [mean annual temperature (MAT) estimate 19.2° ± 2.4°C] and humid [mean annual precipitation (MAP) estimate 2000 to 2500 mm] climatic conditions, supporting a diverse subtropical vegetation on the northwestern Patagonian region (11), perhaps with some patches of drier areas (12). The identification of the asteracean fossil provides an important addition to the diversity of the Eocene subtropical flora. Members of Asteraceae probably inhabited dry or transitional zones between humid and dry areas, as the majority of current species do.

The Palaeogene record of Asteraceae is so sparse that the discovery of one new fossil can have a substantial effect on known time ranges in the phylogenetic tree. Fossils from unequivocally Middle Eocene deposits of Patagonia allow us to assume that the divergence age of Mutisioideae s. l. and Carduoideae from Barnadesioideae is at least 47.5 Ma. This age is older than that estimated by

the last molecular clock for the Mutisioideae s. l.–Carduoideae origin (Late Eocene, 38 to 42 Ma) (13) but may be consistent with the age of origin estimated for the whole family (Early Eocene, 50 Ma) (14).

This finding of Eocene fossils with Mutisioideae–Carduoideae affinities in southern South America, together with those reported from Africa (4, 5) and Australia (6), suggests that an ancestral stock of Asteraceae may have formed part of a geoflora widespread across southern Gondwana before the establishment of effective dispersal barriers within this landmass.

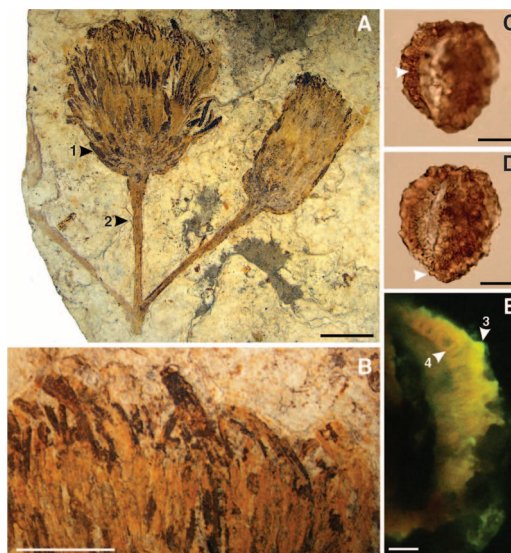
## References and Notes

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## Supporting Online Material

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Materials and Methods

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**Fig. 1.** Fossil Asteraceae. (A) Capitulescence under transmitted white light. Label 1 indicates involucre bracts (arrow); 2, peduncle (arrow). (B) Flowers. (C and D) Pollen grains at equatorial view under transmitted white light: (C) exine structure (arrow) and (D) spines arrangement (arrow). (E) Optical section of the pollen grain under fluorescent light with confocal microscope; 3, spines (arrow); 4, columellae (arrow). Scale bar in (A) and (B) equals 1 cm; in (C) and (D), 10  $\mu$ m; and in (E), 5  $\mu$ m.

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