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A Phylogeny of the Monocots, as Inferred from *rbcL* and *atpA* Sequence Variation, and a Comparison of Methods for Calculating Jackknife and Bootstrap Values

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ABSTRACT. A phylogenetic analysis of the monocots was conducted on the basis of nucleotide sequence variation in two genes (*atpA*, encoded in the mitochondrial genome, and *rbcL*, encoded in the plastid genome). The taxon sample of 218 angiosperm terminals included 177 monocots and 41 dicots. Among the major results of the analysis are the resolution of a clade comprising four magnoliid lineages (Canellales, Piperales, Magnoliales, and Laurales) as sister of the monocots, with the deepest branch within the monocots between a clade consisting of Araceae, Tofieldiaceae, *Acorus*, and Alismatales, and a clade that includes all other monocots. Nartheciaceae are placed as the sister of Pandanales, and Corsiaceae as the sister of Liliales. The Triuridaceae, represented by three genera, including *Lacandonia*, are resolved as monophyletic and placed in a range of positions, generally within Pandanales. Dasypogonaceae and Arecaceae diverge sequentially from a clade that includes all other commelinid taxa, and within the latter group Poales s. lat. are sister of a clade in which Zingiberales and Commelinales are sisters. Within Poales s. lat., *Trithuria* (Hydatellaceae) and *Mayaca* appear to be closely related to some or all elements of Xyridaceae. A comparison was conducted of jackknife and bootstrap values, as computed using strict-consensus (SC) and frequency-within-replicates (FWR) approaches. Jackknife values tend to be higher than bootstrap values, and for each of these methods support values obtained with the FWR approach tend to exceed those obtained with the SC approach.

The monocots, an angiosperm group with about 100 families (Kubitzki 1998a, b), have been the subject of numerous phylogenetic analyses (Wilson and Morrison 2000, and citations therein), variously focused on particular subgroups or on the overall phylogenetic structure of the group as a whole. An early and critical set of contributions in this area was generated by Rolf Dahlgren and colleagues (Dahlgren and Clifford 1982; Dahlgren and Rasmussen 1983; Dahlgren et al. 1985), who assembled a comprehensive suite of structural characters for the monocots, surveyed the group for variation in these characters, and applied formal cladistic logic to the analysis of relationships among the monocots using these characters. After the last of these works was published, nucleotide sequence variation in *rbcL* was brought to bear on the problem of relationships in the monocots (Duvall et al. 1993a, b) and in the angiosperms as a whole (Chase et al. 1993), including a broad sampling of monocots. Many additional studies along these lines have since been conducted (cited below), as various investigators have sampled particular lineages in greater depth, and have generated DNA sequence data sets based on additional genes plus combined matrices that included structural and sequence characters.

In a recent review and new analysis, Chase et al. (2000) described a mixed state of affairs. Although several major lineages within the monocots have been identified, with varying degrees of confidence, and some relationships among these groups appear to have been well established, several areas of instability remain. Chase et al. (2000) analyzed relationships among 126 monocot terminals, which had been sampled for nucleotide sequences in three genes (*rbcL* and *atpB* from the plastid genome, and 18S ribosomal DNA from the nuclear genome), and they framed much of their discussion in terms of relationships within and among a set of 12 major lineages. While there was robust support for the monophyly of most of these groups, most relationships among them had only weak

to moderate support. In the present analysis we examine relationships among 177 monocot taxa, on the basis of nucleotide sequences of two genes, *rbcL* from the plastid genome and *atpA* from the mitochondrial genome. To accommodate differences between the results reported here and those reported previously, higher-level relationships are discussed in terms of 15 principal lineages that collectively include all monocots in the sample.

Most discussions of support for groups in a phylogenetic framework involve resampling procedures such as the bootstrap (Felsenstein 1985) and the jackknife (Farris et al. 1996). Although these procedures have been used widely, the numbers that they generate can vary according to the manner in which the procedures are implemented, and current implementations vary in important ways. One important aspect of variation lies in the method that is used to assess the occurrence of each clade among the trees derived from each replicate analysis. The results of each replicate of a bootstrap or jackknife analysis can be assessed with a ''strict-consensus'' (SC) or ''frequency-within-replicates'' (FWR) approach (Soreng and Davis 1998; Grass Phylogeny Working Group 2001). With the SC approach, a clade is regarded as having been resolved in a particular replicate only if the group occurs in all most-parsimonious trees obtained by that replicate; when a group occurs in the consensus tree it receives a score of 1 for that replicate, and in all other cases it receives a score of 0. With the FWR approach, the score that is assigned to each clade following each replicate is proportional to the frequency of occurrence of the clade among most-parsimonious trees for that replicate. Thus, a clade that occurs in some but not all trees obtained in a given replicate will have an FWR score greater than 0 and less than 1. The distinction in scoring between these approaches disappears if only one tree is retained within each replicate analysis, but if multiple trees are obtained, it is to be expected that the overall FWR score for a group will be equal to or greater than the SC score if all other aspects of the analysis are identical. PAUP* (Swofford 2001) employs the FWR approach, and WinClada (Nixon 2002) employs the SC approach. Therefore, the support levels reported by these programs for identical matrices should differ in a predictable way (i.e., PAUP* may report generally higher scores than WinClada). In the context of our analysis of monocot relationships we have examined this matter by conducting both forms of bootstrap and jackknife analysis, and analyzing variation patterns among the results. Results are compared in terms of overall means of support values for groups resolved by the basic analysis, and in terms of variance patterns of these values.

Materials and Methods

Molecular Methods. Variation was examined at two loci, *atpA* (from the mitochondrial genome, encoding the alpha subunit of F-1-ATPase) and *rbcL* (from the plastid genome, encoding the large subunit of ribulose 1,5-bisphosphate carboxylase). Sequence data were generated by the authors from total genomic DNA isolations, following standard PCR and automated cycle sequencing protocols, or obtained either from GenBank (where some *atpA* sequences are listed as *atp1*) or directly from other investigators. Most primers used for amplification and sequencing have been published previously (*atpA*: Eyre-Walker and Gaut 1997; Davis et al. 1998; *rbcL*: Chase et al. 1993; Asmussen and Chase 2001), but two new primers also were developed for *atpA*, specifically for the amplification of alismatid taxa. They are *atpA*-F-A1 (5′-cagttggagatgggattgcacg-3′), a forward-priming sequence that corresponds to sites 104–125 of the reference *Oryza* sequence (see below), and *atpA*-B-A1 (5′-ggcagtggttcatattgtggttg-3′), a reverse-priming sequence that corresponds to sites 1,297–1,319 of the *Oryza* sequence. In some cases, where PCR amplification yielded only faint bands, PCR-generated DNA fragments were cloned with an Invitrogen TOPO TA Cloning® Kit (Invitrogen Corporation, Carlsbad, California). Fragments were ligated into the pCR® 2.1-TOPO® vector and introduced into chemically competent *Escherichia coli* cells of strain DH5 α-T1®. Plasmid DNA then was extracted using a QIAprep® Spin Miniprep Kit (Qiagen Inc., Valencia, California) and sequenced, either with the original amplification primers or with the M13 plasmid primers supplied with the cloning kit.

The sequenced portion of *atpA* comprises 1,277 aligned nucleotides corresponding to a region of length 1,259 (sites 98–1,356) in the *atp1* coding sequence in GenBank accession AB076666 (*Oryza sativa*). Within this range, alignment was regarded as ambiguous in the region from site 581 to site 604, and this section was excluded from all cladistic analyses. Two additional sites also were excluded (220 and 255), because sequencing of the two DNA strands often yielded conflicting results at these sites. Artifacts of this sort, reflecting imperfections in sequencing accuracy, can occur when certain combinations of nucleotides lie in close proximity to each other within a sequence (Parker et al. 1995). In addition to the *atpA* nucleotide-site characters, two informative insertion/deletion (indel) characters were included in the matrix. The sequenced portion of *rbcL* comprises 1,371 nucleotides, corresponding to sites 31–1,401 in the *rbcL* coding sequence in GenBank accession NC001879 (*Nicotiana tabacum*), with no length variation observed among the taxa. Three data matrices used in the analysis are available from the senior author and from TreeBASE (study accession number S951; matrices M1576 and M1577 are the aligned *rbcL* and *atpA* matrices, respectively; matrix M1575 is the combined matrix, minus ambiguously aligned and uninformative characters).

Taxon Sampling. The taxon set includes 177 monocots and 41 dicots, for a total of 218 terminals (Appendix I). All major lineages of monocots identified in recent analyses are represented, and the dicots include representatives of putatively early-diverging angiosperm lineages (e.g., *Amborella*, Nymphaeaceae, Illiciaceae), early-diverging elements within the major tricolpate angiosperm lineage (e.g., *Cercidiphyllum*, *Platanus*, *Nelumbo*, Berberidaceae), and various additional ''magnoliid'' lineages for which there is evidence of a close affinity with monocots (e.g., Piperales [including Aristolochiales], Laurales, Magnoliales, and Canellales). To facilitate comparisons with previous classifications, provisional assignments of genera to families follow Kubitzki et al. (1993) and Kubitzki (1998a, b), except as noted, and provisional assignments of families to orders and other higher-level groupings follow the revised classification of the Angiosperm Phylogeny Group (i.e., the APG II system; Angiosperm Phylogeny Group 2003). Kubitzki's taxonomic system for monocot genera and families is comprehensive, for every accepted monocot genus is assigned to a family with the exception of two families of uncontroversial circumscription (Orchidaceae and Poaceae) that have not been treated. The provisional assignment of each genus to a family differed from the treatment by Kubitzki with respect to the circumscription of Nartheciaceae,

which, as treated by Tamura (1998) in that work, includes six genera in the present analysis. Two of these six genera (*Aletris* and *Narthecium*) are recognized here as elements of Nartheciaceae, and the remaining four are assigned to two other families (*Pleea* and *Tofieldia* to Tofieldiaceae, *Japonolirion* and *Petrosavia* to Petrosaviaceae; cf. Chase et al. 2000; Fuse and Tamura 2000; Soltis et al. 2000; Hilu et al. 2003). Multiple genera were sampled from several families, and multiple species were sampled from each of three genera; the sample includes three species of *Acorus* and two each of *Eichhornia* and *Xyris*. The isolated genus *Acorus* is represented by three species as a test of the accuracy of previously available sequences, which in several instances have placed this genus on a long branch as the sister of all other monocots (e.g., Duvall et al. 1993a, b; Chase et al. 1993, 2000). The simultaneous inclusion of three putative species of this genus represents an attempt to subdivide a long branch, which might provide a more robust test of the placement of this genus than is provided when only one representative is included (Hendy and Penny 1989; Graybeal 1998; Poe and Swofford 1999; Poe 2003), because the synapomorphies of the genus are captured and the effects of autapomorphies of a single species are minimized. Two species of *Xyris* were sampled for similar reasons, and two species of *Eichhornia* were sampled to test previous reports that the genus is not monophyletic, and specifically that the two species included in the present analysis belong to different major lineages within Pontederiaceae (Graham et al. 1998). For each species sampled from these three genera, sequences of both genes were obtained from the same species, and in most cases from the same DNA isolation. Each of the other genera in the analysis is represented by only one terminal, and for many genera the available *atpA* and *rbcL* sequences represent different species.

Data Analysis. All characters, including the two *atpA* indels (one of which has three recognized states) were weighted equally and treated as nonadditive (i.e., the states unordered) during tree searches. Parsimony searches were conducted using conventional search strategies and the parsimony ratchet (Nixon 1999). Searches were conducted with the multi-thread version of NONA vers. 1.6 (i.e., ''PARANONA'', compiled February 26, 1998; Goloboff 1993), except as noted otherwise. Searches conducted with NONA used the default polytomy settings, which allow polytomies to occur (*poly=*), and which resolve a clade, rather than a polytomy, only when support for the resolution is unambiguous (*amb-*; i.e., ambiguous support is insufficient for resolution). The precise criterion of unambiguous support for a group is that the group's branch length is greater than zero under all possible character optimizations; conversely, support for a group is regarded as ambiguous when its minimum length is zero, and in these cases it is determined that the group is not resolved.

Conventional searches involved 1,000 individual subsearches, with partial results saved periodically to avoid their loss in case of interruption. Each subsearch was initiated by the construction of a Wagner tree, using a random taxon entry sequence, and this tree then was subjected to TBR swapping, with up to 20 shortest trees retained and subjected to additional branch swapping, using the command *mult**, preceded by *rs 0* and *hold/20.* All most-parsimonious trees accumulated by the 1,000 search initiations were pooled, and TBR swapping was conducted on these and all additional trees propagated during this phase of the search, with up to 100,000 trees retained and swapped, using the commands *hold 100000* and *max**.

Ratchet searches were conducted with WinClada vers. 1.00.08 (Nixon 2002), with NONA invoked as a daughter process for cladistic analysis. Ten ratchet searches were conducted, each initiated with the generation of a Wagner tree, using a random taxon entry sequence, followed by TBR branch swapping with one tree retained (*rs 0, hold/1, mult*1*) and used as the starting point for 500 ratchet cycles. In the weighted/constrained half of each ratchet cycle, a randomly selected set of 10% of the characters were resampled, and a randomly selected set of 10% of the resolved clades were constrained. All most-parsimonious trees accumulated by the 10 ratchet searches were pooled, and TBR swapping was conducted on these and all additional trees propagated during this phase of the search, with up to 100,000 trees retained and swapped, using the commands *hold 100000* and *max**.

Incongruence between the two single-gene matrices was assessed with the incongruence length difference test of Farris et al. (1995), as implemented in WinClada, with NONA invoked as a daughter process for cladistic analysis. Five hundred paired replicate analyses of random character partitions were conducted, with each replicate comprising four search initiations and up to 20 trees retained during TBR swapping after each initiation (*hold/20; mult*4*), followed by TBR swapping of all shortest trees from each set of four initiations, including those generated during this phase of swapping, with up to 100 trees retained (*hold 100; max**).

Support for clades resolved by the ''principal analysis'' (see below) was assessed by bootstrap and jackknife analyses, with each of these two procedures conducted with both PAUP* (vers. 4.0b10; Swofford 2001), which employs an FWR approach, and WinClada/NONA, which employs an SC approach. Thus, analyses were conducted with all four permutations of two factors (bootstrap vs. jackknife, and SC vs. FWR). A single analysis of each type was conducted, with the exception of the SC jackknife analysis, of which two complete analyses were conducted, for a total of five analyses of clade support, each consisting of 1,000 replicates. All five analyses were conducted with the same matrix used for the principal analysis, which includes no uninformative characters. For the analyses conducted with WinClada and NONA, the same character and polytomy settings were used as in the basic analyses of relationships, and each of the 1,000 replicates within each analysis consisted of four subsearches, with up to 20 trees retained during TBR swapping after each search initiation (*hold/20; mult*4*), followed by additional TBR swapping of all shortest trees, including those generated during this phase of swapping, with up to 100 trees retained (*hold 100; max**). Character sampling for each replicate jackknife search was implemented in WinClada as described by Farris et al. (1996), with each character individually considered for deletion, with a deletion probability of e^{-1} (ca. 37%), so the number of characters can vary among the matrices used for the various replicates. For the analyses conducted with PAUP*, the same character and polytomy settings were used as in the other analyses (all characters equally weighted, states unordered, branches of zero minimum length collapsed). Multiple trees were allowed, and each replicate consisted of four searches, with each search initiated with a random taxon addition sequence and followed by TBR swapping, with up to 20 trees retained per search, and with the steepest-descent option not applied. PAUP* retains records of all groups with support frequencies greater than or equal to a user-specified number, and this was set at 1%. The jackknife analysis conducted with PAUP* utilized the ''emulate JAC'' command, which (as in WinClada) causes each character to be considered individually for deletion according to a particular probability, which was set at 37%.

For each of the five support analyses, the mean support frequency was determined for the 201 clades resolved by the principal analysis. Pairwise comparisons among the results of the various support analyses were conducted in terms of mean support values for the 201 clades. Also, for each pairwise combination of methods, the average variance (σ^2) of the two available scores (one from each support analysis), across the 201 clades, was computed. The purpose of these calculations is to detect variation among the estimates provided by the various methods, irrespective of differences or similarities in mean support values. For example, two methods might provide substantially different estimates of support for many individual clades, while still detecting approximately the same overall average support levels. Average variance levels were separately calculated on the basis of the raw support numbers for the clades, and on the basis of the natural logarithms (ln) of the raw support values. Because the clades have support values that range from a few to 100%, the range of means for the 201 clades span nearly two orders of magnitude. Because proportionally equal differences among higher numbers yield substantially higher variances than among lower numbers (e.g., σ^2 of 6 and 8 is 2, and σ^2 of 60 and 80 is 200), the average variances based on raw support numbers are disproportionately affected by

clades with higher support values. This effect of differences in magnitude is eliminated by logarithmic transformation (Lewontin 1966), and this transformation therefore removes the dominance of clades with higher support numbers in the computation of these averages (σ^2 of the ln of 6 and the ln of 8 (0.04) is equal to that of the ln of 60 and the ln of 80). It might be argued that groups with higher support levels are of greater intrinsic interest or importance to systematists, and that the use of the ln transformation therefore is inadvisable. Also, if stochastic factors influence all support levels by similar absolute amounts (i.e., by a few percentage points), it may be inappropriate to magnify the influence of clades with low support numbers, in which numerically small but proportionally large differences among analyses can occur. We cannot settle these matters here, and therefore present both sets of numbers; ultimately, the two calculations yielded similar results.

The phylogenetic implications of certain groups of interest that were not resolved by unconstrained analysis were examined by conducting constrained analyses in which these groups were forced to be resolved. Each constrained analysis was conducted by conventional parsimony analysis following addition to the matrix of a heavily-weighted dummy character consistent with the target constraint group. This method allows one set of terminals to be forced to fall within the constrained group (e.g., those scored as state 1 for the constraint character), while those of another set, including the outgroup (scored as state 0), are forced to be excluded from the constrained group, and those of an optional third set (scored as unknown) are allowed to fall either within or outside of the constrained group. The constrained analyses were conducted using the same tree-search methods described above for conventional unconstrained analyses. For comparison with the results of unconstrained analyses, calculations of tree lengths, CIs, and RIs for the constrained analyses exclude the dummy characters. Levels of support by the unconstrained data set for groups resolved only by the constrained analyses (the constrained groups themselves, plus other groups that occur in the resulting trees) were assessed in terms of the SC jackknife frequencies obtained for these groups from the unconstrained jackknife analysis described above.

RESULTS

Data Matrix. With two genes and 218 terminals (Appendix 1), the data matrix potentially included 436 sequences. However, despite repeated attempts to obtain a sequence for each gene from each taxon, five achlorophyllous taxa (*Arachnitis*, *Thismia*, *Lacandonia*, *Sciaphila*, and *Triuris*) did not yield any *rbcL* sequences, and one taxon (*Trithuria*) did not yield an *atpA* sequence. Thus, the complete matrix comprises 213 *rbcL* sequences and 217 *atpA* sequences, with sequences of both genes available for only 212 of the 218 taxa. Of the 430 sequences, 255 (59%) were generated by the authors, and 175 (41%) were obtained either from GenBank or directly from other investigators. Of the 255 sequences generated by the authors, 196 are *atpA* sequences, and 59 are *rbcL* sequences.

Following exclusion of the two ambiguously aligned regions and the two ambiguously read sites in *atpA*, this portion of the matrix consisted of 1,236 aligned sites, of which 418 (34%) are cladistically informative for the complete set of 218 taxa. Of the 1,371 *rbcL* sites, 582 (42%) are informative for the complete set of 218 taxa. Thus, the informative portion of the matrix for the 218 taxa comprises 1,000 nucleotide sites (42% from *atpA*, 58% from *rbcL*), plus two *atpA* indel characters.

Preliminary analyses of the complete matrix and various subsets of it demonstrated that inclusion of the three representatives of Triuridaceae (all of which lack *rbcL* sequences) results in a substantial decrease in resolution, relative to what is obtained when they are excluded. Below we describe results obtained with various subsets of the taxa and characters, including the complete matrix. For purposes of discussion, we designate the unconstrained analysis of the 215-taxon by two-gene matrix that is obtained when the three representatives of Triuridaceae are excluded as the ''principal analysis.'' With the three elements of Triuridaceae excluded, the matrix used in the principal analysis still includes one taxon that lacks an *atpA* sequence (*Trithuria*), and two that lack *rbcL* sequences (*Arachnitis* and *Thismia*). The informative portion of the character set for this matrix consists of 414 *atpA* nucleotide sites (of the 418 in the complete matrix), both of the *atpA* indel characters, and all 582 *rbcL* nucleotide sites that are informative for the complete set of 218 taxa, for a total of 998 characters and 214,570 cells. Of these cells, 206,184 (96.1%) are scored as individual states, 8,216 (3.8%) as missing or unknown, and 170 (0.1%) as subset polymorphisms (actually, subset ambiguities, for the most part, because these polymorphisms usually represent ambiguity in the available DNA sequences, rather than actual polymorphisms within the individual plants that were sampled). Of the 8,216 cells scored as missing or unknown, 1,619 (19.7% of the total) occur in the three taxa that each lack a complete gene sequence. In the complete matrix of 218 taxa and 1,002 informative characters there are 218,436 cells, of which 10,023 (4.6%) are scored as missing or unknown. Of these 10,023 cells, 3,379 (33.7% of all such scores in the matrix) occur in the six taxa that each lack a gene sequence.

Principal Combined Analysis, and Single-Gene Analyses. Conventional searches and parsimony ratchet searches of the matrix used in the principal analysis detected an identical set of 768 most-parsimonious trees of length 8,590, with a CI of 0.20 and an RI of 0.62 (all consistency indices reported in this paper were computed on the basis of informative characters only). With the arbitrary basal dichotomy between *Amborella* and all other taxa collapsed, there are 201 clades resolved in the consensus tree. The *atpA* portion of this matrix, including the two indel characters, consists of 214 sequences and 416 informative characters (42% of the total number of informative characters in the matrix), while the *rbcL* portion consists of 213 sequences and 582 informative characters (the remaining 58% of the characters). Among most-parsimonious trees derived from the principal analysis there are between 2,471 and 2,475 steps in the *atpA*

portion of the matrix (ca. 5.9 steps per character, and ca. 29% of the total, with a CI of ca. 0.29 and an RI of ca. 0.70), and there are between 6,115 and 6,119 steps in the *rbcL* portion (ca. 10.5 steps per character, and ca. 71% of the total, with a CI of ca. 0.17 and an RI of ca. 0.59.

The incongruence length difference D_{XY} (Farris et al. 1995) for the *atpA* and *rbcL* partitions of the matrix used in the principal analysis is 8,590 − (2,404 + 6,073) = 113 steps. None of the 500 random-partition replicates yielded a length difference of this magnitude, so the two single-gene matrices are determined to be incongruent, with $p < 0.002$.

Two analyses based solely on *atpA* data were conducted. The first of these, designated the ''*atpA*-214 analysis,'' included just the 214 taxa from the principal analysis for which *atpA* sequences are available, and the second, designated the ''*atpA*-217 analysis,'' included these 214 taxa plus the three representatives of Triuridaceae, which were excluded from the principal analysis. Both of these analyses yielded 100,000 most-parsimonious trees, the predetermined maximum number that was allowed to accumulate, so the actual number of most-parsimonious trees for these two matrices is not known. Trees from the *atpA*-214 analysis, with 416 informative characters, are of length 2,404, with a CI of 0.30 and an RI of 0.71, and trees from the *atpA*-217 analysis, with 420 informative characters, are of length 2,464, with a CI of 0.29 and an RI of 0.70. There are 143 clades in the consensus tree for the *atpA*-214 analysis, and 156 clades in the consensus tree from the *atpA*-217 analysis. Analysis of just the *rbcL* portion of the matrix from the principal analysis, with 582 informative characters, yielded 10,548 most-parsimonious trees of length 6,073, with a CI of 0.17 and an RI of 0.59. There are 191 clades resolved in the consensus tree.

CLADE SUPPORT. The consensus of the 768 most-parsimonious trees derived from the principal analysis is depicted in Fig. 1. A summary figure of relationships resolved among 15 major monocot lineages (discussed below) also is presented as Fig. 2A. Results of two of the five support analyses that were conducted (the first of the two SC jackknife analyses, and the FWR bootstrap analysis) are presented for each clade in Fig. 1, and results of the first of the two SC jackknife analyses also are presented in Fig. 2. Groups that occur in the consensus tree from the principal analysis, and that also are resolved in the consensus trees of the single-gene analyses (for *atpA,* the *atpA*-214 analysis), are labelled as such in Fig. 1. It should be noted that because the *atpA*-214 analysis does not include *Trithuria*, and because the *rbcL* analysis does not include *Arachnitis* or *Thismia*, the placement of each these taxa in the principal analysis was excluded from consideration when determining whether a clade resolved by the principal analysis also was resolved by a single-gene analysis that did not include the taxon.

The average support values for the 201 clades in the consensus tree, as determined by each of the five support analyses, are presented in Table 1. Summary comparisons of support values for the 201 clades also are presented in Table 1, for all pairwise combinations among the five analyses, except that the second SC jackknife analysis is compared only with the first SC jackknife analysis (the second SC jackknife analysis was conducted only for comparison with the first, to provide an estimate of the magnitude of stochastic variation among the results of support analyses conducted with identical software settings). Average support values for the 201 clades differ between the two SC jackknife analyses by 0.1% (74.4% vs. 74.5%), with 109 clades having been assigned different scores by these two analyses, with a maximum difference in score of 5%, an average variance of 1.07 for the raw support values, and an average variance for the ln-transformed values of $1.07*10^{-3}$. As in a conventional analysis of variance, these values represent the magnitude of stochastic variation between two analyses conducted with identical settings, and the corresponding results for pairwise comparisons among the various methods can be described with reference to these values.

Differences between the FWR and SC approaches can be discerned in comparisons between the FWR and SC jackknife analyses, and between the FWR and SC bootstrap analyses. Average support values from the FWR jackknife analysis exceed those from the first SC jackknife analysis by 4.6%, with the FWR jackknife score exceeding the SC jackknife score for 136 of the 201 clades, in 40 cases by 10% or more, and in one case by 24%. In contrast, none of the 201 clades has an SC jackknife score that exceeds its FWR jackknife score. The average variance of support values for these two methods, whether calculated on the basis of the raw scores or the ln-transformed scores, is greater than the corresponding average variance for the two SC jackknife analyses by a factor greater than 10. A similar though less pronounced relationship is observed in the comparison of FWR bootstrap scores to SC bootstrap scores, where the average support value for the former exceeds that of the latter by 2.4%. The FWR bootstrap score exceeds the SC bootstrap score for 131 of the 201 clades, in 10 cases by 10% or more, and with a maximum difference of 11%, while the latter yields a higher score for 8 clades, with a maximum difference of 2%. The average variance of support values for these two methods, whether calculated on the basis of the raw scores or the ln-transformed scores, exceeds the corresponding average variance for the two SC jackknife analyses by a factor of approximately 6.

Differences between the bootstrap and jackknife approaches can be discerned in comparisons between the

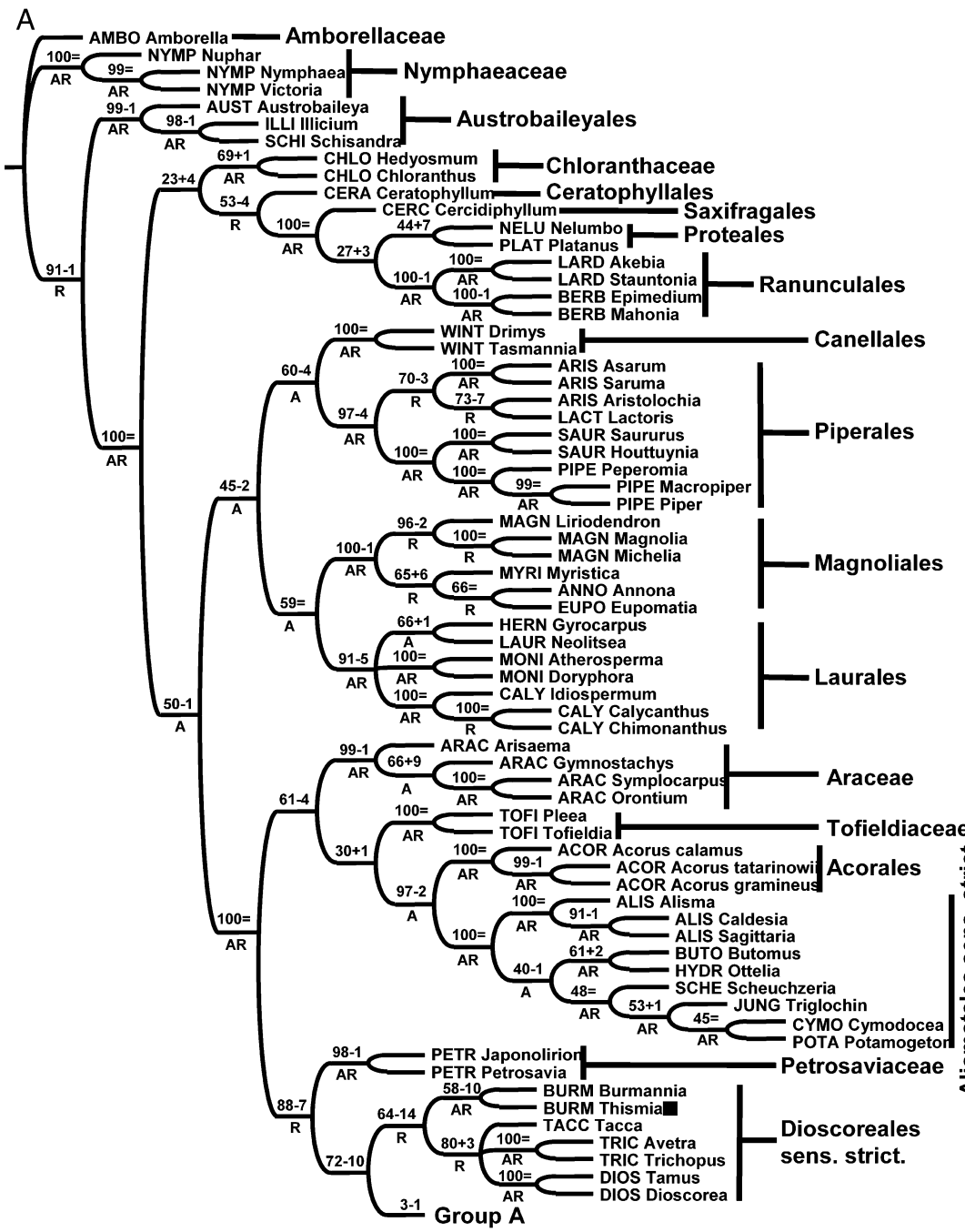

FIG. 1. Strict consensus of 768 most-parsimonious trees for 215 angiosperm terminals. Each terminal's name is preceded by a four-letter family code (cf. Appendix I). Fifteen major monocot lineages that encompass all monocots in the taxon sample, and that are mutually exclusive in membership, are labelled at right, as are ordinal assignments of dicots. One terminal that lacks an *atpA* sequence (*Trithuria*) is marked with a solid circle, and two that lack *rbcL* sequences (*Arachnitis* and *Thismia*) are marked with solid squares. The first number above each branch is the SC jackknife percentage from the initial jackknife analysis (see text). The FWR bootstrap percentage for each group is indicated just afterward by its relationship to the jackknife percentage, either by an equal sign (if the score is equal) or by a plus or minus sign and a second number (e.g., 97-4 denotes a jackknife percentage of 97 and a bootstrap percentage of 93). Letters below branches mark groups that are resolved by separate analyses of the *atpA* (A) or *rbcL* (R) subsets of the matrix used in the principal analysis. A. Basal region of tree.

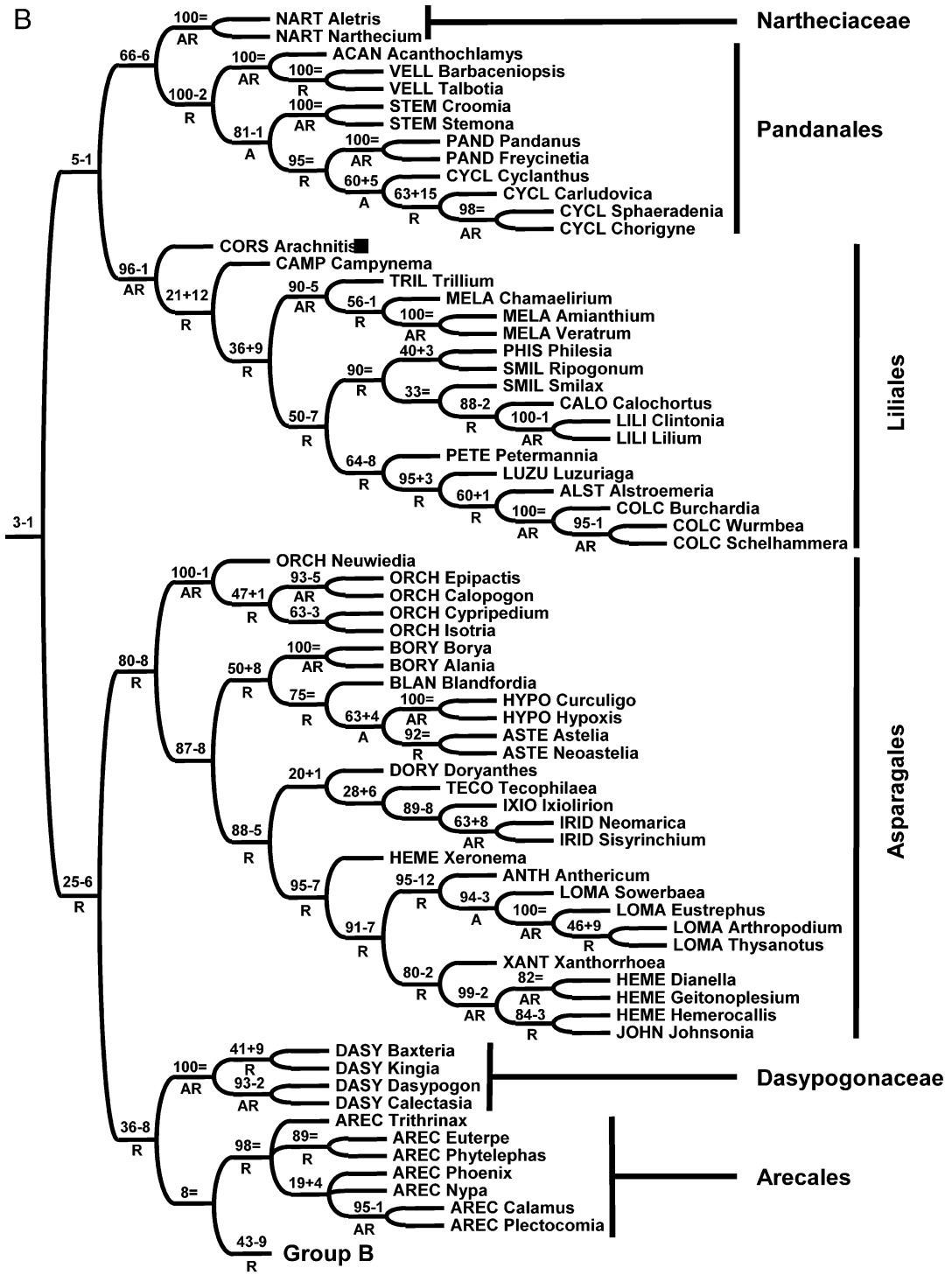

FIG. 1. (continued) B. Structure of Group A from Fig. 1A.

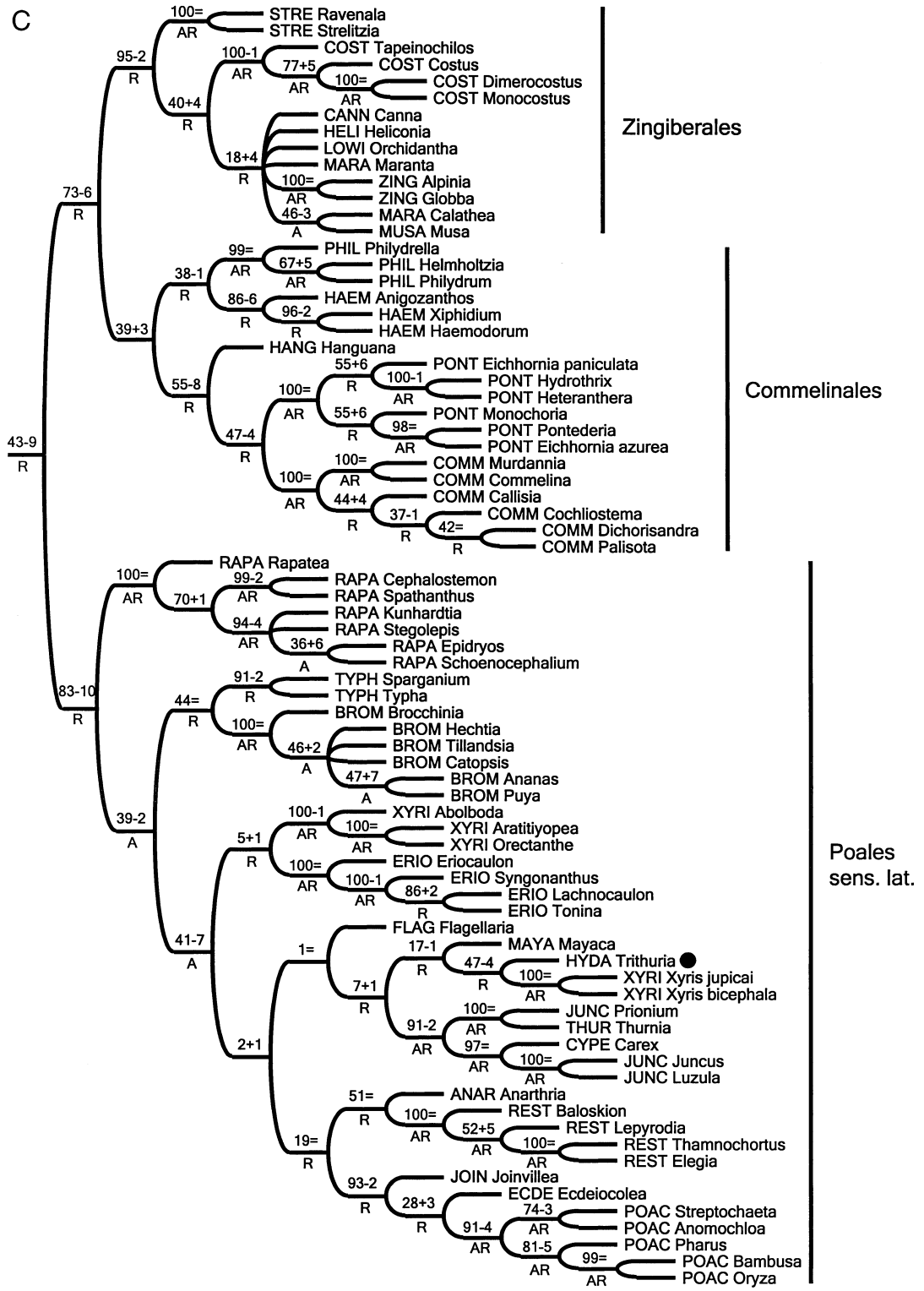

FIG. 1. (continued) C. Structure of Group B from Fig. 1B.

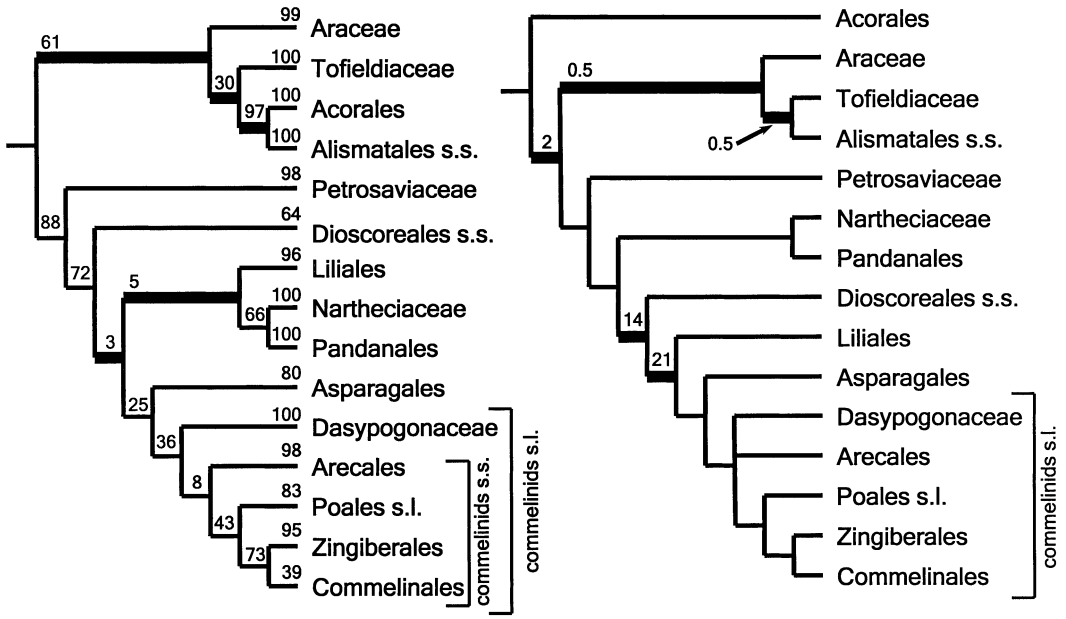

FIG. 2. Summary relationships among 15 major lineages of monocots, as resolved by the principal analysis (2A) and by a constrained analysis in which a clade consisting of all monocots except Acorales is forced to be monophyletic (2B). Each tree is a portion of more inclusive tree that includes the dicot outgroups, and in both cases the monocots as a whole and each of the 15 major monocot groups are resolved as monophyletic. 2A. SC jackknife frequencies from the initial jackknife analysis are provided for all groups, and correspond to those in Fig. 1; bolded lines identify five clades that are inconsistent with relationships in Fig. 2B. 2B. Five clades that are inconsistent with relationships in Fig. 1 and 2A are indicated with bolded lines, and SC jackknife frequencies from unconstrained analysis of the data are provided for these groups.

SC bootstrap and jackknife analyses, as well as between the FWR bootstrap and jackknife analyses. Average support values from the SC jackknife analysis exceed those from the SC bootstrap analysis by 2.9%, with the SC jackknife score exceeding the SC bootstrap score for 128 of the 201 clades, in 20 cases by 10% or more, and in one case by 19%. In contrast, the SC bootstrap score exceeds the SC jackknife score for 17 clades, with a maximum difference of 7%. The average variance of support values for these two methods, whether calculated on the basis of the raw scores or the ln-transformed scores, exceeds that of the two SC jack-

TABLE 1. Relative support values obtained by four methods for 201 clades resolved in the consensus tree from the principal analysis. One method (SC jackknife) was used twice. The average support value obtained by each method for the 201 clades is indicated in parentheses in the first column. Pairwise comparisons among support analyses are provided in the body of the table. In each case, the first of the unparenthesized numbers is the number of clades for which the first analysis (named in column 1 of the row) yields a higher support value than the second (named in the column heading), the second is the number of clades for which the first analysis yields a support value that exceeds that of the second by 10 percentage points or more, and the third is the maximum number of percentage points by which the first analysis exceeds the second, among the 201 clades. The average variance (σ^2) of the two reference scores for each of the 201 groups (one from each of the two methods compared) is provided in parentheses in the upper right sector of the matrix; the first of the two parenthesized numbers is the average variance of the raw support numbers, and the second is the average variance of ln-transformed support numbers. Results of the second SC jackknife analysis were compared only to those of the first.

First analysis in two-way comparison	Second analysis in two-way comparison				
	SC jackknife #1	SC jackknife #2	SC bootstrap	FWR jackknife	FWR bootstrap
SC jackknife #1 (74.4%)	—	51, 0, 5 (1.07; $1.07*10^{-3}$)	128, 20, 19 (13.34; $1.04*10^{-2}$)	0, 0, 0 (22.65; $1.48*10^{-2}$)	84, 5, 14 (8.23; $4.45*10^{-3}$)
SC jackknife #2 (74.5%)	58, 0, 5	—	—	—	—
SC bootstrap (71.5%)	17, 0, 7	—	—	0, 0, 0, (53.16; $3.77*10^{-2}$)	8, 0, 2 (6.84; $6.79*10^{-3}$)
FWR jackknife (79.0%)	136, 40, 24	—	154, 71, 29	—	149, 39, 24 (26.4; $1.50*10^{-2}$)
FWR bootstrap (73.9%)	45, 2, 15	—	131, 5, 11	0, 0, 0	—

knife analyses by a factor of nearly 10 (ln-transformed) or more than 10 (raw scores). A similar relationship is observed in the comparison of FWR jackknife scores to FWR bootstrap scores, where the average support value for the former exceeds that of the latter by 2.4%. Also, the FWR jackknife score exceeds the FWR bootstrap score for 149 clades, in 39 cases by 10% or more, with a maximum difference of 24%, while there is no clade for which the latter yields a higher score than the former. The average variance of support values for these two methods, whether calculated on the basis of the raw or ln-transformed scores, exceeds that of the two SC jackknife analyses by a factor greater than 10.

In the following descriptions of groups resolved by the principal analysis, SC jackknife scores and FWR bootstrap scores are reported for various clades, and the terms used to describe various levels of support conform to the conventions of Chase et al. (2000). These categories are ''strong'' (≥ 85%), ''moderate'' (75–84%), ''weak'' (50–74%), and either ''lacking'' or ''absent'' (less than 50%). These categories differ from those used by Soltis et al. (2000), who delimit strong, moderate, and weak jackknife support as ≥85%, 63–84%, and 50–62%, respectively. In text below this point, all descriptions of support for specific groups, either in terms of support frequencies or in terms of these four categories, refer to SC jackknife support, except as otherwise indicated, and descriptions of bootstrap support refer to FWR bootstrap frequencies, except as otherwise indicated. In general, bootstrap support usually is mentioned only when it falls within a different category than the level of SC jackknife support.

Of the 201 resolved groups in the consensus tree of the principal analysis, 92 are resolved independently by both *atpA* and *rbcL*, 87 by one gene or the other, but not by both, and 22 by neither gene alone. Of the 92 that are resolved independently by both genes, 79 have strong jackknife support, support is lacking for two, and support is weak to moderate for the remaining 11 groups. Of the 87 clades that are resolved by one gene or the other, but not both, 69 are resolved only by *rbcL*, and 18 only by *atpA*; of these 87 clades, 26 have strong jackknife support in the combined analysis, support is lacking for 30, and support is weak to moderate for the remaining 31 clades. Of the 22 clades that are not resolved independently by either gene, two have strong jackknife support, support is lacking for 15 and support is weak to moderate for the remaining five clades.

MONOPHYLY OF GENERA AND FAMILIES. Two of the three genera that are represented in the principal analysis by more than one terminal, *Acorus* and *Xyris*, are resolved as monophyletic, each with 100% jackknife support; each of these genera also is resolved by the separate *atpA* and *rbcL* analyses (Figs. 1A, C). The third genus that is represented by more than one terminal, *Eichhornia*, is not resolved as monophyletic because *E. paniculata* is placed with *Hydrothrix* and *Heteranthera*, and *E. azurea* is placed with *Monochoria* and *Pontederia* (Fig. 1C). Jackknife support is weak for each of these two groups of three terminals (55% in both cases), but it is strong (98%) for the placement of *E. azurea* with *Pontederia*. The latter group, which is resolved independently by each gene, is inconsistent with a monophyletic *Eichhornia*.

Of 11 dicot families represented by more than one genus, 10 are resolved as monophyletic by the combined analysis, and of these 10, all but one (Magnoliaceae) are resolved independently by both genes (Fig. 1A). The one dicot family that is not resolved by the principal combined analysis, Aristolochiaceae, is rendered nonmonophyletic by the placement of *Lactoris* (Lactoridaceae) as the sister of *Aristolochia*. This grouping of two terminals is resolved by the *rbcL* analysis (e.g., Fig. 3). It occurs in some but not all most-parsimonious trees from each of the *atpA* analyses (e.g., Fig. 4), and therefore is lacking in the consensus trees of these analyses (not illustrated), both of which include a polytomy in which the following four groups emerge from a common point: *Aristolochia*; *Lactoris*; *Asarum* + *Saruma*; and Saururaceae + Piperaceae. Among individual trees from the two *atpA* analyses, the three representatives of Aristolochiaceae never constitute a monophyletic group. *Lactoris* is placed in a variety of positions, including sister of *Aristolochia* and sister of *Asarum* + *Saruma*.

Forty-three of the monocot families in the sample (as circumscribed in Kubitzki 1998a, b) are represented by more than one terminal each, though one of these families, Triuridaceae, was not included in the principal analysis. Of the 42 that were included in the principal analysis, and therefore subject to testing for monophyly, 37 were resolved as monophyletic and five were not. Smilacaceae are not monophyletic because one representative, *Ripogonum*, is placed as the sister of *Philesia* (Philesiaceae), while the other, *Smilax*, is placed in a neighboring group with *Calochortus* and Liliaceae (Fig. 1B). Hemerocallidaceae are not monophyletic because *Johnsonia* (Johnsoniaceae) is nested among three representatives of this family, and the fourth representative, *Xeronema*, is placed a few nodes away, as sister of the group that includes the aforementioned taxa plus *Anthericum* and Lomandraceae (Fig. 1B). Marantaceae are not monophyletic because *Calathea* is placed as the sister of *Musa* (Musaceae), while *Maranta* is one element of a more inclusive unresolved group that includes the *Calathea*/*Musa* group (Fig. 1C). Xyridaceae are not monophyletic because the two representatives of *Xyris* are placed in a clade with *Trithuria* (Hydatellaceae) and *Mayaca* (Mayacaceae), among representatives of several other families, while the other three genera of Xyridaceae (*Abolboda*, *Orectanthe*, and *Arati-*

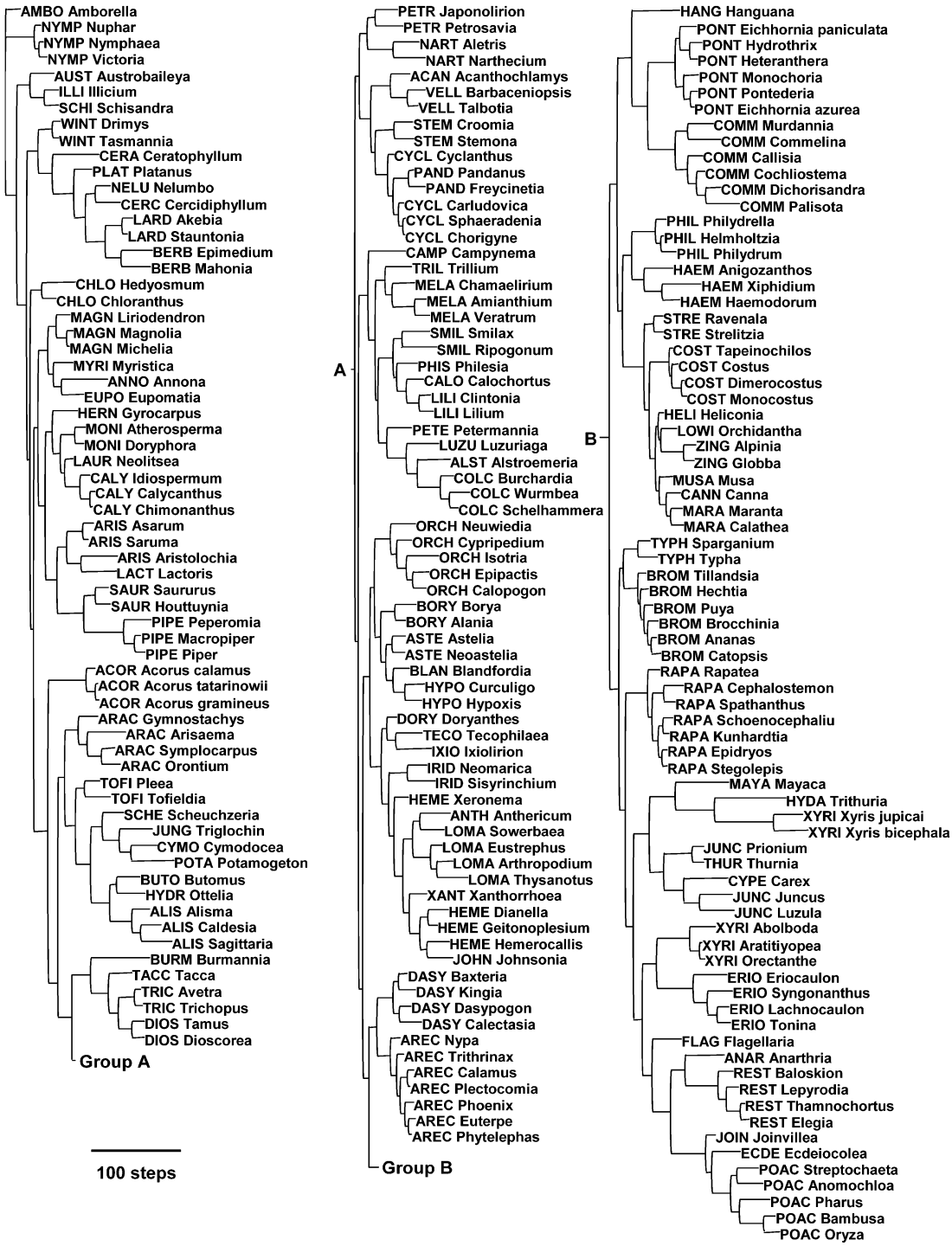

FIG. 3. One randomly selected most-parsimonious tree for the *rbcL* portion of the matrix used in the principal analysis. Branch lengths are approximately proportional to the number of steps on each branch, as in Fig. 4, and the scale is identical in the two figures.

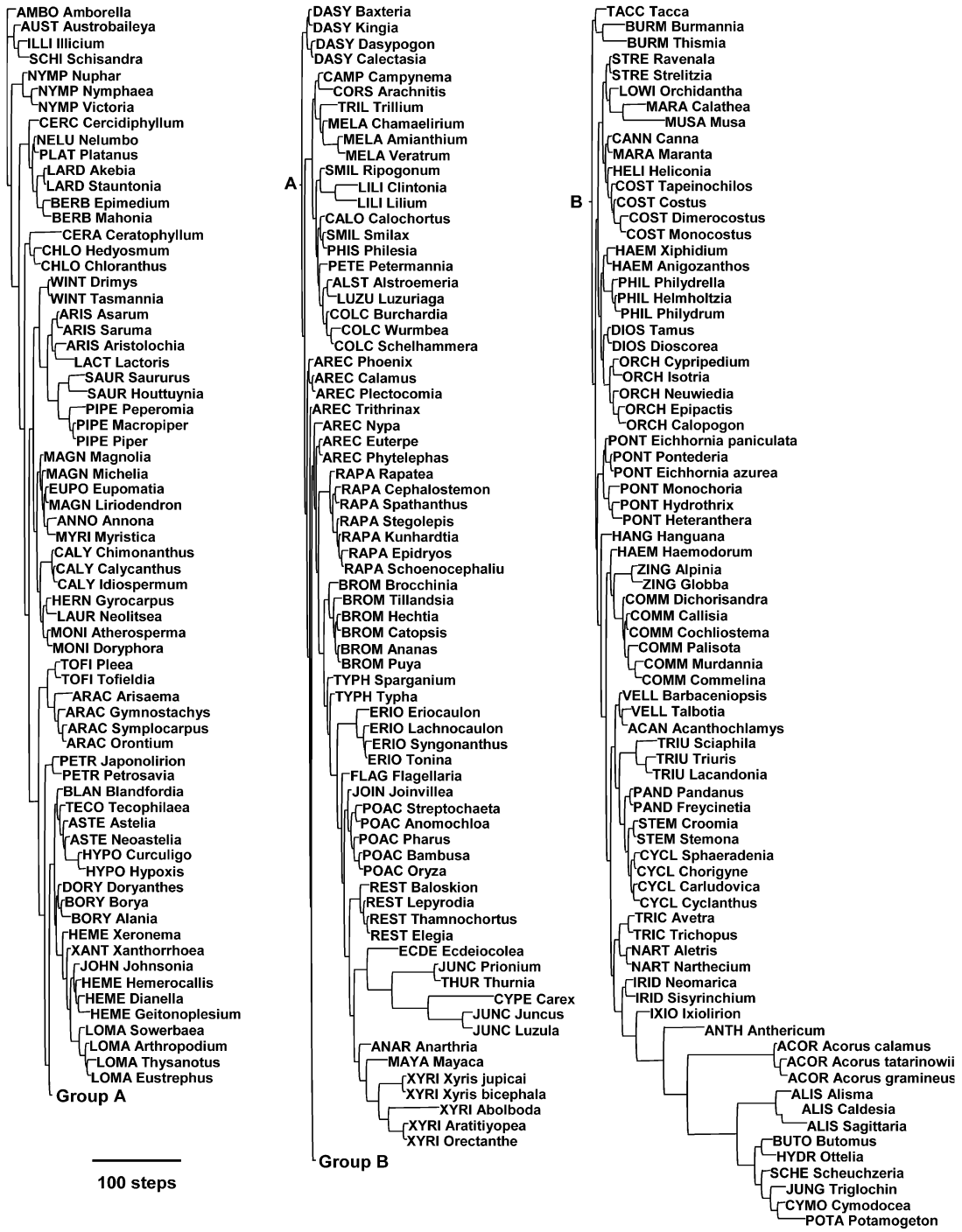

FIG. 4. One randomly selected most-parsimonious tree for the *atpA*-217 data set (see text). Branch lengths are approximately proportional to the number of steps on each branch under accelerated-transformation optimization, with all characters (informative or not) included in the matrix; scale bar represents 100 character transformations.

tiyopea) are resolved as a clade that is the sister of Eriocaulaceae (Fig. 1C). Among the nodes that are inconsistent with monophyly of Xyridaceae (i.e., those along the track between the two resolved portions of the family), the greatest jackknife support is for the placement of *Trithuria* as the sister of *Xyris* (47%, here regarded as absence of support), while the group with the next strongest support is the one that includes

these two genera plus *Mayaca* (17%). Jackknife support for the monophyly of Xyridaceae (a group that does not occur in the consensus tree) is 40%. Finally, Juncaceae are not monophyletic because *Prionium* is placed as the sister of *Thurnia* (Thurniaceae), while *Juncus* and *Luzula* are placed with *Carex* (Cyperaceae; Fig. 1C). Of the 37 monocot families that are resolved as monophyletic, 29 are independently resolved by both *atpA* and *rbcL,* and each of the other eight families is resolved either by *atpA* alone (two families) or by *rbcL* alone (six families).

MAJOR GROUPS OF MONOCOTS AND RELATIONSHIPS AMONG THEM. With the consensus tree for the principal analysis rooted between *Amborella* and all other taxa, and with the arbitrary grouping of all taxa other than *Amborella* collapsed, the three lineages that arise from the obligatory basal trichotomy are *Amborella*, Nymphaeaceae, and a clade that includes all other taxa in the analysis (Fig. 1A). The latter group has strong jackknife support (91%). The deepest branch within the clade that includes all remaining taxa is a dichotomy in which the Austrobaileyales are the sister of all other taxa. Within the latter group, which is strongly supported (100%), there is a dichotomy between a clade that includes most of the remaining elements, and a clade that consists of Chloranthaceae, Ceratophyllales (i.e., *Ceratophyllum*), and a monophyletic grouping of seven tricolpate taxa, within which the Saxifragales (i.e., *Cercidiphyllum*) are sister of the other six, with Proteales (i.e., *Platanus* + *Nelumbo*) sister of Ranunculales (i.e., Lardizabalaceae + Berberidaceae). Support is strong (100%) for the grouping of tricolpate taxa, and for the Ranunculales (100%). Jackknife support is weak (53%), and bootstrap support is lacking (49%) for the placement of *Ceratophyllum* as sister of the tricolpate group. All remaining taxa in the analysis fall into two sister clades, with one including all of the remaining dicots and the other including all of the monocots in the analysis. The dicot group, which lacks jackknife support (45%), comprises four orders, with a dichotomy between a weakly supported clade (60%) in which Canellales and Piperales are sister groups, and a weakly supported clade (59%) in which Magnoliales and Laurales are sister groups. Support is strong for all four of these orders.

Further description of the results of the principal analysis, with respect to higher-level relationships within the monocots, is facilitated by the enumeration of 15 mutually exclusive groups that collectively include all monocots in the sample. Eight of these groups correspond to orders in the APG II system (Angiosperm Phylogeny Group 2003); these are **Acorales** (i.e., *Acorus*), **Arecales** (i.e., Arecaceae), **Asparagales, Commelinales, Liliales, Pandanales,** Poales (referred to here as **Poales s. lat.**), and **Zingiberales.** Two of the 15 groups are orders that are delimited more narrowly here than in the APG II system, by the exclusion of certain families, and three of the 15 groups are the families that are removed from these two orders; the two orders are **Alismatales s. str.** and **Dioscoreales s. str.** The three families that have been removed from them are **Araceae** and **Tofieldiaceae** (from Alismatales s. lat.), and **Nartheciaceae** (from Dioscoreales s. lat.). The two remaining groups, of the 15, are families that were not assigned to orders in the APG II system (**Dasypogonaceae** and **Petrosaviaceae**). All 15 of these groups are resolved as monophyletic by the principal analysis, 11 of them with strong jackknife support (Figs. 1, 2A). Of the four remaining groups, support is moderate for two (Asparagales and Poales s. lat.), weak for one (Dioscoreales s. str.), and lacking for one (Commelinales). Of the 15 groups, eight are independently resolved by *atpA* and *rbcL,* six by *rbcL* but not by *atpA,* and one (Commelinales) by neither gene alone. None of these groups is resolved by *atpA* but not by *rbcL.*

Relationships among the 15 major monocot lineages are fully resolved in the consensus tree of the principal analysis (Figs. 1, 2A). Of the 14 total groups that are resolved among these lineages, only the most inclusive one, the group that consists of all monocots, is resolved independently by both *atpA* and *rbcL.* Of the remaining 13, one is resolved only by *atpA,* five are resolved only by *rbcL,* and seven are not resolved independently by either gene. Of the 14 resolved groups, three have strong jackknife support (Figs. 1A, 2A). These three groups are the clade that includes all monocots (and which is resolved by each gene independently, as already noted); the placement of Acorales with Alismatales s. str. (which is resolved by *atpA* but not by *rbcL*), and the grouping of all monocots except Araceae, Tofieldiaceae, Acorales, and Alismatales s. str. (which is resolved by *rbcL* but not by *atpA,* and which has moderate bootstrap support). Of the 11 remaining groupings among the major monocot lineages, four have weak jackknife support and seven have none. Detailed descriptions of relationships among and within the major monocot groups follow.

The deepest branch resolved within the monocots is between a clade that includes four of the 15 major groups, and another that includes the remaining 11 (Figs. 1A, 2A). Within the first of these groups, which is weakly supported (61%), *Acorus* (i.e. Acorales) and Alismatales s. str. are sister groups (with strong support, 97%), the sister of this pair is Tofieldiaceae, and the sister of this set of three groups is Araceae. Within the clade that includes the remaining 11 groups, which has strong jackknife support (88%) and moderate bootstrap support (81%), the deepest branch is between Petrosaviaceae and a clade that includes the other 10 groups. Within the latter group, which has weak support (72%), Dioscoreales s. str. are the sister of a clade

that includes the nine remaining groups. Among the remaining nine, a clade that consists of three groups is sister of a clade that includes the remaining six (Figs. 1B, 2A). Within the assemblage of three groups, which lacks support, Liliales are the sister of a clade in which Nartheciaceae and Pandanales are sisters (with weak support, 66%). Within the assemblage that includes the remaining six groups (which lacks support) there is a pectinate structure, with Asparagales, Dasypogonaceae, Arecales, and Poales diverging sequentially from a lineage in which the remaining two groups, Commelinales and Zingiberales, are sisters (Figs. 1B, C, 2A). Support is lacking for all relationships among these six lineages, except that there is weak support (73%) for the grouping of Commelinales and Zingiberales.

In addition to the 15 major groups mentioned above, the status of three other major groupings is of interest. Discussion of these three groups is separated from that of the 15 major groups, because these three are not mutually exclusive in membership relative to each other or to the other major groups. The first of these groups, **Poales s. str.** (as distinguished from Poales s. lat., as mentioned above), includes the seven families assigned by Dahlgren et al. (1985) to Poales (Flagellariaceae, Joinvilleaceae, Poaceae, Restionaceae, Ecdeiocoleaceae, Anarthriaceae, and Centrolepidaceae), plus Lyginiaceae and Hopkinsiaceae, which were segregated recently from Restionaceae (Briggs and Johnson 2000), and are not included in the present analysis. The principal analysis resolves a clade that includes all of the sampled taxa of Poales s. str., except *Flagellaria* (Fig. 1C); this clade lacks jackknife support (19%). *Flagellaria* is the first group to diverge within the sister group of this clade, and that placement also lacks jackknife support (1%). Jackknife support is 9% for Poales s. str. (including *Flagellaria*), a group that is not resolved by the principal analysis.

The two additional monocot groups of interest are the **commelinids s. str.** and the **commelinids s. lat.** In terms of the major groups described above, the commelinids s. str. include the Arecales, Commelinales, Zingiberales, and Poales s. lat. This group corresponds closely in membership to the ''commelinids'' of Linder and Kellogg (1995). The commelinids s. lat. comprise the commelinids s. str. plus Dasypogonaceae, and correspond to the ''commelinids'' as delimited in the APG II system (Angiosperm Phylogeny Group 2003). The principal analysis resolves both of these groups, with jackknife support lacking in both cases (8% for the commelinids s. str., 36% for the commelinids s. lat.).

RELATIONSHIPS WITHIN MAJOR MONOCOT GROUPS. The four taxa of Araceae (Fig. 1A) represent three subfamilies sensu Mayo et al. (1997), with Aroideae (*Arisaema*) sister of a clade with weak jackknife support (66%) and moderate bootstrap support (75%), which includes Gymnostachydoideae (*Gymnostachys*) as sister of a strongly supported Orontioideae (*Orontium* and *Symplocarpus*). Within Alismatales s. str., there is strong support for the monophyly of Alismataceae and for the grouping of *Caldesia* and *Sagittaria* as sisters within this family. The sister of Alismataceae includes the six remaining families of Alismatales s. str., each represented by a single taxon; this group lacks jackknife support (40%).

The deepest branch resolved within the Dioscoreales s. str. is between Burmanniaceae and a clade with moderate jackknife support (80%) that includes Taccaceae, Trichopodaceae, and Dioscoreaceae. Relationships among the latter three families are unresolved.

Within the clade that consists of Nartheciaceae and Pandanales (Fig. 1B), Pandanaceae and Cyclanthaceae are united, with strong jackknife support (95%), and support for the placement of Stemonaceae as sister of this group is moderate (81%). There is strong jackknife support (100%) for the placement of Acanthochlamydaceae as sister of Velloziaceae.

The deepest branches within Liliales lack jackknife support. The placement of Trilliaceae with Melanthiaceae is strongly supported (90%), as is the clade that consists of Philesiaceae, Smilacaceae, Calochortaceae, and Liliaceae (90%). There is strong support (95%) for the clade that consists of Luzuriagaceae, Alstroemeriaceae, and Colchicaceae, and weak support for the placement of Petermanniaceae as sister of this group.

Within Asparagales, there is strong jackknife support (87%) and moderate bootstrap support (79%) for the clade that includes all taxa in the order except Orchidaceae. Support is moderate (80%) for the clade that includes Xanthorrhoeaceae, Johnsoniaceae, and all elements of Hemerocallidaceae except *Xeronema*, while the grouping of Anthericaceae and Lomandraceae has strong support (95%), but moderate bootstrap support (83%), as does the grouping of these two clades (jackknife support 91%, bootstrap support 84%). The placement of *Xeronema* with this entire group has strong jackknife support (95%). Doryanthaceae and Tecophilaeaceae diverge sequentially from a group in which Ixioliriaceae and Iridaceae are sister taxa; jackknife support is lacking for the monophyly of this group, and for the subgroup that includes all elements of it except Doryanthaceae, but the sister group relationship between Ixioliriaceae and Iridaceae has strong jackknife support (89%) and moderate bootstrap support (81%). Asteliaceae and Hypoxidaceae are sister groups (with weak support, 63%), and their sister group is Blandfordiaceae (with moderate support, at 75%). The placement of Boryaceae as the sister group of this lineage has weak jackknife support (50%).

Within Zingiberales (Fig. 1C), the only relationships with jackknife support, apart from monophyly of individual families, are two internal nodes within Cos-

taceae. The least resolved region of the entire tree lies within Zingiberales, where relationships are mostly unresolved within a clade of eight terminals that includes all representatives of Cannaceae, Musaceae, Zingiberaceae, Lowiaceae, Heliconiaceae, and Marantaceae; jackknife support for this clade is lacking. The Strelitziaceae are placed as the sister of a group that includes all other elements of Zingiberales, though jackknife support for the latter grouping is lacking.

Within Commelinales, Pontederiaceae and Commelinaceae are resolved as sister taxa, though jackknife support for this clade is lacking. The sister of this clade is the single terminal that represents Hanguanaceae. This clade of three families is the only multi-family grouping within the order that has jackknife support, and this support is weak (55%), while bootstrap support for this clade is lacking (47%). This clade is resolved as sister of a clade in which Philydraceae and Haemodoraceae are sisters. Within Commelinaceae, the clade consisting of *Commelina* and *Murdannia* is resolved with strong jackknife support (100%), and it is placed as sister of a clade that includes all other elements of the family. The latter group, which includes four genera, lacks jackknife support (44%). Within the group of four genera there is a pectinate structure, with *Callisia* and *Cochliostema* diverging in succession from a clade that consists of *Dichorisandra* and *Palisota*; jackknife support is lacking for all resolved clades within this group. The six terminals representing Pontederiaceae are resolved as a strongly supported clade (100%) that includes two sister clades of three terminals each. Each of these smaller groups has weak jackknife support (55% in both cases), but there is a strongly supported structure within each group. Within Philydraceae, *Helmholtzia* and *Philydrum* are resolved as sister taxa, with moderate jackknife support (67%), and with *Philydrella* resolved as their sister group. Within Haemodoraceae, *Xiphidium* and *Haemodorum* are resolved as sister taxa, with strong jackknife support (96%), and with *Anigozanthos* resolved as their sister group.

Within Poales, Rapateaceae are resolved as the sister of a clade that includes all other taxa; the latter group lacks jackknife support (39%). Within Rapateaceae, *Rapatea* is resolved as sister of the rest of the family, and the latter group has weak jackknife support (70%). Within this group, *Cephalostemon* and *Spathanthus* are placed together as a group that is the sister of a group that includes all remaining members of the family. Both of these groups have strong jackknife support (99% and 94%, respectively). Typhaceae and Bromeliaceae are resolved as sister groups, but the grouping of these two families lacks jackknife support. Within Bromeliaceae, *Brocchinia* (Pitcairnioideae) is sister of a clade that includes all other representatives of the family, and relationships are largely unresolved within the latter group, though *Puya* (Pitcairnioideae) and *Ananas* (Bromelioideae) are united; no aspect of the internal structure of Bromeliaceae has jackknife support, but the association of *Ananas* with *Puya* has weak bootstrap support (54%). All remaining elements of Poales s. lat. are placed in a group that lacks jackknife support (41%), and some aspects of the internal structure of this group have jackknife percentages in single digits. One strongly supported set of relationships within this group, involving elements of more than one family, is the placement of all elements of Cyperaceae, Juncaceae, and Thurniaceae within a clade (91% jackknife support). Within this group, there is strong support (97%) for the placement of two genera of Juncaceae (*Juncus* and *Luzula*, but not *Prionium*) with *Carex* (the only representative of Cyperaceae), and for the placement of *Prionium* with *Thurnia* (100%). Within the lineage that includes all elements of Poales s. str. except *Flagellaria* (described above), the deepest division is between a group in which *Anarthria* is sister of Restionaceae (weak jackknife support, 51%), and a strongly supported group (93%) that includes Joinvilleaceae, Ecdeiocoleaceae, and Poaceae. Within the latter group, Ecdeiocoleaceae and Poaceae are resolved as sister groups, though jackknife support for this group is lacking (28%).

One randomly selected most-parsimonious tree from the analysis of the *rbcL* portion of the principal analysis, and one from the *atpA*-217 analysis, are presented in Figs. 3 and 4, respectively. Relatively long branches are evident in the *atpA* tree for several individual taxa and groups, including *Ceratophyllum*; Piperales; Liliaceae; Eriocaulaceae; the clade that includes *Ecdeiocolea*, Juncaceae, *Thurnia*, and *Carex*; *Mayaca*; Xyridaceae; the clade that includes *Tacca* and Burmanniaceae; *Calathea*; *Musa*; Triuridaceae; *Anthericum*; *Acorus*; and Alismatales s. str. In the *rbcL* tree, relatively long branches are evident in the clade that includes *Ceratophyllum*, *Platanus*, *Nelumbo*, *Cercidiphyllum*, Lardizabalaceae, and Berberidaceae; *Annona*; Piperales; *Acorus*; the clade that includes Araceae, Tofieldiaceae, and Alismatales s. str.; Dioscoreales s. str.; Liliales; and the clade that includes *Mayaca*, *Trithuria*, Xyridaceae, Juncaceae, *Thurnia*, *Carex*, Eriocaulaceae, and most families within Poales s. str. These observations are general and nonquantitative.

Groups resolved by the principal analysis and also by the *atpA*-214 analysis or by the analysis of the *rbcL* data have been described, and are indicated in Fig. 1. Consensus trees for the single gene analyses are not presented here, but there are several groups of interest that are not resolved by the principal analysis, but are resolved by the *atpA* analyses or by the *rbcL* analysis: Some groups of interest that are in the consensus tree from the *atpA*-217 analysis, but not in the consensus tree from the principal analysis, are a clade that in-

cludes all taxa except *Amborella* and Austrobaileyales; a clade consisting of Araceae and Tofieldiaceae; a clade consisting of all five representatives of Xyridaceae, with *Mayaca* the sister of this clade. Another group that is resolved by the *atpA*-217 analysis but not by the principal analysis is a clade that consists of all representatives of Pandanales, including the three representatives of Triuridaceae. Within this clade, Stemonaceae, Pandanaceae, and Cyclanthaceae are placed together as a clade, with Triuridaceae the sister of this group, and with a clade consisting of *Acanthochlamys* and Velloziaceae as the sister of this group of four families. Within Triuridaceae, *Triuris* and *Lacandonia* are sister taxa, with *Sciaphila* placed as the sister of this pair. All of the groups described in this paragraph as resolved by the *atpA*-217 analysis also are resolved by the *atpA*-214 analysis, except for the Pandanales. Because Triuridaceae were not included in the *atpA*-214 analysis, they, of course, are absent, but the remaining representatives fail to be resolved as a monophyletic group. Three of the families (Stemonaceae, Pandanaceae, and Cyclanthaceae) are resolved as a clade by the *atpA*-214 analysis, and two others (Acanthochlamydaceae and Velloziaceae) are resolved as a clade, but these two clades are not placed together in a more inclusive group that excludes all other taxa in the analysis. Thus, a group that corresponds to the Pandanales is resolved by *atpA* only when the three representatives of Triuridaceae are included in the analysis.

Some groups of interest that are in the consensus tree from the *rbcL* analysis, but not in the consensus tree from the principal analysis, are a clade that includes Winteraceae as sister of a clade that includes *Ceratophyllum*, *Cercidiphyllum*, Proteales, and Ranunculales; a group in which Laurales and Piperales are sisters, with Magnoliales the sister of this group; a group that includes all monocots except *Acorus*, with *Acorus* the sister of this group (i.e., monocots resolved as monophyletic, as in the principal analysis, but *Acorus* placed as the first lineage to diverge from a group that includes all other monocots); a group consisting of Araceae, Tofieldiaceae, and Alismatales s. str.; a group, within Asparagales, consisting of Orchidaceae, Boryaceae, Asteliaceae, Blandfordiaceae, and Hypoxidaceae, as sister of a clade that includes all other taxa of the order; a group consisting of Dasypogonaceae and Arecaceae; and a group that includes all elements of Poales s. str.

Insertion/Deletion Zones. Of the two informative *atpA* indel characters, one occurs as two states, with 199 of the 215 taxa in the principal analysis (including *Oryza*) exhibiting the undeleted state, five having a deletion of six nucleotides corresponding approximately to sites 581–586 of the *Oryza* sequence, and 11 scored as unknown (in some cases because the taxa lack an *atpA* sequence, in others because of ambiguity of alignment in this region). The five taxa with this deletion are *Arisaema*, *Neuwiedia*, *Ixiolirion*, and two of the achlorophyllous taxa, *Arachnitis* and *Thismia*. Close relationships are not resolved among any of these taxa in the optimal trees, so one step is associated with each occurrence, the CI is 0.2, and the RI is 0. The three representatives of Triuridaceae, which were not included in the principal analysis, are undeleted in this region.

The second of the informative indel characters occurs in an ambiguously aligned position between sites 585 and 597 of the reference *Oryza* sequence. In this region, 156 taxa in the principal analysis are undeleted, including *Oryza*, 29 have a deletion of three nucleotides, 25 have a deletion of six nucleotides, and five are scored as unknown. Among taxa in the principal analysis, the three-nucleotide deletion occurs in *Gyrocarpus*, *Carex*, *Thurnia*, all three representatives of *Acorus*, all elements of Alismatales s. str. except *Cymodocea*, and in all sampled elements of Typhaceae, Bromeliaceae, Eriocaulaceae, and Juncaceae. The six-nucleotide deletion occurs in *Arisaema*, all elements of Pandanales except *Talbotia*, and all elements of Zingiberales. There are 10 steps in this character, including a reversion from a three-nucleotide deletion to the undeleted state in *Cymodocea* and a reversion from a six-nucleotide deletion to the undeleted state in *Talbotia*; the CI is 0.2, and the RI is 0.84. The three representatives of Triuridaceae, which were not included in the principal analysis, also have the six-nucleotide deletion, a feature in which they resemble most other members of Pandanales.

Relationships Resolved with Alternative Data Sets. ALTERNATIVE *BURMANNIA RBCL* SEQUENCES. Alternative *atpA* and *rbcL* sequences are available in GenBank for many of the taxa in the analysis, including several of the taxa for which new sequences were generated for this analysis. In selecting among available sequences, one goal was for both sequences of each terminal to represent the same species, and another was to use sequences that were as complete as possible. In some instances these criteria favored different available sequences. In most cases only minor differences were observed among the results of analyses conducted with alternative sequences, but an exception was observed for *Burmannia*, for which five *rbcL* sequences were available in GenBank. Of these five, one (*B. lutescens*) is derived from an achlorophyllous species, and the remaining four (*B. biflora*, *B. coelestis*, *B. longifolia*, and *B. madagascariensis*) from chlorophyllous species (Caddick et al. 2002; Lewis 2002). The *rbcL* sequence of *B. coelestis* lacks an internal region that is 367 nucleotides in length, and it was eliminated from consideration for that reason. The *atpA* sequence generated for this analysis was obtained from *B. lutescens*, which is one of species for which an *rbcL* sequence is available, but the available *rbcL* sequence for this species is only 1,040

nucleotides in length, as it lacks 284 nucleotides at the 5′ end of the gene, and 47 nucleotides at the 3′ end, relative to the endpoints used for other sequences in the analysis. Hence, this sequence was regarded as a potentially suboptimal choice for inclusion in the analysis, but was retained provisionally for consideration. To examine this situation, an analysis was conducted using only *rbcL* sequences, including the four most complete sequences from *Burmannia* (i.e., all except *B. coelestis*), plus all other *rbcL* sequences in the complete matrix. In the resulting trees, the sequence from *B. lutescens* was placed among several dicot lineages as the sister of *Cercidiphyllum*, while those of the other three species of *Burmannia* (*B. longifolia*, *B. biflora*, and *B. madagascariensis*) were resolved as a clade within a more inclusive group that consisted of all other members of Dioscoreales s. str. in the sample. Because the *rbcL* sequence from the achlorophyllous species *B. lutescens* was not placed with the other available *rbcL* sequences of *Burmannia* or Dioscoreales s. str., it was regarded as an inappropriate choice for an analysis of higher-level relationships, and therefore eliminated from consideration. Of the three remaining *rbcL* sequences, which were resolved as a clade, the sequence from *B. longifolia* was placed on the shortest branch in the resulting trees, and on that basis it was selected for use in the analysis. Among various additional analyses that were conducted, a provisional analysis was run with a matrix identical to the one used in the principal analysis, except that it included the *rbcL* sequence of *B. biflora*, rather than that of *B. longifolia*. The resulting trees were similar in many respects to those obtained by the principal analysis, but the Dioscoreales s. str. were placed among the commelinid families, as the sister of Arecales.

Alternative Character Subsets. Removal of the two indel characters from the matrix used in the principal analysis leaves 996 characters for 215 taxa. Analysis of this matrix yielded the same set of 768 most-parsimonious trees that were resolved by the principal analysis.

RNA editing of *atpA* transcripts has been reported in *Oenothera* (Schuster et al. 1991), *Beta* (Senda et al. 1993), triticale (Laser et al. 1995), *Arabidopsis* (Giegé and Brennicke 1999), and *Oryza* (Notsu et al. 2002). These reports collectively identify seven edited sites within the region of *atpA* that was sampled for the present study, corresponding to the following numbered sites in the reference *Oryza* sequence in GenBank accession AB076666: 246 (*Oenothera*), 393 (triticale), 971 (triticale), 1,110 (*Arabidopsis*), 1,178 (*Beta*, *Oryza*, triticale, *Arabidopsis*), 1,291 (*Oryza*), and 1,292 (*Beta*, triticale, *Arabidopsis*). All of these sites except one (1,291) are cladistically informative in the data matrix assembled for the present study, as well as in the subset used in the principal analysis. The observed states for the seven edited sites, across the 217 taxa for which *atpA* sequences are available (1,519 cells of the matrix) include 38 scores of unknown and two subset ambiguities. Of the remaining 1,479 cells, which are scored as individual nucleotides, 1,118 (76%) are scored as C, 349 (24%) as T, seven (< 1%) as G, and five (< 1%) as A. Corresponding percentages of C, T, G, and A in the complete set of 217 *atpA* sequences, including informative and uninformative characters, are 21%, 26%, 25%, and 28%, respectively. Of the 217 taxa for which there are *atpA* sequences, 195 are scored as individual nucleotides for all seven of the edited sites, and of these 195, the number of taxa with a C at each of the seven sites, in order from the 5′ to the 3′ end of *atpA,* is 190, 189, 115, 42, 148, 195, and 160.

The data set obtained from the matrix used in the principal analysis by removing the six informative *atpA* nucleotide sites for which RNA editing has been observed has 215 taxa and 992 informative characters, though there are *atpA* sequences for only 214 of these taxa (i.e., all but *Trithuria*). Analysis of this matrix yielded 1,536 most-parsimonious trees (twice as many as were resolved by the principal matrix) of length 8,520, with a CI of 0.20 and an RI of 0.62. Among the six edited sites that are cladistically informative, and which were excluded from this analysis, there are 70 steps in half of the most-parsimonious trees, and 71 in the other half, and the ensemble CI and RI for this set of five characters are ca. 0.13 and 0.73, respectively. Among the 1,536 most-parsimonious trees, the 768 trees with 70 steps among the edited sites (i.e., those with 8,590 steps when those characters are included) are identical to the set of trees obtained by the principal analysis. All relationships in the consensus tree, except one, are identical to those resolved by the principal analysis. The exception lies in the presence of a trichotomy, with the following three groups emerging from a common point: Araceae, Tofieldiaceae, and a clade that consists of Acorales and Alismatales s. str. Because half of the most-parsimonious trees from this analysis are identical to those resolved by the primary analysis, these trees resolve the same relationships, with the first of the three groups sister of a clade in which the latter two are sisters (Fig. 1A). In the remaining trees, Tofieldiaceae are sister of a clade in which Araceae and the Acorales/Alismatales s. str. clade are sisters.

The matrix obtained by removing all taxa that lack one or the other of the two genes includes 212 terminals and 998 informative characters. It differs from the matrix used in the principal analysis in the exclusion of *Arachnitis*, *Thismia*, and *Trithuria*. Analysis of this matrix yielded 1,536 most-parsimonious trees (twice as many as were resolved by the principal matrix) of length 8,477, CI 0.21, and RI 0.62. With the positions of the three excluded genera removed from consider-

ation, the consensus of these trees (not illustrated) is identical to that of the principal analysis with respect to relationships among dicots, and monophyly of the monocots. Also, relationships are identical to those resolved by the principal analysis (both within and among groups) for the first two monocot lineages to diverge in succession from the line that includes all other monocots. These two lineages encompass five of the 15 mutually exclusive clades of monocots delimited above (Araceae, Tofieldiaceae, Acorales, Alismatales s. str., and Petrosaviaceae). The results of this analysis differ, however, in the presence of a trichotomy at the base of the group that is the sister of Petrosaviaceae. One clade that diverges from this point corresponds to Liliales (minus *Arachnitis*, which is not in this analysis), and has an internal structure that is identical to that of Liliales in the principal analysis. The second clade that diverges from this point includes Dioscoreales s. str. (minus *Thismia*, which is not in this analysis) as the sister of a clade in which Nartheciaceae and Pandanales are sister taxa. Relationships within these groups are identical to those in the principal analysis, except within Dioscoreales s. str., where *Burmannia* (the only remaining representative of Burmanniaceae) is the sister of the clade that includes all other members of the group, within which *Tacca* is the sister of Dioscoreaceae, with Trichopodaceae the sister of this pair. The last of the three groups that diverge at the polytomy includes all remaining monocots. This clade includes the six remaining major lineages of monocots (Asparagales, Dasypogonaceae, Arecales, Zingiberales, Commelinales, and Poales s. str., with *Trithuria* not represented). Most relationships within and among these groups are identical to those resolved by the principal analysis, but there are some exceptions. First, there is a loss of resolution within Asparagales, with a polytomy now present from which four groups emerge (*Doryanthes*, *Tecophilaea*, the *Ixiolirion* + Iridaceae clade, and the clade in which *Xeronema* is sister of a set of 10 other taxa). Second, there is a trichotomy at the base of the commelinids s. str., with Dasypogonaceae, Arecales, and a clade that includes all other commelinid taxa (except *Trithuria*) diverging from a common point. Third, there is a loss of resolution within Arecales (i.e., Arecaceae), with all terminals arising from a common basal polytomy, except that *Calamus* and *Plectocomia* are resolved as sisters, as are *Euterpe* and *Phytelephas*. Fourth, there is a rearrangement within Poales s. lat., with the clade consisting of two species of *Xyris* shifted from its placement with *Mayaca* to one in which it is the sister of the clade that includes the other three representatives of Xyridaceae. Thus, Xyridaceae are resolved as monophyletic, and Xyridaceae and Eriocaulaceae are sister groups.

Analysis of the complete data matrix for 218 taxa (the matrix used in the principal analysis plus the three representatives of Triuridaceae, each represented only by an *atpA* sequence) yielded 1,632 trees of length 8,652 and approximately the same CI and RI as obtained with the principal analysis (0.20 and 0.62, respectively). The consensus of these trees (not illustrated) is identical to that of the principal analysis with respect to relationships among the dicots, and in resolving the monocots as monophyletic. Also, relationships are identical to those resolved by the principal analysis (both within and among groups) for the first three monocot lineages to diverge in succession from the line that includes all others. The first three lineages include six of the 15 mutually exclusive clades of monocots delimited above (Araceae, Tofieldiaceae, Acorales, Alismatales s. str., Petrosaviaceae, and Dioscoreales s. str.). The results of this analysis differ, however, in the presence of a polytomy at the base of the group that is the sister of Dioscoreales s. str. Within this group, which includes the nine remaining monocot lineages, seven of the groups (Nartheciaceae, Liliales, Asparagales, Dasypogonaceae, Arecaceae, Commelinales, and Poales s. lat.) have identical internal structures as in the principal analysis, but relationships among these groups are unresolved. These seven groups, and elements of the remaining two (Pandanales and Zingiberales), plus a clade consisting of the three representatives of Triuridaceae, which were not included in the principal analysis, diverge from a single point in the consensus tree. Within Triuridaceae, *Triuris* and *Lacandonia* are sister taxa, with *Sciaphila* placed as the sister of this pair, as in the *atpA*-217 analysis. The breakup of Pandanales and Zingiberales in the consensus tree is a consequence of instability in placement of the Triuridaceae. A group corresponding to Pandanales, including Triuridaceae, occurs in 94% of most-parsimonious trees. Stemonaceae, Pandanaceae, and Cyclanthaceae together constitute a clade in all of these trees. In half of these trees (i.e., in 47% of all trees) Triuridaceae and Velloziaceae are sister taxa, with this clade placed as sister of the Stemonaceae + Pandanaceae + Cyclanthaceae clade. In the remaining half of these trees, Triuridaceae are the sister of the Stemonaceae + Pandanaceae + Cyclanthaceae clade, with Velloziaceae the sister of this entire group. In all of the trees in which Triuridaceae are placed in Pandanales, the relationships within Zingiberales are resolved as in the principal analysis. In the remaining 6% of the optimal trees, in which the three representatives of Triuridaceae are not placed in Pandanales, they are placed as the sister of Zingiberaceae within an otherwise conventionally circumscribed Zingiberales, and the internal structure of Pandanales is identical to that in the principal analysis. Thus, apart from the placement of Triuridaceae, the Pandanales and Zingiberales are resolved in all trees, and Triuridaceae al-

ways are placed within one or the other of these two groups.

Constrained Analyses of the Principal Data Matrix. One group of interest that was not resolved by the principal analysis is Xyridaceae. A constrained analysis was conducted, using the same matrix of 215 taxa that was used in the principal analysis, except that the five representatives of this family were scored as having one state for the constraint character and all other taxa were scored as having an alternative state for this character. This analysis yielded 8,960 most-parsimonious trees of length 8,592 (two steps, or 0.02% longer than the trees obtained by the principal analysis). In the consensus of these trees (not illustrated) the five representatives of Xyridaceae constitute a monophyletic grouping, consistent with the constraint. The Xyridaceae clade is one of seven that diverge from a polytomy, the other six groups being *Flagellaria*; *Mayaca*; Eriocaulaceae; a clade consisting of *Thurnia*, *Carex*, and Juncaceae, within which *Prionium* and *Thurnia* are sister taxa; a clade consisting of *Anarthria* and Restionaceae; and a clade consisting of *Trithuria*, *Ecdeiocolea*, *Joinvillea*, and Poaceae.

A second constrained analysis involving Xyridaceae also was conducted, using the same scores as in the first constrained analysis, except that *Mayaca* and *Trithuria* were scored as unknown for the constraint character. This analysis yielded 11,776 most-parsimonious trees of length 8,591 (one step, or 0.01% longer than the trees obtained by unconstrained analysis of this matrix). As in the consensus of the unconstrained analysis, the Xyridaceae are not resolved as monophyletic in the consensus of these trees (not illustrated). Also as in the unconstrained analysis, the two species of *Xyris* are sisters, with *Trithuria* the sister of this pair, and *Aratitiyopea* and *Orectanthe* are sisters, with *Abolboda* the sister of this pair. A clade of six terminals, in which these two sets of three taxa are sisters, occurs in 89% of the most-parsimonious trees. In the other 11% of the most-parsimonious trees, *Mayaca* is the sister of the *Trithuria* + *Xyris* clade, and this group of four terminals is sister of the clade that includes the other three elements of Xyridaceae. Thus, when this constraint is applied, the smallest group that includes all elements of Xyridaceae also includes *Trithuria*, and it includes *Mayaca* in some but not all trees.

Among the various groups resolved by the first two constrained analyses, and other combinations of these taxa, jackknife support in the data set used for the principal analysis (i.e., without any constraint applied) is lacking (40%) for a monophyletic Xyridaceae, as it is for a clade that includes just *Trithuria* and the five representatives of Xyridaceae (22%), for a clade that includes *Trithuria*, *Mayaca*, and all five representatives of Xyridaceae (12%), for a clade that includes just *Mayaca* and the five representatives of Xyridaceae (10%), and for a clade consisting of *Trithuria* and *Mayaca* (9%).

Another relationship of interest that was not resolved by the principal analysis is the placement of *Acorus* as the sister of all other monocots. This relationship was examined by constraining monophyly of a group that consists of all monocots except the three representatives of *Acorus*. This constraint does not force the three representatives of *Acorus* to be a monophyletic group, nor does it force *Acorus* to be placed as the sister of the constrained group, but both of these results were obtained when the matrix was analyzed, and therefore resolved the monocots as monophyletic, with a monophyletic *Acorus* as the sister of all other monocots. This analysis yielded 1,152 most-parsimonious trees of length 8,602 (12 steps, or 0.14% longer than the trees obtained by the principal analysis). Relationships resolved among the dicots are identical to those resolved by the principal analysis. Within the monocots, all 15 of the major lineages also were resolved as monophyletic by the constrained analysis, as they were by the principal analysis. In addition to the difference that is specifically constrained (exclusion of *Acorus* from a clade that includes all other monocots), the consensus of these trees also differs in other respects from the one that is obtained by the unconstrained analysis (cf. Figs. 2A vs. 2B). Araceae, Tofieldiaceae, and Alismatales s. str. have the same relationships to each other when the constraint is applied as when it is not, but under the constraint *Acorus* is absent (as forced by the constraint) from the group that includes these four lineages in the unconstrained analysis. Jackknife support (as measured in the unconstrained analysis) is 2% or less for each of the three relationships among these groups that are present when the constraint is applied but not in the results of the unconstrained analysis (2% for monophyly of all monocots except *Acorus*, 0.5% for the placement of Tofieldiaceae with Alismatales s. str., and 0.5% for the alliance of Araceae with these two groups). Petrosaviaceae continue to be resolved as the sister of a clade that includes all remaining monocots, but additional differences are observed within the sister group of Petrosaviaceae. The deepest branch within this group is between a clade that consists of Nartheciaceae and Pandanales, and a clade that includes all remaining taxa, the latter of which lacks jackknife support (its jackknife percentage is 14% in the unconstrained analysis). The Dioscoreales s. str. are the next group to diverge from a clade that includes all remaining taxa, and jackknife support for the latter group is 21% in the unconstrained analysis. Finally, the commelinids s. lat. are resolved in the consensus tree, but the commelinids s. str. are not. The commelinids s. str. are resolved in 33% of the most-parsimonious trees, as in the unconstrained trees, with Dasypogonaceae placed as the

sister of this group, and with Arecales resolved as the sister of a clade that includes all other elements of the group. However, Dasypogonaceae and Arecales are resolved as sister taxa in the other 67% of most-parsimonious trees, resulting in a polytomy at this point (Fig. 2B).

Discussion

***Comparative Attributes of* atpA *and* rbcL.** The sequenced portion of *rbcL* in the present study (1,371 sites) is longer than that of *atpA* (1,277 aligned sites, representing between 1,247 and 1,265 actual nucleotide sites among the various taxa), and a greater percentage of *rbcL* characters are informative (42% vs. 34% in the matrix used for the principal analysis). Consequently, the total number of informative *rbcL* characters substantially exceeds that of *atpA* (582 vs. 418, respectively, with two of the latter being indel characters). Analysis of just the *rbcL* portion of the matrix used in the principal analysis yields trees of length 6,073 (corresponding to an average of 10.4 steps per informative character, and a CI and RI of 0.17 and 0.59, respectively), while analysis of just the *atpA* portion of the matrix (i.e., the *atpA*-214 analysis) yields trees of length 2,404 (for an average of 5.8 steps per informative character, and a CI and RI of 0.30 and 0.71, respectively). Thus, the general pattern that emerges is that *rbcL* is both more variable and more homoplasious than *atpA.* These attributes alone would result in a greater total number of steps in *rbcL* characters than in *atpA* characters, even if the number of sequenced sites was equal for these genes, but because more *rbcL* sites were sequenced the disparity in the overall number of steps, if not in CI and RI, is further increased. Notably, the *rbcL* portion of the matrix used in the principal analysis, which includes a greater number of characters than the *atpA* portion, and which exhibits a greater number of steps per character, also provides a greater deal of resolution (191 clades resolved in the consensus tree of the *rbcL* analysis vs. 143 for the *atpA* analysis). The superior resolving power of the more variable and homoplasious portion of the overall matrix is consistent with the observations of Källersjö et al. (1999), though in the present instance the distinction is between two genes, rather than among various character partitions of a single gene.

The occurrence of greater homoplasy in *rbcL* is evident in combined analyses as well. For example, in most-parsimonious trees from the principal analysis, *rbcL* exhibits a greater number of steps per informative character than *atpA* (10.5 vs. 5.9, respectively), and therefore a greater total number of steps among most-parsimonious trees (6,115 to 6,119 for *rbcL* vs. 2,471 to 2,475 for *atpA*), a greater percentage of the total number of steps in these trees (71% vs. 29%), and a lower CI (0.17 vs. 0.29) and RI (0.59 vs. 0.70). The two single-gene matrices are incongruent, as is evident in the different relationships they support, and in the results of the incongruence length difference test of Farris et al. (1995), with 113 steps in the combined tree attributable to incongruence between the two genes, representing a 1.3% increase in length, relative to the numbers of steps in the separate analyses. The combined analysis adds 42 to 46 steps to the *rbcL* characters (a minimum of 0.7%, relative to the number of steps in the *rbcL* analysis), and between 67 and 71 steps to the *atpA* characters (a minimum of 2.8%). Thus, the *atpA* portion of the combined matrix includes fewer characters than the *rbcL* portion, and is less homoplasious than the *rbcL* portion, even in the combined tree, but it is within the *atpA* portion of the combined matrix that the greatest increase in number of steps occurs when the matrices are combined, as measured either in absolute or proportional terms. By these various measures, the *rbcL* portion of the matrix can be regarded as dominating the *atpA* portion in the combined analysis.

The relative dominance of the *rbcL* matrix in the results of the combined analysis also is evident in terms of the number of groups that are resolved by the combined analysis and that also are resolved by each of the two genes when analyzed separately. Of the 201 clades resolved by the combined matrix used in the principal analysis, 92 are resolved by both *atpA* and *rbcL* when these two portions of the matrix are analyzed separately. An additional 69 clades from the principal analysis are resolved only by *rbcL,* so this gene resolves a total of 161 (80%) of the 201 clades that are resolved by the combined analysis. In contrast, 18 clades in the combined tree are resolved only by *atpA,* so this gene resolves a total of 110 (55%) of the 201 clades that are resolved by the combined analysis.

Although these numbers indicate that the results of the combined analysis more closely reflect those supported by *rbcL* than those by *atpA,* the effects of the latter portion of the matrix on the results of the combined analysis are not trivial. The 69 clades that are resolved by *rbcL* and by the combined analysis, but not by *atpA,* are scattered throughout the overall tree, and many critical groups fall within this category. The 18 clades that are resolved by *atpA* and by the combined analysis, but not by *rbcL,* also occur throughout the tree, but there are two principal areas in which they are concentrated. One of these areas, which includes eight such groups, is in the dicot group that is sister of the monocots, and within the smaller of the two clades that diverge at the base of the monocots. Among the groups that are resolved by *atpA* and by the combined analysis, but not by *rbcL,* are: 1) the clade that includes Canellales, Piperales, Magnoliales, and Laurales (Fig. 1A), 2) the two major subclades within this group (Canellales + Piperales, and Magnoliales +

Laurales), 3) the clade that consists of this dicot group and the monocots, and 4) within the monocots, the clade that includes *Acorus* and Alismatales s. str. (Fig. 1A). The second area of concentration of such groups lies among the early-diverging groups within Poales s. lat. (Fig. 1C). The group that consists of all elements of Poales s. lat. except Rapateaceae, and the group that is the sister of Typhaceae + Bromeliaceae, are resolved by *atpA* but not by *rbcL,* as are two clades within Bromeliaceae and one within Rapateaceae.

Another dimension of the overall pattern of conflict between the two genes is seen in the number of clades that are not resolved by the combined analysis, but are resolved by one gene or the other when they are analyzed separately. With 191 clades resolved by *rbcL* alone, and 161 of these also resolved by the combined analysis, there are 30 clades (16% of all of those that are resolved by *rbcL*) that are resolved by *rbcL,* but not by the combined matrix. With 143 clades resolved by the *atpA*-214 analysis, and 110 of these also resolved by the combined analysis, there are 33 clades (23% of those that are resolved by *atpA*) that are resolved by *atpA,* but not by the combined matrix. Thus, there are fewer clades that are resolved by *rbcL,* but not by the combined analysis, in both absolute and relative terms, than the number resolved by *atpA,* but not by the combined analysis. This distinction is not an extreme one, but it provides an indication of the degree to which the *rbcL* portion of the data matrix dominates the results of the combined tree. One complication lies in the fact that so many single-gene and multi-gene analyses (including the present analysis) include *rbcL.* For groups that are favored by the present *rbcL* analysis, but not by the combined analysis, previous occurrences of these groups in other analyses that also include *rbcL* cannot be taken as independent evidence of the veracity of these groups.

While the relationships supported by *atpA* and *rbcL* are demonstrably incongruent, it should be noted that the degree of resolution in the consensus tree for the combined analysis (201 clades resolved) exceeds that of either of the separate analyses. Thus, while there is a statistically significant incongruence between the two genes, and there are many groups that are resolved by one gene, but not by the other, including some that are not resolved by the combined analysis, there are 22 clades that are resolved by the combined analysis, but not by either of the genes alone. Among the groups in this category are the clade that includes Nartheciaceae and Pandanales; the clade that includes these two groups plus Liliales; the clade that includes all elements of Asparagales except Orchidaceae; the commelinids s. str.; and the Commelinales. Two large groups in this category are the clade that is the sister of Dioscoreales, and the clade that includes this group plus Dioscoreales.

Among groups that are resolved by the combined analysis, but not by either of the single-gene analyses, there are two in particular that involve the placement of *Acorus*. As noted above, the clade that consists of *Acorus* and Alismatales s. str. is resolved by *atpA,* but not by *rbcL.* The slightly more inclusive clade that consists of this group plus Tofieldiaceae is resolved only by the combined analysis, as is the clade that consists of these three groups plus Araceae. Also striking in this regard is a nested series of groups that are resolved by the combined analysis within the Nartheciaeae + Pandanales clade (Fig. 1B). The clade consisting of *Sphaeradenia* and *Chorigyne* is resolved by both of the single-gene analyses. The placement of *Carludovica* as sister of this group is resolved by *rbcL,* but not by *atpA,* while the group that consists of these three genera plus *Cyclanthus* (i.e., Cyclanthaceae) is resolved by *atpA,* but not by *rbcL.* Three successively more inclusive clades also are resolved, in an alternating sequence, either by *atpA* or *rbcL,* but in no case individually by both, and the next most inclusive group, Nartheciaceae + Pandanales, is resolved by neither of the genes alone. Thus, *rbcL* can be interpreted as dominating the results of the combined analysis, in terms of the number of extra steps attributable to incongruence, and in terms of the number of groups that are resolved by each of the genes alone. However, at least with respect to the second of these criteria, there are regions in the combined tree in which the *atpA* signal may be regarded as dominant, and others in which the signals in the two genes interact in a complex pattern to produce a mosaic of groups that are or are not supported by each of the genes alone.

Insertion/Deletions. Analysis of the data set used in the principal analysis, modified only by removal of the two *atpA* indel characters, resolved the same set of most-parsimonious trees as were resolved when the indels were included. Therefore, the same conclusions are drawn regarding the evolutionary history of the DNA regions affected by the indels, regardless of whether they are included in the analysis. The three-nucleotide indel that occurs in the region corresponding approximately to sites 581–586 of the *Oryza* sequence is completely homoplasious in these analyses (RI = 0), because the five occurrences of the deleted state are in taxa that are not closely related to each other. This character may prove useful if additional taxa are examined (e.g., other representatives of Araceae or Orchidaceae). The indel that occurs in the region corresponding approximately to sites 585–597 of the *Oryza* sequence, which exists in three states (undeleted and three- and six-nucleotide deletions), exhibits 10 transformations on most-parsimonious trees, two of which are autapomorphic deletions, six of which are synapomorphic deletions for various groups, and two of which are reversions to the undeleted state within

two of these six groups. A three-nucleotide deletion is a synapomorphy of the clade that consists of *Acorus* and Alismatales s. str., but reversion to the undeleted state occurs in *Cymodocea*. Similarly, a six-nucleotide deletion is a synapomorphy of the Pandanales (and also occurs in the three sampled elements of Triuridaceae, which were not included in the principal analysis), but reversion to the undeleted state occurs in *Talbotia*. In the case of *Cymodocea*, the three nucleotides in the position that is deleted in relatives are GAA, and the closest relatives that lack the deletion (both representatives of Tofieldiaceae, and three of the four representatives of Araceae) have a TCT triplet in the corresponding location. The fourth element of Araceae (*Arisaema*), also has a TCT triplet that can be aligned in this location, but this taxon is scored as having a six-nucleotide deletion because six nucleotides are absent and it is possible to align the deletion so as to be in the same location as that of other taxa. Thus, *Arisaema* may share a common set of three nucleotides with other elements of Araceae and Tofieldiaceae. The occurrence of a string of three different nucleotides in *Cymodocea*, which is nested among taxa with the deletion, is consistent with the interpretation that three nucleotides were deleted, and three nucleotides that are not homologous with the original three were later inserted. This point is made here because the situation is different in *Talbotia*.

In the case of *Talbotia*, the closest relatives that lack the deletion are the two representatives of Nartheciaceae (*Aletris* and *Narthecium*), and in the six-nucleotide region that is deleted in most elements of Pandanales these two taxa have the following nucleotides: GAGAGT. The seven nucleotides that follow these six are GAGACAT in *Narthecium*, and GACACAT in *Aletris*. The resulting 13-nucleotide string in this region in *Narthecium* (GAGAGTGAGACAT) is identical to the sequence that occurs in most taxa in the sample, and of these 13 nucleotides it is the first six or others that may have been deleted in all elements of Pandanales except *Talbotia*, because these elements have the GAGACAT string. The three taxa of Triuridaceae, also interpreted as having a six-nucleotide deletion, differ slightly from this pattern, with two of them exhibiting a string of seven nucleotides (GAAACAT) that differs from the common sequence at one site, while the third differs at two sites (GAAACGT). What is remarkable about *Talbotia* is that it is nested among elements that have a deletion, yet it lacks a deletion. Furthermore, the six-nucleotide sequence that occurs in *Talbotia* in the location in which its closest relatives are deleted (GAGACT) is nearly identical to the sequence that occurs in this location in most other undeleted taxa in the sample, including the closest relatives of Pandanales (GAGAGT). It is possible that the apparent reversion in *Talbotia* to a six-nucleotide sequence that closely resembles that of many other taxa in the sample can be explained in part by reference to the seven nucleotides that follow in *Talbotia* and most other taxa (GAGACAT). Just as the previous six nucleotides in *Talbotia* differ from those of most other taxa in the occurrence of a C in place of a G (GAGACT vs. GAGAGT), the seven nucleotides that follow, in *Talbotia* and most other taxa, differ from the six preceding ones in most taxa by the occurrence of a C in place of a G, as well as in the presence of an A (GAGACAT vs. GAGAGT). In light of these patterns, one plausible explanation for the observed nucleotide sequence in *Talbotia* is that an ancestor that had the six-nucleotide deletion experienced an imperfect duplication event involving the following seven nucleotides, so that all except the third A in GAGACAT were duplicated, leaving GAGACT-GAGACAT in place of this sequence and preserving the reading frame by inserting only six nucleotides. It should be emphasized that although the indels in this region were used as characters in the principal analysis and others, the nucleotides in this region were not, because of the ambiguity of alignment.

Apart from this occurrence of a six-nucleotide deletion in Pandanales, and an isolated occurrence in *Arisaema*, a six-nucleotide deletion also occurs as an apparent synapomorphy of the Zingiberales. Although there is little evidence to suggest a close affinity between the Pandanales and Zingiberales, it is notable that these are the two groups with which the Triuridaceae are affiliated in the analysis of 218 taxa (the 215 taxa of the principal analysis plus the three representatives of Triuridaceae). Consequently, it may not be appropriate to dismiss the possibility of previously unsuspected affinities among these taxa, at least with respect to their genomic history.

The three-nucleotide deletion occurs in three groups within the Poales s. lat., and also in *Gyrocarpus* and the *Acorus*/Alismatales s. str. group. Within Poales, the deletion occurs in Eriocaulaceae, the Typhaceae/Bromeliaceae group, and the group that consists of Juncaceae, Cyperaceae, and Thurniaceae. The phylogenetic structure resolved by the present analysis is consistent with the interpretation of these three occurrences of the deletion as the results of independent deletion events. However, higher-level relationships within Poales are not well understood, and it is possible that two or all three of these groups are more closely related to each other than is suggested by the present results.

Alternative Data Matrices. ALTERNATIVE *BURMANNIA RBCL* SEQUENCE. Several aspects of the overall pattern of interaction among characters within and between the *atpA* and *rbcL* data partitions are evident in differences in the results obtained with various subsets of the data. One general result of these alternative analyses is the demonstration of how fragile are many of the higher-level relationships resolved by the prin-

cipal analysis, as evidenced by major changes in the relationships that are resolved when relatively small changes are made in the data set. A particularly striking case is seen in the dramatic differences resulting from the replacement of the *rbcL* sequence of *Burmannia longifolia* by that of *B. biflora*. Both of these species are chlorophyllous, and they are placed together in a clade, along with a third chlorophyllous species, *B. madagascariensis*, in an *rbcL*-only analysis. Hence, there is no reason to believe that the available *rbcL* sequence of any of these three taxa actually represents another taxon, as might be the case if a sample had been mislabelled or contaminated. However, replacement of the *rbcL* sequence of *B. biflora* with that of *B. longifolia* in the combined matrix used in the principal analysis causes the Dioscoreales to move from their position near Petrosaviaceae to a placement among the commelinid taxa. This example alone should be sufficient to cast serious doubt on any assumptions that higher level relationships resolved by analyses of this sort are immune to major changes as more data accumulate.

REMOVAL OF RNA-EDITED SITES. Of the five reports of RNA editing of *atpA* transcripts mentioned above, two are from monocots, and both of these monocots are grasses (triticale and *Oryza*). A total of five *atpA* sites are reported as being edited in these two grasses, but only one of these sites is edited in both of them. This site (number 1,178 in the reference *Oryza* sequence), also is edited in *Beta* and *Arabidopsis*. Another site (1,291), though known to be edited in *Oryza*, is adjacent to another site (1,292) that is edited in triticale, *Beta*, and *Arabidopsis*. Each of the other sites that is known to be edited is reported as such in just one of the five taxa, including two in triticale and one in *Oryza*. The taxonomic sampling represented in these reports is sparse, but the outline of a pattern appears, in which RNA editing is taxonomically widespread at one site, as well as within a region that is two nucleotides in length, while it also occurs sporadically elsewhere in the gene. Another aspect of this pattern is that all of the sites known to be edited in any of the seven taxa, including those known to be edited only in one dicot taxon, such as *Oenothera* and *Arabidopsis*, are G/C rich across the taxon sample in this analysis, with about 76% of all scores for these sites being a C or a G. However, both G and A are rare in the coding strand (i.e., the mRNA-like strand), so the G/C richness at these sites is exhibited in the form of a high frequency of C in this strand (ca. 76%), a lower frequency of T (ca. 24%), and only rare occurrences of G or A. RNA editing of plant mitochondrial transcripts generally takes the form of C to U editing in messenger RNAs, with U to C editing occurring less frequently (e.g., Binder and Brennicke 2003; Gray 2003; and citations therein). The reported occurrence of editing at these RNA sites does not by itself imply that sites that are known to be subjected to editing must be G/C rich across large numbers of taxa, including those in which editing has been examined and has not been observed at these sites. However, the near constancy of G/C richness throughout the taxon set, at sites known to be edited in only one or a few taxa, coupled with the near absence of G and A in the coding strand, suggests that there may be a relationship between these phenomena. On the one hand, RNA editing may be particularly likely to occur at sites that are highly conserved for G/C richness. In this case, G/C richness might be maintained at these sites across large taxonomic assemblages by some unspecified process, and the sporadic occurrence of RNA editing at these sites, and not at others, might be a secondary effect of whatever process maintains the G/C richness. Alternatively, RNA editing might contribute in some way to the maintenance of G/C richness at particular sites. Under this hypothesis, RNA editing itself, or a consequence of it, would play a role in the maintenance of the G/C richness that is observed. However, if this were the case, the observed occurrence of this G/C richness across the vast majority of taxa in the present sample would imply that editing occurs in all or most of these taxa at all seven sites that have been identified, despite that fact that it has not been detected at all of these sites in all of the taxa that have been examined. This might be the case if these sites are edited in all or most of the taxa in the sample but only a portion of the transcripts are edited in any particular plant, in which case editing might occur at some sites in some of the taxa that have been screened for it yet remain undetected.

The removal from the matrix (i.e., from all taxa in the matrix) of six cladistically informative sites, each of which is known to be edited in at least one taxon, resulted in the loss of one node in the consensus tree, and in no other changes. Of course, the removal of any six informative characters from a matrix of 998 characters has a certain chance of altering the results of an analysis, so it cannot be concluded from this result that it was improper to have included these sites in the first place. While RNA editing is known to occur in some taxa in this analysis, and may occur in others, this is just one of many factors that may contribute to the overall pattern of DNA evolution in plants. All *atpA* sequences used in this analysis were derived by direct sequencing of genomic DNA, so RNA editing would not be expected to affect these sequences directly, though it might affect the evolutionary dynamics of these sites. However, all characters are evolving under a variety of forces that influence evolutionary rates and patterns, and that vary among sites, lineages, and time periods. In light of these facts, and because no sequences in the present matrix were generated from cDNA, we would argue that there is no reason to elim-

inate from the analysis the six characters that are known to be edited in some taxa. It is curious, though, that the clade that is lost when these characters are removed is in close proximity to the placement of *Acorus*, a group that is placed in quite different locations by *atpA* and *rbcL*. However, the loss of resolution in this part of the tree may have nothing to do with the fact that the six sites removed from the matrix are known to be edited in some taxa. Because the sites that were removed are all *atpA* sites, and because *atpA* and *rbcL* are known to favor different structures in this region of the tree, it should not be surprising that this part of the tree is affected by the removal of a subset of the *atpA* characters.

ALTERNATIVE TAXON SAMPLES. Three of the 215 taxa in the principal analysis lacked the sequence of one or the other of the two genes (*Trithuria* lacks an *atpA* sequence and *Arachnitis* and *Thismia* lack *rbcL* sequences). Removal of these three taxa resulted in the destabilization of several parts of the tree, as well as in the resolution of alternative and conflicting relationships, even within clades that do not include any of these three taxa. For example, none of the three taxa removed from the analysis lies within the Asparagales or Arecales, and although each of these groups continues to be resolved as monophyletic when these three taxa are removed, much of the resolution is lost within each of them. Another difference that is attributable to the exclusion of these three taxa lies in the resolution of Xyridaceae as monophyletic, and in the resolution of a group that consists of Xyridaceae and Eriocaulaceae. In this case, one of the groups affected by the exclusion of the three taxa is a close relative of one of the three excluded taxa in the results of the principal analysis (i.e., *Trithuria* is the sister of *Xyris*). Regardless of one's notions concerning the actual phylogenetic relationships among the taxa in the principal analysis, it is clear that the three taxa that each lack a DNA sequence provide critical elements of support for several groups that are resolved by that analysis.

Conversely, the addition of three Triuridaceae taxa (each with *atpA* only) to the matrix used in the principal analysis results in a loss of resolution relative to what is obtained by the principal analysis. When included in the analysis, the three representatives of Triuridaceae constitute a monophyletic group in all most-parsimonious trees, yet this group is placed in different locations among the set of most-parsimonious trees. Evidently, there is conflicting and evenly balanced evidence for the placement of Triuridaceae either in the Pandanales or in the Zingiberales, for these are the only two groups in which the family is placed, and because these two orders are placed distantly from each other, a considerable amount of resolution is lost in the strict consensus tree. As already noted, the six-nucleotide state of the indel that is located approximately between sites 585 and 597 of the reference *Oryza atpA* sequence occurs only in *Arisaema*, Triuridaceae, Zingiberales, and the remaining taxa of Pandanales, except for *Talbotia*. This character therefore contributes to the placement of Triuridaceae in these two alternative positions. In order to determine whether the nucleotide sequences also favor these two placements, an additional analysis was conducted, in this case with the 218-taxon matrix (i.e., including Triuridaceae), and with the two indel characters deleted. The results are similar to those obtained with the indel characters included, with the same number of most-parsimonious trees (1,632), and with most but not all of these trees identical to those obtained with the indels included. However, as with the analysis that included the indels, the three taxa of Triuridaceae are a monophyletic group in all of these trees, and this family always is placed within the Pandanales or the Zingiberales.

Constrained Analyses. The overall weakness of support for many relationships resolved by the principal analysis is evident in results of the constrained analyses, as it is in results of analyses with slightly different data matrices. The two constrained analyses involving Xyridaceae demonstrate that Xyridaceae are monophyletic in trees that are scarcely longer than those obtained by unconstrained analysis, in which elements of this family are separate by several nodes. Two additional steps are required for the five representatives of Xyridaceae s. str. to constitute a monophyletic group, and only one additional step is required for a monophyletic Xyridaceae that includes *Trithuria* or both *Trithuria* and *Mayaca*. In light of these results, and as discussed in more detail below, the potential inclusion of these two genera with Xyridaceae deserves continued attention.

The final constrained analysis involved the placement of *Acorus*. A minimum of 12 extra steps are required for a monophyletic group consisting of all monocots except *Acorus* to be resolved. The forced removal of *Acorus* from the group that also includes Araceae, Tofieldiaceae, and Alismatales s. str. does not alter the placement of Petrosaviaceae as the sister of all remaining monocots, but it does affect relationships within the latter group, notably including the placement of Liliales and the internal structure of the commelinids s. lat. (cf. Fig. 2A vs. 2B). Under this constraint, the commelinids s. str. no longer are resolved. It should also be noted that jackknife support is quite small ($< 1\%$) for the clade that consists of Araceae, Tofieldiaceae, and Alismatales s. str., as it is for the clade that consists of the latter two of these three groups (Fig. 2B). These results also provide an example of the manner in which a forced change at one point in a tree results in changes far from this point. This is a particularly striking case, because only one

small clade of three terminals was shifted in position, yet there were ripple effects of this change throughout the superstructure of the monocots.

Support Analyses. With the results of five support analyses in hand it is possible to dissect some of the underlying differences between these approaches by conducting pairwise comparisons of the support values that they provide for various clades. It would not be appropriate to conduct a formal analysis of variance (ANOVA) with the various analytical methods as the factors and levels of clade support calculated with these methods as the underlying data, because the clades that are resolved and their degrees of support are not independent of each other. However, variance levels were calculated for the support numbers for each clade resolved by the principal analysis, for all pairwise combinations of methods, in order to facilitate informal comparisons among the results of the various analyses. Comparisons of the variance levels provide a means for assessing differences among the methods that is not provided by simple comparisons of mean support values alone. This is because it is possible for two methods to provide widely varying estimates of support for many or all groups, or even for a narrow subset of groups, while still returning support values with similar averages across all groups. Thus, even if the mean levels of support provided by two methods were identical for a group of clades, high levels of variance between the sets of support values still could exist, and would indicate that the two methods recognize substantially different levels of support for at least some of the groups. In terms of analysis of variance, the two principal factors that underlie any differences that might exist among the analyses that were conducted, apart from random variation, are the distinction between the SC and FWR approaches, and the distinction between the jackknife and the bootstrap. Because two SC jackknife analyses were conducted (corresponding to replicates within treatments in a formal ANOVA), an estimate of the level of stochastic variation is available, though it should be recognized that this calculation is specific to the SC jackknife analysis, and it may not provide an accurate indication of the level of random variation for the three other analytical methods. Another complication inherent in the comparisons that have been made lies in the fact that all SC analyses were conducted with WinClada and NONA, and all FWR analyses were conducted with PAUP*, so differences between the SC and FWR approaches cannot be disentangled from differences between the software packages. If there are differences in the results of these analyses that are attributable to differences between the software platforms from which they were obtained, these software-specific differences could be caused by intrinsic differences in the manner in which tree searches are conducted and the results evaluated (e.g., ambiguity of clade support might be determined according to different rules in the two platforms, TBR swapping might be implemented differently, etc.). Other potential causes of software-specific differences might lie in user-determined attributes of the analyses such as the number of trees retained for swapping, and saved, in each replicate. In the present case, an additional round of branch swapping was conducted in NONA, but not in PAUP*, following the set of four search initiations within each bootstrap and jackknife replicate. Also, it should be recognized that the differences observed here are specific to the data matrix used in this analysis, and that different patterns might be observed with other data sets. It should be noted as well that the presence of uninformative characters can influence the support values that are calculated (Harshman 1994; Carpenter 1996). In the present case, all of the support analyses were conducted with a matrix from which all parsimony-uninformative characters had been removed.

Levels of variation between the results of the two SC jackknife analyses, conducted with the same software and using identical settings, provide an estimate of the repeatability of these results (Table 1). The maximum difference in jackknife frequency for any group between the two SC jackknife analyses was five percentage points, and there were only two groups with differences of this magnitude (one clade had a higher score in the first analysis, and another clade had a higher score in the second analysis). Freudenstein et al. (2004) found a similar range of variation in their study of jackknife support when ten replicates were compared. Thus, with the present data matrix, and with the analytical methods that were used, it seems likely that nearly all of the calculated SC jackknife frequencies lie within a few percentage points of those that would be obtained by more extensive analyses. Therefore, the average SC jackknife frequency for all 201 groups is likely to be very close to the calculated mean of 74.45%, which is the average of the results obtained by the two SC jackknife analyses. If the three other support analyses that were conducted are regarded as being similarly accurate, with respect to the results that would have been obtained by more thorough analyses, it can be concluded that the observed differences among the various analyses are largely attributable to real differences between the methods and/or software platforms, rather than to random variation.

An SC jackknife analysis should yield frequencies that are equal to or lower than those obtained by an FWR jackknife, and similarly, an SC bootstrap should yield frequencies equal to or lower than those obtained from an FWR bootstrap, if search conditions otherwise are identical (Soreng and Davis 1998; Grass Phylogeny Working Group 2001). This relationship is expected be-

cause under the SC approach a clade is recognized as having been resolved in a particular replicate analysis only if it occurs in all most-parsimonious trees obtained for that replicate. Thus, a group that occurs in all trees obtained by a given replicate analysis receives a score of one with both approaches, but a group that occurs in some but not all trees obtained receives a score of zero under the SC approach, and a score between zero and one (proportional to its frequency of occurrence among trees discovered by that replicate) under the FWR approach. Deviations from the predicted pattern may occur because of differences in the manners in which character weightings and tree searches are conducted, differences in tree-search efficiency among software packages, and random variation among sets of replicates. Also, differences may occur between bootstrap and jackknife numbers simply because of intrinsic differences in these approaches.

Observed differences between support values from the SC and FWR jackknife analyses, and between the SC and FWR bootstrap analyses, are consistent with expectations and with previous results. In both cases (jackknife and bootstrap), the average support frequency obtained with an FWR analysis exceeds that obtained with an SC analysis by a few percentage points (Table 1). The magnitude of the difference is greater for the jackknife (4.6%) than for the bootstrap (2.4%). For the jackknife, FWR scores exceed SC scores for 154 of the 201 groups, by as many as 29 percentage points, while no group has an SC jackknife score that exceeds its FWR jackknife score. A similar relationship is observed between scores for the FWR and SC bootstrap analyses, but again, the difference is less than for the jackknife. Of the 201 groups, 131 have higher scores from the FWR bootstrap than from the SC bootstrap, with a maximum difference of 11 points, and eight groups have higher scores for the SC bootstrap than for the FWR bootstrap, with the SC scores never more than two percentage points higher than the FWR scores. Also, the average variance among jackknife scores for the 201 clades (SC vs. FWR) is more than five times greater than the average variance among the corresponding bootstrap scores. If the observed patterns signify real differences between the underlying analyses, it would appear that the distinction between the FWR and SC approaches is greater for the jackknife than for the bootstrap.

Consistent differences also are observed between the jackknife and the bootstrap, on both software platforms, with jackknife scores generally exceeding bootstrap scores. The average SC jackknife value for the 201 clades exceeds the average SC bootstrap value by 4.6%, with the jackknife value exceeding the bootstrap value for 128 of the clades, in 20 cases by 10 percentage points or more, while the SC bootstrap value exceeds the SC jackknife value for 17 clades, and never by more than 7 points. Similarly, the average FWR jackknife value exceeds the average FWR bootstrap value by 5.1% with the jackknife value exceeding the bootstrap value for 149 clades, in 39 cases by 10 points or more, while there is no clade for which the FWR bootstrap frequency exceeds the FWR jackknife frequency. The disparity between jackknife and bootstrap values also is evident in the average variance levels, which in both cases (SC jackknife vs. SC bootstrap, and FWR jackknife vs. FWR bootstrap; Table 1) exceed the base level observed for the two SC jackknife analyses by factors ranging from just less than 10 to more than 24. Because these differences are pronounced and are observed on both platforms, with both an SC and FWR approach, it seems likely that they reflect real differences between the jackknife and the bootstrap, at least as applied to this data set.

It is not clear why jackknife values consistently exceed bootstrap values, when other attributes of these analyses are held constant. In fact, Mort et al. (2000) predicted the opposite because of the smaller size of the resampled matrix in jackknife as opposed to bootstrap analyses, yielding fewer phylogenetically informative characters. It is not that simple however, because their analyses showed that mean support values for particular nodes obtained with 33% and 50% deletion for fast jackknife bracketed those obtained with fast bootstrap, the jackknife values with 33% deletion being consistently higher than the bootstrap values. Salamin et al. (2003) found no significant differences in support values when they compared 50% jackknife deletion to bootstrap using various swapping strategies. Clearly, percentage deletion in the jackknife is an important factor, and it has been discussed by Farris et al. (1996) and Felsenstein (2004).

In terms of the difference observed in the present study between jackknife and bootstrap values, it is important to note that the universe in which this disparity is observed is the set of 201 clades that are resolved in the strict consensus tree. Although SC jackknife support exceeds SC bootstrap support for these groups, just as FWR jackknife support exceeds FWR bootstrap support, it is possible that these differences are more pronounced among groups that occur in the consensus tree than among groups that do not. In other words, there are many other groups that occur among the bootstrap and jackknife replicates, and it is possible that the relatively higher levels of jackknife support among groups that occur in the consensus tree are offset by higher levels of support in other groups. This might be the case if bootstrap support were distributed among a greater number of groups than jackknife support. WinClada and PAUP* provide the results of support analyses in different ways, and this possible explanation is consistent with the results obtained

from both programs. WinClada provides a complete enumeration of clades that occur among the consensus trees generated by an SC support analysis, and the two replicate SC jackknife analyses detected nonzero support for 1,833 and 1,873 unique groups, respectively, while the SC bootstrap analysis detected some support for 3,715 unique groups, approximately twice as many. PAUP* provides a catalog of groups with support greater than or equal to a user-set percentage (1% in the present case), and the FWR jackknife analysis detected 766 unique groups with 1% or greater support, while the FWR bootstrap analysis detected 984 such groups. Thus, bootstrap support was detected for a greater number of groups than jackknife support on both platforms, and the generally lower bootstrap frequencies observed for the groups in the consensus tree may be a consequence of this phenomenon.

In interpreting these results, it may be useful to note that bootstrap analysis, by its nature, can assign a weight greater than one to any given character in any given replicate analysis (i.e., a character can be selected more than once), while the weight of each character can be no greater than one in any given jackknife replicate (i.e., each character either is included or excluded). If, for any particular matrix, there are clades that can be resolved only when certain characters are selected more than once, or that are more likely to be resolved when this occurs, bootstrap analyses may tend to detect support for more groups than do jackknife analyses. Indeed, there may be groups that cannot be resolved by jackknife analysis, but can be resolved by bootstrap analysis, because they depend upon particular combinations of character weights that can occur only in a bootstrap replicate. Thus, the bootstrap, in a general sense, may cast a broader net than the jackknife, in terms of the groups for which support is detected. This tendency would be consistent with the notion that if one character with a particular distribution has been detected, it is appropriate to consider the possibility that other characters with the same distribution may exist, and should be considered when support is analyzed. Some systematists may agree with this proposition, while others may not. We would argue that a support analysis that is focused on a particular data set should not invoke unobserved characters, and note that further investigation of these matters is warranted.

Regardless of the underlying causes, the pattern that emerges from these analyses is one in which FWR values exceed SC values, for both the jackknife and the bootstrap, and jackknife values exceed bootstrap values, in both FWR and SC analyses. Thus, the average support value obtained with the FWR jackknife (79.0%) is the highest of the four combinations of these factors, and the average obtained with the SC bootstrap (71.5%) is the lowest. This disparity also is exhibited in other aspects of this pairwise combination, such as the average variance among the 201 clades, which is greater for this pair than for any other (Table 1), whether calculated on the basis of raw or ln-transformed data. The other two combinations of these factors, as manifested in the SC jackknife and FWR bootstrap analyses, yielded the least extreme results of the four analyses, with the average score from the former slightly exceeding that of the latter (74.4% vs. 73.9%, respectively), though there are 45 clades that have higher scores from the FWR bootstrap than from the SC jackknife (e.g., the clade that includes all representatives of Liliales except *Arachnitis*).

It is noteworthy that several of the clades that are resolved in the consensus tree have extremely low support values (seven with SC jackknife and FWR bootstrap frequencies less than 10%, and one group, comprising *Flagellaria* and its sister group, with 1% support by both measures). As demonstrated by these examples, there are real data sets in which groups with jackknife and bootstrap frequencies in the single digits occur in all most-parsimonious trees. It should be noted as well that there are two groups that have strong jackknife and bootstrap support in the combined (principal) analysis, yet are resolved by neither gene alone, and there are two other groups that are supported independently by both genes, yet have jackknife and bootstrap support below 50%. These occurrences are not surprising, since they can be explained in terms of character conflict within and between the two single-gene matrices. However, they highlight the complexity of interactions among characters within the overall matrix, in the resolution of particular groups, and in the overall pattern of support for those groups.

The SC jackknife was chosen as the principal measure of support for this analysis. The jackknife is preferred over the bootstrap because the former measures support in terms of randomly selected subsets of the actual data, without increasing the weight of any character, and thereby positing character combinations that do not actually occur in the available data. The SC approach is preferred because it does not rely on a majority-rule approach within each replicate in the calculation of clade support. However, a scan of the recent literature suggests that the FWR bootstrap is the most widely used method by systematists for the estimation of support, and for purposes of comparison with other analyses we present scores obtained with these two methods for all 201 clades (Fig. 1).

Phylogenetic Relationships. SISTER GROUP OF THE MONOCOTS. The focus of the present analysis is on relationships among monocots, but with 41 dicot taxa included as outgroups the results also provide a phylogenetic hypothesis regarding relationships among the major lineages of magnoliid dicots, tricolpate dicots, and monocots. The results of the present analysis

resemble those of the parsimony analysis of the three-gene data set by Soltis et al. (2000) in placing the monocots as sister of a clade that comprises four magnoliid groups (Piperales, Laurales, Magnoliales, and Winterales, the latter corresponding to the Canellales of the present analysis). The three-gene analysis places Chloranthaceae as the sister of this clade (i.e., the clade of four magnoliid lineages plus monocots), while the present analysis places Chloranthaceae with *Ceratophyllum* and a clade of tricolpate dicots. Although the present analysis agrees with the three-gene analysis in identifying the same dicot lineage as sister of the monocots, relationships within that group are more fully resolved by the present analysis, for Canellales and Piperales are resolved as sister taxa by the present analysis, as are Magnoliales and Laurales, and these two pairs of orders are resolved as sisters of each other, while relationships among these four groups are unresolved in the consensus tree of the three-gene analysis. Results of a five-gene analysis by Qiu et al. (2000) resemble those of the present analysis in yielding a clade that consists of representatives of four magnoliid dicot orders, with Laurales sister of Magnoliales, and Piperales sister of Winterales (again, with the latter group corresponding to Canellales in the present treatment). However, relationships were unresolved among this clade of four magnoliid orders and four other major clades, one of which was the monocots. Thus, the analysis of Qiu et al. (2000) resolved a major clade of magnoliid dicots that is also resolved by the present analysis, but did not identify this clade, or any other specific clade, as the sister of the monocots. The combined analysis of *atpB* and *rbcL* by Savolainen et al. (2000) placed monocots as the sister of a clade that consists of the same four magnoliid orders as in the present results, but Piperales and Laurales were sister taxa in the *atpB*/*rbcL* trees, as were Magnoliales and Canellales. Moreover, the Chloranthaceae were placed as the sister of the clade that consists of monocots and these four magnoliid orders, and the sister of this overall group included Amborellaceae, Nymphaeaceae, and other early-diverging angiosperm lineages, but not *Ceratophyllum* or the major lineage of tricolpate dicots.

Mathews and Donoghue (2000) conducted a series of analyses with sequences of phytochromes A and C. In their parsimony analysis of the combined two-gene data set, with species as terminals, the sister of the monocots was a group of tricolpate dicots, while *Ceratophyllum* was placed with the Nymphaeales. Graham and Olmstead (2000) and Graham et al. (2000) obtained similar results with a matrix of nucleotide sequences of 17 plastid-encoded genes, plus indel data. Their analyses resolved a clade consisting of monocots and tricolpate dicots (each of these groups monophyletic), plus *Ceratophyllum*. In one case (Graham and Olmstead 2000), tricolpate dicots were placed as sister of *Ceratophyllum* + monocots, and in the other (Graham et al. 2000), monocots were placed as sister of *Ceratophyllum* + tricolpate dicots. The morphological matrix of Doyle and Endress (2000) placed Nymphaeales as sister of the monocots, and their combined morphological and molecular analysis identified Piperales as sister of the monocots. Parsimony analysis of the *matK* matrix of Hilu et al. (2003) placed Chloranthaceae as sister of the monocots, with a clade consisting of Piperales, Canellales, Laurales, and Magnoliales in an unresolved relationship relative to the monocots + Chloranthaceae clade and a large clade including *Ceratophyllum* and the tricolpate dicots. Relationships among the four named magnoliid orders were identical to those obtained by the present analysis. Hilu et al. obtained similar results when analyzing their matrix using Bayesian inference, but, in that case, the clade of four magnoliid orders was supported as the sister of Chloranthaceae + monocots, and relationships among the four magnoliid orders differed.

In the analysis by Chase et al. (2000), which focused on monocot relationships, the only dicots in the sample were those of the ''eumagnoliids'' of Soltis et al. (2000), including Chloranthaceae. We restrict our discussion of their analysis to the results they obtained with characters equally weighted. Their trees are rooted between dicots and monocots, with both groups represented as monophyletic. Some relationships among the dicot groups are unresolved in their first analysis (which included only those taxa for which sequences of all three genes were available), but relationships are fully resolved in this section of the tree in their second analysis (which also included some taxa that were incomplete for all three genes). In the latter, rerooting of the cladogram between Chloranthaceae and all other taxa would result in a tree in which the remaining dicots were placed in one clade, and all monocots in another, though the absence of additional outgroups precludes recognition of these two groups as sister taxa. To this extent the present results are consistent with those of Chase et al. (2000), with respect to the sister-group of the monocots. However, Winteracae and Canellaceae (of which the latter is not sampled in the present analysis) constitute a clade in their tree that is the sister of Magnoliales, with Laurales the sister of this group, and Piperales the sister of this more inclusive group. Thus, even with Chloranthaceae and Canellaceae removed from consideration, internal relationships among these dicot groups differ from those resolved by the present analysis. Clearly, recent analyses have differed widely in terms of relationships among early-diverging dicot lineages, and in terms of the placement of monocots among these lineages, with the placement of *Ceratophyllum* and Chloranthaceae being among of the areas of least agreement.

EARLY-DIVERGING LINEAGES WITHIN THE MONOCOTS, AND THE POSITION OF *ACORUS*. Within the monocots, the resolution by the present analysis of a group that includes *Acorus* and three other lineages is inconsistent with several previous analyses, which have placed *Acorus* as the sister of all other monocots, on the basis of *rbcL* (Duvall et al. 1993a, b; Chase et al. 1993); *rbcL* and morphology (Chase et al. 1995b); *rbcL* and *atpA* with fewer taxa than in the present analysis (Davis et al. 1998); *rbcL, atpB,* and 18S rDNA (Chase et al. 2000), *rbcL, atpB,* 18S rDNA, and morphology (Doyle and Endress 2000), a set of 17 plastid-encoded genes (Graham and Olmstead 2000; Graham et al. 2000), and *matK* (Hilu et al. 2003). However, other recent analyses have placed *Acorus* differently. Phytochromes A and C placed *Acorus* with Poaceae and Araceae (Mathews and Donoghue 2000), while a morphological data set (Doyle and Endress 2000) and a five-gene data set (Qiu et al. 2000) both placed *Acorus* with Araceae, Tofieldiaceae, and Alismatales s. str., as does the present analysis. A sister group relationship between *Acorus* and Alismatales s. str. also was detected in a combined analysis of *rbcL, atpA,* restriction sites, and morphology (Stevenson et al. 2000), which placed the clade consisting of these two groups as sister of all other monocots, with Araceae the next group to diverge from the clade that included all other monocots (Tofieldiaceae were not included in that analysis).

These four groups (Araceae, Tofieldiaceae, Alismatales s. str., and *Acorus*) are among the earliest lineages to diverge from the line that includes all other monocots in the analyses of Chase et al. (2000). In those analyses, however, *Acorus* is the sister of all other monocots, and a clade consisting of the three other groups is sister of a group that includes all remaining monocots. There is little support for these alternative groupings by the matrix analyzed in the principal analysis of the present study, in which jackknife support is 2% for a group that includes all monocots except *Acorus*, and less than 1% for a group that consists of Araceae, Alismatales s. str., and Tofieldiaceae, but not *Acorus* (Fig. 2B). As indicated by the single-gene analyses, and as might be expected on the basis of previously reported results with *rbcL,* the placement of *Acorus* as the sister of all other monocots is supported predominantly by this gene, while its placement in the clade with three other monocot groups is supported predominantly by *atpA.* This conclusion also is supported by an enumeration of character transformations on the branches in this region of the tree. For example, in most of the trees resulting from the principal analysis there are 42 steps in *atpA* characters on the branch that leads to *Acorus* and Alismatales s. str. under accelerated transformation optimization, and only 13 *rbcL* transformations, while under delayed character transformation there are 21 steps in *atpA,* and only 3 in *rbcL.* Thus, although *atpA* accounts for 29% of the steps in the overall tree, it accounts for between 76% and 88% of the steps on this branch. The placement of *Acorus* clearly is a point of conflict between the two genes, but this fact alone does not indicate which of the two placements might be correct, if indeed either of them is.

The grouping of *Acorus*, Alismatales s. str., and Araceae is consistent with recent interpretations of floral characters and floral development in *Acorus* and genera of Alismatales and Araceae (Buzgo 2001), who concluded that *Acorus* and representatives of Alismatales s. str. share bract-like abaxial tepals, unidirectional floral development, and similarities in other characters related to gynoecium and inflorescence development.

The conflicting placements of *Acorus* by the two genes in the present analysis, and the general correspondence of results of the combined analysis with the relationships supported by *atpA* could be interpreted as evidence of mutually supporting secondary signals in the two genes, but this need not be the case. Clearly, it is possible for one portion of a matrix that consists of two or more natural subsets (e.g., two genes) to provide support for a particular group with sufficient strength that this group is resolved by the overall matrix, despite a complete absence of support for this group elsewhere in the matrix. In such cases, the other portions of the data may resolve any number of other relationships that are consistent with the group in question, and these may lack support within the data subset that is responsible for resolving the specified group. Similar observations also can be made in terms of the role of long branch attraction in the resolution of particular groups. One may argue that the branch that leads to *Acorus* and the branch that leads to Alismatales s. str. are sufficiently long in the combined analysis that they attract each other, but the same could be said of the branch that leads to *Acorus* and the branch that lies between dicots and all other monocots in the *rbcL* tree.

Relationships detected by this study within Alismatales s. str. are largely congruent with those detected by Les et al. (1997), on the basis of *rbcL* sequences from numerous taxa representing all alismatid families. The only deviation is in the placement of a group consisting of Butomaceae and Hydrocharitaceae, which in the analysis of Les et al. (1997) is the sister group of Alismataceae. In the present analysis this group is sister of a clade consisting of Scheuchzeriaceae, Juncaginaceae, Cymodoceaceae, and Potamogetonaceae, though jackknife support for this relationship is lacking.

Relationships among four representatives of Araceae, as resolved by the present analysis, are congruent with results of previous and more comprehensive phylogenetic analyses of plastid restriction site data

(French et al. 1995) and morphological characters (Mayo et al. 1997). Gymnostachydoideae (represented by *Gymnostachys*) and Orontioideae (represented by *Orontium* and *Symplocarpus*) form the monophyletic, species-poor group of ''proto-Araceae'' sensu Mayo et al. (1997), and the species-rich group of ''true Araceae'' sensu Mayo et al. (1997) is represented only by *Arisaema* (Aroideae).

PETROSAVIACEAE. The present analysis, like previous ones (see Cameron et al. 2003 and citations therein) supports the taxonomic disintegration of a formerly heterogeneous Nartheciaceae s. lat. Among the groups that often have been included in Nartheciaceae (e.g., Tamura 1998) are *Petrosavia* and *Japonolirion* (collectively Petrosaviaceae), which are placed together as the sister group of a clade that includes Dioscoreales s. str. and the nine remaining major groups of monocots (Fig. 1A). In the first APG classification (Angiosperm Phylogeny Group 1998) these two genera were assigned to different families, and neither was assigned to an order. In the classification by Chase et al. (2000), and in the APG II system (Angiosperm Phylogeny group 2003), both genera are included in Petrosaviaceae, and this family remains unassigned to an order. The inclusion of *Japonolirion* within Petrosaviaceae is supported by molecular as well as morphological data (Cameron et al. 2003), and the present analysis confirms this relationship. The morphological analysis of Stevenson and Loconte (1995) placed a narrowly defined Petrosaviaceae (i.e., excluding *Japonolirion*) in an achlorophyllous clade with Triuridaceae (see below), while molecular analyses have variously placed Petrosaviaceae as sister of the Pandanales or sister of a clade that includes all monocots except *Acorus* and Alismatales s. lat. (Chase et al. 2000; Soltis et al. 2000; Fuse and Tamura 2000). The present analysis supports the latter placement.

DIOSCOREALES S. STR., NARTHECIACEAE, PANDANALES, AND TRIURIDACEAE. In the present analysis Dioscoreales s. str. are monophyletic (Fig. 1A), but the sister of this group is not Nartheciaceae, as in the analyses of Caddick et al. (2000, 2002) and Chase et al. (2000). Those authors, partly on basis of their phylogenetic results, included Nartheciaceae in a broadly defined Dioscoreales, as did the Angiosperm Phylogeny Group (2003), who previously (1998) had not assigned this family to an order. The analyses of Caddick et al. (2000, 2002) and Hilu et al. (2003) placed Pandanales as the sister of this broadly defined Dioscoreales s. lat., while that of Chase et al. (2000) placed Pandanales nearby, but not as the sister group of Dioscoreales. In particular, Caddick et al. (2002), using a matrix of three genes and morphology, identified the presence of glandular hairs on the ovary as a synapomorphy that linked Nartheciaceae with the rest of the Dioscoreales, yet this grouping lacked bootstrap support. The relationships supported by the present analysis, with weak jackknife and bootstrap support, are similar to those of Caddick et al. and Chase et al. in placing Pandanales and Dioscoreales in proximity to each other, but differ in placing Nartheciaceae with Pandanales, rather than with Dioscoreales. With regard to this placement, it is notable that Behnke (2000) has identified similarities between the sieve-element plastid inclusions of *Aletris* and *Narthecium* (Nartheciaceae), and those of some elements of Velloziaceae (Pandanales). However, these features also occur in other taxa, including elements of Petrosaviaceae, and these characters remain to be tested by formal cladistic analysis. A combined analysis of all available data, and possibly new data as well, may be needed to resolve the relationships among these groups, and patterns of incongruence among individual portions of the available data also should be explored. Relationships resolved within Dioscoreales s. str. by the present analysis are congruent with those resolved by the combined analysis of Caddick et al. (2002), except for the presence of a trichotomy from which Taccaceae, Trichopodaceae, and Dioscoreaceae emerge. With respect to these three groups, the analysis of Caddick et al. placed Taccaceae as the sister of a clade in which the other two families were sisters.

In this analysis we have included three genera (*Triuris*, *Lacandonia* and *Sciaphila*) of the eight that are recognized in the family Triuridaceae. This is noteworthy, since only one genus (*Sciaphila*) was represented in the only previous molecular analysis that included a representative of this family (Chase et al. 2000). In the present analysis there are two members of tribe Triurideae (*Triuris* and *Lacandonia*) and one of tribe Sciaphileae (*Sciaphila*). Of special interest is the inclusion of *Lacandonia*, because its placement within the family still is in dispute. *Lacandonia* is characterized by an inverted arrangement of the stamens and carpels (the stamens are enclosed by the carpels). Martínez and Ramos (1989), Márquez-Guzmán et al. (1989, 1993) and Vázquez-Santana et al. (1998) noted that there are numerous differences between *Lacandonia* and other taxa of the family, and recognized *Lacandonia* as the only member of the family Lacandoniaceae. However, Maas-van der Kamer and Mass (1994), Maas-van der Kamer (1995), and Maas-van der Kamer and Weustendeld (1998) placed *Lacandonia* within Triuridaceae, in the tribe Triurideae, and authors such as Stevens (1991) and Takhtajan (1997) have suggested that this genus represents a case of homeotic mutation, but have not suggested that it be removed from Triuridaceae. Gandolfo et al. (2002) conducted a phylogenetic analysis, based on morphological characters, and including all extant and fossil genera of the family. Their analysis resolved two major clades within the family, one including all members of tribe Sciaphileae, and the other

including both of the fossil genera, plus all extant members of tribe Triurideae, and *Lacandonia*. In the latter clade, the fossil taxa constitute a monophyletic group that is the sister of a group that includes the remaining genera, and within the latter group, *Lacandonia* is the sister of all extant Triurideae. The present results, though including only three genera of Triuridaceae, are consistent with those of Gandolfo et al. (2002) in confirming the placement of *Lacandonia* within this family, and within a clade that corresponds to tribe Triurideae.

Since the family initially was described by Miers (1845), the phylogenetic relationships and appropriate taxonomic placement of Triuridaceae have remained obscure. Bentham and Hooker (1883) and Engler and Prantl (see treatment by Engler 1889) suggested a close relationship between Triuridaceae and Liliaceae. Hutchinson (1934) erected the order Triuridales to accommodate this family alongside the Alismatales. Tomlinson (1982) proposed the elevation of this group to a subclass, and established the subclass Triurididae, which also included the family Petrosaviaceae. On the basis of a variety of morphological characters, several investigators such as Cronquist (1981), Thorne (1992), Rübsamen-Weustenfeld (1991), and Stevenson and Loconte (1995) have variously proposed relationships between the Triuridaceae and Petrosaviaceae, Liliaceae, Burmanniaceae, and Alismatales, and the family also has been compared with dicots. Dahlgren and Rasmussen (1983) placed the Triuridaceae within the Ariflorae-Triuridiflorae-Alismatiflorae complex, and Dahlgren et al. (1985) noted that although this family shares several characters with Alismatiflorae and Liliiflorae, it also differs from them in numerous features. In the original APG system (Angiosperm Phylogeny Group 1998), several families were left unclassified in order to avoid nonmonophyletic higher groups; among these families were Triuridaceae, Petrosaviaceae, and Nartheciaceae. In their revised classification the Angiosperm Phylogeny group (2003) placed the Triuridaceae within the Pandanales (see below).

Stevenson and Loconte (1995) included Triuridaceae in a phylogenetic analysis based on morphological and anatomical characters, and Chase et al. (1995b) included it in a combined analysis of morphological and anatomical characters plus *rbcL,* though there was no *rbcL* sequence available for Triuridaceae. Chase et al. (2000) were the first to conduct a molecular analysis that included molecular data for a representative of Triuridaceae. The analysis of Loconte and Stevenson (1995) placed Triuridaceae as the sister of Petrosaviaceae, in a clade supported by features such as apocarpous gynoecia and folliculate fruits, and this achlorophyllous clade was placed as the sister group of a clade that included the Liliidae and the ABC clade (Bromeliiflorae + Alismatidae + Commelinidae). The combined analysis of Chase et al. (1995b) placed Triuridaceae among alismatid taxa, and the molecular analysis of Chase et al. (2000) placed *Sciaphila* (the sole representative of Triuridaceae) within Pandanales, as the sister of *Freycinetia* (the sole representative of Pandanaceae). The molecular analysis of Vergara-Silva et al. (2003) also placed Triuridaceae in Pandanales, but as the sister of Velloziaceae.

Triuridaceae are included in two of the analyses presented here. In one (the *atpA*-217 analysis), Triuridaceae are placed within Pandanales in all most-parsimonious trees, as they were by Chase et al. (2000) and Vergara-Silva et al. (2003). Within this order the present analysis places Triuridaceae as the sister of a clade that includes Stemonaceae, Pandanaceae, and Cyclanthaceae, rather than as the sister of Pandanaceae or Velloziaceae. In another of the analyses presented here (the analysis of all 218 taxa, based on data from both genes), Triuridaceae are placed within Pandanales in some most-parsimonious trees, and within Zingiberales, as sister of Zingiberaceae, in others. When placed in Pandanales, the Triuridaceae are sister of the Stemonaceae + Pandanaceae + Cyclanthaceae clade in some trees, and sister of Velloziaceae in others. Thus, the present results consistently resolve Triuridaceae as monophyletic, but are ambiguous with respect to the placement of this group. It appears that more work is needed to understand the relationships and evolutionary history of the Triuridaceae.

Corsiaceae and Liliales. Historically, Corsiaceae have been placed most often within Burmanniales (e.g., Dahlgren et al. 1985), and a phylogenetic analysis of morphological characters supported this placement (Stevenson and Loconte 1995). In the classification of Chase et al. (2000), Corsiaceae were left unplaced. The results of the present analysis, in placing this family as sister of a conventionally defined order Liliales, is consistent with the recognition of Corsiaceae as the sole element of an order that is the sister of Liliales, or with the expansion of Liliales to include this family. This placement agrees with results of a phylogenetic analysis of 26S rDNA sequences (Neyland 2002). Among other taxa of Liliales, Chase et al. (2000) and Rudall et al. (2000) included Trilliaceae in Melanthiaceae, which otherwise would have been paraphyletic in their analyses, and Hilu et al. (2003) also found Trilliaceae to be nested within Melanthiaceae. In the present analysis the two families are sister groups that together constitute a strongly supported monophyletic group. Rudall et al. (2000), based on a combined analysis of molecular and morphological characters, suggested that Ripogonaceae and Philesiaceae should be included in Smilacaceae. In our analysis Ripogonaceae and Philesiaceae are sister taxa, whereas Smilacaceae are the sister group of Liliaceae (though neither of these pairs has jackknife support). The relationships

detected by the present analysis among Luzuriagaceae, Alstroemeriaceae, and Colchicaceae are in agreement with those resolved by Rudall et al. (2000), with the exception of the position of *Petermannia*. The combined analysis of Rudall et al. (2000) placed *Petermannia* within Colchicaceae, a position supported by the molecular data from the plastid genome, but not by the morphological data. However, the molecular data for *Petermannia* in that study were derived from a misidentified specimen (M. Chase, pers. comm.). The present analysis, using molecular data derived from a different plant accession, places *Petermannia* as the sister of this set of three families, and hence is consistent with the recognition of Petermanniaceae as a separate family.

ASPARAGALES. The placement of Orchidaceae as sister of a group that includes all other representatives of Asparagales agrees with the results of Fay et al. (2000), but not with those of Chase et al. (2000) or Hilu et al. (2003). In the present case, jackknife support is moderate (and bootstrap support is weak) for monophyly of Asparagales, and jackknife support is strong (and bootstrap support moderate) for monophyly of the group that includes all elements of Asparagales except Orchidaceae. Within Orchidaceae, the unexpected placement of *Isotria* from the Vanilloideae as the sister of *Cypripedium* from the Cypripedioideae (cf. Cameron et al. 1999; Cameron and Chase 2000) perhaps is attributable to poor taxon sampling in the present study. Rudall et al. (1998) and Fay et al. (2000) also found the relationship between Boryaceae, Hypoxidaceae, Asteliaceae, and Blandfordiaceae that is detected here. Some critical details of the internal structure of the well-supported clade consisting of Anthericaceae, Lomandraceae, Xanthorrhoeaceae, Johnsoniaceae, and Hemerocallidaceae (including *Xeronema*) are strongly supported by the jackknife analysis, but the limited taxon sampling of Asparagales in the present analysis hampers any precise indication of the relationships. One strongly supported relationship in the present analysis, which is inconsistent with the analysis of Fay et al. (2000), is the placement of Iridaceae and Ixioliriaceae as sister taxa.

ARECALES, DASYPOGONACEAE, AND THE COMMELINID ALLIANCE. The palms (Arecales) were placed in a variety of positions in pre-cladistic angiosperm classifications (see review by Uhl et al. 1995). Some authors (e.g., Cronquist 1981) grouped them with various arboreal and subarboreal monocots, while others (e.g., Dahlgren et al. 1985) recognized them as an isolated group of uncertain affinity, though Dahlgren et al. did suggest a possible relationship with taxa that are now recognized as elements of the commelinid alliance. Early phylogenetic analyses of *rbcL* (Chase et al. 1993; Clark et al. 1993; Duvall et al. 1993a, b) placed the palms with the commelinids, as sister of a clade that included the rest of the group, and a phylogenetic analysis of morphological characters placed the palms among other commelinid elements, as sister of Poales s. str. (Stevenson and Loconte 1995). A more recent *rbcL* analysis (Chase et al. 1995b) also placed the palms among the commelinids, rather than as sister of the rest of the group, with a clade consisting of Dasypogonaceae and Zingiberales as the sister of all other commelinid elements. Thus, the Dasypogonaceae and Arecaceae came to be associated with the commelinids, and a combined analysis of *rbcL* and morphological data (Chase et al. 1995b) placed these two families together, in a clade that also included *Hanguana*, and that also was the sister of all other taxa of the commelinid alliance. Both of the three gene analyses of Chase et al. (2000) placed Dasypogonaceae and Arecaceae with the commelinids, and in both cases these two families were the earliest lineages to diverge from a clade that included the rest of the group. However, in one of the analyses these two families were resolved as sister taxa, and in the other they diverged in succession (first Arecaceae, then Dasypogonaceae) from the group that included the remaining commelinids. The present analysis yields a third structure, in which these two families again are placed with the remaining commelinid elements, as the earliest groups to emerge from a clade that includes the rest of the group, but in this case the Dasypogonaceae are the first of the two groups to diverge from this line, and the Arecaceae are the second. Jackknife support for this structure is lacking, just as bootstrap support was lacking for the alternative structures resolved by Chase et al. An alternative placement for Arecaceae is seen in the analysis of Hilu et al. (2003), in which this family is the sister of a clade that includes taxa of Commelinales and Zingiberales.

ZINGIBERALES. The monophyly of Zingiberales as recovered in the principal analysis (which did not include the three representatives of Triuridaceae) is consistent with a long history of the recognition of this group in traditional classifications (e.g., Cronquist 1981; Dahlgren et al. 1985) and by recent cladistic analyses (e.g., Kress 1990; Stevenson and Loconte 1995; Rudall et al. 1999; Chase et al. 2000; Kress et al. 2001). While monophyly of the Zingiberales is widely accepted, the position of this group within the monocots has been enigmatic. Dahlgren et al. (1985) suggested that the sister of Zingiberales was Bromelianae, a group that consisted of Velloziaceae, Bromeliaceae, Philydraceae, Haemodoraceae, Pontederiaceae, Sparganiaceae, and Typhaceae. Except for Velloziaceae, which now appear to belong in Pandanales, all of these families, like Zingiberales, belong to the commelinid alliance, so their suggestion was prescient. Cladistic analyses that include morphological data sets have placed Zingiberales as sister of Pontederiales (Steven-

son et al. 2000), or as sister of Hanguanales within a larger Liliidae clade (Stevenson and Loconte 1995; Rudall et al. 1999). In a study based on *rbcL,* Duvall et al. (1993b) found Zingiberales to be sister of a clade that included Philydraceae, Haemodoraceae, and Pontederiaceae (part of Bromelianae sensu Dahlgren et al. 1985) as well as Commelinaceae (part of Commelinanae sensu Dahlgren et al. 1985). These four families plus Hanguanaceae have been recovered as a well-supported sister to Zingiberales in more recent studies (Chase et al. 1995a, 2000; Givnish et al. 1999), though not in all (e.g., Chase et al. 1995b). In the present analysis the Zingiberales again are recovered as sister of a clade that consists of these five families (i.e., Commelinales sensu Chase et al. 2000), and it has a similar level of support (bootstrap 71% in Chase et al. 2000; jackknife 73% and bootstrap 67% in the present analysis). Various attributes were listed by Dahlgren and Clifford (1982) as supporting this relationship, including zygomorphic flowers often with a petaloid inner whorl, presence of raphides, amoeboid tapetum, binucleate pollen grains, pistil with a branched style, crassinucellate ovules, and axile placentation. However, many morphological characters conflict with the alliance of these two clades, as evidenced by the results of morphology-based cladistic analyses, which do not recover the Zingiberales-Commelinales sister relationship (Stevenson and Loconte 1995; Rudall et al. 1999; Stevenson et al. 2000). Detailed morphological analyses that focus on conflicting characters will be required to determine whether there is support for this relationship in morphological characters, and if so, which morphological synapomorphies support this sister relationship. It is notable that while molecular studies have been useful in suggesting a sister relationship of Zingiberales with Commelinales sensu Chase et al. (2000), the relationship remains only weakly supported.

Within the Zingiberales, only Strelitziaceae, Costaceae, Marantaceae, and Zingiberaceae are represented by more than one taxon in the present analysis, and thus testable for monophyly. Of these four families, all but Marantaceae were found to be monophyletic, with strong jackknife support, but Marantaceae are rendered nonmonophyletic by the placement of *Calathea* (Marantaceae) with *Musa* (Musaceae), rather than with *Maranta*. In the analysis of Chase et al. (2000), where multiple exemplars were included from each family, all families were found to be monophyletic. However, support for all relationships among the families was lacking (less than 50% bootstrap support within the order), except for the strong support exhibited for the placement of Lowiaceae with Strelitziaceae (a relationship that is not recovered by the present analysis). In the current analysis, no relationships among the eight families have jackknife support. The majority of the families are united in a group that has an internal polytomy, with Costaceae sister of this group and Strelitziaceae as sister of the rest of the Zingiberales. These relationships differ fundamentally from those detected by more focused cladistic studies (Kress 1990, 1995; Kress et al. 2001) or by earlier analyses of morphological patterns. A close relationship among the ''ginger families'' (i.e., Zingiberaceae, Costaceae, Marantaceae, and Cannaceae), based on reduction in the number of fertile stamens to one, and modification of the remaining sterile stamens into petaloid staminodia, has long been recognized (Tomlinson 1962; Dahlgren and Rasmussen 1983; Kirchoff 1988; Kress 1990, 1995; Kress et al. 2001), and these families have been segregated from the four ''banana families'' (i.e., Musaceae, Strelitziaceae, Lowiaceae, and Heliconiaceae). Among the ginger families, Costaceae have been supported as the sister of Zingiberaceae, and Marantaceae as the sister of Cannaceae. Determining relationships of the banana families has been a more elusive task, despite substantial efforts (Kress 1990, 1995; Kress et al. 2001). Relationships detected among these four families seem to be highly dependent on the outgroups that are used, especially in the case of morphological analyses (Kress 1995). The most recent analysis (Kress et al. 2001), upon which the current classification of Zingiberales is based, places Heliconiaceae (*Heliconia*) as sister of the ginger family clade. A clade including the monophyletic Strelitziaceae (three genera) and Lowiaceae (*Orchidantha*) is sister to Heliconiaceae plus the ginger families, with Musaceae the earliest-diverging lineage. The analysis presented here does not recover these relationships. However, the weak support found within the order does not support any alternative relationships either. More intensive sampling within the families may help to recover the relationships supported in ordinal level analyses, or at least recover all families as monophyletic, as found by Chase et al. (2000). However, the lack of support for interfamilial relationships in Chase et al. (2000) is consistent with our findings, suggesting that only the inclusion of characters from faster evolving genes would provide support in this region. Only Costaceae is sampled in sufficient depth to determine some generic relationships within the family; however, the relationships recovered in this analysis are not fully concordant with more detailed analyses of the family (Specht et al. 2001; Specht, 2004). Additional sampling within the family is needed to investigate generic relationships. Additional sampling within Marantaceae may also help to resolve the issue of nonmonophyly in this analysis.

Recent studies by Pederson (2003) have resolved alternative relationships within the Zingiberales. According to this latest study, Lowiaceae (*Orchidantha*) is the first family to diverge, followed by the Strelitziaceae, leaving a clade containing Musaceae plus Heliconiaceae as sister families and another clade contain-

ing the four ginger families in the same relationships recovered by Kress et al. (2001; i.e. Costaceae sister to Zingiberaceae and Marantaceae sister to Cannaceae). In the present analysis the Lowiaceae (*Orchidantha*) are not the earliest lineage to diverge within the order, but rather are part of the large polytomy that includes all Zingiberales minus Costaceae and Strelitziaceae. Thus the current analysis does not support the novel phylogenetic relationships reported by Pederson any more than it does the Kress et al. (2001) phylogeny.

COMMELINALES. Cladistic analyses of morphological and anatomical data (Stevenson and Loconte 1995; Rudall et al. 1999) have supported an alliance of Commelinaceae with a range of families, including Eriocaulaceae, Mayacaeae, Rapateaceae, and Xyridaceae, thus supporting the Commelinales sensu Dahlgren et al. (1985), and similar groupings by Cronquist (1981) and Takhtajan (1997). In contrast, the present analysis, like other recent molecular phylogenetic studies (e.g., Givnish et al. 1999; Chase et al. 2000), resolves a clade comprising Commelinaceae, Haemodoraceae, Hanguanaceae, Philydraceae, and Pontederiaceae (i.e., the Commelinales sensu Chase et al. 2000 and the Angiosperm Phylogeny Group 2003). Thus, sequence data indicate that the Commelinales of Dahlgren et al. (1985) are an unnatural assemblage and that, having excluded the Commelinaceae, the remaining elements of this alliance are nested within the Poales s. lat. of the Angiosperm Phylogeny Group (2003). Nevertheless, the discordance between the circumscriptions of the Commelinales by Dahlgren et al. and APG II cannot be portrayed accurately as simply an instance of conflict between morphology and DNA sequence data. A survey of more than a century's worth of morphology-based systems of monocot classification (reviewed in part by Dahlgren and Clifford 1982) reveals varying amounts of both of these apparently contrasting concepts of relationships, depending on the system and the particular author's bias in the weighting of characters.

The precise systematic position of *Hanguana* within the monocotyledons has historically been problematic (Rudall et al. 1999). Likewise, inclusion of Hanguanaceae in the Commelinales sensu Chase et al. (2000) has been viewed with some skepticism. Givnish et al. (1999) noted that Hanguanaceae were unusual among the Commelinales (and the larger Commelinales-Zingiberales alliance) in that they lacked raphides and a showy perianth. However, perianth showiness is somewhat difficult to qualify, and not all Zingiberalean taxa possess raphides, nor are raphides wholly absent from Hanguanaceae (Prychid and Rudall 1999). Perhaps the strongest evidence that Hanguanaceae do not belong within the Commelinales lies in the palynological and floral anatomical characters that support a closer alliance to the Zingiberales (Rudall et al. 1999). Nevertheless, Tillich (1997) maintains that Hanguanaceae are allied most closely to the Commelinaceae, primarily in terms of seed and seedling structure. The hypothesis of Tillich is corroborated by the sister-group relationship resolved between these two families in the codon-weighted analysis of *rbcL* sequence variation by Givnish et al. (1999), while the present analysis, like that of Chase et al. (2000), resolves Hanguanaceae as sister of a clade that includes both Commelinaceae and Pontederiaceae. Jackknife and bootstrap support for either set of relationships is weak to lacking, however, so the precise position of *Hanguana* within the Commelinales, if at all, is in need of further attention. Beyond the issue of the placement of Hanguanaceae, robust interfamilial relationships within the Commelinales as a whole also have been elusive. Although the Commelinaceae and Pontederiaceae are resolved as sister taxa here, as they were by Chase et al. (2000), jackknife and bootstrap support for this relationship are lacking. This topology also is inconsistent with the findings of Givnish et al. (1999; but also with very weak support) and some palynological, morphological, and embryological studies (Simpson 1987; Steinecke and Hamann 1989; Tillich 1995) that indicate a closer relationship of Pontederiaceae to Philydraceae and Haemodoraceae. Graham et al. (2002) recently suggested that the recurring phenomenon of weakly supported interfamilial relationships in the order may be a secondary effect of the long evolutionary branches that subtend the surviving lineages of these five distinctive families.

With just a single representative terminal, the monophyly of Hanguanaceae could not be tested. Nevertheless, there are only one or two recognized species in the family, so its monophyly may be a moot issue. The monophyly of each of the other four families of Commelinales, as sampled, is strongly supported (with jackknife values ranging from 86% to 100%). Within Commelinaceae, the first dichotomy is between the sets of terminals representing the predominantly Old World tribe Commelineae (*Commelina* and *Murdannia*) and the mostly New World tribe Tradescantieae sensu Faden (1998). A much more detailed analysis of relationships within Commelinaceae was conducted by Evans et al. (2003). With the exception of the root, the topology of the Pontederiaceae, as sampled, is consistent with the results of Graham et al. (1998), including the nonmonophyly of *Eichhornia*. With just three representative terminals each, topologies of the Haemodoraceae and Philydraceae are each restricted to a single three-taxon statement, and little can be concluded regarding the phylogenetic structures of these families, so they will not be discussed further.

POALES S. LAT. The position of Rapateaceae as sister of a group that includes all other taxa of Poales s. lat., as resolved here, has been supported by some previous molecular analyses (e.g., Chase et al. 2000; Bre-

mer 2002). In other analyses, *rbcL* sequence data alone and in combination with morphological data has supported a sister group relationship of Rapateaceae and Bromeliaceae (Clark et al. 1993; Chase et al. 1995b; Linder and Kellogg 1995), but some analyses of morphological data alone, or of morphology and molecular data, have placed Rapateaceae with families assigned by Dahlgren et al. (1985) to Commelinales (Chase et al. 1995b; Stevenson and Loconte 1995; Rudall et al. 1999; Michelangeli et al. 2003), or with Cyperaceae and Juncaceae (Linder and Kellogg 1995). A sister-group relationship of Rapateaceae with Mayacaceae plus Bromeliaceae was recovered in a codon-weighted analysis of *rbcL* data (Givnish et al. 1999). Within the Rapateaceae, two subfamilies (Rapateoideae and Saxofridericioideae) have been recognized (Maguire 1965; Stevenson et al. 1998). We resolve a monophyletic Saxofridericioideae (the clade including *Kunhardtia* and *Epidryos*) and a nonmonophyletic Rapateoideae, with *Rapatea* as sister of the rest of the family (Fig. 1C). The structure resolved here is similar to that obtained from *ndhF* sequence data and a broader sampling of Rapateaceae (Givnish et al. 2000), except that *Spathanthus*, rather than *Rapatea*, was resolved as sister of the rest of the family.

The placement here of Bromeliaceae as sister of Typhaceae (i.e., *Typha* and *Sparganium*) was also resolved in one recent analysis of Poales s. lat. (Bremer 2002). This precise relationship was not recovered by Michelangeli et al. (2003), although these two families were placed as successively diverging lines in a larger, more inclusive clade in their analysis. The general lack of resolution within Bromeliaceae in the present analysis provides little information regarding relationships among the sublineages of this family (Gilmartin and Brown 1987; Ranker et al. 1990; Horres et al. 2000). There is a general consensus that the Bromeliaceae subfamilies Bromelioideae and Tillandsioideae are monophyletic, while Pitcairnioideae, as traditionally circumscribed, are not (but see Smith and Till 1998). Anomalous attributes, such as the placement of *Brocchinia* among Pitcairnioideae, have been discussed (Gilmartin and Brown 1987; Varadarajan and Gilmartin 1988a, b; Givnish et al. 1997). The position of *Brocchinia* (currently classified in Pitcairnioideae) as sister of the rest of Bromeliaceae, as resolved by the present analysis, agrees with previous studies based on morphological or sequence data (Varadarajan and Gilmartin 1988a, Terry et al. 1997), although other relationships have been proposed (Givnish et al. 1997; Horres et al. 2000). A sister-group relationship of *Puya* (formerly Pitcairnioideae) to Bromelioideae (represented by *Ananas*) was also found in an analysis of *ndh*F sequence data (Terry et al. 1997; see Horres et al. 2000).

Xyridaceae and Eriocaulaceae often have been regarded as closely related (Dahlgren et al. 1985; Stützel 1998). Other authors, however, noting the complex floral morphology in Eriocaulaceae, have interpreted this group as an isolated lineage, and treated it as a separate order, while placing Xyridaceae more closely to Rapateaceae (Hutchinson 1959; Hamann 1961). Results of the principal analysis of the present contribution are equivocal, for they divide Xyridaceae into two groups, and place the portion of the family that sometimes is recognized as Abolbodaceae (e.g., Angiosperm Phylogeny Group 1998) with Eriocaulaceae, while placing *Xyris* with *Flagellaria*, *Mayaca*, *Trithuria*, and Cyperales sensu Dahlgren et al. (1985; i.e., Juncaceae, Cyperaceae, and Thurniaceae). As demonstrated by the two constrained analyses involving Xyridaceae, trees with this family constrained to be monophyletic are one step longer than those obtained by unconstrained analysis if *Trithuria* and *Mayaca* are allowed to fall within the family, and they are two steps longer than those obtained by unconstrained analysis if these two genera are excluded from the family. A putative synapomorphy that may support a relationship of *Trithuria* and *Mayaca* with Xyridaceae is the presence of an embryostega formed from the inner integument instead of from the outer integument as in the Commelinaceae. Possible synapomorphies of *Mayaca* and *Xyris* include an anther exothecium instead of an endothecium, and marginal, parietal placentation. It is interesting to note that Cronquist (1981) suggested a relationship of *Trithuria* with the Commelinales, and Takhtajan (1997) suggested a relationship with Commelinaceae. Both authors based their inferences upon seed morphology, i.e., the presence of an operculum (embryostega). Both authors also considered the Xyridaceae and Commelinaceae to be closely related, and one basis for that was the presence of the embryostega. As mentioned above, it is now believed that the embryostega has two origins, with that of *Trithuria* being similar in development to that of Xyridaceae.

Apart from the question of whether *Trithuria* and *Mayaca* belong within Xyridaceae, the placement of this group in the constrained trees is ambiguous, for it is variously associated with Eriocaulaceae, Cyperales sensu Dahlgren et al. (1985), and other families. *Mayaca* and *Trithuria* are discussed further below. A sister-group relationship between *Trithuria* and *Xyris* also was detected by Stevenson et al. (2000), in an analysis that did not include *Mayaca* or other elements of Xyridaceae. Bremer (2002) found *Xyris*, *Mayaca*, and *Trithuria* to lie on long branches, and favored exclusion of the latter two from analysis, as they destabilized the structure in this region of the tree. The relationship of *Abolboda* and close relatives with Eriocaulaceae is supported by features of the gynoecium, pollen, and habit, which have been invoked in prior discussions of the relationship of Xyridaceae to Eriocaulaceae. A close relationship between Xyridaceae and Eriocaulaceae has

been supported by previous parsimony analyses (e.g., Linder and Kellogg 1995; Stevenson and Loconte 1995; Rudall et al. 1999; Givnish et al. 1999; Bremer 2002), but not by others (e.g., some analyses in Chase et al. 1995b; Stevenson et al. 2000). Michelangeli et al. (2003), using morphology plus the same two genes as in the present analysis, detected a clade comprising *Mayaca*, *Trithuria*, and all representatives of Xyridaceae and Eriocaulaceae, and as in this analysis, Xyridaceae were not monophyletic. This family generally has been recognized as comprising two groups that correspond to subfamilies (Suessenguth and Beyerle 1935; Xyridoideae [including *Achlyphila*] and Abolbodoideae) or families. The heterogeneity of Xyridaceae has long been discussed (Carlquist 1960; Dahlgren et al. 1985; Rudall and Sajo 1999), and it appears that any complete evaluation of this group must include an assessment of Mayacaceae and Hydatellaceae.

The infrafamilial classification of Eriocaulaceae still is in a state of flux, and is complicated by the possibility that *Paepalanthus*, the largest and most widely distributed genus, may be a polyphyletic assemblage (Stützel 1998; Giulietti et al. 2000). Monophyly of the two traditional subfamilies, Eriocauloideae (*Eriocaulon* and *Mesanthemum*), and Paepalanthoideae (the remaining genera of the family), has been questioned (Stützel 1998; Giulietti et al. 2000), but cannot be addressed adequately by the taxonomic sampling used here. The pairing of *Tonina* with *Lachnocaulon* corresponds to Hamann's (1964) tribe Toninеae, but the tribe has not been accepted in subsequent studies (Stützel 1998; Giulietti et al. 2000). The analyses of morphological data by Giulietti et al. (2000) placed *Tonina* as the sister of all other Eriocaulaceae, or of *Philodice*. The placement by the present analysis of *Eriocaulon* as sister of the rest of the family is consistent with some interpretations of relationships within the family (Stützel 1985; 1998; Hensold and Giulietti 1991), though a phylogenetic analysis based on morphological and anatomical characters placed *Eriocaulon* elsewhere (Giulietti et al. 2000).

Hydatellaceae (*Hydatella* and *Trithuria*) are reduced, aquatic plants, whose relationships have been unclear. The family formerly was included in Centrolepidaceae, but Dahlgren et al. (1985), noting several morphological differences, placed Hydatellaceae in a separate order. *Trithuria* was found to be the sister of *Xyris*, within a clade that also included *Eriocaulon* and *Carex*, on the basis of morphological and sequence data (Stevenson et al. 2000). Problematic character scoring resulting in the placement of Hydatellaceae as sister of a grouping of *Typha* and *Sparganium* (Chase et al. 1995b; Stevenson and Loconte 1995) is discussed by Stevenson et al. (2000).

An association of Mayacaceae with a clade that also includes Thurniaceae, Cyperaceae, and Juncaceae was detected by Chase et al. (2000). This small, monogeneric family of aquatic herbs has been hypothesized to be most closely related to *Flagellaria* and Commelinaceae (Hutchinson 1959), Commelinaceae (Dahlgren et al. 1985), Eriocaulaceae (Campbell et al. 2001), or Xyridaceae (Venturelli and Bouman 1986; Stevenson and Loconte 1995; Takhtajan 1997; Stevenson 1998; Rudall et al. 1999). The latter relationship was found in a cladistic analysis of morphological data alone (Stevenson and Loconte 1995), and in combination with *rbcL* sequence data (Chase et al. 1995b). With different taxon sampling, and using codon-weighted parsimony analysis, an analysis of *rbcL* sequence variation supported a sister-group relationship between *Mayaca* and Bromeliaceae, with Rapateaceae placed as the sister of this group (Givnish et al. 1999).

Thurniaceae sometimes is recognized as including two genera, *Thurnia* and *Prionium. Thurnia* includes robust (except *T. jenmani* Hook. f.), seasonally inundated, aquatic (emergent at anthesis) plants from the Guayana Shield and adjacent northwestern Amazonia, and *Prionium* is a woody hydrophyte from South Africa. The affinities of these genera have not always been clear. *Prionium* has at times been included as an unusual member of Juncaceae, but Cutler (1969) proposed its exclusion. The removal of *Prionium* from Juncaceae was formalized by Munro and Linder (1998), who proposed the family Prioniaceae, in part on the basis of the results of their parsimony analysis of morphology and *rbcL* sequence data; however, sequence data from *Thurnia* was not available for that study. *Thurnia* has been treated as a monogeneric family of Juncales (Cutler 1969, Cronquist 1981), with morphological analyses placing it as sister of Juncaceae (Stevenson and Loconte 1995; Rudall et al. 1999), and it also has been allied with Rapateaceae (Dahlgren et al. 1985; Tiemann 1985) and Xyridaceae (Dahlgren et al. 1985). With more inclusive sampling, *Prionium* and *Thurnia* have been resolved as sister taxa, as they are here, either within Juncaceae (Simpson 1995), or as a closely related group (Givnish et al. 1999; Chase et al. 2000).

Flagellariaceae, a small family of vines, often has been considered an isolated family. Hutchinson (1959) suggested a relationship to Mayacaceae and Commelinaceae, and Dahlgren et al. (1985) included the family in Poales. In an early analysis of *rbcL* sequence data (Chase et al. 1993), *Flagellaria* was variously placed as sister of a clade corresponding to Cyperales sensu Dahlgren et al. (1985), or in an unresolved position among the Cyperales group and elements of Eriocaulaceae, Restionaceae, Poaceae, *Typha*, and *Sparganium*. In another *rbcL* analysis (Duvall et al. 1993b), *Flagellaria* was placed with Restionaceae and Poaceae, in a group that corresponds to Poales sensu Dahlgren et al. (1985). In subsequent phylogenetic analyses Flagellariaceae have remained with Poales, often as the sister of a

clade that includes all other elements of the group (Clark et al. 1993; Davis 1995; Linder and Kellogg 1995; Stevenson and Loconte 1995; Rudall et al. 1999; Givnish et al. 1999; Chase et al. 2000; Stevenson et al. 2000; Bremer 2002; Michelangeli et al. 2003). The present analysis, however, does not place *Flagellaria* with the rest of the Poales s. str. (i.e., sensu Dahlgren et al. 1985), though jackknife support for its placement in the sister group of this clade is less than 1%.

Apart from the placement of *Flagellaria*, monophyly of Poales sensu Dahlgren et al. (1985) is supported by the present analysis. The placement of *Anarthria* as sister of Restionaceae is consistent with the results of Briggs et al. (2000) and Linder et al. (2000). Ecdeiocoleaceae have long been associated with Poales, within which they were considered a close relative of Restionaceae (e.g., Dahlgren et al. 1985). Phylogenetic analyses based on morphology generally confirmed this placement (Kellogg and Linder 1995; Stevenson and Loconte 1995). However, it is becoming increasingly likely that *Ecdeiocolea* is more closely related to Poaceae than to Restionaceae. The placement of *Ecdeiocolea* by the present analysis, as the sister of Poaceae, with *Joinvillea* the sister of this pair, is consistent with the distribution of a 6-kb inversion in the plastid genome, which is present in all taxa sampled from these three families, and absent in all other taxa that have been examined (Hiratsuka et al. 1989; Shimada and Sugiura 1991; Doyle et al. 1992; Katayama and Ogihara 1996; Michelangeli et al. 2003). Briggs et al. (2000) detected a close relationship between Ecdeiocoleaceae and Poaceae, but that analysis did not include Joinvilleaceae. The relationship detected here among these three families was resolved previously by Bremer (2002) and Michelangeli et al. (2003). Relationships resolved within Poaceae by the present analysis are congruent with current understandings of the family (Grass Phylogeny Working Group 2001, and citations within).

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APPENDIX I

Taxa sampled for *atpA* and *rbcL,* sources of DNA isolations and sequences, and GenBank accession numbers of sequences. Genera are assigned to families according to Kubitzki (1998a, 1998b) and Kubitzki et al. (1993), except as noted in text. Families are assigned to orders according to the Angiosperm Phylogeny Group (2003), and are listed alphabetically within each order. Family names are accompanied by four-letter codes that also are used in figures. For each sequence generated by the authors, accession information is provided for the DNA sample that was used, including species name and taxonomic authority (or genus name if species is undetermined), collection information, acronym of the herbarium in which the voucher specimen is deposited (absence of an herbarium acronym denotes absence of a known voucher); and (for each DNA isolation from a plant in a curated living collection) the name of the institution and accession number of the living plant. A GenBank accession number is provided, without parentheses, for each sequence generated by the authors from a described DNA isolation, and in parentheses for each sequence obtained from GenBank. In the latter case, the species name as listed in Genbank (without taxonomic authority) is provided if it differs from that of a DNA accession used by the authors for a species of the same genus. For unpublished sequences obtained directly from other persons, the donor's name and other available information are provided, in parentheses. Institutions providing plant materials, with abbreviations used in the table, are as follows: Aarhus Universitet (Aarhus); Adelaide Botanic Garden (Adelaide Bot. Gard.); University of Copenhagen Botanic Garden (Copenhagen Bot. Gard.); Cornell University Campus (Cornell); Fairchild Tropical Garden (Fairchild Trop. Gard.); Harold L. Lyon Arboretum (Lyon Arb.); Herrick Conservatory, Kent State University (Herrick Conserv.); L. H. Bailey Hortorium Conservatory (Bailey Conserv.); Missouri Botanical Garden (Mo. Bot. Gard.); Smithsonian Institution, National Museum of Natural History (NMNH); New York Botanical Garden (NYBG); Royal Botanic Gardens, Kew (RBG Kew); Royal Botanic Gardens Melbourne (RBG Melbourne); Royal Botanic Gardens

Sydney (RBG Sydney); University of Melbourne (University of Melbourne).

DICOTYLEDONS

No Ordinal Assignment. Amborellaceae (AMBO). *Amborella trichopoda*; (*atpA* AY009407); (*rbcL* L12628). **Chloranthaceae (CHLO).** *Chloranthus spicatus* (Thunb.) Makino, NYBG 732/89, NY; *atpA* AY299746; (*rbcL* AY236835). *Hedyosmum* sp., D. Stevenson 1188, NY; *atpA* AY299777; *Hedyosmum orientale* (*rbcL* AY236848). **Nymphaeaceae (NYMP).** *Nuphar* sp. (*atpA* AF197638); *Nuphar variegata* (*rbcL* M77029). *Nymphaea odorata* Aiton, K. Hansen s.n., June 1993, BH; *atpA* AY299814; (*rbcL* M77034). *Victoria cruziana* Orb., Copenhagen Bot. Gard.; *atpA* AY299855; (*rbcL* M77036).

AUSTROBAILEYALES. Austrobaileyaceae (AUST). *Austrobaileya scandens* C.T. White, NYBG 371/82A, NY; *atpA* AY299723; (*rbcL* L12632). **Illiciaceae (ILLI).** *Illicium anisatum* L., NYBG 206/80A, NY; *atpA* AY299786; *Illicium parviflorum* (*rbcL* L12652). **Schisandraceae (SCHI).** *Schisandra sphenanthera*; (*atpA* AF197662); (*rbcL* L12665).

CERATOPHYLLALES. Ceratophyllaceae (CERA). *Ceratophyllum demersum* L., J. Freudenstein 2555, OS; *atpA* AY299743; (*rbcL* D89473).

CANELLALES. Winteraceae (WINT). *Drimys winteri* J.R. Forst. & G. Forst., RBG Melbourne, A. Doust 1125, MELU; *atpA* AY299761; (*rbcL* AF093734). *Tasmannia lanceolata* (Poir.) A.C. Sm., RBG Melbourne, J. Grimes 3528, MEL; *atpA* AY299847; *rbcL* AY298851.

LAURALES. Calycanthaceae (CALY). *Calycanthus occidentalis* Hook. & Arn., Cornell, M. Simmons 1899, BH; *atpA* AY299739; (*rbcL* AF022951). *Chimonanthus praecox*; (*atpA* AF197679); (*rbcL* L12639). *Idiospermum australiense* (Diels) S.T. Blake, NYBG 870/79A, NY; *atpA* AY299785; (*rbcL* L12651). **Hernandiaceae (HERN).** *Gyrocarpus americanus* Jacq., NYBG 732/89, D. Stevenson s.n., NY; *atpA* AY299773; *Gyrocarpus* sp. (*rbcL* L12647). **Lauraceae (LAUR).** *Neolitsea cassia* (L.) Kosterm., NYBG 245/85A, NY; *atpA* AY299811; *rbcL* AY298841. **Monimiaceae (MONI).** *Atherosperma moschatum*; (*atpA* AF197683); (*rbcL* AF121362). *Doryphora sassafras* (*atpA* AF197688); *Doryphora aromatica* (*rbcL* L77211).

MAGNOLIALES. Annonaceae (ANNO). *Annona muricata* L., NYBG 921/92A, NY; *atpA* AY299712; (*rbcL* L12629). **Eupomatiaceae (EUPO).** *Eupomatia laurina* R. Br., RBG Sydney 884938, NSW (484292); *atpA* AY299767; *Eupomatia bennettii* (*rbcL* L12644). **Magnoliaceae (MAGN).** *Liriodendron chinense*; (*atpA* AF197690); (*rbcL* L12654). *Magnolia grandiflora* L. cv. Edith Bogue, M. Simmons 1902, BH; *atpA* AY299800; *rbcL* AY298837. *Michelia figo* (Lour.) Spreng., Cornell, M. Simmons 1898, BH; *atpA* AY299802; (*rbcL* L12659). **Myristicaceae (MYRI).** *Myristica fragrans* Houtt., NYBG 3/95B, NY; *atpA* AY299808; *rbcL* AY298839.

PIPERALES. Aristolochiaceae (ARIS). *Aristolochia gigantea* Mart. & Zucc., NYBG 1677/94, NY; *atpA* AY299718; *Aristolochia macrophylla* (*rbcL* L12630). *Asarum canadense*; (*atpA* AF197671); (*rbcL* L14290). *Saruma henryi*; (*atpA* AF197672); (*rbcL* L12664). **Lactoridaceae (LACT).** *Lactoris fernandeziana*; (*atpA* AF197710); (*rbcL* L08763). **Piperaceae (PIPE).** *Macropiper excelsum* (Forster f.) Miq., Univ. of Melbourne, A. Doust 1126, MELU; *atpA* AY299799; *rbcL* AY298836. *Peperomia polybotrya* Kunth, NYBG 380/49, NY; *atpA* AY299819; *Peperomia* sp. (*rbcL* L12661). *Piper betle* (*atpA* AF197630); *Piper nigrum* L., L.H. Bailey Conserv. 68-334, K. Hansen s.n., BH; *rbcL* AY298847. **Saururaceae (SAUR).** *Houttuynia cordata*; (*atpA* AF197632); (*rbcL* L08762). *Saururus cernuus* L., K. Hansen & J. Davis s.n., June 1994, BH; *atpA* AY299833; (*rbcL* L14294).

PROTEALES. Nelumbonaceae (NELU). *Nelumbo lutea*; (*atpA* AY009420); (*rbcL* M77032). **Platanaceae (PLAT).** *Platanus occidentalis*; (*atpA* AF197655); (*rbcL* AF081073).

RANUNCULALES. Berberidaceae (BERB). *Epimedium grandiflorum* Morr., Cornell, J. Davis s.n., September 1999, BH; *atpA* AY299765; *Epimedium koreanum* (*rbcL* L75869). *Mahonia bealei*; (*atpA* AF197659); (*rbcL* L75871). **Lardizabalaceae (LARD).** *Akebia quinata* (Houtt.) Decne., from cultivation, J. Davis s.n., BH; *atpA* AY299704; (*rbcL* L12627). *Stauntonia hexaphylla* Decne., NYBG 4225/95B, NY; *atpA* AY299841; (*rbcL* L37922).

SAXIFRAGALES. Cercidiphyllaceae (CERC). *Cercidiphyllum japonicum* Siebold & Zucc., Cornell, J. Davis s.n., September 1999, BH; *atpA* AY299744; (*rbcL* L11673).

MONOCOTYLEDONS

No Ordinal Assignment. Petrosaviaceae (PETR). *Japonolirion osense* Nakai, M. Chase 3000, K; *atpA* AY299790; (*rbcL* AF206784). *Petrosavia stellaris* Becc., K. Cameron 2154, NY, K; *atpA* AY299821; (*rbcL* AF206806).

ACORALES. Acoraceae (ACOR). *Acorus calamus* L., R. Dirig 2990, BH; *atpA* AF039256; (*rbcL* M91625). *Acorus gramineus* Aiton, Herrick Conserv., J. Freudenstein s.n., OS; *atpA* AY299699; (*rbcL* D28866). *Acorus tatarinowii* Schott, RBG Sydney 933022, NSW (492836); *atpA* AY299700; *rbcL* AY298815.

ALISMATALES. Alismataceae (ALIS). *Alisma plantago-aquatica*; (*atpA* AF197717); (*rbcL* L08759). *Caldesia oligococca* (F. Von Mueller) Buche, F. Rasmussen et al. C-246, 26 September 1998, C; *atpA* AY277800; *rbcL* AY277799. *Sagittaria latifolia* Willd., K. Hansen 93-08, BH; *atpA* AY299832; (*rbcL* L08767). **Araceae (ARAC).** *Arisaema triphyllum* (L.) Schott, N. Uhl 93-03, BH; *atpA* AY299717; *rbcL* AY298817. *Gymnostachys anceps* R. Br., Bailey Conserv. 95-101, K. Hansen s.n., BH; *atpA* AF039244; (*rbcL* M91629). *Orontium aquaticum* L., NYBG 49/80, NY; *atpA* AY299816; (*rbcL* AJ005632). *Symplocarpus foetidus* (L.) W. Barton, N. Uhl 92–01, BH; *atpA* AF039245; (*rbcL* L10247). **Butomaceae (BUTO).** *Butomus umbellatus* L., N. Uhl 92-05, BH; *atpA* AY299733; (*rbcL* U80685). **Cymodoceaceae (CYMO).** *Cymodocea serrulata* (R. Br.) Ascherson & Magh., O'Donohue 21395, BRN; *atpA* AY277801; (*rbcL* U80687). **Hydrocharitaceae (HYDR).** *Ottelia ovalifolia* (R.Br.) Rich., F. Rasmussen et al. C-245, 26 September 1998, C; *atpA* AY277802; *Ottelia alismoides* (*rbcL* U80707). **Juncaginaceae (JUNG).** *Triglochin maritima* L., D. Goldman s.n., June 1993, BH; *atpA* AY299852; *Triglochin maritimum* (*rbcL* U80714). **Potamogetonaceae (POTA).** *Potamogeton natans* L., K. Hansen s.n., 1992, BH; *atpA* AY299829; *Potamogeton richardsonii* (*rbcL* U03730). **Scheuchzeriaceae (SCHE).** *Scheuchzeria palustris* L., G. Petersen C-522, 1 August 1999, C; *atpA* AY277803; (*rbcL* U03728). **Tofieldiaceae (TOFI).** *Pleea tenuifolia* Michx., M. Chase 152, NCU; *atpA* AY299827; (*rbcL* AJ131774). *Tofieldia calyculata* (L.) Wheldon, M. Chase 1851, K; *atpA* AY299851; *Tofieldia pusilla* (*rbcL* AJ286562).

ASPARAGALES. Anthericaceae (ANTH). *Anthericum* sp., Weigend & Weigend 2000/154, NY, HUSA; *atpA* AY299713; *Anthericum liliago* (*rbcL* Z69225). **Asteliaceae (ASTE).** *Astelia* sp., RBG Melbourne, J. Grimes 3525, MEL; *atpA* AY299722; *Astelia pumila* (*rbcL* AF307906). *Neoastelia spectabilis* J. B. Williams, RBG Melbourne 941074 DGR095, J. Grimes 3529, MEL; *atpA* AY299810; *rbcL* AY298840. **Blandfordiaceae (BLAN).** *Blandfordia grandiflora* R. Br., RBG Melbourne 821598 Z2833; *atpA* AY299727; *Blandfordia punicea* (*rbcL* Z73694). **Boryaceae (BORY).** *Alania endlicheri* Kunth, J. Freudenstein 2554, OS; *atpA* AY299705; (*rbcL* Y14982). *Borya* aff. *sphaerocephala* R. Br., J. Conran et al. 944, PERTH, ADU; *atpA* AY299728; *Borya septentrionalis* (*rbcL* Y14985). **Doryanthaceae (DORY).** *Doryanthes excelsa* Corrêa, M. Chase 188, NCU; *atpA* AY299760; (*rbcL* Z73697). **Hemerocallidaceae (HEME).** *Dianella caerulea* Sims, NYBG 88/3, J. Davis s.n., BH; *atpA* AY299756; *Dianella ensifolia* (*rbcL* M96960). *Geitonoplesium cymosum* (R. Br.) A. Cunn. ex Hook., Adelaide Bot. Gard., J. Conran et al. 970, ADU; *atpA* AY299771; *rbcL* AY298833. *Hemerocallis* sp. cv. Stella d'Oro, K. Hansen s.n., September 1992, BH; *atpA* AY299780; *Hemerocallis fulva* (*rbcL* L05036). *Xeronema callistemon* W.R.B. Oliv., M. Chase 653, K; *atpA* AY299857; (*rbcL* Z69235). **Hypoxidaceae (HYPO).** *Curculigo capitulata* (Lour.) Kuntze, Bailey Conserv. 95-103, K. Hansen & J. Davis s.n., BH; *atpA* AF039249; (*rbcL* Z73701). *Hypoxis occidentalis* Benth. var. *occidentalis*, J. Conran et al. 919, PERTH, ADU; *atpA* AY299784; *Hypoxis glabella* (*rbcL* Y14989). **Iridaceae (IRID).** *Neomarica northi-*

ana (Schneev.) Sprague, Bailey Conserv., D. Goldman 1758, BH; *atpA* AY299812; *rbcL* AY298842. *Sisyrinchium angustifolium* Mill., K. Hansen 92-05, BH; *atpA* AY299837; *Sisyrinchium micranthum* (*rbcL* Z77290). **Ixioliriaceae (IXIO).** *Ixiolirion tataricum* (Pall.) Herb., M. Chase 489, K; *atpA* AY299789; (*rbcL* Z73704). **Johnsoniaceae (JOHN).** *Johnsonia lupulina* R. Br., J. Conran et al. 901, PERTH, ADU; *atpA* AY299791; *Johnsonia pubescens* (*rbcL* Z77304). **Lomandraceae (LOMA).** *Arthropodium cirratum* (G. Frost.) R. Br., J. Grimes 3256, MEL; *atpA* AY299719; (*rbcL* Z69233). *Eustrephus latifolius* R. Br., Adelaide Bot. Gard. G880587, J. Conran et al. 969, ADU; *atpA* AY299768; *rbcL* AY298831. *Sowerbaea laxiflora* Lindl., J. Conran et al. 897A, PERTH, ADU; *atpA* AY299838; *Sowerbaea juncea* (*rbcL* Z69234). *Thysanotus thyrsoideus* Baker, J. Conran et al. 925, PERTH, ADU; *atpA* AY299850; *Thysanotus spiniger* (*rbcL* Z69236). **Orchidaceae (ORCH).** *Calopogon tuberosus* (L.) Britton, Sterns & Poggenb., D. Goldman 532, TEX, BH, GH; *atpA* AY299738; (*rbcL* AF074119). *Cypripedium calceolus* L. var. *pubescens* (Willd.) Correll, J. Morris 3A, KE; *atpA* AY299755; *Cypripedium passerinum* (*rbcL* AF074142). *Epipactis helleborine* (L.) Crantz, D. Potter s.n., OS; *atpA* AY299766; (*rbcL* Z73707). *Isotria verticillata* (Muhl. ex Willd.) Raf., J. Freudenstein 2402, OS; *atpA* AY299788; (*rbcL* AF074180). *Neuwiedia veratrifolia* Blume, M. Chase O-883, K; *atpA* AY299813; (*rbcL* AF074200). **Tecophilaeaceae (TECO).** *Tecophilaea cyanocrocus* Leyb., M. Chase 447, K; *atpA* AY299848; (*rbcL* Z73709). **Xanthorrhoeaceae (XANT).** *Xanthorrhoea australis* R. Br., RBG Kew 1985-708, K; *atpA* AF039250; *Xanthorrhoea hostilis* (*rbcL* Z73710).

DIOSCOREALES. Burmanniaceae (BURM). *Burmannia lutescens* Becc., L. Caddick 352, K; *atpA* AY299732; *Burmannia longifolia* (*rbcL* AF307484). *Thismia rodwayi* F. Muell., P. Garnock-Jones 2218, WELTU; *atpA* AY299849; no *rbcL* sequence. **Dioscoreaceae (DIOS).** *Dioscorea retusa* Mast., Bailey Conserv. 91-058, K. Hansen s.n., BH; *atpA* AY299759; *Dioscorea polygonoides* (*rbcL* AJ235803). *Tamus communis* L., F. & H. Rasmussen, C-1170, C; *atpA* AY277804; (*rbcL* AF307474). **Nartheciaceae (NART).** *Aletris farinosa* L., M. Chase 105, NCU; *atpA* AY299706; (*rbcL* provided by M. Chase, sequenced from same DNA isolation as *atpA*). *Narthecium ossifragum* (L.) Huds., M. Chase 610, K; *atpA* AY299809; (*rbcL* AJ286560). **Taccaceae (TACC).** *Tacca parkeri* Seem., R. Schultes 9298b, NY; *atpA* AY299845; *Tacca chantrieri* (*rbcL* AJ235810). **Trichopodaceae (TRIC).** *Avetra sempervirens* H. Perrier, L. Caddick 304, K; *atpA* AY299724; *rbcL* AY298818. *Trichopus zeylanicus* Gaertn., L. Caddick 346 (MWC6634), K; *atpA* AY277805; (*rbcL* AF307477).

LILIALES. Alstroemeriaceae (ALST). *Alstroemeria caryophyllaea* Jacq., Fairchild Trop. Gard. 81-563, FTG; *atpA* AF039254; *Alstroemeria* sp. (*rbcL* Z77254). **Calochortaceae (CALO).** *Calochortus minimus* Ownbey, Ness 606, PUA; *atpA* AY299737; (*rbcL* Z77263). **Campynemataceae (CAMP).** *Campynema lineare* Labill., Walsh 3488, MEL; *atpA* AY299740; *Campynema linearis* (*rbcL* Z77264). **Colchicaceae (COLC).** *Burchardia multiflora* Lindl., J. Conran et al. 890A, PERTH, ADU; *atpA* AY299731; *Burchardia umbellata* (*rbcL* Z77266). *Schelhammera multiflora* R. Br., NYBG 2555/93A, MASS; *atpA* AY299834; *rbcL* AY298849. *Wurmbea* sp., J. Conran et al. 899, PERTH, ADU; *atpA* AY299856; *rbcL* AY298853. **Corsiaceae (CORS).** *Arachnitis uniflora* Phil., L. Aagesen s.n., 18 December 1998, C; *atpA* AY299715; no *rbcL* sequence. **Liliaceae (LILI).** *Clintonia borealis* (Aiton) Raf., M. Chase 498, K; *atpA* AY299748; (*rbcL* D17372). *Lilium superbum* L., M. Chase 112, NCU; *atpA* AY299797; (*rbcL* L12682). **Luzuriagaceae (LUZU).** *Luzuriaga radicans* Ruiz & Pav., RBG Kew 1961-64905, M. Chase 499, K; *atpA* AY299798; (*rbcL* Z77300). **Melanthiaceae (MELA).** *Amianthium muscaetoxicum* (Walter) A. Gray, N. Uhl 92-06, BH; *atpA* AY299709; (*rbcL* AJ417895). *Chamaelirium luteum* (L.) A. Gray, M. Chase 224, NCU; *atpA* AY299745; (*rbcL* AJ276347). *Veratrum viride* Aiton, N. Uhl 92–02, BH; *atpA* AF039255; *Veratrum album* (*rbcL* D28168). **Petermanniaceae (PETE).** *Petermannia cirrosa* F. Muell., S. Frederiksen et al. s.n., 4 October 1998, C; *atpA* AY299820; *rbcL* AY298844. **Philesiaceae (PHIS).** *Philesia buxifolia* Lam., RBG Kew 1965-68407, M. Chase 545, K; *atpA* AY299822; (*rbcL* Z77302). **Smilacaceae (SMIL).** *Ripogonum discolor* F. Muell., S. Frederiksen et al. s.n., 5 October 1998, C; *atpA* AY299831; *Ripogonum elseyanum* (*rbcL* Z77309). *Smilax rotundifolia* L., N. Uhl 92-07, BH; *atpA* AF039251; *Smilax glauca* (*rbcL* Z77310). **Trilliaceae (TRIL).** *Trillium grandiflorum* (Michx.) Salisb., N. Uhl s.n., 1993, BH; *atpA* AF039253; (*rbcL* D28164).

PANDANALES. Acanthochlamydaceae (ACAN). *Acanthochlamys bracteata* P.C. Kao, P. Kao 1993, K; *atpA* AY299698; (*rbcL* provided by M. Chase, sequenced from same DNA isolation as *atpA*). **Cyclanthaceae (CYCL).** *Carludovica palmata*; (*atpA* AF197707); (*rbcL* AF197596). *Chorigyne cylindrica* R. Erikss., Mo. Bot. Gard. 891186, MO; *atpA* AY299747; *rbcL* AY298823. *Cyclanthus bipartitus* Poit. ex A. Rich., Mo. Bot. Gard. 891177, MO; *atpA* AY299754; (*rbcL* AY007660). *Sphaeradenia stenosperma* Harling, Mo. Bot. Gard. U-910, MO; *atpA* AY299840; *Sphaeradenia pendula* (*rbcL* AJ235808). **Pandanaceae (PAND).** *Freycinetia multiflora* Merrill, Mo. Bot. Gard. 811323, MO; *atpA* AY299770; *Freycinetia scandens* (*rbcL* AF206770). *Pandanus copelandii* Merr., Mo. Bot. Gard. 801094, MO; *atpA* AY299818; *Pandanus veitchii* (*rbcL* M91632). **Stemonaceae (STEM).** *Croomia pauciflora* (Nutt.) Torr., A. Gholson, Jr. 10360, Florida 4/83, FLAS; (*atpA* AF197708); *rbcL* AY298827. *Stemona javanica* (Kunth) Engl., M. Chase 2156, K; *atpA* AY299842; *Stemona japonica* (*rbcL* AJ131948). **Triuridaceae (TRIU).** *Lacandonia schismatica* E. Martínez & Ramos, F. Vergara Silva s.n., MEXU; *atpA* AY299794; no *rbcL* sequence. *Sciaphila albescens* Benth., B. Ambrose s.n., MEXU; *atpA* AY299835; no *rbcL* sequence. *Triuris* sp., F. Vergara Silva s.n., MEXU; *atpA* AY299854; no *rbcL* sequence. **Velloziaceae (VELL).** *Barbaceniopsis* sp., Weigend & Weigend 2000/318, NY, HUSA; *atpA* AY299725; *rbcL* AY298819. *Talbotia elegans* Balf., Bailey Conserv. 91-069, BH; *atpA* AF039247; "*Barbacenia elegans*" in GenBank (*rbcL* AJ131946).

No Ordinal Assignment. Dasypogonaceae (DASY). *Baxteria australis* R. Br. ex Hook., J. Conran et al. 906, PERTH, ADU; *atpA* AY124504; *rbcL* AY123230. *Calectasia cyanea* R. Br., J. Conran et al. 928, PERTH, ADU; *atpA* AY124505; *rbcL* AY123231. *Dasypogon hookeri* J.R. Drumm., J. Conran et al. 917, PERTH, ADU; *atpA* AY124503; *rbcL* AY123229. *Kingia australis* R. Br., J. Conran et al. 922, PERTH, ADU; *atpA* AY124506; *rbcL* AY123232.

ARECALES. Arecaceae (AREC). *Calamus caryotoides* A. Cunn. ex Mart., NYBG 454/84, NY; *atpA* AY299734; *Calamus hollrungii* (*rbcL* AJ404775). *Euterpe oleracea* Mart., Lyon Arb. L-70.0017, BH; *atpA* AY299769; *rbcL* AY298832. *Nypa fruticans*; (*atpA* U58833); (*rbcL* M81813). *Phoenix reclinata*; (*atpA* U58831); (*rbcL* M81814). *Phytelephas aequatorialis* Spruce, Aarhus 87BI00261, BH; *atpA* AY299825; *rbcL* AY298846. *Plectocomia elongata* Mart. ex. Blume, RBG Kew 1984-4821, K; *atpA* AY299826; *rbcL* AY298848. *Trithrinax acanthocoma* Drude, N. Uhl s.n., BH; *atpA* AY299853; *rbcL* AY298852.

COMMELINALES. Commelinaceae (COMM). *Callisia warszewicziana* (Kunth & Bouché) D.R. Hunt, Bailey Conserv. 60-511, BH; *atpA* AY299736; *rbcL* AY298821. *Cochliostema odoratissimum* Lem., Bailey Conserv. 64-502, H. Moore 7537, BH; *atpA* AY299750; *rbcL* AY298824. *Commelina communis* L., C. Hardy 267, NY; *atpA* AY299751; *rbcL* AY298825. *Dichorisandra thyrsiflora* J.C. Mikan, NYBG 407/65, C. Hardy 228, NY; *atpA* AY299757; *rbcL* AY298828. *Murdannia* sp., Bailey Conserv. 75-650, BH; *atpA* AY299805; *rbcL* AY298838. *Palisota bracteosa* C.B. Clarke, Bailey Conserv., C. Hardy 95, BH; *atpA* AY299817; *rbcL* AY298843. **Haemodoraceae (HAEM).** *Anigozanthos flavidus* DC. in Redouté, Bailey Conserv. 95-102, K. Hansen & J. Davis s.n., BH; *atpA* AF039246; (*rbcL* AJ404843). *Haemodorum simulans* F. Muell., J. Conran et al. 936, PERTH, ADU; *atpA* AY299774; (*rbcL* provided by M. Chase, *Haemodorum spicatum* R. Br., Dixon s.n., KPBG). *Xiphidium caeruleum* Aubl., NYBG 1415/89, NY; *atpA* AY299858; (*rbcL* provided by M. Chase, *Xiphidium caeruleum* Aubl., Chase 221, NCU). **Hanguanaceae (HANG).** *Hanguana malayana* Merr., P. Rudall s.n., K; *atpA* AY299775; (*rbcL* AJ417896). **Philydraceae (PHIL).** *Helmholtzia glaberrima* (Hook. f.) Caruel, RBG Melbourne; *atpA* AY299779; *rbcL* AY298834. *Philydrella pygmaea* (R. Br.) Caruel, J. Conran et al. 915, PERTH, ADU; *atpA* AY299823; *rbcL* AY298845. *Philydrum lanuginosum* Banks & Sol. ex Gaertn., RBG Kew 1987-8002, K; *atpA* AY299824; (*rbcL* U41596). **Ponteder-**

iaceae (PONT). *Eichhornia azurea* (Sw.) Kunth, RBG Kew 1991-1656, K; *atpA* AY299762; (*rbcL* U41573). *Eichhornia paniculata* (Spreng.) Solms, S. Barrett 1401, TRT; *atpA* AY299763; (*rbcL* U41578). *Heteranthera rotundifolia* (Kunth) Griseb., S. Barrett 1411, TRT; *atpA* AY299782; (*rbcL* U41585). *Hydrothrix gardneri* Hook. f., RBG Kew 1991-1141, K; *atpA* AY299783; (*rbcL* U41582). *Monochoria korsakowii* Regel & Maack, S. Barrett 1415, TRT; *atpA* AY299803; *Monochoria korsakovii* (*rbcL* U41590). *Pontederia cordata* L., NYBG 2844/95, L. Campbell 755, NY; *atpA* AY299828; *Pontederia cordata* var. *cordata* (*rbcL* U41592).

POALES. Anarthriaceae (ANAR). *Anarthria prolifera* R. Brown, J. Conran et al. 902, PERTH, ADU; *atpA* AY124513; *Anarthria polyphylla* (*rbcL* AF148760). **Bromeliaceae (BROM).** *Ananas comosus* (L.) Merr., Bailey Conserv.; *atpA* AY299710; (*rbcL* L19977). *Brocchinia reducta* Baker, F. Michelangeli 525, VEN; *atpA* AY299729; *rbcL* AY298820. *Catopsis nutans* (Sw.) Griseb., Bailey Conserv. 72-783, BH; *atpA* AF039257; *Catopsis montana* (*rbcL* L19976). *Hechtia texensis* S. Watson, NYBG 135/80, NY; *atpA* AY299776; *Hechtia montana* (*rbcL* L19974). *Puya berteroniana* Mez, NYBG 30/77A, NY; *atpA* AY124508; *Puya dyckioides* (*rbcL* L19973). *Tillandsia usneoides* (L.) L., Bailey Conserv.; *atpA* AY124507; *Tillandsia elizabethae* (*rbcL* L19971). **Cyperaceae (CYPE).** *Carex interior* L.H. Bailey, K. Hansen 93-06, BH; *atpA* AY124514; *Carex monostachya* (*rbcL* Y12998). **Ecdeiocoleaceae (ECDE).** *Ecdeiocolea monostachya* F. Muell., J. Conran et al. 943, PERTH, ADU; *atpA* AY124516; *rbcL* AY123235. **Eriocaulaceae (ERIO).** *Eriocaulon humboldtii* Kunth, F. Michelangeli 542, VEN; *atpA* AY124517; *rbcL* AY123236. *Lachnocaulon anceps* (Walter) Morong, S. Orzell 25895, USF, BH; *atpA* AY299795; *rbcL* AY298835. *Syngonanthus flavidulus* (Michx.) Ruhland, S. Orzell 25894, USF, BH; *atpA* AY299844; *rbcL* AY298850. *Tonina fluviatilis* Aubl., D. Stevenson 1067, NY; *atpA* AY124518; *rbcL* AY123237. **Flagellariaceae (FLAG).** *Flagellaria indica* L., Bailey Conserv. 77-394, K. Hansen s.n., May 1994, BH; *atpA* AF039248; (*rbcL* L12678). **Hydatellaceae (HYDA).** *Trithuria submersa* Hook. f., A. Doust 1123, MELU; no *atpA* sequence; *rbcL* AF458076. **Joinvilleaceae (JOIN).** *Joinvillea ascendens* Gaudich. ex Brongn. & Gris, A. Bruneau s.n., August 1992, BH; *atpA* AY124519; *Joinvillea plicata* (*rbcL* L01471). **Juncaceae (JUNC).** *Juncus* sp., K. Hansen s.n., BH; *atpA* AY124520; *Juncus effusus* (*rbcL* L12681). *Luzula acuminata* Raf., F. Michelangeli 543, BH; *atpA* AY124521; *Luzula multiflora* (*rbcL* AJ419945). *Prionium serratum* (L. f.) Drège ex E. Mey., Copenhagen Bot. Gard., O. Seberg s.n., C; *atpA* AY124527; (*rbcL* U49223). **Mayacaceae (MAYA).** *Mayaca sellowiana* Kunth, J. Steyermark 58451, NY; *atpA* AY124522; *Mayaca fluviatilis* (*rbcL* AJ419948). **Poaceae (POAC).** *Anomochloa marantoidea* Brongn., Bailey Conserv., K. Hansen & J. Davis s.n., BH; *atpA* AY124526; (*rbcL* AF021875). *Bambusa multiplex* (Lour.) Raeusch. ex Schult. & Schult. f., Bailey Conserv. 71-470, R. Soreng s.n., BH; *atpA* AY124525; (*rbcL* M91626). *Oryza sativa*; (*atpA* X51422); (*rbcL* D00207). *Pharus latifolius* L., Bailey Conserv., K. Hansen s.n., 29 July 92; *atpA* AY124524; (*rbcL* AY357724). *Streptochaeta angustifolia* Soderstr., Bailey Conserv., BH; *atpA* AY124523; *Streptochaeta spicata* (*rbcL* AJ419949). **Rapateaceae (RAPA).** *Cephalostemon flavus* (Link) Steyerm., B. Maguire 29321, NY; *atpA* AY299742; *rbcL* AY298822. *Epidryos allenii* (Steyerm.) Maguire, D. Stevenson 1210, NY; *atpA* AY299764; *rbcL* AY298830. *Kunhardtia radiata* Maguire & Steyerm., B. Maguire 31834, NY; *atpA* AY299793; (*rbcL* AF036883). *Rapatea xiphoides* Sandwith, C. Kelloff 975, BH; *atpA* AY124511; *rbcL* AF460969. *Schoenocephalium cucullatum* Maguire, B. Maguire 37631, NY; *atpA* AY124512; *rbcL* AF460970. *Spathanthus bicolor* Ducke, R. Schultes 17980, NY; *atpA* AY299839; *rbcL* AF460971. *Stegolepis parvipetala* Steyerm., F. Michelangeli 513, VEN; *atpA* AY124535; *rbcL* AY123242. **Restionaceae (REST).** *Baloskion tetraphyllum* (Labill.) B.G. Briggs & L.A.S. Johnson, RBG Kew 1977-6565, J. Davis s.n., M. Chase 560, K; *atpA* AY124529; (*rbcL* AF148761). *Elegia fenestrata* Pillans, NYBG 1697/95, NY; *atpA* AY124530; *rbcL* AY123238. *Lepyrodia scariosa* R. Br., M. Crisp 8400, CANB; *atpA* AY124528; *Lepyrodia glauca* (*rbcL* AF148785). *Thamnochortus cinereus* H.P. Linder, NYBG 227/86A, NY; *atpA* AY124531; (*rbcL* provided by H. Linder, *Thamnochortus cinereus* H.P. Linder, H. Linder et al. 7281, Z). **Thurniaceae (THUR).** *Thurnia polycephala* Schnee, B. Maguire 35629, NY; *atpA* AY124532; *rbcL* AY123239. **Typhaceae (TYPH).** *Sparganium eurycarpum* Engelm., K. Hansen s.n., June 1993, BH; *atpA* AY124509; *Sparganium americanum* (*rbcL* M91633). *Typha latifolia* L., N. Uhl 92-04, BH; *atpA* AY124510; (*rbcL* M91634). **Xyridaceae (XYRI).** *Abolboda macrostachya* Spruce ex Malme var. *macrostachya*, B. Maguire 36287, NY; *atpA* AY124533; *rbcL* AY123240. *Aratitiyopea lopezii* (L.B. Sm.) Steyerm. & P.E. Berry, B. Maguire 28276, NY; *atpA* AY299716; *rbcL* AF461418. *Orectanthe sceptrum* (Oliv. ex Thurn) Maguire, B. Maguire 33680, NY; *atpA* AY124534; *rbcL* AY123241. *Xyris bicephala* Gleason, F. Michelangeli 524, VEN; *atpA* AY124536; *rbcL* AY123243. *Xyris jupicai* Rich., D. Goldman 1766, BH; *atpA* AY299859; *rbcL* AY298854.

ZINGIBERALES. Cannaceae (CANN). *Canna indica* L., Bailey Conserv. 72-117, BH; *atpA* AY299741; (*rbcL* AF378763). **Costaceae (COST).** *Costus lateriflorus* Baker, NMNH 98–224, W.J. Kress 00-6599, US; *atpA* AY299753; *rbcL* AY298826. *Dimerocostus argenteus* (Ruiz & Pav.) Maas, C. Specht 98-190, NY; *atpA* AY299758; *rbcL* AY298829. *Monocostus uniflorus* (Poepp. ex Petersen) Maas, C. Specht 01-280, NY; *atpA* AY299804; (*rbcL* AF243839). *Tapeinochilos* sp., Lyon Arb. L-86.0039; *atpA* AY299846; *Tapeinochilos ananassae* (*rbcL* AF243840). **Heliconiaceae (HELI).** *Heliconia rostrata* Ruiz & Pav., NYBG 1380/91A, NY; *atpA* AY299778; *Heliconia indica* (*rbcL* AF378765). **Lowiaceae (LOWI).** *Orchidantha maxillarioides* K. Schum., NYBG 1639/91, NY; *atpA* AY299815; *Orchidantha fimbriata* (*rbcL* AF243841). **Marantaceae (MARA).** *Calathea loeseneri* J.F. Macbr., NYBG 345/95A, NY; *atpA* AY299735; (*rbcL* AF243842). *Maranta leuconeura* E. Morren, Bailey Conserv. 84-107; *atpA* AY299801; *Maranta bicolor* (*rbcL* AF378768). **Musaceae (MUSA).** *Musa textilis* Née, NYBG 1682/77, NY; *atpA* AY299806; *Musa acuminata* (*rbcL* AF378770). **Strelitziaceae (STRE).** *Ravenala madagascariensis* Sonn., NYBG 331/99, NY; *atpA* AY299830; *Ravenala madagascarensis* (*rbcL* L20138). *Strelitzia nicolai* Regel & Körn., NYBG 400/56, NY; *atpA* AY299843; (*rbcL* AF243846). **Zingiberaceae (ZING).** *Alpinia purpurata* (Vieill.) K. Schum., Bailey Conserv. 72-114, BH; *atpA* AY299708; *rbcL* AY298816. *Globba winittii* C.H. Wright, NYBG 358/95, NY; *atpA* AY299772; *Globba atrosanguinea* (*rbcL* AF378777).