



Angiosperm phylogeny inferred from 18S rDNA, *rbcL*, and *atpB* sequences

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A phylogenetic analysis of a combined data set for 560 angiosperms and seven outgroups based on three genes, 18S rDNA (1855 bp), *rbcL* (1428 bp), and *atpB* (1450 bp) representing a total of 4733 bp is presented. Parsimony analysis was expedited by use of a new computer program, the RATCHET. Parsimony jackknifing was performed to assess the support of clades. The combination of three data sets for numerous species has resulted in the most highly resolved and strongly supported topology yet obtained for angiosperms. In contrast to previous analyses based on single genes, much of the spine of the tree and most of the larger clades receive jackknife support $\geq 50\%$. Some of the noneudicots form a grade followed by a strongly supported eudicot clade. The early-branching angiosperms are Amborellaceae, Nymphaeaceae, and a clade of Austrobaileyaceae, Illiciaceae, and Schisandraceae. The remaining noneudicots, except Ceratophyllaceae, form a weakly supported core eumagnoliid clade comprising six well-supported subclades: Chloranthaceae, monocots, Winteraceae/Canellaceae, Piperales, Laurales, and Magnoliales. Ceratophyllaceae are sister to the eudicots. Within the well-supported eudicot clade, the early-diverging eudicots (e.g. Proteales, Ranunculales, Trochodendraceae, Sabiaceae) form a grade, followed by the core eudicots, the monophyly of which is also strongly supported. The core eudicots comprise

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six well-supported subclades: (1) Berberidopsidaceae/Aextoxicaceae; (2) Myrothamnaceae/Gunneraceae; (3) Saxifragales, which are the sister to Vitaceae (including *Leea*) plus a strongly supported eurosoid clade; (4) Santalales; (5) Caryophyllales, to which Dilleniaceae are sister; and (6) an asterid clade. The relationships among these six subclades of core eudicots do not receive strong support. This large data set has also helped place a number of enigmatic angiosperm families, including Podostemaceae, Aphloiaceae, and Ixerbaceae. This analysis further illustrates the tractability of large data sets and supports a recent, phylogenetically based, ordinal-level reclassification of the angiosperms based largely, but not exclusively, on molecular (DNA sequence) data.

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INTRODUCTION

Recent analyses have greatly improved our understanding of phylogenetic relationships among flowering plants (Chase *et al.*, 1993; Nandi, Chase & Endress, 1998; Savolainen *et al.*, 2000a, b; Soltis *et al.*, 1997a). All of these studies, based on plastid *rbcL* (Chase *et al.*, 1993), 18S rDNA (Soltis *et al.*, 1997a), *rbcL* plus morphology, chemistry, and other non-DNA characters (Nandi *et al.*, 1998), and combined plastid *atpB* and *rbcL* (Savolainen *et al.*, 2000a), included hundreds of species and more than 1000 characters, placing them among the largest phylogenetic analyses yet conducted. Despite striking overall similarity among the topologies obtained from these analyses (reviewed in Soltis *et al.*, 1997b; Chase & Albert, 1998; Chase & Cox, 1998) and strong internal support for many of the smaller clades located near the tips, the spine of the angiosperm tree has remained poorly resolved and weakly supported. Furthermore, only a few large clades received strong support (i.e. >85%) from bootstrap or jackknife analyses. Hence, internal support was lacking in those areas most essential for understanding general angiosperm relationships on a broad scale.

Although the feasibility of analyses of large data sets has been questioned (e.g. Graur *et al.*, 1996; Hillis, Huelsenbeck & Swofford, 1994), recent simulations (Graybeal, 1998; Hillis, 1996) and empirical studies (Chase & Cox, 1998; Soltis *et al.*, 1998) have indicated that one solution to the computational difficulties large data sets pose is, ironically, the addition of both taxa and characters. A recent study employing three genes (*rbcL*, *atpB*, and 18S rDNA) sequenced for a similar suite of

190 angiosperms and three outgroups provided enormous improvements in computer run time, as well as greatly enhanced internal support for clades compared to phylogenetic analyses of the individual data sets or even data sets combined in pairs (Soltis *et al.*, 1998). Based on the success of this and other analyses of large combined data sets for angiosperms (e.g. Chase & Cox, 1998; Savolainen *et al.*, 2000a; Soltis *et al.*, 1997b), we compiled an angiosperm data set with additional taxa for these same three genes. We report here the results of a phylogenetic analysis of a three-gene data set of 18S rDNA (1855 bp), *rbcL* (1428 bp), and *atpB* (1450 bp) sequences (a total of 4733 bp/taxon) for 560 angiosperms, plus seven gymnosperm outgroups.

MATERIAL AND METHODS

Data sets

DNA samples for most of the species included were extracted from fresh material or tissue dried in silica gel following the 2X CTAB method of Doyle & Doyle (1987) and modifications thereof using liquid nitrogen and/or higher CTAB concentrations (e.g. Soltis *et al.*, 1991). Microprep methods that require small amounts of tissue (e.g. Cullings, 1992) were used for some herbarium or pressed specimens. In many cases different placeholder species or genera were used as representatives of families in previous analyses. In this study, we attempted to use the same species for each family represented; in many cases the same DNA was used (Appendix). In several instances, different congeneric species were used to represent a given genus; in only two instances were different genera used as placeholders for a family. For Melastomataceae, *Clidemia* was sequenced for *atpB*, whereas *Osbeckia* was used for both *rbcL* and 18S rDNA; for Urticaceae, *Urtica* was sequenced for *atpB*, and *Boehmeria* was included for both *rbcL* and 18S rDNA (Appendix). DNAs and leaf material were exchanged to generate all three gene sequences from the same source. In addition to ensuring greater uniformity among the samples included for all three genes, we also improved the taxon sampling and increased the representation of many clades relative to earlier phylogenetic efforts (e.g. Chase *et al.*, 1993; Soltis *et al.*, 1997a; Savolainen *et al.*, 2000a). General collection and voucher information has been provided for many of these samples in previous publications, including Chase *et al.* (1993), Hoot, Megallon & Crane (1999), Savolainen *et al.* (2000a), and Soltis *et al.* (1997a, 1998).

We used seven outgroups representing three gymnosperm lineages: *Ephedra sinica* C. A. Mey., *Gnetum gnemon* L., and *Welwitschia mirabilis* Hook. (Gnetophyta), *Ginkgo biloba* L. (Ginkgophyta), and *Pinus*, *Podocarpus*, and *Taxus* (Pinophyta).

The sequences generated earlier for the large data sets of 18S rDNA (Soltis *et al.*, 1997a), *rbcL* (Chase *et al.*, 1993), and *atpB* (Savolainen *et al.*, 2000a) formed the foundation for the large data set compiled here. New sequences for 18S rDNA, *rbcL*, and *atpB* were generated using previously published primers and approaches (e.g. 18S rDNA, Soltis & Soltis, 1997, Soltis *et al.*, 1997a, Johnson *et al.*, 1999; *rbcL*, Chase *et al.*, 1993, and Lledó *et al.*, 1998; *atpB*, Hoot, Culham & Crane, 1995a, b and Savolainen *et al.*, 2000a). All of the new sequences for 18S rDNA, *rbcL*, and *atpB* were generated via automated sequencing. Alignment of sequences for these three genes was easily achieved by eye; no insertions or deletions occur in *rbcL*, and

they are extremely rare in *atpB*. With the exception of four small, well-defined regions, alignment of the 18S rDNA sequences was also easily accomplished; these four regions correspond to positions 230–237, 496–501, 666–672, and 1363–1369 on the reference sequence of *Glycine max* (L.) Merr. (see Soltis *et al.*, 1997a). As in Soltis *et al.* (1997a), no attempt was made to align these four regions across the angiosperms, and they were excluded from phylogenetic analyses. The difficulty in aligning these four small regions across all angiosperms has been reviewed elsewhere (Soltis *et al.*, 1997a; Soltis & Soltis, 1998).

The molecular evolution of all three genes (18S rDNA, *rbcL*, and *atpB*) in the angiosperms has been discussed in detail previously, and the relative rates of evolution of these genes have also been provided (e.g. Chase & Cox, 1998; Hoot *et al.*, 1995a; Savolainen *et al.*, 2000a; Soltis & Soltis, 1998). The strong overall similarity of the topologies based on analyses of the individual genes has also been discussed, as have issues of congruence and the suitability of combining these three data sets into a single matrix for use in a combined analysis (Hoot *et al.*, 1997, 1999; Soltis *et al.*, 1997b, 1998; Chase & Cox, 1998). Hence, none of these issues will be dealt with here. All previous studies indicated that data from these three genes can be combined, and we view such a combined analysis as the best way to reconstruct angiosperm phylogeny. For a review of issues surrounding direct combination of matrices, see Wiens (1998); the procedure used for these matrices, developed independently, parallels his recommendations of direct combination in spite of potential conflicts. We believe that all available tests of incongruence are too coarse to be useful and that the best way to detect true incongruence is by examination of results, expecting lower internal support and perhaps less resolution in groups in which hard incongruence occurs (*sensu* Seelanan, Schnabel & Wendel, 1997).

Phylogenetic analysis

Several approaches were used to analyse the three-gene, 567-taxon data set assembled here. Parsimony searches were conducted using PAUP* 4.0 (Swofford, 1998). These analyses followed the general approach applied in previous analyses of large data sets (e.g. Savolainen *et al.*, 2000a; Soltis *et al.*, 1997a, 1997b, 1998). This approach was ultimately abandoned, however, in favour of a second approach, the RATCHET method (Nixon, 1999), which quickly found trees shorter than those obtained with PAUP* 4.0. The RATCHET, which is employed with NONA (Goloboff, 1993), uses TBR branch swapping and saves shortest trees; this is followed by the use of random weighting, which finds shorter trees; this is then followed by TBR branch swapping, and the process is repeated. The RATCHET/NONA analyses were conducted by K. Nixon.

Parsimony jackknifing (Farris *et al.*, 1996) was used to provide estimates of internal support for clades. The version of the *Jac* program employed has a faster tree-building algorithm than the original *Jac* program, and it also performs branch swapping. In this analysis, only clades with support $\geq 50\%$ were saved; 1000 replicates were conducted and were completed in 60.63 hours. The parsimony jackknife analysis was conducted by S. Farris. Farris *et al.* (1996) considered a jackknife value of 63% to represent the breakpoint at which at least one unambiguous character supports the clade in question. Mort *et al.* (2000) determined that fast jackknife estimates are generally lower than estimates of support obtained with

standard, branch-swapping bootstrap analyses. As in previous analyses employing the jackknife (e.g. Soltis *et al.*, 1997a), we will use the following terminology to describe levels of jackknife support: weak 50–62%; moderate 63–84%; strong (or well supported) $\geq 85\%$.

RESULTS

The RATCHET/NONA quickly found trees shorter than those recovered by PAUP* 4.0d64 (Swofford, 1998). After several weeks, searches with PAUP* 4.0 found trees of 45 107 steps whereas the RATCHET found trees of length 45 101 steps (that is, six steps shorter than the trees found using PAUP*) in only a few hours, and subsequent analyses found trees of 45 100 steps. In addition to being fast, the RATCHET method makes it possible to consider large numbers of trees from multiple islands, decreasing chances of being marooned on a single island of trees and improving the reliability of the consensus of the shortest trees. For example, with the 567-taxon, three-gene data set, PAUP* found approximately 1600 trees of length 45 107, all on one island, over the course of several weeks, whereas the RATCHET recovered nearly 5000 trees of length 45 101 in approximately 24 hours. The shortest recovered trees (45 100 steps) have a consistency index of 0.12 (0.11 excluding uninformative sites) and a retention index of 0.59.

We present these results in 12 figures composed of two series (A, B). Series A is the jackknife consensus tree indicating all groups recovered in 50% or more of the replicates; series B is one of the 8000 shortest trees (the first one found in the search) with branch lengths indicated above the branches (ACCTRAN optimization) and with all clades not found in the strict consensus indicated by arrowheads. The former series indicates patterns of internal support as assessed with the jackknife, and the latter illustrates relative levels of divergence and patterns of nucleotide changes among and within lineages. In nearly all cases, lack of resolution and low internal support are associated with low levels of nucleotide change.

As is evident from series A, the trees obtained are well supported; much of the spine of the tree and most major clades receive support $\geq 50\%$. Below we discuss our results in detail, beginning with the noneudicot or basal angiosperms and then considering the eudicots and all major clades therein. The ordinal names used here correspond to those used in APG (1998) and in nearly all instances are identical in circumscription. Deviations from the APG classification (1998) are noted, and some amendments to this classification are suggested. In addition, we address the uneven pattern of molecular divergence observed in all three gene trees (see Chase *et al.*, 1993, and Savolainen *et al.*, 2000a, for the individual plastid trees; see Soltis *et al.*, 1997a, and Soltis & Soltis, 1998 for the rDNA tree), as well as in the combined trees.

DISCUSSION

For convenience and to facilitate comparison with earlier analyses (e.g. Chase *et al.*, 1993; Soltis *et al.*, 1997a; Savolainen *et al.*, 2000a), we will divide our discussion

into two portions, the first dealing with the noneudicots (including the monocotyledons) and the second with the eudicots. As reviewed in earlier analyses (e.g. Chase *et al.*, 1993; Soltis *et al.*, 1997a; Savolainen *et al.*, 2000a), the noneudicots have uniaperturate or uniaperturate-derived pollen. The eudicots have triaperturate or triaperturate-derived pollen.

Noneudicots

The noneudicots form a grade in these three-gene trees, a result similar to those obtained in analyses of morphological data (e.g. Donoghue & Doyle, 1989; Loconte & Stevenson, 1990; Nandi *et al.*, 1998) and of 18S rDNA and *atpB* sequences alone (Soltis *et al.*, 1997a; Savolainen *et al.*, 2000a). In contrast, analyses of *rbcL* (Chase *et al.*, 1993) and *rbcL/atpB* (Savolainen *et al.*, 2000a) revealed a noneudicot clade, excluding Ceratophyllaceae, which appeared as the sister to all other angiosperms in these two studies.

In this analysis, Amborellaceae are sister to all other angiosperms, followed in succession by Nymphaeaceae, and a small clade of Austrobaileyaceae/Illiciaceae/Schisandraceae. With the exception of Ceratophyllaceae, the remaining noneudicots form a weakly supported eumagnoliid clade (56%) that comprises six well-supported subclades: Chloranthaceae (hereafter Chloranthales), monocots, Piperales, Laurales, Winteraceae/Canellaceae (hereafter Winterales), and Magnoliales. Ceratophyllaceae appear as sister to the eudicots, a relationship that also receives only weak support (53%).

Early-branching taxa

Amborellaceae are the first-branching angiosperms, followed successively by a well-supported Nymphaeaceae (100%) and a strongly supported clade (100%) composed of Austrobaileyaceae as sister to Illiciaceae/Schisandraceae (100%). Analyses of *rbcL* sequence data (Renner, 1999), as well as a five gene analysis (Qiu *et al.*, 1999) and a six-gene analysis (Zanis *et al.*, submitted) focused on the noneudicots and including additional taxa indicate that Trimeniaceae are also part of this clade with Austrobaileyaceae, Illiciaceae, and Schisandraceae.

In contrast to previous analyses, the basal nodes of the tree receive internal support >50% (Figs 1, 2). The node indicating the monophyly of all angiosperms, excluding Amborellaceae, receives 65%. The node excluding the grade of Amborellaceae and Nymphaeaceae has jackknife support of 72%, and the subsequent node 71% (Fig. 1A). Although these taxa form a grade here, in some previous analyses, such as those based on *rbcL*, *rbcL/atpB*, and *rbcL/nonDNA* characters, they formed a clade (Qiu *et al.*, 1993; Nandi *et al.*, 1998; Savolainen *et al.*, 2000a). The monophyly of these taxa in some analyses prompted Savolainen *et al.* (2000a) and Nandi *et al.* (1998) to refer to them as magnoliid II, although in Nandi *et al.* Winteraceae were included in this clade.

The grade obtained here at the base of the angiosperm tree is similar to that retrieved in analyses of 18S rDNA (Soltis *et al.*, 1997a) and *atpB* sequences alone (Savolainen *et al.*, 2000a). Several recent studies provided strong support for these same first-branching angiosperms. An analysis focused on noneudicots involving five mitochondrial, plastid, and nuclear genes (total aligned length 8733 bp) similarly

demonstrated with strong support that *Amborella*, Nymphaeales, and Illiciales-Trieniaceae-*Austrobaileya* represent the first branches of angiosperm phylogeny (Qiu *et al.*, 1999). In an independent analysis of five genes representing the mitochondrial, plastid, and nuclear genomes, Parkinson *et al.* (1999) also found the same first-branching angiosperms. Significantly, levels of internal support for these first-branching angiosperms were even higher in Qiu *et al.* (1999) and Parkinson *et al.* (1999) than the values reported here. A novel approach that involved analysis of duplicate phytochrome genes (*PHYA* and *PHYC*) by Mathews and Donoghue (1999) also found a grade of these same taxa as the early-diverging angiosperms, but they were unable to include *Ceratophyllum* (due to issues of homology of the single *PHYA* copy amplified) and so their study cannot be considered a valid evaluation of the issue of the root for the angiosperms. Finally, sequences of numerous, slowly evolving plastid genes also revealed the same branching order (Graham & Olmstead, unpubl.). Thus, the basal branches of the angiosperm tree now seem clear.

Although some earlier analyses indicated Ceratophyllaceae to be the sister to all other angiosperms, the network produced in all published analyses is actually the same. That is, if the *rbcL* trees were rooted between Amborellaceae and all the rest of the angiosperms, instead of between Ceratophyllaceae and all the rest, they would produce the same result obtained here. Thus, the discrepancy between the *rbcL* tree and our three-gene tree is simply a matter of where the root is positioned. We note the frequency with which a rooting within these same first-branching taxa (Amborellaceae, Nymphaeaceae, Austrobaileyaceae/Illiciaceae/Schisandraceae) has occurred in several recent studies, whereas the Ceratophyllaceae rooting has only occurred with the *rbcL* and the *rbcL/atpB* trees. In all trees published so far (except Mathews & Donoghue, 1999, from which it is absent), *Ceratophyllum* has been an isolated genus situated as sister to a major clade of angiosperms (either all other angiosperms, the eudicots, or the monocots) and should be accorded ordinal status in future revisions of the APG classification.

Eumagnoliids

Our analyses reveal a weakly supported clade (56%) comprising all of the remaining noneudicots, except Ceratophyllaceae. This large clade, referred to here informally as the eumagnoliids, has been referred to in earlier analyses as magnoliid I (Nandi *et al.*, 1998). The eumagnoliid clade is composed of six well-supported subclades, all with jackknife support $\geq 95\%$: monocots (including *Acorus*), Winterales, Piperales, Laurales, Magnoliales, and Chloranthales. Earlier analyses of *rbcL* alone and *rbcL/atpB* indicated a similar clade of eumagnoliids, albeit without support $\geq 50\%$ (Chase *et al.*, 1993; Qiu *et al.*, 1993; Savolainen *et al.*, in press). In Chase *et al.* (1993) and Qiu *et al.* (1993), the magnoliid II grade families (see above) were embedded within the magnoliid I clade, but this eumagnoliid clade was still present. Analyses of 18S rDNA alone (Soltis *et al.*, 1997a, did not recover this eumagnoliid clade.

As noted, Nandi *et al.* (1998) referred to this core eumagnoliid group as magnoliid I, although the circumscription of this clade was not consistent in these earlier analyses. Savolainen *et al.*'s magnoliid I clade consists of Magnoliales, Laurales, Piperales, monocots, and perhaps also Winterales and Chloranthales. Our three-gene analysis strengthens the concept of a eumagnoliid clade that consists of all six of these subclades. A suite of morphological and chemical features is shared by members of the eumagnoliids (summarized in Nandi *et al.*, 1998 and Savolainen *et al.*, 2000a; Doyle & Endress, in press).

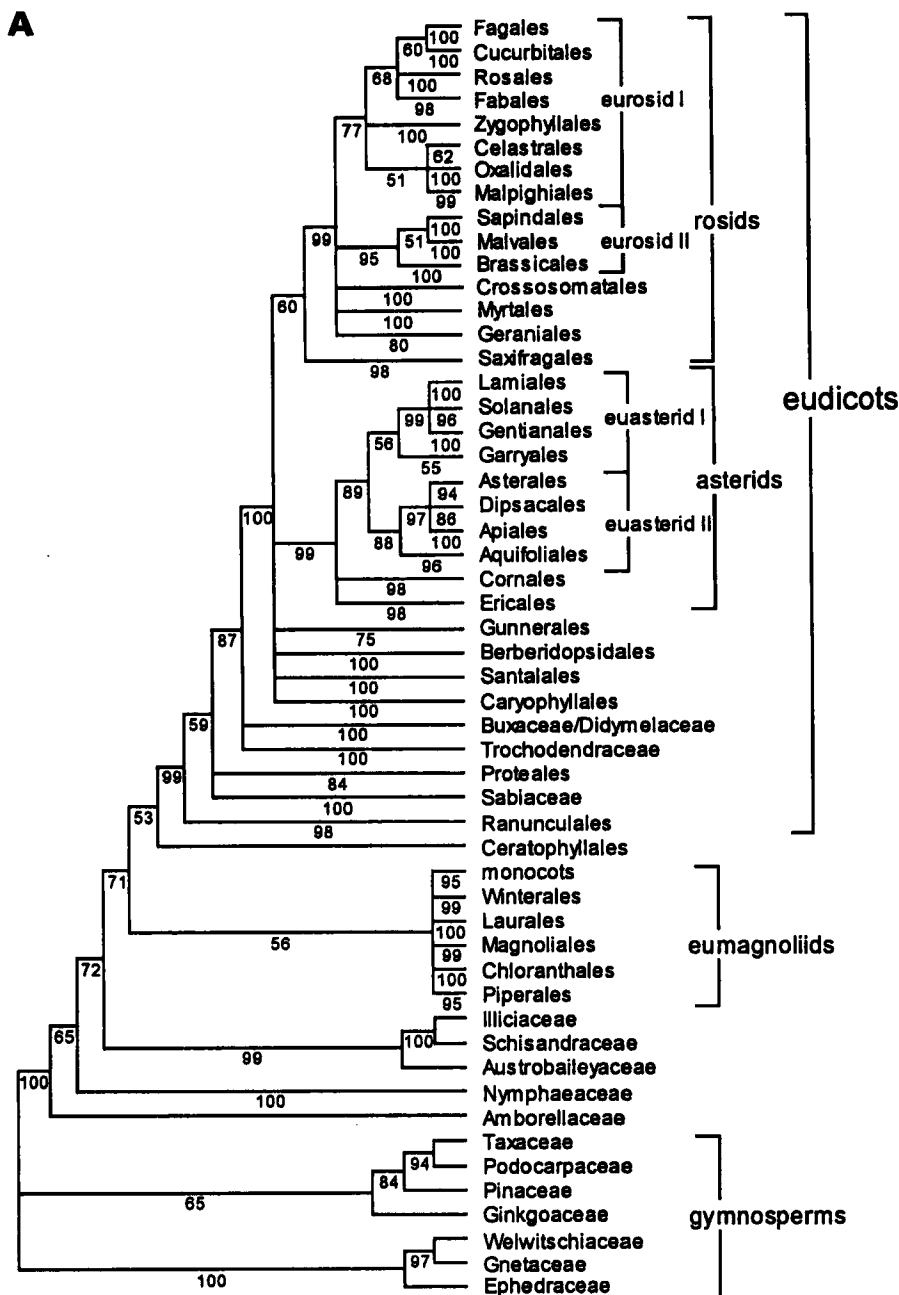
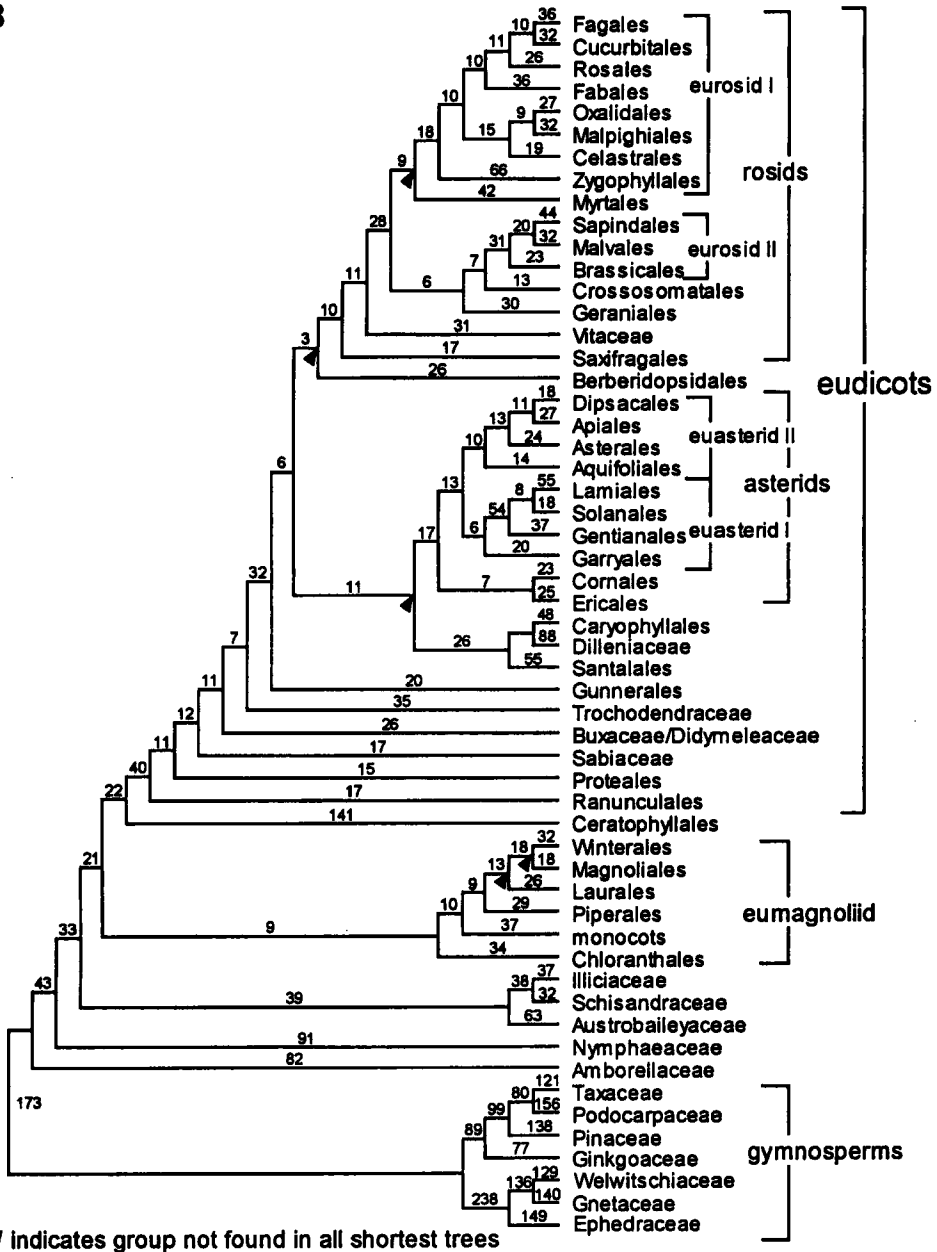


Figure 1. (A) The 'A series' of figures all illustrate the jackknife consensus tree; this first one is a summary of the major groups that occurred in greater than 50% of the 1000 jackknife replicates; orders and informal names are more or less those of the APG system (1998; see text for exceptions). The gymnosperms are not arranged to reflect relationships, but rather they were collectively specified as the outgroups without any attempt to estimate which, if any, were closest to the angiosperms.

B



(B) The 'B series' of figures illustrate one of the shortest trees from the more than 8000 shortest trees found with the ratchet method (Nixon, 2000); the first is a summary of this same single tree. Branch lengths (ACCTRAN optimization) are indicated so that patterns of character support can be discussed; clades not consistently placed in all shortest trees are marked with arrowheads. Names are those of the APG system (1998). The gymnosperms were specified as a monophyletic group sister to the angiosperms, so these relationships are not evaluated by this study.

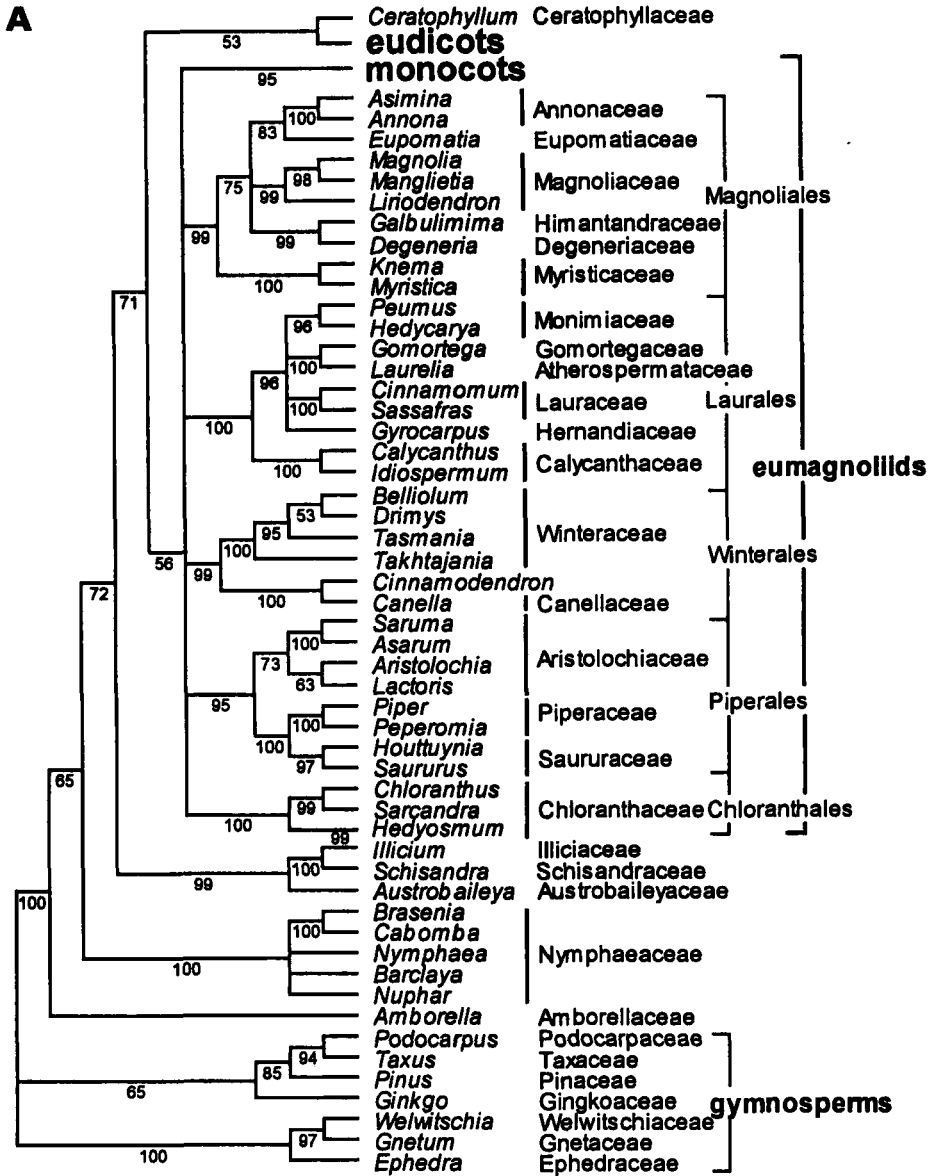


Figure 2. The jackknife consensus tree (A) focusing on the basal-most branches within the angiosperms (monocots and eudicots are shown as single terminals); (B) the same set of taxa from the single tree with branch lengths illustrated (ACCTRAN optimization); arrowheads indicate groups not found in all shortest trees. Note that Amborellaceae, Austrobaileyaceae, Ceratophyllaceae, Illiciaceae, Nymphaeaceae, and Schisandraceae are unplaced to order.

Although each of the six subclades of eumagnoliids receives strong internal support, relationships among these subclades are not clear. All of our shortest trees (Figs 1B, 2B) show Chloranthaceae as sister to the remaining subclades, followed by the monocots (including *Acorus*). However, none of these placements receives support $\geq 50\%$. The remaining four subclades (Piperales, Laurales, Winterales, and Magnoliales) form an unresolved polytomy.

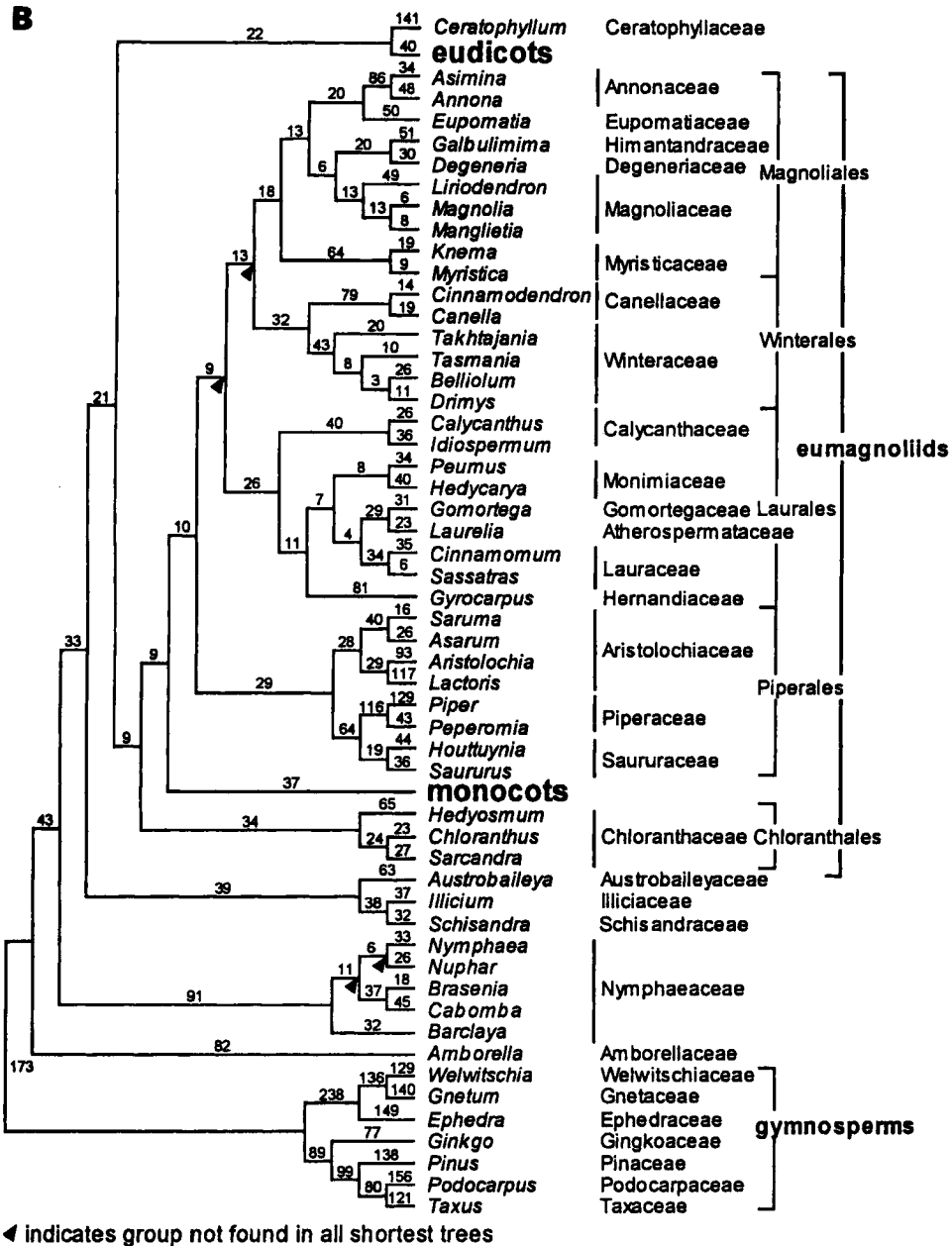


Figure 2. See caption on facing page.

Chloranthaceae, represented here by three genera, from a strongly supported clade (100%) that is sister to the remaining eumagnoliid clade (justifying elevation to Chloranthales). The monocots also form a well-supported clade (95%), which is discussed in more detail below. Piperales comprise two well-supported sister groups, Aristolochiaceae, including *Lactoris* (72%), and Saururaceae/Piperaceae (100%). Within Laurales, a clade of Calycanthaceae (100%) is sister to the remainder of the

clade; the remaining Laurales form a strongly supported clade (96%) consisting of Hernandiaceae, Monimiaceae, Lauraceae, Gomortegaceae and Athero-spermataceae. Canellaceae and Winteraceae are sister groups and form a well-supported clade (100%) that should be accorded ordinal status (Winterales) in future revisions of the APG classification. Of the four genera of Winteraceae sampled, *Takhtajania* is sister to the rest, in agreement with more thorough analyses using additional genes and involving all genera of Winteraceae (Zimmer *et al.*, in prep). Magnoliales consist of Myristicaceae as sister to a moderately well-supported subclade (75%) of Eupomatiaceae/Annonaceae (83%), Degeneriaceae/Himantandraceae (100%), and Magnoliaceae (99%).

Monocots. The relationships among the monocots discussed here are consistent with those of Chase *et al.* (2000), who provided a phylogenetic analysis of the monocots that is based on these same three genes (18S rDNA, *rbcL*, *atpB*). However, Chase *et al.* employed a larger sampling of monocot taxa. To increase taxon density and place problematic monocots, Chase *et al.* also included exemplars of additional families sequenced for only one or two of these three genes (for example, sequences for the plastid genes *atpB* and *rbcL* could not be obtained for some achlorophyllous taxa; hence, only 18S rDNA was used). Chase *et al.* (2000) presented the most thorough phylogenetic analysis of monocots so far undertaken.

A well-supported sister group for the monocots is not identified here. However, our results place the monocots in a large clade with Chloranthales first-branching, followed by the monocots, which in turn are sister to Piperales, Laurales, Winterales, and Magnoliales. This analysis is the first to provide any measure of internal support for this large clade (eumagnoliids). If the shortest trees are accurate, then the sister group of the monocots is a clade composed of both woody and herbaceous taxa rather than a single family or order. The similarities of the monocots to taxa such as Aristolochiaceae and Chloranthaceae likely developed in parallel rather than through common ancestry.

The monocots form a well-supported clade (95%; Fig. 3A). Following *Acorus*, the monophyly of the remaining monocots is also strongly supported by a jackknife of 99%. After *Acorus*, a strongly supported (99%) Alismatales appear as the sister to the remaining monocots. Alismatales, including Tofieldiaceae, Araceae, and a strongly supported (100%) subclade of Zosteraceae, Hydrocharitaceae and Aponogetonaceae, are sister to the remaining monocots. These remaining monocots also form a well-supported clade (99%) and, in turn, comprise several subclades, all with jackknife support $\geq 50\%$, that correspond to the circumscriptions given in APG (1998) and Chase *et al.* (2000): commelinoids (68%); Dioscoreales (96%), Petrosaviaceae (99%; including *Japonolirion*, as in Chase *et al.*, 2000), Pandanales (99%), Liliales (84%), and Asparagales (56%). Relationships among these major subclades of monocots do not receive jackknife support $\geq 50\%$, and in the strict consensus of all shortest trees, the relationships of Asparagales, Dioscoreales, Liliales, Pandanales, and commelinoids are unresolved (Fig. 3B). In contrast, in the analyses of Chase *et al.* (2000) the branching order above Alismatales in all shortest trees is: Dioscoreales, Pandanales, Liliales, and Asparagales/commelinoids.

Our interpretation of this different result with similar, although not identical, sampling is that in the present larger analysis we have not obtained the shortest trees for the monocot portion of the tree. However, it is also possible that the additional taxa in Chase *et al.* (2000) caused a greater level of resolution. The major

issue for this analysis is that our results do not contradict those of Chase *et al.* (2000), and those of the latter are highly similar to previous analyses of *rbcL* alone for the monocots (Duvall *et al.*, 1993; Chase *et al.*, 1995). The tree illustrated here (Fig. 3B) is in agreement with the strict consensus tree of Chase *et al.* (2000), and the lack of resolution is again centred around the shortest branches (all of these have 10–16 steps whereas those branches nearby with jackknife support all have 21 or more steps; Fig. 3B), leading us to conclude that obtaining a robust assessment of the branching order simply requires more data.

The monophyly of Asparagales receives low jackknife support (56%; Fig. 3A), but if the Orchidaceae clade (Fig. 3B; Asteliaceae, Blandfordiaceae, Boryaceae, Hypoxidaceae, and Orchidaceae) is excluded, then support for the rest of Asparagales rises to 81%. Even though there is weak support for inclusion of the orchid clade in Asparagales, in the strict consensus of the shortest trees the orchid clade is not associated with the rest of Asparagales. In contrast, in all shortest trees found in Chase *et al.* (2000), the orchid clade is associated with the rest of Asparagales, but again Asparagales receive only weak support (56% bootstrap). In Fay *et al.* (2000) who employed *rbcL*, *atpB*, and *trnL-F* sequences, Asparagales received strong support (87% bootstrap), although the number of outgroups used was not as great as here. Within Asparagales, however, there is considerable structure, with many relationships receiving jackknife support $\geq 50\%$. As noted, with the exception of the orchid clade, the remaining families of Asparagales form a moderately supported clade (81%). Within this large core of Asparagales, Ixioliriaceae appear as sister to Tecophilaeaceae (55%). These two families are, in turn, sister to a clade (73%) that includes Iridaceae, Xeronemataceae, Anthericaceae, Behniaceae, Agavaceae, Laxmanniaceae, Asphodeliaceae, Xanthorrhoeaceae, Amaryllidaceae, Alliaceae, Asparagaceae, Hyacinthaceae and Convallariaceae. After the analysis was completed, it was noticed that the taxon labelled in the matrix as '*Luzuriaga*' fell within Asparagales; the *rbcL* sequence alone for this terminal appears in Liliales (as in Chase *et al.*, 1995). The identity of the specimen used for the *atpB* and 18S rDNA sequences was originally determined to be *Luzuriaga latifolia* (W. Hahn, pers. comm.), which is now known to be a member of genus *Eustephus* (*E. latifolius*), a member of Laxmanniaceae. Luzuriagaceae and Laxmanniaceae are members of Liliales and Asparagales, respectively (Rudall *et al.*, 1997). We could not correct this problem without repeating the entire analysis, which we felt was unwarranted due to the minor nature of this problem and the great length of time involved in reanalyzing data sets of this size. The most likely effect of this misidentification would be lowering of jackknife support within Asparagales; Chase *et al.* (2000) excluded this 'hybrid' sequence, and it is possible that this conflicting signal in our study is one reason why Asparagales are not resolved as monophyletic in the strict consensus tree. Other noteworthy relationships within Asparagales include Agavaceae/Anthericaceae/Behniaceae (100%), Asphodeliaceae/Xanthorrhoeaceae (76%), and Convallariaceae, including *Nolina* and *Ruscus* (100%).

Liliales are strongly supported (96%) and comprise three well-supported subclades: Melanthiaceae, including *Trillium* (100%), Alstroemeriaceae/Colchicaceae (100%), and Smilacaceae/Liliaceae (100%). In addition to *Lilium*, Liliaceae (97%) here include the sampled genera *Clintonia*, *Scoliopus*, and *Tricyrtis*, all of which have sometimes been included in separate families.

Burmanniaceae, Taccaceae, and Dioscoreaceae form a well-supported (96%)

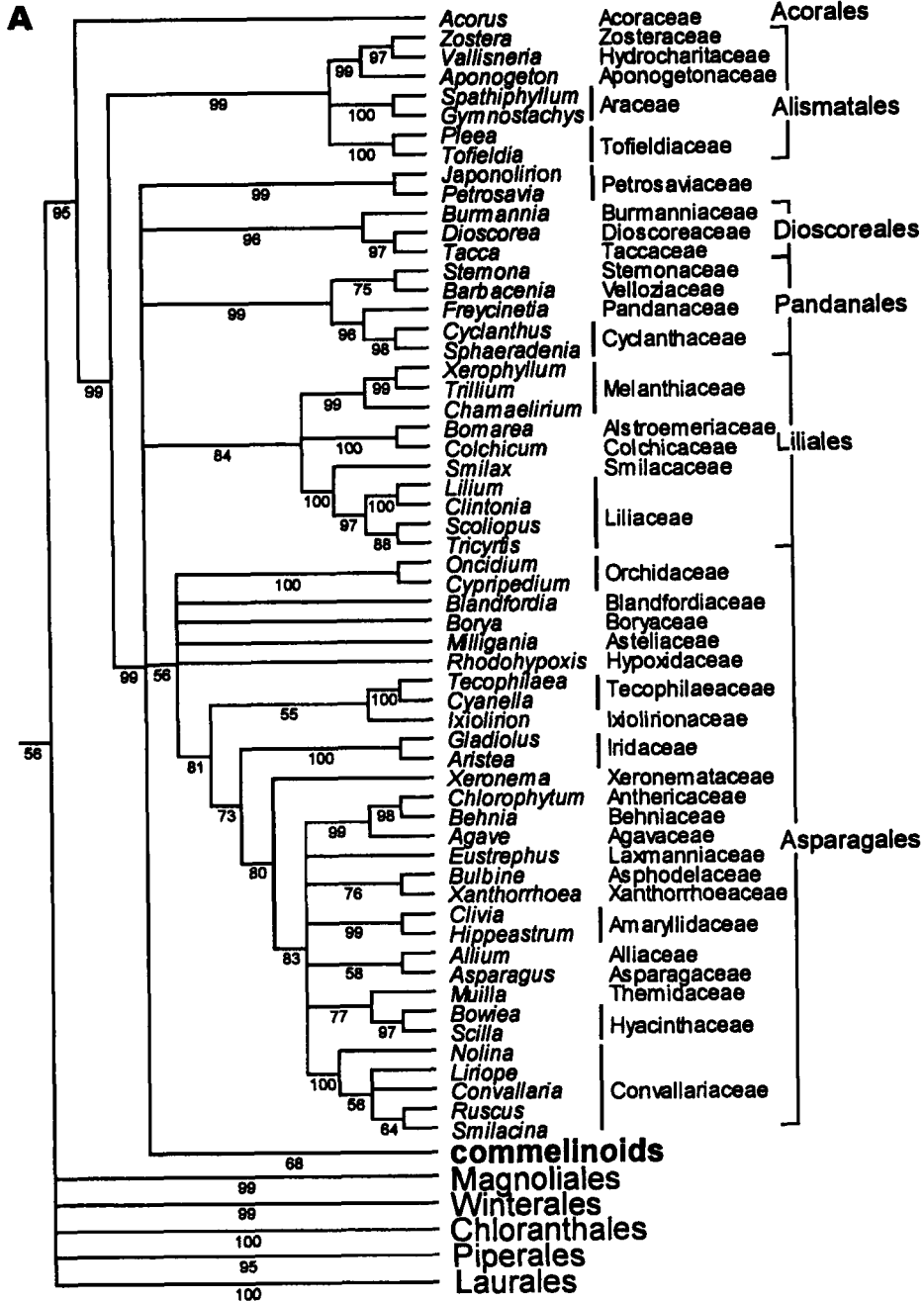


Figure 3. The jackknife consensus tree (A) focusing on the basal-most branches within the monocots and nearest eumagnoliid relatives; (B) the same set of taxa from the single tree with branch lengths illustrated (ACCTRAN optimization); arrowheads indicate groups not found in all shortest trees. The commelinoid orders and families are represented as a single terminal. Note that Petrosaviaceae are unplaced to order.

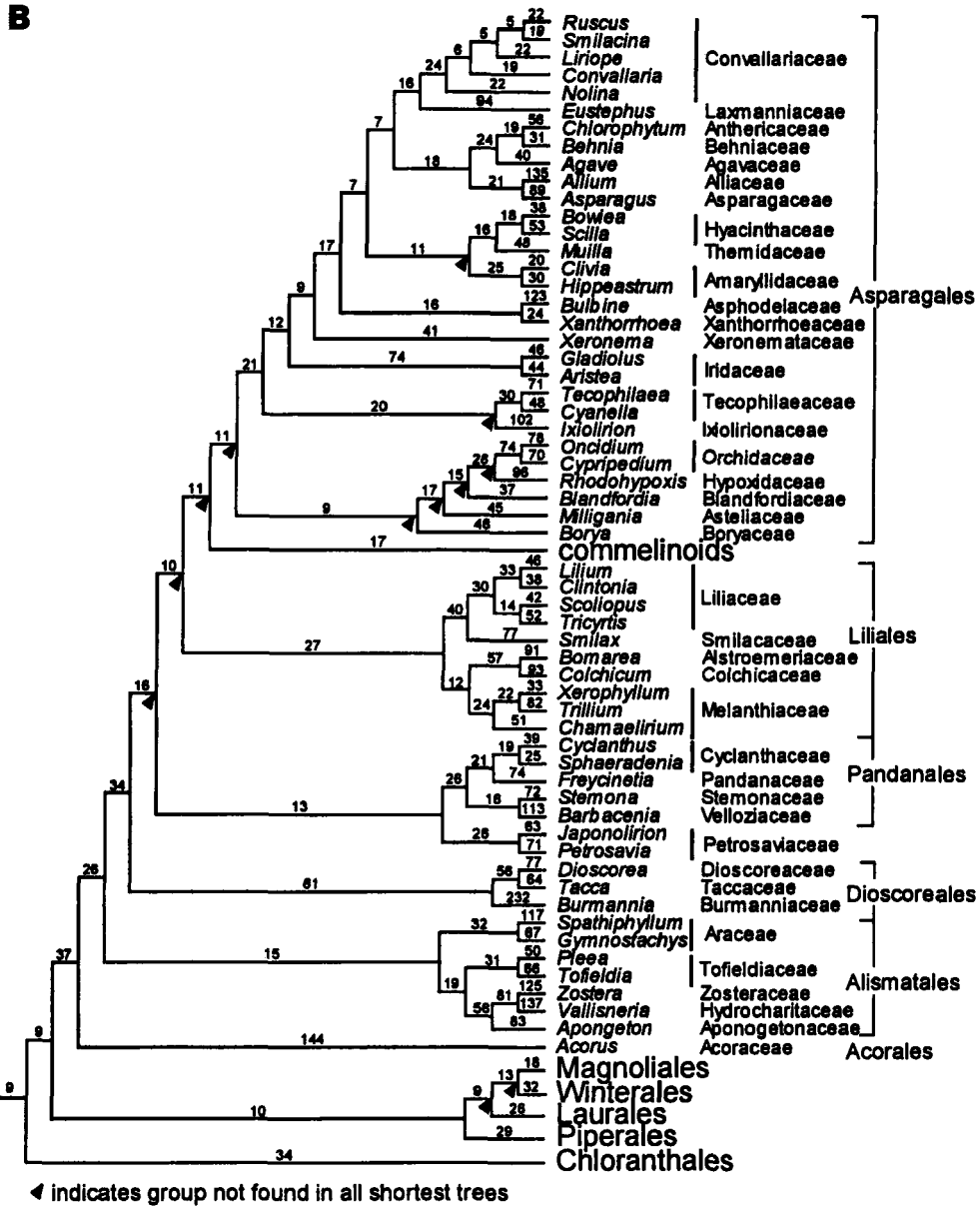


Figure 3. See caption on facing page.

Dioscoreales. Pandanales are also strongly supported (99%), consisting of Velloziaceae/Stemonaceae (75%) as sister to a strongly supported clade (96%) of Pandanaceae/Cyclanthaceae. *Sciaphila* (Triuridaceae) also appears to be a member of this clade (Chase *et al.*, 2000), although this placement is based only on an 18S rDNA sequence because plastid loci failed to amplify.

The commelinoids form a large clade with jackknife support of 68% (Fig. 4A). Within this clade, a tetrachotomy exists in the jackknife tree of: (1) Poales plus Bromeliaceae (98%); (2) Commelinales/Zingiberales (82%); (3) Arecaceae (100%);

and (4) Dasypogonaceae (100%). Hence, several critical relationships remain unsupported in the commelinoids. The branching order in all shortest trees is: Areaceae, Dasypogonaceae, and Commelinales/Zingiberales as sister to Poales plus Bromeliaceae. As above, the branches with support <50% have just slightly fewer optimised substitutions (13–16 steps) than those that are supported at $\geq 50\%$ (16 or more steps), so it would appear again that obtaining a well-supported tree will require only slightly more information. Within some of the subclades of commelinoids, however, there is considerable phylogenetic structure. Both Bromeliaceae and Poales are monophyletic (100% and 67% jackknife values, respectively); Chase *et al.* (2000) recommended including Bromeliaceae within Poales. Within this order, Sparganiaceae are sister to the remaining families, which are strongly supported as a clade (86%). Within this core of Poales, Xyridaceae are the sister to Juncaceae/Cyperaceae (86%), and Flagellariaceae and Restionaceae are supported as successive sisters to Poaceae. The sisters (82%) Commelinales and Zingiberales are each strongly supported as monophyletic (jackknife values of 95% and 100%, respectively). Within Commelinales, a well-supported clade (95%) of Commelinaceae/Pontederiaceae is sister to Philydraceae. Within Zingiberales, the monophyly of each family is supported, but the only interfamilial relationship to receive jackknife support $\geq 50\%$ is Lowiaceae/Strelitziaceae (96%). Each of the families is highly divergent from the others, but all branches connecting them are extremely short (6–13 steps; Fig. 4B), which probably is why support is lacking for these relationships.

Ceratophyllaceae

As noted above, Ceratophyllaceae have attracted considerable attention in previous molecular analyses due to their appearance as the sister to all remaining angiosperms (e.g. Chase *et al.*, 1993; Savolainen *et al.*, 2000a). In contrast, other genes alone, such as 18S rDNA and *atpB*, have indicated different placements for this enigmatic family. The 18S rDNA data (Soltis *et al.*, 1997a) placed Ceratophyllaceae as sister to the monocots and *atpB* sequence data (Savolainen *et al.*, 2000a) indicated a similar position (sister to *Acorus*; the two together are in turn sister to the monocots). The five-gene analysis of Qiu *et al.* (1999) similarly suggested a close relationship of *Ceratophyllum* with monocots, albeit without strong support. With a more complete set of monocot *atpB* sequences than were used in Savolainen *et al.* (2000a), Ceratophyllaceae are excluded from the monocots and fall as sister to the eudicots (Chase, unpubl.). In this three-gene analysis, Ceratophyllaceae are sister to the eudicots, a relationship that receives only weak jackknife support (53%; Fig. 2A). At this point, therefore, the position of *Ceratophyllum* is uncertain, although the recent six-gene analysis of Zanis *et al.* (submitted) placed *Ceratophyllum* with the monocots with strong support.

Eudicots

The monophyly of the eudicots is strongly supported (100%; fig. 5A). Whereas previous studies using individual genes have all retrieved a eudicot clade (e.g. Chase *et al.*, 1993; Soltis *et al.*, 1997a; Savolainen *et al.*, 2000a), only *rbcL* has provided jackknife support $\geq 50\%$ (72%; Savolainen *et al.*, 2000a). Combining *rbcL* and *atpB* (Soltis *et al.*, 1998; Savolainen *et al.*, 2000a) also provided only moderate support for

the monophyly of the eudicots (73%). Analysis of three genes, however, has established the monophyly of the eudicots with a high degree of confidence (100%; see also Soltis *et al.*, 1998 and Hoot *et al.*, 1999). Some of the morphological features, in addition to triaperturate pollen, that are shared by many eudicots are reviewed in Nandi *et al.* (1998) and Savolainen *et al.* (2000a).

Within the eudicot clade is a basal grade (Figs 1, 2) followed by a strongly supported clade (100%) of 'core' eudicots. The early-diverging eudicots and core eudicots are discussed, in turn, below.

Early-diverging eudicots

The relationships reported here for the lower eudicots are consistent with those of Hoot *et al.* (1999), who employed the same three genes but different sampling. The early-diverging eudicots are Ranunculales, Proteales, Sabiaceae, Didymelaceae/Buxaceae, and Trochodendraceae (including *Tetracentron*, Figs 1A, B; 5A, B). A well-supported Ranunculales (98%) are sister to the remaining eudicots, but the monophyly of all remaining eudicots receives low jackknife support (59%). Proteales (85%) and Sabiaceae (99%) are both well supported and follow Ranunculales. The monophyly of all remaining eudicots receives high jackknife support (87%); two small clades then appear as successive sister groups to the core eudicots, Didymelaceae/Buxaceae (100%) and Trochodendraceae (including *Tetracentron*; 100%). This grade of early-diverging eudicots agrees with previous analyses (Chase *et al.*, 1993; Soltis *et al.*, 1997a; Qiu *et al.*, 1998; Savolainen *et al.*, 2000a, b), although the Hoot *et al.* (1999) analysis and this study are the first to provide internal support $\geq 50\%$ for many of these relationships, particularly along the spine of the tree (Fig. 5A).

Ranunculales have appeared as the first-branching eudicots in separate analyses of 18S rDNA (Soltis *et al.*, 1997a), *rbcL* (Chase *et al.*, 1993), and *atpB* (Savolainen *et al.*, 2000a) sequences. Ranunculales are represented here by Ranunculaceae, Berberidaceae, Eupteleaceae, Menispermaceae, Circaeasteraceae, Lardizabalaceae (including *Sargentodoxa*) and Papaveraceae. These results further confirm the position of *Sargentodoxa* within Ranunculales; the placement of *Sargentodoxa* near Fabaceae in Chase *et al.* (1993) was based on misidentified plant material (see Hoot *et al.*, 1995b; Soltis *et al.*, 1997a). Relationships within Ranunculales are also well resolved and generally strongly supported. Papaveraceae appear as sister to the remaining Ranunculales, which form a weakly supported core (53%). Eupteleaceae are sister to the remaining taxa, which form a strongly supported monophyletic group (99%). Lardizabalaceae are a strongly supported clade (100%) that forms a trichotomy with Circaeasteraceae (100%) and a clade (70%) of Menispermaceae, Berberidaceae, and Ranunculaceae; a clear sister-group relationship is indicated for Berberidaceae and Ranunculaceae (92%). These results are in general agreement with other recent analyses involving Ranunculales (e.g. Hoot & Crane, 1995; Hoot *et al.*, 1999).

Proteales are strongly supported (85%), comprising three families nearly always previously considered distantly related: Proteaceae, Platanaceae, and Nelumbonaceae. Within this clade, Nelumbonaceae are sister to the strongly supported (93%) sister pair of Platanaceae and Proteaceae. A close relationship among these three families was previously indicated by separate analyses of *rbcL*, *atpB*, and 18S rDNA sequences, albeit without support $\geq 50\%$ except for 60% with *atpB/rbcL* combined (Chase *et al.*, 1993; Soltis *et al.*, 1997a; Savolainen *et al.*, 2000a, b); *rbcL* and *atpB* each identified a Proteales clade; 18S rDNA showed a grade for these

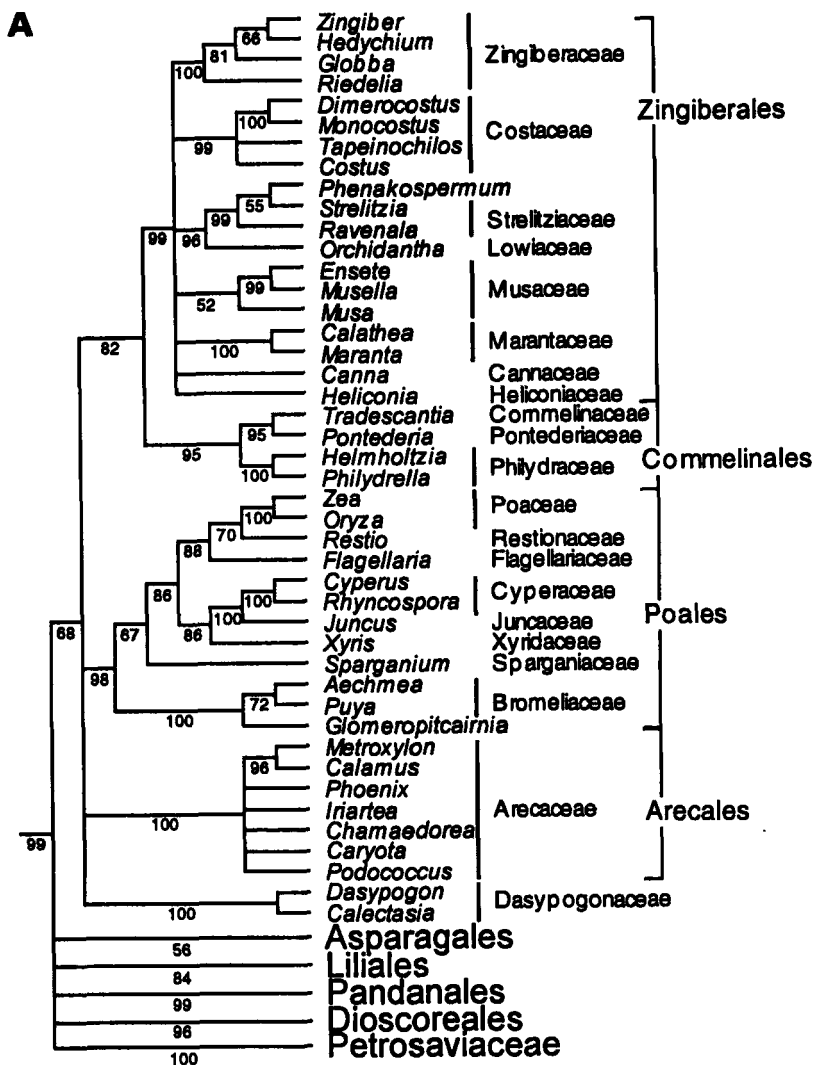


Figure 4. The jackknife consensus tree (A) focusing on the commelinoid monocots; (B) the same set of taxa from the single tree with branch lengths illustrated (ACCTRAN optimization); arrowheads indicate groups not found in all shortest trees. Note that Dasypogonaceae are unplaced to order.

families. Although the composition of Proteales has to be one of the major surprises of molecular phylogenetics, this study and Hoot *et al.* (1999) provide very strong support for this clade; furthermore, the monophyly of this clade is supported by several morphological and anatomical features (Nandi *et al.*, 1998; Savolainen *et al.*, 2000a).

The monophyly of Sabiaceae is strongly supported (99%); however, the placement of Sabiaceae relative to Proteales is not well supported in our three-gene analysis (Fig. 5A) or in Hoot *et al.* (1999). In all shortest trees, Proteales branch first, followed by Sabiaceae, but this relationship receives support <50%. Earlier analyses based on the individual genes (18S rDNA, *rbcL*, and *atpB*) also indicated a close placement

B

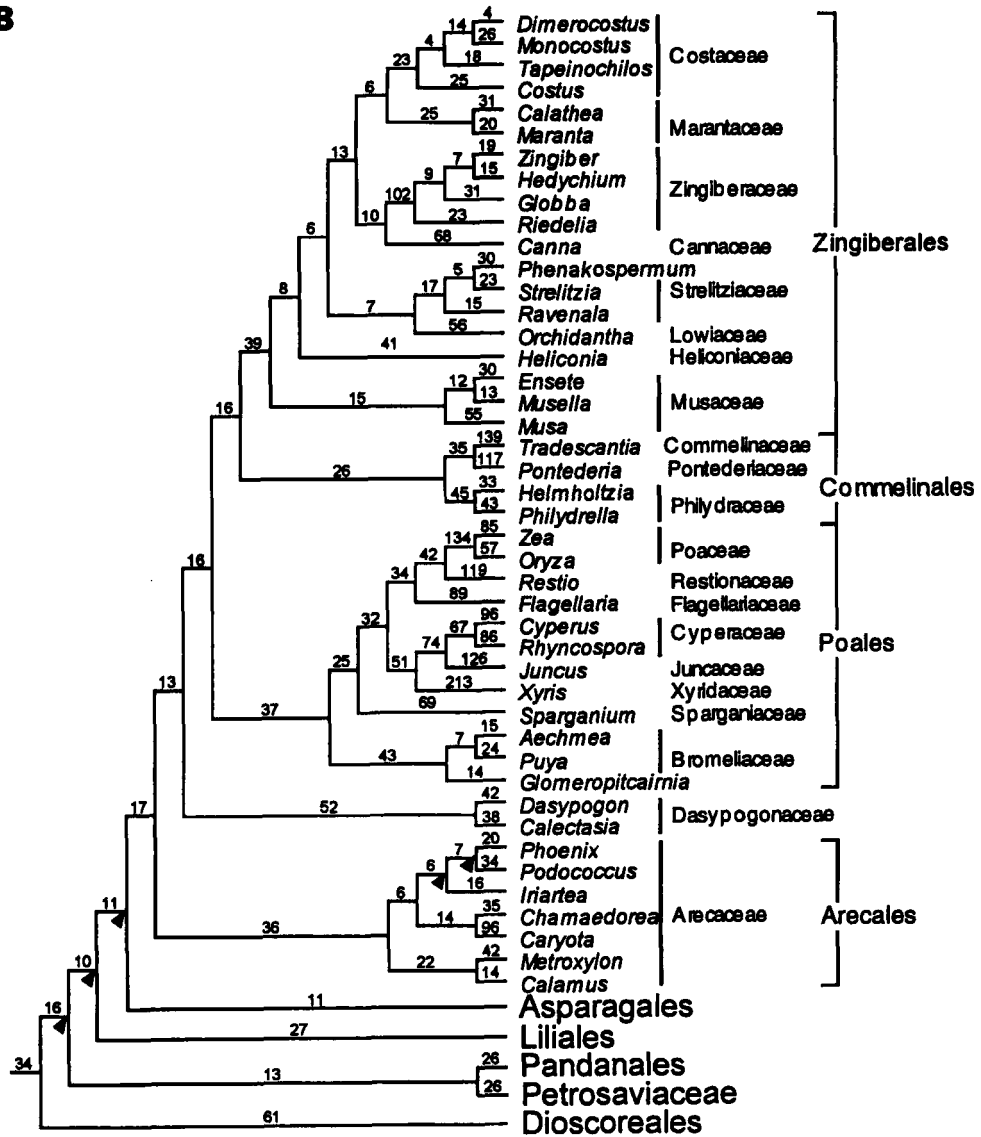


Figure 4. See caption on facing page.

of Sabiaceae and Proteales, although it has never been clear whether they are a clade or grade (Chase *et al.*, 1993; Savolainen *et al.*, 2000a, b; Soltis *et al.*, 1997a).

Didymelaceae/Buxaceae and Trochodendraceae (including *Tetracentron*) complete the early-diverging eudicot grade (Fig. 5; the recent APG classification combined Trochodendraceae and Tetracentraceae into a single family, Trochodendraceae). The monophyly of Didymelaceae/Buxaceae and Trochodendraceae is each strongly supported (100%), in agreement with previous broad analyses. The placement of these families in an unresolved trichotomy with the core eudicots receives strong jackknife support (87%), but in all shortest trees Trochodendraceae alone are sister

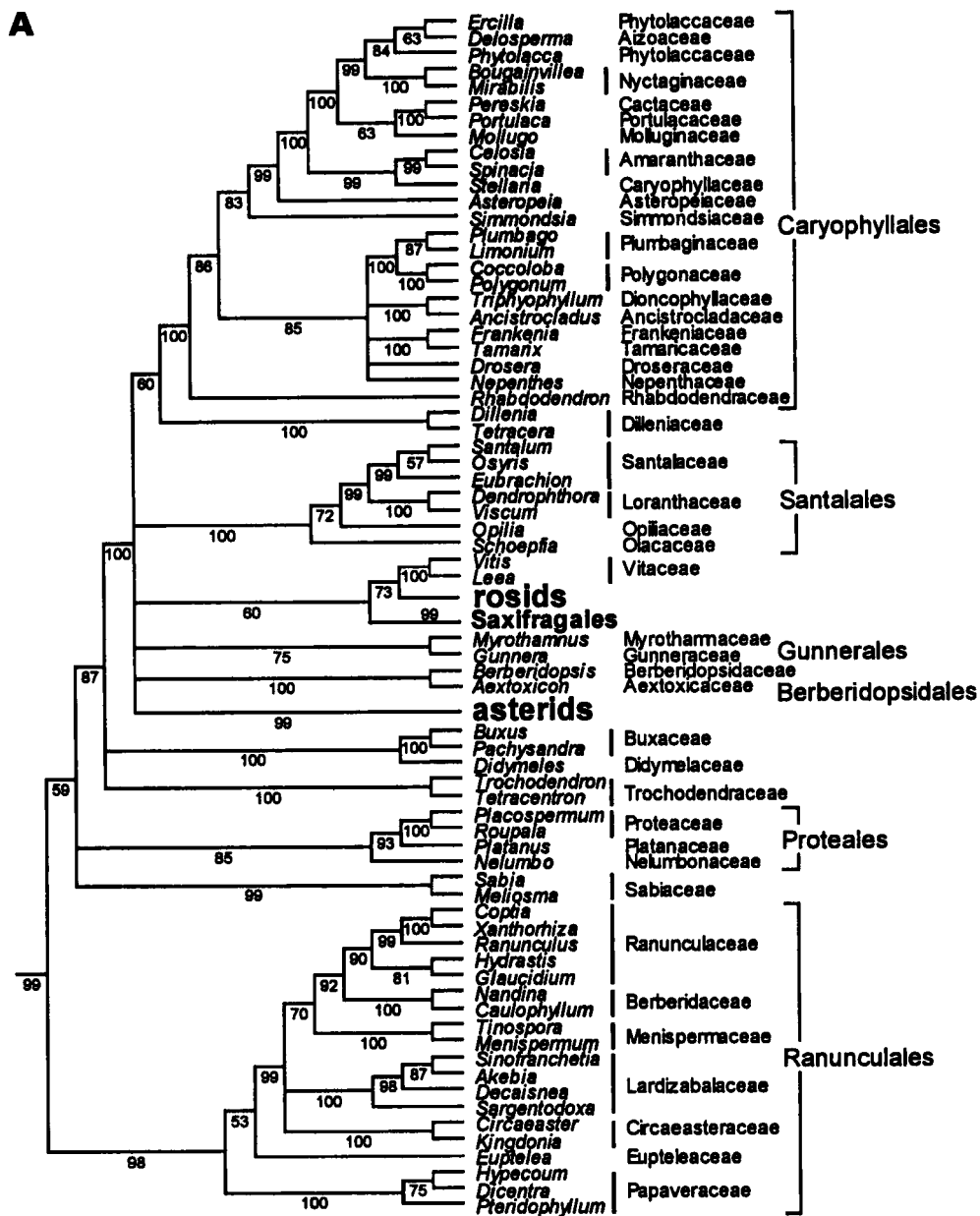


Figure 5. The jackknife consensus tree (A) focusing on the basal-most groups of eudicots; (B) the same set of taxa from the single tree with branch lengths illustrated (ACCTRAN optimization); arrowheads indicate groups not found in all shortest trees. Asterisks and rosids (as well as Saxifragales) as illustrated as single terminals. Note that Buxaceae, Didymelaceae, Dilleniaceae, Sabiaceae, Trochodendraceae, and Vitaceae are unplaced to order.

to the core eudicots (Fig. 5B); the exact relationship between Didymelaceae/Buxaceae and Trochodendraceae fails to receive greater than 50% jackknife support (Fig. 5B see also Hoot *et al.*, 1999). Phylogenetic trees based on *atpB*, as well as *atpB/rbcL*,

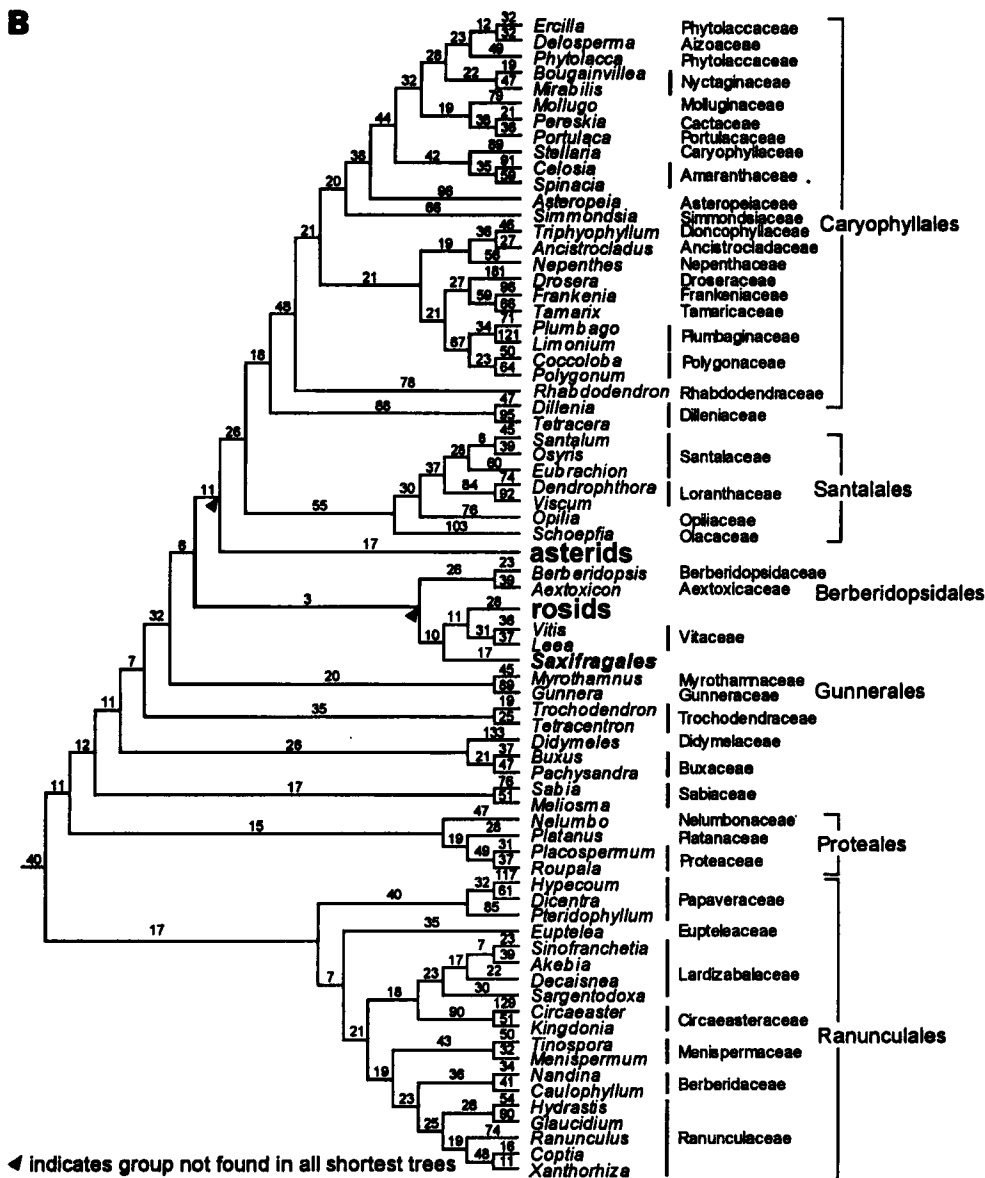


Figure 5. See caption on facing page.

produced the same relationships found here (Savolainen *et al.*, 2000a), whereas, in contrast, *rbcL* alone retrieved a clade of Didymelaceae/Buxaceae and Trochodendraceae (Qiu *et al.*, 1998; Savolainen *et al.*, 2000a, b); 18S rDNA alone also revealed a grade of Buxaceae followed by Trochodendraceae as sister to all remaining angiosperms, but Didymelaceae were not included (Soltis *et al.*, 1997a).

Core eudicots

Monophyly of the core eudicots is strongly supported (100%; Fig. 5A). Whereas previous broad analyses that have employed 200 or more taxa have all indicated

the monophyly of the core eudicots, only combined *atpB/rbcL* has provided strong support for this clade (91%; Savolainen *et al.*, 2000a). A number of morphological and chemical features is shared by most core eudicots, including ellagic acid (replaced in the core asterids, euasterid I and II, by iridoids and other compounds), non-laminar/marginal placentation and calyx/corolla differentiation; these features are discussed in Nandi *et al.* (1998) and Savolainen *et al.* (2000a).

The core eudicot clade comprises six subclades, each receiving jackknife support $\geq 50\%$: (1) Berberidopsidales (composed of only Berberidopsidaceae and Aextoxicaceae); (2) Gunnerales (Myrothamnaceae and Gunneraceae); (3) Saxifragales/Vitaceae (including *Leea*)/eurosids; (4) Santalales; (5) Dilleniaceae/Caryophyllales; and (6) asterids (Figs 1A, 5A). Although the monophyly of each of these six subclades is well supported, relationships among them are not clear. Our shortest trees indicate that Gunneraceae/Myrothamnaceae are sister to the remaining core eudicots, followed by Berberidopsidaceae/Aextoxicaceae (Figs 1B, 5B). Santalales appear as the sister group to Dilleniaceae/Caryophyllales, all of which are in turn sister to the asterids. This large Santalales plus Dilleniaceae/Caryophyllales plus asterid clade is, in turn, sister to the large Saxifragales/Vitaceae/eurosid clade (Figs 1B, 5B). Resolving relationships among these six clades of core eudicots now represents one of the major remaining questions of phylogenetic inference in the angiosperms. Each of these six clades is discussed below, but because of their small size, Berberidopsidaceae/Aextoxicaceae and Myrothamnaceae/Gunneraceae are discussed together.

Berberidopsidaceae/Aextoxicaceae; Myrothamnaceae/Gunneraceae. The sister pairs Berberidopsidaceae/Aextoxicaceae and Myrothamnaceae/Gunneraceae each receive support $\geq 50\%$ (100% and 75%, respectively; Figs 1A, 5A). A close relationship between the members of each sister pair was indicated in recent molecular phylogenetic analyses (e.g. Hoot *et al.*, 1999; Qiu *et al.*, 1998; Savolainen *et al.*, 2000a, b). However, phylogenetic analysis of non-DNA characters, including chemistry, morphology and anatomy (Nandi *et al.*, 1998), indicated that Myrothamnaceae, Didymelaceae, and Buxaceae form part of a small clade that also includes Proteaceae and Platanaceae, whereas Gunneraceae appear within the asterids. As noted, our shortest trees indicate that Gunneraceae/Myrothamnaceae are the sister to the remaining core eudicots, followed by Berberidopsidaceae/Aextoxicaceae, but none of these phylogenetic positions receives jackknife support $\geq 50\%$. However, these two pairs of monogeneric families (Berberidopsidaceae are sometimes split into two genera, *Berberidopsis* and *Streptothamnus*) are strongly excluded from all other higher eudicot clades (Fig. 2A), reinforcing the impression of their isolated status. It is thus most appropriate to treat them both as orders, Berberidopsidales and Gunnerales. Recent analyses of *rbcL*, *atpB*, and *rbcL/atpB* sequences similarly indicated that at least some of these taxa are early-branching core eudicots (e.g. Qiu *et al.*, 1998; Savolainen *et al.*, 2000a). For example, analyses of combined *rbcL/atpB* (Savolainen *et al.*, 2000a) sequences and a much smaller (75 taxa) data set of *rbcL/atpB*/18S rDNA sequences similarly placed Gunneraceae/Myrothamnaceae as sister to all other core eudicots.

Santalales. Santalales form a well-supported clade (100%), in agreement with a number of previous phylogenetic analyses (e.g. Chase *et al.*, 1993; Soltis *et al.*, 1997a; Savolainen *et al.*, 2000a, b; Nickrent *et al.*, 1998). The composition of Santalales revealed here agrees with those earlier studies. Included in our analysis are Olacaceae,

which appear as sister to a clade (72%) of Opiliaceae and a broadly defined Santalaceae (including Viscaceae); Loranthaceae and Misodendraceae were not sampled in this study. More detailed analyses of relationships within Santalales are provided by Nickrent *et al.* (1998).

Whereas the monophyly of Santalales is strongly supported (100%), the relationships of the order to other core eudicots remain unclear. In our shortest trees, Santalales are sister to a clade of Dilleniaceae plus Caryophyllales, but without support $\geq 50\%$. This large clade is, in turn, sister to the asterids, but again without support $\geq 50\%$. The position of Santalales has varied in each broad phylogenetic survey so far conducted; placement of Santalales even differed between the two *rbcL* searches conducted by Chase *et al.* (1993). Search 1 placed Santalales within the asterid clade, with *Paonia* and *Gunnera* (asterid V), whereas search 2 placed Santalales as sister to the caryophyllids. Analysis of *atpB/rbcL* sequences (Savolainen *et al.*, 2000a) placed Santalales as sister to Dilleniaceae, and these two clades together were, in turn, sister to the asterids. There are, therefore, some similarities and overlap among these analyses. Santalales and Caryophyllales may indeed be related and in turn closely related to asterids. However, additional characters (e.g. sequences from an additional gene or genes) will be needed to address these questions adequately (see below). The lack of a stable placement for both Santalales and Caryophyllales is largely due to the short branches in the core eudicots (only 3–6 steps; Fig. 5B).

Dilleniaceae/Caryophyllales. Dilleniaceae appear as the sister to a broadly defined caryophyllid clade (or Caryophyllales *sensu* APG, 1998) with 60% jackknife support (Fig. 5A); the monophyly of Caryophyllales is also strongly supported (100%) by our three-gene analysis. Several previous analyses similarly placed Dilleniaceae as sister to this clade. For example, search 2 of Chase *et al.* (1993) placed Caryophyllales together with Dilleniaceae, but without support $\geq 50\%$ (Chase & Albert, 1998). However, analyses of a combined *rbcL/atpB* data set did not place Dilleniaceae with Caryophyllales (Savolainen *et al.*, 2000a).

A broadly defined Caryophyllales has been indicated by all previous large analyses of angiosperms, but with strong support only in Savolainen *et al.* (2000a; *rbcL* with 84% bootstrap, *atpB* with 74%, and combined *rbcL/atpB* with 97%). Such an expanded concept of the order has not been suggested in any previous classification, even though a number of chemical, morphological, and anatomical features link the members of this group (Nandi *et al.*, 1998), and many of these same satellite families formed a clade with the core Caryophyllales in the results of the non-molecular analyses in Nandi *et al.* (1998).

In our analyses, Caryophyllales have Rhabdodendraceae as sister to the rest of the clade (Ledó *et al.*, 1998), the monophyly of which is strongly supported (86%). The remainder of Caryophyllales comprises two well-supported clades: (1) Dioncophyllaceae, Ancistrocladaceae, Droseraceae, Nepenthaceae, Frankeniaceae, Tamaricaceae, Plumbaginaceae and Polygonaceae (85%); and (2) Phytolaccaceae, Aizoaceae, Nyctaginaceae, Cactaceae, Portulacaceae, Molluginaceae, Amaranthaceae, Caryophyllaceae (Caryophyllales *sensu* Cronquist, 1981), Asteropeiaceae and Simmondsiaceae (83%). Within the first of these two clades, several strongly supported sister pairs are evident: Dioncophyllaceae/Ancistrocladaceae (100%), Frankeniaceae/Tamaricaceae (100%) and Plumbaginaceae/Polygonaceae (100%). In the second of the two major clades, Simmondsiaceae are sister to a well-supported clade (100%) of Asteropeiaceae and a core clade of Phytolaccaceae, Aizoaceae,

Nyctaginaceae, Cactaceae, Portulacaceae, Molluginaceae, Amaranthaceae, Caryophyllaceae (Caryophyllales *sensu* Cronquist, 1981) that is also well supported (100%). Caryophyllales *sensu* Cronquist comprise two additional subclades: (1) Amaranthaceae and Caryophyllaceae (99%); and (2) Aizoaceae, Phytolaccaceae, Nyctaginaceae, Molluginaceae, Cactaceae and Portulacaceae (94%). *Delosperma* (Aizoaceae) is nested within Phytolaccaceae, appearing as sister to *Ercilla*.

Saxifragales/Vitaceae/eurosids. Saxifragales plus Vitaceae (including *Leea*) and the eurosids form a weakly supported clade (60%). Within this clade, the monophyly of Saxifragales is strongly supported (98%); Saxifragales are the sister group to a clade (73%) consisting of Vitaceae (including *Leea* as in Ingrouille *et al.*, submitted) as sister to the large, well-supported (99%) eurosid clade. The monophyly of both Saxifragales and eurosids has been indicated previously, and both received measures of internal support greater than 50% in earlier analyses (e.g. Soltis *et al.*, 1997a, 1997b, 1998; Soltis & Soltis, 1997; Savolainen *et al.*, 2000a, b). Analyses of *rbcL* and *rbcL/atpB* sequences similarly indicated that Saxifragales are sister to Vitaceae and in turn sister to the eurosids, but without support $\geq 50\%$ for these relationships. Analysis of *atpB* alone indicated that *Leea* and Vitaceae are sisters (again without support $\geq 50\%$) but placed this pair as sister to Saxifragales; these in turn were sister to a clade of eurosids, asterids, and caryophyllids. Hence, this three-gene analysis is the first to support these large-scale relationships among Saxifragales, Vitaceae, and the eurosids.

Saxifragales. This eclectic assemblage of herbaceous and woody taxa (placed in three subclasses in recent classifications) has emerged as a very strongly supported clade (98%; Fig. 6A). Saxifragales comprise Altingiaceae, Hamamelidaceae, Cercidiphyllaceae and Daphniphyllaceae, all previously Hamamelidaceae, as well as Saxifragaceae *s.s.*, Iteaceae, Pterostemonaceae, Grossulariaceae (*Ribes*), Crassulaceae, Tetracarpaceae, Penthoraceae, Haloragaceae, all traditional Rosidae, plus Paeoniaceae, variously placed near Ranunculaceae or in Dilleniidae (reviewed in Cronquist, 1981). Analysis of *rbcL* sequences first indicated the presence of this Saxifragales clade (Chase *et al.*, 1993; Morgan & Soltis, 1993), but without support $\geq 50\%$ (Chase & Albert, 1998). Analyses of *atpB* alone, as well as *atpB/rbcL*, also indicated a monophyletic Saxifragales, but again without support $\geq 50\%$ (Savolainen *et al.*, 2000a). In contrast, 18S rDNA alone and 18S rDNA/*rbcL* have previously shown a Saxifragales clade with moderate jackknife support (e.g. Soltis *et al.*, 1997a, 1998; Soltis & Soltis, 1997). Hence, the combination of all three genes has yielded, by far, the highest support for this clade.

Within Saxifragales, Daphniphyllaceae, Hamamelidaceae, Cercidiphyllaceae and Altingiaceae form a grade (Fig. 6B), but the branching order is not supported by jackknife values $\geq 50\%$ (Fig. 6A). A number of subclades within Saxifragales, however, do receive support $\geq 50\%$. Hamamelidaceae form a monophyletic group (58%) and include *Exbucklandia* as their first-branching member. Altingiaceae and Saxifragaceae are each strongly supported as monophyletic (100%). Iteaceae and Pterostemonaceae are strongly supported sister families (100%); they form a clade with *Ribes* (Grossulariaceae) and Saxifragaceae *s.s.*, but without support $\geq 50\%$. Crassulaceae are monophyletic (100%) and together with Penthoraceae, Tetracarpaceae, and Haloragaceae form a moderately supported clade (80%). The relationships of Paeoniaceae within Saxifragales remain obscure, although all shortest

trees place the family in the Crassulaceae/Penthoraceae/Tetracarpaceae/Haloragaceae subclade.

The composition of Saxifragales and the relationships within this clade depicted here generally agree with those based on 18S rDNA/*rbcL* and *rbcL* (e.g. Soltis & Soltis, 1997; Qiu *et al.*, 1998), although our three-gene topology is much better resolved and supported than trees obtained in earlier studies. Saxifragales have been the recent focus of a more detailed analysis based on sequences of five genes, 18S rDNA, 26S rDNA, *matK*, *rbcL*, and *atpB* (Fishbein *et al.*, in press).

Eurosids. The monophyly of a large eurosid clade receives strong jackknife support (99%; Fig. 1A). Although earlier analyses based on *rbcL* (Chase *et al.*, 1993), *atpB* alone, *atpB/rbcL* (Savolainen *et al.*, 2000a), 18S rDNA (Soltis *et al.*, 1997a), and non-DNA characters (Nandi *et al.*, 1998) all recovered this large eurosid clade, only *atpB/rbcL* provided even weak support (61%) for this large assemblage of angiosperms. Previous studies also found two large subclades of eurosids, termed eurosid I and II, but again without support $\geq 50\%$ (e.g. Chase *et al.*, 1993; Savolainen *et al.*, 2000a). Our three-gene analysis provides moderate support for eurosid I (77%); eurosid II (composed here of Brassicales, Tapisciaceae, Malvales and Sapindales) is recovered in all shortest trees and has jackknife support of 95%. Several morphological and anatomical features are shared by many eurosids, including nuclear endosperm development, reticulate pollen sexine, generally simple perforations of vessel end-walls, mucilaginous epidermis, and often two or more whorls of stamens (obdiplostemony). Similarly, a suite of non-DNA characters is shared by many members of the two subclades, eurosid I and eurosid II (Nandi *et al.*, 1998; Savolainen *et al.*, 2000a).

Eurosid I. Eurosid I comprises three major subclades, all with jackknife support $\geq 50\%$ (Fig. 7A): (1) a nitrogen-fixing clade (68%; see Soltis *et al.*, 1995) consisting of Rosales, Fabales, Cucurbitales and Fagales (68%); (2) a small clade (100%) of Krameriaceae and Zygophyllaceae (100%); and (3) a large clade (51%) of Malpighiales, Oxalidales and celastroids plus Huaceae (51%).

The monophyly of all angiosperms that form symbiotic associations with nitrogen-fixing bacteria involving root nodules had been indicated previously based on *rbcL* sequence data (Soltis *et al.*, 1995) but without bootstrap support greater than 50%. Although the monophyly of Rosales, Cucurbitales and Fagales was apparent with 18S rDNA sequence data alone, the inclusion of Fabales in the same clade was less certain (Soltis *et al.*, 1997a). Phylogenetic analyses of *atpB* and *atpB/rbcL* also indicated a monophyletic nitrogen-fixing clade, but again without strong internal support. Hence, this study provides the strongest evidence yet for a monophyletic group containing all angiosperms engaged in nitrogen-fixing symbioses in root nodules, reinforcing the hypothesis of a single origin of the predisposition of nitrogen-fixing symbiosis (Soltis *et al.*, 1995). A suite of chemical, palynological and anatomical features are shared by many members of these nitrogen-fixing orders (Nandi *et al.*, 1998).

Within the nitrogen-fixing clade, the monophyly of each of the four subclades also receives strong support, Rosales (100%), Fabales (98%), Cucurbitales (100%) and Fagales (100%); also supported is a sister-group relationship between Cucurbitales and Fagales (60%). Within Rosales, a strongly supported Rosaceae (100%) are sister to the remainder of the order, which comprises a well-supported clade (99%) of three subgroups: a monophyletic Rhamnaceae (64%); Barbeyaceae/

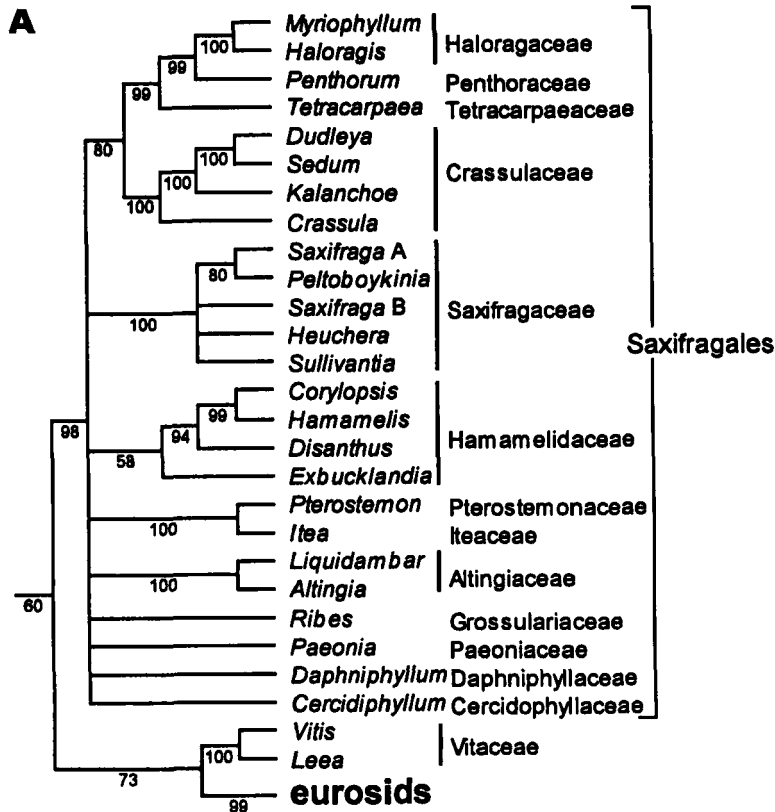


Figure 6. The jackknife consensus tree (A) focusing on Saxifragales; (B) the same set of taxa from the single tree with branch lengths illustrated (ACCTRAN optimization); arrowheads indicate groups not found in all shortest trees. The eurosids are indicated as a single terminal, to which Vitaceae (including *Leea*) are the sister group.

Elaeagnaceae (69%); and a clade of *Zelkova* (Ulmaceae), Urticaceae, Moraceae, *Humulus* (Cannabaceae), *Celtis* and *Trema* (Celtidaceae; see Wiegrefe, Systema & Guries, 1998, for recognition of Celtidaceae and Ulmaceae as distinct families). Within the latter subclade, *Zelkova* is sister to the remaining taxa, which form a well-supported monophyletic group (99%); Urticaceae are then sister to a weakly supported clade (52%) of Moraceae, Cannabaceae and Celtidaceae. Within Fabales, the three subfamilies of Fabaceae form a clade (80%) and are sister to a clade (69%) of Surianaceae/Polygalaceae. Within Cucurbitales, only the monophyly of Cucurbitaceae (100%) and the sister relationship of Coriariaceae/Corynocarpaceae (94%) receive support $\geq 50\%$. Within Fagales, Fagaceae (100%) appear as sister to a strongly supported clade (100%) of Myricaceae/Juglandaceae (92%) plus Casuarinaceae/Betulaceae (100%).

Krameriaceae/Zygophyllaceae form a strongly supported (100%) clade within eurosid I. A close relationship between these two families had previously received strong support based on *rbcL/atpB* sequences (e.g. Savolainen *et al.*, 2000a). The close relationship between Krameriaceae and Zygophyllaceae, as well as their highly divergent morphologies, are discussed in Sheahan & Chase (1996, 2000). The recent

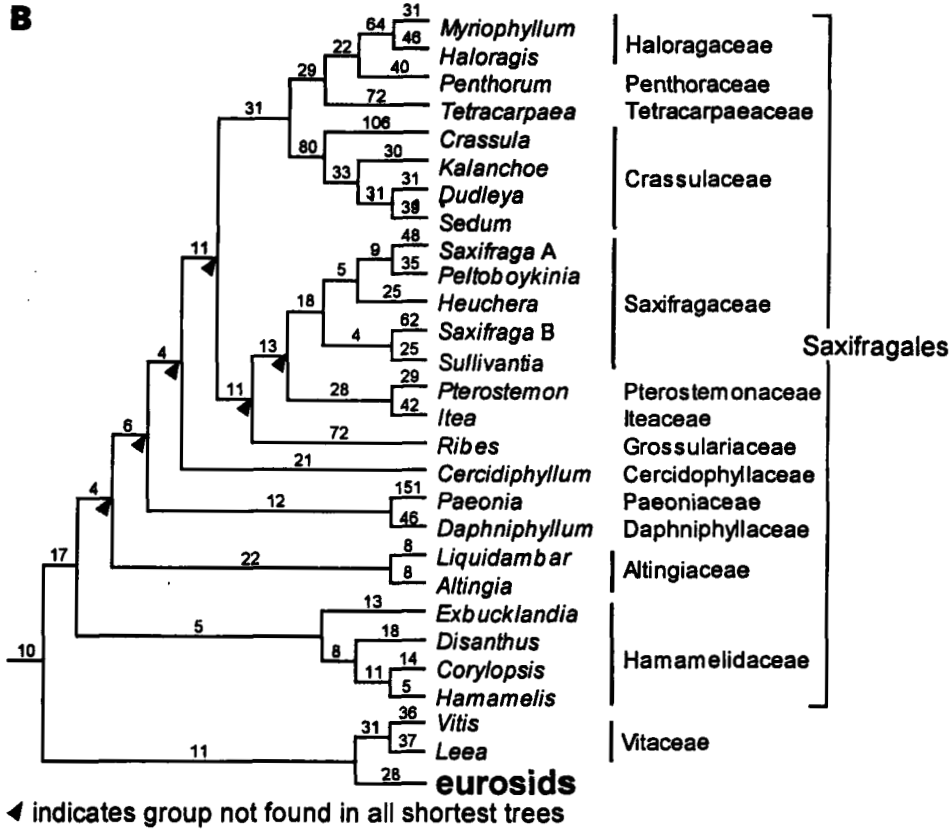


Figure 6. See caption on facing page.

APG (1998) classification did not recognise this family pair as a discrete order of angiosperms because their exact relationships were not clear. The strong internal support obtained here for their exclusion from the other orders of eurosid I indicates that in subsequent updates of the APG classification *Zygophyllales* (comprising *Krameriaceae* and *Zygophyllaceae*) should be recognized. They are an isolated clade that is sister to the rest of the eurosid I clade.

The remaining members of eurosid I form a large, weakly supported subclade (51%) consisting of *Malpighiales*, *Oxalidales* and a celastroid group plus *Huaceae*. Monophyly of *Malpighiales* and *Oxalidales* is each well supported (100%). The sister-group relationship of *Huaceae* to core celastroids is weakly supported (62%). As with the *Zygophyllaceae*/*Krameriaceae* clade, it is now clear that the celastroids are excluded from both *Malpighiales* and *Oxalidales*, making appropriate their recognition as the order *Celastrales* that consists of three families, a broadly defined *Celastraceae*, *Parnassiaceae* (including *Lepuropetalon*) and *Huaceae*.

Malpighiales form a large clade comprising a number of well-supported subclades, the relationships among which do not receive jackknife support $\geq 50\%$ (Fig. 8A). The first several dichotomies within *Malpighiales* are extremely short (3–6 steps; Fig. 8B), so it is not surprising that jackknife support is low. These subclades include: *Balanopaceae* (100%) as sister to a well-supported clade (99%) of *Chrysobalanaceae*

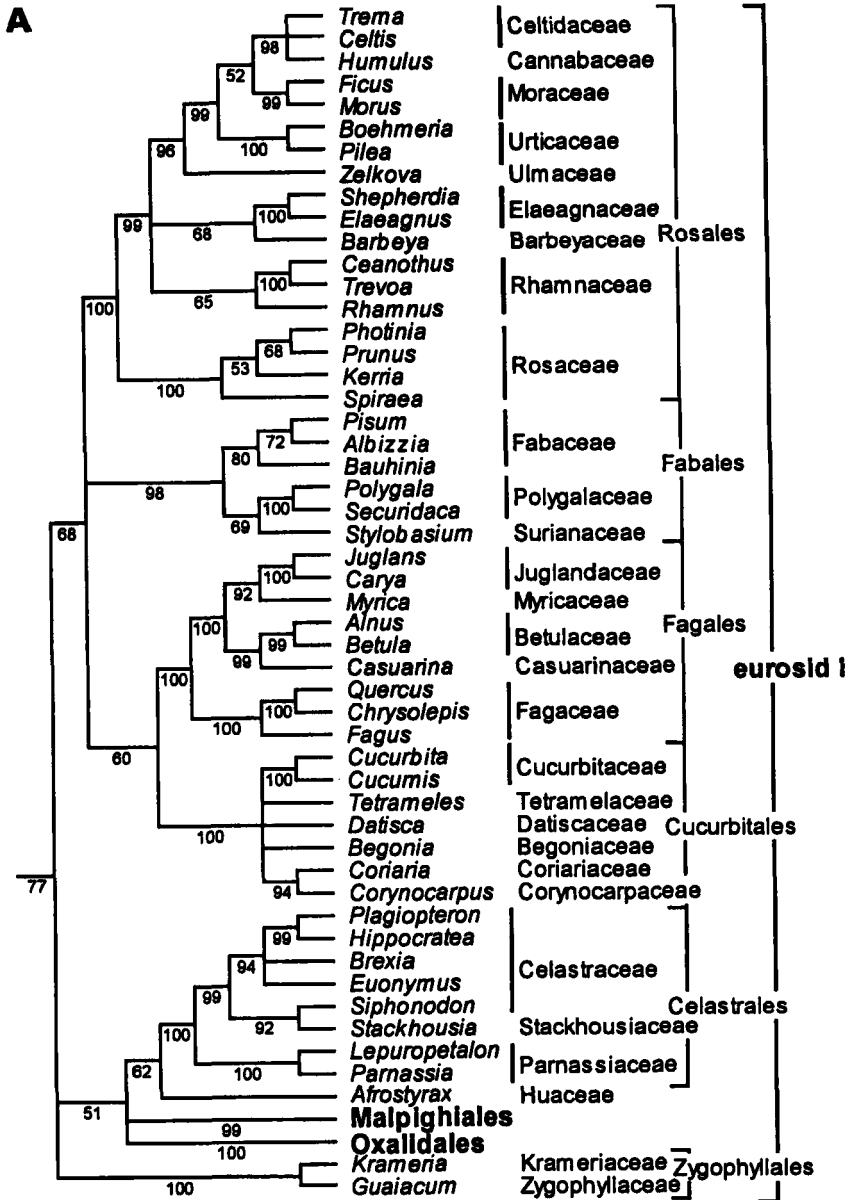


Figure 7. The jackknife consensus tree (A) focusing on a portion of the eurosid I clade; (B) the same set of taxa from the single tree with branch lengths illustrated (ACCTRAN optimization); arrowheads indicate groups not found in all shortest trees. Malpighiales and Oxalidales are each indicated as single terminals. Note that Huaceae are unplaced to order.

plus Trigoniaceae/Dichapetalaceae (98%). Euphorbiaceae are not monophyletic in our analyses. Instead, *Androstachys* and *Stachystemon* (Oldfieldioideae) form a well-supported clade (100%; recognition of Pseudanthaceae would be appropriate), whereas *Drypetes* (Putranjivaceae) and *Euphorbia* each have allies elsewhere (Humiriaceae and Linaceae, respectively), based on the shortest trees obtained (Fig. 8B).

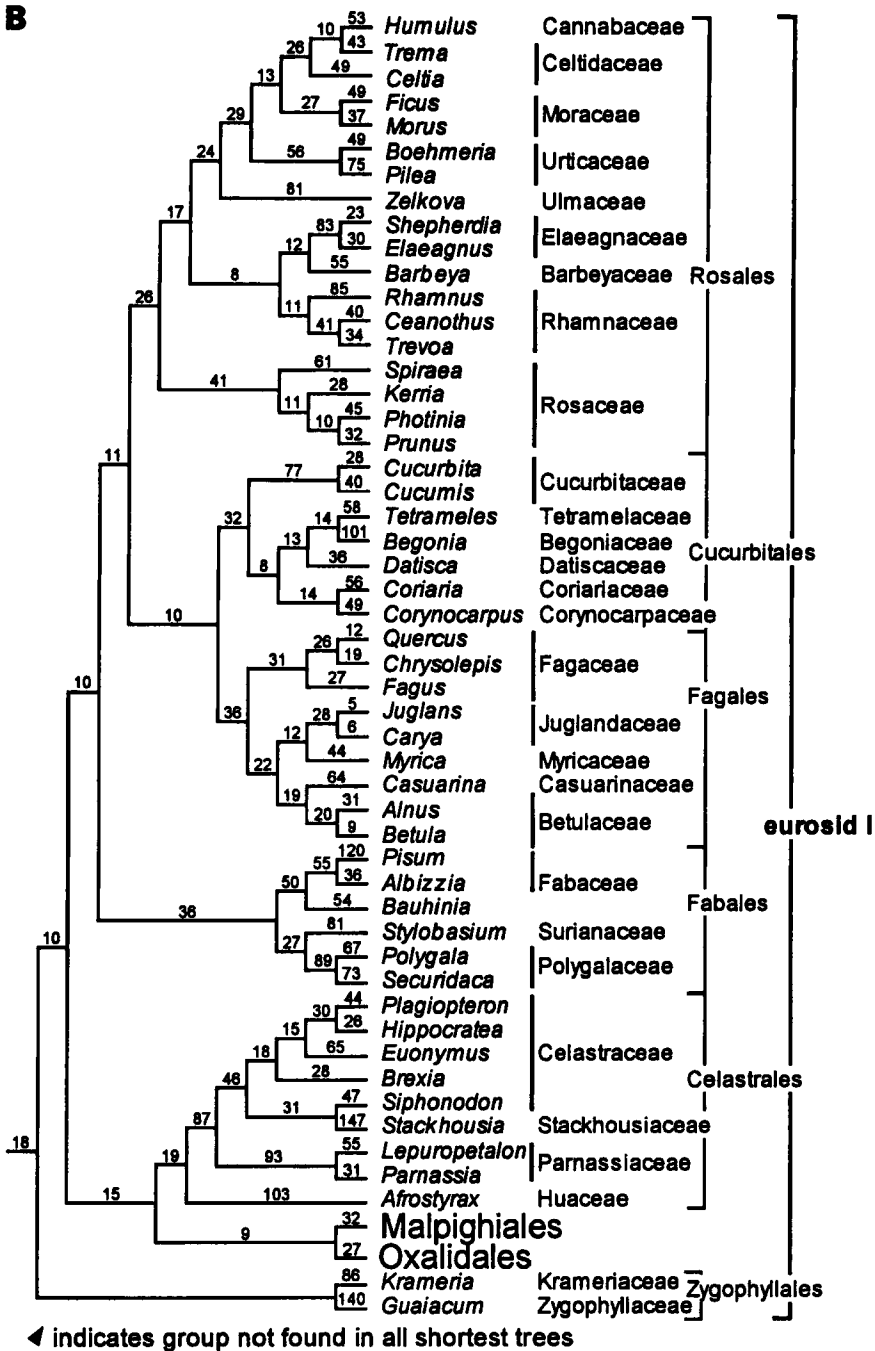


Figure 7. See caption on facing page.

A well-supported clade (100%) of Erythroxylaceae as sister to Rhizophoraceae is revealed. Also retrieved is a strongly supported clade (100%) of Quinaceae as sister to a clade (60%) of Medusagnaceae/Ochnaceae (see also Fay, Swensen & Chase,

1997). Violaceae are sister (79%) to a clade (100%) of Passifloraceae plus a family pair (65%) of Malsherbiaceae/Turneraceae.

Delimitation of Flacourtiaceae has long been problematic (see Lemke, 1988), and so we purposely sampled many taxa that have in the past been referred to the family. *Muntingia* is a member of Malvales, and Bayer, Chase & Fay (1998) described it and two other genera as Muntingiaceae because they were not, on morphological grounds, members of any other family in Malvales. *Berberidopsis* (here treated as Berberidopsidaceae) has always been considered the most archaic member of Flacourtiaceae (Hutchinson (1967), and it is indeed an isolated taxon that has *Aextoxicon* (Aextoxicaceae) as its closest relative; the pair falls entirely outside of the eurosids (see above). *Aphloia* (here treated as Aphloiaceae) is placed with *Ixerba* (Ixerbaceae), and the pair is weakly supported (56%) as sister to Crossosomatales (see below). *Plagiopteron* (sometimes also recognized as a distinct family, Plagiopteridaceae; Airy Shaw, 1985) appears here in Celastraceae (Fig. 7), and we consider it to be a member of that family, with which it fits well on vegetative terms (Baas *et al.*, 1979). *Asteropeia* (also considered to be its own family as here, Asteropeiaceae, or referred to Theaceae; Cronquist, 1981) falls with *Physena* (Morton, Chase & Karol, 1997b), and the pair is sister to the core Caryophyllales (see above; Fig. 5). Tribes Paropsieae and Abatieae have been treated as members of both Flacourtiaceae and Passifloraceae (in the latter because they both have an extrastaminal corona but in the former because they are trees or shrubs rather than vines), and some authors have stated that these two tribes are 'transitional' between the two families (De Wilde, 1971; Keating, 1973). We sampled *Abatia* and *Paropsia*, and the former occurs with *Flacourtia* and the latter with *Passiflora*, and thus neither habit nor the presence of an extrastaminal corona is always reliable here. Floral development (Bernhard, 1999) clearly supports the placements obtained here for these two tribes in that *Abatia* is completely unlike that of Passifloraceae whereas Paropsieae and Passifloraceae are similar. *Lacistema* (often tribe Lacistemataceae; Sleumer, 1980, or family Lacistemataceae with two genera, *Lacistema* and *Lozania*) falls in all shortest trees (Fig. 8B) as sister to Flacourtiaceae/Salicaceae but with jackknife support <50%. Flacourtiaceae *s.l.* (Lemke, 1988) are not monophyletic in the shortest trees (Fig. 8B) but rather fall into two well-supported clades (99%) that differ in their chemistry (cyanogenic glycosides versus tannins) and the presence of a salicoid tooth (Nandi *et al.*, 1998). We recognize the cyanogenic glycoside group here as Kiggelariaceae (*Hydnocarpus*, *Pangium*, *Kiggelaria*), which form a clade (99%) with a taxon originally labelled as *Ixonanthes* (Ixonantheae) and *Acharia* (Achariaceae). The plant in question was obtained from the living collection at Kebun Raya (Bogor, Indonesia) and is clearly not a species of *Ixonanthes* (as recently determined by comparing the voucher to collections of the genus in the Herbarium, RBG Kew), but the voucher is sterile; although we can refute it as being a species of *Ixonanthes*, we have been unable to determine what it is. Based on its sequences, it is a member of Kiggelariaceae. However, Kiggelariaceae are not monophyletic, with *Hydnocarpus* sister to a clade (100%) of *Pangium*-Achariaceae/*Kiggelaria*. Additional taxon sampling is needed to clarify relationships within this subclade of Malpighiales. Achariaceae are South African herbaceous climbers or shrublets and are so highly modified that their relationships have been unclear. In another well-supported clade (100%), the four representatives of Flacourtiaceae sampled (*Casearia*, *Flacourtia*, *Abatia*, *Idesia*) are paraphyletic relative to Salicaceae; *Casearia* is sister to a clade (100%) of *Flacourtia*/

Abatia, *Idesia* and Salicaceae. This clade will be formally proposed as Salicaceae (Zmarzty & Chase, in prep.).

Malpighiales also illustrate the value of broad phylogenetic analyses in placing enigmatic taxa. The relationship of Medusagynaceae is but one example (see Fay *et al.*, 1997). Other such examples of small, enigmatic families that appear as part of a well-supported Malpighiales include Goupiaceae, Irvingiaceae, Balanopaceae, and Caryocaraceae. A particularly noteworthy example of the value of this large data matrix in placing problematic families involves Podostemaceae, variously associated with Piperaceae, Nepenthaceae, Polygonaceae, Caryophyllaceae, Scrophulariaceae, Rosaceae, Crassulaceae and Saxifragaceae (reviewed in Les, Philbrick & Novelo, 1997; Ueda *et al.*, 1997; Soltis *et al.*, 1999). Our phylogenetic analyses place Podostemaceae in Malpighiales as part of a strongly supported Clusiaceae clade (99%) that consists of *Mesua* as sister to a clade (100%) of *Hypericum*/Podostemaceae. A relationship of Podostemaceae with Malpighiales was first indicated in an analysis of over 250 angiosperms using 18S rDNA and 18S rDNA/*rbcL* sequences, but without strong internal support (Soltis *et al.*, 1999); this relationship of Podostemaceae with Malpighiales was not indicated, however, by analyses of *rbcL* sequences alone (Les *et al.*, 1997; Ueda *et al.*, 1997). However, neither of these previous analyses included enough taxa to get an accurate placement; members of Malpighiales were noteworthy in their absence. Reduction of the number of taxa so that a more rigorous analysis can be performed is not a solution to the placement of problematic taxa, particularly if in this process the close relatives are omitted.

Oxalidales comprise Oxalidaceae as sister to a clade (99%) consisting of a broadly defined and strongly supported (100%) Cunoniaceae (that includes *Bauera* and *Davidsonia*), that is in turn sister to a clade (76%) consisting of members of Elaeocarpaceae and Tremandraceae. Elaeocarpaceae, represented here by *Crinodendron*, *Elaeocarpus* and *Sloanea*, are paraphyletic relative to *Platytheca* (Tremandraceae), with *Sloanea* sister to a well-supported clade (95%) of *Crinodendron*/*Elaeocarpus*/*Platytheca*. Tremandraceae (three genera confined to Australia and Tasmania) differ only from Elaeocarpaceae in having two distinct whorls of four or five stamens, whereas the latter have many stamens. However, the stamens in Elaeocarpaceae are often clearly arranged in bundles, so Tremandraceae merely having a definite number is not so significantly different (although different enough to cause Cronquist, 1981, to put them into different subclasses). As with many Australasian plants, Tremandraceae are xeromorphic in habit, but even the micromorphological details of the plants, for example commonly arillate seeds with a straight embryo immersed in an abundant and oily endosperm, compare well with those described for Elaeocarpaceae (Cronquist, 1981). Tremandraceae should be considered members of Elaeocarpaceae.

The problematic *Afrostyrax* (Huaceae) appears as sister (with 62% support) to a strongly supported (100%) core celastroid clade. Although a Celastrales clade was not recognised in the reclassification of angiosperms proposed by APG (1998), our data support ordinal recognition of Parnassiaceae, Celastraceae and Huaceae as an order, Celastrales. It also seems apparent that Celastraceae should be broadly defined (Celastraceae *s.l.*) to include *Euonymus*, as well as *Brexia*, *Hippocratea*, *Plagiopterum* and *Stackhousia*, each of which has previously been placed in a distinct family (Brexiaceae, Hippocrateaceae, Plagiopteridaceae and Stackhousiaceae, respectively). Stackhousiaceae, for example only differ from Celastraceae, as previously recognized, in being mostly herbaceous and having a better developed hypanthium (Cronquist, 1981). Celastraceae *s.l.* are monophyletic, and *Siphonodon* is sister to *Stackhousia* with

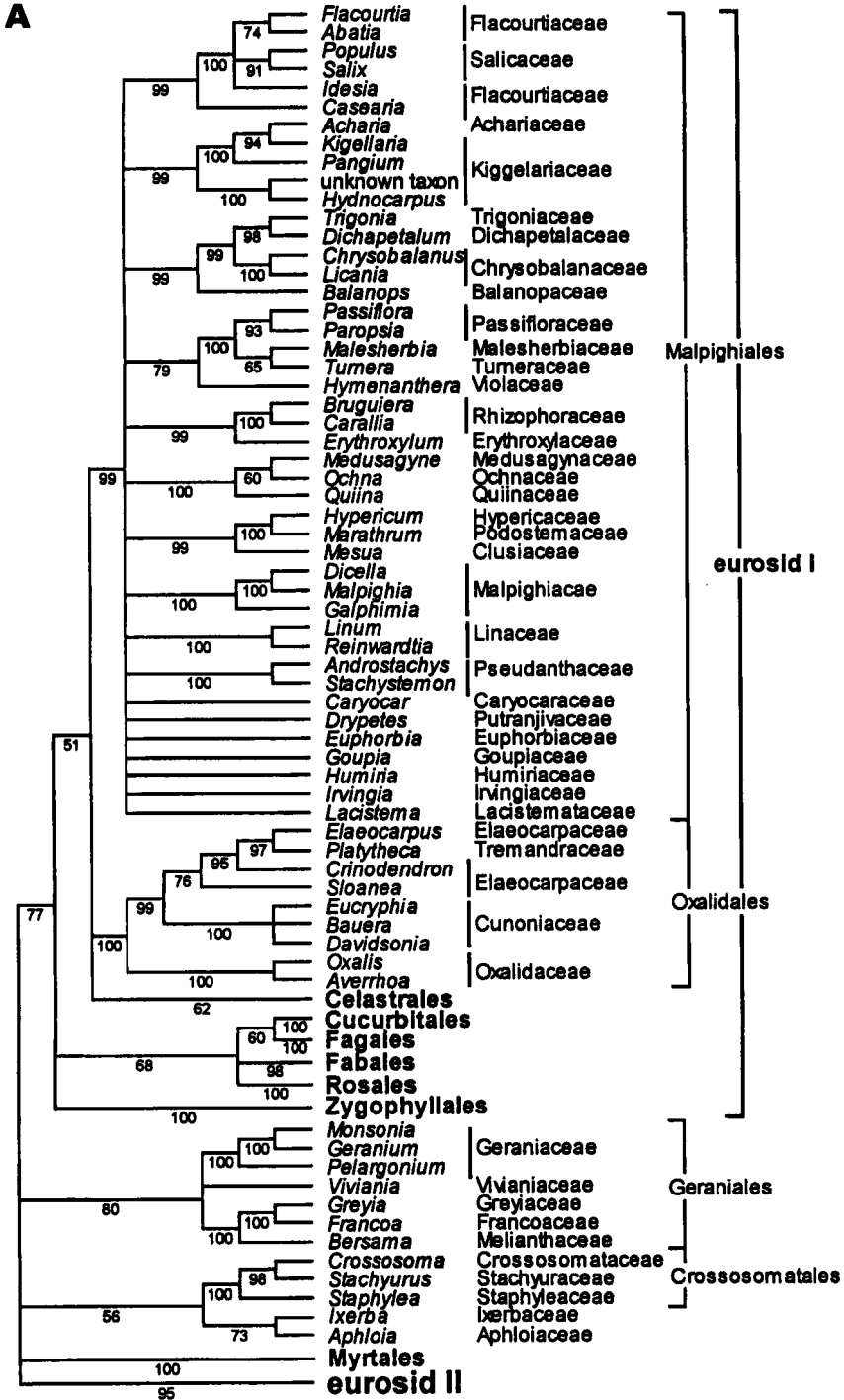


Figure 8. The jackknife consensus tree (A) focusing on a portion of the eurosid I clade plus the unplaced eurosid orders and families; (B) the same set of taxa from the single tree with branch lengths illustrated (ACCTRAN optimization); arrowheads indicate groups not found in all shortest trees. Celastrales, Cucurbitales, Fagales, Fabales, Myrtales, Rosales, and Zygophyllales are each indicated as single terminals. Note that Aphloiaceae and Ixerbaceae are unplaced to order.

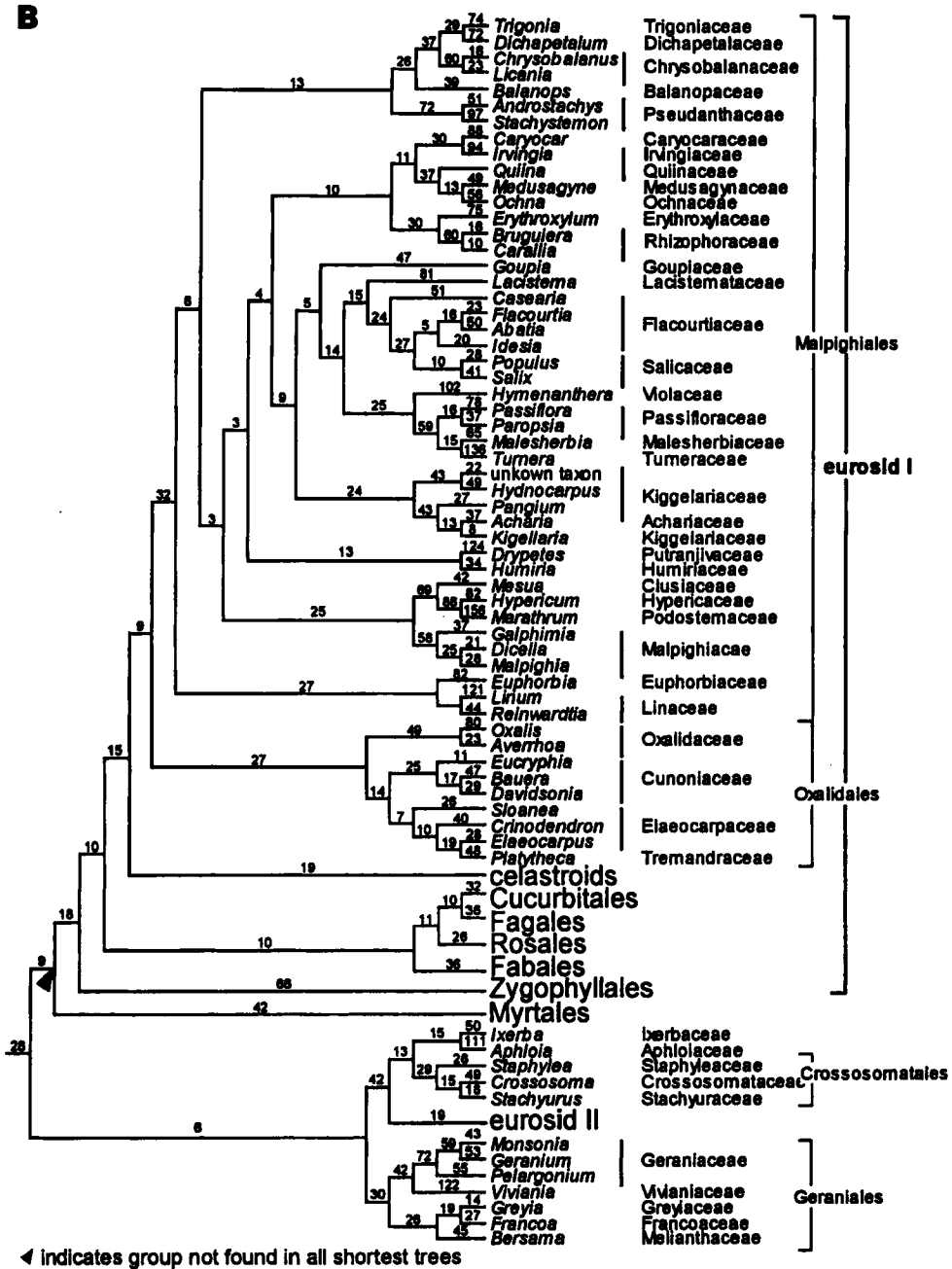


Figure 8. See caption on facing page.

strong support (92%). Celastraceae, Parnassiaceae and Stackhousiaceae formed a well-supported clade within eurosid I in previous studies (e.g. Savolainen *et al.*, 2000a). Although analyses of *rbcL/atpB* placed Huaceae as sister to Celastrales, there was no bootstrap support $\geq 50\%$. Hence, our three-gene analysis strengthens the support of the placement of another enigmatic family, Huaceae.

Eurosid II. As noted, eurosid II including Myrtales is not present as a distinct clade in our shortest trees, as was previously found with *rbcl* alone, although without jackknife support $\geq 50\%$ (Fig. 9A). With this sampling of taxa and genes, Myrtales are sister in all shortest trees to the eurosid I clade (Fig. 9A, B), but Geraniales and Crossosomatales (Crossosomataceae, Stachyuraceae, Staphyleaceae and perhaps Aploiaceae and Ixerbaceae; see below) are allied to the well-supported core orders of eurosid II. At this point, therefore, eurosid II is restricted to Brassicales (100%), Tapisciaceae, Sapindales (100%) and Malvales (100%). All shortest trees place Geraniales and Crossosomatales with the strongly supported core eurosid II clade (Figs 8B, 9B), but with support of less than 50%, so it is still premature to assign a position for these orders, as well as for Myrtales.

Previous studies of single genes have consistently recovered a clade of Brassicales, Sapindales and Malvales (Savolainen *et al.*, 2000a, b), but without internal support $\geq 50\%$; Savolainen *et al.* found weak support (62%) for a sister-group relationship of Brassicales/Malvales with combined *rbcl/atpB* data, although this position is here reversed such that the pair Malvales/Sapindales has weak support (51%). Our study indicates that these three orders, plus the enigmatic Tapisciaceae, are strongly supported clade (95%). Within this clade, Brassicales are strongly supported, as are Sapindales and Malvales (each with 100%). The relationship of Tapisciaceae in all shortest trees is as sister to these three orders collectively, but this does not receive support $\geq 50\%$ (Fig. 9A, B).

The composition and relationships depicted here for Brassicales are similar to those recently reported based on *rbcl*/18S rDNA sequence data (Rodman *et al.*, 1998). Three strongly supported subclades are present within Brassicales: Tropaeolaceae/Akaniaceae/Bretschneideraceae (100%); Moringaceae/Caricaceae (94%); and a large clade (100%) in which *Setchellanthus* (Setchellanthaceae) is sister to a clade (61%) of the remaining members of Brassicales sampled (i.e. Limnanthaceae, Koeberliniaceae, Bataceae, Resedaceae and Brassicaceae, including Capparaceae). Among these remaining families, Limnanthaceae are sister to a clade (79%) of Bataceae/Koeberliniaceae (64%), which in turn are sister to Resedaceae and a broadly defined Brassicaceae represented by *Capparis*, *Brassica* and *Cleome*. *Drypetes* (Putranjivaceae, formerly in Euphorbiaceae), another glucosinolate-producing taxon, is not part of this Brassicales clade, but instead is part of well-supported Malpighiales in the eurosid I clade (see above). Hence, the three-gene topology reinforces the hypothesis that the 'mustard oil bomb', a defence mechanism, was invented only twice (Rodman *et al.*, 1993, 1998).

Sapindales consist of three well-supported subclades: (1) a broadly defined Sapindaceae (see APG, 1998) that includes both *Aesculus* (Hippocastanaceae) and *Acer* (Aceraceae); (2) a strongly supported (97%) sister group of Anacardiaceae/Burseraceae; and (3) a well-supported clade (99%) of Meliaceae, Simaroubaceae and (98%) Rutaceae, which includes *Cneorum* (Cneoraceae; Chase, Morton & Kallunki, 1999, also included Ptaeroxylaceae in Rutaceae). Relationships within Sapindales inferred from *rbcl* sequences were discussed in more detail by Gadek *et al.* (1996) and from combined *rbcl/atpB* data by Chase *et al.* (1999).

Malvales comprise a weakly supported clade (66%) with Muntingiaceae as sister to a clade (100%) of Cistaceae and Sarcocaulaceae/Dipterocarpaceae. Also part of Malvales are Thymelaeaceae and Bixaceae (Alverson *et al.*, 1998; Fay *et al.*, 1998), but the relationships of these two families within the order are not clear. A broadly defined Malvaceae receives strong support (100%); in addition to Malvaceae in the

strict sense, this family also includes former members of Bombacaceae, Sterculiaceae and Tiliaceae (Judd & Manchester, 1997; Bayer *et al.*, 1999). Our results also support the polyphyly of both Sterculiaceae and Tiliaceae (*Theobroma* of Sterculiaceae is strongly supported as sister to *Grewia* of Tiliaceae, and *Tilia* is strongly supported as sister of a clade containing both *Durio* and *Sterculia* of Sterculiaceae).

Myrtales consist of three subclades each having support $\geq 50\%$ (Fig. 9A). One of these is only weakly supported (58%) and consists of Melastomataceae/Mecycylaceae as sister to a clade (54%) of Heteropixidaceae/Vochysiaceae. The second subclade consists of Combretaceae (100%); the third subclade (95%) comprises a broadly defined Lythraceae (that also include Punicaceae) as the strongly supported sister (95%) of Onagraceae. These relationships are in agreement with the results of Savolainen *et al.* (2000a) based on *atpB/rbcL*, as well as those of Conti, Litt & Sytsma (1996) based on *rbcL* alone.

The composition and placement of Geraniales remain unsupported (Fig. 8A, B). Our three-gene analysis provides strong support (80%) for the monophyly of a core Geraniales clade consisting of Geraniaceae, Vivianiaceae, Melianthaceae, Francoaceae and Greyiaceae. The last three are strongly supported as a clade (100%) and could well be considered a single family, Melianthaceae; *Bersama* and *Greyia* have highly similar pollen (Cronquist, 1981), but *Francoa* (from Chile and the only member of this clade outside eastern and southern Africa) is herbaceous and otherwise dissimilar to the other woody taxa of this group. Previous studies have indicated a close relationship among some of Geraniales, albeit without strong internal support (e.g. Morgan & Soltis, 1993; Price & Palmer, 1993; Savolainen *et al.*, 2000a, b).

Our results also indicate a broadly defined Crossosomatales clade (56%) consisting of Staphyleaceae, Crossosomataceae and Stachyuraceae (100%) and perhaps as well Ixerbaceae/Aphloiaceae (73%), to which they are sister (with weak support, 56%). Crossosomatales and Geraniales are successive sisters to eurosid II, but without support $\geq 50\%$ (Crossosomatales were not recognized in the APG, 1998, classification, but we propose that they should be in future versions).

Within eurosid II, additional enigmatic taxa have been placed. For example, *Ixerba* has variously been placed in its own family, or with *Brexia* and *Roussea* in Brexiaceae (Takhtajan, 1987). However, these three genera are not closely related, but instead are members of distantly related clades (eurosid II, Crossosomatales and euasterid II, respectively), in agreement with a recent analysis based on *rbcL* and 18S rDNA data (Koontz & Soltis, 1999). In addition, our results provide support for a sister-group relationship of *Ixerba* and *Aphloia* (73%), both of which have also been problematic in their placements. Many authors have treated *Aphloia* as a member of Flacourtiaceae, to which it is clearly only distantly related.

Asterids. The monophyly of a broadly defined asterid clade (Asteridae *s.l.* of Olmstead *et al.*, 1992, 1993) is strongly supported (100%; Fig. 10A). Ericales and Cornales are the sister groups to the two clades of euasterids (euasterid I and II) in all shortest trees (Fig. 10B), but without jackknife support $\geq 50\%$. The monophyly of both Ericales and Cornales is strongly supported (each with 98%). The remaining asterids form a well-supported clade (89%) and, in turn, form two subclades, euasterid I (56%) and euasterid II (88%). Although euasterid I and II have been recovered in earlier phylogenetic analyses of individual genes, such as *rbcL* (search 2 of Chase *et al.*, 1993), *atpB* and *atpB/rbcL* (Savolainen *et al.*, 2000a), and 18S rDNA (Soltis *et al.*,

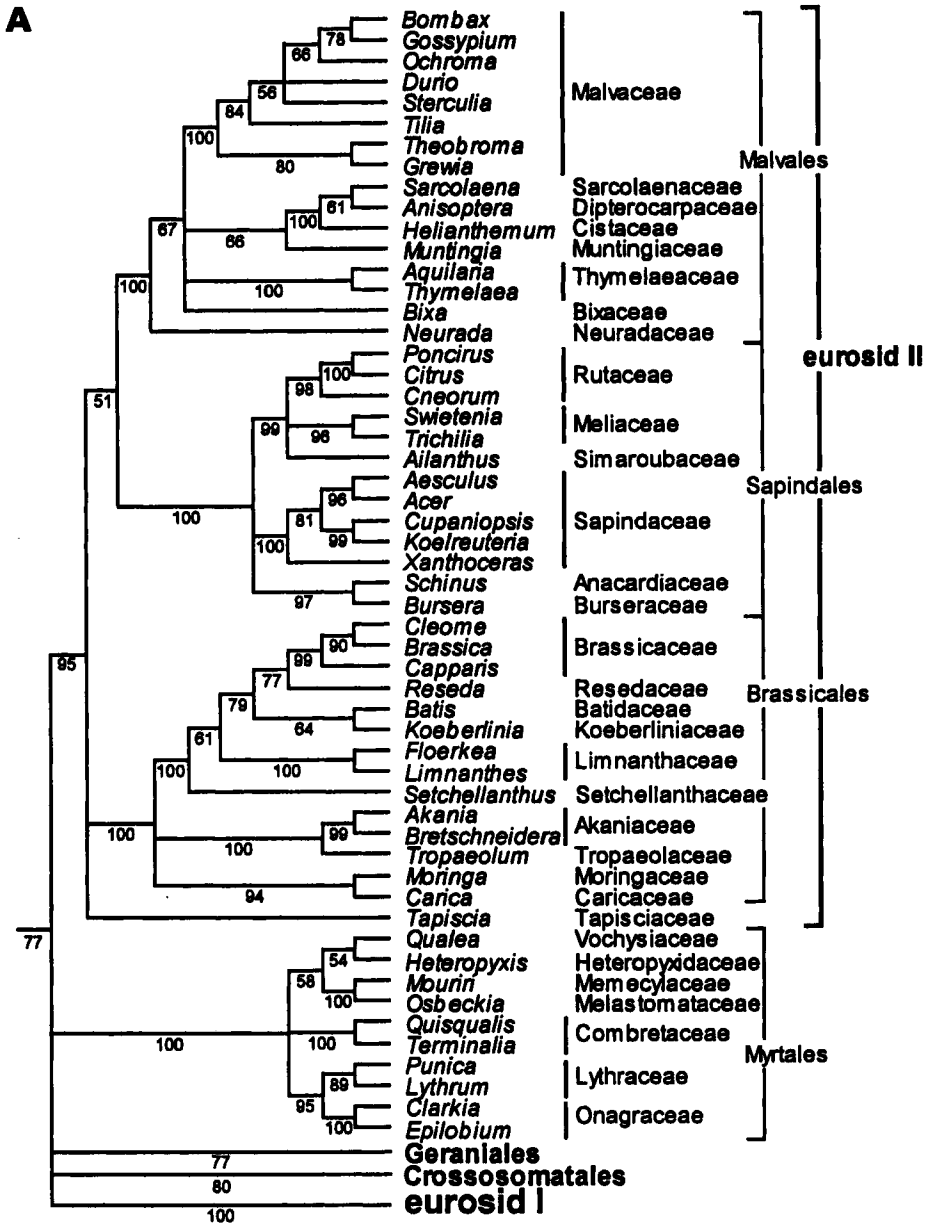


Figure 9. The jackknife consensus tree (A) focusing on the eurosid II clade plus Myrtales; (B) the same set of taxa from the single tree with branch lengths illustrated (ACCTRAN optimization); arrowheads indicate groups not found in all shortest trees. Crossosomatales, eurosid I, and Geraniales are each indicated as single terminals. Note that Tapisciaceae are unplaced to order.

1997a), this is the first time these two large subclades of asterids have received support $\geq 50\%$. The morphological and chemical features shared by members of this asterid clade, as well as non-DNA characters supporting each of euasterid I and II, have been discussed elsewhere (e.g. Olmstead *et al.*, 1993; Nandi *et al.*, 1998; Albach *et al.*, in press).

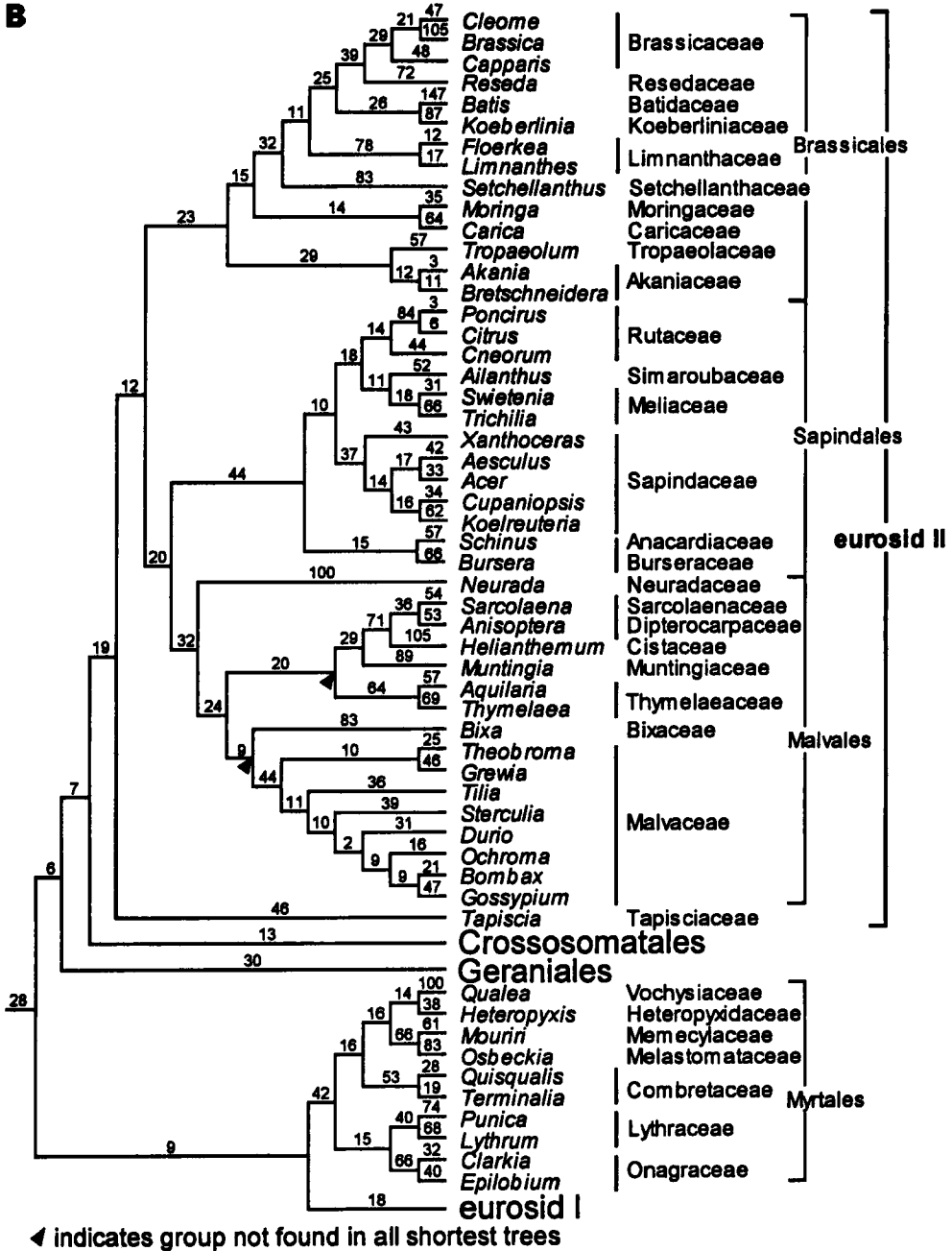


Figure 9. See caption on facing page.

Other recent analyses have focused on the asterid clade in greater detail (e.g. Olmstead *et al.*, in prep.; Albach *et al.*, in press), and a detailed analysis of the asterid clade involving four genes (*atpB*, *rbcL*, *ndhF*, 18S rDNA; Albach *et al.*, in press) provides greater support for the relationships within asterids noted here. Furthermore, the four-gene analysis provides additional insights, including at least weak bootstrap

support for a large clade of Apiales/Dipsacales and Asterales, a monophyletic group found in our shortest trees (see below) but without support $\geq 50\%$.

Cornales comprise three subclades, Nyssaceae (including *Camptotheca*), Cornaceae (including *Alangium*), and a third clade (91%) that includes Loasaceae as sister to a monophyletic Hydrangeaceae that also includes Hydrostachyaceae. These relationships are in general agreement with previous analyses of Cornales (e.g. Hempel *et al.*, 1995; Soltis, Xiang & Hufford, 1995; Xiang *et al.*, 1993; Xiang, Soltis & Soltis, 1998).

The composition of Cornales inferred here illustrates again the value of this large data set in placing enigmatic taxa. Hydrostachyaceae are another problematic aquatic family variously placed with another enigmatic aquatic, Podostemaceae (see above), or asterids such as Hydrophyllaceae. In our three-gene analysis, Hydrostachyaceae appear within the well-supported Cornales clade as part of a Hydrangeaceae clade that receives moderate support (71%; see also Hempel *et al.*, 1995). Although more work is needed to establish the robustness of the relationship of Hydrostachyaceae to Hydrangeaceae, the support for placement of Hydrostachyaceae within Cornales is strong.

Although the monophyly of Ericales is strongly supported (98%), there are few major groups within Ericales that receive support $\geq 50\%$ due to the unusually short branches at the base of this clade. One strongly supported clade (100%) consists of Balsaminaceae as sister to a clade (74%) of Marcgraviaceae/Pellicieraceae/Tetrameristaceae. Another strongly supported clade (100%) comprises *Maesa* (Myrsinaceae) as sister to a well-supported clade (87%) of Theophrastaceae/Primulaceae. Included within a strongly supported Primulaceae (100%) is *Ardisia* (Myrsinaceae) as sister to *Anagalis*. The relationships of Myrsinaceae, Primulaceae and Theophrastaceae need detailed attention because the two former families do not appear to be monophyletic as currently circumscribed. *Maesa* in particular is morphologically out of place within Myrsinaceae (Anderberg, Stahl & Kallersjo, 1998). Diapensiaceae form a moderately supported clade (71%) with Styracaceae (including Halesiaceae). Theaceae *s.l.* do not form a clade in our analysis. Although *Eurya* and *Ternstroemia*, treated as Ternstroemiaceae in the APG (1998) classification, form a strongly supported (97%) group, *Camellia* of Theaceae *s.s.* is not closely related to these genera in the shortest trees obtained, and *Asteropeia*, treated as Asteropeiaceae (APG, 1998), falls in Caryophyllales. The last commonly recognized subfamily of Theaceae, Bonnetioideae, falls into Malpighiales next to Clusiaceae and Hypericaceae (Savolainen *et al.*, 2000b). Relationships within Ericales are in general agreement with earlier studies (e.g. Olmstead *et al.*, 1993; Kron & Chase, 1993; Morton *et al.*, 1997a). As in Malpighiales, the first few branches within the clade are short (3–7 steps; Fig. 10B), none of these has jackknife support $>50\%$, and some of these are not consistent in all shortest trees.

Euasterid I. This large group of asterids comprises a trichotomy in the jackknife consensus tree (Fig. 11A): (1) Oncothecaceae (55%), (2) Garryales and (3) a large, well-supported monophyletic group (99%) consisting primarily of three well-supported orders, Lamiales (99%), Gentianales (100%) and Solanales (96%), plus Vahliaceae and Boraginaceae. In the shortest trees obtained, Garryales and Oncothecaceae are successive sister groups to the large Lamiales/Gentianales/Solanales clade.

Icacina is sister to the remaining Garryales. Icacinaceae are shown here to be diphyletic in that the other two representatives of the family sampled (*Gonocaryum*,

Irvingbaileya) are part of eurastrid II (see below). Cardiopteridaceae (with a single genus *Peripterygium*) and the euasterid II members of Icacinaceae form a clade (Savolainen *et al.*, 2000b), so no new family will need to be described to clarify this taxonomic issue. *Peripterygium* closely resembles Icacinaceae (Cronquist, 1981), and both are clearly asterid in their characters: production of iridoid compounds, haplostemonous flowers typically with fused corolla (often forming a long floral tube) and unitegmic, tenuinucellate ovules. They are clearly not related to Celastraceae, with which they have been associated in many systems, and merit more detailed study. The remainder of Garryales forms a clade (82%) consisting of Eucommiaceae as sister to a strongly supported (100%) Garryaceae/Aucubaceae.

By far the largest clade of euasterid I comprises Lamiales, Gentianales and Solanales. Although the monophyly of each of these three subclades is strongly supported, relationships among them do not have jackknife support $\geq 50\%$ (Fig. 11A). In the shortest trees (Fig. 11B), Vahliaceae and then Boraginaceae consistently appear as immediate sister groups to Lamiales, followed by Solanales and then Gentianales. Placements of both Vahliaceae and Boraginaceae have been variable in previous analyses. Vahliaceae have often appeared (as in this analysis) as sister to Lamiales based on individual genes (e.g. Morgan & Soltis, 1993; Chase *et al.*, 1993; Soltis & Soltis, 1997). In contrast, Boraginaceae appeared as part of Solanales in some recent analyses, such as those based on *rbcL* sequences (e.g. Chase *et al.*, 1993; Savolainen *et al.*, 2000a, b); as with Vahliaceae, Boraginaceae were placed without specific alliance to order as members of euasterid I by APG (1998). A 158-taxon, four-gene analysis (Albach *et al.*, in press) revealed identical relationships of Vahliaceae and Boraginaceae to Lamiales but again without support $\geq 50\%$. Both this study and that of Albach *et al.* have increased sampling of Solanales, Gentianales and Lamiales compared to earlier analyses. Other studies have also not placed Boraginaceae within Solanales: *atpB* (Savolainen *et al.*, 2000a) and 18S rDNA (Soltis & Soltis, 1997).

Although Lamiales form a well-supported clade, few relationships within the order receive support $\geq 50\%$ other than the monophyly of a few families, such as Gesneriaceae, Acanthaceae and Lentibulariaceae. Even with sequences of three genes, the branches within this clade are very short (1–9 steps; Fig. 11B), so a great deal more sequence data will be needed before relationships in Lamiales can be confidently estimated. Lamiaceae, including *Callicarpa* (formerly Verbenaceae), are a strongly supported lineage (86%). Other members of Verbenaceae (*Verbena*, *Lantana*) form a distinct, well-supported clade. Members of Scrophulariaceae sampled form several, separate clades. One such clade with weak support (51%) includes *Anthrimum*, *Digitalis*, *Callitriche* (Callitrichaceae) and *Plantago* (Plantaginaceae). *Verbascum* and *Scrophularia* form a separate well-supported (100%) clade. These results for Scrophulariaceae and Lamiaceae plus Verbenaceae are in agreement with the results of more focused analyses involving many more taxa (e.g. Wagstaff & Olmstead, 1997; Olmstead & Reeves, 1995; Reeves & Olmstead, 1998); readers should consult these papers for a more comprehensive look at these families. What is clear from these results is that a complete overhaul of families in Lamiales is required. After the analyses were completed, we discovered that the terminal labelled as 'Phyla' was composed of hybrid set of sequences; it contained an *atpB* sequence of *Pedicularis*, whereas those for *rbcL* and 18S rDNA were from *Phyla*; however, removing the *atpB* sequence and replacing it with question marks did not change the placement of this terminal.

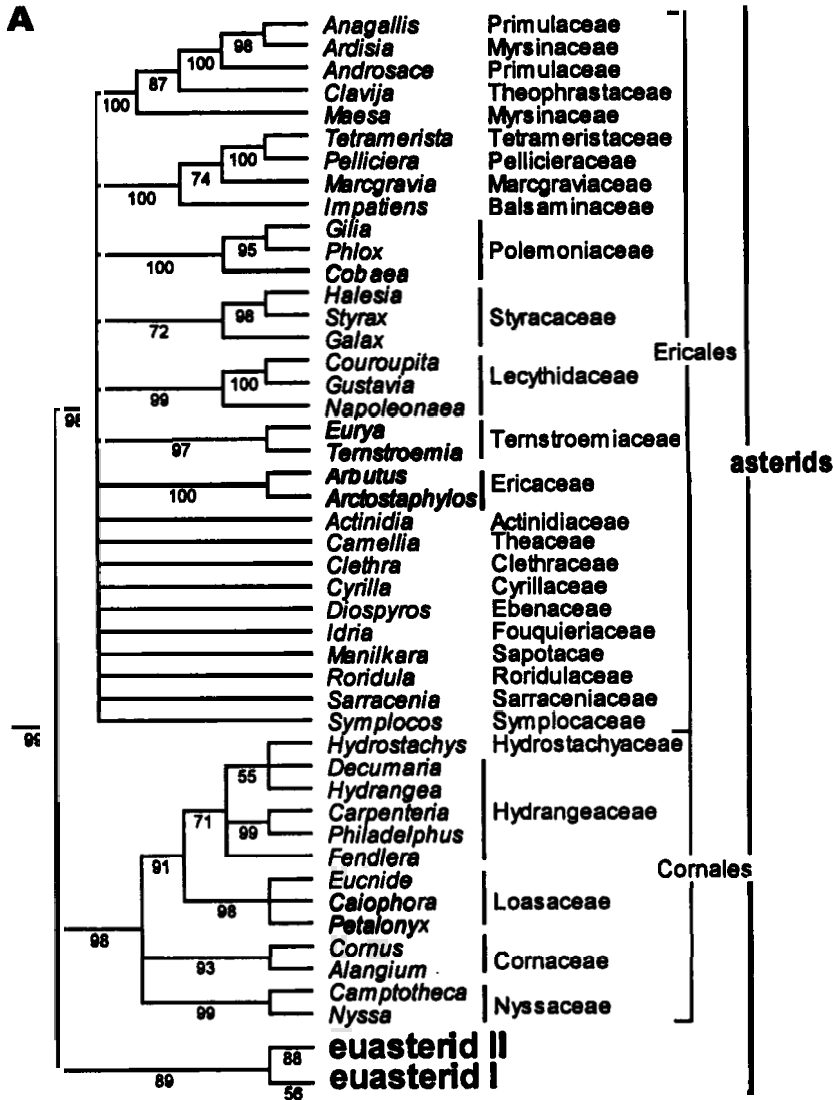


Figure 10. The jackknife consensus tree (A) focusing on the base of the asterids; (B) the same set of taxa from the single tree with branch lengths illustrated (ACCTRAN optimization); arrowheads indicate groups not found in all shortest trees. Note that in these shortest trees Cornales and Ericales form sister groups. Euasterid I and II are each indicated as single terminals.

Gentianales consist of a weakly supported Rubiaceae (58%) that is sister to a clade (78%) of Gentianaceae as sister to Loganiaceae/Apocynaceae. *Dialypetalanthus*, usually *Dialypetalanthaceae*, falls either as sister to Rubiaceae with weak support in the jackknife consensus tree or as sister to the whole of Gentianales, as in the shortest trees found. After this analysis was completed, it was discovered that the *rbcL* sequence used for *Dialypetalanthus* was a chimera of two sequences: the front half (700 bp) is from *Dialypetalanthus*, whereas the second half of the sequence was from an unknown contaminating angiosperm DNA. This mix-up is probably the reason

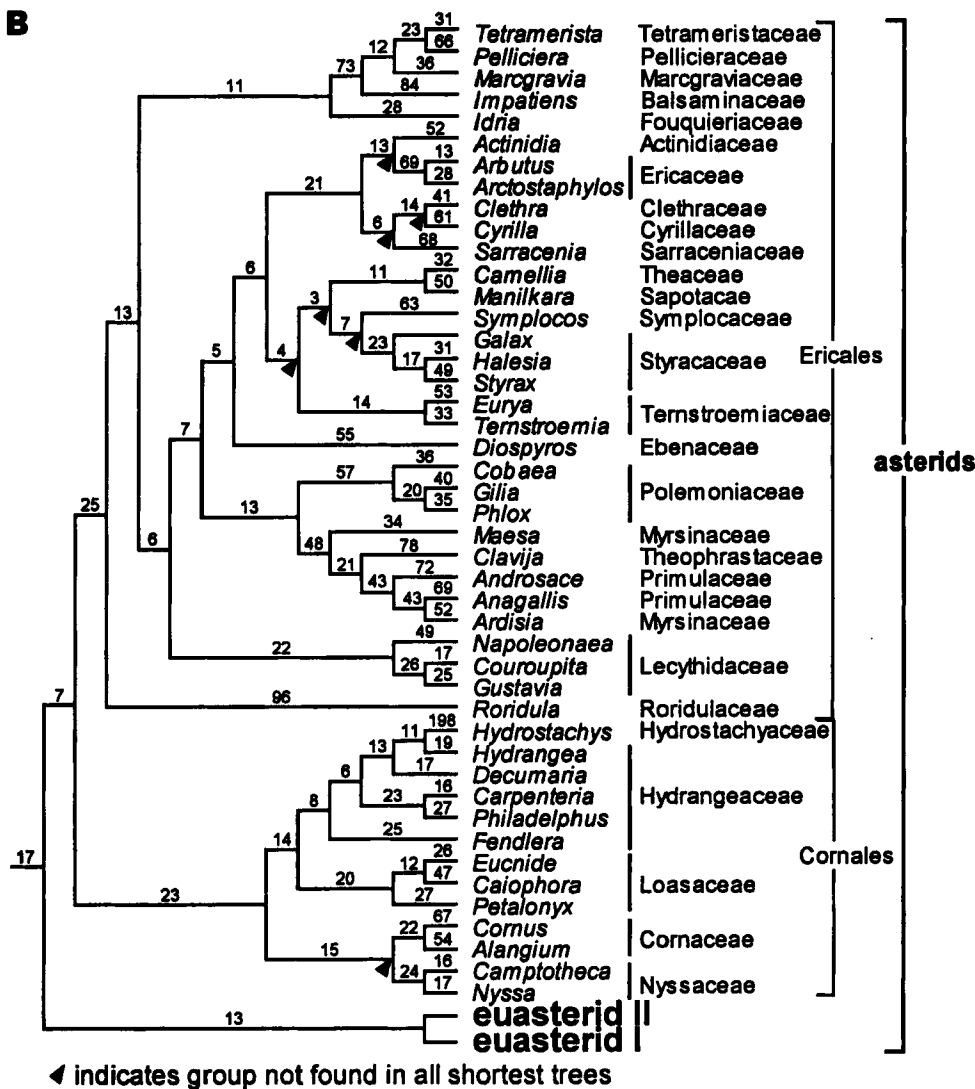


Figure 10. See caption on facing page.

that the shortest trees and the jackknife tree disagree. As noted earlier, because of the length of time required to conduct rigorous phylogenetic analyses of such a large data set, we did not feel it necessary to repeat our analyses with a corrected sequence. We now have a complete *rbcL* sequence for *Dialypetalanthus*, and it falls deeply into Rubiaceae, which eliminates the need for a separate family (Fay *et al.*, in press). Solanales comprise a well-supported (99%) family pair of Montiniaceae/Hydrroleaceae as sister to a broadly defined Solanaceae that includes *Nolana* (sometimes placed in Nolanaceae).

Euasterid II. Euasterid II consists of well-supported Aquifoliales (96%) as sister to a second large clade (97%) that contains all remaining members of euasterid II (Fig. 12A). This second clade within euasterid II comprises three major subclades that

A

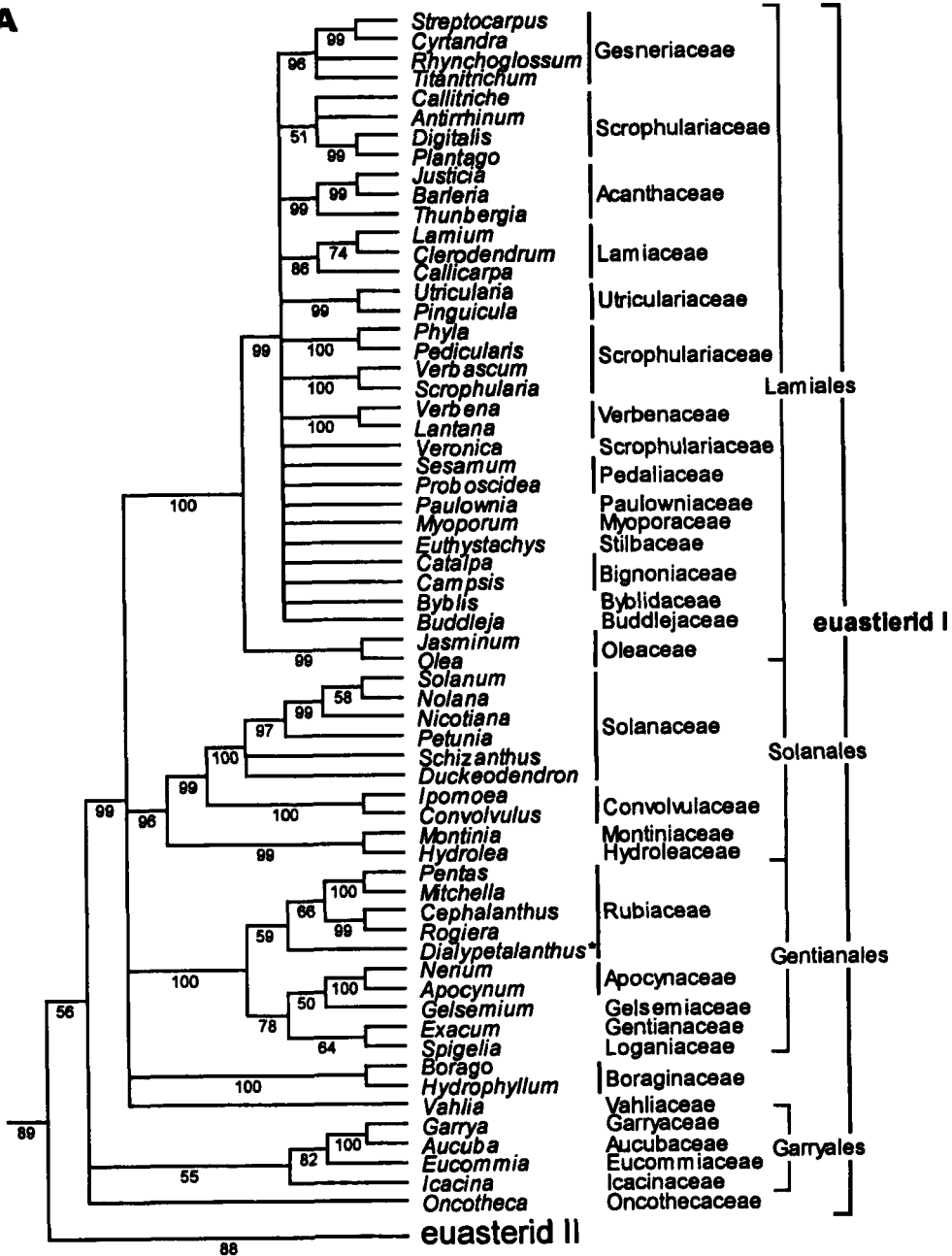


Figure 11. The jackknife consensus tree (A) focusing on the euasterid I clade; (B) the same set of taxa from the single tree with branch lengths illustrated (ACCTRAN optimization); arrowheads indicate groups not found in all shortest trees. Euasterid II are indicated as a single terminal. Note that Boraginaceae, Oncothecaceae, and Vahliaceae are unplaced to order.

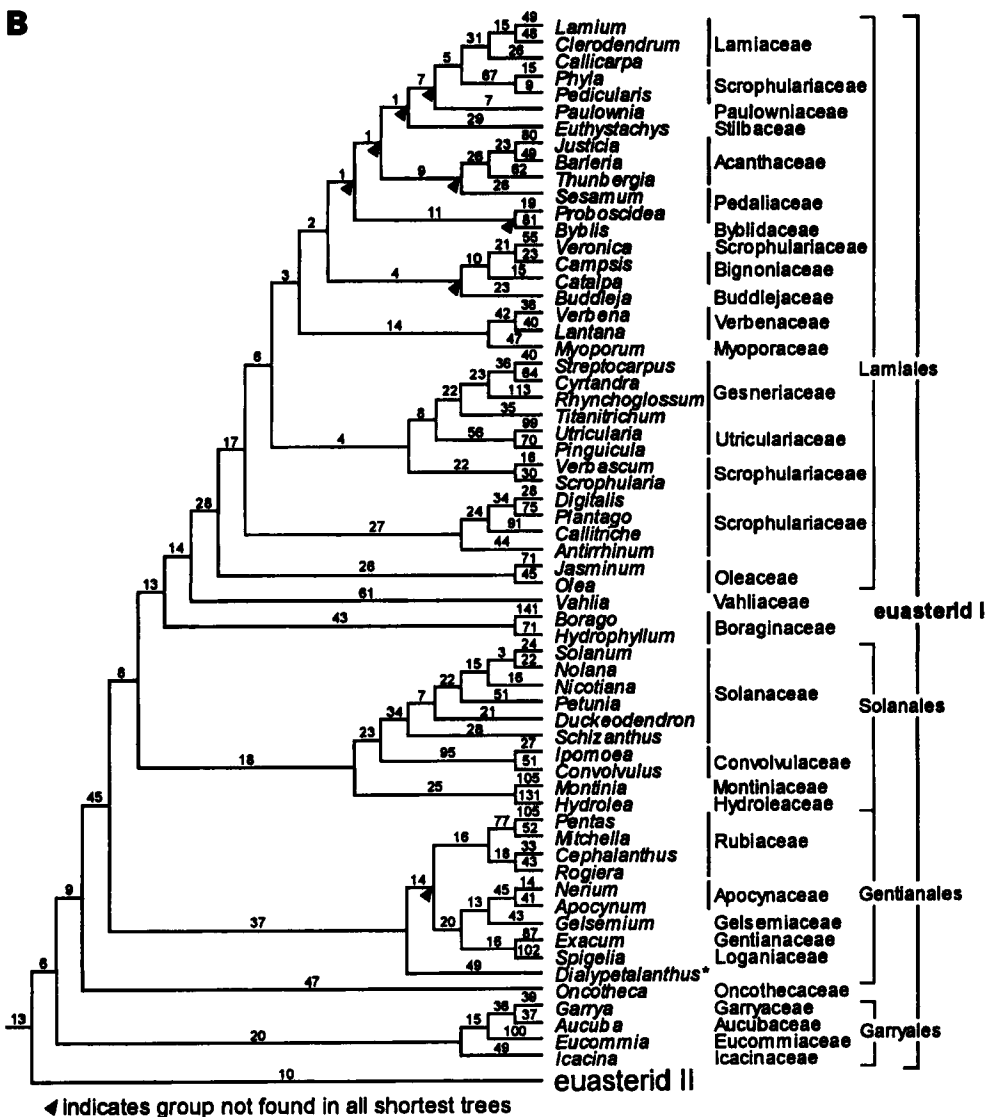


Figure 11. See caption on facing page.

are well supported, Apiales (100%), Dipsacales (86%) and Asterales (95%), as well as several taxa for which the closest relatives have >50% jackknife support, Eremosynaceae/Escalloniaceae and Bruniaceae.

Following APG (1998), Aquifoliales consist of Phyllonomaceae, Helwingiaceae and Aquifoliaceae, which form a well-supported clade (100%). Our study also reveals that two members of Icacinaceae, *Irvingbaileya* and *Gonocaryum*, are sister to this clade. As noted above, *Icacina*, a third genus of Icacinaceae sampled here, is part of euosid I. Together, Phyllonomaceae, Helwingiaceae, Aquifoliaceae and *Irvingbaileya*/*Gonocaryum* (Icacinaceae) form a well-supported Aquifoliales *s.l.* clade (96%); in future revisions of the APG classification, a broader circumscription of

Aquifoliales that includes some members of former Icacinaceae (probably to be called Cardiopteridaceae; see above; Savolainen *et al.*, 2000b) seems warranted.

Dipsacales consist of Adoxaceae as sister to a well-supported clade (100%) of Valerianaceae, Linnaeaceae, Caprifoliaceae and Dipsacaceae (see also Donoghue *et al.*, 1992). Valerianaceae are sister to a clade (80%) of *Abelia* (Linnaeaceae), which is in turn sister to a moderately supported (65%) Caprifoliaceae/Dipsacaceae. Our results for Dipsacales are in general agreement with those of Backlund and Bremer (1997), who discuss these relationships in more detail.

Adoxaceae represent another example of the value of this three-gene matrix in placing problematic families. Adoxaceae were considered a family of uncertain position (APG, 1998), but this three-gene analysis provides strong support (86%) for the inclusion of Adoxaceae within Dipsacales.

Apiales consist of Griselinaceae and Melanophyllaceae as sisters to a strongly supported (100%) core clade that is a trichotomy of Pittosporaceae, Araliaceae and Apiaceae. These results mirror those recently reported for Apiales based on a thorough sampling of taxa and *matK/rbcL* sequence data (e.g. Plunkett, Soltis & Soltis, 1997).

There is considerable phylogenetic structure within Asterales that also receives jackknife support $\geq 50\%$ (Fig. 12A). A weakly supported clade (58%) of Rouseaceae/Campanulaceae (including *Lobelia*) is sister to the remainder of Asterales, which form a weakly supported clade (61%). Within this portion of Asterales, a family pair (56%) of Donatiaceae/Stylidiaceae is sister to a clade (55%) of Phellinaceae, Alseuosmiaceae, *Corokia* (Argophyllaceae) and a strongly supported clade (100%) of Calyceraceae/Goodeniaceae and Asteraceae. These relationships within Asterales agree with phylogenetic analyses that have focused on this clade or portions of it (e.g. Cosner, Jansen & Lammers, 1994; Backlund & Bremer, 1997).

The relationships of *Escallonia/Eremosyne* and *Berzelia* (Bruniaceae) within euasterid II do not receive jackknife support $\geq 50\%$. *Escallonia* (Escalloniaceae) and *Eremosyne* (Eremosynaceae) form a well-supported clade (90%), in agreement with previous analyses (e.g. Hibsich-Jetter, Soltis & MacFarlane, 1997; Soltis & Soltis, 1997). In the shortest trees (Fig. 12B), they appear in a clade with Apiales and Dipsacales, but without support $\geq 50\%$; this placement is in general agreement with earlier analyses (e.g. Hibsich-Jetter *et al.*, 1997; Soltis & Soltis, 1997; Albach *et al.*, in press). Likewise, in our shortest trees, *Berzelia* also appears, along with *Escallonia/Eremosyne*, in a clade with Apiales and Dipsacales. An analysis of asterids based on four genes (*atpB*, *rbcL*, *ndhF*, 18S rDNA) places *Berzelia* as sister to *Escallonia/Eremosyne*, with this small clade as the sister group to Apiales and Dipsacales (Albach *et al.*, in press).

PATTERNS OF SEQUENCE VARIATION

One of the most striking aspects of this and other gene trees for the angiosperms is the highly uneven pattern of branch lengths. Groups that are highly divergent for plastid genes are also highly divergent for nuclear genes and vice versa, and this pattern extends as well to non-coding regions such as plastid *trnL-F* (Reeves *et al.*, submitted; Sheahan & Chase, 2000) and nuclear ITS (Whitten *et al.*, 2000). Groups with unusual or atypical life-history strategies (e.g. parasites, mycotrophs, xerophytes, aquatics) seem to have higher rates of sequence divergence than close relatives with

more typical or 'standard' life histories (e.g. Nickrent *et al.*, 1998). There are many such examples in the gene trees presented here, including: *Ceratophyllum* relative to all other angiosperms (Fig. 1B); *Burmannia* (Burmanniaceae) relative to *Tacca* and *Dioscorea* (both Dioscoreaceae; Fig. 3B; Caddick *et al.*, 2000); the whole of Caryophyllales *s.l.* and other orders (*rbcL*, for example, can be used at the species level within Droseraceae and Plumbaginaceae; Williams *et al.*, 1994; Lledó *et al.*, 1998; Fig. 3B); *Stackhousia* and *Siphonodon* (Celastraceae; Fig. 7B); *Marathrum* (Podostemaceae) and Clusiaceae (Fig. 8B); *Hydrostachys* and Hydrangeaceae (Fig. 10B); *Callitriche* and other members of its clade of Scrophulariaceae (Fig. 11B); and *Nymphoides* and *Menyanthes* (Menyanthaceae; Fig. 12B). Molecular evolution is clearly not consistent across all lineages of the angiosperms; it is much faster in taxa that have undergone reorganization of vegetative organs, leaving the impression that both morphological and molecular evolution experience episodic bursts in parallel.

Apart from such exceptional cases, there is also evidence that change at some loci is nearly clock-like or 'quasi-ultrametric' (Albert *et al.*, 1994). If the genes of most taxa are evolving at nearly constant rates over time, then we must also seek a biological explanation for the mixture of long and short branches that mark the major groups of taxa (i.e. clades such as euasterid I, eurosids and asterids, clades recognized as orders and families, as well as intrafamilial clades, e.g. Jansen & Kim, 1996; Cameron *et al.*, 1999; Richardson *et al.*, in press). The general pattern is indicative of episodic phyletic radiations (short branches) producing lineages that exist for long periods (long branches), followed by another phyletic burst, and so on. This contrasts with the red algae (Freshwater *et al.*, 1994), in which the pattern of change in *rbcL* across all branches gives the appearance of slow and clock-like lineage production without the periodic 'starbursts' present in the angiosperm tree. This difference could be due simply to differences in patterns of speciation between marine (stable) and terrestrial (unstable) environments or reflect differences in the complexity of both the organisms and their interactions with other organisms. Whatever the reasons, the uneven pattern of nucleotide change exists and begs for an explanation.

PATTERNS OF EVOLUTION

We have not sampled intensively within families, and so it is on this effectively lowest taxonomic category present in these trees we will first focus. If one examines the complete range of morphological/anatomical/biochemical characters that exist within the angiosperms, then it quickly becomes apparent that many possible combinations of angiosperm traits do not exist or are rare. For example, the combination of two whorls of five perianth parts with stamens arranged in a spiral does not exist (although the reverse does in a few genera of Kiggelariaceae in tribe Erythrospermeae), and the combination of unitegmic/tenuinucellate ovules and diplostemonous flowers is largely unknown outside of Santalales, in which a large range of variability in these and other characters exists (Santalales are difficult to place using DNA sequences as well; see above section on Santalales). Clades that systematists have named 'families' are highly canalized in their traits, which is of course one of the reasons why they have a long history of being recognized as some form of higher taxonomic category. Most families are easily and accurately

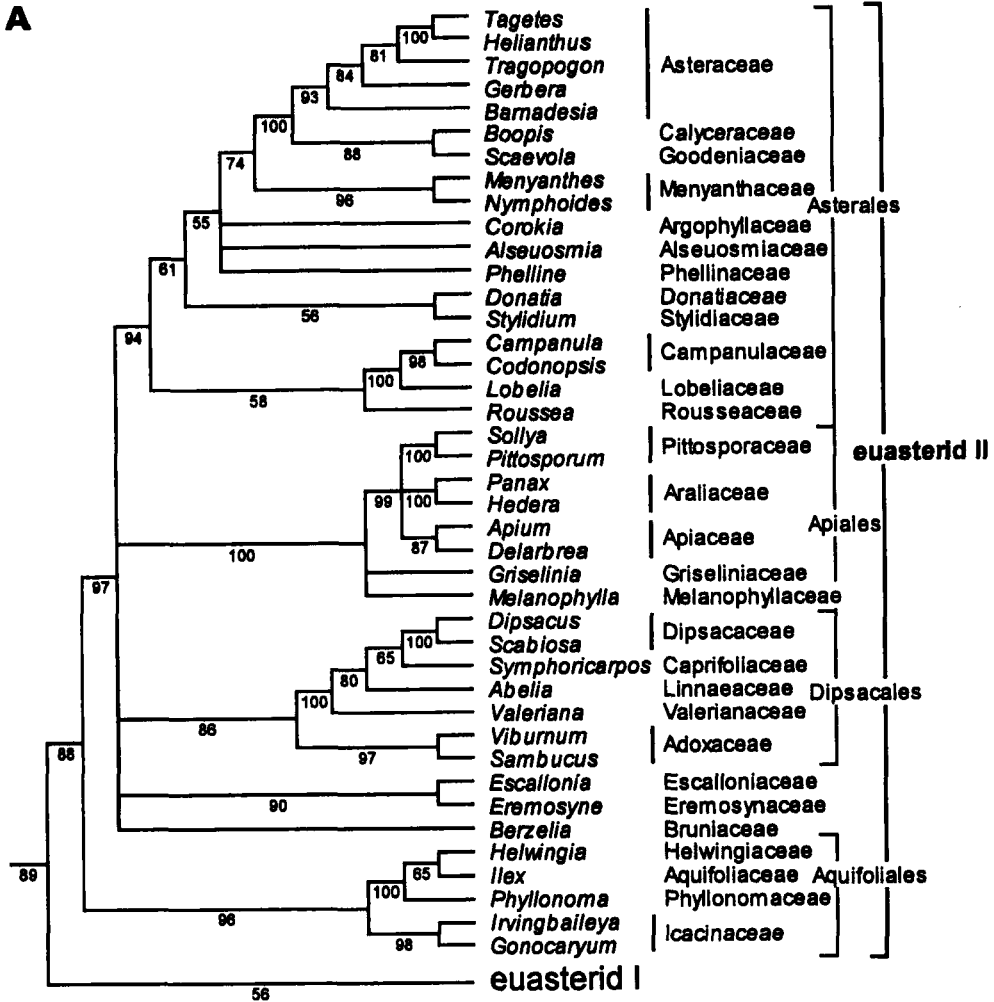


Figure 12. The jackknife consensus tree (A) focusing on the euasterid II clade; (B) the same set of taxa from the single tree with branch lengths illustrated (ACCTRAN optimization); arrowheads indicate groups not found in all shortest trees. Euasterid I are indicated as a single terminal. Note that Bruniaceae, Eremosynaceae, and Escalloniaceae are unplaced to order.

diagnosable with multiple characters (there are notable exceptions, Flacourtiaceae, for example, and the single-character families that were artificially circumscribed in Lamiales, Liliales and Asparagales), and they have been equally easy to identify in molecular systematic studies. In most cases, one gene (typically *rbcL*) contained enough variable sites to ‘find’ the great majority of families.

The reason why most angiosperm families have been easy to find in DNA studies is that they are marked by the ‘long branch’ portions of the angiosperm tree. For example, within Zingiberales (Fig. 4B) all of the families recognized on morphological grounds have long branches and have been easily identified by DNA studies (e.g. Smith, Kress & Zimmer, 1993). The sister-family pairs Costaceae/Marantaceae differ by 48 assessed substitutions and Cannaceae/Zingiberaceae differ by 170,

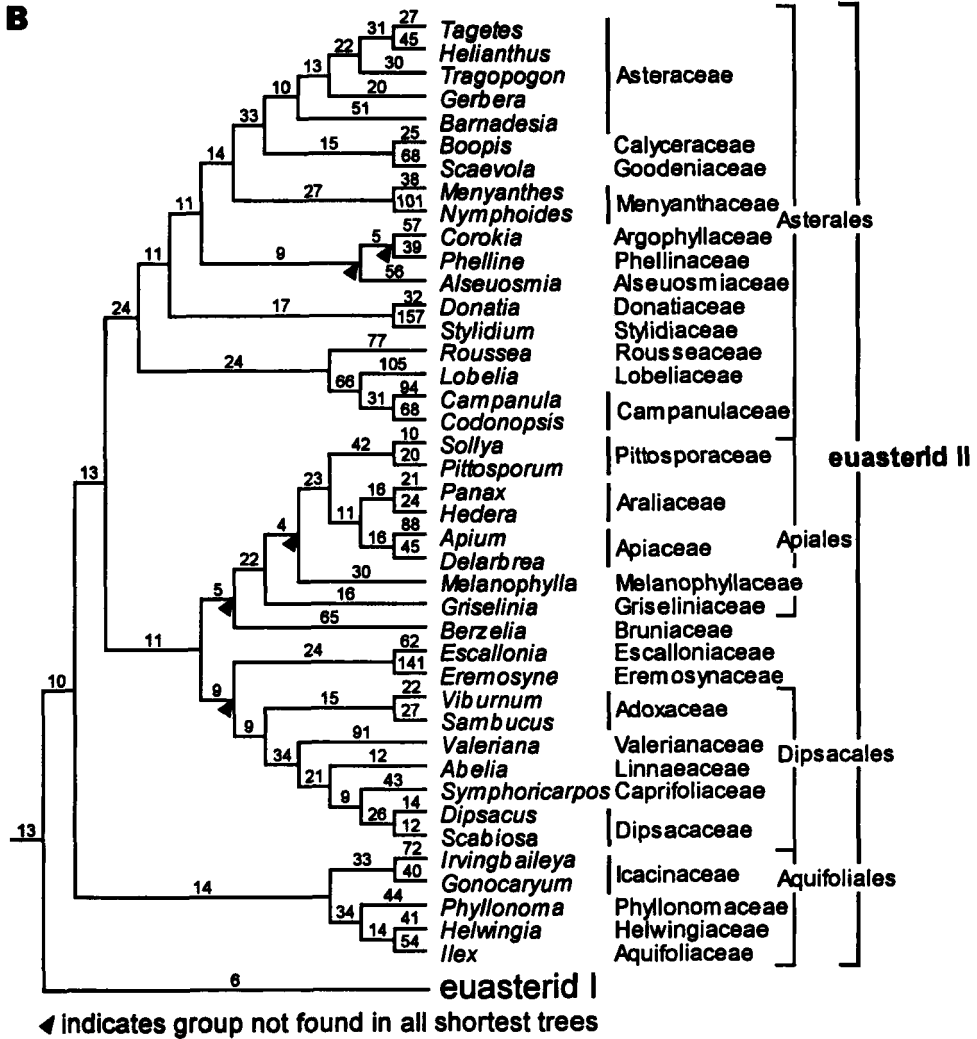


Figure 12. See caption on facing page.

whereas the two pairs of families, Costaceae/Marantaceae and Cannaceae/Zingiberaceae, differ by only 16; the families are clearly separated, but the sets of families are not. This same sort of pattern occurs throughout the angiosperms at this level in the hierarchy. Those lineages that we recognize as families are not a random division of morphological/anatomical possibilities, and the fact that these taxonomic categories and longer branches coincide is not due to chance. They are the result of the canalization of suites of traits within lineages over long periods of time; thus, they are as easy to find with DNA data as they generally are with morphological data because they have existed long enough to have accumulated a large number of substitutions.

This same pattern also is evident at deeper levels within the angiosperms. For example, within the eurosid I clade (Fig. 7B), we observe that detecting clades that correspond to recognized orders has been relatively straightforward; nearly all of

these were obvious in the first large analysis of *rbcL* data (Chase *et al.*, 1993). The APG classification of families arranged in orders was largely a simple matter of naming well-supported groups, and the well-supported groups are those with long branches. Regardless of the hierarchical level at which they were recognized, these were easily found with a minimal amount of DNA data. However, above the level of family (which are also well-supported) there are generally few other levels within most of these orders that we could confidently name because the branches are short and cannot be 'found' with even three genes. For example, branch-length patterns and support within Malpighiales and Ericales (Figs 8, 10) are repeated in nearly all the clades recognized as orders. Many orders are not as poorly resolved internally in the jackknife tree as are Malpighiales and Ericales, but the pattern of groups with 95–100% jackknife support tracks branch length, and branch lengths track in a most uncanny way clades that have long been recognized as families and then again larger sets of families (which the APG system, 1998, recognized as orders).

Family names have therefore been assigned to groups with canalized suites of traits, most of which are easily observed with the unassisted eye, but those clades recognized as orders are not so easily diagnosed morphologically; many of the orders recognized on the basis of DNA studies were not present in any previous classification based on morphology. The reason for this could be fact that the phyletic radiation that produced clades we recognize as orders has been obscured by the subsequent radiations that produced clades we recognize as families, producing a 'saturation' of morphological characters that is similar to the way that highly variable base positions in genes can be saturated and become difficult to sort out at great phylogenetic distances. Larger clades corresponding to the higher categories (e.g. eurosids and euasterids) are even more difficult to decipher morphologically for the same reason: phyletic radiations are working with the same suites of gross morphological traits that interact with the environment. Perhaps the evidence for the existence of the earlier phyletic radiations can be found in characters that have not been widely used in higher-level angiosperm classification, such as biochemical pathways, developmental traits and micromorphological details. These traits cannot be observed without technological assistance, and assessing them in any statistically meaningful percentage of taxa is a lengthy and expensive undertaking. Only rarely do we have a clear picture of synapomorphies for clades recognized as orders and higher categories (still recognized here informally; i.e. eurosids, etc.); for example, mustard-oil synthesis for Brassicales (Rodman *et al.*, 1993) and mucilage in special cells, cavities or canals for Malvales (Nandi *et al.*, 1998). With our present knowledge, we have little idea of the potential synapomorphies that may exist for many orders (Nandi *et al.*, 1998).

Fortunately, DNA sequencing is neither time consuming nor expensive with automated technology, so systematic botanists and other evolutionary biologists have a much better chance of detecting these patterns, but until we produced multiple, large nucleotide data sets we could not have predicted how congruent nor consistent phylogenetic and branch-length patterns would be. We suggest that patterns of change in molecules and morphology (broadly defined) are correlated. Deep-level clades are canalized lineages that represent the end products of periodic rapid bursts of reorganization of gross morphology. The causes of these episodes are unknown but of great evolutionary significance. Our best chance of understanding such phenomena is closely tied to how accurate our estimates of relationships of these

taxa are, and we hope that congruent independent and well-supported combined data sets will be the means to this end.

FUTURE PROSPECTS

The resolution and support of relationships revealed by this three-gene analysis based on 567 taxa represent a dramatic improvement over previous analyses, which were all based on fewer taxa and either one data set (e.g. Chase *et al.*, 1993; Soltis *et al.*, 1997a) or two data sets combined (e.g. Nandi *et al.*, 1998; Savolainen *et al.*, 2000a). Much of the big picture of angiosperm phylogeny is now well resolved and well supported. Future work should concentrate on the following key issues.

Several major questions of angiosperm phylogeny remain at higher levels, and a number of these involve relationships within the noneudicots. Although the initial branching order in the angiosperms now appears well established with strong support (Mathews & Donoghue, 1999; Parkinson *et al.*, 1999; Qiu *et al.*, 1999), additional studies are also needed to ascertain relationships among the six subclades of eumagnoliids: Chloranthales, monocots, Piperales, Laurales, Winterales and Magnoliales. The placement of Ceratophyllaceae also remains a major question. Within the monocots, the relationships of the orders within the commelinoids are uncertain, as are the relationships of the orders Asparagales, Dioscoreales, Liliales and Pandanales.

The relationships among the six major clades of core eudicots also require further data collection to resolve. The current three-gene analysis essentially depicts a polytomy among six subclades: (1) Berberidopsidales (Berberidopsidaceae/Aextoxicaceae), (2) Gunnerales (Gunneraceae/Myrothamnaceae), (3) Saxifragales/Vitaceae/eurosids, (4) Santalales, (5) Dilleniaceae/Caryophyllales and (6) asterids. Within some of the larger eudicot clades, relationships among some of the orders also require clarification. For example, within eurosid I, the relationship among Rosales, Fabales and Cucurbitales/Fagales requires study. The relationships of Geraniales, Crossosomatales and Myrtales to the other eurosid orders are also not determined with confidence.

Most of these large-scale questions can best be addressed via the sequencing of additional genes—in many of these cases, it may not be necessary or desirable to add more taxa. Several sequencing efforts are presently underway to resolve phylogenetic relationship within the noneudicots; the entire 26S rDNA and two mitochondrial genes are now being sequenced. The phylogenetic utility of 26S rDNA sequence data in the angiosperms has recently been demonstrated (Kuzoff *et al.*, 1998; Fishbein *et al.*, in press). Sequencing of the entire 26S rDNA, or perhaps only a portion of this large gene (approx. 3400 bp in length), may be useful in resolving relationships among the clades of eumagnoliids, as well as among the core eudicots.

On a finer scale, the composition of several proposed orders of angiosperms needs clarification, such as the relationship of Boraginaceae to Solanales and the circumscription of Crossosomatales. Addressing these questions may require more focused analyses of euasterid I and eurosid II, respectively; these analyses also require the addition of characters (e.g. additional gene sequence data), and might also benefit from the addition of taxa. For example, additional genera of Boraginaceae

could be included to help place this family. Similarly, clarifying the circumscription of Geraniales may require the addition of more representatives of Staphyleaceae.

The relationships of a number of enigmatic families remain uncertain (APG, 1998). Most of these small families have been rarely studied and have not been included in the large phylogenetic analyses conducted to date. This three-gene analysis, and other recent studies involving the *rbcL* and 18S rDNA data sets, have demonstrated the great value of obtaining sequence data for these problematic groups and then adding those sequences to the large data base currently available.

Lastly, these phylogenetic trees for angiosperms and the consequent reclassification of flowering plants should play a pivotal role in comparative studies in diverse fields from ecology to molecular evolution (Soltis, Soltis & Chase, 1999). The well resolved and strongly supported topology shown here provides the framework needed for evolutionary examination of a diverse array of traits in a phylogenetic context.

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APPENDIX: LIST OF TAXA SEQUENCED

FAMILY	SPECIES (atpB)	VOUCHER (atpB)	CITATION (atpB)	EMBL (atpB)
Acanthaceae	<i>Barleria prionitis</i> L.	Scotland 18	this paper	AJ236179
Acanthaceae	<i>Justicia americana</i> (L.) Vahl.	Olmstead 90-011 WTU	this paper	AJ236178
Acanthaceae	<i>Thunbergia coccinea</i> Wall.	Chase 2539 K	Savolainen et al. 2000a	AJ235625
Achariaceae	<i>Acharia tragodes</i>	Chase 812 NCU	this paper	AF209520
Acoraceae	<i>Acorus calamus</i> L.	Chase 2758 K	Savolainen et al. 2000a	AJ235381
Actinidiaceae	<i>Actinidia chinensis</i> Planch.	Kron 2117 NCU	Savolainen et al. 2000a	AJ235382
Adoxaceae	<i>Sambucus nigra</i> L.	Chase 2509 K	Savolainen et al. 2000a	AJ235591
Adoxaceae	<i>Viburnum opulus</i> L.	Chase 2519 K	Savolainen et al. 2000a	AJ235640
Aextoxicaceae	<i>Aextoxicon punctatum</i> Ruiz & Pav.	Chase 959 K	Savolainen et al. 2000a	AJ235384
Agavaceae	<i>Agave ghesbreghtii</i> C. Koch	Chase 3467 K	this paper	AF209521
Aizoaceae	<i>Delosperma echinatum</i> (Lam.) Schwantes	Chase 2539 K	Savolainen et al. 2000a	AJ235452
Akaniaceae	<i>Akania bidwillii</i> (Hogg) Mabf.	Fernando & Quinn s.n. UNSW	this paper	AF209522
Alliaceae	<i>Allium altaicum</i> Pall.	Chase 834 K	this paper	AF209525
Alseuosmiaceae	<i>Alseuosmia macrophylla</i> A. Gunn.	Morgan 2141 WS	this paper	AJ236198
Alstroemeriaceae	<i>Bomarea hirtella</i> Herb.	Chase 520 K	Savolainen et al. 2000a	AJ235413
Altingiaceae	<i>Altingia excelsa</i> Noronha	Hoot 9225 UWM	Hoot et al. 1999	AF092103
Altingiaceae	<i>Liquidambar styraciflua</i> L.	Kron 162 NCU	Hoot et al. 1999	AF092104
Amaranthaceae	<i>Celosia argentea</i> L.	none	this paper	AF209559
Amaranthaceae	<i>Spinacia oleracea</i> L.	none	Chase et al. 1993	U23082
Amaryllidaceae	<i>Clivia nobilis</i> Lindl.	Chase 3080 K	this paper	AF209566
Amaryllidaceae	<i>Hippeastrum papilio</i> (Ravenne) J. Van Scheepen	Hahn s.n. US	this paper	AF168924
Amborellaceae	<i>Amborella trichopoda</i> Baill.	Thien 500 NCU	Savolainen et al. 2000a	AJ235389
Anacardiaceae	<i>Schinus molle</i> L.	Anderson 13601 MICH	Bakker et al. 1998	AF035914
Ancistrocladaceae	<i>Ancistrocladus korupensis</i> D. W. Thomas & R. E. Gereau	Gereau et al. 5203 MO	this paper	AF209526
Annonaceae	<i>Annona muricata</i> L.	Qiu 90031 NCU	Savolainen et al. 2000a	AJ235393
Annonaceae	<i>Asimina triloba</i> (L.) Dunal	Qiu 15 NCU	this paper	AF209532
Anthericaceae	<i>Chlorophytum comosum</i> Baker	Kress 92 3434 US	this paper	AF168894
Aphloiaceae	<i>Aphloia theaeformis</i> Benn.	Prance 30804 K	this paper	AF209528
Apiaceae	<i>Apium graveolens</i> L.	Chase 2523 K	Savolainen et al. 2000a	AJ235396
Apiaceae	<i>Melanophylla alnifolia</i> Baker	Schatz 3552 MO	this paper	AF209625
Apocynaceae	<i>Apocynum androsaemifolium</i> L.	Soltis & Soltis 2534 WS	this paper	AF209529
Apocynaceae	<i>Nerium oleander</i> L.	Albach 3 WS	this paper	AJ236189
Aponogetonaceae	<i>Aponogeton elongatus</i> Benth.	Hahn s.n., WIS	this paper	AF168887
Aquifoliaceae	<i>Ilex crenata</i> Thunb.	Chase 119 NCU	Savolainen et al. 2000a	AJ235502
Araceae	<i>Gymnostachys anceps</i> R. Br.	Kress 92-3417, US	this paper	AF168915
Araceae	<i>Spathiphyllum wallisii</i> Hort.	Chase 201 NCU	Savolainen et al. 2000a	AJ235606
Araliaceae	<i>Delarbrea michieana</i> F. v. Muell.	Plunkett 1366 WS	this paper	AJ236211
Araliaceae	<i>Hedera helix</i> L.	Chase 2743 K	Savolainen et al. 2000a	AJ235488
Araliaceae	<i>Panax quinquefolium</i> L.	Ware 10046 WILLI	this paper	AJ236210
Areceaceae	<i>Calamus</i> sp.	Fairchild Trop Garden 64-129 C	this paper	AF233081
Areceaceae	<i>Caryota mitis</i> Lour.	Hahn 6627 WIS	this paper	AF233083
Areceaceae	<i>Chamaedorea sieffrizii</i> Burret	Hahn 6897 WIS	this paper	AF233083
Areceaceae	<i>Iriartea deltoidea</i> Ruiz & Pavon	Grifo s.n. WIS	this paper	AF233084
Areceaceae	<i>Metroxylon vitiense</i> (H.A. Wendl.) Benth. & J.D. Hook.	Fairchild Trop Garden 89-197	this paper	AF233086
Areceaceae	<i>Phoenix canariensis</i> Chabaud	Chase 1396 K	this paper	AF209652

VOUCHERS, AND LITERATURE CITATIONS

SPECIES (rbcL)	CITATION (rbcL)	EMBL (rbcL)	SPECIES (18S)	VOUCHER (18S)	CITATION (18S)	EMBL (18S)
same species	Chase et al. 1993	L01886	same DNA as for atpB	same as for atpB	this paper	AF107567
same DNA	Chase et al. 1993	L14401	same DNA	same	this paper	AF107568
<i>T. usambarica</i> Lindau	Chase et al. 1993	L12956	<i>T. alata</i>	Olmstead 93-045 WTU	this paper	AF107569
same DNA	this paper	AF206728	same DNA	same	this paper	AF206837
same species	Duvall et al. 1993	M901625	same species	Nickrent 2941 SIU	Nickrent & Soltis 1995	L24078
same DNA	Chase et al. 1993	L01882	<i>Actinidia</i> sp.	Morgan WS	Soltis et al. 1997a	U42495
<i>S. racemosa</i> L.	Donoghue et al. 1992	L14066	<i>S. ehulus</i>	Albach 11 WS	this paper	AJ236005
<i>V. acerifolia</i> L.	Olmstead et al. 1992	L01959	<i>V. acerifolia</i> L.	Soltis 2561 WS	this paper	AJ236007
same DNA	Alverson et al. 1998	X83986	same DNA	same	this paper	AF206839
<i>Agave</i> sp.	Chase et al. 1993	AF206729	same DNA as for atpB	same	this paper	AF206841
same DNA	Savolainen et al. 2000a	AJ235778	same DNA	same	this paper	AF206899
same DNA	Gadek et al. 1992	L12568	same DNA	same	Rodman et al. 1998	L12568
same DNA	this paper	AF206731	<i>A. thunbergii</i> G. Don	NA 55049 US	Soltis et al. 1997a	U42071
same DNA	this paper	X87377	same DNA	same	this paper	AF206844
same DNA	Chase et al. 1995	Z77255	same DNA	same	this paper	AF206871
unknown	Chase et al. 1993	AF206732	same DNA	same as rbcL	Soltis et al. 1997a	U42552
<i>L. formosana</i> Hance	Chase et al. 1993	M58394	<i>L. styraciflua</i> L.	Soltis & Soltis 2516 WS	Soltis et al. 1997a	U42553
same DNA	this paper	AF206747	same DNA	same	this paper	AF206883
same species	Chase et al. 1993	J01443	same species	Nickrent 2896 SIU	Nickrent & Soltis 1995	L24420
<i>C. miniata</i> Regel	Duvall et al. 1993	L05032	same DNA as for atpB	same as for atpB	this paper	AF206889
same DNA	this paper	AF206776	<i>Hippeastrum</i> sp.	Hahn 6875 WIS	Soltis et al. 1997a	U42065
same DNA	Qiu et al. 1993	L12628	same species	Suh 44 US	Soltis et al. 1997a	U42497
same DNA	Gadek et al. 1996	U39270	same DNA	same	Soltis et al. 1999	AF207015
same DNA	this paper	AF206733	same DNA	same	this paper	AF206846
same DNA	Qiu et al. 1993	L12629	same DNA	same	this paper	AF206850
same DNA	Qiu et al. 1993	L12631	same DNA	same	this paper	AF206856
<i>C. comosum</i> Baker	Chase et al. 1993	L05031	same DNA as for atpB	same as for atpB	Soltis et al. 1997a	U42066
same DNA	this paper	AF206735	same DNA	same	this paper	AF206851
same species	Chase et al. 1993	L01885	same species	Plunkett 1332 WS	this paper	AF206852
same DNA	Plunkett et al. 1997	U50254	same DNA	same	this paper	AF206960
<i>A. cannabinum</i> L.	Olmstead et al. 1992	L11678	same DNA as for atpB	same as for atpB	this paper	AF107571
same DNA	this paper	AF206799	same DNA	same	this paper	AF107572
same species	Les et al. 1997	U80683	same DNA as for atpB	same as for atpB	this paper	AF168826
same DNA	Chase et al. 1993	L01928	<i>I. opaca</i> Ait.	Soltis & Soltis 2552	Soltis et al. 1999	AF206938
same species	Duvall et al. 1993	M91629	same DNA as for atpB	same as for atpB	Hershkovitz et al. 1999	AF069200
same DNA	Chase et al. 1993	AJ235807	same DNA	same	this paper	AF207023
same DNA	Plunkett et al. 1997	U50243	same DNA	same	this paper	AF107573
same species	Xiang et al. 1993	L01924	same species	Plunkett 1368 WS	Soltis et al. 1997a	U42500
same DNA	Plunkett et al. 1997	U50250	same DNA	same	this paper	AF107574
<i>C. usitatus</i> Mart.	Chase et al. 1993	M81810	same DNA as for atpB	same as for atpB	this paper	AF168828
same species	Chase et al. 1993	M81811	same DNA as for atpB	same as for atpB	this paper	AF168831
<i>C. costaricana</i> Oerst.	Chase et al. 1993	AF206748	same DNA as for atpB	same as for atpB	Hershkovitz et al. 1999	AF069209
same DNA	this paper	AF233088	same DNA	same	this paper	AF168854
same DNA	this paper	AF233089	same DNA	same	this paper	AF168860
<i>P. reclinata</i> Jacq.	Chase et al. 1993	M81814	same DNA as for atpB	same as for atpB	this paper	AF206991

continued

APPENDIX—

FAMILY	SPECIES (atpB)	VOUCHER (atpB)	CITATION (atpB)	EMBL (atpB)
Arecaceae	<i>Podococcus barteri</i> G. Mann & H.A. Wendl.	Fairchild Trop Garden 88-480	this paper	AF233086
Argophyllaceae	<i>Corokia cotoneaster</i> Raoul	Chase 2752 K	Savolainen et al. 2000a	AJ235445
Aristolochiaceae	<i>Aristolochia macrophylla</i> Lam.	Qju 91019 NCU	Savolainen et al. 2000a	AJ235399
Aristolochiaceae	<i>Asarum canadense</i> L.	Hoot 923 UWM	Hoot et al. 1999	U86383
Aristolochiaceae	<i>Saruma henryi</i> Oliv.	Chase 3077 K	Savolainen et al. 2000a	AJ235595
Aristolochiaceae	<i>Lactoris fernandeziana</i> Phil.	Steussy 11335 OS	Savolainen et al. 2000a	AJ235515
Asparagaceae	<i>Asparagus officinalis</i> L.	Duvall 19920604 UCR	Savolainen et al. 2000a	AJ235400
Asphodelaceae	<i>Bulbine succulenta</i> Compton	UCJ Arb. 7174	Savolainen et al. 2000a	AJ235421
Asteliaceae	<i>Milligania stylolosa</i>	Chase 511 K	this paper	AF209628
Asteraceae	<i>Barnadesia caryophylla</i> (Vell.) S.F. Blake	Jansen 911 MICH	this paper	AF209537
Asteraceae	<i>Gerbera</i> sp.	Albach 22 WS	this paper	AJ236200
Asteraceae	<i>Helianthus annuus</i> L.	Albach 4 WS	this paper	AJ236205
Asteraceae	<i>Tagetes</i> sp.	Nickrent 3061 SIU	this paper	AJ236206
Asteraceae	<i>Tragopogon dubius</i> Scop.	Soltis 2472 WS	this paper	AJ236197
Asteropeiaceae	<i>Asteropeia micrastra</i> H. Halier	Civeyrel s.n. K	this paper	AF209533
Atherospermataceae	<i>Laurelia novae-zelandiae</i> A. Cunn.	Strybing Arb.	this paper	AF209615
Aucubaceae	<i>Aucuba japonica</i> Thunb.	Chase 1095 K	Savolainen et al. 2000a	AJ235402
Austrobaileyaaceae	<i>Austrobaileya scandens</i> C.T.White	Qju 90030 NCU	Savolainen et al. 2000a	AJ235403
Balanopaceae	<i>Balanops viellardii</i> Baill.	Chase 1816	this paper	AF209534
Balsaminaceae	<i>Impatiens repens</i> Moon	Chase 901 K	Savolainen et al. 2000a	AJ235503
Barbeyaceae	<i>Barbeya oleoides</i> Schwein.	Collenette 1/93 K	this paper	AF209535
Bataceae	<i>Batis maritima</i> L.	Itlis 30500 WIS	this paper	AF209538
Begoniaceae	<i>Begonia metallica</i> x <i>sanguinea</i>	Chase 225 NCU	this paper	AF209541
Behniaceae	<i>Behnia reticulata</i> F. Didrichs	Goldblatt 9273 MO	this paper	AF209542
Berberidaceae	<i>Caulophyllum thalictroides</i> (L.) Michx.	Hoot 925 UWM	Hoot et al. 1999	AF092108
Berberidaceae	<i>Nandina domestica</i> Thunb.	Hoot 922 UWM	Hoot et al. 1999	L37930
Berberidopsidaceae	<i>Berberidopsis corallina</i> Hook.	Chase 555 K	Savolainen et al. 2000a	AJ235409
Betulaceae	<i>Alnus incana</i> Moench	unknown	?	X56618
Betulaceae	<i>Betula pendula</i> Roth	Chase 2539 K	Savolainen et al. 2000a	AJ235411
Bignoniaceae	<i>Campsis radicans</i> Seem.	Course 0295a OS	this paper	AJ236168
Bignoniaceae	<i>Catalpa bignonioides</i> Walt.	Chase 2539 K	Savolainen et al. 2000a	AJ235428
Bixaceae	<i>Bixa orellana</i> L.	Chase 243 NCU	Bakker et al. 1998	AF035897
Blandfordiaceae	<i>Blandfordia punicea</i> Sweet	Chase 519 K	Savolainen et al. 2000a	AJ235412
Boraginaceae	<i>Borago officinalis</i> L.	Chase 2746 K	Savolainen et al. 2000a	AJ235498
Boraginaceae	<i>Hydrophyllum canadense</i> L.	Chase 2548 K	Savolainen et al. 2000a	AJ235498
Boryaceae	<i>Borya septentrionalis</i> F. Muell.	Chase 2205 K	this paper	AF209543
Brassicaceae	<i>Brassica balearica</i> Pers.	Chase 1534 K	Bayer et al. 1999	AF209545
Brassicaceae	<i>Capparis spinosa</i> L.	Chase 2751 K	Bakker et al. 1998	AF035900
Brassicaceae	<i>Cleome hassleriana</i> Chodat	Al-Shebaz s.n. MO	this paper	AF209565
Bretschneideraceae	<i>Bretschneidera sinensis</i> Hemsl.	Leu & Lin 726 WIS	this paper	AF209546
Bromeliaceae	<i>Aechmea chantinii</i> (Carriere) Baker	Hahn 6942 WIS	this paper	AF168885
Bromeliaceae	<i>Glomeropitcairnia penduliflora</i> (Grisebach) Mez	Kress 92-3466 US	this paper	AF168914
Bromeliaceae	<i>Puya raimondii</i> Harms	Chase 2847 K	this paper	AF209661
Bruniaceae	<i>Berzelia lanuginosa</i> Brongn.	Kirstenbosch 7589	Hoot et al. 1999	AF095731

continued

SPECIES (rbcL)	CITATION (rbcL)	EMBL (rbcL)	SPECIES (18S)	VOUCHER (18S)	CITATION (18S)	EMBL (18S)
same DNA	this paper	AF233090	same DNA	same	this paper	AF168870
same species	Xiang et al. 1993	L11221	same DNA as for rbcL	same as for rbcL	Soltis et al. 1997a	U42523
same DNA	Qju et al. 1993	L12630	same DNA	same	this paper	AF206855
same species	Chase et al. 1993	L14290	same DNA	Nickrent 2888 SIU	Soltis et al. 1997	L24043
same species	Qju et al. 1993	L12664	same DNA as for rbcL	same as for rbcL	Nickrent & Soltis 1995	L24417
same species	Chase et al. 1993	L08763	same species	Steussy et al. 11784 OS	Soltis et al. 1997a	U42783
same species	Duvall et al. 1993	L05028	<i>A. falcatus</i> L.	Hahn 6881 WIS	Hershkovitz et al. 1999	AF069205
same DNA	Chase et al. 1995	AJ131947	same DNA	same	this paper	AF206876
same DNA	this paper	AF206795	same DNA	same	this paper	AF206963
same DNA	Chase et al. 1993	L13859	same DNA	same	this paper	AF107575
<i>G. jamesonii</i> Bolus	Chase et al. 1993	L13643	same DNA as for atpB	same as for atpB	this paper	AF107576
same species	Chase et al. 1993	L13929	same DNA as for atpB	same as for atpB	this paper	AF107577
<i>T. erecta</i> L.	Chase et al. 1993	L13637	same DNA as for atpB	same as for atpB	Soltis et al. 1997a	U42501
<i>T. porrifolius</i> L.	Chase et al. 1993	L13647	same DNA as for atpB	same as for atpB	Soltis et al. 1997a	U42502
same DNA	this paper	AF206737	same DNA	same	this paper	AF206857
same DNA	this paper	AF206788	same DNA	same	this paper	AF206950
same species	Xiang et al. 1993	L11210	same species	US National Arb.	Soltis et al. 1997a	U42522
same DNA	Qju et al. 1993	L12632	same species	Nickrent 2953 SIU	Soltis et al. 1997a	U42503
same DNA	this paper	AF206738	same DNA	same	this paper	AF206860
<i>I. capensis</i> Meerb.	Chase et al. 1993	Z83142	<i>I. wallerana</i> Hook.	Johnson 95-071 WS	Soltis et al. 1997a	L49285
same DNA	Qju et al. 1998	U60314	same DNA	same	this paper	AF206862
same species	Chase et al. 1993	M88341	same DNA as for atpB	same as for atpB	Soltis et al. 1997a	U42504
same DNA	Chase et al. 1993	L01888	same DNA	same	Soltis et al. 1997a	U42506
same DNA	this paper	AF206740	same DNA	same	this paper	AF206864
same species	Chase et al. 1993	L08760	same DNA as for atpB	same as for atpB	Soltis et al. 1997a	L54064
same DNA	Hoot et al. 1995a	L37920	same DNA	same	Hoot et al. 1999	L37911
same DNA	Savolainen et al. 2000a	AJ235773	same DNA	same	this paper	AF206866
<i>A. rubra</i> Bong.	this paper	AF132889	<i>A. glutinosa</i> L. Gaertn.	unknown	Soltis et al. 1997a	X59984
<i>B. nigra</i> L.	Chase et al. 1993	L01889	<i>B. papyrifera</i> Marsh	unknown	Savard et al. 1994	L00971
same DNA	this paper	AF156737	same DNA	same	this paper	AF107578
same species	Olmstead et al. 1992	L11679	same species	Olmstead 92-099 WTU	this paper	AF107579
same DNA	Fay et al. 1998	Y15139	same DNA	same	this paper	AF206868
same DNA	Chase et al. 1995	Z73694	same DNA	same	this paper	AF206869
same species	Olmstead et al. 1992	L11680	same species	Olmstead 96-062 WTU	this paper	AF107580
<i>H. virginianum</i> L.	Olmstead et al. 1992	L01927	<i>H. fendleri</i> (Gray) Heller	Olmstead 957 WTU	this paper	AJ236019
same DNA	this paper	AF206741	same DNA	same	this paper	AF206872
<i>B. oleracea</i> L.	Rodman et al. 1993	M88342	<i>B. hirta</i> Moench	unknown	Soltis et al. 1997a	X17062
<i>C. hastata</i> Jacq.	Rodman et al. 1993	M95755	<i>C. sandwichiana</i> DC.	Ilitis 30502 WIS	Rodman et al. 1998	
same DNA	Chase et al. 1993	M95755	same DNA	same	Soltis et al. 1997a	U42511
same DNA	Chase et al. 1993	M95753	same DNA	same	Rodman et al. 1998	
same species	Chase et al. 1993	L19978	same DNA as for atpB	same as for atpB	Hershkovitz et al. 1999	AF069212
same species	Chase et al. 1993	L19975	same species	same as for atpB	Soltis et al. 1997a	U42075
<i>P. dyckoides</i> (Baker) Mez	Duvall et al. 1993	AF206814	same DNA as for atpB	same as for atpB	this paper	AF207001
same species	Olmstead et al. 1993	L14391	same DNA as for rbcL	same as for rbcL	Soltis et al. 1997a	U42508

continued

APPENDIX—

FAMILY	SPECIES (atpB)	VOUCHER (atpB)	CITATION (atpB)	EMBL (atpB)
Buddlejaceae	<i>Buddleja auriculata</i> Benth.	Chase 2467 K	Savolainen et al. 2000a	AJ235420
Burmanniaceae	<i>Burmannia biflora</i> L.	Chase 157 NCU	this paper	AF209548
Burseraceae	<i>Bursera inaguensis</i> Britton	Fairchild Trop Garden 64-269 D	Bakker et al. 1998	AF035899
Buxaceae	<i>Buxus sempervirens</i> L.	Hoot 921 UWM	Hoot et al. 1999	AF092110
Buxaceae	<i>Pachysandra procumbens</i> Michx.	Hoot 917 UWM	Hoot et al. 1999	AF092111
Byblidaceae	<i>Byblis gigantea</i> Lindl.	Palmengarten BG	this paper	AJ236181
Cabombaceae	<i>Brasenia schreberi</i> J.F. Gmelin in L.	Qju 91031 NCU	this paper	AJ235418
Cabombaceae	<i>Cabomba caroliniana</i> A. Gray	Les s.n. CONN	this paper	AF209549
Cactaceae	<i>Pereskia aculeata</i> Mill.	Soltis & Soltis sn	this paper	AF209648
Calycanthaceae	<i>Calycanthus floridus</i> L.	Qju 94155 NCU	Savolainen et al. 2000a	AJ235422
Calycanthaceae	<i>Idiospermum australiense</i> Blake	Qju 91042 NCU	Savolainen et al. 2000a	AJ235500
Calyceraceae	<i>Boopis graminea</i> Phil.	Palmer 904 IND	this paper	AJ236199
Campanulaceae	<i>Campanula trachelium</i> Brot.	Chase 2546 K	Savolainen et al. 2000a	AJ235423
Campanulaceae	<i>Codonopsis pilosula</i> Nannf.	Albach 10 WS	this paper	AJ236203
Campanulaceae	<i>Lobelia angulata</i> Forst.	Chase 2540 K	Savolainen et al. 2000a	AJ235524
Canellaceae	<i>Canella winteriana</i> (L.) Gaertn.	Qju 90017 NCU	Savolainen et al. 2000a	AJ235424
Canellaceae	<i>Cinnamodendron ekmanii</i> Sleumer	Qju 47067 NCU	Savolainen et al. 2000a	AJ235435
Cannabaceae	<i>Humulus lupulus</i> L.	Qju 92004 NCU	this paper	AF209599
Cannaceae	<i>Canna indica</i> L.	Kress 80-1124 US	this paper	AF168892
Caprifoliaceae	<i>Symphoricarpos albus</i> (L.) Blake	Olmstead s.n. COLO	this paper	AJ236208
Caricaceae	<i>Carica papaya</i> L.	Chase 2508 K	Bakker et al. 1998	AF035901
Caryocaraceae	<i>Caryocar glabrum</i> Pers.	Mori 22997 NY	this paper	AF209556
Caryophyllaceae	<i>Stellaria media</i> (L.) Cyrill.	Mort s.n. WS	this paper	AF209680
Casuarinaceae	<i>Casuarina litorea</i> L.	Chase 215 NCU	Savolainen et al. 2000a	AJ235427
Celastraceae	<i>Euonymus alatus</i> Siebold	Chase 137 NCU	Savolainen et al. 2000a	AJ235471
Celastraceae	<i>Siphonodon celastrineus</i> Griff.	Chase 2097 K	this paper	AF209676
Celastraceae	<i>Brexia madagascariensis</i> Thouars	Schwerdtfeger 25471 B	Savolainen et al. 2000a	AJ235419
Celastraceae	<i>Hippocratea barbata</i> Muell.	Chase 2971 K	Savolainen et al. 2000a	AJ235493
Celastraceae	<i>Plagiopteron suaveolens</i> Griff.	Chase 1335 K	Savolainen et al. 2000a	AJ235562
Celtidaceae	<i>Celtis yunnanensis</i> C.K. Schneid.	Qju P90002 NCU	this paper	AF209560
Ceratophyllaceae	<i>Ceratophyllum demersum</i> L.	Qju 91027 NCU	Savolainen et al. 2000a	AJ235430
Cercidiphyllaceae	<i>Cercidiphyllum japonicum</i> Siebold & Zucc.	Olmstead 90-016 COLO	Hoot et al. 1999	AF092112
Chloranthaceae	<i>Chloranthus japonicus</i> Siebold	Chase 204 NCU	Savolainen et al. 2000a	AJ235431
Chloranthaceae	<i>Hedyosmum arborescens</i> Sw.	Chase 338 NCU	Savolainen et al. 2000a	AJ235490
Chloranthaceae	<i>Sarcandra grandiflora</i> Subr. & Henry	Qju 92002 NCU	Savolainen et al. 2000a	AJ235593
Chrysobalanaceae	<i>Chrysobalanus icaco</i> L.	Fairchild Trop G 76-311	this paper	AF209562
Chrysobalanaceae	<i>Licania tomentosa</i> Fritsch	Fairchild Trop G 64-734	this paper	AF209617
Circaeasteraceae	<i>Circaeaster agrestis</i> Maxim.	Chase 506 K	Hoot & Crane 1995	AF092116
Circaeasteraceae	<i>Kingdonia uniflora</i> Balf. f. & W.W. Sm.	Qjn s.n. PE	Hoot & Crane 1995	AF092115
Cistaceae	<i>Helianthemum grandiflorum</i> DC.	Chase 524 K	Bakker et al. 1998	AF035907
Clethraceae	<i>Clethra arborea</i> Vent.	Chase 902 K	Savolainen et al. 2000a	AJ235438
Clusiaceae	<i>Hypericum perforatum</i> L.	unknown	this paper	AF209602
Clusiaceae	<i>Mesua</i> sp.	Chase 677 K	this paper	AF209627
Colchicaceae	<i>Colchicum speciosum</i> Steven.	Chase 109 NCU	this paper	AF209569
Combretaceae	<i>Quisqualis indica</i> L.	Chase 128 NCU	Savolainen et al. 2000a	AJ235576
Combretaceae	<i>Terminalia boivinii</i>	Chase 5956 K	this paper	AF209686

continued

SPECIES (rbcl)	CITATION (rbcl)	EMBL (rbcl)	SPECIES (18S)	VOUCHER (18S)	CITATION (18S)	EMBL (18S)
<i>B. davidii</i> Franch	Olmstead et al. 1993	L14392	same species as for rbcl	Johnson 95-031 WS	Soltis et al. 1997a	L49275
same DNA	Olmstead et al. 1992	AF206742	same DNA	same	this paper	AF168827
same DNA	Chase et al. 1993	L01890	same DNA	same	Soltis et al. 1999	AF206877
same species	Hoot et al. 1999	AF093717	same DNA as for rbcl	same as for rbcl	Soltis et al. 1997a	L54065
same DNA	Chase et al. 1993	AF093718	same DNA	same	Hoot et al. 1999	AF094533
<i>B. liniflora</i> Salisb.	Chase et al. 1993	L01891	same DNA as for atpB	same as for atpB	Soltis et al. 1997a	U42509
same DNA	Chase et al. 1993	M77028	same DNA	same	Les et al. 1999	AF096693
same DNA ?	Chase et al. 1993	M77029	same DNA	same	Les et al. 1999	AF206878
same DNA	this paper	AF206805	same DNA	same	this paper	AF206986
same DNA	Chase et al. 1993	L14291	same species	Nickrent 2893 SIU	Soltis et al. 1997a	U38318
same DNA	Qiu et al. 1993	L12651	same DNA	same	this paper	AF206937
<i>B. anthemoides</i> Juss.	Olmstead et al. 1993	L13860	same DNA as for atpB	same as for atpB	this paper	AF107583
<i>C. ramulosa</i> Wall.	Olmstead et al. 1992	L13861	same DNA as for rbcl	same as for rbcl	Soltis et al. 1997a	U42510
<i>C. ovata</i> Benth.	Albach et al. 2000a	L18797	same DNA as for atpB	same as for atpB	this paper	AF107584
<i>L. erinus</i> L.	Chase et al. 1993	L01931	same DNA as for rbcl	same as for rbcl	Soltis et al. 1997a	U42785
same DNA	Qiu et al. 1993	AJ131928	same DNA	same	this paper	AF206879
same DNA	Savolainen et al. 2000a	AJ235776	same DNA	same	this paper	AF206887
same DNA	Chase et al. 1993	U02729	same DNA	same	this paper	AF206931
same DNA as for atpB	Smith et al. 1993	L05445	<i>C. coccinea</i> Mill.	Chaw 1371 HAST	Soltis et al. 1997a	D29784
same DNA	Olmstead et al. 1992	L11682	same DNA	same	Soltis et al. 1997a	U42513
same species	Rodman et al. 1993	M95671	same DNA as for rbcl	same as for rbcl	Soltis et al. 1997a	U42514
same DNA	this paper	AF206745	same DNA	same	this paper	AF206881
same DNA	this paper	AF206823	same DNA	same	this paper	AF207027
same DNA	Chase et al. 1993	L01893	<i>C. equisetifolia</i> L.	Nickrent 2977 SIU	Soltis et al. 1997a	U42515
same DNA	Chase et al. 1993	L13184	same species	Nickrent 2894 SIU	Nickrent & Franchina 1990	X16600
same DNA	this paper	AF206821	same DNA	same	this paper	AF207021
same species	Morgan & Soltis 1993	L11176	same species	Kew 1977-14901	Soltis et al. 1997a	U42543
<i>H. richardiana</i> Cambess.	Savolainen et al. 2000a	X69740	same DNA as for atpB	same as for atpB	this paper	AF206928
same DNA	Savolainen et al. 2000a	AJ235787	same DNA	same	this paper	AF206993
same DNA	Chase et al. 1993	L12638	same DNA	same	Soltis et al. 1997a	U42818
same species	Chase et al. 1993	M77030	same DNA as for atpB	same as for atpB	Soltis et al. 1997a	U42517
same species	Olmstead et al. 1992	L11673	same species	Soltis 2540 WS	Soltis et al. 1997a	U42518
same DNA	Qiu et al. 1993	L12640	<i>C. multistachys</i>	Wurdack 92-0010 US	this paper	AF206885
same DNA	Qiu et al. 1993	L12649	same DNA	same	this paper	AF206925
same DNA	Qiu et al. 1993	L12663	same DNA	same	this paper	AF207012
same DNA	Morgan & Soltis 1993	L11178	same DNA	same	Soltis et al. 1997a	U42519
same DNA	Morgan & Soltis 1993	L11193	same DNA	same	Soltis et al. 1997a	U42520
same DNA	Hoot & Crane 1995	AF092116	same DNA	same	Hoot & Crane 1995	AF094538
same DNA	Hoot & Crane 1995	AF093719	same DNA	same	Hoot & Crane 1995	AF094537
same DNA	Fay et al. 1998	Y15141	same DNA	same	this paper	AF206926
<i>C. alnifolia</i> L.	Kron & Chase 1993	L12609	same DNA as for rbcl	same as for rbcl	Soltis et al. 1997a	U42521
<i>H. empetrifolia</i> Willd.	this paper	AF206779	same DNA as for atpB	same as for atpB	this paper	AF206934
same DNA	this paper	AF206794	same DNA	same	this paper	AF206962
same DNA?	Chase et al. 1993	L12673	<i>C. autumnale</i> L.	Hahn 6864 WIS	Soltis et al. 1997a	U42072
same DNA	Chase et al. 1993	L01948	same DNA	same	this paper	AF207004
<i>T. catappa</i> L.	Chase et al. 1993	AF206826	same DNA as for rbcl	same	Soltis et al. 1999	AF207037

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APPENDIX—

FAMILY	SPECIES (atpB)	VOUCHER (atpB)	CITATION (atpB)	EMBL (atpB)
Commelinaceae	<i>Tradescantia ohiensis</i> Raf.	Hahn 6854 WIS	this paper	AF168950
Convallariaceae	<i>Convallaria majalis</i> L.	Hahn 6867 WIS	this paper	AF168897
Convallariaceae	<i>Liriope muscari</i> (Decne.) L.H. Bailey	Hahn 6992 WIS	this paper	AF168926
Convallariaceae	<i>Ruscus aculeatus</i> L.	Hahn 6871 WIS	this paper	AF168942
Convallariaceae	<i>Smilacina racemosa</i> (L.) Desf.	Hahn 6878 WIS	this paper	AF168945
Convallariaceae	<i>Nolina recurvata</i> Hemsl.	Chase 3466	this paper	AF209639
Convolvulaceae	<i>Convolvulus arvensis</i> L.	Soltis 2581 WS	this paper	AJ236186
Convolvulaceae	<i>Ipomoea mauritiana</i> Jacq.	Chase 2525 K	Savolainen et al. 2000a	AJ235505
Coriariaceae	<i>Coriaria myrtifolia</i> L.	Chase 245 NCU	Savolainen et al. 2000a	AJ235443
Cornaceae	<i>Alangium</i> sp.	Chase 2541 K	Savolainen et al. 2000a	AJ235386
Cornaceae	<i>Cornus officinalis</i> Sieb et Zucc.	Arnold Arb. 8156-A	this paper	AJ236229
Cornaceae	<i>Camptotheca acuminata</i> Decne.	Strybing Arb. 74–180	this paper	AF209554
Cornaceae	<i>Griselinia lucida</i> G. Forst.	Cameron s.n. AKU	this paper	AF209595
Cornaceae	<i>Helwingia japonica</i> (Thunb.) F. Dieter	Kew 1953–24705	this paper	AF209596
Cornaceae	<i>Nyssa sylvatica</i> Marsh	Chase 2530 K	Savolainen et al. 2000a	AJ235545
Corynocarpaceae	<i>Corynocarpus laevigatus</i> Forst.	Chase 236 NCU	Savolainen et al. 2000a	AJ235446
Costaceae	<i>Costus barbatus</i> Suess.	Kress 94–3710 US	this paper	AF168898
Costaceae	<i>Dimerocostus strobilaceous</i> Kuntze	Kress 94–3601 US	this paper	AF168909
Costaceae	<i>Monocostus uniflorus</i> (Poepp. Ex Petersen) Maas	Kress 79–1112 SEL	this paper	AF168930
Costaceae	<i>Tapeinochilos ananassae</i> K. Schum.	Kress 79–1114, SEL	this paper	AF168949
Crassulaceae	<i>Crassula marnierana</i> Huber & Jacobsen	Morgan 2152 WS	Savolainen et al. 2000a	AJ235447
Crassulaceae	<i>Dudleya viscida</i> Moran	Huntington 62801 BG	Savolainen et al. 2000a	AJ235461
Crassulaceae	<i>Kalanchoe daigremontana</i> Hamet & Perrier	Morgan 2151 WS	Savolainen et al. 2000a	AJ235510
Crassulaceae	<i>Sedum nudum</i> Aiton	Chase 2459 K	Savolainen et al. 2000a	AJ235600
Crossosomataceae	<i>Crossosoma californicum</i> Nutt.	Rancho Santa Ana Bot Gard	this paper	AF209571
Cucurbitaceae	<i>Cucumis sativus</i> L.	Soltis s.n. WS	this paper	AF209572
Cucurbitaceae	<i>Cucurbita pepo</i> L.	Soltis s.n. WS	this paper	AF209573
Cunoniaceae	<i>Bauera rubioides</i> Andrews	Kew 1977–6377 K	this paper	AF209539
Cunoniaceae	<i>Davidsonia puriens</i> F. Muell.	Hufford 1687 WS	this paper	AF209574
Cunoniaceae	<i>Eucryphia lucida</i> Druce	Strybing Arb 86–0250	this paper	AF209584
Cyclanthaceae	<i>Cyclanthes bipartitus</i> Poit.	Hammel 15585 MO	this paper	AF168904
Cyclanthaceae	<i>Sphaeradenia pendula</i> Hammel	Chase 222 NCU	Savolainen et al. 2000a	AJ235607
Cyperaceae	<i>Cyperus albobistriatus</i> Scradler	Kress 92–3463 US	this paper	AF168906
Cyperaceae	<i>Rhynchospora nervosa</i>	Chase 787 K	this paper	AF209667
Cyrtillaceae	<i>Cyrtilla racemiflora</i> L.	Chase 2531 K	Savolainen et al. 2000a	AJ235449
Daphniphyllaceae	<i>Daphniphyllum</i> sp.	Wagner et al. 6599 HAST	Hoot et al. 1999	AF092118
Dasypogonaceae	<i>Calectasia intermedia</i> Behr & F. Muell. Ex Sond.	Chase 456 K	this paper	AF168891
Dasypogonaceae	<i>Dasypogon bromeliifolius</i> R. Br.	Chase 430 K	this paper	AF168907
Datisceae	<i>Datisca cannabina</i> L.	Chase 2745 K	Savolainen et al. 2000a	AJ235450
Datisceae	<i>Tetrameles nudiflora</i> R. Br.	Philbrick 2272 RSA	this paper	AF209689
Degeneriaceae	<i>Degeneria vitiensis</i> , I. W. Bailey & A. C. Smith	Qju 1202–55 NCU	Savolainen et al. 2000a	AJ235451
Diapensiaceae	<i>Galax urceolata</i> L.	Kron 163 NCU	this paper	AJ236223
Dichapetalaceae	<i>Dichapetalum brownii</i> Baill.	Fison s.n. 10/8/93 K	Savolainen et al. 2000a	AJ235455
Didymeleaceae	<i>Didymeles perrieri</i> Leandri	Andrianantonnina 387 MO	Hoot et al. 1999	AF092119

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SPECIES (rbcL)	CITATION (rbcL)	EMBL (rbcL)	SPECIES (18S)	VOUCHER (18S)	CITATION (18S)	EMBL (18S)
<i>T. soconuscana</i> Matuda	Smith et al. 1993	L05463	same DNA as for atpB	same as for atpB	Hershkovitz et al. 1999	AF069213
same species	Savolainen et al. 2000a	D28334	same DNA as for atpB	same as for atpB	this paper	X16600
same species	Rudall et al. 2000a	Z77271	same DNA as for atpB	same as for atpB	this paper	AF168856
same species	Rudall et al. 2000a	Z77274	same species	same as for atpB	this paper	AF168873
<i>S. hondoensis</i> Ohwi	Shinwari et al. 1994	D17380	same DNA as for atpB	same as for atpB	this paper	AF168874
same species	Duvall et al. 1993	L05030	same DNA as for atpB	same as for atpB	this paper	AF206971
<i>C. tricolor</i> L.	Olmstead et al. 1992	L11683	same DNA as for atpB	same as for atpB	this paper	AJ236013
<i>I. coccinea</i> L.	Olmstead et al. 1993	L14400	<i>I. hederacea</i> Jacq.	Colwell s.n. MO	Soltis et al. 1997a	U38310
same DNA	Chase et al. 1993	L01897	same DNA	same	Soltis et al. 1999	AF206891
<i>A. chinense</i> Harms	Xiang et al. 1993	L11209	same DNA as for rbcL	same as for rbcL	this paper	AF206843
same DNA	Xiang et al. 1993	L11216	same DNA	same	Soltis & Soltis 1997	U52033
same DNA	Xiang et al. 1993	L01937	same DNA	same	Soltis et al. 1997a	U42789
same DNA	Xiang et al. 1993	L11225	same DNA	same	this paper	AF206922
same species	Xiang et al. 1993	L11226	same DNA as for rbcL	same as for rbcL	this paper	U42524
<i>N. ogeshe</i> Marsh	Xiang et al. 1993	L11228	same DNA as for rbcL	same as for rbcL	Soltis & Soltis 1997	U52032
same DNA	Savolainen et al. 2000a	X69731	same DNA	same	this paper	AF206892
same DNA	this paper	AF243510	same DNA	same	Soltis & Soltis 1997	U42080
same DNA	this paper	AF243838	same DNA	same	this paper	AF168839
same DNA	this paper	AF243839	same DNA	same	this paper	AF168861
same DNA	this paper	AF243840	same DNA	same	this paper	AF168877
same DNA	Savolainen et al. 2000a	L01899	same DNA	same	Soltis et al. 1997a	U42525
same DNA	Morgan & Soltis 1993	L11182	same DNA	same	Soltis et al. 1997a	U42526
same DNA	Morgan & Soltis 1993	L11189	same DNA	same	Soltis et al. 1997a	U42527
<i>S. rubrotinctum</i> Clausen	Chase et al. 1993	L01956	same DNA as for rbcL	same as for rbcL	Soltis et al. 1997a	U42528
same DNA	Morgan & Soltis 1993	L11179	same DNA	same	Soltis et al. 1997a	U42529
same species	Chase et al. 1993	AF206755	same DNA as for atpB	same as for atpB	Soltis et al. 1999	AF206894
same species	Chase et al. 1993	AF206756	same DNA as for atpB	same as for atpB	this paper	AF206895
same species	Morgan & Soltis 1993	L11174	same DNA as for atpB	same as for atpB	Soltis et al. 1997a	U42505
same DNA	this paper	AF206759	same DNA	same	this paper	AF206897
same species	Chase et al. 1993	L01918	same DNA as for atpB	same	Soltis et al. 1997a	U42533
same DNA as 18S	this paper		same DNA as for atpB	same as for atpB	this paper	AF168837
same DNA	Chase et al. 1993	AJ235808	same DNA	same	this paper	AF207024
<i>C. alternifolius</i> L.	Duvall et al. 1993	M91627	same DNA as for atpB	same as for atpB	Soltis et al. 1997a	U42077
same DNA?	this paper	AF206818	same DNA	same	this paper	AF207009
same species	Albert et al. 1992	L01900	same species	Kron s.n. NCU	Soltis et al. 1997a	U43294
same species	Albert et al. 1992	L01901	same DNA as for rbcL	same as for rbcL	Soltis et al. 1997a	U42531
same DNA	Chase et al. 1995	AF206743	same DNA as for atpB	same as for atpB	Hershkovitz et al. 1999	AF069209
same DNA	Chase et al. 1995	AF206758	same DNA as for atpB	same as for atpB	this paper	
same species	Chase et al. 1993	L21939	<i>D. glomerata</i> (Presl) Baill.	Rancho Santa Ana Bot Gard	Soltis et al. 1997a	U42426
same DNA	Chase et al. 1993	AF206828	same DNA	same	Soltis et al. 1997a	U41502
same DNA	Chase et al. 1993	L12643	same DNA	same	this paper	AF206898
same DNA	this paper	Z80184	same DNA	same	Soltis et al. 1997a	L49281
<i>D. crassifolium</i> Chod.	Savolainen et al. 2000a	X69733	<i>D. macrocarpum</i> Engl.	Fison s.n. K	this paper	AF206902
same DNA	Hoot et al. 1999	AF094541	same DNA	same	this paper	AF092119

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APPENDIX—

FAMILY	SPECIES (atpB)	VOUCHER (atpB)	CITATION (atpB)	EMBL (atpB)
Dilleniaceae	<i>Dillenia retusa</i> Thunb.	Chase 2103 K	Savolainen et al. 2000a	AF095732
Dilleniaceae	<i>Tetracera asiatica</i> Hoogl.	Chase 1238 K	Savolainen et al. 2000a	AJ235622
Dioncophyllaceae	<i>Triphophyllum pelatum</i> (Hutch. & Dalziel) Airy Shaw	Chase 663 K	this paper	AF209693
Dioscoreaceae	<i>Dioscorea polygonoides</i> Plum. & Bompl.	Chase 197 NCU	Savolainen et al. 2000a	AJ235456
Dipsacaceae	<i>Dipsacus sativus</i> (L.) Honck.	Jansen 931 MICH	this paper	AF209577
Dipsacaceae	<i>Scabiosa</i> sp.	Albach 39 WS	this paper	AJ236207
Dipterocarpaceae	<i>Anisoptera marginata</i> Korth	Chase 2486 K	Bakker et al. 1998	AF035918
Donatiaceae	<i>Donatia</i> sp.	Morgan 2142 WS	this paper	AJ236203
Droseraceae	<i>Drosera communis</i> A.St.-Hil.	Chase 2582 K	Savolainen et al. 2000a	AJ235459
Ebenaceae	<i>Diospyros kaki</i> Thunb.	Chase 920 K	Savolainen et al. 2000a	AJ235457
Elaeagnaceae	<i>Elaeagnus</i> sp.	Chase 2414 K	Savolainen et al. 2000a	AJ235462
Elaeagnaceae	<i>Shepherdia canadensis</i> (L.) Nutt.	Brunsfeld s.n.	this paper	AF209675
Elaeocarpaceae	<i>Crinodendron hookerianum</i>	Chase 909	this paper	AF209570
Elaeocarpaceae	<i>Elaeocarpus sphaericus</i> Schum.	Alverson s.n. WIS	this paper	AF209581
Elaeocarpaceae	<i>Sloanea berteriana</i> Choisy	Chase 343 NCU	Savolainen et al. 2000a	AJ235603
Ephedraceae	<i>Ephedra tweediana</i> C.A.Mey.	none	Savolainen et al. 2000a	AJ235463
Eremosynaceae	<i>Eremosyne pectinata</i> Endl.	Annels & Hearn 4795 PERTH?	this paper	AJ236215
Ericaceae	<i>Arbutus unedo</i> L.	652–60 Seattle Arb	this paper	MWC/VVS
Ericaceae	<i>Arctostaphylos uva-ursi</i> (L.) Spreng.	Johnson 94-085 WS	this paper	AJ236225
Erythroxylaceae	<i>Erythroxylum confusum</i> Britton	Fairchild Trop Garden 63–251E	Savolainen et al. 2000a	AJ235466
Escalloniaceae	<i>Escallonia</i> sp.	Chase 2499 K	Savolainen et al. 2000a	AJ235467
Eucommiaceae	<i>Eucommia ulmoides</i> Oliv.	Chase 2755 K	Savolainen et al. 2000a	AJ235469
Euphorbiaceae	<i>Euphorbia polychroma</i> Kerner	Chase 102 NCU	Savolainen et al. 2000a	AJ235472
Eupomatiaceae	<i>Eupomatia bennetti</i> Muell.	Qiu 90022 NCU	Savolainen et al. 2000a	AJ235473
Eupteleaceae	<i>Euptelea polyandra</i> Siebold et Zucc.	Qiu 90026 NCU	Hoot et al. 1997	U86384
Fabaceae	<i>Albizia julibrissin</i> Durazz.	Doyle 1526 BH	this paper	AF209524
Fabaceae	<i>Bauhinia</i> sp.	Doyle s.n. MSU	this paper	AF209540
Fabaceae	<i>Pisum sativum</i> L.	unknown	Chase et al. 1993	X03852
Fagaceae	<i>Chrysolepis sempervirens</i> (Kellogg) Hjelmq.	Qiu P90007 NCU	this paper	AF209563
Fagaceae	<i>Quercus rubra</i>	Swensen sn IND	this paper	AF209663
Fagaceae	<i>Trigonobalanus verticillatus</i> Forman	Chase 595 K	Savolainen et al. 2000a	AJ235631
Flacourtiaceae	<i>Abatia parviflora</i> Ruiz et Pav.	Pennington 676 K	this paper	AF209519
Flacourtiaceae	<i>Casearia sylvestris</i> Sw.	Chase 337 K	this paper	AF209557
Flacourtiaceae	<i>Flacourtia jangomas</i> Steud.	Chase 2150 K	this paper	AF209588
Flacourtiaceae	<i>Idesia polycarpa</i> Maxim.	Chase 561 K	this paper	AF209604
Flagellariaceae	<i>Flagellaria indica</i> L.	Chase 206 NCU	this paper	AF209589
Fouquieriaceae	<i>Idria columnaria</i> Kellogg	Chase 269 NCU	Savolainen et al. 2000a	AJ235501
Francoaceae	<i>Francoa appendiculata</i> A.Juss.	Chase 2502 K	Bakker et al. 1998	AF035905
Frankeniaceae	<i>Frankenia pulverulenta</i> L.	Collenette 6/93 K	Savolainen et al. 2000a	AJ235475
Garryaceae	<i>Garrya elliptica</i> Douglas	Kew 1969-17852	this paper	AJ235478
Gelsemiaceae	<i>Gelsemium sempervivens</i> (L.) Pers.	Longwood BG 860395	this paper	AJ236193
Gentianaceae	<i>Exacum affine</i> Balf. f. ex Regel	none	this paper	AJ236195
Geraniaceae	<i>Geranium sanguineum</i> L.	Chase 125 NCU	Bakker et al. 1998	AF035906
Geraniaceae	<i>Monsonia emarginata</i> (L.) L' Herit.	Price s.n. IND	this paper	AF209632
Geraniaceae	<i>Pelargonium cotyledonis</i> L' Herit.	Chase 1098 K	Savolainen et al. 2000a	AF035911

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SPECIES (rbcL)	CITATION (rbcL)	EMBL (rbcL)	SPECIES (18S)	VOUCHER (18S)	CITATION (18S)	EMBL (18S)
<i>D. indica</i> L.	Chase et al. 1993	L01903	<i>D. alata</i> (DC) Mart.	Nickrent 2956 SIU	Soltis et al. 1997a	U38314
same DNA	Savolainen et al. 2000a	AJ235796	same DNA	same	this paper	AJ235982
same DNA	Lledo et al. 1998	Z97637	same DNA	same	this paper	AF207049
same DNA	Chase et al. 1993	AF206762	same DNA	same	this paper	AF206903
same DNA	Olmstead et al. 1992	L13824	same DNA	same	Soltis et al. 1997a	U43150
same DNA	this paper	AF156734	same DNA	same	this paper	AJ236006
same DNA	Fay et al. 1998	Y15144	same DNA	same	this paper	AF206849
<i>D. fascicularis</i> Forst.	this paper	X87385	same DNA as for atpB	same	this paper	AJ236012
<i>D. spathulata</i> Labill.	Chase et al. 1993	L13168	<i>D. capensis</i>	Palmengarten Bot Gard	Soltis et al. 1997a	U42532
<i>D. virginiana</i> L.	Kron & Chase 1993	L12613	same species	Johnson 95015 WS	Johnson et al. 1999	L49279
<i>E. angustifolia</i> L.	Soltis et al. 1995	V17038	<i>E. umbellata</i> Thunb.	Nickrent 2898 SIU	Soltis et al. 1997a	L24090
same DNA	Soltis et al. 1995	V17039	same DNA	same	this paper	AF207020
same DNA	this paper	AF206754	same DNA	same	this paper	AF206893
<i>Elaeocarpus</i> sp.	this paper	AF206765	same DNA as for atpB	same as for atpB	this paper	AF206906
<i>S. latifolia</i> (Rich.) Schumann	Alverson et al. 1998	AF022131	same DNA as for rbcL	same as for rbcL	Soltis et al. 1997a	U42826
same DNA	Chase et al. 1993	L12677	<i>Ephedra sinica</i> Stapf	TI-9297 TI	Soltis et al. 1997a	D38242
same DNA	Hibsch-Jetter et al. 1997	L47969	same DNA	same	this paper	U42807
<i>A. canariensis</i> Duhamel	Kron & Chase 1993	L12597	same DNA as for atpB	same as for atpB	this paper	AF206853
same species	Kron & Chase 1993	L12598	same DNA as for atpB	same as for atpB	Soltis et al. 1997a	L49272
same DNA	Chase et al. 1993	L13183	same species	Chase 134	this paper	AF206909
<i>E. coquimbensis</i> RemyChase	Morgan & Soltis 1993	L11183	same DNA as for rbcL	same as for rbcL	Soltis et al. 1997a	U42544
same species	Chase et al. 1993	L01917	same DNA as for rbcL	same as for rbcL	Soltis et al. 1997a	L54066
same DNA	Chase et al. 1993	L13183	same DNA	same	Soltis et al. 1997a	L13183
same DNA	Qju et al. 1993	L12644	same DNA	same	Soltis et al. 1997a	L12644
same DNA	Chase et al. 1993	L12645	same DNA	same	Soltis et al. 1997a	L12645
same species	Chase et al. 1993	AF206730	same DNA as for atpB	same as for atpB	Soltis et al. 1997a	U42536
<i>Bauhinia</i> sp.	Chase et al. 1993	AF206739	same DNA as for atpB	same as for atpB	Soltis et al. 1997a	U42537
same species	Chase et al. 1993	X03853	same species	no voucher	Soltis et al. 1997a	U43011
same DNA	Chase et al. 1993	AF206750	same DNA	same	Soltis et al. 1999	AF206886
same DNA	this paper	AF132888	same DNA	same	this paper	AF132892
<i>F. americanus</i> Sweet	Chase et al. 1993	L13338	<i>F. grandifolia</i> Ehrh.	Soltis 2521 WS	Soltis et al. 1999	AF206910
same DNA	this paper	AF206726	same DNA	same	this paper	AF206836
same DNA	this paper	AF206746	same DNA	same	this paper	AF206882
same DNA	this paper	AF206768	same DNA	same	this paper	AF206912
same DNA	this paper	AF206781	same DNA	same	this paper	AF206936
same DNA	this paper	AF206769	same DNA	same	this paper	AF168845
same DNA	Morton et al. 1997a	Z80210	same species	U.C. Berkeley Bot. G	Johnson et al. 1999	AF003961
<i>F. sonchifolia</i> Cav.	Soltis et al. 1990	L11184	same DNA as for rbcL	same as for rbcL	Nickrent & Soltis 1995	L28137
same DNA	Fay et al. 1997	Z97638	same DNA	same	this paper	AF206914
same species	Morgan & Soltis 1993	L01919	same DNA as for rbcL	same as for rbcL	Soltis et al. 1997a	U42540
same DNA	Olmstead et al. 1993	L14397	same DNA	same	this paper	AJ236025
same DNA	Olmstead et al. 1992	L11684	same DNA	same	this paper	AJ236023
<i>G. cinereum</i> Cav.	Price & Palmer 1993	L14695	same DNA as for rbcL	same as for rbcL	Soltis et al. 1997a	U42541
same DNA	Price & Palmer 1993	L14701	same DNA	same	this paper	AF206964
same species	Chase et al. 1993	L01919	same DNA as for rbcL	same as for rbcL	Soltis et al. 1999	AF206982

continued

APPENDIX—

FAMILY	SPECIES (atpB)	VOUCHER (atpB)	CITATION (atpB)	EMBL (atpB)
Gesneriaceae	<i>Cyrtandra hawaiiensis</i>	Wagner 6753 BISH	this paper	AJ236172
Gesneriaceae	<i>RhynchoGLOSSUM notonianum</i>	SI 94-378	this paper	AJ236170
Gesneriaceae	<i>Saintpaulia</i> sp.	Franceschi s.n.	this paper	AJ235588
Gesneriaceae	<i>Titanotrichum oldhamii</i> (Hemsl.) Solered.	SI 86-106	this paper	AJ236171
Ginkgoaceae	<i>Ginkgo biloba</i> L.	Chase 2489 K	Savolainen et al. 2000a	AJ235480
Gnetaceae	<i>Gnetum gemon</i> L.	Chase 208 NCU	Savolainen et al. 2000a	AJ235482
Gomortegaceae	<i>Gomortega keule</i> (Molina) I.M. Johnston	Ueda	this paper	AF209593
Goodeniaceae	<i>Scaevola aemula</i> R. Br.	D. Albach 18 WS	this paper	AF209670
Goupiaceae	<i>Goupia glabra</i> Aubl.	Prevost 3031 CAY	Savolainen et al. 2000a	AJ235484
Greyiaceae	<i>Greyia radlkoferi</i> Szyszyl	Strybing Arb. 640406	this paper	AF209594
Grossulariaceae	<i>Ribes speciosum</i> Pursh.	Chase 2542 K	Savolainen et al. 2000a	AJ235583
Gunneraceae	<i>Gunnera hamiltonii</i> Kirk. ex W.S.Ham.	Chase 562 K	Hoot et al. 1999	AF093374
Haloragaceae	<i>Haloragis aspera</i> Lindl.	Chase 453 K	Savolainen et al. 2000a	AJ235487
Haloragaceae	<i>Myriophyllum exalbescens</i> Fernald	Broch 30 Aug 1991 WS	Savolainen et al. 2000a	AJ235538
Hamamelidaceae	<i>Corylopsis pauciflora</i> Siebold & Zucc.	Reznicek 9239 MICH	Hoot et al. 1999	AF093377
Hamamelidaceae	<i>Disanthus cercidifolia</i> Maxim.	Hoot 9221 UWM	Hoot et al. 1999	AF093378
Hamamelidaceae	<i>Exbucklandia populnea</i> R. Br. ex Griffith	Chase 619 K	Hoot et al. 1999	AF93379
Hamamelidaceae	<i>Hamamelis virginiana</i> L.	Hoot 910 UWM	Hoot et al. 1999	AF093380
Heliconiaceae	<i>Heliconia indica</i> Lam.	Kress 80-1118 SEL	this paper	AF168917
Hernandiaceae	<i>Gyrocarpus americana</i> Jacq.	Chase 317 NCU	Savolainen et al. 2000a	AJ235486
Himantandraceae	<i>Galbulimima belgraveana</i> Sprague	Qju 90034 NCU	Savolainen et al. 2000a	AJ235477
Huaceae	<i>Afrostryax</i> sp.	Check 5007 K	Savolainen et al. 2000a	AJ235385
Humiriaceae	<i>Humiria balsamifera</i> Aubl.	Anderson 13654 MICH	Savolainen et al. 2000a	AJ235494
Hyacinthaceae	<i>Bowiea volubilis</i> Harv. ex Hook. f.	Hahn 6882 WIS	this paper	AF168889
Hydrangeaceae	<i>Carpenteria californica</i> Torr.	Chase 2497 K	Savolainen et al. 2000a	AJ235426
Hydrangeaceae	<i>Decumaria barbara</i> L.	Kew 1969-50409	this paper	AJ236233
Hydrangeaceae	<i>Fendlera rupicola</i> Engelm. et Gray	Abott 216 UC	this paper	AJ236234
Hydrangeaceae	<i>Hydrangea macrophylla</i> Torr.	Chase 2537 K	Savolainen et al. 2000a	AJ235497
Hydrangeaceae	<i>Philadelphus lewisii</i> Pursh	Soltis & Soltis 2411 WS	this paper	AJ236231
Hydrocharitaceae	<i>Vallisneria</i> sp.	Chase 6018 K	this paper	AF209694
Hydroleaceae	<i>Hydrolea ovata</i> Nutt. ex Choisy	Olmstead 89-009 COLO	this paper	AJ236184
Hydrostachyaceae	<i>Hydrostachys imbricata</i> Thou.	Schatz 3414 MO	this paper	AJ236230
Hypoxidaceae	<i>Rhodohypoxis milloides</i> (Baker) Hilliard & B.L.Burtt	Chase 479 K	Savolainen et al. 2000a	AJ235582
Icacinaeae	<i>Gonocaryum litorale</i> Sleum.	Chase 1294 K	Savolainen et al. 2000a	AJ235483
Icacinaeae	<i>Icacina manii</i> Oliver	Chase 2244 K	this paper	AF209603
Icacinaeae	<i>Irvingbaileya</i> sp	Plunkett 1510 WS	this paper	AJ236219
Illiciaceae	<i>Illicium parviflorum</i> Michx.	Naczi 2784 MICH	Hoot et al. 1997	U86385
Iridaceae	<i>Aristea glauca</i> Klatt	Goldblatt 9500 MO	this paper	AF209531
Iridaceae	<i>Gladiolus buckevildii</i> (L. Bol.) Goldblatt	Goldblatt & Manning 9504 MO	this paper	AF209592
Irvingiaceae	<i>Irvingia malayana</i> Oliver	Chase 2574 K	this paper	AF209605
Iteaceae	<i>Itea virginica</i> L.	Ware 9401 WS	Hoot et al. 1999	AF093383
Ixerbaceae	<i>Ixerba brexioides</i> A. Cunn.	Small s.n. WS	this paper	AF209606
Ixioliriaceae	<i>Ixiolirion tataricum</i> Herb.	Chase 489 K	Savolainen et al. 2000a	AJ235007
Juglandaceae	<i>Carya glabra</i> (Miller) Sweet	Chase 254 NCU	this paper	AF209555
Juglandaceae	<i>Juglans nigra</i> L.	Albach s.n. WS	this paper	AF209609

continued

SPECIES (rbcL)	CITATION (rbcL)	EMBL (rbcL)	SPECIES (18S)	VOUCHER (18S)	CITATION (18S)	EMBL (18S)
same species	Smith et al. 1993	AF206757	same DNA as for atpB	same as for atpB	this paper	AJ236053
same species	Albach et al. 2000a	AF206817	same DNA as for atpB	same as for atpB	this paper	AJ236052
<i>Streptocarpus holstii</i> Engl.	Olmstead et al. 1993	L14409	same DNA as for rbcL	same	this paper	AJ236038
same species	Albach et al. 2000a	AF206829	same DNA as for atpB	same as for atpB	this paper	AJ236054
same species	Chase et al. 1993	AJ235804	same species	Chaw 1347	Chaw et al. 1993	D16448
same DNA	Chase et al. 1993	L12680	same species	Gillespie 4212 US	Soltis et al. 1997a	U42416
same DNA	this paper	AF206773	same DNA	same	this paper	AF206918
<i>S. frutescens</i> Krause	Chase et al. 1993	L13932	same DNA as for atpB	same as for atpB	this paper	AJ236008
same DNA	Savolainen et al. 2000a	AJ235780	same DNA	same	this paper	AF206920
same DNA	Morgan & Soltis 1993	L11185	same DNA	same	Soltis et al. 1997a	U43151
<i>R. aureum</i> Pursh	Morgan & Soltis 1993	L11204	same DNA as for rbcL	same as for rbcL	Soltis et al. 1997a	L28143
<i>G. manicata</i> Linden	Morgan & Soltis 1993	L11186	same DNA as for rbcL	same as for rbcL	Soltis et al. 1997a	U43787
<i>H. serra</i> Brongn.	Conti et al. 1996	U26325	same DNA as for atpB	same as for atpB	Soltis et al. 1997a	U42550
same DNA	Morgan & Soltis 1993	L11195	same DNA	same	Soltis et al. 1997a	L11195
same DNA	Hoot et al. 1999	AF094548	same DNA	same	Hoot et al. 1999	AF094548
same DNA	Hoot et al. 1999	AF094549	same DNA	same	Hoot et al. 1999	AF094549
same DNA	Qiu et al. 1998	AF060708	same DNA	same	Hoot et al. 1999	AF094550
<i>H. mollis</i> Oliv.	Chase et al. 1993	L01922	same DNA as for atpB	same as for atpB	Hoot et al. 1999	AF094551
<i>H. latispatha</i> Benth.	Smith et al. 1993	L05451	same DNA as for atpB	same as for atpB	this paper	AF168849
same DNA	Qiu et al. 1993	L12647	same DNA	same	this paper	AF206923
same DNA	Qiu et al. 1993	L12646	same DNA	same	this paper	AF206916
same DNA	Savolainen et al. 2000a	AJ235771	same DNA	same	this paper	AF206840
same DNA	Chase et al. 1993	L01926	same DNA	same	Soltis et al. in press	AF206930
same species	Chase et al. 1993	Z69237	same DNA as for atpB	same as for atpB	Soltis et al. 1997a	U42067
same species	Chase et al. 1993	L11177	same DNA as for rbcL	same as for rbcL	this paper	AJ235992
<i>Decurmaria</i> sp.	Chase et al. 1993	AF206760	same DNA as for atpB	same as for atpB	this paper	AJ235985
same DNA	Soltis et al. 1995	AF206766	same DNA	same	this paper	AJ235986
same species	Morgan & Soltis 1993	L11187	same DNA as for rbcL	same as for rbcL	Soltis et al. 1997a	U42781
same DNA	Morgan & Soltis 1993	L11198	same DNA	same	Soltis et al. 1997a	U42782
same DNA	?	AF206832	same DNA	same	this paper	AF207050
same DNA	Chase et al. 1993	L14293	same DNA	same	this paper	AJ236014
<i>H. multifida</i> A. Juss.	Hempel et al. 1995	U17879	same DNA as for atpB	same as for atpB	this paper	AJ235983
same DNA	Chase et al. 1995	Z77280	same DNA	same	this paper	AF207008
same DNA	Savolainen et al. 2000a	AJ235779	same DNA	same	this paper	AF206919
same DNA	this paper	AF206780	same DNA	same	this paper	AF206935
same DNA	this paper	AF156733	same DNA	same	this paper	AJ235999
same species	Qiu et al. 1993	L12652	same DNA as for atpB	same as for atpB	Soltis et al. 1997a	L75832
same DNA?	this paper	AF206736	same DNA	same	this paper	AF206854
same DNA?	this paper	AF206772	same DNA	same	Soltis et al. 1997a	L54062
same DNA	this paper	AF206782	same DNA	same	this paper	AF206939
same DNA	Chase et al. 1993	L11188	same DNA	same	Soltis et al. 1997a	U42545
same DNA	Koontz & Soltis 1999	AF084475	same DNA	same	Koontz & Soltis 1999	AF084476
same DNA	Chase et al. 1995	Z73704	same DNA	same	this paper	AF206940
same DNA	Chase et al. 1993	L12637	same DNA	same	Soltis et al. 1999	AF206880
same species	this paper	AF206785	same species	Soltis 2520 WS	this paper	AF206943

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APPENDIX—

FAMILY	SPECIES (atpB)	VOUCHER (atpB)	CITATION (atpB)	EMBL (atpB)
Juncaceae	<i>Juncus effusus</i> L.	Chase 200 NCU	Savolainen et al. 2000a	AJ235509
Kiggelariaceae	<i>Kiggelaria africana</i> L.	Chase 5607 K	this paper	AF209610
Kiggelariaceae	<i>Pangium edule</i> Reinw.	Chase 1285 K	this paper	AF209644
Kiggelariaceae	<i>Hydnocarpus heterophyllum</i> Blume	Chase 1278 K	this paper	AJ235496
Kiggelariaceae	unknown	Chase 1301 K	this paper	AF209607
Koerberliniaceae	<i>Koerberlinia spinosa</i> Zucc.	Al-Shebaz s.n. MO	this paper	AF209612
Krameriaceae	<i>Krameria ixine</i> L.	Litt 1 NY	Savolainen et al. 2000a	AJ235514
Lacistemataceae	<i>Lacistema aggregatum</i> Rusby	Chase 1600	this paper	AF209613
Lamiaceae	<i>Clerodendrum chinense</i> (Osb.) Mabb.	Matthaei Bot. Gard. MICH	this paper	AJ236033
Lamiaceae	<i>Lamium amplexicaule</i> L.	Mort s. n. WS	this paper	AJ236165
Lardizabalaceae	<i>Akebia quinata</i> (Houtt.) Decne	Qju 91020 NCU	Hoot et al. 1995a	AF209523
Lardizabalaceae	<i>Decaisnea fargesii</i> Franchet	Reznicek 9236 MICH	Hoot et al. 1995a	L37926
Lardizabalaceae	<i>Sinofranchetia chinensis</i> Hemsley	Edinburgh 831635 F	Hoot et al. 1995a	L37931
Lardizabalaceae	<i>Sargentodoxa cuneata</i> Rehder & E. Wilson	Qin s.n. PE	Hoot et al. 1995a	AF903396
Lauraceae	<i>Cinnamomum camphora</i> Nees & Eberm.	Qju 102 NCU	Savolainen et al. 2000a	AJ235436
Lauraceae	<i>Sassafras albidum</i> (Nutt.) Nees	Soltis & Soltis 2518 WS	this paper	AF209668
Laxmanniaceae	<i>Eustrephus latifolius</i> R.Br.	Kress s.n. US	this paper	AF233085
Lecythydaceae	<i>Couropita guianensis</i> Aubl.	Fairchild Trop. Bot Gard	this paper	AJ236224
Lecythydaceae	<i>Gustavia superba</i> Berg	Fairchild Trop. Bot Gard	this paper	AJ236222
Lecythydaceae	<i>Napoleonaea vogelii</i> Hook. & Planch.	Chase 329 K	Savolainen et al. 2000a	AJ235540
Lentibulariaceae	<i>Pinguicula lutea</i> Walt.	Albach 1 WS	this paper	AF209655
Lentibulariaceae	<i>Utricularia biflora</i> Roxb.	Chase 143 NCU	Savolainen et al. 2000a	AJ235636
Liliaceae	<i>Clintonia borealis</i> (Aiton) Raf.	Hahn 6962 WIS	this paper	
Liliaceae	<i>Lilium superbum</i> L.	Chase 112 NCU	this paper	AF209618
Liliaceae	<i>Scilla</i> sp.	Hahn s.n. WIS	this paper	AF069206
Liliaceae	<i>Scoliopus hallii</i> Wats.	Chase 3468 K	this paper	AF209672
Liliaceae	<i>Tricyrtis latifolia</i> Maxim.	Chase 548 K	Savolainen et al. 2000a	AJ235630
Limnanthaceae	<i>Floerkea proserpinoides</i> Willd.	Reznicek 8609 MICH	Bakker et al. 1998	AF035904
Limnanthaceae	<i>Limnantes douglassii</i> R. Br.	Price s.n. IND	this paper	AF209619
Linaceae	<i>Linum perene</i> Guss.	Chase 111 NCU	Savolainen et al. 2000a	AJ235521
Linaceae	<i>Reinwardtia indica</i> Dumort.	Chase 230 NCU	Savolainen et al. 2000a	AJ235577
Linnaeaceae	<i>Abelia triflora</i> R.Br.	2009-45 Seattle Arb	this paper	AJ236209
Loasaceae	<i>Loasa acuminata</i> Wedd.	Albach 56 WS	this paper	AF209550
Loasaceae	<i>Eucnide bartonioides</i> Zucc.	Albach 55 WS	this paper	AJ236227
Loasaceae	<i>Petalonyx nitidus</i> S. Wats.	Hufford 554 DUL	this paper	AJ236232
Loganiaceae	<i>Spigelia marilandica</i> L.	none	this paper	AF209679
Lowiaceae	<i>Orchidantha fimbriata</i> Holtum	Kress & Beach 87-2159 US	this paper	AF168933
Lythraceae	<i>Lythrum salicaria</i> L.	Soltis & Soltis WS	this paper	AF209621
Lythraceae	<i>Punica protopunica</i> Balf.	Chase 1905 K	Savolainen et al. 2000a	AJ235574
Magnoliaceae	<i>Liriodendron tulipifera</i> L.	Qju 94126 NCU	Savolainen et al. 2000a	AJ235522
Magnoliaceae	<i>Magnolia tripetala</i> L.	Qju 3 NCU	Savolainen et al. 2000a	AJ235526
Magnoliaceae	<i>Manglietia fordiana</i> Oliver	Qju 26 NCU	this paper	AF209623
Malesherbiaceae	<i>Malesherbia linearifolia</i> Poir.	Gengler 23 OS	this paper	AF209622
Malpighiaceae	<i>Dicella nucifera</i> Chodat	Anderson 13607 MICH	Savolainen et al. 2000a	AJ235453
Malpighiaceae	<i>Galphimia gracilis</i> Bart.	Adelson 13580 MICH	this paper	AF209591
Malpighiaceae	<i>Malpighia coccigera</i> L.	Matthaei BG 20626 MICH	Savolainen et al. 2000a	AJ235527

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SPECIES (rbcL)	CITATION (rbcL)	EMBL (rbcL)	SPECIES (18S)	VOUCHER (18S)	CITATION (18S)	EMBL (18S)
same DNA	Chase et al. 1993	L12681	same DNA	same	this paper	AF206944
same DNA	this paper	AF206786	same DNA	same	this paper	AF206945
same DNA	this paper	AF206801	same DNA	same	this paper	AF206979
same DNA	this paper	AJ235781	same DNA	same	this paper	AF206932
same DNA	this paper	AF206783	same DNA	same	this paper	AF206941
same DNA	Rodman et al. 1993	L14600	same DNA	same	Soltis et al. 1997a	U42512
<i>K. lanceolata</i> Torr.	Chase et al. 1993	Y15032	same DNA as for atpB	same as for atpB	Soltis et al. 1999	AF206948
same DNA	this paper	AF206787	same DNA	same	this paper	AF206949
<i>C. fragrans</i> R. Br.	Olmstead et al. 1992	L11689	same DNA as atpB	same	this paper	AJ236033
<i>L. purpureum</i> L.	Olmstead et al. 1993	U75702	same species as for atpB	Johnson 95-001 WS	Soltis et al. 1997a	L49278
same DNA	Hoot et al. 1995a	L12627	same species	Nickrent 2945 SIU	Soltis et al. 1997a	L31795
same DNA	Hoot et al. 1995a	L37907	same DNA	same	Hoot et al. 1995a	L37916
same DNA	Hoot et al. 1995a	L37912	same DNA	same	Hoot et al. 1995a	L37921
same DNA	Hoot et al. 1995a	AF093731	same DNA	same	Hoot et al. 1995a	L75841
same DNA	Qiu et al. 1993	L12641	same DNA	same	this paper	AF206888
same DNA	this paper	AF206790	same DNA as for atpB	same as for atpB	this paper	AF233091
same DNA	this paper	AF206819	same DNA	same	Soltis et al. 1997a	AF207014
same species	Morton et al. 1997a	Z80181	same DNA as for atpB	same as for atpB	this paper	AJ235993
<i>G. poeppigiana</i> Berg	Morton et al. 1997	Z80175	same DNA as for atpB	same as for atpB	this paper	AJ235994
same DNA	Morton et al. 1997a	Z80173	same DNA	same	this paper	AF206969
<i>P. caerulea</i> Walt.	Chase et al. 1993	L01942	same DNA as for atpB	same as for atpB	this paper	AJ236043
same DNA	Chase et al. 1993	L13190	<i>Utricularia</i> sp.	Albach 5 WS	this paper	AJ236044
same species	this paper	AF206751	same DNA as for atpB	same as for atpB	this paper	AF168833
same DNA	Chase et al. 1995	Z77295	same DNA	same	this paper	AF206952
same DNA	this paper	L05038	same DNA	same	this paper	AF069206
same DNA	this paper	AF206820	same DNA	same	this paper	AF207018
<i>T. affinis</i> Makino	Savolainen et al. 2000a	D17382	same DNA as for rbcL	Chase 2777 K	this paper	AF207046
same DNA	Chase et al. 1993	L12679	same DNA	same	Soltis et al. 1997a	U42784
same DNA	Rodman et al. 1993	L14700	same DNA	same	Rodman et al. 1998	
same DNA	Fay et al. 1997	Z75681	same species	Nickrent 2900 SIU	Soltis et al. 1997a	L24401
same DNA	Fay et al. 1997	Z13188	same DNA	same	Soltis et al. 1999	AF207005
<i>Abelia</i> sp.	Olmstead	AF206727	same DNA as for atpB	same as for atpB	this paper	AJ236004
<i>Caiphora laterita</i> Klotzsch	Hempel et al. 1995	U17872	same DNA as for atpB	same as for atpB	this paper	AJ235990
<i>E. lobata</i> A. Gray	Hempel et al. 1995	U17874	same DNA as for atpB	same as for atpB	this paper	AJ235988
same DNA	Xiang et al. 1998	U96904	same DNA	same	this paper	AJ235959
same DNA	Olmstead et al. 1993	L14410	same DNA	same	this paper	AJ236024
same DNA	this paper	L05457	same DNA	same	Hershkovitz et al. 1999	AF069223
<i>L. hyssopifolia</i> L.	Conti et al. 1993	L10218	same DNA as for atpB	same as for atpB	Soltis et al. 1999	AF206955
<i>P. granatum</i> L.	Conti et al. 1993	L10223	same species as for rbcL	Nickrent 2931 SIU	Soltis et al. 1997a	U38311
same species	Chase et al. 1993	X54346	<i>L. chinense</i>	Qiu 28 NCU	this paper	AF206954
same DNA	Qiu et al. 1993	AF206791	same species	same	this paper	AF206956
same DNA	Chase et al. 1993	L12658	same DNA	same	this paper	
same species	this paper	AF206792	same DNA as for atpB	same as for atpB	this paper	AF206957
same DNA	Chase et al. 1993	AJ235802	same species	Chase 148 NCU	Soltis et al. 1999	AF206901
same species	Chase et al. 1993	AF206771	same DNA as for atpB	same as for atpB	this paper	AF206917
same DNA	Savolainen et al. 2000a	AJ235784	same species	Nickrent 2905 SIU	Soltis et al. 1997a	L24046

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APPENDIX—

FAMILY	SPECIES (atpB)	VOUCHER (atpB)	CITATION (atpB)	EMBL (atpB)
Malvaceae	<i>Gossypium hirsutum</i> L.	Chase 3014 K	Bayer et al. 1999	AJ233052
Malvaceae	<i>Ochroma pyramidale</i> (Cav. ex Lam.) Urb.	Chase 244 NCU	Bayer et al. 1999	AF035910
Malvaceae	<i>Bombax malabarica</i> DC.	Chase 3049 K	Bayer et al. 1999	AJ233051
Malvaceae	<i>Durio zibethinus</i> Murray	Alverson 2180 WIS	Alverson et al. 1998	AF022119
Malvaceae	<i>Grewia occidentalis</i> L.	Chase 3042 K	Bayer et al. 1999	AJ233105
Malvaceae	<i>Sterculia apetala</i> Karsten	Chase 352 K	Bayer et al. 1999	AJ233089
Malvaceae	<i>Theobroma cacao</i> L.	Chase 3016 K	Bayer et al. 1999	AJ233090
Malvaceae	<i>Tilia americana</i> L.	Chase 3018 K	Bayer et al. 1999	AJ233113
Marantaceae	<i>Calathea loeseneri</i> J. F. Macb.	Kress 94-3722 US	this paper	AF168890
Marantaceae	<i>Maranta bicolor</i> Vell.	Kress 94-3724 US	this paper	AF168927
Marcgraviaceae	<i>Marcgravia rectiflora</i> Triana & Planch.	Chase 331 NCU	Savolainen et al. 2000a	AJ235529
Medusagynaceae	<i>Medusagyne oppositifolia</i> Baker	Chase 670 K	Savolainen et al. 2000a	AJ235530
Melanthiaceae	<i>Chamaelirium luteum</i> Willd.	Chase 224 NCU	this paper	AF209561
Melanthiaceae	<i>Xerophyllum tenax</i> Nutt.	Chase 527 K	Savolainen et al. 2000a	AJ132285
Melastomataceae	<i>Clidemia petiolaris</i> Triana	Chase 2534 K	Savolainen et al. 2000a	AJ235439
Meliaceae	<i>Swietenia macrophylla</i> King	Chase 250 K	Savolainen et al. 2000a	AJ235616
Meliaceae	<i>Trichilia emetica</i> Vahl	Chase 552 K	Savolainen et al. 2000a	AJ235629
Meliantaceae	<i>Bersama lucens</i> Szyszyl.	Chase 1125 K	Savolainen et al. 2000a	AJ235410
Memecylaceae	<i>Mouriri cyphocarpa</i> Standl.	Chase 2534 K	this paper	AF209634
Menispermaceae	<i>Menispermum canadensis</i> L.	Naczi 2837 MICH	Hoot et al. 1999	AF093384
Menispermaceae	<i>Tinospora caffra</i> Miers	Jaarsveld 2131 NBG	Hoot et al. 1995a	L37933
Menyanthaceae	<i>Menyanthes trifoliata</i> L.	Chase 3501 K	Savolainen et al. 2000a	AJ235533
Menyanthaceae	<i>Nymphoides geminata</i> (R.Br.) Kuntze	Albach 61 WS	this paper	AJ236204
Molluginaceae	<i>Mollugo verticillata</i> L.	Hershkovitz 37 WS	this paper	AF209631
Monimiaceae	<i>Hedycarya arborea</i> Forst.	Qju 90028 NCU	Savolainen et al. 2000a	AJ235489
Monimiaceae	<i>Peumus boldus</i> Molina	Strybing Arb.	this paper	AF209650
Montiniaceae	<i>Montinia caryophyllacea</i> Thunb.	Williams 2833 MO	this paper	AJ236187
Moraceae	<i>Ficus</i> sp.	Soltis s.n. WS	this paper	AF209587
Moraceae	<i>Morus nigra</i> L.	Chase 2512 K	Savolainen et al. 2000a	AJ235536
Moringaceae	<i>Moringa oleifera</i> Lam.	Iltis 30501 WIS	this paper	AF209633
Muntingiaceae	<i>Muntingia calabura</i> L.	Chase 346 NCU	Bakker et al. 1998	AF035908
Musaceae	<i>Ensete ventricosum</i> (Welw.) Cheesman	Kress s.n. US	this paper	AF168910
Musaceae	<i>Musa acuminata</i> Colla	U.S. Bot Gard. s.n. US	this paper	AF168931
Musaceae	<i>Musella lasiocarpa</i> (Franch.) C.Y. Wu	Kress US	this paper	AF168932
Myoporaceae	<i>Myoporum mauritanum</i> A. de Candolle	RBG Kew 1984-4220	this paper	AJ236166
Myricaceae	<i>Myrica cerifera</i> L.	Chase 2500 K	Savolainen et al. 2000a	AJ233068
Myristicaceae	<i>Knema latericia</i> Elmer	Qju 91014 NCU	this paper	AF209611
Myristicaceae	<i>Myristica fragrans</i> Hout.	Qju 92014 NCU	this paper	AJ235539
Myrothamnaceae	<i>Myrothamnus flabellifolius</i> Welw.	Winter 72 RAV	Hoot et al. 1999	AF093386
Myrsinaceae	<i>Ardisia</i> sp.	Albach 5 WS	this paper	AF209530
Myrsinaceae	<i>Maesa myrsinoides</i> L.	Chase 309 K	Savolainen et al. 2000a	AJ235525
Myrtaceae	<i>Heteropyxis natalensis</i> Harv.	Conti 1002 WIS	this paper	AF209597
Nelumbonaceae	<i>Nelumbo lutea</i> Pers.	Hoot 9212 UWM	Hoot et al. 1999	AF093387
Nepenthaceae	<i>Nepenthes alata</i> Blanco	Chase 145 NCU	Savolainen et al. 2000a	AJ235542
Neuradaceae	<i>Neurada procumbens</i> L.	Collenette 8193 K	this paper	AF209637
Nyctaginaceae	<i>Bougainvillea glabra</i> Choisy	Chase 2485 K	Savolainen et al. 2000a	AJ235415

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SPECIES (rbcL)	CITATION (rbcL)	EMBL (rbcL)	SPECIES (18S)	VOUCHER (18S)	CITATION (18S)	EMBL (18S)
<i>G. robinsoni</i> F.Muell.	Chase et al. 1993	L13186	same species as for atpB	Alverson s.n. WIS	Soltis et al. 1997a	U42827
same DNA	Bayer et al. 1999	AF206800	same DNA	same	this paper	AF206975
<i>B. buonopozense</i> P.Beauv.	Chase et al. 1993	AF022118	<i>B. ceiba</i> Burm.	Alverson s.n. WIS	Soltis et al. 1997a	U42507
same species	Bayer et al. 1999	AJ233053	same DNA as for atpB	same as for atpB	this paper	AF206905
same DNA	Bayer et al. 1999	AJ233152	same DNA	same	this paper	AF206921
<i>S. tragacantha</i> Lindl.	Alverson et al. 1998	AF022126	<i>S. recordiana</i>	Alverson 2184 WIS	Soltis et al. 1999	AF207029
same species	Chase et al. 1993	AF022125	same species	Hunter 698 WIS	this paper	AF207040
<i>T. americana</i> L.	Chase et al. 1993	AF022127	same species	Soltis 2538 WS	this paper	AF207042
same DNA	this paper	AF243842	same DNA	same	Hershkovitz et al. 1999	AF069224
same species	Duval et al. 1993	L05040	same DNA as for atpB	same as for atpB	Soltis et al. 1997a	U42079
same DNA	Morton et al. 1997a	Z83148	same DNA	same	Kron 1996	Z83148
same DNA	Fay et al. 1997	Z75670	same DNA	same	this paper	AF206959
same DNA	this paper	AF206749	same DNA	same	this paper	AF206884
same DNA	Chase et al. 1995	AJ1311949	same DNA	same	this paper	AF207057
<i>Osbeckia stellata</i> Wall.	Chase et al. 1993	AJ235777	same DNA as for rbcL	Conti 1004 WIS	this paper	AF206977
same DNA	Gadek et al. 1996	U39080	same DNA	same	this paper	AF207031
same DNA	Gadek et al. 1996	U39082	same DNA	same	this paper	AF207045
same DNA	Savolainen et al. 2000a	AJ235774	<i>B. abyssinica</i> Fres.	Knox 2563 K	this paper	AF206867
same DNA	this paper	AF206796	same DNA	same	Soltis et al. 1999	AF206965
same species	Hoot et al. 1999	AF093726	same DNA	same	Soltis et al. 1997a	L75834
same DNA	Hoot et al. 1995a	L37923	same DNA	same	Hoot et al. 1995a	L37914
same species	Olmstead et al. 1993	L14006	same species	Peterson & Arnabe 3810 WS	this paper	AJ236009
<i>N.peltatum</i> Britt & Rendle	this paper	X87392	same DNA as for atpB	same as for atpB	this paper	AJ236010
same species	Chase et al. 1993	M62566	same DNA as for atpB	same as for atpB	Soltis et al. 1997a	U42828
same DNA	Qiu et al. 1993	L12648	same DNA	same	this paper	AF206924
same DNA	this paper	AF206807	same DNA	same	this paper	AF206988
same DNA	Morgan & Soltis 1993	L11194	same DNA	same	Soltis et al. 1997a	U42808
<i>F. trigonata</i> L.	Chase et al. 1993	AF206767	same DNA as for atpB	same as for atpB	this paper	AF206911
<i>M. alba</i> L.	Chase et al. 1993	L01933	same species as for rbcL	Nickrent 2924 SIU	Soltis et al. 1997a	L24398
same DNA	Rodman et al. 1993	L11359	same DNA	same	Soltis et al. 1997a	U42786
same DNA	Fay et al. 1998	Y15146	same species	Alverson 2172 WIS	Soltis et al. 1997a	U42539
same DNA	this paper	AF243843	same DNA	same	this paper	AF168842
same DNA	Smith et al. 1993	L05455	same DNA	same	Soltis et al. 1997a	U42083
same DNA	this paper	AF243844	same DNA	same	this paper	AF168862
same species	Olmstead & Reeves 1995	L36403	same DNA as for atpB	same as for atpB	this paper	AJ236036
same species	Chase et al. 1993	L01934	same DNA as for rbcL	same as for rbcL	Soltis et al. 1999	AF206967
same DNA	Qiu et al. 1993	L12653	same DNA	same	this paper	AF206946
same DNA	this paper	AF206798	same DNA	same	this paper	AF206968
same DNA	Qiu et al. 1998	AF060707	same DNA	same	Hoot et al. 1999	AF094555
<i>A. crenata</i> Sims.	Kron & Chase 1993	L12599	same DNA as for atpB	same as for atpB	this paper	AJ235997
same DNA	Morton et al. 1997a	Z80203	same DNA	same	this paper	AJ235997
same DNA	this paper	AF206775	same DNA	same	this paper	AF206927
same species	Chase et al. 1993	M77032	same DNA as for atpB	same as for atpB	Soltis et al. 1997a	L75835
same DNA	Chase et al. 1993	L01935	<i>Nepenthes</i> sp.	Nickrent 3056 SIU	Soltis et al. 1997a	U42787
same DNA	Morgan et al. 1993	U06814	same DNA	same	this paper	AF206970
same species	Manhart et al. unpubl.	M88340	same species	Soltis s.n. WS	this paper	AF206873

continued

APPENDIX—

FAMILY	SPECIES (atpB)	VOUCHER (atpB)	CITATION (atpB)	EMBL (atpB)
Nyctaginaceae	<i>Mirabilis jalapa</i> L.	Hershkovitz 60 WS	this paper	AF209629
Nymphaeaceae	<i>Nuphar variegata</i> Durand	Schneider s. n. SBBG	this paper	AF209640
Nymphaeaceae	<i>Nymphaea odorata</i> Aiton	Qui 91029 NCU	Savolainen et al. 2000a	AJ235544
Nymphaeaceae	<i>Barclaya longifolia</i> Wall.	Schneider and Vaughan SBBG	this paper	AF209536
Ochnaceae	<i>Ochna multiflora</i> DC.	Chase 229 NCU	Savolainen et al. 2000a	AJ235546
Oleaceae	<i>Schoepfia schreberi</i> J. F. Gmel.	Nickrent 2599 ILL	this paper	AF209671
Oleaceae	<i>Jasminum polyanthum</i> Franch.	Chase 2474 K	Savolainen et al. 2000a	AJ235508
Oleaceae	<i>Olea europaea</i> L.	Johnson 95-004 WS	this paper	AJ236163
Onagraceae	<i>Clarkia xantiana</i> A. Gray	Gotlieb 7346 DAV	this paper	AF209564
Onagraceae	<i>Epilobium angustifolium</i> L.	Soltis & Soltis 2521 WS	this paper	AF209582
Oncothecaceae	<i>Oncotheca balansae</i> Baill.	Jaffre 3238 NOU	Savolainen et al. 2000a	AJ235549
Opiliaceae	<i>Opilia amentacea</i> Roxb.	Chase 1902 K	Savolainen et al. 2000a	AJ235550
Orchidaceae	<i>Cypripedium calceolus</i> Walt.	Chase O-714 K	Savolainen et al. 2000a	AJ235448
Orchidaceae	<i>Oncidium excavatum</i> Lindl.	Chase O-86 K	Savolainen et al. 2000a	AJ235548
Oxalidaceae	<i>Averrhoa carambola</i> L.	Chase 214 NCU	Savolainen et al. 2000a	AJ235404
Oxalidaceae	<i>Oxalis dillenii</i> Jacq.	Soltis & Soltis 2548 WS	this paper	AF209642
Paeoniaceae	<i>Paeonia suffruticosa</i> Andr.	Reznicek 9235 MICH	Hoot et al. 1999	AF093389
Pandanaceae	<i>Freycinetia scandens</i> Gaudich	Chase 191 NCU	this paper	AF209590
Papaveraceae	<i>Hypocoum imberbe</i> Sm.	Chase 528 K	Hoot & Crane 1995	U86398
Papaveraceae	<i>Dicentra chrysantha</i> Walp.	Chase 534 K	Savolainen et al. 2000a	AJ235454
Papaveraceae	<i>Pteridophyllum racemosum</i> Sieb. et Zucc.	Chase 531 K	Hoot & Crane 1995	U86400
Parnassiaceae	<i>Lepuropetalon spathulatum</i> (Muhl.) Elliott	Thomas s.n. NLU	this paper	AF209616
Parnassiaceae	<i>Parnassia palustris</i> L.	Fay sn K	Savolainen et al. 2000a	AJ235552
Passifloraceae	<i>Paropsia madagascariensis</i> (Baill.) H. Perrier	Chase 3761 K	this paper	AF209645
Passifloraceae	<i>Passiflora coccinea</i> Aubl.	Chase 2475 K	Savolainen et al. 2000a	AJ235553
Paulowniaceae	<i>Paulownia tomentosa</i> (Thunb.) Steud.	Olmstead 88-008 WTU	this paper	AJ236174
Pedaliaceae	<i>Proboscidea louisianica</i> Thell.	Morden 857 IND	this paper	AJ236161
Pedaliaceae	<i>Sesamum indicum</i> L.	Wagstaff 92-239 COLO	this paper	AJ236176
Pellicieraceae	<i>Pelliciera rhizophorae</i> Planch. & Triana	Pennington et al. 586 INB, CR, E, K	this paper	AF209647
Penthoraceae	<i>Penthorum sedoides</i> L.	Hayden 2232 WS	Savolainen et al. 2000a	AJ235555
Petrosaviaceae	<i>Japonolirion osense</i> Nakai	Chase 3000 K	this paper	AF209608
Petrosaviaceae	<i>Petrosavia stellaris</i> Becc.	Chase 1933 K	this paper	AF209649
Phellinaceae	<i>Phelline comosa</i> Labill.	Savolainen pco1 G	Savolainen et al. 2000a	AJ235557
Phylidraceae	<i>Helmholtzia acrifolia</i> F. Muell.	Kress 92-3505 US	this paper	AF168922
Phylidraceae	<i>Philydrella pygmaea</i>	Chase 2236 K	this paper	AF209651
Phyllonomaceae	<i>Phyllonoma laticuspus</i> (Turcz.) Engl.	Morgan 2124 WS	this paper	AJ236216
Phytolaccaceae	<i>Ercilla volubilis</i> A.Juss.	Chase 2526 K	Savolainen et al. 2000a	AJ235464
Phytolaccaceae	<i>Phytolacca dioica</i> L.	Chase 2535 K	Savolainen et al. 2000a	AJ235558
Finaceae	<i>Pinus thunbergiana</i> Franco	unknown	Savolainen et al. 2000a	D17510
Piperaceae	<i>Peperomia obtusifolia</i> Miq.	Qju 94135 NCU	Savolainen et al. 2000a	AJ235556
Piperaceae	<i>Piper betel</i> L.	Qju 91048 NCU	Savolainen et al. 2000a	AJ235560
Pittosporaceae	<i>Pittosporum fairchildii</i> Cheeseman	Chase 2468 K	Savolainen et al. 2000a	AJ235561
Pittosporaceae	<i>Sollya heterophylla</i> Lindl.	Plunkett 1361 WS	this paper	AJ236214
Plantaginaceae	<i>Plantago lanceolata</i> L.	Albach 13 WS	this paper	AF209656
Platanaceae	<i>Platanus occidentalis</i> L.	Qju P90005 NCU	Hoot et al. 1997	U86386
Plumbaginaceae	<i>Limonium dendroides</i> Svent.	Chase 706 K	this paper	AF209620

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SPECIES (rbcL)	CITATION (rbcL)	EMBL (rbcL)	SPECIES (18S)	VOUCHER (18S)	CITATION (18S)	EMBL (18S)
same species	Chase et al. 1993	M62565	same DNA as for atpB	same as for atpB	Soltis et al. 1997a	U42788
<i>N. variegata</i> Padget	Chase et al. 1993	AF096695	same DNA as for atpB	same as atpB	this paper	AF206972
same species	Chase et al. 1993	M77031	<i>Nymphaea</i> sp.	Qiu 91029 NCU	this paper	AF096696
same species	Chase et al. 1993	M77027	same DNA as for atpB	Zanis WS	this paper	AF096692
<i>O. serratula</i> Walp	Chase et al. 1993	Z75273	same DNA as for atpB	same as for atpB	Soltis et al. 1999	AF206974
same DNA	Chase et al. 1993	L11205	same DNA	same	this paper	AF207017
<i>J. suavissimum</i> Lindl.	Chase et al. 1993	L01929	same DNA as for rbcL	same as for rbcL	this paper	AJ236035
same species	Savolainen et al. 2000a	AJ001766	same DNA as for atpB	same as for atpB	Soltis et al. 1997a	L49289
same DNA	Olmstead et al. 1992	L10896	same DNA	same	Soltis et al. 1997a	U67930
same species	Conti et al. 1993	L10217	same DNA as for atpB	same as for atpB	Soltis et al. 1999	AF206907
same DNA	Savolainen et al. 2000a	AJ131950	same species	Chase 2392 K	this paper	AF206976
same DNA	Savolainen et al. 2000a	AJ131773	same species	Nickrent 2816 SIU	Soltis et al. 1997a	U42790
<i>C. irapeanum</i> Lex.	Chase et al. 1993	Z73706	same species as atpB	Hahn s.n. WIS	Hershkovitz et al. 1999	AF069208
same DNA	Olmstead et al. 1992	AF074201	same DNA	same	Soltis et al. 1997a	U42791
same species	Chase et al. 1993	L14692	same DNA as for rbcL	same as for rbcL	Soltis et al. 1999	AF206859
same species	Chase et al. 1993	L01938	same DNA as for atpB	same as for atpB	this paper	AF206978
<i>P. tenuifolia</i> L.	Chase et al. 1993	L13687	same DNA as for atpB	same as for atpB	Soltis et al. 1997a	U42792
same DNA	Chase et al. 1993	AF206770	same DNA	same	this paper	AF206915
same DNA	Hoot & Crane 1995	U86628	same DNA	same	Soltis et al. 1997a	L75836
<i>D. spectabilis</i> (L.) Lem.	Chase et al. 1993	L08761	<i>D. exima</i> Torrey	Reznicek 9756 MICH	Soltis et al. 1997a	L37908
same DNA	Hoot & Crane 1995	U86631	same DNA	same	Hoot & Crane 1995	AF094560
same species	Morgan & Soltis 1993	L11192	same DNA as for rbcL	same as for rbcL	Soltis et al. 1997a	L28141
<i>P. fimbriata</i> Banks	Chase et al. 1993	L01939	same DNA as for rbcL	same as for rbcL	Soltis et al. 1997a	U42809
same DNA	this paper	AF206802	same DNA	same	this paper	AF206980
<i>P. quadrangalis</i> L.	Chase et al. 1993	L01940	<i>P. standleyi</i> Killip	MO 876630	Soltis et al. 1999	AF206981
same DNA	Olmstead & Reeves 1995	L36447	same DNA	same	this paper	AJ236039
same DNA	Chase et al. 1993	L01946	same DNA	same	this paper	AJ236040
same species	Olmstead et al. 1993	L14408	same DNA as for atpB	same as for atpB	this paper	AJ236041
same DNA	this paper	AF206804	same DNA	same	this paper	AF206983
same DNA	Chase et al. 1993	L11197	same DNA	same	Soltis et al. 1997a	U25660
same DNA	this paper	AF206784	same DNA	same	this paper	AF206942
same DNA	this paper	AF206806	same DNA	same	this paper	AF206987
same DNA	Savolainen et al. 2000a	X69748	<i>P. billardieri</i>	Van Balgooy 7013 L	this paper	AF206989
same DNA	this paper	AF206774	same DNA	same	Soltis et al. 1997a	U42074
same DNA	this paper	AF206808	same DNA	same	this paper	AF206990
same DNA	Morgan & Soltis 1993	L11201	same DNA	same	Soltis et al. 1997a	U42546
same DNA	Savolainen et al. 2000a	AJ235800	same DNA	same	this paper	AF206908
<i>P. americana</i> L.	Chase et al. 1993	M62567	same species as for rbcL	Hershkovitz 38 WS	Soltis et al. 1997a	U42793
same species	Savolainen et al. 2000a	D17510	<i>Pinus ellioti</i>	Chaw 1394	Chaw et al. 1995	D38245
<i>P. obtusifolia</i> Miq.	Qiu et al. 1993	L12661	same DNA	same	this paper	AF206985
same DNA	Qiu et al. 1993	L12660	same DNA	same	this paper	AF206992
<i>P. japonicum</i> Hort.	Morgan & Soltis 1993	L11202	same species as for rbcL	Rieseberg sn RSA	Soltis et al. 1997a	L28142
same DNA	Plunkett et al. 1997	U50262	same DNA	same	this paper	AJ236001
same species	Olmstead & Reeves 1995	L36454	same DNA as for atpB	same as for atpB	this paper	AJ236046
same DNA	Chase et al. 1993	L01943	same species	Soltis & Soltis 2514 WS	Soltis et al. 1997a	U42794
same DNA	this paper	AF206789	same DNA	Chase 1649 K	this paper	AF206953

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APPENDIX—

FAMILY	SPECIES (atpB)	VOUCHER (atpB)	CITATION (atpB)	EMBL (atpB)
Plumbaginaceae	<i>Plumbago zeylanica</i> L.	Chase 994 K	Savolainen et al. 2000a	AJ235565
Poaceae	<i>Oryza sativa</i> L.	unknown	Chase et al. 1993	X15901
Poaceae	<i>Zea mays</i> L.	unknown	Savolainen et al. 2000a	X86563
Podocarpaceae	<i>Podocarpus milanjanus</i> Rendl.	Chase 2482 K	Savolainen et al. 2000a	AJ235567
Podostemaceae	<i>Maranthrum rubrum</i> Novelo & Philbrick	Philbrick sn CONN	this paper	AF209624
Polemoniaceae	<i>Cobaea scandens</i> Cav.	Chase 961 K	Savolainen et al. 2000a	AJ235440
Polemoniaceae	<i>Gilia capitata</i> Sims.	Johnson 92-15 WS	this paper	AJ236220
Polemoniaceae	<i>Phlox longifolia</i> Nutt.	Albach 20 WS	this paper	AJ236221
Polygalaceae	<i>Polygala cruciata</i> L.	Chase 155 NCU	Savolainen et al. 2000a	AJ235568
Polygalaceae	<i>Securidaca diversifolia</i> (L.) S. F. Blake	Chase 2998 K	this paper	AF209673
Polygonaceae	<i>Coccoloba uvifera</i> L.	Nickrent 2927 SIU	this paper	AF209568
Polygonaceae	<i>Polygonum sachalinense</i> Schmidt	Chase 896 K	Savolainen et al. 2000a	AJ235569
Pontederiaceae	<i>Pontederia cordata</i> L.	Chase 2996 K	this paper	AF209657
Portulacaceae	<i>Portulaca grandiflora</i> Hook.	Soltis sn WS	this paper	AF209659
Primulaceae	<i>Anagallis tenella</i> L.	Chase 1910 K	Savolainen et al. 2000a	AJ235390
Primulaceae	<i>Androsace spinulifera</i> Knuth	Chase 954 K	Savolainen et al. 2000a	AJ235392
Proteaceae	<i>Placospermum coriaceum</i> C.T.White & W.D. Francis	Douglas 110 MEL	Savolainen et al. 2000a	AF060391
Proteaceae	<i>Roupala macrophylla</i> Pohl	Douglas 131 MEL	Savolainen et al. 2000a	AF060416
Pseudanthaceae	<i>Androstachys johnsonii</i> Prain	Chase 1904 K	this paper	AF209527
Pseudanthaceae	<i>Stachystemon axillaris</i> A. S. George	Chase 2165 K	this paper	
Pterostemonaceae	<i>Pterostemon rotundifolius</i> Ramirez	Jordan s.n. HO	Savolainen et al. 2000a	AJ235573
Putranjivaceae	<i>Drypetes roxburghii</i> (Wall.) Hurus.	FTG-83463A K	this paper	AF209578
Quinaceae	<i>Quina pteridophylla</i> (Radlk.) Pires	J. Murca Pires CPATU	this paper	AF209664
Ranunculaceae	<i>Coptis trifoliata</i> (L.) Salisb.	Voss & Howard sn MICH	Hoot et al. 1999	AF093393
Ranunculaceae	<i>Glaucidium palmatum</i> Siebold & Zucc.	Hoot 924 UWM	Hoot & Crane 1995	AF093375
Ranunculaceae	<i>Hydrastis canadense</i> L.	Naczi 2883 MICH	Hoot & Crane 1995	AF093382
Ranunculaceae	<i>Ranunculus</i> sp.	Hoot	this paper	
Ranunculaceae	<i>Xanthorhiza simplissima</i> Marshall	Qiu 91030 NCU	Hoot et al. 1999	AF093394
Resedaceae	<i>Reseda alba</i> L.	Price sn IND	this paper	AF209665
Restionaceae	<i>Restio tetraphyllus</i> Labill.	Chase 560 K	this paper	AF209666
Rhabdodendraceae	<i>Rhabdodendron amazonicum</i> Huber	Ribeiro 1187 K	Savolainen et al. 2000a	AJ235578
Rhamnaceae	<i>Ceanothus sanguineus</i> Pursh	Morgan 2155 WS	this paper	AF209558
Rhamnaceae	<i>Rhamnus cathartica</i> L.	Chase 100 NCU	Savolainen et al. 2000a	AJ235579
Rhamnaceae	<i>Trevoa trinervis</i>	Berry s.n. UC Davis	this paper	AF209690
Rhizophoraceae	<i>Brugiera gymnorrhiza</i> (L.) Savigny	Conti sn WIS	this paper	AF209547
Rhizophoraceae	<i>Carallia brachiata</i> Merrill.	Chase 2151 K	Savolainen et al. 2000a	AJ235425
Roridulaceae	<i>Roridula gorgonias</i> Planchon	Goldblatt 5393 MO	this paper	AJ236180
Rosaceae	<i>Kerria japonica</i> (Thunb.) DC.	Henrickson 97-102 CAL	this paper	AF132893
Rosaceae	<i>Photinia fraseri</i> Dress	Morgan 2131 WS	this paper	AF209653
Rosaceae	<i>Prunus persica</i> (L.) Batsch	Dickson sn BH	this paper	AF209660
Rosaceae	<i>Spirea betulifolia</i> Pall.	Chase 2503 K	Savolainen et al. 2000a	AJ235608
Rousseaceae	<i>Roussea simplex</i> Sm.	Mauritius Sugar Res. Inst.	Savolainen et al. 2000a	AJ235586
Rubiaceae	<i>Cephalanthus occidentalis</i> L.	Forbes sn UC 82.0070	this paper	AJ236190
Rubiaceae	<i>Mitchella repens</i> L.	Xiang sn OSU	this paper	AF209630
Rubiaceae	<i>Pentas lanceolata</i> (Forsk.) K. Schum.	Bremer 2702 CONN	this paper	AJ236194

continued

SPECIES (rbcl)	CITATION (rbcl)	EMBL (rbcl)	SPECIES (18S)	VOUCHER (18S)	CITATION (18S)	EMBL (18S)
<i>P. capensis</i> Thunb.	Chase et al. 1993	M77701	<i>P. auriculata</i> Lam.	Nickrent sn SIU	Soltis et al. 1997a	U42795
same species	Chase et al. 1993	X15901	same species	unknown	Soltis et al. 1997a	X00755
same species	Savolainen et al. 2000a	X86563	same species	none	Soltis et al. 1997a	U42796
<i>P. gracilior</i> Pilg.	Chase et al. 1993	X58135	<i>P. costalis</i>	Chaw 1396 TW	Chaw et al. 1995	D38473
same DNA	Les et al. 1997	U68086	same DNA	same	Soltis et al. 1999	AF206958
same DNA	Morton et al. 1996	Z83143	same species	Patterson sn WS	Soltis et al. 1997a	L49277
<i>G. aggregata</i> (Pursh) Spreng.	Morton et al. 1996	Z83144	same DNA as for atpB	same as for atpB	Soltis et al. 1997a	L24143
same DNA	this paper	AF206809	same DNA	same	this paper	AJ235996
same DNA	Chase et al. 1993	L01945	<i>P. pauciflora</i> Willd.	Doyle 1567 BH	Soltis et al. 1997a	U42797
same species	Olmstead et al. 1992	L01955	same DNA as for atpB	same as for atpB	this paper	AF207019
same species	this paper	AF206753	same DNA as for atpB	same as for atpB	Soltis et al. 1997a	U42798
same DNA	Savolainen et al. 2000a	AJ235789	<i>Polygonum</i> sp.	Soltis s.n. WS	this paper	AF206996
<i>P. sagittata</i> C. Presl.	Chase et al. 1993	L20128	same DNA as for atpB	same as for atpB	this paper	AF168871
same species	Chase et al. 1993	M62568	same DNA as for atpB	same as for atpB	this paper	AF207000
<i>A. arvensis</i> L.	Chase et al. 1993	M88343	same DNA as for atpB	same as for atpB	this paper	AF206845
same DNA	Savolainen et al. 2000a	AJ235772	same DNA as for atpB	same as for atpB	this paper	AF206847
same DNA	Hoot et al. 1999	AF093729	same DNA	same	Soltis et al. 1997a	L75837
same DNA	Hoot et al. 1999	AF093728	same DNA	same	Hoot et al. 1999	AF094559
same DNA	this paper	AF206734	same DNA	same	this paper	AF206848
same DNA	this paper	AJ402922	same DNA	same	this paper	
same DNA	Morgan & Soltis 1993	L11203	same species	Sanchez 259 TEX	Soltis et al. 1997a	U42547
same species	Rodman et al. 1993	M95757	same DNA as for atpB	same as for atpB	Soltis et al. 1997a	U42534
same DNA	this paper	AF206815	same DNA	same	this paper	AF207003
same DNA	Hoot et al. 1999	AF093730	same DNA	same	Soltis et al. 1997a	L75838
same DNA ?	Hoot & Crane 1995	AF206772	same DNA	same	Hoot & Crane 1995	AF093374
same DNA	Hoot & Crane 1995	L75849	same DNA	same	Hoot & Crane 1995	L75828
<i>R. trichophyllus</i> Chaix	Chase et al. 1993	L08766	<i>R. sardous</i> Crantz	Nickrent 2932 SIU	Soltis et al. 1997a	L24092
same DNA	Chase et al. 1993	L12669	same DNA	same	Soltis et al. 1997a	L75839
same DNA	Rodman et al. 1993	M95756	same DNA	same	Rodman et al. 1998	AF070973
same DNA	this paper	AF206816	same DNA	same	this paper	AF207006
same DNA	Fay et al. 1997	Z97649	same DNA	same	this paper	AF207007
same DNA	Soltis et al. 1995	U06795	same DNA	same	Soltis et al. 1997a	U42799
same DNA	Chase et al. 1993	L13189	same DNA	same	this paper	AJ235979
same DNA	this paper	AF132887	same DNA	same	this paper	AF132891
same DNA	Conti et al. 1996	U26230	same DNA	same	this paper	AF206875
same DNA	this paper	AF206744	same DNA	same	this paper	
same DNA	Chase et al. 1993	L01950	same DNA	same	this paper	AF207010
same DNA	this paper	AF132886	same DNA	same	this paper	AF132890
same DNA	Morgan & Soltis 1993	L11200	same DNA	same	Soltis et al. 1997a	U42800
<i>P. virginiana</i> L.	Morgan & Soltis 1993	L01947	same DNA as for atpB	same	Soltis et al. 1997a	L28749
<i>S. vanhouttei</i> Zabel	Morgan & Soltis 1993	L11206	same DNA as for rbcL	Morgan 2130 WS	Soltis et al. 1997a	U42801
same DNA	Savolainen et al. 2000a	AJ235792	same DNA	same	Soltis et al. 1997a	U42528
same DNA	this paper	X83629	same DNA	same	this paper	AJ236021
same DNA	this paper	Z68805	same DNA	same	Soltis et al. 1997a	U42802
same DNA	this paper	L13931	same DNA	same	this paper	AJ236027

continued

APPENDIX—

FAMILY	SPECIES (atpB)	VOUCHER (atpB)	CITATION (atpB)	EMBL (atpB)
Rubiaceae	<i>Rogieria suffrutescens</i> (Brand.) A. Borhidi	Bremer 2712 CONN	this paper	AJ236191
Rubiaceae	<i>Dialypetalanthus fuscescens</i>	Chase 3950 K	this paper	AF209576
Rutaceae	<i>Citrus paradisi</i> Macfad.	Chase 2473 K	Chase et al. 1999	AJ238408
Rutaceae	<i>Cneorum pulverulentum</i> Vent.	Chase 3428 K	this paper	AF209567
Rutaceae	<i>Poncirus trifoliata</i> Raf.	Chase 117 NCU	Chase et al. 1999	AJ238409
Sabiaceae	<i>Meliosma veitchiorum</i> Hemsl.	Chase 2989 K	this paper	AF209626
Sabiaceae	<i>Sabia swinhoei</i> Hemsl. ex F.B.Forbes & Hemsl.	Wagner 6518 HAST	Hoot et al. 1999	AF093395
Salicaceae	<i>Populus tremuloides</i> Michx.	Soltis & Soltis 2551 WS	this paper	AF209658
Salicaceae	<i>Salix reticulata</i> L.	Chase 840 K	Savolainen et al. 2000a	AJ235590
Santalaceae	<i>Osyris lanceolata</i> Hochst. & Steud	Nickrent 2731 SIU	this paper	AF209641
Santalaceae	<i>Santalum album</i> L.	Chase 1349 K	Savolainen et al. 2000a	AJ235592
Santalaceae	<i>Dendrophthora clavata</i> (Benth.) Urban	Nickrent 2182 SIU	this paper	AF209575
Santalaceae	<i>Eubrachion ambiguum</i> (Hook. & Arnott) Engler	Nickrent 2699 SIU	this paper	AF209583
Santalaceae	<i>Viscum album</i> L.	Nickrent 2253 SIU	this paper	AF209695
Sapindaceae	<i>Aesculus pavia</i> Castigl.	Chase 503 K	Savolainen et al. 2000a	AF035894
Sapindaceae	<i>Cupaniopsis anacardioides</i> Radl.	Chase 217 NCU	Bakker et al. 1998	AF035903
Sapindaceae	<i>Koelreuteria paniculata</i> Laxm.	Chase 115 NCU	Savolainen et al. 2000a	AJ235513
Sapindaceae	<i>Xanthoceras sorbifolia</i> Bunge	Chase 2866 K	this paper	AF209697
Sapindaceae	<i>Acer saccharum</i> L.	Chase 106 NCU	Savolainen et al. 2000a	AF035893
Sapotaceae	<i>Manilkara zapota</i> Royen	Chase 129 NCU	Savolainen et al. 2000a	AJ235528
Sarcocaulaceae	<i>Sarcocaula</i> sp.	Chase 903 K	Bayer et al. 1999	AJ233070
Sarraceniaceae	<i>Sarracenia flava</i> L.	Chase 144 NCU	Savolainen et al. 2000a	AJ235594
Saururaceae	<i>Houttuynia cordata</i> Thunb.	Reznicek 9238 MICH	Hoot et al. 1999	AF093397
Saururaceae	<i>Saururus chinensis</i> Hort. ex Lond.	Qju 91023 NCU	Savolainen et al. 2000a	AJ235595
Saxifragaceae	<i>Heuchera micrantha</i> Douglas	Soltis & Soltis 2477 WS	Savolainen et al. 2000a	AF093399
Saxifragaceae	<i>Peltoboykinia tellimoides</i> Hara	Nikko Bot. Gard. Japan	Savolainen et al. 2000a	AJ235554
Saxifragaceae	<i>Saxifraga mertensiana</i> Bong.	Grable 11586 WS	this paper	AF209669
Saxifragaceae	<i>Saxifraga retusa</i> Gouan	Soltis and Soltis 2253 WS	this paper	AJ235597
Saxifragaceae	<i>Sullivantia oregana</i> Wats.	Grable 11598 WS	this paper	AF209682
Schisandraceae	<i>Schisandra sphenanthera</i> Rehder & Wilson	Qju 94165 NCU	Savolainen et al. 2000a	AJ235599
Scrophulariaceae	<i>Antirrhinum majus</i> L.	Chase 2570 K	Savolainen et al. 2000a	AJ235395
Scrophulariaceae	<i>Callitriche heterophylla</i> Pursh. emend Darby	Jansen 512 CONN	this paper	AF209552
Scrophulariaceae	<i>Digitalis grandiflora</i> Mill.	Olmstead 92-015 WTU	this paper	AJ236167
Scrophulariaceae	<i>Pedicularis coronensis</i> Schur.	Albach 29 WS	this paper	AF209646
Scrophulariaceae	<i>Scrophularia californica</i> Cham. & Schlecht	Olmstead 93-89 WTU	this paper	AJ236175
Scrophulariaceae	<i>Verbascum thapsus</i> L.	Olmstead 92 133 WTU	this paper	AJ236177
Scrophulariaceae	<i>Veronica anagallis-aquatica</i> L.	Albach 37 WS	this paper	AJ236169
Setchellanthaceae	<i>Setchellanthus caeruleus</i> T. Brandeg.	Iltis & Lasseigne 100 WIS	this paper	AF209674
Simaroubaceae	<i>Ailanthus altissima</i> L.	Chase 126 NCU	Savolainen et al. 2000a	AF035895
Simmondsiaceae	<i>Simmondsia chinensis</i> C.K.Schneid.	Boyd et al. 3355 F	Hoot et al. 1999	AF093401
Smilacaceae	<i>Smilax glauca</i> Walt.	Chase 107 NCU	this paper	AF209677
Solanaceae	<i>Lycopersicon esculentum</i> Mill.	Albach 53 WS	this paper	AJ236188
Solanaceae	<i>Nicotiana tabacum</i> L.	unknown	Deno et al. 1983	V00162
Solanaceae	<i>Petunia axillaris</i> (Lam.) Juss.	Olmstead S-60 WTU	this paper	AJ236182

continued

SPECIES (rbcL)	CITATION (rbcL)	EMBL (rbcL)	SPECIES (18S)	VOUCHER (18S)	CITATION (18S)	EMBL (18S)
same DNA	Albach et al. 2000a	X83665	same DNA	same	this paper	AJ236030
same DNA	this paper	AF206761	same DNA	same	this paper	AF206900
same DNA	Chase et al. 1999	AJ238407	<i>C. aurantium</i> L.	Nickrent 2977 SIU	Soltis et al. 1997a	U38312
same DNA	this paper	AF206752	same DNA	same	this paper	AF206890
same DNA	Chase et al. 1993	AJ235806	same DNA	same	Soltis et al. 1999	AF206997
same DNA	this paper	AF206793	same DNA	same	this paper	AF206961
<i>Sabia</i> sp.	Chase et al. 1993	L12662	same DNA as for atpB	same as for atpB	Soltis et al. 1997a	L75840
same species	Savolainen et al. 2000a	AF206812	same DNA as for atpB	same as for atpB	Soltis et al. 1999	AF206999
same DNA	Savolainen et al. 2000a	AJ235793	same DNA	same	this paper	AF207011
same DNA	Morgan & Soltis 1993	L11196	same DNA	same	Soltis et al. 1997a	U42803
same species	Nickrent & Soltis 1995	L26077	same DNA as for rbcL	Nickrent 2734 SIU	Nickrent & Soltis 1995	L24416
same DNA	Nickrent & Soltis 1995	L26069	same DNA	same	Nickrent & Soltis 1995	L24068
same DNA	Nickrent & Soltis 1995	L26071	same DNA	same	Nickrent & Soltis 1995	L24141
same DNA	Nickrent & Soltis 1995	L26078	same DNA	same	Soltis et al. 1997a	U42821
same DNA	Gadek et al. 1996	U39277	<i>A. hippocastaneum</i> L.	Soltis & Soltis 2547 WS	Soltis et al. 1999	AF206838
same DNA	Chase et al. 1993	L13182	same DNA	same	Soltis et al. 1999	AF206896
same DNA	Gadek et al. 1996	U39283	same DNA	same	Soltis et al. 1999	AF206947
same DNA	this paper	AF206833	same DNA	same	this paper	AF207055
same DNA	Chase et al. 1993	L01881	<i>Acer rubrum</i> L.	Soltis & Soltis 2515 WS	Soltis et al. 1997a	U42494
same DNA	Chase et al. 1993	L01932	same DNA	same	Soltis et al. 1997a	U43080
same DNA	Fay et al. 1998	Y15147	same DNA	same	this paper	submitted
same DNA	Chase et al. 1993	L01952	<i>S. pupurea</i> L.	Morgan sn WS	Soltis et al. 1997a	U42804
same species	Chase et al. 1993	L08762	same species	Nickrent 2940 SIU	Nickrent & Soltis 1995	AF206929
<i>S. cernuus</i> L.	Chase et al. 1993	L14924	same species as for rbcL	Suh 128 US	Soltis et al. 1997a	U42805
same DNA	Chase et al. 1993	L11173	same DNA	same	Soltis et al. 1997a	X28139
same DNA	Soltis et al. 1993	U06213	same DNA	same	Soltis & Soltis 1997	AF206984
same DNA	this paper	U06216	same DNA	same	Soltis & Soltis 1997	U42811
<i>S. integrifolia</i> Hook	Morgan & Soltis 1993	L01953	same DNA	same	Soltis et al. 1997a	U42810
same DNA	Soltis et al. 1993	U06219	same DNA	same	Soltis & Soltis 1997	U42812
same DNA	Qiu et al. 1993	L12665	<i>S. chinensis</i> (Turcz.) Baill.	Reznicek sn MICH	Soltis & Soltis 1997	L75842
same DNA	Olmstead et al. 1992	L11688	same species	Albach 57 WS	this paper	AJ236047
same species	Olmstead et al. 1992	L11681	same DNA as for atpB	same as for atpB	this paper	AF107582
<i>D. purpurea</i> L.	Chase et al. 1993	L01902	same DNA as for atpB	same as for atpB	this paper	AJ236045
<i>P. foliosa</i> L.	this paper	AF206803	<i>P. lanceolata</i> Michx.	Colwell MO	Soltis et al. 1997a	U38317
<i>Scrophularia</i> sp.	Olmstead & Reeves 1995	L36449	same DNA as for atpB	same as for atpB	this paper	AJ236031
same species	Olmstead & Reeves 1995	L36452	same DNA as for atpB	same as for atpB	this paper	AF207051
<i>V. catenata</i> Pennell	Olmstead & Reeves 1995	L36453	same DNA as for atpB	same as for atpB	this paper	AJ236055
same DNA	Rodman et al. 1993	U41455	same DNA	same	Rodman et al. 1997	
same DNA	Chase et al. 1993	L12566	same DNA	same	Soltis et al. 1999	AF206842
same DNA	Fay et al. 1997	AF093732	same DNA	same	Hoot et al. 1999	AF094562
same DNA	Chase et al. 1993	AF206822	same DNA	same	this paper	AF207022
same species	Olmstead et al. 1993	L14403	same DNA as for atpB	same as for atpB	this paper	AJ236017
same species	Chase et al. 1993	Z00044	same species	Albach 53 WS	this paper	AJ236016
<i>P. hybrida</i> (Hook. f.) Vilm.	Chase et al. 1993	X04976	same DNA as for atpB	same as for atpB	same as for atpB	AJ236020

continued

APPENDIX—

FAMILY	SPECIES (atpB)	VOUCHER (atpB)	CITATION (atpB)	EMBL (atpB)
Solanaceae	Schizanthus sp.	Albach WS	this paper	AJ236185
Solanaceae	Duckeodendron cestoides Kuhlman.	Ribeiro 1189 K	this paper	AF209579
Solanaceae	Nolana humifusa I. M. Johnston	Albach 19 WS	this paper	AF209638
Sparganiaceae	Sparganium americanum Nutt.	Chase 257 NCU	this paper	AF209678
Stachyuraceae	Stachyurus praecox Siebold & Zucc.	Chase 900 K	Savolainen et al. 2000a	AJ235609
Stackhousiaceae	Stackhousia minima Hook.f.	Molloy s.n. CHR	Savolainen et al. 2000a	AJ235610
Staphyleaceae	Staphylea trifoliata Marsh	Chase 116 NCU	Savolainen et al. 2000a	AJ235611
Stemoneaceae	Stemona japonica Franch. & Sav.	Chase 258 NCU	Savolainen et al. 2000a	AJ235612
Strelitziaceae	Phenakospermum guyanense (Rich.) Miq.	Kress 86-2099D US	this paper	AF168938
Strelitziaceae	Ravenala madagascariensis J. F. Gmel.	Kress 92-3504 US	this paper	AF168939
Strelitziaceae	Strelitzia nicolae Regel & Koch	Kress 91-3169 US	this paper	AF168948
Stylidiaceae	Stylidium graminifolium Sw.	MFD 386 Bremer UPS	this paper	AJ236201
Styracaceae	Halesia diptera Ellis	U.S. Nat. Arb.	this paper	AJ236226
Styracaceae	Styrax japonica Siebold & Zucc.	Chase 960 K	Savolainen et al. 2000a	AJ235615
Surianaceae	Stylobasium spatulatum Desf.	Prendergast Aug 1991 PERTH	this paper	AF209681
Symplocaceae	Symplocos costata Choisy	Chase 1374 K	Savolainen et al. 2000a	AJ235617
Taccaceae	Tacca chantrieri André	Chase 175 NCU	Savolainen et al. 2000a	AJ235618
Tamaricaceae	Tamarix pentandra Hampe ex Bunge	Chase 252 NCU	this paper	AF209684
Tapisciaceae	Tapiscia sinensis Oliver	Chase 1021 K	this paper	AF209685
Taxaceae	Taxus baccata L.	Chase 2527 K	Savolainen et al. 2000a	AJ235619
Tecophilaeaceae	Cyanella capensis L.	Hahn 6966 WIS	this paper	AF168903
Tecophilaeaceae	Tecophilaea cyanocrocus Leyb.	Chase 447 K	Savolainen et al. 2000a	AJ235620
Ternstroemiaceae	Ternstroemia stahlii Krug & Urb.	Axelrod 4538 UPR	this paper	AF209687
Ternstroemiaceae	Eurya japonica Thunb.	Kew 1992-1192	this paper	AF209585
Tetracarpaceae	Tetracarpacea tasmanica Hook. f.	Jordan sn HO	this paper	AF209688
Tetrameristaceae	Tetramerista sp.	Coode 7925 K	Savolainen et al. 2000a	AJ235623
Theaceae	Camellia japonica L.	Nickrent 2929 SIU	this paper	AF209553
Themidaceae	Muilla maritima S. Wats.	Chase 779 K	this paper	AF209635
Theophrastaceae	Clavija eggertiana Mez.	Chase 216 NCU	Savolainen et al. 2000a	AJ235437
Thymelaeaceae	Aquilaria beccariana Tiegh.	Chase 1380 K	Bayer et al. 1999	AJ233079
Thymelaeaceae	Thymelaea hirsuta Endl.	Chase 1882 K	Savolainen et al. 2000a	AJ235626
Tofieldiaceae	Pleea tenuifolia Michx.	Chase 152 NCU	Savolainen et al. 2000a	AJ235564
Tofieldiaceae	Tofieldia calyculata Wahlenb.	Fay sn K (= Chase 1581 K????)	Savolainen et al. 2000a	AJ235627
Tremandraceae	Platytheca verticellata Baill.	Chase 179 NCU	Savolainen et al. 2000a	AJ235563
Trigonaceae	Trigonia sp.	Chase 166 NCU	this paper	AF209691
Trilliaceae	Trillium erectum v. album	Chase 444 K	this paper	AF209692
Trochodendraceae	Trochodendron aralioides Siebold	Qju 90026 NCU	Hoot et al. 1999	AF093423
Trochodendraceae	Tetracentron sinensis Oliv.	Qju 90009 NCU	Hoot et al. 1999	AF093422
Tropaeolaceae	Tropaeolum tricolor Lindl.	Chase 2518 K	Bakker et al. 1998	AF035917
Turneraceae	Turnera ulmifolia L.	Chase 220 NCU	Savolainen et al. 2000a	AJ235634
Ulmaceae	Trema micrantha Blume	Chase 335 NCU	Savolainen et al. 2000a	AJ235628
Ulmaceae	Zelkova serrata Makino	Soltis & Soltis 2517 WS	this paper	AF209699
Urticaceae	Pilea cadierei Gagnep. & Guillam.	Nickrent 2972 SIU	this paper	AF209654
Urticaceae	Urtica dioica L. (Boehmeria for rbcL and 18S)	Chase 2754 K	Savolainen et al. 2000a	AJ235635

continued

SPECIES (rbcL)	CITATION (rbcL)	EMBL (rbcL)	SPECIES (18S)	VOUCHER (18S)	CITATION (18S)	EMBL (18S)
<i>S. pinnatus</i>	Savolainen et al. 2000a	U08619	same DNA as for atpB	same as for atpB	same as for atpB	AF207016
same DNA	this paper	AF206763	same DNA	same	this paper	AF206904
<i>N. spathulata</i> Ruiz & Pau.	Savolainen et al. 2000a	U08616	same DNA as for atpB	same as for atpB	this paper	AJ236017
same DNA	Duval et al. 1993	M91633	<i>S. eurycarpum</i> Engl.	Nickrent 2943 SIU	Soltis et al. 1997a	L24419
same DNA	Savolainen et al. 2000a	AJ235794	same DNA	same	this paper	AF207025
same DNA	Savolainen et al. 2000a	AJ235795	same DNA	same	this paper	AF207026
same DNA	Gadek et al. 1996	AJ238406	same DNA	same	this paper	AJ235978
same DNA	Chase et al. 1995	AJ131948	same DNA	same	this paper	AF207028
same DNA	this paper	AF243845	same DNA	same	Hershkovitz et al. 1999	AF069227
same DNA	Smith et al. 1993	L05459	same DNA	same	Hershkovitz et al. 1999	AF069228
Duke Univ. GH 78-044D	this paper	AF243846	same DNA	same	Hershkovitz et al. 1999	AF069229
same DNA	Albach et al. 2000a	L18790	same DNA	same	this paper	AJ236011
<i>H. carolina</i> Ellis	Savolainen et al. 2000a	Z80190	same DNA as for atpB	same as for atpB	Johnson et al. 1999	L49284
<i>S. americana</i> Lam.	Kron & Chase 1993	L12623	same DNA as for rbcL	Kron 3002 NCU	Soltis et al. 1997a	U43296
same DNA	Morgan et al. 1995	U06828	same DNA	same	this paper	AF207030
<i>S. paniculata</i> Miq.	Kron & Chase 1993	L12624	same DNA as for rbcL	Kron 3005	Soltis et al. 1997a	U43297
same DNA	Chase et al. 1993	AJ235810	<i>Tacca</i> sp.	Mo Bot Gard 894904 US	Soltis et al. 1997a	U42063
same DNA	Fay et al. 1997	Z97650	same DNA	same	this paper	AF207033
same DNA	this paper	AF206825	same DNA	same	this paper	AF207034
<i>T. media</i> Rehder	Chase et al. 1993	AJ235811	<i>Taxus mairei</i>	Chaw 1345	Chaw et al. 1993	D16445
<i>C. hyacinthoides</i> L.	Brummitt et al. 1998	Z77312	same DNA as atpB	same	Soltis et al. 1997a	U42078
same DNA	Chase et al. 1995	Z73709	same DNA	same	this paper	AF207036
same DNA	this paper	AF206827	same DNA	same	this paper	AF207038
same DNA	Morton et al. 1997a	Z80207	<i>E. emarginata</i> (Thunb.) Makhm.	Albach s.n. WS	this paper	AJ235995
same DNA	Morgan & Soltis 1993	L11207	same DNA	same	Soltis et al. 1997a	U42549
same DNA	Morton et al. 1997a	Z80199	same DNA	same	this paper	AF207039
same species	Kron & Chase 1993	L12602	same DNA as for atpB	same as for atpB	Soltis et al. 1997a	U42815
same DNA	this paper	AF206797	same DNA	same	this paper	AF206966
same DNA	Kron & Chase 1993	L12608	same species	Fairchild Trop Gard	this paper	AJ235998
same DNA	Fay et al. 1998	Y15149	same DNA	same	this paper	submitted
same DNA	Fay et al. 1998	Y152151	same DNA	same	this paper	AF207041
same DNA	Chase et al. 1993	AJ131774	same DNA	same	this paper	AF206995
same DNA	Savolainen et al. 2000a	AJ235798	same DNA	same	this paper	AF207043
same DNA	Chase et al. 1993	L01944	same DNA	same	Soltis et al. 1999	AF206994
<i>T. nivea</i> Cambess.	Chase et al. 1993	AF206830	same DNA as for atpB	same as for atpB	Soltis et al. 1999	AF207047
same DNA	this paper	AF206831	same DNA	same	this paper	AF168879
same species	Chase et al. 1993	L01958	same DNA	same	Soltis et al. 1997a	U42816
same species	Chase et al. 1993	L12668	same DNA	same	Soltis et al. 1997a	U42814
<i>T. majus</i> L.	Price & Palmer 1993	L14706	same DNA as for rbcL	Chase 113 NCU	Nickrent & Soltis 1995	L31796
same DNA	Fay et al. 1997	Z75691	same DNA	same	Soltis et al. 1997a	U42817
same DNA	Chase et al. 1993	U03844	same DNA	same	Soltis et al. 1999	AF207044
same species	this paper	AF206835	same DNA as for atpB	same as for atpB	Soltis et al. 1997a	U42819
<i>Pilea pumila</i> (L.) Gray	S. et al. 2000a	AF206811	same DNA as for atpB	same as for atpB	Soltis et al. 1997a	U42820
<i>Boehmeria nivea</i> Gaudich.	Chase et al. 1993	AF062005	same DNA as for rbcL	Qju 91049 NCU	this paper	AF206870

continued

APPENDIX—

FAMILY	SPECIES (atpB)	VOUCHER (atpB)	CITATION (atpB)	EMBL (atpB)
Vahliaceae	<i>Vahlia capensis</i> Thunb.	Van Wyk 10-579 PUR	this paper	AJ236217
Valerianaceae	<i>Valeriana officinalis</i> L.	Chase 2524 K	Savolainen et al. 2000a	AJ235637
Velloziaceae	<i>Barbacenia elegans</i> Pax	Chase 253 K	Savolainen et al. 2000a	AJ235406
Verbenaceae	<i>Callicarpa dichotoma</i> (Lour.) K. Koch	Olmstead 88-012 COLO	this paper	AF209551
Verbenaceae	<i>Lantana</i> sp.	Albach 12 WS	this paper	AF209614
Verbenaceae	<i>Phyla lanceolata</i> (Michx.) Greene	McCormac 4090 OSU	this paper	AJ236162
Verbenaceae	<i>Verbena scabrido-glandulosa</i> Turrill.	Chase 2460 K	Savolainen et al. 2000a	AJ235639
Verbenaceae	<i>Euthystachys abbreviata</i> (E. Mey) A. DC.	McDonald 92-288	this paper	AJ236173
Violaceae	<i>Hymenanthera alpina</i> Oliv.	Chase 501 K	Savolainen et al. 2000a	AJ235499
Vitaceae	<i>Vitis aestivalis</i> Michx.	Chase 226 NCU	Savolainen et al. 2000a	AJ235643
Vitaceae	<i>Leca guineensis</i> G.Don.	Chase 712 K	Savolainen et al. 2000a	AJ235520
Vivianiaceae	<i>Viviania marifolia</i> Cav.	Penalillo 91000 IND	this paper	AF209696
Vochysiaceae	<i>Qualea</i> sp.	Anderson 13660 MICH	this paper	AF209662
Welwitschiaceae	<i>Welwitschia mirabilis</i> Hook.	Geneva BG	Savolainen et al. 2000a	AJ235645
Winteraceae	<i>Bellium</i> sp.	Qju 90025 NCU	Savolainen et al. 2000a	AJ235408
Winteraceae	<i>Drimys winteri</i> J.R.Forster & G.Forster	Nickrent 3013 SIU	Hoot et al. 1999	AF093425
Winteraceae	<i>Takhtajania perrieri</i> (Capuron) J.F. Leroy & Baranova	Rakotomalaza et al. 1342 MO	this paper	AF209683
Winteraceae	<i>Tasmania lanceolata</i> Smith	Raleigh 109 MEL	Hoot et al. 1999	AF093424
Xanthorrhoeaceae	<i>Xanthorrhoea quadrangulata</i> F. Muell.	Kress 92-3422 US	this paper	AF168952
Xeronemaceae	<i>Xeronema callistema</i> Oliv.	Chase 653 K	Savolainen et al. 2000a	AJ235647
Xyridaceae	<i>Xyris</i> sp.	Chase 154 NCU	this paper	AF209698
Zingiberaceae	<i>Globba curtisii</i> Holttum	Kress 99-6347 US	this paper	AF168913
Zingiberaceae	<i>Hedychium flavum</i> Rodb.	Kress 94-3733 US	this paper	AF168916
Zingiberaceae	<i>Riedelia</i> sp.	Selby Bot Gard 83-203 SEL.	this paper	AF168940
Zingiberaceae	<i>Zingiber gramineum</i> Noronha	Kress 91-3266 US	this paper	AF168953
Zosteraceae	<i>Zostera noltei</i> Hornem.	Chase 2789 K	this paper	AF209700
Zygophyllaceae	<i>Guaicum sanctum</i> L.	Chase 133 NCU	Savolainen et al. 2000a	AJ235485

continued

SPECIES (rbcL)	CITATION (rbcL)	EMBL (rbcL)	SPECIES (18S)	VOUCHER (18S)	CITATION (18S)	EMBL (18S)
same DNA	Morgan & Soltis 1993	L11208	same DNA	same	Soltis et al. 1997a	U42813
same species	Olmstead et al. 1992	L13934	same species	Albach 2 WS	this paper	AJ236003
same DNA	Chase et al. 1995	AJ131946	same DNA	same	this paper	AF206861
same DNA	Olmstead et al. 1993	L14393	same DNA	same	this paper	AJ236048
same DNA	this paper	AF156736	same DNA	same	this paper	AJ236049
same DNA	this paper		same DNA	same	this paper	AJ236051
<i>V. bonariensis</i> L.	Olmstead et al. 1993	L14412	<i>V. bracteata</i> Lag. & Rodr.	Olmstead 92-131 WTU	this paper	AJ236042
same DNA	Savolainen et al. 2000a	Z29671	same DNA	same	this paper	AJ236034
same DNA	Fay et al. 1997	Z75692	same DNA	same	this paper	AF206933
same DNA	Chase et al. 1993	L01960	<i>Vitis</i> sp.	Soltis & Soltis 2519	Soltis et al. 1999	AF207053
same DNA	Savolainen et al. 2000a	AJ235783	same DNA	same	this paper	AF206951
same DNA	Price & Palmer 1993	L14707	same DNA	same	this paper	AF207054
same DNA	Olmstead et al. 1992	U02730	same DNA	same	Soltis et al. 1999	AF207002
same species	Chase et al. 1993	AJ235814	same species	Sweere	Soltis et al. 1999	AF207059
same DNA	Qju et al. 1993	L12633	same DNA	same	this paper	AF206865
same DNA	Chase et al. 1993	L01905	same species	Suh 47 US	Soltis et al. 1997a	U42823
same DNA	this paper	AF206824	same DNA as for atpB	same	this paper	AF207032
<i>T. insipida</i> DC.	Chase et al. 1993	L01957	<i>T. insipida</i>	Qju 90032 NCU	this paper	AF207035
<i>X. hostilis</i> R. Br.	Duvall et al. 1993	Z73710	same DNA as for atpB	same as for atpB	Soltis et al. 1997a	U42606
same DNA	Chase et al. 1995	Z69235	same DNA	same	this paper	AF207056
same DNA	this paper	AF206834	<i>Xyris</i> sp.	Hahn 7263 WIS	this paper	AF168881
same DNA	this paper	AF243847	same DNA	same	this paper	AF168846
same DNA	this paper	AF243848	same DNA	same	this paper	AF168848
Same DNA	this paper	AF243849	same DNA	same	this paper	AF168872
Same species	this paper	AF243850	same DNA	same	Soltis et al. 1997a	U42081
same DNA	this paper	U80733	same DNA as for atpB	same	Les et al. 1997	AF207058
same DNA	Chase et al. 1993	AJ1311770	same DNA	same	Soltis et al. 1997a	U42824