

## A MIDDLE-LATE EOCENE INFLORESCENCE OF CARYOPHYLLACEAE FROM TASMANIA, AUSTRALIA<sup>1</sup>

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A new genus and species (*Caryophylloflora paleogenica* genus and species nova G. J. Jord. & Macphail) are proposed for a fossil inflorescence found in Middle-Late Eocene sediments at Locharbour, northeastern Tasmania, Australia. A parsimony analysis of 75 extant species of the order Caryophyllales and five outgroups placed the fossil within Caryophyllaceae, either subfamily Alsinoideae or Caryophylloideae. The analysis used molecular (*rbcL* and/or *matK*), morphological, and anatomical data for the extant species and morphological data for the fossil. Tests on extant species imply that the placement of the fossil should be convincing. The fossil appears to be of a lineage distinct from any extant Australian Caryophyllaceae. In situ pollen are consistent with the form species, *Periporopollenites polyoratus*. This relatively simple pollen type first appears in Australia and New Zealand in the Late Cretaceous, the oldest known record of the Caryophyllaceae. The last appearance of *P. polyoratus* in Australia is in the Oligocene, and extant Australian members of the Caryophyllaceae are best interpreted as having evolved from species that dispersed from elsewhere during the Neogene or Quaternary.

**Key words:** Antarctica; Australia; Caryophyllaceae; Centrospermae; Eocene; fossil; Paleogene; phylogeny; pollen.

The Caryophyllaceae is a large, cosmopolitan family of 86 genera and about 2200 species of herbs and small shrubs (Bittrich, 1993). Only three of the genera are large shrubs or small trees, *Sanctambrosia*, endemic to San Ambrosio Island, Chile, and the Hawaiian endemics, *Alsinidendron* and *Schiedea* (Bittrich, 1993). The family is included in the order Caryophyllales, which Cronquist (1981) defined to contain about 600 genera and 10 000 species. This is a monophyletic group (Cuenod et al., 2002). Cactaceae, Aizoaceae, Amaranthaceae, and Portulacaceae are other large families in the same order. Savolainen et al. (2000) defined Caryophyllales more broadly but this work will use Cronquist's (1981) narrow definition.

The fossil record of the family is sparse, with published pre-Pleistocene records consisting almost exclusively of pollen. Most Caryophyllaceae have more or less spherical, periporate, spinulose, microechinate or microreticulate annular perforate or punctate pollen with simple apertures (Nowicke, 1994; Punt and Höen, 1995). Fossil pollen matching this description are included in *Periporopollenites* Pflug & Thompson in Thompson & Pflug 1953, *Malvacipollis* and *Chenopodipollis* Krutzsch 1966. *Periporopollenites* includes pollen previously assigned to *Periporites* Van der Hammen 1956, *Caryophyllidites* Couper 1960, *Parsonsidites* Couper 1960, *Liquidambarpollenites* Ratz 1937 ex Potonié 1960, *Polyporina* Naumova 1939 ex Potonié 1960, *Caryophyllaceapites* Biswas 1962, and *Chenopodipollis*. *Malvacipollis* and *Chenopodipollis* are still in use, but now only encompasses pollen of Euphorbiaceae and Amaranthaceae (defined to include Chenopodiaceae), respectively (Truswell et al., 1985).

*Periporopollenites polyoratus* (Couper 1960) Stover and

Partridge 1973 has the longest geological range of fossil pollen types assigned to Caryophyllaceae. Its earliest record is Late Campanian from the Gippsland and Otway Basins in southeast Australia (Stover and Partridge, 1973) and South Island, New Zealand (Raine, 1984). Its last recorded appearance is Oligocene. Younger records of *Periporopollenites* that may be derived from members of Caryophyllaceae are morphologically distinct species. They include Oligocene specimens of *P. pallidus* and *P. vesicus* (Nott and Owen, 1992), Early Miocene specimens of *P. vesicus* and two undescribed *Periporopollenites* species (Owen, 1988), and an undescribed Early-?Middle Miocene grain (Tulip et al., 1982).

Caryophyllaceae-type pollen first appears in Europe in the Miocene (Muller, 1981). This late appearance is surprising considering the much higher diversity of the family in the Northern Hemisphere (Bittrich, 1993) and the earlier Southern Hemisphere records. Eocene seeds from England, *Hantsia pulchra* and *H. glabra* (Chandler, 1961, 1963), have been attributed to the family. These are the only macrofossil records of the family, but their taxonomic status is uncertain (Chandler, 1961).

Morphological convergence means that the pollen records of Caryophyllaceae need to be interpreted carefully. All the features of typical Caryophyllaceae pollen occur in other families of the order, notably Amaranthaceae, Rivinaceae, and Nyctaginaceae. Periporate pollen also occurs in unrelated families such as Papaveraceae, Convolvulaceae, Euphorbiaceae, and Hamamelidaceae.

This work describes a fossil inflorescence from Middle-Late Eocene sediments at Locharbour, northwestern Tasmania, Australia, and the relationships of the in situ pollen with dispersed fossil pollen types. Recent progress in understanding angiosperm evolution has been made by determining the relationships of extinct species to living taxa without forcing fossils into extant genera or families (Dilcher, 2000). This work therefore uses a phylogenetic analysis to determine the relationships of the fossil to extant groups. Formal phylogenetic analysis was necessary because of extensive morphological homoplasy within the order.

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TABLE 1. Morphological, anatomical, and biochemical characters and states. All multistate characters were treated as unordered.

Character	States
1. Inflorescence	0 = not dichasial 1 = dichasial
2. Paired floral bracts	0 = absent 1 = present
3. Flowers	0 = bisexual 1 = unisexual
4. Perianth	0 = with both petals and sepals 1 = with sepals only
5. Calyx merosity	0 = pentamerous 1 = pleiomerous 2 = trimerous 3 = tetramerous
6. Calyx parts	0 = free 1 = fused
7. Stamen position	0 = unassociated with calyx 1 = episepalous/pseudo-obdiplostemonous 2 = alternisepalous
8. Androecium	0 = numerous parts 1 = same number of elements as calyx 2 = twice as many elements as calyx
9. Filaments	0 = filiform 1 = subulate/tapering
10. Stamens	0 = all free 1 = fused into bundles
11. Stamen number	0 = multiple of calyx elements 1 = number reduced 2 = indeterminate
12. Anther attachment	0 = dorsifixed 1 = basifixed
13. Fusion of floral whorls	0 = free 1 = anthers fused to free perianth parts 2 = perigynous 3 = epigynous
14. Pollen aperture type	0 = furrows (colpi) 1 = pores
15. Pollen aperture number	0 = three 1 = 4–7 2 = more than seven
16. Pollen	0 = not spinulose or echinate 1 = spinulose or echinate
17. Pollen	0 = punctate or perforate 1 = not punctate or perforate
18. Carpel number	0 = indefinitely large 1 = four or five 2 = two or three 3 = one
19. Styles	0 = free 1 = fused 2 = one carpel
20. Leaves	0 = alternate 1 = opposite, not connate around stem 2 = opposite, connate around stem
21. Pigments	0 = anthocyanin type 1 = betalaine type

TABLE 1. Continued.

Character	States
22. Sieve element plastid	0 = without protein filaments 1 = peripheral ring of protein filaments present
23. Sieve element plastid crystals	0 = absent 1 = globular 2 = polygonal/angular/cuboidal

## MATERIALS AND METHODS

**Fossil site and paleoenvironmental context**—The fossil came from a lens of laminated siltstone in gravel exposed in the Locharbour tin mine in north-eastern Tasmania (40°56'16" S, 148°0'34" E, 60 m a.s.l.). The siltstone is consistent with a cut-off channel in a braided stream deposit. The sediments are part of extensive mid-Cretaceous-early Neogene freshwater deposits in the region (Baillie, 1989). The associated palynoflora falls in the Lower *Nothofagidites asperus* zone of Stover and Partridge (1973), implying a Middle or possibly Late Eocene age.

The living relatives of fossil species at Locharbour and coeval sites suggest that floristically the vegetation at the time of deposition was diverse, cool climate rainforest dominated by genera with extant species in temperate and tropic-montane rainforests (Carpenter et al., 1994; Macphail et al., 1994). The Locharbour fossil flora includes the conifers *Phyllocladus aberensis* (Hill, 1989), *Willungia oppositifolia* (Hill and Pole, 1992), *Acropyle tasmanica*, *Dacrycarpus mucronatus* (Hill and Carpenter, 1991), and *Araucaria* (Carpenter et al., 1994), and the angiosperms *Eucryphia aberensis* (Barnes and Jordan, 2000) and *Banksiaephyllum attenuatum* (Hill and Christophel, 1988).

**Specimen preparation**—One partial inflorescence was found by manually splitting a block of sediment. Brushing the block with a fine brush under running water exposed this fossil progressively. Some individual anthers were squashed on glass slides and mounted in phenol glycerine jelly for light microscopy. Others were soaked in 50% hydrofluoric acid for approximately 1 h to remove residual sediments, then placed on double-sided conductive tape on aluminum stubs. These were sputter coated with gold to approximately 40 nm thick and observed under high vacuum with an ESEM 2020 Environmental Scanning Electron Microscope (ElectroScan, Wilmington, Massachusetts, USA).

**Data for cladistic analyses**—This work seeks the most parsimonious phylogeny of extant species and the fossil (e.g., Jordan and Hill, 2000). Molecular and morphological data were used for extant species and only morphological data for the fossil. Eighty extant genera with published *rbcl* or *matK* nucleotide sequences were used (Appendix 1, archived at the Botanical Society of America website [http://ajbsupp.botany.org/V90/]). They were 75 genera of Caryophyllales and genera from five families chosen as outgroups based on Savolainen et al. (2000) and Cuenod et al. (2002). All recognized families of the order were represented.

In total 41 *rbcl* and 69 *matK* sequences were used, with both *rbcl* and *matK* sequences for 30 genera. For 76 genera only one species was used. In 14 genera the *rbcl* and *matK* sequences were from different species, and the sequences were combined to minimize the sparsity of the data matrices. This approach could cause misinterpretation if the relevant pairs of species were not monophyletic with regard to the other species analyzed. However, the sparse sampling of taxa makes this unlikely. Scoring of morphological characters allowed for polymorphism in these genera.

After alignment the *rbcl* sequences were trimmed to 1389 sites. Two sequences for *Halophytum ameghinoi* were combined to produce a usable length of 1187 sites. The *matK* alignments followed Cuenod et al. (2002). Ten informative presence/absence characters from *rbcl* sequences and five from *matK* sequences were created for indels. The missing nucleotides were treated as missing values (Simmons and Ochoterena, 2000).

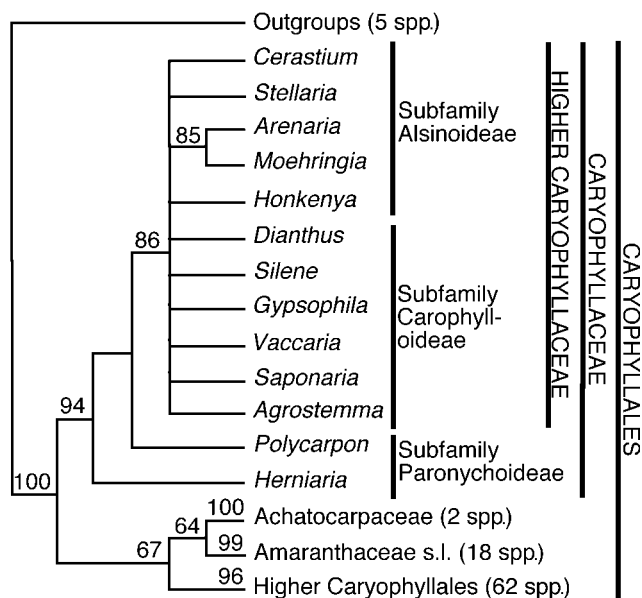


Fig. 1. A strict consensus of 513 parsimonious trees of 3647 steps (excluding uninformative characters, with a consistency index of 0.383) from analysis of 80 extant species based on 810 informative characters. Bootstrap percentages are shown above branches. Some well-supported branches have been collapsed, even though significant structure occurred within these clades. For each of these groups the number of species analyzed is indicated.

Most morphological/anatomical characters (Table 1) were derived from Rodman's (1994) characters, but were scored following an exemplar approach (Prendini, 2001) rather than inferring basal states for families. Preference was given to characters that could be scored unambiguously on the fossil. The data included 23 characters. Twenty morphological characters were compiled from Ross-Craig (1951), Roles (1957), Davis (1967), Dyer (1975), Nowicke and Skvarla (1979), Manly and Hutchins (1980), Cronquist (1981), Correa (1984), Eliasson (1993), Kubitzki et al. (1993), Nowicke (1994, 1996), Hofmann (1994), and Punt and Höen (1995). Of these, 19 could be scored on the fossil. One character was biochemical (pigment type; scored from Clements et al. [1994] and Cuenod et al. [2002]). Two characters described sieve element plastids (Behnke, 1994).

**Cladistic analyses**—PAUP version 4.0 (Swofford, 2000) was used to seek most-parsimonious trees. All characters were analyzed both for extant species only and for extant species and the fossil (Appendix 2, archived at the Botanical Society of America website [http://ajbsupp.botany.org/V90/]). These analyses used random addition sequences replicated 100 times, with tree bisection-reconnection, saving multiple trees. Branch support for the analysis of extant species was assessed by bootstrap with 1000 replicate heuristic searches, each using simple addition sequence, saving a single tree at each step and, because of memory limitations, restricting each replicate to 10<sup>8</sup> rearrangements.

The power of phylogenetic placements using the limited data available on the fossil was tested following Jordan and Hill (2000). For each extant species, a matrix (Appendix 3, archived at the Botanical Society of America website [http://ajbsupp.botany.org/V90/]) was created. The relevant species was coded only for characters that could be scored on the fossil (thus simulating a fossil). All characters were coded for the other 79 extant species. The most-parsimonious phylogenetic placement of each extant species using this restricted data was then compared with its placement based on the complete data.

## RESULTS

The analysis of extant species alone (Fig. 1), produced a moderately well-resolved consensus. Four major clades were

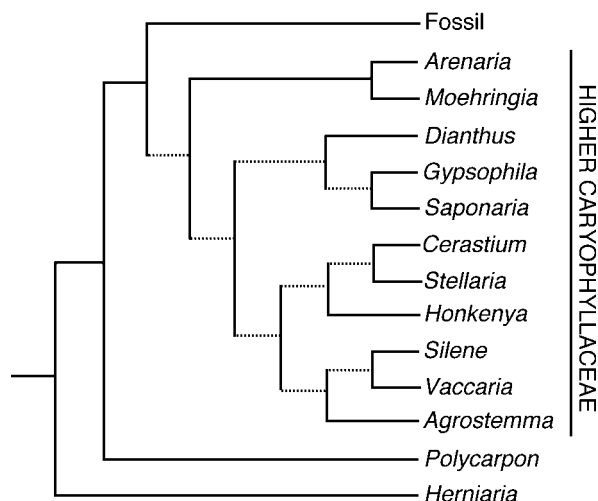


Fig. 2. Part of one of 6609 equally parsimonious trees from analysis of the fossil and 80 extant species. Branches with dashed lines collapsed in the strict consensus. The remainder of the consensus tree had the same topology as in Fig. 1. The trees were 3648 steps long (excluding uninformative characters), with a consistency index of 0.383.

well supported: (1) Caryophyllales sensu stricto; (2) higher Caryophyllales, i.e., Phytolaccaceae, Agdestidaceae, Rivinaeae, Nyctaginaceae, Cactaceae, Aizoaceae, Didiereaceae, Bassellaceae, Portulacaceae, Stegnospermataceae, Halophytaceae, Barbeuiaceae, and Molluginaceae; (3) Caryophyllaceae; and (4) the higher Caryophyllaceae, i.e., subfamilies Caryophyllaceae and Alsinoideae.

The fossil was most parsimoniously placed in a polytomy within, or as sister to, the higher Caryophyllaceae (Fig. 2). Trees only two steps longer than the most-parsimonious trees placed the fossil outside higher Caryophyllaceae, suggesting that support for the placement of the fossil within higher Caryophyllaceae was not strong (Källersjö et al., 1992). The placement within Caryophyllaceae is better supported: the shortest trees placing the fossil outside the family were three steps longer. These placed the fossil in a number of basal positions with the Caryophyllales.

**The power to identify fossils**—The analyses of extant species in which data for one species was restricted to characters that could be measured on fossils are too complex to present here in detail. The following is a summary. For each of the 11 extant species of the higher Caryophyllaceae in the data used here, the strict consensus tree unambiguously placed the relevant species with the other species of that clade. None of the 67 nonmembers of this clade was placed within it. Both sampled members of Caryophyllaceae subfamily Paronychoideae were placed within a clade containing the other members of Caryophyllaceae. No nonmember of Caryophyllaceae was placed within the Caryophyllaceae clade. These data imply that, given only the characters measured on the fossil, species of Caryophyllaceae would be correctly identified as members of that family, and similarly, species of higher Caryophyllaceae would be correctly placed within that clade. Furthermore, the data suggests that placement of any nonmember of Caryophyllaceae as a member of that family is unlikely.



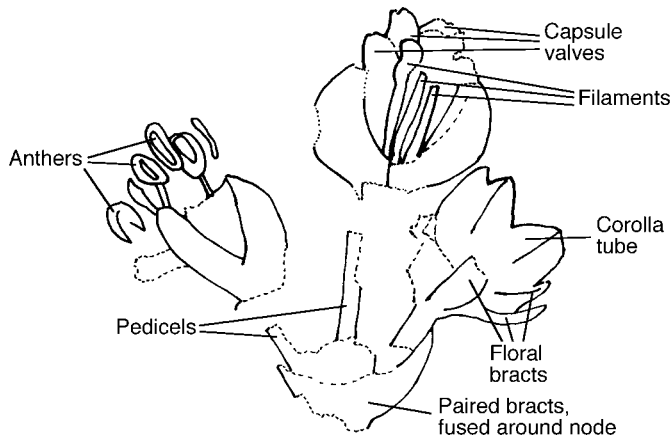


Fig. 3. Line drawing of holotype of *Caryophylloflora paleogenica* G. J. Jord. & Macphail, sp. nov. (LA218). See also Figs. 4–7.

### SYSTEMATIC DESCRIPTION

**Class**—Magnoliopsida.

**Order**—Caryophyllales.

**Family**—Caryophyllaceae.

**Genus**—*Caryophylloflora* G. J. Jord. & Macphail genus nov.

**Etymology**—In reference to the association with Caryophyllaceae.

**Diagnosis**—Inflorescence dichasial, bracts fused around each node. Flowers with several bracts appressed to the calyx. Calyx a five-lobed tube. Stamens free, five opposite and five alternate to the sepals. Ovary syncarpous, superior. Pollen a sphaeroidal, periporate monad with nonannulate, circular pores; exine perforate, tectate with clearly visible columellae.

**Species**—*Caryophylloflora paleogenica* G. J. Jord. & Macphail sp. nov. (Figs. 3–22).

**Holotype**—Specimen LA218, stored in the School of Plant Science, University of Tasmania.

**Locality**—Locharbour mine, northeastern Tasmania, Australia 40°56'16" S, 148°0'34" E.

**Age**—Middle to Late Eocene.

**Etymology**—In reference to the Paleogene age of the fossil.

**Diagnosis**—Inflorescence an open dichasium with at least three flowers. Flowers hermaphrodite or unisexual. Pedicels 5–10 mm long, subtended by acute bracts, pairs of bracts fused around the peduncle. Floral bracts acute, imbricate, about as long as the calyx tube. Calyx tube approximately 3 mm long, lobes triangular, obtuse, approximately two-thirds as long as the tube. Stamens slightly exserted, filaments tapering slightly towards the apex. Anthers approximately 1 mm long, dorsifixed, tetrasporangiate, opening latrorsely by longitudinal slits.

Ovary opening by five valves. Pollen 24–(30)–32  $\mu\text{m}$  in diameter; amb circular; pores approximately 16, 3–3.5  $\mu\text{m}$  in diameter, with or without a pore membrane; exine 2–2.5  $\mu\text{m}$  thick, sexine approximately 1.5  $\mu\text{m}$  thick, microreticulate-microechinate, thinner around pores, nexine  $\ll 1$   $\mu\text{m}$  thick, protruding through or invaginated within pores.

### DISCUSSION

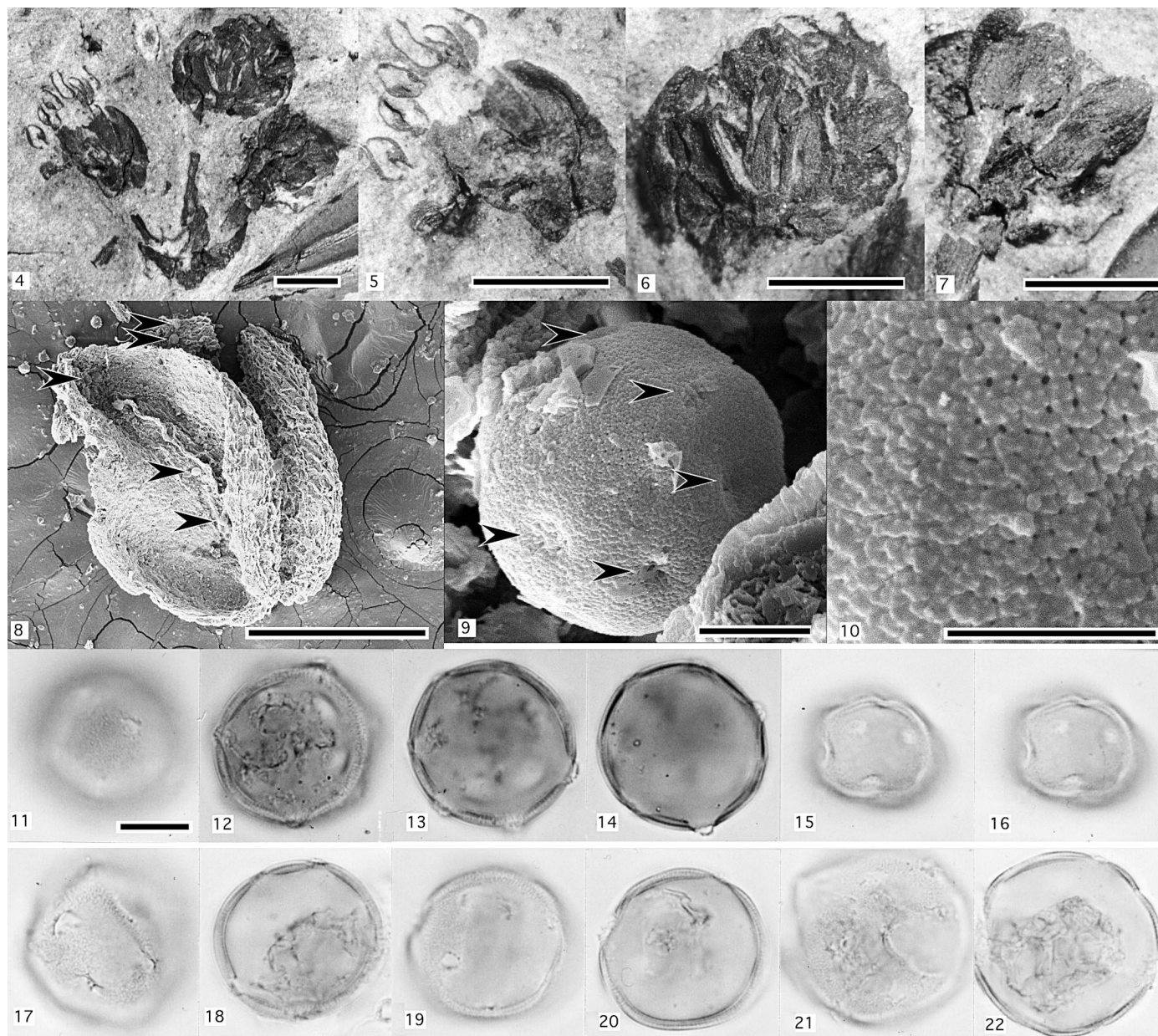
**Phylogeny of extant species**—The most parsimonious phylogeny was broadly consistent with those of Cuenod et al. (2002). The four major clades, Caryophyllales, higher Caryophyllales, Caryophyllaceae, and higher Caryophyllaceae (Fig. 1), were also strongly supported by earlier analyses (Downie and Palmer, 1994; Manhart and Rettig, 1994; Savolainen et al., 2000; Cuenod et al., 2002; Smissen et al., 2002).

In the most parsimonious trees (Fig. 1), all morphological characters are homoplasious, including some traditionally considered to be of taxonomic significance. Pollen ornamentation, aperture number and shape, stamen number and arrangement, perianth merosity and fusion all appear to have converged or reverted in several clades. For example, tricolpate and periporate pollen occur in both Caryophyllaceae and higher Caryophyllales. The strong support for these clades implies convergence in aperture shape and number.

**Phylogenetic placement of the fossil**—The analyses of the power to correctly classify fossils suggest that, given the characters available on the fossil, the approach used here would place only members of higher Caryophyllaceae within that clade. Combined with the additional numbers of steps required to place the fossil outside the clade, this makes the placement of *C. paleogenica* as a member of higher Caryophyllaceae (Fig. 2) convincing, in spite of extensive homoplasy. These interpretations assume that the fossil is a member of the order. However, the combination of periporate pollen, cymose inflorescence, fused calyx, and pentamerous flowers, with five stamens opposite the sepals and five alternate, makes placement in other groups unlikely.

The pollen grains of *C. paleogenica* (Figs. 9–22) are consistent with dispersed grains of *Periporopollenites polyoratus* from Australia and East Antarctica (Figs. 23–33). The dispersed grains are larger (39  $\mu\text{m}$  vs. 30  $\mu\text{m}$ ), but this is probably due to oxidization from weathering and palynological preparation. The grains of *C. paleogenica* differ from other *Periporopollenites* species described in Australia. They have larger and more pores than *P. demarcatus* Stover & Partridge 1973 (Figs. 34–41) and *P. hexaporus* Macphail & Hill 1994 (Figs. 43–45). They are smaller than *P. vesicus* Stover & Partridge 1973, which does not have distinctly defined columellae. *Periporopollenites pallidus* Truswell & Owen 1988 has more pores (20–30) and a thinner exine (1–1.3  $\mu\text{m}$ ) that does not decrease in thickness around the pores.

The grains of *C. paleogenica* differ from all published extant Caryophyllaceae pollen (Heusser, 1971; Nowicke and Skvarla, 1979; Moar, 1993; Nowicke, 1994, 1996; Punt and Höen, 1995). Most extant Caryophyllaceae (e.g., Figs. 46–53) have (1) spinulose, not echinate pollen, (2) conspicuous spinulose opercula over the apertures, and (3) conspicuous perforations (Nowicke, 1994; Punt and Höen, 1995). Many have much larger perforations through the sexine (Nowicke, 1994; Punt and Höen, 1995). Some species, such as *Melandrium apricum* and *Silene aperta*, are finely reticulate (Nowicke,



Figs. 4–22. Holotype of *Caryophylloflora paleogenica* G. J. Jord. & Macphail, sp. nov. (LA218). 4. Fossil inflorescence (compare with Fig. 3). 5. Left-hand flower (staminate). 6. Middle flower (hermaphrodite). 7. Right-hand flower (pistillate). 8. Scanning electron micrograph of an anther. Note the two chambers and in situ pollen grains (indicated by arrows). 9. Scanning electron micrograph of an in situ pollen grain. Arrows indicate pores. 10. Detail of the grain illustrated in Fig. 9. Note the perforations and spinules. 11–22. Optical sections through unoxidized pollen grains from a crushed anther. Fig. 4, scale bar = 2 mm; Figs. 5–7, scale bar = 1 mm; Fig. 8, scale bar = 500  $\mu$ m; Figs. 9, 11–22, scale bar = 10  $\mu$ m; Fig. 10, scale bar = 5  $\mu$ m.

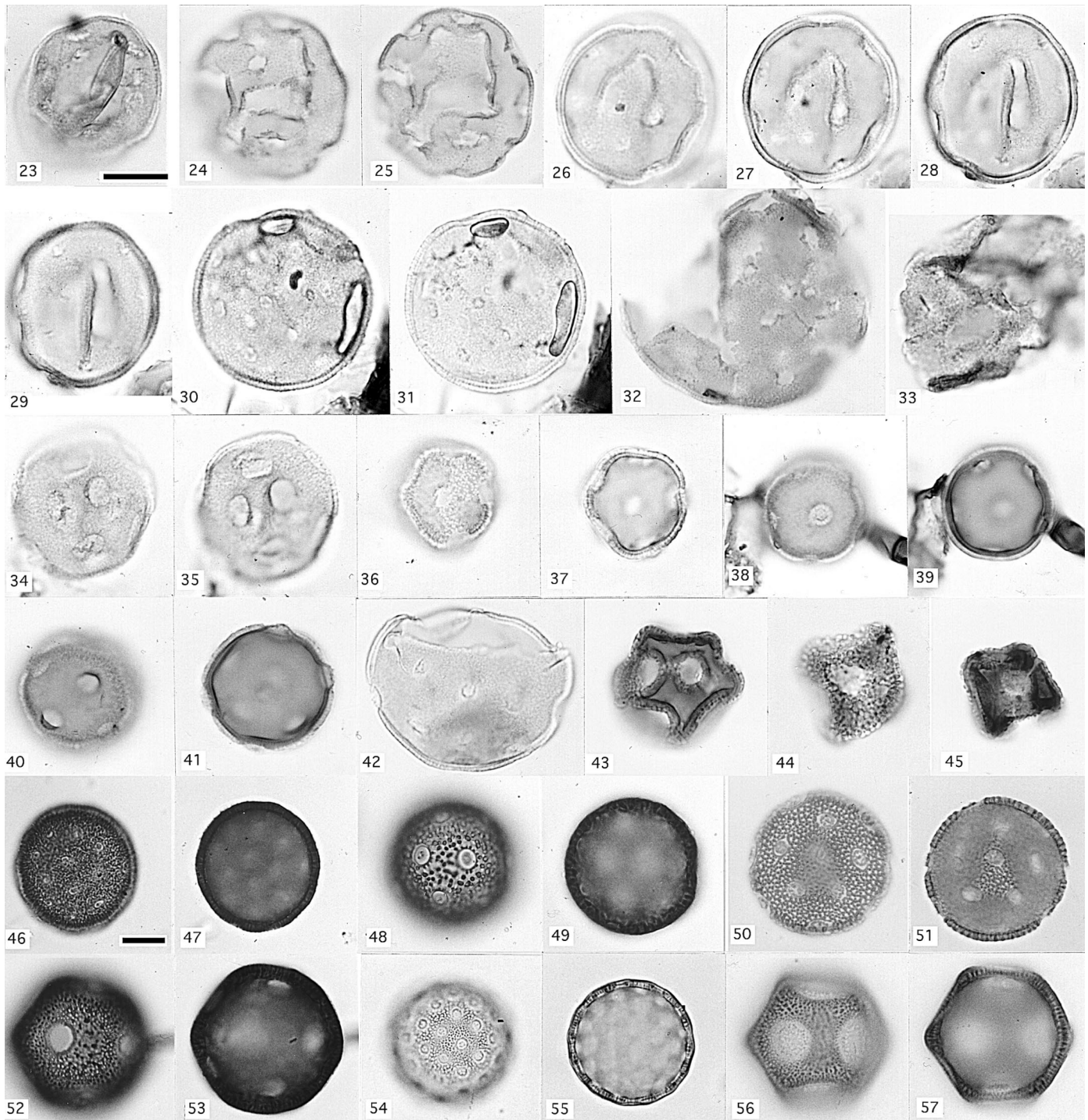
1994; Punt and Höen, 1995), but this is due to large perforations unlike the fine ones of the fossil (Fig. 10). *Illecebrum verticillatum*, like the fossil, has echinate grains with fine perforations and little elaboration of the exine over the apertures, but has only 6–9 pores (Punt and Höen, 1995). The pollen is also distinct from other periporate Caryophyllales (e.g., Figs. 54–57). In particular, Amaranthaceae (including Chenopodiaceae) have annulate pores.

*Caryophylloflora paleogenica* is clearly distinct in floral form from any of the eight genera and 40 or so species of Caryophyllaceae native to Australia (Hnatiuk, 1990). *Gypsophila* lacks bracts appressed to the calyx. *Arenaria*, *Stellaria*,

*Spergularia*, *Colobanthus*, *Polycarpea*, and *Drymaria* have free sepals. In *Scleranthus* the stamens arise from the top of a hypanthium. *Caryophylloflora paleogenica* is therefore best considered as a member of an extinct genus. To establish the relationships of *C. paleogenica* within Caryophyllaceae more precisely would require a detailed phylogeny. This may be indecisive considering the morphological convergence in the order and lack of resolution among extant species (Fig. 1; Smissen et al., 2002).

**Evolutionary and biogeographic implications**—*Caryophylloflora paleogenica* implies that Caryophyllaceae were in Aus-





Figs. 23–57. Light micrographs of pollen grains of fossil *Periporopollenites* species (Figs. 23–45) and extant species of Caryophyllales (Figs. 46–57). Multiple images of specimens represent optical sections. 23–25. *Periporopollenites polyoratus* from latest Middle-Late Eocene glacio-marine sediments, 148.36 m, ODP Leg 188, Site 1166, Prydz Bay, East Antarctica. 26–31. *Periporopollenites polyoratus* from a Middle-Late Eocene backswamp deposit, Tallong, Southern Highlands, New South Wales, Australia. 32. Fragmented grain of *Periporopollenites* sp. cf. *P. polyoratus* from an Early Oligocene tillite, 39.93 m in Lemonthyme Creek DDH 5825, Northwest Tasmania, Australia. 33. Poorly preserved grain of *P. polyoratus* from Late Paleocene fluvio-deltaic sediments, 1923 m, Esso-BHP Snapper-1 Well, Gippsland Basin, southeast Australia. 34–37. *Periporopollenites demarcatus* from the Middle-Late Eocene Tallong sediments. 38–41. *Periporopollenites demarcatus* from Middle Eocene backswamp sediment, Nelly Creek, Lake Eyre Basin, Central Australia. 42. Fragmented grain of *Periporopollenites* sp. cf. *P. polyoratus* from the Middle-Late Eocene Tallong sediments. 43. *Periporopollenites hexaporus* from an Early Oligocene tillite, 21.34 m, Wilmot Dam DDH 4558, Northwest Tasmania. 44–45. *Periporopollenites hexaporus* from latest Middle-Late Eocene marginal marine sediments, 156.99 m, ODP Leg 188, Site 1166, Prydz Bay, East Antarctica. 46–47. *Colobanthus apetalus* (Caryophyllaceae). 48–49. *Lychnis coronata* (Caryophyllaceae). 50–51. *Scleranthus diander* (Caryophyllaceae). 52–53. *Stellaria flaccida* (Caryophyllaceae). 54–55. *Suaeda australis* (Amaranthaceae). 56–57. *Hemichroa pentandra* (Amaranthaceae). Scale bars = 10  $\mu$ m. The larger bar applies to Figs. 23–45, the smaller to Figs. 46–57.

tralia by the Late Eocene. It also confirms that at least some fossil pollen assigned to *Periporopollenites polyoratus* was produced by Caryophyllaceae. The placement of the fossil among or as sister to the higher Caryophyllaceae suggests that considerable divergence had occurred within the family by the Late Eocene. Furthermore, the distinct nature of *C. paleogenica* and the absence of *P. polyoratus* after the Oligocene implies that Paleogene Caryophyllaceae in Australia may not have been closely related to extant Australian members of the family.

Most extant Australian genera of Caryophyllaceae are best interpreted as having arrived during the Neogene or Quaternary. *Arenaria*, *Gypsophila*, *Stellaria*, and *Spergularia* are cosmopolitan or primarily Eurasian, and the Australian species are identical to or closely related to temperate Eurasian species. Fossil pollen closely resembling that produced by *Stellaria* (*Polyporina granulatus* Martin 1973) and *Silene* (*Polyporina reticulata* Martin 1973) first appear in southern Australia during the Late Miocene-Early Pliocene (Macphail, 1997). This suggests relatively recent dispersal. *Polycarpea* and the Australian species of *Drymaria*, *D. cordata*, are more or less pantropical (Bittrich, 1993). Transoceanic dispersal appears to have been significant in both *Colobanthus* and *Scleranthus*. The former occurs on isolated islands of relatively recent origin (e.g., Macquarie Island), and species of the latter (*S. biflorus* and *S. brockei*) occur in both Tasmania and New Zealand, a distribution unlikely to have arisen through vicariance (see Jordan, 2001). Thus, although *C. paleogenica* demonstrates that the family grew in the Southern Hemisphere by the Middle-Late Eocene, modern Australian Caryophyllaceae appear to be independent, recent arrivals.

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