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ASSEMBLING THE TREE OF THE MONOCOTYLEDONS: PLASTOME SEQUENCE PHYLOGENY AND EVOLUTION OF POALES[1]

Thomas J. Givnish,[2] Mercedes Ames,[2] Joel R. McNeal,[3] Michael R. McKain,[3] P. Roxanne Steele,[4] Claude W. dePamphilis,[5] Sean W. Graham,[6] J. Chris Pires,[4] Dennis W. Stevenson,[7] Wendy B. Zomlefer,[3] Barbara G. Briggs,[8] Melvin R. Duvall,[9] Michael J. Moore,[10] J. Michael Heaney,[11] Douglas E. Soltis,[11] Pamela S. Soltis,[12] Kevin Thiele,[13] and James H. Leebens-Mack[3]

Abstract

The order Poales comprises a substantial portion of plant life (7% of all angiosperms and 33% of monocots) and includes taxa of enormous economic and ecological significance. Molecular and morphological studies over the past two decades, however, leave uncertain many relationships within Poales and among allied commelinid orders. Here we present the results of an initial project by the Monocot AToL (Angiosperm Tree of Life) team on phylogeny and evolution in Poales, using sequence data for 81 plastid genes (exceeding 101 aligned kb) from 83 species of angiosperms. We recovered highly concordant relationships using maximum likelihood (ML) and maximum parsimony (MP), with 98.2% mean ML bootstrap support across monocots. For the first time, ML resolves ties among Poales and other commelinid orders with moderate to strong support. Analyses provide strong support for Bromeliaceae being sister to the rest of Poales; Typhaceae, Rapateaceae, and cyperids (sedges, rushes, and their allies) emerge next along the phylogenetic spine. Graminids (grasses and their allies) and restiids (Restionaceae and its allies) are well supported as sister taxa. MP identifies a xyrid clade (Eriocaulaceae, Mayacaceae, Xyridaceae) sister to cyperids, but ML (with much stronger support) places them as a grade with respect to restiids + graminids. The conflict in resolution between these analyses likely reflects long-branch attraction and highly elevated substitution rates in some Poales. All other familial relationships within the order are strongly supported by both MP and ML analyses. Character-state mapping implies that ancestral Poales lived in sunny, fire-prone, at least seasonally damp/wet, and possibly nutrient-poor sites, and were animal pollinated. Five subsequent shifts to wind pollination—in Typhaceae, cyperids, restiids, Ecdeiocoleaceae, and the vast PACCMAD-BEP clade of grasses—are significantly correlated with shifts to open habitats and small, inconspicuous, unisexual, and nectar-free flowers. Prime ecological movers driving the repeated evolution of wind pollination in Poales appear to include open habitats combined with the high local dominance of conspecific taxa, with the latter resulting from large-scale disturbances, combined with tall plant stature, vigorous vegetative

[1] This research was supported by National Science Foundation (NSF) grants DEB-0829762, DEB-0829849, DEB-0829868, DEB-0830009, DEB-0830020, and DEB-0830036 to members of the Monocot AToL Team, and by the Hertel Gift Fund of the University of Wisconsin-Madison to T.J.G. Jannice Friedman, Jana Vamosi, Spencer Barrett, and Kathleen Kay kindly provided access to data sets on wind pollination and related traits across angiosperms, and George Weiblen graciously let us use his data set on the occurrence of dioecy across monocots. Lynn Clark kindly shared information on bamboo seeds and pollination. Marco Duretto and Greg Jordan helped provide permits and suggest collecting locations in Tasmania; Joanne Birch provided assistance and camaraderie while collecting at Cradle Mountain. Godfrey Bourne and Margaret Chan-a-Sue were especially generous in helping to obtain research permits and organize transport to and from Kaieteur Falls National Park in Guyana. We would like to thank Frank Zich of the Australian Tropical Herbarium and Mark Clements of the Centre for Biodiversity Research for providing access to *Apostasia* Blume, and Jeremy Bruhl for sending material of *Neoastelia* J. B. Williams. Andrew Meade, Mark Pagel, Mark Chase, Ken Sytsma, Marie Adams, and Eric Cabot kindly provided technical assistance. Mike Havey generously provided access to important lab equipment. Chang Liu helped prepare DNA samples for sequencing. Raj Ayyampalayam wrote Perl scripts and Aakrosh Ratan provided early access to the YASRA assembler. Kandis Elliott worked her digital magic with the illustrations; Catherine Wardrop contributed the beautiful drawings of *Georgeantha* B. G. Briggs & L. A. S. Johnson and *Hypolaena* R. Br. Many thanks to Peter Stevens for having organized a highly stimulating symposium on plant diversification, to Peter Stevens and Victoria Hollowell for providing several helpful comments, and to Victoria Hollowell for her many contributions during editing.

[2] Department of Botany, University of Wisconsin, Madison, Wisconsin 53706, U.S.A. givnish@wisc.edu.
[3] Department of Plant Biology, University of Georgia, Athens, Georgia 30602, U.S.A.
[4] Department of Biological Sciences, University of Missouri, Columbia, Missouri 65211, U.S.A.
[5] Department of Biology, Pennsylvania State University, University Park, Pennsylvania 16802, U.S.A.
[6] Botanical Garden and Centre for Plant Research, University of British Columbia, Vancouver BC, Canada V6T 1Z4.
[7] New York Botanical Garden, Bronx, New York 10458, U.S.A.
[8] Botanic Gardens Trust, Sydney, New South Wales 2000, Australia.
[9] Department of Biological Sciences, Northern Illinois University, DeKalb, Illinois 60115, U.S.A.
[10] Department of Biology, Oberlin College, Oberlin, Ohio 44074, U.S.A.
[11] Department of Botany, University of Florida, Gainesville, Florida 32611, U.S.A.
[12] Florida Museum of Natural History, University of Florida, Gainesville, Florida 32611, U.S.A.
[13] Western Australian Herbarium, Perth, Western Australia 6983, Australia.
doi: 10.3417/2010023

spread, and positive ecological feedback. Reproductive assurance in the absence of reliable animal visitation probably favored wind pollination in annuals and short-statured perennials of Centrolepidaceae in ephemerally wet depressions and windswept alpine sites.

Key words: Commelinids, correlated evolution, cyperids, graminids, long-branch attraction, molecular systematics, monocots, plastid, plastome, restiids, xyrids.

Monocots—with ca. 65,000 species in 82 families and 12 orders (Cameron et al., 2003; Givnish et al., 2006; Saarela et al., 2007; Angiosperm Phylogeny Group, 2009), and including such groups as the grasses, sedges, bromeliads, palms, gingers, bananas, orchids, irises, onions, asparagus, lilies, yams, pondweeds, aroids, and seagrasses—are one of the most diverse, morphologically varied, ecologically successful, and economically important clades of angiosperms. Since monocotyledons arose in the early Cretaceous (Herendeen & Crane, 1995; Bremer, 2000; Friis et al., 2004; Ramirez et al., 2007; Conran et al., 2009), they have radiated into almost every habitat on earth. Today, they dominate many terrestrial and aquatic ecosystems, display kaleidoscopic variation in vegetative and floral form, provide the basis for most of the human diet, support a huge horticultural industry, include large numbers of endangered taxa, and comprise nearly one fourth of all species and families of flowering plants. Understanding their origin, phylogeny, and patterns of morphological evolution, geographic diversification, and ecological radiation is thus a grand challenge and opportunity for evolutionary biologists.

Over the past 18 years, molecular systematics has revolutionized our understanding of monocot relationships (Chase et al., 1993, 1995a, b, 2000, 2006; Duvall et al., 1993a, b; Les et al., 1997; Givnish et al., 1999, 2005; Bremer, 2000, 2002; Kress et al., 2001; Hahn, 2002; Cameron et al., 2003; Michelangeli et al., 2003; Davis et al., 2004; Graham et al., 2006; Pires et al., 2006; Saarela et al., 2008). Such studies have led to a dramatic reclassification of the monocots (Angiosperm Phylogeny Group, 1998, 2003, 2009), with an ever-increasing understanding of relationships within and among the 12 orders currently recognized. Triumphs of monocot molecular systematics have included, first and foremost, the recognition of the commelinid clade (Chase et al., 1993, 1995a) composed of the orders Poales (the grasses, sedges, bromeliads, and their allies), Commelinales (the dayflowers, water hyacinths, and relatives), Zingiberales (the gingers, bananas, and related tropical monocots), Arecales (the palms), and the Australian Dasypogonales (Dasypogonaceae, Angiosperm Phylogeny Group, 2009, here recognized as an order following Givnish et al., 1999). This finding was buttressed by the demonstration that all five orders share UV-fluorescent ferulic acid bound to cell walls (Harris & Hartley, 1980; Dahlgren et al., 1985; Rudall & Caddick, 1994; Harris & Tretheway, 2009) despite their otherwise great divergence in form and despite their relationships to each other that remain enigmatic based on molecular and morphological data (Chase, 2004; Graham et al., 2006). Other key advances have included the validation, to a large degree, of many of the orders inferred cladistically from morphology by Dahlgren et al. (1985); the identification of relationships among those orders; the placement of *Acorus* L. as sister to all other monocots (Duvall et al., 1993a); and the discovery that several genera, originally placed in Melanthiales based on morphology by Dahlgren et al. (1985) and Tamura (1998), actually belong to three other orders—including *Tofieldia* Huds. in Alismatales, *Narthecium* Huds. in Dioscoreales, and *Japonolirion* Nakai in Petrosaviales (Chase et al., 1995a, b, 2000, 2006; Zomlefer, 1999; Tamura et al., 2004). Perhaps most remarkably, Saarela et al. (2007) recently showed that highly reduced members of the aquatic family Hydatellaceae were not—as had long been believed (Hamann, 1976; Dahlgren et al., 1985; Angiosperm Phylogeny Group, 1998, 2003; Davis et al., 2004)—members of order Poales, and not even monocots, but were instead sister to waterlilies and other Nymphaeales, one of the earliest divergent clades of angiosperms (see Bosch et al., 2008, and Rudall et al., 2009, for corroborating morphological evidence).

Chase et al. (2006) provided the most powerful study of relationships across monocots to date, in terms of its combination of extensive taxon sampling (125 species stratified across 77 of 82 families) and sequence data per taxon (four plastid genes, two mitochondrial genes, one nuclear ribosomal gene). Based on their maximum parsimony (MP) analysis, *Acorus* is sister to all other monocots, followed by the successive divergence of Alismatales, Petrosaviales, Dioscoreales–Pandanales, Liliales, Asparagales, and the commelinids (Fig. 1). Based on Chase et al. (2006), all orders appear to be strongly supported, and all relationships among orders are resolved and—outside the commelinids—moderately to strongly supported. Yet, the MP strict consensus tree resulting from that study left many relationships within orders weakly supported, as well as a few of those among orders. Areas of substantial uncertainty include

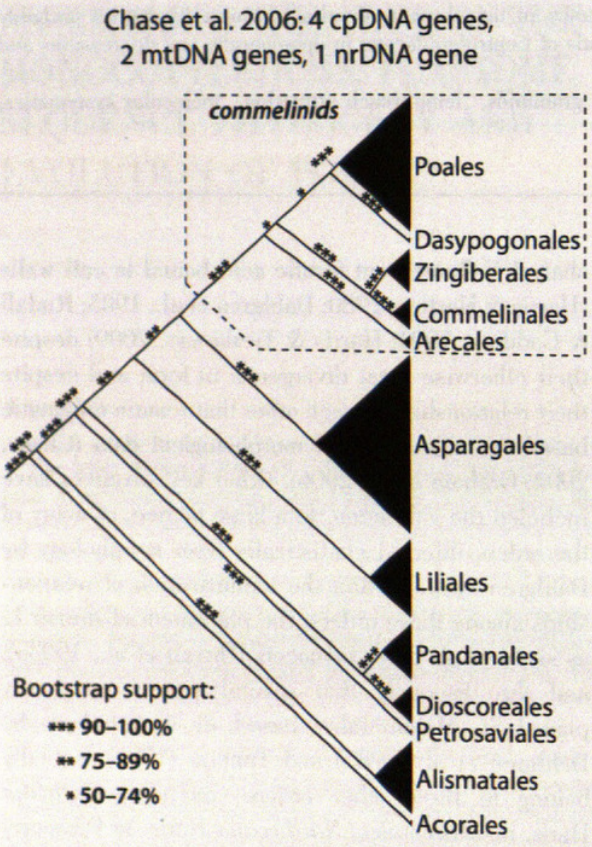

Figure 1. Branching topology and support at the ordinal level in monocots, based on an analysis of four plastid genes, two mitochondrial genes, and one nuclear ribosomal gene (4777 informative sites, or 34.9 informative sites/taxon). Adapted from Chase et al. (2006).

relationships among many families within Poales, and among the five orders of commelinids; the positions of Asparagales and Liliales relative to the commelinids; and affinities of several families in Asparagales, Zingiberales, Dioscoreales, Pandanales, and Alismatales. In addition, relationships among commelinid orders found by Chase et al. (2006) weakly conflict with those identified by Graham et al. (2006) based on 16 kb of sequences for coding and noncoding plastid regions from 69 monocots representing 53 of 82 families. Research on relationships among various monocot groups has made enormous progress (see symposia volumes edited by Rudall et al., 1995; Wilson & Morrison, 2000; Columbus et al., 2006, 2007; Seberg et al., 2010). Yet much remains to be learned, perhaps because so many groups appear to have diverged more than 90 million years ago (Bremer, 2000, 2002; Givnish et al., 2000, 2005; Wikström et al., 2001; Jannsen & Bremer, 2004), leaving only subtle traces of deep relationships in their current form and genetic sequences.

To address these uncertainities, develop a better understanding of broadscale relationships in monocots, and provide a strong basis for comparative studies of morphological, developmental, ecological, and geographic differentiation in this important group, the National Science Foundation–funded Monocot AToL (Assembling the Tree of Life) project (<http://www.botany.wisc./monatol/>) is conducting a 5-year investigation of monocot evolution, building on the strong foundation of previous research by the international botanical community. Our aims are to: (1) develop a fully resolved, strongly supported, highly inclusive broadscale phylogeny for the monocots, based on sequencing transcriptomes of young leaf tissue for several dozen species, and whole-plastid genomes and targeted mitochondrial and nuclear genes for a few hundred species representing all monocot families and subfamilies; (2) score more than 200 morphological characters for the same extant species and 75 fossil taxa; (3) reassess the stratigraphy and classification of several fossil monocots and develop a new timeline for monocot evolution; (4) identify morphological synapomorphies to permit diagnosis of all major monocot clades, in both extant and fossil plants; (5) use the resulting phylogeny to conduct analyses of morphological, developmental, ecological, and biogeographic evolution using hundreds of taxa stratified across the monocots (e.g., see Davies et al., 2004; Givnish et al., 2005; Dunn et al., 2007); and ultimately (6) help train and inspire a new generation of monocot systematists in phylogenetics, genomics, and evolutionary biology. As a key part of this effort, we will sequence and analyze hundreds of complete plastid genome sequences. Almost all studies to date using DNA to infer relationships among monocots and other angiosperms have been phylogenetic, relying on sequences of only one or a few genes or gene spacers. Our approach will be phylogenomic, ultimately providing sequences for more than 100 chloroplast genes and the spacers between these genes, and generating an avalanche of new data with which to assess evolutionary relationships. This approach has proved fruitful in broadscale investigations of relationships among angiosperms and land plants (Leebens-Mack et al., 2005; Cai et al., 2006; Jansen et al., 2007; Moore et al., 2007; Wang et al., 2009). However, high data density per taxon must be complemented with a reasonably dense stratification of taxon sampling across the range of organisms being investigated in order to minimize errors in phylogenetic inference due to long-branch attraction (e.g., see Goremykin et al., 2003, vs. Soltis & Soltis, 2004; Leebens-Mack et al., 2005).

In sequencing plastomes and targeted mitochondrial and nuclear genes, we are collaborating closely with members of the Angiosperm AToL team (<http://www.flmnh.ufl.edu/angiospermATOL>), who have already sequenced more than 30 plastomes and several mitochondrial and nuclear genes for nonmonocots.

We are also coordinating our efforts with members of the European monocot initiative (supported by a grant from the Leverhulme Trust) who are sequencing two plastid genes (*rbcL* and *matK*) for representatives of all ca. 2400 monocot genera. These efforts are complementary, in taxonomic coverage for the Angiosperm AToL, and in our resolution of deep monocot nodes while the Europeans link our backbone phylogeny to the remaining monocot genera. We are also collaborating with the 1000 Plants Initiative (<http://www.onekp.com>) to sequence shoot transcriptomes for several dozen species. We believe that the unparalleled amount of genetic information from all three plant genomes obtained in our AToL project should provide the most powerful analysis of relationships for any major plant group studied to date.

In this paper, we present a demonstration of the utility of a plastome-based phylogenomic approach, focusing on relationships among families of Poales and their immediate relatives among the commelinids. Poales is the second largest order of monocots, and economically surely the most important, as a consequence of its including the cereal and pasture grasses, which contribute so much to the human diet, directly or indirectly; the bamboos, a key source of building materials; and the restioids, sedges, rushes, cattails, and bur reeds, which form such key components of wetland ecosystems locally and worldwide. Poales and the commelinids include many of the nodes in the monocot tree of life that have proven most difficult to resolve using traditional phylogenetic techniques. Here we present a new, plastome-based phylogeny for the monocots and discuss its implications for relationships among families of Poales and its immediate commelinid relatives. We then use this phylogeny to analyze broadscale evolutionary patterns within Poales, including habitat diversification and, especially, the pattern and potential causes of multiple origins of wind pollination, an otherwise fairly uncommon mechanism in the monocots. We conclude with a brief discussion of some of the limitations of plastome-based phylogenomics for understanding monocot phylogeny and evolution.

Methods

Taxon and Gene Sampling

The 83 taxa included in our study represent most major clades of angiosperms sensu Angiosperm Phylogeny Group (2009) (Appendix 1). New draft plastid genome sequences were generated for 44 of the 83 taxa included in the study (Appendix 1). These new data greatly increase the number of monocot sequences included in plastid phylogenomic analyses. Sixty-four species acted as placeholders for 11 monocot orders and 32 of 82 monocot families. Taxon sampling is concentrated on Poales and, to a lesser extent, its putative relatives among the commelinids and Asparagales. Commelinids sequenced included members of 15 of 16 families of order Poales (Anarthriaceae not sampled); one of five families of Commelinales; two of eight families of Zingiberales; and the single families in Arecales and Dasypogonales (Dasypogonaceae sensu Angiosperm Phylogeny Group, 2009). Nonmonocot angiosperms included representatives of an additional 18 orders of flowering plants (Appendix 1). We used *Amborella* Baill., the consensus sister taxon to all other angiosperms (Jansen et al., 2007; Moore et al., 2007) as the outgroup.

Plastome Sequencing

We used next-generation sequencing to generate 44 plastid genomes sequences (Appendix 1) using one of two strategies. Following methods described by Jansen et al. (2005), plastids of *Lilium* L., *Hosta* Tratt., *Tradescantia* L., *Brocchinia* Schult. f., *Neoregelia* L. B. Sm., *Pitcairnia* L'Hér., and *Puya* Molina were isolated on a sucrose gradient and used as templates for rolling circle DNA amplification. Plastome-enriched amplicons were sequenced on a Roche GS-FLX sequencer (Roche, Branford, Connecticut, U.S.A.) using 454 pyrosequencing technology (Moore et al., 2007). The remaining 37 draft plastome sequences were assembled from whole-genome shotgun sequences generated on an Illumina GS sequencer (Illumina, Inc., San Diego, California, U.S.A.). The proportion of plastid DNA in isolated DNAs was estimated through quantitative real-time PCR amplification of a 150-bp portion of the *rbcL* gene. Samples estimated to have at least 5% plastid DNA were prepared for whole-genome shotgun sequencing on the Illumina sequencing platform, following the manufacturer's protocol. Bar codes were ligated to templates, and at least one million 75-bp reads were generated for each taxon. De novo assemblies of sequences generated on the 454 platform were constructed using the manufacturer's Newbler assembler (<http://www.454.com>) and the MIRA assembler (<http://www.chevreux.org/projects_mira.html>; Chevreux et al., 2004). Resulting assemblies were inspected using Consed (Gordon et al., 1998) and Sequencher (<http://www.genecodes.com/>). Genes were annotated and gene sequences were extracted from assemblies using the DOGMA webserver (<http://dogma.ccbb.utexas.edu>, Wyman et al., 2004, and see below). Sequences generated using the Illumina short-read platform were subjected to reference-based assembly using the YASRA assembler (Ratan, 2009;

download available with documentation at <http://www.bx.psu.edu/miller_lab>) to layer short reads on a reference genome while allowing substantial sequence divergence (< 85% sequence identity). For each taxon, the most closely related plastome genome sequence available in GenBank was initially used as the reference genome. In addition, our draft genome sequences were used as alternative references for assembly of related genomes. For example, the *Cyperus alternifolius* L. draft plastome was used as a reference for *Juncus effusus* L. and *Thurnia sphaerocephala* Hook. f. plastome assembly and vice versa. Final assemblies for each taxon were compiled in Sequencher. As described above, genes were annotated and extracted from the resulting contigs using DOGMA. DOGMA identifies genes through BLASTX searches against a database of amino acid sequences extracted from exemplar plastid genomes. As a consequence, gaps in the assemblies, rare sequencing errors, and assembly errors that introduce frame shifts or stop codons may result in annotation of gene fragments rather than full-length genes. Only full- or near-full-length gene annotations were included in alignments and phylogenetic analyses. Therefore, individual taxa may be missing genes due to low sequencing coverage, assembly errors, or evolutionary loss (e.g., the loss of the *ycf2* gene in the inverted repeat [IR] region of the plastome on the branch leading to Poaceae/Ecdeiocoleaceae/Joinvilleaceae). The only taxa with substantial numbers of missing genes were those with less than 15× coverage under next-generation sequencing, including *Abolboda macrostachya* Spruce ex Malme, *Mayaca fluviatilis* Aubl., and *Syngonanthus chrysanthus* Ruhland, and *Joinvillea plicata* (Hook. f.) Newell & B. C. Stone under ordinary direct sequencing. All gene sequences included in alignments and phylogenetic analyses have been deposited into GenBank. All analyses were based on the exons of 77 protein-coding plastid genes and four ribosomal RNAs (rRNAs), with a total of 109,134 aligned bases. This set of 81 plastid genes was also used by Jansen et al. (2007) to resolve broadscale relationships across flowering plants.

SEQUENCE ALIGNMENT

Following Jansen et al. (2007), 81 plastome-encoded gene sequences were aligned individually and alignments concatenated into a single nexus file for phylogenetic analyses; the file is posted at the Monocot AToL project website (see <http://chloroplast.cbio.psu.edu/supplement.html>). Perl scripts were written to sort gene sequences extracted from DOGMA annotations for each taxon into multitaxon fasta files for each gene, to align gene sequences using MUSCLE (Edgar, 2004), and to concatenate alignments in a Nexus file. Missing genes were filled with Ns in the concatenated alignment.

PHYLOGENETIC ANALYSES

We inferred relationships among taxa from the nucleotide data using MP and maximum likelihood (ML). MP analyses were run using PAUP* 4.0d102 (Swofford, 2002). Individual nucleotides were considered to be multistate, unordered characters of equal weight; unknown bases were treated as uncertainties. Gapped cells were treated as missing data and we did not attempt to score indels. To evaluate the possibility of multiple islands of equally most parsimonious trees (Maddison, 1991), we ran heuristic searches seeded with 100 random-addition sequences, employing tree bisection-reconnection (TBR) swapping while retaining up to 100 trees per iteration. Bootstrap analysis (Felsenstein, 1985) was used to assess the relative support for each node in the single shortest tree found, using 200 random resamplings of the data and retaining up to 100 trees per resampling. Consistency indices, including autapomorphies (CI) and excluding them (CI′), were calculated to measure the relative extent of homoplasy in the data (Givnish & Sytsma, 1997).

ML analyses were performed on concatenated alignments using RAxML version 7.0.4 (Stamatakis, 2004). A single substitution process was modeled as general time reversible (GTR) plus gamma for the entire concatenated alignment (i.e., data were not partitioned). Among-site variation in substitution rates was modeled using the discrete approximation of the gamma distribution (Yang, 1994) with 25 rate classes. The ML bootstrap analysis included 250 pseudoreplicates drawn from the concatenated alignment.

ANCESTRAL HABITAT RECONSTRUCTION

To trace patterns of habitat evolution within the order Poales, we overlaid various environmental characteristics on the commelinid portion of the ML cladogram, simplified to the family level, using parsimony as implemented in MacClade 4.0 (Maddison & Maddison, 1992) to infer ancestral states, resolving all of the most parsimonious states at each node. Given their distinctive ecologies, we separated subfamily Anomochlooideae from the other Poaceae sampled (a subset of the bistigmatic clade = subfamily Puelioideae + the PACCMAD-BEP clade of grasses; the latter consists of Panicoideae, Arundinoideae, Chloridoideae, Centothecoideae, Micrairoideae, Aristidoideae, Danthonioideae–Bambusoideae, Ehrhartoideae, and Pooideae (Sánchez-Ken et al., 2007). We interpolated the subfamily Phar-

oideae (unsampled in our phylogenetic study) between Anomochlooideae and Puelioideae, given that recent molecular studies place them there with high support, and given the distinctive ecology of pharoids and puelioids versus most members of the huge PACC-MAD-BEP clade, which includes 99% of all grass genera and species (Soderstrom & Calderón, 1971; Clark et al., 1995, 2000; Grass Phylogeny Working Group I, 2001; Hodkinson et al., 2007a, b; Bouchenak-Khelladi et al., 2008). Characteristics overlaid include: (a) light availability (sunny vs. shady); (b) moisture supply (soil wet or inundated vs. well drained or dry); (c) soil fertility (highly infertile [e.g., sand or sandstone] vs. fertile); and (d) fire prevalence (high vs. low/absent). Data on ecology were drawn from summaries in Dahlgren et al. (1985), Givnish et al. (1999, 2000, 2004, 2007), Linder and Rudall (2005), and Sokoloff et al. (2009). We used the ML phylogeny, including Poales and families of the other commelinids studied as ingroups and *Apostasia* Blume of Orchidaceae as the outgroup, because it resolves a few crucial nodes differently and with far higher support than the MP tree, and because ML generally is less susceptible to problems caused by extensive change in evolutionary rates over time (i.e., heterotachy) and long-branch attraction (e.g., Huelsenbeck & Hillis, 1993; Huelsenbeck, 1995; Chang, 1996; Swofford et al., 2001; Gadagkar & Kumar, 2005; Leebens-Mack et al., 2005; Jansen et al., 2007; Moore et al., 2007; Whitfield & Lockhart, 2007; Wang et al., 2009). Where necessary in large, ecologically diverse groups represented by single taxa, we overlaid the ancestral conditions previously inferred for such families based on detailed infrafamilial molecular studies (e.g., Givnish et al., 2000, 2004, 2007) or inferred what those ancestral conditions would have been, given the habitats of the first several earliest-divergent lineages within those families (Appendix 2).

ORIGINS OF WIND POLLINATION AND PATTERNS OF CORRELATED EVOLUTION

We also overlaid wind versus animal pollination on the simplified Poales tree using MacClade, following earlier analyses by Givnish et al. (1999) and Linder and Rudall (2005). We drew data from those papers and from Newell (1969), Soderstrom and Calderón (1971, 1979), Henderson (1986), Stützel (1986, 1990), Listabarth (1992), Soreng and Davis (1998), Rosa and Scatena (2003, 2007), Blüthgen et al. (2004a, b), Blüthgen and Fiedler (2004), Ramos et al. (2005), Moura et al. (2008), Oriani et al. (2009), and Sokoloff et al. (2009) (see Appendix 2, Table A2). Previous authors have argued that wind pollination should be positively associated with visually inconspicuous, unisexual flowers; an absence of nectar; single ovules; growth in open or seasonally open, windy environments; and a taxon's local abundance (see Faegri & van der Pijl, 1979; Regal, 1982; Cox, 1991; Linder, 1998; Weller et al., 1998; Givnish et al., 1999; Cully et al., 2002; Friedman & Barrett, 2008). To evaluate how these ideas apply to Poales, we conducted formal tests of correlated evolution of pollination mechanism (wind vs. animal) with plant habitat, nectaries (presence or absence), floral sexuality (hermaphroditic vs. unisexual flowers), sexual system (cosexuality vs. dioecy), ovule number (one vs. many), floral size (small vs. large petals or other visual displays), and floral showiness (nonshowy vs. showy colors) using the BayesDiscrete module of BayesTraits (available at <http://www.evolution.rdg.ac.uk>). BayesDiscrete tests for significant patterns of correlated evolution of two binary traits by comparing the fit (ln likelihood) to models that assume their independent versus dependent evolution on the phylogeny provided using continuous-time Markov models (Pagel & Meade, 2006). For each trait, we conducted two sets of nested ML analyses, either setting the branch-length parameter κ equal to 1 or allowing it to assume its optimal value under ML analysis. Values of $\kappa < 1$ result in a scaling that reduces the length of longer branches more than shorter branches. Our approach directly parallels that used by Friedman and Barrett (2008) to test for correlated evolutionary patterns involving wind pollination across angiosperms. We used the nonsimplified commelinid portion of our ML tree for topology and branch lengths. Character states for all taxa in the ML tree (see Appendix 2) were drawn from the pollination references previously cited and from two data sets kindly provided by Jannice Friedman, Jana Vamosi, and Spencer Barrett, and by George Weiblen. We scored the highly unusual (if not, indeed, unique) case of *Chamaedorea* Willd. in which thrips are involved in releasing clouds of pollen that move from staminate plants to pistillate plants via the wind (Listabarth, 1992), as animal pollinated, given the role that animals play in this case of animal-induced wind pollination.

RESULTS

PHYLOGENY

MP yielded a single, fully resolved tree of length 152,366 steps (Fig. 2). Overall, there were 25,107 parsimony-informative characters, of which 22,156 were informative within the monocots. Across all taxa, 12,634 characters were variable but uninformative and 71,834 were constant. Monocots were monophyletic and

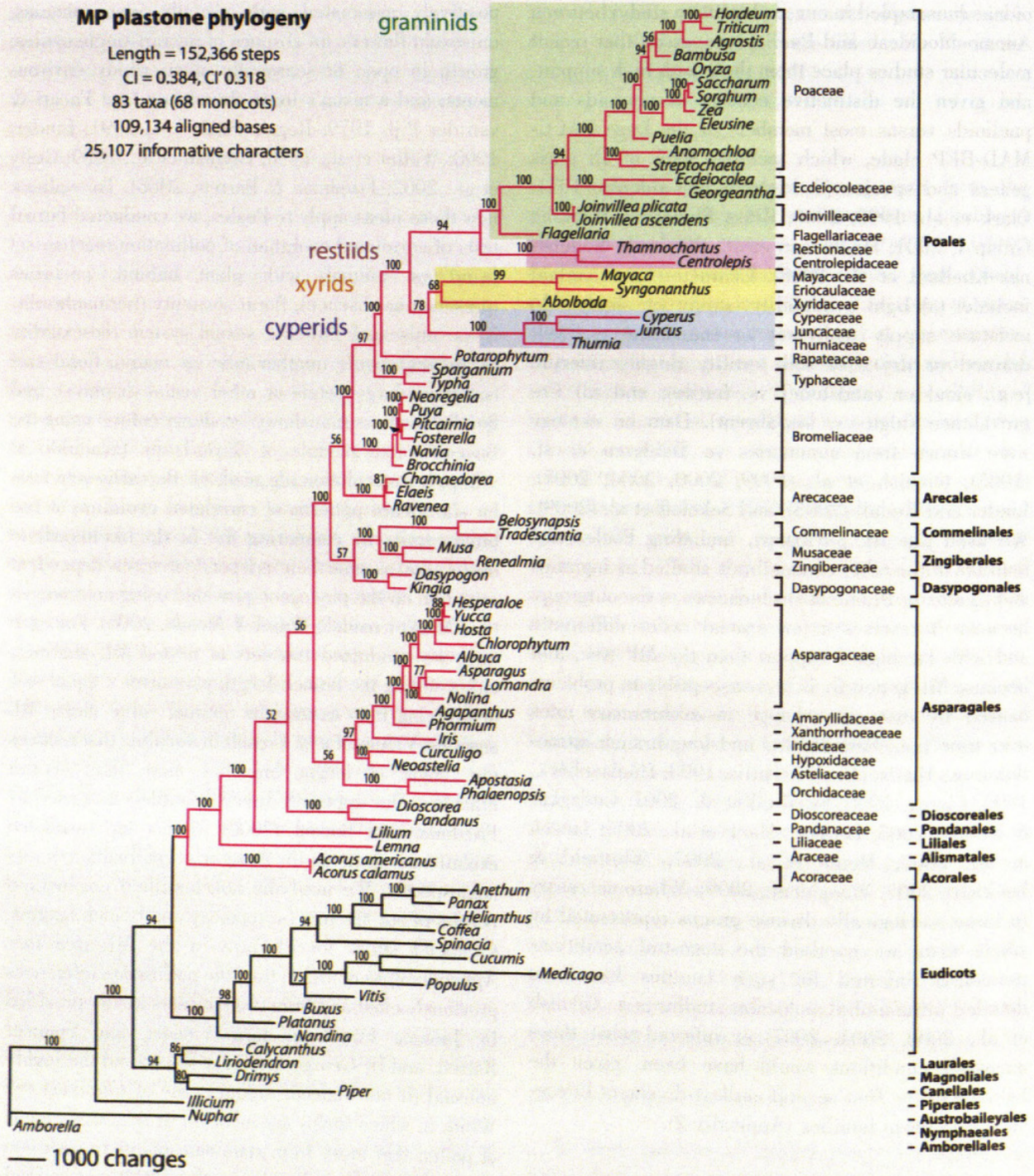

Figure 2. Phylogram for the single MP tree resulting from analysis of the plastome data, rooted using *Amborella* Baill. Branch lengths are proportional to the number of inferred substitutions down each branch. Bootstrap support for each node is shown above the corresponding branch. Monocots are highlighted with magenta branches; cyperids, xyrids, restiids, and graminids, with colored boxes. Full scientific names and authorities for the exemplars shown are given in Appendix 1.

Acorus was sister to all other taxa, both with 100% bootstrap support. At the ordinal level, Alismatales (*Lemna* L.), Liliales (*Lilium*), Dioscoreales–Pandanales (*Dioscorea* L.–*Pandanus* Parkinson), and finally Asparagales and the commelinids diverged from progressively more recent nodes. Bootstrap support for the branching sequence of Liliales, Dioscoreales–Pandanales, and Asparagales was, however, weak (52%–56%), as was that for the monophyly of Asparagales (Fig. 2). The commelinids as a whole, and each of their five orders, had 100% bootstrap support. Poales was resolved as sister to Arecales, and Dasypogonales as sister to Commelinales–Zingiberales, but both relationships had weak support.

Within Poales, Bromeliaceae were sister to all other taxa, with 100% bootstrap support, followed by the divergence of Typhaceae and Rapateaceae at the two succeeding nodes, with 97% and 100% support,

respectively (Fig. 2). The MP tree recovered the xyrids (Eriocaulaceae, Mayacaceae, Xyridaceae) as monophyletic with 68% bootstrap support and placed them sister to the cyperids (Cyperaceae, Juncaceae, Thurniaceae) with 78% bootstrap support. Within the xyrids, *Mayaca* Aubl. was placed sister to *Syngonanthus* Ruhland of Eriocaulaceae with 99% bootstrap support. Branches among the cyperids all had 100% bootstrap support. The restiids (Restionaceae Centrolepidaceae, and Anathriaceae, with the last small family unsampled here) were monophyletic, with 100% bootstrap support, and were sister (with 94% bootstrap support) to the graminid clade of grasses and their allies. Within the graminids, *Flagellaria* L. was sister to all other taxa with 100% support; *Joinvillea* Gaudich. ex Brongn. & Gris was sister to the remaining taxa, also with 100% support. Finally, Ecdeiocoleaceae was resolved as monophyletic (100% support) and sister to the grasses (94% support).

Across monocots, inferred branch lengths were especially short in Acoraceae, Arecaceae, Bromeliaceae, and Typhaceae, and especially long in the graminids, restiids, xyrids, and cyperids (Fig. 2). Seven of these eight clades are part of the commelinids. Relative to the commelinid crown-group root node, branch lengths averaged 1734 ± 170 (mean ± SD) steps for palms, 2112 ± 103 for bromeliads, and 2701 ± 67 for cattails and bur-reeds, compared with 7027 ± 1062 for xyrids, 7821 ± 1102 for cyperids, 8644 ± 1210 for restiids, and 9152 ± 1416 for graminids. Rates of plastid sequence evolution thus vary by as much as 5.2-fold within the commelinids, based on MP analysis.

ML produced a single, fully resolved, well-supported phylogeny (Fig. 3). This tree is strikingly similar in most regards to the MP tree, with four key exceptions. First, *Lilium* (Liliales) was resolved as sister to the Asparagales–commelinid clade; this position has 94% bootstrap support. Second, Asparagales had 100% bootstrap support as being monophyletic and 99% support as being sister to the commelinids in the ML tree, versus 56% for both conditions in the MP tree. Support for the topology of the ML tree was generally higher than that for the MP tree, with 63 of 67 nodes within the monocots having ≥ 94% bootstrap support, and all 18 nodes outside the monocots having 100% support (Fig. 3). Third, ML provided a different and much more strongly supported resolution of the commelinid orders, with Poales being sister to Commelinales–Zingiberales with 93% bootstrap support, and Arecales being sister to Dasypogonales with 86% bootstrap support. Finally, in the ML tree, the xyrids formed a grade, not a clade, and were associated with the graminid–restiid clade, not the cyperids. *Abolboda* Bonpl. of Xyridaceae was sister to the restiid–graminid clade with 100% bootstrap support; *Mayaca* of Mayacaceae and *Syngonanthus* of Eriocaulaceae were sister to *Abolboda* plus the restiid–graminid clade (Fig. 3).

ANCESTRAL HABITAT RECONSTRUCTION

We infer that the ancestral Poales occupied habitats that were sunny, wet, possibly nutrient poor, and fireswept (Figs. 4, 5), much like the conditions occupied by *Brocchinia prismatica* L. B. Sm., *B. melanacra* L. B. Sm., *B. reducta* Baker, *Lindmania guianensis* (Beer) Mez, and other early divergent members of Bromeliaceae today (Givnish et al., 1997, 2007). Low-nutrient conditions characterize the ancestral Poales only under ACCTRAN. However, infertile soils are more likely than fertile soils to favor fire (Givnish, 1980), the inferred condition for ancestral Poalean habitats (Fig. 5B). Both ACCTRAN and DELTAN reconstruct infertile soils as the ancestral state for the clade including Rapateaceae and its sister (Fig. 5A). Open habitats typify most of the early divergent families—from bromeliads to the restiids—although bromeliads and rapateads include a number of reinvasions of shaded sites (Givnish et al., 2000, 2004, 2007), as do sedges (e.g., in *Becquerelia* Brongn. and *Carex* L.) and rushes (e.g., in *Luzula* DC.), which can be inferred from the phylogenies provided by Drábková and Vlček (2009) and Muasya et al. (2009). Shady habitats were reinvaded by members of a grade running from *Flagellaria* and *Joinvillea* through the anomochlooid and pharoid grasses, with reinvasions of sunny habitats in Ecdeiocoleaceae and the PACCMAD-BEP grasses (Fig. 4A). Damp or wet soils appear to be the ancestral condition in Poales from bromeliads (e.g., *Brocchinia*, *Lindmania* Mez) through at least Xyridaceae (*Abolboda*), with a transition to well-drained rainforest soils for *Flagellaria*, *Joinvillea*, Anomochlooideae, and Pharoideae (Fig. 4B). Several Centrolepidaceae and Restionaceae grow in permanently or seasonally inundated soils, but others occupy well-drained sites.

If we assume that the ancestral habitat of Poales had highly infertile soils (see above), then such soils would have characterized all families and ancestors from Bromeliaceae through the restiids, with the exception of Typhaceae, Cyperaceae, and Juncaceae on richer soils, although some members of the latter two families now occupy highly infertile substrates as well. The terminal clade of Poales (Flagellariaceae through Poaceae) typically occupies more fertile substrates, with the exception of Ecdeiocoleaceae. Finally, fireswept habitats characterized families from Bromeliaceae through Xyridaceae and possibly the restiids, with such disturbance being lost in the aquatic *Thurnia* Hook. f. (but perhaps not in *Prionium* E. Mey.), the aquatic *Mayaca*, the aquatic and alpine

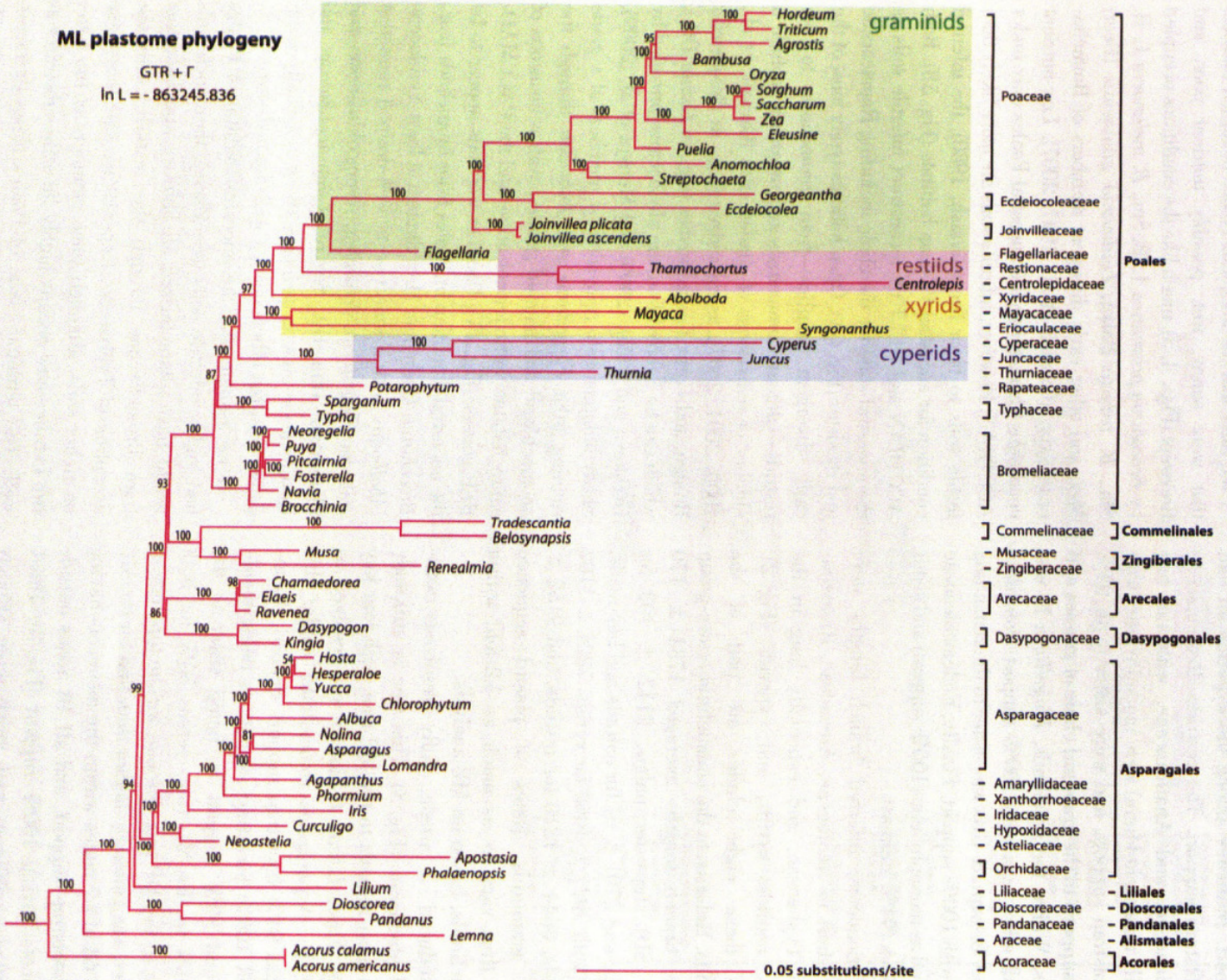

Figure 3. Phylogram for the single ML tree. The nonmonocot portion of the tree is not shown. The resolution of that portion is, however, identical to that shown in Figure 1, with 100% bootstrap for all nodes. Bootstrap support for each node within the monocots is shown above the corresponding branch. Cyperids, xyrids, restiids, and graminids are highlighted with colored boxes.

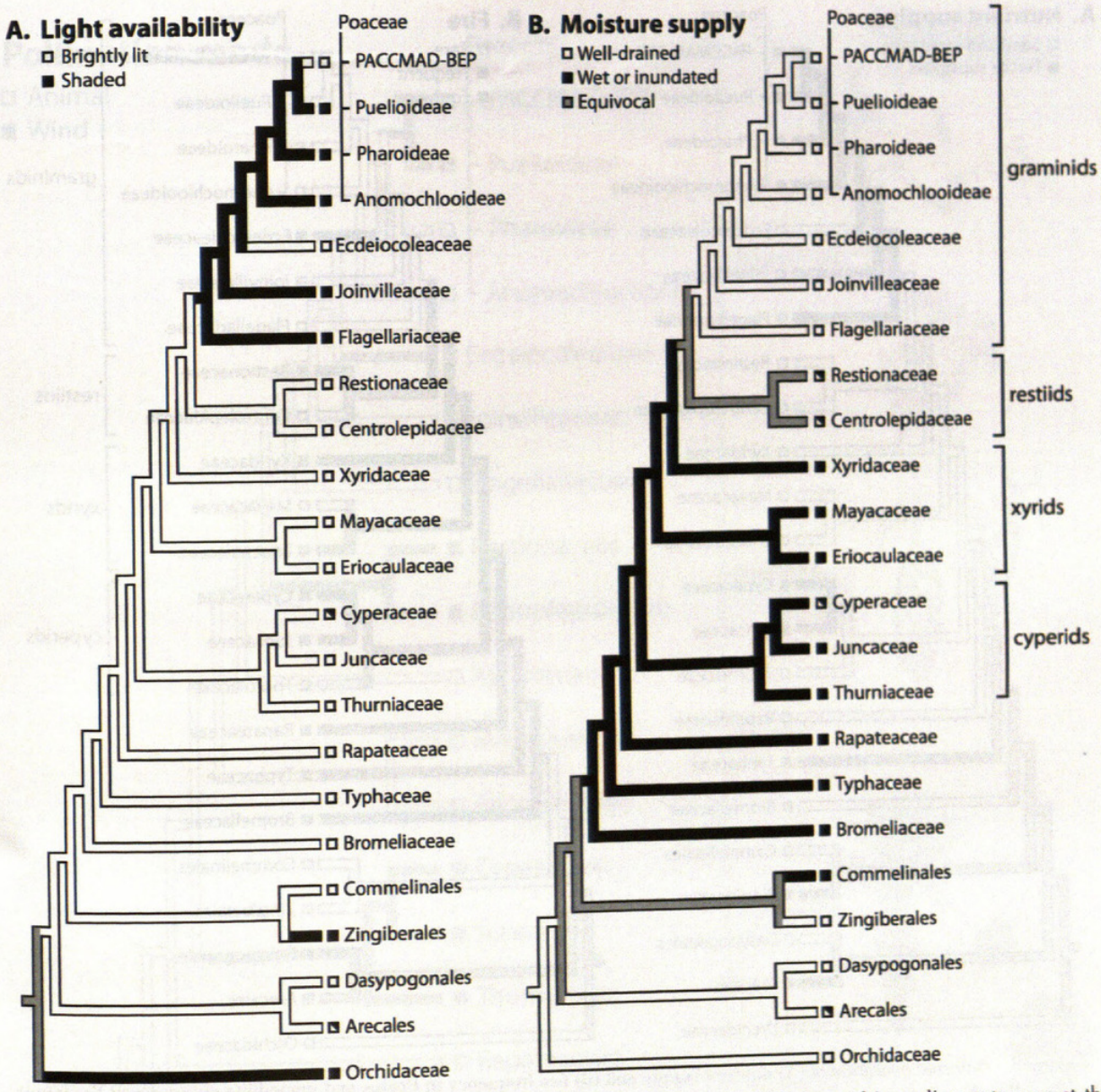

Figure 4. Inferred evolution of (A) light availability and (B) moisture supply in Poales and immediate outgroups at the family level under parsimony. Cases in which the ancestral character state for a family could not be inferred unequivocally (see text) were coded as polymorphic, and both character states for the current-day, terminal taxa are indicated in the split box. Gray branches indicate equivocal resolution of character states in ancestral taxa.

Centrolepidaceae, and the forest-inhabiting grade from *Flagellaria* through the early divergent grass families, with fire ecology recurring in Ecdeiocoleaceae and Poaceae (Fig. 5B). If Anarthriaceae had been included in this analysis, sister to the other restiid subfamilies as in other recent analyses (e.g., Chase et al., 2006), then Restionaceae would have been resolved as retaining fireswept habitats rather than invading them anew.

MULTIPLE ORIGINS OF WIND POLLINATION AND CORRELATED TRAITS

Ancestral character-state reconstruction using the ML tree implies that wind pollination evolved at least five times in Poales: in Typhaceae, cyperids, restiids, Ecdeiocoleaceae, and the PACCMAD-BEP clade of Poaceae (Fig. 6). Animal pollination is inferred to be homologous across the commelinids.

Based on ML testing in BayesTraits, pollination mechanisms in Poales and its immediate relatives showed correlated evolution with (1) floral showiness, (2) flower size, (3) floral sexuality, (4) nectar production, and (5) habitat openness (Table 1). Wind pollination was, as expected, associated with smaller, less conspicuous, often unisexual flowers and with open habitats. In Poales and its immediate relatives, there was no evidence for correlated evolution between pollination mechanism and ovule number or sexual system (cosexuality vs. dioecy); the latter finding

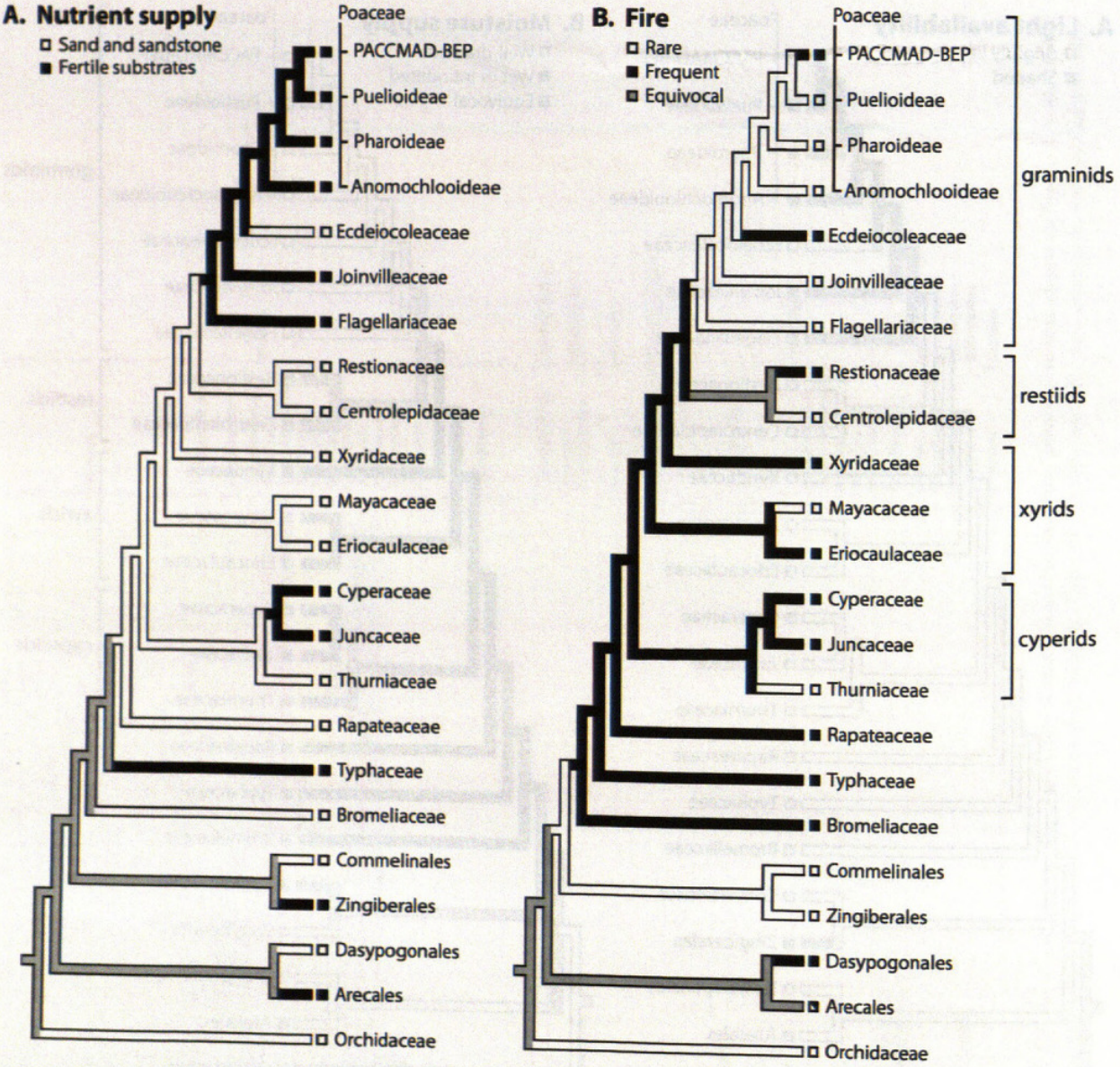

Figure 5. Inferred evolution of (A) nutrient supply and (B) fire frequency in Poales and immediate outgroups at the family level (see Fig. 4).

implies that unisexual flowers associated with wind pollination are typically found in cosexual plants.

Discussion

Phylogeny

ML analysis of 81 coding regions from the plastid genome produced—within the limits of taxon sampling—the best resolved and most strongly supported phylogeny to date of Poales, the commelinids, and the monocots as whole, with a mean bootstrap support of 98.2% for all monocot nodes (Fig. 3). We focus on the ML tree because it had much higher bootstrap support for several crucial nodes within and outside Poales than the MP tree, including some that differ between the two trees; because Poales exhibits striking rate heterogeneity and a combination of very short and very long branches in close proximity; and because ML generally outperforms MP in reconstructing phylogenies when faced with rate heterogeneity and long-branch attraction. The nodes at which the ML and MP trees differ are just those with very short and very long branches immediately juxtaposed, where long-branch attraction might be expected to be especially likely to distort phylogenetic reconstruction via parsimony. This was seen in the placement of the xyrids within Poales, the monophyly of the xyrids, the sister group to the Poales, relationships among the other commelinid orders, and the placement of Liliales (Fig. 3). The much higher rates of evolutionary divergence of plastid coding regions in Poaceae and allied families versus Arecaceae and Bromeliaceae have long been recognized (Gaut et al., 1992, 1996; Givnish et al., 1999, 2004; Smith & Donoghue, 2008).

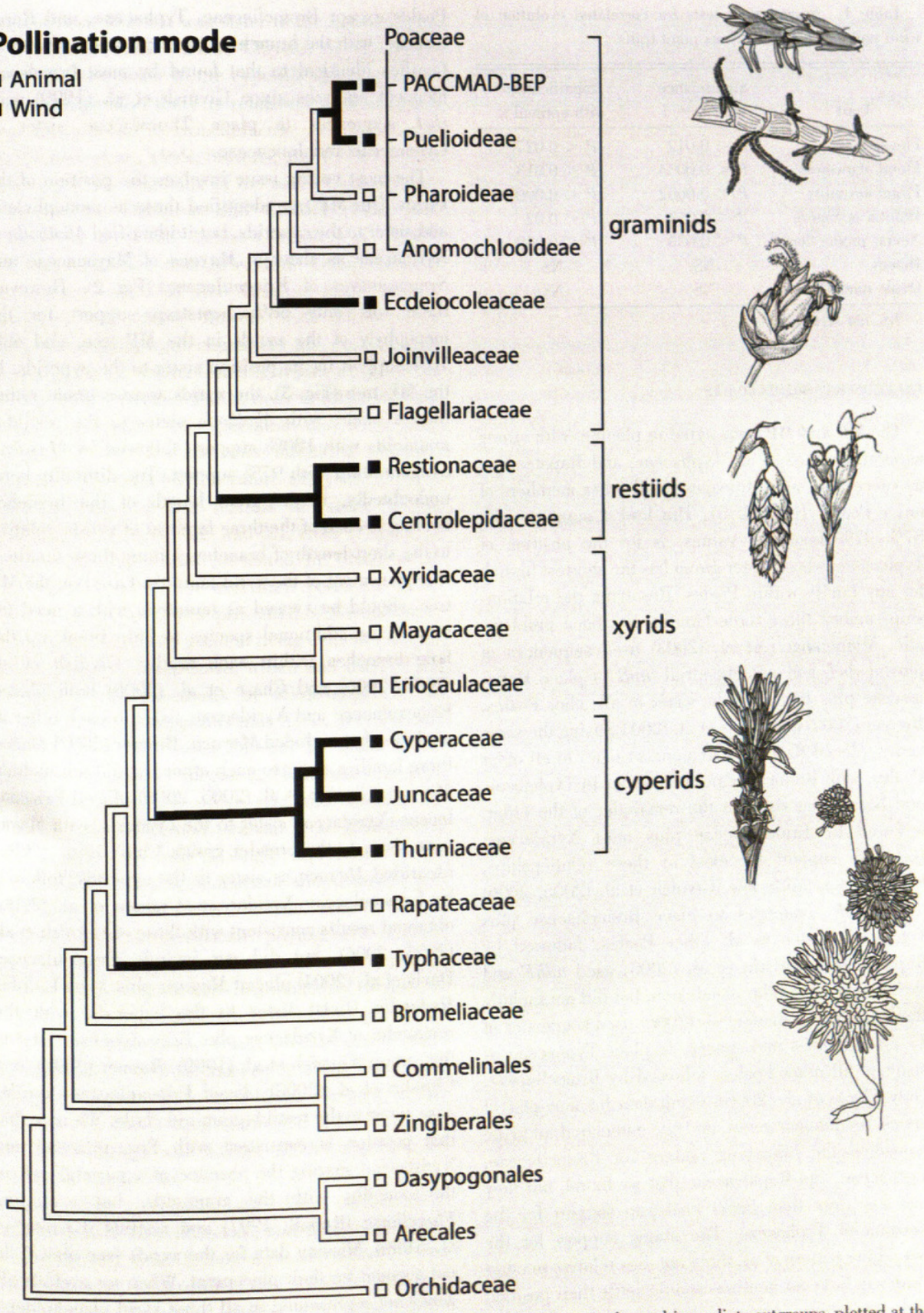

Figure 6. Minimum of five independent origins of wind pollination within Poales and immediate outgroups, plotted at the family level. Drawings show typical floral and/or inflorescence form for each origin. From top to bottom: *Tripsacum dactyloides* L. (Poaceae), staminate and pistillate portions of inflorescence; *Georgeantha hexandra* B. G. Briggs & L. A. S. Johnson (Ecdeiocoleaceae), floral spike with zones of male and female flowers; *Hypolaena fastigiata* R. Br. (Restionaceae), staminate and pistillate inflorescences borne on separate plants; *Carex pilulifera* Willd. ex Kunth (Cyperaceae), staminate and pistillate portions of inflorescence; and *Sparganium emersum* Rehm. (Typhaceae), staminate and pistillate portions of inflorescence. Note long and/or plumose branches of styles in each case and mostly large, dangling (often centrally attached) anthers.

Table 1. Summary of tests for correlated evolution of wind pollination with various plant traits.

Trait	Significance with $\kappa = 1$	Significance with optimal κ
Flower size	$P < 0.012$	$P < 0.027$
Floral showiness	$P < 0.0034$	$P < 0.013$
Floral sexuality	$P < 0.0002$	$P < 0.0005$
Habitat openness	$P < 0.013$	$P < 0.02$
Nectar production	$P < 0.035$	$P < 0.038$
Dioecy	NS	NS
Ovule number	NS	NS

NS, not significant.

RELATIONSHIPS WITHIN POALES

The ML and MP trees agree in placing, with strong support, Bromeliaceae, Typhaceae, and Rapateaceae as successive sister lineages to all other members of order Poales (Figs. 2, 3). The lowest support, with 87%–97% bootstrap values, is for the position of Typhaceae, whose sister group has the shortest branch for any family within Poales. Resolving the relationships among these three families has been problematic. Michelangeli et al. (2003) used sequences of plastid *rbcL* and mitochondrial *atpB* to place Rapateaceae plus the xyrids as sister to all other Poales. Bremer (2002) and Davis et al. (2004), using the same genes, placed Rapateaceae alone as sister to all other Poales, with Bromeliaceae being sister to Typhaceae, and both being sister to the remainder of the order, followed by Eriocaulaceae plus most Xyridaceae; jackknife support for most of these relationships, however, was quite low. Givnish et al. (2005, 2006) used *ndhF* sequences to place Bromeliaceae plus Typhaceae sister to all other Poales, followed by Rapateaceae. Christin et al. (2008) used *ndhF* and *rbcL* to reach a similar conclusion, but did not include Rapateaceae. Graham et al. (2006) used sequences of 17 plastid genes and spacers to place Typhaceae as sister to all other Poales, followed by Bromeliaceae. Only Chase et al. (2006), using data for four plastid genes, two nuclear genes, and one mitochondrial gene, recovered the branching pattern for Bromeliaceae, Typhaceae, and Rapateaceae that we found, but they had low (less than 50%) bootstrap support for the position of Typhaceae. The strong support for the branching pattern of all three families relative to other Poales in both our analyses should settle their position and branching pattern. The absence of septal nectaries from all Poales except Bromeliaceae and a few derived Rapateaceae (where such nectaries have apparently reevolved [Givnish et al., 2000]) helps support the placement of Bromeliaceae at the base of the order. ML placed the cyperids sister to all other Poales except Bromeliaceae, Typhaceae, and Rapateaceae, with the branching topology among the three families identical to that found by most broadscale monocot analyses since Givnish et al. (1999) used *rbcL* sequences to place Thurniaceae sister to Cyperaceae and Juncaceae.

The most vexing issue involves the position of the xyrids. Our MP tree identified these as monophyletic and sister to the cyperids, but it identified *Abolboda* of Xyridaceae as sister to *Mayaca* of Mayacaceae and *Syngonanthus* of Eriocaulaceae (Fig. 2). However, there was only 68% bootstrap support for the monophyly of the xyrids in the MP tree, and only 78% support for its position sister to the cyperids. In the ML tree (Fig. 3), the xyrids were a grade rather than a clade, with *Abolboda* sister to the restiids–graminids with 100% support, followed by *Mayaca–Syngonanthus* with 97% support. The difficulty here, undoubtedly, is the great length of the branches leading to each of the three families of xyrids, relative to the short length of branches joining those families. Our placement of the xyrid families, based on the ML tree, should be viewed as tentative, with a need for sequencing additional species to help break up the long branches within each family. Givnish et al. (2005, 2006) and Chase et al. (2006) both placed Eriocaulaceae and Xyridaceae sister to each other in analyses that included *Mayaca*; Bremer (2002) placed these families sister to each other but did not include *Mayaca*. Givnish et al. (2005, 2006) placed Eriocaulaceae–Xyridaceae sister to the cyperids, with Mayaceae sister to the broader group; Chase et al. (2006) identified *Mayaca* as sister to the cyperids, followed by Eriocaulaceae–Xyridaceae. Graham et al. (2006) obtained results consistent with those of Givnish et al. (2005, 2006), but did not include Eriocaulaceae. Davis et al. (2004) placed *Mayaca* plus *Xyris* L. (plus *Hydatella* Diels) sister to the cyperids, with the remainder of Xyridaceae plus Eriocaulaceae sister to that group. Givnish et al. (1999), Bremer (2002), and Christin et al. (2008) placed Eriocaulaceae–Xyridaceae sister to the restiid–graminid clade. We note that that position is consistent with Eriocaulaceae and Xyridaceae sharing the absence of a parietal cell in the nucellus with the graminids, but excluding *Flagellaria* (Rudall, 1997) and restiids (Givnish et al., 1999). Missing data for the xyrids (see above) do not account for their placement. When we exclude all genes not represented in all three xyrid placeholders, ML yields exactly the same branching topology (albeit with weaker support) within Poales. Placement of the xyrids should not be viewed simply as a choice between being sister to the cyperids versus the restiid–graminid clade. When we included *Mayaca* while excluding *Abolboda* and *Syngonanthus* in our

own analyses, *Mayaca* was sister to the cyperids plus the restiid–graminid clade. Christin et al. (2008) placed *Mayaca* sister to the cyperids alone.

Morphologically, there is relatively little evidence tying Mayacaceae to Eriocaulaceae and Xyridaceae (see Givnish et al., 1999; Stevens, 2009). These three families are the remnants of the order Commelinales recognized by Dahlgren and Clifford (1982) and Dahlgren et al. (1985) before Givnish et al. (1999) used *rbcL* sequence data to exclude Commelinaceae and Rapateaceae. All five families share nuclear endosperm and showy flowers with differentiated petals and sepals; both characters are more broadly plesiomorphic in commelinids (Givnish et al., 1999; Stevens, 2009). In other words, there is relatively little evidence to support an expectation that these three families will form a clade when additional plastome sequence data are added to future analyses.

The position of the restiids as sister to the graminids in both the MP and ML trees (Figs. 2, 3) accords with the results presented by Chase et al. (2006) and is consistent with their positions in the incompletely resolved tree presented by Givnish et al. (2005, 2006). The only point of disagreement involves the placement of *Flagellaria*, which was sister to the restiids and the graminids by Michelangeli et al. (2003), sister to the cyperids plus *Xyris*, *Mayaca*, and *Trithuria* Hook. f. (Hydatellaceae) by Davis et al. (2004), and sister to *Elegia* L. (Restionaceae) plus representatives of the other graminid families by Givnish et al. (1999) and Graham et al. (2006). Our sampling includes only a single representative for each of the families Restionaceae and Centrolepidaceae, with none for Anarthriaceae. Anarthriaceae, when included in broadscale phylogenetic studies based on molecular data, has usually been placed sister to Centrolepidaceae–Restionaceae (Briggs et al., 2000; Bremer, 2002; Michelangeli et al., 2003; Davis et al., 2004; Chase et al., 2006). Centrolepidaceae was sister to Restionaceae in most broadscale molecular studies, but some (e.g., Bremer, 2002; Briggs et al., 2010) have embedded it in Restionaceae, while Briggs and Linder (2009) regarded its position as unresolved.

Within the graminids, our data confirm that Flagellariaceae, Joinvilleaceae, and Ecdeiocoleaceae are successively sister to ever-narrower subsets of the graminids, with Ecdeiocoleaceae sister to Poaceae. This branching topology concurs with those documented by Bremer (2002), Chase et al. (2006), and Graham et al. (2006), but conflicts with those of Marchant and Briggs (2007), Christin et al. (2008), and others that place *Joinvillea* sister to Ecdeiocoleaceae, with both sister to Poaceae. Early studies based on morphological or molecular data either assumed or concluded that *Joinvillea* was sister to the grasses (e.g., Campbell & Kellogg, 1987; Chase et al., 1995a, b; Clark et al., 1995; Kellogg & Linder, 1995; Stevenson & Loconte, 1995; Soreng & Davis, 1998; Grass Phylogeny Working Group I, 2001). Briggs et al. (2010) were unable to resolve a trichotomy involving the grasses, *Joinvillea*, and Ecdeiocoleaceae. Doyle et al. (1992) discovered a 28-kb inversion in the chloroplast genome that united Joinvilleaceae, Ecdeiocoleaceae, and Poaceae; they detected a 6-kb inversion in Joinvilleaceae and Poaceae, but were unable to amplify the region in question for Ecdeiocoleaceae. Several subsequent authors confused the absence of data on the 6-kb inversion with absence of that inversion in Ecdeiocoleaceae, until Michelangeli et al. (2003) demonstrated that the inversion was indeed present in that family, and that *rbcL* and *atpB* sequence data supported (albeit quite weakly) a sister-group relationship between *Ecdeiocolea* F. Muell. and the grasses. In retrospect, a key morphological character used by Campbell and Kellogg (1987), Kellogg and Linder (1995), and Kellogg (2000) as a synapomorphy to unite Joinvilleaceae and Poaceae—namely, the presence of long and short cells in the leaf epidermis—may be seen to exclude Ecdeiocoleaceae. Although adult plants of *Ecdeiocolea* have scarcely any development of leaf blades, juvenile plants of *Ecdeiocolea* and adult *Georgeantha* B. G. Briggs & L. A. S. Johnson (Briggs & Johnson, 1998) show substantial leaf blades with no evidence of a long and short cell pattern (Briggs, pers. obs.). Thus, the presence of long and short cells in the leaf epidermis either evolved twice (in Poaceae and Joinvilleaceae) or—perhaps more likely—arose once in the common ancestor of Joinvilleaceae–(Ecdeiocoleaceae–Poaceae) and subsequently was lost in the highly reduced Ecdeiocoleaceae.

Within Poaceae, our data confirm that *Anomochloa* Brongn. and *Streptochaeta* Schrad. ex Nees are sister taxa, forming subfamily Anomochlooideae; this subfamily is, in turn, sister to the remainder of the family (see Clark et al., 1995; Grass Phylogeny Working Group I, 2001; Christin et al., 2008). The latter lineage is characterized by the presence of the typical grass-type spikelet found in all grasses except Anomochlooideae, and is therefore termed the spikelet clade (Grass Phylogeny Working Group I, 2001). Relationships among the remaining grasses generally accord with those found using molecular data by Grass Phylogeny Working Group I (2001), Hodkinson et al. (2007a, b), Bouchenak-Khelladi et al. (2008), and Saarela and Graham (2010). We hope to add several additional plastome sequences in the near future to permit detailed analyses of evolution within the Poaceae.

RELATIONSHIPS AMONG COMMELINID ORDERS

The ML phylogeny presented provides the first well-supported (93% bootstrap) evidence for the sister group to Poales, identifying the Commelinales–Zingiberales clade as the closest relative to the grasses, bromeliads, and their allies (Fig. 3). The two remaining commelinid orders, Arecales and Dasypogonales, also form a clade with relatively strong (87% bootstrap) support, which is sister to the clade formed by the previous three orders. None of the recent analyses of broadscale relationships among monocots found this branching topology. Givnish et al. (1999) and Davis et al. (2004) came closest, placing Arecales or Dasypogonales sister to Commelinales–Zingiberales plus Poales. Given that our MP analysis retrieved an alternative, albeit weakly supported topology (Fig. 2), our conclusions regarding ordinal relationships among commelinids should be viewed somewhat tentatively. We plan to include multiple representatives of each family in analyses in the near future, using increased taxon sampling density to confront the difficulties caused by long-branch attraction and striking variation in evolutionary rates within the commelinids. For now, however, we note that the sister-group relationship between Poales and Commelinales–Zingiberales is supported by possession of (1) starchy endosperm across all taxa surveyed and (2) a distichous or tristichous phyllotaxy across most families (except for Bromeliaceae, Mayacaceae, Cannaceae, Costaceae, Musaceae, and scattered cases in other families, e.g., *Palisota* Rchb. ex Endl. in Commelinaceae [Faden, 1988; Givnish et al., 1999]). The sister-group relationship of Arecales and Dasypogonales is supported by the possession of a woody habit in all of the former and most of the latter. Identification of woodiness as a synapomorphy for Arecales–Dasypogonales must await further evidence on relationships within Dasypogonaceae.

ANCESTRAL HABITAT RECONSTRUCTIONS

The ancestral habitat of Poales appears to have been sunny, damp to wet, highly infertile, and fireswept (see also Givnish et al., 1999; Linder & Rudall, 2005). Today, these conditions typify the family, either as a whole or in early divergent members (e.g., *Brocchinia*) in six cases: Bromeliaceae, Rapateaceae, Eriocaulaceae, Xyridaceae, Ecdeiocoleaceae, and Restionaceae (see Figs. 4, 5). However, the most species-rich families, Poaceae and Cyperaceae, often occur on more fertile substrates. Relatively few families and species are associated with forest understory environments (Fig. 4A), which helps to explain the high frequency of wind pollination within the order.

REPEATED EVOLUTION OF WIND POLLINATION IN POALES

Analyses based on our ML phylogeny indicate that wind pollination has arisen at least five times within Poales—in Typhaceae, the cyperids, the restiids, Ecdeiocoleaceae, and the PACCMAD-BEP clade of Poaceae (Fig. 6). This contrasts with three origins of wind pollination in Poales as inferred by Givnish et al. (1999) and Linder and Rudall (2005). Partly, this difference in conclusions is a result of different branching topologies, and partly, of different assumptions as to which taxa are wind pollinated. We assumed that insects pollinate *Flagellaria* and *Joinvillea*, based on arguments by Soreng and Davis (1998). We also assumed that insects pollinate *Anomochloa*, *Streptochaeta*, and *Pharus* P. Browne in Poaceae. Nothing certain is known about the pollination of these grasses. But the fact that all three lack feathery stigmas and versatile anthers on slender stamen filaments, both of which are usually associated with wind pollination, argues for their pollination by animals (Soderstrom, 1981; Soreng & Davis, 1998). In addition, *Anomochloa*, *Streptochaeta*, and at least one member of Pharoideae have grouped pollen granules with high exine relief, characters that are not associated with wind pollination in Poaceae (Page, 1978). Insect pollination has also been observed or inferred in a number of forest-dwelling bamboo grasses in herbaceous tribes Olyreae, Parianeae, and woody Bambuseae (Soderstrom & Calderón, 1971, 1979; Chapman, 1990; Salgado-Labouriau et al., 1992; Soreng & Davis, 1998); the placement of bamboos in the BEP clade (Grass Phylogeny Working Group I, 2001; Bouchenak-Khelladi et al., 2008) suggests this represents at least one secondary origin of animal pollination within the PACCMAD-BEP clade. The phyletic gap between the wind-pollinated graminids and the restiids of open habitats—involving animal-pollinated *Flagellaria* and *Joinvillea* in rainforest understories and light gaps—clearly argues that any additional case of wind pollination in the graminids would be an additional independent origin. In addition, animal pollination in Anomochlooideae and Pharoideae supports separate origins of wind pollination in Ecdeiocoleaceae and the PACCMAD-BEP clade of Poaceae based on our phylogeny (Fig. 6).

As predicted by several investigators and demonstrated across a wide sampling of angiosperms by Friedman and Barrett (2008), we found that animal pollination showed a significant correlation with floral showiness, flower size, floral sexuality, nectar production, and habitat openness (Table 1). Wind pollination was strongly associated, as predicted, with smaller, less conspicuous, often unisexual flowers, absence of nectar, and open habitats. Smaller and less

brightly colored flowers, often involving the loss of petals and/or sepals and nectar, are expected in wind-pollinated species given the energetic costs of these attractive structures, as well as the lack of utility of such structures in wind-pollinated taxa, and the possibility that the presence of petals and/or sepals, especially large ones, might interfere with the arrival of wind-borne pollen to stigmatic surfaces (see Linder, 1998; Culley et al., 2002; Linder & Rudall, 2005; Friedman & Barrett, 2008). It should be recognized that there is no need to invoke reevolution of petals and/or sepals in *Flagellaria* and *Joinvillea*, given the continuity of an ancestral line pollinated by animals up to the PACCMAD-BEP clade (Fig. 6).

Wind pollination and unisexual flowers—and their inverse, animal pollination with hermaphroditic flowers—should be associated because the reduced cost and increased benefits of attractive structures for attracting and dispersing pollen in hermaphroditic flowers applies only to animal-pollinated taxa (Givnish, 1980; Lloyd, 1982), and because unisexuality could help reduce self-pollination and stigma clogging in wind-pollinated taxa, given that the latter produce large amounts of pollen (Givnish, 1980; Lloyd & Webb, 1986; Charlesworth, 1993). The exceptional statistical significance of correlated evolution between wind pollination and unisexual flowers in analyses that include or exclude optimization of κ ($P < 0.0005$ and $P < 0.0002$, respectively) most likely has to do with the widespread occurrence of unisexual flowers in Poales, in nine of 16 families and a total of at least six clades.

Habitats that are open and windswept—even if only seasonally, as in the canopy of temperate deciduous forests—clearly favor wind pollination; conversely, windless understories favor animal pollination (Linder, 1998; Culley et al., 2002; Friedman & Barrett, 2008). However, the large number of animal-pollinated families of Poales found ancestrally in open habitats (Bromeliaceae, Eriocaulaceae, Mayacaceae, Xyridaceae) reduces the strength of the evolutionary correlation between habitat and pollination mechanism in the order. There is, however, a nearly perfect association of wind pollination with open habitats, including Typhaceae and the cyperids in open wetlands, and restiids, Ecdeiocoleaceae, and the PACCMAD-BEP clade of Poaceae in open, often seasonally arid or fireswept upland habitats. Note the association of putative insect pollination with tropical forest understories and edges in *Flagellaria*, *Joinvillea*, and anomoochloid, pharoid, and olyroid grasses (see Soderstrom & Calderón, 1971, and preceding discussion). Within-family reversions to insect pollination (not shown in Fig. 6) have occurred in scattered species in several genera of Cyperaceae with brightly colored or fragrant inflorescences (e.g., *Ascolepis* Nees ex Steud., *Carex*, *Eleocharis* R. Br., *Hypolytrum* Rich., *Mapania* Aubl., *Rhynchospora* Vahl sect. *Dichromena* (Michx.) Griseb. [Goetghebeur, 1998; Magalhães et al., 2009]); several of these taxa grow in forest understories.

Nectar production should be negatively associated with wind pollination given the costs of producing nectar and its lack of utility in anemophilous species. Conversely, in some (but not all) animal-pollinated species, nectar serves as an attractant. The correlation between nectar production and pollination mechanism in Poales is significant but surprisingly weak (Table 1), with the latter probably reflecting the near absence of nectaries in the order outside the bromeliads. Even though Friedman and Barrett (2008) found that nectar production had the strongest pattern of correlated evolution with pollination mechanism of any factor they surveyed across the angiosperms, it would be difficult for such a pattern to occur in any lineage that is nearly uniform in nectar production or its absence. We coded *Potarophytum* Sandwith, the placeholder for Rapateaceae, as having septal nectaries, based on their presence in *Spathanthus* Desv. (Venturelli & Bouman, 1988) of tribe Rapateeae and in *Guacamaya* Maguire, *Kunhardtia* Maguire, and *Schoenocephalium* Seub. of tribe Schoenocephalieae (Givnish et al., 2004). However, such nectaries are probably only of sporadic occurrence in Rapateaceae; they have not been observed as yet in other members of the family, and Renner (1989) described buzz pollination for *Saxo-fridericia* R. H. Schomb. (tribe Saxofridericieae) and *Stegolepis* Klotzsch ex Körn. (tribe Stegolepideae). If we assume that the ancestral condition for Rapateaceae is a lack of nectaries, then the correlation betweeen pollination mechanism and nectar production remains weakly significant ($P < 0.045$ for $\kappa = 1$ and $P < 0.032$ for optimal κ).

Nectaries appear to have evolved independently in Eriocaulaceae, variously associated with petal appendages, staminodes, pistillodes, and pistils (Stützel, 1986; Rosa & Scatena, 2003, 2007; Ramos et al., 2005; Oriani et al., 2009), and in Xyridaceae, associated with stylar appendages in *Abolboda* (Stützel, 1990). *Flagellaria* secretes large amounts of nectar, with high concentrations of sugar and amino acids, from extrafloral nectaries and attracts large numbers of ants (Blüthgen et al., 2004a, b; Blüthgen & Fiedler, 2004); the ants observed to visit the flowers (Newell, 1969) almost surely are attracted by these extrafloral nectaries. Scoring *Flagellaria* as lacking nectar production (it has no floral nectaries) has almost no effect on the significance of correlated evolution between pollination mechanism and nectar

production, with $P < 0.047$ for tests with and without optimization of κ. If scoring were reversed for both *Flagellaria* and Rapateaceae, the correlation between pollination mechanism and nectar production would be marginally nonsignificant ($P < 0.058$ for $\kappa = 1$ and $P < 0.064$ for optimal κ).

The near absence of dioecy in Poales outside the restiids probably explains the nonsignificance of correlated evolution between wind pollination and dioecy in the order (Table 1). Although such a pattern is manifest across angiosperms, only the restiids show a high proportion of dioecious species within Poales, with scattered dioecious species or populations—not likely to be scored in an analysis involving so few terminals as the current study—in Cyperaceae, Eriocaulaceae, Poaceae, and Typhaceae (Connor, 1981; Linder & Rudall, 2005). Low levels of dioecy at the familial level in Poales might be expected as based on the near absence of the woody habit and fleshy fruits at that level, given that both traits are strongly associated with dioecy across angiosperms and gymnosperms (Givnish, 1980; Renner & Ricklefs, 1995).

Finally, phylogenetic conservatism appears to account for the lack of a significant correlation between wind pollination and ovule number. Reduction to a single ovule is expected in wind-pollinated taxa given the presumed low probability of multiple pollen grains arriving on a single stigma (Dowding, 1987; Linder, 1998; Friedman & Barrett, 2008; but see Friedman & Barrett, 2009). However, in Poales, single ovules per carpel characterize the entire restiid–graminid clade irrespective of pollination mode, while multiple ovules characterize many of the taxa in the grade including Rapateaceae, the cyperids, and xyrids, again largely independent of pollination mode.

Two general questions that have not been satisfactorily addressed by previous authors remain: (1) why is wind pollination so widespread in Poales? and (2) why has wind pollination evolved five times independently in a single monocot order, when wind pollination is so rare in monocots? Of the factors just tested for correlated evolution with wind pollination, only one—open habitats—could be considered a prime mover, an external set of conditions that would drive the evolution of wind pollination and the many traits associated with the syndrome, namely, unisexual flowers, lack of nectar, reduced perianth, feathery stigma, versatile anthers, reduction in carpel and ovule number, and abundant, smooth, ulcerate pollen (Faegri & van der Pijl, 1979; Dahlgren & Clifford, 1982; Dahlgren et al., 1985; Linder, 1998; Friedman & Barrett, 2009). Potential factors favoring wind pollination identified by previous authors include open, windswept habitats (see above), local dominance by conspecifics (Regal, 1982), and the absence or inefficiency of animal pollinators or the low quality of pollen delivered by them (Whitehead, 1983; Berry & Calvo, 1989; Cox, 1991; Weller et al., 1998; Culley et al., 2002). Strongly windswept habitats might also have poor animal visitation, so the first and third of these mechanisms are partly linked. Regal (1982) argued that high densities of conspecifics would favor wind-pollinated species, given the inherent inefficiencies of pollen delivery to conspecific stigmas in anemophily versus the higher costs of attractive structures or secretions in animal pollination. Indeed, several studies show that pollen delivery to conspecific stigmas drops rapidly with decreasing conspecific density in wind-pollinated taxa (Friedman & Barrett, 2009), and that such taxa have very high pollen:ovule ratios (Cruden, 1977, 2000).

But why have Poales evolved and retained wind pollination so frequently? One factor surely is that many early divergent lineages occupied habitats kept open by flooding, fire, and/or extreme soil infertility, and that open habitats were reinvaded by two additional lineages, Ecdeiocoleaceae and the PACC-MAD-BEP clade of Poaceae (Figs. 4–6). In addition, we propose that four additional prime movers favor wind pollination in herbs, including (1) tall stature, (2) vigorous vegetative spread, (3) adaptation to patchy disturbance by fire and/or flooding, and (4) positive feedback on conspecific abundance. These traits would all help generate high local dominance—and (1) through (3) above characterize all lineages that evolved or retained wind pollination in Poales, except for Ecdeiocoleaceae and Centrolepidaceae. Wind pollination in the latter two families may have been favored selection for reproductive assurance in the harsh, windswept alpine habitats and extremely infertile, fireswept, or seasonally inundated microsites they occupy. Goodwillie (1999) argued that wind pollination could provide such assurance—without the disadvantage of inbreeding associated with self-pollination—in open, harsh environments where pollinator abundance can vary greatly through time and space. Such assurance may be especially important for annual plants, given their need to produce seeds at the end of each growing season if an individual's genes are to enter the next generation, and given the likely spatial autocorrelation of poor conditions for pollinators.

Tall stature, vigorous vegetative spread, adaptation to patchy disturbances, and/or positive feedback on conspecific abundance—coupled with occupancy of open habitats—appear to provide a logical explanation for the distribution of wind pollination in other members of Poales. Typhaceae grow in open, fertile

habitats subject to frequent flooding and siltation, which are inimical to seedling establishment in most species, and to which few other species are adapted; Typhaceae gain high local dominance through advantages in height, rapid rhizomatous spread, and their ability to grow in wet, anoxic soils. Many bromeliads and rapateads lack rhizomatous growth or grow below closed canopies, where wind pollination should be a disadvantage. However, there are some genera (e.g., *Brocchinia* [Bromeliaceae] and *Stegolepis* [Rapateaceae]) in these two families that spread and form extensive, dense colonies on wet soil or rock surfaces, and it is not clear why wind pollination has not evolved in them. Extremely low growth rates in such habitats might prevent such plants from spreading and reaching local dominance for a substantial period after initial colonization of area, working against wind pollination. The origin of wind pollination in the cyperids may be related to invasion and rapid rhizomatous spread within frequently flooded or burnt areas. *Thurnia* of Thurniaceae forms massive colonies in streams on the Guayana Shield where few other plants grow; *Prionium* of the same family forms large monocultures in seasonal streambeds on sandstone in South Africa, which are flooded and burnt at frequent intervals.

Retention of animal pollination by Eriocaulaceae, Xyridaceae, and Mayacaceae despite their occurrence in frequently flooded or burnt sites may be related to their short stature and limited ability to achieve local dominance and spread laterally for any substantial distance. Their small size and slow growth almost surely reflect their occurrence in areas with wet, exceedingly poor soil. They usually inhabit sandy seepage zones and seasonal ponds where nutrients are not delivered in substantial amounts of transported sediment, unlike large-statured *Thurnia* and *Prionium* found in streams on similar sand or sandstone substrates.

Invasion of fire-prone, summer-dry upland habitats over infertile soils, as well as seasonally flooded microsites, by the restiids may help account for their local dominance and evolution of wind pollination (Linder & Rudall, 2005). Frequent, heavy rainfall and strong winds in some parts of western and montane Tasmania—where several early divergent taxa occur—might also favor wind pollination in restiids for pollination assurance. We argue (see above) that pollinator assurance was the primary driver toward anemophily in annual Centrolepidaceae that inhabit extremely infertile, seasonally wet depressions and rock pockets in southern Australia (Pignatti & Pignatti, 1994, 2005; Cooke, 2010). Pollination assurance probably also drove the origin and maintenance of wind pollination in tiny, perennial centrolepid cushion plants at high elevations in Tasmania and New Guinea, given the harsh conditions for pollinators there and the extremely short stature and lack of local dominance of the centrolepids. Interestingly, both kinds of communities are also inhabited by strikingly convergent species of *Trithuria* (Nymphaeales: Hydatellaceae). Preliminary studies suggest that at least one of these (*T. submersa* Hook. f., in Western Australia) is also wind pollinated (Taylor & Williams, 2009).

Reinvasion of shaded habitats on more fertile, well-drained, unburnt sites by *Flagellaria* and *Joinvillea* favored reevolution of animal pollination, accompanied in *Flagellaria* by a small but conspicuously white corolla and scented flowers (Backer, 1951), abundant supply of extrafloral nectar (Blüthgen et al., 2004a, b; Blüthgen & Fiedler, 2004), and visitation by ants (Newell, 1969). Apparent retention of animal pollination in the anomoochloid and pharoid grasses presumably was favored by their restriction to forest understories. Finally, evolution and retention of wind pollination in the vast PACCMAD-BEP clade of Poaceae appear to have been favored by invasion of open habitats and achievement of high local dominance. Factors promoting such dominance might include (1) moderate to tall stature, usually combined with rapid rhizomatous spread; (2) morphological and physiological adaptations of grasses (e.g., narrow, erect foliage, C_4 photosynthesis) to widespread drought under bright, warm conditions starting in the Eocene and intensifying in the Miocene (Kellogg, 2000; Edwards & Smith, 2010); (3) positive feedback among grasses, fire, and nitrogen, given the low nitrogen content and decomposition rate of C_4 grasses and thus their flammability, the tolerance of grasses to fire due to their basal leaf meristems, the volatilization of nitrogen during fires, and the low nitrogen requirement of C_4 grasses (Seastedt et al., 1991; Wedin, 1995; Blair, 1997; Knapp et al., 1998; Reed et al., 2005); (4) positive feedback between grasses and grazers, given the attractiveness of grasses to many grazers, their resistance to grazing damage conferred by basal meristems, and collateral damage by grazers to other plants while seeking grasses (Archibald, 2008); and (5) positive feedback between grasses and their horizontally and vertically transmitted fungal endophytes (e.g., *Epichloë* Tul. & C. Tul., Clavicipitaceae, Ascomycota), based on protection against herbivores provided by the alkaloids secreted by the endophytes, resulting increases in the local frequency of infected grasses, and consequent increases in transmission of the endophytes to uninfected grasses (see Rudgers et al., 2009). An additional factor favoring at least temporary local dominance in grasses may involve (6) the negative effect that certain grasses have on nongrasses, at least in the short term, via the very large absorptive root surface developed by

grasses and their consequent ability to reduce the levels of soil nitrate available to other plants (see Craine, 2006; Dybzinski & Tilman, 2007). The great dominance of pooid grasses in cool areas (Edwards & Smith, 2010) might reflect (1), (4), (5), and/or (6), or some as yet unidentified ecological advantage of that group; the dominance of panicoid grasses in warmer, dryer areas probably reflects at least factors (1) through (4). Clearly, however, none of the proposed factors would have operated in early divergent grasses native to tropical forest understories. Wind pollination in most woody bamboos probably reflects its origin in the PACCMAD-BEP clade (Fig. 6). The alternative—that it represents yet another gain (i.e., a transition from animal-pollinated bamboos)—seems unlikely, given the restriction of known instances of animal pollination to a few understory genera of herbaceous bamboos, such as *Eremitis* Döll, *Olyra* L., *Pariana* Aubl., and *Piresia* Swallen (Gagné, 1969; Soderstrom & Calderón, 1971, 1979), which appear to be sister to the woody bamboos (see Bouchenak-Khelladi et al., 2008). Animal pollination might occur in a few woody bamboos (e.g., *Chusquea* Kunth; Janzen, 1976). If it does, it might represent a secondary gain of animal pollination, but our knowledge of bamboo pollination is far too rudimentary to hazard any analysis at this time. The retention of wind pollination in woody bamboos might be due to (7) their inability to sustain animal pollinators over the multi-year intervals between mass flowering events, driven by selection to satiate seed predators that feed on the unusually numerous (and sometimes unusually large) bamboo seeds, which like other grass seeds are nutritious and chemically unprotected (Janzen, 1976).

Our reanalysis of the evolution of wind pollination in Poales has thus produced several new insights, including a revision upward from three to five independent origins of wind pollination. In addition, we have shown that some traits that show a significant correlation with wind pollination across the angiosperms fail to do so within Poales, apparently due to phylogenetic conservatism in ovule number and nondioecious breeding systems. Our analyses confirm that open habitats, lack of nectar production, and small, nonshowy, unisexual flowers show significant patterns of correlated evolution with wind pollination. Finally, we have proposed specific mechanisms—including several new ideas regarding the potential significance of plant stature, vegetative spread, and local positive feedback—to account for each of the five origins of wind pollination in Poales. Our predictions call for several new tests and for rigorous studies of pollination biology in some critical taxa (e.g., *Flagellaria*, *Joinvillea*, and the anomochlooid, pharoid, puelioid, and bambusoid grasses). Lynn Clark (pers. comm.) suggests that pollination studies on relatively widespread *Pharus* might be especially interesting.

Conclusion

Deriving a monocot phylogeny based on plastomes—a core goal of the Monocot AToL Team—is designed to increase, to the maximum extent possible, the amount of phylogenetic information that can be wrung from the plastid genome. Sampling ever-greater numbers of bases per taxon should increase the resolution and likely accuracy of the resulting estimates of phylogenetic relationships in large taxonomic groups when combined with a reasonably dense and well-stratified sampling of taxa (Hillis, 1996; Givnish & Sytsma, 1997; Graybeal, 1998; Soltis et al., 1998; Hillis et al., 2003; Graham et al., 2006; Jansen et al., 2007). Our plastid data, including 25,107 informative sites, represent a 38-fold increase in the number of such sites over the pioneering study of monocot phylogeny by Duvall et al. (1993b), based on sequences of the single plastid gene *rbcL* and a comparable number of taxa. In the intervening years, monocot researchers increased the number of informative characters by sequencing genes that evolve faster (e.g., Fuse & Tamura, 2000, for *matK*; Givnish et al., 2005, for *ndhF*) or by concatenating and analyzing the sequences of several genes. The latter, multigene strategy has proven the more productive approach (e.g., see Chase et al., 2000; Soltis et al., 2000; Qiu et al., 2005), partly due to the difficulty of aligning rapidly evolving regions across highly divergent taxa, and to the inherently higher rate of homoplasy associated with such regions (Givnish & Sytsma, 1997). Chase et al. (2006) used 4777 informative sites from seven genes from the plastid, nuclear, and mitochondrial genomes to reconstruct relationships among 136 monocot taxa; Graham et al. (2006) used 5617 informative sites from 17 plastid genes and spacers to reconstruct ties among 94 monocot taxa. These studies increased the number of informative characters 5.3- to 8.6-fold over Duvall et al. (1993b) and increased the number of informative characters per taxon from 6.3 to 26 to 60.

The study presented here—using 81 plastid genes and over 100 kb of aligned sequence data per taxon—represents a further increase of fourfold to sixfold in data density per taxon, resulting in a ratio of 302 informative sites per taxon. Our study, and similar ones recently using 61 to 81 plastid gene sequences (Goremykin et al., 2003, 2004; Leebens-Mack et al., 2005; Cai et al., 2006; Jansen et al., 2007; Moore et al., 2007) to address angiosperm and land-plant relationships, mark the transition from plant multigene phylogenetics to phylogenomics. However, it

must be recognized that obtaining an avalanche of data—by sequencing plastomes in this project and, ultimately, transcriptomes and whole nuclear genomes in future analyses—will not relieve us of the need to complement large amounts of data per taxon with adequate taxon sampling. Long-branch attraction is a challenge that must constantly be kept in mind (Soltis & Soltis, 2004; Leebens-Mack et al., 2005; Whitfield & Lockhart, 2007). In the current study, given the more than fivefold variation in evolutionary rates in commelinids, the presence of numerous very long and very short branches in immediate proximity to each other, the conflict between the results of MP and ML analyses, and the current density of taxon sampling, long-branch attraction is clearly an issue. Relationships of the xyrids to each other, and to other members of the order, manifestly need additional taxon sampling and analysis to resolve. The appropriate level of taxon sampling density required to complement ever-rising amounts of sequence data per taxon is a central issue that must continue to be confronted theoretically (e.g., Geuten et al., 2007) and empirically (e.g., Soltis & Soltis, 2004; Leebens-Mack et al., 2005). To address these and other concerns, in the near future we plan to increase taxon sampling in Poales several-fold, and to explore additional analytical techniques (e.g., Lartillot et al., 2007) that may be less sensitive to long-branch attraction. Increased taxon sampling will also increase the power of comparative studies and of searches for morphological and anatomical synapomorphies for individual clades, and make careful calibration of our molecular tree and biogeographic analyses possible. The results presented here, however, show that even with the existing extent of taxon sampling, inferring a phylogeny based on whole plastid genomes can produce numerous new insights into monocot relationships and patterns of adaptive evolution at broad scales. The future of such studies—coupling a greatly increased number of plastomes with the sequencing of transcriptomes, the scoring and analysis of hundreds of morphological characters across representatives of all monocot families and subfamlies, the refinement of a timeline for monocot evolution, and analysis of broadscale patterns of monocot historical biogeography and adaptive evolution—appears very bright.

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Appendix 1. Taxa included in study, with GenBank accession numbers and voucher data.

Major clade	Order	Family	Species	GenBank accession numbers*	Voucher data†
Basal angiosperms	Amborellales	Amborellaceae	*Amborella trichopoda* Baill.	NC_005086	Goremykin et al., 2003a
	Nymphaeales	Nymphaeaceae	*Nuphar advena* Aiton	NC_008788	Raubeson et al., 2007
	Austrobaileyales	Schisandraceae	*Illicium oligandrum* Merr. & Chun	NC_009600	Hansen et al., 2007
Magnoliids	Canellales	Winteraceae	*Drimys granadensis* L. f.	NC_008456	Cai et al., 2006
	Laurales	Calycanthaceae	*Calycanthus floridus* L.	NC_004993	Goremykin et al., 2003b
	Magnoliales	Magnoliaceae	*Liriodendron tulipifera* L.	NC_008326	Cai et al., 2006
	Piperales	Piperaceae	*Piper cenocladum* Diels	NC_008457	Cai et al., 2006
Eudicots	Ranunculales	Berberidaceae	*Nandina domestica* Thunb.	NC_008336	Raubeson et al., 2007
	Proteales	Platanaceae	*Platanus occidentalis* L.	NC_008335	Moore et al., 2006
	Buxales	Buxaceae	*Buxus microphylla* Siebold & Zucc.	NC_009599	Hansen et al., 2007
	Cucurbitales	Cucurbitaceae	*Cucumis sativus* L.	NC_007144	Plader et al., 2007
	Fabales	Fabaceae	*Medicago truncatula* Gaertn.	NC_003119	Matsushima et al., 2008
	Malpighiales	Salicaceae	*Populus alba* L.	NC_008235	Okumura et al., 2007
	Vitales	Vitaceae	*Vitis vinifera* L.	NC_007957	Jansen et al., 2006
	Caryophyllales	Amaranthaceae	*Spinacia oleracea* L.	NC_002202	Schmitz-Linneweber et al., 2001
	Gentianales	Rubiaceae	*Coffea arabica* L.	NC_008535	Samson et al., 2007
	Asterales	Asteraceae	*Helianthus annuus* L.	NC_007977	Jansen et al., 2007
	Apiales	Apiaceae	*Anethum graveolens* L.	EU016721–EU016801	Jansen et al., 2007
	Apiales	Araliaceae	*Panax ginseng* C. A. Mey.	NC_006290	Kim & Lee, 2004
Monocots	Acorales	Acoraceae	*Acorus americanus* (Raf.) Raf.	DQ069337–DQ069702, EU0167701–EU016720	Leebens-Mack et al., 2005
	Alismatales	Araceae	*Acorus calamus* L.	NC_007407	Goremykin et al., 2005
			Lemna minor L.	NC_010109	Mardanov et al., 2008
	Dioscoreales	Dioscoreaceae	*Dioscorea elephantipes* (L'Hér.) Engl.	NC_009601	Hansen et al., 2007
	Pandanales	Pandanaceae	*Pandanus utilis* Bory	this study*	*Zomlefer 2348* (GA)
	Liliales	Liliaceae	*Lilium superbum* L.	this study*	*Givnish UW-8-2009-1* (WIS)
	Asparagales	Amaryllidaceae	*Agapanthus praecox* Willd.	this study*	*Zomlefer 2311* (GA)
		Asparagaceae	*Albuca kirkii* (Baker) Brenan	this study*	*McKain 111* (GA)
			Asparagus officinalis L.	this study*	*Leebens-Mack 1001-2010* (GA)

Appendix 1. Continued.

Major clade	Order	Family	Species	GenBank accession numbers*	Voucher data†
			Chlorophytum rhizopendulum Bjorå & Hemp	this study*	*McKain 110* (GA)
			Hesperaloe parviflora (Torr.) J. M. Coult.	this study*	*McKain 102* (GA)
			Hosta ventricosa (Salisb.) Stearn	this study*	*McKain 106* (GA)
			Lomandra longifolia Labill.	this study*	*Steele 1087* (UMO)
			Nolina atopocarpa Bartlett	this study*	*McKain 114* (GA)
			Yucca schidigera Ortgies	DQ069337–DQ069702, EU016681–EU016700	Leebens-Mack et al., 2005
		Asteliaceae	*Neoastelia spectabilis* J. B. Williams	this study*	*Bruhl 2767, Quinn 95289* (NE)
		Hypoxidaceae	*Curculigo capitulata* (Lour.) Kuntze	this study*	*Steele 1081* (UMO)
		Iridaceae	*Iris virginica* L.	this study*	*Pires 2009-101* (UMO)
		Orchidaceae	*Apostasia wallichii* R. Br.	this study*	*Zich 634*; CNS130807 (CNS)
			Phalaenopsis aphrodite Rchb. f.	NC_007499	Chang et al., 2006
		Xanthorrhoeaceae	*Phormium tenax* J. R. Forst. & G. Forst.	this study*	*Givnish Tas-2009-5* (WIS)
	Arecales	Arecaceae	*Chamaedorea seifrizii* Burret	this study*	*Zomlefer 2358* (GA)
			Elaeis oleifera (Kunth) Cortés	EU016883–EU016962	Leebens-Mack et al., 2005
			Ravenea hildebrandtii C. D. Bouché	this study*	*Zomlefer 2357* (GA)
	Dasypogonales	Dasypogonaceae	*Dasypogon bromeliifolius* R. Br.	this study*	KRT3702 (PERTH)
			Kingia australis R. Br.	this study*	KRT3703 (PERTH)
	Commelinales	Commelinaceae	*Belosynapsis ciliata* (Blume) R. S. Rao	this study*	*Winters, Higgins & Higgins 186, pl 2; SI 1982-232* (SI)
			Tradescantia ohiensis Raf.	this study*	*Moore 337* (FLA)
	Zingiberales	Musaceae	*Musa acuminata* Colla	EU016983–EU017063	Leebens-Mack et al., 2005
		Zingiberaceae	*Renealmia alpinia* (Rottb.) Maas	this study*	*Zomlefer 2322* (GA)
	Poales	Bromeliaceae	*Brocchinia micrantha* (Baker) Mez	this study*	*Givnish UW-8-2009-2* (WIS)
			Fosterella caulescens Rauh	this study*	*Rauh 40573A* (SEL)
			Navia saxicola L. B. Sm.	this study*	*Givnish 3/16/1987* (WIS)
			Neoregelia carolinae (Beer) L. B. Sm. 'Argentea'	this study*	*McKain 112* (GA)
			Pitcairnia feliciana (A. Chev.) Harms & Mildbr.	this study*	*Luther 28 Aug 2000* (SEL)
			Puya laxa L. B. Sm.	this study*	*Leebens-Mack 1003-2010* (GA)

Appendix 1. Continued.

Major clade	Order	Family	Species	GenBank accession numbers*	Voucher data†
		Centrolepidaceae	*Centrolepis monogyna* Benth.	this study*	*McKain 116* (GA)
		Cyperaceae	*Cyperus alternifolius* L.	this study*	*Leebens-Mack 1002-2010* (GA)
		Ecdeiocoleaceae	*Ecdeiocolea monostachya* F. Muell.	this study*	KRT3786 (PERTH)
			Georgeantha hexandra B. G. Briggs & L. A. S. Johnson	this study*	KRT3775 (PERTH)
		Eriocaulaceae	*Syngonanthus chrysanthus* Ruhland	this study*	*M. Ames 10/15/2009* (WIS)
		Flagellariaceae	*Flagellaria indica* L.	this study*	*K. Hansen 77-394* (BH)
		Joinvilleaceae	*Joinvillea ascendens* Gaudich. ex Brongn. & Gris	this study*	*Lorence 9066* (NTBG), *800379* (NTBG)
			Joinvillea plicata (Hook. f.) Newell & B. C. Stone	FJ486219–FJ486269	Leseberg & Duvall, 2009
		Juncaceae	*Juncus effusus* L.	this study*	*McKain 113* (GA)
		Mayacaceae	*Mayaca fluviatilis* Aubl.	this study*	*McKain 118* (GA)
		Poaceae	*Agrostis stolonifera* L.	NC_008591	Saski et al., 2007
			Anomochloa marantoidea Brongn.	NC_014062	Morris & Duvall, 2010
			Bambusa oldhamii Munro	NC_012927	Wu et al., 2009
			Eleusine coracana (L.) Gaertn.	this study*	*Leebens-Mack 1003-2010* (GA)
			Hordeum vulgare L.	NC_008590	Saski et al., 2007
			Oryza sativa L.	NC_001320	Hiratsuka et al., 1989
			Puelia olyriformis (Franch.) Clayton		*Clayton 1060* (MO)
			Saccharum officinarum L.	NC_006084	Asano et al., 2004
			Sorghum bicolor (L.) Moench	NC_008602	Saski et al., 2007
			Streptochaeta angustifolia Soderstr.	this study*	*J. I. Davis 757* (BH)
			Triticum aestivum L.	NC_002762	Ogihara et al., 2002
			Zea mays L.	NC_001666	Maier et al., 1995
		Rapateaceae	*Potarophytum riparium* Sandwith	this study*	*Givnish GUY-09-2* (BRG)
		Restionaceae	*Thamnochortus insignis* Mast.	this study*	*Givnish UW-8-2009-3* (WIS)
		Sparganiaceae	*Sparganium eurycarpum* Engelm.	this study*	*Ames 10/21/2009* (WIS)
		Thurniaceae	*Thurnia sphaerocephala* Hook. f.	this study*	*Givnish GUY-09-5* (BRG)
		Typhaceae	*Typha latifolia* L.	NC_013823	Guisinger et al., 2010
		Xyridaceae	*Abolboda macrostachya* Spruce ex Malme	this study*	*Givnish GUY-09-7* (BRG)

* GenBank accession numbers for plastid genes newly sequenced in this study are HQ180399–HQ183709. A spreadsheet listing individual accession number for each region and species is available at <http://chloroplast.cbio.psu.edu/supplement.html>.

† Voucher specimen (collector and number, with acronym for herbarium of deposit, or citation for sequences previously published elsewhere).