

# Early evolution of the angiosperm clade Asteraceae in the Cretaceous of Antarctica

Viviana D. Barreda<sup>a,1,2</sup>, Luis Palazzesi<sup>a,b,1</sup>, Maria C. Tellería<sup>c</sup>, Eduardo B. Olivero<sup>d</sup>, J. Ian Raine<sup>e</sup>, and Félix Forest<sup>b</sup>

<sup>a</sup>División Paleobotánica, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia,” Consejo Nacional de Investigaciones Científicas y Técnicas, Buenos Aires C1405DJR, Argentina; <sup>b</sup>Jodrell Laboratory, Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3DS, United Kingdom; <sup>c</sup>Laboratorio de Sistemática y Biología Evolutiva, Museo de La Plata, La Plata B1900FWA, Argentina; <sup>d</sup>Centro Austral de Investigaciones Científicas, Consejo Nacional de Investigaciones Científicas y Técnicas, 9410 Ushuaia, Tierra del Fuego, Argentina; and <sup>e</sup>Department of Palaeontology, GNS Science, Lower Hutt 5040, New Zealand

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The Asteraceae (sunflowers and daisies) are the most diverse family of flowering plants. Despite their prominent role in extant terrestrial ecosystems, the early evolutionary history of this family remains poorly understood. Here we report the discovery of a number of fossil pollen grains preserved in dinosaur-bearing deposits from the Late Cretaceous of Antarctica that drastically pushes back the timing of assumed origin of the family. Reliably dated to ~76–66 Mya, these specimens are about 20 million years older than previously known records for the Asteraceae. Using a phylogenetic approach, we interpreted these fossil specimens as members of an extinct early diverging clade of the family, associated with subfamily Barnadesioideae. Based on a molecular phylogenetic tree calibrated using fossils, including the ones reported here, we estimated that the most recent common ancestor of the family lived at least 80 Mya in Gondwana, well before the thermal and biogeographical isolation of Antarctica. Most of the early diverging lineages of the family originated in a narrow time interval after the K/P boundary, 60–50 Mya, coinciding with a pronounced climatic warming during the Late Paleocene and Early Eocene, and the scene of a dramatic rise in flowering plant diversity. Our age estimates reduce earlier discrepancies between the age of the fossil record and previous molecular estimates for the origin of the family, bearing important implications in the evolution of flowering plants in general.

Asteraceae | evolution | Antarctica | fossil | phylogenetics

Flowering plants underwent a rapid ecological radiation and taxonomic diversification in the Early Cretaceous, about 121–99 Mya (1). Asterids, in particular, represent an extraordinarily diverse clade of extant angiosperms that includes more than 80,000 species. This clade contains the most species-rich angiosperm family, the Asteraceae, with 23,000 species, many of which are economically important taxa, such as sunflowers, lettuce, and gerberas. The origin and early diversification of family Asteraceae were important events in the history of life largely because this lineage has been a dominant component for the past several millions of years in numerous biomes around the world, primarily in open habitat ecosystems. Particularly, the evolution of Asteraceae, typically characterized by bearing attractive inflorescences (or capitula), may have promoted the radiation of insect pollinators (e.g., solitary bees) that heavily rely on this family to feed and reproduce (2). To date, the oldest fossil confidently assigned to Asteraceae is from the Middle Eocene of Patagonia. It consists of an inflorescence and associated pollen grains assigned to an extinct clade of Asteraceae, phylogenetically placed at a moderately derived position within the phylogenetic tree of the family (3). The discovery of these Eocene specimens indicated that the crucial split between subfamily Barnadesioideae, the earliest diverging branch of the family, and the rest of Asteraceae occurred even earlier, either during the early Paleogene or Late Cretaceous (4, 5). Recent molecular dating analyses support a Late Cretaceous origin for the crown group Asterales (4, 6), whereas the emergence of Asteraceae was estimated to have occurred in the Early Eocene (4).

Here we report fossil pollen evidence from exposed Campanian/Maastrichtian sediments from the Antarctic Peninsula (Fig. 1, Fig. S1, and *SI Materials and Methods, Fossiliferous Localities*) (7) that radically changes our understanding of the early evolution of Asteraceae.

## Results and Discussion

The pollen grains reported here and discovered in the Late Cretaceous of Antarctica are tricolporate, microechinate, with long colpi and rimmed margins. We placed these specimens within the wide-ranging variable fossil species *Tubulifloridites lilliei* (Couper) Farabee and Canright previously recorded in a restricted time interval within the Late Cretaceous of western Gondwana (8, 9) (see also *Supporting Data, Systematic Remarks*). It has been botanically related to a number of eudicot families (*Supporting Data, Systematic Remarks*; see also Figs. S2B and S3F for comparison) based on superficial similarities of the pollen grains or considered as an angiosperm of uncertain position (9). We assembled our specimens from Antarctica as a subgroup of the polymorphic *T. lilliei* that here we informally denominate as *T. lilliei* type A, which is distinguished from other *T. lilliei* specimens by several specific morphological characters (e.g., clearly tricolporate pollen grains with well-defined lalongate ora and intercolpal depressions) (see *Supporting Data, Systematic Remarks* for a full description). Morphologically identical specimens of *T. lilliei* type A were also recovered in the Late Cretaceous of New Zealand (Fig. S4). *Tubulifloridites lilliei*, including *T. lilliei* type A, disappeared almost simultaneously from Antarctica, Australia, Patagonia, and New Zealand about 66 Mya (K/P boundary) (see *Supporting Data, Systematic Remarks*).

## Significance

The flowering plant family Asteraceae (e.g. sunflowers, daisies, chrysanthemums), with about 23,000 species, is found almost everywhere in the world except in Antarctica. Asteraceae (or Compositae) are regarded as one of the most influential families in the diversification and evolution of a large number of animals that heavily depends on their inflorescences to survive (e.g. bees, hummingbirds, wasps). Here we report the discovery of pollen grains unambiguously assigned to Asteraceae that remained buried in Antarctic deposits for more than 65 million years along with other extinct groups (e.g. Dinosaurs, Ammonites). Our discovery drastically pushes back the assumed origin of Asteraceae, because these pollen grains are the oldest fossils ever found for the family.

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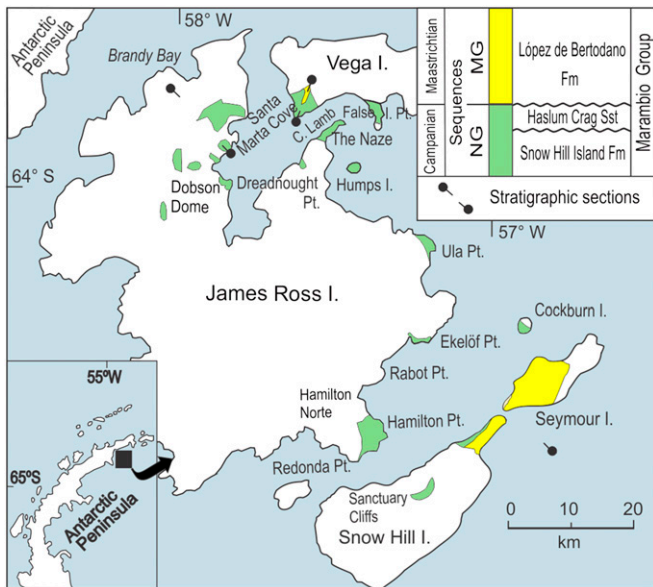
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<sup>1</sup>V.D.B. and L.P. contributed equally to this work.

<sup>2</sup>To whom correspondence should be addressed. Email: vbarreda@macn.gov.ar.

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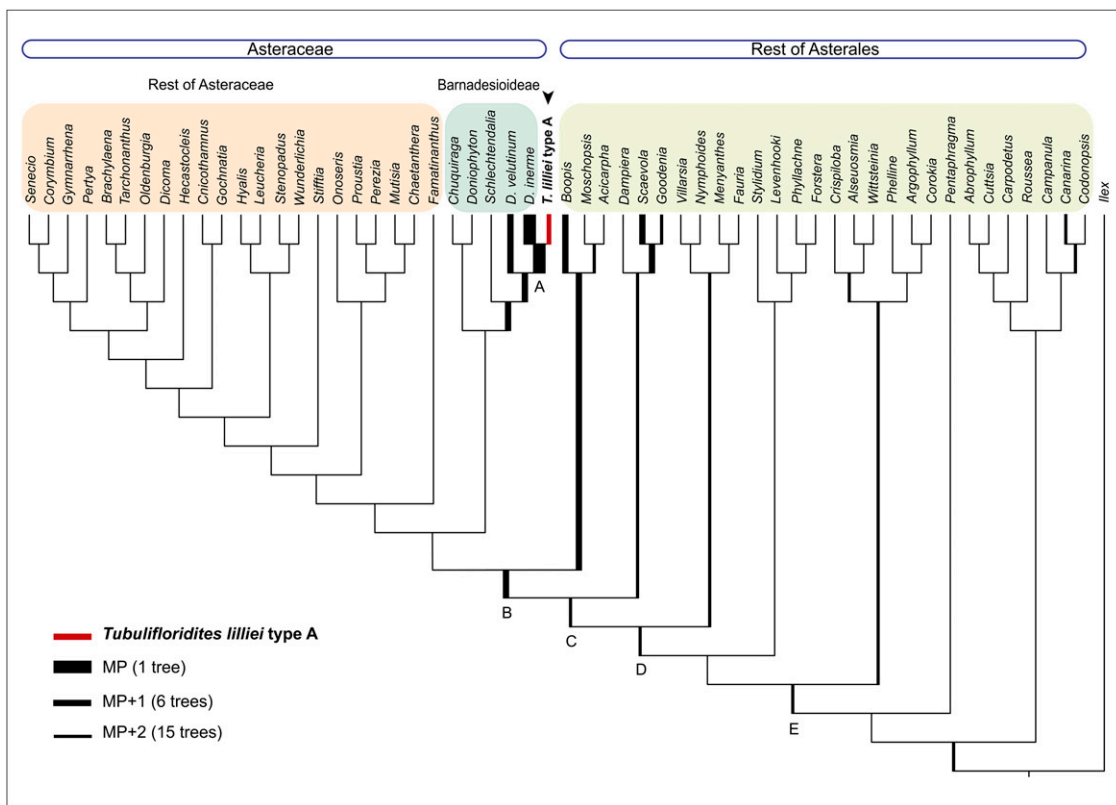


**Fig. 1.** Map showing distribution of Upper Cretaceous rocks of the Snow Hill Island and López de Bertodano Formations. The studied sections in Brandy Bay–Santa Marta Cove (James Ross Island) and Cape Lamb (Vega Island) are also indicated. Adapted from Olivero (7).

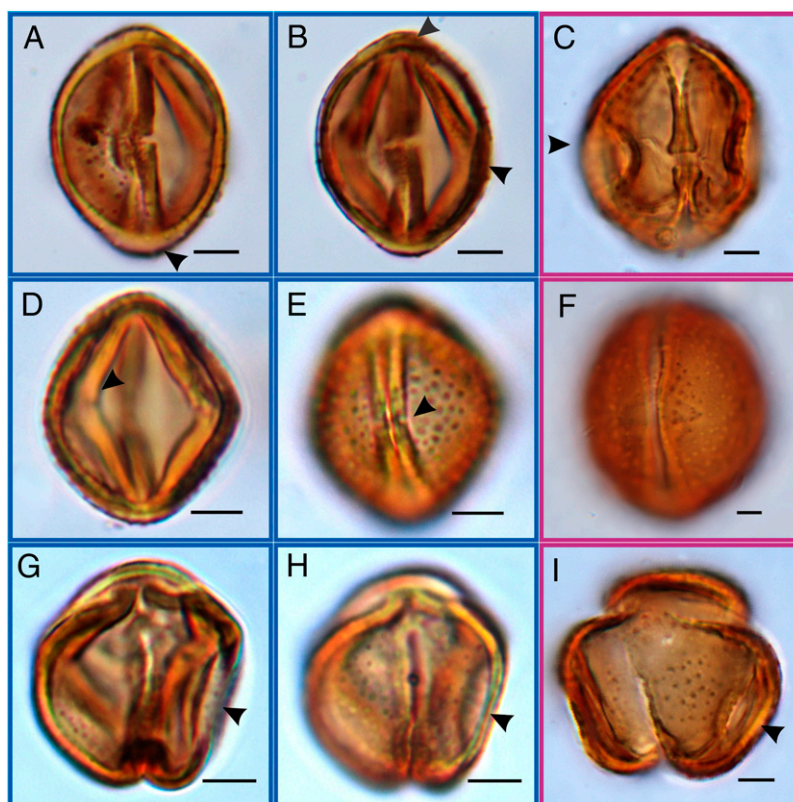
Using an apomorphy-based method [in the sense of Sauquet et al. (10)] as a first attempt at comparing the Antarctic fossils (*T. lilliei* type A) and the pollen produced by extant eudicots (all

supported by a single morphological synapomorphy: triaperturate pollen), we found strong morphological similarities between *T. lilliei* type A and some members of Asterales (Supporting Data and Figs. S24 and S3C). We explored further the phylogenetic placement of *T. lilliei* type A within Asterales in a parsimonious framework by using a matrix of pollen morphological characters (Supporting Data, List of Characters and Character State Definitions Used to Compile a Matrix Used as Input in Parsimony Analyses Aimed at Placing the Fossil Taxa and Table S1) and a phylogenetic tree of Asterales as backbone constraint (Fig. 2). After conducting a sensitivity analysis (see SI Materials and Methods, Estimation of Divergence Times) we found one position suitable for calibration based on the single most-parsimonious tree (188 steps). This single most-parsimonious tree places *T. lilliei* type A within *Dasyphyllum* of the Barnadesioideae (Fig. 2), the earliest diverging subfamily of the Asteraceae; the fossil possesses most of the derived morphological character states of the *Dasyphyllum* pollen (Figs. 3 and 4 and Fig. S3 A, B, D, and E). We also explored other scenarios, assuming *T. lilliei* type A was either an extinct stem relative of Asteraceae or more closely related to other members of the Asterales (Fig. S5 and Table S2). Here, we discuss the age of the origin of the daisy family considering *T. lilliei* type A as a crown group member (i.e., nested within *Dasyphyllum*).

The crown of Asteraceae [i.e., the most recent common ancestor (MRCA) of the family plus all extant and extinct lineages that descended from it] is inferred to have been present from the Late Cretaceous, estimated here at 85.9 Mya [95% highest posterior density (HPD) interval: 82.3–91.5 Mya] (Fig. 5), coinciding in part with the expansion of other eudicot lineages, herbivorous and social insects, birds, mammals, and some dinosaur groups (1, 11–14). The MRCA of Asteraceae other than



**Fig. 2.** Phylogenetic analyses of the fossil taxa. Branching positions of the fossil *T. lilliei* type A mapped onto a backbone tree derived from a molecular analysis of Beaulieu et al. (4), with some asteracean taxa added, following a recent comprehensive analyses of Panero et al. (24). Thicker black lines indicate the most parsimonious (MP), one step less parsimonious (MP + 1), and two steps less parsimonious (MP + 2) positions for *T. lilliei* type A. Letters indicate the nodes used to calibrate alternative scenarios, A: Fig. 5; B–E: Fig. S5 and Table S2.

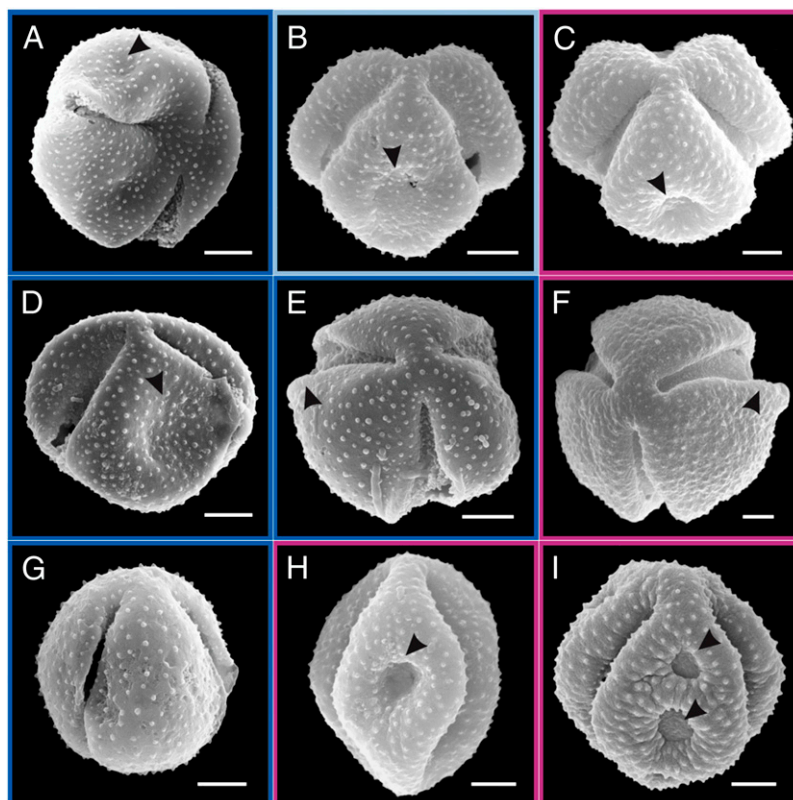


**Fig. 3.** Fossil and extant representatives of Asteraceae observed by light microscopy. (A, B, D, E, G, H) Specimens of *Tubulifloridites lilliei* type A from the Late Cretaceous of Antarctica (blue frames). Specimens on slide BAPal. ex CIRGEO Palin 963b; (A and B) N42(4); (D and E) L36(0); (G and H) P57(1). (A, B, D, E) Equatorial view. (G and H) Subpolar view. (A and B) Exine thickened at the poles (arrowhead). (A, E, and H) Microechinate-baculate sculpture. (D and E) Thickened exine at apertures level (arrowhead). (B, G, and H) Poorly defined intercolpal depressions (arrowhead). (G and H) Rounded colpi ends. (C, F, and I) Pollen of extant species for comparison (pink frames). (C and I) Extant *Dasyphyllum inerme* (Rusby) Cabrera, with well-defined intercolpal depressions and rounded colpi ends comparable to those of *T. lilliei* type A (arrowheads). (F) Extant *Dasyphyllum velutinum* (Baker) Cabrera, with microechinate-baculate exine surface similar to that of *T. lilliei* type A. (Scale bars, 5  $\mu$ m.)

Barnadesioideae is estimated to have evolved about 60 Mya during the Paleocene. Interestingly, the major clades of the family diverged from this common ancestor after the K–P mass extinction event and during a relatively short time interval during the late Paleocene–early Eocene, the Cenozoic’s most pronounced warm interval (59–52 Mya) (15), which was in turn associated with a dramatic rise in flowering plant diversity and a sharp increase in insect herbivory (6, 16, 17). The analysis, assuming that the fossil is a stem relative of Asteraceae, indicated an age for Asteraceae of 67.9 Mya, also within the Late Cretaceous (Fig. S5A and Table S2).

The tolerance of some of the early diverging taxa of Asteraceae, and most members of its sister family Calyceraceae, to extreme environmental and ecological conditions leads us to believe that this resistance might have played a major role in the early evolution of Asteraceae. The earliest lineage of Asteraceae and Calyceraceae occur today in a limited number of restricted regions in South America (18), and several of their members can tolerate the extreme climatic conditions that characterize the Patagonian desert of today (e.g., intense winds, droughts, salt-sprays). Assuming that *T. lilliei* type A pollen grains might represent a member of the crown Barnadesioideae, their parent plants may have been able to cope with environmental stress. We infer that *T. lilliei* type A parent plants occupied a wide geographic range, as suggested by their distribution across western Gondwana during the Late Cretaceous, but may have become drastically reduced close to the K/P boundary, with persistence only in some areas of western Gondwana. Their descendants survived and expanded in South America, probably during the Miocene, as indicated by several fossil pollen

records (19). It is assumed that plant lineages characterized by higher adaptability and increased tolerance to harsh environmental conditions (e.g., earliest branches of Asteraceae and sister Calyceraceae) were probably less affected during global extinction events. It has also been observed that the survival probability in these severe conditions would have been better for plants with polyploid genomes (20). Polyploidy is common in Asteraceae and occurs in virtually all species of subfamily Barnadesioideae (21) and family Calyceraceae (22); thus, polyploidization in the early-diverging lineages of Asteraceae may also have contributed to the survival of this group across the K–P extinction event. The pronounced climatic warming during the Late Paleocene and the Early Eocene Climatic Optimum might have also influenced the diversification of Asteraceae. We show here that most of the major lineages of Asteraceae, which mainly occur today in South America, diverged during this period of global warmth (Fig. 5) and later became isolated when cool-temperate conditions were established in the more austral regions during the Oligocene. For example, in the Guyana Highlands of northeastern South America some species of the earliest-diverging lineages (e.g., *Stenopadus* group) coexist as relictual patches (23). The presence in Patagonia of an Eocene inflorescence and pollen grains displaying some of the characters of this *Stenopadus* group (5) supports the notion that the MRCA of Asteraceae, excluding Barnadesioideae, existed in the southernmost latitudes of South America, and began to diverge and disperse northward following the equable conditions of the early Cenozoic. The global drop in temperatures during the late Cenozoic may have caused the local extinction of these Guyana



**Fig. 4.** Fossil and extant representatives of Asteraceae observed by scanning electron microscopy. (A, D, E, G) Specimens of *Tubulifloridites lilliei* type A from the Late Cretaceous of Antarctica (blue frames). (A) Subpolar view showing details of sculpture and poorly defined depressions (arrowhead); note the microgranulate apertural membrane. (D) Subequatorial view showing a poorly defined depression (arrowhead). (E) Polar view with small apocolpium and thickened colpi margins. (G) Equatorial view showing the microechinate-baculate- verrucate sculpture. (B) Specimen of *Quilembaypollis tayuoides* Barreda and Palazzesi from the Miocene of Patagonia (light blue frame) that shares morphological features with both the Cretaceous and extant asteraceous specimens; note the microechinate-baculate sculpture. (C, F, H, I) Extant species of *Dasyphyllum* (pink frames) showing variations in the development and number of intercolpal depressions. (C and H) *Dasyphyllum inerme* (Rusby) Cabrera. (F) *Dasyphyllum latifolium* (Gardner) Cabrera. (I) *Dasyphyllum leptacanthum* (Gardner) Cabrera. (Scale bars, 5  $\mu$ m.)

Highland-centered genera from the higher latitudes and their consequent restriction in low latitudes of South America.

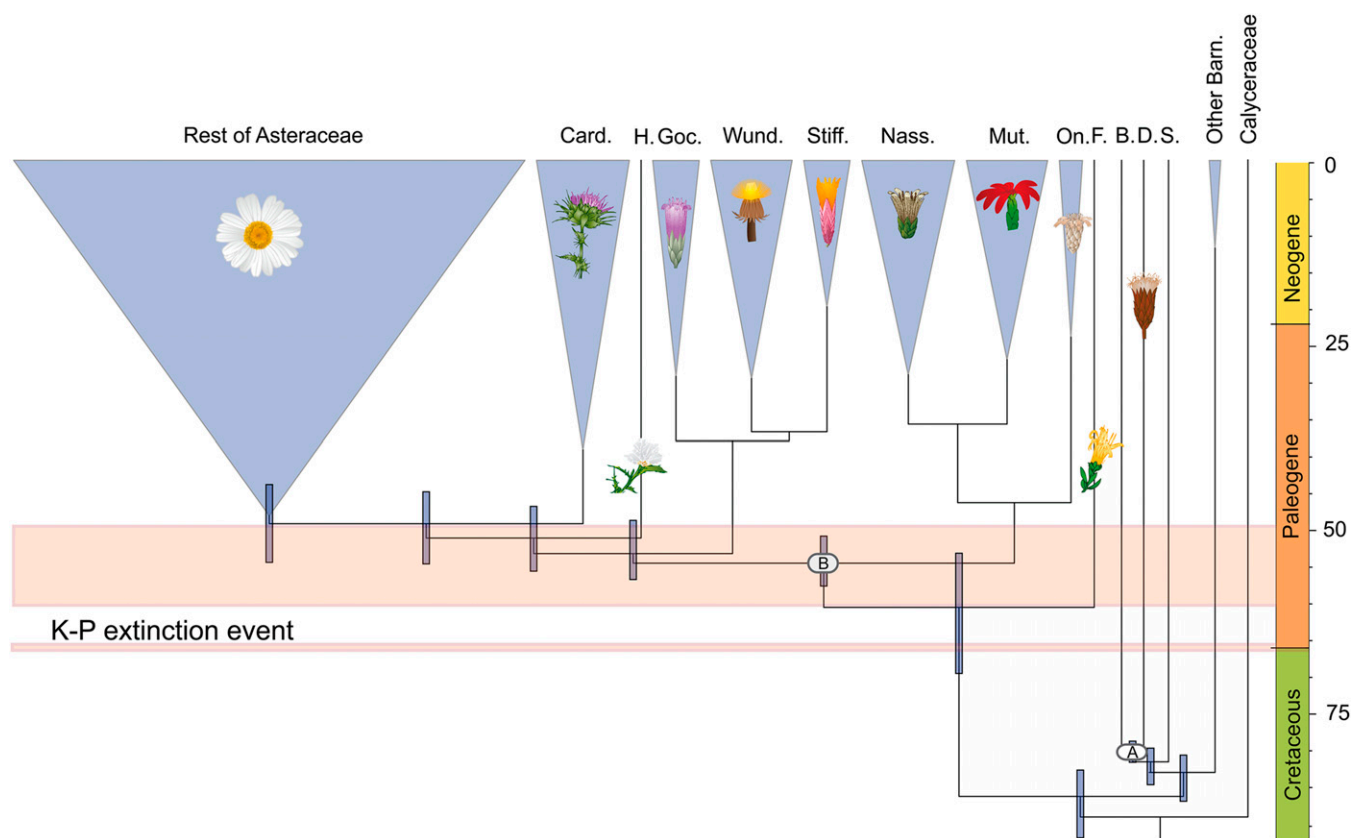
Our new divergence time-estimate analysis contradicts some previous assumptions about a geologically recent origin of the Asteraceae (18), indicating instead that the MRCA of the family existed far back into the Late Cretaceous. However, we also infer that the vast majority of the present-day diversity of the Asteraceae is the result of a radiation event that took place during the early Cenozoic, several millions of years after the origin of the family. This finding has important implications for our understanding of the evolution of this highly diverse and ecologically important family. The Cretaceous record from Antarctica is still poorly explored and much evidence on the early evolution of the Asterales, and potentially other groups, probably remains buried beneath present-day ice sheets. From our present knowledge, however, we estimate that the world's highest Southern Hemisphere latitudes (i.e., Patagonia, New Zealand, Antarctica, and Australia) witnessed the emergence and early evolution of what is today the most diverse flowering plant family.

### Materials and Methods

**Fossil Samples.** Rock samples were recovered from the Campanian/Maastrichtian Snow Hill and López de Bertodano Formations on the James Ross and Vega islands, in Antarctica by E.B.O. Samples were chemically treated following standard palynological techniques (*SI Materials and Methods, Fossiliferous Localities and Fossil Pollen Morphotypes*, and Fig. S1). The slides are housed in the palynological collection of the Museo Argentino de

Ciencias Naturales (Buenos Aires, Argentina): BAPal, ex CIRGEO Palin 605–613, 962–965.

**Phylogenetic Placement of the Fossil.** The apomorphy-based method was used first to compare the fossil *T. lilliei* type A with extant angiosperm families, particularly those having triaperturate microechinate pollen grains (e.g., Ranunculaceae, Rubiaceae, Euphorbiaceae, Campanulaceae, Calyceraceae, Asteraceae) by using information available in the literature. We observed strong morphological similarities between *T. lilliei* type A and some members of Asterales. To increase the taxonomic resolution of this assignment we conducted a parsimony analysis to evaluate the placement of the fossils from Antarctica within the order. Pollen characters for 55 extant species of Asterales were scored (*SI Materials and Methods, Extant Reference Samples, and Supporting Data, List of Characters and Character State Definitions Used to Compile a Matrix Used as Input in Parsimony Analyses Aimed at Placing the Fossil Taxa and Details of the Extant Material Examined for Morphological Characters Provided in Data Matrix and References for Scoring*). The morphological matrix comprises 26 binary and multistate pollen characters, and 55 taxa chosen to represent all families and tribes in Asterales, along with one outgroup taxon, *Ilex* from family Aquifoliaceae (*Supporting Data, Details of the Extant Material Examined for Morphological Characters Provided in Data Matrix and References for Scoring* and Table S1). We used a backbone tree derived from a molecular analysis of Beaulieu et al. (4), with some additional taxa, following the recent comprehensive analysis of Panero et al. (24). We conducted the analyses using the parsimony criterion as implemented in the software PAUP (25), enforcing the topological constraint, with the heuristic search option of 1,000 random addition replicates and tree bisection and reconnection branch swapping. Alternative phylogenetic positions of *T. lilliei* type A were evaluated by searching for the bootstrap consensus tree, the most parsimonious tree, and by searching for trees one and two steps longer than the most parsimonious tree



**Fig. 5.** Evolutionary timescale of the diversification of Asteraceae. Chronogram (scale on the right in Mya) estimated using a Bayesian relaxed clock calibrated with a previously described fossil inflorescence from the Eocene ("B") and our newly discovered specimens from the Cretaceous of Antarctica ("A"). We assume that this Cretaceous species (*T. lilliei* type A) represents an extinct branch nested within *Dasyphyllum* (crown representative). Other possible calibration scenarios are illustrated in Fig. S5. Light-blue bars at nodes represent 95% credibility intervals on estimates of divergence times. Orange horizontal lines indicate the timing of the K-P extinction event and the Cenozoic's warmest interval. Most subfamilies of Asteraceae diverged during the Paleogene, but the earliest divergence occurred in the Late Cretaceous. B., *Barnadesia*; Barn., Barnadesioideae (91 species); Card., Carduoideae (2,500+ species); D., *Dasyphyllum*; F., Famatinanthoideae (1 species); Goc., Gochnatioideae (90 species); H., Hecastocleidoideae (1 species); Mut., Mutisieae (254 species); Nass., Nassauvieae (313 species); On., Onoserideae (52 species); S., *Schlechtendalia*; Stiff., Stifftioideae (44 species); Wund., Wunderlichioideae (41 species); rest of Asteraceae (19,600 + species).

(SI Materials and Methods, Estimation of Divergence Times) and by assigning the fossil manually to different branches with MacClade (26), following the approach of Doyle and Endress (27).

**Divergence Time Estimates.** We selected DNA sequences of 101 species of Asteraceae, with an additional 36 species used as outgroup taxa. Three protein-coding genes from the plastid genome (*ndhF*, *rbcL*, *matK*) were obtained for all taxa from GenBank (Table S3). Alignment of individual regions was completed using default settings in MAFFT v.7 (28).

Divergence time estimates and phylogenetic relationships were inferred using Markov Chain-Monte Carlo methods implemented in BEAST2 (29). A GTR +  $\Gamma$  substitution model applied to the entire dataset, and the birth-death model of speciation and an uncorrelated lognormal-relaxed molecular clock model were used. Prior distributions on the root and two other nodes were applied based on the interpretation from the fossil record of Asteraceae. A complete list of the fossil species used to calibrate the tree, geologic ages, and citations is given in Table S4 and Fig. S6, and a list of the explored calibration scenarios is given in Table S2 and illustrated in Fig. S5. We ran

four independent chains for each calibration scenario, each for 100 million iterations, sampling every 1,000th generation using the CIPRES Science Gateway. The program Tracer (29) was used to confirm that the four independent runs converged on the same stationary distribution. Post burn-in samples from the marginal posterior distribution were combined using LogCombiner v1.5.4 (29) and trees summarized with TreeAnnotator (29). The topology of the tree broadly corresponds with that obtained by Panero et al. (24).

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1. Friis EM, Crane PR, Pedersen KR (2011) *Early Flowers and Angiosperm Evolution* (Cambridge Univ Press, Cambridge, UK).
2. Funk VA, et al. (2009) Compositae metatrees: The next generation. *Systematics, Evolution, and Biogeography of Compositae*, eds Funk VA, Susanna A, Stuessy TF, Bayer RJ (IAPT, Vienna, Austria), pp 747–777.
3. Barreda VD, et al. (2010) Eocene Patagonia fossils of the daisy family. *Science* 329(5999):1621.
4. Beaulieu JM, Tank DC, Donoghue MJ (2013) A Southern Hemisphere origin for campanulid angiosperms, with traces of the break-up of Gondwana. *BMC Evol Biol* 13:80.
5. Barreda VD, et al. (2012) An extinct Eocene taxon of the daisy family (Asteraceae): Evolutionary, ecological and biogeographical implications. *Ann Bot (Lond)* 109(1):127–134.

6. Magallón S, Castillo A (2009) Angiosperm diversification through time. *Am J Bot* 96(1):349–365.
7. Olivero EB (2012) Sedimentary cycles, ammonite diversity and palaeoenvironmental changes in the Upper Cretaceous Marambio Group, Antarctica. *Cretac Res* 34(4):348–366.
8. Raine JL, Speden IG, Strong CP (1981) New Zealand. *Aspects of Mid-Cretaceous Regional Geology*, eds Reymont RA, Bengtson P (Academic, London), pp 221–267.
9. Dettmann ME, Jarzen DM (1988) Angiosperm pollen from uppermost Cretaceous strata of southeastern Australia and the Antarctic Peninsula. *Memoir of the Association Australasian Palaeontologists* 5:217–237.
10. Sauquet H, et al. (2012) Testing the impact of calibration on molecular divergence times using a fossil-rich group: The case of *Nothofagus* (Fagales). *Syst Biol* 61(2):289–313.

11. Cardinal S, Danforth BN (2013) Bees diversified in the age of eudicots. *Proc Biol Sci* 280(1755):20122686.
12. Ericson PG, et al. (2006) Diversification of Neoaves: Integration of molecular sequence data and fossils. *Biol Lett* 2(4):543–547.
13. Lloyd GT, et al. (2008) Dinosaurs and the Cretaceous terrestrial revolution. *Proc Biol Sci* 275(1650):2483–2490.
14. Ho SYW (2014) The changing face of the molecular evolutionary clock. *Trends Ecol Evol* 29(9):496–503.
15. Zachos J, Pagani M, Sloan L, Thomas E, Billups K (2001) Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science* 292(5517):686–693.
16. Wilf P, et al. (2005) Eocene plant diversity at Laguna del Hunco and Río Pichileufú, Patagonia, Argentina. *Am Nat* 165(6):634–650.
17. Currano ED, et al. (2008) Sharply increased insect herbivory during the Paleocene-Eocene Thermal Maximum. *Proc Natl Acad Sci USA* 105(6):1960–1964.
18. Stuessy TF, Sang T, DeVore ML (1996) Phylogeny and biogeography of the subfamily Barnadesioideae with implications for early evolution of the Compositae. *Compositae: Systematic*, eds Hind DNN, Beentje H (Royal Botanical Gardens, Kew, UK), pp 463–490.
19. Palazzesi L, Barreda VD, Telleria MC (2009) Fossil pollen grains of Asteraceae from the Miocene of Patagonia: Barnadesioideae affinity. *Rev Palaeobot Palynol* 155:83–88.
20. Fawcett JA, Maere S, Van de Peer Y (2009) Plants with double genomes might have had a better chance to survive the Cretaceous-Tertiary extinction event. *Proc Natl Acad Sci USA* 106(14):5737–5742.
21. Semple JC, Watanabe K (2009) A review of chromosome numbers in Asteraceae with hypotheses on chromosomal base number evolution. *Systematics, Evolution and Biogeography of Compositae*, eds Funk VA, Susanna A, Stuessy TF, Bayer RJ (IAPT, Vienna), pp 61–72.
22. Hellwig FH (2007) Calyceraceae. *The Families and Genera of Vascular Plants. Flowering Plants—Eudicots. Asterales*, eds Kubitzki K, Kadereit JW, Jeffrey C (Springer, Berlin), pp 19–25.
23. Bremer K (1993) Intercontinental relationships of African and South American Asteraceae: A cladistic biogeographic analysis. *Biological Relationships Between Africa and South America*, ed Goldblatt P (Yale Univ Press, New Haven, CT), pp 104–135.
24. Panero JL, et al. (2014) Resolution of deep nodes yields an improved backbone phylogeny and a new basal lineage to study early evolution of Asteraceae. *Mol Phylogenet Evol* 80:43–53.
25. Swofford D (2002) *PAUP\* Phylogenetic Analysis Using Parsimony (\* and other methods). Version 4* (Sinauer Associates, Sunderland, MA).
26. Maddison DR, Maddison WP (2003) *MacClade 4: Analysis of Phylogeny and Character Evolution, Version 4.06* (Sinauer Associates, Sunderland, MA).
27. Doyle JA, Endress PK (2010) Integrating Early Cretaceous fossils into the phylogeny of living angiosperms: Magnoliidae and eudicots. *J Syst Evol* 48(1):1–35.
28. Katoh K, Standley DM (2013) MAFFT multiple sequence alignment software version 7: Improvements in performance and usability. *Mol Biol Evol* 30(4):772–780.
29. Rambaut A, Suchard MA, Xie D, Drummond AJ (2014) Tracer v1.6. Available at [bio.ed.ac.uk/Tracer](http://bio.ed.ac.uk/Tracer). Accessed July 15, 2014.
30. Salgado L, Gasparini Z (2006) Reappraisal of an ankylosaurian dinosaur from the Upper Cretaceous of James Ross Island (Antarctica). *Geodiversitas* 28(1):119–135.
31. Coria RA, Moly JJ, Reguero M, Santillana S, Marensi S (2013) A new ornithomimid (Dinosauria, Ornithischia) from Antarctica. *Cretac Res* 41:186–193.
32. Pirrie D, Crame JA, Riding JB (1991) Late Cretaceous stratigraphy and sedimentology of Cape Lamb, Vega Island, Antarctica. *Cretac Res* 12(3):227–258.
33. Roberts EM, et al. (2014) Stratigraphy and vertebrate paleoecology of Upper Cretaceous—? Lowest Paleogene strata on Vega Island, Antarctica. *Palaeogeogr Palaeoclimatol Palaeoecol* 402:55–72.
34. Traverso A (1988) *Paleopalynology* (Unwin Hyman, Boston).
35. Punt W, Hoen PP, Blackmore S, Nilsson S, Le Thomas A (2007) Glossary of pollen and spore terminology. *Rev Palaeobot Palynol* 143(1–2):1–81.
36. Urtubey E, Telleria MC (1998) Pollen morphology of the subfamily Barnadesioideae (Asteraceae) and its phylogenetic and taxonomic significance. *Rev Palaeobot Palynol* 104(1):19–37.
37. Telleria MC (2008) Taxonomic significance of pollen types in the Guayana Highland-centred composite genera of Mutisioideae (Asteraceae). *Bot J Linn Soc* 156(2):327–340.
38. Telleria MC, Katinas L (2004) A palynologic and comparative study of *Chaetanthera* (Asteraceae, Mutisieae) and allied genera. *Syst Bot* 29(3):752–773.
39. Telleria MC, Katinas L (2005) The unusual occurrence of tricolpate pollen within Mutisieae (Asteraceae). *Grana* 44(2):91–97.
40. Telleria MC, Katinas L (2009) New insights into the pollen morphology of *Mutisia* (Asteraceae, Mutisieae). *Plant Syst Evol* 280(3–4):229–241.
41. Telleria MC, Sancho G, Funk VA, Ventosa I, Roque N (2013) Pollen morphology and its taxonomic significance in the tribe Gochnatieae (Compositae, Gochnatioideae). *Plant Syst Evol* 299(5):935–948.
42. Erdtman G (1960) The acetolysis method, a revised description. *Sven Bot Tidskr* 54:561–564.
43. Doyle J (2012) Molecular and fossil evidence on the origin of Angiosperms. *Annu Rev Earth Planet Sci* 40(1):301–326.
44. Gradstein FM, Ogg JG, Schmitz MD, Ogg GM (2012) *The Geologic Time Scale 2012* (Elsevier, Amsterdam, The Netherlands).
45. Couper RA (1953) Upper Mesozoic and Cainozoic spores and pollen grains from New Zealand. *New Zealand Geological Survey Palaeontological Bulletin* 22:1–77.
46. Wilson GJ (1975) Palynology of deep-sea cores from DSDP site 275, southeast Campbell Plateau. *Initial Reports Deep Sea Drilling Project 29*, eds Kennett JP, et al. (US Government Printing Office, Washington, DC), pp 1031–1035.
47. Barreda VD, et al. (2012) Cretaceous/Paleogene floral turnover in Patagonia: Drop in diversity, low extinction, and a *Classopollis* spike. *PLoS One* 7(12):e52455.
48. Specht RL, Dettmann ME, Jarzen DM (1992) Community associations and structure in the Late Cretaceous vegetation of southeast Australasia and Antarctica. *Palaeogeogr Palaeoclimatol Palaeoecol* 94(3–4):283–309.
49. Macphail M, Hill RS, Partridge AD, Jordan GJ (2014) Geo-botany of the Cretaceous to Neogene. *Geological Evolution of Tasmania*, eds Corbett KD, Quilty PG, Calver CR (Geological Society of Australia Inc, Special Publication 24, Canberra, Australia), pp 495–507.
50. Heusser CJ (1971) *Pollen and Spores of Chile* (Univ of Arizona Press, Tucson, AZ).
51. Skvarla JJ, Turner BL, Patel VC, Tomb AS (1977) Pollen morphology in the Compositae and in morphologically related families. *The Biology and Chemistry of the Compositae*, eds Heywood VH, Harborne JB, Turner BL (Academic, London), pp 141–265.
52. Clarke GCS, Punt W, Hoen PP (1991) The Northwest European pollen flora, Ranunculaceae. *Rev Palaeobot Palynol* 69(1–3):117–271.
53. Raj B (1983) A contribution to the pollen morphology of Verbenaceae. *Rev Palaeobot Palynol* 39(3–4):343–422.
54. Moar NT (1993) *Pollen Grains of New Zealand Dicotyledonous Plants* (Manaaki Whenua Press, Lincoln, New Zealand).
55. Xie L, Li LQ (2012) Variation of pollen morphology, and its implications in the phylogeny of *Clematis* (Ranunculaceae). *Plant Syst Evol* 298(8):1437–1453.
56. Huysmans S, Robbrecht E, Delprete P, Smets E (1999) Pollen morphological support for the Catesbaeeae-Chiococceae-Exostema-complex (Rubiaceae). *Grana* 38(6):325–338.
57. Takahashi M, Nowicki JW, Webster GLA (1995) Note on remarkable exines in Acalyphoideae (Euphorbiaceae). *Grana* 34(5):282–290.
58. De-Yuan H, Kai-Yu P (2012) Pollen morphology of the platycodonoid group (Campanulaceae s. str.) and its systematic implications. *J Integr Plant Biol* 54(10):773–789.
59. Gustafsson MHG, Grafström E, Nilsson S (1997) Pollen morphology of the Goodeniaceae and comparisons with related families. *Grana* 36(4):185–207.
60. DeVore ML, Zhao Z, Jansen RK, Skvarla JJ (2007) Pollen morphology and ultrastructure of Calyceraceae. *Lundellia (Austin, Tex)* 10:32–48.
61. Karehed J (1965) Alseuosmiaceae Airy Shaw. *Kew Bull* 18(249):7–12.
62. Karehed J, Lundberg J, Bremer B, Bremer K (1999) Evolution of the Australasian families Alseuosmiaceae, Argophyllaceae, and Phellinaceae. *Syst Bot* 24(4):660–682.
63. Rowley JR, Nilsson S (1972) Structural stabilization for electron microscopy of pollen from herbarium specimens. *Grana* 12(1):23–30.
64. Bronckers F, Stainier F (1972) Contribution à l'étude morphologique du pollen de la famille des Styliidiaceae. *Grana* 12(1):1–22.
65. Nilsson S (1973) Menyanthaceae Dum. Taxonomy by Robert Ornduff. *World Pollen and Spore Flora* 2:1–20.
66. Martin HA (1977) The history of *Ilex* (Aquifoliaceae) with special reference to Australia: Evidence from Pollen. *Aust J Bot* 25(6):655–673.
67. Lobreau-Callen D (1977) Les pollens des Celastrales. *Mémoires et Travaux de l'Institut de Montpellier (l'École Pratique des Hautes Études, Montpellier, France)* 3:1–116.
68. Ferguson IK, Hideux MJ (1978) Some aspects of the pollen morphology and its taxonomic significance in Cornaceae sens. lat. *Proceedings of the Fourth International Palynological Conference, Lucknow, India (1976–1977)*. 1:240–249.
69. Dunbar A (1978) Pollen morphology and taxonomic position of the genus *Pentaphragma* Wall. (Pentaphragmataceae). *Grana* 17(3):141–147.
70. Pragłowski J, Grafström E (1985) The genus *Carpodetus* (Escalloniaceae): A pollen morphological enigma. *Grana* 24(1):11–22.
71. Cilliers SS (1991) Pollen morphology and its taxonomic value in *Brachylaena* (Asteraceae) in southern Africa. *S Afr J Bot* 57(6):325–330.
72. Hansen HV (1991) SEM-studies and general comments on pollen in tribe Mutisieae (Compositae) sensu Cabrera. *Nord J Bot* 10(6):607–623.
73. Lundberg J (2001) The asteralean affinity of the Mauritian *Roussea* (Rousseaceae). *Bot J Linn Soc* 137(4):267–276.
74. Telleria MC, Urtubey E, Katinas L (2003) *Prostia* and *Lophopappus* (Asteraceae, Mutisieae): Generic and subtribal relationships based on pollen morphology. *Rev Palaeobot Palynol* 123(3–4):237–246.
75. Polevova SV (2006) Review of the sporoderm ultrastructure of members of the Asterales. *Paleontol J* 40(5):656–663.
76. Wortley AH, et al. (2007) A search for pollen morphological synapomorphies to classify rogete genera in Compositae (Asteraceae). *Rev Palaeobot Palynol* 146(1–4):169–181.
77. Blackmore S, Wortley AH, Skvarla JJ, Gabarayeva NI, Rowley JR (2010) Developmental origins of structural diversity in pollen walls of Compositae. *Plant Syst Evol* 284(1–2):17–32.
78. Pereira Coutinho A, Almeida da Silva R, Sá da Bandeira D, Ortiz S (2012) Pollen morphology in tribe Dicomeae Panero and Funk (Asteraceae). *Plant Syst Evol* 298(10):1851–1865.
79. Freire SE, Barboza GE, Cantero JJ, Ariza Espinar L (2014) *Famatinanthus*, a new Andean genus segregated from *Aphyllocladus* (Asteraceae). *Syst Bot* 39(1):349–360.
80. Crame JA, Francis JE, Cantrill DJ, Pirrie D (2004) Maastrichtian stratigraphy of Antarctica. *Cretac Res* 25(5):411–423.
81. Crampton JS, et al. (2000) Revision of the Piripauan and Haumurian local stages and correlation of the Santonian-Maastrichtian (Late Cretaceous) in New Zealand. *NZ J Geol Geophys* 43(3):309–333.
82. Partridge AD (2006) *Australian Mesozoic and Cenozoic Palynology Zonations—Updated to the 2004 Geologic Time*, coord. Monteil E (Geoscience Australia Record 2006/23 Chart 4, Canberra, Australia).

# Supporting Information

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## SI Materials and Methods

**Fossiliferous Localities.** Samples were collected by E.B.O. in Snow Hill Island and López de Bertodano Formations on James Ross and Vega islands, Antarctica (Fig. 1) during several summer field trips. These units constitute the middle and upper parts (Campanian–Danian) of the Marambio Group, which include two major shallowing-upwards depositional sequences (1). These sequences are denominated the NG Sequence (Snow Hill Island and Haslum Crag Formations, mid–late Campanian–early Maastrichtian) and the MG Sequence (López de Bertodano Formation, early–late Maastrichtian–Danian).

In the studied section near Santa Marta Cove, James Ross Island, the outcrops of the Snow Hill Island Formation are included in the Gamma Member. This member consists of a lower sandstone-dominated package with lenticular coquinas, approximately 120 m thick, and an upper mudstone-dominated package, approximately 50 m thick (Fig. S1A). Both packages represent the transgressive system tract of the NG Sequence, with proximal, sandstone-dominated shore–face deposits at the base, followed by prodelta mudstones interbedded with sandy tempestites at the top (7). The lower package of the Gamma Member bears important fossil vertebrates, including a partial skeleton of the ankylosaur *Antarctopelta oliveroi* (30) and the ornithopod *Trinisauras antartaricensis* (31). Ammonites are scarce, but the basal conglomerate bears a reworked ammonite fauna, including diagnostic mid Campanian taxa, such as *Baculites subanceps*, *Metaplacenticerias subtilistriatum*, and *Hoplitoplacenticerias* sp., and several horizons, including the kosmaticeratid *Neogrammites primus*, which defines the mid–Campanian Ammonite Assemblage 8-1 (7). The studied samples in this package were recovered within the Ammonite Assemblage 8.1 *Neogrammites primus*, and include samples D8-1, D10-8, D11-1, D12-8, and D13-3b (Fig. S1A). The upper mudstone-dominated package of the Gamma Member is more fossiliferous and bears, in stratigraphic order, the Ammonite Assemblage 8-2 *Neogrammites cf. kiliani*, late Campanian, and the Ammonite Assemblage 9 *Neogrammites–Gunnarites*, latest Campanian–early Maastrichtian. The studied samples 14S-4d, Hy-20, and Hy were recovered within the Ammonite Assemblage 8-2, and the sample 14S within the Ammonite Assemblage 9 (7) (Fig. S1A).

The mudstone-dominated package of the Gamma Member crops out also on Hump Island and southern Cape Lamb on Vega Island (7). At Cape Lamb, it is transitionally covered by a coarsening-upward succession of silty mudstones and sandstones referred to the Cape Lamb Member of the Snow Hill Island Formation (7). The Cape Lamb Member is interpreted as a prograding deltaic wedge (7). The ammonite genus *Gunnarites* is very abundant throughout the member characterizing the Ammonite Assemblage 10 *Gunnarites* of early Maastrichtian (latest Campanian?) age (ref. 7 and references therein). The studied samples V6-10 and V8-8 were recovered from this interval (Fig. S1B). In Cape Lamb, Vega Island, the Snow Hill Island Formation is unconformably covered by the López de Bertodano Formation (Fig. S1B). The López de Bertodano Formation consists of a basal conglomerate followed by a mudstone-dominated succession with abundant ammonites, dominated by *Maorites densicostatus*, which are interpreted as offshore deposits representing a transgressive system tract. Based on sequence stratigraphy (7), these offshore mudstones are correlated with the late Maastrichtian deposits of the López de Bertodano Formation on Seymour Island, which bear the Ammonite Assemblages 12, 13, and 14 of Olivero (7). The studied samples V10-12, and V10-24 were recovered from the mudstone-dominated

interval of the López de Bertodano Formation (Fig. S1B). The upper part of the López de Bertodano Formation at Cape Lamb consists of regressive sandstone and conglomerates included in the Sandwich Bluff Member of latest Maastrichtian age (32). Thin conglomerates at the top, possibly Paleocene, were referred to the Sobral Formation (33).

**Fossil Pollen Morphotypes.** The samples were treated following standard palynological techniques (34). Fossil pollen grains were examined under transmitted white light with a Leica microscope and photomicrographs were taken with a Leica camera DFC 290. SEM photographs were included to illustrate the superficial morphological features of the pollen morphotypes. Specimen coordinates are referred to the England Finder. Pollen terminology follows Punt et al. (35).

**Extant Reference Samples.** Pollen characters were obtained from the examination of slides of acetolyzed pollen grains from 368 species representing all families of extant Asterales. Pollen of *Ilex*, chosen as an outgroup taxon, was also included. The specimens are deposited in the herbaria ALCB, B, BAF, C, CANB, CBG, FM, G, GÖTT, HAC, HAJB, HUT, K, LP, MO, S, US, WIS ([sweetgum.nybg.org/ih/](http://sweetgum.nybg.org/ih/)). Most pollen slides were used in previous studies, mainly those of Asteraceae (36–41), but additional specimens were included. For the specimens examined specifically for the present study under scanning electron microscope, pollen grains were acetolyzed (42), suspended in 90% (vol/vol) ethanol, and mounted on stubs. The samples were sputter-coated with gold-palladium and details of the exine sculpture were examined using a JEOL JSM T-100 SEM. A list of the specimens investigated is provided in *Supporting Data*, below. Additional information was obtained from the literature (*Supporting Data*).

**Estimation of Divergence Times.** We selected two fossil taxa for the estimation of the divergence times for the Asteralean lineages: one pollen morphotype placed on the phylogenetic tree using characters of extant clades (*Tubulifloridites lilliei* type A), and one macrofossil (capitulum) and associated pollen (*Raiguenrayun cura* + *Mutisiapollis telleriae*) related to extant Asteraceae (3, 5). Finally, the origin of the crown eudicots with fossil records (tricolpate pollen) near the late Barremian/early Aptian was used as a maximum age constraint (ref. 43, and references therein) on the root node of the phylogenetic tree (Table S4). The geologic age of each fossil was determined with precision. All stratigraphic ages were converted into absolute ages by using the geological timescale of Gradstein et al. (44). The late Campanian–early Maastrichtian to late Maastrichtian age range of the fossil *T. lilliei* type A translated into an absolute age of 76.4–72.1/66.0 Ma. This fossil provides a safe minimum age of 72.1 Myr for node A (Fig. S6 and Table S4).

We explored a number of alternative calibration scenarios based on the position of *T. lilliei* type A in the backbone tree of Asterales (Fig. 2, Fig. S5, and Table S1). The most parsimonious reconstruction placed this fossil within the extant genus *Dasyphyllum* (Fig. 2). We also studied other possible placements of *T. lilliei* type A by randomly sampling all 26 characters from our original matrix with replacement (5,000 replicates) with the aim of simulating the variability that we would get if we could have sampled more characters. The resulted bootstrap consensus tree placed *T. lilliei* type A next to all living Asteraceae (Fig. S5A and calibration scenario 2 in Table S2) as an extinct stem relative. The age of the origin of the crown Asteraceae occurred during the Late Cretaceous either using *T. lilliei* type A as a crown

relative (i.e., nested within *Dasyphyllum*) (Fig. 5 and calibration scenario 1 in Table S2) or as a stem relative (i.e., sister to all Asteraceae) (Fig. S5A and calibration scenario 2 in Table S2). We also analyzed the impact on the age of origin of Asteraceae, MGCA (Menyanthaceae, Goodeniaceae, Calyceraceae, and Asteraceae) and Asterales when calibrating the tree using the deepest placements in next-best parsimonious positions (MP+1 and MP+2) of the parsimony analysis (Fig. S5 B–E and calibration scenarios 3–6 in Table S2).

## Supporting Data

### Systematic Remarks.

**Comments on *T. lilliei* (Couper) Farabee and Canright 1986.**

**General morphology.** This species assembles tricolporate, oblate to subspheroidal pollen grains characterized by having microechinate sculpture. The exine is faintly stratified (0.8–1.5  $\mu\text{m}$  thick), the colpi are long, often with rimmed margins, and the ora are irregular in outline with ragged margins. However, this species shows variation in colpi development, density of spines and clarity of the ora (ref. 9, and references therein).

**Stratigraphic distribution.** *T. lilliei* was widely reported in the Late Cretaceous of New Zealand, Australia, Antarctica, and southern South America [e.g., Couper (45); Raine et al. (8); Dettmann and Jarzen (9); Wilson (46); Barreda et al. (47)].

**Botanical affinity.** *T. lilliei* was botanically related to Ranunculaceae [*Clematis* (45, 48)], Euphorbiaceae [*Neoscortechinia* (49)], or considered as an unknown angiosperm group (9).

**Specimens from Antarctica.** The specimens recovered from the Campanian-Maastrichtian of Antarctica fit with the general diagnosis of *T. lilliei* and support the polymorphic features of this morphospecies. However, some of these specimens, in particular, show consistent and well defined characters that lead us to circumscribe them within a new morphotype that we retained within *T. lilliei* and informally named as *T. lilliei* type A. A formal definition should wait until a complete study of most *T. lilliei* specimens recorded in the Late Cretaceous of southern Gondwana (Australia, Patagonia, New Zealand, Antarctica) are carried out. *T. lilliei* type A.

**Description.** Pollen grain tricolporate, isopolar, subspheroidal to subprolate; amb circular to subcircular and elliptic outline in equatorial view. Colpi long with rounded ends and rimmed margins, colp membrane microgranulate, ora well defined, lalongate. Exine faintly stratified (1.2–2  $\mu\text{m}$  thick), thickened at poles; nexine equal to or thinner than sexine. Exine surface microechinate, sometimes interspersed with microbacula and small verrucae, 0.2–0.5  $\mu\text{m}$  in basal diameter, 0.3–0.8  $\mu\text{m}$  in height, and spaced 2–4  $\mu\text{m}$  apart. Intercolpal depressions often present but poorly defined.

**Dimensions.** Equatorial diameter 18–22  $\mu\text{m}$ ; polar diameter 20–25  $\mu\text{m}$ .

**Main studied material.** Specimens on slide BAPal. ex CIRGEO Palin 963b: N42(4), L36(0), P57(1).

**Distribution.** Occurs in trace amounts in late Campanian-late Maastrichtian sequences of Snow Hill Island and Lopez de Bertodano Formations, Snow Hill and Vega Islands, Antarctica.

**Remarks and comparisons.** This new type fits with the broad diagnosis of *T. lilliei* but it shows variations in general shape (subspheroidal to subprolate), clarity of apertures (with well-defined lalongate ora), and exine structure (thickened at poles and with intercolpal depressions). Some specimens reported from the Late Cretaceous of Papanoa Coal Measures, Westland, New Zealand (8) bear strong similarities with *T. lilliei* type A, as they have a thick exine and poorly defined intercolpal depressions (Fig. S4).

**Botanical affinity.** Several angiosperm families produce triaperturate pollen grains with microechinate exine sculpture. Here we used the apomorphy-based method [in the sense of Sauquet et al. (10)] as a first attempt to estimate the closest living relatives of the fossil *T. lilliei* type A, conducting exhaustive comparisons with members of Lamiaceae, Ranunculaceae, Cleomaceae, Sol-

anaceae, Hectorellaceae, Rhamnaceae, Euphorbiaceae, Rubiaceae, Caprifoliaceae, and families of Asterales (Stylidiaceae, Campanulaceae, Goodeniaceae, Calyceraceae and Asteraceae) by using information available in the literature (36, 50–60). Despite gross similarities, however, most of these families have significant differences in apertures, structure, or sculpture with *T. lilliei* type A: Lamiaceae (*Clerodendrum* type) are tricolpate, have short colpi, uniformly microechinate sculpture, and perforate tectum (53); Ranunculaceae (*Clematis*) are larger (approximately 40  $\mu\text{m}$ ), oblate to spheroidal, tricolpate, have a clearly columellate exine structure and variable sculpture (microechinate-microgranulate), with minutely perforate tectum (52, 54, 55); Cleomaceae (*Cleome*) are tricolporoidate, with thin exine (< 1  $\mu\text{m}$ ) and conspicuous columellae (50); Solanaceae (*Latua*) have indistinct ora and very thin exine (< 1  $\mu\text{m}$ ) (50); Hectorellaceae (*Hectorella*) are tricolpate, larger (approximately 40  $\mu\text{m}$ ), clearly columellate and with perforate tectum (54); Rhamnaceae (*Pomaderris*) have circular ora and sparingly perforate tectum (54); Euphorbiaceae (*Neoscortechinia*) differ in having shorter colpi, clearly columellate exine, and stout microspines with acute ends (57); Rubiaceae, (*Bikkia*) have shorter colpi with poorly defined margins (56); Caprifoliaceae (*Symphoricarpos*, *Plectritis*) have tricolporate apertures, but with short colpi, clearly columellate exine, and conical microspines with acute ends (51). The strong morphological similarities from *T. lilliei* type A occur within the members of Asterales. In particular, the phylogenetic method we conducted to evaluate the accurate placement of the fossils from Antarctica within the order indicate the genus *Dasyphyllum* of the Barnadesioideae (Asteraceae) as the closest living relative of *T. lilliei* type A.

**List of Characters and Character State Definitions Used to Compile a Matrix Used as Input in Parsimony Analyses Aimed at Placing the Fossil Taxa (Table S1).** Pollen characters are as follows: 1- Pollen units: single monads (0), tetrads (1). 2- Pollen size (average): small (< 20  $\mu\text{m}$ ) (0), medium (20–40  $\mu\text{m}$ ) (1), large (>40  $\mu\text{m}$ ) (2). 3- Shape (P/E index): peroblate (0), oblate-suboblate (1), spheroidal (2), subprolate (3), prolate (4). 4- Outline in equatorial view: circular-subcircular (0), elliptic (1), rhomboid-subrhomboid (2), rectangular-subrectangular (3). 5- Outline in polar view (Amb): circular-subcircular (0), subangular (1), angular (2). 6- Aperture number: three (triaperturate) (0), many (polyaperturate) (1). 7- Aperture type: porate (0), colpate (1), colporate (2). 8- Aperture fusion: syncolpate (0), nonsyncolpate (1). 9- Endoaperture shape: circular to subcircular (0), lalongate (1). 10- Apocolpia size: small (equatorial diameter/apocolpium ratio > 5) (0), medium (equatorial diameter/apocolpium ratio between 3–5) (1), large (equatorial diameter/apocolpium ratio <3) (2). 11- Colpi ends: rounded (0) yes, acute (1). 12- Sculpture of the apertural membrane: psilate (0), microgranulate (1), scabrate (2), verrucate (3), microechinate (4). 13- Exine sculpture: microechinate (0), echinate (spines longer than 1  $\mu\text{m}$ ) (1), striate-rugulate (2), striate (3), clavate (4), punctate (with sparse puncta) (5), rugulate (6), verrucate (7), microgranulate (8), baculate (9). 14- Sculpture size (observations under light microscopy): sculpture visible in optical section (approximately >0.8  $\mu\text{m}$ ) (0), sculpture faintly visible in optical section (approximately 0.8–0.4  $\mu\text{m}$ ) (1), sculpture not visible in optical section (approximately < 0.4  $\mu\text{m}$ ) (2). 15- Tip of spine: acute (0), rounded (1). 16- Tectal surface among major sculptural elements (observations under SEM): psilate (0), scabrate (1), striate (2), microperforate (3), rugulate (4). 17- Intercolpal depressions: absent (0), present (1). 18- Intercolpal depressions development: well defined (1), poorly defined (0). 19- Columellate layer (observations under light microscopy): columellae clearly distinguishable (0), columellae poorly distinguishable (1), columellae not distinguishable (2). 20- Internal tectum: present (1) yes, absent (0). 21- Ectexine layers (observations under light microscopy): one layer (0), two layers (1), three layers (2). 22- Exine



thickness at the mid-mesocolpium:  $\leq 1 \mu\text{m}$  (0), between 1 and  $3 \mu\text{m}$  (1),  $> 3 \mu\text{m}$  (2). 23- Exine thickened at the poles: thickened (1), nonthickened (0). 24- Exine thickened at the equator: thickened (1), nonthickened (0). 25- Nexine/sexine ratio:  $> 2$  (0), between 1 and 2 (1),  $< 1$  (2). 26- Exine thickened at apertures level: thickened (1), nonthickened (0).

**Details of the Extant Material Examined for Morphological Characters Provided in Data Matrix and References for Scoring.** Specimens examined specifically for the present study are identified with an asterisk (\*).

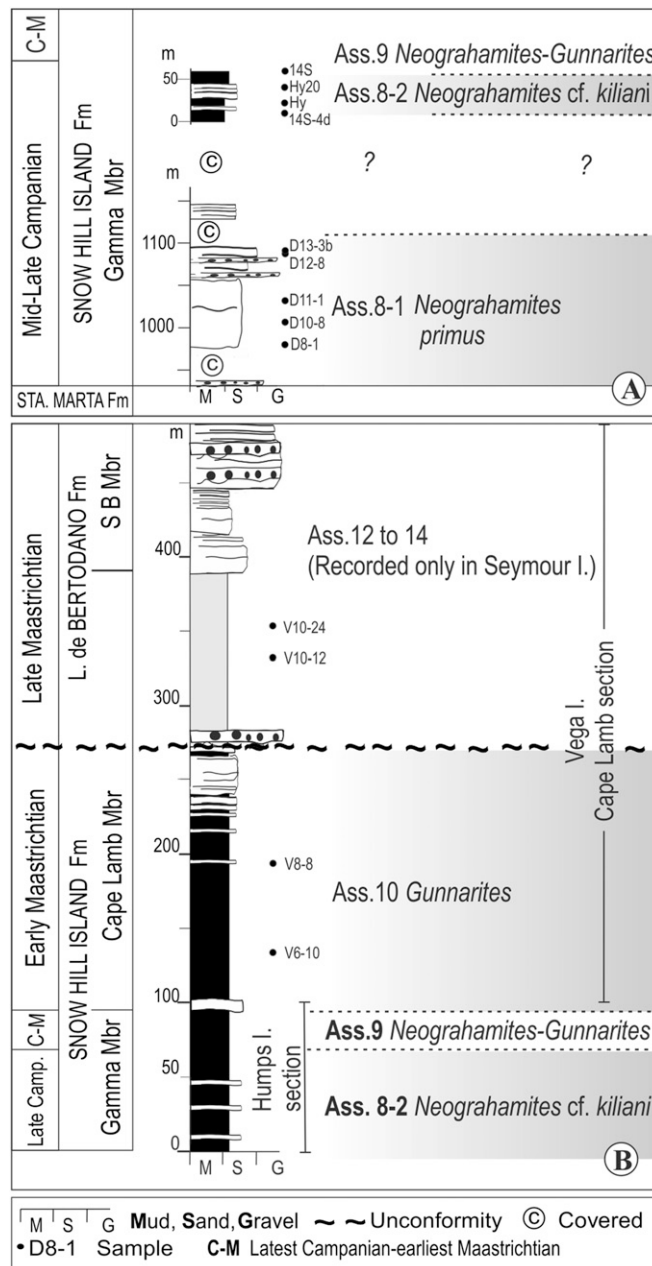
**Extant specimens investigated.** ALSEUOSMIACEAE: *Alseuosmia*. *A. macrophylla* A. Cunn.: \*Chapman 258560 (K); *A. quercifolia* A. Cunn.: \*Melville 1665 (K). *Crispiloba*. *C. disperma* (S. Moore) Steenis: \*Arboretum 1501 (K), \*Gray 1904 (K). ARGOPHYLLACEAE: *Argophyllum*. *A. lejourdanii* F. Muell.: \*Forster 9487 (K). *Corokia*. *C. buddleioides* A. Cunn.: \*S. Andreos s/n° (K). ASTERACEAE: *Brachylaena*. *B. discolor* DC.: Mogg 16165 (US). *Chaetanthera*. *C. acerosa* (Remy) Benth. & Hook. f.: Ruiz Leal 24661 (LP), Cabrera 3525 (LP); *C. apiculata* (Remy) F. Meigen: Werdermann 627 (LP), Philippi, s/n° (LP 66472); *C. australis* Cabrera: Böcher et al., 1658 (LP); *C. brachylepis* Phil.: 9842 (LP), Barros 7443 (LP); *C. chilensis* DC.: Barros 7441 (LP), Riera s/n° (LP 66820); *C. chiquianensis* Ferreyra: Cerrate 1323 (LP); *C. ciliata* Ruiz & Pav.: Brochers 1071c (LP), Landbeck s.n. (LP 66975); *C. cochlearifolia* (A. Gray) B. L. Robinson: Macbride & Featherstone 845 (LP); *C. dioica* (Remy) B. L. Robinson: Kurtz 13717 (LP), Jörgensen 1325 (LP); *C. elegans* Phil.: without leg. (ex LPS 1592 in LP), Barros 2410 (LP); *C. euphrasioides* (DC.) F. Meigen: Spegazzini (ex LPS 2542 in LP), Looser 5751 (LP); *C. flabellata* D. Don: Pisano et al., 1641 (LP), Zöllner 660 (LP); *C. flabellifolia* Cabrera: Werdermann 189 (LP), Rossow & Rizzo 5642 (LP); *C. glabrata* (DC.) F. Meigen: Looser 4389 (LP), Jiles 2363 (LP); *C. glandulosa* Remy: Jiles 1237 (LP); *C. gnaphalioides* (Remy) I.M. Johnst.: Wagenknecht 4388 (LP), Jiles 1237a (LP); *C. incana* Poepp. ex Less.: Jiles 2326 (LP), without leg. (LP 66959). *C. lanata* I. M. Johnst.: Cabrera 3550 (LP), Gijoux s.n. (LP 66804); *C. leptoccephala* Cabrera: Muñoz & Johnson 2192 (LP); *C. limbata* (D. Don) Less.: Germain s/n° (LP 66884), Barros 2402 (LP); *C. linearis* Poepp. Ex Less.: Montero O. 293 (LP), Looser 5214 (LP); *C. hypodioides* (Remy) Cabrera: Boelcke 2468 (LP), Looser 2150 (LP); *C. microphylla* (Cass.) Hook. & Arn.: Cabrera 11120 (LP), Mahu 1040 (LP); *C. minuta* (Phil.) Cabrera: Cabrera 3568 (LP), Krapovickas & Hunziker 5700 (LP); *C. moenchioides* Less.: without leg. (LP 67034), without leg. (LP 67033); *C. pentacaenoides* (Phil.) Hauman: King 336 (LP), Ruiz Leal & Roig 23617 (LP); *C. peruviana* A. Gray: Cerrate et al., 6490 (LP), Weberbauer 6876 (LP); *C. planiseta* Cabrera: without leg. (LP 66498), Barros 9849 (LP); *C. pulvinata* (Phil.) Hauman: Pérez Moreau 158 (LP), Ruiz Leal 3182 (LP); *C. pusilla* (D. Don) Hook. & Arn.: Germain s/n° (LP 66621), without leg. (LP 6371); *C. renifolia* (Remy) Cabrera: Philippi s/n° (LP 66746), Philippi s/n° (LP 6370); *C. revoluta* (Phil.) Cabrera: Cabrera 8372 (LP), Cabrera 8874 (LP); *C. serrata* Ruiz & Pav.: Junge 1282 (LP), Gunckel 432 (LP); *C. spathulifolia* Cabrera: Pérez Moreau s/n° (LP 66809), Spegazzini s/n° (ex LPS 1600 in LP); *C. sphaeroidalis* (Reiche) Hicken: Werdermann 253 (LP), *C. splendens* (Remy) B. L. Robinson: Jiles 1567 (LP), Reiche s/n° (LP 66742); *C. stuebelii* Hieron.: Rohmeder T-18 (LP), Krapovickas & Hunziker 5332 (LP); *C. valdiviana* Phil.: Philippi 1068 (LP); Barros 178 (LP). *Chuquiraga*. *C. acanthophylla* Weddell: Cabrera 7721 (LP), Cabrera 9468, 7721 (LP); *C. arcuata* Harling: Asplund 17679 (S); *C. atacamensis* Kuntze: Budins 5 (LP), Cabrera 8288 (LP); *C. aurea* Skottsberg: Castellanos 7927 (LP), Birabén & Birabén 1 (LP); *C. avellanadae* Lorentz: Boelcke 1687 (LP), Morello 34 (LP); *C. calchaquina* Cabrera: Novara 1123 (MCNS), 1283 (LP); *C. echeagarayi* Hieronymus: Roig 13026 (LP), Zardini & Volponi 100 (LP); *C. erinaceae* D. Don.: Cabrera 9036 (LP); *C. jussieu* J.F. Gmelin: Cañigueral 280 (LP), Herzog 2477 (LP); *G. kuschelii*

Acevedo: Ricardi et al., 110 (LP), Ricardi and Silva 3362 (LP); *C. longiflora* (Grisebach) Hieronymus: Fabris 1361, 1385 (LP), Rodríguez 1411 (LP); *C. morenonis* (Kuntze) Ezcurra: Ruiz Leal 26876 (LP), Ameghino s/n; *C. oblongifolia* Sagástegui: Sánchez et al., 6076 (HAO), Sánchez & Briones 3761 (HAO); *C. oppositifolia* D. Don.: Ruiz Leal 153, 27159 (LP); *C. parviflora* (Grisebach) Hieronymus: Schikendantz 152, 278 (LP); *C. rosulata* Gaspar: Cabrera 19533 (LP), Pérez Moreau 3018 (LP), Ruiz et Leal 16057 (LP), *C. ruscifolia* D. Don.: Ruiz Leal 1838 (LP), Botino 85 (LP); *C. spinosa* subs. *huamapinta* Ezcurra: López et al., 8327 (HUT); *C. straminea* Sandwith: Cabrera 20574 (LP); *C. ulicina* (Hook. et Arn.) Hook & Arn.: Barros 2075 (LP), Cabrera 12674 (LP); *C. weberbaueri* Tovar: López et Sagástegui 3229 (HUT), Sánchez Vega 1146 (LP). *Cnicothamnus* *lorentzii* Griseb.: Maldonado 408 (LP), Cabrera et al., 14497 (LP). *Cyclolepis* *genistoides* D. Don, Zardini & Kiesling 114 (LP); Ruiz Leal 4055 (LP). *Dasyphyllum*. *D. argenteum* Kunth: Rose 23055 (US), *D. armatum* (Koster) Cabrera: Cárdenas 4805 (US); *D. brasiliense* Cabrera: Glaziou 14948 (LP), Rojas 4645 (LP); *D. brevispinum* Sagástegui & M.O. Dillon: Sagástegui et al., 14277, 14454 (HAO); *D. cabreriae* Sagástegui: Díaz et al., 1105 (HUT); *D. candolleianum* (Gardner) Cabrera: Lima 49163 (LP); *D. colombianum* (Cuatrecasas) Cabrera: Killip & Smith 19690 (US); *D. cryptocephalum* (Baker) Cabrera: Santos Lima & Brade 14194 (LP); *D. diacanthoides* (Lessing) Cabrera: Cabrera 11495 (LP), Boelcke 1798 (LP); *D. donianum* (Gardner) Cabrera: Gardner 4946 (LP), Duarte 8169 (LP); *D. excelsum* (Don) Cabrera: Garavente 4146 (LP); *D. ferox* (Weddell) Cabrera: López 1121 (LP), Isern 475 (LP); *D. flagellare* (Cassaretto) Cabrera: Duarte 2633 (LP), Hatschbach 38797 (LP); *D. floribundum* (Gardner) Cabrera: Hassler 11251 (LP); *D. horridum* (Muschler) Cabrera: Weberbauer 5847 (LP); *D. hystrix* Weddell: López & Sagástegui 8065 (HUT), Smith et al., 12019 (HUT); *D. inerme* (Rusby) Cabrera: Tolaba et al., 1844 (LP), Cabrera 3100 (LP), Ragonese 268 (LP); *D. infundibulare* (Baker) Cabrera: Pohl 344 (K); *D. lanceolatum* (Lessing) Cabrera: Hoehne 2348 (BAF); *D. lanosum* Cabrera: Glaziou 19571 (LP); *D. latifolium* Rojas 10533 (LP), 10484 (LP); *D. leioccephalum* (Weddell) Cabrera: Samaloa 56, 68 (LP), Marín 2053 (LP); *D. leptacanthum* (Gardner) Cabrera: Occhioni 1023 (LP), Cabrera 12256 (LP); *D. marialianae* Zardini et Soria: Guerrero 13263 (MO), Soria 7047 (LP); *D. orthacanthum* (De Candolle) Cabrera: Glaziou 5912 (US); *D. popayanense* (Hieronymus) Cabrera: Lehmann 6231 (US); *D. reticulatum* (De Candolle) Cabrera: Pereira Duarte 2400 (LP), Hatschbach 29840 (LP); *D. retinens* (S. Moore) Cabrera: Malme 2117 (LP); *D. spinescens* (Lessing) Cabrera: Sehnen 2514 (LP), Kuhlman s/n° (LP), *D. sprengelianum* (Gardner) Cabrera: Duarte 2660 (LP), Hatschbach 32099 (LP); *D. synacanthum* (Baker) Cabrera: Rambo 45445 (LP), Reitz 1528 (LP); *D. tomentosum* (Sprengel) Cabrera: Hunziker 926 (LP), Rambo 47174 (LP); *D. trichophyllum* (Baker) Cabrera: Damazio s/n° (LP); *D. vagans* (Gardner) Cabrera: Glaziou 11059 (LP), Melo Barreto 3766 (LP); *D. velutinum* (Baker) Cabrera: Duarte 2906 (LP), Melo Barreto 10884 (LP); *D. vepreculatum* (D. Don) Cabrera: Williams & Alston 243 (LP), Steyermark 61092 (F); *D. weberbaueri* (Tovar) Cabrera: López et al., 7805 (HUT). *Dicoma*. *D. anomala* Chisumpa 26 (LP). *Doniophyton*. *D. anomalum* (D. Don) Kurtz: Buenanueva s/n° (LP); King 648 (LP); Maldonado 1448 (LP), Bonifacino et al., 96 (LP); *D. weddellii* Katinas et Stuessy: Ruiz Leal 2093 (LP). *Gochmatia*. *G. arborescens* T. S. Brandege: Keid Moran 9538 (US), Spjut & Edson 6085 (US); *G. argyrea* (Dusén) Cabrera, Smith, Klein & Hatschbach 14460 (LP); *G. attenuata* (Britton) R. N. Jervis & Alain: Bisse et al. s/n° 50424 (HAJB); *G. arequipensis* Sandw.: Eyerden & Beetle 22120 (LP); *G. barrosoae* Cabrera: Macedo 5574 (US), Cabrera 12313 (LP), Mantovani 503 (LP); Mathes 3 (LP); *G. boliviana* S. F. Blake: Beck 6264 (LP); Herzog 1757 (LP), *G. buchii* (Urb.) J. Jiménez Alm.: Jiménez & Holdridge 2039 (US), Jiménez 3613 (LP), Leonard & Leonard 11858 (US); *G. calcicola* (Britton) R. N. Jervis & Alain: del Risco et al. s/n° (HAC 27561); *G. crassifolia* (Britton)

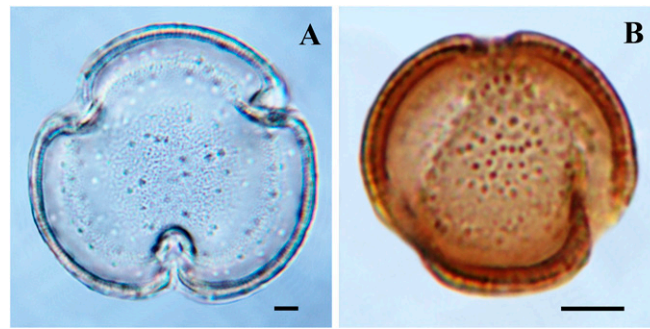
- R. N. Jervis & Alain: Arias et al. s/n° (HAJB 58526); *G. cordata* Less.: Burkart & Crespo 23169 (LP), 19951 (US); *G. cowellii* (Britton) R. N. Jervis & Alain: Howard 5098 (US), Ventosa s/n° (HAJB); *G. cubensis* (Carabia) R. N. Jervis & Alain: López Figueras 1692 (HAC); *G. curviflora* (Griseb.) O. Hoffm.: Jerez et al., 4912 (LP), Fiebrig s/n° (C); *G. densicephala* Sancho: Assis & Williams 7393 (LP), Glaziou 11072 (K); *G. discolor* Baker: Clausen 1301 (NY); *G. ekmanii* (Urb.) R. N. Jervis & Alain: Ekman 13865 (S), Ekman 16865 (S); *G. elliptica* (León) Alain: Valentín Montero 21269 (HAC); *G. floribunda* Cabrera: Roque et al., 281 (LP); *G. foliolosa* (D. Don) Hook. & Arn.: Boelcke 3887 (LP), Marticorena et al., 25217 (LP), Jiles 1693 (S); *G. gardneri* (Baker) Cabrera: 4183 (K, G), *G. glutinosa* (D. Don) Hook. & Arn.: Simon & Bonifacino 509 (LP), Navarro & Bruno 9228 (S); *G. gomezii* (León) R. N. Jervis & Alain: León 20876 (HAC); *G. hatschbachii* Cabrera: Maguire et al., 49149 (US); *G. haumaniana* Cabrera: Maguire et al., 49194 (US), Rojas 10391 (K); *G. ilicifolia* Less.: Eggers 4473 (C), Small & Carter 8526 (US), Ventosa, Oviedo & Fuentes 42615 (HAC); *G. intertexa* (Griseb.) R. N. Jervis & Alain: Bisse et al. s/n° (HAJB 41557). *G. magna* Cabrera: Cronquist 11277 (NY); *G. mantuensis* (Griseb.) R. N. Jervis & Alain: Shafer 11208 (LP), Wright 2876 (HAC); *G. microcephala* (Griseb.) R. N. Jervis & Alain: Ekman H- 9280 (S); *G. maisiana* (León) R. N. Jervis & Alain: La Salle 17576 (HAC); *G. montana* (Britton) R. N. Jervis & Alain: Ekman 18725 (S); *G. obovata* (Urb. & Ekman) J. Jiménez Alm.: Ekman 5366 (S); *G. obtusifolia* (Britton) R. N. Jervis & Alain: Acuña & Díaz Barreto 17456 (HAC); *G. oligocephala* (Gardner) Cabrera: Menezes s/n° (59198 LP); *G. orbiculata* (Malme) Cabrera: Handro 156 (US); *G. palosanto* Cabrera, Ventura 9793 (LP), Wood 12696 (US); *G. parvifolia* (Britton) R. N. Jervis & Alain: Bisse et al. s/n° (HAJB 38075); *G. patazina* Cabrera: Velande Nuñez 3178 (LP); *G. pauciflosculosa* (Wight) R. N. Jervis: Eggers 3866 (C), Brace 4019 (US); *G. picardae* (Urb.) J. Jiménez Alm.: Ekman 5385 (US); *G. polymorpha* (Less.) Cabrera: Harley et al., 26 497 (US), Woolston 808 (S), Blanchet 3251 (LP), Glaziou 3039 (LP); *G. ramboi* Cabrera: Rambo 51161 (LP); *G. recurva* (Britton) R. N. Jervis & Alain: Bisse et al. s/n° (HAJB 21657), Alvarez et al. s/n° (HAJB 56472), Acuña 12788 (US); *G. rotundifolia* Less.: Hoehne 3411273 (US), Brade 5346 (S); *G. sagreana* R. N. Jervis & Alain: Britton et al., 13981 (US), Bisse et al. s/n° (HAJB 42105); *G. shaferi* (Britton) R. N. Jervis & Alain: Bisse et al. s/n° (HAJB 35368); *G. tortuensis* (Urb.) J. Jiménez Alm.: Ekman H-4313 (S); *G. veronioides* Kunth.: López et al., 3354 (LP), Becker & Torrones 1391 (US), López Sagástegui 3354 (LP); *Hecastocleis shockleyi* A. Gray: Train 3973 (LP), A. Kellogg 5301 (US). *Hyalis argentea* D. Don: Daciuk (LP), \*Pertusi 259 (LP). *Mutisia*. *M. acerosa* Poepp.: Cabrera 3463 (LP); *M. acuminata* var. *paucijuga*: Cabrera et al., 13894 (LP); *M. alata* Hieron.: A. López et al., 6719 (LP); *M. andersonii* Sodiro: Scolniek 1532 (LP); *M. arequipensis* Cabrera: Treacy 840, 829 (WIS); *M. brachyantha* Phil.: Wederman 541 (LP); *M. campanulata* Less.: G. Hatschbach 4058 (LP); *M. cana* Poepp. Et Endl.: Jiles 2710; *M. clematis* L.: F. Fosberg 22294 (LP); *M. coccinea* St. Hil.: Krapovickas et al., 22993 (LP); *M. cochabambensis* Hieron.: Cañigueral 11 (LP); Zamaloa 2033 (LP); *M. comptoniafolia* Rusby: Krach 7178 (SI); *M. decurens* Cav.: Grüner 132 (LP), Soriano 4294 (LP); *M. friesiana* Cabrera: Cabrera et al., 22501 (LP); *M. hamata* Reiche: Cabrera et al., 22495 (LP); *M. homoeantha* Wedd.: Meyer 17565 (LP); *M. ilicifolia* Phil.: Jiles 1871 (LP); *M. involucrata* Phil.: Barros 3804 (LP); *M. latifolia* D. Don.: Jiles 3139 (LP); *M. ledifolia* Decaisne: Cabrera 9438 (LP); *M. kurtzii*: Fabris et al., 4082 (LP); var. *anomala*: Cabrera 9001 (LP), Rodríguez 320 (LP); *M. linearifolia* Cav.: Marticorena & Matthei 947 (LP); *M. linifolia* Hook.: Dawson & Pujals 1611 (LP); *M. macrophylla* Phil.: Barros 7552, 1772 (LP); *M. mandoniana* Wedd.: Beck & Seidel 14549 (SI); G. & D. Schmitt 123 (FM); Cárdenas 4869 (FM); *M. manigera* Wedd.: Riccardi & Marticorena 25468 (LP); *M. mathewsii* var. *anomala* Cabrera: Macbride & Featherstone 907 (LP); *M. retrorsa* M. A. Vignati 420 (LP), *M. saltensis* Cabrera: Cabrera et al., 25519 (LP). *M. sinuata* Cav.: Fabris & Marchionni 2344 (LP), King 334 (LP), Ruiz Leal 2146 (LP); *M. spectabilis* Phil.: C. Jiles P. 1834 (LP); *M. subspinoso* Cav.: Ruiz Leal 1051 (LP); Villavicencio, O'Donell 1331(LP); *M. subulata* R. & P.: Jiles 4189, 2586 (LP); *M. orbignyana* Wedd.: Meyer, Cuezzo & Legname 20888 (LP), Isern 394 (LP); *M. grandiflora* Humb. & Bonpl.: Cuatrecasas 20917 (FM), Acosta Solís 5442 (FM); *M. hamata* Reiche: Cabrera et al., 22495 (LP); *M. intermedia* Hieron.: Sodiro (BAF); *M. lanata* Weddell 2314 (LP); Scolnik & Luti 519 (LP); *M. lehmannii* Hieron.: Jaramillo 5415 (FM), Dorr & Valdespino 6382 (FM); *M. microphylla* Willd ex C.D.: Sodiro (BAF); Zak 715 (FM), Romoleroux 297 (FM), Firmin 524 (FM); *M. oligodon* Popp. Et Endl.: Cabrera 6090 (LP), Ledezma 650 (LP); *M. pulcherima* Muschl.: Sagástegui 7469 (LP); *M. retrorsa* Cav.: M. A. Vignati 420 (LP); *M. rimbachii* Sodiro ex Harris: Villacrés 234 (FM); *M. sodiroi* Hieron.: Sodiro (BAF), Fosberg 21188 (FM); *M. speciosa* Ait.: Grüner 1077 (LP), Rodríguez 1265 (LP), T. Rojas 4042 (LP); *M. spectabilis* Phil.: Carlos Jiles 1834 (LP), Zorrilla & Jiles 1816 (LP); *M. spinosa* R. & P.: Hollermayer 725 (LP); *M. stuebelii* Hieron.: Cuatrecasas 19156 (FM). *M. venusta* Blake: Vargas 4420 (LP); *M. vicia* Koster: 2256 (LP); *M. wurdackii* Cabrera: López, Sagástegui & Kollantes 4303 (LP). *Onoseris*. *O. alata* Rusby: Cabrera 15862 (LP); Cabrera et al., 14525 (LP); *O. odorata* Hook. & Arn.: Scolnick 1013 (LP); Cabrera & Fabris 13427 (LP). *Perezia*. *P. atacamensis* (Phil.) Reiche: \*Cabrera et al., 22482 (LP); *P. bellidifolia* (Phil.) Reiche: \*Eskuche 599–20 (LP); *P. recurvata* Less.: \*1493 (LP). *Pertya*. *P. scandens* (Thunb. Ex Thunb) Sch. Bip.: Steward & Cheo 972 (NY); *P. discolor* Rheder: Smith 5786 (MO). *Proustia*. *P. cuneifolia* D. Don: Burkart & Troncoso 11974 (LP), \*Fabris & Zuloaga 8466 (LP). *Stenopadus*. *S. huachamacari* Maguire: Maguire et al., 30116 (MO); *S. affinis* Maguire et al.: Liesner 18346 (MO); *S. connellii* (N.E.Br.) S. Blake: Liesner 23109 (MO); *Schlechtendalia*. *S. luzulaefolia* Less.: Rosengurt B-4507 (LP); \*Pereira 8490 (LP). *Senecio*. \**S. pampeanus* Boffa 1087 (LP). *Stiffia*. *S. chrysantha* J.C. Mikan: Cabrera 12242 (LP). *S. parviflora* (Leandro) D. Don: Hering 7680 (LP); *S. uniflora* Ducke: Ducke s/n° (LP). *Tarchoanthus*. *T. camphoratus* Regmen 501 (US). *Wunderlichia*. *W. azulensis* Maguire & G.M. Barroso: Harleg et al., 25209 (MO); *W. crulsiana* Taubert: Ratter et al., 2615 (MO); *W. mirabilis* Riedel ex Baker: Ratter et al., 2621 (MO). CAMPANULACEAE: *Canarina*. *C. campanula* (L.) Vatke: \*s/n° (GÖTT). *Campanula*. *C. barbata* L.: \*Pedersen 6779 (LP).
- CALYCERACEAE: *Boopis*. *B. anthemoides* Juss.: \*Bottino 437 (LP). *bM. fuensis*: \*Neumeyen n° 20 (LP). ESCALLONIA-CEAE: *Carpodetus*. *C. arboreus* (Lauterb. & K. Schum.) Schltr.: \*30638 (K); *C. major* Schltr.: \*Regdado 1145 (K). *Pentaphragma*. *P. decurrens* Airy Shaw: \*Christensen 1055 (K). GOODENIACEAE: *Cooperookia*. *C. polygalaceae* (de Vriese) Carolin: \*Jackson 1432 (CANB). *Dampiera*. *D. lanceolata* A. Cunn.: \*Wheeler 454 (GÖTT). *Goodenia*. *G. ovata* Sm.: \*Wolls (GÖTT); *G. incana* R. Br.: \*Von Müeller (GÖTT). ICACINACEAE: *Ilex*. *I. paraguayensis* A. St.-Hil.: \*Zardini et al., 727 (LP). MENYANTHACEAE: *Menyanthes*. *M. trifoliata* L.: \*2263, Vöhrnm (Gött). *Nymphoides*. *N. aquatica* (J.F. Gmel.) Kuntze: \*Nelson 23881 B); *N. brevipedicelata* (Vatke) A. Raynal: \*4576 (B); *N. peltata* (s.G. Gmel.) Kuntze: \*Fratiles (B). *Liparophyllum*. *L. capitatum* (Ness) Tippery & Les.: \*Pritzel 108 (B). RANUNCULACEAE: *Clematis*. *C. montevidensis* Spreng.: \*Torres Robles 1613 (LP). ROUSSEACEAE: *Abrophyllum*. *A. ornans* var. *microcarpum* F.M. Bailey: \*Wannana (K), Arbo-retum (K). *Cuttsia*. *C. viburnea* F. Muell.: \*Telford 2623 (CBG). *Roussea*. *R. simplex* Sm.: \*Botana 1483 (K). STYLIDIACEAE: *Levenhookia*. *L. preisii* (Sond) F. Muell.: \*Wrigley s/n° (CBG); *L. stipitata* F. Muell. *Phyllachne*. *P. uliginosa* J.R. Forst & G. Forst: \*Reed s/n° (K). *Stylidium*. *S. inundatum* R. Br.: \*Kennally 11435 (CANB); *S. preisii* (Sond) F. Muell.: \*Carquist 4013 (CANB).
- Specific literature used.** Karehed, 1965 (61); Karehed et al., 1999 (62); Rowley and Nilsson, 1972 (63); Bronckers and Stainier, 1972 (64); Nilsson, 1973 (65); Martin, 1977 (66); Lobreau-Callen, 1977 (67); Skavarla et al., 1977 (51); Ferguson and Hideux, 1978 (68);

Dunbar 1978 (69); Prąglowsky and Grafström, 1985 (70); Cilliers, 1991 (71); Hansen, 1991 (72); Moar, 1993 (54); Gustafsson et al., 1997 (59); Urtubey and Tellería, 1998 (36); Lundberg, 2001 (73); Tellería et al., 2003 (74), Tellería et al.,

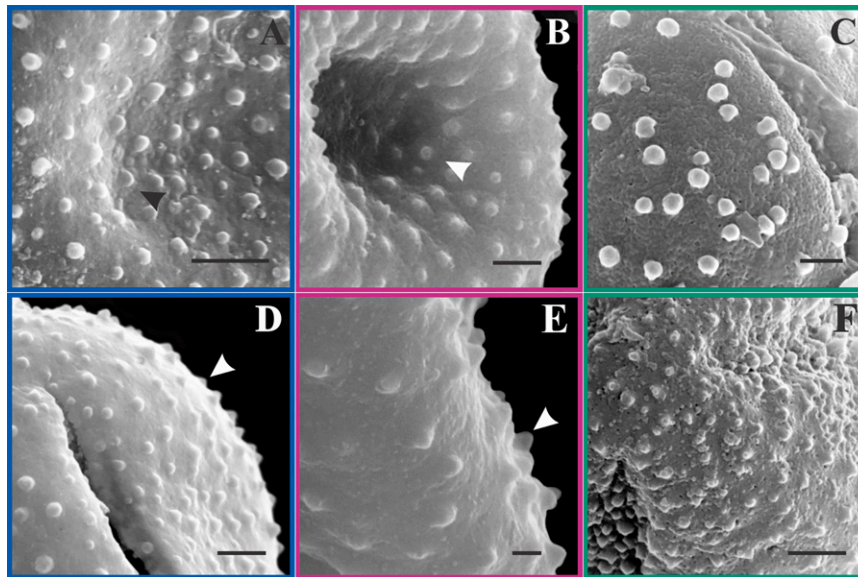
2013 (41); Tellería, 2008 (37); Polevova, 2006 (75); Wortley et al., 2007 (76); DeVore et al., 2007 (60); Blackmore et al., 2010 (77); Pereira Coutinho et al., 2012 (78); Hong and Pan, 2012 (58); Freire et al., 2014 (79).



**Fig. S1.** Stratigraphic sections of the Upper Cretaceous Snow Hill Island and López de Bertodano Formations. (A) Stratigraphic section of the Snow Hill Island Formation at Santa Marta Cove, James Ross Island with the situation of the studied samples and Ammonite Assemblages [Assemblages 8–9, adapted from Olivero (7)]. (B) Stratigraphic section of the Snow Hill Island and López de Bertodano Formations at Cape Lamb, Vega Island with the situation of the studied samples. To highlight the stratigraphic continuity of the samples, the lower 100 m of the section includes the Gamma Member of the Snow Hill Island Formation exposed on Humps Island, which bear the same Ammonite Assemblages 8-2 and 9 (Assemblages 8-2 and 9) recorded in Santa Marta Cove area (see A).



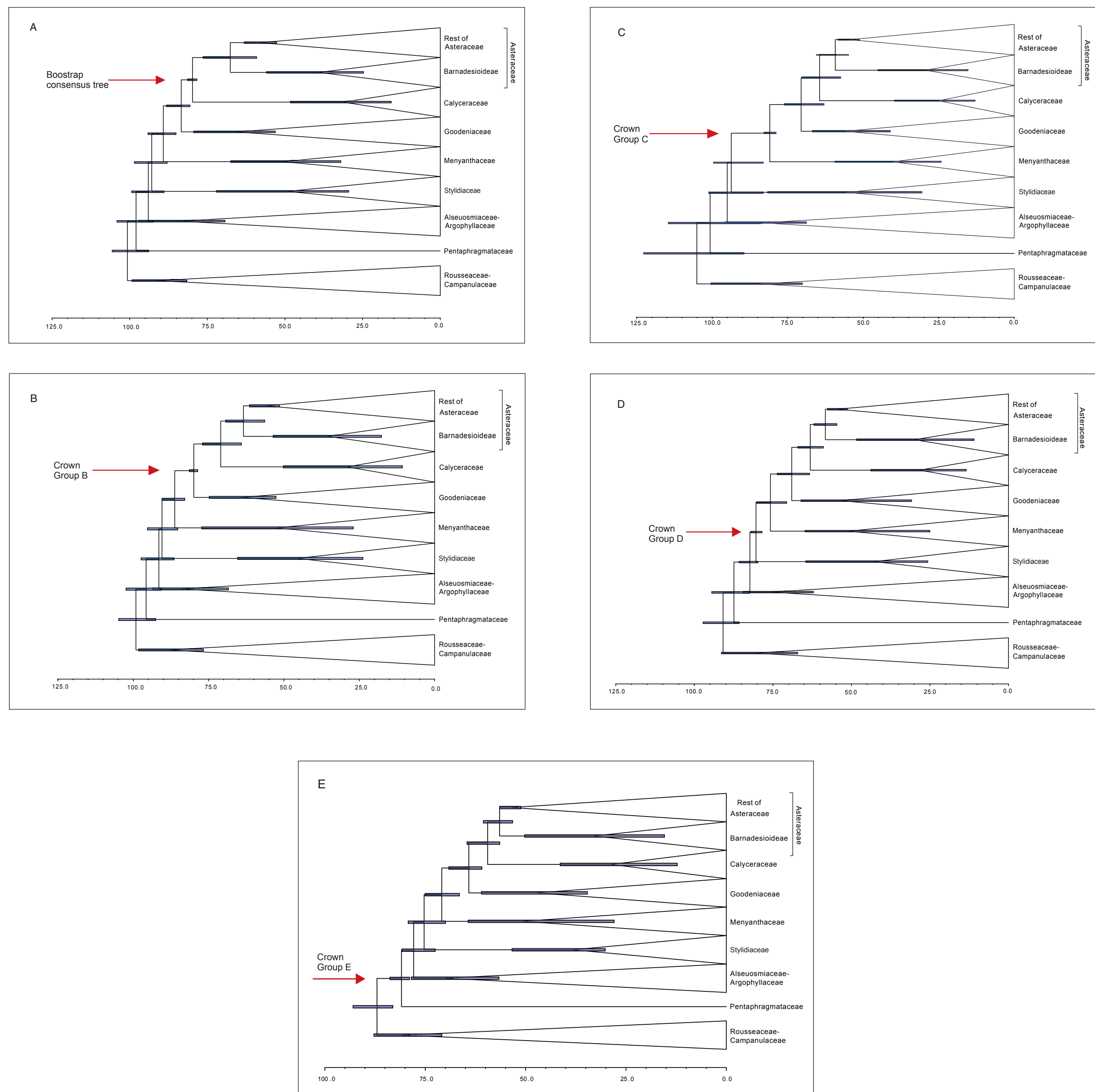
**Fig. 52.** Extant species of Campanulaceae and Ranunculaceae that bear superficial similarities with the fossil *T. lilliei* type A. (A) *Canarina canariensis* (L.) Vatke shows a general resemblance to *T. lilliei*. (B) *Clematis montevicensis* Spreng., family Ranunculaceae, has been previously considered related to *T. lilliei*. Both *Canarina* and *Clematis*, show marked differences in exine structure and sculpture. Note the clearly columellate exine structure (see *Supporting Data, Systematic Remarks*). (Scale bars, 5 µm.)



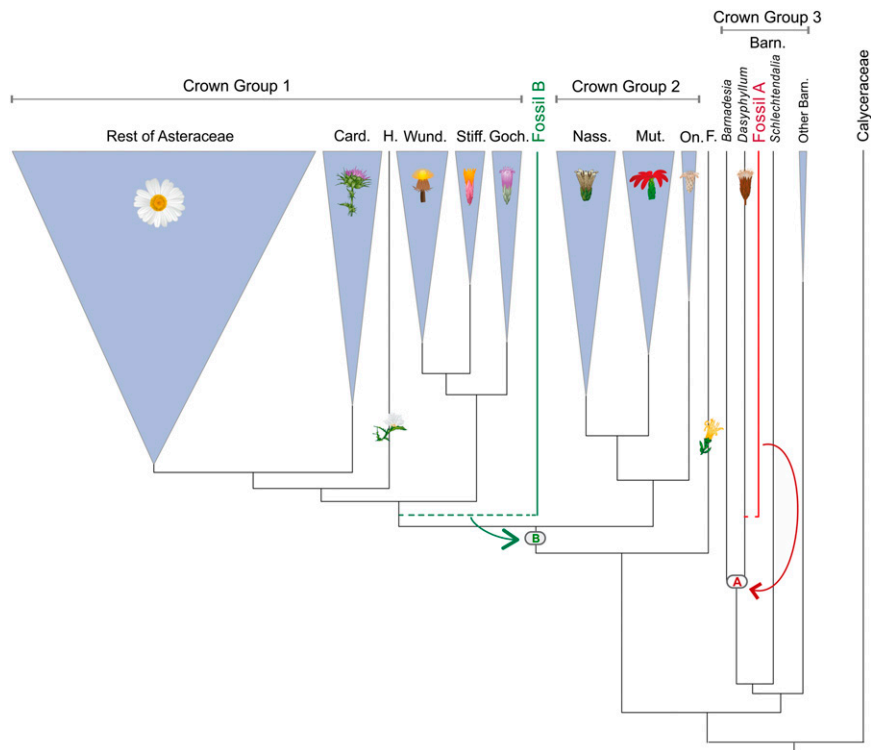
**Fig. 53.** Details (SEM) of the fossil *T. lilliei* type A from the Late Cretaceous of Antarctica and extant representatives of Asteraceae, Campanulaceae, and Ranunculaceae. (A and D) Specimens of *Tubulifloridites lilliei* type A (blue frames). (A) Poorly defined intercolpal depression (arrowhead); (D) detail of sculpture, note microspine (arrowhead) and bacula. (B and E) Extant *Dasyphyllum inerme* (Barnadesioideae subfamily, Asteraceae, pink frames). (B) Well-defined intercolpal depression (arrowhead); (E) microspines and baculum (arrowhead). (C) *Canarina canariensis* (L.) Vatke (Campanulaceae, green square), verrucate-perforate sculpture. (F) *Clematis montevicensis* (Ranunculaceae, green square) details of the microechinate-microgranulate-punctate sculpture. (Scale bars, 2 µm.)



**Fig. 54.** Specimens of *Tubulifloridites lilliei* (Couper) Farabee & Canright from the Late Cretaceous of New Zealand that bear strong similarities with *T. lilliei* type A. (*Supporting Data, Systematic Remarks*). Specimens on slide L5664/3 (Paparua Coal Measures, Westland Plate VI, figures 17–18 in ref. 8). (A) Specimens in equatorial view with a poorly defined intercolpal depression (arrowhead), L40(1). (B) Specimen in subpolar view, Q40(0). (Scale bars, 5 µm.)



**Fig. 55.** Timing of diversification of Asterales using different calibration scenarios. Chronograms (A–E, scale at the bottom in Mya) estimated using a Bayesian relaxed clock calibrated with a previously described fossil inflorescence and pollen from the Eocene (crown Asteraceae, except Barnadesioideae and Faminanthoideae) and the oldest eudicot records (ref. 43, and references therein) from the Cretaceous (see Table S4). Our newly discovered specimens from the Cretaceous of Antarctica (red arrow) were used to calibrate alternative nodes according to the results of our sensitivity analysis (see *SI Materials and Methods, Estimation of Divergence Times*, and Table S2).



**Fig. S6.** Placement of the fossils used in the calibration scenario 1. Fossils A (*T. lilliei* type A) is an extinct species of *Dasyphyllum* in the Crown Group 3 and hence we used the age of this Fossil A to calibrate the split between *Dasyphyllum* and its sister genus *Barnadesia*. Fossils B (*Raiguenrayun cura* + *Mutisiapollis telleriae*) are extinct taxa that we identified as stem relatives of Crown Group 1. We used its age to calibrate the split between Crown Group 1 (Stifftioideae; Wunderlichioideae; Gochnatioideae; Hecastocleidoideae; Carduoideae subfamilies and rest of Asteraceae) and Crown Group 2 (Onoserideae; Mutisioideae; Nassauvieae subfamilies). Barn., Barnadesioideae; Card., Carduoideae; F., Famatinanthoideae; Goch., Gochnatioideae; H., Hecastocleidoideae; Mut., Mutisioideae; Nass., Nassauvieae; On., Onoserideae; Stiff., Stifftioideae; Wund., Wunderlichioideae.

**Table S1. Pollen morphological data matrix of extant and fossil taxa**

[Table S1](#)

**Table S2. Calibration scenarios**

[Table S2](#)

**Table S3. GenBank accession numbers**

[Table S3](#)

**Table S4. Fossil data**

[Table S4](#)