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EVOLUTION OF ANGIOSPERM POLLEN. 3. MONOCOTS¹

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ABSTRACT

Monocots, with ca. 65,000 species in 78 families and 12 orders as classified by the Angiosperm Phylogeny Group (Angiosperm Phylogeny Group III, 2009), have traditionally been known as a distinct assemblage from dicots within angiosperms and are now seen as a lineage that diverged from within the more basal of the angiosperm groupings. In this study, the third in a series analyzing pollen characters across the angiosperms, we illustrate the pollen morphological diversity of monocots and analyze 19 palynological and two ecological characters for 120 taxa in 71 families covering the 12 monocot orders and 16 taxa of nine orders in basal angiosperms. Pollen morphological data from previous works and our investigations were optimized onto a new maximum likelihood tree reconstructed from an existing DNA matrix of Chase et al. (2006) using Fitch parsimony, maximum likelihood, and hierarchical Bayesian analysis. From these analyses we infer evolutionary patterns in palynological characters, assess their systematic value, and investigate two aspects (pollination type and habitat moisture) of their ecological adaptation. The highest levels of pollen variation were shown to exist in the Alismatales and Commelinales, with lower levels seen in the Asparagales, Dasygogonales, and Zingiberales; the most variable characters across the phylogeny were found to be pollen outline in polar view, size, and tectum extent. We infer unambiguous plesiomorphic states for monocots and report significant transitions in character states at various levels within the monocot assemblage. Analyses of correlated evolution reconfirmed the hypothesis of an association between exine reduction (or complete loss) and habitat moisture and found significant correlations between various states of exine loss and habitat for hydrophytic–helophytic plants. The presence or absence of the exine itself was found to be more significantly correlated than individual structures, in terms of association with hydrophytic–helophytic plants. The most rapid rate of state changes in pollen characters, in the evolutionary history of monocots, is estimated to have occurred during the Albian-Turonian stage; our work may provide insights into the identification of enigmatic fossil pollen grains from this geological time.

Key words: Character evolution, correlated evolution, exine stratification, habitat moisture, monocots, pollen morphology, pollination type, systematic significance.

Monocotyledonous plants have been recognized as a distinct group, based principally on the single cotyledon of the seed, since the 18th century (Ray, 1703). Monocots are one of the most distinctive major lineages of angiosperms, with ca. 65,000 known species in 78 families and 12 orders, representing ca. 25% of the total diversity of angiosperms (Angiosperm Phylogeny Group III, 2009; Reveal & Chase, 2011). Cladistic studies based on morphological data have indicated putative synapomorphies for monocots that include an adventitious root system, parallel-

veined leaves, scattered vascular bundles in the shoots, cambium presence, and successive microsporogenesis (Donoghue & Doyle, 1989a, 1989b; Loconte & Stevenson, 1991; Doyle & Donoghue, 1992; Doyle & Endress, 2000). Tomlinson (1995) stated that the uniqueness of the monocot vascular system among seed plants and the lack of homology in organization between the primary vascular systems of monocots and other angiosperms might suggest an independent origin of monocots from other angiosperms. However, Tomlinson's observations are

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inconsistent with other morphological characters and molecular data. Scattered vascular bundles and monocotyledonoid floral features are found elsewhere in angiosperms, among basal lineages (Soltis et al., 2005), and the monocots are now known to nest within angiosperms, closely related to the magnoliids (a clade comprising Canellales, Laurales, Magnoliales, and Piperales), as supported by analyses of several nucleotide sequences (Chase et al., 1993; Soltis et al., 1997; Qiu et al., 1999, 2000, 2005, 2006, 2010). Thus, monocots currently form one of the best supported major clades within angiosperms (Chase, 2004; Chase et al., 2006).

Phylogenetic studies of the monocots have made immense strides over the past 20 years, through increasingly extensive taxon sampling and the application of molecular data from plastid, nuclear, and mitochondrial genomic regions (e.g., Chase et al., 1993, 2006; Duvall et al., 1993a, 1993b, 2006; Bremer, 2000; Davis et al., 2004; Tamura et al., 2004; Givnish et al., 2006, 2010; Graham et al., 2006; Petersen et al., 2006; Li & Zhou, 2007). The most basally branching monocots have been considered, from morphological inference, to be the aquatic alismatids (a clade including all families of Alismatales except Araceae and Tofieldiaceae; Hutchinson, 1934; Cronquist, 1968, 1981; Takhtajan, 1969, 1991; Stebbins, 1974; Thorne, 1976), Dioscoreales (Dahlgren et al., 1985) or Melanthiales (Thorne, 1992a, 1992b). Since some of the first molecular studies of monocots (Chase et al., 1993; Duvall et al., 1993a, 1993b), *Acorus* L. has been inferred as the basalmost branching taxon and sister to all other monocots, a finding that has received support from almost all subsequent DNA-based analyses.

The most recent angiosperm classification provided by the Angiosperm Phylogeny Group III (2009) recognized 12 monocot orders: Acorales, Alismatales, Asparagales, Dioscoreales, Liliales, Pandanales, Petrosaviales, and the commelinid orders Arecales, Commelinales, Dasygogonales (Dasygogonaceae, Angiosperm Phylogeny Group III, 2009, here recognized as an order following Reveal & Chase, 2011), Poales, and Zingiberales. In this scheme, Acorales are the first branch to diverge from the rest of the group, with the Alismatales second, followed by Petrosaviales and Dioscoreales–Pandanales. Liliales are sister to a large clade of all other core monocots (i.e., Asparagales and the commelinid orders). Although this phylogenetic framework for monocots is mostly well supported at the ordinal level by nuclear, plastid, and mitochondrial data (Chase et al., 2006), the relationships among some lineages have remained controversial. For instance, the positions of the

Dasygogonales and Arecales, relative to other commelinids, are ambiguous, and relationships remain unresolved in Zingiberales, in particular the placements of the Heliconiaceae and Musaceae, as well as in the most basal branches of the Poales (e.g., Kress et al., 2001; Davis et al., 2004; Tamura et al., 2004; Givnish et al., 2006, 2010; Graham et al., 2006; Petersen et al., 2006; Barrett et al., 2014).

Pollen can play a key role in studies of angiosperm evolution due to its morphological variability and its potential to fossilize (Jones & Rowe, 1999). Multiple studies have indicated the taxonomic significance of pollen morphology in monocots, including investigations in Alismataceae (Argue, 1974, 1976), Araceae (Grayum, 1992; Weber et al., 1999; Hesse, 2006), Arecaceae (Thanikaimoni, 1970; Sowunmi, 1972; Ferguson, 1986; Ferguson & Harley, 1993; Harley & Baker, 2001), Cyperaceae (Van Wichelen et al., 1999; Simpson et al., 2003), Dioscoreales (Caddick et al., 1998), Eriocaulaceae (Thanikaimoni, 1965; de Borges et al., 2009), Liliaceae (Nair & Sharma, 1965; Kosenko, 1999), Smilacaceae (Chen et al., 2006), and Tecophilaeaceae (Simpson, 1985b). Similarities in pollen wall structure provided evidence for a close relationship between Lemnaceae and Araceae (the former treated as a subfamily within the latter in the Angiosperm Phylogeny Group III; Hesse, 2006), supporting the recent molecular results of Barabé et al. (2002) and Cabrera et al. (2003). Distinctive aperture patterns and tectum sculptures have supported the combination of *Heterosmilax* Kunth and *Smilax* L. in the Smilacaceae and the removal of *Rhipogonum* J. R. Forst. & G. Forst. from Smilacaceae (Chen et al., 2006). Pollen characters, such as aperture pattern and spine type, are also consistent with treatment of the Eriocaulaceae at various taxonomic levels (de Borges et al., 2009). Pollen evolution across the monocots was previously summarized in detail by Zavada (1983), who proposed evolutionary trends in pollen aperture and wall structure parallel to those proposed for other angiosperms by Walker (1974, 1976): this suggested similar selective pressures on pollen characters in monocots and other angiosperms. Increases in the number and number of types of apertures in the pollen grains of the Alismatales, Arecidae, and Liliales, and a reduction of the sulcus among many monocot groups, are obvious trends that, however, have not been investigated in a modern phylogenetic context but, so far, only under traditional classification systems such as that of Cronquist (1981).

The monocots are commonly considered to have originated by the Early Cretaceous (146–100 million years ago [Ma]) and diversified into the major extant

lineages during the Late Cretaceous (100–66 Ma), contemporaneously with other basal angiosperm groups (Herendeen & Crane, 1995; Bremer, 2000; Gandolfo et al., 2000; Chaw et al., 2004; Janssen & Bremer, 2004; Bell et al., 2010; Smith et al., 2010). Pollen grains of monocots from the Early Cretaceous, such as *Liliacidites* Couper and other types with a distinct graded reticulum, have long been regarded as evidence of early monocots (Doyle, 1973; Walker & Walker, 1984, 1986). On the other hand, Gandolfo et al. (2000) questioned all Early Cretaceous records of monocots and stated that the earliest unequivocal monocot fossils are from the Turonian. The apparently sparse fossil record of monocots is probably due to this group's fundamentally herbaceous habit and the fact that some monocot pollen is hard to distinguish from the monosulcate pollen of some basal angiosperms (e.g., Magnoliales; Friis et al., 2006). Friis et al. (2004) argued that the earliest proposed unequivocal monocot fossil was *Mayoa portugallica* Friis, Pedersen & Crane, with polyplicate and inaperturate pollen grains, which was placed in the Araceae (Pothoideae). However, Hofmann and Zetter (2010) suggested that this placement may be incorrect, based on similarities to the far older Triassic spore taxon *Lagenella martinii* (Leschik) Klaus. The incompleteness and insufficiency of the fossil record have limited our understanding of the evolutionary links between extinct and extant taxa and present obstacles to identifying early fossil monocot pollen grains. Therefore, determining plesiomorphic pollen states and pollen evolutionary patterns from extant taxa in a phylogenetic context may provide new insights into the palynological characters of the earliest monocots.

Evidence from phylogenetics has indicated that pollinators played an important role in angiosperm diversification (Johnson, 2006; Armbruster & Muchhala, 2009; Kay & Sargent, 2009). Pollen grains of angiosperms may be transported to the stigma by a variety of biotic and abiotic mechanisms for which pollen structures are adapted (Ackerman, 2000; Dobson & Bergstrom, 2000; Lunau, 2000; cf. Edlund et al., 2004). Relationships have been observed between pollination strategies and pollen features (e.g., Skvarla et al., 1978; Grayum, 1986; Linder, 1998, 2000; Hesse, 2000; Tanaka et al., 2004; Sannier et al., 2009; Wang et al., 2014); pollen wall stratification may be affected by pollination syndrome (reviewed in Hesse, 2000), and reduced exine structures may be associated with hypohydrophily (i.e., underwater cross pollination, Tanaka et al., 2004). Similarly, characteristics such as small grain size appear to be linked to pollen delivery by abiotic

vectors (wind or water; Ackerman, 2000). Aspects of the habitat features (e.g., moisture) have also likely played a substantial role in the evolution of pollen morphology (Ackerman, 2000; Franchi et al., 2002). For instance, "harmomegathy," a term introduced by Wodehouse (1935) to describe alterations in form that accompany changes in the degree of hydration of pollen grains, allows grains to respond and adapt to their environment. Both aperture closure and pollen-wall folding act to accommodate a decrease in cellular volume due to water loss (Katifori et al., 2010).

The loss or reduction of the exine has been a particularly prevalent and interesting feature of monocots. Pollen grains with a partially or fully reduced exine are typically found in moist environments (such as marshes, swamps, and bogs), where the pollen can remain viable without investing in a protective exine, and especially in the evolution of aquatic groups (Wodehouse, 1935). Exineless or exine-reduced pollen has been found in a large number of monocot families including Araceae (Weber et al., 1998; Hesse et al., 1999; Weber et al., 1999), Asparagaceae and Cannaceae (Erdtman, 1952, 1963; Skvarla & Rowley, 1970; Rowley & Skvarla, 1986), Costaceae (Stone et al., 1981), Cymodoceaceae (Pettitt, 1976, 1981, 1984; Ducker et al., 1978; McConchie et al., 1982; Harris et al., 1994), Haemodoraceae (Simpson, 1989), Heliconiaceae (Kress et al., 1978; Stone et al., 1979; Kress & Stone, 1983), Hydrocharitaceae (Pettitt, 1981; Tanaka et al., 2004), Lowiaceae (Kamelina & Raven, 1997), Marantaceae (Erdtman, 1952; Sharma, 1968; Furness & Rudall, 1999), Melanthiaceae (Takahashi, 1987), Musaceae (Erdtman, 1952; Sharma, 1968), Strelitziaceae (Hesse & Waha, 1983; Kronstedt-Robards & Rowley, 1989; Rowley et al., 1997), Zingiberaceae (Theilade & Theilade, 1996), and Zosteraceae (Pettitt & Jermy, 1975; Pettitt, 1976). Elsewhere in angiosperms, exineless or exine-reduced pollen is almost entirely restricted to basal-branching groups such as Annonaceae (Waha, 1987), Ceratophyllaceae (Takahashi, 1995), Degeneriaceae and Gomortegaceae (Rowley & Vasanthy, 1980; Kubitzki, 1981; Hesse & Kubitzki, 1983; Rowley & Vasanthy, 1993), Hernandiaceae (Rowley & Vasanthy, 1980; Kubitzki, 1981; Hesse & Kubitzki, 1983), and Lauraceae (Rowley & Vasanthy, 1980; Kubitzki, 1981; Hesse & Kubitzki, 1983; Gabarayeva et al., 2010), with an exception being the obligate aquatic species of *Callitriche* L. in Plantaginaceae (Osborn et al., 2001). For a fuller listing of exineless taxa, see Furness and Rudall (1999), and for reviews of aquatic taxa in particular, see Cox (1988), Osborn and Philbrick (1994), Philbrick and Les (1996), and

Cooper et al. (2000). Hesse and Kubitzki (1983) claimed that truly exineless pollen is found only in the seagrass taxa of Alismatales, *Amphibolis* C. Agardh (Cymodoceaceae), *Halophila* Thouars (Hydrocharitaceae), and *Thalassodendron* Hartog (Cymodoceaceae), with other taxa (e.g., *Canna* L., *Heliconia* L., and *Strelitzia* Aiton in Zingiberales) retaining at least vestiges of exine. However, Cooper et al. (2000) stated that fully exineless pollen can also be found in some aquatic species of *Callitriche*.

Exine reduction has been described (Furness & Rudall, 1999) as analogous to aperture formation. Since apertures are defined as an opening or thinning within the exine, exineless pollen grains may be functionally either monoaperturate or omniaperturate (in this case, the single aperture covering the entire surface of the grain). However, exineless taxa exhibit a wide range of developmental pathways, in contrast to the single pathway commonly described for aperture formation, by the deposition of apertural shields of endoplasmic reticulum that block the deposition of sporopollenin. Since exine may be laid down on a fibrillar layer (primexine) within the callose wall during the tetrad period of microsporogenesis, or mediated earlier by the plasma membrane and glycocalyx (Takahashi, 1987), exineless pollen grains may be generated either by a lack of primexine (perhaps as in *Ceratophyllum* L., Ceratophyllaceae, Ceratophyllales [Takahashi, 1995] and partially in *Canna*, Cannaceae, Zingiberales [Skvarla & Rowley, 1970; Rowley & Skvarla, 1986]), callose (perhaps the case in *Callitriche*; Osborn et al., 2001), or exine, or by subsequent loss of exine (e.g., *Zingiber* Mill., Zingiberaceae, Zingiberales; Theilade & Theilade, 1996). However, *Canna* does have primexine in the shape of the spines, which do not become exine. Also, within the primexine of typical pollen grains, sporopollenin only polymerizes at specific sites—the parts of the primexine that do not accumulate sporopollenin are later dispersed—appearing as empty voids in the mature pollen wall, such as the spaces between columellae. Frequently, exine loss is accompanied by some degree of compensation in other layers, such as the retention of the primexine or the thickening and elaboration of the intine (Kress & Stone, 1982; Theilade & Theilade, 1996; Franchi et al., 2002).

The extensive accumulation of pollen morphological data and an increasingly robust phylogenetic framework for angiosperms based on advanced molecular analyses together allow for more reliable reconstruction of morphological character states for extant flowering plants and their evolution in a phylogenetic context (Endress & Doyle, 2009; Wortley et al., 2015). The pollen morphology and evolution of monocots are integral to our understand-

ing of morphological evolution in the angiosperms as a whole. In this paper, we survey variation in pollen characters and infer key character state transitions in various lineages based on the most up-to-date phylogenetic framework, using Fitch parsimony (FP), maximum likelihood (ML), and hierarchical Bayesian inference (HB), in order to reveal pollen evolutionary patterns and trends throughout the monocots and to assess the systematic value of pollen characters as evidence for hitherto uncertain relationships within this group. We also perform correlated evolution analyses between pollen traits and ecological characters, to provide further insights into adaptive evolutionary mechanisms and driving forces for pollen character state changes in monocots, as corroborated with data on divergence times for the lineage from previous works. The integration of pollen data and analysis in this study may also facilitate the interpretation of early fossil monocot pollen grains.

MATERIALS AND METHODS

POLLEN DATA COLLECTION

Pollen grains from 20 species in 20 families covering all 12 orders within monocots were examined by LM and SEM to demonstrate the pollen variability of monocots. Pollen samples were collected from the living collections of the Kunming Botanic Garden (KBG) and Xishuangbanna Tropical Botanical Garden (XTBG), China, and from herbarium specimens of the Kunming Institute of Botany (KUN), China, Royal Botanic Garden Edinburgh (E), U.K., and Australian National Herbarium (CANB; for voucher details see Appendix 1). Anthers from herbarium material for LM and SEM observation were softened in warm water for 5 to 10 minutes and then dehydrated through an ethanol series to 100% ethanol. The acetolysis method was inapplicable because most pollen grains of monocots are fragile and liable to collapse. For SEM, anthers were mounted on specimen stubs with double-sided sticky tape and then carefully dissected to expose the pollen grains. The stubs were sputter-coated with gold. Pollen morphology was examined using a Hitachi (Tokyo, Japan) S-4800 SEM at 10.0 kV (KUN). To dry extremely delicate pollen grains (such as those with a very thin pollen wall) while preserving their surface structure for SEM observation, treatment with 2,2-dimethoxypropane (DMP) and critical-point drying (SPI-DRY Critical Point Dryer, No. 13200-AB Manual CPD; SPI Supplies, West Chester, Pennsylvania, U.S.A.) was performed according to Halbritter (1998). Pollen size (the maximum diameter of a single grain) was measured under LM. Note that, due to our

preparation methods, sizes may not be directly comparable with those in the literature derived from acetolyzed grains.

POLLEN CHARACTERS AND CODING STRATEGY

Pollen data were extracted from the literature (primarily SEM and transmission electron microscopy [TEM] observations), online databases, and new observations presented in this paper (see Appendix 1). Palynological terminology follows that of Punt et al. (2007) and Wortley et al. (2015).

The character selection and coding strategy followed those of Wortley et al. (2015) and Harley and Zavada (2000). For reconstruction of character evolution, 19 pollen characters were selected for coding: dispersal unit, polarity, symmetry (in polar view), basic shape, shape class, outline in polar view (amb), size (diameter of largest axis), aperture number, aperture position, aperture membrane, aperture shape, annulus, exine extent, tectum extent, supratectal element presence/absence, supratectal element shape, tectum sculpture, infratectum structure, and foot layer presence/absence (see Table 1 for coded character states). Two ecological characters, pollination type and habitat moisture, were also coded (see Table 1 for coded character states). Characters were treated as unordered binary or multistate characters, with inapplicable states coded as “-” and unknown data as “?” We adopted two coding methods, the comprehensive method sensu Wortley et al. (2015), which includes polymorphic states, and the democratic method (coding for the most common state; Bininda-Emonds et al., 1998). We adopted the composite coding strategy (incorporating inapplicable states into a more inclusive multistate character) advocated by Maddison (1993) for dealing with the inapplicable states. Data matrices are presented in Appendices 2 and 3.

For studies of correlated evolution, seven pairs of palynological character states and one pair of ecological character states, selected on the basis of previous hypotheses of correlation (Kress & Stone, 1982; Theilade & Theilade, 1996; Ackerman, 2000; Franchi et al., 2002; Katifori et al., 2010), were coded as binary presence/absence characters (see Part II of Table 1 for coded character states). Correlations were tested between six exine stratification characters: exine, tectum, eutectum (whether the tectum provides an effective seal against water loss), infratectum (presence of alveolar, granular, columellate, or structureless material beneath the tectum and above the foot layer or endexine), columellate infratectum, and granular infratectum, and two ecological characteristics: helo-hydrophytes or hy-

drophytes (hydrophytes are defined as plants adapted to aquatic environments, and helophytes to wet but marshy habitats; McDonald et al., 2002). This data matrix is presented in Appendix 4.

ANALYSES OF CHARACTER EVOLUTION

Of recent phylogenetic investigations focused on monocots (Davis et al., 2004; Tamura et al., 2004; Chase et al., 2006; Givnish et al., 2006, 2010; Graham et al., 2006; Petersen et al., 2006), the seven-gene phylogenetic tree of Chase et al. (2006) provides the most powerful study of relationships across the group to date (Givnish et al., 2010), with the broadest taxonomic coverage across the widest range of genetic loci (nuclear, mitochondrial, and chloroplast regions). The results were highly congruent with those of other recent phylogenetic studies.

To enable comparative studies based on a phylogenetic tree with branch lengths, a tree was generated based on the original DNA matrix of Chase et al. (2006), obtained from Mark Chase, containing 120 taxa in 71 families covering all 12 orders of monocots (following the Angiosperm Phylogeny Group III system) plus 16 outgroups of nine orders of the basal angiosperms, using maximum likelihood (ML) inference in RAxML (Stamatakis, 2006), including a simultaneous bootstrap analysis of 2000 replicates, under the GTRGAMMA model.

Two strategies for optimization of pollen characters were used: (1) analysis of the comprehensive dataset with Fitch parsimony and hierarchical Bayesian inference (abbreviated as CFP and CHB, respectively) and (2) analysis of the democratic dataset with Fitch parsimony, maximum likelihood, and hierarchical Bayesian inference (hereafter abbreviated as DFP, DML, and DHB, respectively). The ML method as implemented in Mesquite does not accept polymorphisms, which were numerous in our comprehensive dataset; therefore, only the democratic matrix was analyzed under ML. Ecological characters were analyzed only under CFP and CHB. A series of CFP analyses were conducted to determine differences in pollen evolutionary pattern on the much-debated alternative topologies within commelinids and Poales (Janssen & Bremer, 2004; Chase et al., 2006; Graham et al., 2006; Petersen et al., 2006; Givnish et al., 2006, 2010; Soltis et al., 2011; Barrett et al., 2012; Davis et al., 2012; see Fig. 1), with the same number of terminals as that of Chase et al. (2006) but in different phylogenetic skeletons as above.

FP and ML (using the Mk-1 model) optimizations were performed in Mesquite 2.75 (Maddison & Maddison, 2011), and HB optimizations using

Table 1. Pollen and ecological characters and their states used in analyses of character optimization and as defined in this study. Part I indicates character states for 19 pollen characters (1–19) and two ecological characters (20 and 21), which are mapped in Figure 7A, B. Part II indicates binary characters of pollen morphology (a1 to a6) and ecology (b1 and b2) that were used in analyses of correlated evolution. Part II is not mapped on Figure 7A, B.

Part I

1. Dispersal unit: 0, monad; 1, permanent tetrad (includes pseudomonads)
2. Polarity: 0, apolar; 1, heteropolar; 2, isopolar (or subisopolar)
3. Symmetry (in polar view): 0, bilateral; 1, radial; 2, asymmetrical
4. Basic shape: 0, boat-shaped; 1, globose; 2, filiform
5. Shape class: 0, oblate; 1, spheroidal; 2, prolate
6. Outline in polar view (amb), states as defined by Walker & Doyle (1975): 0, circular (longest equatorial axis [LA]/shortest equatorial axis [SEA] = 1); 1, elliptic ($1 < LA/SEA < 1.5$); 2, oblong ($1.5 \leq LA/SEA < 2$); 3, elongate ($LA/SEA \geq 2$)
7. Size (diameter of longest axis), states as defined by Walker & Doyle (1975): 0, small (10–24 μm); 1, medium (25–49 μm); 2, large (50–99 μm); 3, very large (100–199 μm); 4, gigantic ($> 200 \mu\text{m}$)
8. Aperture number: 0, zero; 1, one; 2, two; 3, three; 4, more than three
9. Aperture position: 0, polar: distal; 1, polar: proximal; 2, equatorial; 3, global
10. Aperture membrane: 0, smooth (without ectexine); 1, sculptured (with numerous ectexine elements but not operculate); 2, with operculum
11. Aperture shape: 0, colpate (when at the distal or proximal pole of a pollen grain, we usually term it sulcate); 1, porate; 2, zonate; 3, spiral; 4, syncolpate
12. Annulus: 0, absent; 1, present
13. Exine extent: 0, none or merely small patches appearing as sculpture (exineless); 1, homogeneous exine (atectate); 2, fully present
14. Tectum extent: 0, intectate (without a tectum but with sculpturing); 1, semitectate; 2, eutectate
15. Supratectal elements: 0, absent; 1, present
16. Supratectal element shape: 0, gemmate; 1, echinate; 2, verrucate
17. Tectum sculpture: 0, imperforate; 1, perforate (micro- and macro-); 2, reticulate (foveolate); 3, rugulate; 4, striate; 5, fossulate; 6, areolate; 7, cupulate
18. Infratectum structure: 0, columellate; 1, granulate; 2, intermediate between granulate and columellate. Terminology is taken from Doyle (2005).
19. Foot layer: 0, absent; 1, present
20. Pollination type: 0, self-pollination; 1, wind pollination; 2, insect pollination; 3, water pollination; 4, bat pollination; 5, bird pollination; 6, non-flying mammal pollination
21. Habitat moisture; states as defined by McDonald et al. (2002): 0, xerophytic (adapted to arid and low water availability soils); 1, mesophytic (adapted to soils of moderate moisture content); 2, helophytic (adapted to wet but marshy habitats); 3, hydrophytic (adapted to aquatic environments).

Part II

- a1. Exine: 0, absent; 1, present
- a2. Tectum: 0, absent; 1, present
- a3. Eutectum: 0, absent; 1, present
- a4. Infratectum: 0, absent; 1, present
- a5. Columellae: 0, absent (all other infratectum types); 1, present
- a6. Granules: 0, absent (all other infratectum types); 1, present
- b1. Helo-hydrophytes: 0, absent (all other habitat types); 1, present (plant adapted to wet and marsh or aquatic habitat)
- b2. Hydrophytes: 0, absent (all other plant types); 1, present (plant adapted to aquatic habitat)

BayesTraits 1.0 (available from <http://www.evolution.rdg.ac.uk/BayesTraits.html>). Both CHB and DHB analyses were run in BayesTraits using BayesMultistate with empirically selected, most appropriate settings: a reversible-jump hyperprior model, prior distribution range for uniform seeding distribution (0–10 distribution, 0–20 distribution, or 0–30 distribution depending on the character), rate variations ranging from 5 to 35, a sampling frequency of 300 to 800 generations, a burn-in of 10,000 generations, and a total of 5,000,000 generations.

In the discussion that follows, the state of the most recent common ancestor (MRCA) was presented only for derived states, in contrast to the plesiomorphic states of the monocots. For ML and HB analyses, we took the state with the highest likelihood or probability at each node to represent the state of this node on the phylogeny.

TESTS OF CORRELATED EVOLUTION

BayesDiscrete tests for correlated evolution on 12 pairs of character states from the palynological and

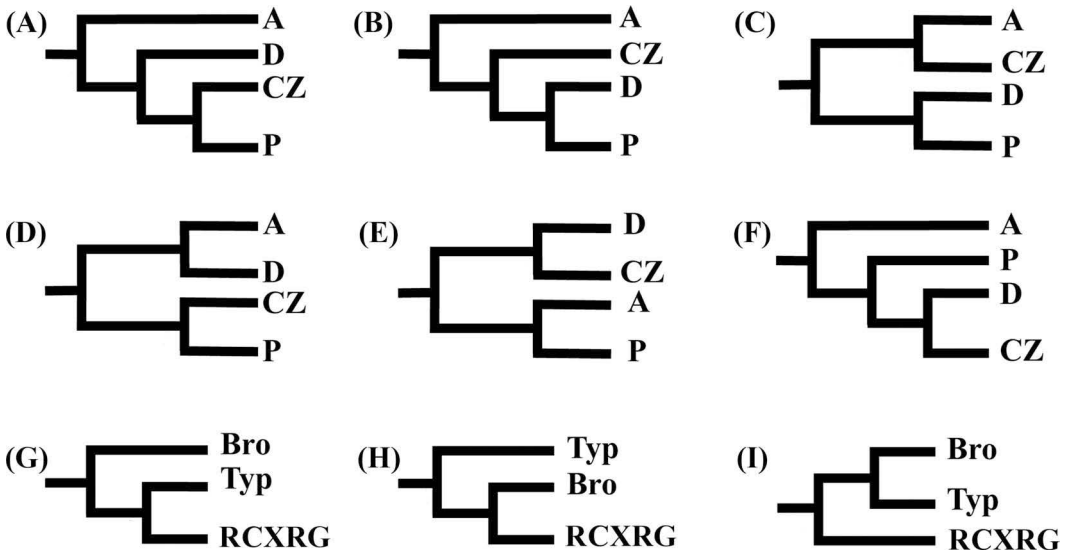


Figure 1. Nine alternative topologies (differing in terms of the internal relationships among commelinids and the basalmost branching group of Poales). A indicates the Arecales; D, Dasypogonales; P, Poales; CZ, Commelinales–Zingiberales; Bro, Bromeliaceae; Typ, Typhaceae; and RCXRG indicates Rapateaceae and the clade comprising the cyperids, xyrids, restiids, and graminids within Poales. The nine topologies correspond to the following recent phylogenetic studies: —A. Janssen & Bremer (2004, p. 390), maximum likelihood (ML) tree in this study. —B. Chase et al. (2006, seven-gene maximum parsimony [MP] tree, pp. 67–68), Peterson et al. (2006, four-gene summarized tree, p. 56, fig. 2A). —C. Chase et al. (2006, four-gene MP tree, pp. 69–70). —D. Givnish et al. (2010, ML tree, p. 592), Barrett et al. (2012, pp. 9, 12), Davis et al. (2012, p. 329). —E. Graham et al. (2006, p. 6), Givnish et al. (2010, MP tree, p. 590). —F. Givnish et al. (2006, p. 39). —G. Chase et al. (2006, seven-gene MP tree, pp. 67–68), Givnish et al. (2010, pp. 590, 592). —H. Graham et al. (2006, p. 6). —I. Chase et al. (2006, four-gene MP tree, pp. 69–70), ML tree in this study, Soltis et al. (2011, p. 7).

ecological data were conducted under ML models (an independent model, I, and a dependent model, D) using the Markov chain Monte Carlo (MCMC) method under the Discrete option in BayesTraits 1.0. A likelihood score representing goodness of fit was calculated for the two models (Table 1, Part II). The likelihood ratio (LR) was determined by $LR = 2$ (likelihood [dependent model]-likelihood [independent model]) and was tested against a χ^2 distribution with four degrees of freedom (following Pagel, 1994). Transition rates for correlated characters were estimated following Pagel and Meade (2006), with eight possible character transitions for each of the six pairs of traits (Fig. 2).

A total of 5,000,000 generations with a burn-in period of 10,000 generations and a sampling frequency of 100 generations was used for both dependent and independent models, using a reversible-jump hyperprior model, exponential prior distribution, and rate variations ranging from 8 to 20. The difference in the harmonic means of the log-likelihoods between the two models was calculated twice. The log Bayes factor value (log BF) was calculated to indicate the degree of evolutionary correlation between two characters: with values of two to five representing a positive correlation, greater

than five a strong correlation, and greater than 10 a very strong correlation (Pagel & Meade, 2006).

We then tested specific hypotheses of contingent evolution by restricting two of the rates to be equal following the method of Pagel (1994) and Schmitt et al. (2009) to test if the loss/gain of a palynological character is related to the absence/presence of an ecological character (Table 1, Part II). The two rate coefficients per trait were created from a model that allows the characters to evolve independently on the tree in the BayesDiscrete tests for correlated evolution. We compared this seven-parameter restricted dependent model to a full dependent model using the likelihood ratio test with one degree of freedom based on Pagel (1994). That is, a significant likelihood ratio would indicate that the parameters were significantly different from one another, demonstrating that the state of one trait influences the direction of evolution of the other. Finally, the exclusiveness of character state changes was tested by restricting one of the rates to zero and recalculating the likelihood ratio of the model. We then compared the restricted seven-parameter model to the unrestricted dependent model using a χ^2 test with one degree of freedom. A significant value would suggest

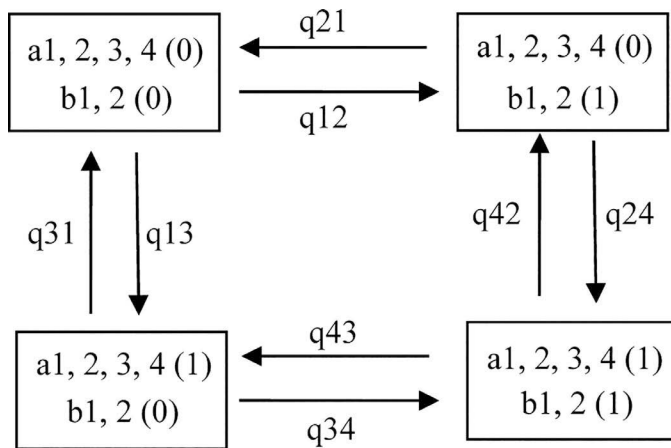


Figure 2. Rate parameters for the eight possible transitions between four pairs of binary pollen characters and binary ecological characters under a model of dependent evolution, exine (character [char.] a1) and helo-hydrophytes (char. b1) or hydrophytes (char. b2), tectum (char. a2) and helo-hydrophytes (char. b1) or hydrophytes (char. b2), ectectum (char. a3) and helo-hydrophytes (char. b1) or hydrophytes (char. b2), infractectum (char. a4) and helo-hydrophytes (char. b1) or hydrophytes (char. b2); characters and states follow Table 1. Arrows indicate direction of transition (only one state transfer while another is stable).

that a character trait was not gained or lost in the presence of another character trait.

Three pollen binary characters, ectectum, columellate infractectum, and granular infractectum, were not analyzed by the contingent evolution test because they were confirmed to be negatively correlated with helo-hydrophyte plants in the BayesDiscrete test.

RESULTS

PALYNOLOGICAL OBSERVATIONS

The pollen morphology of 20 representative taxa observed under LM and SEM is described below to exemplify the diversity of pollen characters and their states in the monocots (Figs. 3–6). The species are presented in phylogenetic order, corresponding to their placement in Figure 7.

Acorus gramineus Sol. ex Aiton (Acoraceae, Acorales, Fig. 3A–C) has pollen dispersed as monads; grains heteropolar, bilaterally symmetrical, boat-shaped, amb usually elliptic; size small (ca. 13–20 μm); monosulcate, aperture distal, with sculptured aperture membrane; tectum with scattered perforations.

Epipremnum pinnatum (L.) Engl. (Araceae, Alismatales, Fig. 3D–F) has pollen dispersed as monads; grains heteropolar, radially symmetrical, globose (spheroidal), amb circular; size medium (ca. 26–30 μm); zonate, aperture equatorial; tectum perforate to fossulate.

Alisma orientale (Sam.) Juz. (Alismataceae, Alismatales, Fig. 3G, H) has pollen dispersed as monads;

grains apolar, asymmetrical, globose (spheroidal), amb circular; size small to medium (ca. 18–22 μm); pantoporate, apertures global, with sculptured aperture membrane; supractectal elements echinate; tectum perforate.

Zostera marina L. (Zosteraceae, Alismatales, Fig. 3I, J) has pollen dispersed as monads; grains apolar, filiform; size gigantic (> 1000 μm long); inaperturate; without exine.

Petrosavia stellaris Becc. (Petrosaviaceae, Petrosaviales, Fig. 3K, L) has pollen dispersed as monads; grains heteropolar, bilaterally symmetrical, boat-shaped, amb elliptic; size small (ca. 16–22 μm); monosulcate, aperture distal; tectum reticulate.

Dioscorea melanophyma Prain & Burkill (Dioscoreaceae, Dioscoreales, Fig. 4A, B) has pollen dispersed as monads; grains subisopolar, bilaterally symmetrical, globose (oblate), amb elliptic; size small (ca. 14–17 μm); disulculate not situated at a pole, apertures equatorial; tectum fossulate to reticulate.

Stemona tuberosa Lour. (Stemonaceae, Pandanales, Fig. 4C, D) has pollen dispersed as monads; grains heteropolar, bilaterally symmetrical, boat-shaped, amb elliptic; size medium (ca. 26–30 μm); monosulcate, aperture distal; tectum rugulate.

Trillium maculatum Raf. (Melanthiaceae, Liliales, Fig. 4E, F) has pollen dispersed as monads; grains apolar, radially symmetrical, globose (spheroidal), amb circular; size medium (ca. 33–40 μm); inaperturate; tectum rugulate.

Tulipa iliensis Regel (Liliaceae, Liliales, Fig. 4G–I) has pollen dispersed as monads; grains heteropolar,

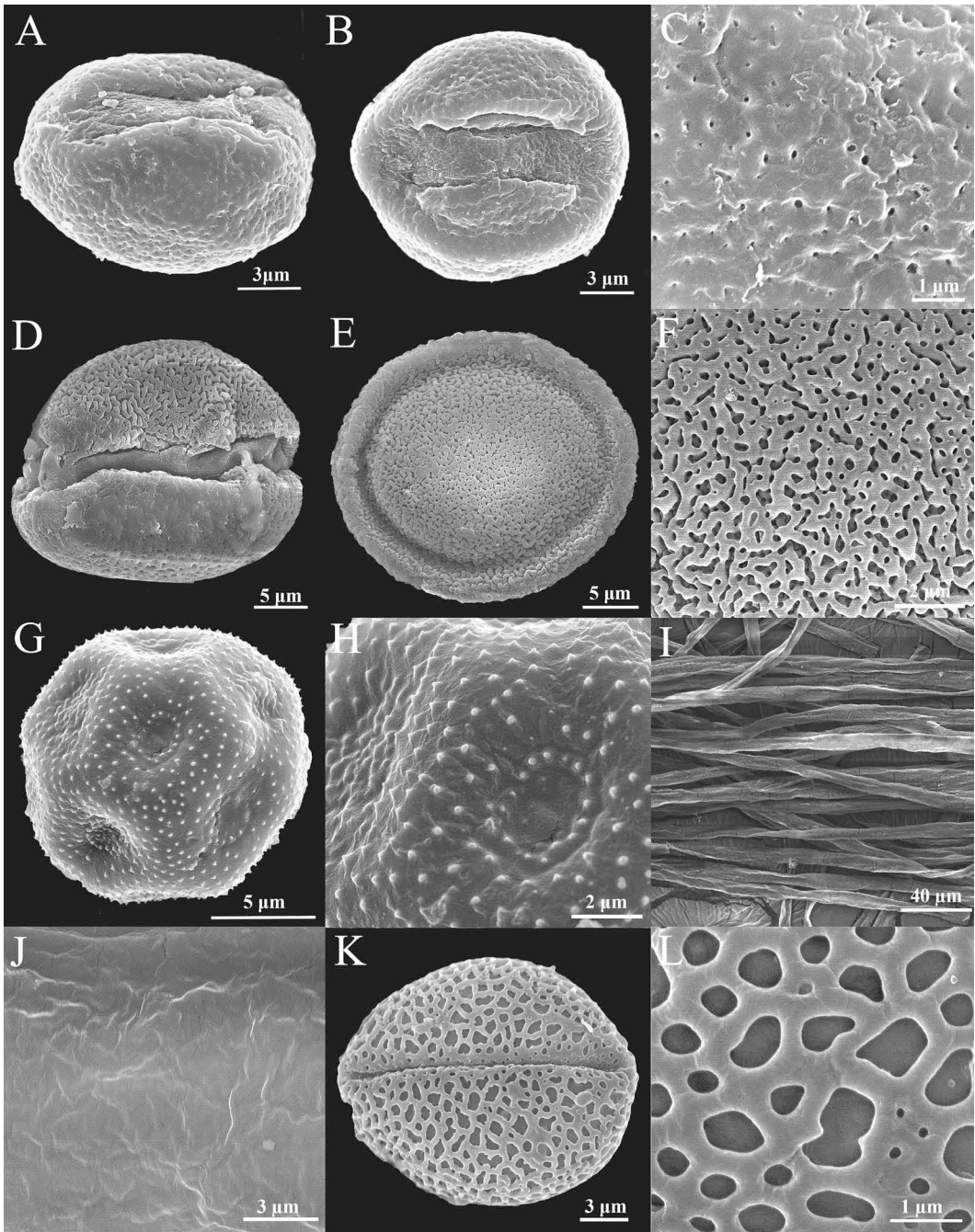


Figure 3. SEMs of monocot pollen, arranged following the topology of Chase et al. (2006). A–C. *Acorus gramineus* Sol. ex Aiton, Acoraceae, Acorales. —A. Equatorial view, showing monad, boat-shaped pollen grain, of small size, with monosulcate aperture. —B. Distal view. —C. Detail of tectum with scattered perforations. D–F. *Epipremnum pinnatum* (L.) Engl., Araceae, Alismatiales. —D. Equatorial view, showing expanded apertural ring (zonate pollen). —E. Polar view. —F. Detail of fossulate to reticulate tectum. G, H. *Alisma orientale* (Sam.) Juz., Alismataceae, Alismatales. —G. Whole grain, pantoporate pollen. —H. Detail of echinate supratectal elements. I, J. *Zostera marina* L., Zosteraceae, Alismatales. —I. Filiform, inaperturate pollen grain. —J. Detail of unsculptured, very thin, and highly reduced exine. K, L. *Petrosavia stellaris* Becc., Petrosaviaceae, Petrosaviales. —K. Polar view, showing boat-shaped pollen grain of small size. —L. Detail of reticulate tectum.

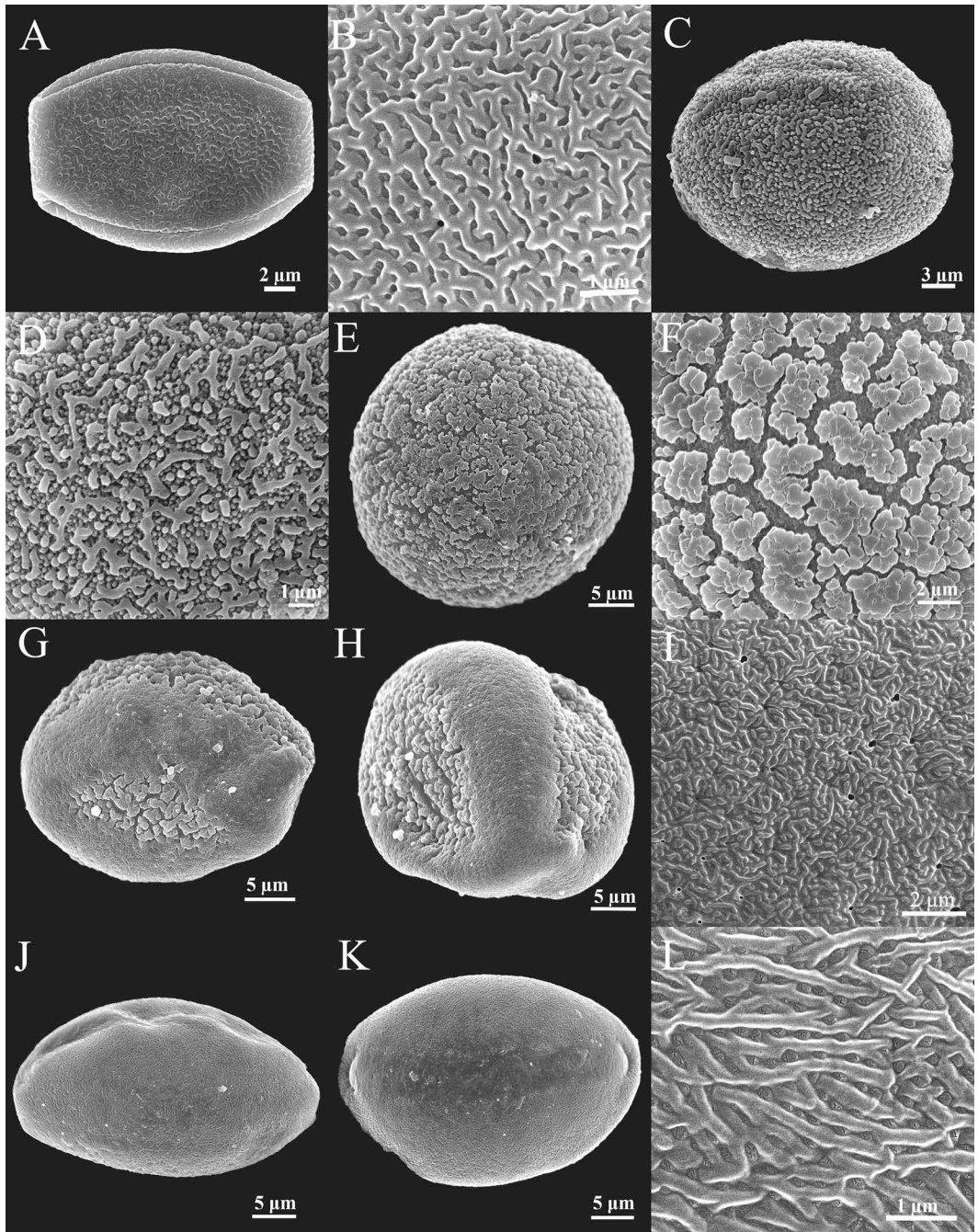


Figure 4. SEMs of monocot pollen, arranged following the topology of Chase et al. (2006). A, B. *Dioscorea melanophyma* Prain & Burkill, Dioscoraceae, Dioscoreales. —A. Polar view, showing disulculate apertures. Note that the pollen grain shown here is rather anomalous; grains of most examples of this taxon are rather more globose. —B. Detail of fossulate to reticulate tectum. C, D. *Stemona tuberosa* Lour., Stemonaceae, Pandanales. —C. Equatorial view, showing monosulcate aperture. —D. Detail of rugulate tectum. E, F. *Trillium maculatum* Raf., Melanthiaceae, Liliales. —E. Spheroidal and inaperturate pollen grain. —F. Detail of rugulate tectum. G–I. *Tulipa iliensis* Regel, Liliaceae, Liliales. —G. Equatorial view, showing colpi located at distal and proximal poles. —H. Oblique equatorial view, showing two colpi located at the proximal pole. —I. Detail of rugulate tectum. J–L. *Allium cyaneum* Regel, Liliaceae, Liliales. —J. Equatorial view, pollen grain of medium size. —K. Distal polar view. —L. Detail of striate tectum.

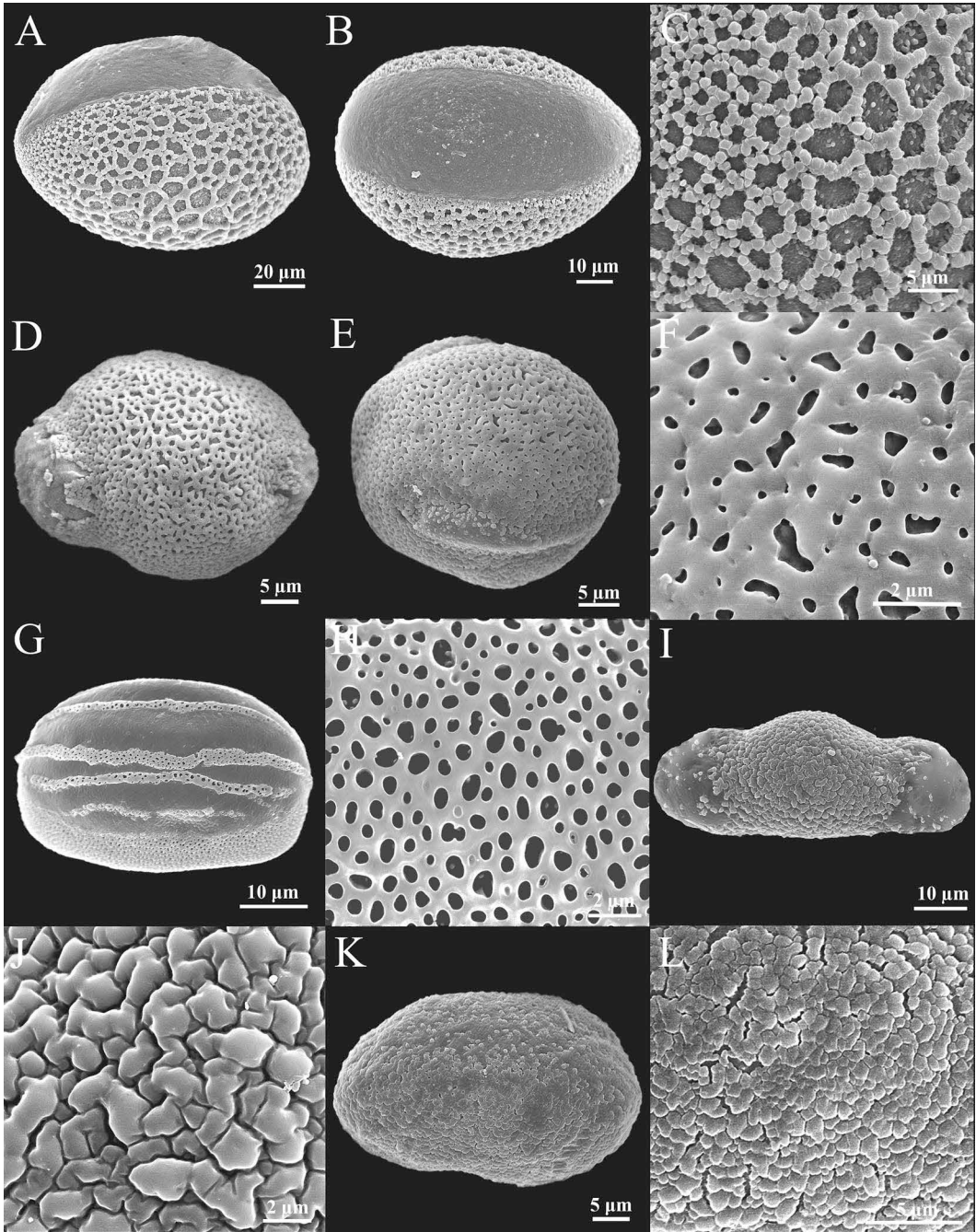


Figure 5. SEMs of monocot pollen, arranged following the topology of Chase et al. (2006). A–C. *Hemerocallis fulva* (L.) L., Xanthorrhoeaceae, Asparagales. —A. Equatorial view, showing very large-size grain. —B. Distal polar view. —C. Detail of reticulate tectum. D–F. *Calamus nambariensis* Becc., Arecaceae, Arecales. —D. Equatorial view. —E. Polar view, showing two equatorially located colpi. —F. Detail of perforate to reticulate tectum. G, H. *Calectasia cyanea* R. Br., Dasypogonaceae, Dasypogonales. —G. Distal polar view, showing monosulcate, operculate aperture. —H. Detail of foveolate tectum. I, J. *Anigozanthos viridis* Endl., Haemodoraceae, Commelinales. —I. Polar view, showing two equatorially located pores. —J. Detail of rugulate tectum. K, L. *Cartonema parviflorum* Hassk., Commelinaceae, Commelinales. —K. Distal polar view, showing sculptured aperture membrane. —L. Detail of areolate to rugulate tectum.

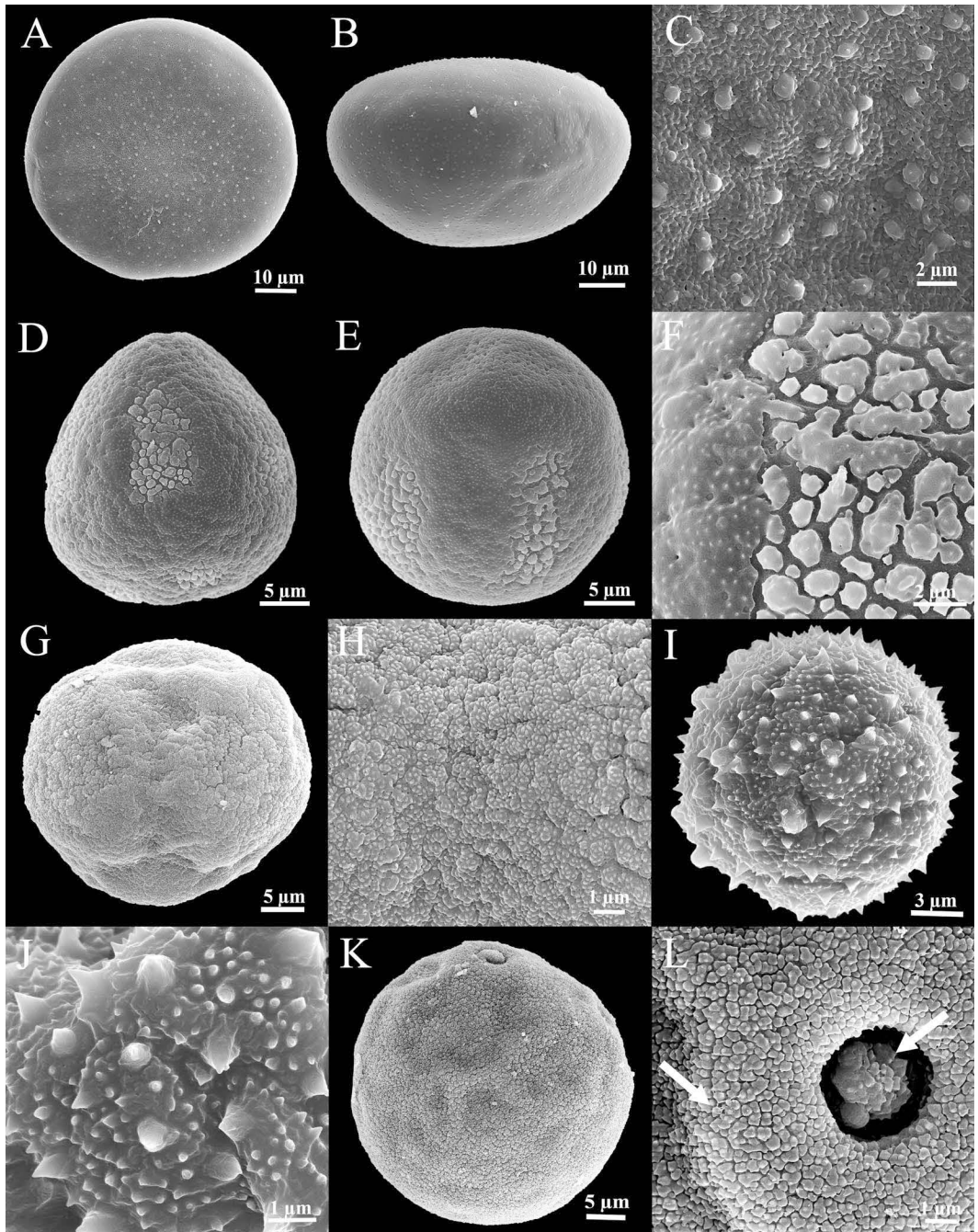


Figure 6. SEMs of monocot pollen, arranged following the topology of Chase et al. (2006). A–C. *Heliconia subulata* Ruiz & Pav., Heliconiaceae, Zingiberales. —A. Distal polar view. —B. Heteropolar, oblate, large, inaperturate pollen grain. —C. Surface of distal polar view, showing granular exinous residues. D–F. *Carex scaposa* C. B. Clarke, Cyperaceae, Poales. —D. Equatorial view, showing single poroid aperture at the distal pole and four to five apertures in the equatorial region. —E. Proximal polar view. —F. Detail of gemmate suprategumentary elements. G, H. *Juncus sikkimensis* Hook. f., Juncaceae, Poales. —G. Entire tetrad. —H. Detail of areolate tectum and gemmate suprategumentary elements. I, J. *Eriocaulon cristatum* Mart., Eriocaulaceae, Poales. —I. Small, spiral pollen grain. —J. Detail of echinate suprategumentary elements. K, L. *Dendrocalamopsis beecheyana* (Munro) Keng f. var. *pubescens* (P. F. Li) Keng f., Poaceae, Poales. —K. Equatorial view, showing single aperture at the distal pole. —L. Detail of areolate tectum; arrows indicate pore with an operculum and annulus.

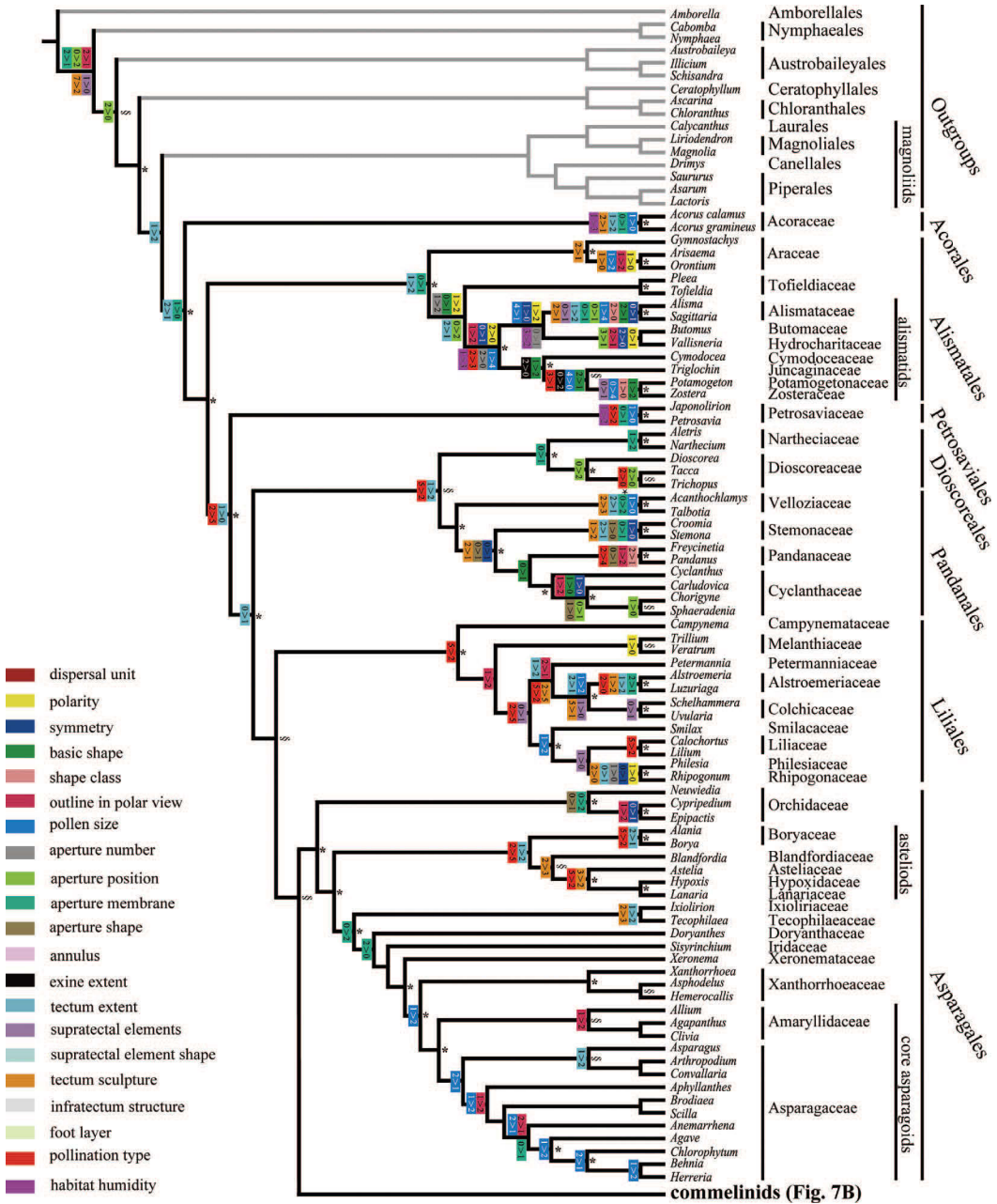


Figure 7. Inferences of character state change for 19 pollen characters and two ecological characters reconstructed with hierarchical Bayesian inference using comprehensive coding on a maximum likelihood phylogeny, based on the molecular data of Chase et al. (2006). Character state changes assume a single transition between differing states at adjacent nodes. Changes on terminal branches are not shown. Numbers on bars indicate the character state transition from the lower to upper node. Character boxes and the number within indicate character state change, following Table 1. §, bootstrap (BP) = 100; *, BP 90%–99%. —A. Seven orders (Acorales, Alismatales, Petrosaviales, Dioscoreales, Pandanales, Liliales, and Asparagales) and outgroups are shown.

B

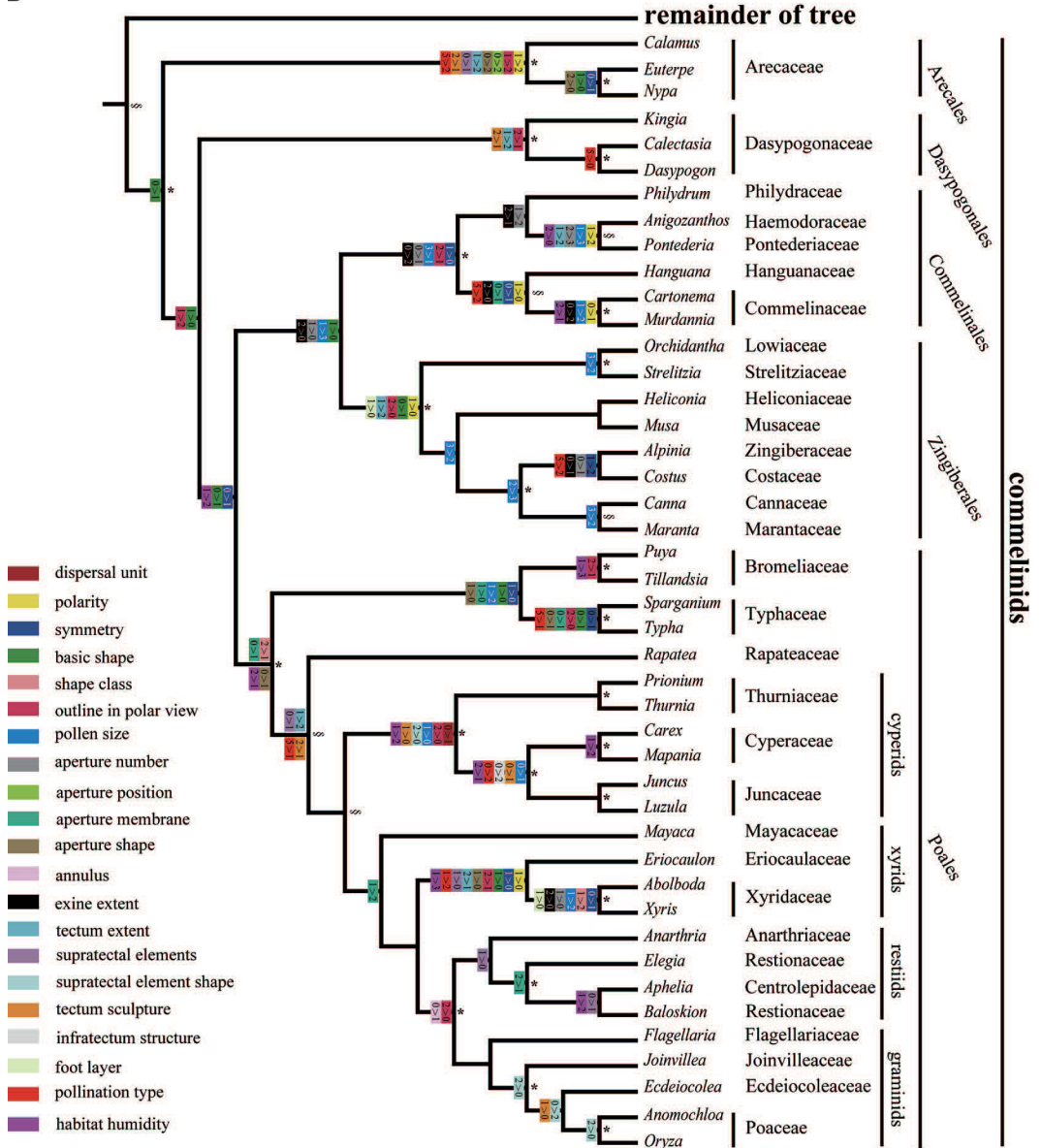


Figure 7. Continued. —B. The commelinid clade is shown.

bilaterally symmetrical, boat-shaped, amb elongate; size medium (ca. 40–45 μm); trisulcate, one aperture distal, two apertures proximal, with sculptured aperture membrane; tectum rugulate.

Allium cyaneum Regel (Amaryllidaceae, Asparagales, Fig. 4J–L) has pollen dispersed as monads; grains heteropolar, bilaterally symmetrical, boat-shaped, amb elliptic; size medium (ca. 28–40 μm); monosulcate, aperture distal; tectum striate.

Hemerocallis fulva (L.) L. (Xanthorrhoeaceae, Asparagales, Fig. 5A–C) has pollen dispersed as monads; grains heteropolar, bilaterally symmetrical, boat-shaped, amb oblong; size large to very large (ca. 85–105 μm); monosulcate, aperture distal; tectum reticulate.

Calamus nambariensis Becc. (Arecaceae, Arecales, Fig. 5D–F) has pollen dispersed as monads; grains heteropolar, bilaterally symmetrical, globose

(spheroidal), amb elliptic; size medium (ca. 30–38 μm); disulcate, aperture equatorial; tectum perforate-reticulate.

Calcectasia cyanea R. Br. (Dasypogonaceae, Dasypogonales, Fig. 5G, H) has pollen dispersed as monads; grains heteropolar, bilaterally symmetrical, boat-shaped, amb oblong; size medium to large (ca. 38–56 μm); monosulcate, aperture distal with a unique operculum, not reported elsewhere in angiosperms, comprising a sulcus provided with three elongated, more or less parallel strips of membrane (Chanda & Ghosh, 1976); tectum foveolate-reticulate.

Anigozanthos viridis Endl. (Haemodoraceae, Commelinales, Fig. 5I, J) has pollen dispersed as monads; grains subisopolar, bilaterally symmetrical, globose (oblate), amb elongate; size medium to large (ca. 45–65 μm); diporate, apertures equatorial; tectum rugulate.

Cartonema parviflorum Hassk. (Commelinaceae, Commelinales, Fig. 5K, L) has pollen dispersed as monads; grains heteropolar, bilaterally symmetrical, boat-shaped, amb oblong; size medium (ca. 35–42 μm); monosulcate, aperture distal; tectum areolate to rugulate.

Heliconia subulata Ruiz & Pav. (Heliconiaceae, Zingiberales, Fig. 6A–C) has pollen dispersed as monads; grains heteropolar, radially symmetrical, globose (oblate), amb circular; size large (ca. 64–68 μm); inaperturate; exineless with granulate elements.

Carex scaposa C. B. Clarke (Cyperaceae, Poales, Fig. 6D–F) has pollen grains dispersed as “pseudomonads” (permanent tetrads with three rudimentary grains); grains heteropolar, asymmetrical, globose (prolate), amb circular; size medium (ca. 24–28 μm); polyporate (usually with five or six poroids), apertures distal or equatorial, respectively; suprategal elements gemmate; tectum perforate.

Juncus sikkimensis Hook. f. (Juncaceae, Poales, Fig. 6G, H) has pollen dispersed as tetrads; tetrads radially symmetrical and globose (spheroidal); tetrads of medium size (ca. 34–38 μm); individual grains heteropolar and radially symmetrical, globose (spheroidal), amb circular; monoporate, aperture distal; suprategal elements gemmate; tectum areolate with gemmae and perforations.

Eriocaulon cristatum Mart. (Eriocaulaceae, Poales, Fig. 6I, J) has pollen dispersed as monads; grains apolar, asymmetrical, globose (spheroidal), amb circular; size small (ca. 16–18 μm); aperture spiral; suprategal elements echinate; tectum perforate.

Dendrocalamopsis becheyana (Munro) Keng f. var. *pubescens* (P. F. Li) Keng f. (Poaceae, Poales, Fig. 6K, L) has pollen dispersed as monads; grains heteropolar, radially symmetrical, globose (spheroidal), amb

circular; size medium (ca. 30–34 μm); monoporate, operculate, with a surrounding annulus, aperture distal; suprategal elements gemmate; tectum areolate.

POLLEN VARIATION

Most of the monocots studied possess heteropolar pollen grains dispersed as monads, with distal monosulcate or monosulcate-derived (e.g., a sulcus reduced to a pore) apertures, and a columellate infrategal, with an exine and foot layer but without an operculum or annulus. In addition to these generally consistent character states, apertural characters in particular show taxonomically ordered patterns of variation: inaperturate pollen predominates in the orders Alismatales and Zingiberales, whereas monosulcate pollen occurs in most taxa within the Liliales and Asparagales, in near-basal lineages such as *Butomus* L. (Butomaceae, Alismatales), in *Gymnostachys* R. Br. and *Orontium* L. (Araceae, Alismatales), and in some genera of Bromeliaceae (Poales). Highly specialized and unique pollen shapes (such as filiform in *Zostera* L.) with a highly reduced exine occur in the seagrass families (Cymodoceaceae, Potamogetonaceae, and Zosteraceae). Pollen morphological variation was observed to exist even within genera (in our comprehensive dataset for monocots, Appendix 2), with especially high variation found in *Dioscorea* L. (Dioscoreales), *Pandanus* Parkinson, and *Stemona* Lour. (both in Pandanales), as well as *Trillium* L. (Liliales), with lower variability seen in *Alisma* L. (Alismatales), *Canna* (Zingiberales), *Juncus* L., and *Typha* L. (both Poales).

ANCESTRAL STATE RECONSTRUCTION

The topology of the new ML tree based on DNA data from Chase et al. (2006) used for character optimization showed some incongruence with the original seven-gene tree derived from maximum parsimony (MP) analysis (Chase et al., 2006). Discrepancies included the positions of Boryaceae, Campynemataceae, Dasypogonaceae, Doryanthaceae, Heliconiaceae, Ixioliriaceae, Mayacaceae, Musaceae, and Typhaceae, for the clade comprising Eriocaulaceae and Xyridaceae, for the position of the genera *Aphelia* R. Br., *Baloskion* Raf., and *Elegia* L., as well as internal relationships within the Asparagaceae s.l., which includes Agavaceae, Aphyllanthaceae, Hyacinthaceae, Laxmanniaceae, Ruscaceae, and Themidaceae (Angiosperm Phylogeny Group III, 2009). Nevertheless, these conflicts were not well supported, with mainly low (bootstrap values below 50%) or

moderate (bootstrap values 50%–80%) support in one or both trees (cf. Fig. 7).

Pollen characters. Of the 19 pollen characters studied, only pollen dispersal unit (cf. Table 1, character [char.] 1) evolved unequivocally throughout all nodes with all five methods. Almost all pollen characters displayed unambiguous plesiomorphic states for monocots as a whole in all five methods (17 characters in analysis of the comprehensive dataset with Fitch parsimony inference [CFP], 19 in analysis of the comprehensive dataset with hierarchical Bayesian inference [CHB], 17 in analysis of the democratic dataset with Fitch parsimony inference [DFP], 19 in analysis of the democratic dataset with maximum likelihood inference [DML], and 18 in analysis of the democratic dataset with hierarchical Bayesian inference [DHB]). The most consistent plesiomorphic states across all five methods were dispersal unit (char. 1) as monad, polarity (char. 2) as heteropolar, pollen size (char. 7) as medium, aperture number (char. 8) as one, aperture membrane (char. 10) as sculptured, aperture shape (char. 11) as colpate, annulus (char. 12) as absent, exine extent (char. 13) as fully present, supratectal elements (char. 15) as absent, infratectum structure (char. 18) as columellate, and foot layer (char. 19) as present. Unambiguous (or probable) plesiomorphic states for the remaining seven characters were not consistently reconstructed across all five methods (char. 5, shape class, and char. 16, supratectal element shape, are inapplicable states for this node). For symmetry in polar view (char. 3), pollen grains were bilateral using CFP, CHB, DML, and DHB, and bilateral or radial under DFP. For basic pollen shape (char. 4), the plesiomorphic state was found to be boat shaped using CHB, DFP, DML, and DHB, and boat shaped or globose under CFP. For outline in polar view (char. 6), pollen grains were found to be circular using DFP and DML, elliptic under CHB, oblong under DHB, and circular or elliptic under CFP. For aperture position (char. 9), a distal position was recovered using DFP, DML, CFP, and CHB, and an equatorial one under DHB; for tectum (char. 14), pollen was semitectate using CFP, DFP, DML, and DHB, and eutectate under CHB. For tectum sculpture (char. 17), pollen was recovered as reticulate using CHB, DFP, DML, and DHB, and perforate or reticulate under CFP.

All 19 pollen characters studied were inferred to exhibit unambiguous state changes on at least one lineage of monocots, using all five analytical methods. The state changes observed at family level or above are summarized in Table 2. Tectum sculpture, aperture membrane, and pollen size for

characters 17, 10, and 7, respectively, had the greatest number of inferred state changes. Pollen dispersal unit (char. 1), annulus (char. 12), infratectum structure (char. 18), and foot layer (char. 19) had the fewest number of changes. Of the 12 orders of monocots investigated, Zingiberales were subtended by the greatest number of state changes (9), Alismatales and Asparagales by the fewest (zero).

Ecological characters. The two ecological characters, pollination type and habitat moisture, were optimized onto the new ML tree using CFP and CHB methods. For pollination type (char. 20), the plesiomorphic state for monocots was found to be wind pollination (under both CFP and CHB). Water pollination was inferred to have evolved on the lineage leading to alismatids (CHB). Herein, alismatids we sampled include the Alismataceae, Butomaceae, Hydrocharitaceae, Cymodoceaceae, Juncaginaceae, Potamogetonaceae, and Zosteraceae (Fig. 7). Shifts to wind pollination occurred in the clade comprising the alismatid families Juncaginaceae, Potamogetonaceae, and Zosteraceae (CHB), in the graminid–restiid clade (CFP), in the Poales excluding Bromeliaceae and Typhaceae (CHB), Typhaceae (CFP, CHB), and Thurniaceae (CFP). Beyond the Poaceae, graminids include the Ecdeiocoleaceae, Joinvilleaceae, and Flagellariaceae; restiids encompass the Anarthriaceae, Centrolepidaceae, and Res-toniaceae.

For habitat moisture (char. 21), the plesiomorphic state for monocots was inferred as mesic (CFP and CHB). Xeric or drier habitats evolved on the clade comprising Haemodoraceae and Pontederiaceae (CHB). Wetter habitats were found to evolve on six lineages including the clade comprising Commelinales and Zingiberales, and Thurniaceae (Poales; CFP or CHB). Wet habitats evolved on four lineages, i.e., Acorales, core alismatids (Alismatales), Typhaceae (Poales), and the clade comprising Eriocaulaceae and Xyridaceae (CFP and/or CHB; cf. Table 2).

POLLEN CHARACTER STATE CHANGES

The minimum number of state change steps of each of the 19 pollen characters optimizing on the nine alternative topologies tested (Fig. 1) were counted in the CFP analysis. Fifteen characters (excluding symmetry, basic shape, shape class, and outline in polar view [amb]) possessed the same minimum number of steps throughout all nine topologies. Within the topologies, A through F focus on the controversial relationships among major clades within commelinids, and topologies A, D, and E yield the fewest steps for symmetry and basic shape.

Table 2. Pollen character state changes inferred from comprehensive and democratic datasets of 19 pollen morphological and two ecological characters for lineages at or above family level in monocots analyzed with Fitch parsimony (FP), maximum likelihood (ML), and hierarchical Bayesian inference (HB). Pollen characters and their states (in brackets) correspond to Table 1. Superscripts refer to the number of the method used: ¹CFP, ²CHB, ³DFP, ⁴DML, and ⁵DHB.

Taxon	Characters and states	
	Pollen characters	Ecological characters
Acorales	7 (0 ¹²⁴), 14 (2 ¹³⁴⁵), 17 (1 ²³⁴⁵)	21 (3 ²)
Alismataceae	3 (2 ⁴), 4 (1 ²⁵), 5 (1 ²⁵), 6 (0 ²⁵), 7 (0 ⁵), 8 (4 ²⁴⁵), 11 (1 ²⁵), 14 (2 ¹³⁵), 15 (1 ¹²³⁴⁵), 17 (1 ²³⁴⁵)	
Alismatales	None	
Alismatids	2 (0 ²⁴⁵), 3 (1 ²), 4 (1 ³), 6 (0 ⁵ , 2 ²), 7 (4 ²⁵), 8 (0 ²⁴⁵)	20 (3 ²), 21 (3 ²)
Alstroemeriaceae	7 (2 ³), 17 (3 ⁵)	
Amaryllidaceae	6 (2 ²), 7 (2 ³)	
Araceae	14 (2 ¹³⁴⁵), 17 (1 ²³⁴⁵)	
Arecales	2 (2 ²⁴⁵), 4 (1 ⁴), 6 (2 ²), 9 (2 ²⁴), 11 (2 ²), 14 (2 ³), 15 (1 ²), 17 (1 ²⁵)	
Asparagaceae	None	
Asparagales	None	
Asparagales–commelinids	10 (0 ⁴)	
Asparagales with Orchidaceae excluded	None	
Asteliods	None	20 (5 ²)
Boryaceae	14 (1 ²)	
Bromeliaceae	6 (1 ²⁴), 7 (2 ³)	20 (5 ¹)
Colchicaceae	15 (1 ²⁵), 17 (1 ³)	
Commelinaceae	7 (2 ²⁵)	
Commelinaceae–Hanguanaceae	2 (0 ³), 3 (1 ²⁵), 7 (0 ³), 13 (0 ²⁵)	
Commelinales	6 (1 ³)	
Commelinales–Zingiberales	7 (2 ³ , 3 ²), 8 (0 ³), 13 (0 ²⁵)	21 (2 ¹)
Commelinales–Zingiberales–Poales	3 (1 ²⁵), 4 (1 ²⁴), 5 (0 ²⁵)	21 (2 ¹)
Commelinids	4 (1 ²⁵), 10 (0 ¹³)	
Commelinids with Arecales excluded	6 (2 ²), 7 (2 ³), 9 (0 ³), 14 (2 ⁴)	
Core asparagoid	None	
Cyclanthaceae	None	
Cyclanthaceae–Pandanaeae	3 (1 ¹⁴), 4 (1 ¹²³⁴), 5 (0 ³), 10 (0 ¹³⁴), 11 (1 ¹³⁴), 14 (2 ³⁴), 17 (1 ³⁴)	
Cyperaceae	3 (2 ²⁵)	21 (2 ²)
Cyperids	1 (1 ¹²³⁴⁵), 6 (0 ²), 7 (0 ²⁵), 11 (1 ¹³), 14 (2 ⁴), 15 (1 ⁴), 16 (0 ²⁵), 17 (0 ²⁵ , 1 ⁴)	21 (2 ²)
Dasypogonales	7 (2 ⁴), 14 (2 ⁴⁵), 17 (1 ²⁴⁵)	
Dioscoreaceae	9 (2 ²), 14 (2 ²⁴⁵), 17 (1 ³)	
Dioscoreales	5 (1 ³), 9 (2 ²⁵), 10 (1 ³ , 2 ²), 16 (1 ³)	
Dioscoreales–Pandanales	None	
Eriocaulaceae–Xyridaceae	2 (0 ²⁵), 6 (1 ³), 14 (1 ³)	21 (3 ²)
Graminids	None	
Haemodoraceae–Pontederiaceae	2 (2 ²⁵), 7 (2 ⁵ , 3 ²), 8 (2 ³⁴ , 3 ²), 14 (2 ⁵)	21 (0 ²)
Ixioliriaceae–Tecophilaeaceae	6 (1 ³), 10 (2 ⁴), 14 (2 ³), 17 (3 ²⁵)	
Juncaceae	None	
Liliaceae	6 (2 ⁴)	
Liliales	6 (2 ¹³)	
Lowiaceae–Strelitziaceae	7 (2 ² , 3 ⁴⁵)	
Melanthiaceae	2 (0 ²⁵), 13 (0 ³), 19 (0 ³)	
Monocots	6 (1 ²⁴⁵), 7 (0 ²⁵), 9 (0 ³), 10 (0 ²⁵), 14 (1 ²)	
Monocots–magnoliids	6 (2 ²)	
Musaceae–Heliconiaceae	None	
Nartheciaceae	7 (0 ³), 10 (2 ²⁵), 17 (1 ²)	
Orchidaceae	10 (2 ²⁵), 11 (1 ³)	
Pandanaceae	5 (1 ³ , 2 ²), 6 (2 ²), 7 (0 ²⁴⁵), 12 (1 ²⁵), 13 (1 ³), 17 (0 ²)	20 (4 ²)
Pandanales	14 (2 ⁵)	

Table 2. Continued.

Taxon	Characters and states	
	Pollen characters	Ecological characters
Petermanniaceae–Alstroemeriaceae– Colchicaceae	17 (5 ²⁵)	
Petrosaviales	7 (0 ²⁵), 14 (0 ³)	21 (2 ³)
Philesiaceae–Rhipogonaceae	2 (0 ²⁵), 3 (1 ²⁵), 4 (1 ³), 6 (1 ³), 8 (0 ²), 15 (1 ²), 17 (0 ²⁵)	
Philydraceae–Haemodoraceae– Pontederiaceae	8 (2 ²⁵), 13 (1 ³)	
Poaceae	10 (2 ⁴), 16 (0 ²⁵), 17 (0 ⁴)	
Poales	3 (1 ⁴), 5 (1 ²⁵), 6 (0 ³), 11 (1 ²⁵)	
Poales with Bromeliaceae and Typhaceae excluded	11 (1 ⁴), 14 (2 ³), 15 (1 ²⁵), 17 (1 ²⁵)	20(1 ³)
Restiids	10 (2 ³), 17 (1 ³)	
Restiids–graminids	6 (0 ³), 11 (1 ¹³), 12 (1 ¹²³⁴⁵), 15 (1 ⁴), 17 (1 ⁴)	20(1 ¹)
Stemonaceae	14 (0 ³ , 1 ³)	
Thurniaceae	7 (0 ¹⁴), 16 (1 ³), 17 (0 ⁴)	20(1 ¹), 21(2 ¹)
Tofieldiaceae	2 (2 ⁴), 8 (2 ⁴)	
Typhaceae	3 (1 ²⁵), 4 (1 ²⁵), 6 (0 ²⁵), 11 (1 ¹²³⁴⁵)	20(1 ³), 21(3 ¹³)
Velloziaceae	7 (0 ¹²³⁴⁵), 10 (2 ²⁵), 14 (1 ³), 17 (3 ⁴)	
Xanthorrhoeaceae	6 (1 ³)	
Xyridaceae	3 (1 ³), 5 (2 ³), 7 (2 ²⁵), 8 (0 ²⁵), 13 (0 ²⁵), 19 (1 ²⁵)	
Zingiberaceae–Costaceae	3 (2 ²⁵), 7 (3 ³), 8 (4 ³), 13 (1 ²⁵)	
Zingiberales	2 (0 ²⁵), 3 (1 ⁴), 4 (1 ³ , 2 ³), 6 (0 ²⁵), 7 (2 ⁴), 8 (0 ¹³⁴⁵), 13 (0 ¹³⁴), 14 (2 ³), 19 (0 ¹²³⁴⁵)	

Topology G possesses the fewest steps for basic shape, shape class, and outline in polar view (amb), of the three topologies (G–I) that focus on the basalmost branching group of Poales.

To illustrate character state changes throughout the phylogeny of monocots, we mapped the unambiguous character state changes in the 19 pollen characters and two ecological characters (Table 1) at internal nodes based on CHB optimization (Fig. 7), the method that tends to produce the fewest equivocal states at internal nodes in our analysis (Fig. 7). Changes in pollen character states were not distributed regularly but were clustered in certain lineages. While most nodes were associated with five or fewer changes, 14 internal nodes displayed at least five inferred changes; 10 nodes were seen with five changes, one node with six changes, two nodes with seven changes, and one node with nine changes. The 10 nodes with five changes include the root nodes of alismatids, the Stemonaceae, Commelinales, Zingiberales, and Typhaceae. The one node with six changes was the root of Xyridaceae. The two nodes with seven changes were the clade comprising Eriocaulaceae and Xyridaceae, and the Arecales. The root node of Alismataceae displayed nine changes.

Five orders displayed more than 20 internal pollen character state changes: Alismatales (41 changes), Asparagales (24), Liliales (21), Pandanales (22), and

Poales (45). In contrast, the Dioscoreales, Arecales, and Dasygogonales possessed very few or no changes: four, three, and zero, respectively. Taking the relative sampling and taxonomic size of a lineage into account (pollen character state changes per internal node within a clade), the highest relative rate of pollen character state changes was found in Alismatales, Commelinales, and Arecales (3.73, 3.25, and 3, respectively), while Zingiberales, Asparagales, and Dasygogonales had the lowest relative rate of pollen character change (1.17, 0.83, and 0, respectively).

Thus, these 19 pollen characters (Table 1) showed variable frequencies of state change during the evolution of monocots. Changes of character state at internal nodes were found to be more frequent in pollen size (char. 7, with 29 changes), pollen outline in polar view (char. 6, 22 changes), and tectum sculpture (char. 17, 23 changes), whereas pollen dispersal unit (char. 1, one change), annulus (char. 12, two changes), infratectum structure (char. 18, one change), and pollen foot layer (char. 19, two changes) had far fewer (Fig. 7).

ANALYSES OF CORRELATED EVOLUTION

With the exception of exine presence (MCMC method, log Bayes factor value [log BF] = 3.19), we failed to find positive correlations between exine stratification states and hydrophytes using ML and

Table 3. Results of correlated evolution analyses using maximum likelihood (ML) and Markov chain Monte Carlo (MCMC) methods. Characters and character states are numbered, following Table 1.

Trait pair (pollen and ecological character)	ML			MCMC		
	Likelihood			Harmonic mean of log-likelihood		
	Independent model	Dependent model	Likelihood ratio (LR)	Independent model	Dependent model	Log Bayes factor (LBF)
Exine stratification and helo-hydrophytes						
Exine (character [char.] a1) and helo-hydrophytes (char. b1)	-94.01	-87.12	13.77 [†]	-99.27	-92.71	13.12 [‡]
Tectum (char. a2) and helo-hydrophytes (char. b1)	-102.50	-95.33	14.33 [†]	-106.99	-102.53	8.93 [†]
Eutectum (char. a3) and helo-hydrophytes (char. b1)	-146.43	-142.33	8.22	-150.63	-149.21	2.85*
Infrapectum (char. a4) and helo-hydrophytes (char. b1)	-98.90	-92.20	13.40 [†]	-104.04	-101.73	4.62*
Columellae (char. a5) and helo-hydrophytes (char. b1)	-109.91	-105.22	9.38	-113.62	-113.72	-0.20
Granules (char. a6) and helo-hydrophytes (char. b1)	-82.80	-82.33	0.93	-89.06	-88.87	0.39
Exine stratification and hydrophytes						
Exine (char. b1) and hydrophytes (char. b2)	-68.09	-63.61	8.96	-71.20	-69.60	3.19*
Tectum (char. a2) and hydrophytes (char. b2)	-76.58	-73.15	6.86	-78.49	-78.20	0.57
Eutectum (char. a3) and hydrophytes (char. b2)	-120.51	-118.61	3.82	-126.46	-125.69	1.54
Infrapectum (char. a4) and hydrophytes (char. b2)	-72.97	-70.11	5.74	-75.75	-75.33	0.83
Columellae (char. a5) and hydrophytes (char. b2)	-83.99	-81.69	4.60	-87.19	-87.59	-0.81
Granules (char. a6) and hydrophytes (char. b2)	-56.88	-56.63	0.49	-61.87	-62.19	-0.65

* $P < 0.05$, LBF > 2 .† $P < 0.01$, LBF > 5 .‡ $P < 0.005$, LBF > 10 .

MCMC analysis methods (Table 3). ML and MCMC analyses of correlation for the eutectum and helo-hydrophyly yielded inconsistent results ($P > 0.05$, log BF = 2.85, Table 3).

There was very strong or strong support for correlated evolution between exine presence and habitat for helo-hydrophytes (both with significance of $P < 0.01$ and log BF > 10), and strong or positive support for correlated evolution between three exine characters (presence of tectum, eutectum, and infrapectum) and helo-hydrophyly ($P < 0.01$, log BF = 5–10). The remaining two pollen traits tested (columellate infrapectum and granular infrapectum) were not significantly correlated with helo-hydrophyly (a negative correlation with $P > 0.05$ and log BF < 2). Results of correlated evolution analyses for the seven pairs of traits are shown in Table 3.

In a test of specific hypotheses with regard to contingent evolution, significant support was found: the presence of pollen exine was not gained preferentially in helo-hydrophytes compared to those

that were not helo-hydrophytes (hypothesis q24 $<$ q13, probability values 0.02). Meanwhile, in a test of specific hypotheses of exclusiveness evolution, the loss of pollen exine was not significant in plants that were not helo-hydrophytes (hypothesis q31 = 0, probability values 0.1304) but was significant in helo-hydrophytes (hypothesis q42 = 0, probability values 0.0120). The losses of pollen tectum and infrapectum were significant in both helo-hydrophytes and those that were not helo-hydrophytes (hypothesis q31 = 0 rejected, probability values 0.0347 and 0.0262 respectively, $P < 0.005$).

DISCUSSION

SYSTEMATIC SIGNIFICANCE OF POLLEN MORPHOLOGY IN MONOCOTS

Our optimizations using five methods (analysis of a comprehensive dataset with Fitch parsimony and hierarchical Bayesian inference [abbreviated as CFP

and CHB] and analysis of a democratic dataset with Fitch parsimony, maximum likelihood, and hierarchical Bayesian inference [abbreviated as DFP, DML, and DHB respectively]) allowed us to infer the pollen morphological state changes or synapomorphies for multiple branches within the monocot phylogenetic tree. We found that pollen characters may be of systematic value for delimiting lineages and may provide clues to controversial relationships within monocots (cf. Table 2). Each of the major lineages of monocots is discussed below.

Acorales. The order Acorales was recognized in both Angiosperm Phylogeny Group II (2003) and Angiosperm Phylogeny Group III (2009) classifications. *Acorus*, the single genus in the order, was previously placed in Araceae (reviewed in Grayum, 1987) but later found to be sister to the rest of the monocots based on molecular data (e.g., Chase et al., 1993; Duvall et al., 1993a, 1993b; Chase et al., 2006; Graham et al., 2006). Its isolated position is strongly congruent with several synapomorphies, including small size (char. 7, CFP, CHB, and DML), eutectate pollen (char. 14, CFP, DFP, DML, and DHB), and perforate tectum (char. 17, CHB, DFP, DML, and DHB) (Table 2).

Alismatales. The large order Alismatales comprises ca. 4560 herbaceous species of aquatic and moist habitats and is the second-diverging clade within the monocots (Angiosperm Phylogeny Group III, 2009). No unambiguous pollen synapomorphies were found for the Alismatales. Recent molecular phylogenetic estimates have identified three major clades within Alismatales: Araceae, Tofieldiaceae, and the alismatid aquatic families (Chen et al., 2004a, 2004b; Chase et al., 2006), all of which are characterized by character state changes. For Araceae, states include pollen eutectate (char. 14, CFP, DFP, DML, and DHB) with perforate tectum (char. 17, CHB, DFP, DML, and DHB); Tofieldiaceae are characterized by isopolar and diaphragm pollen (char. 2 and char. 8, DML). Character states identified for the aquatic alismatid families are pollen apolar (char. 2, CHB, DML, and DHB), radially symmetrical in polar view (char. 3, CHB), globose (char. 4, CHB and DHB), circular in polar view (char. 6, DHB), gigantic in size (char. 7, CHB and DHB), and lacking apertures (char. 8, CHB, DML, and DHB; Table 2).

Petrosaviales. The family Petrosaviaceae (Kubitzki, 1998a) was newly recognized as the order Petrosaviales in Angiosperm Phylogeny Group III (2009). Most members of the group were previously

treated as belonging to a diversity of families including Liliaceae (Ohba, 1984), Nartheciaceae, Tofieldiaceae, and Melianthaceae (Dahlgren et al., 1985). The isolated position of this order is characterized by two pollen character state changes, to small pollen size (char. 7, CHB, DML, and DHB) and intectate pollen (char. 14, DHB; Table 2).

Dioscoreales and Pandanales. Dioscoreales are moderately supported as sister to Pandanales based on molecular evidence (Chase et al., 2006; Graham et al., 2006; Petersen et al., 2006). We found no palynological characters to support this relationship. The Dioscoreales themselves were characterized by three pollen character state changes, to spheroidal pollen (char. 5, DHB), equatorial apertures (char. 9, CHB and DHB), and echinate suprategular elements (char. 16, CHB). The monophyly of the Dioscoreaceae s.l. (including the former Taccaceae and Trichopodaceae, as accepted by the Angiosperm Phylogeny Group II based on the combined molecular-morphological analyses of Caddick et al. [2000, 2002a, 2002b]) is congruent with state changes to equatorial apertures (char. 9, CHB), eutectate pollen (char. 14, DFP, DML, and DHB), and perforate tectum sculpture (char. 17, DHB). Pollen morphology is particularly congruent with known systematic relationships within Pandanales. The sister relationship between Cyclanthaceae and Pandanaceae is congruent with pollen character state transitions to radial symmetry (char. 3, CFP and DML), globose shape (char. 4, CFP, CHB, DFP, and DML), oblate pollen (char. 5, CHB), smooth aperture membrane (char. 10, CFP, DFP, and DML), porate apertures (char. 11, CFP, DFP, and DML), eutectate pollen (char. 14, DFP and DML), and a perforate tectum (char. 14, DFP and DML). Pandanaceae as a group are defined by oblong outline in polar view (char. 6, CHB), small size (char. 7, DFP, DML, and DHB), annulus present (char. 12, CHB and DHB), atectate pollen (char. 13, DHB), and imperforate tectum sculpture (char. 17, DHB). Stemonaceae received no defining pollen character states, while Velloziaceae are characterized by small pollen size (char. 7, all five methods) with an operculum (char. 10, CHB and DHB), semitectate (char. 14, CHB), and rugulate tectum (char. 17, CHB; Table 2).

Liliales. Only one pollen character state change, to oblong outline in polar view (char. 6, CFP and DFP), is found on the stem of Liliales. The recent merger of Luzuriagaceae into Alstroemeriaceae (Mabberley, 2008; Angiosperm Phylogeny Group III, 2009) is congruent with both large pollen size (char. 7, DHB) and rugulate tectum (char. 17, DHB).

The placement of Uvulariaceae within Colchicaceae (Fay et al., 2006) is congruent with supratectal elements present (char. 15, CHB and DHB) and perforate tectum sculpture (char. 17, DHB). The placement of the Petermanniaceae has been debated for some time (Angiosperm Phylogeny Group II, 2003; Janssen & Bremer, 2004; Fay et al., 2006). The topology we used in our study, in which it is sister to the clade comprising Alstroemeriaceae and Colchicaceae (Fay et al., 2006), is congruent with two pollen character state transitions, to large size (char. 7, DHB) and fossulate tectum (char. 17, CHB and DHB; Table 2).

Asparagales. The placement of Asparagales as sister to commelinids has been moderately supported by Chase et al. (2006) and strongly by Graham et al. (2006). In our study, this relationship is congruent with only one pollen state (char. 10, smooth aperture membrane, DHB). No state change was found to occur on the branch leading to Asparagales. The monophyly of the astelioid clade (including Asteliaceae, Blandfordiaceae, Boryaceae, Hypoxidaceae, and Lanariaceae) has been well supported in recent phylogenetic studies (Seberg et al., 2012; Chen et al., 2013); however, no pollen character state changes were found for this clade. The placement of Ixioliriaceae as sister to Tecophilaeaceae was strongly supported in the study of Chen et al. (2013) and is congruent with transitions to elliptic pollen outline in polar view (char. 6, DHB), operculate aperture (char. 10, DML), eutectate pollen (char. 14, DHB), and regulate tectum (char. 17, CHB and DHB; Table 2).

Commelinids. The commelinid clade is strongly supported in molecular studies (reviewed in Chase et al., 2006), and the monophyly of each of the five commelinid orders is well established (e.g., Davis et al., 2004; Chase et al., 2006). However, internal relationships among its five major groups remain controversial, particularly the positions of Dasypogonales and Arecales (e.g., Chase et al., 2006; Graham et al., 2006; Givnish et al., 2006, 2010; Angiosperm Phylogeny Group III, 2009; Soltis et al., 2011; Barrett et al., 2012; Davis et al., 2012). Six main conflicting topologies within the commelinids are summarized in Figure 1.

Among the six alternative topologies tested (A–F), topologies A, D, and E produced the minimum number of pollen character state change steps in the CFP analysis, and, thus, they are inferred to be favored by pollen morphology based on the parsimony theory, i.e., ((Arecales (Dasypogonales (Commeliniales–Zingiberales, Poales))), ((Arecales, Dasypogonales) (Commeliniales–Zingiberales, Poales))), and

((Arecales, Poales) (Commeliniales–Zingiberales, Dasypogonales))), respectively (Fig. 1). It is noteworthy that the latest phylogenetic studies using plastid genes and genomes (Givnish et al., 2010; Barrett et al., 2012; Davis et al., 2012) support Arecales plus Dasypogonales as sister to the rest of the commelinid monocots (topology D).

The sister relationship between Commeliniales and Zingiberales has been well supported (Chase et al., 2006; Givnish et al., 2006, 2010; Graham et al., 2006; Soltis et al., 2007, 2011; Qiu et al., 2010) and is also congruent with transitions to very large or large size (char. 7, CHB and DHB, respectively), inaperturate (char. 8, CHB) and exineless pollen (char. 13, CHB and DHB; Table 2). Both topologies A and D contain a clade comprising Commeliniales and Zingiberales as sister to Poales, which is characterized by radial symmetry (char. 3) in both.

The studies of both Givnish et al. (2006) and Chase et al. (2006) presented consistent sister relationships between Haemodoraceae and Pontederiaceae. The clade comprising Haemodoraceae and Pontederiaceae is congruent with multiple pollen character state changes, to isopolar pollen (char. 2, CHB and DHB), very large size or large size (char. 7, CHB and DHB, respectively), two apertures (char. 8, DFP and DML), and eutectate grains (char. 13, DHB; Tables 1, 2).

The Zingiberales are a well-characterized clade with nine inferred shared pollen character states: apolar (char. 2, CHB, DML, and DHB), radially symmetrical (char. 3, DML), globose pollen (char. 4, CHB), circular outline in polar view (char. 6, CHB and DHB), large size (char. 7, DML), no apertures (char. 8, CFP, DFP, and DML), no exine (char. 13, CFP, DFP, and DML), eutectate pollen (char. 14, DHB), and no foot layer (char. 19, all five methods). Two pairs of sister families are found within the order: Costaceae and Zingiberaceae, and Lowiaceae and Strelitziaceae (Kress et al., 2001; Chase et al., 2006; Givnish et al., 2006). The former pairing is congruent with transitions to asymmetrical pollen (char. 3, CHB and DHB), very large size (char. 7, DHB), more than three apertures (char. 8, CFP, DFP, DML, and DHB), exineless (char. 13, CFP, DFP, and DML) and eutectate pollen (char. 14, DHB), and absence of the foot layer (char. 19, all five methods); the latter pairing is congruent only with very large pollen size (char. 7, DML and DHB). The monophyletic group including Cannaceae, Marantaceae, Costaceae, and Zingiberaceae among other Zingiberales is congruent with one pollen character state change, to large pollen size (char. 7, CHB; cf. Fig. 1, Tables 1, 2).

Within Poales, the basalmost branching group has variously been recovered as Bromeliaceae, Typhaceae, or Bromeliaceae–Typhaceae (Davis et al., 2004; Chase et al., 2006; Givnish et al., 2006, 2010; Graham et al., 2006). These three conflicting basal topologies within Poales are shown in Figure 1G–I. Of these, topology G, with Bromeliaceae as the first lineage to diverge, and Typhaceae sister to the remaining Poales (including Rapateaceae and the graminid, restiid, cyperid, and xyrid clades) requires the fewest pollen character state changes (cf. Fig. 1G–I, Table 1). This topology, which is consistent with the phylogenetic work of Givnish et al. (2010), is inferred to be favored by pollen morphology.

The cyperid clade (including Cyperaceae, Junceaceae, and Thuriaceae) has been well supported by molecular data (Chase et al., 2006; Givnish et al., 2010) and can be characterized by pollen states including grains borne in tetrads (char. 1, all five methods), pollen circular outline in polar view (char. 6, CHB), small grain size (char. 7, CHB and DHB), porate aperture (char. 11, CFP and DFP), supratpectal elements present (char. 15, DML), gemmate supratpectal element shape (char. 16, CHB and DHB), and imperforate tectum (char. 17, CHB and DHB). Herein, the pseudomonads of Cyperaceae are treated as hidden tetrads. The xyrids (including Eriocaulaceae, Mayacaceae, and Xyridaceae) did not form a monophyletic group in Chase et al. (2006) and our study (Fig. 7). We found that a sister relationship between Eriocaulaceae and Xyridaceae would be characterized by apolar pollen (char. 2, CHB and DHB), elliptic outline in polar view (char. 6, DHB), and semitectate pollen (char. 14, CHB). Mayacaceae can be distinguished from the other two families by its monosulcate and tectate to intectate pollen (Zavada, 1983), while there is no pollen character linking it with Eriocaulaceae and Xyridaceae. A sister relationship between the restiid and graminid clades is found to be congruent with pollen character state changes to circular outline in polar view (char. 6, CHB), porate aperture (char. 11, CFP and DFP) with an annulus (char. 12, all five methods), supratpectal elements present (char. 15, DML), and perforate tectum sculpture (char. 17, DML; cf. Fig. 7, Tables 1, 2).

THE RELATIONSHIP BETWEEN MONOCOTS AND BASALLY BRANCHING ANGIOSPERMS

The Chloranthaceae, magnoliids, monocots, Ceratophyllaceae, and eudicots are all well supported as major lineages within angiosperms, but the relationships among them remain unclear (e.g., Qiu et al., 2005, 2006, 2010; Soltis et al., 2005, 2008, 2011;

Moore et al., 2007). Studies have suggested several alternatives for the closest relatives of monocots, ranging from magnoliids (Hilu et al., 2003; Duvall et al., 2006) to the aquatic Ceratophyllaceae (Qiu et al., 1999, 2005; Zanis et al., 2002), Ceratophyllaceae–eudicots (Moore et al., 2007; Soltis et al., 2011), Piperales (Duvall, 2000), or Laurales (Parkinson et al., 1999). In our study, although a sister relationship between monocots and magnoliids is congruent with shared pollen character states including oblong outline in polar view (char. 6, DHB; cf. Fig. 7, Table 1), an affinity of monocots to basal eudicots or Ceratophyllaceae has also been supported by pollen characters (Lu et al., 2015).

Our studies suggest that convergent evolution in pollen character states occurs commonly between some monocots and basally branching angiosperms. Both Lu et al. (2015) and the present study suggest that both groups contain taxa with inaperturate pollen grains with a highly reduced exine and thick channeled intine (Zingiberales and Lauraceae; Stone, 1987), trichotomosulcate pollen (Iridaceae, Arecaceae, and Chloranthaceae; Chapman, 1987; Goldblatt & Le Thomas, 1992, 1997; Harley, 1999) or pollen with zonate apertures (Araceae, Arecaceae, Nymphaeaceae, and Eupomatiaceae; Woodland & Garlick, 1982; Grayum, 1992; Gabarayeva & Rowley, 1994; Hesse et al., 2001; Harley & Dransfield, 2003). Polyplacate striae are found in Araceae, Zingiberaceae, and Lauraceae (Hesse et al., 2000), and loss or reduction of exine is also common in both monocots and basal angiosperms.

EVOLUTION OF POLLEN IN MONOCOTS

In this study, plesiomorphic pollen morphological states for monocots were unambiguously inferred under all five optimization methods to include pollen dispersal as monads (char. 1, Table 1, Fig. 7), pollen heteropolarity (char. 2), medium size (char. 7), monosulcate apertures (characters 8 and 11) with a sculptured aperture membrane (char. 10) and lacking an annulus (char. 12), exine fully present (char. 13), supratpectal elements absent (char. 15), infratpectum structure columellate (char. 18), and foot layer present (char. 19). The earliest monocot pollen is therefore likely to have been characterized by most of these pollen features.

Distal monosulcate pollen has long been considered an ancestral state for both basal angiosperms and monocots (Wodehouse, 1936; Takhtajan, 1969; Zavada, 1983; Sampson, 2000; Doyle, 2005; Lu et al., 2015). This character is also shown unambiguously to be plesiomorphic in monocots under four of our five methods (the exception being DHB, which

inferred an equatorial aperture position to be plesiomorphic, and this is in agreement with previous studies (Penet et al., 2005; Ressayre et al., 2005).

Evolution of the pollen dispersal unit (char. 1, Table 1, Fig. 7), infratectum structure (char. 18), and foot layer presence (char. 19) has been relatively conservative throughout the angiosperms (Wortley et al., 2015). These three pollen characters were found to be similarly stable in the evolution of monocots, having the lowest frequency of character state changes, despite the Orchidaceae (although here with only three taxa sampled) being noted as most diverse for pollen dispersal unit among angiosperms (Pacini & Hesse, 2002). Thus, the states dispersal as monads, columellate infratectum structure, and presence of a foot layer are found in the overwhelming majority of monocots. Other character states are less commonly reported (e.g., granulate infratectum) or are restricted to certain derived, monophyletic groups (e.g., absence of the foot layer in Haemodoraceae; Simpson, 1983). In contrast, pollen size (char. 7) and tectum sculpture (char. 17) displayed greater frequency of change among monocots, as has also been the case throughout angiosperms (Wortley et al., 2015).

Pollen aperture characters have displayed frequent state changes throughout the phylogeny of monocots. Although the range of aperture types in monocots is fewer than that observed for other angiosperms (Harley & Zavada, 2000), apertures are key to the evolution of monocot pollen morphology. Two aperture character state shifts, from a proximal to a distal position in early seed plant evolution and to an equatorial position seen at the base of the eudicot clade, have been regarded as some of the most striking innovations in the evolutionary history of seed plants (Muller, 1970; Walker & Doyle, 1975; Chanda & Ghosh, 1979; Zavada, 1983, 1984a; Rudall & Bateman, 2007). There is no intermediate position of apertures between distal and equatorial, and the switch in position reflects developmental changes expressed during meiosis (Blackmore & Crane, 1998). In our analyses for monocots, under CHB, a further transition from distal to equatorial apertures is inferred at the root of the Areaceae. Pollen grains ascribed to Areaceae are abundant and widely distributed from the Late Cretaceous (Burnham & Johnson, 2004; Nichols & Johnson, 2008) and include all four types of equatorial aperture found among monocots, from disulcate, found, for example, in Tofieldiaceae, Dioscoreaceae, and Liliaceae; to diporate, as seen in Bromeliaceae and Haemodoraceae; zonate, observed in Araceae,

Iridaceae, and Rapateaceae (Hesse & Zetter, 2005); and triaperturate, observed in Iridaceae, Commelinaceae, and Orchidaceae (Harley, 2004). Further extensive sampling and analysis of pollen morphology of the Areaceae and related taxa will provide valuable clues to our understanding of distal/equatorial aperture transitions within angiosperms.

Zavada (1983) identified a number of evolutionary trends in aperture type in the monocots, such as the loss of a sulcus and an increase in the number and types of apertures. The trend of loss of sulcus was further exemplified by both Furness and Rudall (2006) and our CHB analysis. Furness and Rudall (2006) revealed that there are apparently homoplastic trends in each family toward either reduction in aperture size (e.g., from sulci to pores) or to coverage of the aperture with exine (e.g., from monosulcate to monosulcate-operculate) within Pandanales. In our analysis, monosulcate apertures were inferred unambiguously as plesiomorphic for monocots, whereas monoporate and inaperturate types were derived within the group. Monoporate pollen (char. 8 and char. 11) is inferred to have evolved on the branches leading to Cyclanthaceae–Pandanales (CFP, DFP, and DML), Typhaceae (all five methods), cyperids (CFP and DFP), and the graminid–restiid clade (CFP and DFP; Table 2). Within the clade comprising Philydraceae, Haemodoraceae, and Pontederiaceae, monosulcate pollen reoccurs in all taxa of the basally placed family Philydraceae (Simpson, 1985a), with diaperturate (char. 8, DFP and DML) or triaperturate pollen (char. 8, CHB) evolving in the more derived Haemodoraceae–Pontederiaceae (Table 2). Alismatales, among the later-diverging lineages of Alismatales, are characterized by pantoporate pollen (char. 8, CFP, CHB, DFP, and DML). Inaperturate pollen (char. 8, Fig. 7, Table 1) evolved more frequently on lineages with helo–hydrophytic plants, such as alismatids (CHB, DML, and DHB) and within Zingiberales (CFP, DFP, DML, and DHB).

ECOLOGICAL ADAPTATIONS IN POLLEN MORPHOLOGY

Monocots display a high diversity of pollination types, including wind pollination (Poaceae and Cyperaceae, exceptionally insect pollination in bamboo grasses; Soderstrom & Calderon, 1971), water pollination (diverse seagrass lineages in Alismatales), and bird pollination (widespread across the eight families of the Zingiberales; Nur, 1976), as well as dispersal of aggregated pollen, usually by animal vectors (Orchidaceae; Harder, 2000). Each of these pollination types corresponds to a series of distinct pollen features. For example, bird-pollinated Zingiberales possess exineless pollen with a thick-

ened, elaborated intine to preserve water (Kress & Stone, 1982; Theilade & Theilade, 1996); the water-pollinated seagrasses in Alismatales have filiform and exineless pollen (Ackerman, 1995, 2000); and the wind-pollinated graminid clade of Poales have typically distally monoporate pollen with an operculum and annulus (Linder & Rudall, 2005). It is interesting to note that the entomophilous bamboo genus, *Pariana* Aubl., has a unique pollen type without an annulus, which may imply a further possible association between pollen morphology and pollination type (Skvarla et al., 2003). In our CHB analysis, four internal nodes having not less than five changes in pollen character state were found to be closely associated with pollinator shifts: the root of the alismatids (from entomophily to hydrophily), the root of the Arecales (a reversal from ornithophily to entomophily), the root of Typhaceae (from ornithophily to anemophily), and the root of the clade comprising Eriocaulaceae and Xyridaceae (a reversal from anemophily to entomophily; see Fig. 7). The interesting results here indicate that the transitions in pollen morphological states may be potentially correlated with the shifts in pollination type.

Asparagales have the second highest diversification rate in monocots (Magallón & Castillo, 2009) yet the lowest average frequency of pollen character state changes at internal nodes among all orders except Dasygogonales (0.76). We found only 22 state changes across all 19 pollen characters studied in this clade: seven in pollen size (char. 7), four in outline in polar view (char. 6), three in aperture membrane (char. 6), four in tectum (char. 14), three in tectum sculpture (char. 17), and one in symmetry (char. 3), indicating that Asparagales pollen morphology has been consistent and comparatively stable during evolution (Fig. 7). In terms of ecological characters, habitat moisture (char. 21) was found to change frequently (seven times) within the core asparagoids, whereas pollination type (char. 20) did not change (Fig. 7): entomophily is consistently the most probable state under CHB at all internal nodes within Asparagales excluding the astelioids and Orchidaceae (Fig. 7). These observations suggest that changes in ecological interactions, particularly pollination type, may have remarkable impact as drivers of pollen morphological change within monocots, while pollen characters can remain remarkably stable under changing habitat moisture.

Fourteen internal nodes in the phylogeny of monocots were found to be characterized by a high number of pollen morphological state changes under CHB (Fig. 7, Table 1), including the root node of Alismataceae (nine changes); the root nodes of

Arecales (seven changes); the clade comprising Eriocaulaceae and Xyridaceae (seven changes); Xyridaceae (six changes); 10 further nodes have five changes, including the roots of alismatids, Stemonaceae, Commelinales, Zingiberales, and Typhaceae. Based on divergence time data for monocots provided by recent studies (Janssen & Bremer, 2004; Merckx et al., 2008; Bell et al., 2010; Smith et al., 2010; Bouchenak-Khelladi et al., 2014; Magallón et al., 2015), the crown or stem node ages of 10 of these 14 major clades are all dated to between 90 and 114 million years ago, approximately corresponding to the Albian-Turonian stage of the Middle Cretaceous. Although many monocot orders are unrepresented by fossil records during the Late Cretaceous, there is clear evidence that monocots were both diverse and widespread in the middle of the Late Cretaceous (Herendeen & Crane, 1995). The dramatic pollen character transformations in the Albian-Turonian seen in our analysis occurred contemporaneously with the rise of angiosperm-dominated ecosystems (Lidgard & Crane, 1990; Coiffard et al., 2006).

The functions of exine architecture in angiosperms are considered to be mainly protection (against adverse atmospheric conditions such as desiccation and UV radiation), storage of physiologically active substances, pollen grain clustering, and harmomegathy (Muller, 1979). It is likely in the near future that we will gain a fuller understanding of Heslop-Harrison's (1969, 1972) insights that pollen wall patterning is not directly coded by genes but involves an interplay between the products of gene expression and the influence of physical forces (Blackmore et al., 2007). Water content status influences not only the survival, longevity, and germination ability of angiosperm pollen (Franchi et al., 2002; Aylor, 2003), but also their exine stratification: exine reduction or loss in monocots has been associated with moist or aquatic environments (Heslop-Harrison, 1976; Philbrick, 1991; Furness & Rudall, 1999; Tanaka et al., 2004), such as those frequented by many alismatids (Thanikaimoni, 1978). However, the complexity of the exine and the development of its stratification under physical stress may limit our understanding of the associations between exine architecture and habitat moisture. We confirmed that three exine stratification traits (exine, tectum, and infratectum) are correlated with the evolution of helo-hydrophytic habitat (Table 3, Fig. 2). The presence or absence of exine is most strongly correlated with helo-hydrophytic habitat rather than hydrophytic habitat among six exine structures (Table 3, Fig. 2). Furthermore, tests of contingent evolution indicated that exine absence was not preferentially lost in helo-

hydrophytes of moist to wet habitats. All of these results indicate that habitat moisture may provide a selective pressure that crucially affects the evolution of pollen morphology in monocots.

Granular infratectum structure appears to be derived within monocots, as the more basally branching lines have a columellate infratectum (Doyle, 2009).

We confirmed that a columellate infratectum is unambiguously plesiomorphic under all five optimization methods. However, neither the ancestral columellate infratectum nor the derived granulate version is found to be significantly correlated with preference for a helo–hydrophytic habitat (Table 3, Fig. 2). Zavada (1983) proposed that a primitive tectate-columellate (perforate or imperforate) wall structure type gave rise to monocotyledonous atectate walls or granular infratectum and finally extreme reduction of the exine, in which it may be completely absent. Our results indicate that the loss of infratectum structure may play a part in the *process* of exine reduction, which leads to subsequent morphological adaptations to helo–hydrophytic habitat.

FUTURE PROSPECTS

Although more extant and fossil pollen morphological data may facilitate a better understanding of pollen evolution and diversification, a more robust phylogenetic framework for monocots based on increased genetic data and denser taxon sampling may also be required for future reconstruction of pollen characters. In particular, there is a need for a better resolution of the positions of Dasypogonales and Arecales, as well as for internal relationships within Commelinales and Zingiberales, and the basalmost-branching group of Poales. In this paper, evolutionary patterns have emerged with respect to pollen characters of monocots, identifying a number of unambiguous pollen plesiomorphies and character state changes, revealing correlations with pollination type and habitat moisture using FP, ML, and HB methods. Substantial clues to the understanding of pollen morphological transformations during the evolution of monocots (e.g., pollen polarity transitions within Areaceae) may help in elucidating correlations between exine reduction or loss and helo–hydrophytes in moist to wet habitats in the evolution of monocots (as well as in other angiosperms). Past interpretations of the evolutionary significance of fossil pollen have relied heavily on comparative morphological studies of extant pollen (Zavada, 1983). Our optimization techniques demonstrate that dramatic state changes in pollen morphology oc-

curred across the monocot phylogeny in the Albian–Turonian stage, which may provide insights for interpreting enigmatic early monocot pollen evolution.

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Appendix 1. Phylogenetic position and terminal taxa used in the phylogenetic analyses (in order to be consistent with the taxa used in Chase et al. [2006], both *Acorus calamus* L. and *A. gramineus* Sol. ex Aiton are listed). Generic totals for families are sensu the Angiosperm Phylogeny Group III (2009) and Chase et al. (2006). One hundred twenty taxa represent the 12 orders and 71 families of monocots, and 16 outgroup taxa represent the nine orders and 13 families of basal angiosperms considered in analysis. Twenty species are vouchers for pollen exemplars seen in Figures 3–6.

Taxonomic classification	Total # of genera per family (total # of genera sampled)	Taxon name, with species voucher	References and voucher information	
			References used for palynological data	References used for ecological data
Monocots				
ACORALES				
Acoraceae	1 (1)	<i>Acorus calamus</i> L.	Grayum, 1992; Rudall & Furness, 1997	Cook, 1990; Kubitzki, 1998b; Buzgo & Endress, 2000
		<i>A. gramineus</i> Sol. ex Aiton	Grayum, 1992; Rudall & Furness, 1997	Cook, 1990; Kubitzki, 1998b; Buzgo & Endress, 2000
ALISMATALES				
Alismataceae	15 (2)	<i>Alisma</i> L.	Argue, 1971, 1974, 1976; Punt & Reumer, 1981; Zavada, 1983; Chanda et al., 1988	Daumann, 1965; Björqvist, 1967; Cook, 1990; Kubitzki, 1998b
		<i>A. orientale</i> (Sam.) Juz. (Fig. 3G, H)	China, Shanxi. <i>L. Zhang & K. M. Lian Zhang f0031</i> (KUN)	
		<i>Sagittaria</i> L.	Argue, 1971, 1974, 1976; Punt & Reumer, 1981; Zavada, 1983; Chanda et al., 1988	Cook, 1990; Kubitzki, 1998b
		<i>Gymnostachys</i> R. Br.	Grayum, 1992; Hesse, 2006	Kubitzki, 1998b
	117 (3)	<i>Arisaema</i> Mart.	Wang & Zhao, 2002; Wang et al., 2002	Kubitzki, 1998b
		<i>Oronitium</i> L.	Grayum, 1992; Weber et al., 1999; Hesse, 2006	Cook, 1990; Kubitzki, 1998b
		<i>Epipremnum pinnatum</i> (L.) Engl. (Fig. 1D–F)	Australia, Queensland. <i>L. J. Brass 19829</i> (CANB)	
		<i>Butomus</i> L.	Argue, 1971; Zavada, 1983; Chanda et al., 1988; Grayum, 1992; Perveen & Qaiser, 2003; Furness & Banks, 2010	Cook, 1990; Kubitzki, 1998b
	1 (1)		Li & Zhou, 2009	
Cymodoceaceae	5 (1)	<i>Cymodocea</i> K. D. Koenig	Sharma, 1968; Sun et al., 2002; Tanaka et al., 2004	Cook, 1990; Kubitzki, 1998b
Hydrocharitaceae	18 (1)	<i>Vallisneria</i> L.		Cook, 1990; Kubitzki, 1998b; Tanaka et al., 2004
Juncaginaceae	3 (1)	<i>Triglochin</i> L.	Cranwell, 1953; Wang, 1990; Grayum, 1992	Charlton, 1981; Cook, 1990; Kubitzki, 1998b
Potamogetonaceae	4 (1)	<i>Potamogeton</i> L.	Cranwell, 1953; Wang, 1990; Grayum, 1992; Perveen, 1999	Posluszny & Sattler, 1974; Cook, 1990; Kubitzki, 1998b
Tofieldiaceae	3 (2)	<i>Pilea</i> Michx.	Kosenko, 1987; Takahashi & Kawano, 1989	Kubitzki, 1998a; Li & Zhou, 2006

Appendix 1. Continued.

Taxonomic classification	Total # of genera per family (total # of genera sampled)	Taxon name, with species voucher	References and voucher information	
			References used for palynological data	References used for ecological data
Zosteraceae	1 (1)	<i>Tofieldia</i> Huuds. <i>Zostera</i> L.	Huynh, 1976; Schulze, 1978; Kosenko, 1987; Takahashi & Kawano, 1989; Díaz et al., 1990; Furness & Banks, 2010 Pettitt et al., 1984; Díez et al., 1988; Furness & Banks, 2010	Kubitzki, 1998a; Li & Zhou, 2006 Cook, 1990; Kubitzki, 1998b
PETROSAVIALES Petrosaviaceae	2 (2)	<i>Z. marina</i> L. (Fig. 3I, J) <i>Japonolirion</i> Nakai <i>Petrosavia</i> Becc.	Denmark, Zealand Island, <i>N. Jacobse & J. Srensdse 48A</i> (E) Kosenko, 1987; Takahashi & Kawano, 1989; Caddick et al., 1998; Furness & Banks, 2010 Caddick et al., 1998; Handa et al., 2001; Furness & Banks, 2010	Kubitzki, 1998a Kubitzki, 1998a
DIOSCOREALES Dioscoreaceae	4 (3)	<i>P. stellaris</i> Becc. (Fig. 3K, L) <i>Dioscorea</i> L. <i>D. melanophyma</i> Prain & Burkill (Fig. 4A, B) <i>Tacca</i> J. R. Forst. & G. Forst.	Malaysia, Sarawak, <i>B. L. Burt & A. M. Martin B5277</i> (E) Radulescu, 1973; Zavada, 1983; Caddick et al., 1998; Schols et al., 2001, 2003, 2005 China, Yunnan, <i>the Altaoshan expedition team XPALSG550</i> (KUN) Zavada, 1983; Caddick et al., 1998; Schols et al., 2005	Fatokun et al., 1992; Kubitzki, 1998b Zhang et al., 2005
Nartheciaceae	4 or 5 (2)	<i>Trichopus</i> Gaertn. <i>Aletris</i> L. <i>Narthecium</i> Huuds.	Caddick et al., 1998 Kosenko, 1987; Takahashi & Kawano, 1989 Takahashi & Kawano, 1989; Caddick et al., 1998; Handa et al., 2001; Schols et al., 2005	Kubitzki, 1998b Sullivan, 1973; Kubitzki, 1998a Jacquemart, 1996; Kubitzki, 1998a
PANDANALES Cyclanthaceae	12 (4)	<i>Cyclanthus</i> Poit. ex A. Rich. <i>Carludonica</i> Ruiz & Pav. <i>Chorigyne</i> R. Eriks. <i>Sphaeradenia</i> Harling	Harling, 1958; Eriksson, 1994a; Kubitzki, 1998a; Furness & Rudall, 2006 Harling, 1958; Eriksson, 1994a; Kubitzki, 1998a; Furness & Rudall, 2006 Eriksson, 1989, 1994a; Kubitzki, 1998a Harling, 1958; Zavada, 1983; Eriksson, 1994a; Furness & Rudall, 2006	Beach, 1982; Kubitzki, 1998a Eriksson, 1994b; Kubitzki, 1998a Kubitzki, 1998a Kubitzki, 1998a
Pandanaceae	4 (2)	<i>Freycinetia</i> Gaudich. <i>Pandanus</i> Parkinson	Hotton et al., 1994; Furness & Rudall, 2006 Huynh, 1980; Hotton et al., 1994	Cox, 1990; Kubitzki, 1998a Cox, 1990; Kubitzki, 1998a

Appendix 1. Continued.

Taxonomic classification	Total # of genera per family (total # of genera sampled)	Taxon name, with species voucher	References and voucher information	
			References used for palynological data	References used for ecological data
Stemonaceae	4 (2)	<i>Croonia</i> Torr. <i>Stemona</i> Lour. <i>S. tuberosa</i> Lour. (Fig. 4C, D) <i>Acanthochlamys</i> P. C. Kao <i>Talbotia</i> Balf.	Van der Ham, 1991 Van der Ham, 1991; Furness & Rudall, 2006 China, Yunnan, <i>S. D. Zhang et al. APE-LY-017</i> (KUN, living collection from KBC) Gao, 1987 Furness & Rudall, 2006	Rogers, 1982; Kubitzki, 1998a Rogers, 1982; Kubitzki, 1998a Kubitzki, 1998a Kubitzki, 1998a
LILIALES				
Alstroemeriaceae	5 (2)	<i>Alstroemeria</i> L. <i>Luzuriaga</i> Ruiz & Pav. <i>Campynema</i> Labill.	Sarwar et al., 2010 Schulze, 1982a; Kosenko, 1994a Erdtman, 1952; Dutt, 1970; Goldblatt, 1986; Kosenko, 1987	Kubitzki, 1998a Kubitzki, 1998a Kubitzki, 1998a
Campynemataceae	2 (1)		Kosenko, 1987	
Colchicaceae	15 (2)	<i>Schelhammera</i> R. Br. <i>Uvularia</i> L.	Kosenko, 1988 Radulescu, 1973; Buchner & Weber, 2000 onwards	Kubitzki, 1998a Kubitzki, 1998a
Liliaceae	19 (2)	<i>Calochortus</i> Pursh <i>Lilium</i> L. <i>Tulipa iliensis</i> Regel (Fig. 4G–I) <i>Trillium</i> L.	Heusser, 1971; Radulescu, 1973; Schulze, 1980b; Halbritter & Hesse, 1993; Kosenko, 1999 Radulescu, 1973; Schulze, 1980b; Halbritter & Hesse, 1993; Kosenko, 1999 China, Xinjiang, <i>D. Y. Tan DY0180</i> (KUN)	Kubitzki, 1998a; Dilley, 1999 Kubitzki, 1998a
Melanthiaceae	16 (2)	<i>T. maculatum</i> Raf. (Fig. 4E, F) <i>Veratrum</i> L. <i>Petermannia</i> F. Muell. <i>Philestia</i> Comm. ex Juss. <i>Rhipogonum</i> J. R. Forst. & G. Forst. <i>Smilax</i> L. <i>Allium</i> L.	Takahashi, 1982, 1983; Buchner & Weber, 2000 onwards U.S.A., Oklahoma, <i>R. K. Godfrey 84058</i> (IBSC) Buchner & Weber, 2000 onwards Erdtman, 1952; Schulze, 1982a Erdtman, 1952; Cranwell, 1953; Heusser, 1971; Schulze, 1982a; Cauneau-Pigot, 1988 Schulze, 1982b; Furness & Rudall, 1999; Chen et al., 2006 Chen et al., 2006; Kodala, 2006	Kubitzki, 1998a; Irwin, 2000 Kubitzki, 1998a; Mulligan & Munro, 1987; Kubitzki, 1998a Kubitzki, 1998a Kubitzki, 1998a Macmillan, 1972; Kubitzki, 1998a Kevan et al., 1991; Kubitzki, 1998a
Smilacaceae ASPARAGALES	1 (1)			
Amaryllidaceae	73 (3)	<i>A. cyaneum</i> Regel (Fig. 4J–L)	Nair & Sharma, 1965; Radulescu, 1973; Schulze, 1980a; Buchner & Weber, 2000 onwards; Guler & Pehlivan, 2006 China, Qinghai, <i>Y. H. Wu LJQ-QLS-2008-0158</i> (KUN)	Kubitzki, 1998a

Appendix 1. Continued.

Taxonomic classification	Total # of genera per family (total # of genera sampled)	Taxon name, with species voucher	References and voucher information	
			References used for palynological data	References used for ecological data
Asparagaceae	153 (11)	<i>Agapanthus</i> L. Her. <i>Clivia</i> Lindl. <i>Asparagus</i> L. <i>Artropodium</i> R. Br. <i>Convallaria</i> L. <i>Aphyllanthes</i> L. <i>Brodiaea</i> Sm. <i>Scilla</i> L. <i>Anemarrhena</i> Bunge <i>Agave</i> L. <i>Chlorophytum</i> Ker Gawl. <i>Behnia</i> Ditr. <i>Hesperia</i> Ruiz & Pav. <i>Astelia</i> Banks & Sol. ex R. Br. <i>Blanfordia</i> Sm. <i>Alania</i> Endl. <i>Borya</i> Labill. <i>Doryanthes</i> Corrêa <i>Hypoxis</i> L. <i>Sisyrinchium</i> L. <i>Ixolirion</i> Fisch. ex Herb. <i>Lanaria</i> Aiton <i>Neuwiedia</i> Blume <i>Cypripedium</i> L. <i>Epipactis</i> Zinn <i>Tecophilaea</i> Bertero ex Colla <i>Xanthorrhoea</i> Sm.	Nair & Sharma, 1965; Radulescu, 1973; Buchner & Weber, 2000 onwards Alzelius, 1955; Gullvåg, 1964 Nair & Sharma, 1965; Buchner & Weber, 2000 onwards; Özler & Pehlivan, 2008 Radulescu, 1973 Ma & Hong, 1990 Radulescu, 1973; Furness, 1985; Lifante et al., 1990 Schulze, 1980a Radulescu, 1973; Schulze, 1980b; Ghavami et al., 2009 Chen & Qiao, 2000 Alvarez & Köhler, 1987; Stroo, 2000 Nair & Sharma, 1965; Buchner & Weber, 2000 onwards Schulze, 1982a; Conran, 1999 Kosenko, 2001 Cranwell, 1953; Radulescu, 1973; Kosenko, 2001; APSA, 2007 Schulze, 1982b; Kosenko, 1994b Erdtman, 1952; Schulze, 1982b; APSA, 2007 Erdtman, 1952; APSA, 2007 Schulze, 1982b; Buchner & Weber, 2000 onwards Cranwell, 1953 Schulze, 1971; Nadot et al., 2006 Schulze, 1983; Donmez & Isik, 2008 Erdtman, 1952 Schill, 1978 Burns-Balogh & Hesse, 1988 Ackeman & Williams, 1980 Erdtman, 1952; Simpson, 1985b Chanda & Ghosh, 1976	Leighton, 1965; Kubitzki, 1998a Kubitzki, 1998a; Meerow & Clayton, 2004 Kubitzki, 1998a Kubitzki, 1998a Kubitzki, 1998a Kubitzki, 1998a; Araki et al., 2005 Kubitzki, 1998 Han et al., 1991 Kubitzki, 1998a Kubitzki, 1998a Gentry, 1982; Kubitzki, 1998a Kubitzki, 1998a; Poulsen & Nordal, 2005 Kubitzki, 1998a Kubitzki, 1998a Moore, 1966; Kubitzki, 1998a Zimmerman & Pyke, 1988; Kubitzki, 1998a Kubitzki, 1998a; Western Australian Herbarium, 1998 onwards Keighery, 1984; Kubitzki, 1998a Newman, 1929; Kubitzki, 1998a Cook, 1990; Kubitzki, 1998a Kubitzki, 1998a; Freitas & Sazima, 2003 Kubitzki, 1998a; Li & Zhou, 2006 Kubitzki, 1998a Benzing & Atwood, 1984; Okada et al., 1996 Benzing & Atwood, 1984; Davis, 1986 Brantjes, 1981; Benzing & Atwood, 1984 Kubitzki, 1998a Keighery, 1980; Kubitzki, 1998a
Asteliaceae	1 (1)			
Blanfordiaceae	1 (1)			
Boyaceae	2 (2)			
Doryanthaceae	1 (1)			
Hypoxidaceae	7 to 9 (1)			
Iridaceae	66 (1)			
Ixoliaceae	1 (1)			
Lanariaceae	1 (1)			
Orchidaceae	880 (3)			
Tecophilaceae	7 (1)			
Xanthorrhoeaceae	35 (3)			

Appendix 1. Continued.

Taxonomic classification	Total # of genera per family (total # of genera sampled)	Taxon name, with species voucher	References and voucher information	
			References used for palynological data	References used for ecological data
Xeromataceae ARECALES	1 (1)	<i>Asphodelus</i> L. <i>Hemerocallis</i> L. <i>H. fulva</i> (L.) L. (Fig. 5A-C) <i>Xeromena</i> Brongn. & Gris	Lifante, 1996; Kosenko & Sventozhetskaya, 1999 Takahashi, 1980; Xiong et al., 1998 China, Yunnan, <i>S. D. Zhang et al. APE-LY-038</i> (KUN, living collection from KBC) Cranwell, 1953	Obeso, 1992; Kubitzki, 1998a Hotta et al., 1985; Kubitzki, 1998a Wardle, 1991; Chase et al., 2000
Areaceae	183 (3)	<i>Calamus</i> L. <i>C. nambariensis</i> Becc. (Fig. 5D-F) <i>Euterpe</i> Mart. <i>Nypa</i> Steck	Sovunmi, 1972; Zhang & Liu, 1983; Ferguson & Harley, 1993 China, Yunnan, <i>S. Y. Chen et al. I4369</i> (KUN)	Essig, 1973; Henderson, 1986; Kubitzki, 1998b
DASYPOGONALES				
Dasyogonaceae	4 (3)	<i>Kingia</i> R. Br. <i>Calcectasia</i> R. Br. <i>C. cyanea</i> R. Br. (Fig. 5G, H) <i>Dasyogon</i> R. Br.	Sovunmi, 1972; Henderson & Galeano, 1996 Sovunmi, 1972; Harley & Baker, 2001 Chanda & Ghosh, 1976 Chanda & Ghosh, 1976; Chanda et al., 1978 Australia, Western Australia, <i>A. Morrison s.n.</i> (E) Chanda & Ghosh, 1976	Essig, 1973; Henderson, 1986; Kubitzki, 1998b Essig, 1973; Henderson, 1986; Kubitzki, 1998b Kubitzki, 1998b Kubitzki, 1998b Kubitzki, 1998b
COMMELINALES				
Commelinaceae	40 (2)	<i>Cartonema</i> R. Br. <i>C. parviflorum</i> Hassk. (Fig. 5K, L) <i>Murdannia</i> Royle <i>Anigozanthos</i> Labill.	none Australia, Northern Territory, <i>R. Jensen 1837</i> (CANB)	Kubitzki, 1998b
Haemodoraceae	14 (1)	<i>A. viridis</i> Endl. (Fig. 5I, J) <i>Hanguana</i> Blume	Poole & Hunt, 1980; Yang et al., 2005 Simpson, 1983; Harley, 2004; Preece & Simpson, 2009 Australia, Western Australia, <i>A. Morrison s.n.</i> (E) Linder & Ferguson, 1985; Furness & Rudall, 1999	Cook, 1990; Kubitzki, 1998b Keighery, 1980; Western Australian Herbarium, 1998 onwards Maury, 1888; Cook, 1990; Kubitzki, 1998b
Hanguanaceae	1 (1)	<i>Philydrum</i> Banks ex Gaertn. <i>Pontederia</i> L.	Hamann, 1966; Simpson, 1985a Simpson, 1987	Cook, 1990; Kubitzki, 1998b Cook, 1990; Kubitzki, 1998b
ZINGIBERALES				
Cannaceae	1 (1)	<i>Canna</i> L.	Skvarla & Rowley, 1970; Kress & Stone, 1982; Ludlow-Wiechers, 1982; Rowley & Skvarla, 1986	Cook, 1990; Kubitzki, 1998b

Appendix 1. Continued.

Taxonomic classification	Total # of genera per family (total # of genera sampled)	Taxon name, with species voucher	References and voucher information	
			References used for palynological data	References used for ecological data
Costaceae	6 (1)	<i>Costus</i> L.	Sharma, 1968; Furness, 1985; Liang, 1988; Mangaly & Nayyar, 1990; Buchner & Weber, 2000 onwards	Kubitzki, 1998b
Heliconiaceae	1 (1)	<i>Heliconia</i> L. <i>H. subulata</i> Ruiz & Pav. (Fig. 6A–C)	Erdtman, 1952; Kress et al., 1978; Stone et al., 1979; Kress & Stone, 1982, 1983 China, Yunman, <i>L. Zhang ZL07</i> (KUN, living collection from XTBC)	Kress, 1985a, 1985b; Kubitzki, 1998b
Lowiaceae	1 (1)	<i>Orchidantha</i> N. E. Br.	Long & Wen, 1997; Buchner & Weber, 2000 onwards	Kubitzki, 1998b; Sakai & Inoue, 1999
Marantaceae	31 (1)	<i>Maranta</i> L.	Erdtman, 1952	Kennedy, 2000
Musaceae	2 (1)	<i>Musa</i> L.	Erdtman, 1952; Sharma, 1968; Stroo, 2000	Kubitzki, 1998b
Strelitziaceae	3 (1)	<i>Strelitzia</i> Aiton	Hesse & Waha, 1983; Kromstedt-Robards & Rowley, 1989; Rowley et al., 1997; Furness & Rudall, 1999	Frost & Frost, 1981; Kubitzki, 1998b
Zingiberaceae	46 to 52 (1)	<i>Alpinia</i> Roxb.	Sharma, 1968; Liang, 1988; Mangaly & Nayyar, 1990	Kubitzki, 1998b
POALES	3 (1)	<i>Anarthria</i> R. Br.	Ladd, 1977	Kubitzki, 1998b; Meney & Pate, 1999
Bromeliaceae	57 (2)	<i>Puya</i> Molina <i>Tillandsia</i> L.	Halbritter, 1992; Halbritter & Hesse, 1993; Stroo, 2000 Halbritter, 1992; Halbritter & Hesse, 1993; Albert et al., 2010	Ortiz Crespo, 1973; Kubitzki, 1998b Kubitzki, 1998b
Centropodiaceae	3 (1)	<i>Aphelia</i> R. Br.	Chanda, 1966; Ladd, 1977	Kubitzki, 1998b
Cyperaceae	98 (2)	<i>Carex</i> L. <i>C. scaposa</i> C. B. Clarke (Fig. 6D–F) <i>Mapania</i> Aubl.	Van Wichelen et al., 1999; Nagels et al., 2009; Halbritter et al., 2010; Wronska-Pilarek et al., 2010 China, Yunman, <i>S. D. Zhang et al. APE-LY-030</i> (KUN, living collection from KBC) Van Wichelen et al., 1999; Simpson et al., 2003; Nagels et al., 2009	Cook, 1990; Kubitzki, 1998b
Ecdeteooleaceae	2 (1)	<i>Ecdeteoolea</i> F. Muell.	Chanda, 1966; Chanda & Rowley, 1967; Ladd, 1977; Linder & Ferguson, 1985	Cook, 1990; Kubitzki, 1998b
Eriocaulaceae	10 (1)	<i>Eriocaulon</i> L. <i>E. cristatum</i> Mart. (Fig. 6I, J)	Thanikaimoni, 1965; Furness, 1985, 1988; De Borges et al., 2009 China, Yunman, <i>S. K. Wu et al. 3024</i> (KUN)	Kubitzki, 1998b

Appendix 1. Continued.

Taxonomic classification	Total # of genera per family (total # of genera sampled)	Taxon name, with species voucher	References and voucher information	
			References used for palynological data	References used for ecological data
Flagellariaceae	1 (1)	<i>Flagellaria</i> L.	Chanda, 1966; Chanda & Rowley, 1967; Ladd, 1977; Linder & Ferguson, 1985	Linder, 1987; Kubitzki, 1998b
Joinvilleaceae	1 (1)	<i>Joinvillea</i> Gaudich. ex Brongn. & Gris	Chanda, 1966; Chanda & Rowley, 1967	Kubitzki, 1998b
Juncaceae	7 (2)	<i>Juncus</i> L. <i>J. sikhimensis</i> Hook. f. (Fig. 6G, H)	Cramwell, 1953; Perveen, 1999; Buchner & Weber, 2000 onwards China, Yunman, X. X. <i>Zhu APE-LY-037</i> (KUN)	Cook, 1990; Kubitzki, 1998b
Mayacaceae	1 (1)	<i>Luzula</i> DC.	Cranwell, 1953; Buchner & Weber, 2000 onwards	Cook, 1990; Kubitzki, 1998b
Poaceae	668 (2)	<i>Mayaca</i> Aubl. <i>Anomochloa</i> Brongn. <i>Oryza</i> L. <i>Dendrocalamopsis beecheyana</i> (Munro) Keng f. var. <i>pubescens</i> (P. F. Li) Keng f. (Fig. 6K, L) <i>Rapatea</i> Aubl. <i>Elegia</i> L. <i>Balioskion</i> Raf. <i>Prionium</i> E. Mey. <i>Thurmtia</i> Hook. f. <i>Sparganium</i> L. <i>Typha</i> L. <i>Abolboda</i> Bonpl. <i>Xyris</i> L.	Page, 1978; Michelangeli et al., 2003 Sharma, 1968; Page, 1978; Chaturvedi et al., 1998 China, Yunman, S. D. <i>Zhang et al. APE-LY-22</i> (KUN, living collection from KBG) Carlquist, 1961; Zavada, 1983; Triemann, 1985 Chanda, 1966 Chanda, 1966; Briggs et al., 1999 Munro & Linder, 1997 Zavada, 1983 Nilsson et al., 1977; Zhang & Chen, 1984 Nilsson et al., 1977; Zhang & Chen, 1984; Perveen, 1999 Carlquist, 1960; Straka & Friedrich, 1984; Furness & Rudall, 1999; Campbell, 2012 Straka & Friedrich, 1984; Rudall & Sajo, 1999; Campbell, 2012	Cook, 1990; Kubitzki, 1998b Cook, 1990; Kubitzki, 1998b Clayton & Renvoize, 1986; Judziewicz & Soderstrom, 1989; Givnish et al., 2010 Clayton & Renvoize, 1986; Givnish et al., 2010 Kubitzki, 1998b Kubitzki, 1998b Kubitzki, 1998b Cook, 1990; Kubitzki, 1998b Cook, 1990; Kubitzki, 1998b Cook, 1990; Kubitzki, 1998b Cook, 1990; Kubitzki, 1998b Cook, 1990; Kubitzki, 1998b; Oriani & Scatena, 2011 Cook, 1990; Kubitzki, 1998b
Xyridaceae	5 (2)			
Outgroups AMBORELLES Amborellaceae	1 (1)	<i>Amborella</i> Baill.	Sampson, 1993, 2000; Hesse, 2001	Kubitzki et al., 1993; Thien et al., 2003

Appendix 1. Continued.

Taxonomic classification	Total # of genera per family (total # of genera sampled)	Taxon name, with species voucher	References and voucher information	
			References used for palynological data	References used for ecological data
NYMPHAEALES				
Cambaceae	2 (1)	<i>Cabomba</i> Aubl.	Walker, 1974, 1976; Osborn et al., 1991	Schneider & Jeter, 1982; Kubitzki et al., 1993
Nymphaeaceae	6 (1)	<i>Nymphaea</i> L.	Meyer, 1964; Gabarayeva & El-Ghazaly, 1997; Sampson, 2000; Gabarayeva et al., 2001	Meeuse & Schneider, 1979; Cook, 1990; Kubitzki et al., 1993; Evik & Knudsen, 2003
AUSTROBAILEYALES				
Austrobaileyaceae	1 (1)	<i>Austrobaileya</i> C. T. White	Endress & Honegger, 1980; Zavada, 1984b; Sampson, 2000	Endress, 1990, 2001; Kubitzki et al., 1993
Schisandraceae	3 (2)	<i>Illicium</i> L. <i>Schisandra</i> Michx.	Lin, 1989; Liu & Yang, 1989; Takahashi, 1994; Sampson, 2000; Wang et al., 2010 Walker, 1974; Sampson, 2000; Sun, 2000; Wang et al., 2010	Thien et al., 1983, 2000; Kubitzki et al., 1993; Dieringer et al., 1999 Kubitzki et al., 1993; Thien et al., 2000; Yuan et al., 2007
CERATOPHYLLALES				
Ceratophyllaceae	1 (1)	<i>Ceratophyllum</i> L.	Díez et al., 1988; Takahashi, 1995	Cook, 1990; Kubitzki et al., 1993
CHLORANTHALES				
Chloranthaceae	4 (2)	<i>Ascarina</i> J. R. Forst. & G. Forst. <i>Chloranthus</i> Sw.	Kuprianova, 1967; Eklund et al., 2004 Kuprianova, 1967; Eklund et al., 2004	Kubitzki et al., 1993; Thien et al., 2000 Kubitzki et al., 1993; Thien et al., 2000
LAURALES				
Calycanthaceae	4 (1)	<i>Calycanthus</i> L.	Nicely, 1965; Li, 1990; Sampson, 2000; Staedler et al., 2009	Kubitzki et al., 1993
MAGNOLIALES				
Magnoliaceae	2 (2)	<i>Liriodendron</i> L. <i>Magnolia</i> L.	Canright, 1953; Agababian, 1972; Wei & Wu, 1993 Canright, 1953; Agababian, 1972; Sampson, 2000; Xu & Kirchoff, 2008	Kubitzki et al., 1993 Kubitzki et al., 1993; Dieringer et al., 1999
CANELLALES				
Winteraceae	5 (1)	<i>Drimys</i> J. R. Forst. & G. Forst.	Walker, 1974; Zavada & Taylor, 1986; Sampson, 1995	Bernhardt & Thien, 1987; Kubitzki et al., 1993
PIPERALES				
Aristolochiaceae	5 to 8 (1)	<i>Asarum</i> L.	Mi & Yang, 1991; Sampson, 2000; Mulder, 2003; Perveen & Qaiser, 2008	Kubitzki et al., 1993; Kelly, 1997
LACTIORDACEAE				
Saururaceae	1 (1) 5 (1)	<i>Lactoris</i> Phil. <i>Saururus</i> L.	Zavada & Taylor, 1986; Sampson, 1995, 2000 Sampson, 2000; Smith & Stockey, 2007	Kubitzki et al., 1993 Cook, 1990; Kubitzki et al., 1993

Appendix 2. Comprehensive data matrix of pollen morphological and ecological characters analyzed in this study (see text and Table 1 for details). Taxon names are the same as those in Chase et al. (2006) throughout. One hundred twenty monocots and 16 outgroups are scored, and outgroup taxa are represented in italics. Inapplicable states are coded as “-” and unknown states as “?”. Polymorphic states are enclosed in curly brackets.

Abolboda	00111020--00-0---022
Acanthochlamys	0100-2010?0021122??21
Acorus calamus	0100-1010100220-10122
Acorus gramineus	0100-1010100220-10122
Agapanthus	0100-{1,2}210000210-20?21
Agave	0100-12{1,2}0{0,1,2}00210-20?{2,4}0
Alania	0100-1110?00211120?21
Aletris	0100-11101002{0,1,2}0-{1,2}0121
Alisma	002110{0,1}431102211101{1,2}2
Allium	0100-{1,2}110{0,1}00220-{1,3,4}0120
Alpinia	00111020--0221100022
Alstroemeria	0100-1210{1,2}00220-{1,3,4}0?2{0,1,2}
<i>Amborella</i>	0{0,1}{0,1}1{0,1}0{0,1}{0,1}02{0,1}02111701{1,2}2
Anarthria	0111{0,1}01102112212{1,3}011{1,2}
Anemarrhena	0100-2110?00210-20?20
Anigozanthos	0201-22{2,3}00101-0--050
Anomochloa	011110?10211221000?21
Aphelia	0111{0,1}0{0,1}10111221031?11
Aphyllanthes	0??11021-13022111??20
Arisaema	001110{0,1}0--022110-022
Arthropodium	0100-{1,2}110000210-2??21
<i>Asarum</i>	0211{0,1}0{1,2}{0,2,3,4}21{0,1}02{1,2}1{0,1,2}{1,2}0{0,1}22
<i>Ascarina</i>	011001{0,1}10100211020112
Asparagus	0100-{1,2}110{0,1}002{1,2}0-{1,2,3}012{0,1}
Asphodelus	0100-1210{0,1}002{1,2}0-{0,1,2}0121
Astelia	0100-{1,2}{0,1}10?002?11?0?2{1,2}
<i>Austrobaileya</i>	0100-11101002{1,2}0-{2,3}0122
Baloskion	011110?1011122??10112
Behnia	0100-?210?00210-2??2{1,2}
Blandfordia	0100-1110000220-3??5{1,2}
Borya	0100-{1,2}{0,1}10?00210-2??20
Brodiaea	0100-2210?00210-2??21
Butomus	0100-1110000210-20123
<i>Cabomba</i>	0100-2{1,2}10{1,2}00221210123
Calamus	0201-1{0,1}220002{1,2}{0,1}{1,2}{1,2,5}0122
Calectasia	0100-2,3{1,2}10200210-{1,2}0101
Calochortus	0100-2{1,2}{1,2}0000210-2??2{0,1,2}
<i>Calycanthus</i>	0200-{0,1}{1,2}{1,2}{0,2}1002{1,2}0-{1,2,3,5}0122
Campynema	0100-2110?00210-{1,2}0??1
Canna	00111020--00-0---0{4,5}2
Carex	1121{1,2}014{0,2}110221{0,1,2}{1,5}212{1,2}
Carludovica	01112{0,1}111?1?220-10122
Cartonema	0110-1210100210-6??21
<i>Ceratophyllum</i>	00111010--00-0---033
Chloranthus	0200-0{0,1}421{0,1}021{0,1}120122
Chlorophytum	0100-{1,2}110100220-1??{0,2}0
Chorigyne	0100-??10?00220-1?122
Clivia	0100-2210000210-20?{2,5}0
Convallaria	0100-{1,2}110000220-10122
Costus	0?211{0,1}3{1,4}30{1,3}01-0-0-0{2,5}2
Croomia	0100-1110100210-20121
Cyclanthus	0111{0,1}1{0,1}10010220-10122
Cymodocea	00-2--40--00-0---033
Cypripedium	0100-1110200220-{0,1}0021
Dasyopogon	0100-1110000220-101{2,5}1
Dioscorea	0{1,2}01-{1,2,3}{0,1}{1,2,3}21002{1,2}0-{1,2,3,4}012{1,2}

Appendix 2. Continued.

Doryanthes	0100-{1,2}110200210-2??{2,5}1
<i>Drimys</i>	111100{0,1}10111210-2012{1,2}
Ecdeiocollea	011110110211221210111
Elegia	011110110?11220-1?112
Epipactis	111110110{0,1}10210-2?122
Eriocaulon	0??110{0,1}{1,2,3}?130221{0,1}{0,1,3}012{1,2}
Euterpe	0100-2{1,2}101002{1,2}0-{1,2}0?2{1,2}
Flagellaria	0111101101112212{1,3}011{1,2}
Freyinetia	0111{0,1}1{0,1}1001122{0,1}0{0,1}01{4,6}2
Gymnostachys	0100-1110100220-{1,5}0122
Hanguana	001110{0,1}0---00-0---022
Heliconia	0111{0,1}020---00-0---0{4,5}2
Hemeroallis	0100-{2,3}{2,3}10000210-20121
Herreria	0100-?110?00210-20??2
Hypoxis	0100-{1,2}110100210-20?2{1,2}
<i>Illicium</i>	0211{0,1}01321{0,4}0210-20121
Ixiolirion	0100-2{1,2}10200210-20?20
Japonolirion	0100-1010?00200--01?2
Joinvillea	011110110111221011011
Juncus	111110{0,1}101102210{0,1}??{1,2}{1,2}
Kingia	0100-1{1,2}10000220-{0,1}01{2,5}1
<i>Lactoris</i>	11{0,1}{0,1}{0,1}0{0,1}101{0,1}0210-{1,3}{0,1}111
Lanaria	0100-1{0,1}10000220-10121
Lilium	01{0,1}0-{1,2}{2,3}{1,2,3}01{0,1}0210-20121
<i>Liriodendron</i>	0100-{1,2}{1,2}101002{1,2}0-{1,2,3}012{1,2}
Luzula	1111101101102210{0,1}??{1,2}{1,2}
Luzuriaga	0100-1{0,1}10100210-2??02
<i>Magnolia</i>	0100-{1,2}{1,2}1010022{0,1}0{1,3}{0,1,2}12{1,2}
Mapania	111110{0,1}101112{1,2}{0,1}{0,1}{1,2,5}0122
Maranta	001110?0---00-0---022
Mayaca	0100-1?101002{0,1}0-20122
Murdannia	0100-2110100221{0,2}10121
Musa	001110{2,3}0---00-0---0{4,5}2
Narthecium	0100-1{0,1}102002{1,2}0-{1,2}0122
Neuwiedia	0100-1010200210-20122
<i>Nymphaea</i>	0{1,2}{0,1}{0,1}{0,1}{0,1}{1,2}12{0,1}{0,2}0221{0,1,2}{0,2}{0,1,2}122
Nypa	021110112020{1,2}11{1,2}0122
Orchidantha	01012030---00-0---022
Orontium	0100-{1,2}210100220-{1,5}0122
Oryza	011110110211211{0,1}{0,6}0?11
Pandanus	0111{1,2}0{0,1}1001{0,1}{1,2}{1,2}{0,1}{0,1,2}{0,1,2,5}{0,2}{0,1}{1,2,4}2
Petermannia	0100-2110?0022115??22
Petrosavia	0100-2{0,1}10100210-{1,2}0?{0,2}{1,2}
Philesia	00110020---021110??5{1,2}
Philydrum	1100-1110000210-20122
Pleea	0201-1{0,1}2??00210-20121
Pontederia	0100-21{2,3}{0,2}000220-{0,3,5}0123
Potamogeton	{0,1}011{0,1}0{0,1}0---0211120113
Pronium	11111001011022100??12
Puya	0100-1210000210-201{4,5}1
Rapatea	0211101121202{1,2}0-{1,2}012{1,2}
Rhipogonum	0100-{1,2}110?0021{0,1}120122
Sagittaria	002110{0,1}43110221{0,1}101{1,2}3
<i>Saururus</i>	0100-2010100221010122
Schelhammera	0100-{1,2}210?002???0?22
<i>Schisandra</i>	011100{0,1}{3,4}{0,2}1{0,4}0210-20121
Scilla	0100-{1,2}1100002{1,2}0-{1,2}0121
Sisyrinchium	0100-2{1,2}10000210-20121
Smilax	001110{0,1}0---02{0,2}1131022
Sparganium	011110110110210-20?12

Appendix 2. Continued.

Sphaeradenia	01{0,1}{0,1}{0,1}21100{0,1}02{1,2}0-{1,2}012{1,2}
Stemona	0100-1{0,1}101002{0,1,2}0-{0,1,2,3,5}{0,1,2}12{0,1}
Strelitzia	00111030---00-0---052
Tacca	0100-{1,2}1101002{1,2}0-{2,3}01{0,2}2
Talbotia	0100-1010200220-301?2
Tecophilaea	0100-1110200220-301?1
Thurnia	111110010110211160?12
Tillandsia	0100-{1,2}{1,2}1{0,1}{1,2}002{1,2}0-{1,2}01{2,5}{0,1}
Tofieldia	0201-1{0,1}2210021{0,1}{0,2}{1,2}012{1,2}
Trichopus	0100-10101002211???02
Triglochin	001110{0,1}0---0210-20112
Trillium	001110{0,1}0---0{0,2}{0,1}0-30{0,1}2{1,2}
Typha	{0,1}11110{0,1}10110210-20?12
Uvularia	0100-{1,2}1{1,2}0200211{0,1}10?2{1,2}
Vallisneria	00111030---00-0---033
Veratrum	0100-{1,2}110200210-2??22
Xanthorrhoea	0100-{1,2}110?00210-201{2,5}1
Xeronema	0100-1110000210-2?1{2,5}0
Xyris	0100-11{1,2}0{1,2}00210-2??2{1,2}
Zostera	00-2--40---00-0---033

Appendix 3. Democratic data matrix of pollen morphological and ecological characters analyzed in this study (see text and Table 1 for details). Taxon names are the same as those in Chase et al. (2006) throughout. One hundred twenty monocots and 16 outgroups are scored, and outgroup taxa are represented in italics. Inapplicable states are coded as “-” and unknown states as “?”.

Abolboda	00111020--00-0---0
Acanthochlamys	0100-2010?0021122??
Acorus_calamus	0100-1010100220-101
Acorus_gramineus	0100-1010100220-101
Agapanthus	0100-2210000210-20?
Agave	0100-1210100210-20?
Alania	0100-1110?00211120?
Aletris	0100-1110100210-201
Alisma	0021100431102211101
Allium	0100-1110100220-401
Alpinia	00111020--02211000
Alstroemeria	0100-1210100220-30?
Amborella	0111000102102111701
Anarthria	011101102112212301
Anemarrhena	0100-2110?00210-20?
Anigozanthos	0200-22200101-0--0
Anomochloa	011110?10211221000?
Aphelia	011110010111221031?
Aphyllanthes	0??11021-1302211??
Arisaema	00111000--022110-0
Arthropodium	0100-2110000210-2??
Asarum	0211102321002112201
Ascarina	0110010101002110201
Asparagus	0100-2110100220-101
Asphodelus	0100-1210100220-101
Astelia	0100-1010?002?11?0?
Austrobaileya	0100-1110100210-201
Baloskion	011110?1011122??101
Behnia	0100-?210?00210-2??
Blandfordia	0100-1110000220-3??
Borya	0100-2110?00210-2??
Brodiaea	0100-2210?00210-2??
Butomus	0100-1110000210-201
Cabomba	0100-22102002212101
Calamus	0201-1122000210-201
Calectasia	0100-2210200210-201
Calochortus	0100-2110000210-2??
Calycanthus	0200-0122100210-201
Campynema	0100-2110?00210-20?
Canna	00111020--00-0---0
Carex	1121101401102210121
Carludovica	011120111?1?220-101
Cartonema	0110-1210100210-6??
Ceratophyllum	00111010--00-0---0
Chloranthus	0200-00421002101201
Chlorophytum	0100-2110100220-1??
Chorigyne	0100-??10?00220-1?1
Clivia	0100-2210000210-20?
Convallaria	0100-2110000220-101
Costus	0?21103430101-0-0-0
Croonia	0100-1110100210-201
Cyclanthus	011101110010220-101
Cymodocea	00-2--40--00-0---0
Cypripedium	0100-1110200220-000

Appendix 3. Continued.

Dasypogon	0100-1110000220-101
Dioscorea	0200-1122100220-101
Doryanthes	0100-2110200210-2??
<i>Drimys</i>	111100110111210-201
Ecdiocola	0111101102112212101
Elegia	011110110?11220-1?1
Epipactis	111110110010210-2?1
Eriocaulon	0??11011?1302211101
Euterpe	0100-2110100220-10?
Flagellaria	0111101101112212301
Freycinetia	011101010011220-101
Gymnostachys	0100-1110100220-101
Hanguana	00111000--00-0---0
Heliconia	01111020--00-0---0
Hemerocallis	0100-3310000210-201
Herreria	0100-?110?00210-20?
Hypoxis	0100-2110100210-20?
<i>Illicium</i>	021110132100210-201
Ixiolirion	0100-2110200210-20?
Japonolirion	0100-1010?00200--01
Joinvillea	0111101101112210110
Juncus	11111001011022101??
Kingia	0100-1210000220-101
<i>Lactoris</i>	111110110100210-311
Lanaria	0100-1110000220-101
Lilium	0100-2210100210-201
<i>Liriodendron</i>	0100-2210100220-101
Luzula	11111011011022101??
Luzuriaga	0100-1110100210-2??
<i>Magnolia</i>	0100-2210100220-101
Mapania	1111100101112210101
Maranta	001110?0--00-0---0
Mayaca	0100-1?101002-0-201
Murdannia	0100-21101002212101
Musa	00111020--00-0---0
Narthecium	0100-1010200210-201
Neuwiedia	0100-1010200210-201
<i>Nymphaea</i>	0211101120202212011
Nypa	0211101120202211101
Orchidantha	01012030--00-0---0
Orontium	0100-2210100220-101
Oryza	011110110211211060?
Pandanus	0111200100101-0--0
Petermannia	0100-2110?0022115??
Petrosavia	0100-2010100210-20?
Philesia	00110020--0-01110??
Phylidrum	1100-1110000210-201
Pleea	0200-102??00210-201
Pontederia	0100-2122000220-301
Potamogeton	00111000--02111201
Prionium	11111001011022100??
Puya	0100-2210000210-201
Rapatea	021110112120210-201
Rhipogonum	0100-1110?00210-201
Sagittaria	0021100431102211101
<i>Saururus</i>	0100-22101002210101
Schellhammera	0100-2210?002??0???
<i>Schisandra</i>	011100142140210-201
Scilla	0100-2110000210-201
Sisyrinchium	0100-2110000210-201

Appendix 3. Continued.

Smilax	00111000---0200--10
Sparganium	011110110110210-20?
Sphaeradenia	0101-2110000220-101
Stemona	0100-1110100200--11
Strelitzia	00111030---00-0---0
Tacca	0100-2110100220-301
Talbotia	0100-1010200220-301
Tecophilaea	0100-1110200220-301
Thurnia	111110010110211160?
Tillandsia	0100-1110100210-201
Tofieldia	0200-1022100210-201
Trichopus	0100-10101002211???
Triglochin	00111000---0210-201
Trillium	00111010---00-0---0
Typha	111110110110210-20?
Uvularia	0100-1110200211110?
Vallisneria	00111030---00-0---0
Veratrum	0100-2110200210-2??
Xanthorrhoea	0100-1110?00210-201
Xeronema	0100-1110000210-2?1
Xyris	0100-1110200210-2??
Zostera	00-2--40---00-0---0

Appendix 4. Data matrix of pollen morphological and ecological characters used in analyses of correlated evolution (see text and Table 1 for details). Taxon names used are the same as those in Chase et al. (2006) throughout. One hundred twenty monocots and 16 outgroups are scored, and outgroup taxa are represented in italics. Unknown states are coded as "?."

Abolboda	00000010
Acanthochlamys	11011000
Acorus_calamus	11111011
Acorus_gramineus	11111011
Agapanthus	11011000
Agave	11011000
Alania	11011000
Aletris	11011000
Alisma	11111011
Allium	11111000
Alpinia	11111000
Alstroemeria	11111000
<i>Amborella</i>	11111000
Anarthria	11111000
Anemarrhena	11011000
Anigozanthos	10000000
Anomochloa	11111000
Aphelia	11110100
Aphyllanthes	11111000
Arisaema	11111000
Arthropodium	11011000
<i>Asarum</i>	11011000
<i>Ascarina</i>	11011000
Asparagus	11011000
Asphodelus	11011000
Astelia	11?11000
<i>Austrobaileya</i>	11011000
Baloskion	11111010
Behnia	11011000
Blandfordia	11111000
Borya	11011000
Brodiaea	11011000
Butomus	11011011
<i>Cabomba</i>	11111011
Calamus	11011000
Calectasia	11011000
Calochortus	11011000
<i>Calycanthus</i>	11011000
Campynema	11011000
Canna	00000010
Carex	11111010
Carludovica	11111000
Cartonema	11011000
<i>Ceratophyllum</i>	00000011
<i>Chloranthus</i>	11011000
Chlorophytum	11111000
Chorigyne	11111000
Clivia	11011000
Convallaria	11111000
Costus	10000010
Croomia	11011000
Cyclanthus	11111010
Cymodocea	00000011

Appendix 4. Continued.		Appendix 4. Continued.	
Cypripedium	11111000	Rhipogonum	11011000
Dasyogon	11111000	Sagittaria	11111011
Dioscorea	11111000	<i>Saururus</i>	11111010
Doryanthes	11011000	Schelhammera	11?11000
Drimys	11011000	Schisandra	11011000
Ecdeiocolea	11111000	Scilla	11011000
Elegia	1111??00	Sisyrinchium	11011000
Epipactis	1101??00	Smilax	10010100
Eriocaulon	11111010	Sparganium	11011011
Euterpe	11111000	Sphaeradenia	11111000
Flagellaria	11111000	Stemona	11011000
Freycinetia	11111000	Strelitzia	00000010
Gymnostachys	11111000	Tacca	11111000
Hanguana	00000011	Talbotia	11111000
Heliconia	00000010	Tecophilaea	11111000
Hemero callis	11011000	Thurnia	11011011
Herreria	11011000	Tillandsia	11011000
Hypoxis	11011010	Tofieldia	11011000
<i>Illicium</i>	11011000	Trichopus	11?11010
Ixiolirion	11011000	Triglochin	11011010
Japonolirion	10011010	Trillium	00000000
Joinvillea	11110100	Typha	11011011
Juncus	1111??10	Uvularia	11111000
Kingia	11111000	Vallisneria	00000011
Lactoris	11110100	Veratrum	11011000
Lanaria	11111000	Xanthorrhoea	11011000
Lilium	11011000	Xeronema	11011000
<i>Liriodendron</i>	11111000	Xyris	11011010
Luzula	1111??00	Zostera	00000011
Luzuriaga	11011000		
<i>Magnolia</i>	11111000		
Mapania	11111000		
Maranta	00000010		
Mayaca	10011011		
Murdannia	11111010		
Musa	00000010		
Narthecium	11011010		
Neuwiedia	11011000		
<i>Nymphaea</i>	11110111		
Nypa	11111000		
Orchidantha	00000010		
Orontium	11111011		
Oryza	11011010		
Pandanus	11000000		
Petermannia	11111000		
Petrosavia	11011000		
Philesia	11111000		
Philydrum	11011010		
Pleea	11011000		
Pontederia	11111011		
Potamogeton	11011011		
Prionium	1111??10		
Puya	11011000		
Rapatea	11011000		

