American Journal of Botany 91(10): 1645–1655. 2004.

MONOCOT RELATIONSHIPS: AN OVERVIEW[1]

MARK W. CHASE[2,3]

[2]Molecular Systematics Section, Jodrell Laboratory, Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3DS, UK

In 10 years, the monocots have gone from being one of the least studied and most phylogenetically misunderstood groups of the angiosperms to one of the best characterized. Based on analyses of seven genes representing all three genomes, the following clades have high bootstrap support: Acorales (with the single genus *Acorus*) is sister to the rest of the monocots, followed successively by Alismatales (including Araceae and Tofieldiaceae), Petrosaviales, Dioscoreales/Pandanales, Liliales, Asparagales, and finally a polytomy of Arecales, Commelinales/Zingiberales, Dasypogonaceae, and Poales. Many of these results also have support from at least some morphological data, but some are unique to the trees created from DNA sequence data. Monocots have been shown in molecular clock studies to be at least 140 million years old, and all major clades and most families date to well before the end of the Cretaceous. More data are required to clarify the positions of the remaining unclearly placed orders, Asparagles, Liliales, and Arecales, as well as Dasypogonaceae. More sequences from the nuclear and mitochondrial genomes are also needed to complement those from the plastid genome, which is the most sampled and thus far most pattern-rich.

Key words: *Acorus*; angiosperms; classification; molecular clock; monocot classification; monocot phylogenetics; mycoparasitic angiosperm phylogeny.

Monocotyledons (monocots) are one of the major radiations of angiosperms, and they have been recognized as a group since studies of seed structure by John Ray (1682, 1696, 1703) in the seventeenth century. This long history of recognition is in direct contrast to nearly all other major angiosperm clades, which have been drastically reorganized as a result of DNA studies (e.g., asterids, rosids, and Caryophyllales). One of the primary differences between the monocots and other angiosperms is their possession of a single cotyledon (vs. usually two in other angiosperms). Many systems of classification have emphasized this trait and erected two subclasses based on this difference in seed leaf number (e.g., Cronquist, 1981). There are other, perhaps more significant differences in their vegetative architecture (Tomlinson, 1995), which made it likely that the monocots would turn out to be monophyletic. Most monocots have parallel leaf venation (except in Dioscoreales and several other unrelated genera and families, which have net-veined leaves), floral parts in threes (rather than fours and fives as in most eudicots, but several members of the magnoliids, such as Annonaceae and Aristolochiaceae, also have trimerous flowers, so this is clearly not a trait unique to the monocots), sieve-tube plastids with several cuneate protein crystals, scattered vascular bundles in their stems (atactostely, as opposed to bundles in a cylinder), and, probably as a direct result of the last, no vascular-cambium-producing secondary phloem and secondary xylem. In spite of their lack of a vascular cambium, some monocots (e.g., *Yucca*, *Aloe*, *Dracaena*, and *Cordyline*), nevertheless can become trees through increases in stem diameter via a novel process, usually termed ''anomalous'' secondary growth. In this case, plants are able to add new vascular bundles and parenchyma to the primary body (Zimmerman and Tomlinson, 1970), thus increasing their girth. Other monocot trees, such as the palms (Arecaceae), screwpines (Pandaceae), and bananas (Musaceae), are incapable of adding new bundles. Thus, these ''trees'' are merely overgrown herbs. The root systems of monocots are also distinctive in that the radical aborts at an early stage and the root system of the adult plants develop adventitiously.

[1] Manuscript received 2 January 2004; revision accepted 29 June 2004.

[3] Reprint requests (e-mail: m.chase@kew.org).

Monocots are relatively uniform for the characters described and differ from the other major clade of angiosperms, the eudicots, in their possession of uniaperturate, most commonly monosulcate, pollen, but within the seed plants only triaperturate pollen is a clear synapomorphy (i.e., of eudicots). Monocots share their plesiomorphic pollen condition and floral traits with many of the magnoliids, and it is only their habit (roots, stems, cotyledonary condition, and leaves) and sieve-cell plastids (Behnke, 1969) that represent potential synapomorphies. However, even these are homoplasious to a degree. For example, multiple, cuneate sieve-cell plastids also occur in some genera of Aristolochiaceae (*Saruma* and *Asarum*), and scattered bundles and an abortive primary root radical are present in Nymphaeaceae and some Piperaceae. Even before the age of DNA systematics, these traits were thought likely to be due to convergence (Dahlgren et al., 1985), and phylogenetic studies of DNA sequences have supported these conclusions and demonstrated that none of these taxa and the monocots are related to the exclusion of other groups (Soltis et al., 1999).

Likewise, some monocots (e.g., *Dioscorea*, *Trillium*, *Smilax*, and *Pogonia*) have net-veined rather than parallel-veined leaves, which have presumably evolved as convergent adaptations to forest understory conditions (Givnish, 1979; Chase et al., 1995a, b). Monocots with these traits are widely dispersed among nearly all orders, particularly in the petaloid or liliid monocots, so it is clear that net-veined leaves have evolved repeatedly from taxa with parallel venation.

The monocot habit represents a major reorganization of angiosperm vegetative conditions. Tomlinson (1995) took this argument of reorganization a step further and stated that the vascular system of monocots is so highly modified that it is not homologous to that of dicots and unlikely to have been derived from that of dicots. This statement is difficult to reconcile with the position of monocots within the angiosperms; monocots are clearly angiosperms, but although their exact position is not yet clear, it is nonetheless apparent that they are embedded within a grade of plants that are in the most general terms ''dicots'' (e.g., Amborellaceae, Austrobaileyales, Ceratophyllales, Chloranthaceae, eudicots, Nymphaeales, magnoliids). In this sense, monocots are derived from some sort of primitive ''dicot.'' However, the distinction between

monocots and dicots is most apparent when considering eudicots vs. monocots and less clear against the background of the highly heterogeneous ''primitive'' dicots (i.e., Amborellaceae, Austrobaileyales, Chloranthaceae, Canellales, Laurales, Magnoliales, Nymphaeales, and Piperales).

Although the general patterns would hold given a variety of topologies, let us suppose that monocots are sister to *Ceratophyllum* (Ceratophyllaceae; Ceratophyllales) and then that this pair of taxa is sister to magnoliids, eudicots, plus Chloranthaceae (not unlike the tree presented in Zanis et al., 2002). This places them away from nearly all groups that could in any way be considered typical dicots and among the clades for which there is a high degree of heterogeneity in habit and vegetative organization. Such a position opens the possibility that when the monocots evolved, the typical angiosperm habit was not yet canalized, and this lack of canalization made possible the ''drastic reorganization'' to the condition that Tomlinson stated to be nonhomologous with that in dicots.

Burger (1981) took the idea that monocots were derived from dicots and turned it upside down, thus providing us with an alternative to the most commonly held hypothesis. Although the early angiosperms may have been atypical and developmentally uncanalized, it is difficult to imagine how a vascular cambium can be reinvented from an atactostele. It is far easier to hypothesize that, as occurred independently in Piperales and Nymphaeales, monocots are secondarily herbaceous. A similar situation occurs in Ranunculales, in which an atactostele occurs, and some taxa can become woody without having a vascular cambium. Although members of the eudicots, Ranunculales are sister to the remaining members of this clade and may also have diverged before the canalization of typical eudicot traits. The most parsimonious explanation of this situation, based on the tree topology from analyses of DNA sequence data, is that a vascular cambium was likely inherited by the angiosperms from the common ancestor they shared with the gymnosperms (Pryer et al., 2001). The common ancestor of all extant monocots then lost this ability, but the similar structure found in Piperales and Nymphaeales is due to convergence, not shared ancestry.

In summary, there was previously clear information to indicate that the monocots were a natural group, but dicots as a whole lacked clear evidence of monophyly relative to monocots. That is, some ''dicots''(e.g., magnoliids and perhaps Ceratophyllaceae) were more closely related to the monocots than to the rest of the ''dicots'' (e.g., eudicots). How the monocots fit into the larger angiosperm tree is covered in Soltis and Soltis (2004, this volume), but it is now clear on the basis of molecular (DNA sequence) studies that monocots are related in some way to magnoliids, eudicots, Chloranthaceae, and Ceratophyllaceae (Zanis et al., 2002). All DNA studies, except for those of 18S rDNA (Bharathan and Zimmer, 1995; Soltis et al., 1997), have demonstrated that the monocots are monophyletic. In the Bharathan and Zimmer (1995) study, only *Acorus* was not placed with the other monocots (it fell with Aristolochiaceae), but this result lacked bootstrap support (greater than 50%); in the Soltis et al. (1997) analysis, *Acorus* also fell in an isolated position away from the monocots. In both studies, the remainder of monocots were monophyletic. Analyses of single genes (plastid *rbcL*, Chase et al., 1995a; plastid *atpB*, Savolainen et al., 2000; plastid *matK*, Hilu et al., 2003; and mitochondrial *atpA*, Davis et al., 1998, in press) and combined data (Chase et al., 2000b, in press; Savolainen et al., 2000; Graham et al., in press) have consistently shown monocots, including *Acorus*, to be monophyletic.

Monocot phylogenetic relationships have been extensively studied with DNA data (Chase et al., 1993, 1995a, in press; Davis et al., 1998, in press; Duvall et al., 1993b; Hilu et al., 2003; Graham et al., in press) and are now among the best understood of the major clades in the angiosperms. Three major international conferences have focused attention on monocot phylogenetics, and each has seen a marked improvement. The first symposium was held at the Royal Botanic Gardens, Kew, UK, in 1993 (Rudall et al., 1995). The second was held at the Royal Botanic Garden, Sydney, Australia, in 1998 (Wilson and Morrison, 2000), and the third was held in 2003 at the Rancho Santa Ana Botanical Garden, Claremont, California, USA (Columbus et al., in press). In the following sections, I review the evidence of relationships of the major groups of monocots and comment upon phylogenetic analyses relative to recent classifications. Unless otherwise noted, the taxonomic circumscriptions are those of APG II (APG II, 2003). In this paper, I routinely use the broader circumscriptions of families that are considered optional in APG II (2003) and denote this by the use of ''s. l.'' Table 1 indicates both these broad and narrow optional circumscriptions of APG II (2003).

Root node within the monocots—Morphological analyses of monocots (Stevenson and Loconte, 1995) placed the root of the monocot tree in a grade of taxa with net-veined leaves: Dioscoreaceae, Luzuriagaceae, Petermanniacae, Philesiaceae, Stemonaceae, Taccaceae, Trichopodaceae, and Trilliaceae (APG II lumps Taccaceae and Trichopodaceae in Dioscoreaceae and Trilliaceae in Melanthiaceae). DNA analyses of *rbcL* data (Chase et al., 1993, 1995a; Duvall et al., 1993a, b) instead placed the root between *Acorus* (Acoraceae; Acorales) and the rest and scattered the net-veined taxa among families with more typical parallel venation. Although the morphological data placed *Acorus* far away from the root node with Typhaceae and Hydatellaceae, a combined analysis of *rbcL* and morphological data (Chase et al., 1995b) again placed the root in the same position as the *rbcL*-alone analysis. Analyses of 18S rDNA data (Bharathan and Zimmer, 1995; Soltis et al., 1997), as mentioned earlier, placed *Acorus* among the magnoliids and the root between the Alismatales sensu lato (s. l.) (sensu APG II, including Araceae and Tolfieldiaceae) and the rest; essentially, this is similar to that of *rbcL* except that *Acorus* was not with the rest of the monocots. Combined analyses consistently have placed the root as in the *rbcL* tree or in the case of combined mitochondrial *atpA* and plastid *rbcL* (Davis et al., in press) between the alismatid clade, including *Acorus*, and the rest (see later). In relative terms, assignment of the root among the monocots has been relatively consistent and strongly supported (Chase et al., 2000b, in press; Graham et al., in press), except for the topology produced by the combined *atpA/rbcL* matrix. I would argue that this last result is due to some sort of spurious interaction between *atpA* and *rbcL* because neither gene analyzed alone produced such a rooting, and mitochondrial genes are known to have highly uneven rates of change in different lineages of monocots as well as having lineage-specific biases (Petersen et al., in press). Such patterns produce unreliable results; combining *atpA* with yet more genes (seven; Chase et al., in press) produced the same rooting as originally seen with *rbcL*, but in the last case, this relationship is well supported by the bootstrap (Fig. 1).

In the paper in which the position of *Acorus* was first de-

TABLE 1. List of families and order of monocots from Angiosperm Phylogeny Group (AGP II) (2003). Families of Asparagales that could optionally be combined into larger units are indicated in brackets. Sparganiaceae are included in Typhaceae here, although in APG II (2003) they were separate, which was a mistake. Petrosaviales is used here because their position as sister to a clade composed of several families already recognized in APG (II) is well supported in Chase et al. (in press) and Graham et al. (in press).

Acorales
Acoraceae Martynov
Alismatales
Alismataceae Vent.
Aponogetonaceae J. Agardh
Araceae Juss.
Butomaceae Mirb.
Cymodoceaceae N. Taylor
Hydrocharitaceae Juss.
Juncaginaceae Rich.
Limnocharitaceae Takht. ex Cronquist
Posidoniaceae Hutch.
Potamogetonaceae Rchb.
Ruppiaceae Horan.
Scheuchzeriaceae F. Rudolphi
Tofieldiaceae Takht.
Zosteraceae Dumort.
Asparagales
Alliaceae Batsch ex Borkh.
[+Agapanthaceae F. Voigt]
[+Amaryllidaceae J. St.-Hil.]
Asparagaceae Juss.
[+Agavaceae Dumort.]
[+Aphyllanthaceae Burnett]
[+Hesperocallidaceae Traub]
[+Hyacinthaceae Batsch ex Borkh.]
[+Laxmanniaceae Bubani]
[+Ruscaceae Spreng.]
[+Themidaceae Salisb.]
Asteliaceae Dumort.
Blandfordiaceae R. Dahlgren & Clifford
Boryaceae (Baker) M.W. Chase, Rudall & Conran
Doryanthaceae R. Dahlg. & Clifford
Hypoxidaceae R. Br.
Iridaceae Juss.
Ixioliriaceae Nakai
Lanariaceae H. Huber ex R. Dahlgren & A.E. vanWyk
Orchidaceae Juss.
Tecophilaeaceae Leyb.
Xanthorrhoeaceae Dumort.
[+Asphodelaceae Juss.]
[+Hemerocallidaceae R. Br.]
Xeronemataceae M.W. Chase, Rudall & M.F. Fay
Dioscoreales
Burmanniaceae Blume
Dioscoreaceae R. Br.
Nartheciaceae Fr. ex Bjurzon
Liliales
Alstroemeriaceae Dumort
Campynemataceae Dumort
Colchicaceae DC.
Corsiaceae Becc.
Liliaceae Juss.
Luzuriagaceae
Melanthiaceae Batsch
Philesiaceae Dumort.
Rhipogonaceae Conran & Clifford
Smilacaceae Vent.
Pandanales
Cyclanthaceae Poit. ex A. Rich.
Pandanaceae R. Br.
Stemonaceae Caruel
Triuridaceae Gardner
Velloziaceae Hook.
Petrosaviales
Petrosaviaceae Hutch.
COMMELINIDS
Dasypogonaceae Dumort.
Arecales
Arecaceae Schultz
Commelinales
Commelinaceae Mirb.
Haemodoraceae R. Br.
Hanguanaceae Airy Shaw
Philydraceae Link
Pontederiaceae Kunth
Poales
Anarthriaceae D.F. Cutler & Airy Shaw
Bromeliaceae Juss.
Centrolepidaceae Endl.
Cyperaceae Juss.
Ecdeiocoleaceae D.F. Cutler & Airy Shaw
Eriocaulaceae Martynov
Flagellariaceae Dumort.
Hydatellaceae U. Hamann
Joinvilleaceae Toml. & A.C. Sm.
Juncaceae Juss.
Mayacaceae Kunth
Poaceae (R. Br.) Barnh.
Rapateaceae Dumort.
Restionaceae R. Br.
Thurniaceae Engl.
Typhaceae Juss.
Xyridaceae C. Agardh
Zingiberales
Cannaceae Juss.
Costaceae Nakai
Heliconiaceae Nakai
Lowiaceae Ridl.
Marantaceae R. Br.
Musaceae Juss.
Strelitziaceae Hutch.
Zingiberaceae Martynov

scribed, Duvall et al. (1993a) developed the Acoranan hypothesis, which posited that ancestral monocots would have been similar to *Acorus*, a genus of plants growing in freshwater wet sites in the northern temperate zone. The position of *Acorus* alone as sister to the rest of monocots does not support the Acoranan hypothesis of Duvall et al. (1993a); primitive traits for monocots could just as likely be retained in the sister clade of *Acorus*. However, the combination of the two basalmost nodes (*Acorus* and Alismatales) with predominantly aquatic (both submerged and emergent) taxa does support the hypothesis that monocots were primitively aquatic or at least associated with wet habitats. Aquatic angiosperms, such as Nymphaeales, also have scattered vascular bundles (atactosteles), vessels in the vascular tissue are also absent from aquatic taxa, and this syndrome is present in both Acorales and Alismatales. Other traits exhibited by *Acorus* (e.g., unifacial leaves) are

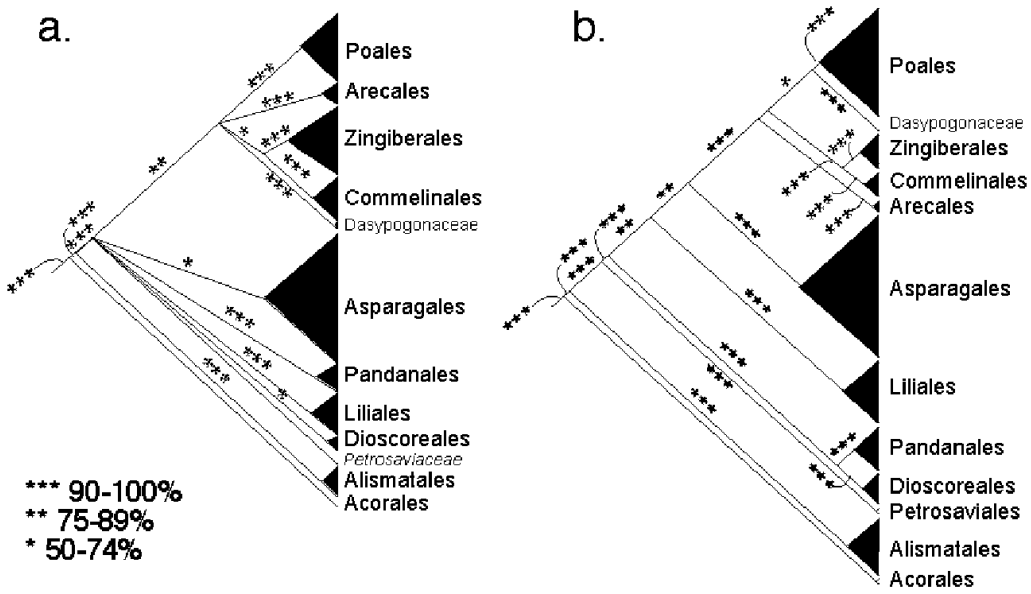

Fig. 1. Bootstrap 50% consensus trees of phylogenetic analyses of monocot relationships. a. Modified from Chase et al. (2000), based on plastid *atpB* and *rbcL* and nuclear 18S rDNA; b. modified from Chase et al. (in press), based on plastid *atpB*, *rbcL*, *matK*, and *ndhF*, mitochondrial *atpA*, and nuclear 18S and 26S rDNA. Number of asterisks indicates general ranges of bootstrap percentages. Names of orders follows APG II (2003), except for that of Petrosaviales. Size of triangles indicates roughly the size of clades in terms of species.

unlikely to be ancestral for monocots, and one should in turn look for such characters among the families of Alismatales and Dioscoreales/Pandanales. Taxa with parallel venation are uncommon among clades attached to the basal nodes of the monocot tree, although this condition does appear in *Acorus*, Tofieldiaceae, a few aroids and alismatids, and *Japonolirion* (one of the two genera of Petrosaviales; see later).

Higher-level relationships among the monocots—The first DNA sequence studies of monocots were those of Chase et al. (1993) and Duvall et al. (1993b) with the plastid gene *rbcL*, although neither of these was sampled extensively (94 and 78 species of monocots, respectively). Chase et al. (1995a), again using *rbcL*, sampled 175 taxa and was particularly focused on relationships among liliid families. Using parsimony and maximum likelihood analyses for tree construction and the bootstrap (Felsenstein, 1985) and Bremer support (decay of parsimony; Bremer, 1994) for estimating internal support, these three papers demonstrated that the higher-level relationships were only weakly supported, although all analyses converged on similar tree topologies with *Acorus* sister to the rest of monocots (73% bootstrap support, Duvall et al., 1993b; one step less parsimonious, Chase et al., 1995a). Savolainen et al. (2000) and Soltis et al. (2000) both used more genes (plastid *rbcL* and *atpB*, and these two genes plus nuclear 18S rDNA, respectively) but with fewer taxa. Their results supported the clades obtained with *rbcL* and provided higher levels of internal support, as estimated with the bootstrap and jackknife (Farris et al., 1996). Chase et al. (2000b) used the data from these two studies plus increased the taxon sampling (135 taxa) and again demonstrated relationships similar to those found with just *rbcL*. *Acorus* was excluded from the clade with the rest of the monocots with high support (99% bootstrap). Likewise, Alismatales were sister to the remainder (excluded from) with high support (95%). Ordinal relationships for most families were also clear in this analysis with three genes (Fig. 1a); Arecales, Commelinales, Liliales, Pandanales, Poales, and Zingiberales all received greater than 90% bootstrap support, but their interrelationships and those of Asparagales and Dioscoreales were weakly supported (less than 77% bootstrap). Thus, the Chase et al. (2000b) analysis was unable to robustly address higher-level relatinships for the majority of taxa.

In an analysis with two additional plastid genes, *matK* and *ndhF*, one mitochondrial gene, *atpA*, and two nuclear ribosomal genes, 18S and 26S, Chase et al. (in press) achieved a much improved estimate of relationships at higher levels in the monocots (Fig. 1b). The addition of the two plastid genes that both have more variable sites than the others previously analyzed (*atpB* and *rbcL*) made the biggest overall improvement. Chase et al. (in press) also reported that addition of the mitochondrial *atpA* sequences for several nonphotosynthetic genera (e.g., *Sciaphila*, Triuridaceae; *Thismia* and *Burmannia*, Burmanniaceae; and *Arachnitis*, Corsiaceae) resulted in lower bootstrap support for much of the tree, presumably from higher rates of sequence divergence and inconsistent/biased patterns of molecular evolution in these taxa (see also Petersen et al., in press, for an examination of this problem with both *atpA* and *cob*). Addition of the two ribosomal DNA regions, which individually have little pattern (Soltis and Soltis, 1998), improved bootstrap percentages (Soltis et al., 1998), so the combined gene approach, which has been used successfully in many groups of land plants (Pryer et al., 2001; Qiu et al., 2000; Soltis et al., 2000; Zanis et al., 2002), appears to be well suited to analysis of phylogenetic relationships in the monocots. Graham et al. (in press), using many additional plastid genes, also achieved much higher levels of bootstrap support for much of the monocot tree. I will now focus on each of the monocot orders, starting with the basal nodes and finishing with Poales, providing comments on results and implications.

Acorales—As mentioned earlier, Acoraceae with a single, North Temperate genus, *Acorus*, is the sole member of Acor-

ales. For many years, it was considered to be a member of Araceae, but in recent years, it had become clear that it deviated substantially from that family (Grayum, 1987) and should at least be considered a distinct, but perhaps allied family. The Duvall et al. (1993a) analysis of *rbcL* sequences demonstrated that such a conclusion had been appropriate and furthermore that *Acorus* was alone sister to the rest of the monocots. This position now appears to be well founded, in spite of the combined analysis of *rbcL* and *atpA* in Davis et al. (in press), which placed *Acorus* within Alismatales. There are reasons to be skeptical of this result (see previous comments). The isolated position of *Acorus* and its unusual mixture of traits may not have many implications for ancestral characteristics of the monocots, and I would caution readers not to be led astray by comments (e.g., Duvall et al., 1993a, b and others) that *Acorus* is ''basal'' within the monocots; this not particularly accurate description has been taken by some workers to mean that this genus has primitive traits for monocots, which of course is not necessarily true. No a priori reason exists for one of a pair of sister taxa to always represent ancestral traits for the larger group; hence the term ''basal'' is meaningless, unless it is understood simply to mean that ''*Acorus* is sister to the rest of monocots,'' in which case, it is better to state the latter so it does not confuse the issue of what is being discussed—phylogenetic positions or character states.

Acorus grows in wet sites, often as an emergent aquatic, and has morphological traits typical for aquatics, such as air canals in its leaves. Morphological analyses using paleoherb magnoliids (such as Aristolochiaceae) as outgroups could never achieve this rooting within monocots because none of the outgroups has many traits in common with *Acorus* (Chase et al., 1995b). This is one clear case in which only molecular data could help us arrive at this conclusion.

Similarities in floral development and leaf morphology of *Acorus* to species in Juncaginaceae (Alismatales) were noted by Buzgo (2001) and Rudall and Buzgo (2002), respectively. Similarity in morphology between these two taxa does not necessarily imply a unique relationship; it could mean as well that these correspondences are symplesiomorphies for monocots in general. Similarity, noted in isolation, could also be a result of convergence between these taxa. Without study of other taxa in Alismatales and Petrosaviales (Fig. 1), we cannot interpret such findings in a robust framework.

Alismatales—A taxon with nearly this circumscription has been a feature of several previous classifications (e.g., Cronquist, 1981, as subclass Alismatidae; Dahlgren et al., 1985, as superorder Alismatiflorae), but in the DNA analyses, two additional families have consistently had a strongly supported position as close relatives of the alismatid families. The first was no particular surprise because Araceae had previously been thought to be related to the alismatid families (Dahlgren et al., 1985), but the second, Tofieldiaceae, was unexpected; the three genera of this family had previously been placed in the melanthioid lilies, Melanthiaceae (Liliales; see later). Many Araceae and some Tofieldiaceae are marsh plants or aquatics, so Alismatales are prime examples of the aquatic nature of many groups near the basal nodes of the monocot tree. Additionally, Tofieldiaceae share several features of flowers and inflorescences that are either unique or otherwise rare among monocots, supporting the broader circumscription of Alismatales (APG II, 2003; Remizova and Sokoloff, 2003).

Nearly all previous authors have recognized the world's smallest angiosperms, Lemnaceae, as separate from Araceae because of their distinct appearance. APG (1998) did not do so because it was clear that they were embedded in the latter. In the lemnids, the plant body is reduced and thallus-like, and it functions in both photosynthesis and assimilation because there are no leaves and few true roots. Flowers are similarly reduced (to a single anther or ovary), but the majority of their reproduction is asexual. Lemnids are related to the ''protoaroids'' (L. Cabrera et al., Royal Botanic Gardens, Kew, and UNAM, Mexico, unpublished data), which include *Lysichiton*, *Symplocarpus*, *Orontium*, and *Gymnostachys*, which also have atypical vegetative and floral features for Araceae (e.g., spadices without a spathe and unifacial leaves in *Gymnostachys*). These taxa all evolved before traits considered the hallmark of the aroids became canalized. None of these aroids attached at the first several nodes of the Araceae tree has many species, but the lemnids with approximately 30 species are more or less cosmopolitan.

The families of the alismatid clade (Alismatanae sensu Dahlgren et al., 1985) are submerged or emergent aquatics. They share with Araceae the lack of vessels in their stems, leaves with a distinct petiole, intravaginal squamules (not present in all Araceae), an inflorescence with a spathe and spadix, lacticifers, and extrorse anthers (these last three not present in some members of both groups). In Tofieldiaceae, a ''calyculus,'' which has characteristics of both a spathe and a floral whorl, subtends the flower (Remizova and Sokolof, 2003). Alismatales thus have many taxa with some extrafloral structures, and this complex nature of these organs makes it difficult to determine what is a flower and what is an inflorescence. This situation is met with again in Pandanales (discussed later) and is a good example of how many angiosperms outside the core eudicots have reproductive organs of unclear homology. Inflorescence/floral structure of all of these families requires a great deal more study.

Petrosaviales—This order was not recognized in APG II (APG, 2003) because at that time the position of this bigeneric family was still somewhat unclear (Fig. 1a). With the additional information available in Chase et al. (in press; Fig. 1b) and Graham et al. (in press), their position is now clear: they are sister to the liliid/commelinid clade. Because they are sister to a clade composed of many orders, they must therefore also be accepted as an order (APG II, 2003). Although there are only two genera in the family, their position in the monocot tree makes them more important than their numbers would indicate. They are also worthy of additional study because they are a closely related pair of taxa, one of which is photosynthetic, *Japonolirion*, and the other an achlorophyllous mycoparasite, *Petrosavia*. Comparative studies of Acorales and families of Alismatales should also include Petrosaviales because similarities within these three orders will likely provide clues about ancestral traits in monocots in general. Cameron et al. (2003) studied the morphology of these plants and proposed to include *Japonolirion* in Petrosaviaceae. Like Tofieldiaceae these two genera had previously been included in Melanthiaceae (Dahlgren et al., 1985) or Melanthioideae of Liliaceae s. l. (Ambrose, 1980).

Dioscoreales—Dioscoreales and Pandanales are strongly supported as sister clades in the combined analysis of Chase et al. (in press; Fig. 1b) and Graham et al. (in press), but these are the first analyses in which they have had this relationship.

In Chase et al. (2000b; Fig. 1b), both orders were supported, but there was no bootstrap support (>50%) for any specific relationship of either order. Some concept of Dioscoreales has been a feature of several previous classifications (e.g., Thorne, 1976, 1992; Dahlgren et al., 1985), but in general, other authors have circumscribed them with many more families than did APG II (2003), in which there were only three: Burmanniaceae, Dioscoreaceae, and Nartheciaceae. Characters associated with their net-veined leaves were used as the basis to ally Petermanniaceae, Stemonaceae, Trilliaceae, and Smilacaceae with Dioscoreaceae, Taccaceae, and Trichopodaceae (all three now part of Dioscoreaceae s. l.; Caddick et al., 2002a). Burmanniaceae and Nartheciaceae have never before been associated with Dioscoreacae, but there are morphological characters that support this alliance (Caddick et al., 2002a, b). Burmanniaceae were previously placed near the orchids (Orchidaceae), largely due to their shared mycoparasitic life history traits, but these similarities were suspected to be convergent because characters of these two groups are otherwise dissimilar (Dahlgren et al., 1985). Molecular evolution in Burmanniaceae is unusual in that these taxa are clearly evolving at a faster rate than their close relatives (Caddick et al., 2002a), and this poses problems for obtaining a clear answer about their relationships (Petersen et al., in press). Nartheciaceae were previously considered members of Melanthiaceae or Liliaceae, but they were known to be divergent members of these families (Ambrose, 1980).

Many previous authors considered Dioscoreales or some component of the order to be the most ''archaic'' or ancestral monocots (Huber, 1969; Dahlgren et al., 1985). The cladogram of Stevenson and Loconte (1995) also placed Dioscoreales s. l. (i.e., including nearly all net-veined monocots) at the basal nodes, largely because they included only several of the paleoherb families as outgroups (i.e., Aristolochiaceae, Nymphaeaceae, and Piperaceae), and these inhabit similar habitats, such as forest understories and margins. As indicated earlier, Dioscoreales in this wider circumscription was demonstrated to be polyphyletic (Chase et al., 1993; Duvall et al., 1993b).

Pandanales—This order was one of the major surprises of the earliest molecular results because it placed with two families long thought to be related, Cyclanthaceae and Pandanaceae, two others that had never before been associated with them, Velloziaceae (Chase et al., 1993; Duvall et al., 1993b) and Stemonaceae (Chase et al., 1995a). There is still little morphological evidence known to support such a set of relationships, but the DNA data are clear about this result. At least, tetramerous flowers, which are rare in the monocots, are uniquely shared by Cyclanthaceae and Stemonaceae. Ribosomal DNA sequences also support the placement of the achlorophyllous (mycoparasitic) family Triuridaceae with Pandanales (Chase et al., 2000b). Previously, Stemonaceae were most often associated with Dioscoreaceae (both are vining taxa with net-veined leaves), but Velloziaceae have been more problematic in their affinities. Dahlgren et al. (1985) associated them with Bromeliaceae, but they expressed doubts about this relationship. On the basis of their more or less separate and numerous carpels, many authors have associated Triuridaceae with the alismatid families (Cronquist, 1981; Dahlgren et al., 1985).

Rudall (2003) has hypothesized that the flowers of Triuridaceae are instead an inflorescence, which would account for the peculiar arrangement of the stamens inside a whorl of carpels in *Lacandonia* (Marquez Guzman et al., 1989). Similar inflorescence-like flowers occur in Cyclanthaceae and Pandanaceae. Pseudanthia have evolved several times in the angiosperms. The flowers of several clades of monocots (e.g., Alismatales, Pandanales), as well as most other groups of angiosperms except the core eudicots (Soltis et al., 2003), would perhaps be best viewed as structures with aspects of both flowers and inflorescences, which might explain why some floral genes are also involved in inflorescence induction (e.g., *LEAFY*; Irish, 1999).

Liliales—Like most of the previous orders, some concept of this order was present in most previous systems of classification that recognized more than one family, Liliaceae s. l. Their circumscription was variable, and even the system of Dahlgren et al. (1985) placed some families there that belonged in other orders (e.g., Iridaceae) and left out others (e.g., Smilacaceae, Philesiaceae). Liliales now are composed of 11 families, most of which are geophytes or rhizomatous perennials. As compared to Asparagales, they have perigonal nectaries and successive microsporogenesis and lack phytomelan in their seed coats. Some are vines, such as *Smilax* and *Petermannia* (the latter was included as a synonym of Colchicaceae in APG, 1998; APG II, 2003, but the voucher for this plant has now been determined to be another vining genus, *Tripladenia*, of Colchicaceae). The mycoparasitic family Corsiaceae also belongs to Liliales, based on nuclear ribosomal DNA data (18S and 26S) and mitochondrial *atpA* (Chase et al., in press)

Asparagales—This last order of liliids is the largest of the monocots (in terms of the number species) and contains the largest family of monocots, Orchidaceae. The position of orchids among monocots has been the subject of a great deal of speculation (Dressler and Chase, 1995; Rasmussen, 1995), and in terms of DNA data, orchids have also been difficult to clearly place. The early work with *rbcL* (Chase et al., 1993; Duvall et al., 1993b) placed them with Asparagales, but other data sets (e.g., *atpB*, Savolainen et al., 2000; *atpA*, Davis et al., in press; and some analyses of *matK*, Hilu et al., 2003) have placed them elsewhere, but always with weak bootstrap support. With a limited sampling of outgroup monocots, Fay et al. (2000) found high bootstrap support for the monophyly of Asparagales including Orchidaceae, and Chase et al. (in press), Graham et al. (in press), and Pires et al. (in press) found that orchids were sister to the rest of Asparagales. Morphologically, orchids fit well in this position; they are among a grade of families at the basal nodes that have simultaneous microsporogenesis and inferior ovaries. Phytomelan is commonly found in seeds of the dry-fruited members of the order, but some of those with hairy seeds (e.g., *Eriospermum*, Asparagaceae s. l.), berries (e.g., *Maianthemum*, Asparagaceae s. l.), or highly reduced seeds (e.g., orchids) lack this dark pigment in their seed coats. Phytomelan is not a synapomorphy for Asparagales, but it is common in these families and rare outside the order.

Most relationships within Asparagales are now well established (Pires et al., in press; Graham et al., in press), but circumscriptions of several of the families have varied. Of course, the great majority of these taxa were included in the grossly polyphyletic Liliaceae (Cronquist, 1981), but the treatment of Dahlgren et al. (1985) attempted to delimit monophyletic groups, treated as families, and in so doing circumscribed them narrowly. As a result, APG (1998) recognized 28 fami-

lies in Asparagales. Although such narrow treatments were an appropriate way to deal with a taxonomically problematic set of taxa, this narrow set of family limits was not a necessity once relationships were better understood. APG II (2003) thus optionally reduced the number of families to just 14, mostly by condensing several clades of multiple families into single ones. For example, Alliaceae s. l. consist of Alliaceae sensu stricto (s. s.), Agapanthaceae, and Amaryllidaceae, and Xanthorrhoeaceae s. l. of Asphodelaceae, Hemerocallidaceae, and Xanthorrhoeaceae s. s. This move also reduced the number of small families, which are undesirable in classification because they make the classification complicated. A further move may be to reduce the asteliid families (i.e., Asteliaceae, Hypoxidaceae, Lanariaceae, and perhaps Blandfordiaceae) to a single family, Hypoxidaceae s. l.; it has previously been demonstrated that there are some shared morphological characters for all but Blandfordiaceae (Rudall et al., 1998). Such condensations were largely motivated by the problems in teaching such a complicated taxonomic scheme; these changes make it much more likely that students will learn families that comprise more of the genera that they commonly encounter (at least in the temperate zones and in horticulture).

Arecales—The larger commelinid clade (previously termed ''commelinoids,'' a name considered to be easily confused with subfamily Commelinoideae, Commelinaceae; APG II, 2003) was recognized by several earlier authors because of their shared silica bodies, starchy endosperms, epicuticular waxes of the *Strelitzia* type, and cell walls with UV-fluorescent ferulic acids (Dahlgren et al., 1985). However, Arecales (single family, Arecaceae, the palms) were not included in this concept of the commelinids, although Dahlgren et al. (1985) noted that palms shared these characters with those families. Instead, most authors preferred to consider palms related to a set of families with which they appeared to share habits and spathe-bearing inflorescences. However, Dahlgren et al. (1985, p. 105) stated that relationships of Arecaceae vis-à-vis Pandanaceae/Cyclanthaceae were ''undoubtedly two of greatest problems in monocot evolution.'' Thorne (1983) and other authors saw the connection of Arecaceae to Pandanaceae and Cyclanthaceae as so tenuous that three monofamilial orders were an appropriate taxonomic treatment; such unclear ideas about relationships were often used as an argument to justify creation of small orders. DNA sequences have indicated that similarities in habit and inflorescence are parallelisms because palms are members of the commelinid clade and Pandanaceae/Cyclanthaceae are only distantly related to them. Within commelinids, there is still no clear picture (e.g., a relationship with high bootstrap support) of where the palms fit (Fig. 1b). All shortest trees in Chase et al. (in press) placed Arecales as sister to the rest of the commelinids. Graham et al. (in press) placed the palms as sister to Poales but with less than 50% bootstrap support. Although we do not yet have a firm idea of where palms fit exactly in the commelinids, DNA data have at least gone a long way to sorting out these ''two major problems'' in higher-level relationships among monocots.

Dasypogonaceae—The four genera of this family confined to Australia were previously considered anomalous members of several other families. Most authors have recently treated them as either members of Xanthorrhoeaceae s. l. (Cronquist, 1981) or Dasypogonaceae (Dahlgren et al., 1985) and generally have considered them somehow related to Agavaceae because at least some members were arborescent. The discovery that some contained ferulic acids in their cell walls (Rudall and Caddick, 1994; Rudall and Chase, 1996), whereas others did not, completely changed the assumptions about relationships of these taxa. DNA data confirmed that Dasypogonaceae should not be included in Xanthorrhoeaceae (Asparagales; Chase et al., 1995a) and are related to the commelinids, supporting the cell-wall character as a synapomorphy of commelinids. Further weight to this placement was given by the discovery in Dasypogonaceae of silica bodies (Rudall and Chase, 1996), which are found only in the orchids outside the commelinid clade. Like Arecaceae, exact placement within the commelinid clade is not yet clear. Chase et al. (in press) found them to be sister to Poales, but with only 58% bootstrap support (Fig. 1b), and Graham et al. (in press) placed them as sister to Commelinales/Zingiberales but with less than 50% bootstrap support.

Commelinales—A relationship of Commelinaceae to families of Zingiberales was noted by Dahlgren et al. (1985, p. 377) on the basis of similarities in seed morphology (e.g., the presence of an operculum). Other characters have not been considered in the light of the DNA data, which now strongly support Commelinales and Zingiberales as sister taxa. The other families of Commelinales, Haemodoraceae, Hanguanaceae, Philydraceae, and Pontederiaceae were not ever associated prior to the DNA sequence data. There were seed structural data (Dahlgren et al., 1985) to support a relationship of Haemodoraceae, Philydraceae, and Pontederiaceae, but little evidence is known to support a relationship to Hanguanaceae and Commelinaceae. Dahlgren et al. (1985) stated that Commelinaceae were instead related to the families of Commelinales (Poales sensu APG) but were ''less specialized.'' *Hanguana* had been hypothesized to be sister to Zingiberales based on morphological cladistic studies (Rudall et al., 1999), but DNA analyses placed them with Commelinaceae, Haemodoraceae, and Philydraceae (100% bootstrap; Chase et al., in press).

Zingiberales—The eight families of this order have nearly always been recognized at some level of the taxonomic hierarchy. They are easily recognized by their inferior ovaries, inaperturate pollen (except in Costaceae), reduced numbers of functional stamens (except in *Ensete* and *Ravenala*), often highly modified staminodes (often petaloid), and essential oils. They formed a clade in the morphological analyses of Stevenson and Loconte (1995) and Chase et al. (1995b).

DNA studies have always demonstrated Zingiberales to be monophyletic with high bootstrap support (Chase et al., 1995a, b; Givnish et al., 1999). The order has a number of small families that have been kept distinct from their larger sister families as a matter of tradition, but it seems clear that *Canna* (Cannaceae) could easily be included in Marantaceae (Andersson and Chase, 2001), Costaceae in Zingiberaceae (Kress et al., 2002), and *Orchidantha* (Lowiaceae) in Heliconiaceae (Kress et al., 2001; Chase et al., in press). Combining Musaceae with either Strelitziaceae or Heliconiaceae, as suggested by Dahlgren et al. (1985), has not been justified on the basis of molecular studies (Kress et al., 2001; Chase et al., in press). Studies of floral development (Kirchoff, 1992; Kirchoff and Kunze, 1995) have provided important insights into homologies of the various floral parts of these often highly modified taxa.

Poales—The 17 families of this order are dominated by the sedge and grass families and their close relatives. Most of these families have been thought to be related and have been treated as a superorder (Thorne, 1983, 1992; Dahlgren et al., 1985) or subclass (Cronquist, 1981; Takhtajan, 1997), usually named for Commelinaceae (e.g., Commelininae or Commelinidae). Sparganiaceae (monogeneric) were recognized in APG II (2003), but this was a mistake and they should have been included in Typhaceae (also monogeneric, if the two families are recognized); they have always been highly supported as a clade in DNA studies. Inclusion of Bromeliaceae and Typhaceae in this order (APG, 1998; APG II, 2003) was not part of most previous systems (e.g., Dahlgren et al., 1985). Dahlgren et al. (1985) placed Bromeliaceae and Typhaceae in the same superorder based on their general syndrome of shared traits, but so far no molecular study has obtained this result. They both retain soluble starch in several parts of the plant and have similar seed structure (Dahlgren et al., 1985).

The major split in Poales is that into the graminid and cyperid clades. Cyperaceae and Juncaceae are sister taxa (Jones et al., in press) and not intermingled as in some previous studies (Muasya et al., 1998). Thurniaceae are then their sister. Poaceae are sister to the poorly known Australian family, Ecdeiocoleaceae (Bremer, 2002), and then these two join Joinvilleaceae, Flagellariaceae, and the restio clade, Anarthriaceae, Centrolepidaceae, and Restionaceae as successive sister taxa.

Sister clades of unequal sizes—One of the more significant patterns that has been detected in angiosperm phylogenetic studies has been that of successive, insignificant, and small sets of taxa that are sister to large, species-rich clades. These small groups generally have some, but not all, of the traits associated with their species-rich sister clades, and they often lack what have become known as ''key characters'' (Bateman, 1999), which often turn out to be nothing more than the final trait that makes up what then appears to be the ''successful, canalized syndrome.'' The relatives of Poaceae are one such example (Chase et al., 2000a; Kellogg, 2000); they are species-poor in spite of having some of the traits that make up the successful syndrome. The key trait is just one of these, which would have been unlikely on its own to confer evolutionary success on the group. Other monocot examples of this phenomenon include Orchidaceae and Araceae. In the former, subfamilies Apostasioideae, Cypripedioideae, Vanilloideae, and Orchidoideae are successive sister taxa to the species-rich subfamily Epidendroideae (Chase et al., 2003), and they demonstrate an increasing number of the traits that make up the syndrome of Epidendroideae. Likewise, ''proto-aroids'' (see earlier) exhibit a similar syndrome relative to the canalized set of traits that most people think of as ''typical'' aroids (spathe, spadix, unisexual flowers, etc.). In evolutionary developmental studies, more attention should be paid to these insignificant groups because it is in these plants that the evolutionary context of individual components can be made clearer because they are not associated with the full morphological suite typical of most members of their families.

Molecular clock studies of the monocots—Two studies have been published that examined the age of the monocots from the perspective of relatively well-sampled phylogenetic trees, Wikström et al. (2001) and Bremer (2002). Although the latter focused on Poales, from it we can extrapolate an age for the monocots as a whole. The Wikström et al. (2001) paper used a calibration point well outside the monocots (within the eudicot order Fagales), and this was criticized by Bremer (2002) as introducing an error into the calculations. The Wikström et al. paper produced an age for extant (crown group node) monocots of 127–141 million years ago (mya) and Poales of 69–72 mya. Bremer (2002) calculated the age of Poales using several calibration points within Poales to be 115 mya, which if we then extrapolate to the monocot crown node would mean that they are approximately 162–176 mya, which is older than the Wikström et al. estimate for the age of the angiosperms. Of course, this is far older than the fossil record indicates for the angiosperms. I am not trying to say that one of these estimates is correct; they may both be incorrect. I would argue instead that we can draw some generalities about ages of monocot orders and families from these studies, but if we try to get into too many specifics, then we will have to choose between the age estimates in the Bremer and Wikström et al. studies, which would be unwise. Given the problems with the Wikström et al. calibration point and the apparently excessively old estimates of Bremer, we can imagine that the truth may lie somewhere in between. To get better age estimates from molecular clocks, we need improved methods of calibrating trees based on DNA sequence data.

The oldest fossil monocots are those of the palms, aroids, and Triuridaceae (Christopher, 1979; Herendeen and Crane, 1995; Gandolfo et al., 2002), all of which occurred around the mid-Cretaceous. It is clear from this and the molecular clock studies that the monocots were among the first lineages of angiosperms to diversify. All orders and the great majority of families appeared well before the end of the Cretaceous; even if we take the crown nodes of most families rather than the root nodes, we still have evidence that these clades existed before the end of the age of dinosaurs, 65 mya. In contrast, the ages of most eudicot orders and families are much younger than similar taxa in the monocots.

Monocot phylogenetics: problems and prospects—Progress in our understanding of the basic phylogenetic framework for the monocots has been rapid. The first analyses were published just about ten years ago (Chase et al., 1993; Duvall et al., 1993a, b), and now with the exception of three nodes, two of them fairly minor, we have high confidence in the spine of the monocot tree. The position of Liliales relative to Dioscoreales/Pandanales and Asparagales to commelinids are the biggest points of uncertainty. We also do not as yet have a clear position for either Arecales or Dasypogonaceae relative to the other clades of the commelinids. I expect that, by continuing to collect additional data, the positions of these taxa can be made clear. Within several of the orders, the positions of some families also require more than the seven genes we have now (Chase et al., in press).

There are several more plastid genes that could be added to improve the situation (e.g., Graham et al., in press), but it is also important to incorporate information from both the mitochondrial and nuclear genomes. These are needed in particular to better estimate the relationships of the achlorophyllous, mycoparasitic families, Burmanniacae, Corsiaceae, and Triuridacae. The mitochondrial genes currently available, *atpA* and *cob*, have both proven problematic, at least in some taxa, with respect to patterns and rates of change; these genes in some taxa also may have been transferred to the nucleus, giving them highly unusual patterns of change relative to copies still residing in the mitochondrial genome (Petersen et al., in

press). In general, mitochondrial genes are plagued by horizontal gene transfer in ways that plastid and nuclear rDNA genes seem not to be (Bergthorrson et al., 2003; Won and Renner, 2003).

The two ribosomal DNA genes, 18S and 26S rDNA, are thus far the only evidence available for the nuclear genome of a broad sampling of monocots, but these two are not particularly good sources of phylogenetic information (i.e., they produce only low bootstrap percentages; Soltis et al., 1997). We need sequences from low-copy protein-coding genes, such as have been developed for eudicot groups (Mathews and Donoghue, 1999; Simmons et al., 2001). The approach of Fulton et al. (2002) for eudicots would also be worthwhile carrying out for monocots. Developing broadly useful PCR primers for such genes is also difficult, and some critical taxa appear to have lost or modified some of these (e.g., *Ceratophyllum* had a single copy of the phytochrome gene, which was difficult to assign to either of two phytochrome genes, *PHYB* or *PHYC*; Mathews and Donoghue, 1999). Although adding information from both the mitochondrial and nuclear genomes is highly desirable, there is good evidence that the current trees based largely on the patterns present in plastid DNA (Chase et al., in press) are reliable when the accuracy of predicting (based on these trees) the distribution of additional traits has been evaluated in other studies (e.g., Adams et al., 2001; Sykorova et al., 2003). Therefore, there is no reason to think that evidence from other genomes will be vastly different than the estimates of phylogeny thus far produced.

The problems posed by the work of Tomlinson (1995) on habit, especially the vascular system, and Rudall (2003) on flowers/inflorescences of monocots, both require more investigation, particularly with respect to genes controlling their development. Understanding the re-patterning of the vascular system in monocots involves understanding how it is controlled in dicots, so both of these areas of study are larger than just monocots. Monocots exhibit some forms of floral mutation that have never been observed in eudicot flowers, such as extra whorls of perianth (e.g., in *Hippeastrum*, *Lilium*, and *Hemerocallis*) without the corresponding conversion of stamens into petals, such as occurs in *Rosa* hybrids, petaloid sepals (tepals), and fusion of sepals and petals into a floral tube (e.g., in *Sandersonia*). Thus, it seems clear that the genes controlling monocot floral development are not exactly those observed in eudicots.

Unlike the eudicots in which there are major model species in at least two of the largest clades, in the monocots we have only the grasses in which model species have been developed. In a clade as large and diverse as the monocots, this presents some problems, particularly because the model species we have (grasses) are themselves so highly modified, including at the molecular level (Gaut et al., 1992, 1993, 1996). This both calls into question the homology of structures and also makes much more difficult the use of tools developed in the grasses on other, more ''typical'' monocots, such as lilies, yams, and daffodils. There is clearly a need to broaden the picture in the monocots, and work such as that proposed in Pires et al. (in press) will move us in that direction.

Now that a broad picture of monocot relationships has been established, the first thing that is clear is how much we do not know about the biology of monocots. When we could only speculate on monocot relationships, we could only hypothesize about many other possible topics for research. Now we have the tools to carry out such research and a well-founded assessment of relationships to help focus our questions in the most reliable manner, which bodes well for greatly improving our understanding of the peculiarities of the monocots.

LITERATURE CITED

ADAMS, S. P., T. P. V. HARTMAN, K. Y. LIM, M. W. CHASE, M. D. BENNETT, I. J. LEITCH, AND A. R. LEITCH. 2001. Loss and recovery of *Arabidopsis*-type telomere repeat sequences 5′-(TTTAGGG)n-3′ in the evolution of a major radiation of flowering plants. *Proceedings of the Royal Society of London, series B* 268: 1541–1546.

AMBROSE, J. D. 1980. A re-evaluation fo the Melanthioideae (Liliaceae) using numerical analyses. *In* C. D. Brickell, D. F. Cutler, and M. Gregory [eds.], Petaloid monocotyledons, 65–81. Academic Press, London, UK.

ANDERSSON, L., AND M. W. CHASE. 2001. Phylogeny, relationships and classification of Marantaceae. *Botanical Journal of the Linnean Society* 135: 275–287.

APG. 1998. An ordinal classification for the families of flowering plants. *Annals of the Missouri Botanical Garden* 85: 531–553.

APG II. 2003. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG II. *Botanical Journal of the Linnean Society* 141: 399–436.

BATEMAN, R. M. 1999. Integrating molecular and morphological evidence of evolutionary radiations. *In* P. M. Hollingsworth, R. M. Bateman, and R. J. Gornall [eds.], Molecular systematics and plant evolution, 432–471. Taylor and Francis, London, UK.

BERGTHORSSON, U., K. L. ADAMS, B. THOMASON, AND J. D. PALMER. 2003. Widespread horizontal transfer of mitochondrial genes in flowering plants. *Nature* 424: 197–201.

BEHNKE, H.-D. 1969. Die Siebrohren-Plastiden bei Monocotlen. *Naturwissenschaften* 55: 140–141.

BHARATHAN, G., AND E. A. ZIMMER. 1995. Early branching events in monocotyledons—partial 18S ribosomal DNA sequence analysis. *In* P. J. Rudall, P. J. Cribb, D. F. Cutler, and C. J. Humphries [eds.], Moncotcotyledons: systematics and evolution, 81–107. Royal Botanic Gardens, Kew, London, UK.

BREMER, K. 1994. Branch support and tree stability. *Cladistics* 10: 295–304.

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

BURGER, W. C. 1981. Heresy revived: the monocot theory of angiosperm evolution. *Evolutionary Theory* 5: 189–225.

BUZGO, M. 2001. Flower structure and development of Araceae compared with alismatids and Acoraceae. *Botanical Journal of the Linnean Society* 136: 393–425.

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

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

CAMERON, K. M., M. W. CHASE, AND P. J. RUDALL. 2003. Recognition and recircumscription of Petrosaviales to include *Petrosavia* and *Japanolirion* (Petrosaviaceae s.l.). *Brittonia* 55: 214–225.

CHASE, M. W., R. L. BARRETT, K. M. CAMERON, AND J. V. FREUDENSTEIN. 2003. DNA data and Orchidaceae systematics: a new phylogenetic classification. *In* K. M. Dixon, S. P. Kell, R. L. Barrett, and P. J. Cribb [eds.], Orchid conservation, 69–89. Natural History Publications, Kota Kinabalu, Sabah, Malaysia.

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

CHASE, M. W., M. F. FAY, D. S. DEVEY, N. RØNSTED, J. DAVIES, Y. PILLON, G. PETERSEN, O. SEBERG, M. N. TAMURA, C. B. ASMUSSEN, K. HILU, T. BORSCH, J. I. DAVIS, D. W. STEVENSON, J. C. PIRES, T. J. GIVNISH, K. J. SYTSMA, AND S. W. GRAHAM. In press. Multi-gene analyses of monocot relationships: a summary. *In* J. T. Columbus, E. A. Friar, C. W. Hamilton, J. M. Porter, L. M. Prince, and M. G. Simpson [eds.], Monocots: Comparative biology and evolution. Rancho Santa Ana Botanic Garden, Claremont, California, USA.

CHASE, M. W., M. F. FAY, AND V. SAVOLAINEN. 2000a. Higher-level classification in the angiosperms: new insights from the perspective of DNA sequence data. *Taxon* 49: 685–704.

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

CHASE, M. W., D. E. SOLTIS, P. S. SOLTIS, P. J. RUDALL, M. F. FAY, W. H. HAHN, S. SULLIVAN, J. JOSEPH, T. GIVNISH, K. J. SYTSMA, AND J. C. PIRES. 2000b. Higher-level systematics of the monocotyledons: an assessment of current knowledge and a new classification. *In* K. L. Wilson and D. A. Morrison [eds.], Monocots systematics and evolution, 3–16. CSIRO, Melbourne, Australia.

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

CHRISTOPHER, R. A. 1979. *Normapolles* and triporate pollen assemblages from the Raritan and Magothy formations (Upper Cretaceous) of New Jersey. *Palynology* 3: 73–122.

COLUMBUS, J. T., E. A. FRIAR, C. W. HAMILTON, J. M. PORTER, L. M. PRINCE, AND M. G. SIMPSON [EDS.]. In press. Monocots: comparative biology and evolution. Rancho Santa Ana Botanic Garden, Claremont, California, USA.

CRONQUIST, A. 1981. An integrated system of classification of flowering plants. Columbia University Press, New York, New York, USA.

DAHLGREN, R. M. T., H. T. CLIFFORD, AND P. F. YEO. 1985. The families of the monocotyledons: structure, evolution and taxonomy. Springer, Berlin, Germany.

DAVIS, J. I., M. P. SIMMONS, D. W. STEVENSON, AND J. F. WENDEL. 1998. Data decisiveness, data quality, and incongruence in phylogenetic analysis: an example from the monocotyledons using mitochondrial *atpA* sequences. *Systematic Biology* 47: 282–310.

DAVIS, J. I., D. W. STEVENSON, G. PETERSEN, O. SEBERG, L. M. CAMPBELL, J. V. FREUDENSTEIN, D. H. GOLDMAN, C. R. HARDY, F. A. MICHELANGELI, M. P. SIMMONS, C. D. SPECHT, F. VERGARA-SILVA, AND M. A. GANDOLFO. In press. A phylogeny of the monocots, as inferred from *rbcL* and *atpA* sequence variation. *Systematic Botany*.

DRESSLER, R. L., AND M. W. CHASE. 1995. Whence the orchids? *In* P. J. Rudall, P. J. Cribb, D. F. Cutler, and C. J. Humphries [eds.], Monocotyledons: systematics and evolution, 217–226. Royal Botanic Gardens, Kew, London, UK.

DUVALL, M. R., M. T. CLEGG, M. W. CHASE, W. D. LARK, W. J. KRESS, H. G. HILLS, L. E. EGUIARTE, J. F. SMITH, B. S. GAUT, E. A. ZIMMER, AND G. H. LEARN, JR. 1993a. Phylogenetic hypotheses for the monocotyledons constructed form *rbcL* sequences. *Annals of Missouri Botanical Garden* 80: 607–619.

DUVALL, M. R., G. H. LEARN, L. E. EGUIARTE, AND M. T. CLEGG. 1993b. Phylogenetic analysis of *rbcL* sequences identifies *Acorus calamus* as the primal extant monocotyledon. *Proceedings of the National Academy of Sciences, USA* 90: 4611–4644.

FARRIS, J. S., V. A. ALBERT, M. KÄLLERSJÖ, D. LIPSCOMB, AND A. G. KLUGE. 1996. Parsimony jackknifing outperforms neighbor-joining. *Cladistics* 12: 99–124.

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

FELSENSTEIN, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* 39: 783–791.

FULTON, T. M., R. VAN DER HOEVEN, N. T. EANNETTA, AND S. D. TANKSLEY. 2002. Identification, analysis, and utilization of conserved ortholog set markers for comparative genomics in higher plants. *Plant Cell* 14: 1457–1467.

GANDOLFO, M. A., K. C. NIXON, AND W. L. CREPET. 2002. Triuridaceae fossil flowers from the Upper Cretaceous of New Jersey. *American Journal of Botany* 89: 1940–1957.

GAUT, B., S. V. MUSE, W. D. CLARK, AND M. T. CLEGG. 1992. Relative rates of nucleotide substitution at the *rbcL* locus in monocotyledonous plants. *Journal of Molecular Evolution* 35: 292–303.

GAUT, B. S., B. R. MORTON, B. C. MCCAIG, AND M. T. CLEGG. 1996. Substitution rate comparisons between grasses and palms: synonymous rate differences at the nuclear gene *Adh* parallel rate differences at the plastid gene *rbcL*. *Proceedings of the National Academy of Sciences, USA* 93: 10274–10279.

GAUT, B. S., S. V. MUSE, AND M. T. CLEGG. 1993. Relative rates of nucleotide substitution in the chloroplast genome. *Molecular Phylogenetics and Evolution* 2: 89–96.

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

GIVNISH, T. J., T. M. EVANS, J. C. PIRES, AND K. J. SYTSMA. 1999. Polyphyly and convergent morphological evolution in Commelinales and Commelinidae: evidence from *rbcL* sequence data. *Molecular Phylogenetics and Evolution* 12: 360–385.

GRAHAM, S. W., J. M. ZGURSKI, M. A. MCPHERSON, D. M. CHERNIAWSKY, J. M. SAARELA, E. S. C. HORNE, S. Y. SMITH, W. A. WONG, H. E. O'BRIEN, V. L. BIRON, J. C. PIRES, RICHARD G. OLMSTEAD, M. W. CHASE, AND H. S. RAI. In press. Robust inference of monocot deep phylogeny using an expanded multigene plastid data set. *In* J. T. Columbus, E. A. Friar, C. W. Hamilton, J. M. Porter, L. M. Prince, and M. G. Simpson [eds.], Monocots: comparative biology and evolution. Rancho Santa Ana Botanic Garden, Claremont, California, USA.

GRAYUM, M. H. 1987. A summary of evidence and arguments supporting the removal of *Acorus* from the Araceae. *Taxon* 36: 723–729.

HERENDEEN, P. S., AND P. R. CRANE. 1995. The fossil history of the monocotyledons. *In* P. J. Rudall, P. J. Cribb, D. F. Cutler, and C. J. Humphries [eds.], Monocotyledons: systematics and evolution, 570. Royal Botanic Gardens, Kew, London, UK.

HILU, K., T. BORSCH, K. MÜLLER, D. E. SOLTIS, P. S. SOLTIS, V. SAVOLAINEN, M. W. CHASE, L. ALICE, R. EVANS, H. SAUQUET, C. NEINHUIS, T. SLOTTA, J. ROHWER, AND L. CHATROU. 2003. Angiosperm phylogeny based on *matK* sequence information. *American Journal of Botany* 90: 1758–1776.

HUBER, H. 1969. Die Sammenmerkmale und Verwandschaftsverhältnisse der Liliifloren. *Mittellungen der Botanischen Staatssammlung München* 8: 219–538.

IRISH, V. L. 1999. Patterning the flower. *Developmental Biology* 209: 211–220.

JONES, E., T. HODKINSON, J. PARNELL, AND M. W. CHASE. In press. The Juncaceae-Cyperaceae interface: a combined plastid gene analysis. *In* J. T. Columbus, E. A. Friar, C. W. Hamilton, J. M. Porter, L. M. Prince, and M. G. Simpson [eds.], Monocots: comparative biology and evolution. Rancho Santa Ana Botanic Garden, Claremont, California, USA.

KELLOGG, E. A. 2000. The grasses: a case study in macroevolution. *Annual Review of Ecology and Systematics* 31: 217–238.

KIRCHOFF, B. K. 1992. Ovary structure and anatomy in the Heliconiaceae and Musaceae (Zingiberales). *Canadian Journal of Botany* 70: 2490–2508.

KIRCHOFF, B. K., AND H. KUNZE. 1995. Inflorescence and floral development in *Orchidantha maxillarioides* (Lowiaceae). *International Journal of Plant Science* 156: 159–171.

KRESS, W. J., L. M. PRINCE, W. J. HAHN, AND E. A. ZIMMER. 2001. Unraveling the evolutionary radiation of the families of the Zingiberales using morphological and molecular evidence. *Systematic Biology* 50: 926–944.

KRESS, W. J., L. M. PRINCE, AND K. J. WILLIAMS. 2002. The phylogeny and a new classification of gingers (Zingiberaceae): evidence from molecular data. *American Journal of Botany* 89: 1682–1696.

MARQUEZ GUZMAN, J., M. ENGLEMAN, A. MARTINEZ MENA, E. MARTÍNEZ, AND C. RAMOS. 1989. Anatomia reproductiva de *Lacandonia schismatica* (Lacandoniaceae). *Annals of the Missouri Botanical Garden* 76: 124–127.

MATHEWS, S., AND M. J. DONOGHUE. 1999. The root of angiosperm phylogeny inferred from duplicate phytochrome genes. *Science* 286: 947–950.

MUASYA, A., D. A. SIMPSON, A. CULHAM, AND M. W. CHASE. 1998. An

assessment of suprageneric phylogeny in Cyperaceae using *rbcL* DNA sequences. *Plant Systematics and Evolution* 211: 257–271.

PETERSEN, G., O. SEBERG, J. I. DAVIS, D. H. GOLDMAN, D. W. STEVENSON, L. M. CAMPBELL, F. A. MICHELANGELI, C. D. SPECHT, M. W. CHASE, M. F. FAY, J. C. PIRES, J. V. FREUDENSTEIN, C. R. HARDY, AND M. P. SIMMONS. In press. Mitochondrial data in monocot phylogenetics. *In* J. T. Columbus, E. A. Friar, C. W. Hamilton, J. M. Porter, L. M. Prince, and M. G. Simpson [eds.], Monocots: comparative biology and evolution. Rancho Santa Ana Botanic Garden, Claremont, California, USA.

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

PRYER, K. M., H. SCHNEIDER, A. M. SMITH, R. CRANFILL, P. G. WOLF, J. S. HUNT, AND S. D. SIPES. 2001. Horsetails and ferns are a monophyletic group and the closest living relatives to the seed plants. *Nature* 409: 618–622.

QIU, Y.-L., J. LEE, F. BERNASCONI-QUADRONI, D. E. SOLTIS, P. S. SOLTIS, M. ZANIS, Z. CHEN, V. SAVOLAINEN, AND M. W. CHASE. 2000. Phylogeny of basal angiosperms: analysis of five genes from three genomes. *International Journal of Plant Sciences* (Supplement) 161: S3–S27.

RASMUSSEN, F. N. 1995. Relationships of Burmanniales and Orchidales. *In* P. J. Rudall, P. J. Cribb, D. F. Cutler, and C. J. Humphries [eds.], Monocotyledons: systematics and evolution, 227–241. Royal Botanic Gardens, Kew, London, UK.

RAY, J. 1682. Methodus plantarum nova. Faithorne and Kersey, London, UK.

RAY, J. 1696. De variis plantarum methodis dissertatio brevis. Smith and Walford, London, UK.

RAY, J. 1703. Methodus plantarum emendata et aucta. Smith and Walford, London, UK.

REMIZOVA, M., AND D. SOKOLOFF. 2003. Inflorescence and floral morphology in *Tofieldia* (Tofieldiaceae) compared with Araceae, Acoraceae and Alismatales s.str. *Botanisches Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 124: 255–271.

RUDALL, P. J. 2003. Monocot pseudanthia revisited: floral structure of the mycoheterotrophic family Triuridaceae. *International Journal of Plant Sciences* 164(Supplement): S307–S320.

RUDALL, P. J., AND M. BUZGO. 2002. Evolutionary history of the monocot leaf. *In* C. B. Q. Cronk, R. Bateman, and J. Hawkins [eds.], Developmental genetics and plant evolution, 432–458. Taylor and Francis, London, UK.

RUDALL, P. J., AND E. CADDICK. 1994. Investigation of the presence of phenolic compounds in monocot cell walls, using UV fluorescence microscopy? *Annals of Botany (London)* 75: 483–491.

RUDALL, P. J., AND M. W. CHASE. 1996. Systematics of Xanthorrhoeaceae sensu lato: evidence for polyphyly. *Telopea* 6: 629–647.

RUDALL, P. J., M. W. CHASE, D. F. CUTLER, J. RUSBY, AND A. Y. DE BRUIJN. 1998. Anatomical and molecular systematics of Asteliaceae and Hypoxidaceae. *Botanical Journal of the Linnean Society* 127: 1–42.

RUDALL, P. J., P. J. CRIBB, D. F. CUTLER, AND C. J. HUMPHRIES. 1995. Monocotyledons: systematics and evolution. Royal Botanic Gardens, Kew, London, UK.

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

SAVOLAINEN, V., M. W. CHASE, C. M. MORTON, S. B. HOOT, D. E. SOLTIS, C. BAYER, M. F. FAY, A. DE BRUIJN, S. SULLIVAN, AND Y.-L. QIU. 2000. Phylogenetics of flowering plants based upon a combined analysis of plastid *atpB* and *rbcL* gene sequences. *Systematic Biology* 49: 306–362.

SIMMONS, M. P., C. C. CLEVINGER, V. SAVOLAINEN, R. H. ARCHER, S. MATHEWS, AND J. J. DOYLE. 2001. Phylogeny of the Celastraceae inferred from phytochrome B and morphology. *American Journal of Botany* 88: 313–325.

SOLTIS, D. E., A. E. SENTERS, M. J. ZANIS, S. KIM, J. D. THOMPSON, P. S. SOLTIS, L. P. RONSE DE CRAENE, P. K. ENDRESS, AND J. S. FARRIS. 2003. Gunnerales are sister to the other core eudicots: implications for the evolution of pentamery. *American Journal of Botany* 90: 461–470.

SOLTIS, D. E., P. S. SOLTIS, M. W. CHASE, M. E. MORT, D. C. ALBACH, M. ZANIS, V. SAVOLAINEN, W. H. HAHN, S. B. HOOT, M. F. FAY, M. AXTELL, S. M. SWENSEN, K. C. NIXON, AND J. S. FARRIS. 2000. Angiosperm phylogeny inferred from a combined data set of 18S rDNA, *rbcL*, and *atpB* sequences. *Botanical Journal of the Linnean Society of London* 133: 381–461.

SOLTIS, D. E., P. S. SOLTIS, M. E. MORT, M. W. CHASE, V. SAVOLAINEN, S. B. HOOT, AND C. M. MORTON. 1998. Inferring complex phylogenies using parsimony: an empirical approach using three large DNA data sets for angiosperms. *Systematic Biology* 47: 32–42.

SOLTIS, D. E., P. S. SOLTIS, D. L. NICKRENT, L. A. JOHNSON, W. J. HAHN, S. B. HOOT, J. A. SWEERE, R. K. KUZOFF, K. A. KRON, AND M. W. CHASE. 1997. Angiosperm phylogeny inferred from 18S ribosomal DNA sequences. *Annals of the Missouri Botanical Garden* 84: 1–49.

SOLTIS, P. S., AND D. E. SOLTIS. 1998. Molecular evolution of 18S rDNA in angiosperms: implications for character weighting in phylogenetic analysis. *In* D. E. Soltis, P. S. Soltis, and J. J. Doyle [eds.], Molecular systematics of plants, vol. 2, DNA sequencing, 188–210. Kluwer Academic, Dordrecht, Netherlands.

SOLTIS, P. S., D. E. SOLTIS, AND M. W. CHASE. 1999. Angiosperm phylogeny inferred from multiple genes as a tool for comparative biology. *Nature* 402: 402–404.

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

SYKOROVA, E., K. Y. LIM, Z. KUNICKA, M. W. CHASE, M. D. BENNETT, J. FAJKUS, AND A. R. LEITCH. 2003. Telomere variability in the monocotyledonous plant order Asparagales. *Proceedings of the Royal Society of London, B, Biological Sciences*, 270: 1893–1904.

TAKHTAJAN, A. 1997. Diversity and classification of flowering plants. Columbia University Press, New York, New York, USA.

THORNE, R. F. 1976. A phylogenetic classification of the Angiospermae. *Evolutionary Biology* 9: 35–106.

THORNE, R. F. 1983. Proposed new realignments in the angiosperms. *Nordic Journal of Botany* 3: 85–117.

THORNE, R. F. 1992. An updated phylogenetic classification of the flowering plants. *Aliso* 13: 365–389.

TOMLINSON, P. B. 1995. Non-homology of vascular organisation in monocotyledons and dicotyledons. *In* P. J. Rudall, P. J. Cribb, D. F. Cutler, and C. J. Humphries [eds.], Moncotyledons: systematics and evolution, 589–622. Royal Botanic Gardens, Kew, London, UK.

WIKSTRÖM, N., V. SAVOLAINEN, AND M. W. CHASE. 2001. Evolution of the angiosperms: calibrating the family tree. *Proceedings of the Royal Society of London, B, Biological Sciences* 268: 2211–2220.

WILSON, K. L., AND D. A. MORRISON. 2000. Monocots: systematics and evolution. CSIRO Publishing, Collingwood, Victoria, Australia.

WON, H., AND S. S. RENNER. 2003. Horizontal gene transfer from flowering plants to *Gnetum*. *Proceedings of the National Academy of Sciences, USA* 100: 10824–10829.

ZANIS, M. J., D. E. SOLTIS, P. S. SOLTIS, S. MATHEWS, AND M. J. DONOGHUE. 2002. The root of the angiosperms revisited. *Proceedings of the National Academy of Sciences, USA* 99: 6848–6853.

ZIMMERMAN, M. H., AND P. B. TOMLINSON. 1970. The vascular systems in the axis of *Dracaena fragrans*. II. Distribution and development of secondary vascular tissue. *Journal of the Arnold Arboretum* 51: 478–491.