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Phylogenetic Relationships in the Commelinaceae: II. A Cladistic Analysis of *rbcL* Sequences and Morphology

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ABSTRACT. The chloroplast-encoded gene *rbcL* was sequenced in 30 genera of Commelinaceae to evaluate intergeneric relationships within the family. The Australian *Cartonema* was consistently placed as sister to the rest of the family. The Commelineae is monophyletic, while the monophyly of Tradescantieae is in question, due to the position of *Palisota* as sister to all other Tradescantieae plus Commelineae. The phylogeny supports the most recent classification of the family with monophyletic tribes Tradescantieae (minus *Palisota*) and Commelineae, but is highly incongruent with a morphology-based phylogeny. This incongruence is attributed to convergent evolution of morphological characters associated with pollination strategies, especially those of the androecium and inflorescence. Analysis of the combined data sets produced a phylogeny similar to the *rbcL* phylogeny. The combined analysis differed from the molecular one, however, in supporting the monophyly of Dichorisandrinae. The family appears to have arisen in the Old World, with one or possibly two movements to the New World in the Tradescantieae, and two (or possibly one) subsequent movements back to the Old World; the latter are required to account for the Old World distribution of Coleotrypinae and Cyanotinae, which are nested within a New World clade.

The Commelinaceae, a well defined family of 41 genera and about 650 species (Cronquist 1981; Faden 1985; Faden and Hunt 1991; Evans 1995; Faden 1998), is of considerable interest from biogeographic, evolutionary, and systematic perspectives. The family is diverse both in the Paleo- and Neotropics, with some genera distributed in both (Faden 1983). The species exhibit remarkable morphological variation, particularly in floral and inflorescence features (e.g., Brenan 1966; Evans et al. 2000a, b; Faden 2000). The family has radiated extensively in response to non-nectar seeking pollinators with changes in floral symmetry, stamen number, structure, and position, and inflorescence size and arrangement being the most pronounced (Faden 2000). The broad range of morphological variation has made interpretation of homology of these characters difficult and has led to differing interpretations of relationships and thus classifications for the family (e.g., Brückner 1930; Pichon 1946; Rohweder 1956; Brenan 1966; Faden and Hunt 1991; Faden 1998). Evans et al. (2000a) conducted a cladistic analysis of 47 morphological and anatomical characters to determine phylogenetic relationships among 40 of the 41 genera. The resulting phylogeny (Figure 1) placed the Australian-endemic *Cartonema* R. Brown sister to the rest of the family (in agreement with Faden and Hunt [1991] and Faden [1998]). Most of the other groups that had been proposed in these most recent classifications of the Commelinaceae, especially the tribes Commelineae (Meisner) Faden & D. R. Hunt and Tradescantieae (Meisner) Faden & D. R. Hunt, were not supported.

A molecular phylogenetic analysis of the Commelinaceae is thus both timely and necessary. Presented here are phylogenetic analyses of the Commelinaceae based on chloroplast-encoded gene *rbcL* and on combined *rbcL*/morphology data sets. At higher taxonomic levels, *rbcL* has been useful for evaluating phylogenetic relationships (e.g., Chase et al. 1993; Duvall et al. 1993; Conti et al. 1997; Lewis et al. 1997; Rodman et al. 1998; Chase and Albert 1998; Qiu et al. 1998; Soltis et al. 1998; Givnish et al. 1999; Savolainen et al. 2000). However, an increasing number of studies have found *rbcL* useful at the family or even generic levels (e.g., Doebley et al. 1990; Plunkett et al. 1995; Muasya et al. 1998; Setoguchi et al. 1998; Cameron et al. 1999; Chase et al. 1995; Chen et al. 1999; Korall et al. 1999; Les et al. 1999; Meerow et al. 1999; Nepokroeff et al. 1999; Azuma et al. 2000; see reviews in Soltis and Soltis 1998, and Sytsma and Hahn 1996, 2001).

DNA sequences are ideal for phylogenetic analyses of Commelinaceae because: (1) the family belongs to a larger group of monocots where results from cladistic analysis of morphology and DNA have been at odds due to floral evolution in response to pollinator shifts (Givnish et al. 1999)—responses that may well have occurred in the evolution of Commelinaceae; (2) DNA sequences show significantly less homoplasy than morphology when the taxonomic level and comparable numbers of taxa are considered (Givnish and Sytsma 1997a,b; contra earlier and less-sampled surveys of Sanderson and Donoghue 1989, Donoghue and Sanderson 1992); and (3) a morphological cladistic analysis has been completed prior to the DNA analysis (see Fig. 1)—ensuring complete independence of the morphological analysis, permitting direct comparisons of the results of the two classes of data, and allowing for

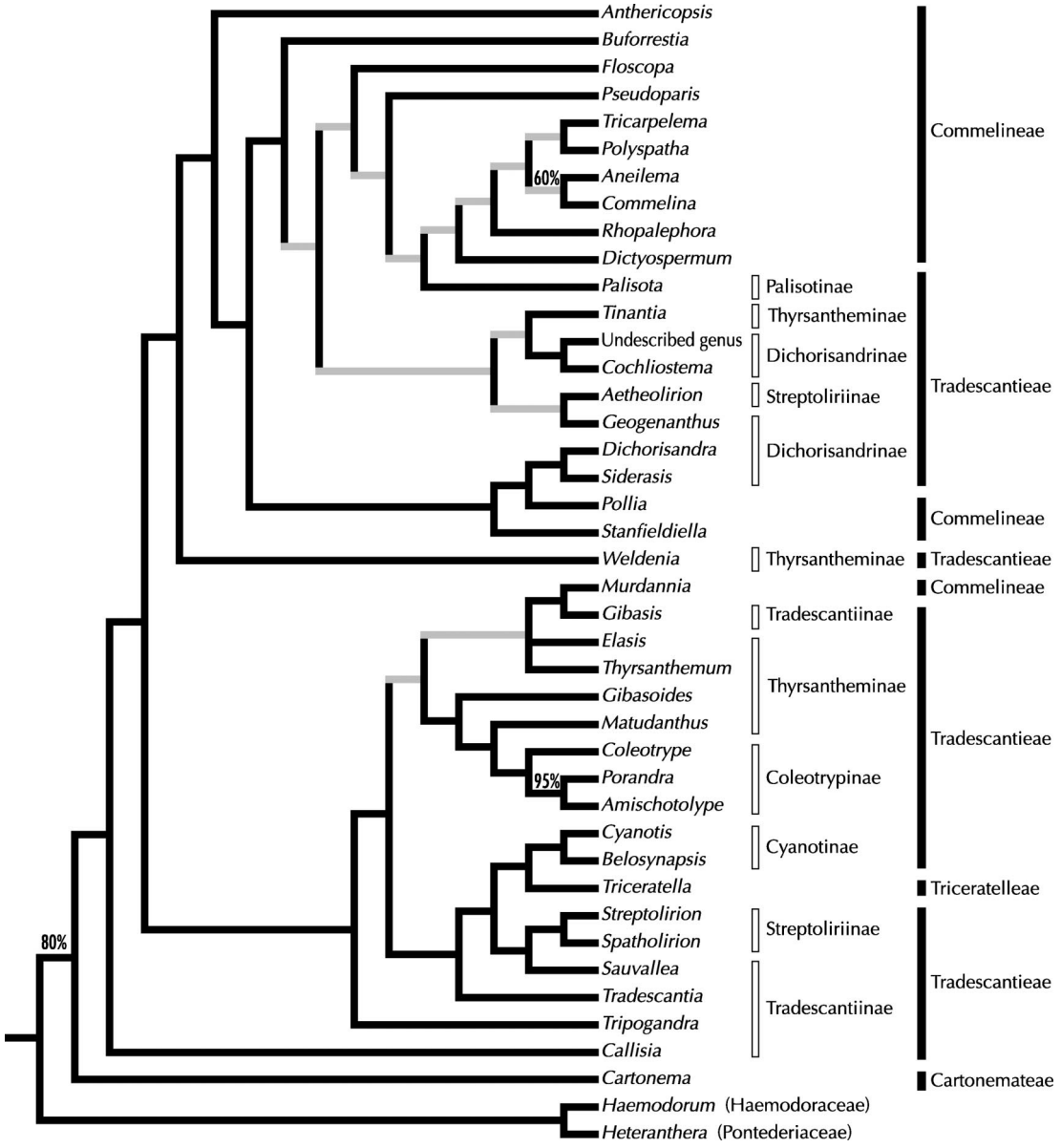

FIG. 1. A representative of the 154 equally most parsimonious trees found in the unordered analysis of 47 morphological characters in Commelinaceae using *Haemodorum* and *Heteranthera* as outgroups (from Evans et al. 2000a; Length = 239, CI′ = 0.43, RI = 0.63). Grey lines represent branches that collapse in the strict consensus of most parsimonious trees. Bootstrap values greater than 50% are shown above branches. Subtribal and tribal affinities are indicated with the bars to the right of the cladogram.

a combined data approach. Although arguments (philosophical and practical) can be made for advantages and disadvantages of the consensus, combined, and conditional combination approaches (see review in Soltis and Soltis 1998), we explore here multiple taxonomic and character congruence approaches to obtain additional information about both character evolution and phylogenetic relationships.

The goals of this study are to: (1) use *rbcL* sequence data to evaluate the phylogenetic relationships among genera in Commelinaceae; (2) compare results obtained from morphology with DNA sequences to assess whether there is significant incongruence between the two, whether there is greater homoplasy in the morphological data, and what classes of morphological characters contribute most to any incongruence between data sets; (3) determine whether analysis of the combined data provides additional phylogenetic infor-

TABLE 1. Taxa for which *rbcL* was sequenced in this study, with GenBank accession numbers. * indicates taxa for which sequence was obtained from GenBank.

Amischotolype monosperma (C. B. Clarke) I. M. Turner *Bogner 1811*, AF312239; *Aneilema calceolus* Brenan *Faden and Faden 77/565,* AF036889; *Aneilema clarkei* Rendle *Faden and Beentje 85/49,* AF312253; *Aneilema neocaledonicum* Schltr. *McPherson 6842,* AF312252; *Anthericopsis sepalosa* (C. B. Clarke) Engl. *Faden 74/504,* AF312259; *Belosynapsis kewensis* Hassk. *Hort. U. Chicago Greenhouse s.n.,* AF312257; *Buforrestia obovata* Brenan *Hall s.n.,* AF036886; *Callisia navicularis* (Ortgies) D. R. Hunt *Fryxell s.n.,* AF312248; *Callisia repens* (Jacq.) L. *A. B. Graf s.n.,* AF312247; *Cartonema philydroides* F. Muell. *Hort. Munich Bot. Gard. s.n.,* AF036890; *Cochliostema odoratissimum* Lem. *Ex. Marie Selby Bot. Gard. s.n.,* AF312244; *Coleotrype natalensis* C. B. Clarke *Goldblatt 6587,* AF312243; *Commelina congesta* C. B. Clarke *Faden 86/68,* AF036888; * *Commelina benghalensis* L. Duvall et al. 1995, L05033; *Cyanotis* sp. *A. Faden 8/82,* AF312241; *Dichorisandra thyrsiflora* Mikan *Hort. Mo. Bot. Gard. s.n.,* AF312242; *Elasis hirsuta* (Kunth) D. R. Hunt *MacDougal and Lalumondier 4953,* AF312251; *Floscopa scandens* Lour. *Chu 23,* AF312255; *Geogenanthus poeppigii* (Miq.) Faden *Des Moines Botanical Center,* AF312261; *Gibasis geniculata* (Jacq.) Rohweder *Hort. Mo. Bot. Gard. s.n.,* AF312250; *Murdannia clarkeana* Brenan *Faden 87/59,* AF312256; *Palisota ambigua* (P. Beauv.) C. B. Clarke *Faden 86/55,* AF312240; *Pollia hasskarlii* R. S. Rao *Chu s.n.,* AF312262; *Polyspatha hirsuta* Mildbr. *Kahn 92/1,* AF312263; *Rhopalephora scaberrima* (Bl.) Hassk. *Hahn 5948,* AF312264; *Siderasis fuscata* (Lodd.) H. E. Moore *Hort. Mo. Bot. Gard. s.n.,* AF312254; *Spatholirion longifolium* Dunn *M. Chase 593,* AF036887; *Stanfieldiella imperforata* (C. B. Clarke) Brenan *Keating 89/6,* AF312265; *Tradescantia soconuscana* Matuda *Faden 76/98,* AF312238; * *Tradescantia zebrina* Hort. ex Bosse Duvall et al. 1995, L05042; *Thyrsanthemum* sp. *M. Chase 606,* AF312246; *Tinantia leiocalyx* C. B. Clarke *Iltis 3065,* AF312260; *Tripogandra diuretica* (Martius) Handlos *Plowman 10102,* AF312249; Undescribed genus *Encarnación et al. 93-542,* AF312258; *Weldenia candida* Schult. f. *M. Chase 592,* AF312245

Outgroups: **Anigozanthos flavida* DC. (Haemodoraceae) Chase et al. 1993, AJ404843; **Hanguana malayana* Merr. (Hanguanaceae) Chase et al. 1995, AF036877; **Philydrum lanuginosum* Banks & Sol. ex Gaertn. (Philydraceae) Graham 1995, U41596; **Pontederia cordata* L. (Pontederiaceae) Graham 1995, U41592; *Wachendorfia thyrsiflora* (Haemodoraceae) L. *M. Chase 263,* AF312266; **Zingiber gramineum* Noronha (Zingiberaceae) Smith et al. 1993, L05465

mation beyond that obtained from either morphology or molecules alone; and (4) reconstruct patterns of biogeographical diversification and ecological specialization in Commelinaceae.

MATERIALS AND METHODS

New sequences for *rbcL* were obtained for 32 species representing 30 genera of Commelinaceae (Table 1). Sequences for four additional species of Commelinaceae (see Table 1) were obtained from GenBank. Six sequences were included as part of a global outgroup approach (Maddison et al. 1984; see below). The data matrix contains 3.0% missing data.

Total DNA was isolated from fresh or frozen leaf material using the CTAB procedure of Doyle and Doyle (1987) as modified by Smith et al. (1991). *rbcL* was amplified using oligonucleotide primers that anneal to the first 26 nucleotides of the 5′ end of the gene and slightly downstream of the 3′ end. Amplifications were done on a Perkin Elmer Cetus DNA Thermocycler using dGTP nucleotides from United States Biochemical (USB) and either *Taq* polymerase or *Tfl* DNA polymerase from Promega. Sequences were obtained from double-stranded amplified products as described by Gyllensten (1989), using the Sanger dideoxy method (Sanger et al. 1977). The sequencing reactions were executed as described in the USB-Sequenase kit protocol, with the cold-shock modification recommended by Conti et al. (1993). The amplification primers, as well as internal primers (see Conti et al. 1993, 1997), spaced approximately 300 bases apart from one another, were used to obtain sequence from all but the first ca. 26 nucleotides of *rbcL*. Between 75 and 100% overlap of the two strands was obtained with these primers. DNA fragments were separated on a 6% polyacrylamide gel and exposed to Kodak X-OMAT AR X-ray film for a minimum of 12 hours. Sequences were aligned to a template of the *Tradescantia zebrina rbcL* sequence and entered manually into a computer file using MacClade version 3.0 (Maddison and Maddison 1992).

Outgroup Selection. The relationships of Commelinaceae with other monocot families have been widely debated (Cronquist 1981; Dahlgren et al. 1985; Clark et al. 1993; Duvall et al. 1993; Stevenson and Laconte 1995; Givnish et al. 1999); thus, the more global *rbcL* analysis of commelinoid monocots (Givnish et al. 1999) was used to select appropriate outgroups for a cladistic analysis within the family. That study consistently identified a well-supported clade consisting of Commelinaceae, Hanguanaceae, Pontederiaceae, Philydraceae, and Haemodoraceae. The other families traditionally placed with Commelinaceae in the order Commelinales on morphological grounds—Eriocaulaceae, Mayacaceae, Rapateaceae, and Xyridaceae (Dahlgren et al. 1985; Stevenson and Laconte 1995)—were placed elsewhere in three other monocot clades (Givnish et al. 1999). We therefore included outgroup representatives of Haemodoraceae, Hanguanaceae, Pontederiaceae, and Philydraceae, as well as one representative of the more distantly related Zingiberaceae used to root the tree.

Phylogenetic Analyses. All phylogenetic analyses used PAUP* vers. 4.0b4a (Swofford 1999). Two search strategies were employed to find the most parsimonious trees: (1) a multiple-islands approach (Maddison 1991) modified from Olmstead et al. (1993) and Olmstead and Palmer (1994), and (2) a simple search involving 1,000 random-addition sequences and TBR swapping, with steepest descent and MULPARS activated. Bootstrap analyses were conducted to evaluate internal support for each node. One thousand replicate searches were performed on informative characters using TBR branch-swapping. The possible misuses and misinterpretations of bootstrap values are well understood (Sanderson 1989; Wendel and Albert 1992; Felsenstein and Kishino 1993; Hillis and Bull 1993), but bootstrap values still provide useful information about the relative degree of support of individual clades. Support for each clade within phylogenies was also evaluated using decay analysis (Bremer 1988). The decay values were determined using AutoDecay vers. 2.4 (Eriksson and Wilkström 1995) and executed in PAUP* 4.0 using 10 replicate random-addition sequences, heuristic search, and TBR branch-swapping. Two additional analyses were conducted in PAUP* 4.0 to explore how character-state weighting or alternative optimality strategies might affect phylogenetic relationships, using (1) maximum parsimony analysis using codon weighting of nucleotide sequence data (Albert and Mishler 1992; Albert et al. 1993) and (2) a maximum likelihood analysis using a transition/transversion ratio of 2.0 and empirical frequencies of individual nucleotides.

Integration of Molecular and Morphological Data. To evaluate whether the morphological and molecular data sets are congruent, we employed approaches based on both tree topology and character congruence, to permit the most effective assessment of divergence and agreement in the phylogenetic information con-

tained in the two data sets (Larson 1994, Mason-Gamer and Kellogg 1996, Johnson and Soltis 1998, and de Queiroz 2000). For all comparisons between *rbcL* and morphology, the morphological data set was taken from Evans et al. (2000a). As a preliminary indication of taxonomic congruence (agreement between tree topologies produced by the different data sets separately), a strict consensus tree was constructed for all most parsimonious trees produced from Fitch analysis of molecular data and unordered analysis of morphological data. As there was not complete duplication in taxon sampling, taxa that were not included in one or the other analysis were pruned from the trees before they were combined. When taxa not present in both the *rbcL* and morphology analyses were pruned from the most parsimonious trees, 80 of the original 154 morphological trees and 4 of the 15 molecular trees were retained. As a quantitative index for assessing topological congruence between the morphology and DNA trees, the partition metric based on tree interconversion was used following the recommendations of Johnson and Soltis (1998; their Box 11.1). The partition metric index was calculated by PAUP* 4.0 (using symmetrical differences) and probabilities assigned based on comparisons with random pairs of trees generated from each data set (following the procedure in Johnson and Soltis 1998, Box 11.9).

To assess character congruence, we combined the two data sets and searched for the most parsimonious tree(s) using the multiple-island search strategy. Because different outgroup genera were used in the morphological and molecular analyses, only taxa of Commelinaceae were included in the combined analysis. However, because both molecular and morphological analyses strongly place *Cartonema* as being sister to all other Commelinaceae, *Cartonema* can justifiably be used as an outgroup. Four genera (*Aneilema*, *Callisia*, *Commelina*, and *Tradescantia*) were scored for multiple species in the molecular study but only for a single species in the morphological analysis. Combined analyses included all of the species that were present in the molecular study. As the morphological data are specific to a given species from a genus (see Evans 1995; Evans et al. 2000a) and the possibility is great that some of the larger genera are not monophyletic (see Results), we followed the conservative approach and scored morphological characters as missing for other species of a genus in the combined data set.

Character congruence was quantified by calculating both I_{MF} (Mickevich and Farris 1981) and I_M (Miyamoto, in Swofford 1991). The first index uses both the separate analyses and the combined analysis to determine what proportion of the incongruence is due to within-data set conflict, and what proportion is due to between-data set conflict (see Swofford 1991; Johnson and Soltis 1998). The second index determines how much of the character incongruence is due to within-data set incongruence, but does not involve comparison with a combined analysis. As a statistical measure of conflict between the two data sets, the Partition Homogeneity Test (Farris et al. 1994, 1995) was employed using PAUP* 4.0. One thousand replicates of this test were performed using TBR branch-swapping, simple addition sequence, and steepest descent. Given the large amount of computer time required to run the Partition Homogeneity Test, the maximum number of trees retained for each replicate was limited to 100. Although setting the maximum number of trees to 100 may reduce the chance of finding the most parsimonious topologies, Farris et al. (1994) note that even a single pass through the data should be sufficient, as the exact tree-lengths are not critical to the test.

Assessment of Character Evolution and Homoplasy. To further evaluate character congruence between the morphological and molecular data sets, we employed the Wilcoxon signed-ranks test (Templeton 1983; see implementation in Larson 1994 and Johnson and Soltis 1998). This approach not only provides a statistical measure of how well characters from one data set map onto specified trees obtained from a second data set, it also permits a more detailed analysis of how individual (morphological) characters are behaving. We also determined the consistency index (CI) for each morphological character when mapped onto the morphology, *rbcL,* and combined data set trees. To compare the performance of morphological characters on each of the three sets of trees, we regressed the CI of individual characters on the morphology tree against (1) the CI of the same characters on the molecular tree, and (2) the CI of the same characters on the combined-data tree; the least-mean-squares (Model I) approach was taken. Analysis of covariance was used to determine whether the slopes of the regression lines varied significantly from the expected value of 1.0. Regression analysis and analysis of covariance were conducted with the Systat 5.2 computer statistical software package. Categories of characters (anatomy, floral, androecium, floral minus androecium, fruit/seed, and inflorescence) defined by Evans et al. (2000b) were examined for significant differences in CI when mapped onto the morphology, molecular, and combined data trees, using the Bonferroni test of pairwise mean comparison. The Bonferroni method allows for multiple mean comparisons while guaranteeing that no single mean differs from the others by chance alone (see Moore and McCabe 1989).

Character State Mapping. To reconstruct historical shifts in morphology and biogeography, we overlaid characters onto a representative tree from the combined data set, assuming accelerated transformation (ACCTRAN) in MacClade 3.0 (Maddison and Maddison 1992; delayed transformation [DELTRAN] was also evaluated in cases where alternate optimizations may affect conclusions). For the purposes of character-state reconstruction, we focused on evolution at the generic level and above, and therefore used a tree in which all but one species per genus had been pruned. We examined the evolution of (1) geographic distribution (Old World vs. New World); (2) seed dispersal mechanism (animal dispersal of fleshy fruits vs. wind or gravity dispersal of seeds); and (3) inflorescence position (axillary vs. terminal).

Molecular Clock. The likelihood ratio test (Felsenstein 1981, 1994; Huelsenbeck and Rannala 1997) was used to test the assumption of a molecular clock, in order to explore the possibility of establishing a range of divergence times for lineages within Commelinaceae. The null hypothesis for this test is that the rate of nucleotide substitutions is constant along all branches of the phylogeny. If a molecular clock is operating, then the likelihood score (L) for an optimal phylogeny in which no molecular clock is enforced will not differ significantly from the likelihood of a phylogeny in which a molecular clock is enforced. For implementation of the likelihood ratio test, outgroup taxa were pruned from the maximum parsimony phylogenies, and *Cartonema* was used as a functional outgroup. Log likelihood scores (lnL) were determined for all of the most parsimonious trees, first without a molecular clock and then with enforcement of a molecular clock. The likelihood ratio, $2(-\ln L_{\text{no clock}} + \ln L_{\text{clock}})$ for each of the 15 trees was compared with the X^2 distribution with 34 degrees of freedom (number of taxa − 2) to test for significant departure from a molecular clock (Felsenstein 1994).

RESULTS

Molecular Analyses. The unweighted analysis yielded 15 most parsimonious trees of 974 steps without autapomorphies (CI′=0.42) and 1149 steps with autapomorphies (CI=0.51). When codon weighting was employed, a single most parsimonious tree emerged (Fig. 2), representing one of the 15 trees in the unweighted analysis. Maximum likelihood analysis yielded a single tree that was also one of the 15 trees produced by the unweighted cladistic analysis. This tree (not shown) differed from the codon-weighted tree in the positions of *Buforrestia* and *Tradescantia socunuscana*. Relationships among the outgroup taxa are weak, as also seen in the broader Commelinidae analysis of Givnish et al. (1999). All analyses, however, placed the largely Australian endemic *Cartonema* sister to the rest of Commelinaceae. *Palisota* Reichb., from tropical Africa, is sister to the remaining genera, which

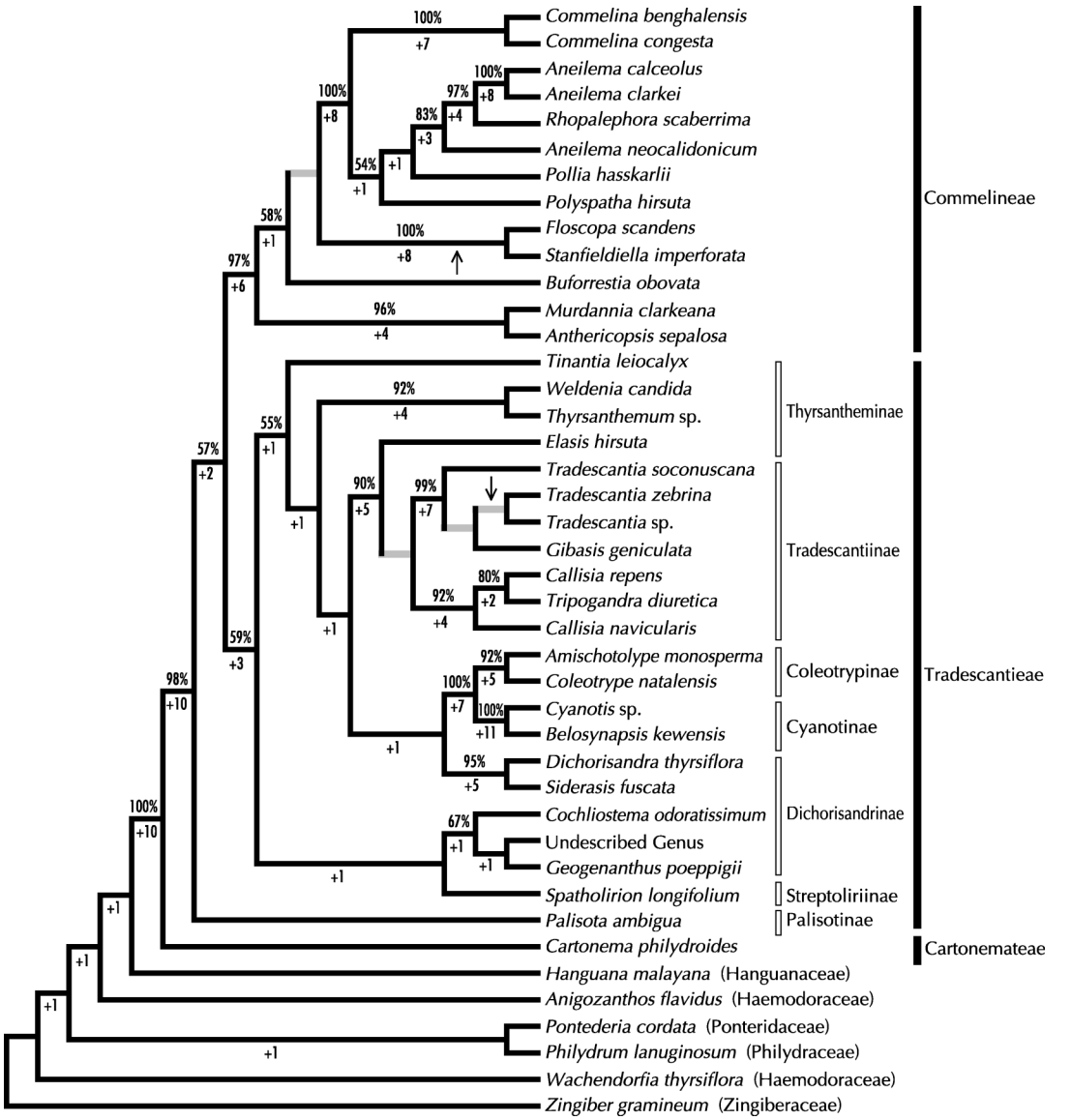

FIG. 2. Single most parsimonious tree produced in the codon weighted cladistic analysis of *rbcL* sequences in the Commelinaceae and one of the 15 most parsimonious trees in the unweighted analysis (Length = 974, CI′ = 0.42, RI = 0.60). Grey lines represent branches that collapse in the strict consensus of the 15 most parsimonious trees. Numbers below each branch indicate the number of additional steps required before that branch collapses (decay value); numbers above each branch indicate bootstrap support. Arrows indicate shift of branches in the maximum likelihood tree. Subtribal and tribal affinities are indicated with the bars to the right of the cladogram.

form two large clades corresponding to tribe Commelineae and tribe Tradescantieae minus *Palisota*. Two extra steps are required to place *Palisota* within a monophyletic Tradescantieae. Two subtribes within Tradescantieae are not resolved as monophyletic: Dichorisandrinae [Pichon] Faden and D. R. Hunt, and Thyrsantheminae Faden and D. R. Hunt. A monophyletic Dichorisandrinae is recovered in trees one step longer. Thyrsantheminae, however, appears to be strongly polyphyletic, with monophyly requiring seven additional steps.

rbcL/Morphology Combined Analyses. After pruning taxa for which only molecular or morphological data were available, we obtained 80 morphological trees and 4 molecular trees. A strict consensus of these trees (not shown)—that is, taxonomic congruence—resolves only five clades: *Cartonema*; the rest of the family; *Cyanotis* and *Belosynapsis*; *Coleotrype* and *Amischo-*

TABLE 2. Partition metric indices for topological incongruence within and between morphological and molecular tree sets as compared to between random tree sets generated from each data set. The normalized distance values are given in parentheses.

Tree comparison	Mean partition metric	Range partition metric
Morphology–Morphology	7 (0.106)	1 (0.015)–15 (0.227)
DNA–DNA	4 (0.061)	2 (0.030)–8 (0.121)
Morphology–DNA	59 (0.894)	55 (0.833)–61 (0.924)
Random–Random	65 (0.985)	51 (0.773)–66 (1.000)

tolype; and *Dichorisandra* and *Siderasis*. The analysis of partition metric indices (Table 2) indicates little incongruence **within** either the morphology or DNA tree sets, but substantial incongruence **between** these two sets of trees. The mean partition metric index between morphology and molecular trees (59) is close to the mean index (65) between 1,000 random trees generated from each data set and well within the range of these random tree indices (51–66).

When the data sets were combined for a ''total data'' analysis, five trees of 832 steps and a CI' of 0.41 were produced (999 steps with autapomorphies, CI = 0.51). One of these five trees, showing branches collapsed in the strict consensus tree, is shown in Figure 3. The character incongruence analyses demonstrated moderate to substantial incongruence between the morphological and molecular data sets (Table 3). The I_{MF} index (0.081) indicated that less than 10% of the incongruence was due to conflict between data sets, whereas the I_M index (0.487) indicated that nearly 50% of the conflict was between data sets. The Partition Homogeneity Test indicated that the molecular and morphological data sets have significantly different phylogenetic structure. The null hypothesis that the two data sets are homogeneous was rejected ($P = 0.001$). When using the combined data sets, the Templeton test (Wilcoxon signed ranks test) indicated significant differences ($P < 0.0001$) in pair-wise comparisons of morphology trees with either molecular or combined trees, but not ($P > 0.1$) in comparisons of molecular with combined trees. Thus, with both taxonomic and character incongruence tests, the morphological and molecular data sets for Commelinaceae are providing significantly different phylogenetic estimates of generic relationships.

As perhaps expected with 409 informative character state changes possible in *rbcL* and 107 possible in the morphological data set (some of the 47 characters have more than 2 states), the phylogenetic trees from the combined data set (Fig. 3) were far more similar to the DNA trees than to the morphology trees. Of the total 27 resolved clades in the combined data strict consensus tree, 21 are maintained from the *rbcL* strict consensus tree and only 5 from the morphological strict consensus tree. *Cartonema*, again, represents the early diverging lineage in the family and sister to the remainder of Commelinaceae. Likewise, *Palisota* is placed as sister to the clade comprising the tribes Tradescantieae (minus *Palisota*) and Commelineae, as seen in the molecular data. Interestingly, as opposed to the DNA results, now only one of the subtribes within Tradescantieae is not monophyletic (Thyrsantheminae) with Dichorisandrinae now forming a monophyletic group (although it was monophyletic in one-step longer DNA trees). Relationships within Commelineae are somewhat different from the DNA results, but most differences between the combined data trees and the DNA trees in this tribe are in clades poorly supported by either *rbcL* or the combined data as indicated by low bootstrap and decay support (Figs. 2–3).

CI values for morphological characters mapped onto the morphological phylogeny showed significant correlations with the corresponding values for the same characers mapped onto the *rbcL* phylogeny (Fig. 4a) or the combined tree (Fig. 4b). However, in each case, the LMS slope was significantly less than the slope of 1.0 expected if the two data sets were completely congruent. For the morphology/DNA comparison, the least mean squares regression analysis yielded a slope of 0.2, significantly less than the expected value of 1.0 ($P < 0.001$). Similarly, for the morphology/combined data comparison, the LMS analysis yielded a slope of 0.33, significantly less than the expected value of 1.0 ($P < 0.001$).

The mean CI for the six categories of morphological characters when mapped onto the (1) morphological tree, (2) DNA tree, and (3) combined data tree revealed differences in performance of some character classes (Fig. 5; Tables 4 and 5). No statistical difference was found among the CIs of character classes when mapped onto the morphological tree (Fig. 5a; Table 5). However, significant differences were found in CIs among classes when mapped onto either the DNA or the combined data trees. For example, on the DNA trees, the mean CI for vegetative anatomical characters is significantly greater than for androecial, floral, and fruit/seed characters (Fig. 5b; Table 5). Likewise, anatomical characters performed significantly better on the combined phylogeny than all classes of characters except inflorescence characters (Fig. 5b; Table 5).

Character State Mapping. When geographical distribution is overlaid onto the combined phylogeny, New World members of tribe Tradescantieae are found in two separate lineages (Fig. 6). Within the tribe, the two Old World subtribes, Coleotrypineae and Cyanotineae, are nested well within New World taxa. Thus, it appears that evolution of Tradescantieae involved one movement from the Old World to the New World, followed by a reintroduction from New to Old (using

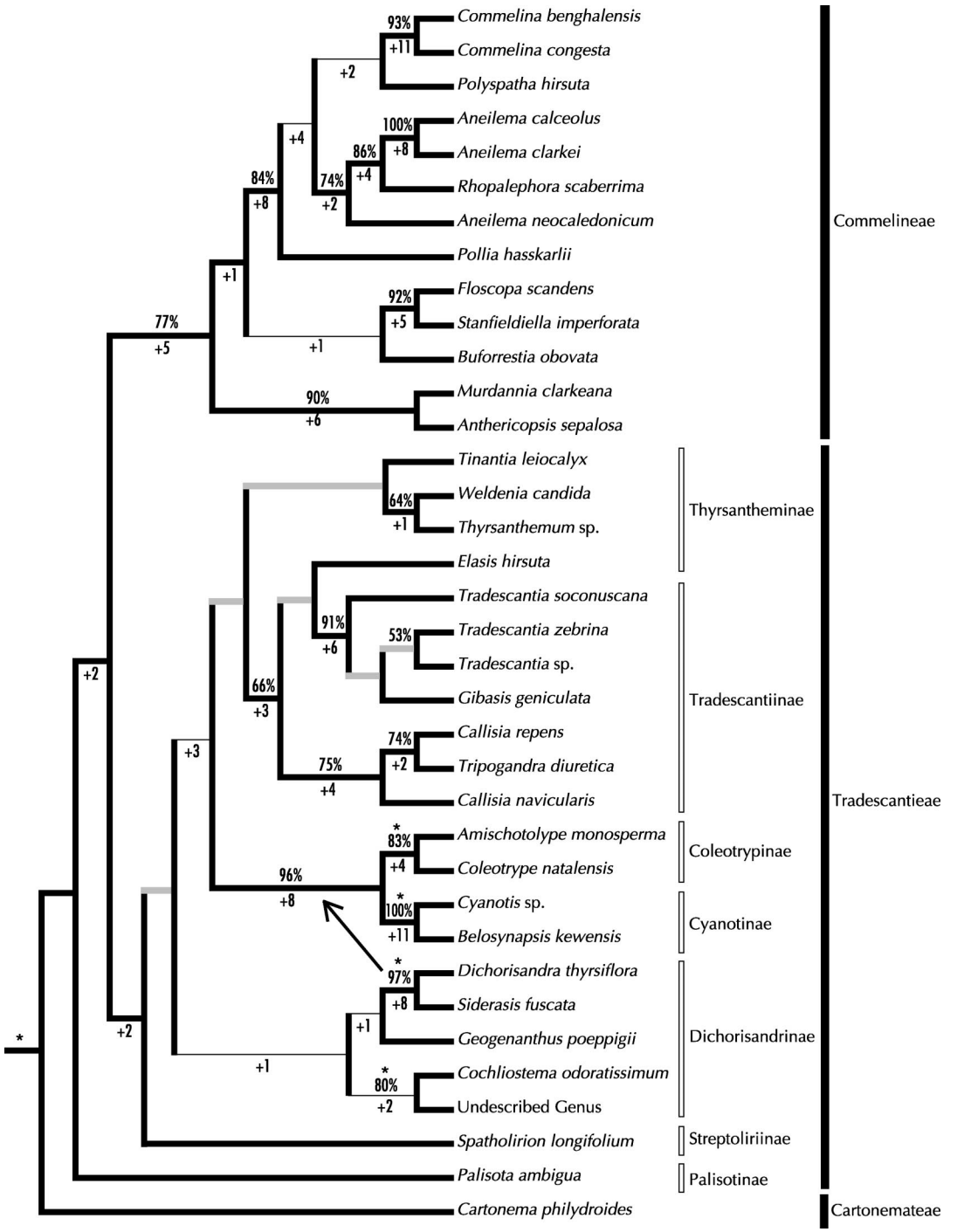

FIG. 3. One of five most parsimonious trees produced by combined morphology/*rbcL* data sets (Length = 832, CI′ = 0.41, RI = 0.61). Grey lines represent branches that collapse in the strict consensus of the five most parsimonious trees. Numbers below each branch indicate the number of additional steps required before that branch collapses (decay value); numbers above each branch indicate bootstrap support. Subtribal and tribal affinities are indicated with the bars to the right of the cladogram. Twenty-one branches in bold are congruent with *rbcL* strict consensus tree; five branches indicated with an asterisk are congruent with the morphological strict consensus tree. Note that subtribe Dichorisandrineae is monophyletic in the combined analysis but not with either of the two separate analyses. Arrow indicates placement of portion of the subtribe Dichorisandrineae in the *rbcL* tree; this one shift would allow two other clades to be congruent with the *rbcL* strict consensus tree.

TABLE 3. Values used for calculating character congruency indices for comparisons of the morphology and *rbcL* data sets (after reducing number of taxa to match overlap). All values were determined with autapomorphies excluded. I_{MF} index = 0.081; I_M index = 0.487.

	Minimum tree length	Actual tree length	Number of extra steps	CI
Morphology	minL{a} = 61	LenA{a} = 156	95	0.391
Molecular	minL{b} = 444	LenB{b} = 803	359	0.553
Combined	minL{a,b} = 505	LenAB{a,b} = 999	494	0.506
Morphology data on molecular trees	n.a.	LenB{a} = 1188	n.a.	n.a.
Molecular data on morphology trees	n.a.	LenA{b} = 202	n.a.	n.a.

ACCTRANS optimization), or two movements from the Old World to the New World (using DELTRANS optimization). The distribution of seed dispersal mechanism and inflorescence position showed these two characters to be homoplasious within the family (Fig. 7 and 8). Distributions of these characters, however, were associated with ecological factors, such as habitat type, pollination syndrome, and dispersal mechanism.

Molecular Clock. The likelihood ratio test strongly rejected the assumption of a molecular clock for all most parsimonious trees (Table 6). The likelihood ratio ($2[-\ln L_{\text{no clock}} + \ln L_{\text{clock}}]$) was 176.98. Assuming a X^2 distribution and 34 degrees of freedom, the likelihood ratio indicates that the molecular clock may be rejected for each most parsimonious tree with a probability of $P<0.0001$.

DISCUSSION

Six important conclusions emerge from this analysis of *rbcL* sequence and morphological variation in Commelinaceae: (1) DNA and morphological results are incongruent; (2) the total evidence phylogeny largely matches the DNA phylogeny, supports monophyly of an additional subtribe not seen with DNA alone, and is closely congruent with the most recent classfication for Commelinaceae; (3) *Cartonema* is sister to the remainder of the family; (4) tribes Commelineae and Tradescantieae (excluding *Palisota*) are monophyletic and contain strongly supported clades; (5) an Old World origin of the family is supported with several subsequent shifts between the Paleotropics and Neotropics; (6) ecological specialization and convergence

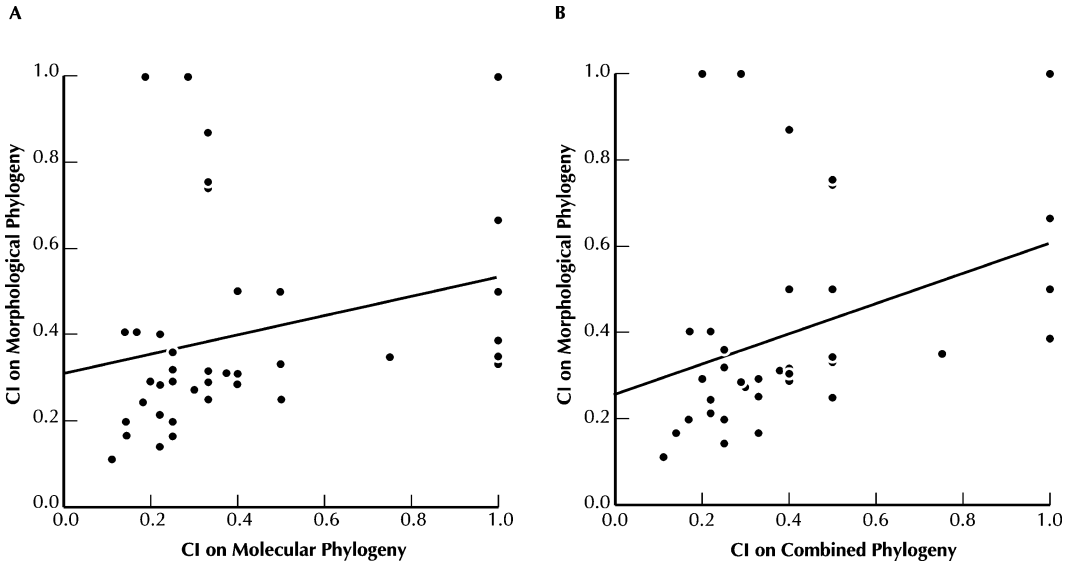

FIG. 4. Consistency index (CI) of each morphological character (from Evans et al. 2000a) mapped onto the most parsimonious trees from the morphological data set versus its CI when mapped onto the most parsimonious trees of the (A) *rbcL* data set and (B) combined data set. Analysis of covariance indicates that the slope of each regression line varies significantly from the expected value of 1.0, barring any incongruence between the data sets (slope in graph A = 0.2, $p<0.001$; slope in graph B = 0.33, p,0.001).

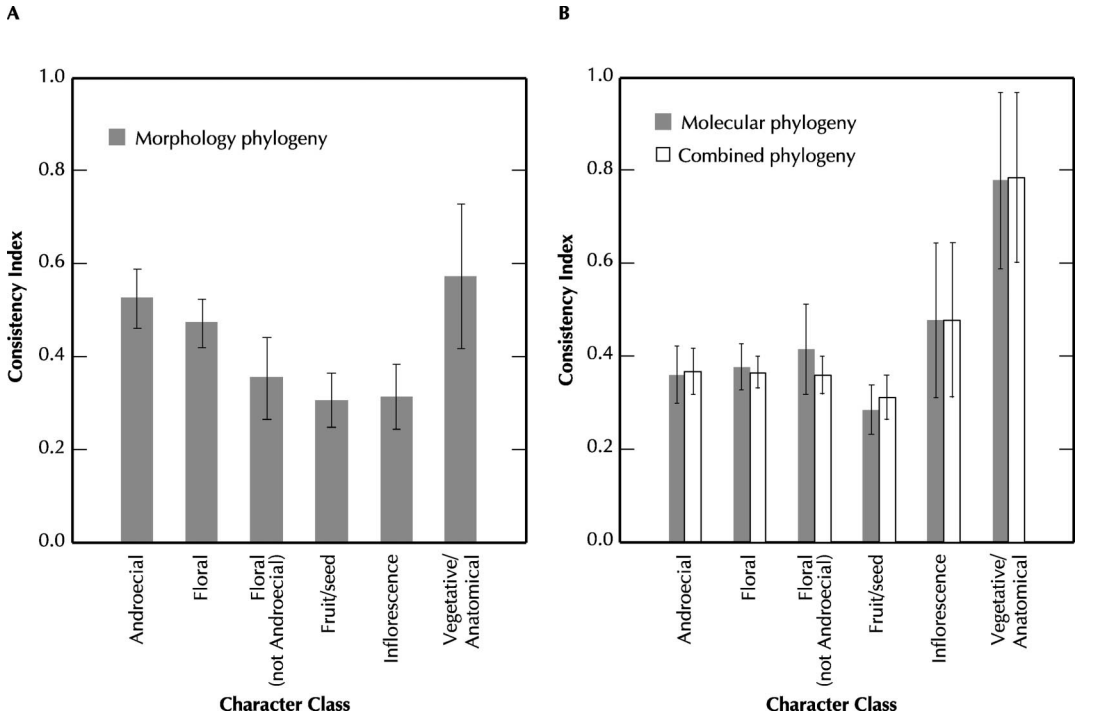

FIG. 5. Histogram showing the mean consistency index (CI) for six categories of morphological characters (see Evans et al. 2000b for discussion of these categories). (A) CIs mapped onto a representative morphology tree. No statistical difference was found between any two character classes. (B) CIs mapped onto a representative *rbcL* tree and onto a combined data set tree. Anatomical characters showed statistically greater support for both molecular and combined trees than did any other character class ($P = 0.002$).

in floral and inflorescence characters contribute to the long-standing systematic issues in the family and incongruence between morphology and DNA.

DNA and Morphology are Incongruent in Commelinaceae. With the increasingly common practice of obtaining both morphological and molecular data for groups of organisms, more rigorous comparisons of congruence are now possible. The results often indicate substantial agreement between morphology and molecules (e.g., Bousquet et al. 1992; Eldenäs and Linder 2000; see recent reviews in Sytsma and Hahn 1996, 2001). Examples abound, however, where the molecular and morphological data sets (or even different molecular data sets) provide incongruent hypotheses of phylogenetic relationships (e.g., Qiu et al. 1993; Mishler et al. 1994; Olmstead and Sweere 1994; Linder and Kellogg 1995; Eriksson and Donoghue 1997; Normark and Lanteri 1998; Givnish et al. 1999; McCracken et al. 1999; Quicke and Belshaw 1999; Wiens and Hollingsworth 2000). One might argue that such incongruence is biologically more interesting as it provides a window into genome or phenotypic evolution (Wendel and Doyle 1998).

The appropriate treatment of multiple independent data sets is currently an area of debate in systematics (Cracraft and Mindell 1989; Kluge 1989; Sytsma 1990; Barrett et al. 1991; Swofford 1991; Donoghue and Sanderson 1992; Bull et al. 1993; de Queiroz 1993; de Quei-

TABLE 4. Mean CI values for each class of morphological characters as mapped onto the morphological, *rbcL*, or combined phylogeny. [a] Numbers indicate characters as listed in Table 1.

Class	Number of characters (N)	Mean CI (morphology)	Mean CI (molecular)	Mean CI (combined)
Vegetative/Anatomical	5	0.57 ± 0.10	0.78 ± 0.12	0.78 ± 0.09
Androecial	17	0.56 ± 0.06	0.37 ± 0.06	0.37 ± 0.05
Floral (including androecial)	26	0.47 ± 0.05	0.37 ± 0.05	0.36 ± 0.04
Floral (excluding androecial)	9	0.28 ± 0.09	0.40 ± 0.09	0.35 ± 0.07
Fruit/seed	7	0.31 ± 0.10	0.29 ± 0.10	0.31 ± 0.08
Inflorescence	5	0.55 ± 0.09	0.48 ± 0.12	0.48 ± 0.09

TABLE 5. Bonferroni adjusted probabilities for pairwise comparisons of mean CI value of morphological characters mapped onto the morphological, *rbcL*, and combined phylogenies. Values indicate the probability (P) that the mean CI values for each class of characters are statistically the same. Values to the left of the diagonal represent characters mapped onto morphological phylogeny. Values to the right of the diagonal represent characters mapped onto the *rbcL* (left of slash) and combined (right of slash) phylogenies.

	Vegetative/ anatomical	Androecial	Floral (all)	Floral (minus androecium)	Fruit/seed	Inflorescence
Vegetative/Anatomical	**1.000**	0.037/0.003	0.032/0.001	0.146/0.004	0.026/0.003	1.000/0.300
Androecial	1.000	**1.000**	1.000/1.000	1.000/1.000	1.000/1.000	1.000/1.000
Floral (all)	1.000	1.000	**1.000**	1.000/1.000	1.000/1.000	1.000/1.000
Floral (minus androecium)	0.491	0.122	**0.782**	**1.000**	1.000/1.000	1.000/1.000
Fruit/seed	0.976	0.415	1.000	1.000	**1.000**	1.000
Inflorescence	1.000	0.894	1.000	1.000	1.000	**1.000**

roz et al. 1995; Miyamoto and Fitch 1995; Huelsenbeck et al. 1996; Givnish and Sytsma 1997a,b; Luckow and Bruneau 1997). The main justifications for keeping data sets separate are (1) they allow for consensus procedures that will produce the most conservative estimate of relationships by accepting only those groups that are produced by each data set (Hillis 1987); (2) each provides independent verification of a particular phylogeny and assumptions of character homology and evolution (Sytsma 1990; Swofford 1991; Bull et al. 1993, Lanyon 1993; Miyamoto and Fitch 1995); and (3) a more selectively neutral (at least to ecological forces) DNA dataset can be used to evaluate convergence in strongly selected morphological characters—especially where suites of characters may be involved (Sytsma et al. 1991; Givnish and Sytsma 1997a,b; Givnish 1998; Givnish et al. 1999). Likewise, justifications for combining data include: (1) combined data sets produce trees directly from the data while consensus trees are one step removed from the total data (Kluge 1989; Kluge and Wolf 1993) and thus can produce trees that may actually contradict the tree produced by the combined data sets, indicating that consensus procedures are not necessarily conservative (Cracraft and Mindell 1989; Barrett et al. 1991; Ernisse and Kluge 1993); and (2) the assumption that all data are equivalent and therefore that partitions among different ''sets'' of data are artificial (Ernisse and Kluge 1993; Kluge and Wolf 1993).

The consensus tree of the two sets of trees derived from morphological and *rbcL* analyses for Commelinaceae is almost totally unresolved, and may suggest substantial incongruence between the morphological and molecular data sets. Although both the morphological and *rbcL* data sets divide the family into two large clades, there are substantial differences in the composition of those clades. While the major clades in the *rbcL* tree correspond closely to the tribes Commelineae and Tradescantieae (with the exception of *Palisota*), the two large clades in the morphological tree are a mixture of taxa from both tribes. Thus, the issue of consensus techniques in the analysis of two data sets for Commelinaceae was not in the formation of spurious clades within the new consensus tree, but rather in the nearly complete lack of structure within the resulting consensus tree. The same difficulty with consensus techniques was found in *Columnea* (Smith and Sytsma 1994) and would suggest that consensus techniques may have little utility when even moderate amounts of incongruence are seen between data sets (see further discussion in Johnson and Soltis 1998). The partition metric indices for tree distances between the morphological and molecular trees are in the range of those seen for random trees; thus the trees from morphology and DNA are not more similar than expected by chance alone.

The I_{MF} index, which estimates character congruency based on a total combined data analysis, indicates that about 8% of the total incongruence in the combined analysis is due to incongruence between data sets (Table 3). One of the weaknesses of this index, however, is that it is dependent on the relative size of the different data sets; a much larger data set (such as the *rbcL* data set) can overwhelm a smaller one, and thus it can bias the amount of observed incongruence (Miyamoto 1985; Swofford 1991). The I_M index, however, is not dependent upon a combined data analysis; each data set is analyzed separately and then the characters of each set of data are mapped onto the trees produced by the other data. The I_M index for morphology and *rbcL* in Commelinaceae indicates that nearly 50% of the incongruence for these two data sets is due to between-data set conflict. The I_M value in Commelinaceae suggests a high degree of conflict between the data sets, higher than that reported for an analysis with some of the highest incongruence yet seen (*Krigia*, $I_{MF} = 0.114$, $I_M = 0.225$; Kim and Jansen 1994).

The Partition Homogeneity Test provides a statistical measurement of character incongruence between multiple data sets. The results from this analysis in Commelinaceae indicate that the morphological and *rbcL* data sets are significantly different from each other with a probability of 99% (P=0.01). The phylogeny produced by the original (non-randomized) data sets is significantly shorter than the trees produced when the two data sets were randomly recombined. In other

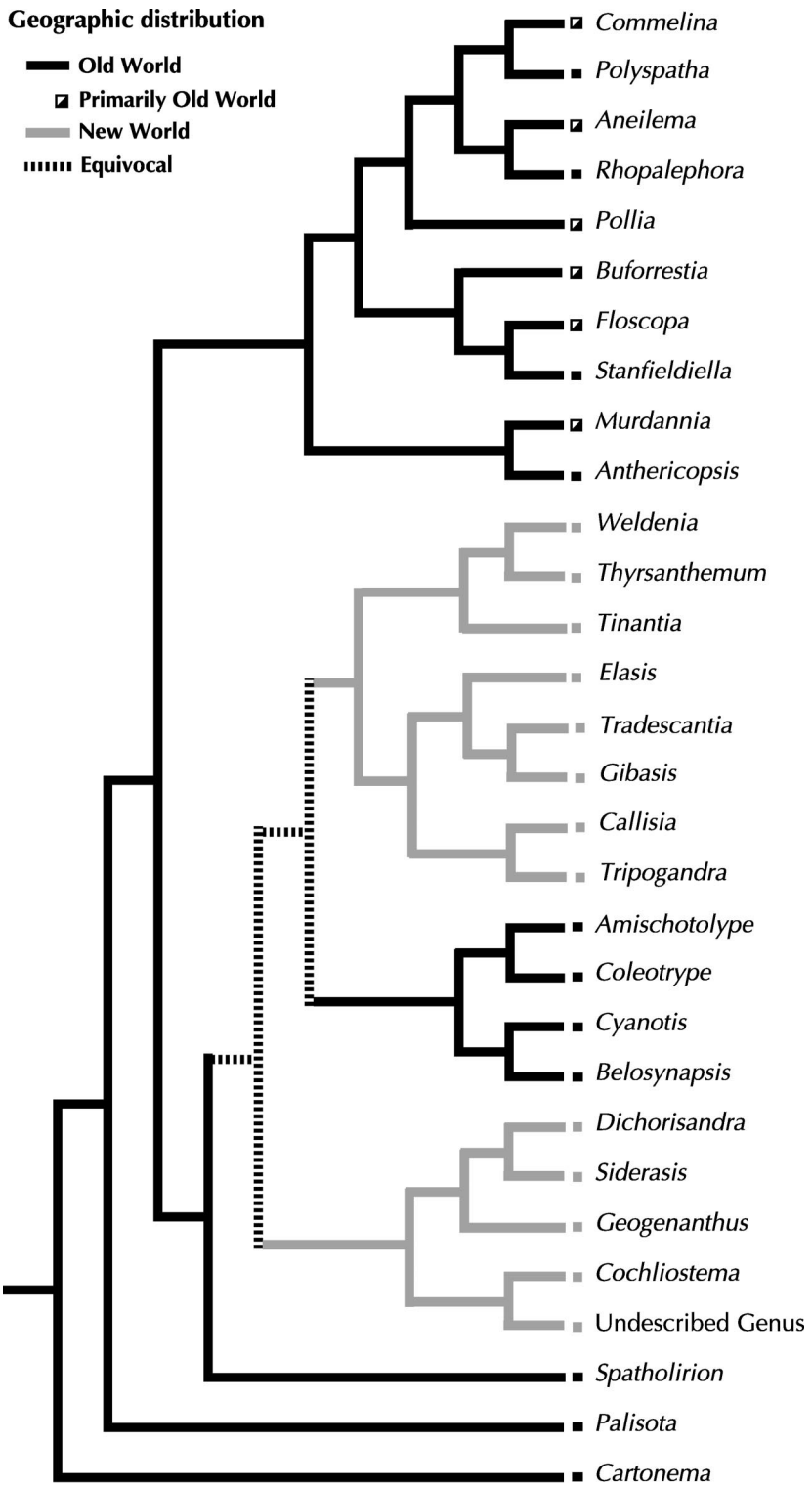

FIG. 6. Geographic distributions mapped onto a representative cladogram from the combined morphology/*rbcL* phylogeny, illustrating likely Old World origin for Commelinaceae. Although several genera are found in both the western and eastern hemispheres, the placement of the strictly Old World subtribes Coleotrypinae and Cyanotinae nested among New World genera suggests either a secondary introduction from the New World back to Africa or Asia or at least two introductions from the Old World to the New World.

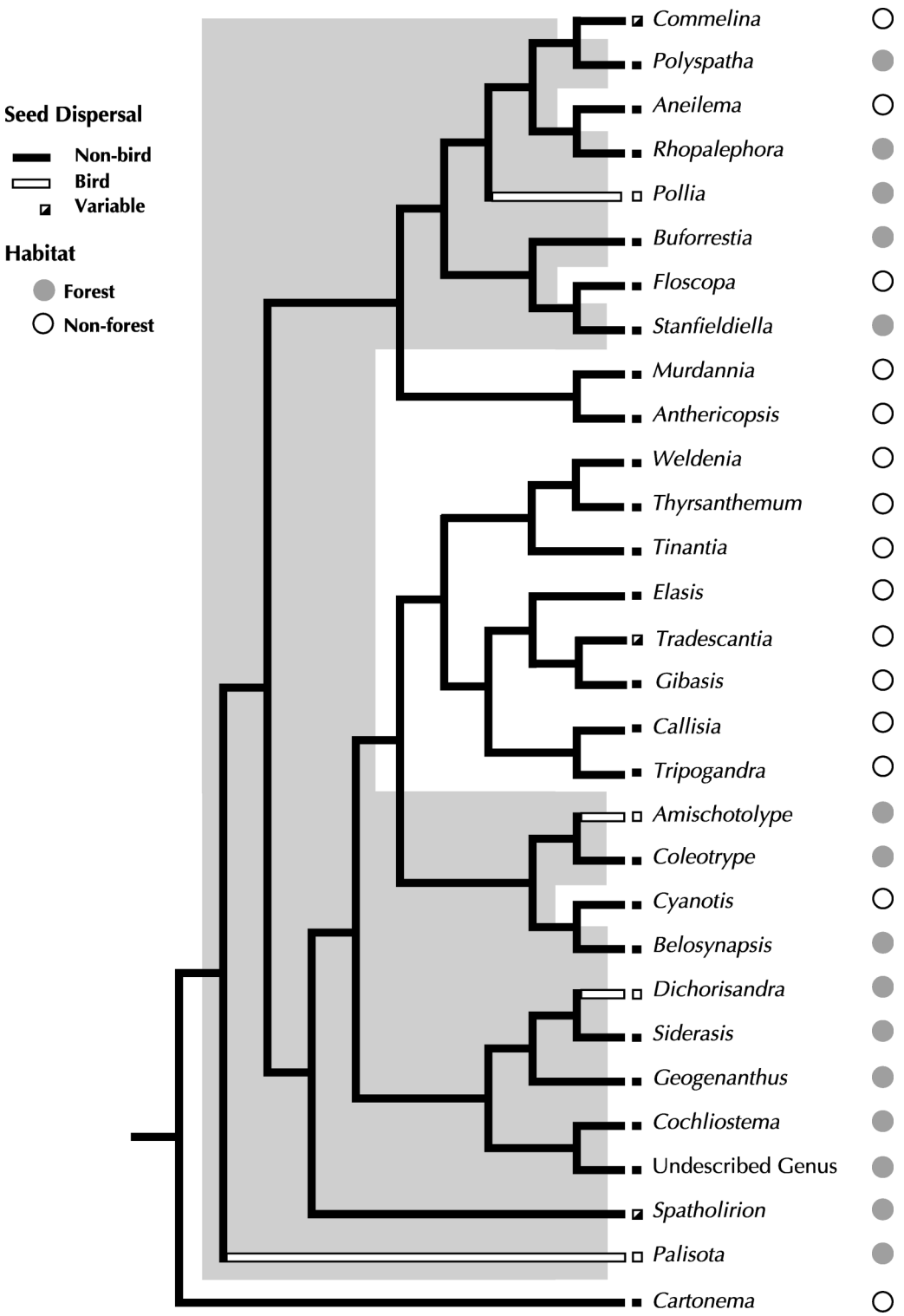

FIG. 7. Distribution of seed dispersal syndromes and habitat mapped onto a representative cladogram from the combined morphology/*rbcL* phylogeny. Habitat designation of forest or non-forest is according to Faden (1988). Note that all separate origins of seed dispersal by birds correlate with the forest habitat.

TABLE 6. Negative log maximum likelihood values for each of the 15 most parsimonious trees produced from a cladistic analysis of *rbcL* data in Commelinaceae, with and without enforcement of a molecular clock. P indicates the probability that the likelihood scores with and without enforcement of a molecular clock do not differ (Chi square distribution, 32 degrees of freedom).

Phylogeny	−1nL no clock	−1nL clock	$2(-1nL_{no\ clock} + 1nL_{clock})$	P
1	7026.07	7148.92	245.71	6.54×10^{-34}
2	7026.33	7149.20	245.75	6.40×10^{-34}
3	7026.09	7148.93	245.68	6.61×10^{-34}
4	7026.68	7146.14	238.91	1.25×10^{-32}
5	7030.42	7153.79	246.74	4.17×10^{-34}
6	7026.49	7146.06	239.15	1.13×10^{-32}
7	7026.35	7149.21	245.73	6.47×10^{-34}
8	7026.09	7148.93	245.68	6.61×10^{-34}
9	7026.70	7146.14	238.88	1.27×10^{-32}
10	7030.44	7153.79	246.71	4.22×10^{-34}
11	7026.51	7146.07	239.13	1.14×10^{-32}
12	7026.35	7149.21	245.73	6.47×10^{-34}
13	7026.70	7146.14	238.88	1.27×10^{-32}
14	7030.44	7153.79	246.71	4.22×10^{-34}
15	7026.51	7146.07	239.13	1.14×10^{-32}

words, a given character from one data set tends to support other characters from the same data set more strongly than it supports characters from the other data set. Thus, consensus approaches, I_M values, and Partition Homogeneity Testing indicate substantial incongruence between the morphology and *rbcL* data sets. Specific morphological characters contributing to this incongruence are examined later.

The Combined Data Tree is Similar to the DNA Tree. Maximum parsimony analysis of the combined data produced a topology (Fig. 3) that was only slightly more resolved than that based on *rbcL* alone (three unresolved nodes, versus four in the *rbcL* consensus tree). The combined data topology strongly resembles the tree produced by the molecular data, particularly in the placements of *Cartonema* (also seen in the morphological phylogeny) and *Palisota* at the base of Commelinaceae, and in the circumscription of the two main clades of tribes Commelineae and Tradescantieae. As is evident in Figure 3, a high proportion of the ingroup clades in the combined analysis (21 of 27 resolved clades indicated in bold) are seen in the *rbcL* tree alone.

One interesting feature of the combined data analysis, however, is the clade containing *Dichorisandra*, *Siderasis*, *Cochliostema*, *Geogenanthus*, and an undescribed genus—the subtribe Dichorisandrinae (Fig. 3). The morphological data set alone produced a highly polyphyletic Dichorisandrinae, uniting *Cochliostema* and the undescribed genus in one clade, and *Siderasis* and *Dichorisandra* in a second clade (Fig. 1); a monophyletic Dichorisandrinae is not obtained with the morphological analysis until parsimony is relaxed three extra steps. *rbcL* sequence data united *Cochliostema*, *Geogenanthus*, and the undescribed genus, while *Siderasis* and *Dichorisandra* were placed in a separate clade, also showing a polyphyletic Dichorisandrinae (Fig. 2). By combining the molecular and morphological data, these two groups are united into a single clade, and a set of relationships not seen in the analysis of either data set alone is produced. However, a monophyletic Dichorisandrinae is recovered in *rbcL* analyses by relaxing parsimony by only one extra step, suggesting that this seemingly striking difference between the molecular and combined analyses is simply incongruence in a weakly supported area of the molecular tree. A shift in placement of *Dichorisandra* and *Siderasis* in the combined tree to the position seen in the *rbcL* trees (see arrow in Fig. 3) requires one extra step and would then make an additional two clades congruent between the two analyses (see arrow in Fig. 3), for a total of 23 congruent clades out of 27 resolved clades.

Similar results where clades unique to the combined data set and absent in the two being combined have been found in the Solanaceae (Olmstead and Sweere 1994) and *Columnea* (Smith and Sytsma 1994). Those results, as well as those obtained in this study, suggest that combining different data sets may reveal phylogenetic signal that is masked in either data set alone. In the case of the subtribe Dichorisandrinae as with *Gossypium* (Seelanan et al. 1997), ''soft'' incongruence is presumably operating, with clades in question weakly supported and alternative resolutions only slightly less parsimonious (Hillis 1987). The results presented here suggest that even if one of the data sets has a low ''signal to noise'' ratio, so that the phylogenetic signal is effectively masked by noise in the analysis of that data set alone, it can still help to resolve relationships in a combined analysis (see Barrett et al. [1991] and Chippindale and Weins [1994] for discussion on the emergence of phylogenetic signal in combined analyses). These results are also consistent with studies that have demonstrated that the likelihood of estimating the correct phylogeny increases with the number of variable or informative characters (Givnish and Sytsma 1997a,b).

Cartonema *is the Sister Genus to All Other Commelinaceae.* The family Commelinaceae has historically been considered to be well-defined based on its distinctive stem anatomy, involute ptyxis, thyrsiform inflorescence, deliquescent flowers, distinct calyx and corolla, lack of nectaries, and seeds with a prominent embryotega (Cronquist 1981; Faden 1985; Faden and Hunt 1991). The *rbcL* and combined data sets support the monophyly of the family. Strong support (98% in the *rbcL* tree) is seen for the basal placement of *Cartonema* as the sister to the remainder of the family, followed (but supported less strongly) by *Palisota* (of tribe Tradescantieae [sensu Faden and Hunt 1991; Faden 1998]). Likewise, the morphological analysis (Evans et al. 2000a) places *Cartonema* at the base of Commeli-

naceae. *Cartonema*—nearly endemic to Australia (one species has been reported from Trangan Island, Indonesia; Faden 1998)—is morphologically isolated from the rest of the family by glandular hairs covering its vegetative parts (a rare occurrence in the family), the lack of both glandular microhairs and raphide canals, and non-succulent leaves. The inflorescence of *Cartonema* has been termed a raceme, although Brenan (1966) re-interpreted it as a thyrse with reduced, one-flowered cymes (cincinni) arranged along a central axis. Its flowers are usually yellow, a condition otherwise rare in the rest of the family. The seeds possess only a poorly delimited embryotega (Grootjen 1983), shared only with *Triceratella* (Barker et al. 2001), while the embryotega is very distinct in the seeds of the rest of the family.

These features compelled Pichon (1946) to assign the genus to its own family, Cartonemataceae, a decision that was supported by Hutchinson (1959). Tomlinson (1966) used anatomical data to place *Cartonema* back into the Commelinaceae, although with some doubt, and he later accepted Cartonemataceae (Tomlinson 1969). Brenan (1966) rejected the segregation of *Cartonema* into a separate family based largely on his reinterpretation of the inflorescence. He assigned *Cartonema* to its own ''Group'' (''Group II''), and suggested it might be a highly specialized derivative of his ''Group I'', which contained *Stanfieldiella* Brenan, *Thyrsanthemum* Pichon, *Forrestia* (= *Amischotolype* Hassk.), *Geogenanthus*, *Murdannia* Royle, *Floscopa* Lour., *Tinantia* Scheidw., *Aneilema*, and *Ballya* (= *Aneilema*). Faden and Hunt (1991) and Faden (1998) recognized *Cartonema*'s unique morphology and anatomy and placed it along with *Triceratella* Brenan into a separate subfamily—the Cartonematoideae (Brückner) Faden & D. R. Hunt—apart from the remainder of the family—the Commelinoideae. Thus, with respect to *Cartonema*, all cladistic analyses to date in Commelinaceae are consistent with this most recent classfication and the separation of the genus from the remainder of the family. The position of *Cartonema* in these analyses implies that it would be phylogenetically defensible to either recognize it as a genus within Commelinaceae or as its own monogeneric family. Based on the strong support of the branch uniting *Cartonema* with the rest of the Commelinaceae (decay value of 10 additional steps and bootstrap value of 100% for molecular analysis; Fig. 2), as well as the inflorescence and anatomical characters described by Brenan (1966) and Tomlinson (1966, 1969), respectively, there is no compelling reason to separate *Cartonema* from Commelinaceae.

One factor that might ultimately affect the taxonomic circumscription of Commelinaceae with respect to *Cartonema* is the inclusion of *Triceratella* in a cladistic analysis of molecular data. Like *Cartonema*, *Triceratella* is morphologically isolated from the rest of the Commelinaceae. *Triceratella* is similar to *Cartonema* in possessing glandular pubescence and yellow flowers, and lacking glandular microhairs. Although it possesses raphide canals (which are absent in *Cartonema*), these are located next to veins of the lamina rather than between veins as in all other Commelinaceae (Tomlinson 1964). Morphological analyses place *Triceratella* as the sister genus to the Cyanotinae (Pichon) Faden and D. R. Hunt (Evans et al. 2000a), based upon the presence of a punctiform hilum. Tomlinson (1964) suggested that *Triceratella* might be intermediate between *Cartonema* and the rest of the Commelinaceae, a view that is shared by Faden and Hunt (1991) and Faden (1998). Thus, *Triceratella* is critical for inclusion in a DNA analysis to ascertain relationships at the base of Commelinaceae. Unfortunately, *Triceratella* is known only from two collections (Barker et al. 2001), and DNA material was not available for this study.

Monophyly of Tribes Commelineae and Tradescantieae. The *rbcL* and combined data sets support the monophyly of the tribe Commelineae (greater than 95% bootstrap) and Tradescantieae (59% if *Palisota* is excluded). *Palisota* was consistently placed sister to the clade containing the tribe Commelineae and the remaining members of Tradescantieae; by contrast, Faden and Hunt (1991) and Faden (1998) included *Palisota* in Tradescantieae on morphological grounds. *Palisota* is unusual in the Commelinaceae for its unique stamen and staminode arrangement, a fleshy berry as a fruit, a complex reproductive system that includes dimorphic stamens and dimorphic pollen, two types of hairs on its vegetative parts peculiar to the genus, and a basic chromosome number ($x = 20$) that does not occur in any other genus of Commelinaceae (Tomlinson 1966, 1969; Faden unpubl. data). It clearly stands morphologically apart from the other genera and its placement as sister to the tribe Commelineae and other Tradescantieae as seen in both the *rbcL* and combined data analyses is perhaps not surprising. Cladistic analysis of morphological data places *Palisota* within the Commelineae clade (Fig. 1) due to the presence of a zygomorphic androecium. Androecial characters are labile in the family as a whole, however, and the placement of *Palisota* within Commelineae is only weakly supported. Likewise, stomatal features differentiate *Palisota* from members of Commelineae, making its position in the morphological phylogeny highly suspect (see Evans et al. 2000a for further discussion). Despite the unique morphology of *Palisota* and its placement sister to the rest of subfamily Commelinoideae in the DNA and combined analyses, its exact relationship to the other members of the subfamily is still unclear. Only two additional steps in the DNA or combined data analyses are required to produce a monophyletic Tradescantieae (i.e., in which *Palisota* is included). Until additional data lend stronger support to the placement

of this genus, modifications to the current taxonomy would be premature.

The six remaining subtribes within the Tradescantieae are, with a few modifications, largely supported by *rbcL* and combined data. Subtribe Tradescantiinae consists of four genera: *Callisia* Loefl., *Gibasis* Raf., *Tradescantia* L. (including segregates such as *Campelia* Rich. and *Zebrina* Schnizl.), and *Tripogandra* Raf. Each method of phylogeny reconstruction grouped these taxa together, but they also included *Elasis* (Figs. 2 and 3). Faden and Hunt defined this subtribe based on a unique inflorescence consisting of a pair of cincinni that are fused back-to-back (or of two to several stipitate cincinni in a pseudo-umbel). All members of this clade possess this inflorescence type except *Elasis*. Although the DNA data show strong support for the inclusion of *Elasis* within tribe Tradescantiinae (decay value of five additional steps and bootstrap value of 90%; Fig. 2), at this time no morphological characters are apparent that unite *Elasis* with the rest of the subtribe. *Elasis* might represent a morphologically reduced member of the tribe, in which one cincinnus of the cincinnus-pair has been lost.

Two of the genera in Tradescantiinae (*Tradescantia* and *Callisia*) are composed of numerous segregates that have at times been placed into different genera. Two species of *Tradescantia* that have at times been placed into segregate genera were included in this study (*T. soconuscana* [*Campelia standleyi*] and *T. zebrina* [*Zebrina pendula*]), and the genus appears to be monophyletic only with the addition of *Gibasis*. Representatives from two different sections of *Callisia* (sects. *Callisia* and *Brachyphylla* D. R. Hunt; Hunt 1986) were sampled as well. The *rbcL* data suggest that *Callisia* is paraphyletic, with *Tripogandra* being a derivative of the genus. Alternatively, *Callisia* could be polyphyletic and require splitting into segregate genera. It should be noted, however, that *rbcL* evolves too slowly to evaluate relationships at this level with confidence and a more quickly evolving region of DNA should be sequenced to address these issues.

The second major clade within the tribe Tradescantieae includes subtribes Coleotrypinae Faden and D. R. Hunt and Cyanotinae (as well as part of the Dichorisandrinae [*Dichorisandra* Mikan and *Siderasis* Raf.] in the *rbcL* trees). The Coleotrypinae, Cyanotinae, Streptoliriinae, and Palisotinae (only genus *Palisota*), are the only African/Asian subtribes in the tribe Tradescantieae. Each of these subtribes is well defined on morphological grounds. Members of the Coleotrypinae possess axillary perforating inflorescences with congested cincinni. The Cyanotinae possess seeds with a terminal embryotega. The Streptoliriinae are mainly twiners. The Palisotinae have distinctive floral morphology and a berry fruit. While biogeography might suggest that the Coleotrypinae and Cyanotinae are related, we have found no morphological synapomorphies.

Subtribe Dichorisandrinae consists of five genera: *Dichorisandra*, *Siderasis*, *Geogenanthus*, *Cochliostema*, and an undescribed genus. Both the molecular and morphological analyses produced a polyphyletic Dichorisandrinae (Figs. 1, 2), whereas the combined analysis supported monophyly for the subtribe (Fig. 3). In the molecular analysis, *Geogenanthus* was placed sister to the undescribed genus (Fig. 2) while it is sister to the clade containing *Dichorisandra* and *Siderasis* in the combined analysis (Fig. 3). *Geogenanthus*, *Cochliostema*, and the undescribed genus are the only genera in the Commelinaceae with fringed petal margins. It is difficult, however, to identify a morphological synapomorphy that unambiguously unites *Dichorisandra* and *Siderasis* with the rest of the subtribe, although the genera are united by karyotype: 19 pairs of large chromosomes (Faden and Hunt 1991; Faden 1998). It is apparent that the subtribe Dichorisandrinae consists of two distinct groups (one group with fringed petal margins and one without), but the relationship between these groups, and therefore the monophyly of the subtribe as a whole, is not clear (see above for further discussion on the monophyly of this subtribe). Likewise, the placement of *Geogenanthus* is ambiguous due to its shift in placement between the maximum parsimony and combined analyses (Figs. 2 and 3).

Maximum parsimony analyses of the *rbcL* and combined data sets indicate that the subtribe Thyrsantheminae Faden and D. R. Hunt is polyphyletic or paraphyletic, due to the more basal position of *Tinantia*, as well as the placement of *Elasis* (the only strictly South American genus in the Thyrsantheminae) within the Tradescantiinae. The non-monophyly of subtribe Thyrsantheminae is not surprising. Members of this subtribe are defined on the basis of the absence of petal fringing, unpaired cincinni, longitudinal anther dehiscence, and uniseriate seed arrangement. Thus, its circumscription is based largely on the absence of derived characters and the presence of putatively primitive characters (based on overall trends in monocots) instead of any synapomorphic features. Although molecular data may aid in determining phylogenetic relationships among genera of Thyrsantheminae, applying morphological characters that reflect those relationships has proven difficult. While the monophyly of the subtribe is strongly suspect, neither morphology nor *rbcL* sequence data have reliably resolved the relationships among the genera to justify a taxonomic revision of the subtribe. Examination of a more quickly evolving region of DNA, as well as inclusion of *Gibasoides* D. R. Hunt and *Matudanthus* D. R. Hunt (not included in the present study), should help to resolve relationships among these genera. It is noteworthy that with

the exception of *Elasis*, all the genera of Thyrsanthemineae examined are mainly Mexican.

The composition of the second major clade is in complete agreement with the circumscription of the tribe Commelineae (Faden and Hunt 1991; Faden 1998). Faden and Hunt defined this tribe based on anatomical characters, particularly the stomatal apparatus consisting of six subsidiary cells with relatively small terminal cells (see Fig. 3 of Evans et al. 2000a). Additionally, all members of this tribe that have been examined possess a spinulose pollen exine, while spines are lacking on the exine of other genera of Commelinaceae (except for *Tripogandra*; Sharma 1968; Poole and Hunt 1980; Faden and Hunt 1991; Faden 1998). While it is believed that pollen characters hold great promise for phylogenetic studies in the Commelinaceae, pollen features have not yet been explored in enough detail to be incorporated into a cladistic analysis.

Although Faden and Hunt (1991) were successful in identifying the tribe Commelineae as a natural group, they were unable to divide it into smaller segregates due to a lack of useful characters. They point out that chromosome characters may show a relationship between *Aneilema* and *Pollia* (Faden and Suda 1980), and mention a particular chemical character (an anthocyanidin) that appears to be present only in *Buforrestia* C. B. Clarke and *Polyspatha* Benth., but they are unable to hypothesize any other taxonomic affinities within the tribe. The *rbcL* and combined data support a close relationship among *Aneilema*, *Rhopalephora*, and *Pollia* (Figs. 2–3). All analyses place *Rhopalephora* nested within *Aneilema*, making *Aneilema* paraphyletic. The nested position of *Rhopalephora* within *Aneilema* is not surprising considering that the two genera are quite similar morphologically, and no single morphological character separates them, although *Rhopalephora* does appear to have a unique basic chromosome number of $x=29$ (Faden 1991, 1998).

The molecular and combined analyses also identified a clade containing *Aneilema*, *Commelina*, *Pollia*, *Polyspatha*, and *Rhopalephora*. Although the morphological cladistic analysis did not produce this clade (Evans et al. 2000a), these are the only genera that have three fertile stamens below three staminodes (except some species of *Pollia*). Anatomical evidence also supports this clade in that all five genera, as well as *Dictyospermum* Wight (not included in this study), possess a particular type of trichome (''hook-hair'', sensu Tomlinson 1966) that is not found in other genera in the family. Inclusion of *Dictyospermum* in a future molecular analysis should help test whether the presence of hook-hairs is a reliable synapomorphy for this group.

More problematic is the *Stanfieldiella*, *Buforrestia*, and *Floscopa* group, which can be characterized only by having all stamens fertile (a plesiomorphic character also present in some species of *Pollia* of the *Commelina* group) and by the absences of hook-hairs and a continuous hypodermis. The three genera form a clade in the maximum likelihood analysis of *rbcL* and in the combined data analysis, but not in the parsimony analysis of *rbcL* alone. *Floscopa* and *Stanfieldiella* are sister taxa in the molecular and combined trees, but not in the morphology trees. As with other clades within the Commelineae, a paucity of morphological characters supports these relationships, or else different characters suggest alternate relationships. *Stanfieldiella* and *Floscopa* share a common cincinnus bract development, wherein there is a gradation of large bracts at the lowermost cincinni to smaller bracts subtending the uppermost cincinni, but the bracts in *Buforrestia* are more nearly uniform in size. The flowers of *Floscopa* and *Buforrestia* produce one petal that is different from the other two petals, but in *Stanfieldiella* all three petals are equal. A unique type of glandular hair has been found in *Buforrestia* and apparently in *Floscopa*, but not in *Stanfieldiella* (Faden, unpublished). It appears that morphological characters are only able to unite this group when a combination of characters is used, due to the absence of one or more unambiguous synapomorphies.

The final clade within the Commelineae is composed of *Murdannia* and *Anthericopsis* Engl., and is resolved in both the molecular and combined analyses. Cladistic analysis of morphological data alone do not unite these two genera (Fig. 1; Evans et al. 2000a) until parsimony is relaxed three additional steps. The two genera differ from the rest of the Commelineae by typically having the antesepalous stamens fertile and the antepetalous staminodial, which is a unique arrangement in the family (Faden and Inman 1996). *Murdannia* and *Anthericopsis* also share several anatomical features that distinguish them from the other genera of the tribe Commelineae (Faden and Inman 1996), but those features have not been examined across the entire family, and thus were not included in the morphological cladistic analysis. It appears that this clade is well supported by morphological, anatomical, and sequence data.

Biogeography of Commelinaceae. A sharp division between Old and New World taxa can be seen in the Commelinaceae (Fig. 6). Of the 41 genera, only six occur in both the Old World and New World (*Aneilema*, *Commelina*, *Buforrestia*, *Floscopa*, *Murdannia*, and *Pollia*; Faden 1983), all of which are members of the tribe Commelineae. The remaining eight genera of the tribe Commelineae are found exclusively in Africa, Asia, and Australia, suggesting an Old World origin of the tribe. In the tribe Tradescantieae, four subtribes (Palisotinae Faden and D. R. Hunt, Streptoliriinae, Cyanotinae, and Coleotrypinae), containing nine genera, are exclusively Paleotropical (Faden and Hunt 1991; Faden

1998), and three subtribes (Dichorisandrinae, Thyrsantheminae, and Tradescantiinae) consisting of 16 genera, are found only in the Americas (Faden and Hunt 1991; Hunt 1993, 1994; Faden 1998).

The sister genus to the rest of the family, *Cartonema*, is nearly endemic to Australia, and its purported closest relative, *Triceratella* (sensu Faden and Hunt 1991 and Faden 1998, but not sensu morphological cladistic analysis), is endemic to south tropical Africa (Zimbabwe and Mozambique). Likewise, *Palisota*, sister to all remaining Commelinaceae, is restricted to Africa. Thus, the distributions of the major early clades suggest an eastern Gondwanan origin for Commelinaceae (Fig. 6). This is in agreement with Givnish et al. (1999), who examined biogeographic patterns among commelinoid monocots as a whole, and suggested an eastern Gondwanan origin for Commelinaceae and its closest families. The early branching of *Cartonema* from the rest of the family seen with all data sets (Figs. 1–3), as well as the morphological and geographical isolation of the genus, suggest an ancient split from the rest of the Commelinaceae. The apparently relictual distribution of *Triceratella*, the genus probably most closely related to *Cartonema*, also suggests an early separation from other Commelinaceae. The fossil record for Commelinaceae is extremely poor, however, and the rejection of a molecular clock prohibits the inference of divergence times based on *rbcL* sequences, making it difficult to determine the absolute timing of early branching events in the family.

It is noteworthy that the six genera with both Old and New World distributions (*Aneilema*, *Commelina*, *Buforrestia*, *Floscopa*, *Murdannia*, and *Pollia*) are confined to the well-supported clade of tribe Commelineae (Fig. 6). We see no obvious long-distance dispersal mechanisms within most of these genera, with the exception of the berry-like fruits of *Pollia*, that would facilitate greater widespread dispersal than the genera of Tradescantieae (see ''Ecological Specializations'' below). One possibility, other than multiple long distance dispersal events, is that these disjunct generic distributions in Commelineae reflect a single, more ancient, vicariant event. In all likelihood, no single cause or event can explain all of these distributions.

In any case, one or two shifts (equivocal in Fig. 6) from the Old World to the New World occur in the tribe Tradescantieae. The position of the primarily Asian and African subtribes Coleotrypinae and Cyanotinae nested well within the predominantly western hemisphere tribe Tradescantieae (Fig. 6) poses some interesting questions regarding the biogeographic history of these taxa. The inclusion of these strictly Old World genera among (but not basal to) the strictly American genera is somewhat surprising, and could be explained by a single long-distance dispersal event from the New World to the Old World (using ACCTRANS optimization). Alternatively, two independent introductions from the Old World to the New World (the clade containing Dichorisandreae followed by the Thyrsantheminae/Tradescantiinae clade; using DELTRANS optimization) could account for the distribution. A final possible explanation for this distribution is the Boreotropical Flora hypothesis (Wolfe 1975), in which tropical New World and Old World floristic elements represent relictual distributions of a formerly widespread northern temperate distribution. The relatively derived position of Tradescantiinae (the main subtribe represented in temperate North America), as well as the relatively early divergence of Dichorisandrinae (which has its center of diversity in South America) from other members of the tribe Tradescantieae, however, makes the last scenario unlikely.

Ecological Specialization and Morphological Convergence in Commelinaceae. Members of the Commelinaceae are found in a broad range of habitats, from closed forest to semi-desert. Faden (1988) recognized forest and non-forest genera, based on the habitat of the majority of species in a genus. He proposed that similar suites of characters evolved in different lineages in response to similar ecology. For example, forest genera developed convergent features as adaptations to low light intensities: broad, spirally arranged leaves to efficiently capture light; axillary inflorescences requiring less vegetative growth in connection with sexual reproduction; and white flowers for better visibility under low light conditions. In contrast, non-forest genera demonstrated convergent adaptations for limited water availability during a dry season, including annual habit, underground storage organs, and succulence. Faden and Evans (1999) re-examined these characters in light of the *rbcL* phylogeny and found several instances in which convergence was apparent. Bird-dispersed seeds (either via fleshy fruit or arillate or otherwise showy seeds, thus clearly not a single character), which are commonly associated with forest habitats in flowering plants (Givnish 1998; Givnish et al. 1999), were found to occur almost exclusively in forest genera, such as *Palisota* and *Pollia*, plus a few forest species of non-forest genera (*Commelina* and *Tradescantia* in Fig. 7). Under closed canopies where wind speeds are reduced, endozoochory (internal transport by animals) and fleshy fruits should be favored (see Givnish [1998] and Givnish et al. [1999] for other examples in which fleshy fruits are associated with the rain forest habitat). Likewise, the presence of all axillary or basal inflorescences has arisen primarily in forest genera (Fig. 8).

Some instances of convergence are not related to habitat. For example, characters of the androecium are adaptations for pollination (see below). The appearance of these similar character types in separate lineages illustrates the difficulty in assessing homology of

some morphological characters in this family undergoing repeated specialization to distinct habitats (Givnish and Sytsma 1997b) or selection pressures.

To understand in more detail the evolution and possible convergence of specific morphological characters and suites of characters in Commelinaceae, consistency indices of each morphological character were obtained for the morphological, molecular, and combined trees (Figs. 4–5). The relative performance of a character on the different trees provides information about its contribution toward the conflict between data sets. As examples, consider an anatomical character (presence/absence of glandular microhairs; character 45 of Evans et al. 2000a) and outer antesepalous staminal fertility (character 18 of Evans et al. 2000a). The anatomical character is perfectly congruent (CI = 1) on both the molecular and combined trees, but is highly incongruent on the morphological trees (CI = 0.5). However, the staminal character has a CI of 0.76 on the morphological trees but only 0.33 on the molecular trees.

In general, the suites of characters showing the most CI reduction going from morphological to molecular (and combined) trees include androecial features (Fig. 5). In contrast, vegetative anatomical, and to a lesser extent inflorescence, characters fit significantly better on the molecular (and combined) trees relative to their performance on the morphological trees. While it is not the intent in this paper to discuss all of the factors that may affect homoplasy in phylogenetic studies (see Sanderson and Donoghue 1989; Donoghue and Sanderson 1994; Givnish 1997; Givnish and Sytsma 1997b), specific causes may be attributed to the differences seen here. Organisms operating under similar, context-specific selective pressures may express suites of similar morphological characteristics (e.g., see Givnish et al. 1999; McCracken et al. 1999). Flowers in the Commelinaceae are visited by a wide range of insect pollinators, and the androecium has been highly modified in some genera for the attraction of pollinators (Faden 1991, 1992, 2000). Because there is no nectar reward for pollinators, modifications of the stamens (i.e., large, showy antherodes; filament hairs) may be deceptive mechanisms to attract insects (Vogel 1978; Faden 1992). The strong selective pressures involved in the attraction of insect pollinators, in addition to the lack of nectar reward, may greatly increase the incidence of parallel evolution and convergence in staminal characters, rendering them highly homoplasious in a phylogenetic analysis. Faden (2000) concluded that heteranthery—the division of the stamens into two sets—has evolved in at least seven clades in the family: four of the seven subtribes of Tradescantieae recognized by Faden and Hunt (1991) and all three major clades of tribe Commelineae.

Vegetative anatomical characters, however, may not be under such strong selective constraints; alternatively, the selection pressures involved may not be context-specific, which would favor similar characteristics across the lineage and no independent origins of convergent traits. When vegetative anatomical characters are mapped onto the *rbcL*-based or combined tree, the average CI is 0.78 (Fig.5; Table 4), much higher than any other class of characters on any set of trees. Assuming that the *rbcL* and combined trees are a reliable estimate of phylogenetic relationships within Commelinaceae, the strong support provided by the vegetative anatomical characters suggests that the selective and/or developmental constraints upon these characters are less severe—or at the very least, less context-specific—than those acting upon features relating to pollination.

Based on our phylogeny and the ecology of the genera, there was an early split between forest and non-forest genera in Commelinaceae (the ancestral state for habitat, forest versus non-forest, is ambiguous; Fig. 7, 8). Both the basal genus *Cartonema* and the unstudied *Triceratella* (Barker et al. 2001) are non-forest genera, whereas *Palisota* and *Spatholirion* appear to have spread to forests in Africa (*Palisota*) and Asia (*Spathlolirion*). The two remaining large clades both contain forest and non-forest genera. In the tribe Tradescantieae (minus *Palisota* and *Spatholirion*) the three major lineages show different patterns. The genera of subtribe Dichorisandrinae are mainly South American and are all forest genera. The paleotropical Cyanotinae plus Coleotrypinae comprise forest genera, except for the largest genus *Cyanotis*, but the most basal species of that genus may be forest species, with a secondary adaptation to drier conditions (Faden, unpublished). Except for the monospecific and South American *Elasis*, the clade comprising subtribes Tradescantiinae plus Thysantheminae is mainly Mexican and Central American, and all of the genera are non-forest genera.

In tribe Commelineae, which is mainly paleotropical, the pattern is more complex. Both genera of the basal clade, *Murdannia* and *Anthericopsis*, are non-forest genera. However, the other two clades contain both forest and non-forest genera. The general pattern in tropical Africa is that the smaller genera, such as *Buforrestia*, *Polyspatha* and *Stanfieldiella*, are largely restricted to rainforests of West and Central Africa, whereas the larger genera, particularly *Commelina* and *Aneilema*, are most diverse in the grasslands, bushlands and open woodlands of eastern and southcentral Africa. This pattern suggests an aridification in tropical Africa, during which the forest decreased and non-forest habitats expanded (Richardson and Richardson 1972; Axelrod and Raven 1978; Faden, 2001). Genera with adaptations to withstand dessication, such as the spathes in *Commelina* and glandular bracteoles and sepals in *Aneilema*, were able to radiate in the drier areas, whereas the forest genera, lacking such adaptations,

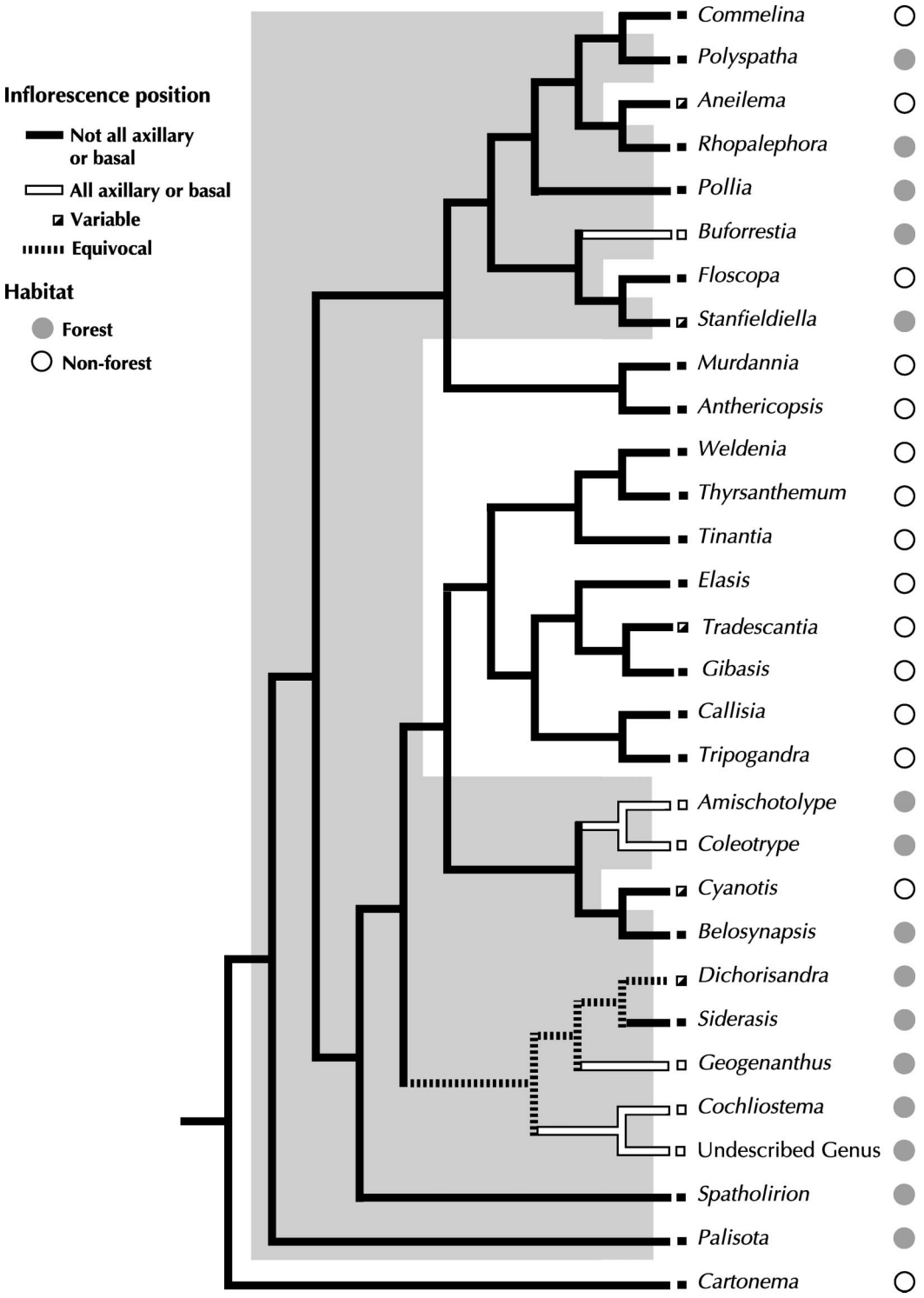

FIG. 8. Distribution of inflorescence position characters and habitat mapped onto a representative cladogram from the combined morphology/*rbcL* phylogeny. Habitat designation of forest or non-forest is according to Faden (1988). Note that all genera that have only axillary inflorescences correlate with the forest habitat.

became more restricted in their distribution and perhaps less diverse (Faden 2001).

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