

Evolution of Angiosperm Pollen. 5. Early Diverging Superasteridae (Berberidopsidales, Caryophyllales, Cornales, Ericales, and Santalales) Plus Dilleniales

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EVOLUTION OF ANGIOSPERM
POLLEN. 5. EARLY DIVERGING
SUPERASTERIDAE
(BERBERIDOPSIDALES,
CARYOPHYLLALES, CORNALES,
ERICALES, AND SANTALALES)
PLUS DILLENIALES¹

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ABSTRACT

This study, the fifth in a series investigating palynological characters in angiosperms, aims to explore the distribution of states for 19 pollen characters on five early diverging orders of Superasteridae (Berberidopsidales, Caryophyllales, Comales, Ericales, and Santalales) plus Dilleniales. To illustrate the character states found in the pollen of this group, we examined pollen grains of 15 species exemplifying 15 families across all studied orders using light, scanning, and transmission electron microscopy. We reconstructed the phylogeny of the early diverging Superasteridae and related taxa with eight genetic markers for 172 genera, using maximum likelihood (ML) analysis. Nineteen pollen characters were coded for the genera used in this phylogeny and compiled into two morphological matrices using two coding strategies. The characters were then optimized on the newly generated ML tree plus two constrained trees differing in the position of Dilleniales, using three methods of inference. Taxa in this grade show a striking diversity of pollen morphologies, particularly in certain characters such as size, tectum sculpture, and aperture number. The plesiomorphic condition for the early diverging Superasteridae is unambiguously and consistently inferred to comprise monad-dispersed, isopolar, spheroidal, circular in outline, equatorially arranged, tricolpate pollen grains with granular aperture membranes, a smooth tectum, and endexine present. We identify diagnostic character states and synapomorphies for several monophyletic groups, and explore the palynological evidence that may shed light on some unresolved relationships. For example, the hypothesis that Dilleniales is sister to Superosidae is better supported than alternative hypotheses, being consistent with a number of shared palynological state changes including transitions to presence of costae, reticulate tectum, and columellar infratectum structure. Across this part of the angiosperm phylogeny, most state transitions occur repeatedly, and their frequency varies among both clades and characters. We discuss the impact of optimization method, tree topology, and coding strategy upon ancestral state reconstruction.

Key words: Ancestral state reconstruction, character state distribution, character variability, convergence, palynology, phylogeny, tree topology.

This study is the fifth in a series investigating pollen evolution across angiosperm groups in a phylogenetic context (Fig. 1 shows a simplified current phylogeny of the angiosperm orders used in this series; see also Wortley et al., 2015). In it, we aim to analyze the distribution patterns of pollen character states in five independent lineages branching basally within Superasteridae, plus Dilleniales. These early diverging superasterid orders (Berberidopsidales, Caryophyllales, Cornales, Ericales, Santalales, and perhaps Dilleniales)

are interesting not only for their remarkable diversity of species (the grade comprises 83 currently recognized families and approximately 25,000 species in the recent APG IV (2016) classification, accounting for 9.5% of extant angiosperms), morphologies, and ecological preferences (Kubitzki & Bayer, 2003; Kubitzki, 2004, 2007; Kuijt & Hansen, 2015), but also for their phylogenetically significant position within eudicots (Moore et al., 2010, 2011; Soltis et al., 2011). The group is notable for several long-standing unresolved systematic issues, such as the

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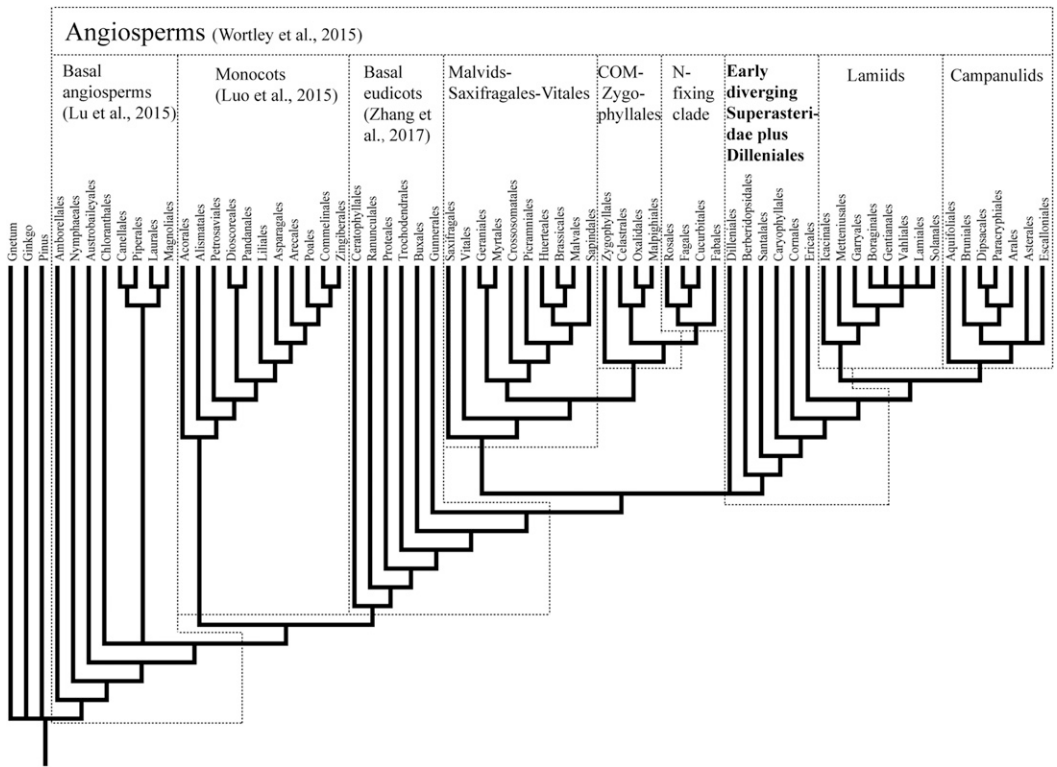


Figure 1. Phylogeny of angiosperm orders as proposed in APG IV (2016), showing the nine groups analyzed in this series of studies. Four papers—one general introduction to the series and three focused on basal angiosperms, monocots, and basal eudicots—have previously been published. The target grade of the present study is highlighted in boldface type. COM, Celastrales, Oxalidales, and Malpighiales.

placement of Dilleniales and relationships within Ericales (Anderberg et al., 2002; Soltis et al., 2011).

Over the past two decades, our understanding of phylogenetic relationships within and between the early diverging superasterid orders has greatly improved through numerous molecular studies (e.g., Soltis et al., 1997, 1999, 2000, 2002, 2003, 2007, 2011; Fan & Xiang, 2003; Fior et al., 2006; Der & Nickrent, 2008; Malécot & Nickrent, 2008; Horn, 2009; Burke et al., 2010; Gillespie & Kron, 2010; Harbaugh et al., 2010; Moore et al., 2010, 2011; Xiang et al., 2011; summarized in APG I [1998], Stevens [2001 onwards], APG II [2003], APG III [2009], and APG IV [2016]). Amongst these studies, a consensus has emerged that the lineage leading to Santalales separated from the remaining Superasteridae first, followed by those leading to Berberidopsidales, Caryophyllales, Cornales, and Ericales.

At the time of this writing, three alternative phylogenetic hypotheses have been proposed for the position of Dilleniales in molecular phylogenetic studies using different taxon samples and genetic markers (e.g., Soltis et al., 2003, 2011; Ruhfel et al., 2014; Zeng et al., 2017). Firstly, in some studies with relatively limited taxon

sampling, Dilleniales was resolved as sister to Caryophyllales (e.g., Soltis et al. [2003]: 206 taxa and three plastid and nuclear genes, bootstrap support (BS) = 83%; Zeng et al. [2017]: 161, 216, and 504 nuclear genes from transcriptomic and genomic datasets), an affinity that is also congruent with the distribution of some morphological characters, such as deep-seated phellogen initiation, successive cambia, persistent calyces, and campylotropous ovules (Kubitzki, 2007). Secondly, in recent large trees, Dilleniales has been placed as sister to Superasteridae using a combination of nuclear and plastid gene markers (Soltis et al. [2011]: 640 taxa, 17 plastid and nuclear genes, BS = 97%), or thirdly, as sister to Superrosidae using exclusively plastid DNA data (Ruhfel et al. [2014]: 360 taxa, 78 plastid genes, BS = 95%). Aside from this, a few other phylogenetic relationships within the early diverging Superasteridae remain problematic, particularly the delimitation of certain paraphyletic families, such as Olacaceae s.l. and Santalaceae s.l. (Der & Nickrent, 2008; Malécot & Nickrent, 2008).

Pollen morphology has been widely used as a source of taxonomic characters, not only providing morphological evidence to support monophyletic groups and clarify uncertain relationships (e.g., Abu-Asab et al., 1993; Chung

et al., 2010; Oswald et al., 2011), but also helping to elucidate the affinities of some enigmatic and/or extinct groups (e.g., Tekleva & Krassilov, 2009; Doyle & Endress, 2010). The most obvious case is the traditional division of flowering plants based on the presence of a single distal aperture versus three equatorial apertures (Erdtman, 1960; Donoghue & Doyle, 1989; Doyle & Hotton, 1991). This division is consistent with recent molecular phylogenetic studies, with the mono-aperturate taxa forming a paraphyletic group (monosulcate grains being found in both basal angiosperms and monocots; Chase et al. [1993]; Soltis et al. [1999]), and the tri-zono-aperturate taxa (with some reversals or subsequent modifications) being resolved as the monophyletic eudicots.

The early diverging Superasteridae plus Dilleniales are particularly notable for their pollen morphological diversity. In 1952, Erdtman documented the pollen diversity of angiosperms using light microscopy (LM), including all early diverging superasterid orders and Dilleniales. Later, Nowicke and colleagues carried out palynological studies in Caryophyllales (e.g., Skvarla & Nowicke, 1976; Nowicke & Skvarla, 1977, 1979) and Cornales (e.g., Poston & Nowicke, 1993) using LM, SEM, and transmission electron microscopy (TEM). Feuer and co-workers published a series of studies regarding the pollen morphology of the families Olacaceae and Santalaceae, also using LM, SEM, and TEM (e.g., Feuer, 1977; Feuer & Kuijt, 1980, 1985). Dickison et al. (1982) have studied the pollen morphology of Dilleniales extensively, and the pollen diversity of Ericales has been surveyed in a large number of reports, such as those by Muller (1973: Lecythidaceae), Harley (1991: Sapotaceae), Janssens et al. (2005: Balsaminaceae), Lens et al. (2005: Marcgraviaceae), and Sarwar (2007: Ericaceae). Although the diversity of pollen morphology in the present grade has thus been widely investigated, few studies have explored how this morphological diversity is distributed on a phylogeny, and how it might have been generated (for exceptions, see Furness & Rudall, 2004; Doyle, 2005, 2009; Müller & Borsch, 2005).

In light of previous molecular-phylogenetic studies (Fan & Xiang, 2003; Hilu et al., 2003; Brockington et al., 2009; Soltis et al., 2011; Xiang et al., 2011), we reconstructed a large-scale phylogeny of the early diverging Superasteridae plus Dilleniales using eight nuclear and plastid genetic markers for 172 genera. Taking advantage of the availability and accessibility of substantial amounts of DNA sequence data, our sampling was designed not only to represent the morphological variation seen in superasterid pollen, but also to cover all major clades (at least at family level). To illustrate the states of the 19 pollen characters analyzed in the grade, we examined pollen grains of 15 species representing all studied orders using LM, SEM, and TEM. Subsequently, we compiled two morphological matrices using comprehensive coding (displaying all

observed states within a genus) and democratic coding (a matrix comprising the most common state for each genus; Bininda-Emonds et al. [1998]) as described in Wortley et al. (2015), and optimized these on the maximum likelihood (ML) tree plus two constrained trees to infer the distribution patterns of pollen features. Our aim was to estimate the potential systematic value of palynological characters across the phylogeny, with particular focus on their significance for defining monophyletic groups or clarifying relationships unresolved in present phylogenies. The results shed light upon some long-standing systematic questions, such as which phylogenetic hypothesis for Dilleniales is better supported, and which palynological character states favor the separation of Nyssaceae from Cornaceae.

MATERIALS AND METHODS

TAXON SELECTION AND PHYLOGENY RECONSTRUCTION

We reconstructed a new phylogeny for the early diverging Superasteridae plus Dilleniales using 150 ingroup genera representing 82 families (APG IV, 2016) from the six studied orders (almost 99% of total family diversity in early diverging Superasteridae; only the poorly understood family Microteaceae was excluded because DNA sequence data for this family were largely missing) and covering a diversity of pollen types. In addition, five genera of basal eudicots were selected as outgroups, and seven genera from Lamiidae and Campanulidae and 10 from Superrosidae as nested ingroups, on the basis of several previous phylogenies (Moore et al., 2010, 2011; Soltis et al., 2011; Ruhfel et al., 2014). In total, 1003 sequences for six plastid (*atpB*, *rbcL*, *matK*, *atp1*, *nad5*, and *matR*) and two nuclear markers (18S and 26S) were downloaded from GenBank (for accession information, see Appendix 1; alignment and trees are deposited in TreeBASE; see <<http://treebase.org/treebase-web/phyloWS/study/TB2:S20606>>) and aligned using PhyDE v0.9971 (<<http://www.phyde.de>>). We inferred phylogenetic hypotheses using ML analysis in RAxML on the Cipres portal (Miller et al., 2010). The optimum model GTR+Gamma+I was selected using both the Akaike information criterion and Bayesian information criterion in jModeltest v2.1.1 (Darriba et al., 2012). Bootstrap values for ML analyses were obtained via 100 bootstrap replicates in RAxML using the same model and parameters as in the optimal tree search. Other parameters were set at default values.

Our ML analysis resulted in a phylogeny of the early diverging Superasteridae (see Fig. 2, tree A) congruent with previous studies except in the placement of Dilleniales. To test the effect of uncertainty in topology upon inferences of pollen character state distribution, we produced constrained phylogenies fixing the placement of Dilleniales as sister to Superasteridae (see Fig. 2, tree

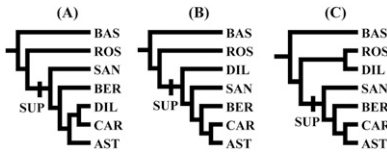


Figure 2. Simplified diagrams showing the three alternative topologies for early diverging Superasteridae generated in the present study, differing in the position of Dilleniales. —A. Maximum likelihood (ML) tree reconstructed for 172 genera using eight plastid and nuclear markers. —B. Constrained ML tree fixing the position of Dilleniales as sister to remaining Superasteridae, following Soltis et al. (2011). —C. Constrained ML tree fixing the position of Dilleniales as sister to Superosidae, following Ruhfel et al. (2014). AST, Asteridae; BAS, basal eudicots; BER, Berberidopsidales; CAR, Caryophyllales; DIL, Dilleniales; ROS, Superosidae; SAN, Santalales; SUP, Superasteridae.

B; a hypothesis supported by Soltis et al., 2011), and to Superosidae (see Fig. 2, tree C; a hypothesis supported by Ruhfel et al., 2014). Both constrained trees were reconstructed using RAxML as before, and all three ML trees were used in the following optimization analyses.

COLLECTION AND CODING OF PALYNOLOGICAL DATA

For the same set of taxa as in the molecular tree, we collected information on 19 pollen traits (Table 1) from

both palynological descriptions and images in the literature (see Appendix 2), as well as our own observations of acetolyzed pollen grains examined under LM, SEM, and TEM. We compiled two morphological matrices using comprehensive and democratic coding strategies as described in Wortley et al. (2015); for the two morphological matrices see Appendices 3 and 4. Palynological terminology follows Punt et al. (2007).

To illustrate some of our pollen characters for the reader, we created images of pollen grains from 15 species in 15 families covering all studied orders, using LM, SEM, and TEM. For these taxa, pollen samples were collected from herbarium specimens (for voucher information, see Appendix 2). Anthers were removed from samples and softened in warm water for 5–10 min. Pollen grains were treated by acetolysis following Erdtman (1966) for LM and SEM observations. For LM, pollen grains were then stained using Calberla’s solution (Bernhardt & Dafni, 2000) for 1–2 min. before examining under an Axio Lab.A1 microscope (Carl Zeiss AG, Oberkochen, Germany), and images were taken using an Axio CamI Cc 1 Rev.4 digital camera (Carl Zeiss AG). For SEM, pollen grains were sputter-coated with gold before examining under a Hitachi S-4800 SEM (Hitachi, Ltd., Tokyo, Japan) at 10.0 kV. For TEM, anthers were embedded in 5% agar and then fixed

Table 1. The 19 palynological characters and their states as used in optimization analyses.

1. Dispersal unit: 0, monad; 1, tetrad
2. Polarity: 0, isopolar; 1, apolar; 2, heteropolar
3. Shape class: 0, peroblate ($P/E < 0.5$); 1, oblate ($P/E = 0.5-0.75$); 2, \pm spheroidal ($P/E = 0.75-1.33$); 3, prolate ($P/E = 1.33-2$)
4. Outline in polar view: 0, \pm circular; 1, polygonal; 2, lobate (generally lobate in outline, with indentations indicating the positions of the apertures); 3, trilobate (deeply curved in outline, with apertures located on the three lobes, usually syncolpate; following Feuer & Kuijt [1980]); 4, elliptic
5. Size (diameter of longest axis): 0, small (10–24 μm); 1, medium (25–49 μm); 2, large (50–99 μm); 3, very large (100–199 μm) (states for this character follow Walker & Doyle [1975])
6. Aperture number: 0, zero; 1, usually three (rarely two or four); 2, usually four; 3, six; 4, > six
7. Aperture position: 0, equatorial; 1, global; 2, polar (proximal and/or distal); 3, at the center of four projections in tetrahedral grains (unique to <i>Schoepfia</i> Schreb.)
8. Ectoaperture shape: 0, colpate; 1, porate; 2, syncolpate; 3, channeled (used specifically for <i>Drosera</i> L., which has a complex aperture system comprising a large proximal central pore and 10 to 15 channels radiating from the central pore; following Takahashi & Sohma [1982]; Takahashi [1988])
9. Endoaperture: 0, absent; 1, present
10. Endoaperture shape: 0, \pm circular; 1, lalongate; 2, lolongate
11. Aperture membrane ornamentation: 0, granular; 1, smooth
12. Costae: 0, absent; 1, present
13. Supratectal elements: 0, absent; 1, present
14. Supratectal element shape: 0, echinate; 1, verrucate; 2, gemmate
15. Supratectal element size: 0, < 1 μm ; 1, > 1 μm
16. Tectum: 0, absent; 1, present
17. Tectum sculpture: 0, perforate; 1, imperforate; 2, reticulate; 3, <i>Croton</i> -patterned (“crotonoid”); 4, striate (\pm perforate); 5, rugulate (\pm perforate); 6, striato-reticulate; 7, fossulate
18. Infratectum structure: 0, columellar; 1, granular; 2, intermediate (comprising irregular radial elements mixed with apparent granules; following Doyle & Endress [2000])
19. Endexine: 0, absent; 1, present

with 2% glutaraldehyde in 0.05 mol/L sodium cacodylate buffer at pH 7.4. Subsequently, the material was dehydrated in a graded ethanol series and stained with 1% phosphotungstic acid (PTA) in 100% ethanol before embedding in LR white resin. Ultra-thin (670 nm) sections were stained with uranyl acetate and lead citrate in an LKB 2168 Ultrastainer (LKB-Produkter AB, Bromma, Sweden) and were observed in a JEOL JEM-1011 transmission electron microscope (JEOL, Inc., Peabody, Massachusetts, U.S.A.).

ANCESTRAL STATE RECONSTRUCTION

We reconstructed hypothesized ancestral states for selected pollen characters across all ingroups, nested ingroups (derived core eudicots), and outgroups (basal eudicots) to enable the most comprehensive exploration of the origin and distribution of pollen character states in early diverging Superasteridae in its proper phylogenetic context. We used three optimization methods: Fitch parsimony (FP), ML, and hierarchical Bayesian inference (HB). We conducted a total of five sets of analysis, namely, analysis of the comprehensive matrix using FP (comprehensive FP [CFP]) and HB (comprehensive HB [CHB]), and of the democratic matrix using FP (democratic FP [DFP]), ML (democratic ML [DML]), and HB (democratic HB [DHB]); ML analyses in Mesquite cannot at present tolerate polymorphic cells and therefore were unable to be performed on the comprehensive dataset. All FP and ML analyses were performed using Mesquite v3.03 (Maddison & Maddison, 2015), while all HB analyses were carried out using BayesTraits (<<http://www.evolution.rdg.ac.uk/BayesTraits.html>>). Each HB analysis used a reversible-jump hyperprior method with an exponential prior drawn from a uniform 0–80 distribution and rate deviations ranging from six to 48 for five million iterations. The burn-in phase and sampling frequency were set at 50,000 and 1000 generations, respectively. In ML and HB analyses, the most probable state for a given node was taken as the one with the highest probability value, but if this value was shared by two or more states, we treated the ancestral state at this node as uncertain. To reduce biases introduced by confounding missing data with inapplicable states, we coded “inapplicable” as an additional state for the optimizations (this applied to character 4 [outline in polar view], character 10 [endoaperture shape], character 14 [supratpectal element shape], and character 15 [supratpectal element size]).

RESULTS

EXEMPLAR PALYNOLOGICAL OBSERVATIONS

The pollen morphology of 15 taxa representing 15 families in six studied orders is described below and illustrated using LM, SEM, and TEM (Figs. 3–7) to

exemplify the diversity of pollen character states found in the early diverging Superasteridae plus Dilleniales. Species are presented in alphabetical order.

Actinidia arguta (Siebold & Zucc.) Planch. ex Miq. (Actinidiaceae, Ericales, Fig. 3A–E). Pollen grains dispersed as monads; isopolar, prolate, amb usually sublobate; size medium (ca. 26–30 μm); tricolporate (i.e., with three compound apertures, each aperture comprising an ectocolpus with one or more endoapertures; Punt et al. [2007]), apertures equatorial, aperture membranes granular, endoapertures circular; costae absent; tectum microrugulate-microperforate, supratpectal elements absent; infratectum structure columellar; foot layer and endexine present.

Arbutus menziesii Pursh (Ericaceae, Ericales, Fig. 3F–J). Pollen grains dispersed as tetrads; grains heteropolar, spheroidal, outline in polar view usually circular; size small (ca. 12–14 μm for single pollen grains); tricolporate, apertures equatorial, aperture membranes granular, endoapertures alongate; costae present; tectum fossulate-perforate, supratpectal elements absent; infratectum structure columellar; foot layer and endexine present.

Basella alba L. (Basellaceae, Caryophyllales, Fig. 3K–O). Pollen grains dispersed as monads; apolar, cuboid; size medium (ca. 25–46 μm); hexacolpate, apertures distributed globally, aperture membranes granular; costae absent; tectum sculpture perforate alongside apertures and coarsely reticulate in mesocolpi, supratpectal elements absent; infratectum structure columellar; foot layer present; endexine absent.

Berberidopsis corallina Hook. f. (Berberidopsidaceae, Berberidopsidales, Fig. 4A–E). Pollen grains dispersed as monads; isopolar, oblate, amb circular; size medium (ca. 30–33 μm); tricolpate, apertures equatorial, aperture membranes granular; costae absent; tectum microrugulate-microperforate, supratpectal elements absent; infratectum structure columellar; foot layer and endexine present.

Dillenia pentagyna Roxb. (Dilleniaceae, Dilleniales, Fig. 4F–J). Pollen grains dispersed as monads; isopolar, oblate-spheroidal, amb circular; size medium (ca. 15–32 μm); tricolpate, apertures equatorial, aperture membranes granular; costae absent; tectum reticulate or punctate-reticulate (polymorphism consistent across multiple collections of this species), supratpectal elements absent; infratectum structure columellar; foot layer and endexine present.

Diospyros kaki Thunb. (Ebenaceae, Ericales, Fig. 4K–O). Pollen grains dispersed as monads; grains isopolar, prolate-spheroidal, amb circular; size medium (ca. 33–40 μm); tricolporate, apertures equatorial, aperture membranes granular, endoapertures alongate; costae absent; tectum imperforate, supratpectal elements

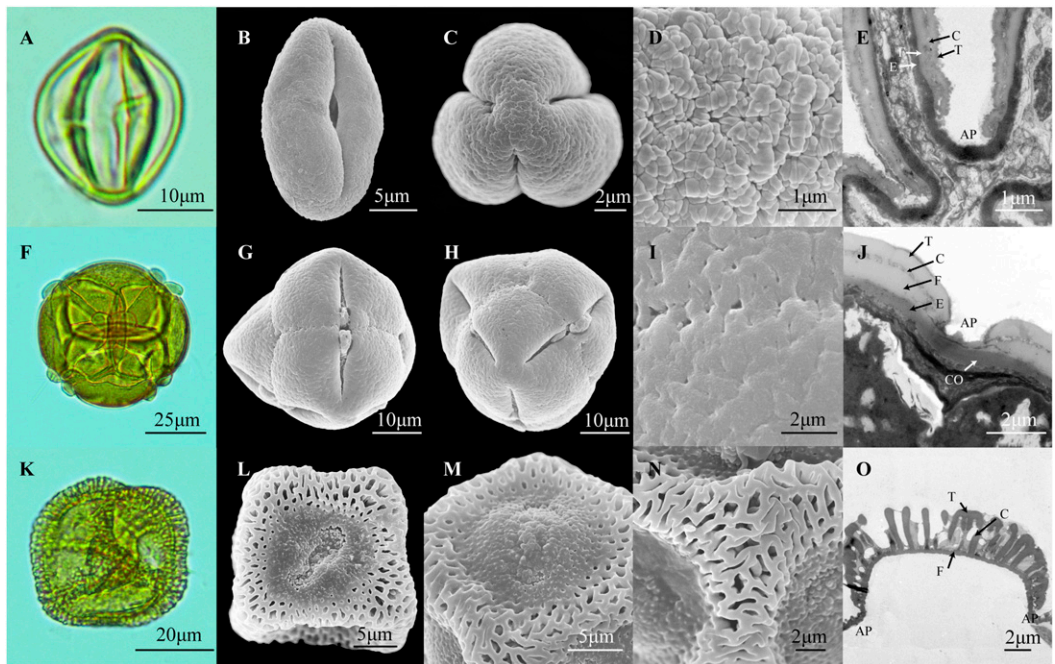


Figure 3. Light, scanning, and transmission electron micrographs of early diverging Superasteridae pollen, arranged alphabetically. A–E. *Actinidia arguta* (Siebold & Zucc.) Planch. ex Miq. —A. Equatorial view (LM). —B. Equatorial view (SEM). —C. Polar view, showing sublobate outline and three colpate apertures (SEM). —D. Detail of microrugulate-perforate tectum (SEM). —E. Mesocolpial and mesoaperturate exines, the former showing tectum (T) with microrugules, columellae (C), foot layer (F), and endexine (E), the latter (AP) showing thin foot layer and a little thickening of endexine (TEM). F–J. *Arbutus menziesii* Pursh. —F. Overall view of tetrad (LM). —G. Overall view of tetrad (SEM). —H. Overall view of tetrad (looking down on single grain; SEM). —I. Detail of microperforate tectum (SEM). —J. Mesocolpial and mesoaperturate exines, the former showing tectum (T), columellae (C), foot layer (F), and endexine (E), the latter (AP) showing very thin foot layer and thickenings of endexine (costae [CO]; TEM). K–O. *Basella alba* L. —K. Overall view (LM). —L. Overall view, showing cuboid shape with one aperture situated at the center of each surface (SEM). —M. Detail of aperture, showing granular aperture membrane (SEM). —N. Detail of coarsely reticulate tectum in mesocolpial region (SEM). —O. Mesocolpial and mesoaperturate exines, the former showing tectum (T), columellae (C), and foot layer of even thickness (F), the latter (AP) showing foot layer; endexine is absent (TEM).

absent; infratectum structure granular; foot layer and endexine present.

Drosera peltata Thunb. (Droseraceae, Caryophyllales, Fig. 5A–D). Pollen grains dispersed as tetrads (note that Takahashi & Sohma [1982] observed the tetrads to be united by cross-wall cohesion); grains heteropolar, mushroom-shaped, outline in polar view usually circular; size small (ca. 6–9 µm for single grains); aperture system complex (aperture area defined as the proximally thinned part of the exine [Kuprianova, 1973; Takahashi, 1988]), each grain having a large proximal central pore with 13 to 16 channels radially extending from the central pore to the exterior of the tetrad, aperture membranes not seen; intectate, sexine spinuliferous with spines 2–3 µm and spinules less than 1 µm; foot layer and endexine present.

Impatiens delavayi Franch. (Balsaminaceae, Ericales, Fig. 5E–H). Pollen grains dispersed as monads; isopolar, oblate, amb usually elliptic; size medium (ca. 26–50 µm); tetracolpate, apertures equatorial, aperture

membranes smooth; costae absent; tectum reticulate, microfossulate in the lumina, supracteal elements absent; infratectum structure columellar; foot layer and very thin endexine present.

Mentzelia involucreta S. Watson (Loasaceae, Cornales, Fig. 5I–L). Pollen grains dispersed as monads; isopolar, prolate, amb circular; size medium (ca. 22–29 µm); tricolpate, apertures equatorial, aperture membranes granular, endoaperture circular (seen in LM and SEM); costae present; tectum striato-microperforate, supracteal elements absent; infratectum structure columellar; foot layer and endexine present.

Mirabilis himalaica (Edgew.) Heimerl (Nyctaginaceae, Caryophyllales, Fig. 6A–D). Pollen grains dispersed as monads; apolar, oblate; size very large (ca. 136–144 µm); 38- to 134-porate, apertures distributed globally, aperture membranes granular; costae absent; tectum perforate, supracteal elements echinate, size less than 1 µm; infratectum structure columellar; foot layer and endexine present.

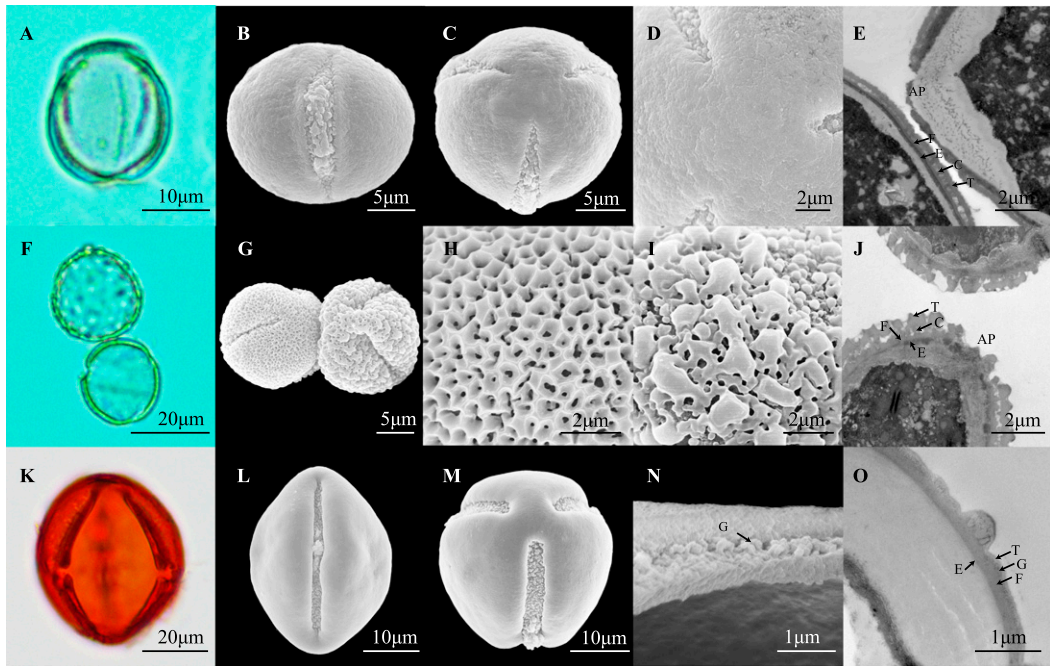


Figure 4. Light, scanning, and transmission electron micrographs of early diverging Superasteridae pollen, continued. A–E. *Berberidopsis corallina* Hook. f. —A. Equatorial view (LM). —B. Equatorial view, showing granular aperture membrane (SEM). —C. Polar view (SEM). —D. Detail of microrugulate-microporate tectum (SEM). —E. Mesocolpial and mesoaperturate exines, the former showing tectum (T), columellae (C), foot layer (F), and endexine (E), the latter (AP) showing thin foot layer and endexine (TEM). F–J. *Dillenia pentagyna* Roxb. —F. Polar view of two pollen grain subtypes (LM). —G. Overall view, showing two subtypes found within one collection. Type I: reticulate tectum. Type II: punctate-reticulate tectum (SEM). —H. Detail of reticulate tectum in type I (SEM). —I. Detail of punctate-reticulate tectum in type II (SEM). —J. Mesocolpial and mesoaperturate exines, the former showing tectum (T), columellae (C), foot layer (F), and endexine (E), the latter (AP) showing foot layer and apparently discontinuous endexine (TEM). K–O. *Diospyros kaki* Thunb. —K. Equatorial view (LM). —L. Equatorial view (SEM). —M. Polar view, showing three colporate apertures with granular aperture membranes (SEM). —N. Cross section through exine, showing granular infratectum structure (G; SEM). —O. Mesocolpial exine showing tectum (T), granular infratectum structure (G), foot layer (F), and thin endexine (E; TEM).

Nepenthes mirabilis (Lour.) Druce (Nepenthaceae, Caryophyllales, Fig. 6E–H). Pollen grains dispersed as tetrads; grains apolar, oblate; size small (ca. 17–19 μm for single grains); inaperturate; intectate, sexine microrugulate-verrucate with spines 2–3 μm and verrucae less than 1 μm ; foot layer and very thin endexine present.

Phanerodiscus diospyroidea Capuron (Aptandraceae, Santalales, Fig. 6I–L). Pollen grains dispersed as monads; isopolar, peroblate, amb usually polygonal; size small (ca. 14–30 μm); hexaporate with three apertures in the proximal hemisphere and three in the distal hemisphere, aperture membranes granular; costae absent; tectum imperforate or microporate, supracteal elements absent; infratectum structure intermediate (granular with a few columellae); foot layer and endexine present.

Polemonium L. sp. (Polemoniaceae, Ericales, Fig. 7E–H). Pollen grains dispersed as monads; apolar, spheroidal; size medium (ca. 36–45 μm); 60- to 70-porate, apertures distributed globally, aperture membranes smooth; costae present; tectum striato-reticulate,

supracteal elements microechinate, size less than 1 μm ; infratectum structure columellar; foot layer and endexine present.

Psittacanthus calyculatus (DC.) G. Don (Loranthaceae, Santalales, Fig. 7A–D). Pollen grains dispersed as monads; isopolar, peroblate, amb trilobate; size large (ca. 33–78 μm); trisyncolpate, apertures equatorial, aperture membranes granular; costae absent; tectum perforate, supracteal elements verrucate, size less than 1 μm ; infratectum structure columellar; foot layer and endexine present.

Schoepfia fragrans Wall. (Schoepfiaceae, Santalales, Fig. 7I–L). Pollen grains dispersed as monads; heteropolar, tetrahedral, amb usually polygonal; size small (ca. 18–25 μm); tetraporate, the four apertures positioned at the center of four projections, aperture membranes smooth; costae absent; tectum microrugulate-microporate, supracteal elements absent; infratectum structure columellar; foot layer and thin endexine present.

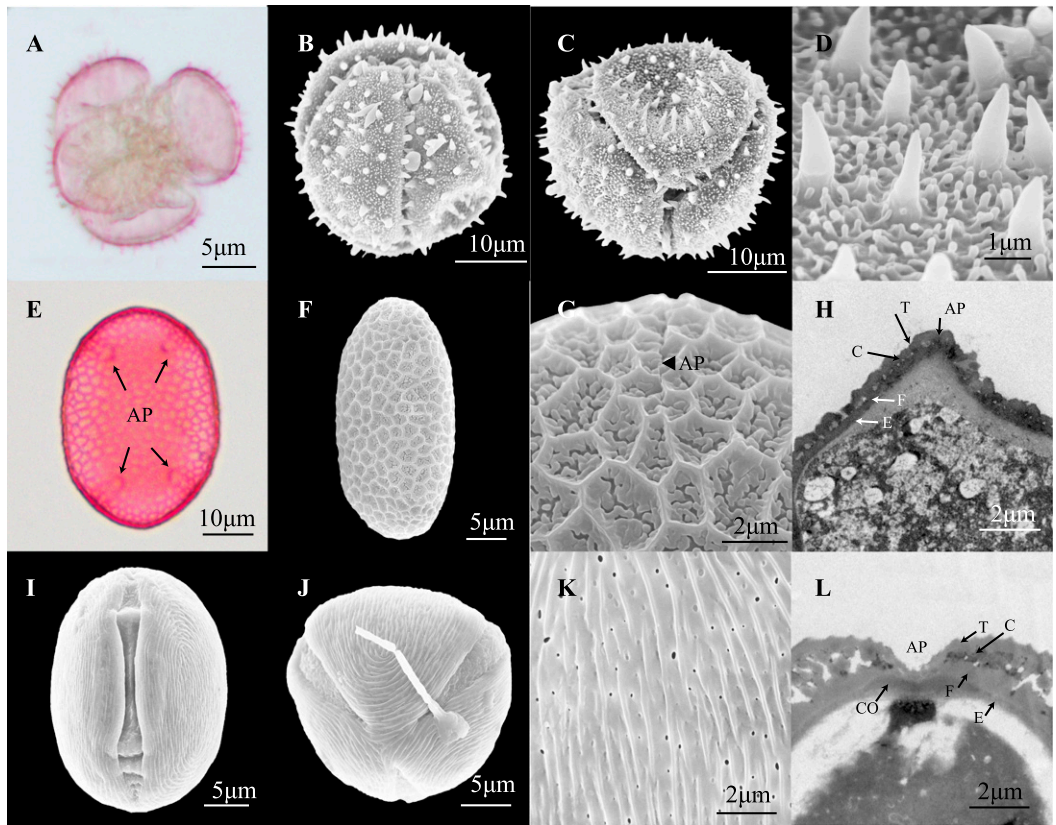


Figure 5. Light, scanning, and transmission electron micrographs of early diverging Superasteridae pollen, continued. A–D. *Drosera peltata* Thunb. —A. Overall view of tetrad showing more or less mushroom-shaped monads and some aspects of the complex aperture system (LM). —B. Overall view of tetrad (SEM). —C. Overall view of tetrad (SEM). —D. Detail of dimorphic sexine elements (grains are intact; SEM). E–H. *Impatiens delavayi* Franch. —E. Overall view (LM), showing four colpate apertures (AP, arrowed). —F. Polar view, showing bilateral symmetry (SEM). —G. Detail of reticulate tectum; arrow (AP) indicates a colpate aperture (SEM). —H. Mesocolpial and mesoaperturate exines, the former showing tectum (T), columellae (C), foot layer (F), and thin endexine (E), the latter (AP, apertural region is narrow) showing foot layer and a little thickening of endexine (TEM). I–L. *Mentzelia involucrata* S. Watson. —I. Overall view (SEM). —J. Equatorial view, showing colpate ectoaperture (SEM). —K. Detail of striate-microporate tectum (SEM). —L. Mesocolpial and mesoaperturate exines, the former showing tectum (T), columellae (C), foot layer (F), and endexine (E), the latter (AP) showing foot layer and thickenings of endexine (costae [CO]; TEM).

ANCESTRAL STATE RECONSTRUCTION

We optimized our two morphological matrices on three ML trees (differing in the position of Dilleniales; simplified topologies of the trees are shown in Fig. 2) using three methods of inference. The results of these optimizations varied with all parameters (tree topologies, coding strategies, and optimization methods), with variation being particularly great among methods (see Appendix 5). The state changes inferred in the 19 pollen characters are shown in Figure 3 for the example of the CHB analysis on tree B, while the most probable state changes inferred at family level across all optimizations are summarized in Table 2.

For Superasteridae as a whole, plesiomorphic states for many pollen characters were inferred unambiguously and consistently in all analyses, including monad dispersal

unit (char. 1), isopolar polarity (char. 2), spheroidal shape (char. 3), circular outline in polar view (char. 4), equatorially positioned, tricolpate apertures (chars. 6, 7, and 8) with granular membranes (char. 11), smooth tectum (chars. 13 and 16), and presence of endexine (char. 19). Plesiomorphic states for the remaining characters were inferred inconsistently among the five analyses and on the three trees (see Table 2, Fig. 8). A few shared character state changes were inferred to support two of the three phylogenetic hypotheses for the position of Dilleniales, i.e., the affinity of Dilleniales and Caryophyllales (tree A) is supported by shared transitions to simple apertures (char. 9: DML, CHB, and DHB), granular aperture membranes (char. 11: DHB), and columellar infratectum structure (char. 18: CHB and DHB), while the sister relationship between Dilleniales and Superrosidae

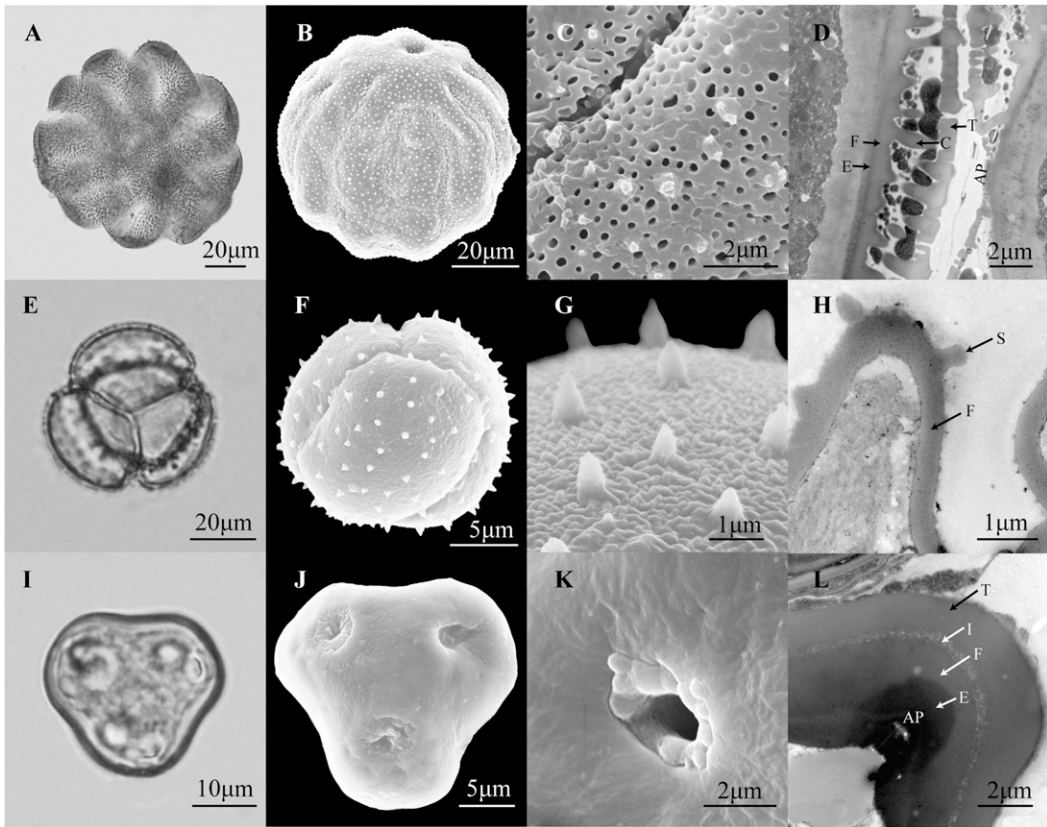


Figure 6. Light, scanning, and transmission electron micrographs of early diverging Superasteridae pollen, continued. A–D. *Mirabilis himalaica* (Edgew.) Heimerl. —A. Overall view of pantoporate grain (LM). —B. Overall view of pantoporate grain (SEM). —C. Detail of perforate tectum with supraterectal spinules (SEM). —D. Mesocolpial and mesoaperturate exines, the former showing tectum (T), columellae (C), foot layer (F), and endexine (E), the latter (AP) showing very thin foot layer and endexine (TEM). E–H. *Nepenthes mirabilis* (Lour.) Druce. —E. Overall view of tetrad, showing oblate shape of monads (LM). —F. Overall view of tetrad (SEM). —G. Detail of microrugulate-verrucate sexine (grains are intectate) with large echinae and small verrucae (SEM). —H. Exine showing echinate sexine elements (S), thick foot layer (F), and very thin endexine (E; TEM). I–L. *Phanerodiscus diospyroides* Capuron. —I. Overall view (LM). —J. Polar view, showing the three pori of one hemisphere and triangular amb (SEM). —K. Detail of imperforate tectum around an aperture with granules (SEM). —L. Mesoaperturate exine (AP) showing tectum (T), intermediate infratectum structure (granules mixed with a few columellae, I), foot layer (F), and endexine (E; TEM).

(tree C) is supported by transitions to presence of costae (char. 12: DFP and CHB), reticulate tectum (char. 17: CHB and DHB), and columellar infratectum structure (char. 18: CHB and DHB). In contrast, we did not find shared states to support the separation of Dilleniaceae and the remaining Superasteridae from Superrosidae (tree B).

Apart from supraterectal element shape (invariable under CFP, DFP, and DML; all trees) and infratectum structure (invariable under CFP, DFP, and DML; all trees), all pollen characters displayed state changes across the phylogeny, with the rate of change varying among characters, analyses, and trees (see Appendix 5). Among the five analyses, CHB and DHB showed a relatively higher rate of state changes than CFP, DFP, and DML analyses. Compared to the variability in state changes among characters and analyses, that among trees is lower. For example, we inferred a rate of

0.103, 0.101, and 0.100 state transitions per character per branch on trees A, B, and C, respectively, in the CHB analysis. Of all nonterminal branches, 17 display at least five state changes, with the largest numbers found in the lineages leading to Misodendraceae–Schoepfiaceae and Polemoniaceae, both displaying eight state transitions each. In contrast, some families, such as Cactaceae, Didiereaceae, and Nyctaginaceae, showed comparatively few state changes (Fig. 8).

DISCUSSION

SYSTEMATIC SIGNIFICANCE OF PALYNOLOGICAL CHARACTERS

A general survey of the literature regarding pollen morphology in the early diverging Superasteridae plus

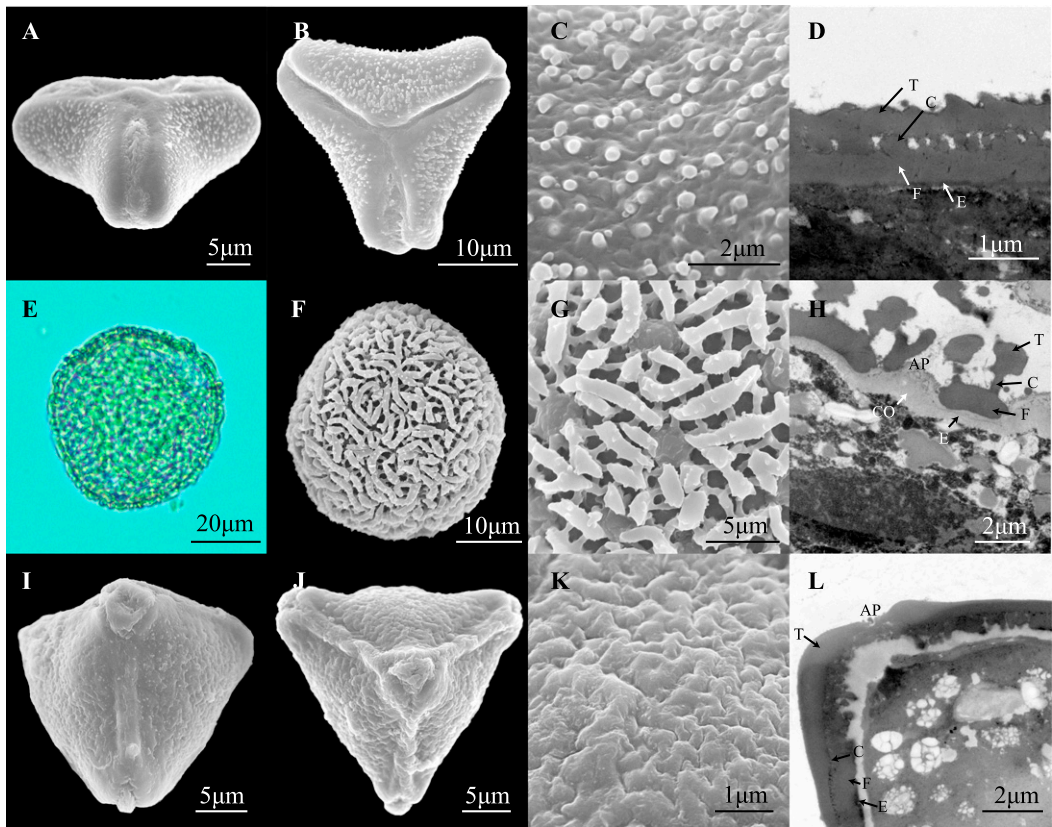


Figure 7. Light, scanning, and transmission electron micrographs of early diverging Superasteridae pollen, continued. A–D. *Psittacanthus calyculatus* (DC.) G. Don. —A. Equatorial view, showing peroblate shape (SEM). —B. Polar view, showing three syncolpi and trilobate outline (SEM). —C. Detail of perforate tectum with suprategular verrucae (SEM). —D. Mesocolpial exine showing tectum (T), columellae (C), foot layer (F), and very thin endexine (E; TEM). E–H. *Polemonium* L. sp. —E. Overall view of grain (LM). —F. Overall view of grain (SEM). —G. Detail of striato-reticulate tectum with granular suprategular elements (SEM). —H. Mesocolpial and mesoaperturate exines, the former showing tectum (T) with striate-reticulate ornamentation, columellae (C), foot layer (F), and endexine (E), the latter (AP) showing very thin foot layer and thickenings of endexine; costae (CO) also shown (TEM). I–L. *Schoepfia fragrans* Wall. —I. Equatorial view, showing tetrahedral shape (SEM). —J. View of one projection, with aperture situated at its center (SEM). —K. Detail of microrugulate-microperforate tectum (SEM). —L. Mesocolpial and mesoaperturate exines, the former showing tectum (T) with striate-reticulate, columellae (C), foot layer (F), and discontinuous endexine (E), the latter (AP) showing granular foot layer (TEM).

Dilleniales reveals a wide range of variation in pollen character states as illustrated here (Figs. 3–7). Variation is particularly great in certain characters, such as size, with a range of 6–216 μm (for single grains), outline in polar view (i.e., circular, polygonal, lobate, elliptic, and trilobate), and tectum sculpture (i.e., imperforate, perforate, reticulate, striate, striato-reticulate, and microfossulate-perforate). The level of pollen morphological diversity also varies markedly among clades, with comparatively high levels in large and diverse groups, such as Caryophyllales and Ericales. Several character states appeared clustered at family or even ordinal level across the phylogeny (for instance, tetrad dispersal units [char. 1] occurring in Ericaceae and Droseraceae–Nepenthaceae, and apolar grains [char. 2]

in Polemoniaceae and Caryophyllales), suggesting potential systematic usefulness.

As in our earlier studies in this series (Lu et al., 2015; Luo et al., 2015; Zhang et al., 2017), our optimizations illustrate that palynological characters are useful for diagnosing a range of clades and may provide supportive evidence for resolving enigmatic groups or poorly known relationships in the early diverging Superasteridae and their relatives. Below, we discuss briefly the congruence of palynological evidence with phylogenetic relationships drawn from molecular data for clades in the present grade. In particular we focus on lineages for which the placement is not yet certain, or with unique pollen types, pollination syndromes, and/or habitat preferences.

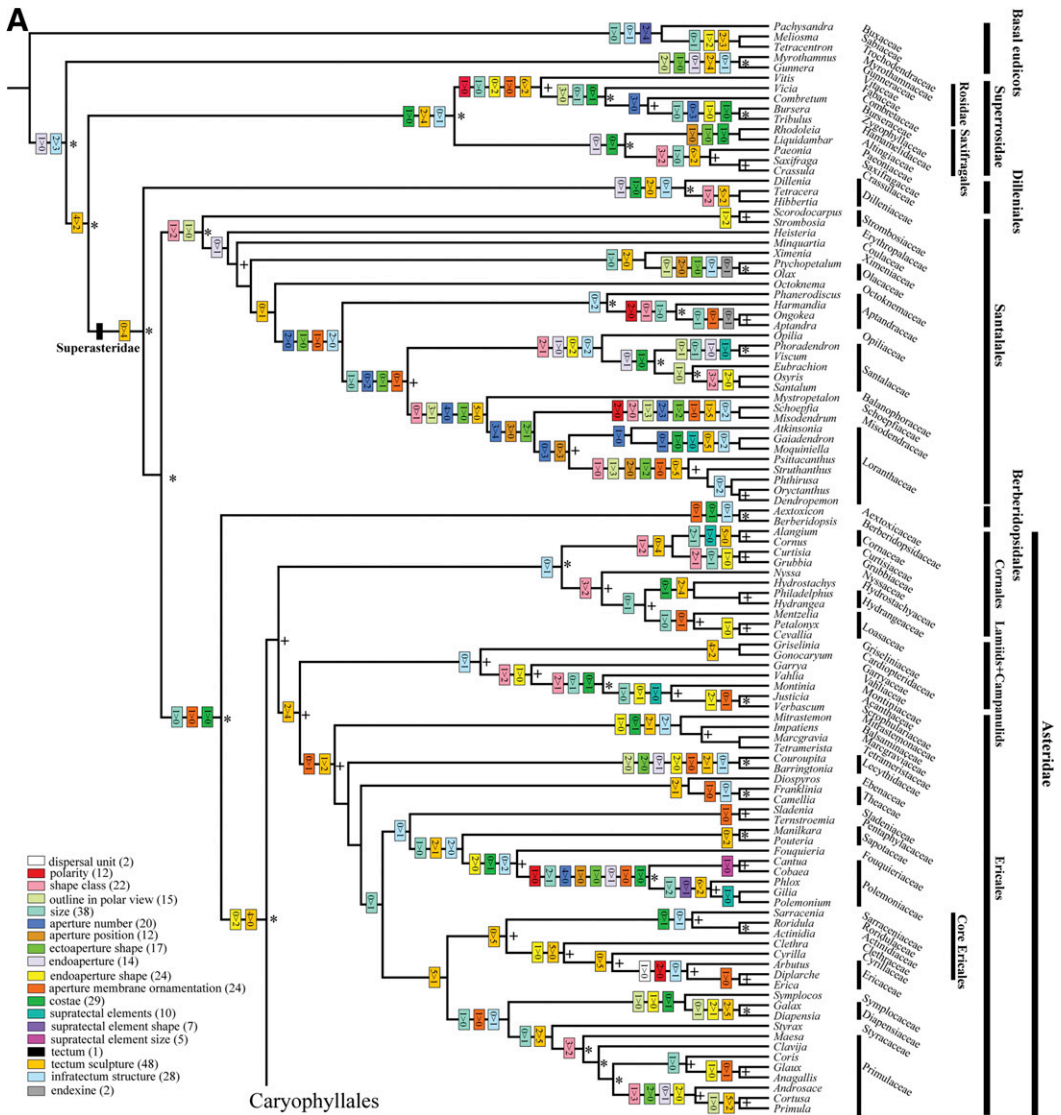


Figure 8. —A, B. State changes (shown in rectangles) inferred for 19 comprehensively coded pollen characters mapped using hierarchical Bayesian (HB) inference on a maximum likelihood (ML) tree with the position of Dilleniales constrained as sister to Superasteridae. The legend shows pollen traits (colored rectangles) and the number of state changes (in parentheses following the character). Bootstrap support values of 100% are indicated by an asterisk (*), and values of 80%–99% by a plus sign (+).

Dilleniales

The monofamilial order Dilleniales, consisting of 10 to 14 genera and ca. 500 species, is recognized as one of the most distinctive lineages of eudicots based on both morphological and molecular evidence (Horn, 2009; Moore et al., 2010, 2011; Soltis et al., 2011). The position of this order in eudicots remains controversial. In this study, we inferred some shared state changes congruent with two of three proposed placements of Dilleniales, i.e., transitions to simple apertures, granular aperture membranes, and columellar infratectum

structure for the affinity of Dilleniales and Caryophyllales (tree A), and to presence of costae, reticulate tectum, and columellar infratectum structure for the affinity of Dilleniales and Superrosidae (tree C). Soltis et al. (2011) pointed out that the close relationship of Dilleniales and Caryophyllales, frequently found in trees with small sampling, may be an artifact of reduced sampling density. This may also explain why Dilleniales was placed as sister to Caryophyllales in our newly generated phylogeny (tree A) for 172 genera—a relatively small sample size compared to recent phylogenies comprising more than 300 taxa

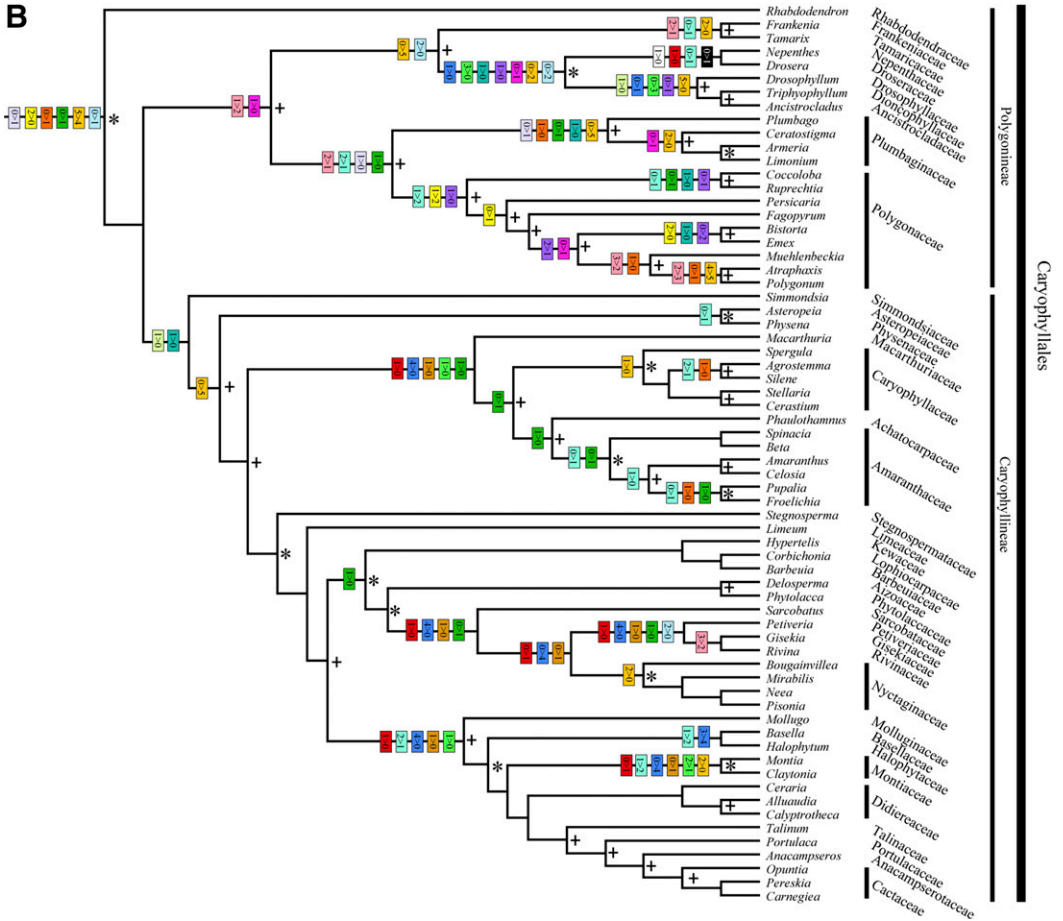


Figure 8. Continued.

(e.g., Soltis et al., 2011). Since palynological characters provide some support for both tree A and tree C, further studies integrating larger morphological and molecular data sets are required to finalize the position of Dilleniales.

Santalales

The monophyletic nature of Santalales has previously been strongly supported using molecular data (Soltis et al., 2000, 2003; Hilu et al., 2003; Moore et al., 2010) and is also supported by one pollen synapomorphy: polygonal outline in polar view (char. 4; DML, CHB, and DHB; all trees). Although recent phylogenetic investigations have greatly improved our understanding of inter- and supra-specific relationships in this order (Nickrent & Franchina, 1990; Vidal-Russell & Nickrent, 2007, 2008; Der & Nickrent, 2008; Malécot & Nickrent, 2008), the exact delimitations of its families remain only partly understood, particularly for Santalaceae s.l. and Olacaceae s.l. In recent molecular phylogenetic studies, these two families have been divided into seven (Santalaceae s. str., Amphorognaceae,

Cervantesiaceae, Comandraceae, Nanodeaceae, Thesiaceae, and Viscaceae; Der & Nickrent, 2008) and eight (Olacaceae s. str., Aptandraceae, Coulaceae, Erythropalaceae, Octoknemaceae, Strombosiaceae, Schoepfiaceae, and Ximeniaceae; Malécot & Nickrent, 2008) family-level groups, respectively, without strong molecular or morphological support for these relationships (summarized in Nickrent et al., 2010). In our study, taxa sampled from Santalaceae s.l. are all nested in a robust clade, which in turn comprises two strongly supported subclades corresponding to Santalaceae s. str. and Viscaceae (Fig. 8). The latter subclade can be distinguished from the former by a transition to presence of supratelical elements (char. 13; all analyses; all trees). As in previous molecular studies, the relationships within Olacaceae s.l. remain weakly supported in our phylogeny (Fig. 8). Correspondingly, we failed to find any palynological synapomorphies to support the segregation of those families previously recognized in Olacaceae s.l., except for Schoepfiaceae, which is characterized by an unusual synapomorphy, four apertures located at the center of four projections producing

Table 2. Summary of state changes inferred for 19 palynological characters at the family level on three topologies for basal Superasteridae. Inferred most probable ancestral states of pollen characters for a given node are shown as X(Y), with X corresponding to the character and Y to the state. Superscripts refer to the methods under which each state was inferred: ¹CFP, comprehensive matrix using Fitch parsimony; ²DFFP, democratic matrix using Fitch parsimony; ³DML, democratic matrix using maximum likelihood; ⁴CHB, comprehensive matrix using hierarchical Bayesian inference; and ⁵DHB, democratic matrix using hierarchical Bayesian inference. Characters and their states follow Table 1. Clades that are unavailable in a given topology are indicated with a dash (-).

Clades	State changes for 19 palynological characters		
	Tree A	Tree B	Tree C
Amaranthaceae	5(0 ⁴⁵), 12(0 ⁴⁵)	5(0 ⁴⁵)	5(0 ⁴⁵), 12(0 ⁴⁵)
Aptandraceae	7(2 ⁴⁵), 8(1 ¹²³⁵), 9(0 ¹²³⁴⁵), 11(1 ⁵)	8(1 ¹²³), 9(0 ¹²³), 18(0 ⁴⁵)	7(2 ⁴), 8(1 ¹²³), 9(0 ¹²³), 18(0 ⁴⁵)
Asteridae	9(1 ²), 11(1 ¹²³), 12(1 ¹³)	11(1 ¹²³), 12(1 ¹³)	11(1 ¹²³), 12(1 ¹²³)
Asteridae, excluding Comales	17(2 ³⁴⁵)	17(2 ³⁴ , 5 ²)	17(2 ³⁴ , 5 ²)
Asteridae–Caryophyllales	10(0 ⁴), 11(1 ⁵), 17(4 ⁴⁵)	10(0 ⁴), 17(4 ⁴⁵)	10(0 ⁴), 17(4 ⁴⁵)
Berberidopsidales	9(0 ³⁵), 10(1 ⁵), 12(0 ⁴⁵), 18(0 ⁴⁵)	9(0 ⁵), 10(1 ⁵), 11(0 ⁴⁵), 12(0 ⁴⁵), 18(0 ⁴⁵)	9(0 ⁵), 10(1 ⁵), 11(0 ⁴⁵), 12(0 ⁴⁵), 18(0 ⁴⁵)
Caryophyllaceae	17(1 ⁴⁵)	17(1 ⁴⁵)	17(1 ⁴⁵)
Caryophyllales	5(1 ⁴⁵), 10(2 ⁴), 13(1 ¹²³), 17(5 ⁴ , 0 ³)	9(0 ³⁴⁵), 10(2 ⁴), 11(0 ⁴⁵), 12(0 ⁴⁵), 13(1 ¹²³), 17(5 ⁴ , 0 ³), 18(0 ⁴⁵)	9(0 ⁴⁵), 10(2 ⁴), 11(0 ⁴⁵), 12(0 ⁴⁵), 13(1 ¹²³), 15(0 ⁴⁵), 17(5 ⁴ , 0 ³), 18(0 ⁴⁵)
Caryophyllineae	4(1 ⁴), 13(1 ¹⁴⁵), 17(0 ⁵)	4(1 ⁴), 13(1 ¹⁴⁵), 17(0 ⁵)	4(1 ⁴), 13(1 ¹⁴⁵), 17(0 ⁵)
Core Ericales	5(0 ¹²³), 17(0 ⁴⁵)	5(0 ¹²³), 17(0 ⁴⁵)	5(0 ¹²³), 17(0 ⁴⁵)
Cornaceae	3(1 ⁵), 4(1 ⁵), 5(2 ⁴⁵), 13(1 ²³⁴⁵), 17(5 ⁴)	3(1 ⁵), 4(1 ⁵), 5(2 ⁴⁵), 13(1 ²³⁴⁵), 17(5 ⁴)	3(1 ⁵), 4(1 ⁵), 5(2 ⁴⁵), 13(1 ²³⁴⁵), 15(0 ⁴), 17(5 ⁴)
Cornales	11(0 ⁴), 18(0 ⁴⁵)	18(0 ⁴⁵)	18(0 ⁴⁵)
Diapensiaceae	3(3 ⁴ , 2 ⁵), 4(0 ⁴⁵), 10(2 ⁴⁵), 11(1 ⁴), 12(0 ⁵), 17(2 ⁴⁵)	3(3 ⁵), 4(0 ⁴⁵), 10(2 ⁴⁵), 12(0 ⁵), 17(2 ⁴⁵)	3(3 ⁴⁵), 4(0 ⁴⁵), 10(2 ⁴⁵), 12(0 ⁵), 17(2 ⁴⁵)
Didiereaceae	none	none	none
Dilleniaceae	5(0 ¹²³), 9(0 ¹²), 11(1 ⁴), 12(1 ³⁴⁵), 17(2 ³⁴⁵)	5(0 ¹²), 9(0 ⁴⁵), 12(1 ³⁴⁵), 17(2 ⁴⁵), 18(0 ⁴⁵)	5(0 ¹²), 12(1 ³)
Dilleniaceae–Caryophyllales	5(0 ⁴⁵), 9(0 ³⁴⁵), 11(0 ⁴⁵), 12(0 ⁴⁵), 17(0 ⁴ , 5 ²), 18(0 ⁴⁵)	–	–
Ericaceae	1(1 ¹²³⁴⁵), 2(2 ¹²³⁴), 18(0 ⁴⁵)	1(1 ¹²³⁴⁵), 2(2 ²³⁴), 18(0 ⁴⁵)	1(1 ¹²³⁴⁵), 2(2 ²³⁴), 18(0 ⁴⁵)
Ericales	11(0 ³⁵), 17(1 ⁴ , 5 ²)	11(0 ³⁴⁵), 17(1 ⁴)	11(0 ³⁴⁵), 17(1 ⁴ , 5 ²)
Hydrangeaceae	5(0 ³), 17(2 ¹²)	5(0 ³), 17(2 ¹²³)	3(2 ⁵), 5(0 ¹²³), 12(0 ⁴⁵), 17(2 ¹²³⁴⁵)
Lamiids–Campanulids	11(0 ⁴), 17(2 ¹²), 18(0 ⁴⁵)	17(2 ¹²⁵), 18(0 ⁴⁵)	17(2 ¹²⁵), 18(0 ⁴⁵)
Lecythidaceae	3(3 ⁴⁵), 4(2 ⁴⁵), 8(2 ⁴⁵), 9(0 ⁴⁵), 10(2 ⁴⁵), 11(1 ⁵), 17(2 ¹²⁴⁵), 18(0 ⁴⁵)	4(2 ⁴⁵), 8(2 ⁴⁵), 9(0 ⁴⁵), 10(2 ⁴⁵), 11(1 ⁴⁵), 17(2 ¹²⁴⁵), 18(0 ⁴⁵)	3(3 ⁴), 4(2 ⁴⁵), 8(2 ⁴⁵), 9(0 ⁴⁵), 10(2 ⁴⁵), 11(1 ⁴⁵), 17(2 ¹²⁴⁵), 18(0 ⁴⁵)
Loasaceae	3(3 ¹²³), 5(1 ⁴⁵), 11(0 ⁵), 17(4 ³)	3(3 ¹²³), 5(1 ⁴⁵), 11(0 ³⁴⁵), 17(4 ³)	3(3 ¹²³), 5(1 ⁴⁵), 11(0 ³⁴⁵), 17(4 ³)
Loranthaceae	3(0 ¹²³), 4(3 ³), 5(1 ¹²³), 6(1 ⁴⁵), 7(0 ⁴⁵), 8(2 ³⁵), 17(0 ⁵)	3(0 ²³), 4(3 ³), 5(1 ¹²³), 6(1 ⁴⁵), 7(0 ⁴⁵), 8(2 ³⁵), 17(5 ²)	3(0 ²³), 4(3 ³), 5(1 ¹²³), 6(0 ⁴⁵), 7(0 ⁴⁵), 8(2 ³), 17(5 ²)
Montiaceae	2(0 ⁴⁵), 5(1 ⁵), 6(1 ⁴⁵), 7(0 ⁴⁵), 8(2 ⁴⁵), 17(2 ⁴⁵)	2(0 ⁴⁵), 5(1 ⁴⁵), 6(1 ⁴⁵), 7(0 ⁴⁵), 8(2 ⁴⁵), 17(2 ⁴⁵)	2(0 ⁴⁵), 5(0 ⁴ , 1 ⁵), 6(1 ⁴⁵), 7(0 ⁴⁵), 8(2 ⁴⁵), 17(2 ⁴⁵)
Nyctaginaceae	17(2 ⁴⁵)	17(2 ⁴⁵)	17(2 ⁴⁵)
Olacaceae	3(1 ¹²³), 4(0 ³⁴⁵), 5(1 ¹²³), 7(2 ⁴⁵), 8(1 ²³⁴), 17(2 ³ , 1 ⁵), 18(0 ⁴⁵), 19(0 ¹²³⁴⁵)	3(1 ¹²³), 4(0 ¹²³⁴⁵), 5(1 ¹²³), 7(2 ⁴⁵), 8(1 ²³⁴), 17(2 ³ , 1 ⁵), 18(0 ⁴⁵), 19(0 ¹²³⁴⁵)	3(1 ¹²³), 4(0 ¹²⁴⁵), 5(1 ¹²³), 7(2 ⁴⁵), 8(1 ²³⁴), 17(2 ³ , 1 ⁵), 18(0 ⁴⁵), 19(0 ¹²³⁴⁵)
Opiliaceae–Loranthaceae	3(1 ⁴), 5(1 ⁴⁵), 9(0 ⁵), 11(0 ⁵), 18(2 ⁴⁵)	5(1 ⁴⁵), 6(0 ⁴⁵), 8(0 ⁴), 9(0 ³), 11(0 ⁴⁵)	3(2 ⁵), 5(1 ⁴⁵), 6(1 ⁴), 8(0 ⁴), 9(0 ³)
Plumbaginaceae	5(2 ¹²³), 11(1 ¹²⁴⁵), 12(0 ⁴⁵), 13(1 ⁴⁵), 17(0 ⁴⁵)	5(2 ¹²³), 9(0 ⁴⁵), 11(1 ¹²³⁴⁵), 12(0 ⁴⁵), 13(1 ⁴⁵), 17(0 ⁴⁵)	5(2 ¹²³), 9(0 ⁴⁵), 11(1 ¹²³⁴⁵), 13(1 ⁴⁵), 17(0 ⁴⁵)

Table 2. Continued.

Clades	State changes for 19 palynological characters		
	Tree A	Tree B	Tree C
Polemoniaceae	2(1 ¹²³⁴⁵), 5(2 ⁴⁵), 6(4 ¹²³⁴⁵), 7(1 ¹²³⁴⁵), 8(1 ¹²³⁴⁵), 9(0 ¹²³⁴⁵), 11(1 ³⁵ , 0 ⁴), 12(1 ⁴⁵)	2(1 ¹²³⁴⁵), 5(2 ⁴⁵), 6(4 ¹²³⁴⁵), 7 (1 ¹²³⁴⁵), 8(1 ¹²³⁴⁵), 9(0 ¹²³⁴⁵), 11(1 ³⁴⁵), 12(1 ⁴⁵)	2(1 ¹²³⁴⁵), 5(2 ⁴⁵), 6(4 ¹²³⁴⁵), 7(1 ¹²³⁴⁵), 8(1 ¹²³⁴⁵), 9(0 ¹²³⁴⁵), 11(1 ³⁴⁵), 12(1 ⁴⁵)
Polygonaceae	5(1 ⁴⁵), 9(1 ³⁴), 10(1 ⁴), 12(1 ²), 14(1 ⁴⁵), 17(5 ²)	5(1 ⁴⁵), 9(1 ²), 10(1 ⁴), 12(1 ²), 14 (1 ⁴ , 0 ²)	5(1 ⁴⁵), 9(1 ²), 10(1 ⁴), 12(1 ³⁴⁵), 14(1 ⁵ , 0 ²), 17(5 ²)
Polygonineae	3(1 ⁴⁵), 17(5 ²), 18(2 ⁴⁵)	3(1 ⁴⁵), 15(1 ⁴), 17(5 ²), 18(2 ²)	3(1 ⁴⁵), 17(5 ²), 18(2 ⁴⁵)
Primulaceae	3(3 ⁴), 5(0 ¹²³), 11(1 ²), 17(2 ³⁵)	3(3 ⁴), 5(0 ¹²³), 11(1 ²), 17(2 ³⁵)	3(3 ⁴), 5(0 ¹²³), 11(1 ²), 17(2 ³⁵)
Santalaceae	4(0 ¹²⁵), 5(1 ³), 9(0 ⁴⁵), 11(0 ⁴)	4(0 ¹²⁵), 5(1 ³), 9(0 ⁴⁵), 12(1 ⁴⁵)	4(0 ¹²⁵), 5(1 ³), 9(0 ⁴⁵), 12(1 ⁴⁵)
Santalales	3(1 ⁴⁵), 4(1 ³⁴⁵), 5(0 ¹²³), 9(1 ²), 10(2 ²)	3(1 ⁴), 4(1 ³⁴⁵), 5(0 ¹²), 10(2 ²)	3(1 ⁴⁵), 4(1 ³⁴⁵), 5(0 ¹²), 10(2 ²)
Sapotaceae	17(0 ⁴⁵)	17(0 ⁴⁵)	17(0 ⁴⁵)
Saxifragales	5(0 ²), 9(0 ⁴⁵)	9(0 ⁴⁵), 12(0 ⁴⁵)	9(0 ⁴⁵), 12(0 ⁴⁵)
Rosids	2(1 ⁴⁵), 5(1 ⁴⁵), 9(1 ¹²), 10(0 ⁴⁵), 11(1 ⁴⁵), 17(6 ²)	2(1 ⁴⁵), 5(1 ³⁴⁵), 9(1 ¹²), 10(0 ⁴⁵), 11(1 ⁴⁵), 17(6 ¹²)	2(1 ⁴⁵), 5(1 ⁴⁵), 9(1 ¹²), 10(0 ⁴⁵), 11(1 ⁴⁵), 17(6 ²)
Strombosiaceae	3(1 ¹²³), 4(1 ¹²), 10(1 ⁴)	3(1 ¹²³), 4(1 ¹²), 10(1 ⁴⁵)	3(1 ¹²³), 4(1 ¹²), 10(1 ⁴⁵)
Superasteridae	9(1 ¹²), 17(0 ⁴⁵)	12(0 ²), 17(0 ⁴⁵)	9(1 ¹²³), 10(1 ²), 17(0 ¹²³⁴⁵)
Superasteridae, excluding Santalales	5(1 ⁴⁵), 10(0 ²), 11(1 ⁴), 12(1 ⁴⁵)	–	5(1 ³⁴⁵), 10(0 ²), 11(1 ⁴⁵), 12(1 ⁴⁵)
Superasteridae, excluding Dilleniales	–	9(1 ¹²³), 10(0 ²), 17(0 ¹²³)	–
Superrosidae	10(2 ²), 12(1 ⁴⁵), 17(2 ⁴⁵), 18(0 ⁴⁵)	10(2 ²), 12(1 ⁴), 17(2 ⁴⁵), 18(0 ⁴⁵)	9(1 ⁴⁵)
Superrosidae–Dilleniales	–	–	9(0 ⁴⁵), 12(1 ²⁴), 17(2 ⁴⁵), 18(0 ⁴⁵)
Superrosidae– Dilleniales–Superasteridae	10(1 ²), 17(4 ⁴)	5(0 ²), 9(1 ²), 10(1 ²)	5(0 ²), 9(1 ²), 12(1 ²)
Theaceae	11(1 ⁴⁵), 18(0 ⁴⁵)	11(1 ⁴⁵), 18(0 ⁴⁵)	11(1 ⁴⁵), 18(0 ⁴⁵)

tetrahedral-shaped grains (char. 7). Additionally, we found some state changes shared across suprageneric groups, including transitions to a reticulate tectum (char. 17: CFP, DFP, and CHB; all trees) for Ximeniaceae–Olacaceae s. str.; polygonal amb (char. 4: CFP and DFP; tree A) for Octoknemaceae–Loranthaceae; porate ectoapertures (char. 8: CFP, DFP, DML, and CHB on tree A and B; all methods on tree C), imperforate tectum (char. 17: CFP, DFP, and CHB; all trees), and columellar infractum structure (char. 18: CHB and DHB on tree A and C; CHB on tree B) for Schoepfiaceae–Misodendraceae.

Caryophyllales

Most phylogenetic studies to date, including this one, have generated a similar topology for Caryophyllales regardless of the sample size and number of genetic markers used (Fay et al., 1997; Applequist & Wallace, 2001; Cuénoud et al., 2002; Hilu et al., 2003; Brockington et al., 2009; Nyffeler & Eggli, 2010). The order is consistently divided into two major subclades, Polygonineae and Caryophyllineae, plus a basally branching

lineage, Rhabdodendraceae. Although we did not find any pollen synapomorphies to distinguish Polygonineae or Rhabdodendraceae, Caryophyllineae is supported by one character state transition: to spinulose supracteal elements (char. 13: CHB and DHB; all trees). In Polygonineae, the positions of Nepenthaceae and Droseraceae are still uncertain (Albert et al., 1992; Fay et al., 1997; Meimberg et al., 2000, 2001; Hilu et al., 2003; Rivadavia et al., 2003; Heubl et al., 2006; Brockington et al., 2009; Soltis et al., 2011). Although a sister relationship between these two families was weakly supported in our phylogeny (BS = 44%), morphologically, they can be united by a remarkable pollen character state: absence of tectum (char. 16: all methods; all trees), with the exception of *Dionaea* Sol. ex J. Ellis in Droseraceae, in which the exine shows the more standard eudicot structure comprising tectum, columellate infractum, and foot layer (Takahashi & Sohma, 1982). A more detailed phylogeny of Droseraceae–Nepenthaceae might be able to determine whether the state seen in *Dionaea* is plesiomorphic, a reversal, or whether there is a

tendency to repeated loss of the tectum in these groups. The atectate state rarely occurs in the early diverging Superasteridae and is apparently confined to these groups plus a few species of *Viscum* L. (Feuer et al.; 1982; Takahashi & Sohma, 1982).

The large clade Caryophyllineae continues to present problems with respect to delimitation of some previously broadly defined families, especially Phytolaccaceae s.l., Portulacaceae s.l., and Molluginaceae s.l. (reviewed in Hernández-Ledesma et al., 2015), though the majority of families are now placed with good support. Genera previously associated with Phytolaccaceae s.l. have been ascribed to many new families, including Stegnospermataceae, Barbeuiaceae, Sarcobataceae, Petiveriaceae, Gisekiaceae, and Rivinaceae. However, we found few pollen character states to distinguish these or to resolve the relationships between them, with the exception of the close relationship between Sarcobataceae and the clade of Petiveriaceae–Gisekiaceae–Rivinaceae, which is supported by shared transitions to apolarity (char. 2: CHB and DHB; all trees), pantoporate, and globally distributed apertures (chars. 6 and 7: CHB and DHB; all trees). The situation is similar for Portulacaceae s.l., now separated into families including Talinaceae and Anacamptserotaceae (Applequist & Wallace, 2001; Nyffeler, 2007; Nyffeler & Eggli, 2010), and Molluginaceae s.l., now separated into families including Macarthuraceae, Limeaceae, Kewaceae, and Lophiocarpaceae (Cuénoud et al., 2002; Schäferhoff et al., 2009; Christenhusz et al., 2014), across both of which palynological characters are remarkably uniform (Fig. 8). Pollen grains in Portulacaceae s.l. are distinguished by their medium size, globally distributed and pantoporate apertures, granular aperture membranes, presence of costae, perforate tectum with microspinules, and columellar infratectum structure, while those of Molluginaceae s.l. differ from Portulacaceae only in tricolpate apertures and absence of costae (Fig. 8).

Cornales and Ericales (Asteridae)

Redefined as a monophyletic group in recent molecular studies (Murrell, 1993; Hempel et al., 1995; Bayer et al., 1996; Savolainen et al., 2000; Anderberg et al., 2002; Bremer et al., 2002; Soltis et al., 2002, 2007; Xiang et al., 2002, 2011; Fan & Xiang, 2003; Geuten et al., 2004; Feng et al., 2009; Bell et al., 2010; Hardy & Cook, 2012), the Asteridae included in our study are united by three shared apomorphies: compound apertures (char. 9: DFP on tree A), smooth aperture membranes (char. 11: CFP, DFP, and DML; all trees), and presence of costae (char. 12: CFP and DML on trees A and B; CFP, DFP, and DML on tree C). Within Cornales, Nyssaceae was previously included in Cornaceae based on morphological evidence (Kubitzki, 2004), but it is now, on the basis of molecular sequence data, segregated from

Cornaceae and instead resolved as sister to the clade comprising Hydrostachyaceae–Hydrangeaceae–Loasaceae (Xiang et al., 2011), which is in agreement with the topology seen in our study. The current position of Nyssaceae as sister to Hydrostachyaceae–Hydrangeaceae–Loasaceae is supported by one pollen state transition: to oblate shape class (char. 3: CHB and DHB; all trees).

Within Ericales, the position of Mitrastemonaceae is not yet finalized. This family has been morphologically and palynologically associated with Rafflesiaceae (Erdtman, 1952, 1986; Cronquist, 1981), but was supported as a member of Ericales in recent molecular phylogenetic studies (Barkman et al., 2004; Hardy & Cook, 2012). Sampling representatives from all families of Ericales, our study resolved Mitrastemonaceae as sister to the Marcgraviaceae–Balsaminaceae–Tetrameristaceae clade with weak support (BS < 80%). However, there is substantial divergence in pollen morphology between Mitrastemonaceae and this sister group. Pollen grains of Mitrastemonaceae are prolate, small, with two or multiple equatorially arranged porate apertures, verrucate supra-ectal elements, and a perforate tectum, while those of Marcgraviaceae–Balsaminaceae–Tetrameristaceae are spheroidal, medium size, with equatorial tricolporate apertures, and a smooth, reticulate tectum (Fig. 8).

PATTERNS OF POLLEN CHARACTER STATE CHANGE

Our optimization analyses consistently suggest that the plesiomorphic states for Superasteridae pollen are monad-dispersed, isopolar, spheroidal, circular in outline, tricolpate grains, with granular aperture membranes, smooth tectum, and endexine. This description fits well with observations of the earliest tricolpate fossil pollen found in the Aptian, except that the latter had a prolate shape (Brenner, 1976; Hickey & Doyle, 1977; Doyle, 1992). These plesiomorphic states presumably gave rise to the more diverse phenotypes observed in extant early diverging Superasteridae taxa, including tetrads, polygonal outlines, pantoaperturate apertures, large size, and striate tecta.

Most of the derived states seen in this study were inferred to have evolved independently multiple times (Fig. 8), reconfirming previous hypotheses of rampant homoplasy in pollen character evolution (by convergent or parallel evolution; Muller, 1979; Doyle, 2005, 2009; Müller & Borsch, 2005; Furness, 2007; Furness et al., 2007; Harder & Johnson, 2008; Verstraete et al., 2011; Doyle & Le Thomas, 2012). However, not all pollen character states appear to show the same level of homoplasy. Taking the CHB analysis on tree B as an example (Fig. 8), some characters, such as pollen grain size and tectum sculpture (chars. 5 and 17, displaying 38 and 48 state transitions, respectively), exhibit more state transitions than others, such as tectum (char. 16),

dispersal unit (char. 1), and endexine (char. 20) (showing one, two, and two state transitions, respectively). This variation also differs from group to group. At suprafamilial level, certain clades, such as Santalales (71 state changes over 28 branches = 2.54 changes per branch; under CHB on tree B) and Polygonineae (52 changes over 19 branches = 2.74 state changes per branch; under CHB on tree B), displayed comparatively higher levels of state change than others, such as Caryophyllineae (48 state transitions over 44 branches = 1.09 state changes per branch; under CHB on tree B). These differences perhaps reflect some aspects of pollen morphological evolution, such as changes in the physical and chemical environmental conditions within which haploid microsporocytes develop into mature pollen (reviewed by Blackmore et al., 2007), pressures imposed by ecological conditions (e.g., reduced exine thickness correlated with hydrophytic-helophytic habitats; Tanaka et al., 2004; Luo et al., 2015), developmental constraints (e.g., the genetic basis for aperture patterns; Shi et al., 2015), and extinction (e.g., loss of particular pollen phenotypes due to extinction of plant lineages; Foote, 1993, 1997; Erwin, 2007).

We now turn to compare the patterns seen in the present grade to those previously observed or proposed in palynological studies from phylogenetic, ecological, and/or ontogenetic perspectives (Wodehouse, 1935; Walker, 1974; Walker & Skvarla, 1975; Muller, 1979; Harley et al., 1986; Pozhidaev, 1998, 2000; Doyle & Endress, 2000; Furness & Rudall, 2004; Furness, 2007; Furness et al., 2007).

Dispersal unit

The distribution of pollen aggregated into tetrads, polyads, or pollinia has been discussed many times in the past, perhaps initiated by the observations of Erdtman (1945) on permanent tetrads. More recently, Harder and Johnson (2008) indicated that aggregated pollen, derived from the monad condition, has evolved independently in angiosperms at least 39 times. In the present grade, aggregated pollen commonly comprises tetrads, which evolved at least six times, i.e., in *Claytonia* L., *Couroupita* Aubl., *Diospyros* L., Droseraceae–Nepenthaceae, Ericaceae, and Hydrostachyaceae. The form in which the tetrad is held together in these lineages appears, however, to differ. For instance, calymmate tetrads are found in Ericaceae (e.g., *Rhododendron* L.; Terzioğlu et al., 2001) while acalymmate tetrads occur in Droseraceae (Takahashi & Sohma, 1982). One particular change in this character, from the plesiomorphic state, monads, to the derived state, tetrads, was consistently inferred across all analyses and all trees on the branches leading to Ericaceae and to Droseraceae–Nepenthaceae (Fig. 8; Table 2). Reversal to monads, however, is less frequent. Two unusual polymorphisms

in dispersal unit are also seen. Firstly, species of *Couroupita* produce both monads and tetrads simultaneously in ring and hood anthers, respectively. This condition is hypothesized to maximize fertilization via insects, with the tetrads being physiologically and functionally specialized to provide food for pollinators and probably sterile (Mori et al., 1980), while the monads act as functional microspores (Ormond et al., 1981; Yarsick et al., 1986). Secondly, some species of Styphelieae produce tetrads in which one to three grains are aborted (e.g., *Brachyloma* Sond.), and in rare cases, these aborted grains are visible and remain adhering to mature fertile ones (e.g., *Acrotriche* R. Br.; Franks & Watson, 1963), analogous to the condition seen more widely in Cyperaceae (Brown & Lemmon, 2000).

Aperture system (polarity, aperture numbers, and position)

Aperture system is a widely discussed feature of pollen biology, with implications for pollen–stigma interactions, germination, and harmomegathy (Muller, 1979; Furness & Rudall, 2004). In the present grade, we observed two main pollen aperture patterns: one with three equatorial colpi or colpori (isopolar grains) occurring in most taxa, the other with multiple and globally distributed pori (apolar grains), restricted to a few families, i.e., Amaranthaceae, Cactaceae, Didiereaceae, Nyctaginaceae, and Polemoniaceae (Fig. 8). The latter type is inferred to have been derived from the former, and to have done so independently at least 10 times across this part of angiosperm phylogeny, including changes within terminal taxa. On internal branches, the frequency of state changes for this character differed among analyses (see Appendix 5; Fig. 8). Using tree B as an example, state changes from tricolpate or tricolporate to pantoporate grains were found on two branches using DML; four using CFP, DFP, and DHB; and six using CHB. The only branch on which this change was consistently inferred in all analyses was the one leading to Polemoniaceae. On the same tree, the reverse transition (from pantoporate to tricolpate or tricolporate apertures) was found on two branches separately leading to Montiaceae and Petiveriaceae–Nyctaginaceae using CHB and DHB, but none using CFP, DFP, and DML.

Aside from the pantoporate state, we also found a few other derived states of aperture system, including the unique and complex aperture system in Droseraceae (Fig. 6A–D), inaperturate grains in three unrelated lineages (*Atkinsonia* F. Muell., *Hydrostachys* Thouars, and Nepenthaceae), and tetra-aperturate grains in *Schoepfia* Schreb. The precise range of aperture systems seen in this grade may be considered to be determined by meiosis (Heslop-Harrison, 1968, 1971; Dover, 1972) and/or as a result of space-filling self-patterning process (Blackmore & Crane, 1988; also reviewed in Blackmore

et al., 2007), but which other processes may constrain the observed patterns remain poorly known.

Surface sculpture

Our optimizations of pollen characters relating to supratectal elements (char. 13) and tectum sculpture (char. 17) indicated that the plesiomorphic states for Superasteridae are a smooth (char. 13: all methods, all trees) and reticulate (char. 17: CFP, DFP, and DML analyses; all trees) or *Croton*-patterned (CHB and DHB analyses; all trees) tectum. These inferences are consistent with the hypothesis proposed by Muller (1979), who suggested that columella-derived structures determined by the pattern of infratectum structure were more concentrated in early diverging taxa than tectum-derived structures (mostly supratectal elements) or combined structures. Within the early diverging Superasteridae, both tectum sculpture and supratectal elements appeared to have changed state more than 20 times, and show particularly high levels of variation at low hierarchical levels. For instance, the pollen grains of *Actinidia* Lindl. exhibit perforate, reticulate, or rugulate tectum sculpture (Dickison et al., 1982; Zhang & Anderberg, 2002), and those of *Alangium* Lam. exhibit reticulate, rugulate, or striato-reticulate sculpture (Reitsma, 1970; Sharma & Gupta, 1996; Li et al., 2010). Even within anthers of *Dillenia* L., pollen grains are found to produce either a reticulate or punctate-reticulate tectum (see Fig. 4G).

Infratectum structure

Our knowledge with respect to the stratification of the pollen grain exine largely comes from developmental studies (Heslop-Harrison, 1968; Gabarayeva & Grigorjeva, 2003; Doyle, 2005, 2009; Gabarayeva & Hemsley, 2006; Gabarayeva et al., 2016). One of the most distinctive layers is the infratectum (char. 18), which lies between the tectum and foot layer. In angiosperms, Doyle and Endress (2000) recognized three infratectum types, granular, intermediate, and columellar, and indicated that the intermediate state may be the plesiomorphic condition for angiosperms as a whole. However, this view was later contradicted by Doyle (2005, 2009) and Lu et al. (2015), who used phylogenetic-based methods to infer that the columellar infratectum structure occurring in basally branching angiosperm groups, such as *Amborella* Baill., Cabombaceae, and *Barclaya* Wall., is plesiomorphic for angiosperms. Here we found all three states in the early diverging Superasteridae, but the plesiomorphic state for this grade was inferred inconsistently across the five analyses, being columellar in CFP, DFP, and DML analyses (all trees) and granular in CHB and DHB analyses (all trees). The columellar state dominates the grade, while the intermediate and granular conditions are restricted to a few lineages: intermediate, for example, in Loranthaceae (e.g., *Atkinsonia*, *Psittacanthus*

Mart., and *Struthanthus* Mart.), Rivinaceae, Sapotaceae (e.g., *Manilkara* Adans.), and Tetrameristaceae, and granular in *Clethra* L., *Cyrilla* Garden, and the grade from Strombosiaceae to Ximeniaceae. Interestingly, we found an imbalance in the frequency of change in different directions among these states. For example, in the CHB analysis on tree B, infratectum structure changed 16 times from granular to columellar, seven times from intermediate to columellar, four times from columellar to intermediate, and once from granular to intermediate.

Shape, outline, and size

Van Campo (1976) and Muller (1979) suggested a general pattern of shape evolution in pollen grains of seed plants, that is, the typically “boat-shaped” pollen coincident with distally monosulcate apertures occurring in gymnosperms and several basal angiosperm taxa evolved toward a more spheroidal shape in eudicots and subsequently became aperturally and structurally modified, leading to oblate or prolate shapes. This hypothesis has been partly confirmed by earlier studies in this series (Lu et al., 2015; Luo et al., 2015; Zhang et al., 2017) and is supported again here. In our group, spheroidal shape was inferred as the plesiomorphic state and gave rise to some derived states, including peroblate, oblate, and prolate, which originated independently at least four, 12, and 22 times, respectively, across the phylogeny. Further detailed information about the pattern of pollen shape evolution can be obtained by estimating the type and number of state transitions. Given the four states of shape coded in this group (char. 3, Table 1), there are a total of 12 putative types of state transition. However, we only inferred a few of them in any analysis, at variable frequencies. For example, we inferred eight transitions using CHB analysis on tree B, with changes from spheroidal or prolate to peroblate shape; oblate or spheroidal to prolate shape was not seen. In the same example, the most frequent state changes inferred were from spheroidal to prolate (six times) or to oblate states (five times), and from oblate to spheroidal (five times).

A circular amb was inferred as the plesiomorphic state for Superasteridae in all analyses and on all trees (Fig. 8, Table 2). In some lineages, this may differentiate into a polygonal (usually triangular; for example, in some Santalales species), lobate (occurring in six separate lineages in the present grade), trilobate (a putative synapomorphy for Loranthaceae, where it is found in *Psittacanthus*, *Moquiniella* Balle, and *Gaiadendron* G. Don), or elliptical state (unique to *Impatiens* L. in our group).

Of all pollen characters studied, size displays one of the highest frequencies of state change (alongside tectum sculpture). The plesiomorphic state for size in Superasteridae was inconsistently inferred, being small using CFP

and DFP but medium using DML, CHB, and DHB (all trees; Fig. 8, Table 2). In either case, large-sized grains (size > 50 μm) are inferred to be derived from smaller ones, a transition that occurred independently at least nine times. Particularly large grains (size > 100 μm) are found in *Cobaea* Cav., *Mirabilis* L., and *Opuntia* Mill. The evolution of this character may be affected by a complex of internal factors, e.g., chromosome numbers (Kapadia & Gould, 1964; Katsiotis & Forsberg, 1995), floral characters (Cruden, 2009; Wang et al., 2016), and pollen grain number (Vonhof & Harder, 1995; Aguilar et al., 2002), and external factors, such as mineral availability (Stanley & Linskens, 1974).

Endexine, costae, and ectoapertures

Endexine is defined as the inner layer of the exine, generated through deposition of sporopollenin on lamellae at the end of the tetrad stage or soon after (Heslop-Harrison, 1968). With few exceptions, endexine is well developed in tricolpate pollen grains (Furness & Rudall, 2006; Furness et al., 2007). Exceptions found in our study included greatly reduced endexine in some typically tricolpate or tricolporate pollen grains, as in *Berberidopsis* Hook. f. (Fig. 4E) and *Diospyros* (Fig. 4O).

Costae are defined as thickenings of the nexine/endexine that follow the outline of the ectoapertures (Punt et al., 2007). Pollen grains of early diverging Superasteridae taxa probably lack this feature (char. 12: CFP, DFP, CHB, and DHB on tree A and B; all analyses on tree C). Costae were gained at least 20 times and subsequently lost three times under CFP, DFP, and DML, or gained 15 times under CHB and 17 times under DHB (on tree B as an example).

Ectoapertures form in the endexine and may involve the development of onci and assembly of pectocellulosic materials (Blackmore & Crane, 1998; Pozhidaev, 1998). Within eudicots, simple apertures have been considered a plesiomorphic state (Blackmore et al., 1995; Zhang et al., 2017), and this is also supported in our study. For the early diverging Superasteridae as a whole, however, simple apertures were inferred as the derived state in all analyses and trees except the DFP analyses on tree A (in which the plesiomorphic state was inferred as uncertain), and may have originated at least six times in this grade.

CODING STRATEGY, OPTIMIZATION METHODS, AND TREE TOPOLOGY

In the first paper in this series, Wortley et al. (2015) empirically tested the influence of three aspects of methodology (optimization method, coding strategy, and tree topology) on optimization of pollen characters and concluded that the impact of these parameters varied partly depending on the level of character

variability relative to any topological discrepancies. A similar pattern was found in the present study (Table 2; Fig. 2; Appendix 5). Of the 19 pollen characters studied, 16 showed variability in optimization results with at least one parameter, and 14 with all three parameters. The remaining three characters, dispersal unit (char. 1), tectum (char. 16), and endexine (char. 19), were relatively robust to changes within all three parameters (see Appendix 5).

The comprehensive coding strategy is expected to result in fewer inferred state changes than the democratic one, because of a greater number of polymorphic data points in the former matrix allowing for state changes not to be required on internal branches but instead assumed to occur within terminal taxa. Our study exemplifies this prediction. For example, CFP analysis results in fewer state changes than DFP on all trees (see Appendix 5). Our study also indicated the limited influence of topological heterogeneity on ancestral state reconstruction. In this study, the instability in topology caused by different placements of Dilleniales resulted in slight differences in optimization at deep nodes (at suprafamilial level), particularly those leading to Dilleniales and its sister clades, but had essentially no effect on inferences at lower taxonomic (generic) levels (see Table 2).

Compared to the above two parameters, optimization method showed a greater impact on the optimization results, and accounts for the majority of variability in state changes inferred for most pollen characters in this study (see Appendix 5). HB methods often lead to larger numbers of state changes than MP or ML, perhaps due to their heavy dependence on the ordering of lineages (determined by models applied in methods, Huelsenbeck & Bollback, 2001; Pagel & Meade, 2006). Aside from this, the difference in results among methods may also be influenced by other factors, such as branch length (Felsenstein, 1978; Graybeal, 1998) and character variability. Here we found no significant difference in the number of state changes on long branches across the three methods (FP, ML, and HB), suggesting a limited effect of long branches. Character variability might be expected to have effects on optimization, perhaps particularly for characters whose values vary in a continuous range, such as shape class (char. 3) and pollen size (char. 5). However, character variability does not completely explain the discrepancies seen between the results of different optimization methods. For example, the two characters aperture position (char. 7) and ectoaperture shape (char. 8) both have four states and similar consistency indices (CI, calculated in Mesquite; CI = 0.367 and 0.375, respectively), but show significantly different levels of variability across methods. For aperture position we inferred three times as many state changes under HB as

under FP or ML, whereas for ectoaperture shape we inferred only twice as many under HB compared to the other methods (see Appendix 5). We suggest that at least some of the variation in state change across methods is due to their variable propensity to site state changes on terminal taxa.

FUTURE PROSPECTS

By integrating comprehensive observations of pollen morphology with recent phylogenetic analyses, this study has explored the distribution patterns of palynological characters across the early diverging Superasteridae and related taxa. The patterns recovered not only indicate the systematic significance of pollen features for diagnosing monophyletic clades and elucidating relationships, but also provide insights into the differentiation of pollen morphology and underlying processes that have shaped the pollen characteristics seen in the grade. We are now more than halfway through our exploration of pollen morphology across angiosperms (for previous studies, see Wortley et al. [2015], Lu et al. [2015], Luo et al. [2015], and Zhang et al. [2017]; also see Fig. 1), which has greatly improved our understanding of pollen character evolution across the phylogeny. The remaining five groups—Malvids–Saxifragales–Vitales, COM (Celastrales, Oxalidales, and Malpighiales)—Zygophyllales, the nitrogen-fixing clade, Lamiales, and Campanulales—will complete this seminal series.

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Appendix 1. Families, species, and GenBank accession numbers for sequences used in phylogenetic analyses, presented in alphabetical order by family.

Families	Species	atpB	rbcL	18S	26S	matK	atp1	nad5	matR
Acanthaceae	<i>Justicia americana</i> (L.) Vahl	AJ236178	L14401	AF107568	AF479165	HQ384510			
Achatocarpaceae	<i>Justicia carnea</i> Lindl.				AY741824				
	<i>Phaulothamnus spinosens</i> A. Gray	HQ843259	M97887	HQ843433	HQ843457	AY514846			
Actinidiaceae	<i>Actinidia arguta</i> (Siebold & Zucc.) Planch. ex Miq.				AY727964		AF420916	GU351330	
	<i>Actinidia chinensis</i> Planch.	AJ235382.2	L01882.2	AF419792		U61324			AY163745
	<i>Actinidia rubricaulis</i> Dunn								
Aextoxicaceae	<i>Aextoxicon punctatum</i> Ruiz & Pav.	AJ235384	X83986	AF206839	AF389239	DQ182342	GU350952	GU351331	GU351143
Aizoaceae	<i>Delosperma deilanthoides</i> S. A. Hammer					HQ620866			
	<i>Delosperma echinatum</i> (Lam.) Schwantes	AJ235452.2	AJ235778	AF206899					
	<i>Delosperma napiforme</i> (N. E. Br.) Schwantes				HQ843446				
Altingiaceae	<i>Liquidambar macrophylla</i> Oerst.		DQ352382						
	<i>Liquidambar styraciflua</i> L.	AF092104		U42553	AF274654	AF133219	EU281013	EF370737	EF370718
Amaranthaceae	<i>Amaranthus caudatus</i> L.		X51964	AH006866		AY514809			
	<i>Amaranthus hypochondriacus</i> L.	AJ235388							
	<i>Beta vulgaris</i> L.	DQ067451	DQ067450	FJ669720		AY514832	47118321	DQ381457	108469695
	<i>Celosia argentea</i> L.	AF209559	AF206747	AF206883	AF479094				
	<i>Celosia cristata</i> L.								
	<i>Celosia trigyna</i> L.								
	<i>Froelichia drummondii</i> Moq.		FR775294			AY514811	GU350985	GU351367	GU351177

Appendix I. Continued.

Families	Species	atpB	rbcL	18S	26S	matK	atp1	nad5	matR
	<i>Pupalia lappacea</i> (L.) Juss.		AY270122			AY514858			
	<i>Spinacia oleracea</i> L.	11497503:51543- 53039	11497503: 53825- 55252 AM235079	L24420	HQ843464	11497503	DQ401287	DQ406883	AY453110
Anacampserotaceae	<i>Anacampseros papyracea</i> E. Mey. ex Fenzl								
	<i>Anacampseros telephiastrum</i> DC.					DQ855862			
Anastrocladaceae	<i>Anastrocladus korupensis</i> D. W. Thomas & Gereau	AF209526	Z97636	AF206846	HQ843441	CQ470536			
	<i>Anastrocladus tectorius</i> (Lour.) Merr.						GU350958	GU351335	GU351148
Aptandraceae	<i>Aptandra tubicina</i> (Poepp.) Benth. ex Miers		DQ790141	DQ790105	DQ790217	DQ790178			
	<i>Harmandia mekongensis</i> Baill.		FJ848842	FJ848849		FJ848846			
	<i>Ongokea gore</i> (Hua) Pierre		DQ790140	DQ790120	DQ790216	DQ790177			DQ110350
	<i>Phanerodiscus capuronii</i> Malécot, G. E. Schatz & Bosser		DQ790143	DQ790122	DQ790219	DQ790180			
Asteropeiaceae	<i>Asteropeta micraster</i> Hallier f.	AF209533	AF206737	AF206857	AF479090	AY042549			AY957449
Balanophoraceae	<i>Mystroptalon thomii</i> Harv.			AY957445					
Balsaminaceae	<i>Impatiens auriculata</i> Wight					AJ429280			AF520117
	<i>Impatiens capensis</i> Meerb.								
	<i>Impatiens pallida</i> Nutt.								
	<i>Impatiens parviflora</i> DC.						AF420933	DQ406952	

Appendix 1. Continued.

Families	Species	atpB	rbcL	18S	26S	matK	atp1	nad5	matR
Barbentaceae	<i>Impatiens repens</i> Moon	AJ235503	Z80197		AF479154				
	<i>Impatiens walleriana</i> Hook. f.			L49285					
Basellaceae	<i>Barbentia madagascariensis</i> Steud.		GQ497673			AY042552	GU350966	GU351344	GU351156
	<i>Basella alba</i> L.	GQ497643	M62564	GQ497567	HQ843442	JQ844148	GU350967	GU351345	AF520150
Berberidopsidaceae	<i>Berberidopsis beckeri</i> (F. Muell.) Veldekamp	AJ235409	AJ235773	AF206866	AF389242	EU002171	DQ401303	DQ406898	DQ401394
	<i>Berberidopsis corallina</i> Hook. f.						AY594462		
Butseraceae	<i>Bursera fagaroides</i> (Kunth) Engl.	AF035899		AF206877	AY17421				
	<i>Bursera inaguensis</i> Britton								
Buxaceae	<i>Bursera simaruba</i> (L.) Sarg.		KJ773325						
	<i>Bursera Jacq. ex L. sp.</i>								
Cactaceae	<i>Pachysandra procumbens</i> Michx. (Engelm.) Britton & Rose	AF092111	AJ235815	AF094533	AF389244	GU266592	GU350975	GU351355	GU351166
	<i>Opuntia dillenii</i> (Ker Gawl.) Haw.		546471556			HM041657	AF197634	DQ406887	AF197784
Cardiopteridaceae	<i>Opuntia microdasys</i> (Lehm.) Pfeiff.	HQ843258		HQ843432	HQ843456	HM041744	GU351076	GU351476	
	<i>Pereskia aculeata</i> Mill.	AF209648	AF206805	AF206986	AF479092	DQ855863	GU351083		GU351274
Cardiopteridaceae	<i>Pereskia grandifolia</i> Haw.								
	<i>Gonocaryum litorale</i> Sleumer	AJ235484	AJ235779	AF206919	AF479201	GQ983654			

Appendix 1. Continued.

Families	Species	atpB	rbcl	18S	26S	matK	atp1	nad5	matR
Caryophyllaceae	<i>Agrostemma githago</i> L.	576303595; 52795-54291	576303595; 55083- 56510				576303595:1941 3452		FJ589241
	<i>Cerastium arcticum</i> Lange			EF127844					
	<i>Cerastium arvense</i> L.	374249929;	JX848446 374249929;	307101719;	307101719;	AY936295 374249929;			HM099797
	<i>Silene latifolia</i> Poir.	51855-53327	54117- 55544	215899- 218029	190407- 193658	1905- 3416			
	<i>Spergula arvensis</i> L.	AF209680	HM850378 AF206823	AF207027	AF479084	JN895158 AY936299	EF547206	GU351519	
	<i>Stellaria media</i> (L.) Vill.						AF420919	GU351376	AF420996
	<i>Stellaria</i> L. sp.		L12609.2	AF419793		AJ429281			
Clethraceae	<i>Clethra alnifolia</i> L.	AJ235438							
	<i>Clethra arborea</i> Aiton								
	<i>Clethra barbinervis</i> Siebold & Zucc.								
	<i>Clethra ferruginea</i> (Ruiz & Pav.) Link ex Spreng.				AY727968				
Combretaceae	<i>Combretum collinum</i> Fresen.					JX495696			
	<i>Combretum indicum</i> (L.) DeFilipps	AJ235576	L01948	AF207004					AF520133
Cornaceae	<i>Alangium chinense</i> Harms		L11209	AF206843	AY260009	FJ64464			AF520122
	<i>Alangium</i> Lam. sp. <i>Cornus chinensis</i> Wangerin	AJ235386							
	<i>Cornus florida</i> L.							DQ407012	
	<i>Cornus officinalis</i> Siebold & Zucc.	AJ236229	L11219	U52033	AF479163				
	<i>Cornus sericea</i> L.								AY725883
Coullaceae	<i>Cornus suecica</i> L. <i>Minquartia guianensis</i> Aubl.		DQ790148	L24396			AF420915 DQ110151		DQ110346

Appendix 1. Continued.

Families	Species	atpB	rbcL	18S	26S	matK	atp1	nad5	matR
Crassulaceae	<i>Crassula helmsii</i> (Kirk) Berger		KT626832				EF370690		
	<i>Crassula marnierana</i> Huber & Jacobsen					AF115601			
	<i>Crassula orbicularis</i> L.								
	<i>Crassula perforata</i> Thunb.	AF274679		AF274604	AF274643				
Curtisiaceae	<i>Curtisia dentata</i> (Burm. f.) C. A. Sm.	JF298838	L11222.2	L16007	AY260012	U96901	GU351003	GU351387	GU351195
Cyrtillaceae	<i>Cyrtilla racemiflora</i> L.	AJ235449.2	L01900.2	U43294	AY727969	AF380080	AF420922	GU351388	AY725892
Diapensiaceae	<i>Diapensia lappionica</i> L.	AF420967	L12612	L49278	AY727986	AJ429283	AF420923		AF421001
	<i>Galax urceolata</i> (Poir.) Brummitt	AY725936	Z80184	L49281	AY727983	L48576	AF420929	GU351410	AF421007
Didiereaceae	<i>Alluaudia ascendens</i> (Drake) Drake				HQ843440		GU350955		AF520129
	<i>Alluaudia humbertii</i> Choux								
	<i>Alluaudia procera</i> (Drake) Drake	GQ497645	M62563			HQ62084			
	<i>Calyptrorhca somalensis</i> Gilg					AY042563	GU350978	GU351358	GU351169
	<i>Ceraria fruticulosa</i> Pearson & Stephens		AY875218			AY875371			
Dilleniaceae	<i>Dillenia alata</i> A. DC.			U38314					
	<i>Dillenia indica</i> L.		L01903			GQ997143	DQ401306	DQ406882	AY163747
	<i>Dillenia retusa</i> Thunb.	AF095732			AF479096				
	<i>Hibbertia cuneiformis</i> Labill.				HQ843451	HQ896421	GU351035	GU351427	GU351224
	<i>Hibbertia volubilis</i> Andrews	AF092120	AF093721	AF094542					
	<i>Tetracera asiatica</i> (Lour.) Hoogland	AJ235622.2	AJ235796	AJ235982	AF479097	AY042665	GU351128	GU351531	AF520094
Dioncophyllaceae	<i>Triphyophyllum peltatum</i> (Hutch. & Dalziel) Airy Shaw	AF209693	Z97637	AF207049	AF479091	AF315940	GU351131	GU351535	GU351319

Appendix I. Continued.

Families	Species	atpB	rbcL	18S	26S	matK	atp1	nad5	matR
Droseraceae	<i>Drosera capensis</i> L.	AY096110	L01909.2	U42532	AF389248				
	<i>Drosera regia</i> Stephens					AF204848	FJ764810	GU351398	GU351201
Drosophyllaceae	<i>Drosophyllum lusitanicum</i> (L.) Link	AY096113	L01907.2	AB072556	HQ843447	AY514860	GU351012	GU351399	GU351202
Ebenaceae	<i>Diospyros lotus</i> L.		Z83133		AY727957				AF520202
	<i>Diospyros multiflora</i> Rehder & E. H. Wilson								
	<i>Diospyros virginiana</i> L.	DQ923957		U43295		AB175002	GU351008	GU351394	
Ericaceae	<i>Arbutus canariensis</i> Veil.	JQ067650.2: 32440-33936	JQ067650.2: 34697- 36124	AF161008	DQ067894	JQ067650: 1915- 3435			
	<i>Arbutus unedo</i> L.		AF419821			AF440418		GU351342	GU351155
	<i>Diplazche multiflora</i> Hook. f. & Thomson								
	<i>Erica carnea</i> L.		AF419823		DQ065768	U61341			
	<i>Erica sicula</i> Guss.	AJ235465					AY725911		
	<i>Rhododendron impeditum</i> Balf. f. & W. W. Sm.								
Erythropalaceae	<i>Heisteria parvifolia</i> Sm.	AJ235492	DQ790163	L24146	DQ790232	DQ790199	GU351032	GU351423	GU351220
Fabaceae	<i>Vicia faba</i> L.							Y12731	
	<i>Vicia sativa</i> L.	827045405:6855- 8507	827045405: 4863- 6290			KJ850242.1 :1833- 3525			
Fouquieriaceae	<i>Vicia villosa</i> Roth		AY725861	KT459214	KT459256	EU628508	AY725902	GU351438	KT459001
	<i>Fouquieria columnaris</i> (Kellogg) Kellogg ex Curran	AJ235501		AF003961	AF479159				GU351234
Frankeniaceae	<i>Frankenia laevis</i> L.		Z97638	AF206914	HQ843448	AY514853			GU351211
Garryaceae	<i>Garrya elliptica</i> Douglas ex Lindl.	AJ235476	L01919.2	U42540	AF47918	AJ429319	GU351022	GU351408	GU351211
	<i>Gisekia africana</i> Kuntze	AJ235479			HQ843449	AY042591	EU280969	HQ384804	AY453095

Appendix 1. Continued.

Families	Species	atpB	rbcL	18S	26S	matK	atp1	nad5	matR
Griselinaceae	<i>Gisekia pharnacoides</i> L.		M97890						
	<i>Griselinia littoralis</i> (Raoul) Raoul							GU351421	
	<i>Griselinia lucida</i> (J. R. Forst. & G. Forst.) G. Forst.	AF209595	L11225	AF206922	AF479197	U58628			
Grubbiaceae	<i>Griselinia racemosa</i> (Phil.) Taub.						EU281012		AY453096
	<i>Grubbia tomentosa</i> Harms	JF298839	Z83141		AY260020	AF323184			
Gunneraceae	<i>Gunnera hamiltonii</i> Kirk ex W. S. Ham.	AF093374	AF093724	AF094546	AF479204	AMB96506	DQ401302	DQ406897	DQ401383
	<i>Halophytum ameghinoi</i> (Speg.) Speg.	GQ497647	AJ403024	GQ497574	HQ848450	AY514852	GU351031	GU351422	GU351219
Hamamelidaceae	<i>Rhodoleia championii</i> Hook. f.	AF274674	DQ352373	AF274599	AF479236	KC737254	EF370703	EF370742	EF370722
	<i>Hydrangea anomala</i> D. Don		AF323202			GU369710			
Hydrangeaceae	<i>Hydrangea arborescens</i> L.	AF093381			AY260032			GU351431	AY453091
	<i>Hydrangea macrophylla</i> (Thunb.) Ser.			U42781					
	<i>Hydrangea seemannii</i> L. Riley						EU280975		
Hydrostachyaceae	<i>Philadelphus tenuis</i> Pursh	AJ26231	L11198	U42782	AF389252	KF202034			
	<i>Hydrostachys imbricata</i> A. Juss.	AJ26230	JF308653	AJ235983	AY260023	FN811268			
Kewaceae	<i>Hypertelis salsoloides</i> (Burch.) Adamson		FN824478			FN825763			
	<i>Barringtonia asiatica</i> (L.) Kurz	AF420962	EU980812	AY289647	AY727949	DQ924095	AY725906		AF420992
Lecythidaceae	<i>Couroupita guianensis</i> Aubl.	AJ236224	AF022134	AJ235993	AY727950		AY725907	GU351382	GU351190
	<i>Lineum africanum</i> L.				HQ848452	JQ844143	GU351051	GU351445	GU351241

Appendix I. Continued.

Families	Species	atpB	rbcL	18S	26S	matK	atp1	nad5	matR
	<i>Lineum arabicum</i>		FN868314						
	Friedrich								
	<i>Lineum</i> L. sp.	AF093385		AF094554		AF503301			
	<i>Cevallia sinuata</i> Lag.		U17873			AY254077			
Loasaceae	<i>Mentzelia decapetala</i> (Pursh) Urb.	JF298868	U17877		AY260030				
	<i>Mentzelia floridana</i> Nutt. ex Torr. & A. Gray						GU351060	GU351457	GU351249
	<i>Mentzelia lindleyi</i> Torr. & A. Gray			AJ235987					
	<i>Petalonyx nitidus</i> S. Watson	AJ236232	U96904	AJ235959	AF479161	AF503296			
Lophiocarpaceae	<i>Corbichonia decumbens</i> (Forssk.) Exell	GQ497648	FN824475	GQ497577		FN825760			
	<i>Atkinsonia ligustrina</i> F. Muell.		EF464526	EF464464	EF464475	DQ787444			
Lorantheaceae	<i>Dendropemon bicolor</i> Krug & Urb.		EU544469	AF039075	EU544365	EU544422			DQ110339
	<i>Gaiadendron punctatum</i> (Ruiz & Pav.) G. Don		L26072	L24143	DQ790209	DQ787445	DQ110147		
	<i>Gaiadendron</i> G. Don sp.								
	<i>Moquinella rubra</i> (A. Spreng.) Balle	GQ497649	AM235021	AF039078	DQ790207	DQ790171		GU351409	
	<i>Oryctanthus cordifolius</i> (C. Presl) Urb.		JQ592409	L24408	EU544389	EU544445			
	<i>Phthirusa pyrifolia</i> (Kunth) Eichler			L24412	EU544392	EU544448			
	<i>Psittacanthus</i> <i>angustifolius</i> Kuijt		L24414						
	<i>Psittacanthus</i> <i>calyculatus</i> (DC.) G. Don				EU544394	EU544450			
	<i>Struthanthus oerstedii</i> (Oliv.) Standl.			L24421	EU544402	EU544457			

Appendix 1. Continued.

Families	Species	atpB	rbL	18S	26S	matK	atp1	nad5	matR
	<i>Struthanthus orbicularis</i> (Kunth) Blume		JQ594621						
Macarthuraceae	<i>Macarthuria australis</i> Hügel ex Endl.		FN824479			323461120: 675-2198			
Marcgraviaceae	<i>Marcgravia rectiflora</i> Triana & Planch.	AJ235529	Z83148		AY727937			GU351453	
Misodendraceae	<i>Marcgravia</i> L. sp. <i>Misodendrum linearifolium</i> DC.		L26074	L24397.2	DQ790211	AJ429289 DQ787438	AF420939		AF421017
Mitrasomonaceae	<i>Mitrasomon kanehirai</i> Yamam.			KC588405					
	<i>Mitrasomon yamanotoi</i> Makino						EU280949		AY739011
Molluginaceae	<i>Mollugo verticillata</i> L.	AF209631	M62566	U42828	AF479088	FN825743	GU351062	GU351460	GU351252
Montiaceae	<i>Claytonia perfoliata</i> Donn ex Willd.		AF132093						
	<i>Claytonia sibirica</i> L.								
	<i>Claytonia virginica</i> L.	HQ843256	JQ933413	HQ843427	HQ843445	JX456286	GU350992	GU351375	GU351184
	<i>Montia fontana</i> L.								
	<i>Montia parvifolia</i> (Moc. ex DC.) Greene					AY042616			
Montiaceae	<i>Montinia caryophyllacea</i> Thunb.	AJ236187	L11194	U42808	AF479175	AJ429359	AY596706	GU351461	HQ384802
Myrothamnaceae	<i>Myrothamnus flabellifolius</i> Welw.	AF093386	AF060707	AF094555	AF479223	AM396507	GU351067	GU351466	GU351258
Nepenthaceae	<i>Nepenthes alata</i> Blanco <i>Nepenthes mirabilis</i> (Lour.) Druce	AJ235542	L01935			AF315891			AF520128
Nyctaginaceae	<i>Nepenthes</i> L. sp. <i>Bougainvillea glabra</i> Choisy	AJ235415	M88340	U42787 AF206873	AF389260 HQ843443	JQ844141	DQ401307 AY818932	DQ406900 GU351351	
	<i>Mirabilis jalapa</i> L. <i>Neea floribunda</i> Poepp. & Endl.	AF209629	M62565 JQ626040	U42788	AF479086	FN868307 JQ626464	EU280980	GU351459	GU351251

Appendix I. Continued.

Families	Species	atpB	rbcL	18S	26S	matK	atp1	nad5	matR
	<i>Pisonia brunoniana</i> Endl.		JQ933356						
	<i>Pisonia rotundata</i> Griseb.					KJ522685			
Nyssaceae	<i>Nyssa ogeche</i> W. Bartram ex Marshall	JF298837	L01937	U52032	AF297545	U96886			
	<i>Nyssa sylvatica</i> Marshall						GU351072	GU351471	GU351263
Octoknemaceae	<i>Octoknema</i> Pierre sp.		DQ790139	DQ790117		DQ790176			
Oleaceae	<i>Oleax aphylla</i> R. Br. <i>Oleax benhamiana</i> Miq. <i>Oleax emirnenis</i> Baker <i>Oleax imbricata</i> Roxb. <i>Psychopetalum</i> <i>olacoides</i> Benth. <i>Psychopetalum</i> <i>petiolatum</i> Oliv.			124405					
	<i>Opilia</i> Roxb. sp.	AJ235550	L26076	U42790	AF479095	AY042621		GU351475	GU351267
Paeoniaceae	<i>Paeonia tenuifolia</i> L.	AF274681	L13187	AF274605	AF274660	AF033609	EF370700	EF370739	EF370720
Pentaphragmaceae	<i>Ternstroemia fragrans</i> (Champ.) Choisy <i>Ternstroemia</i> <i>gymnanthera</i> (Wight & Arn.) Sprague						HQ437919		AY163754
	<i>Ternstroemia stahlii</i> Krug & Urb.	AJ235621	Z80211	AF207038	AY727955	HQ437951			
Physenaceae	<i>Physena</i> <i>madagascariensis</i> Thouars ex Tul.	HQ843260	Y13116	HQ843434	HQ843458		GU351087		
Phytolaccaceae	<i>Petiveria alliacea</i> L. <i>Phytolacca americana</i> L. <i>Phytolacca dioica</i> L.								
	<i>Petiveria alliacea</i> L.	AF09339	AJ402987	U42793	HQ843459	AY042631			
	<i>Phytolacca americana</i> L.		F1860398				DQ401288	DQ406904	DQ401389
Plumbaginaceae	<i>Armeria pubigera</i> Boiss.								
	<i>Armeria pubigera</i> Boiss.					GQ901438			

Appendix 1. Continued.

Families	Species	atpB	rbcl	18S	26S	matK	atp1	nad5	matR
	<i>Armeria splendens</i> Webb		Y16908						
	<i>Ceratostigma minus</i> Stapf ex Prain		Z97641			AY042566			
	<i>Limonium arborescens</i> Kuntze	AF206920	AF206789	AF206953	HQ843453				
	<i>Limonium sinense</i> (Girard) Kuntze					JQ946307			
	<i>Plumbago auriculata</i> Lam.	EU002166	M77701	U42795	AF036492	EU002187			
Polemoniaceae	<i>Cantua buxifolia</i> Juss. ex Lam.	AY725927	AY725864		AY727943		AY725905		AY725889
	<i>Cantua quercifolia</i> Juss.			L49276					
	<i>Cantua volcanica</i> J. M. Porter & Prather					EU628510			
	<i>Cobaea penduliflora</i> (H. Karst.) Hook. f.					EU628511			
	<i>Cobaea scandens</i> Cav.	AJ235440							
	<i>Gilia aggregata</i> (Pursh) Spreng.		Z83143 Z83144	L49277	AY727944		AF420921		AF420999
	<i>Gilia capitata</i> Sims	AJ236220		L24143	AF479155	L34182			
	<i>Phlox divaricata</i> L.				AF148281				
	<i>Phlox glaberrima</i> L.					EU628515			
	<i>Phlox longifolia</i> Nutt.	AJ236221		AJ235996					
	<i>Polemonium caeruleum</i> L.		AF206809	L49294					
	<i>Polemonium</i> <i>pauciflorum</i> S. Watson	AY725925			AY727941	L48602	AF420944		AF421023
	<i>Polemonium reptans</i> L.		L11687						
Polygonaceae	<i>Atraphaxis irtyshensis</i> C. Y. Yang & Y. L. Han		JQ009265						
	<i>Atraphaxis spinosa</i> L.								
	<i>Bistorta amplexicaulis</i> (D. Don) Greene		AF297130			EU840453			

Appendix I. Continued.

Families	Species	atpB	rbcL	18S	26S	matK	atp1	nad5	matR
	<i>Bistorta</i> (L.) Scop. sp.								
	<i>Bistorta vivipara</i> (L.) Delarbre					EU840456		GU351349	GU351161
	<i>Coccoloba mollis</i> Casar.					JQ626541			
	<i>Coccoloba usifera</i> (L.) L.	AF209568		CUU42798		HM851069			
	<i>Emex spinosa</i> (L.) Campd.		HM849974						
	<i>Fagopyrum</i>	189162250:	189162250:						
	<i>crispatifolium</i> J. L.	53772-55268	56062- 57489						
	Liu					JF829975			
	<i>Fagopyrum esculentum</i> Moench subsp.								
	<i>ancestralis</i> Ohnishi					HM851072			
	<i>Muehlenbeckia</i> <i>complexa</i> (A. Cunn.) Meisn.		HM850184						
	<i>Persicaria posumbu</i> (Buch.-Ham. ex D. Don) H. Gross					GU266606			
	<i>Persicaria virginiana</i> (L.) Gaertn.								
	<i>Polygonum aviculare</i> L.								
	<i>Polygonum</i> <i>sachalinense</i> F. Schmidt	AJ235569	AJ235789		AF479085	HM357913			
	<i>Polygonum</i> L. sp.								
	<i>Ruprechtia laxiflora</i> Meisn.		EF437987			FN597637			
Portulacaceae	<i>Portulaca grandiflora</i> Hook.	AF209659	M62568	AF207000	AF479093	EU834751			
	<i>Portulaca oleracea</i> L.								
Primulaceae	<i>Anagallis arvensis</i> L.		HM849771						
	<i>Anagallis foemina</i> Mill.	AJ235390		AF206845	AF479149	HM850731			
	<i>Androsace chamaejasme</i> Wulfen ex Host					DQ378429			
							GU351095	GU351495	GU351284
							DQ401308	DQ406901	DQ401388

Appendix 1. Continued.

Families	Species	atpB	rbcL	18S	26S	matK	atp1	nad5	matR
	<i>Androsace sarmentosa</i> Wall.								
	<i>Androsace spinulifera</i> R.	AJ235392	AJ235772	AF206847	AF479150		GU350959	GU351336	GU351149
	<i>Clavija costaricana</i> Knuth					JQ588865			
	<i>Clavija domingensis</i> Urb. & Ekman						AF420918		AF420995
	<i>Clavija eggersiana</i> Mez	AJ235437	L12608	AJ235998				GU351374	
	<i>Clavija integrifolia</i> Mart. ex Miq.								
	<i>Clavija lancifolia</i> Desf.				AY727962				
	<i>Coris monepaliensis</i> L.	AF213770	U96660			DQ378421			
	<i>Cortusa turkestanica</i> Losinsk.	AF213769	AF213803						
	<i>Glaux maritima</i> L.		AF213821		AY727959	JN895983		GU351450	
	<i>Maesa japonica</i> (Thunb.) Moritzi & Zoll.								
	<i>Maesa myrsinoides</i> H. Lév.	AJ235525	Z80203						
	<i>Maesa tenera</i> Mez					AJ429288	AF420937		AF421015
	<i>Primula cortusoides</i> L.	AF213786	AF213800			DQ378412			
	<i>Primula elatior</i> Hill				AY727960				
	<i>Primula</i> L. sp.			L49295					
Rhabdodendraceae	<i>Rhabdodendron</i> <i>amazonicum</i> (Spruce ex Benth.) Huber	AJ235578	JQ625835	AF207007	AF479087	JQ844136		GU351502	AF520114 GU351291
Rivinaeae	<i>Rivina humilis</i> L.	HQ843261	M62569	HQ843438	HQ843461	AY514850	GU351103	GU351503	GU351292 JQ619025
Roridulaceae	<i>Roridula dentata</i> L.								
	<i>Roridula gorgonias</i> Planch.	AJ236180	L01950	AF207010	AY727965	AJ429294	AY725910		
Sabiaceae	<i>Meliosma squamulata</i> Hance						AF197656	DQ406896	DQ007426

Appendix I. Continued.

Families	Species	atpB	rbcL	18S	26S	matK	atp1	nad5	matR
Santalaceae	<i>Meliosma veitchiorum</i> Hemsl.	AF209626	AF206793	AF206961	AF389271	F1626530			
	<i>Eubrachion ambiguum</i> (Hook. & Arn.) Engl.	AF209583	L26071	L24141	AF389273	EF464498			
	<i>Osyris lanceolata</i> Hochst. & Steud.	AF209641	L11196	U42803	AF389274	EF464506			
	<i>Osyris wightiana</i> Wall. ex Wight								AF520155
	<i>Phoradendron</i> <i>serotinum</i> (Raf.) M. C. Johnst.	GQ997715	L11199.2	X16607	AF181787	GQ997723			
Sapotaceae	<i>Santalum album</i> L.	AJ235592	L26077	L24416	AY957453	AY042650	GU351108	GU351508	JQ613250
	<i>Viscum album</i> L.	AF209695	L26078	U42821	AF389275	EF464496			
	<i>Manilkara zapota</i> (L.) P. Royen	AJ235528	EU980807	U43080	AF479160	AJ429295	AF420938	GU351452	AF421016
	<i>Pouteria campechiana</i> (Kunth) Baehni				AY727948				
Sarcobataceae	<i>Pouteria gongrippii</i> Eyma		JQ626231			JQ626486			
	<i>Pouteria macrantha</i> (Merr.) Baehni	AJ235570							
	<i>Pouteria macropoda</i> (H. J. Lam) Baehni			GU476467			AF420945		AF421024
	<i>Pouteria obovata</i> (R. Br.) Baehni								
Sarraceniaceae	<i>Sarcobatus vermiculatus</i> (Hook.) Torr.	GQ497660	AF132088	GQ497586	HQ843462	AY042652	GU351109	GU351509	GU351298
	<i>Sarracenia alabamensis</i> Case & R. B. Case								JQ218276
Saxifragaceae	<i>Sarracenia flava</i> L.	AJ235594	L01952		JQ519380	JQ619000	AF420947	GU351510	
	<i>Sarracenia purpurea</i> L.		U42804						
	<i>Saxifraga mertensiana</i> Bong.	AF209669	U06216	U42811	AF479224	L34142			
	<i>Saxifraga samentosa</i> L. f.						EF370705	EF370744	EF370724

Appendix 1. Continued.

Families	Species	atpB	rbcL	18S	26S	matK	atp1	nad5	matR
Schoepfiaceae	<i>Schoepfia jasminodora</i> Siebold & Zucc.	AF209671	L11205	L24418	AF389261	DQ787447		GU351512	JQ613252
	<i>Schoepfia schreberi</i> J. F. Gmel.								
Scrophulariaceae	<i>Schoepfia</i> Schreb. sp. <i>Verbascum thapsus</i> L.	AJ236177	L36452	AF161011	AF479168	AF052002	EU280991		
Simmondsiaceae	<i>Simmondsia chinensis</i> (Link) C. K. Schneid.	AF093401	AF093732	AF094562	HQ843463	AY514854	DQ401309	DQ406903	DQ401397
Sladeniaceae	<i>Sladenia celastriifolia</i> Kurz	AF420988	AF320784	AF320782		AJ429297	AF420959		
Stegnospermataceae	<i>Stegnosperma cubense</i> A. Rich.					JQ588612			
	<i>Stegnosperma halimifolium</i> Benth.		M62571		HQ843465		GU351119	GU351518	GU351307
Strombosiaceae	<i>Scorodocarpus borneensis</i> (Baill.) Becc.		DQ790159	U59934	DQ790228	DQ790195			
	<i>Strombosia philippinensis</i> S. Vidal								
	<i>Strombosia pustulata</i> Oliv.		DQ790157	AF039079	DQ790226	DQ790193			DQ110360
Styracaceae	<i>Styrax americanus</i> Lam. <i>Styrax grandiflorus</i> Griff.								
	<i>Styrax japonicus</i> Siebold & Zucc.	AJ235615	L12623	L49296	AF479156			GU351523	AF520205
	<i>Styrax officinalis</i> L.					AJ429300	AF420950		
Symplocaceae	<i>Symplocos paniculata</i> Miq.			U43297		AF440433			
	<i>Symplocos setchuensis</i> Brand								AF520111
	<i>Symplocos zeyphoides</i> Stapf	AY725934	AY725865		AY727978		AY725913		

Appendix I. Continued.

Families	Species	atpB	rbcL	18S	26S	matK	atp1	nad5	matR
Talinaceae	<i>Talinum paniculatum</i> (Jacq.) Gaertn.	HQ843263	AY875214	HQ843439	HQ843466	AY015274	GU351124	GU351526	GU351313
Tamaricaceae	<i>Tamarix parviflora</i> DC. <i>Tamarix pentandra</i> Pall.	AF209684	Z97650	AF207033	AF479083	JQ844134	EU280995		AF520098
Tetrameristaceae	<i>Tamarix</i> L. sp.							GU351527	
Theaceae	<i>Tetramerista</i> Miq. sp. <i>Camellia japonica</i> L. <i>Camellia sinensis</i> (L.) Kuntze <i>Franklinia alatamaha</i> Marshall	AJ235623	Z80199	AF207039	AF479153	AJ429304	AF420958	GU351532 DQ406870	GU351316
	<i>Franklinia alatamaha</i> Marshall	HM100289	AF380037	AB120309	AY727975	AF380077	AF420952		AF421034
Trochodendraceae	<i>Tetracentron sinense</i> Oliv.	AF093422	L12668	U42814	AF274670	AM396504	AF197647	DQ406874	AF197791
Vahliaaceae	<i>Vahlia capensis</i> (L. f.) Thunb.	AJ236217	L11208	U42813	AF479182	AJ429316	HQ385207	HQ384806	HQ384792
Vitaceae	<i>Vitis aestivalis</i> Michx. <i>Vitis riparia</i> Michx. <i>Vitis rupestris</i> Scheele <i>Vitis</i> L. sp. <i>Vitis vinifera</i> L. <i>Vitis vulpina</i> L.				XM002276993	AF542593			
	<i>Ximenea americana</i> L. <i>Tribulus terrestris</i> L.	AM083947 GQ997862 GQ220747	KJ773985 DQ790149 DQ267165	AF321272 I24428	DQ790220	GQ997871 KF224985	EU280996 GU351141	DQ406881 GU351547	FMI 79380 DQ110367 AF520097

Appendix 2. Literature citations for palynological data and specimen information for light (LM), scanning (SEM), and transmission electron microscope (TEM) observations of pollen grains. APSA, Australasian Pollen & Spore Atlas (<http://apsa.anu.edu.au/>); PalDat, Palynological Database (<https://www.paldat.org/>). Species for which pollen was examined using LM and/or SEM and/or TEM are marked with an asterisk (*).

Classification	Total genera per family (total genera sampled)	Genera used in phylogeny and species for which LM, SEM, and TEM were obtained	References for palynological data and species vouchers for LM, SEM, and TEM
BASAL SUPERASTERIDAE			
BERBERIDOPSISDALES			
Aextoxicaceae	1(1)	<i>Aextoxicon</i> Ruiz & Pav.	Erdtman, 1952
Berberidopsidaceae	2(1)	<i>Berberidopsis</i> Hook. f. * <i>Berberidopsis corallina</i> Hook. f. (Fig. 4A–E)	Keating, 1973 Chile, <i>M. F. Gardner et al.</i> 562 (E)
CARYOPHYLLALES			
Achatocarpaceae	2(1)	<i>Phaulothamnus</i> A. Gray	Bortenschlager et al., 1972; Skvarla & Nowicke, 1982
Aizoaceae	123(1)	<i>Delosperma</i> N. E. Br.	PalDat; Nowicke & Skvarla, 1979
Amaranthaceae	174(6)	<i>Amaranthus</i> L. <i>Beta</i> L. <i>Celostia</i> L.	PalDat; Skvarla & Nowicke, 1976 Skvarla & Nowicke, 1976; Nowicke & Skvarla, 1979 Nowicke, 1975; Zandonella & Lecocq, 1977; Chaturvedi et al., 1993; Borsch, 1998
Anacampserotaceae	1(1)	<i>Froelichia</i> Moench	Nowicke, 1975; Zandonella & Lecocq, 1977
Ancistrocladaceae	1(1)	<i>Pupalia</i> Juss. <i>Spinacia</i> L.	Nowicke, 1975; Zandonella & Lecocq, 1977 Olvera et al., 2006
Asteropeiaceae	1(1)	<i>Anacampseros</i> L.	Nyananyo, 1992
Barbeteaceae	1(1)	<i>Ancistrocladus</i> Wall. <i>Asteropeia</i> Thouars <i>Barbeteia</i> Thouars	Erdtman, 1986 Erdtman, 1952; Morton et al., 1997 Nowicke, 1968, 1994; Erdtman, 1986
Basellaceae	4(1)	<i>Bosella</i> L.	Nowicke, 1975, 1994, 1996; Skvarla & Nowicke, 1976; Nowicke & Skvarla, 1979
Cactaceae	131(3)	* <i>Basella alba</i> L. (Fig. 3K–O) <i>Carnegiea</i> Britton & Rose <i>Opuntia</i> Mill. <i>Pereskia</i> Mill. <i>Agrostemma</i> L. <i>Cerastium</i> L. <i>Silene</i> L. <i>Spergula</i> L. <i>Stellaria</i> L.	Vietnam, <i>China – Vietnam Expedition 1735</i> (KUN) Kurtz, 1963; Nowicke, 1975, 1994 PalDat; Kurtz, 1963; Kozar, 1974; Skvarla & Nowicke, 1976; Nowicke & Skvarla, 1979; Garralla & Cuadrado, 2007 PalDat; Nowicke, 1994; Santos et al., 1997 Nowicke, 1994; Punt & Hoen, 1995 Nowicke, 1975, 1994; Al-Eisawi, 1989 Nowicke, 1975, 1994; Punt & Hoen, 1995 Nowicke, 1975; Al-Eisawi, 1989; Punt & Hoen, 1995; Perveen & Qaiser, 2006 Iwarsson, 1977; Al-Eisawi, 1989; Punt & Hoen, 1995; Wei, 2003

Appendix 2. Continued.

Classification	Total genera per family (total genera sampled)	Genera used in phylogeny and species for which LM, SEM, and TEM were obtained	References for palynological data and species vouchers for LM, SEM, and TEM
Didieraceae	7(3)	<i>Alluauadia</i> (Drake) Drake <i>Calypthrotheca</i> Gilg <i>Ceraria</i> Pearson & Stephens <i>Triphyophyllum</i> Airy Shaw <i>Drosera</i> L. <i>*Drosera peltata</i> Thunb. (Fig. 5A–D) <i>Drosophyllum</i> Link <i>Frankenia</i> L. <i>Gisekia</i> L.	Erdtman, 1948; Straka, 1965; Nowicke, 1975; Skvarla & Nowicke, 1976; Nowicke & Skvarla, 1979; Straka & Friedrich, 1983; Nowicke, 1996 Nyananyo, 1992 Nowicke & Skvarla, 1979; Nyananyo, 1992 Erdtman, 1952 SEM; Chanda, 1965; Takahashi & Sohma, 1982; Punt et al., 2003 China, Hong Kong, <i>Hu 9991</i> (CAS) Takahashi & Sohma, 1982 Erdtman, 1952; Perveen & Qaiser, 1999 Behnke, 1977; Nowicke & Skvarla, 1979; Nowicke, 1994; Perveen & Qaiser, 2000a
Halophytaceae	1(1)	<i>Halophytum</i> Speng.	Erdtman, 1986; Skvarla & Nowicke, 1976
Kewaceae	1(1)	<i>Hypertelis</i> E. Mey. ex Fenzl	Nowicke, 1975
Limeaceae	1(1)	<i>Lineum</i> L.	Mitrou, 1971; Nowicke, 1975; Behnke, 1977; Perveen, 1993; Perveen & Qaiser, 2000a
Lophiocarpaceae	2(1)	<i>Corbichonia</i> Scop.	Perveen & Qaiser, 2000a; Osman & Hassan, 2015
Macarthuraceae	1(1)	<i>Macarthuria</i> Hügel ex Endl.	Mitrou, 1971; Nowicke, 1975; Behnke et al., 1983
Molluginaceae	14(1)	<i>Mollugo</i> L.	Mitrou, 1971; Nowicke, 1975; Behnke et al., 1983; Perveen & Qaiser, 2000b
Montiaceae	14(2)	<i>Claytonia</i> L. <i>Montia</i> L.	PalDat; Nilsson, 1967; Nowicke, 1975, 1994; Nowicke & Skvarla, 1979 Nyananyo, 1992
Nepenthaceae	1(1)	<i>Nepenthes</i> L.	Basak & Subramanyam, 1966; Takahashi & Sohma, 1982; Furness, 2007
Nyctaginaceae	38(4)	<i>*Nepenthes mirabilis</i> (Lour.) Druce (Fig. 6E–H) <i>Bougainvillea</i> Comm. ex Juss. <i>Mirabilis</i> L. <i>*Mirabilis himalaica</i> (Edgew.) Heimerl (Fig. 6A–D) <i>Neea</i> Ruiz & Pav. <i>Pisonia</i> L.	China, Hong Kong, <i>Li 21903</i> (KUN) PalDat; Nowicke, 1970; Skvarla & Nowicke, 1976 Nowicke, 1970, 1975, 1994; Wei, 2003 China, <i>Sun et al. SunH-07</i> (KUN) Nowicke, 1975; Reyes-Salas & Martínez-Hernández, 1982 Nowicke, 1975, 1994; Reyes-Salas & Martínez-Hernández, 1982 Nowicke, 1968, 1975, 1994
Petiveriaceae	5(1)	<i>Petiveria</i> L.	Dickison & Miller, 1993; Morton et al., 1997
Physenaceae	1(1)	<i>Physena</i> Noronha ex Thouars	PalDat; Skvarla & Nowicke, 1976; Nowicke & Skvarla, 1979; Wei, 2003
Phytolaccaceae	10(1)	<i>Phytolacca</i> L.	Nowicke & Skvarla, 1977; Turner & Blackmore, 1984
Plumbaginaceae	25(4)	<i>Armeria</i> Willd. <i>Ceratostigma</i> Bunge	Nowicke & Skvarla, 1977, 1979; Turner & Blackmore, 1984

Appendix 2. Continued.

Classification	Total genera per family (total genera sampled)	Genera used in phylogeny and species for which LM, SEM, and TEM were obtained	References for palynological data and species vouchers for LM, SEM, and TEM
		<i>Limonium</i> Mill.	PalDat; Nowicke & Skvarla, 1977; Turner & Blackmore, 1984; Perveen & Qaiser, 2004
		<i>Plumbago</i> L.	PalDat; Erdtman, 1952; Nowicke & Skvarla, 1977, 1979; Weber, 1981; Perveen & Qaiser, 2004
Polygonaceae	49(9)	<i>Atraphaxis</i> L. <i>Bistorta</i> (L.) Scop. <i>Coccoloba</i> P. Browne <i>Emex</i> Neck. ex Campd. <i>Fagopyrum</i> Mill. <i>Muehlenbeckia</i> Meisn. <i>Persicaria</i> Mill. <i>Polygonum</i> L.	Nowicke & Skvarla, 1977; Hong, 1995 Zhou et al., 1999, 2000 Nowicke & Skvarla, 1977; Sánchez-Dzib et al., 2009 Nowicke & Skvarla, 1977 Nowicke & Skvarla, 1977; Van Leeuwen et al., 1988 Nowicke & Skvarla, 1977 Nowicke & Skvarla, 1977; Yasmin et al., 2010 PalDat; Hedberg, 1946; Nowicke & Skvarla, 1977, 1979; Van Leeuwen et al., 1988; Ge, 1993; Wang & Feng, 1994; Zhou et al., 2000, 2002; Wei, 2003; Hong et al., 2005; Yasmin et al., 2010
		<i>Ruprechtia</i> C. A. Mey.	Nowicke & Skvarla, 1977
Portulacaceae	1(1)	<i>Portulaca</i> L.	PalDat; Nowicke & Skvarla, 1979; Nyananyo, 1992; Perveen, 1993
Riviniaceae	1(1)	<i>Rivina</i> L.	Nowicke, 1968; Bortenschlager, 1973
Rhabdodendraaceae	1(1)	<i>Rhabdodendron</i> Gilg & Pilg.	Prance, 1972; Behnke, 1977
Sarcobataceae	1(1)	<i>Sarcobatus</i> Nees	Nowicke, 1975, 1994
Simmondsiaceae	1(1)	<i>Simmondsia</i> Nutt.	Nowicke & Skvarla, 1984
Stegnospermataceae	1(1)	<i>Stegnosperma</i> Benth.	Erdtman, 1952; Skvarla & Nowicke, 1976
Talinaceae	2(1)	<i>Talinum</i> Adans.	Nyananyo, 1992; Nowicke, 1996
Tamaricaceae	5(1)	<i>Tamarix</i> L.	PalDat; Baum et al., 1970, 1971; Xi, 1988; Wei, 2003; Qaiser & Perveen, 2004
CORNIALES			
Comaceae	2(2)	<i>Alangium</i> Lam. <i>Cornus</i> L.	Chao, 1954; Straka, 1954; Reitsma, 1970; Sharma & Gupta, 1996; Perveen & Qaiser, 2002a; Li et al., 2010 PalDat; Chao, 1954; Straka, 1954; Ferguson, 1977; Ludlow-Wiechers & Martínez-Hernández, 1979; Wang & Chen, 1990; Perveen & Qaiser, 2002a
Curtisiaceae	1(1)	<i>Curtisia</i> Aiton	Ferguson, 1977
Grubbiaceae	1(1)	<i>Grubbia</i> P. J. Bergius	Erdtman, 1986
Hydrangeaceae	16(2)	<i>Hydrangea</i> L. <i>Philadelphus</i> L. <i>Hydrostachys</i> Thouars	Hao & Hu, 1996 PalDat; Verbeek-Reuvers, 1977; Hao & Hu, 1996 Erdtman, 1952; Straka, 1988

Appendix 2. Continued.

Classification	Total genera per family (total genera sampled)	Genera used in phylogeny and species for which LM, SEM, and TEM were obtained	References for palynological data and species vouchers for LM, SEM, and TEM
Loasaceae	15(3)	<i>Cevallia</i> Lag. <i>Mentzelia</i> L. * <i>Mentzelia involucreata</i> S. Watson (Fig. 5I-L) <i>Petalonyx</i> A. Gray <i>Nyssa</i> L.	Poston & Nowicke, 1993 Poston & Nowicke, 1993 U.S.A., <i>Woghtum</i> 747 (KUN) Poston & Nowicke, 1993 Chao, 1954; Sohma, 1963, 1967; Erdtman, 1966, 1986
Nyssaceae	1(1)		Erdtman, 1952; Dickison et al., 1982
DILLENALES			
Dilleniaceae	11(3)	<i>Dillenia</i> L. * <i>Dillenia pentagyna</i> Roxb. (Fig. 4F-J; China, <i>Feng</i> 20869)	China (KUN-0671740); China, <i>9213</i> (KUN-0753122); China, <i>Feng</i> 20869 (KUN)
		<i>Hibbertia</i> Andrews <i>Tetracera</i> L.	Dickison et al., 1982 Dickison et al., 1982
ERICALES			
Actinidiaceae	3(1)	<i>Actinidia</i> Lindl. * <i>Actinidia arguta</i> (Siebold & Zucc.) Planch. ex Miq. (Fig. 3A-E)	Dickison et al., 1982; Zhang & Anderberg, 2002; Li et al., 2010 China, <i>Li et al.</i> 1747 (KUN)
Balsaminaceae	2(1)	<i>Impatiens</i> L. * <i>Impatiens delavayi</i> Franch. (Fig. 5E-H)	PalDat; Bhaskar & Razi, 1979; Perveen & Qaiser, 2001; Janssens et al., 2005 China, <i>Xianggelila Expedition 178</i> (KUN)
Clethraceae	2(1)	<i>Clethra</i> L.	Erdtman, 1986; Zhang & Anderberg, 2002; Lu et al., 2005; Li et al., 2010
Cyrillaceae	2(1)	<i>Cyrilla</i> Garden	Zhang & Anderberg, 2002
Diapensiaceae	6(2)	<i>Diapensia</i> L. <i>Galax</i> Sims <i>Diospyros</i> L.	Erdtman, 1952; Xi & Tang, 1990 Xi & Tang, 1990 Sharma & Gupta, 1979; Wallnöfer, 2001; Kodela, 2006; Geeraerts et al., 2009; Li et al., 2010
Ebenaceae	4(1)		
		* <i>Diospyros kaki</i> Thunb. (Fig. 4K-O) <i>Arbutus</i> L. * <i>Arbutus menziesii</i> Pursh (Fig. 3F-J) <i>Diplarche</i> Hook. F. & Thomson <i>Erica</i> L.	China, <i>Yi</i> 378 (KUN) Oldfield, 1959; Mateus, 1989; Sarwar et al., 2008 U.S.A., <i>De Nevers</i> 699 (KUN) Xi & Tang, 1990 Mateus, 1989
Ericaceae	149(3)		
		<i>Fouquieria</i> Kunth <i>Barringtonia</i> J. R. Forst. & G. Forst. <i>Couropitpa</i> Aubl. <i>Maregravia</i> L. <i>Mitrasomon</i> Makino <i>Ternstroemia</i> Mutis ex L. f.	PalDat; Henrickson, 1973 Muller, 1972, 1973; Tsou, 1994 Mori et al., 1980; Tsou, 1994 Lens et al., 2005 Erdtman, 1952 Li et al., 2010; Xu et al., 2011
Fouquieriaceae	1(1)		
Lecythidaceae	25(2)		
Maregraviaceae	5(1)		
Mitrasomonaceae	1(1)		
Pentaplylaceae	14(1)		

Appendix 2. Continued.

Classification	Total genera per family (total genera sampled)	Genera used in phylogeny and species for which LM, SEM, and TEM were obtained	References for palynological data and species vouchers for LM, SEM, and TEM
Polemoniaceae	20(5)	<i>Cantua</i> Juss. ex Lam. <i>Cobaea</i> Cav. <i>Gilia</i> Ruiz & Pav. <i>Phlox</i> L. <i>Polemonium</i> L. * <i>Polemonium</i> L. sp. (Fig. 7E–H) <i>Anagallis</i> L. <i>Androsace</i> L. <i>Clanija</i> Ruiz & Pav. <i>Coris</i> L. <i>Cortusa</i> L. <i>Glaux</i> L. <i>Maesa</i> Forssk. <i>Primula</i> L. <i>Roridula</i> Burm. f. ex L. <i>Manilkara</i> Adans. <i>Pouteria</i> Aubl. <i>Sarracenia</i> L. <i>Sladenia</i> Kurz <i>Syrax</i> L. <i>Symplocos</i> Jacq. <i>Tetramerista</i> Miq. <i>Camellia</i> L. <i>Franklinia</i> W. Bartram ex Marshall	Stuchlik, 1967a, 1967b; Taylor & Levin, 1975; Monfils & Prather, 2004 Stuchlik, 1967a, 1967b; Taylor & Levin, 1975; Ludlow-Wiechers, 1982 Stuchlik, 1967a, 1967b; Taylor & Levin, 1975 Stuchlik, 1967a, 1967b; Taylor & Levin, 1975 Stuchlik, 1967a, 1967b; Taylor & Levin, 1975 China, <i>Zhu et al.</i> 1347 (KUN) Punt et al., 1974; Nowicke & Skvarla, 1979 PalDat; Punt et al., 1974 Erdtman, 1952 Nowicke & Skvarla, 1977, 1979; Carrion et al., 1993 Nowicke & Skvarla, 1977, 1979; Nasir, 1983 Punt et al., 1974; Nowicke & Skvarla, 1977, 1979 PalDat; Erdtman, 1952; Kubitzki, 2004 PalDat; Nowicke & Skvarla, 1977, 1979 Erdtman, 1952; Zhang & Anderberg, 2002 Harley, 1986, 1991; Perveen & Qaiser, 2002b; Aftab & Perveen, 2006 Harley, 1986, 1991 PalDat; Takahashi & Sohma, 1982 Wei et al., 1999 PalDat; Morton & Dickison, 1992 Barth, 1979; Nagamasu, 1989a, 1989b Janssens et al., 2005 PalDat; Zavada & Wei, 1993; Wei, 1997 Wei, 1997
Primulaceae	58(8)		
Roridulaceae	1(1)		
Sapotaceae	53(2)		
Sarraceniaceae	3(1)		
Sladeniaceae	2(1)		
Styracaceae	11(1)		
Symplocaceae	2(1)		
Tetrameristaceae	3(1)		
Theaceae	8(2)		
SANTALES			
Aptandraceae	8(4)	<i>Aptandra</i> Miers <i>Harmandia</i> Baill. <i>Ongokea</i> Pierre <i>Phanerodiscus</i> Cavaco * <i>Phanerodiscus diospyroidea</i> Capuron (Fig. 6L–L) <i>Mystropetalon</i> Harv. <i>Minquartia</i> Aubl.	Erdtman, 1952; Feuer, 1977 Feuer, 1977 Erdtman, 1952; Feuer, 1977 Malécot & Lobreau-Callen, 2005 Madagascar, <i>Rakotonandrasana et al.</i> 1225 (C.AS) Erdtman, 1952; Kuijt & Hansen, 2015 Feuer, 1977; Erdtman, 1986; Colinvaux et al., 1999
Balanophoraceae	20(1)		
Coulaceae	3(1)		

Appendix 2. Continued.

Classification	Total genera per family (total genera sampled)	Genera used in phylogeny and species for which LM, SEM, and TEM were obtained	References for palynological data and species vouchers for LM, SEM, and TEM
Erythropalaceae	4(1)	<i>Heisteria</i> Jacq.	Maguire et al., 1974; Feuer, 1977; Bonnefille et al., 1982; Sleumer, 1984; Erdtman, 1986; Gosling et al., 2013
Loranthaceae	77(8)	<i>Atkinsonia</i> F. Muell. <i>Dendropenon</i> (Blume) Rechb. <i>Gaiadendron</i> G. Don <i>Moquiiniella</i> Balle <i>Oryctanthus</i> (Griseb.) Eichler <i>Plathinusa</i> Mart. <i>Psittacanthus</i> Mart. * <i>Psittacanthus calyculatus</i> (DC.) G. Don (Fig. 7A–D) <i>Struthanthus</i> Mart.	Feuer & Kuijt, 1980 Feuer & Kuijt, 1985 Feuer & Kuijt, 1980 Johri & Raj, 1969 Feuer & Kuijt, 1985 Feuer & Kuijt, 1985 Feuer & Kuijt, 1980 Mexico, <i>Bartholomew et al. 3080B</i> (KUN) Feuer & Kuijt, 1985 Feuer, 1981 Erdtman, 1952; Feuer, 1977 Feuer, 1977 Feuer, 1977 Erdtman, 1952, 1986 Feuer & Kuijt, 1978 Erdtman, 1952; Aronne et al., 1993 Traverse, 2007 Erdtman, 1952 Feuer & Kuijt, 1982; Feuer et al., 1982 Maguire et al., 1974; Feuer, 1977; Sleumer, 1984 China, <i>Liu 1785</i> (KUN) Erdtman, 1952; Feuer, 1977; Bonnefille et al., 1982 Erdtman, 1952; Feuer, 1977 Maguire et al., 1974; Feuer, 1977; Bonnefille et al., 1982
Misodendraceae	1(1)	<i>Misodendrum</i> Banks ex DC.	
Octoknemaceae	1(1)	<i>Octoknema</i> Pierre	
Olacaceae	8(2)	<i>Olax</i> L. <i>Psychopetalum</i> Benth. <i>Opilia</i> Roxb. <i>Eubrachion</i> Hook.f. <i>Osyris</i> L. <i>Phoradendron</i> Nutt.	
Opliaceae	10(1)	<i>Santalum</i> L.	
Santalaceae	42(5)	<i>Viscum</i> L. <i>Schoepfia</i> Schreb. * <i>Schoepfia fragrans</i> Wall. (Fig. 7I–L) <i>Scorodocarpus</i> Becc. <i>Strombosia</i> Blume <i>Ximenia</i> L.	
Schoepfiaceae	3(1)		
Strombosiaceae	6(2)		
Ximeniaceae	4(1)		
OUTGROUPS			
APIALES			
Grisebiniaceae	1(1)	<i>Griselinia</i> J. R. Forst. & G. Forst.	Chao, 1954; Ferguson, 1977
AQUIFOALES			
Cardiopteridaceae	5(1)	<i>Gonocaryum</i> Miq.	APSA; Yang et al. (unpubl. data from SEM)
BUXALES			
Buxaceae	6(1)	<i>Pachysandra</i> Michx.	Nowicke & Skvarla, 1984

Appendix 2. Continued.

Classification	Total genera per family (total genera sampled)	Genera used in phylogeny and species for which LM, SEM, and TEM were obtained	References for palynological data and species vouchers for LM, SEM, and TEM
FABALES			
Fabaceae	745(1)	<i>Vicia</i> L.	Endo & Ohashi, 1996
GARRYALES			
Garryaceae	2(1)	<i>Garrya Douglas</i> ex Lindl.	Chao, 1954; Erdtman, 1986
GUNNERALES			
Gunneraceae	1(1)	<i>Gunnera</i> L.	PalDat; Pragowski, 1970
Myrothamnaceae	2(1)	<i>Myrothamnus</i> Welw.	Zavada & Dilcher, 1986
LAMIALES			
Acanthaceae	220(1)	<i>Justicia</i> L.	PalDat; Graham, 1988; Hilsenbeck, 1990; Ruteangsawang et al., 2013
Scrophulariaceae	65(1)	<i>Verbascum</i> L.	PalDat
MYRTALES			
Combretaceae	14(1)	<i>Combretum</i> Loefl.	Patel, 1982; Krachai & Pompongrungrueng, 2015
PROTEALES			
Sabiaceae	3(1)	<i>Meliosma</i> Blume	Furness et al., 2007; Li et al., 2010
SAPINDALES			
Burseraceae	19(1)	<i>Bursera Jacq.</i> ex L.	Harley et al., 2005
SAXIFRAGALES			
Altingiaceae	1(1)	<i>Liquidambar</i> L.	Ickert-Bond & Wen, 2013
Crassulaceae	34(1)	<i>Crassula</i> L.	PalDat; APSA
Hamamelidaceae	27(1)	<i>Rhodoleia</i> Champ. ex Hook.	Zavada & Dilcher, 1986
Paeoniaceae	1(1)	<i>Paeonia</i> L.	Xi, 1984
Saxifragaceae	33(1)	<i>Saxifraga</i> L.	PalDat; Yao et al., 2014
SOLANALES			
Montiaceae	3(1)	<i>Montinia</i> Thunb.	Erdtman, 1952; Ronse De Craene et al., 2000
TROCHODENDRALES			
Trochodendraceae	2(1)	<i>Tetracentron</i> Oliv.	Zavada & Dilcher, 1986; Li et al., 2010
VITALES			
Vitaceae	14(1)	<i>Vitis</i> L.	Inceoglu & Pinar, 2000
ZYGOPHYLLALES			
Zygophyllaceae	22(1)	<i>Tribulus</i> L.	Pragowski, 1987; Nurbay & Pan, 2003
UNPLACED			
Vahlhiaceae	1(1)	<i>Vahlia</i> Thunb.	Yang et al. (unpubl. data from SEM)

Appendix 3. Comprehensive data matrix of 19 pollen characters for all taxa in our phylogeny. Outgroup and nested ingroup taxa are shown in boldface. Characters and their states follow Table 1. Missing data are indicated with a question mark (?) and inapplicable data with a dash (-).

Taxon	Character coding
<i>Actinidia</i>	00{2,3}{0,2}010010{0,1}00--1{0,2,5}01
<i>Aextoxicon</i>	002001001{1,-}111001001
<i>Agrostemma</i>	012-24110-001001101
<i>Alangium</i>	001021001{0,1,2}0{0,1}{0,1}{1,2,-}{0,1,-}1{2,5,6}01
<i>Alluaudia</i>	012-24110-001011001
<i>Amaranthus</i>	0{0,1}2{0,-}{0,1}{1,4}{0,1}{0,1}0-001001001
<i>Anacampseros</i>	012-24110-001001001
<i>Anagallis</i>	00{2,3}0010011110--12{0,1}1
<i>Ancistrocladus</i>	001011000-0010010??
<i>Androsace</i>	00{2,3}0010010110--1201
<i>Aptandra</i>	0{0,2}{0,1}10{1,4}01--000--1000
<i>Arbutus</i>	122001001101{0,1}0-1701
<i>Armeria</i>	002021000-101001201
<i>Asteropeia</i>	0020?{1,3}00{0,1}{2,-}0?1001001
<i>Atkinsonia</i>	01?-10??-?00--1521
<i>Atropaxxis</i>	0020110{0,2}10010--1401
<i>Barbeuia</i>	002011000-011001001
<i>Barringtonia</i>	0020110212010-1201
<i>Basella</i>	012-1{3,4}10--00{0,1}--1{0,1,2}00
<i>Berberidopsis</i>	00{1,2}01100{0,1}{2,-}000--1{0,1,5}01
<i>Beta</i>	012-04110-001001001
<i>Bistorta</i>	0020110010111001001
<i>Bougainvillea</i>	002011000-101001201
Bursera	0123110011110--1601
<i>Calyptrorhcha</i>	012-24110-001001001
<i>Camellia</i>	00{1,2}01100{0,1}0010001{0,2,5}01
<i>Cantus</i>	012-24110-111111201
<i>Carnegiea</i>	002011000-001001001
<i>Celosia</i>	012-14110-001001001
<i>Ceraria</i>	003011000-001001001
<i>Cerastium</i>	012-14110-001001101
<i>Ceratostigma</i>	0{0,1}3{0,-}2{1,4}{0,1}00-101{0,2}11001
<i>Cevallia</i>	003011001-110--1001
<i>Clavija</i>	00000100111?0--1001

Appendix 3. Continued.

Taxon	Character coding
<i>Claytonia</i>	{0,1}02011020-0{0,1}1001201
<i>Clethra</i>	00{2,3}001001{0,1,2}010--1{1,5}11
<i>Cobaea</i>	012-34110-010--1201
<i>Coccoloba</i>	0030110011011011501
Combretum	0120030{0,2}1{0,1}000--1601
<i>Corbichonia</i>	003011000-001001001
<i>Coris</i>	0030110010110--1201
<i>Cornus</i>	00{1,2}{0,1}110010111001001
<i>Cortusa</i>	001101020-110--1501
<i>Couroupita</i>	{0,1}03211000-1?{0,1}{1,-}{1,-}1201
Crassula	0030010010000--1601
<i>Curtisia</i>	002{0,1}010012110--1001
<i>Cyrilla</i>	00200{1,2,3}0011010--1{0,5}11
<i>Delosperma</i>	002001000-0?1001201
<i>Dendropemon</i>	00{1,2}113210-100--1001
<i>Diapensia</i>	003011001-100--1201
<i>Dillenia</i>	002001000-0{0,1}{0,1}{2,-}{1,-}1{0,2}01
<i>Diospyros</i>	{0,1}0{2,3}{0,1,2}1100{0,1}{0,1,2}000---1{0,1,5}{1,2}1
<i>Diplarche</i>	1220010011110--1001
<i>Drosera</i>	121004230-?0?-0?01
<i>Drosophyllum</i>	012-2411--001001000
<i>Emex</i>	00201100120?{0,1}001501
<i>Erica</i>	122001001201{0,1}--1{0,5}01
<i>Eubranchion</i>	0020110010100--1001
<i>Fagopyrum</i>	0030210010010--1001
<i>Fouquieria</i>	0020{0,1}1001{0,2}000--1201
<i>Frankenia</i>	00{1,2}01{1,2,3}000-001201001
<i>Franklinia</i>	002011001?110--1201
<i>Froelichia</i>	012-14110-101001201
<i>Gaiadendron</i>	000311020-011001001
<i>Galax</i>	00201{1,3}0012010--1001
Garrya	0010110011110--1201
<i>Gilia</i>	012-14101{1,2}{0,1}1{0,1}-{0,-}1{0,6}01
<i>Gisekia</i>	003011000-011001001

Appendix 3. Continued.

Taxon	Character coding
<i>Glaux</i>	0030110011010--1001
Gonocaryum	00201100100?1001201
Griselinia	00{2,3}011001{0,1}110--1401
<i>Grubbia</i>	0030010011?10--1001
Gunnera	00{1,2}211000?110--1201
<i>Halophytum</i>	01?--13110-001001001
<i>Harmandia</i>	020112010-100--1001
<i>Heisteria</i>	0{0,2}20010010000--1011
<i>Hibbertia</i>	001001000-010--1{2,5}01
<i>Hydrangea</i>	0030010010100--1201
<i>Hydrostachys</i>	12?-00??-??100???
<i>Hypertelis</i>	0020?1000-0?1001001
<i>Impatiens</i>	00{1,2}{0,4}1{1,2}000-100-1201
Justicia	00{2,3}{0,4}{1,2}1001{0,1,2}00{0,1}--1{0,2}01
<i>Limeum</i>	002{0,2}01000-001001001
<i>Limonium</i>	002{0,2}21000-101001201
Liquidambar	012-04110-001201001
<i>Macarthuria</i>	002011000-011001001
<i>Maesa</i>	0020010010110--1201
<i>Manilkara</i>	00201{1,2}0010010--1021
<i>Marcgravia</i>	0020110011000--1{0,2,5}01
Meliosma	00{2,3}0110011010--1201
<i>Mentzelia</i>	0030110010010--1{4,6}01
<i>Minuartia</i>	00210100{0,1}2100--1011
<i>Mirabilis</i>	012-341{0,1}0-001001001
<i>Misodendrum</i>	012-04110-011011101
<i>Mitrastemon</i>	003001010-1?11010?1
<i>Mollugo</i>	0{0,1}2{0,-}0{1,4}{0,1}{0,1}0-011001001
<i>Montia</i>	012-1410--101001000
Montinia	00201100111?1001201
<i>Moquiniella</i>	000301020-001001001
<i>Muehlenbeckia</i>	003001001?11{0,1}{2,-}{0,-}1501
Myrothamnus	122001010-001000?01
<i>Mystroptalon</i>	00{1,2}10{2,4}{0,1}00-011011001
<i>Neea</i>	002011000-001001201

Appendix 3. Continued.

Taxon	Character coding
<i>Nepenthes</i>	111-00??-?0?-0?01
<i>Nyssa</i>	002011001111100100?
<i>Octoknema</i>	001101001?000--1001
<i>Olea</i>	00101101--000--1{1,2}00
<i>Ongokea</i>	0{0,2}{0,1}10201--000--1000
<i>Optia</i>	001101001-100--1001
<i>Opuntia</i>	012-{2,3}411{0,-}-00{0,1}--1{0,2}0{0,1}
<i>Oryctanthus</i>	0010132012000--11?1
<i>Osyris</i>	003111000-0?0--1001
<i>Pachysandra</i>	012-14110-100--1301
<i>Paeonia</i>	003011000-0{0,1}0--1201
<i>Pereskia</i>	012-24110-001001001
<i>Persicaria</i>	0{0,1}2{0,-}1{1,4}{0,1}00-010--1201
<i>Petalonyx</i>	00{2,3}0110011010--1401
<i>Petiveria</i>	012-14100-011001001
<i>Phanerodiscus</i>	001103210-100--1{0,1}{0,2}1
<i>Phaulothamnus</i>	012-14110-011001001
<i>Philadelphus</i>	0020010010{0,1}10--1201
<i>Phlox</i>	012-14110-100--1201
<i>Phoradendron</i>	00200100100?1001001
<i>Phthirusa</i>	0{0,2}{1,2}{1,3}132{1,2}0-100--10{0,1}1
<i>Physena</i>	002001000-001001001
<i>Phytolacca</i>	002011000-011001001
<i>Pisonia</i>	0{0,1}2{0,-}1{1,4}{0,1}{0,1}0-0010{0,1}1{0,2}01
<i>Plumbago</i>	00{1,2}{0,2}21000-101{0,2}11001
<i>Polemonium</i>	012-14110-111001601
<i>Polygonum</i>	0{0,1}{2,3}{0,-}1{1,4}{0,1}{0,1}{0,1}{0,1}1{0,1}1 {0,1}-{0,1}-1{0,2}01
<i>Portulaca</i>	012-24000-011011001
<i>Pouteria</i>	00201{1,2}001101{0,1}201{0,2}01
<i>Primula</i>	00{1,2}01{1,3,4}0{0,2}{0,1}{0,-}1{0,1}10--1201
<i>Psittacanthus</i>	000{0,3}210{0,2}0-001101{0,1}{0,2}1
<i>Psychopetalum</i>	0010112{0,1}-000--1200
<i>Pupalia</i>	012-04110-111001001
<i>Rhabdodendron</i>	00200100100?1001001

Appendix 3. Continued.

Taxon	Character coding
Rhodoleia	002001000-010--1201
<i>Rivina</i>	01{2,3}-14100-0?1001021
<i>Roridula</i>	0{0,1}2{1,-}1{1,0}001{0,1}001001001
<i>Ruprechtia</i>	0020010011001011501
<i>Santalum</i>	0020110100010--1001
<i>Sarcobatus</i>	012-04110-001001001
<i>Sarracenia</i>	00{2,3}0041012000--1001
Saxifraga	003011000-001201601
<i>Schoepfia</i>	02?11{2,3}31{0,-}-100--1{1,5}{0,1,2}{0,1}
<i>Scorodocarpus</i>	00110100011000--1001
<i>Silene</i>	012-14110-101001201
<i>Simmondsia</i>	002111010-001011501
<i>Sladenia</i>	0020010012010--1001
<i>Spergula</i>	0{0,1}2{0,-}1{1,4}{0,1}00-001001001
<i>Spinacia</i>	012-14110-001001001
<i>Stegnosperma</i>	00{2,3}011000-011001001
<i>Stellaria</i>	012-04110-001001001
<i>Strombostia</i>	0011010012000--1011
<i>Struthanthus</i>	0{0,2}{1,2}1112{1,2}12100--1{0,1}21
<i>Styrax</i>	002011001{0,1}110--1001
<i>Symphlocos</i>	00{1,2}111001{0,1,2}{0,1}{0,1}{0,1}1{0,1}1501
<i>Talinum</i>	012-24110-001001001
<i>Tamarix</i>	002001000-{0,1}00--1221
<i>Ternstroemia</i>	00{2,3}0010010110--1101
Tetracentron	00{1,2}{0,2}01000?000--1{2,4}01
<i>Tetracera</i>	00200{1,0}??2?10--1001
<i>Tetramerista</i>	0020010012000--1221
Tribulus	012-04110-100--1201
<i>Triphyophyllum</i>	00{1,2}111000-0?10115?1
Valhka	00300100121?0--120?
Verbascum	0020110012{0,1}0{0,1}--1201
<i>Vicia</i>	0130110011010--12{0,1}1
<i>Viscum</i>	002{0,1}1{1,2}0011{0,1}11{0,2,-}{0,1,-}{0,1}0{0,1}1
Vitis	0020110010110--1201
<i>Ximenia</i>	002101000-100--1211

Appendix 4. Democratic data matrix of 19 pollen characters for all taxa in our phylogeny. Outgroup and nested ingroup taxa are shown in boldface. Characters and their states follow Table 1. Missing data are indicated with a question mark (?) and inapplicable data with a dash (-).

Taxon	Democratic coding
<i>Actinidia</i>	0020010010000--1501
<i>Aextoxicon</i>	0020010011111001001
<i>Agrostemma</i>	012-24110-001001101
<i>Alangium</i>	0010210010001--1201
<i>Alluaudia</i>	012-24110-001011001
<i>Amaranthus</i>	012-04110-001001001
<i>Anacampteros</i>	012-24110-001001001
<i>Anagallis</i>	0020010011110--1201
<i>Ancistrocladus</i>	001011000-0010010??
<i>Androsace</i>	0020010010110--1201
<i>Aptandra</i>	00010101--000--1000
<i>Arbutus</i>	12200100110100-1701
<i>Armeria</i>	002021000-101001201
<i>Asteropeia</i>	0020?1000-0?1001001
<i>Atkinsonia</i>	01--10-----00--1521
<i>Atraphaxis</i>	0020110010010--1401
<i>Barbeuia</i>	002011000-011001001
<i>Barringtonia</i>	0020110212010--1201
<i>Basella</i>	01--1310--001--1200
<i>Berberidopsis</i>	002011000-000--1001
<i>Beta</i>	012-04110-001001001
<i>Bistorta</i>	0020110010111001001
<i>Bougainvillea</i>	002011000-101001201
<i>Bursera</i>	0123110011110--1601
<i>Calyptrorhiza</i>	012-24110-001001001
<i>Camellia</i>	0020110010010001501
<i>Cantus</i>	012-24110-111111201
<i>Carnegiea</i>	002011000-001001001
<i>Celosia</i>	012-14110-001001001
<i>Ceraria</i>	003011000-001001001
<i>Cerastium</i>	012-14110-001001101
<i>Ceratostigma</i>	003021000-101211001
<i>Cevallia</i>	003011001-110--1001
<i>Clavija</i>	00000100111?0--1001
<i>Claytonia</i>	002011020-0-1001201
<i>Clethra</i>	0020010010010--1111
<i>Cobaea</i>	012-34110-010--1201
<i>Coccoloba</i>	0030110011011011501
<i>Combretum</i>	0120030011000--1601
<i>Corbichonia</i>	003011000-001001001
<i>Coris</i>	0030110010110--1201
<i>Cornus</i>	0021110010111001001
<i>Cortusa</i>	001101020-111--1501
<i>Couroupita</i>	003211000-1?0--1201
<i>Crassula</i>	0030010010000--1601
<i>Curtisia</i>	0020010012110--1001
<i>Cyrilla</i>	0020010011010--1011
<i>Delosperma</i>	002001000-0?1001201
<i>Dendropemon</i>	001113210-100--1001
<i>Diapensia</i>	003011001-100--1201
<i>Dillenia</i>	002001000-010--1201
<i>Diospyros</i>	0030110010000--1511

Appendix 4. Continued.

Taxon	Democratic coding
<i>Diplarche</i>	1220010011110--1001
<i>Drosera</i>	121004230--0---0-01
<i>Drosophyllum</i>	012-2411--001001000
<i>Emex</i>	00201100120?1001501
<i>Erica</i>	1220010012010--1501
<i>Eubrachion</i>	0020110010100--1001
<i>Fagopyrum</i>	0030210010010--1001
<i>Fouquieria</i>	0020110010000--1201
<i>Frankenia</i>	002011000-001201001
<i>Franklinia</i>	002011001?110--1201
<i>Froelichia</i>	012-14110-101001201
<i>Gaidadron</i>	000311020-011001001
<i>Galax</i>	0020110012010--1001
<i>Garrya</i>	0010110011110--1201
<i>Gilia</i>	012-14101-011--1601
<i>Gisekia</i>	003011000-011001001
<i>Glaux</i>	0030110011010--1001
<i>Gonocaryum</i>	00201100100?1001201
<i>Griselinia</i>	0020110010110--1401
<i>Grubbia</i>	0030010011?10--1001
<i>Gunnera</i>	001211000?110--1201
<i>Halophytum</i>	01--13110-001001001
<i>Harmandia</i>	020112010-100--1001
<i>Heisteria</i>	0020010010000--1011
<i>Hibbertia</i>	001001000-010--1201
<i>Hydrangea</i>	0030010010100--1201
<i>Hydrostachys</i>	12--00-----100----
<i>Hypertelis</i>	0020?1000-0?1001001
<i>Impatiens</i>	001412000-100--1201
<i>Justicia</i>	0030110010000--1201
<i>Limeum</i>	002001000-001001001
<i>Limonium</i>	002021000-101001201
<i>Liquidambar</i>	012-04110-001201001
<i>Macarthuria</i>	002011000-011001001
<i>Maesa</i>	0020010010110--1201
<i>Manilkara</i>	0020110010010--1021
<i>Marcgravia</i>	0020110011000--1-01
<i>Meliosma</i>	0020110011010--1201
<i>Mentzelia</i>	0030110010010--1401
<i>Minuartia</i>	0021010012100--1011
<i>Mirabilis</i>	012-34110-001001001
<i>Misodendrum</i>	012-04110-011011101
<i>Mitrastemon</i>	003001010-1?11010?1
<i>Mollugo</i>	002001000-011001001
<i>Montia</i>	012-1410--101001000
<i>Montinia</i>	00201100111?1001201
<i>Moquiniella</i>	000301020-001001001
<i>Muehlenbeckia</i>	003001001?110--1501
<i>Myrothamnus</i>	122001010-001000-01
<i>Mystropetalon</i>	002104000-011001001
<i>Neea</i>	002011000-001001201
<i>Nepenthes</i>	111-00-----0---0-01
<i>Nyssa</i>	002011001111100100?
<i>Octoknema</i>	001101001?000--1001
<i>Olax</i>	00101101--000--1100
<i>Ongokea</i>	02010201--000--1000

Appendix 4. Continued.

Taxon	Democratic coding
<i>Opilia</i>	001101001-100--1201
<i>Opuntia</i>	012-2411--001--1201
<i>Oryctanthus</i>	0010132012000--11-1
<i>Osyris</i>	003111000-0?0--1001
<i>Pachysandra</i>	012-14110-100--1301
<i>Paeonia</i>	003011000-010--1201
<i>Pereskia</i>	012-24110-001001001
<i>Persicaria</i>	012-14100-010--1201
<i>Petalonyx</i>	0030110011010--1401
<i>Petiveria</i>	012-14100-011001001
<i>Phanerodiscus</i>	001103210-000--1001
<i>Phaulothamnus</i>	012-14110-011001001
<i>Philadelphus</i>	0020010010110--1201
<i>Phlox</i>	012-14110-100--1201
<i>Phoradendron</i>	00200100100?1001001
<i>Phthirusa</i>	001113210-100--1001
<i>Physena</i>	002001000-001001001
<i>Phytolacca</i>	002011000-011001001
<i>Pisonia</i>	002011000-001001001
<i>Plumbago</i>	002021000-101211001
<i>Polemonium</i>	012-14110-111001601
<i>Polygonum</i>	0020110010011001201
<i>Portulaca</i>	012-24000-011011001
<i>Pouteria</i>	0020110011010201001
<i>Primula</i>	002011000-110--1201
<i>Psittacanthus</i>	000321020-001101001
<i>Ptychopetalum</i>	00101121--000--1200
<i>Pupalia</i>	012-04110-111001001
<i>Rhabdodendron</i>	00200100100?1001001
<i>Rhodoleia</i>	002001000-010--1201
<i>Rivina</i>	013-14100-0?1001021
<i>Roridula</i>	0021110011001001001

Appendix 4. Continued.

Taxon	Democratic coding
<i>Ruprechtia</i>	0020010011001011501
<i>Santalum</i>	0020110100010--1001
<i>Sarcobatus</i>	012-04110-001001001
<i>Sarracenia</i>	0030041012000--1001
<i>Saxifraga</i>	003011000-001201601
<i>Schoepfia</i>	02-11231--100--1121
<i>Scorodocarpus</i>	0011010011000--1001
<i>Silene</i>	012-14110-101001201
<i>Simmondsia</i>	002111010-001011501
<i>Sladenia</i>	0020010012010--1001
<i>Spergula</i>	012-14100-001001001
<i>Spinacia</i>	012-14110-001001001
<i>Stegnosperma</i>	002011000-011001001
<i>Stellaria</i>	012-04110-001001001
<i>Strombosia</i>	0011010012000--1011
<i>Struthanthus</i>	0011112112100--1021
<i>Styrax</i>	0020110010110--1001
<i>Symplocos</i>	0011110010-11101501
<i>Talinum</i>	012-24110-001001001
<i>Tamarix</i>	002001000-100--1221
<i>Ternstroemia</i>	0020010010110--1101
<i>Tetracentron</i>	002001000?000--1201
<i>Tetracera</i>	0020010012010--1001
<i>Tetramerista</i>	0020010012000--1221
<i>Tribulus</i>	012-04110-100--1201
<i>Triphyophyllum</i>	001111000-0?10115?1
<i>Vahlia</i>	00300100121?0--120?
<i>Verbascum</i>	0020110012-0--1201
<i>Vicia</i>	0130110011010--1201
<i>Viscum</i>	0020110011011--1001
<i>Vitis</i>	0020110010110--1201
<i>Ximenesia</i>	002101000-100--1211

Appendix 5. Number of state changes calculated for 19 pollen characters across three trees using five analyses. CFP, comprehensive matrix using Fitch parsimony; DFP, democratic matrix using Fitch parsimony; DML, democratic matrix using maximum likelihood; CHB, comprehensive matrix using hierarchical Bayesian inference; DHB, democratic matrix using hierarchical Bayesian inference.

Pollen characters	Tree A					Tree B					Tree C				
	CFP	DFP	DML	CHB	DHB	CFP	DFP	DML	CHB	DHB	CFP	DFP	DML	CHB	DHB
Dispersal unit	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
Polarity	5	5	6	12	13	4	5	5	12	13	5	5	5	12	13
Shape class	8	9	8	25	26	6	8	7	22	22	8	8	7	22	25
Outline in polar view	4	4	6	14	16	4	4	6	15	16	5	5	5	16	16
Size	15	15	12	40	42	14	14	15	38	38	15	15	11	40	39
Aperture number	4	4	6	19	18	5	6	6	20	19	4	5	6	21	19
Aperture position	4	4	4	15	15	4	4	4	12	12	4	4	4	15	12
Ectoaperture shape	8	10	9	16	15	8	10	8	17	15	8	10	8	16	17
Endoapertures	10	10	10	14	17	9	10	9	14	14	9	10	8	14	15
Endoaperture shape	2	2	4	24	27	2	2	4	24	27	2	2	4	24	25
Aperture membrane ornamentation	9	8	5	32	23	9	8	8	24	24	9	8	9	21	22
Costae	8	5	7	27	27	7	5	7	29	31	7	8	7	28	29
Supratracteal elements	4	7	5	10	9	4	7	5	10	10	4	7	5	10	9
Supratracteal element shape	0	0	0	6	3	0	0	0	7	3	0	0	0	7	3
Supratracteal element size	3	3	3	5	4	3	3	3	5	4	3	3	3	5	4
Tectum	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Tectum sculpture	12	12	11	45	51	13	13	12	48	50	13	13	11	43	52
Infrapectum structure	0	0	0	26	26	0	0	0	28	28	0	0	0	27	27
Endexine	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
Total	101	103	101	335	337	97	104	104	330	331	101	108	98	326	332