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PHYLOGENETIC RELATIONSHIPS OF MONOCOTS BASED ON THE HIGHLY INFORMATIVE PLASTID GENE *ndh*F: EVIDENCE FOR WIDESPREAD CONCERTED CONVERGENCE

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ABSTRACT

We used *ndh*F sequence variation to reconstruct relationships across 282 taxa representing 78 monocot families and all 12 orders. The resulting tree is highly resolved and places commelinids sister to Asparagales, with both sister to Liliales–Pandanales in the strict consensus; Pandanales are sister to Dioscoreales in the bootstrap majority-rule tree, just above Petrosaviales. Acorales are sister to all other monocots, with Alismatales sister to all but Acorales. Relationships among the four major clades of commelinids remain unresolved. Relationships within orders are consistent with those based on *rbc*L, alone or in combination with *atp*B and 18S nrDNA, and generally better supported: *ndh*F contributes more than twice as many informative characters as *rbc*L, and nearly as many as *rbc*L, *atp*B, and 18S nrDNA combined. Based on functional arguments, we hypothesized that net venation and fleshy fruits should both evolve—and thus undergo concerted convergence—in shaded habitats, and revert to parallel venation and dry, passively dispersed fruits in open, sunny habitats. Our data show that net venation arose at least 26 times and disappeared 9 times, whereas fleshy fruits arose 22 times and disappeared 11 times. Both traits arose together at least 15 times and disappeared together 5 times. They thus show a highly significant pattern of concerted convergence ($P < 10^{-9}$) and are each even more strongly associated with shaded habitats ($P < 10^{-10}$ to 10^{-23}); net venation is also associated, as predicted, with broad-leaved aquatic plants. Exceptions to this pattern illustrate the importance of other selective constraints and phylogenetic inertia.

Key words: adaptation, biomechanics, correlated evolution, DISCRETE, seed dispersal, submersed plants, tropical forests.

INTRODUCTION

Monocotyledons—with roughly 60,000 species, 92 families, and 12 orders—are the most diverse, morphologically varied, and ecologically successful of the early-divergent angiosperms. Over the past ten years, molecular systematics has revolutionized our understanding of higher-level relationships within the monocots and made them among the best understood in the angiosperms (Chase et al. 1993, 1995*a*, *b*, 2000, 2006; Givnish et al. 1999; Bremer 2000, 2002; Kress et al. 2001; Caddick et al. 2002*a*, *b*; Hahn 2002; Patterson and Givnish 2002; Pires and Sytsma 2002; Michelangeli et al. 2003; Zanis et al. 2003; Graham et al. 2006; McPherson et al. submitted). Such studies have laid the groundwork for rigorous studies of adaptive radiation, geographic diversification, and the evolution of development, independent of phenotypic convergence among distantly related groups or divergence among close relatives.

Based on a cladistic analysis of more than 500 *rbc*L sequences, Chase et al. (1995*a*, *b*) identified six major clades of monocotyledons: commelinids (including Poales, Commelinales, Zingiberales, Dasypogonales, and Arecales), Asparagales, Liliales, Pandanales, Dioscoreales, and Alismatales, with *Acorus* L. sister to all other monocots. However, even when Chase et al. (2000) complemented these data with sequences of *atp*B plastid DNA and 18S nrDNA for a subset

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of 140 species—more than tripling the number of nucleotides scored per taxon—relationships among many major clades remained unresolved or weakly supported, and evolutionary ties among several groups of commelinids and asparagoids remained unclear.

To contribute to efforts to resolve these higher-level relationships and investigate the possibility of widespread concerted convergence and plesiomorphy in ecologically significant traits across the monocots, we decided to produce a well-resolved, highly inclusive monocot phylogenetic analysis based on sequences of the plastid gene *ndh*F. This gene provides abundant data for phylogenetic reconstruction: it is more than 50% larger than *rbc*L (ca. 2200 base pairs [bp] vs. ca. 1428 bp) and has substantially more variable positions (Gaut et al. 1997; Patterson and Givnish 2002). Our *ndh*F tree is also ideally suited for analyzing patterns of repeated convergence and divergence among the monocots: it entails many more characters, better resolution, and higher levels of support for individual clades than phylogenetic trees based on *rbc*L alone (albeit for fewer taxa), while incorporating many more taxa than the existing three-gene tree (Chase et al. 2000) based on *rbc*L, *atp*B, and 18S nuclear ribosomal DNA (nrDNA), or the 7- and 17-gene trees now in preparation (Chase et al. 2006; Graham et al. 2006).

Concerted convergence (Givnish and Sytsma 1997*a*, *b*; Givnish and Patterson 2000; Patterson and Givnish 2002) is the independent rise in different lineages under similar ecological conditions of two or more traits that are genetically, developmentally, and functionally unrelated; *concerted plesiomorphy* involves the retention of the same suite of traits in different lineages under similar conditions (Patterson and Givnish 2002). These phenomena might result from adaptations of unrelated traits to the same environmental conditions, or (possibly more likely) to different components of the shared *set* of conditions. They should be challenging to detect and study using analyses based on phenotypic data, given that multiple (and seemingly independent) characters would carry the same, misleading "signal" regarding evolutionary relationships.

Patterson and Givnish (2002) demonstrated that concerted convergence and plesiomorphy occur among the monocots in the order Liliales. Phylogenetic reconstruction demonstrated that (1) visually showy flowers, capsular fruits, wind-dispersed seeds, narrow leaves, parallel venation, and bulbs arose upon invasion of open seasonal habitats, and (2) visually inconspicuous flowers, fleshy fruits, animal-dispersed seeds, broad thin leaves, net venation, and rhizomes persisted in lineages inhabiting ancestral forest understories. For each trait, the observed variation in phenotype with environment across lineages appeared to be functionally adaptive (Givnish and Patterson 2000; Patterson and Givnish 2002).

Two of these patterns of concerted convergence and plesiomorphy may hold throughout the monocots. Specifically, we predict that net venation and vertebrate-dispersed fleshy fruits should frequently evolve and be retained with each other under shady conditions in forest understories, and that parallel venation and nonfleshy fruits (dispersed by wind, water, or gravity) should frequently evolve and be retained with each other in open habitats. These predictions are based on the biomechanical economy of branched vs. unbranched support networks in thin leaves adapted to shady conditions, and on the efficiency of dispersal via vertebrates vs. more passive means in less windy forest understories.

Shady conditions favor thin, broad leaf laminas, which cannot support themselves mechanically (especially after small losses of turgor pressure), and therefore require longitudinal and lateral reinforcement from primary and secondary veins (Givnish 1979, 1987). The cost per unit length of such veins scales like their diameter squared, whereas their strength scales like diameter cubed, favoring the coalescence of nearby, subparallel veins into one or few branching ribs of lower cost (Givnish 1979, 1995). Thus, the broader and thinner a lamina or its divisions, the greater should be the advantage of net venation and the greater the advantage of a single midrib. Givnish et al. (submitted) argue that soft, thin, broad leaves are also favored in fast-growing, emergent aquatic plants with access to abundant moisture and nutrients (e.g., *Sagittaria* L.), and in filmy-leaved submersed species adapted for photosynthesis underwater (e.g., *Aponogeton* L. f.). Net venation should thus also be selectively favored in such plants. In addition, whereas wind dispersal of seeds is likely to be effective in open, windy habitats, animal dispersal of fleshy fruits should be more effective below closed habitats (Croat 1978; Givnish 1998). In Neotropical rain forests, up to 95% of the woody understory species (mostly dicots) bear fleshy fruits dispersed by birds, bats, or nonvolant mammals (Gentry1982).

In this paper, we evaluate these hypotheses by deriving a well-resolved monocot phylogenetic tree based on *ndh*F sequence variation. We compare the resulting clades with those previously resolved based on *rbc*L, *atp*B and 18S nrDNA sequence variation. Finally, we use the *ndh*F tree to test whether fleshy fruits, net venation, and occurrence in shady forest understories show significant patterns of concerted convergence under shady conditions.

MATERIALS AND METHODS

Phylogenetic Analyses

We included 282 monocot species in our analysis, representing as broad and representative a group of taxa as possible, including members of 78 of 92 families and all 12 orders (Table 1). Families and orders follow APG II (2003), except that we recognize Dasypogonales as equaling Dasypogonaceae (see Givnish et al. 1999; Doweld 2001; Reveal and Pires 2002), and Petrosaviales (Cameron et al. 2003). Most of the families unsampled are small, and several are nonphotosynthetic (e.g., Corsiaceae) or occur in wet or submerged habitats (e.g., Anarthriaceae, Posidoniaceae). The families not represented comprise only 1.2% of all monocot species. Only four (Burmanniaceae, Cyclanthaceae, Hydrocharitaceae, Potamogetonaceae) involve substantial numbers of taxa (100–225 species per family). We used *Ceratophyllum* L. as the outgroup, given its position sister to the monocots in several recent analyses (Soltis et al. 1997, 2000; Graham and Olmstead 2000; Zanis et al. 2002; Borsch et al. 2003). Total DNAs were extracted from fresh, deep-frozen, or silica gel-dried leaf material. We amplified and sequenced *ndh*F for most taxa ourselves following standard techniques (see Patterson and Givnish 2002), obtaining both forward and reverse strands in most cases. New sequences were uploaded to GenBank and accession numbers obtained; se-

Table 1. Classification, GenBank accession numbers, vouchers, and authors for the 283 *ndh*F sequences included in this study. Nomenclature follows Bremer et al. (2002) for orders and families (including "bracketed" taxa), and the International Plant Name Index (2004) for generic names, specific epithets, and taxonomic authorities. Specimens sampled include herbarium vouchers, accessions of living plants provided by various botanical gardens, and, in a few instances, initial citations. Material from curated living collections is designated by institution, followed by accession number. Abbreviations are as follows: ADBG (Adelaide Botanical Garden), ADU (University of Adelaide), NYBG (New York Botanical Garden), SEL (Marie Selby Botanical Garden), SIRG (Smithsonian Institution Research Greenhouses), and UCBG (University of California—Berkeley Botanical Garden).

Order and family	Species	GenBank	Voucher, accession, or citation	Author
Acorales				
Acoraceae	*Acorus calamus* L.	AY007647.2	Denver Botanic Garden, no voucher (RGO 97-149 DNA)	H. O'Brien
	A. gramineus Aiton	AF546992	*Rothwell & McPherson/Williams s. n.*, ALTA	H. O'Brien
Alismatales				
Alismataceae	*Alisma plantago-aquatica* L.	AF546993	*Buzgo 1013*, ALTA	L. Rollins
	Sagittaria latifolia Willd.	AY007657.2	*Barrett s. n.*, TRT	H. O'Brien
Aponogetonaceae	*Aponogeton elongatus* Benth.	AY191195	*Hahn s. n.*, WIS	J. C. Pires
Araceae	*Arisaema fraternum* Schott	AF546995	*Buzgo 953*, ALTA	L. Rollins
	Gymnostachys anceps R. Br.	AY191196	*Chase 3841*, K	J. C. Pires
	Spathiphyllum wallisii Hort.	AY007658.2	*Chase 210*, NCU	H. O'Brien & S. Graham
Butomaceae	*Butomus umbellatus* L.	AF546997	*Chase 6414*, K	L. Rollins
Cymodoceaceae	*Halodule wrightii* Asch.	AY191197	*Kolterman s. n.*, WIS	J. C. Pires
Juncaginaceae	*Triglochin maritimum* L.	AF546998	*Buzgo 1011*, ALTA	L. Rollins
Limnocharitaceae	*Hydrocleys* Rich. sp.	AY191198	U Wisconsin—Madison Botanical Garden	J. C. Pires
Scheuchzeriaceae	*Scheuchzeria palustris* L.	AF547007	*Waterway & Graham 97-60*, ALTA	M. A. McPherson
Tofieldiaceae	*Tofieldia glutinosa* (Michx.) Pers.	AF547023	*Morton & Venn 9282*, ALTA	M. A. McPherson & H. O'Brien
Zosteraceae	*Zostera angustifolia* (Hornem.) Rchb.	AF547022	*Chase 2795-W2*, K	H. Rai & L. Rollins
Petrosaviales				
Petrosaviaceae	*Japonolirion osense* Nakai	AY191199	*Chase 3000*, K	J. C. Pires
Dioscoreales				
Dioscoreaceae	*Dioscorea bulbifera* L.	AY007652.2	EPO Biology, U Colorado—Boulder, no voucher (RGO 97-151 DNA)	H. O'Brien
	Tacca chantieri André	AY191200	*Hahn 6977*, WIS	J. C. Pires
	Trichopus sempervirens (H. Perrier) Caddick & Wilkin	AF546996	*Caddick 304*, K	L. Rollins
Nartheciaceae	*Aletris farinosa* L.	AY191201	*Smith et al. 2263*, WIS	J. C. Pires
	Narthecium ossifragum Huds.	AY191202	*Chase 610*, K	J. C. Pires
Pandanales				
Pandanaceae	*Pandanus utilis* Bory	AY191203	*Hahn 6898*, WIS	J. C. Pires
Stemonaceae	*Croomia japonica* Miq.	AF547002	*Rothwell & Stockey 43*, ALTA	M. A. McPherson
	Stemona tuberosa Lour.	AF547009	*Rothwell & Stockey 46*, ALTA	M. A. McPherson
	Stichoneuron caudatum Ridl.	AF547010	*Rothwell & Stockey 45*, ALTA	M. A. McPherson
Velloziaceae	*Vellozia* Vand. sp.	AF546999	*Kubitzki & Feuerer 97-3*, HBG	L. Rollins
	Talbotia elegans Balf.	AF547011	*Rothwell & Stockey 48*, ALTA	M. A. McPherson
Liliales				
Alstroemeriaceae	*Alstroemeria* L. sp.	AF276011	*Anderson 13653*, MICH	T. B. Patterson
Calochortaceae	*Calochortus albus* Dougl. ex Benth.	AF275994	*Patterson 13*, WIS	T. B. Patterson
	C. apiculatus Baker	AF275995	*Patterson 1060*, WIS	T. B. Patterson
	C. weedii Wood	AF275998	*Patterson 18*, WIS	T. B. Patterson
	Prosartes maculata A. Gray	*AF276015*	*Foster s. n.*, Messiah Coll.	T. B. Patterson
	Scoliopus bigelovii Torr.	*AF276017*	*Kalt 9278*, WIS	T. B. Patterson
	Streptopus amplexifolius DC.	AF276019	*Foster s. n.*, Messiah Coll.	T. B. Patterson
	S. lanceolatus (Aiton) J. L. Reveal	AF276020	*Foster s. n.*, Messiah Coll.	T. B. Patterson
	Tricyrtis affinis Makino	AF276021	*Chase 2777*, K	T. B. Patterson
	T. latifolia Maxim.	AF276022	*Patterson 1070*, WIS	T. B. Patterson
Campynemataceae	*Campynema lineare* Labill.	AF276013	*Walsh 3488*, MEL	T. B. Patterson
Colchicaceae	*Androcymbium ciliolatum* Schltr. & K. Krause	AF276012	*Chase 272*, NCU	T. B. Patterson
	Disporum flavens Kitagawa	AY438618	*Millam 1307*, WIS	K. C. Millam
	Uvularia sessilifolia J. F. Gmel.	AF276023	*Patterson 10*, WIS	T. B. Patterson
	Wurmbea pygmaea (Endl.) Benth.	AF547012	*Case 77*, PERTH	M. A. McPherson

Table 1. Continued.

Order and family	Species	GenBank	Voucher, accession, or citation	Author
Liliaceae	*Cardiocrinum giganteum* Makino	AF275999	*Chase 3689*, K	T. B. Patterson
	var. *yunnanense* Makino	AF276000	*Chase 935*, K	T. B. Patterson
	Clintonia borealis Raf.	AF276001	*Patterson s. n.*, WIS	T. B. Patterson
	Erythronium albidum Nutt.	AF276002	*Patterson 1069*, WIS	T. B. Patterson
	Fritillaria meleagris L.	AF276003	*Patterson 1068*, WIS	T. B. Patterson
	Gagea wilczekii Braun-Blanquet & Maire	AF276004	*Chase 748*, K	T. B. Patterson
	Lilium kelleyanum Lemmon	AF276005	*Felson 13*, WIS	T. B. Patterson
	L. superbum L.	AY007655.2	*Chase 112*, NCU	H. O'Brien
	Lloydia serotina Sweet	AF276006	*Jones s. n.*, K	T. B. Patterson
	Medeola virginiana L.	AF276007	*Patterson 1065*, WIS	T. B. Patterson
	Nomocharis pardanthina Franch.	AF276008	*Chase 934*, K	T. B. Patterson
	Notholirion bulbuliferum (Lingelsh.) Stearn	AF276009	*Patterson s. n.*, WIS	T. B. Patterson
	Tulipa pulchella Fenzl	AF276010	*Patterson 1066*, WIS	T. B. Patterson
Melianthiaceae	*Trillium flexipes* Raf.	AY191205	Givnish, no voucher	J. C. Pires
	Veratrum viride Aiton	AF276024	*Chase 551*, K	T. B. Patterson
	Xerophyllum tenax (Pursh) Nutt.	AY191204	*Pires 99-072*, WIS	J. C. Pires
Philesiaceae	*Philesia buxifolia* Lam. ex Poir.	AF276014	*Chase 545*, K	T. B. Patterson
Ripogonaceae	*Ripogonum elseyanum* F. Muell.	AF276016	*Chase 187*, NCU	T. B. Patterson
Smilacaceae	*Smilax hispida* Muhl.	AF276018	*Givnish s. n.*, WIS	T. B. Patterson
Asparagales				
Agapanthaceae	*Agapanthus africanus* Beauverd	AF508405	UCBG 45.0288, UC	J. C. Pires
Agavaceae	*Agave celsii* Hook.	AF508398	UCBG 65.1883, UC	J. C. Pires
	A. parviflora Torr.	AF508399	UCBG 67.0582, UC	J. C. Pires
	Anemarrhena asphodeloides Bunge	AY191162	*Chase 1022*, K	J. C. Pires
	Anthericum liliago Linn.	AF508402	UCBG 93.0946, UC	J. C. Pires
	Behnia reticulata Didr.	AY191168	*Goldblatt 9273*, MO	J. C. Pires
	Camassia quamash (Pursh) Greene	AF547001	*Coxson & Kuijt 5060*, ALTA	M. A. McPherson
		AF508400	UCBG 86.949, UC	J. C. Pires
	Chlorophytum alismaefolium Baker	AY191163	ADBG G951045, ADU	J. C. Pires
	Herreria salsaparilha Mart.	AY191178	*Chase 2154*, K	J. C. Pires
	Hosta ventricosa (Salisb.) Stearn	AF508401	UCBG 87.0576, UC	J. C. Pires
	Yucca glauca Nutt.	AF547014	Addicott, McPherson, & Hurlburt, no voucher (SWG 00121DNA)	M. A. McPherson
Alliaceae	*Allium haematochiton* S. Watson	AY191160	UCBG 90.0117, UC	J. C. Pires
	A. textile A. Nels. & J. F. Macbr.	AF547000	*McPherson 990704-79*, ALTA	M. A. McPherson
	Ipheion dialystemon Guaglianone	AF508406	UCBG 93.0448, UC	J. C. Pires
	Leucocoryne coquimbensis F. Phil.	AF508407	UCBG 94.1335, UC	J. C. Pires
Amaryllidaceae	*Amaryllis paradisicola* D. A. Snijman	AY191161	*van Jaarsveld 13263*, NBG	J. C. Pires
	Boophone disticha (L. f.) Herb.	AY434486	*Malan 121*, NBG	A. W. Meerow
	Cyrtanthus herrei (Leighton) R. A. Dyer	AY434484	*van Zyl 104*, NBG	A. W. Meerow
	Eustephia darwinii Vargas	AY434479	*Meerow 2436*, FTG	A. W. Meerow
	Griffinia parviflora Ker Gawl.	AY434478	*Meerow 2389*, FTG	A. W. Meerow
	Hippeastrum reticulatum Herb.	AY434481	*Meerow 2407*, FTG	A. W. Meerow
	Hymenocallis tubiflora Salisb.	AY434482	*Meerow 2240*, FTG	A. W. Meerow
	Leucojum aestivum L.	AF547024	*Graham 00-4-2*, ALTA	M. A. McPherson
	Narcissus elegans (Haw.) Spach	U79216	*Barrett 1434*, TRT	S. W. Graham
	Paramongaia weberbaueri Velarde	AY434480	*Meerow 2303*, FTG	A. W. Meerow
	Proiphys cunninghamiana (Lindl.) Habb.	AY434487	*Meerow 1188*, FTG	A. W. Meerow
	Scadoxus membranaceus (Baker) Friis & Nordal	AY434485	*Meerow 2240*, FTG	A. W. Meerow
	Sternbergia lutea Spreng.	U79224	*Barrett 1434*, TRT	M. A. McPherson
	Ungernia flava Boiss. & Haussk. ex Boiss.	AY434483	*Meerow 2436*, FTG	A. W. Meerow
Aphyllanthaceae	*Aphyllanthes monspeliensis* L.	AY191167	*Chase 614*, K	J. C. Pires
Asparagaceae	*Asparagus falcatus* L.	AF508403	*Hahn 6881*, WIS	J. C. Pires
Asteliaceae	*Astelia banksii* A. Cunn.	AY191164	*Chase 1072*, K	J. C. Pires
	A. fragrans Colenso	AY191165	ADBG G900014, ADU	J. C. Pires
	Collospermum hastatum (Colenso) Skottsb.	AY191166	ADBG G87567, ADU	J. C. Pires

Table 1. Continued.

Order and family	Species	GenBank	Voucher, accession, or citation	Author
Asphodelaceae	*Asphodelus* L. sp.	AF508409	*Pires 99-132,* WIS	J. C. Pires
Blandfordiaceae	*Blandfordia punicea* (Labill.) Sweet	AY191169	*Chase 519,* K	J. C. Pires
Boryaceae	*Alania endlicheri* Kunth	AY191170	*Conran 707,* ADU	J. C. Pires
	Borya septentrionalis F. Muell.	AY225959	*Chase 2205,* K	J. C. Pires
Hemerocallidaceae	*Arnocrinum preissii* Lehm.	AY191172	*Conran 953,* ADU	J. C. Pires
	Caesia calliantha R. J. F. Henderson	AY191173	*Conran 826,* ADU	J. C. Pires
	Dianella ensifolia (L.) DC.	DQ058413	*Hahn 6869,* WIS	J. C. Hall
	Geitonoplesium cymosum R. Br.	AY191174	ADBG G880709, ADU	J. C. Pires
	Hensmania turbinata (Endl.) W. Fitzg.	AY191175	*Conran 946,* ADU	J. C. Pires
	Johnsonia pubescens Lindl.	AY191176	*Chase 2213,* K	J. C. Pires
	Phormium cookianum Le Jolis	AY191177	ADBG G881651, ADU	J. C. Pires
	Tricoryne elatior R. Br.	AY191206	*Conran 827,* ADU	J. C. Pires
Hyacinthaceae	*Albuca pendula* B. Mathew	AF508390	*Hannon 94565,* RSA	J. C. Pires
	A. setosa Jacq.	AF508391	UCBG 53.0370, UC	J. C. Pires
	Hyacinthus orientalis Linn.	AF508393	*Hahn 6861,* WIS	J. C. Pires
	Muscari comosum (L.) P. Miller	AF547006	*Harder 000419-1,* ALTA	M. A. McPherson
	Ornithogalum caudatum Aiton	AF508394	Hort. UW Botany	J. C. Pires
	O. juncifolium Jacq.	AF508395	UCBG 96.0458, UC	J. C. Pires
	O. longebractatum Jacq.	AF508396	UCBG 47.0533, UC	J. C. Pires
	Scilla natalensis Planch.	AF508397	UCBG 77.0338, UC	J. C. Pires
Hypoxidaceae	*Hypoxis juncea* Sm.	AJ535775	*Chase DNA 5946,* K	J. C. Pires
Iridaceae	*Gladiolus* L. spp.	AY191180	*Hahn 6970,* WIS	J. C. Pires
	Iris missouriensis Nutt.	AF547003	*McPherson 000707-5a-7,* ALTA	M. A. McPherson
	I. tenax Dougl.	AY191181	*Pires 99-077,* WIS	J. C. Pires
	Sisyrinchium montanum Greene	AF547008	*McPherson 990704-71,* ALTA	M. A. McPherson
Ixioliriaceae	*Ixiolirion tataricum* (Pall.) Herb. & Traub	AY191182	*Chase 489,* K	J. C. Pires
Lanariaceae	*Lanaria lanata* Druce	AY191183	*Goldblatt 9410,* MO	J. C. Pires
Laxmanniaceae	*Arthropodium cirratum* R. Br.	AY191184	*Chase 651,* NCU	J. C. Pires
	Cordyline fruticosa (L.) A. Chev.	AY225023	*Hahn 6932,* WIS	J. C. Pires
	Eustrephus latifolius R. Br.	AY191185	*Chase 193,* NCU	J. C. Pires
	Lomandra longifolia Labill.	AF547004	*Vitt 27411,* ALTA	M. A. McPherson
Orchidaceae	*Diuris laxiflora* Lindl.	AJ535765	*Kores & Molvray 209,* K	P. Kores & M. Molvray
	Epipactis helleborine (L.) Crantz	AJ535763	*Chase 199,* K	P. Kores & M. Molvray
	Neuwiedia veratifolia Blume	U20633	Kew DNA O-460	R. Neyland
	Ridleyella paniculata (Ridl.) Schltr.	AJ535768-70	Hort. Botanicus Leiden 31692	P. Kores & M. Molvray
	Spiranthes cernua (L.) L. C. Rich.	AJ535761	*Chase 81941 402,* K	P. Kores & M. Molvray
	Tropidia effusa Rchb. f.	AJ535766-7	*Kores & Molvray 301,* K	R. Neyland
Ruscaceae	*Convallaria majalis* L.	AF508404	*Hahn 6867,* WIS	J. C. Pires
	Dracaena aubryana Brongn. ex E. Morr.	AY191186	*Chase 1102,* K	J. C. Pires
	Maianthemum racemosum (L.) Link	AF547005	*McPherson 990704-97,* ALTA	M. A. McPherson
	Nolina interrata Gentry	AY191188	ADBG W920633, ADU	J. C. Pires
	Ophiopogon wallichianus (Kunth) Hook. f.	AY191189	*Chase 2865,* K	J. C. Pires
	Polygonatum hookeri Baker	AY191190	*Chase 492,* K	J. C. Pires
	P. pubescens Pursh	AY191191	*Chase 481,* K	J. C. Pires
Tecophilaeaceae	*Cyanastrum cordifolium* Oliv.	U79228	*Graham & Barrett 2,* TRT	M. A. McPherson
	Cyanella hyacinthoides L.	AY191192	ADBG G870862, ADU	J. C. Pires
	Tecophilaea violiflora Bertero ex Colla	AY191193	*Chase 1498,* K	J. C. Pires
Themidaceae	*Bessera elegans* Schult. f.	AF508351	*Pires 99-153,* WIS	J. C. Pires
	Brodiaea elegans Hoover	AF508357	*Pires 96-045,* WIS	J. C. Pires
	Dichelostemma congestum Kunth	AF508366	*Pires 96-030,* WIS	J. C. Pires
	Milla biflora Cav.	AF508371	*Rodriguez 2634,* IBUG	J. C. Pires
	Muilla maritima S. Watson	AF508375	*Pires 98-028,* WIS	J. C. Pires
	Triteleia grandiflora Lindl.	AF508380	*Hufford 2776,* WIS	J. C. Pires
Xanthorrhoeaceae	*Xanthorrhoea semiplana* F. Muell	AY191207	ADBG W922097, ADU	J. C. Pires
Xeronemataceae	*Xeronema callistemon* W. R. B. Oliv.	AY191194	ADBG G850899, ADU	J. C. Pires

Table 1. Continued.

Order and family	Species	GenBank	Voucher, accession, or citation	Author
Arecales				
Arecaceae	*Areca vestiaria* Giseke	AY044535	*Hahn 6363*, WIS	W. Hahn
	Allagoptera arenaria (Gomes) Kuntze	AY044564	*Hahn 7047*, WIS	W. Hahn
	Bactris humilis (Wall.) Burret	AY044558	*Hahn 7384*, WIS	W. Hahn
	Beccariophoenix madagascariensis Jum. & H. Perrier	AY044563	*Hahn 7077*, WIS	W. Hahn
	Calamus caesius Blume	AY044523	*Hahn 6390*, WIS	W. Hahn
	Caryota mitis Lour.	AY044531	*Hahn 6627*, WIS	W. Hahn
	Chamaedorea seifrizii Burret	AY044540	*Hahn 6897*, WIS	W. Hahn
	Drymophloeus litigiosus (Becc.) H. E. Moore	AY044537	*Hahn 6370*, WIS	W. Hahn
	Elaeis oleifera (Kunth) Cortés	AY044562	*Hahn 7085*, WIS	W. Hahn
	Leopoldinia pulchra Mart.	AY044547	*Hahn 7642*, WIS	W. Hahn
	Manicaria saccifera J. Gaertn.	AY044548	*Hahn 7641*, WIS	W. Hahn
	Nypa fruticans Wurmb.	AY044525	*Hahn 7106*, WIS	W. Hahn
	Phoenix dactylifera L.	AY044529	*Hahn 6899*, WIS	W. Hahn
	Ravenea hildebrandtii C. D. Bouché	AY044544	*Hahn 6392*, WIS	W. Hahn
	Reinhardtia simplex (Wendl.) Drude ex Dammer	AY044551	*Hahn 7811*, WIS	W. Hahn
	Serenoa repens (W. Bartram) Small	AY191210	*Hahn 7057*, WIS	J. C. Pires
Dasypogonales				
Dasypogonaceae	*Calectasia intermedia* Sond.	AY191208	*Chase 456*, K	J. C. Pires
	Dasypogon bromeliifolius R. Br.	AY191209	*Rudall 29*, K	J. C. Pires
Commelinales				
Commelinaceae	*Amischotolype monosperma* (C. B. Clarke) I. M. Turner	AY198178	*Bogner 1811*	T. M. Evans
	Aneilema calceolus Brenan	AY198180	*Faden & Faden 77/565*, US	T. M. Evans
	Cartonema philydroides F. Muell.	AY198181	Hort. Munich Bot. Gard. s. n.	T. M. Evans
	Spatholirion longifolium Dunn	AY198179	*Chase 593*, K	T. M. Evans
Haemodoraceae	*Anigozanthos flavidus* DC.	AF546994	*Neyland 1884*, MCN	H. O'Brien
	Lachnanthes Ell. sp.	AY191211	*Hahn 6973*, WIS	J. C. Pires
	Xiphidium caeruleum Aubl.	AF547013	SDSU greenhouse (coll. M. Simpson) SWG 5.7.94 DNA	M. A. McPherson
Hanguanaceae	*Hanguana* Blume sp.	AY125006	*Kress 99-6325*, US	L. M. Prince
	H. malayana (Jack) Merr.	AY007654	*Sirirugsa s. n.*, SONG	S. W. Graham
		AY191212	*Sirirugsa s. n.*, SONG	J. C. Pires
Philydraceae	*Philydrum lanuginosum* Gaertn.	U41622	*Graham & Barrett 1*, TRT	S. W. Graham
Pontederiaceae	*Eichhornia crassipes* (Mart.) Solms	U41599	*Barrett 814*, TRT	S. W. Graham
	Heteranthera limosa (Swartz) Willd.	U41608	*Barrett 1054*, TRT	M. A. McPherson
	Hydrothrix gardneri Hook. f.	U41606	*Barrett 1414*, TRT	M. A. McPherson
	Monochoria korsakovii Reg. & Maack	U41615	*Barrett 1415*, TRT	M. A. McPherson
Zingiberales				
Cannaceae	*Canna polymorpha* Lodd. ex Loud.	AY191214	*Hahn 6912*, WIS	J. C. Pires
Costaceae	*Costus pulverulentus* Presl	AY191215	*Sytsma s. n.*, WIS	J. C. Pires
	Dimerocostus strobilaceus Kuntze	AY124997	*Kress 94-3601*, US	L. M. Prince
	Tapeinochilos Miq. sp.	AY124996	*Kress 90-2984*, US	L. M. Prince
Heliconiaceae	*Heliconia latispatha* Benth.	AY191216	*Hahn 6921*, WIS	J. C. Pires
Lowiaceae	*Orchidantha fimbriata* Holttum	AY191217	*Kress & Beach 87-2159*, US	J. C. Pires
Marantaceae	*Calathea foliosa* Rowlee ex Woodson & Schery	AY125003	Duke 287935	L. M. Prince
	Maranta leuconeura E. Morr.	AY191218	*Kress 94-3724*, US	J. C. Pires
	Marantochloa purpurea (Ridley) Milne-Redhead	AY125004	*Kress 78-0894*, US	L. M. Prince
	Thaumatococcus daniellii (Benn.) Benth. & Hook. f.	AY125005	*Kress 98-6288*, US	L. M. Prince
Musaceae	*Ensete ventricosum* (Welw.) E. E. Cheesm.	AY124993	*Kress 94-5321*, US	L. M. Prince
	Musa L. sp.	AY191219	*Sytsma 7203*, WIS	J. C. Pires
	Musella lasiocarpa (Fr.) Wu ex H. W. Li	AY124992	*Kress 94-3709*, US	L. M. Prince

Table 1. Continued.

Order and family	Species	GenBank	Voucher, accession, or citation	Author
Strelitziaceae	*Phenakospermum guyanense* Endl.	AY124995	*Kress 86-2099D,* US	L. M. Prince
	Ravenala madagascariensis J. F. Gmel.	AY124994	*Kress 92-3504,* US	L. M. Prince
	Strelitzia Aiton sp.	AY191220	*Sytsma 7204,* WIS	J. C. Pires
Zingiberaceae	*Alpinia galanga* (L.) Willd.	AY125002	SIRG 94-753	L. M. Prince
	Globba curtisii Holttum	AY125001	*Kress 99-6347,* US	L. M. Prince
	Hedychium flavescens Carey ex Rosc.	AY124998	*Kress 99-6590,* US	L. M. Prince
	Riedelia Trin. ex Kunth sp.	AY125000	SIRG 98-025	L. M. Prince
	Siphonochilus kirkii (Hook.) B. L. Burtt	AY124999	*Kress 94-3692,* US	L. M. Prince
	Zingiber officinale Roscoe	AY191221	*Sytsma 7205,* WIS	J. C. Pires
Poales				
Bromeliaceae	*Aechmea haltonii* H. Luther	L75844	SEL 85-1447	R. G. Terry et al.
	Ananas ananassoides (Baker) L. B. Sm.	L75845	*Brown 3129,* RM	R. G. Terry et al.
	Brewcaria reflexa (L. B. Sm.) B. K. Holst	AY208982	Givnish et al. 1997	K. C. Millam
	Brocchinia acuminata L. B. Sm.	L75859	SEL 81-1937	R. G. Terry et al.
	B. paniculata Schult. F.	AY208981	*Fernandez 8236,* PORT	K. C. Millam
	Bromelia Adans. sp.	L75860	*Brown 3128,* RM	R. G. Terry et al.
	Canistrum giganteum (Baker) L. B. Sm.	L75861	*Brown 3183,* RM	R. G. Terry et al.
	Catopsis wangerini Mez & Werckle	L75855	*Palací 1235,* RM	R. G. Terry et al.
	Cryptanthus beuckeri E. Morren	L75856	SEL 89-499	R. G. Terry et al.
	Deuterocohnia longipetala Mez	AY208984	Hort. Marnier-Lapostelle s. n.	K. C. Millam
	Dyckia Schult. f. sp.	L75857	*Brown 3131,* RM	R. G. Terry et al.
	Encholirium Mart. ex Schult. sp.	L75862	SEL 1984-0364	R. G. Terry et al.
	Fosterella penduliflora (C. H. Wright) L. B. Sm.	L75863	SEL 69-1976-12	R. G. Terry et al.
	Glomeropitcairnia penduliflora Mez	L75864	*Givnish s. n.,* WIS	R. G. Terry et al.
	Guzmania monostachya Rusby	L75865	SEL 82-225	R. G. Terry et al.
	Hechtia lundelliorum L. B. Sm.	AY208985	SEL 85-1005	K. C. Millam
	Hohenbergia disjuncta L. B. Sm.	L75906	SEL 83-393	R. G. Terry et al.
	Mezobromelia pleiosticha J. F. Utley & H. Luther	L75891	SEL 81-1986	R. G. Terry et al.
	Navia saxicola L. B. Sm.	AY208983	Givnish et al. 1997	K. C. Millam
	Nidularium selloanum (Baker) E. Pereira & Leme	L75894	*Leme 1830,* HB	R. G. Terry et al.
	Pitcairnia carinata Mez	L75902	*Brown 3173,* RM	R. G. Terry et al.
	Puya aequatorialis André	L75903	SEL 93-211	R. G. Terry et al.
	Tillandsia complanata Benth.	L75899	SEL 79-0519	R. G. Terry et al.
	Vriesea viridiflora (Regel) J. R. Grant	L75910	SEL 78-757	R. G. Terry et al.
Cyperaceae	*Carex dioica* L.	AF191808	Royal Botanic Garden, Edinburgh 19851401	A. C. Yen
	Cladium californicum (S. Watson) O'Neill	AY129249	*Swearingen 1596,* RSA	E. H. Roalson
	Dulichium arundinaceum (L.) Britt.	AY129250	*Williams 1441,* RSA	E. H. Roalson
	Eleocharis elegans (Kunth) Roem. & Schult.	AY129258	*Roalson 1458,* WS	E. H. Roalson
	Gahnia deusta (R. Br.) Benth.	AY129253	*Overton 2708,* RSA	E. H. Roalson
	Mapania paradoxa Raynal	AY129256	*Granville 13232,* US	E. H. Roalson
	Rhynchospora corniculata (Lam.) A. Gray	AY129252	*Roalson 1276,* WS	E. H. Roalson
	Scirpus nevadensis S. Watson	AY129254	*Helmkamp s. n.,* RSA	E. H. Roalson
Ecdeiocoleaceae	*Ecdeiocolea monostachya* F. Muell.	AY438617	*Hopper 8531,* K	M. A. McPherson
Eriocaulaceae	*Eriocaulon compressum* Lam.	AF547017	*Unwin 241,* MU	H. Rai
	Tonina fluviatilis Aubl.	AY198182	*Givnish 3109,* WIS	T. M. Evans
Flagellariaceae	*Flagellaria indica* L.	U22008	*Clark & Zhang 1305,* ISC	J. F. Wendel
Joinvilleaceae	*Joinvillea ascendens* Gaudich.	U21973	NYBG 800379	J. F. Wendel
Juncaceae	*Juncus effusus* L.	AF547015	*Rai 1004,* ALTA	H. Rai

Table 1. Continued.

Order and family	Species	GenBank	Voucher, accession, or citation	Author
Mayacaceae	*Mayaca fluviatilis* Aubl.	DQ058414	*Berry 3004*, WIS	J. C. Hall
Poaceae	*Anomochloa marantoidea* Brongn.	U21992	*Clark 1299*, ISC	J. F. Wendel
	Arundo donax L.	U21998	*Clark s. n.*, ISC	J. F. Wendel
	Avena sativa L.	U22000	*Zhang 8400174*, ISC	J. F. Wendel
	Bambusa stenostachya Hack.	U21967	*Zhang 8400174*, ISC	J. F. Wendel
	Brachyelytrum erectum (Schreb.) P. Beauv.	U22005	*Clark 1330*, ISC	J. F. Wendel
	Chusquea circinata Soderstr. & C. E. Calderón	U21990	Quail Botanical Garden	J. F. Wendel
	Coix lacryma-jobi L.	AF117403	USDA Plant Identification Number (MIN)	R. Spangler et al.
	Guaduella marantifolium Franch.	AF164777	*Kobayashi et al. 1539*, ISC	L. G. Clark et al.
	Hordeum vulgare L.	U22003	Wise, no voucher, ISU	J. F. Wendel
	Lithachne pauciflora (Sw.) P. Beauv.	U21978	*Clark 1298*, ISC	J. F. Wendel
	Olyra latifolia L.	U21971	*Londoño & Clark 911*, ISC	J. F. Wendel
	Oryza sativa L.	NC_001320	Hiratsuka et al. 1989	H. Shimada & M. Sugiura
	Panicum virgatum L.	U21986	*Clark 1164*, ISC	J. F. Wendel
	Phaenosperma globosa Munro	U22006	*Clark 1292*, ISC	J. F. Wendel
	Pharus lappulaceus Aubl.	U21994	*Clark 1329*, ISC	J. F. Wendel
	Phyllostachys edulis Mazel ex J. Houz.	U21970	*Clark 1289*, ISC	J. F. Wendel
	Poa pratensis L.	U21980	*Clark 1156*, ISC	J. F. Wendel
	Schizachyrium scoparium Nash	AF117420	*Kellogg V48*, GH	R. Spangler et al.
	Sorghastrum nutans Nash	AF117421	*Clark 1641*, ISC	R. Spangler et al.
	Sporobolus indicus (L.) R. Br.	U21983	*Clark 1293*, ISC	J. F. Wendel
	Tripsacum dactyloides Schltr.	AF117433	*Kellogg V49*, GH	R. Spangler et al.
	Zea mays L.	NC_001666	*Maier et al. 1995*	G. Strittmatter & H. Kossel
	Zoysia matrella Druce	U21975	*Clark 1174*, ISC	J. F. Wendel
Rapateaceae	*Amphiphyllum rigidum* Gleason	AF207638	*Fernández, Stergios, Givnish, & Funk 8061*, PORT	T. M. Evans & M. L. Zjhra
	Cephalostemon flavus (Link) Steyerm.	AF207624	*Smith, Sytsma, & Givnish 303*, WIS	T. M. Evans
	Epidryos guayanensis Maguire	AF207632	*Berry & Brako 5539*, WIS	T. B. Patterson
	Guacamaya superba Maguire	AF207636	*Smith, Sytsma, & Givnish 301*, WIS	T. M. Evans
	Kunhardtia rhodantha Maguire	AF207635	*Smith, Sytsma, & Givnish 300*, WIS	T. M. Evans
	Marahuacaea schomburgkii (Maguire) Maguire	AF207633	*Fernández, Stergios, Givnish, & Funk 8205*, PORT	T. B. Patterson & M. L. Zjhra
	Maschalocephalus dinklagei Gilg & K. Schum.	AF207628	*Assí s. n.*, Côte d'Ivoire 5/95	T. M. Evans
	Monotrema bracteatum Maguire	AF207625	*Smith, Sytsma, & Givnish s. n.*, WIS	T. M. Evans
	Potarophytum riparium Sandwith	AF207627	*Givnish 94-3100*, WIS	T. M. Evans
	Rapatea paludosa Aubl.	AF207623	*Sytsma, Smith, & Givnish 5157*, WIS	T. M. Evans
	Saxofridericia regalis Schomb.	AF207637	*Hahn 4675*, WIS	T. M. Evans & M. L. Zjhra
	Schoenocephalium cucullatum Maguire	AF207634	*Sytsma, Smith, & Givnish* 5116, WIS	T. M. Evans & M. L. Zjhra
	Spathanthus bicolor Ducke	AY438615	*Givnish 89-125*, WIS	K. C. Millam
	S. unilateralis Desv.	AY438613	*Berry & Bachhuber 10 July 2000*, WIS	J. C. Hall
	Stegolepis hitchcockii subsp. *morichensis* Maguire	AF207629	*Smith, Sytsma, & Givnish 297*, WIS	T. M. Evans
Restionaceae	*Elegia fenestrata* Pillans	AF547016	NYBG 1697/95, NY	H. Rai
Thurniaceae	*Prionium serratum* E. Mey.	AF547019		H. Rai
	Thurnia sphaerocephala Hook. f.	AY208986	*Hahn 3999*, US	H. Rai
Typhaceae	*Sparganium* L. sp.	AY191213	*Givnish s. n.*, WIS	J. C. Pires
	Typha angustifolia L.	U79230	*Graham 1040*, TRT	S. W. Graham
Xyridaceae	*Orectanthe sceptrum* (Steyerm.) Maguire	AY438616		K. C. Millam & T. M. Evans
	Xyris jupicai Rich.	AF547017	*Goldman 1766*, BH	H. Rai

quences from previous studies were downloaded from GenBank to complete the data matrix (Table 1). Sequences were visually aligned using MacClade vers. 4 (Maddison and Maddison 2002). Almost all of the 54 indels detected were in-frame and straightforward (albeit laborious) to align, given their general restriction to single species or small sets of close relatives. The aligned data matrix (including 2518 aligned bases) is available upon request from the three senior authors.

Phylogenetic analyses based on maximum parsimony (MP) were conducted using PAUP* vers. 4.0b8 (Swofford 2002). One hundred replicate searches were conducted using tree-bisection-reconnection (TBR) and random stepwise-addition to maximize the chances of detecting multiple islands of trees if they exist. Bootstrap percentages were obtained via TBR searches on 500 random resamplings of the nucleotide data, saving up to 50 trees per replicate. For comparative purposes, an additional MP search was conducted including both nucleotide and indel data; individual indels were treated as equally weighted characters and scored to minimize the number of additional evolutionary events following Baum et al. (1994). We merged our nucleotide data with those analyzed by Chase et al. (2000) to conduct an MP search involving 88 monocot genera for which sequence data are available for 18S nrDNA, *rbc*L, *atp*B, and *ndh*F, using *Acorus* as an outgroup. Based on this analysis, the numbers of informative and variable characters contributed by each of these sequences were calculated.

Calibration of Molecular Phylogenetic Trees Against Time

As previously shown for *rbc*L (Gaut et al. 1992, 1997), *ndh*F displays substantial variation in rates of nucleotide evolution across different groups of monocots, precluding the use of simple molecular clocks to place phylogenetic events and character-state changes on a time line. We therefore used the computer program r8s to transform one of the most-parsimonious *ndh*F trees into ultrametric form—with equal branch lengths from the root after discarding the outgroup *Ceratophyllum*—using cross-verified penalized likelihood (Sanderson 2002). We calibrated this tree against absolute time by fixing the age of the divergence of Acorales from other monocots at 134 million years ago (Mya) (Bremer 2000), while setting the minimum ages of the stem groups of six clades (Poaceae–Joinvilleaceae–Flagellariaceae–Restionaceae, Typhaceae–Sparganiaceae, Zingiberales, Arecales, Araceae, and Tofieldiaceae) equal to 69.5 Mya, 69.5 Mya, 83 Mya, 89.5 Mya, 69.5, and 83 Mya, respectively, based on the estimated ages of the oldest known Cretaceous fossils for these groups (Bremer 2000).

Tests of Concerted Convergence

We used selected *ndh*F trees to test whether fleshy fruits, net venation, and occurrence in shaded understories show correlated evolution employing DISCRETE (Pagel 1994, 1999). DISCRETE uses a continuous Markov model to analyze the evolution of binary characters, incorporating branch lengths and weighting gains and losses equally. We executed separate tests of correlated evolution between (1) fleshy fruits and life in shady habitats; (2) net venation and shady habitats; (3) fleshy fruits and net venation; (4) net venation and shady habitats, emergent broad-leaved aquatics, or submersed broad-leaved aquatics; and (5) fleshy fruits and net venation, excluding emergent and submersed broad-leaved aquatics. DISCRETE produces a likelihood ratio for which the distribution converges on that of χ^2 with 4 degrees of freedom. We tested for correlated evolution—and hence, concerted convergence—by comparing the observed likelihood ratio against critical values of χ^2, a conservative approach (Pagel 1999). We conducted each test on four fully resolved trees, chosen randomly from among the maximum-parsimony trees to represent each of the four resolutions of the major polytomy at the base of the commelinids. The other unresolved nodes are unlikely to have any substantial effect on inferences regarding the correlated evolution of fleshy fruits, net venation, or life in shaded understories. We ran each test using branch lengths (inferred number of substitutions) as measures of the amount of molecular evolution down each branch, reflective of time discounted by the rate of molecular evolution inherent to different lineages. Rates of phenotypic transitions were fitted to a gamma distribution, based on median rates in quartiles across monocots. We conducted each test five times independently because DISCRETE can fit slightly different likelihood models to the data from each random starting point, as a result of nearly flat response surfaces and/or large numbers of species. In a few instances, the first step of a DISCRETE run—which evaluates a model assuming *no* correlated evolution between the given pair of traits—returned a log-likelihood substantially below that of other runs. We discarded such cases a priori because they represent a much worse fit of the independent model than is possible and would bias the dependent test toward higher significance of correlated evolution. This procedure would, if anything, create a bias *against* acceptance of a significant pattern of correlated evolution.

We considered "net venation" to include branching support structures within leaves, including cases of reticulate venation, simple leaves in which the veins diverge from a massive central rib regardless of whether they branch anatomically (e.g., *Musa*), and compound leaves with a branching rachis (palms). "Fleshy fruits" include berries, drupes, and seeds with showy, massive, nutritional arils dispersed by vertebrates. *Proiphys* Herb. (Amaryllidaceae) has brightly colored capsules that seem to mimic fleshy fruits (Meerow and Snijman 1998) and were scored as such. Seeds dispersed by ants, bearing small arils (elaiosomes), occur in forest and nonforest habitats and can serve as adaptations for purposes not directly related to dispersal (e.g., placement in nutrient-rich ant nests, shelter from frequent fire) (Beattie and Culver 1983; Beattie 1985; Hughes and Westoby 1992; Boyd 2001). The fruits of *Acorus* are anatomically berries, but are minute, have a relatively thick, dry coat, and lack the sweet or oily composition usually associated with adaptation for ingestion and dispersal by vertebrates. Other features of its morphology and (especially) its geographic pattern of genetic variation suggest that *Acorus* is water-dispersed (Liao and Hsiao 1998). Thus, we did not score either ant-dispersed seeds or the dry berries of *Acorus* as fleshy fruits. Species were classified as occurring primarily in open, sunny habitats (e.g., tundra, chaparral, desert) or closed, shady habitats (forest understories). For species growing in seasonally deciduous forests, the timing of leaf activity and fruit production rela-

tive to canopy closure was used to categorize the habitats occupied as sunny or shady (see Patterson and Givnish 2002). Assigning species to these two classes was occasionally problematic: light regimes occupied by different species can vary continuously (e.g., see Leach and Givnish 1999; Givnish et al. 2004*b*) and most published accounts of ecological distributions are qualitative. However, no matter how one slices the light availability gradient, taxa like *Schizachyrium* Nees and *Strelitzia* Aiton occur in brightly lit sites, while *Trillium* L. and *Cyanastrum* Cass. occur in shaded understories.

For illustrative purposes, we overlaid net venation, fleshy fruits, and life in shady habitats on an ultrametric tree using MacClade. Accelerated transformation was employed to minimize the number of apparently independent origins of each trait. A complete matrix of venation, fruit, and ecological character states is available upon request from the first author.

RESULTS

Phylogenetic Relationships

Maximum parsimony produced one island of 880 trees, each 16,489 steps in length based on 1727 variable characters, of which 1408 are potentially phylogenetically informative (Fig. 1A–D). Across monocots, *ndh*F strongly supports (85–100% bootstrap) the monophyly of nine of the twelve orders identified by previous molecular studies (Chase et al. 1995*a*, *b*, 2000); support is only modest for Commelinales (52%) and Asparagales (65%), and Petrosaviales are represented by only a single taxon (*Japonolirion* Nakai). Several nodes previously unresolved or weakly supported are resolved in the *ndh*F phylogenetic tree. Our analysis demonstrates that (1) Asparagales are sister to the commelinids; (2) both of these groups are sister to Liliales plus Pandanales; (3) *Japonolirion* (Petrosaviales) and/or Dioscoreales are sister to all preceding groups; (4) Alismatales are strongly supported (99% bootstrap) as sister to the preceding orders; and (5) *Acorus* (Acorales) is sister to all other monocots.

Bootstrap support for individual clades is often substantially higher than that based on *rbc*L, considered alone or in combination with *atp*B and 18S nrDNA (see Chase et al. 1995*a*, *b*, 2000). Even so, support values are still only modest at several points along the backbones of the asparagoid portion of the tree and the monocot tree as a whole (Fig. 1A–D). In a four-gene analysis, *ndh*F contributes 2.2 times as many informative characters as *rbc*L, and 87% as many as *rbc*L, *atp*B, and 18S nrDNA combined. Only nine nodes are unresolved in the *ndh*F strict consensus tree. Of these, only two—involving a four-way polytomy at the base of the commelinids, and a trichotomy involving four families of Zingiberales—involve substantial numbers of taxa. The commelinid polytomy involves unresolved relationships among Poales (P), Zingiberales plus Commelinales (ZC), Dasypogonales (D), and Arecales (A). Each of these clades is strongly supported individually (79–100%), as are the commelinids as a whole (85%). Among the most-parsimonious trees based on *ndh*F sequence variation, we found four different patterns of relationship among the major commelinid clades: ((P,A),(ZC,D)); (P,(ZC,A,D)); ((P,(ZC,D)),A); and ((P,D),A),ZC).

Within Poales, *ndh*F places Bromeliaceae sister to Typhaceae–Sparganiaceae at the base of the order, with this overall group sister to an unresolved trichotomy involving (1) Rapateaceae, (2) the sedge alliance—Cyperaceae–Juncaceae–Thurniaceae, Eriocaulaceae–Xyridaceae, and Mayacaceae, and (3) the grass alliance—Poaceae, Joinvilleaceae, Ecdeiocoleaceae, Flagellariaceae, and Restionaceae (Fig. 1A–B). Rapateaceae are sister to the grass and sedge alliances in the bootstrap consensus (54% support), and are sister to these groups in the strict consensus tree as well if *Ecdeiocolea* F. Muell. is excluded or if nucleotide characters are sequentially reweighted based on their consistency index. Poaceae and Poaceae–Joinvilleaceae–Ecdeiocoleaceae have 100% bootstrap support, with *Elegia* L. (Restionaceae) and/or Flagellariaceae sister to these other elements of the grass alliance. Thurniaceae are sister to Cyperaceae–Juncaceae (93% bootstrap) at the core of the sedge alliance. Eriocaulaceae and Xyridaceae are monophyletic (100% and 84% bootstrap support, respectively) and each other's closest relatives at the base of the sedge alliance minus Mayacaceae (Fig. 1A). The four major subclades of Poales—the grass alliance, sedge alliance, Rapateaceae, and Bromeliaceae—show as much sequence divergence from each other as that seen among the remaining orders of monocots. Members of the grass and sedge alliances show the highest rates of *ndh*F evolution among monocots; bromeliads display unusually low rates, and rapateads are intermediate in this respect (Fig. 1A–D). Resolution of relationships within the latter two families by highly informative *ndh*F indicates that both require new internal classifications, including five new subfamilies and recircumscription of an additional two (Givnish et al. 2004*a*, in press).

Commelinales and Zingiberales are both resolved as sister clades (79% bootstrap support). In Zingiberales, *ndh*F resolves three pairs of sister families—Zingiberaceae–Costaceae (61%), Marantaceae–Cannaceae (80%), and Strelitziaceae–Lowiaceae (89%). Within Commelinales, Pontederiaceae and Haemodoraceae both have 100% bootstrap support as sister taxa. Philydraceae are sister to the rest of Commelinales, but this position is weakly supported (Fig. 1B). One indel supports their placement with Pontederiaceae and Haemodoraceae, and a combined analysis of *ndh*F indels and nucleotides (not shown) places *Philydrum* Banks ex Gaertn. in an unresolved trichotomy with Pontederiaceae–Haemodoraceae and Commelinaceae–Hanguanaceae. *Hanguana* is strongly supported (90%) as being sister to Commelinaceae; *Cartonema* R. Br. is sister to all other members of the latter. Our analysis places the climbing rattan *Calamus* Auct. ex L. sister to the rest of Arecales (98% bootstrap), with the mangrove palm *Nypa* Steck next-divergent. *Dasypogon* R. Br. and *Calectasia* R. Br. are resolved as forming the monophyletic order Dasypogonales (100% bootstrap).

An important finding of this study is that *ndh*F places Asparagales sister to the commelinids rather than Liliales in the strict consensus tree (Fig. 1C). Asparagales are composed of a ladder of eight clades, with Orchidaceae sister to the rest (Fig. 1C). The sequence of families is broadly similar to that seen in recent studies (see Discussion). Hyacinthaceae are sister to Agavaceae rather than Themidaceae,

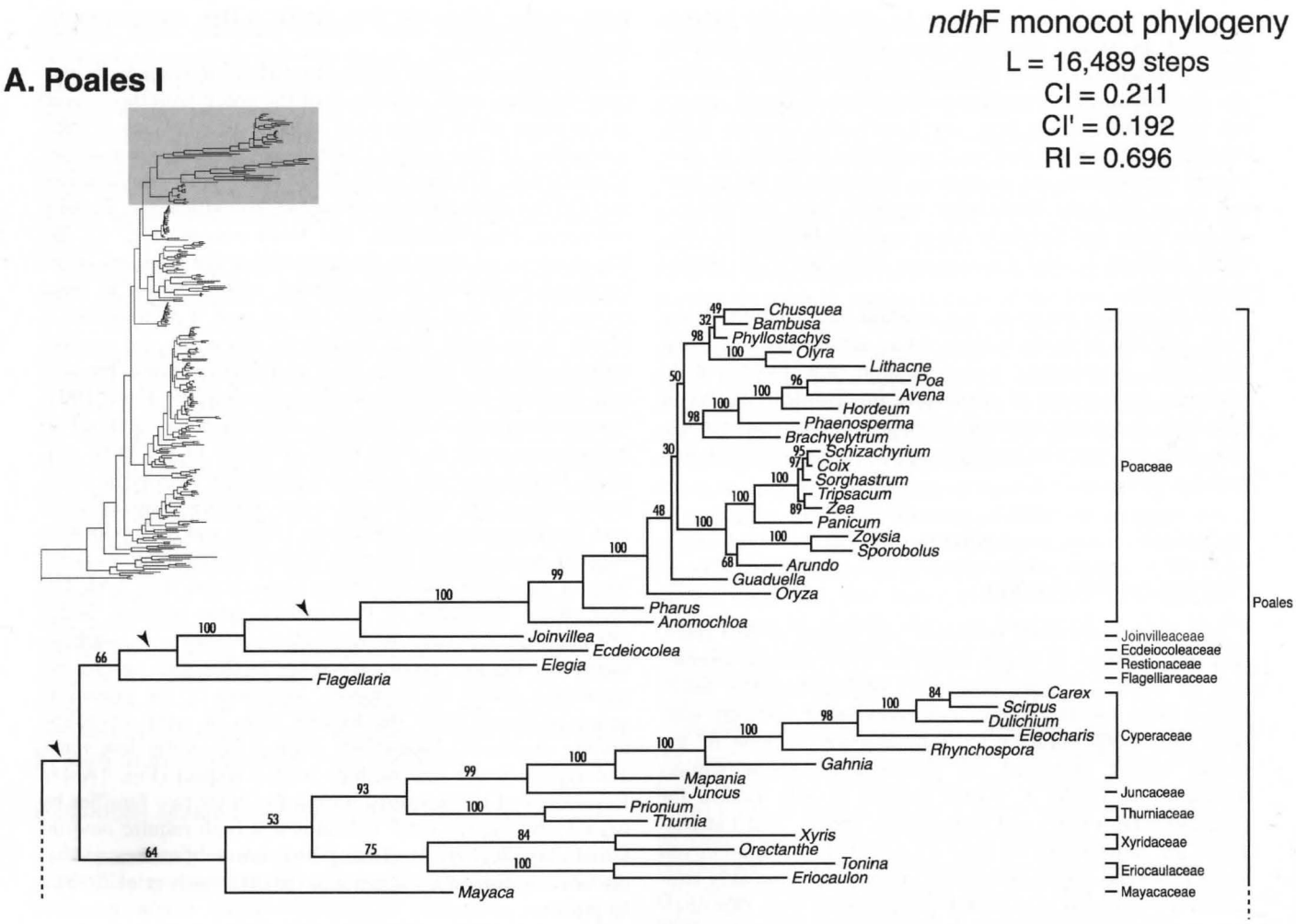

Fig. 1A–D.—Phylogram of one of 874 most parsimonious trees produced by cladistic analysis of *ndh*F sequence variation. CI = consistency index including all variable characters; CI′ = consistency index for informative characters only; RI = retention index. Arrowheads indicate nodes that collapse in the strict consensus tree. Bootstrap values are indicated above each node.—A. Poales I.—B. Poales II, Zingiberales, Commelinales, Dasypogonales, and Arecales.—C. Asparagales.—D. Liliales, Pandanales, Dioscoreales, Petrosaviales, Alismatales, and Acorales.

with which they share bulbs and a similar habit. Agapanthaceae are sister to Amaryllidaceae–Alliaceae. Orchidaceae are strongly supported as monophyletic (100% bootstrap), and are placed sister to all other Asparagales with moderate support (Fig. 1C).

In Liliales, *ndh*F identifies *Campynema* Labill. as earliest divergent, followed successively by Melanthiaceae, Colchicaceae–Alstroemeriaceae, Philesiaceae–Ripogonaceae, Smilacaceae, and Liliaceae (Fig. 1D). The last consists of Calochortaceae and Liliaceae sensu Tamura (1998*a*, *b*), with *Calochortus* Pursh itself embedded in a lineage containing *Prosartes* D. Don, *Scoliopus* Torr., *Streptopus* Michx., and *Tricyrtis* Wall. *Disporum* Salisb. is sister to *Uvularia* L. in Colchicaceae. *Clintonia* Dougl. ex Lindl. and *Medeola* L., with fleshy fruits and broad, net-veined leaves, are strongly supported as each other's closest relatives, forming subfamily Medeoloideae of Liliaceae (Tamura 1998*b*); this group is sister, in turn, to subfamily Lilioideae, characterized by capsular fruits and narrow, parallel-veined leaves excepting forest-dwelling, net-veined *Cardiocrinum* Lindl.

Pandanales are sister to Liliales in the *ndh*F strict consensus tree (Fig. 1D), and to Dioscoreales in the bootstrap majority-rule tree. Among the families sampled, Velloziaceae are sister to Pandanaceae–Stemonaceae in Pandanales, and Nartheciaceae are sister to Dioscoreaceae of Dioscoreales. *Japonolirion* of Petrosaviales is part of an unresolved trichotomy involving itself, Dioscoreales, and commelinids–Asparagales–Liliales–Pandanales; together, these groups form a strongly supported clade (100% bootstrap) consisting of all monocots except Alismatales and Acorales (Fig. 1D).

Araceae (100% bootstrap) are sister to Tofieldiaceae and the remaining Alismatales. The latter form a clade with 100% bootstrap support and two well-marked subclades, including Alismataceae–Limnocharitaceae–Butomaceae (95%), and Aponogetonaceae–Juncaginaceae–Scheuchzeriaceae–Cymodoceaceae–Zosteraceae. Juncaginaceae and Scheuchzeriaceae are resolved as sister groups based on *ndh*F sequence variation. Tofieldiaceae are weakly supported (69%) as sister to the families of the former Najadales (Dahlgren et al. 1985). Finally, *ndh*F provides 100% bootstrap support for the position of *Acorus* sister to all other monocots (Fig. 1D).

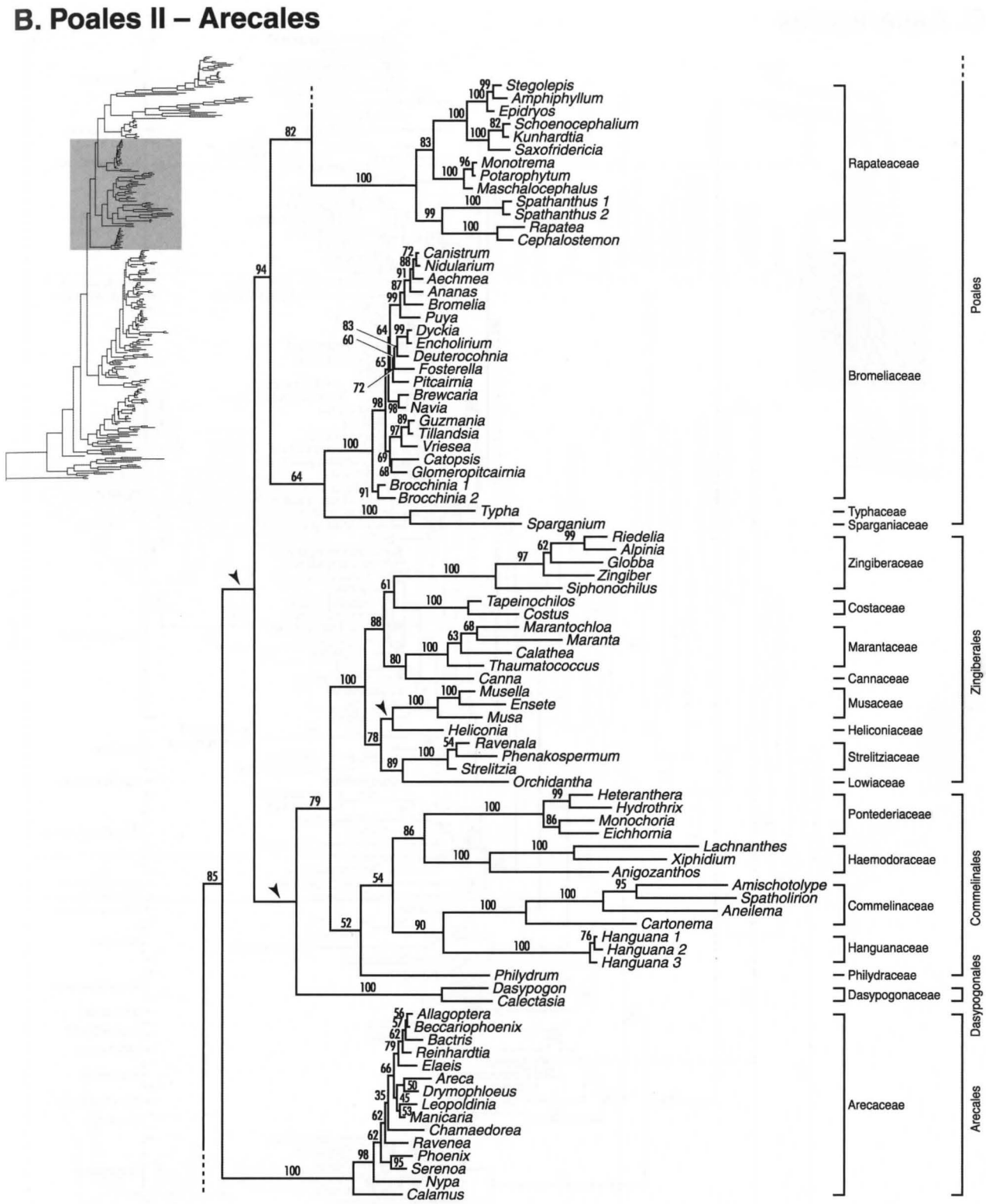

Fig. 1A–D.—Continued.

Concerted Convergence

Based on our *ndh*F data, fleshy fruits appear to have arisen at least 21 times and been lost 11 times, whereas net venation has arisen at least 26 times and been lost 9 times (Table 2; Fig. 2). As predicted, these traits have undergone concerted convergence. They have done so in highly significant fashion ($P < 10^{-9}$, log-likelihood test), with both traits arising together (at the same or adjacent nodes) 15 times and disappearing together 5 times (Table 2; Fig. 2). Fleshy fruits

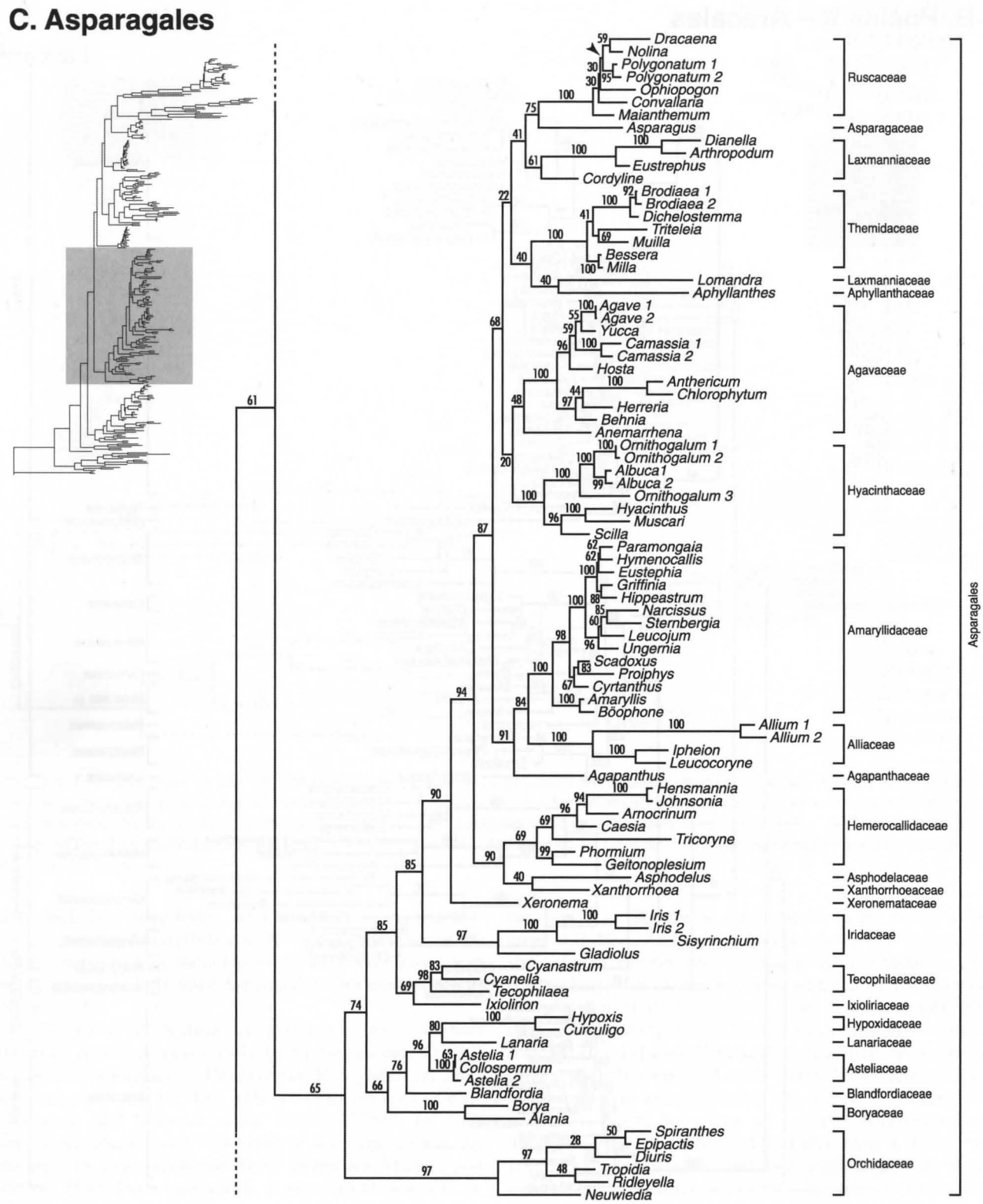

Fig. 1A–D.—Continued.

and net venation arose together in Joinvilleaceae, Flagellariaceae, Hanguanaceae, Arecales, Zingiberales, *Behnia* Didr., two groups of Amaryllidaceae, *Geitonoplesium* A. Cunn., *Curculigo* Gaertn., the core Liliales, *Trillium,* and Araceae, and are associated with each other in Ruscaceae–Laxmanniaceae, *Disporum,* and *Tacca* Forst., with the evolution of fleshy fruits slightly lagging that of net venation among close relatives and inferred ancestors in the last two lines (Fig. 2). Fleshy fruits and net venation were lost together in *Arthropodium* R. Br., *Hypoxis* L.–*Lanaria* Aiton., Lilioideae, and

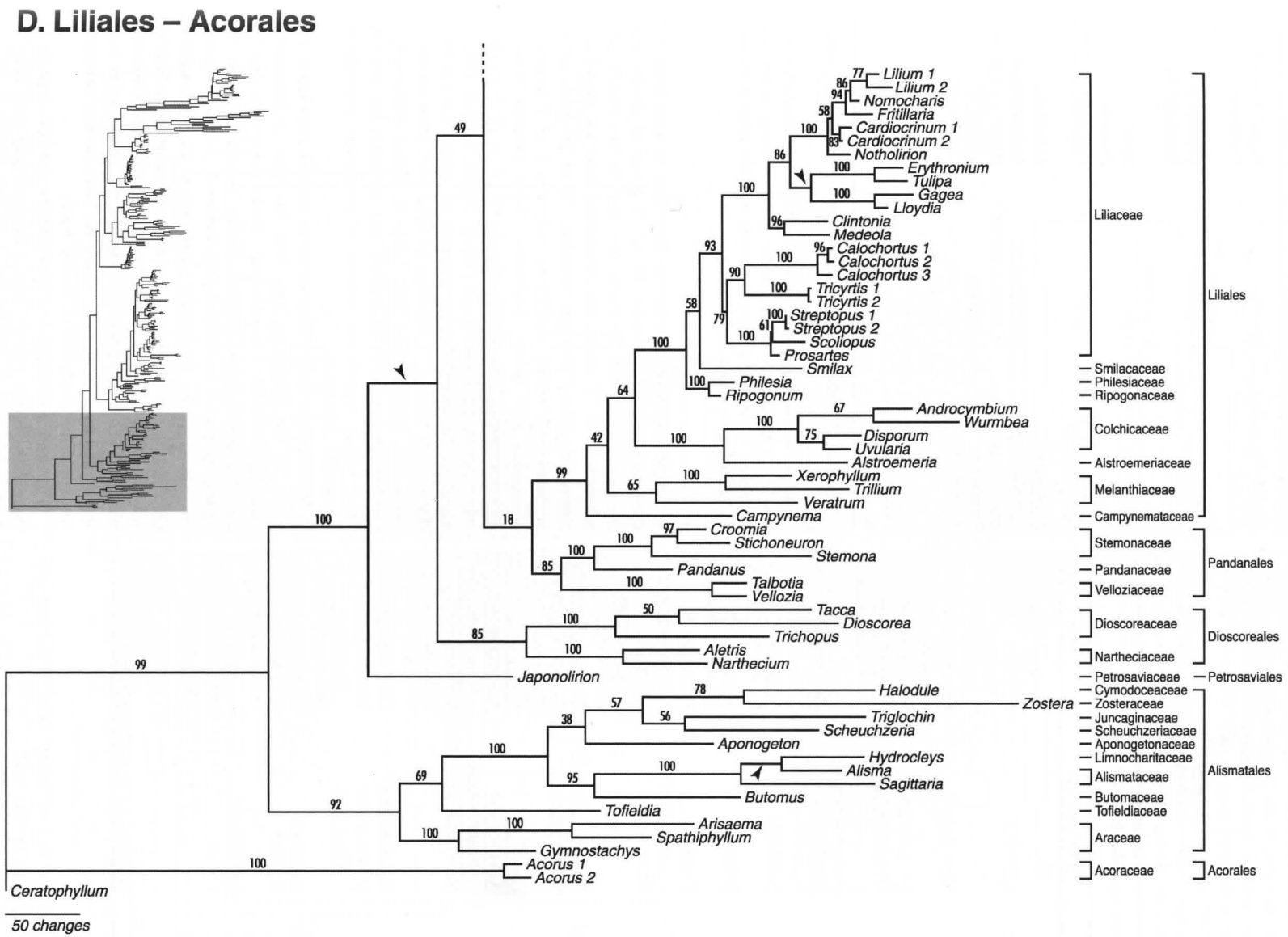

Fig. 1A–D.—Continued.

Table 2. Inferred evolutionary origins of net venation, fleshy fruits, and life in shady habitats, and of parallel venation, passively dispersed fruits and/or seeds, and life in sunny habitats. Most instances of the evolution of the former character states represent initial transitions from the latter, while most instances of the origin of the latter represent reversals from the former. Transitions on the same line occurred at the same node or (in a few cases) adjacent nodes. Instances where all three character states underwent transition at the same or adjacent nodes—involving concerted convergence—are underlined. All calls are based on overlaying characters on a single most-parsimonious tree using accelerated transformation in MacClade (Maddison and Maddison 2002).

Net venation	Fleshy fruits	Shade
Bambusoideae		Bambusoideae
Joinvillea + early-divergent Poaceae	*Joinvillea*	*Joinvillea* + early divergent Poaceae
Flagellaria	*Flagellaria*	*Flagellaria*
		Monotremeae
	Bromelioideae	Bromelioideae
Hanguanaceae	Hanguanaceae	(Hanguanaceae + Commelinaceae)
	Amischotolype	
Zingiberales + Philydraceae[a]	Zingiberales	Zingiberales
Arecaceae	Arecaceae	Arecaceae
Hosta		*Hosta*
Behnia	*Behnia*	*Behnia*
		Chlorophytum
Ruscaceae + Laxmanniaceae	Ruscaceae + Laxmanniaceae	Ruscaceae + Laxmanniaceae
Griffinia	*Hippeastrum*	*Griffinia* + *Hippeastrum*
Hymenocallis		*Hymenocallis*
Proiphys–Scadoxus	*Proiphys–Scadoxus*	*Proiphys–Scadoxus*
Geitonoplesium	*Geitonoplesium*	*Geitonoplesium*
Cyanastrum		*Cyanastrum*
Curculigo	*Curculigo*	*Curculigo*
	Asteliaceae + Blandfordiaceae	Asteliaceae + Blandfordiaceae
	Neuwiedia	*Neuwiedia*
		Epipactis
		Tropidia
Cardiocrinum	[*Cardiocrinum*][b]	*Cardiocrinum*
Liliales above *Alstroemeria*	Liliales above *Ripogonum*	Liliales above *Ripogonum*
		Calochortus albus
Disporum–Uvularia	*Disporum*	*Disporum–Uvularia*
Trillium	*Trillium*	*Trillium*
Stemonaceae		Stemonaceae
	Pandanaceae	
Dioscoreaceae	*Tacca*	Dioscoreaceae
Alismataceae[a]		Alismataceae[a]
Zostera[a]		
Aponogeton[a]		
Araceae	Araceae	Araceae

Table 2. Continued.

Parallel venation	Passively dispersed fruits	Sun
Higher Poaceae	Poaceae	Higher Poaceae
		Cartonema
	Costaceae	
	Cannaceae[a]	Cannaceae
		Strelitziaceae
	Lowiaceae	
	Nypa	*Nypa*
		Phoenix
Dracaena + *Nolina*	*Nolina*	*Dracaena* + *Nolina*
Ophiopogon		
Asparagus		*Asparagus*
Arthropodium	*Arthropodium*	*Arthropodium*
Hypoxis–Lanaria	*Hypoxis–Lanaria*	*Hypoxis–Lanaria*
Lilioideae	Lilioideae	Lilioideae
Calochortus	*Calochortus* + *Tricyrtis*[b]	*Calochortus*
	Scoliopus	
Androcymbium–Wurmbea		

[a] Associated with broad-leaved emergent or submersed aquatic habit.

[b] Associated with retention or origin of passively dispersed fruits adapted to dispersal in autumn under an open canopy in temperate deciduous forests, while leaves have net venation adapted for activity in summer under a closed canopy.

Nolina Michx., with the loss of fleshy fruits in the last lagging that of net venation by one node.

Both fleshy fruits and (especially) net venation show even stronger patterns of correlated evolution with shady conditions than with each other. In almost every case, the evolution of net venation and fleshy fruits is associated with life in forest understories, whereas their loss is associated with open habitats. Specifically, 19 of 21 gains of fleshy fruits are associated with invasion of—or life in—shady sites, whereas 7 of 11 losses are associated with the invasion of sunny conditions. For net venation, 22 of 26 gains are associated with shady conditions, whereas 8 of 9 losses are associated with sunny conditions. These patterns of origin and maintenance are highly significant ($P < 10^{-10}$ to 10^{-30}) when tested in DISCRETE, using branch lengths that are equal to the inferred total amounts of molecular evolution down each lineage, a function of time plus plant characteristics such as generation time; Table 3). These results support our hypotheses about adaptation and establish the existence of a highly significant pattern of concerted convergence across the monocots.

Net venation shows an even more marked association with shade if we factor out the four lineages (Alismataceae, Aponogetonaceae, Philydraceae, Zosteraceae) in which it arose in broad-leaved aquatic plants, mostly near the base of the monocots in Alismatales (Tables 2, 3). All origins of net venation are associated with either shady conditions (85%) or broad leaves in aquatic emergents or submersed species (15%). Fleshy fruits also show a stronger association with net venation if we exclude aquatic plants with broad leaves and net venation, in which we have no a priori reason to expect the evolution of fleshy fruits.

The numerous origins of fleshy fruits and net venation are distributed rather evenly across lineages and time (Fig. 2). Both traits arose nearly 90 Mya ago in Araceae and Arecaceae. The former family is dominated by herbs, vines, and epiphytes of tropical rain-forest understories, together with some temperate forest herbs (e.g., *Arisaema* Mart., *Arum* L.)

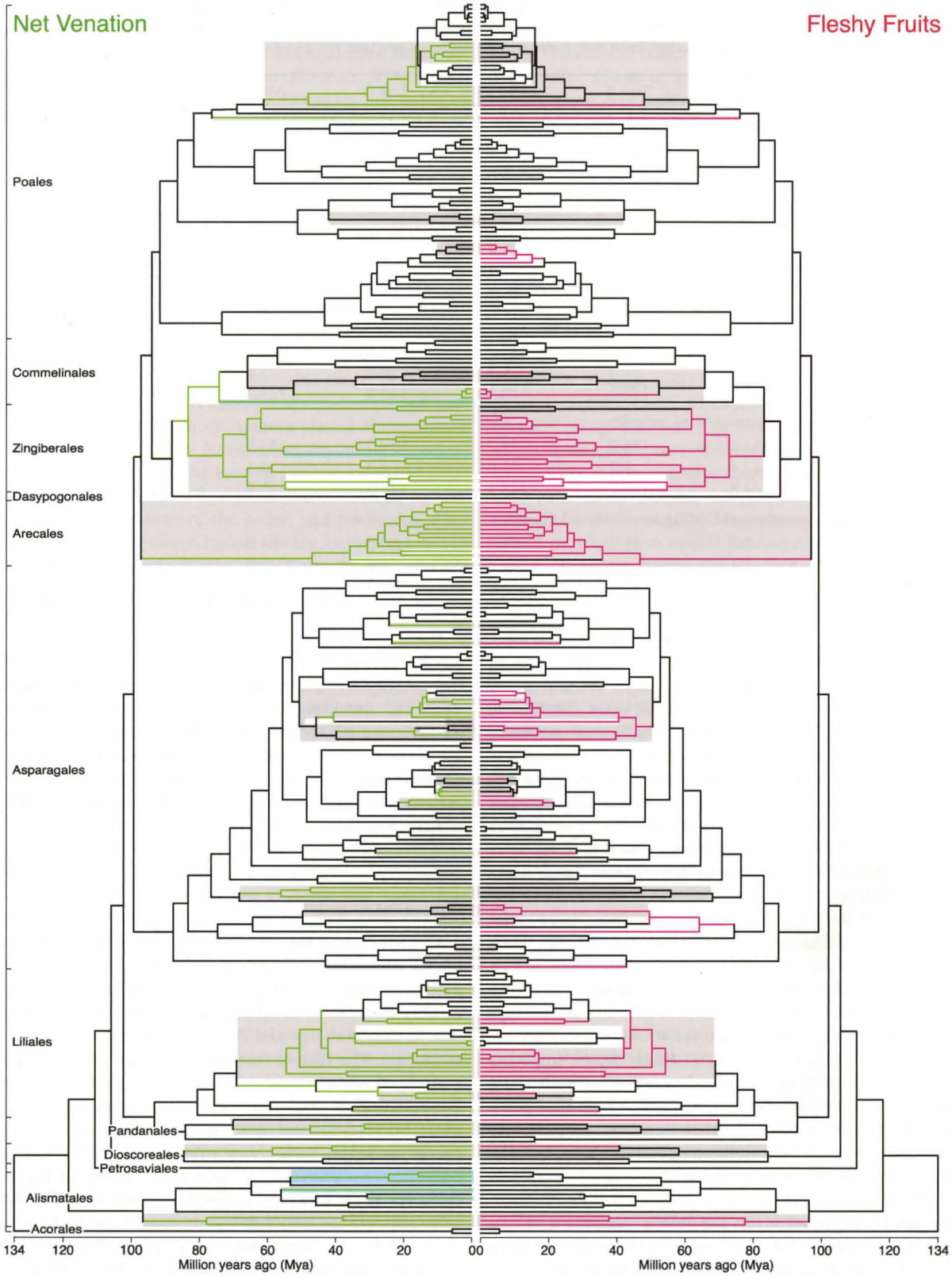

Fig. 2.—Concerted convergence of net venation (green), fleshy fruits (red), shaded habitats (sand boxes), and broad-leaved aquatic habit (blue boxes). Note that almost all transitions to net venation and fleshy fruits occur upon invasion of shaded habitats, and that almost all reversals to parallel venation and dry, passively dispersed seeds or fruits occur upon re-invasion of open, sunny habitats. The tree shown is ultrametric and has been calibrated against the age of six Cretaceous fossils using penalized likelihood, so that the tempo and taxonomic distribution of phenotypic transitions can be visualized. Both net venation and fleshy fruits show somewhat constant rates of ecological evolution over the past 90 million years, with an increase in the absolute number of origins toward the present and a decrease in the number of origins per clade present.

Table 3. Log likelihood ratios (LR) and significance levels (P) resulting from five different tests for correlated evolution across monocots in net venation, fleshy fruits, and life under shaded conditions, conducted on four representative trees using DISCRETE (Pagel 1994, 1999). Mean (±SE) LR represents the average value from five independent analyses per tree per test (see text).

	Tree A	Tree B	Tree C	Tree D	Mean	SE of mean	Significance
1. Fleshy fruits and net venation							
Mean LR	50.6	53.1	59.4	48.1	52.8		
Standard error	0.8	1.4	2.6	0.3	1.3	2.4	
Minimum	48.0	50.7	50.7	47.5	49.2	1.2	$P < 10^{-9}$
2. Fleshy fruits and shade							
Mean LR	74.0	73.4	72.4	66.3	71.5		
Standard error	3.9	2.5	1.4	1.7	1.3	1.8	
Minimum	63.9	65.7	66.8	59.7	64.0	2.2	$P < 10^{-11}$
3. Net venation and shade							
Mean LR	129.8	132.7	120.9	132.1	128.9		
Standard error	3.2	1.3	1.7	0.9	1.8	2.7	
Minimum	117.0	127.5	116.1	128.6	122.3	1.2	$P < 10^{-23}$
4. Net venation and shade + broad-leaved aquatics							
Mean LR	154.3	154.7	154.2	159.3	155.7		
Standard error	2.4	1.7	2.0	3.9	2.5	1.2	
Minimum	144.8	148.2	148.1	146.5	146.9	1.2	$P < 10^{-30}$
5. Fleshy fruits and net venation, excluding broad-leaved aquatics							
Mean LR	63.8	61.2	58.4	60.6	61.0		
Standard error	1.4	1.3	0.9	1.4	1.2	1.1	
Minimum	61.1	56.1	55.0	55.4	56.9	2.0	$P < 10^{-10}$

and broad-leaved submersed aquatics (e.g., *Anubias* Schott, *Cryptocoryne* Fisch. ex Wydler). The palms contain many rain-forest lineages, but have also invaded open subtropical savannas and scrub. The most recent instances of concerted convergence in fleshy fruits (or mimics thereof) and net venation occurred within the last 5 to 10 Mya, in *Griffinia* Ker Gawl. and *Proiphys–Scadoxus* Raf. of Amaryllidaceae and *Curculigo* of Hypoxidaceae. Fleshy fruits arose at least three times in Poales, twice in Commelinales, once in Zingiberales, once in Arecales, eight times in Asparagales, three times in Liliales, once in Pandanales, once in Dioscoreales, and once in Alismatales. Net venation arose at least three times in Poales, once in Commelinales, once in Zingiberales, once in Arecales, eleven times in Asparagales, four times in Liliales, once in Pandanales, once in Dioscoreales, and four times in Alismatales. During 10-Mya intervals, an average of 2.9 ± 0.5 lineages evolved net venation, whereas an average of 2.4 ± 0.4 lineages evolved fleshy fruits, implying a rather clocklike rate of adaptive evolution in both these traits across the monocots. It is important to note that many of the inferred reversals to parallel venation or passively dispersed, dry fruits appear to have occurred quite recently, with the exception of the reversal at the base of subfamily Lilioideae of Liliaceae (Fig. 2).

As might be expected given the relative numbers of origins of net venation and fleshy fruits, there are a number of groups of understory plants in which only net venation, not fleshy fruits, evolved. The net-venation-only syndrome characterizes the bambusoids, early-divergent grasses, Costaceae, *Hosta* Tratt., *Cyanastrum* Oliv., and Stemonaceae. *Cardiocrinum* and *Tricyrtis* of temperate deciduous forests both have net veins only, but are photosynthetically active under shady conditions in summer while releasing seeds after the canopy re-opens in autumn. Net veins also occur in the absence of fleshy fruits in four lineages of broad-leaved aquatics, including Alismataceae, Aponogetonaceae, and Zosteraceae of Alismatales and Philydraceae of Commelinales. Fleshy fruits arose without net venation under shady conditions in bromelioid bromeliads, *Amischotolype* Hassk., Asteliaceae and relatives, and the apostasioid orchid *Neuwiedia* Blume.

DISCUSSION

Phylogenetic Relationships

Cladistic analysis of *ndh*F sequence variation yields a highly resolved, well-supported phylogenetic tree for the monocots (Fig. 1). Relationships among orders are unclear in only two cases, involving the commelinids and the position of Dioscoreales and Pandanales close to the base of the monocots. The lack of resolution among the four major commelinid clades—Poales, Zingiberales plus Commelinales, Dasypogonales, and Arecales—may simply reflect a rapid initial diversification among the commelinids. Analyses based on seven genes (but many fewer taxa) resolve this polytomy by placing Dasypogonales sister to Poales, and Arecales sister to Zingiberales–Commelinales, but the bootstrap support for both relationships is weak (≤51%) (Chase et al. 2006). Analyses based on 17 genes flip these relationships, placing Arecales as sister to Poales and Dasypogonales sister to Zingiberales–Commelinales, and bootstrap support for these relationships is also weak (<50%) (Graham et al. 2006). Here Pandanales are sister to Liliales in the *ndh*F strict consensus, but to Dioscoreales in the bootstrap consensus. The latter position is consistent with that obtained from an analysis based on 7 and 17 genes (Chase et al. 2006;

Graham et al. 2006). Alismatales are sister to a strongly supported clade (100% bootstrap) consisting of all other monocots except Acorales (Fig. 1). Petrosaviales or Dioscoreales are, in turn, sister to all other elements of this large clade; 7- and 17-gene analyses place Petrosaviales sister to all monocots except Alismatales and Acorales, and Dioscoreales sister to Pandanales (Chase et al. 2006; Graham et al. 2006).

Within commelinids, *ndh*F supports many relationships identified previously based on other sequence data (Givnish et al. 1999; Chase et al. 2000; Graham et al. 2003; Michelangeli et al. 2003), and resolves others for the first time. Bromeliaceae and Typhaceae–Sparganiaceae are sister to each other and earliest divergent within Poales, with Rapateaceae being next divergent in the bootstrap consensus and sequentially weighted analyses (see Fig. 1 and Results). Our findings for Poales differ somewhat from those of Michelangeli et al. (2003) based on morphology and sequence variation in *rbc*L and *atp*A. Those authors placed Rapateaceae sister to paraphyletic family Xyridaceae, including Eriocaulaceae and Mayacaceae, at the base of Poales; identified Bromeliaceae, then Typhaceae–Sparganiaceae as sister lineages to the remaining members of the order; and positioned *Flagellaria* L. as sister to two terminal clades, consisting of (1) *Anarthria* R. Br., *Aphelia* R. Br., and Restionaceae, and (2) *Joinvillea* Gaudich., *Ecdeiocolea,* and Poaceae. The nodes at which our results and those of Michelangeli et al. (2003) differ, however, are weakly supported (<50% bootstrap) in their analysis. These include (1) the positions of Bromeliaceae, Rapateaceae, and Typhaceae–Sparganiaceae relative to each other and to Eriocaulaceae, Mayacaceae, and Xyridaceae; (2) the supposed paraphyly of Xyridaceae; and (3) the position of *Flagellaria,* not Restionaceae, as sister to the remainder of the grass alliance. Our *ndh*F analysis resolves both Xyridaceae (including *Orectanthe*) and Eriocaulaceae as being monophyletic with 84–100% bootstrap, and identifies these two families as each other's closest relative (75% bootstrap). We resolve Bromeliaceae as sister to Typhaceae–Sparganiaceae with 64% bootstrap support, and place Rapateaceae as the next-divergent element with 79% support in the bootstrap majority-rule tree, consistent with its strongly supported position in the 7-gene tree (Chase et al. 2006). These relationships are similar to those derived by Bremer (2000) based on *rbc*L, but differ in the placement of the three earliest-divergent clades consisting of Bromeliaceae, Rapateaceae, and Typhaceae–Sparganiaceae. The placement of the last just inside Bromeliaceae–Rapateaceae by Bremer (2000) involves a very short branch, however. We were unable to amplify and sequence *ndh*F for DNAs of *Aphelia* (Centrolepidaceae) and *Trithuria* Hook. f. (Hydatellaceae) kindly provided by J. Davis and D. Stevenson, and so were unable to confirm their strongly supported finding that *Aphelia* is sister to Restionaceae or the more weakly supported association of *Trithuria* with Xyridaceae.

The strongly supported placement of *Thurnia* Hook. f.–*Prionium* E. Mey. sister to Cyperaceae–Juncaceae by *ndh*F is consistent with that of several recent molecular studies (Givnish et al. 1999; Bremer 2000; Chase et al. 2000; Michelangeli et al. 2003). The position of *Mayaca* Aubl. sister to all other elements of the sedge alliance, however, is more weakly supported and problematic. An earlier *ndh*F sequence of this taxon had placed it sister to Bromeliaceae (Givnish et al. 1999), but a new, higher quality sequence from Venezuelan material places it sister to the remainder of the sedge alliance, near Xyridaceae and Eriocaulaceae, which seems more plausible based on morphology and *atp*A and *rbc*L sequence data (Michelangeli et al. 2003); *rbc*L places *Mayaca* immediately sister to Xyridaceae and Eriocaulaceae (Bremer 2000). The possibility that *Mayaca* could act as a "wild card" much like *Ecdeiocolea* (see above) or *Aphyllanthes* Tourn. ex L. in Asparagales (see Fay et al. 2000), should not be overlooked.

The extensive divergence of the grass alliance, sedge alliance, rapateads, and bromeliads from each other is comparable to that among other groups of monocots already recognized at the ordinal level (Fig. 1). The remarkable isolation of both Bromeliaceae and Rapateaceae from other monocots in both morphology and sequence variation appears to reflect 15 to 40 million years between the origins of each group and when present-day lineages began to diverge from each other (Givnish et al. 2004*a*, in press). If support for the four major clades of Poales grows in future multigene analyses, and the position of Eriocaulaceae, Xyridaceae, and (especially) Mayacaceae becomes solidified, it would be prudent to revisit the issue of recognizing the four major clades in Poales—representing 31% of all monocot species—as orders in their own right.

The resolution of Commelinales and Zingiberales as sister taxa is consistent with previous molecular analyses (Givnish et al. 1999; Chase et al. 2000; Evans et al. 2003; Graham et al. 2003). Relationships among families within Zingiberales are largely consistent with a detailed analysis based on morphology and several rapidly evolving stretches of DNA (Kress et al. 2001). Our analysis, however, places Musaceae, Heliconiaceae, and Strelitziaceae–Lowiaceae in an unresolved trichotomy sister to the remaining "ginger" families, rather than in a ladder with Musaceae earliest-divergent as seen in Kress et al. (2001). Our *ndh*F tree identifies Haemodoraceae and Pontederiaceae as each other's closest relatives (Fig. 1B). They fail, however, to provide positive evidence that their immediate sister is Philydraceae, as have other molecular studies (Graham and Barrett 1995; Graham et al. 1998; Chase et al. 1995*a*, 2000; Givnish et al. 1999). However, inclusion of indels places *Philydrum* in a polytomy consistent with a tie to Haemodoraceae and Pontederiaceae (see Results), and thus consistent with previous studies based on morphology (Dahlgren et al. 1985) and molecular variation. Fleshy-fruited, net-veined *Hanguana* is strongly supported as being sister to Commelinaceae, consistent with previous molecular analyses (Givnish et al. 1999; Chase et al. 2000) but not with morphology, which tends to place this genus of southeast Asian rain forests with Zingiberales instead (Rudall et al. 1999).

The placement of *Calamus* as sister to the rest of Arecales, followed by *Nypa,* is consistent with relationships obtained using 5–7 kilobases (kb) of coding and noncoding plastid DNA (Asmussen and Chase 2001; Hahn 2002). Although bootstrap support for relationships within the rest of Arecales based on *ndh*F alone are low (35–95%), the fact that they are fully resolved based on a single gene is promising, given that many similar relationships are unresolved using *rbc*L alone (Uhl et al. 1995). Members of Arecales, Bro-

meliaceae, and Zingiberales display unusually slow rates of plastid DNA evolution (Gaut et al. 1992; Givnish et al. 1999; Fig. 1A–D). It should thus not be surprising that relationships within these groups are much better resolved by *ndh*F than by *rbc*L, with or without *atp*B and 18S nrDNA (see Chase et al. 1995*a*, 2000). Although molecular data (*ndh*F; *rbc*L, *atpB,* 18S nrDNA; and 7- and 17-gene trees in development) do not resolve the relationships among the four major clades of commelinids, certain anatomical and chemical characteristics tend to link Commelinales–Zingiberales to Poales (Stevens 2003).

The placement of Asparagales sister to the commelinids rather than Liliales by *ndh*F (Fig. 1C) runs counter to the previous view that Asparagales and Liliales are sister to each other (Dahlgren et al. 1985). The arrangement of families within Asparagales generally supports that obtained in other recent studies (Fay et al. 2000; Pires et al. 2006; McPherson et al. submitted). Relationships within and near Amaryllidaceae are largely consistent with those obtained by Meerow et al. (1999) based on *rbc*L and the *trn*L–*trn*F region, except that *ndh*F places Agapanthaceae sister to Amaryllidaceae–Alliaceae, rather than Amaryllidaceae alone.

Relationships within Liliales are mostly consistent with those obtained by Vinnersten and Bremer (2001) based on *rbc*L, and by Patterson and Givnish (2002) based on *rbc*L and *ndh*F. Our results differ slightly from the *rbc*L tree, in which Alstroemeriaceae and Colchicaceae are sister to the rest of the order, and in which Liliaceae sensu Tamura (1998*b*), *Calochortus,* and *Scoliopus–Streptopus–Tricyrtis* form a trichotomy at the base of Liliaceae sensu Tamura (1998*a*). Analysis of the combined *rbc*L and *ndh*F data produces a tree identical to that based on *ndh*F alone (Patterson and Givnish 2002). The placement of *Prosartes* in Liliaceae and *Disporum* in Colchicaceae supports previous analyses based on *rbc*L (Shinwari et al. 1994*a*, *b*; Chase et al. 1995*a*, *b*), despite the striking morphological convergence in habit, net venation, and fleshy fruits in these two groups, formerly lumped in *Disporum.*

The position of Pandanales sister to Dioscoreales in the *ndh*F bootstrap majority-rule tree is consistent with analyses of placeholders involving 7 and 17 genes, as is the position of *Japonolirion* (or Dioscoreales) sister to monocots other than Alismatales and Acorales in the strict consensus tree (Chase et al. 2006; Graham et al. 2006). Attempts to sequence *ndh*F for representatives of Burmanniaceae (*Burmannia* L., *Thismia* Griff.) failed despite repeated attempts, preventing us from determining where this family belongs. *Tacca–Dioscorea* L. is sister to *Trichopus* Gaertn. within the dioscorealean taxa sequences surveyed, consistent with the findings of Caddick et al. (2002*a*, *b*) based on *rbc*L, *atp*B, and 18S nrDNA. The isolated position of *Japonolirion* supports the decision to recognize this genus (and achlorophyllous *Petrosavia* Becc.) as constituting Petrosaviales, one of the 12 monocot orders (Cameron et al. 2003).

Relationships among the families of Alismatales based on *ndh*F are broadly similar to those implied by *rbc*L (Les et al. 1997) but differ in detail. Mostly, the divergences between the two trees are not strongly supported in either case. The identification of Juncaginaceae and Scheuchzeriaceae as sister groups by *ndh*F, however, is probably significant, given that these morphologically similar families share a unique cyanogenic glucoside (triglochinin) known in no other angiosperm family (see Haynes et al. 1998). Repeated attempts to amplify and sequence *ndh*F from several of the smallest, aquatic families of Alismatales failed, preventing as detailed an analysis of relationships in this group as desired (D. Les and S. W. Graham pers. comm.). Our results support the important conclusion of Les et al. (1997) that the "aquatic" families of Alismatales fall into two clades, one including Alismataceae, Limnocharitaceae, and Butomaceae, and the other a series of three independently evolved families of seagrasses, with the Madagascar lace-plant family (Aponogetonaceae) closely related to the latter clade.

As noted by Chase et al. (1995*a*) and Zomlefer (1999), several genera once placed in Melanthiaceae in Liliales—including *Japonolirion, Narthecium* Huds., and *Tofieldia* Huds.—are now identified as belonging to three additional orders of monocots, including Petrosaviales, Dioscoreales, and Alismatales. Their growth form, marked by narrow equitant leaves, is also strikingly similar to that of *Acorus* at the base of the monocots (although *Japonolirion* differs from *Narthecium* and *Tofieldia* in having bifacial leaves; M. W. Chase pers. comm.). Our results strongly support this position for *Acorus,* consistent with all recent molecular studies (e.g., Chase et al. 1993, 1995*a*, *b*, 2000, 2006; Bremer 2000; Fuse and Tamura 2000; Graham and Olmstead 2000; Soltis et al. 2000; Borsch et al. 2003; Zanis et al. 2003; Graham et al. 2006).

Concerted Convergence

The independent origin of net venation at least 26 times in the monocots, always in association with invasion of shady conditions (85%) or life as a broad-leaved aquatic plants—as well as the independent origin of fleshy fruits at least 21 times, 19 in association with shaded forest understories—is one of the most remarkable, widespread, and highly significant ($P < 10^{-30}$ to 10^{-30}) cases of convergent evolution ever documented. The joint evolution of fleshy fruits and net venation 15 times across the monocots, and their joint loss five times, is also—by far—the most striking case of concerted convergence and plesiomorphy thus far demonstrated. These patterns are not only highly significant, they have high explanatory value as well. Phylogenetically unstructured correlation coefficients (r) range from 0.54 for the coincidence of net venation and fleshy fruits, to 0.64 and 0.73 for the coincidence of fleshy fruits and net venation with shaded habitats, to 0.77 for the coincidence of net venation with shaded habitats or a broad-leaved aquatic habit, when all traits are scored as binary characters.

In many ways, the contrast between *Trillium* and its closest relatives in Melanthiaceae (represented in this and all other surveys by *Xerophyllum* Michx.) epitomizes the pattern of concerted convergence discussed in this paper. *Trillium* grows in the shaded understories of temperate mesic forests, has broad, thin, soft leaves, net venation, and fleshy fruits, while *Xerophyllum* grows in more open habitats (meadows, fireswept pine glades) and possesses narrow, thick, hard leaves with parallel venation and tiny, wind-dispersed seeds released from dry capsules. It would be difficult, based on gross morphology, to infer that these taxa are actually very close relatives; the demonstration that they are

is one of the triumphs of plant molecular systematics. The contrast between *Trillium* and *Xerophyllum* is paralleled by several other cases, most notably involving the contrast between *Hypoxis* (mostly grass-leaved, capsule-fruited herbs of meadows, prairies, and glades, occasionally found in woodlands) and *Curculigo* (broad-leaved, net veined, fleshy-fruited herbs of tropical forest understories). A few *Hypoxis* occur in tropical forest understories or have broad leaves, and a few *Curculigo* have rather narrow leaves. Fleshy-fruited, net-veined, forest-dwelling *Geitonoplesium* also contrasts sharply with all of its dry-fruited, parallel-veined relatives of open habitats (see Conran 1999). *Cyanastrum* of shady African rain forests and woodlands has broad, cordate leaves with net venation, while confamilial *Cyanella* L. of open South African fynbos and *Tecophilaea* Bert. ex Colla of the Chilean high Andes have narrow, rather fleshy, grasslike foliage that lack cross veins. The difference between forest-dwelling *Hosta* (with thin, broad, net-veined leaves) and *Agave* L., *Yucca* L., and other elements of Agavaceae (mostly with thick, succulent, parallel-veined leaves) to which *Hosta* is sister (Bogler and Simpson 1996) could hardly be more striking, although it does not entail the evolution of different fruit types.

In addition to such cases of divergence among close relatives, striking convergence among distant relatives also supports our case. Asian *Disporum* of Colchicaceae and North American *Prosartes* of Liliaceae both grow in the understories of temperate mesic forests and share net venation and fleshy fruits, as well as many other features of growth form (e.g., arching stems) and floral morphology. They are so similar that both were placed in the same genus, until Shinwari et al. (1994*a*, *b*) used molecular data to demonstrate that the North American taxa were closely related to *Streptopus,* while the Asian taxa were closely related to *Uvularia.* Both of these genera, in turn, are remarkably similar in many ways to *Polygonatum* Miller, *Disporopsis* Hance, and *Smilacina* Desf. (also native to temperate forest understories) of Ruscaceae in order Asparagales; indeed, these genera were grouped with *Disporum* and *Prosartes* in the asparagoid tribe Polygonatae by Krause (1930), Therman (1956), Hutchinson (1959), and La Frankie (1986)!

The joint evolution of fleshy fruits and net venation is not lock-step: by no means is every invasion of forest understories associated with a gain of both traits, nor is every invasion of open sites associated with a loss of both traits. Nevertheless, this pattern is highly significant and some apparent exceptions are illuminating. Bromelioid bromeliads evolved fleshy fruits, but not net venation—which may be understandable, given that they also possess CAM photosynthesis and thus have thick, succulent leaves in which net venation would not be adaptive. CAM photosynthesis seems obviously adaptive in the open, dry habitats (Winter and Smith 1996) in which bromelioids evolved (Givnish et al. in press), but is also advantageous under the constantly damp, rainforest-interior conditions where most other bromelioids grow because it allows CO_2 recycling when the leaf surfaces are occluded with raindrops (Pierce et al. 2002). Vanilloid orchids (not included in our survey) evolved net venation but not fleshy fruits, except *Vanilla* Plum. ex Mill. itself (Cameron and Chase 1998)—which may also be understandable, given that mycotrophy in general appears to favor tiny, exceedingly numerous seeds that are *independently dispersable,* presumably to maximize the chances of contacting a suitable fungal partner. Finally, the retention of net venation in several species of palms (Arecaceae) and yams (Dioscoreaceae) that have invaded open tropical and subtropical habitats speaks for the importance of phylogeny and genetic/developmental heritage, not ecology, in helping maintain this trait. It is true that even yams of open, hot savannas often have thin, soft-textured leaves; presumably this is related to their short leaf lifespans, the ephemeral period of abundant moisture in their savanna habitats, and the widespread trend for specific leaf mass (g m^{-2}) to decline with leaf longevity across biomes and (mainly dicot) lineages (Reich et al. 1997; Ackerly and Reich 1999). However, palms of open savannas and oases often have tough, coriaceous foliage and a relatively compact, palmate form—and yet retain a branching support structure within leaves, strongly supporting a role of phylogenetic morphological conservatism.

There are a few additional cases involving the concerted convergence of net venation and fleshy fruits beyond the monocot taxa we included in our survey. Examples include *Palisota* Rchb. ex Endl. (Commelinaceae), *Vanilla* and *Selenipedium* Rchb. f. (Orchidaceae), *Eucharis* Planch. & Linden (Amaryllidaceae), and Cyclanthaceae of tropical rainforest understories. Perhaps the most striking evidence that selection strongly favors both net venation and fleshy fruits under shaded conditions, however, is provided by *Gnetum* L. This genus of tropical vines and trees is characterized by fleshy fruits and broad, net-veined leaves that strongly resemble those of *Coffea* L. and other understory angiosperms—and yet *Gnetum* is a gymnosperm, closely related to the xeric-adapted *Ephedra* L. and *Welwitschia* Reichb. (Bowe et al. 2000; Chaw et al. 2000). The strong resemblance of *Gnetum* to certain angiosperms helped inspire the hypothesis that the angiosperms were derived from gymnosperms via Gnetales (Doyle and Donoghue 1986; Donoghue 1994). Molecular data do not support that hypothesis, however, indicating that the gymnosperms as a whole are sister to the angiosperms and that Gnetales arose from within the conifers (Bowe et al. 2000; Chaw et al. 2000; Soltis et al. 2002; but see Rydin et al. 2002). Won and Renner (2003) have recently discovered a horizontal transfer of a group II intron (a self-splicing RNA and putative spliceosomal ancestor) and adjacent exons of mitochondrial *nad*I from asterid angiosperms to a few Asian species of *Gnetum.* Although this might seem to open the possibility of a horizontal transfer of genes coding for net venation into *Gnetum,* such a scenario seems highly unlikely, given that the Asian species involved are nested well within *Gnetum,* all of whose species are characterized by net venation.

Phylogenetic analyses indicate that fleshy fruits have evolved repeatedly in association with forest understories in Lobeliaceae (Givnish 1998), Gesneriaceae (Smith 2001), and urticoid Rosales (Sytsma et al. 2002) among the dicots. Givnish (1979) observed that net venation occurs in several monocot groups with thin, broad leaves in forest understories, including *Arisaema, Smilax* L., *Trillium,* and various tropical gingers and their relatives. Conover (1983) and Chase et al. (1995*a*) independently noted similar, qualitative associations of net venation with broad-leaved forest vines; Cameron and Dickison (1998) noted a similar association of

net venation with achlorophyllous vanilloid orchids. The association of net venation with the climbing habit among monocots is well marked. We believe it arises for three reasons: (1) most vines are, perforce, growing in microsites shaded by the hosts they are climbing; (2) species growing directly on tree boles are likely to experience especially dense shade, given that the boles occlude half the sky (Givnish and Vermeij 1976); and (3) the vine habit, by its nature, entails low allocation to support tissue, resulting in more rapid rates of upward growth and self-shading of lower leaves than in self-supporting plants with the same photosynthetic rate, and favoring shorter leaf lifespans and thus thinner, softer leaves with lower specific leaf mass (Givnish 2002). Indeed, a survey of 52 European woody species grown in a common garden showed that climbers/scramblers (6 species) had the lowest specific leaf mass of the species surveyed (Castro-Diez et al. 2000). The association of net veins with the achlorophyllous vanilloid orchids most likely reflects initial adaptation of chlorophyllous ancestors to shady conditions, including the evolution of net venation (seen today in other shade-adapted orchid genera, such as *Goodyera* R. Br. and *Isotria* Raf.). Subsequently, evolution may have favored abandonment of the photosynthetic habit under such unproductive conditions and a focus on carbon input via mycotrophy, with further reduction in leaf size and thickness.

Given that both fleshy fruits and net venation each arose more than 20 times in the monocots, the question immediately arises as to whether the same developmental pathways and underlying genes were involved in each case, or whether these adaptations arose in different ways in different groups (as has occurred in different populations of rock pocket mice that have independently evolved dark pelage on dark-colored soils [Nachman et al. 2003]). The fact that both fleshy fruits and net venation have arisen without the other in some cases demonstrates that they are unlikely to be the pleiotropic effects of a single gene or supergene. Furthermore, given that several groups show obvious differences in the fine details of their pattern of net venation (e.g., see Shinwari et al. 1994*a*, *b*), and that "fleshy fruits" involve the elaboration of different tissues in different groups (e.g., arils vs. capsule walls), it seems unlikely that all of the multiple origins of net venation and fleshy fruits have each depended on the same genes and developmental pathways for each trait. Determining whether or not this has been the case should be a goal of new studies at the interface of ecology, evolution, and development ("eco-evo-devo"; Givnish 2003).

When Patterson and Givnish (2002) demonstrated that net venation, fleshy fruits, inconspicuous flowers, and rhizomes undergo concerted convergence under shady conditions in Liliales, they also showed that these patterns distorted phylogenetic inference based solely on morphology. When morphology was analyzed cladistically, two clades—characterized by the alternative suites of traits undergoing concerted convergence—emerged; when these traits were excluded from analysis, the relationships inferred were nearly identical to those deduced from DNA sequence variation. It would now be worthwhile to see if the same holds true for monocots as a whole: if both fruit and venation type are excluded, does an analysis of relationships across monocots based on morphology more closely approach that based on molecular data? Chase et al. (1995*a*) have already noted that several of the groups placed at the base of the monocots by morphology alone (Stevenson and Loconte 1995) share reticulate venation. It would also be interesting to evaluate whether—as in Liliales—large, visually conspicuous flowers are mainly found in open habitats with strong illumination by broad-spectrum light, and if small, visually inconspicuous flowers are mainly found in shaded sites with low illumination by narrow-spectrum, greenish light. Many forest herbs in eastern North America accord with this prediction (Givnish and Patterson 2000). Across the angiosperms as a whole, this hypothesis may account for the striking increase with rainfall in the fraction of woody species with inconspicuous flowers in tropical forests documented by Gentry (1982), given that most of the tree diversity added in wetter forests are understory species (Givnish 1999*a*). Repeated shifts to visually inconspicuous flowers in shade to visually conspicuous flowers under bright, full-spectrum light may be analogous to the increased sexual selection for bright coloration in African rift-lake cichlids in clearer waters (Seehausen et al. 1997) and the likely role that an analogous process has played in the evolution of bright coloration in tropical coral-reef fish (Givnish 1999*b*).

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LITERATURE CITED

Ackerly, D. D., and P. B. Reich. 1999. Convergence and correlations among leaf size and function in seed plants: a comparative test using independent contrasts. *Amer. J. Bot.* **86**: 1272–1281.

Angiosperm Phylogeny Group II [APG II]. 2003. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG II. *Bot. J. Linn. Soc.* **141**: 399–436.

Asmussen, C. B., and M. W. Chase. 2001. Coding and noncoding plastid DNA in palm systematics. *Amer. J. Bot.* **88**: 1103–1117.

Baum, D. A, K. J. Sytsma, and P. C. Hoch. 1994. A phylogenetic analysis of *Epilobium* (Onagraceae) based on nuclear ribosomal DNA sequences. *Syst. Bot.* **19**: 363–388.

Beattie, A. J. 1985. The evolutionary ecology of ant-plant mutualisms. Cambridge University Press, Cambridge, UK. 182 p.

———, and D. C. Culver. 1983. The nest chemistry of two seed-dispersing ant species. *Oecologia* **56**: 99–103.

Bogler, D. T., and B. B. Simpson. 1996. Phylogeny of Agavaceae based on ITS rDNA sequence variation. *Amer. J. Bot.* **83**: 1225–1235.

Borsch, T., K. W. Hilu, D. Quandt, V. Wilde, C. Neinhuis, and W. Barthlott. 2003. Noncoding plastid *trn*T–*trn*F sequences reveal a well-resolved phylogeny of basal angiosperms. *J. Evol. Biol.* **16**: 558–576.

Bowe, L. M., G. Coat, and C. W. dePamphilis. 2000. Phylogeny of seed plants based on all three genomic compartments: extant

gymnosperms are monophyletic and Gnetales' closest relatives are conifers. *Proc. Natl. Acad. Sci. U.S.A.* **97**: 4092–4097.

BOYD, R. S. 2001. Ecological benefits of myrmecochory for the endangered chaparral shrub *Fremontodendron decumbens* (Sterculiaceae). *Amer. J. Bot.* **88**: 234–241.

BREMER, K. 2000. Early Cretaceous lineages of monocot flowering plants. *Proc. Natl. Acad. Sci. U.S.A.* **97**: 4707–4711.

———. 2002. Gondwanan evolution of the grass alliance of families (Poales). *Evolution* **56**: 1374–1387.

CADDICK, L. R., P. J. RUDALL, P. WILKIN, T. A. J. HEDDERSON, AND M. W. CHASE. 2002*a*. Phylogenetics of Dioscoreales based on combined analyses of morphological and molecular data. *Bot. J. Linn. Soc.* **138**: 123–144.

———, P. WILKIN, P. J. RUDALL, T. A. J. HEDDERSON, AND M. W. CHASE. 2002*b*. Yams reclassified: a recircumscription of Dioscoreaceae and Dioscoreales. *Taxon* **51**: 103–114.

CAMERON, K. M., AND M. W. CHASE. 1998. Seed morphology of vanilloid orchids (Vanilloideae: Orchidaceae). *Lindleyana* **13**: 148–169.

———, ———, AND P. J. RUDALL. 2003. Recircumscription of the monocotyledonous family Petrosaviaceae to include *Japonolirion*. *Brittonia* **55**: 214–225.

———, AND W. C. DICKISON. 1998. Foliar architecture of vanilloid orchids: insights into the evolution of reticulate leaf venation in monocotyledons. *Bot. J. Linn. Soc.* **128**: 45–70.

CASTRO-DIEZ, P., J. P. PUYRAVAUD, AND J. H. C. CORNELISSEN. 2000. Leaf structure and anatomy as related to leaf mass per area variation in seedlings of a wide range of woody plant species and types. *Oecologia* **124**: 476–486.

CHASE, M. W., M. R. DUVALL, H. G. HILLIS, J. G. CONRAN, A. V. COX, L. E. EGUIARTE, J. HARTWELL, M. F. FAY, L. R. CADDICK, K. M. CAMERON, AND S. HOOT. 1995*a*. Molecular phylogenetics of Lilianae, pp. 109–137. *In* P. J. Rudall, P. J. Cribb, D. F. Cutler, and C. J. Humphries [eds.], Monocotyledons: systematics and evolution. Royal Botanic Gardens, Kew, Richmond, Surrey, UK.

———, M. F. FAY, D. S. DEVEY, O. MAURIN, N. RØNSTED, T. J. DAVIES, Y. PILLON, G. PETERSEN, O. SEBERG, M. N. TAMURA, C. B. ASMUSSEN, K. HILU, T. BORSCH, J. I DAVIS, D. W. STEVENSON, J. C. PIRES, T. J. GIVNISH, K. J. SYTSMA, M. A. MCPHERSON, S. W. GRAHAM, AND H. S. RAI. 2006. Multigene analyses of monocot relationships: a summary, pp. 63–75. *In* J. T. Columbus, E. A. Friar, J. M. Porter, L. M. Prince, and M. G. Simpson [eds.], Monocots: comparative biology and evolution (excluding Poales). Rancho Santa Ana Botanic Garden, Claremont, California, USA.

———, D. E. SOLTIS, R. G. OLMSTEAD, D. MORGAN, D. H. LES, B. D. MISHLER, M. R. DUVALL, R. A. PRICE, H. G. HILLS, Y. L. QIU, K. A. KRON, J. H. RETTIG, E. CONTI, J. D. PALMER, J. R. MANHART, K. J. SYTSMA, H. J. MICHAELS, W. J. KRESS, K. G. KAROL, W. D. CLARK, M. HEDRÉN, B. S. GAUT, R. K. JANSEN, K. J. KIM, C. F. WIMPEE, J. F. SMITH, G. R. FURNIER, S. H. STRAUSS, Q. Y. XIANG, G. M. PLUNKETT, P. S. SOLTIS, S. M. SWENSEN, S. E. WILLIAMS, P. A. GADEK, C. J. QUINN, L. E. EGUIARTE, E. GOLENBERG, G. H. LEARN, S. W. GRAHAM, S. C. H. BARRETT, S. DAYANANDAN, AND V. A. ALBERT. 1993. Phylogenetics of seed plants—an analysis of nucleotide sequences from the plastid gene *rbc*L. *Ann. Missouri Bot. Gard.* **80**: 528–580.

———, ———, P. S. SOLTIS, P. J. RUDALL, M. F. FAY, W. H. HAHN, S. SULLIVAN, J. JOSEPH, M. MOLVRAY, P. J. KORES, T. J. GIVNISH, K. J. SYTSMA, AND J. C. PIRES. 2000. Higher-level systematics of the monocotyledons: an assessment of current knowledge and a new classification, pp. 1–16. *In* K. L. Wilson and D. A. Morrison [eds.], Monocots: systematics and evolution. CSIRO Publishing, Collingwood, Victoria, Australia.

———, D. W. STEVENSON, P. WILKIN, AND P. J. RUDALL. 1995*b*. Monocot systematics: a combined analysis, pp. 685–730. *In* P. J. Rudall, P. J. Cribb, D. F. Cutler, and C. J. Humphries [eds.], Monocotyledons: systematics and evolution. Royal Botanic Gardens, Kew, Richmond, Surrey, UK.

CHAW, S. M., C. L. PARKINSON, Y. C. CHENG, T. M. VINCENT, AND J. D. PALMER. 2000. Seed plant phylogeny inferred from all three plant genomes: monophyly of extant gymnosperms and origin of Gnetales from conifers. *Proc. Natl. Acad. Sci. U.S.A.* **97**: 4086–4091.

CONOVER, M. H. 1983. The vegetative morphology of the reticulate-veined Liliiflorae. *Telopea* **2**: 401–412.

CONRAN, J. G. 1999. Anatomy and morphology of *Behnia* (Behniaceae) and its relationships within Lilianae: Asparagales. *Bot. J. Linn. Soc.* **131**: 115–129.

CROAT, T. B. 1978. Flora of Barro Colorado Island. Stanford University Press, Stanford, California, USA. 943 p.

DAHLGREN, R. M. T., H. T. CLIFFORD, AND P. F. YEO. 1985. The families of the monocotyledons. Springer-Verlag, Berlin, Germany. 520 p.

DONOGHUE, M. J. 1994. Progress and prospects in reconstructing plant phylogeny. *Ann. Missouri Bot. Gard.* **81**: 405–418.

DOWELD, A. B. 2001. Prosyllabus tracheophytarum, tentamen systematis plantarum vascularium (tracheophytorum). National Institute of Carpology, Moscow, Russia. 110 p.

DOYLE, J. A., AND M. J. DONOGHUE. 1986. Seed plant phylogeny and the origin of angiosperms: an experimental approach. *Bot. Rev. (Lancaster)* **52**: 32–431.

EVANS, T. M., K. J. SYTSMA, R. B. FADEN, AND T. J. GIVNISH. 2003. Phylogenetic relationships in the Commelinaceae: II. A cladistic analysis of *rbc*L sequences and morphology. *Syst. Bot.* **28**: 270–292.

FAY, M. F., P. J. RUDALL, S. SULLIVAN, K. L. STOBART, A. Y. DE BRUIJN, G. REEVES, F. QAMARUZ-ZAMAN, W.-P. HONG, J. JOSEPH, W. J. HAHN, J. G. CONRAN, AND M. W. CHASE. 2000. Phylogenetic studies of Asparagales based on four plastid DNA regions, pp. 360–371. *In* K. L. Wilson and D. A. Morrison [eds.], Monocots: systematics and evolution. CSIRO Publishing, Collingwood, Victoria, Australia.

FUSE, S., AND M. N. TAMURA. 2000. A phylogenetic analysis of the plastid *mat*K gene with emphasis on Melanthiaceae sensu lato. *Pl. Biol. (New York)* **2**: 415–427.

GAUT, B. S., S. V. MUSE, W. D. CLARK, AND M. T. CLEGG. 1992. Relative rates of nucleotide substitution at the *rbc*L locus of monocotyledonous plants. *J. Molec. Evol.* **35**: 292–303.

———, L. G. CLARK, J. F. WENDEL, AND S. V. MUSE. 1997. Comparisons of the molecular evolutionary process at *rbc*L and *ndh*F in the grass family (Poaceae). *Molec. Biol. Evol.* **14**: 769–777.

GENTRY, A. H. 1982. Patterns of neotropical plant species diversity. *Evol. Biol.* **15**: 1–84.

GIVNISH, T. J. 1979. On the adaptive significance of leaf form, pp. 375–407. *In* O. T. Solbrig, S. Jain, G. B. Johnson, and P. H. Raven [eds.], Topics in plant population biology. Columbia University Press, New York, USA.

———. 1987. Comparative studies of leaf form: assessing the relative roles of selective pressures and phylogenetic constraints. *New Phytol.* **106** (suppl.): 131–160.

———. 1995. Plant stems: biomechanical adaptations for energy capture and influence on species distributions, pp. 3–49. *In* B. L. Gartner [ed.], Plant stems: physiology and functional morphology. Chapman and Hall, New York, USA.

———. 1998. Adaptive radiation of plants on oceanic islands: classical patterns, molecular data, new insights, pp. 281–304. *In* P. Grant [ed.], Evolution on islands. Oxford University Press, New York, USA.

———. 1999*a*. On the causes of gradients in tropical tree diversity. *J. Ecol.* **87**: 193–210.

———. 1999*b*. Adaptive radiation, dispersal, and diversification of the Hawaiian lobeliads, pp. 67–90. *In* M. Kato [ed.], The biology of biodiversity. Springer-Verlag, Tokyo, Japan.

———. 2002. On the adaptive significance of evergreen vs. deciduous leaves: solving the triple paradox. *Silva Fenn.* **36**: 703–743.

———. 2003. How a better understanding of adaptations can yield better use of morphology in plant systematics: towards eco-evo-devo. *Taxon* **53**: 273–296.

———, T. M. Evans, J. C. Pires, and K. J. Sytsma. 1999. Polyphyly and convergent morphological evolution in Commelinales and Commelinidae: evidence from *rbc*L sequence data. *Molec. Phylogen. Evol.* **12**: 360–385.

———, ———, M. L. Zjhra, T. B. Patterson, P. E. Berry, and K. J. Sytsma. 2000. Molecular evolution, adaptive radiation, and geographic diversification in the amphiatlantic family Rapateaceae: evidence from *ndh*F sequences and morphology. *Evolution* **54**: 1915–1937.

———, K. C. Millam, T. M. Evans, J. C. Hall, J. C. Pires, P. E. Berry, and K. J. Sytsma. 2004*a*. Ancient vicariance or recent long-distance dispersal? Inferences about phylogeny and South American–African disjunctions in Rapateaceae and Bromeliaceae based on *ndh*F sequence data. *Int. J. Pl. Sci.* **165**: S35–S54.

———, ———, P. E. Berry, and K. J. Sytsma. In press. Phylogeny, biogeography, and ecological evolution in Bromeliaceae: insights from *ndh*F sequences. *In* J. T. Columbus, E. A. Friar, J. M. Porter, L. M. Prince, and M. G. Simpson [eds.], Monocots: comparative biology and evolution—Poales. Rancho Santa Ana Botanic Garden, Claremont, California, USA.

———, R. A. Montgomery, and G. Goldstein. 2004*b*. Adaptive radiation of photosynthetic physiology in the Hawaiian lobeliads: light regimes, static light responses, and whole-plant compensation points. *Amer. J. Bot.* **91**: 228–246.

———, and T. B. Patterson. 2000. Adaptive radiation: concerted convergence and the crucial contribution of molecular systematics, pp. 97–110. *In* K. Iwatsuki [ed.], IIAS International Symposium on Biodiversity, 3–5 Dec 1998. International Institute for Advanced Studies, Kyoto, Japan.

———, and K. J. Sytsma. 1997*a*. Consistency, characters, and the likelihood of correct phylo-genetic inference. *Molec. Phylogen. Evol.* **7**: 320–330.

———, and ———. 1997*b*. Homoplasy in molecular vs. morphological data: the likelihood of correct phylogenetic inference, pp. 55–101. *In* T. J. Givnish and K. J. Sytsma [eds.], Molecular evolution and adaptive radiation. Cambridge University Press, New York, USA.

———, ———, J. F. Smith, and W. S. Hahn. 1995. Molecular evolution, adaptive radiation, and geographic speciation in *Cyanea* (Campanulaceae, Lobelioideae), pp. 288–337. *In* W. L. Wagner and V. Funk [ed.], Hawaiian biogeography: evolution on a hot spot archipelago. Smithsonian Institution Press, Washington, D.C., USA.

———, and G. J. Vermeij. 1976. Sizes and shapes of liane leaves. *Amer. Naturalist* **110**: 743–778.

Graham, S. W., and S. C. H. Barrett. 1995. Phylogenetic systematics of Pontederiales: implications for breeding-system evolution, pp. 415–441. *In* P. J. Rudall, P. J. Cribb, D. F. Cutler, and C. J. Humphries [eds.], Monocotyledons: systematics and evolution. Royal Botanic Gardens, Kew, Richmond, Surrey, UK.

———, J. R. Kohn, B. R. Morton, J. E. Eckenwalder, and S. C. H. Barrett. 1998. Phylogenetic congruence and discordance among one morphological and three molecular data sets from Pontederiaceae. *Syst. Biol.* **47**: 545–567.

———, and R. G. Olmstead. 2000. Utility of 17 chloroplast genes for inferring the phylogeny of the basal angiosperms. *Amer. J. Bot.* **87**: 1712–1730.

———, ———, and S. C. H. Barrett. 2003. Rooting phylogenetic trees with distant outgroups: a case study from the commelinoid monocots. *Molec. Biol. Evol.* **19**: 1769–1781.

———, J. M. Zgurski, M. A. McPherson, D. M. Cherniawsky, J. M. Saarela, E. F. C. Horne, S. Y. Smith, W. A. Wong, H. E. O'Brien, V. L. Biron, J. C. Pires, R. G. Olmstead, M. W. Chase, and H. S. Rai. 2006. Robust inference of deep monocot phylogeny using an expanded multigene plastid data set, pp. 3–21. *In* J. T. Columbus, E. A. Friar, J. M. Porter, L. M. Prince, and M. G. Simpson [eds.], Monocots: comparative biology and evolution (excluding Poales). Rancho Santa Ana Botanic Garden, Claremont, California, USA.

Hahn, W. J. 2002. A molecular phylogenetic study of the Palmae (Arecaceae) based on *atp*B, *rbc*L and 18S nrDNA sequences. *Syst. Biol.* **51**: 92–112.

Haynes, R. R., D. H. Les, and L. B. Holm-Nielsen. 1998. Juncaginaceae, pp. 260–263. *In* K. Kubitzki [ed.], The families and genera of vascular plants, Vol. 4. Flowering plants, monocotyledons, Alismatanae and Commelinanae (except Gramineae). Springer-Verlag, Berlin, Germany.

Hiratsuka, J., H. Shimada, R. Whittier, T. Ishibashi, M. Sakamoto, M. Mori, C. Kondo, Y. Honji, C. R. Sun, B. Y. Meng, Y. Q. Li, A. Kanno, Y. Nishizawa, A. Hirai, K. Shinozaki, and M. Sugiura. 1989. The complete sequence of the rice (*Oryza sativa*) chloroplast genome—intermolecular recombination between distinct transfer RNA genes accounts for a major plastid DNA inversion during the evolution of the cereals. *Molec. Gen. Genet.* **217**: 185–194.

Hughes, L., and M. Westoby. 1992. Fate of seeds adapted for dispersal by ants in Australian sclerophyll vegetation. *Ecology* **73**: 1285–1299.

Hutchinson, J. 1959. Liliaceae, pp. 591–621. *In* J. Hutchinson [ed.], The families of flowering plants, Vol. 2. Clarendon Press, Oxford, UK.

International Plant Names Index [IPNI]. 2004. *http://www.ipni.org/index.html.*

Krause, K. 1930. Liliaceae, pp. 227–391. *In* A. Engler and K. Prantl [eds.], Die natürlichen Pflanzenfamilien. W. Engelmann, Leipzig, Germany.

Kress, W. J., L. M. Prince, W. J. Hahn, and E. A. Zimmer. 2001. Unraveling the evolutionary radiation of the families of the Zingiberales using morphological and molecular evidence. *Syst. Biol.* **50**: 926–944.

La Frankie, J. V. 1986. Transfer of the species of *Smilacina* to *Maianthemum* (Liliaceae). *Taxon* **35**: 584–589.

Leach, M. K., and T. J. Givnish. 1999. Gradients in the composition, structure, and diversity of remnant oak savannas in southern Wisconsin. *Ecol. Monogr.* **69**: 353–374.

Les, D. H., M. A. Cleland, and M. Waycott. 1997. Phylogenetic studies in Alismatidae, II: Evolution of marine angiosperms (seagrasses) and hydrophily. *Syst. Bot.* **22**: 443–463.

Liao, L. C., and J. Y. Hsiao. 1998. Relationship between population genetic structure and riparian habitat as revealed by RAPD analysis of the rheophyte *Acorus gramineus* Soland. (Araceae) in Taiwan. *Molec. Ecol.* **7**: 1275–1281.

Maddison, W. P., and D. R. Maddison. 2002. MacClade: analysis of phylogeny and character evolution, vers. 4. Sinauer Associates, Inc., Sunderland, Massachusetts, USA.

Maier, R. M., K. Neckermann, G. L. Igloi, and H. Kossel. 1995. Complete sequence of the maize chloroplast genome—gene content, hotspots of divergence and fine-tuning of genetic information by transcript editing. *J. Molec. Biol.* **251**: 614–628.

McPherson, M. A., H. S. Rai, W. A. Wong, and S. W. Graham. In press. Phylogenetic relationships among the major lineages of Asparagales, with a focus on the impact of systematic bias on the placement of Aphyllanthaceae. *Syst. Biol.*

Meerow, A. W., M. F. Fay, C. L. Guy, Q. B. Li, F. Q. Zaman, and M. W. Chase. 1999. Systematics of Amaryllidaceae based on cladistic analysis of plastid *rbc*L and *trn*L–F sequence data. *Amer. J. Bot.* **86**: 1325–1345.

———, and D. A. Snijman. 1998. Amaryllidaceae, pp. 83–110. *In* K. Kubitzki [ed.], Families and genera of vascular plants, Vol. 3.

Flowering plants, monocotyledons, Lilianae (except Orchidaceae). Springer-Verlag, Berlin, Germany.

MICHELANGELI, F. A., J. I DAVIS, AND D. W. STEVENSON. 2003. Phylogenetic relationships among Poaceae and related families as inferred from morphology, inversions in the plastid genome, and sequence data from the mitochondrial and plastid genomes. *Amer. J. Bot.* **90**: 93–106.

NACHMAN, M. W., H. E. HOEKSTRA, S. L. D'AGOSTINO. 2003. The genetic basis of adaptive melanism in pocket mice. *Proc. Natl. Acad. Sci. U.S.A.* **100**: 5268–5273.

PAGEL, M. 1994. Detecting correlated evolution on phylogenies: a general method for the comparative analysis of discrete characters. *Proc. Roy. Soc. London, Ser. B, Biol. Sci.* **255**: 37–45.

———. 1999. Inferring the historical patterns of biological evolution. *Nature* **401**: 877–884.

PATTERSON, T. B., AND T. J. GIVNISH. 2002. Phylogeny, concerted convergence, and phylogenetic niche conservatism in the core Liliales: insights from *rbc*L and *ndh*F sequence data. *Evolution* **56**: 233–252.

PIERCE, S., K. WINTER, AND H. GRIFFITHS. 2002. The role of CAM in high rainfall cloud forests: an in situ comparison of photosynthetic pathways in Bromeliaceae. *Pl. Cell Environm.* **25**: 1181–1189.

PIRES, J. C., I. J. MAUREIRA, T. J. GIVNISH, K. J. SYTSMA, O. SEBERG, G. PETERSEN, J. I DAVIS, D. W. STEVENSON, P. J. RUDALL, M. F. FAY, AND M. W. CHASE. 2006. Phylogeny, genome size, and chromosome evolution of Asparagales, pp. 287–304. *In* J. T. Columbus, E. A. Friar, J. M. Porter, L. M. Prince, and M. G. Simpson [eds.], Monocots: comparative biology and evolution (excluding Poales). Rancho Santa Ana Botanic Garden, Claremont, California, USA.

———, AND K. J. SYTSMA. 2002. A phylogenetic evaluation of a biosystematic framework: *Brodiaea* and related petaloid monocots (Themidaceae). *Amer. J. Bot.* **89**: 1342–1359.

REICH, P. B., M. B. WALTERS, AND D. S. ELLSWORTH. 1997. From tropics to tundra: global convergence in plant functioning. *Proc. Natl. Acad. Sci. U.S.A.* **94**: 13730–13734.

REVEAL, J. L., AND J. C. PIRES. 2002. Phylogenetics and classification of the monocots (Liliopsida), pp. 9–36. *In* Flora of North America Editorial Committee [ed.], Flora of North America north of Mexico, Vol. 26. Oxford University Press, New York, USA.

RUDALL, P. J., D. W. STEVENSON, AND H. P. LINDER. 1999. Structure and systematics of *Hanguana,* a monocotyledon of uncertain affinity. *Austral. Syst. Bot.* **12**: 311–330.

RYDIN, C., M. KÄLLERSJÖ, AND E. M. FRIIST. 2002. Seed plant relationships and the systematic position of Gnetales based on nuclear and chloroplast DNA: conflicting data, rooting problems, and the monophyly of conifers. *Int. J. Pl. Sci.* **163**: 197–214.

SANDERSON, M. J. 2002. Estimating absolute rates of molecular evolution and divergence times: a penalized likelihood approach. *Molec. Biol. Evol.* **19**: 101–109.

SEEHAUSEN, O., J. J. VANALPHEN, AND F. WITTE. 1997. Cichlid fish diversity threatened by eutrophication that curbs sexual selection. *Science* **277**: 1808–1811.

SHINWARI, Z. H., H. KATO, R. TERAUCHI, AND S. KAWANO. 1994*a*. Phylogenetic relationships among genera in the Liliaceae–Asparagoideae–Polygonatae s. l. inferred from *rbc*L gene sequence data. *Pl. Syst. Evol.* **192**: 263–277.

———, R. TERAUCHI, F. H. UTECK, AND S. KAWANO. 1994*b*. Recognition of the New World *Disporum* section *Prosartes* as *Prosartes* (Liliaceae) based on the sequence data of the *rbc*L gene. *Taxon* **43**: 353–366.

SMITH, J. F. 2001. High species diversity in fleshy-fruited tropical understory plants. *Amer. Naturalist* **157**: 646–653.

SOLTIS, D. E., P. S. SOLTIS, M. W. CHASE, M. E. MORT, D. C. ALBACH, M. ZANIS, V. SAVOLAINEN, W. H. HAHN, S. B. HOOT, M. F. FAY, M. AXTELL, S. M. SWENSEN, L. M. PRINCE, W. J. KRESS, K. C. NIXON, AND J. S. FARRIS. 2000. Angiosperm phylogeny inferred from 18S rDNA, *rbc*L, and *atp*B sequences. *Bot. J. Linn. Soc.* **133**: 381–461.

———, ———, D. L. NICKRENT, L. A. JOHNSON, W. J. HAHN, S. B. HOOT, J. A. SWEERE, R. K. KUZOFF, K. A. KRON, M. W. CHASE, S. M. SWENSEN, E. A. ZIMMER, S. M. CHAW, L. J. GILLESPIE, W. J. KRESS, AND K. J. SYTSMA. 1997. Angiosperm phylogeny inferred from 18S ribosomal DNA sequences. *Ann. Missouri Bot. Gard.* **84**: 1–49.

———, ———, AND M. J. ZANIS. 2002. Phylogeny of seed plants based on evidence from eight genes. *Amer. J. Bot.* **89**: 1670–1681.

STEVENS, P. F. 2003. Angiosperm phylogeny website, vers. 4. *http://www.mobot.org/MOBOT/Research/APweb/* (May 2003).

STEVENSON, D. W., AND H. LOCONTE. 1995. Cladistic analysis of monocot families, pp. 543–578. *In* P. J. Rudall, P. J. Cribb, D. F. Cutler, and C. J. Humphries [eds.], Monocotyledons: systematics and evolution. Royal Botanic Gardens, Kew, Richmond, Surrey, UK.

SWOFFORD, D. L. 2002. PAUP*: phylogenetic analysis using parsimony (*and other methods), vers. 4. Sinauer Associates, Inc., Sunderland, Massachusetts, USA.

SYTSMA, K. J., J. MORAWETZ, J. C. PIRES, M. NEPOKROEFF, E. CONTI, M. ZJHRA, J. C. HALL, AND M. W. CHASE. 2002. Urticalean rosids: circumscription, rosid ancestry, and phylogenetics based on *rbc*L, *trn*L–F, and *ndh*F sequences. *Amer. J. Bot.* **89**: 1531–1546.

TAMURA, M. N. 1998*a*. Calochortaceae, pp. 164–172. *In* K. Kubitzki [ed.], The families and genera of vascular plants, Vol. 3. Flowering plants, monocotyledons, Lilianae (except Orchidaceae). Springer-Verlag, Berlin, Germany.

———. 1998*b*. Liliaceae, pp. 343–353. *In* K. Kubitzki [ed.], The families and genera of vascular plants, Vol. 3. Flowering plants, monocotyledons, Lilianae (except Orchidaceae). Springer-Verlag, Berlin, Germany.

THERMAN, E. 1956. Cytotaxonomy of the tribe Polygonatae. *Amer. J. Bot.* **43**: 134–142.

UHL, N. W., J. DRANSFIELD, J. I DAVIS, M. A. LUCKOW, K. S. HANSEN, AND J. J. DOYLE. 1995. Phylogenetic relationships among palms: cladistic analyses of morphological and chloroplast DNA restriction site variation, pp. 623–661. *In* P. J. Rudall, P. J. Cribb, D. F. Cutler, and C. J. Humphries [eds.], Monocotyledons: systematics and evolution. Royal Botanic Gardens, Kew, Richmond, Surrey, UK.

VINNERSTEN, A., AND K. BREMER. 2001. Age and biogeography of major clades in Liliales. *Amer. J. Bot.* **88**: 1695–1703.

WINTER, K., AND J. A. C. SMITH. 1996. An introduction to crassulacean acid metabolism: biochemical principles and ecological diversity, pp. 1–3. *In* K. Winter and J. A. C. Smith [eds.], Crassulacean acid metabolism: biochemistry, ecophysiology and evolution. Springer-Verlag, Berlin, Germany.

WON, H., AND S. S. RENNER. 2003. Horizontal gene transfer from flowering plants to *Gnetum. Proc. Natl. Acad. Sci. U.S.A.* **100**: 10824–10829.

ZANIS, M. J., D. E. SOLTIS, P. S. SOLTIS, S. MATHEWS, AND M. J. DONOGHUE. 2002. The root of the angiosperms revisited. *Proc. Natl. Acad. Sci. U.S.A.* **99**: 6848–6853.

———, P. S. SOLTIS, Y. L. QIU, E. ZIMMER, AND D. E. SOLTIS. 2003. Phylogenetic analyses and perianth evolution in basal angiosperms. *Ann. Missouri Bot. Gard.* **90**: 129–150.

ZOMLEFER, W. B. 1999. Advances in angiosperm systematics: examples from the Liliales and Asparagales. *J. Torrey Bot. Soc.* **126**: 58–62.