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PHYLOGENY, CONCERTED CONVERGENCE, AND PHYLOGENETIC NICHE CONSERVATISM IN THE CORE LILIALES: INSIGHTS FROM *rbc*L AND *ndh*F SEQUENCE DATA

THOMAS B. PATTERSON[1] AND THOMAS J. GIVNISH[1,2]
[1]*Department of Botany, University of Wisconsin, Madison, Wisconsin 53706*
[2]*E-mail: givnish@facstaff.wisc.edu*

Abstract.—*Calochortus* and the family Liliaceae s.s. have often been considered each other's closest relatives, based partly on their shared possession of bulbs, visually showy flowers, winged wind-dispersed seeds, and narrow parallel-veined leaves. We present a well-supported molecular phylogeny for these groups and their close relatives in the core Liliales, based on sequence variation in the chloroplast-encoded *rbc*L and *ndh*F genes. This analysis identifies Liliaceae s.s. as monophyletic, including one clade (((*Lilium*, *Fritillaris*, *Nomocharis*), *Cardiocrinum*), *Notholirion*) that appears to have diversified in the Himalayas roughly 12 million years ago and another ((*Erythronium*, *Tulipa*), (*Gagea*, *Lloydia*)) that arose in East Asia at about the same time. *Medeola* and *Clintonia* are sister to Liliaceae s.s. and bear rhizomes, inconspicuous flowers, fleshy animal-dispersed fruits, and broad reticulate-veined leaves. *Calochortus* is sister to *Tricyrtis*; both *Tricyrtis* and the neighboring clade of *Prosartes-Streptopus-Scoliopus* share several of the traits seen in *Medeola-Clintonia*. The core Liliales thus provide compelling examples of both concerted convergence and phylogenetic niche conservatism. Invasion of open, seasonal habitats was accompanied by the independent evolution of bulbs, showy flowers, wind-dispersed seeds, and narrow parallel-veined leaves in *Calochortus* and Liliaceae s.s. Conversely, persistence in shady habitats was accompanied by the retention of rhizomes, inconspicuous flowers, animal-dispersed seeds, and broad reticulate-veined leaves in their sister groups. We advance arguments for the context-specific adaptive value of each of these traits, as well as evidence of parallel trends in other groups. Concerted convergence—convergence in several different traits, favored by the same shared set of ecological conditions, in two or more lineages—is an important evolutionary process that can mislead evolutionary analyses based solely on phenotypic variation.

Key words.—Calochortaceae, concerted plesiomorphy, evolutionary trends, Liliaceae, phylogenetic inference, Uvulariaceae.

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Based on a cladistic analysis of *rbc*L sequence variation across monocots, Chase et al. (1995a) redefined the order Liliales as comprising parts of four morphologically defined orders recognized by Dahlgren et al. (1985). Within Liliales so defined, the largest clade containing Liliaceae sensu Dahlgren et al. (1985; henceforth Liliaceae s.s.) and composed solely of members of the morphologically defined Liliales also includes Calochortaceae sensu Tamura (1998a; *Calochortus*, *Prosartes*, *Scoliopus*, *Streptopus*, *Tricyrtis*) as well as *Clintonia* and *Medeola* of Liliaceae sensu Tamura (1998b). This clade, which we here term the ''core Liliales,'' corresponds to the expanded Liliaceae recently circumscribed by the Angiosperm Phylogeny Group (1998).

All members of the core Liliales are herbaceous geophytes native to the Northern Hemisphere. They include several beautiful, species-rich, and ecologically diverse genera of bulbous monocotyledons—particularly *Calochortus*, *Fritillaria*, *Lilium*, and *Tulipa*—and range from temperate deciduous forests to Mediterranean scrub, alpine meadows, and arctic tundra. They pose several unresolved taxonomic and biogeographic questions: What are the relationships among genera of Liliaceae s.s.? Is Liliaceae s.s. most closely related to Calochortaceae? What are the affinities of the historically enigmatic genera *Clintonia*, *Medeola*, *Scoliopus*, and *Tricyrtis*? When and where did these groups arise? Answers to these questions are unknown or disputed due to limitations in the resolution, degree of support, and/or taxonomic coverage of previous analyses (Berg 1959, 1962a,b; Björnstad 1970; Dahlgren et al. 1985; Utech 1992; Shinwari et al. 1994a; Chase et al. 1995a,b, 2000; Kato et al. 1995; Stevenson and Loconte 1995; Tamura 1998a,b; Rudall et al. 2000).

More importantly, members of the core Liliales vary in five traits of considerable ecological and evolutionary significance. Storage organs are bulbs or rhizomes, flowers are visually showy or inconspicuous, fruits are capsules or berries, leaves are broad and reticulate-veined or narrow and parallel-veined (Dahlgren et al. 1985; Phillips and Rix 1989; Chase et al. 1995b). Variation in these characters has shaped traditional perspectives on relationships in the core Liliales (Baker 1875; Bentham and Hooker 1883; Ownbey 1940; Berg 1959, 1962a,b; Cronquist 1981; Conover 1983; Dahlgren et al. 1985; Conran 1989; Thorne 1992; Chase et al. 1995b; Stevenson and Loconte 1995) and led many to believe that *Calochortus* and Liliaceae s.s. are each other's closest relatives. Morphological characters are often prone to convergence and other forms of homoplasy (Kadereit 1994; Soltis and Soltis 1995; Givnish and Sytsma 1997a). Such homoplasy can distort phylogenetic inference, and convergence may be especially common in characters that serve important ecological functions (Crisp 1995; Givnish et al. 1995, 1999, 2000; Givnish and Sytsma 1997a; Kirsch and Lapointe 1997; Les et al. 1997; Cameron and Dickson 1998; Evans et al. 2000; Molvray et al. 2000). This problem may become acute if traits show *concerted convergence*, that is, if several different characters each undergo convergence in organisms native to similar habitats, in response to selective pressures imposed by the same shared set of ecological conditions (Givnish 1997; Givnish and Sytsma 1997a,b; Givnish and Patterson 2000).

Here we develop a robust phylogeny for the core Liliales, use it to clarify the evolutionary history of the group, and address several key questions in systematics, morphology, and ecology that involve the phenomenon of concerted convergence. Sequence data for the chloroplast-encoded genes *rbc*L and *ndh*F, which evolve at moderate and relatively rapid rates, respectively (Olmstead and Palmer 1994), provide a tree for the core Liliales that is fully resolved and well supported at all levels. Reconstruction of ancestral character-states suggests that several features of storage organs, flowers, fruits, and leaves underwent concerted convergence with the independent invasion of open seasonal habitats by Liliaceae s.s. and *Calochortus*, favoring a suite of traits that led many to view these two groups as each other's closest relatives.

Materials and Methods

Taxon Sampling

Twenty-three species were used to represent the core Liliales (Table 1). We included each genus that belonged to the order based on a cladistic analysis of morphology (Dahlgren et al. 1985) and that occurred in or had an apparent affinity to the order based on *rbc*L sequence variation (Chase et al. 1995a). The ingroup thus comprised representatives of all nine genera of Liliaceae s.s.; two genera of the polyphyletic Uvulariaceae implicated as their close relatives (Shinwari et al. 1994a,b; Chase et al. 1995a); all major clades of *Calochortus* (Patterson 1998); and the four taxonomically enigmatic genera *Clintonia*, *Medeola*, *Scoliopus*, and *Tricyrtis* (Berg 1959, 1962a; Dahlgren et al. 1985; Utech 1992; Shinwari et al. 1994a,b; Kato et al. 1995). Collectively, these taxa represent all genera of Liliaceae and Calochortaceae sensu Tamura (1998a,b). Eight outgroup taxa represented the other major clades of the molecular Liliales, with *Campynema*, the earliest divergent member of the order (Chase et al. 1995a; Rudall et al. 2000), being used to root the tree (Table 1).

DNA Extraction, Amplification, and Sequencing

Total DNA was isolated from frozen or silica gel–dried leaf tissue using CTAB following Givnish et al. (2000). Total DNA for a number of taxa was generously provided by Dr. Mark Chase from the DNA Bank at the Royal Botanic Garden, Kew (U.K.). Double-stranded templates of the *ndh*F gene were amplified in two segments using the polymerase chain reaction (Mullis et al. 1986). Monocot-specific *ndh*F primers were kindly provided by R. Olmstead and included 032F and 1318R for the first segment and 1318F and 2110R for the second segment. These two amplified segments did not overlap, leaving a small gap (~60 bp) of missing data in each *ndh*F sequence. Attempts to sequence a third polymerase chain reaction (PCR) product spanning this middle region failed.

We amplified *rbc*L in one piece using 3′ and 5′ primers (Olmstead et al. 1992). PCR reactions for both genes included 10% MgCl, 10% reaction buffer (Promega), 3% dNTPs (10 μM), 5% bovine albumin serum (4 μM), 1% Tween 20, 1% each primer (20 μM), 2% total DNA, and 0.25% *Taq* polymerase (Promega, Madison, WI), made up to 100% in dH_20. Reactions were placed in a Perkin-Elmer (Wellesley, MA) thermal cycler and amplified with the following program: one cycle at 94°C for 7 min for initial denaturing; 30 cycles of denaturing at 94°C for 30 sec, annealing at 48°C for 60 sec, and extension at 70°C for 90 sec; terminated by one cycle of extension at 70°C for 7 min.

For *ndh*F, PCR products were cycle-sequenced with the ABI Prism dye-terminator cycle-sequencing reaction kit (Perkin-Elmer). Sequences were generated in five segments of approximately 400 bp each using the primers 032F, 451F, 1318R, 1318F, and 2110R. For *rbc*L, sequences for 14 taxa were downloaded from GenBank (Table 1). The remaining taxa were sequenced in three segments using the *rbc*L primers RH1, 523, and 895. Sequencing reactions included: 1.4 μl dH_2O, 1.6 μl 1 μM primer, 3 μl PCR product, and 4 μl *Fsq* dye terminator mix (Perkin-Elmer). Cycle-sequencing reactions used 25 cycles of denaturing at 96°C for 10 sec, annealing at 48°C for 5 sec, and extension at 60°C for 4 min. To remove excess dye terminators, sequencing products were cleaned by precipitating with ethanol and sodium acetate. Cleaned products were dried, resuspended, and sequenced on an ABI Prism 377 automated DNA sequencer.

Using Sequencher version 3.0 (Gene Codes Corp., Ann Arbor, MI), trace-files were examined for biases and possible errors and corrected using procedures outlined in Perkin-Elmer (1995). To see if sequences of the reverse strand would improve sequence accuracy, we generated reverse-strand sequences for *rbc*L and *ndh*F for some taxa. These data confirmed the original single-strand sequences, suggesting that it was not necessary to obtain data from both strands for all taxa. No stop codons were detected, almost all mutations were silent, and all indels were on-frame; limited sequence divergence facilitated the detection of mutations based on comparisons of trace-files.

Completed sequences were manually aligned. Indels were absent from *rbc*L, but six informative indels were detected in *ndh*F, five near the 3′ end. Indels were aligned to minimize independent evolutionary events using local parsimony (see Baum et al. 1994) but were not coded because they were congruent with nodes well supported by the sequence data alone. The single exception was a six-base insert at the same position in *Alstroemeria*, *Ripogonum*, and *Philesia*, but with a different first nucleotide in *Alstroemera*. All aligned sequences were deposited in GenBank (Table 1) and TreeBase (SN925).

Phenotypic Data

Variation across all taxa in 45 morphological, anatomical, embryological, karyotypic, and chemical characters were compiled from the literature (Table 2). Each was treated as unordered. Base chromosome number was treated as unordered to allow for multiple, effectively simultaneous fusions or fissions, and to avoid giving this character undue weight simply as a result of its large number (nine) of states and potential transitions among states.

Phylogenetic Analyses

Search methods

All phylogenetic studies were conducted using PAUP* version 4.0b8 (Swofford 2001). Separate maximum parsimony

TABLE 1. Voucher/source information and GenBank sequence numbers for survey of core Liliales (§) and outgroups; familial classification follows Dahlgren et al. (1985). Vouchers (including the standard abbreviation for the herbarium where lodged) are cited for all sequences obtained in this study (†); citations are given for previously published sequences from other laboratories for which the same accession was not used in this investigation.

Taxa	Voucher/source	*rbc*L	*ndh*F
Alstroemeriaceae			
Alstroemeria sp.	Anderson 13653, MICH	Z77254	AF276011†
Calochortaceae§			
Calochortus albus	Patterson 13, WIS	AF275983†	AF275994†
Calochortus apiculatus	Patterson 1060, WIS	AF275984†	AF275995†
calochortus balsensis	HP McDonald, s.n. Berkeley CA	AF275985†	AF275996†
Calochortus luteus	Patterson 28, WIS	AF275986†	AF275997†
Calochortus weedii	Patterson 18, WIS	AF275987†	AF275998†
Campynemaceae			
Campynema linearis	Walsh 3488, MEL	Z77264	AF276013†
Colchicaceae			
Androcymbium cilioatum	Chase 272, NCU	Z77265	AF276012†
Liliaceae§			
Cardiocrinum giganteum	Chase 3689, K	AF275988†	AF275999†
Cardiocrinum yunanense	Chase 935, K	AF275989†	AF276000†
Erythronium albidum	Patterson 1069, WIS		AF276002†
Erythronium japonicum	Shinwari et al. (1994a)	D28156	
Fritillaria agrestis	C Baysorder, unpubl.	AF013233	
Fritillaria meleagris	Patterson 1068, WIS		AF276003†
Gagea wilczekii	Chase 748, K	AF275990†	AF276004†
Lilium superbum	Chase et al. (1995a)	L12682	
Lilium kelleyanum	Felson 13, WIS		AF276005†
Lloydia serotina	B Jones s.n., K	Z77294	AF276006†
Nomocharis pardanthina	Chase 934, K	Z77295	AF276008†
Notholirion bulbiferum	Patterson s.n., WIS	AF275991†	AF276009†
Tulipa kolpakowskiana	Chase 438, K	Z77292	AF276010†
Tulipa pulchella	Patterson 1066, WIS		
Melanthiaceae			
Veratrum album	Kato et al. (1995)	D28168	
Veratrum viride	Chase 551, K		AF276024†
Philesiaceae			
Philesia buxifolia	Chase 545, K	Z77302	AF276014†
Smilacaceae			
Ripogonum elseyanum	Chase 187, NCU	Z77309	AF276016†
Smilax glauca	Chase 107, NCU	Z77310	
Smilax hispida	Givnish s. n., WIS		AF276018†
Uvulariaceae			
Clintonia borealis§	Shinwari et al. (1994a)	D17372	
Clintonia borealis§	Patterson s.n., WIS		AF276001†
Medeola virginiana§	Shinwari et al. (1994a)	D28158	
Medeola virginiana§	Patterson 1065, WIS		AF276007†
Prosartes maculata§	Shinwari et al. (1994a)	D17375	
Prosartes maculata§	DK Foster s.n., Messiah College		AF276015†
Scoliopus bigelovii§	Shinwari et al. (1994a)	D28162	
Scoliopus bigelovii§	Kalt 9278, WIS		AF276017†
Streptopus amplexifolius§	Foster, Messiah College	AF275992†	AF276019†
Streptopus roseus§	Shinwari et al. (1994)	D17381	
Streptopus roseus§	DK Foster s.n., Messiah College		AF276020†
Tricyrtis affinis§	Chase 2777, K	D17382	AF276021†
Tricyrtis latifolia§	Patterson 1070, WIS	AF275993†	AF276022†
Uvularia sessilifolia	Shinwari et al. (1994)	AB009948	
Uvularia sessilifolia	Patterson 10, WIS		AF276023†

(MP) analyses were conducted on the *rbc*L, *ndh*F, and phenotypic datasets; 1000 replicates of random addition sequences were performed using the heuristic search option with TBR branch-swapping and steepest descent. All characters and character-state changes were weighted equally under Fitch parsimony (Fitch 1971). For the phenotypic dataset, phylogenies were also derived using the parsimony jackknife (Farris et al. 1996), based on including all characters or deleting those implicated as undergoing concerted convergence (see Discussion). The parsimony jackknife involved random-

TABLE 2. Morphological, anatomical, chemical, and karyotpic character-states used in analyses of evolutionary trends and phylogenetic relationships in the core Liliales. Characters putatively undergoing concerted convergence are 7, 12, 13, 19, and 37.

	Characters[1,2]																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Lilium	0	0	1	0	0&1	1	1	3	0	0	0	0&1	0	1	0&1	1	1	0&1	1	1
Nomocharis	0	0	1	0	1	1	1	3	0	0	0	1	0	1	0	0	1	1	1	1
Fritillaria	0	0	1	0	0	1	1	3	0&1	0	0	1	0	1	0	1	1	0	0&1	1
Cardiocrinum	1	0	1	0	0	1	1	3	1	1	0	0	1	1	1	1	1	1	1	1
Notholirion	1	0	1	0	0	1	1	3	1	1	0	1	0	1	0	1	1	0	1	1
Gagea	0	0	0	0	0	1	1	1	1	0	0	1	0	0	0	1	1	1	1	1
Lloydia	0	0	0	0	0	1	1	1	1	0	0	1	0	0	0	1	1	0&1	1	1
Erythronium	0	0	0	0	0	1	1	1	1	0	0	0	0	0	1	1	0	0	1	1
Tulipa	0	0	0	0	0	1	1	1&3	1	0	0	0	0	0	0	1	1	1	1	1
Clintonia	0	0	0	0	1	1	0	—	—	—	0	0	1	0	1	1	0	0	0	1
Medeola	0	0	1	0	1	1	0	—	—	—	0	0	1	1	1	1	0	0	0	1
Calochortus albus	0	0	2	1	0	1	1	2	1	0	1	1	0	0	0	0	1	0	1	1
Calochortus apiculatus	0	0	0	1	0	1	1	2	1	0	1	1	0	0	0	0	1	1	1	1
Calochortus balsensis	0	0	2	1	0	1	1	2	1	0	1	1	0	0	0	0	1	0	1	1
Calochortus luteus	0	0	1	0&1	0	1	1	2	1	0	1	1	0	0	0	0	1	1	1	1
Calochortus weedii	0	0	1	1	0	1	1	2	1	0	1	1	0	0	0	0	1	1	1	1
Tricyrtis	0	0	2	1	1	1	0	—	—	—	0	0	1	1	0	0	1	0&1	1	1
Prosartes	0	0	2	1	1	1	0	—	—	—	0	0	1	1	0	1	0	1	0	1
Scoliopus	0	0	0	0	0	1	0	—	—	—	0	0	1	0	0	0	0	0	0	1
Streptopus	0	0	2	1	1	1	0	—	—	—	0	0	1	1	0	1	0	0	0	1
Smilax	0	1	3	1	0	1	0	—	—	—	0	0	1	1	1	1	0	0	0	0
Ripogonum	0	1	3	1	0	1	0	—	—	—	0	0	1	1	1	1	0	0	0	0
Philesia	0	1	3	1	0	1	0	—	—	—	0	0	1	1	1	1	0	0	1	0
Alstroemeria	0	0	1	0	0	0	0	—	—	—	0	0	1	1	1	0&1	1	1	1	1
Androcymbium	0	0	0	0	?	0	0	—	—	—	0	0&1	?	0	0	1	1	0&1	0	1
Uvularia	0	0	2	1	1	1	0	—	—	—	0	0	1	1	0	1	0	0	1	1
Veratrum	0	0	1	0	1	0	0	—	—	—	0	1	1	0	1	1	1	1	0	0
Campynema	0	0	1	0	0	0	0	—	—	—	0	1	0	0	0	1	1	1	1	0

[1] Character and character-states (all unordered): 1. Life history: (0) polycarpic, (1) monocarpic; 2. Growth form: (0) herbaceous, (1) woody; 3. Stem: (0) sessile, (1) erect, (2) arching, (3) climbing; 4. Stem architecture: (0) unbranched, (1) branched; 5. Stem pubescence: (0) absent, (1) present; 6. vessels with scalariform plates: (0) absent, (1) present; 7. Bulbs: (0) absent, (1) present; 8. Number of bulb scales: (0) 0, (1) 1, (2) 2, (3) 3 to many; 9. Tunic on storage organ: (0) absent, (1) present; 10. Swollen bases of basal leaves help form bulb; (0) no, (1) yes; 11. Distinctive basal leaf: (0) absent, (1) present; 12. narrow leaves: (0) absent, (1) present; 13. Reticulate venation between major nerves: (0) absent, (1) present; 14. Leaf attachment: (0) sheathing, (1) clasping; 15. Petioles: (0) absent, (1) present; 16. Perianth: (0) heterochlamydeous, (1) homochlamydeous; 17. Floral/inflorescence bracts: (0) absent, (1) present; 18. Flower orientation: (0) nodding, (1) erect; 19. Tepals: (0) short (<2 cm) and visually inconspicuous (green, greenish yellow, brown), (1) long (>2 cm) or visually conspicuous (white, bright yellow, orange, red, blue); 20. Tepal variegation: (0) absent, (1) present; 21. Tepal pubescence: (0) absent, (1) present; 22. Tepals: (0) nonpapillose, (1) papillose; 23. Saccate or depressed nectaries: (0) absent, (1) present; 24. Breeding system: (0) hermaphroditism, (1) dioecy, (2) androdioecy, (3) andromonoecy; 25. Ovary: (0) epigynous, (1) hypogynous; 26. Parietal cells: (0) absent, (1) present; 27. Style: (0) present, (1) obsolete; 28. Stigmatic surface: (0) dry, (1) wet; 29. Stigma: (0) 3-lobed, (1) tripartite, (2) unfused; 30. Anther attachment: (0) basifixed, (1) dorsifixed, (2) pseudo-basifixed (filament tip surrounded by the tubular connective); 31. Anther orientation: (0) extrorse, (1) introrse; 32. Pseudo-staminal column: (0) absent, (1) present; 33. Stamens: (0) free, (1) adnate to petals; 34. Pollen: (0) sulcate, (1) inaperaturate; 35. Embryo-sac formation: (0) *Polygonum* type, (1) *Fritillaria* type, (2) *Clintonia* (modified *Fritallaria*) type, (3) *Allium* type; 36. Endosperm formation: (0) nuclear, (1) helobial; 37. Fruit: (0) capsule, (1) berry; 38. Dehiscence: (0) septicidal, (1) loculicidal, (2) indehiscent, (3) irregular; 39. Fruit orientation at maturity: (0) nodding, (1) erect; 40. Striate seeds: (0) absent, (1) present; 41. Elaisomes: (0) absent, (1) present; 42. Raphides: (0) absent, (1) present; 43. Chelidonic acid: (0) absent, (1) present; 44. Basic chromosome number, *x*: (0) 7, (1) 8, (2) 9, (3) 10, (4) 11, (5) 12, (6) 13, (7) 14, (8) 15, (9) 19; 45. *Clintonia*-type vesicular-arbuscular mycorrhizae: (0) absent, (1) present.

[2] Sources: Dahlgren et al. 1985 (1–8, 11, 12, 14–18, 20–23, 25–31, 33–39, 42, 43); Tamura 1998b (4, 41); Haw 1986 (10); Conover 1983, 1991; Conran 1989; T. B. Patterson and T. J. Givnish, pers. obs. (13); Dahlgren et al. 1985; T. B. Patterson and T. J. Givnish, pers. obs. (19); Wolfe 1998; Jones and Gliddon 1999; Dahlgren et al. 1985 (24); T. B. Patterson, pers. obs. (32); Tamura 1998a (40); Tamura 1998a,b (41); Kubitzki 1998 (44); Widden 1996 (45).

ly deleting 1/*e* (36.8%) of the characters; 1000 replicates were performed using one random addition sequence in each case, with the same heuristic search parameters as those given for the bootstrap analysis below.

For each dataset, the relative support for each node in the corresponding parsimony analysis was assessed via bootstrap and decay analyses (Felsenstein 1985a; Bremer 1988). Bootstrap values were generated by conducting TBR searches on 1000 random resamplings of the sequence data, using random stepwise addition to generate a starting tree for each resampling. To keep search times practical while exploring a large number of equally parsimonious alternatives, no more than 1000 trees of minimum length were held at a time within each bootstrap replicate. Decay values were calculated using AutoDecay (Eriksson 1999). Following Hillis and Bull (1993) and Kellogg et al. (1996), we considered branches with ≥ 70% bootstrap support and decay values ≥ 2 to be well supported.

Parsimony algorithms can lead to long-branch attraction, especially if rates of nucleotide substitution are high and unequal among branches (Felsenstein 1978); maximum-likelihood (ML) algorithms are considered better for overcoming this bias (Huelsenbeck 1995, 1997). We conducted ML searches on the molecular data and compared the resulting phylogenies with those obtained under parsimony to check for long-branch attraction. Analyses used the six-parameter, general time-reversible model (Yang 1994), assuming empirical base frequencies and unequal rates of nucleotide substitution among sites, and estimating the shape parameter α. ML was used as a tie-breaker to decide which of the most

TABLE 2. Extended.

Characters[1,2]																								
21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45
1	1	0	0	1	0	0	1	0	1	0	0	0	0	1	0	0	1	1	0	0	0	0	5	0
1	1	1	0	1	0	0	?	0	1	0	0	0	0	1	0	0	1	1	0	0	0	0	5	0
1	0	1	0	1	0	0	1	0&1	1&2	0	0	0	0	1	0	0	1	1	0	0	0	0	5	0
1	1	0	0	1	0	0	?	0	1	0	0	0	0	1	0	0	1	1	0	0	0	0	5	0
1	1	0	0	1	0	0	0	1	1	0	0	0	0	1	0	0	1	1	0	0	0	0	5	0
1	0	0	1	1	0	0	?	0	2	0	0	0	0	1	0	0	1	1	0	1	0	0	5	0
1	0	0	1	1	0	0	?	0	2	0	0	0	0	1	0	0	1	1	0	0	0	0	5	0
1	0	0	0	1	0	0	0	0	2	0	0	0	0	1	0	0	1	0&1	0	1	0	0	5	0
1	0	0	0	1	0	0	0	0	2	0	0	0	0	1	0	0	1	1	0	0	0	0	5	0
0&1	0	0	0	1	0	0	0	0&1	1	0	0	0	0	1	0	1	2	1	0	0	0	0	7	0
1	0	0	0	1	0	0	?	1	1	0	0	0	?	1	0	1	2	1	0	0	0	0	0	1
0	0	1	0	1	0	1	0	1	2	0	1	0	0	0	0	0	0	0	0	0	0	0	3	0
0	0	1	0	1	0	1	0	1	2	0	1	0	0	0	0	0	0	0	0	0	0	0	3	0
0	0	1	0	1	0	1	0	1	2	0	1	0	0	0	0	0	0	0	0	0	0	0	2	0
0	0	0	0	1	0	1	0	1	2	0	1	0	0	0	0	0	0	1	0	0	0	0	2&3	0
0	0	1	0	1	0	1	0	1	2	0	1	0	0	0	0	0	0	1	0	0	0	0	3	0
0	0	1	0	1	0	0	1	1	1	0	1	0	0	0	0	0	0	1	0	0	0	0	6	0
1	0	0	0	1	0	0	0	0&1	1	0	0	0	0	0	0	1	2	0	0&1	0	0	0	1&2	0
1	0	0	0	1	0	0	?	1	1	0	0	1	?	0	0	0	3	0	1	1	0	0	0&1	0
1	0	0	0	1	0	0	?	0	1	0	0	1	0	0	0	1	2	0	1	0	0	0	1	0
1	0	0	1	1	1	0	0	0	0	1	0	0	1	0	0	1	2	0	0	0	1	1	8	0
1	0	0	1	1	1	0	0	0	0	1	0	0	0	0	0	1	2	?	0	0	1	1	8	0
1	0	1	0	1	1	0	1	0	0	0&1	0	0	1	0	?	1	1&2	?	0	0	1	1	9	0
1	0	0	0	0	0	0	1	?	2	1	0	0	0	0	0	0	1	1	0	0	1	1	1	0
1	0	0	0	1	0	0	?	1	0	0	0	0	0	0	0	0	1	?	0	0	1	1	1&2	0
1	0	0	0	1	0	0	?	0	0	0	0	0	0	0	0	1	1	0	0	1	1	1	0	0
1	0	0	3	1	1	0	0	1	?	0	0	0	?	0	1	1	0	1	0	0	1	1	1	0
1	0	0	0	0	1	0	?	2	0	0	0	0	0	0	1	1	1	?	0	0	1	1	4	0

parsimonious trees is the best point estimate of the phylogeny.

A likelihood-ratio test was used to test whether the combined molecular data evolved in clocklike fashion, after first calculating the likelihoods of the ML tree with and without the molecular clock being enforced. The difference of log-likelihoods was compared with the χ^2 distribution with $n - 2$ degrees of freedom (where n is the number of taxa included in the analysis) to test for significant departures from a molecular clock (Felsenstein 1994). *Campynema* diverged from other Liliales roughly 81 million years ago, based on Bremer's (2000) analysis of diverse rates of *rbc*L sequence evolution across monocots, calibrated against the fossil record. We estimated the age of diversification of each clade in the core Liliales by (1) calculating the average branch length, L, from the terminal taxa in that clade to the basal node joining *Campynema* to other Liliales; (2) measuring the distance, x, from this basal node along the branch to the base of the clade in question; and (3) identifying the estimated age of that clade as $81(1 - x/L)$ million years. This approach can estimate ages even if there is substantial variation in evolutionary rates among branches, by using branch-specific rates (Bremer 2000; Givnish et al. 2000).

Assessment of congruence

The *rbc*L and *ndh*F datasets were compared for phylogenetic congruence via visual inspection and the partition homogeneity test (Farris et al. 1994, 1995) as implemented in PAUP*. Visual inspection permits the precise location of areas of strong discordance (branches conflicting with bootstrap values $\geq$ 70% and decay values $\geq$ 2) between phylogenies generated by different datasets. The partition homogeneity test provides a statistical measure of dataset incongruence and was conducted on informative characters using 100 random-addition replicates with TBR and MULPARS in effect. As with the bootstrap analyses, no more than 1000 equally most parsimonious trees were retained within each PHT replicate. The datasets were combined and analyzed as a unit only if they were found to be congruent (Sytsma 1990; Huelsenbeck et al. 1996; Ballard et al. 1998; Givnish et al. 2000). In a few cases, we had to use different species as placeholders for a given genus in the *rbc*L and *ndh*F datasets (Table 1). We conducted three partition homogeneity tests to determine whether the phenotypic dataset had phylogenetic structure that was congruent with either or both of the cpDNA datasets.

Character-State Mapping and Tests of Correlated Evolution in Relation to Habitat

Phenotypic synapomorphies

Phenotypic characters (Table 2) were mapped onto the molecular phylogeny using MacClade version 3.05 (Maddison and Maddison 1992). Character-state reconstruction assumed Fitch parsimony and accelerated transformation optimization (ACCTRAN). In favoring reversals over parallelisms, ACCTRAN constitutes a conservative approach for estimating independent origins of traits. The molecular MP phylogeny

used for character-state mapping and tests of habitat-specific evolution was pruned to include one representative of each genus, to avoid artifacts introduced by idiosyncrasies in sampling.

Geography, habitat, and ecologically significant characters

Geographic distribution, habitat preference, and four traits of potential ecological importance were also mapped onto the molecular phylogeny using MacClade. Distributions were atomized into continents or into subcontinental biogeographic regions, with the latter including: (1) eastern North America; (2) western North America; (3) eastern Asia (Japan, Korea, eastern China); (4) southeastern Asia; (5) Himalayas; (6) central Asian deserts; (7) boreal and arctic Eurasia; (8) Asia Minor (including the Caucasus); (9) southern Europe; (10) western Europe; and (11) elsewhere (only as part of an outgroup polymorphism). Genera occurring in more than one region were coded explicitly as such.

Habitats were scored as *open* (grasslands; tundra; meadows; Mediterranean scrub; and the spring, fall, or winter phase of temperate deciduous forests), or *closed* (including understory elements active during the summer phase in closed forests and woodlands). Analyses of flower, fruit, or leaf characteristics, respectively, assumed an open habitat for a forest/woodland taxon if it flowers, fruits, or bears foliage only (or mainly) when the canopy is open.

Morphological traits of putative ecological significance that were mapped onto the molecular phylogeny and related to habitat included *storage organ* (bulb vs. rhizome), *floral syndrome* (showy [large, brightly colored] vs. inconspicuous), *fruit type* (capsule vs. berry), and *leaf width/venation* (broad, reticulate-veined vs. narrow, linear-veined). Leaf width and venation were mapped as a single character because both traits are highly correlated in the core Liliales (Conover 1983, 1991; Conran 1989).

Correlated evolution

We tested whether the preceding four traits showed correlated evolution with habitat using DISCRETE (Pagel 1994, 1999). DISCRETE employs a continuous Markov model to examine the evolution of pairs of binary characters on phylogenetic trees, taking branch length into account and weighting gains and losses equally. We set $\kappa = 1$, so that the null Brownian model assumed that character evolution was proportional to branch length on the pruned MP tree used for phenotypic character-state mapping (see above). For each trait, a log-likelihood ratio was calculated to see if the observed rates of evolution conformed significantly better to a model of dependent versus independent character evolution, relative to the outcome of 250 Monte Carlo simulations in which habitat and traits states were assigned randomly and independently to branch tips.

RESULTS

Phylogenetic Analyses

rbcL data

MP produced 321 shortest trees, each 546 steps in length, with a consistency index (CI) of 0.62 ($CI' = 0.52$, excluding autapomorphies). The ML tree was identical to one of these and differed from the strict consensus of the MP trees (Fig. 1A) only in resolving the position of *Calochortus apiculatus* relative to its congeners, suggesting that long-branch attraction is not a major concern. The *rbc*L data strongly supported the monophyly of the core Liliales, identifying three main clades: Liliaceae s.s. plus *Medeola-Clintonia*, *Calochortus*, and the remaining four genera of Calochortaceae sensu Tamura (1998a). Relationships among these three clades, however, were unresolved, and resolution or support for other relationships within Liliaceae s.s. was often weak (Fig. 1A).

ndhF data

Fitch parsimony recovered eight shortest trees, each 1277 steps long (CI = 0.63, $CI' = 0.54$). The ML tree was consistent with the strict consensus of these trees (Fig. 1B) but—at a cost of three additional steps under parsimony—had a zero-length branch at the node tying *Calochortus-Tricyrtis* to *Prosartes-Scoliopus-Streptopus*. The *ndh*F phylogeny differed from that based on *rbc*L mainly in being better resolved and supported. The *ndh*F tree resolved the basal trichotomy in the core Liliales observed in the *rbc*L phylogeny, placing Liliaceae s.s. plus *Clintonia-Medeola* sister to Calochortaceae. Contrary to the *rbc*L tree, however, *Calochortus* and *Tricyrtis* were strongly supported as sister to each other; these taxa were themselves sister to *Prosartes-Scoliopus-Streptopus* (Figs. 1A, B).

Congruency assessment

Based on visual inspection, the only place where the *rbc*L and *ndh*F phylogenies for the core Liliales exhibited discord was in the location of *Tricyrtis* (Figs. 1A, B). The *rbc*L analysis placed *Tricyrtis* sister to *Prosartes-Scoliopus-Streptopus*, whereas *ndh*F placed *Tricyrtis* sister to *Calochortus*. Close inspection suggests that this conflict may be illusory, due to two adjacent and perhaps miscalled bases near the end of the *rbc*L sequences (see Discussion). In addition, the two cpDNA datasets as they stand do not differ significantly in phylogenetic structure based on the partition homogeneity test ($P > 0.79$). We therefore concluded that the *rbc*L and *ndh*F datasets were homogeneous and combined them.

Combined molecular data

Equal weighting of the combined molecular data produced eight most parsimonious trees of length 1829 steps (CI = 0.63, $CI' = 0.53$), the most likely of which is shown in Figure 2. The ML tree was consistent with this tree, but—at a cost of three additional steps, as with the *ndh*F ML tree—failed to resolve the node tying *Calochortus-Tricyrtis* to *Prosartes-Scoliopus-Streptopus*, despite the last group being joined to *Tricyrtis* by both molecular datasets under parsimony. The combined molecular phylogeny was essentially identical to the *ndh*F tree except for the position of *Veratrum* among the outgroups. Most nodes had greater support in the combined tree than in the *ndh*F tree, and most were supported strongly. The single exception involved the position of *Tricyrtis*, which, although identical to that in the *ndh*F tree, had lower support, reflecting its discordant position in the *rbc*L tree.

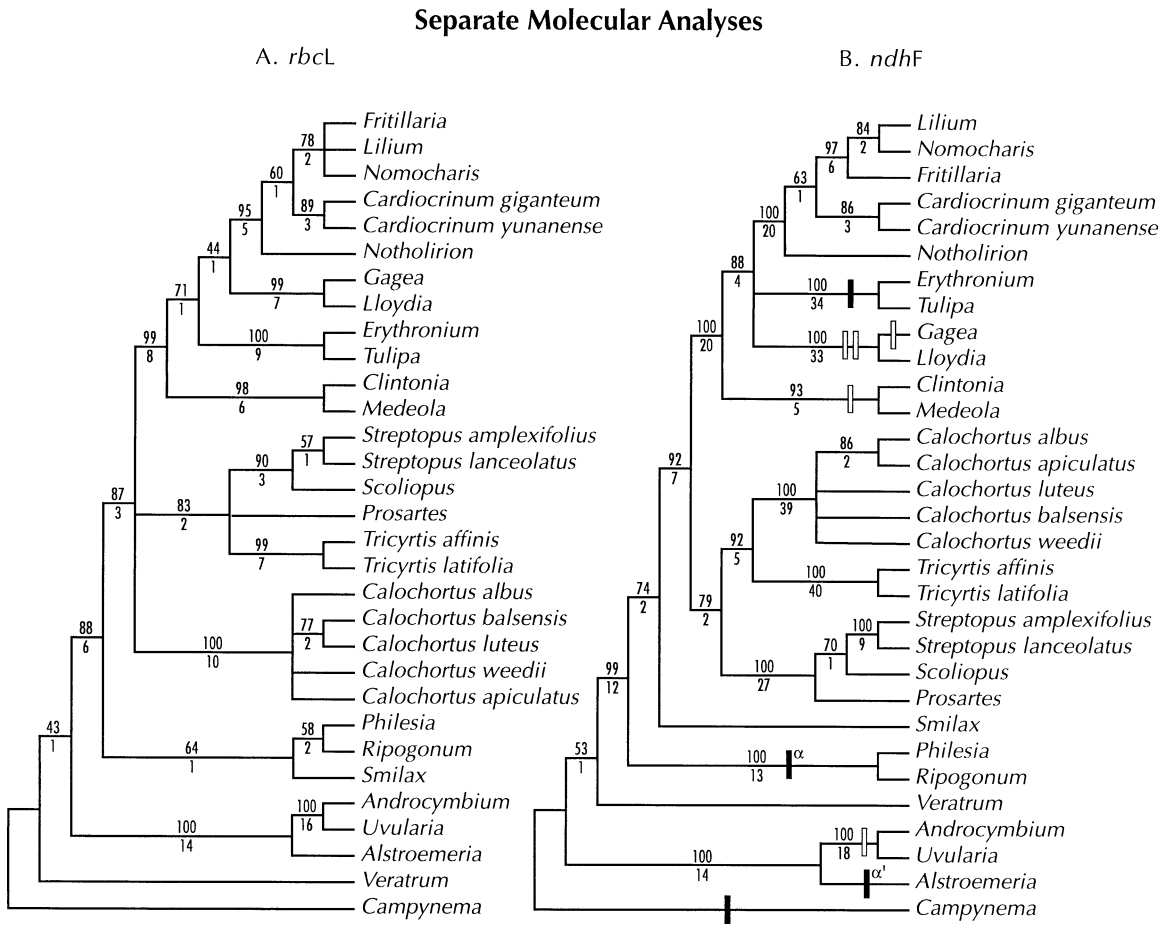

FIG. 1. Maximum-parsimony phylogenies of the core Liliales based on individual chloroplast-encoded gene sequences. Bootstrap values (%) are shown above each node; decay indices, below each node. (A) Strict consensus cladogram of 321 most parsimonious trees based on *rbc*L; (B) strict consensus of eight most parsimonious trees based on *ndh*F.

Within Liliaceae s.s., tribe Tulipeae (*Tulipa*, *Erythronium*, *Gagea*, *Lloydia*) was weakly supported, whereas tribe Lilieae (*Lilium*, *Nomocharis*, *Fritillaria*), *Erythronium-Tulipa*, *Gagea-Lloydia*, and Liliaceae sensu Tamura (1998b) were very strongly supported. In the remainder of the core Liliales, *Calochortus*, *Tricyrtis*, and *Streptopus-Scoliopus-Prosartes* also had exceedingly high support, as did all genera sampled more than once. Rates of evolution within the combined molecular tree were not clocklike ($P < 0.01$, likelihood-ratio test with 29 df), although much of the rate heterogeneity appeared to reside outside the core Liliales (Fig. 2).

Phenotypic data

Fitch parsimony identified 142 shortest trees, each of length 132 steps. The consistency index (CI = CI′ = 0.45) was substantially lower than that for either molecular dataset; the number of binary-equivalent informative characters was only 7.6% of that for the combined molecular data. The strict consensus tree included an unresolved trichotomy among Liliaceae s.s., *Calochortus-Tricyrtis*, and all the fleshy fruited taxa (including *Philesia*, *Ripogonum*, *Smilax*) plus *Scoliopus* and *Uvularia* (Fig. 3). Most nodes were either unresolved or weakly supported (decay index = 1). Based on partition homogeneity tests, the phenotypic data had a phylogenetic structure that was incongruent with that of the *rbc*L, *ndh*F, and combined cpDNA sequence data ($P < 0.01$ in each instance). Based on this finding and the much lower support for nodes in the phenotypic tree, the phenotypic and molecular data were not combined and characters were mapped onto the most likely MP tree derived from the combined molecular data alone. It should be noted, however, that including the phenotypic data would have substantially increased the bootstrap support for *Calochortus-Tricyrtis* (95%), Calochortaceae sensu Tamura (1998a; 87%), and Tulipeae (70%), while otherwise producing essentially the same branching topology in the core Liliales as the combined molecular dataset.

Character-State Mapping

Phenotypic synapomorphies

Several morphological/anatomical characters support clades in the combined molecular phylogeny (Fig. 4). *Tricyrtis* and *Calochortus*, whose association was discordant in the *rbc*L and *ndh*F trees, share four phenotypic synapomorphies: pseudo-staminal column, septicidal dehiscence, sac-

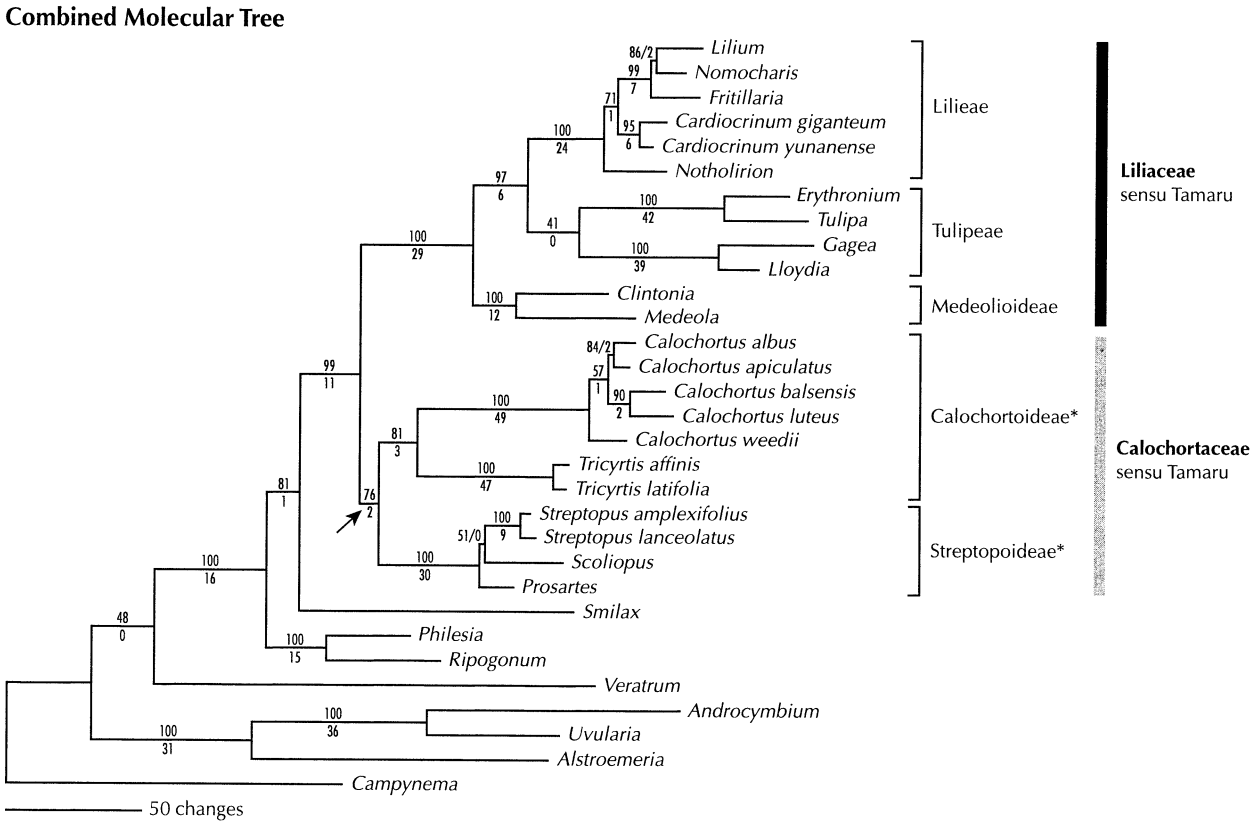

FIG. 2. Molecular phylogeny for the core Liliales based on combined *rbc*L and *ndh*F data. Phylogram shown is the most likely of the eight maximum-parsimony trees. Bootstrap values (%) are shown above each node; decay indices, below each node. Branch lengths are proportional to the number of mutations inferred under ACCTRAN. Solid bars represent in-frame insertions relative to other species; hollow bars, in-frame deletions. Arrow indicates the node that collapses in the maximum-likelihood tree. Subfamilies and tribes are adopted from Tamura (1998a,b), except those indicated by an asterisk, which are proposed or revised in this paper.

cate nectaries (in *Fritillaria* as well), and heavy tepal pubescence. The pseudostaminal column is identified here for the first time, and involves filaments that rise up and around the ovary, contacting each other and the style, but not fusing as they would in a true staminal column. *Calochortus tiburonensis* and *C. weedii* have a pseudo-staminal column that is most similar to that of *Tricyrtis*, but the character is present in all *Calochortus* species. Liliaceae s.s. and *Clintonia-Medeola* share the unique *Fritillaria*-type pattern of embryo-sac development (Berg 1962a,b). Capsules and bulbs were homoplasious, but the specific mechanism of capsular dehiscence and number of bulb scales supported the combined molecular phylogeny without reversal. Septicidal dehiscence characterizes Liliaceae s.s.; loculicidal dehiscence, *Calochortus* and *Tricyrtis*; and irregular dehiscence, *Scoliopus*. Two bulb scales mark *Calochortus*; one scale, the tribe Tulipeae; and numerous scales, the tribe Lilieae (Fig. 4).

Biogeography and times of origin

Based on both continental and subcontinental scoring of distributions, Liliaceae s.s. arose in Eurasia (Fig. 5). Tribe Lilieae appears to have evolved in the Himalayas and undergone an initial radiation there in montane and alpine habitats. The subcontinental analysis implies that *Clintonia-Medeola* arose in North America (with subsequent intercontinental dispersal to account for two species in east Asia and the Himalayas), whereas the continental analysis instead implies that this clade arose in Eurasia. Tribe Tulipeae evolved in east Asia, with subsequent colonization of North America by both *Erythronium* and *Lloydia*. Calochortaceae sensu Tamura (1998a) evolved in western North America, with independent colonizations of east Asia by *Streptopus* and the ancestor of *Tricyrtis*. North America was colonized at least twice within *Lilium* and *Fritillaria,* for a minimum of nine dispersal events between Eurasia and North America in the core Liliales (Fig. 5). This is likely to be an underestimate; detailed phylogenies of genera such as *Lilium* and *Fritillaria,* with large numbers of species on each continent, may imply more dispersal events. Interestingly, seven of nine intercontinental dispersal events appear to have occurred within genera (two of them within individual species, *Streptopus amplexifolius* and *S. streptopoides*), at relatively shallow levels of the molecular phylogeny.

Based on branch-specific rates of molecular evolution, we estimated that members of the core Liliales began diverging from each other 36 million years ago; members of Liliaceae sensu Tamura (1998b) 27 million years ago; members of Liliaceae s.s., 20 million years ago; members of the tribe Lilieae, 12 million years ago; and members of *Calochortus*, 7.3 million years ago.

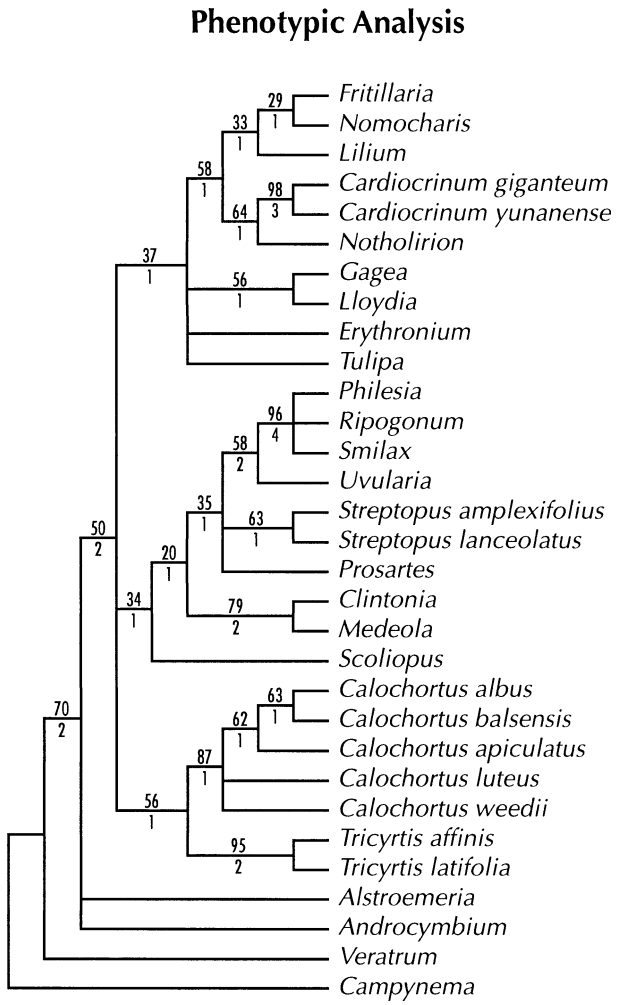

FIG. 3. Strict consensus of 142 most parsimonious trees based on phenotypic data. Bootstrap values (%) are shown above each node; decay indices, below each node.

Habitat and morphology

Character-state reconstructions imply that the core Liliales arose in closed, shaded habitats (Fig. 6). Liliaceae s.s. and *Calochortus* each evolved in conjunction with a shift to open habitats and microsites, but subsequent reversals to shaded conditions occurred in each group (e.g., in *Cardiocrinum*, a few *Lilium*, and a few *Calochortus*). Bulbs appear to have arisen independently in Liliaceae and *Calochortus* from rhizomatous ancestors and are associated significantly ($P < 0.008$, log-likelihood test) with the shift to open habitats and microsites (Fig. 6A). Showy, visually conspicuous flowers arose at least twice—in Liliaceae and *Calochortus-Tricyrtis*—associated significantly ($P < 0.004$) with the invasion of open habitats or (in *Tricyrtis*) the open, autumnal phase of deciduous forest understories (Fig. 6B). Capsular fruits arose from berries three times, in Liliaceae s.s., *Calochortus-Tricyrtis*, and *Scoliopus* (Fig. 6C), significantly associated ($P < 0.004$) with the invasion of open habitats or seasonal phases in the first two instances. In *Scoliopus*, capsules arose in connection with the evolution of myrmecochory (dispersal of individual seeds by ants) in *Scoliopus* (Berg 1959). Myrmecochory also evolved in connection with the retention of capsular fruits in *Erythronium* and *Gagea* subg. *Gagea* (Tamura 1998b). Broad, reticulate-veined leaves characterized the shade-inhabiting ancestor of the core Liliales. Narrow, parallel-veined leaves evolved at least twice—in Liliaceae s.s. and *Calochortus*—significantly associated ($P < 0.04$) with the invasion of open microsites/seasonal phases (Fig. 6D). A secondary reversal to broad, reticulate-veined leaves occurred in *Cardiocrinum* of forest gaps in the Himalayas. Overall, these data suggest a pattern of concerted convergence in storage organs, flower size, fruit type, and leaf form associated with the transition from closed to open habitats.

DISCUSSION

Phylogenetic Relationships

The combined molecular data strongly support the monophyly of the core Liliales (Fig. 2), which is marked by the absence of raphides and chelidonic acid (Fig. 4). Our results imply that the core Liliales is sister to *Smilax*; Chase et al. (1995) inferred that this group was sister to *Smilax-Ripogonum-Philesia-Lapageria* based on *rbc*L variation in a smaller set of taxa. Our inferences of character-state evolution do not depend on *Smilax* or the broader clade recognized by Chase et al. (1995a) being sister to the core Liliales. Both are mainly characterized by small, inconspicuous flowers (not *Philesia*), rhizomes, fleshy fruits, broad reticulate-veined leaves, and growth in closed habitats.

The core Liliales consists of two major clades: Liliaceae sensu Tamura (1998b) and Calochortaceae sensu Tamura (1998a; see Fig. 2). We prefer not to submerge these families in Liliaceae sensu the Angiosperm Phylogeny Group (1998) because both groups are marked by phenotypic synapomorphies (Fig. 4); Liliaceae sensu Tamura is better supported by molecular data than Liliaceae sensu APG; and retaining both families increases the phylogenetic information that the classification can convey with little additional cost. The core Liliales is, however, much more clearly marked by phenotypic characters than either Liliaceae or Calochortaceae sensu Tamura, and the latter is supported by relatively few synapomorphies. Relationships within each of Tamura's families are discussed below.

Liliaceae

The combined molecular data strongly support the monophyly of Liliaceae s.s. (Fig. 2). This clade is marked by loculicidal capsules and a basic chromosome number $x = 12$ (Fig. 4). Our data strongly support *Clintonia* and *Medeola* as part of Liliaceae. The relationships of *Clintonia* and *Medeola* have been contentious (Shinwari et al. 1994a,b; Kato et al. 1995; Tamura 1998a,b). These genera are morphologically distinct from Liliaceae s.s. in having rhizomes instead of bulbs and berries instead of capsules, which may have confounded past attempts based on morphology to assay their relationships. Both genera also share a highly unusual form of vesicular-arbuscular mycorrhizae (Widden 1996). But *Clintonia*, *Medeola*, and all genera of Liliaceae s.s. share the unique *Fritillaria* type of embryo-sac development (Fig. 3). Our results support Tamura's (1998b) decision to recognize

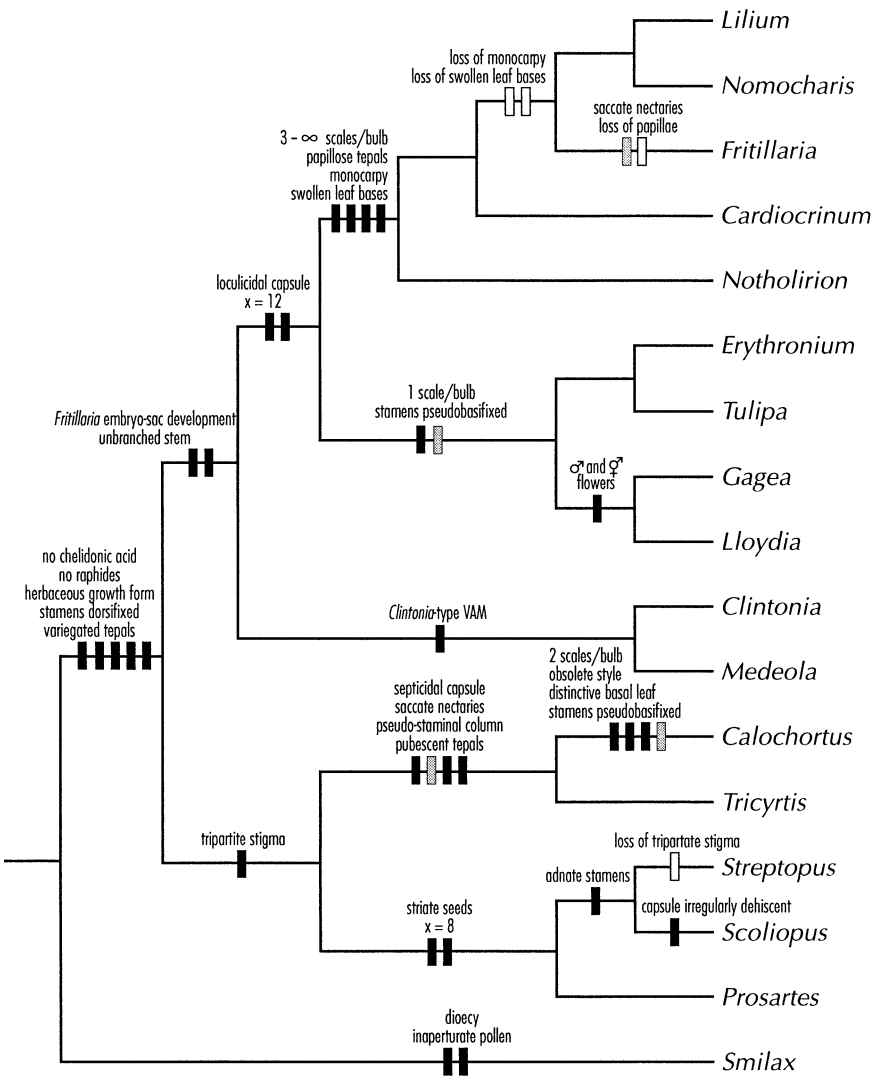

FIG. 4. Phenotypic characters with CI ≥ 0.50 mapped onto the combined molecular phylogeny for the core Liliales under parsimony.

Liliaceae s.s. as the subfamily Lilioideae and *Clintonia-Medeola* as the subfamily Medeolioideae, within his newly circumscribed Liliaceae.

Dahlgren et al. (1985) concluded that Liliaceae s.s. was sister to *Calochortus*, based on their possession of bulbs and pseudo-basifixed anther connectives. However, their analysis did not distinguish bulbs characterized by different numbers of storage scales. The number of storage scales per bulb supports the existence of three separate clades within the core Liliales—Lilieae, Tulipeae, and *Calochortus*—which also emerge in the cpDNA phylogeny (Fig. 4). This is independent evidence that the bulbs in Liliaceae and *Calochortus* are not homologous; on the same grounds, it is possible (although more problematic to argue) that bulbs arose independently in the sister clades Lilieae and Tulipeae.

Subfamily Lilioideae diversified along two main lines. Tribe Lilieae (*Notholirion*, *Cardiocrinum*, *Fritillaria*, *Lilium*, *Nomocharis*) is characterized by papillose tepals (except *Fritillaria*) and numerous fleshy bulb-scales (Fig. 4), as well as a morphologically distinct karyotype composed of two long metacentric chromosomes and 10 telocentrics of medium length (Tamura 1998b). *Notholirion* and *Cardiocrinum* retain basal leaves, and their bulbs are composed largely of the swollen bases of those leaves (Haw 1986). The multiple bulb scales of the three other genera may thus be homologous to the bases of now-vanished basal leaves. *Fritillaria*, *Lilium*, and *Nomocharis* share losses of the bulb tunic and the monocarpic habit ancestral to the tribe (Fig. 4). Tribe Tulipeae (*Tulipa*, *Erythronium*, *Gagea*, *Lloydia*) is supported by the phenotypic synapomorphies of pseudo-basifixed anthers (also in *Calochortus* and *Alstroemeria*) and single bulb scales (Fig. 4). The sister genera *Gagea* and *Lloydia* share andromonoecy (Wolfe 1998; Jones and Gliddon 1999), as well as smaller tepals than most other Liliaceae s.s., associated with much smaller total plant sizes.

Calochortaceae

Our cpDNA phylogeny supports *Tricyrtis* as being sister to *Calochortus* (Fig. 2). This finding casts light on a long-

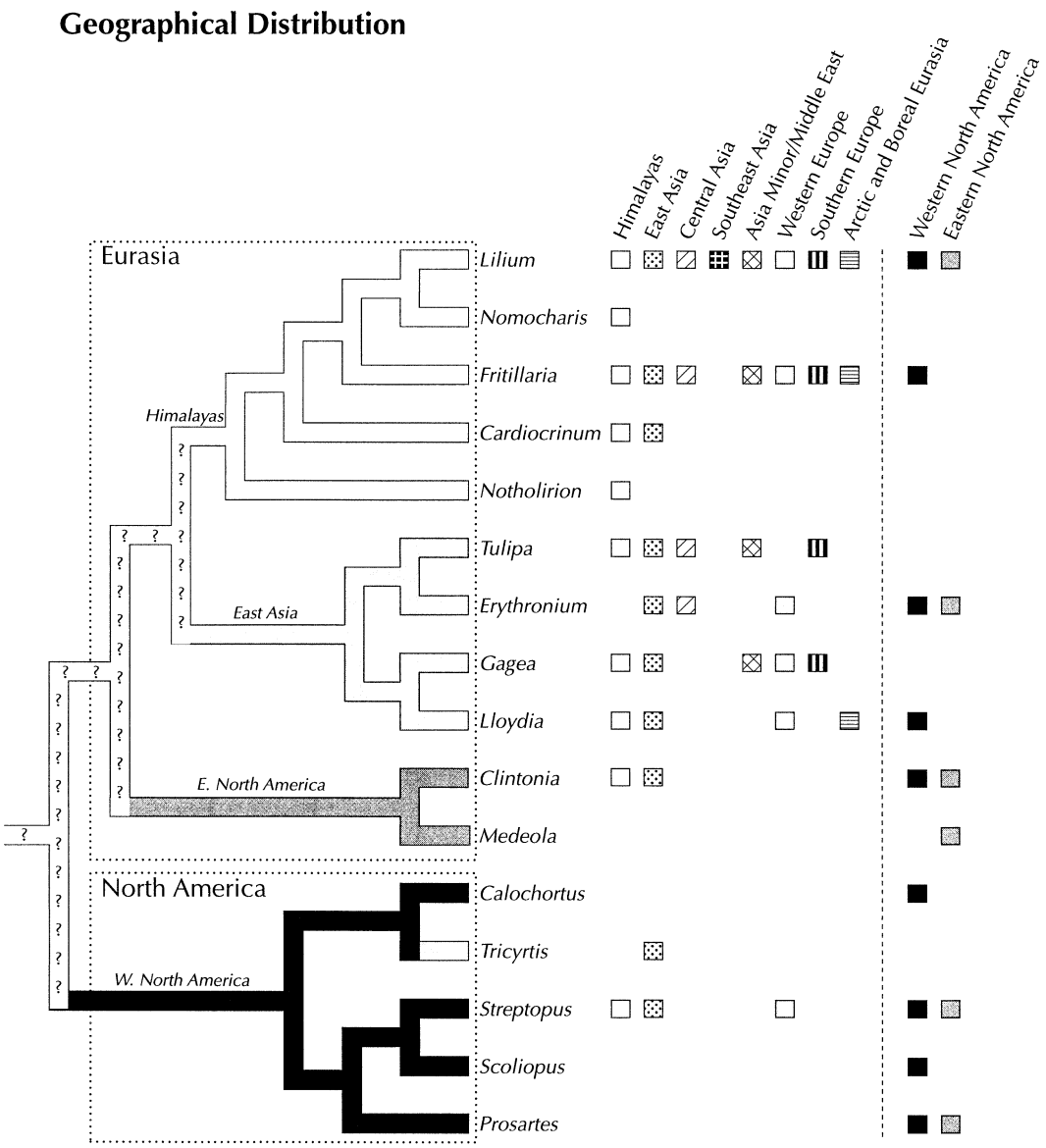

FIG. 5. Reconstructions of inferred geographic distributions of ancestral taxa in the core Liliales, based on atomization of distributions at the subcontinental scale (boxes for occurrences; branches shaded for ancestral states) and continental scale (dashed line separating occurrences in Eurasia vs. North America; dotted line for ancestral states). All taxa included in the combined cpDNA phylogeny were used to establish the polarity of character-states, but only the ingroup taxa are shown. The suggestion that *Clintonia* may have arisen in southern China (based on a noncladistic analysis of karyotypic variation by Li et al. 1996), if proven, would resolve the only conflict between the subcontinental and continental analyses and identify eastern Eurasia as the cradle of Liliaceae.

standing taxonomic mystery regarding the closest relative of *Calochortus* (see Baker 1875; Bentham and Hooker 1883; Ownbey 1940; Cave 1941; Berg 1960; Chase et al. 1995a; Stevenson and Loconte 1995; Tamura 1998a), in which a sister relationship to *Tricyrtis* had never been explicitly suggested. Berg (1960) did, however, discuss similarities in embryology between the two groups (e.g., a very long nucellus rest, early disruption of the nucellus, normal-type embryosac development), and recommended that *Calochortus* be transferred to a position near the tribes Tricyrteae or Uvularieae of Melanthiaceae. Goldblatt (1995) found *Calochortus* and *Tricyrtis* to be members of an unresolved trichotomy including Colchicaceae, supported by the shared possession of septicidal capsules. Tamura (1998a) allied *Tricyrtis* with *Scoliopus*, *Streptopus*, and *Prosartes* in a new subfamily Tricyrtoideae of his Calochortaceae; our results indicate that *Tricyrtis* should instead be included in his subfamily Calochortoideae. We recommend erecting a second subfamily Streptopoideae to recognize the well-supported, previously undescribed clade of *Prosartes*, *Scoliopus*, and *Streptopus* (Fig. 2).

The position of *Tricyrtis* differed in the *rbc*L and *ndh*F phylogenies (Figs. 1A, B). This conflict is troubling because the positions of *Tricyrtis* in both trees had reasonably strong support. Inspection of the sequence data revealed that, among the mutations supporting the different relationships of *Tri-*

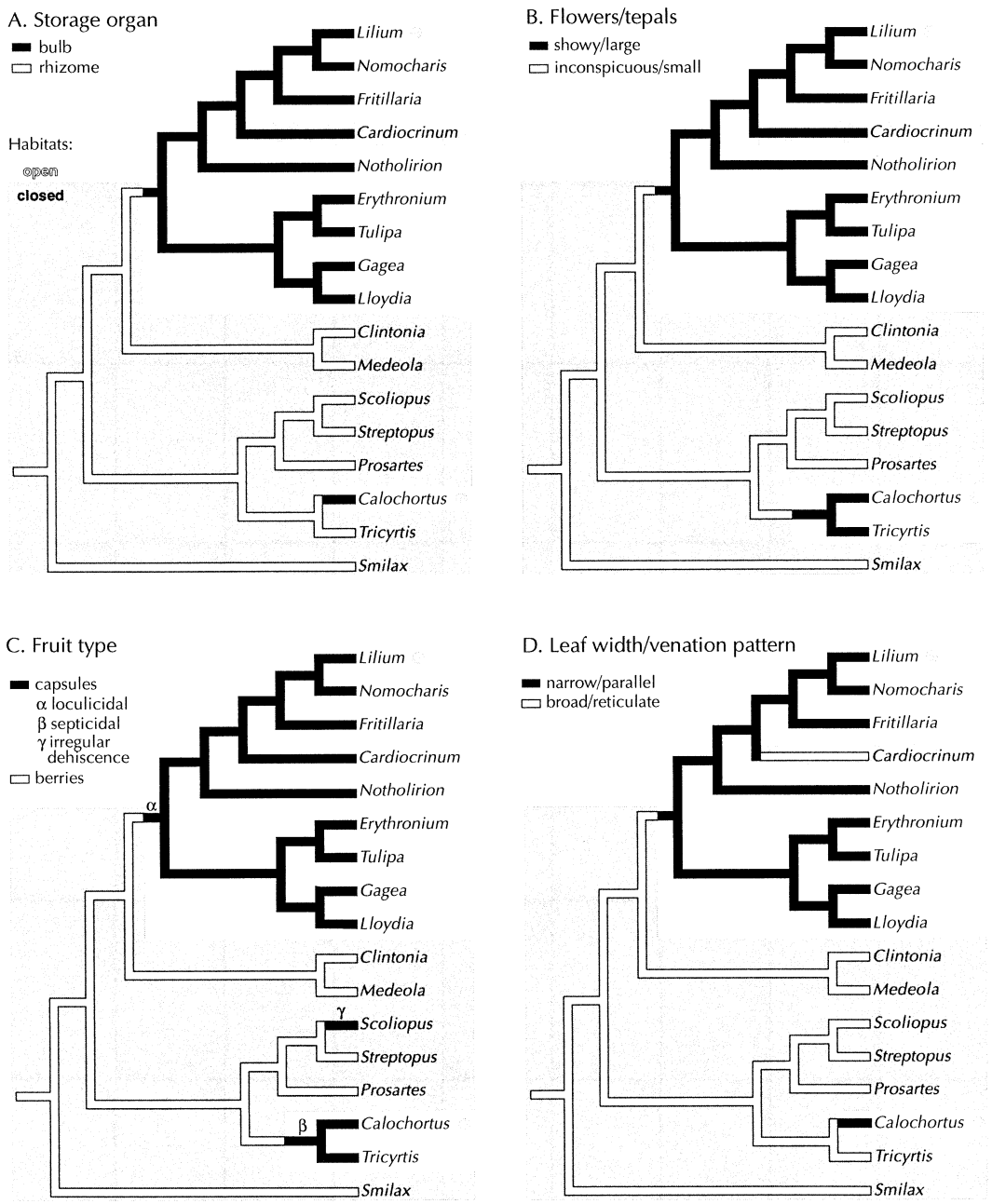

FIG. 6. Reconstructions of character-state evolution in relation to inferred habitat shifts in the core Liliales under parsimony: (A) storage organ (bulb vs. rhizome); (B) floral syndrome (showy: large and/or brightly colored tepals; inconspicuous: small tepals, whitish, cream, or green in color); (C) fruit type (capsule vs. berry); (D) leaf width/venation (leaves narrow and parallel veined vs. leaves broad and reticulate veined). Shaded backgrounds indicate closed habitats (forest gaps in *Cardiocrinum*) for terminal taxa and inferred ancestors; white indicates open habitats. Note differing habitats for vegetative, flowering, and/or fruiting in *Cardiocrinum* and *Tricyrtis* (see text). Dots signify the occurrence of isolated shade species within genera otherwise growing in open habitats.

cyrtis in the *rbc*L and *ndh*F trees, one pair in each dataset involved changes in adjacent nucleotides. Such changes are suspect because they might reflect sequencing error or non-independence of mutations. When each pair was deleted from analysis, the *ndh*F trees were unchanged, but the *rbc*L strict consensus became fully consistent with that for *ndh*F (and hence, the combined analysis) with *Tricyrtis* joining an unresolved polytomy with Liliaceae sensu Tamura (1998a), *Calochortus*, and *Steptopus-Prosartes-Scoliopus*.

Several phenotypic synapomorphies provide additional support for a *Calochortus-Tricyrtis* affiliation (Fig. 4). One particularly striking synapomorphy is the pseudo-staminal column, but the shared possession of septicidal dehiscence, pronounced saccate nectaries (in *Fritillaria* as well), and heavy tepal pubescence also point to a close relationship between the two taxa.

Scoliopus possesses a highly modified suite of fruit and flower characteristics adapted for seed dispersal by ants and

pollination by fungus gnats (Berg 1959; Utech 1992). These unusual features plagued earlier attempts to establish its taxonomic position (Berg 1959, 1962a; Dahlgren et al. 1985; Utech 1992; Shinwari et al. 1994a,b; Kato et al. 1995; but see Tamura 1998a). Our molecular phylogeny places *Scoliopus* in a well-supported clade with *Prosartes* and *Streptopus* (Fig. 2). *Scoliopus* and *Streptopus* share adnate stamens and (with one species of *Prosartes*) striate seeds; all three genera share an inferred ancestral chromosome number of $x = 8$ (Fig. 4). Tamura (1998a) used anatomy to infer a close tie between *Scoliopus* and *Prosartes*, *Streptopus*, and *Tricyrtis*, although he presented no explicit analysis or data matrix.

Biogeography

Evolution in the core Liliales appears to have involved at least nine dispersal events between Eurasia and North America (Fig. 5). Seven of these events occurred within genera (*Lilium*, *Fritillaria*, *Erythronium*, *Clintonia*, *Lloydia*, *Prosartes*, *Streptopus*) over the past 2–14 million years. Many exchanges between Eurasia and North America may thus have occurred recently, probably as a result of the repeated formation of the Bering land bridge over the past 20 million years during the Miocene, Pliocene, and Pleistocene (Tiffney 1985; Graham 1999; Wen 1999). *Streptopus streptopoides* itself has a Beringian distribution on both sides of the current straits.

Definitive conclusions regarding the origin of certain groups must await detailed phylogenetic studies of *Lilium*, *Fritillaria*, *Erythronium*, *Lloydia*, and *Clintonia-Medeola*. The occurrence of several genera in multiple biogeographic regions raises the possibility that their present distributions reflect differences among those regions in the likelihood of extinction as much as past patterns of dispersal. Areas such as the Himalayas, southern China, and Japan, with a wide range of elevations and rainfall, are more likely to retain taxa than areas of lesser relief or more exposure to glaciation. But it seems clear that multiple intercontinental dispersal events occurred and that tribe Lilieae arose in the Himalayas (Fig. 5). According to this scenario, elements of *Fritillaria* and *Lilium* subsequently dispersed from the Himalayas into the rest of Eurasia and North America. This hypothesis is bolstered by the fact that several species of *Lilium* that blur the distinctions among *Lilium*, *Nomocharis*, and *Fritillaria* (e.g., *L. amoenum*, *L. henricii*, *L. nanum*) are today restricted to mountainous portions of Myanmar (Burma), Tibet, and China (Woodcock and Stearn 1950; Haw 1986; McRae 1998). A preliminary internal-transcribed-spacer phylogeny for *Lilium* (Nishikawa et al. 1999) is indeed consistent with a single dispersal event to North America. A new *ndh*F phylogeny for *Erythronium* (Allen et al. 2000) implies two intercontinental dispersal events, not just one; inserting their phylogeny into our analyses leaves our conclusions otherwise unchanged.

Significant uplift of the Himalayas began in the Miocene about 20 million years ago (Johnson 1994; Hodges et al. 1996) and is thought to have greatly intensified the seasonality of monsoonal Asia, especially during the last 7 million years, based on its direct effects on atmospheric circulation and indirect effects on increased carbon burial and silicate weathering (Quade et al. 1995; Fluteau et al. 1999). The latter have also been proposed as potential causes of the general global decrease in temperature and increase in thermal and moisture seasonality at higher latitudes during the Miocene (Raymo and Ruddington 1992; Graham 1999), which would have favored the evolution of bulbous plants like those in Liliaceae s.s. and *Calochortus*.

The tribe Tulipeae appears to have arisen in east Asia (Fig. 5). *Tulipa* is a diverse genus (~100 spp.) of meadows, steppes, Mediterranean scrub, and semideserts ranging from Japan to the Mediterranean, but most diverse in Asia Minor. *Erythronium* (~20 spp.) is concentrated in montane forests and alpine tundra of western North America; three species are spring ephemerals in temperate deciduous forests in eastern North America, and one (*E. dens-canis*, with *E. japonicum* sometimes segregated) is found throughout northern Eurasia (Applegate 1935; Dahlgren et al. 1985). *Gagea* (~90 spp.) occupies rocky meadows and semideserts, has a range similar to *Tulipa*, but is most diverse near the Mediterranean. *Lloydia* (~18 spp.) is found mainly in alpine and arctic tundra habitats, with one species (*L. serotina*) in western North America (Dahlgren et al. 1985; Phillips and Rix 1989).

Concerted Convergence Associated with the Invasion of Open Habitats

Multiple independent origins of a character in conjunction with a particular shift in habitat are strong evidence that the character is adaptive (Felsenstein 1985b; Baum and Larson 1991; Brooks and McLennan 1994; Givnish 1997). Although retained character states (plesiomorphies) under ancestral ecological conditions do not, in and of themselves, constitute evidence of adaptation (particularly in the historical sense; sensu Gould and Vrba 1982), these traits may nevertheless be important ecologically and be maintained by selection (Harvey and Pagel 1991; Lord et al. 1995; Westoby et al. 1995a,b). Thus, devising and testing functional hypotheses for derived *and* plesiomorphic states are needed to understand the directional *and* stabilizing selection pressures that have shaped the morphology of any group. This section examines the potential adaptive significance of four sets of morphological traits—involving storage organs, floral syndrome, fruit type, and leaf form—that appear to have undergone concerted convergence and plesiomorphy in the core Liliales.

Storage organs

Dahlgren et al. (1985) concluded that possession of bulbs was a synapomorphy linking Liliaceae s.s. and *Calochortus*, but our combined cpDNA phylogeny indicated that bulbs arose independently in these two families (Fig. 6A). The origin of bulbs in each case was accompanied by a shift from closed to open photosynthetic habitats. Rundel (1996) observed a similar pattern in California *Iris:* bulbous species were found in open habitats, and rhizomatous ones in shaded habitats. The open habitats occupied by bulbous taxa in the core Liliales are characterized by high light availability and a short season favorable for photosynthetic activity. Bulbous taxa in the core Liliales grow mainly in *Mediterranean scrub or temperate sclerophyll forests* (with a brief period of favorable conditions following winter rains), in *arctic and al-*

pine tundra (with a brief period of favorable conditions between spring thaw and autumn snowfall), or as *spring ephemerals in temperate deciduous forests* (with a brief period of favorable conditions between spring thaw and canopy closure; Raunkiaer 1934; Adamson 1939; Ownbey 1940; Woodcock and Stearn 1950; Stebbins 1974; Pate and Dixon 1982; Dahlgren et al. 1985; Antos 1988; Givnish 1988). This contrasts with the forest habitats occupied by rhizomatous, shade-adapted taxa (e.g., *Clintonia* and *Tricyrtis*) that remain photosynthetically active through a long growing season beneath a closed canopy. A few species of *Lilium* (e.g., *L. canadense*, *L. duchartrei*, *L. pardalinum*) have underground organs that are transitional between bulbs and rhizomes/stolons (McRae 1998). Interestingly, such species are generally found in open woodland and thickets, which are in some ways intermediate between open and closed habitats.

Bulbs or functionally analogous storage organs with preformed shoots (e.g., corms) are generally recognized as adaptations to short growing seasons: they remain dormant during unfavorable conditions, but can rapidly deploy shoots when conditions improve (Rees 1966, 1989; Grime and Mowforth 1982; Pate and Dixon 1982; Eickmeier and Schussler 1993). Massive allocation to storage, however, has an important downside: the opportunity cost (Chapin et al. 1990) of photosynthesis foregone as a consequence of allocation to unproductive storage organs during the favorable period, rather than to additional productive leaves or absorptive roots.

We argue that bulbs or functionally analogous structures are most likely to be favored by a short favorable season involving brightly lit, moist conditions. When photosynthesis is *not* strongly limited by light or moisture availability, the advantage in energetic income caused by rapid leaf deployment and photosynthesis during almost all of a short favorable season is likely to outweigh the energetic disadvantage associated with the storage opportunity cost. Rhizomatous plants tend not to develop preformed shoot apices, perhaps because they would be unable to protect them with the much smaller amount of tissue they cluster around those apices. Horizontally spreading rhizomes may, however, confer a fitness advantage in shaded understories by enabling genets to vegetatively explore the forest floor and forage for light and nutrients, and provide carbon and nutrients to developing ramets to aid their establishment in adverse microsites (Berg 1962b; Cook 1983; Bell 1984; Antos 1988). Massive storage organs might be counterproductive under such conditions, involving large opportunity costs for a relatively small increase in the length of time a plant can be photosynthetically active—and at a relatively low rate.

Floral syndrome

Showy flowers evolved convergently in Liliaceae s.s. and *Calochortus* with movement into sunny, open habitats (Fig. 6B). Many of these habitats are limited in pollinator density as a result of low temperatures in early spring or at high elevations or have a short flowering season as a result of thermal or moisture seasonality (Bliss 1971; Dahlgren et al. 1985; Phillips and Rix 1989; Shmida and Dafni 1989; Dafni et al. 1990). Short flowering seasons and limited numbers of pollinators should select for plants that advertise heavily for pollinators via visual, olfactory, and/or chemical allurements (MacArthur 1972; Shmida and Dafni 1989).

We propose that open habitats—illuminated by bright, broad-spectrum light (Endler 1993)—should select specifically for visually conspicuous flowers, with substantial allocation to large petals, bright colors, and the like. Very small plants (with limited resources) should have flowers that are large relative to their photosynthetic surface, even though such flowers may be small in absolute terms. Conversely, poor illumination by narrow-spectrum light under closed canopies should favor less costly, less visually conspicuous flowers. Research on African rift-lake cichlids has shown that bright colors are indeed most effective as sexual signals under bright, broad-spectrum illumination (Seehausen et al. 1997, 1999).

Within the core Liliales, taxa that inhabit poorly lit forest understories usually have small, whitish or greenish, visually inconspicuous flowers; examples include *Clintonia*, *Medeola*, *Scoliopus*, and many *Streptopus* (flowers borne below the leaves). Similar flowers are seen in *Smilax* and its close relatives (Fig. 6B), and in many other monocots and dicots in eastern North America (e.g., *Disporum*, *Geum*, *Osmorhiza*, *Panax*, *Polygonatum*, *Pyrola*, *Tipularia*) that flower in evergreen forest understories, under closed canopies in deciduous forests, or under their own foliage (T. J. Givnish, pers. obs.). In contrast, most herbaceous genera of deciduous forests that flower before the canopy have large or brightly colored flowers; examples include *Erythronium* as well as *Anemone*, *Dentaria*, *Dicentra*, *Sanguinaria*, *Trillium*, and *Uvularia*. Most core Liliales with large, visually conspicuous flowers grow in open habitats, including most of the Himalayan clade, *Erythronium* and *Lloydia* in alpine meadows, and *Calochortus* and *Tulipa* in Mediterranean scrub and semideserts. *Tricyrtis*, with its rather large (~2–3 cm diameter), brightly colored flowers, blossoms in late summer and autumn (Ohwi 1965) as the canopy thins in Japanese forests. In the core Liliales, exceptions to the generalizations proposed here include a few, closely related species of *Calochortus* in terminal clades that grow in closed woodlands and bear nodding, brightly colored flowers (Jokerst 1981; Patterson 1998); a few species of *Lilium* that grow under closed canopies; and *Clintonia andrewsiana*, which has dull rose-colored flowers in conifer-forest understories. The tepals of *Gagea* and *Lloydia* are somewhat shorter than most other Liliaceae (~1 cm long, similar in length to those of *Clintonia*), but are visually conspicuous (bright yellow or white) and are borne in open habitats. These flowers, however, are much larger relative to their bearers' leaf area than those borne by *Clintonia*, *Medeola*, *Scoliopus*, *Streptopus*, and *Smilax*. Even so, if the flowers of *Gagea* and *Lloydia* were instead coded as visually inconspicuous, the evolution of floral syndrome and habitat openness would remain highly correlated ($P < 0.008$, log-likelihood test).

Cardiocrinum, which grows in open woods and forest openings, presents a special challenge for analysis, in that its habitat is neither open nor closed and would perhaps be best described as a third intermediate state. However, DISCRETE can only analyze the evolution of binary characters. For analytical purposes, we considered *Cardiocrinum* as occupying closed habitats for flowering and leafing (it fruits in

late fall). This is a conservative choice, in that it reduces the likelihood of finding a significant correlation between conspicuous flowers and open habitats. Despite this coding, floral syndrome and habitat in the core Liliales showed a highly significant tendency to evolve in correlated fashion (Fig. 6B).

Fruit morphology

Capsules arose three times from berries in the core Liliales, each time associated with a distinct form of dehiscence, and twice in association with the invasion of open habitats and the evolution of seed dispersal via wind (anemochory; Fig. 6C). Under closed canopies, where wind speeds are reduced, endozoochory (internal transport by animals) and fleshy fruits should be favored; in open, windy habitats, anemochory, winged or plumed seeds, and capsular fruits can be advantageous (Givnish et al. 1995; Givnish 1998). *Tricyrtis* occupies deciduous forest understories, but its capsules dehisce and its seeds disperse via the wind late in the season, after the canopy opens and understory wind speeds increase. In deciduous forests in eastern North America, most herbaceous species that fruit after the canopy opens in fall are wind dispersed (T. J. Givnish, unpubl. data).

Capsular fruits arose in *Scoliopus* in association with myrmecochory. *Scoliopus* has irregularly dehiscent capsules that are moderately fleshy, or ''spongy'' (Utech 1992). Berg (1959) proposed that the *Scoliopus* capsule evolved from loculicidal or septicidal capsules and that irregular dehiscence and fleshiness served to facilitate seed dispersal by ants. Our molecular results suggest another scenario, with capsular fleshiness being a vestige of berrylike fruits in *Scoliopus'* ancestor (Fig. 6C). Dehiscence should aid myrmechory by directly exposing individual seeds and their elaiosomes to ants (Berg 1958, 1959). Most myrmecochorous herbs in temperate forests set fruit early in the growing season, as does *Scoliopus*, when few seed dispersers other than ants are present and effective (Thompson 1981); most of these bear capsular fruits (e.g., *Erythronium*, *Sanguinaria*, *Viola*) or achenes (*Carex*). Berg (1958, 1959) also argued for an evolutionary pathway from bird to ant dispersal in understory herbs: Indeed, bird-dispersed berries, ant-dispersed seeds in capsular fruits, and bird- and ant-dispersed seeds in fleshy berries can all be found within the single genus *Trillium*.

The origin of capsular fruits and wind- or ant-dispersed seeds in Liliaceae s.s., *Calochortus-Tricyrtis*, and *Scoliopus* appears adaptive, as does the retention of fleshy, bird-dispersed berries in other core Liliales. However, it is not evident what adaptive differences, if any, exist among the forms of dehiscence that evolved in this group. We suspect that, in fact, there are no such differences among loculicidal, septicidal, and irregular dehiscence and that they are accidents of history that mark three convergent origins of capsular fruits within the core Liliales.

Leaf venation and shape

Patterns of leaf venation have been used extensively to infer phylogenetic relationships in monocotyledons, in general, and in the Liliales, in particular (Baker 1875; Cronquist 1981; Conover 1983; Dahlgren et al. 1985; Conran 1989; Chase et al. 1995b; Stevenson and Loconte 1995). Yet, Givnish (1979) showed that a branching venation is biomechanically advantageous in broad leaves with a thin cross-section and suggested that its occurrence in many different monocot groups of temperate and tropical forest herbs (e.g., Araceae, Stemonaceae, Trilliaceae, Zingiberales) represents convergence based on selection for broad, thin leaves in shady, moist habitats. Chase et al. (1995a) and Cameron and Dickison (1998) have independently reported an association between reticulate venation and growth in shaded habitats across monocots and vanilloid orchids, respectively.

In the core Liliales, narrow leaves with parallel venation arose twice, in Liliaceae s.s. and *Calochortus*, in conjunction with the invasion of open habitats (Fig. 6D). Broad leaves with reticulate venation (unusual among monocots generally) were retained in other groups found primarily in the shade and evolved again in *Cardiocrinum* when it invaded partly shaded microsites. Narrow leaves are thought to be adaptive in sunlit habitats because they reduce transpiration per unit area and associated energetic costs (e.g., increased root allocation, decreased leaf water potential and photosynthetic capacity) while keeping leaves near air temperature (Givnish 1979, 1987). Broader leaves should be favored by shady and/or moist conditions, given the lower costs associated with transpiration, the lesser increase in leaf temperature with effective leaf width, and the enhancement of photosynthesis at slightly warmer temperatures.

Traditional Taxonomic Perspectives and Confounding Evolutionary Processes

Our molecular phylogeny and interpretations challenge traditional views of relationships within the core Liliales (Baker 1875; Ownbey 1940; Cronquist 1981; Conover 1983; Dahlgren et al. 1985; Conran 1989; Thorne 1992; Zomlefer 1994; but see Cave 1941; Berg 1959). Contrary to many previous views, Liliaceae s.s. and *Calochortus* are not sister to each other, despite similarities in five derived character-states of ecological significance. Both groups evolved in association with the invasion of open, sunny, seasonal habitats and evolved bulbs, visually showy flowers, capsular fruits, narrow leaves, and parallel venation adapted to those habitats. The similarities between these groups thus appears to reflect concerted convergence (Givnish 1997; Givnish and Sytsma 1997a,b), not common descent. *Clintonia-Medeola*, *Tricyrtis*, and *Prosartes-Streptopus-Scolipus*, which have all remained in shaded understories, are not each others' closest relatives, even though they share most or all of the plesiomorphic states for these same characters. Rhizomes, inconspicuous flowers, berries, broad leaves, and reticulate venation were all retained in lineages that adapted to shaded forest understories. Overall, it appears that views of relationships within the core Liliales based on morphology may have been misled by the twin processes of concerted convergence and phylogenetic niche conservatism.

Concerted convergence

Liliaceae s.s and *Calochortus* independently evolved the same suite of character-states—including bulbs, showy flowers, capsules, linear leaves, and parallel leaf venation (Figs. 6A–D)—adapted to open, sunny, seasonal conditions. Con-

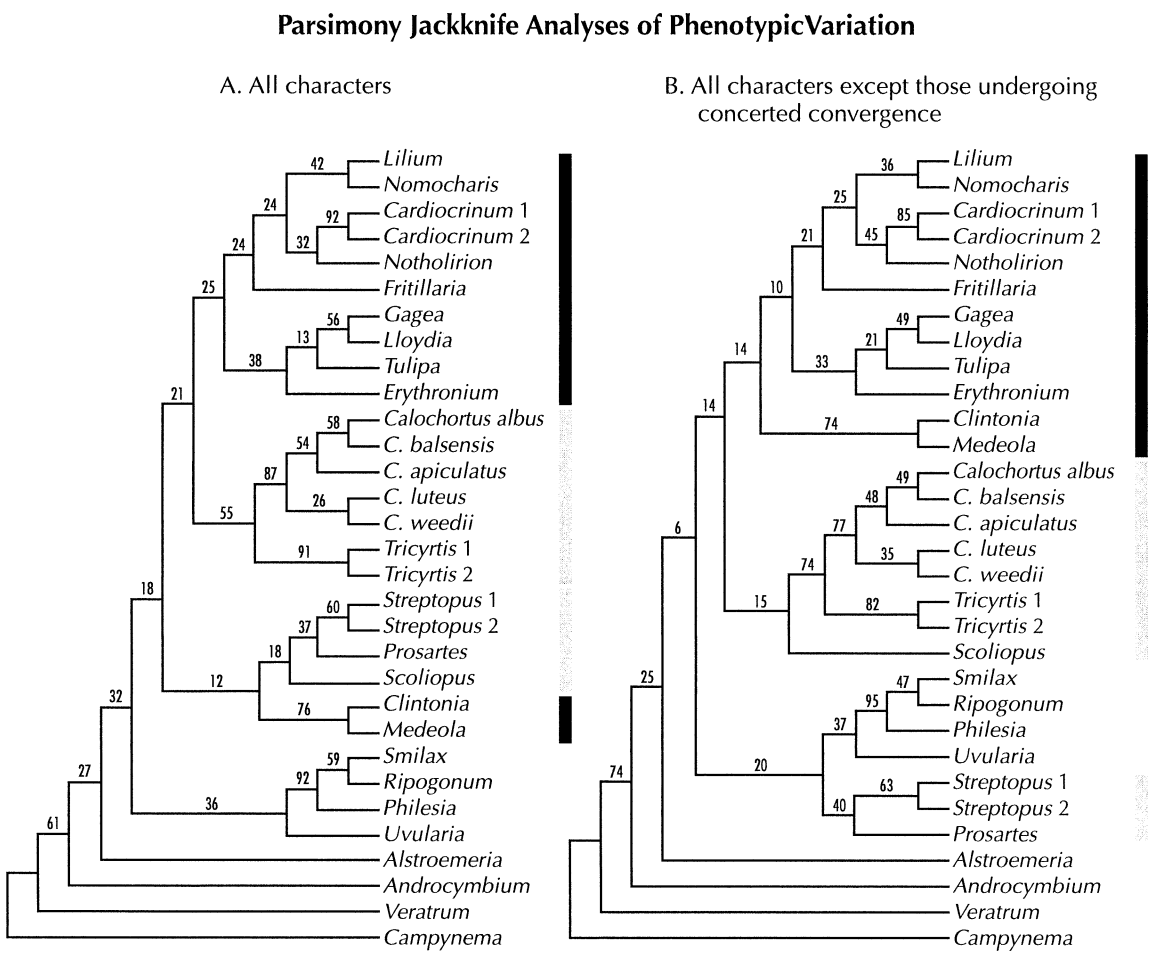

FIG. 7. Jackknife consensus trees for the core Liliales based on phenotypic variation, with and without characters inferred to have undergone concerted convergence. Members of Liliaceae and Calochortaceae are indicated by the black and gray bars, respectively. (A) When all 45 characters are included, Liliaceae s.s and *Calochortus-Tricyrtis* are sister to each other, with *Clintonia-Medeola* and *Scoliopus* at the base of a fleshy fruited clade with *Streptopus* and *Prosartes*. (B) When characters involved in concerted convergence are excluded, *Clintonia-Medeola* becomes sister to Liliaceae s.s. and *Calochortus-Tricyrtis* becomes sister to *Scoliopus*.

certed convergence provides a compelling explanation for the evolution of these traits in both groups: Not only did they arise independently in response to similar conditions, they each appear to confer distinct advantages for survival in their derived habitats. Differences between groups in the nature of capsular dehiscence and the number of scales per bulb (Figs. 6A, C) help confirm that they are not sister taxa.

Phylogenetic niche conservatism

Rhizomes, inconspicuous flowers, berries, and broad leaves with reticulate venation are the plesiomorphic conditions of the core Liliales (Figs. 6A–D). Persistence of plesiomorphic traits within a lineage may be due to either phylogenetic constraint (sensu Brooks and McLennan 1994) or phylogenetic niche conservatism (Harvey and Pagel 1991; Westoby et al. 1995a,b). Phylogenetic constraint involves the presence of lineage-specific, organism-intrinsic barriers to evolutionary change, such as a lack of additive genetic variation for a particular trait, developmental correlations among traits, or genetic burden imposed by coadaptation among traits (Westoby et al. 1995a,b; Givnish 1997). Phylogenetic niche conservatism, in contrast, involves the maintenance of phenotypic traits by stabilizing selection when ancestral ecological roles are conserved within a lineage over time (Lord et al. 1995). An intrinsic capacity to evolve may exist in a lineage, but change may not occur for want of a shift in ecological roles (Westoby 1995a,b).

Our current lack of knowledge regarding potential phylogenetic constraints on phenotypic shifts from rhizomes, inconspicuous flowers, berries, broad leaves, and reticulate venation prevents us from fully differentiating between these two alternative scenarios (see Lord et al. 1995). The large number of shifts across monocots in storage organ type, floral conspicuousness, fruit morphology, and leaf width and venation (T. Givnish, J.C. Pires, S. Graham, L. Prince, M. Mulvray, T. Evans, K. Millam, T. Patterson, J. Kress, and K. Sytsma, unpubl. ms.), however, argue against their being under strong phylogenetic constraints. In our present case, circumstantial evidence suggests that phylogenetic niche conservatism played an important role in maintaining most or all of these characters in *Clintonia-Medeola*, *Tricyrtis*, and *Prosartes-Scoliopus-Streptopus*. First, forest understories

were the ancestral habitat inferred for the core Liliales, and this habitat appears to have been conserved in several subclades until the present day. Second, each of the five plesiomorphic character-states in question has been associated, in both extant taxa and inferred ancestors, with the occupation of closed forest understories. Third, there are compelling functional arguments why each of these character-states should be adaptive (and thus, be maintained by stabilizing selection) under shady conditions. Fourth, many of these character-states occur in other, distantly related genera of shade-adapted forest herbs. Taken together, this evidence suggests that phylogenetic niche conservatism (in essence, concerted plesiomorphy) did help maintain a constellation of five shade-adapted traits within certain lineages of the core Liliales.

Not only do concerted convergence and phylogenetic niche conservatism occur in the core Liliales and not only do they appear to have resulted from selection, they also created a positively misleading signal that can skew at least some analyses of relationships based on phenotype alone. If all 45 phenotypic characters (Table 2) are included in a cladistic analysis, *Calochortus-Tricyrtis* is sister to Liliaceae s.s. in the jackknife consensus tree, with a third clade formed of remaining elements of the core Liliales sister to both groups (Fig. 7A); these three clades form a basal trichotomy in the strict consensus of the eight most parsimonious trees. But when the five characters whose states appear to undergo concerted convergence are excluded, relationships similar to those identified by the molecular data emerge in the jackknife consensus (Fig. 7B), with *Clintonia-Medeola* sister to Liliaceae s.s. and *Calochortus-Tricyrtis* sister to a clade including *Streptopus*, *Uvularia*, and *Prosartes*. It is important to note that phenotypic data recover the *Calochortus-Tricyrtis* clade and that adding them to the molecular datasets increases the support for several clades. Nevertheless, claims that evolutionary convergence is unlikely to mislead phylogenetic analyses, because convergence in one or a few traits is unlikely the overcome the phylogenetic signal in other characters (e.g., Brooks and McLennan 1994; de Queiroz 1996), overlook concerted convergence and concerted plesiomorphy (i.e., phylogenetic niche conservatism). These important phenomena must be considered in analyses of phylogeny and phenotypic evolution.

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