

Phylogenetic Relationships in the Commelinaceae: I. A Cladistic Analysis of Morphological Data

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ABSTRACT. The plant family Commelinaceae displays a wide range of variation in vegetative, floral, and inflorescence morphology. This high degree of variation, particularly among characters operating under strong and similar selective pressures (i.e., flowers), has made the assessment of homology among morphological characters difficult, and has resulted in several discordant classification schemes for the family. Phylogenetic relationships among 40 of the 41 genera in the family were evaluated using cladistic analyses of morphological data. The resulting phylogeny shows some similarity to the most recent classification, but with some notable differences. *Cartonema* (subfamily Cartonematoideae) was placed basal to the rest of the family. *Triceratella* (subfamily Cartonematoideae), however, was placed among genera within tribe Tradescantieae of subfamily Commelinoideae. Likewise, the circumscriptions of tribes Commelineae and Tradescantieae were in disagreement with the most recent classification. The discordance between the phylogeny and the most recent classification is attributed to a high degree of convergence in various morphological characters, particularly those relating to the androecium and the inflorescence. Anatomical characters (i.e., stomatal structure), on the other hand, show promise for resolving phylogenetic relationships within the Commelinaceae, based upon their agreement with the most recent classification.

The Commelinaceae, a well defined family of 41 genera and about 650 species, is characterized by several features including a distinct closed leaf sheath, a succulent leaf blade, and three-merous flowers with distinct petals and sepals (Cronquist 1981; Faden 1985; Faden and Hunt 1991). The genera are largely tropical and subtropical, but several extend into temperate regions. The greatest diversity is in Africa, where, along with Madagascar, nearly half the genera and about 40% of the species are found (Faden 1983a).

There is a natural division of taxa between the Old and the New World. The seven subtribes of tribe Tradescantieae (sensu Faden and Hunt 1991) are each wholly confined to either the Eastern or Western hemisphere, whereas the tribe Commeli-

neae is found mainly in Africa and Asia. Only six genera (*Aneilena*, *Buforessia*, *Commelina*, *Floscopa*, *Murdannia*, and *Pollia*) have indigenous species in both hemispheres.

Older classifications of the Commelinaceae relied heavily on floral features (see Faden and Hunt 1991, for a review). Woodson (1942) first used inflorescence characters for higher-level classification, but he was largely unfamiliar with the Old World genera. Pichon (1946) employed anatomical characters to separate the genus *Cartonema* as the family Cartonemataceae, but he returned to more traditional characters to define his ten tribes of Commelinaceae. Brenan (1966) used a variety of morphological characters to define 15 informal "groups" of genera. These have served as the basis of surveys of

anatomical (Tomlinson 1966, 1969) and cytological (Jones and Jopling 1972) characters in the family, but they have little taxonomic significance.

The most recent classification, which will be used in this study, was put forward by Faden and Hunt (1991). In their classification, the Commelinaceae is divided into two unequal subfamilies (Table 1). Subfamily Cartonematoideae contains the tribes Cartonemateae and Triceratelleae, each comprising a single genus. Subfamily Commelinoideae contains the remaining 38 genera that are arranged in two tribes, Tradescantieae and Commelineae, the former of which is divided into seven subtribes.

Evans (1995) conducted a cladistic analysis of the Commelinaceae using both morphological and molecular characters. This paper represents a modification and expansion of the morphological components of that study.

Relationships of Commelinaceae to other Monocot Families. The family Commelinaceae is the namesake for the order Commelinales. Cronquist (1981) defined the order by the presence of perfect flowers that are adapted for general insect pollination, having showy petals that are differentiated from the sepals. He included three other families in this order: Xyridaceae, Rapateaceae, and Mayacaceae. He separated the Commelinaceae from the other three families by their well-defined and closed leaf sheath, and the succulent blade.

Dahlgren et al. (1985) included the same families in Commelinales as Cronquist, but with the addition of the Eriocaulaceae. Eriocaulaceae was placed in its own order by Cronquist, who maintained that it was most likely derived within Xyridaceae. Dahlgren et al. (1985) distinguished the Commelinaceae from the other commelinoid families by the presence of raphides, an amoeboid tapetum, and the leaf characters used by Cronquist (closed leaf sheath and succulent blade).

Although cladistic analyses of morphological data support a monophyletic Commelinales sensu Dahlgren et al. (1985; Stevenson and Loconte 1995), recently published molecular data suggest otherwise. Nucleotide sequence data from the chloroplast gene *rbcL* (Chase et al. 1993; Clark et al. 1993; Duvall et al. 1993) place the Commelinaceae near the Pontederiaceae, Philydraceae, and Haemodoraceae, all of which are part of a larger clade containing the families of the order Zingiberales. The Rapateaceae (the only other representative of Commelinales included in the previous molecular studies) is placed in a different clade that contains, among other families, Poaceae and Cyperaceae. Combined

molecular and morphological studies are similar to the molecular phylogenies (e.g., Chase et al. 1995; Linder and Kellogg 1995). Recent work by Givnish, Evans, Pires, and Sytsma (Givnish et al. 1995, 1999) generally supports these findings. It also places the Hanguanaceae as the sister family of the Commelinaceae and the Xyridaceae and Eriocaulaceae in the grass/sedge clade.

Certain morphological characters also lend support to the separation of the Commelinaceae from other families of the original Commelinales (sensu Cronquist 1981, or Dahlgren et al. 1985). As discussed above, Dahlgren et al. (1985) separated the Commelinaceae from the other commelinoid families in part by the presence of raphides, which are absent in the Mayacaceae, Rapateaceae, Xyridaceae, and Eriocaulaceae (Dahlgren and Clifford 1982). Raphides are widespread, however, in the Pontederiaceae, Philydraceae, and Haemodoraceae (Dahlgren et al. 1985). Additionally, whereas the Commelinaceae were separated from other families in the Commelinales by the presence of an amoeboid tapetum, the genus *Pontederia* and all investigated members of the Haemodoraceae also have an amoeboid tapetum (Dahlgren and Clifford 1982; Simpson 1988, 1990). Finally, flowers in the Commelinaceae show a strong tendency toward zygomorphy, whereas they are generally actinomorphic in the other members of the Commelinales sensu Cronquist (1981) or Dahlgren et al. (1985). Zygomorphic flowers are common, however, in the Pontederiaceae, Philydraceae, and Haemodoraceae.

Although numerous taxonomic treatments have been produced for the Commelinaceae, there has been little consensus as to which characters should be used to define relationships among the genera. The earlier systems relied heavily upon features of the highly variable androecium, but they ignored characters of the inflorescence. The classification produced by Faden and Hunt (1991), which will be used throughout this study, incorporated a broad range of information, such as characters from morphology, anatomy, and palynology. None of these classifications, however, is rooted in an evolutionary framework. The purpose of this study was to examine the intergeneric relationships in the Commelinaceae using morphological and anatomical characters in a cladistic analysis.

MATERIALS AND METHODS

Operational Taxonomic Units (OTUs). A critical step in any cladistic analysis is the selection of

TABLE 1. Classification of the Commelinaceae (as presented by Faden and Hunt 1991). *indicates Old World subtribe, **indicates New World subtribe.

Family: Commelinaceae R. Br.	
Subfamily:	Cartonematoideae (Pichon) Faden & D. Hunt
Tribe:	Cartonemateae (Pichon) Faden & D. Hunt
	<i>Cartonema</i> R. Brown
Tribe:	Triceratelleae Faden & D. Hunt
	<i>Triceratella</i> Brenan
Subfamily:	Commelinoideae (Brückner) Faden & D. Hunt
Tribe:	Tradescantieae (Meisner) Faden & D. Hunt
Subtribe:	*Palisotinae Faden & D. Hunt
	<i>Palisota</i> Reichb.
Subtribe:	*Streptoliriinae Faden & D. Hunt
	<i>Streptolirion</i> Edgew.
	<i>Spatholirion</i> Ridley
	<i>Aetheolirion</i> Forman
Subtribe:	*Cyanotinae (Pichon) Faden & D. Hunt
	<i>Cyanotis</i> D. Don (Including
	<i>Amischophacelus</i> R. Rao & Kamm.)
	<i>Belosynapsis</i> Hassk.
Subtribe:	*Coleotrypinae Faden & D. Hunt
	<i>Coleotrype</i> C. B. Clarke
	<i>Porandra</i> D. H. Hong
	<i>Amischotolype</i> Hassk.
Subtribe:	**Dichorisandrinae (Pichon) Faden & D. Hunt
	<i>Dichorisandra</i> Mikan
	<i>Siderasis</i> Raf.
	<i>Geogenanthus</i> Ule
	<i>Cochliostema</i> Lem.
	Undescribed genus
Subtribe:	**Thyrsantheminae Faden & D. Hunt
	<i>Thyrsanthemum</i> Pichon
	<i>Gibasoides</i> D. Hunt
	<i>Tinantia</i> Scheidw.
	<i>Elasis</i> D. Hunt
	<i>Matudanthus</i> D. Hunt
	<i>Weldenia</i> Schult. f.
Subtribe:	**Tradescantiinae Rohw.
	<i>Gibasis</i> Raf.
	<i>Tradescantia</i> L. (Including <i>Setcreasea</i> Schumann & Sydow, <i>Separothea</i> Waterf., <i>Cymbispatha</i> Pichon, <i>Campelia</i> Rich., <i>Rhoeo</i> Hance, <i>Zebrina</i> Schnizl.)
	<i>Callisia</i> Loefl. (Including <i>Hadrodemas</i> H. Moore, <i>Cuthbertia</i> Small,
	<i>Aploleia</i> Raf., <i>Leiandra</i> Raf., <i>Phyodina</i> Raf., <i>Leptorhoeo</i> C. B. Clarke ex Hemsley)
	<i>Tripogandra</i> Raf.
	<i>Sauvallea</i> Wright
Tribe:	Commelineae (Meisner) Faden & D. Hunt
	<i>Stanfieldiella</i> Brenan
	<i>Floscopa</i> Lour.
	<i>Buforrestia</i> C. B. Clarke
	<i>Murdannia</i> Royle
	<i>Anthericopsis</i> Engl.
	<i>Tricarpelema</i> J. K. Morton
	<i>Pseudoparis</i> H. Perrier
	<i>Polyspatha</i> Benth.
	<i>Dictyospermum</i> Wight
	<i>Pollia</i> Thunb.
	<i>Aneilema</i> R. Brown
	<i>Rhopalephora</i> Hassk.
	<i>Commelina</i> L. (Including <i>Phaeosphaerion</i> Hassk., <i>Commelinopsis</i> Pichon)

evolutionary units, or operational taxonomic units (OTU's). It is assumed that the units being examined have all descended from a most recent common ancestor, and represent distinct evolutionary entities. If the OTU's are polyphyletic, then inaccurate ("misleading") reconstructions of their evolutionary history may be produced (Nixon and Davis 1991; Donoghue 1994).

Of the 41 genera in the Commelinaceae, ten are monotypic (*Aetheolirion*, *Anthericopsis*, *Elasis*, *Gibbasoides*, *Matudanthus*, *Sauvallea*, *Streptolirion*, *Tapheocarpa* Conran, *Triceratella*, and *Weldenia*), and there is no difficulty in treating each as an OTU. For each of the remaining 31 genera, however, claims of monophyly might be misleading. The genus *Callisia*, for example, as circumscribed by Faden and Hunt (1991), contains 20 species in seven sections (Hunt 1986b). There is no single morphological character that defines the genus, and its questionably monophyletic status (Hunt 1986b) might produce misleading relationships in a cladistic analysis.

Likewise, the genus *Tradescantia* sensu Faden and Hunt (1991) is large (containing about 70 species) and morphologically diverse. Some members of this genus until recently have been placed into as many as six other genera (*Setcreasea*, *Separochea*, *Cymbispatha*, *Campelia*, *Rhoeo*, and *Zebrina*). Hunt (1975, 1980, 1986a) has gradually lumped all of these genera into *Tradescantia*, but the monophyly of the genus is yet to be demonstrated.

Although it is clear that large genera such as *Callisia* and *Tradescantia* must be treated cautiously in a cladistic analysis, the same difficulties may also arise for smaller, more "clearly defined" genera. *Rhopalephora*, for example, is distinguished from *Aneilema* by a combination of characters: inflorescence axis very short, stamen filaments fused basally, ovary and capsule densely covered by hook hairs, and dorsal capsule valve deciduous (Faden 1977). All of these characters occur within *Aneilema*, but not in this combination, and no single morphological character is unique to *Rhopalephora*. The implied hierarchical relationships between the two genera suggests one or the other of them may be paraphyletic.

To avoid the problems discussed above, each OTU should be treated in one of three ways: 1) it should be clearly demonstrated to be monophyletic; 2) if polymorphic for any character, it should be split into smaller groups that are monomorphic (Nixon and Davis 1991); or 3) it should be represented in the analysis by exemplar species (Simp-

son 1990; see also Bininda-Emonds et al. 1998). Some of the difficulties of addressing the first option (monophyly) are discussed above. The theoretical and practical difficulties in dividing all polymorphic OTU's into monomorphic units is discussed in some detail in Donoghue (1994).

Therefore, in this analysis, a single species was scored for each genus where possible (Table 2). Data for individual species of four genera (*Porandra*, *Pseudoparis*, *Rhopalephora*, and an undescribed genus) were unavailable, so they were left as polymorphic to reflect variation within each genus. An attempt was made, whenever possible, to select the same species being used in a complementary molecular cladistic analysis of the Commelinaceae (Evans et al., in prep.) so that the results from the two data sets would be more directly comparable.

On the basis of the recent molecular studies on monocots (Chase et al. 1993; Clark et al. 1993; Duvall et al. 1993; Givnish et al. 1999), representatives of the families Pontederiaceae (*Heteranthera*) and Haemodoraceae (*Haemodorum*) were used as outgroups. These two taxa were selected due to their putatively basal position in their respective families (Simpson 1990; Graham et al. 1998) and availability of morphological data. Forty ingroup and two outgroup genera or exemplars were included in this study (Appendix 1, 2). The recently described genus *Tapheocarpa* Conran (1994) was not included due to insufficient data.

Character Selection. Characters were scored from both living and pressed plants housed at the US National Herbarium (US). Observations were made on living plant material growing in the Smithsonian Institution Botany Research Greenhouses and in the field. Where living or pressed plants were not available for examination, information was taken from published literature (Table 2). Forty seven characters were scored.

Phylogenetic Analysis. Data were entered into a matrix using the computer program MacClade version 3.05 (Maddison and Maddison 1992), and the phylogenetic analyses were performed with PAUP* version 4.0b2a (Swofford 1999). A total of 3.7 percent of the cells of the matrix were scored as "missing," either because the data were unavailable or because particular characters were not applicable to certain taxa.

In an initial analysis, all characters were treated as unordered. A multiple-islands approach was used to find the most parsimonious trees (modified from Olmstead et al. 1993; see also Maddison 1991; Olmstead and Palmer 1994). To evaluate the sup-

TABLE 2. Primary literature sources for information at the species level used in a cladistic analysis of morphological characters in the Commelinaceae.

Species	Source
<i>Aetheolirion stenolobium</i> Forman	Forman 1962
<i>Amischotolype hispida</i> (Lesson & A. Rich.) D. Y. Hong	Clarke 1881
<i>Anthericopsis sepalosa</i> (C. B. Clarke) Engl.	Brenan 1966; Faden, unpubl. data
<i>Aneilema calceolus</i> Brenan	Faden 1991
<i>Belosynapsis keavenis</i> Hassk.	Clarke 1881; Faden, unpubl. data
<i>Buforrestia mannii</i> C. B. Clarke	Brenan 1960; Faden, unpubl. data
<i>Callisia elegans</i> Alexander ex. H. E. Moore	Moore 1958
<i>Cartonema philydroides</i> F. Muell.	Brenan 1966; Faden, unpubl. data
<i>Cochliostema odoratissimum</i> Lemaire	Read 1965; Faden, unpubl. data
<i>Coleotrype natalensis</i> C. B. Clarke	Obermeyer and Faden 1985
<i>Commelina benghalensis</i> L.	Obermeyer and Faden 1985
<i>Cyanotis barbatus</i> D. Don	Brenan 1966
<i>Dichorisandra hexandra</i> (Aubl.) Standl.	Matuda 1955
<i>Dictyospermum montanum</i> Wight	Morton 1966; Faden, unpubl. data
<i>Elasis hirsuta</i> Hunt	Hunt 1978; Faden, unpubl. data
<i>Floscopa africana</i> (P. Beauv.) C. B. Clarke	Berhaut 1988
<i>Geogenanthus poeppigii</i> (Miq.) Faden	Moore 1954
<i>Gibasis geniculata</i> (Jacq.) Rohweder	Hunt 1985
<i>Gibasoides laxiflora</i> (C. B. Clarke) Hunt	Hunt 1978; Faden, unpubl. data
<i>Matudanthus nanus</i> (Martens & Gal.) Hunt	Hunt 1978; Faden, unpubl. data
<i>Murdannia edulis</i> (Stokes) Faden	Faden 1980
<i>Palisota ambigua</i> (P. Beauv.) C. B. Clarke	Clarke 1881
<i>Pollia mannii</i> C. B. Clarke	Brenan 1966
<i>Polyspatha paniculata</i> Benth.	Clarke 1881; Faden, unpubl. data
<i>Porandra</i>	Hong 1974; Faden, unpubl. data
<i>Pseudoparis</i>	Faden, unpubl. data
<i>Rhopalephora</i>	Faden 1975, 1977
<i>Sauvallea</i>	Faden, unpubl. data
<i>Siderasis fuscata</i> (Lodd.) H. E. Moore	Clarke 1881 (as <i>Pyrrhema</i>); Faden, unpubl. data
<i>Spatholirion longifolium</i> (Gagnep.) Dunn	Faden 1985
<i>Stanfieldiella imperforata</i> (C. B. Clarke) Brenan	Brenan 1960
<i>Streptolirion volubile</i> Edgew.	Forman 1962
<i>Thyrsanthemum floribundum</i> (Martens & Galeotti) Pichon	Hunt 1993
<i>Tinantia erecta</i> (Jacq.) Schltld.	Hunt 1993
<i>Tradescantia virginiana</i> L.	Anderson and Woodson 1935
<i>Tricarpelema gigantea</i> (Hassk.) Hara	Morton 1966; Faden, unpubl. data
<i>Triceratella drummondii</i> Brenan	Brenan 1961
<i>Tripogandra amplexicaulis</i> (Klotzsch) Woodson	Hunt 1993
<i>Weldenia candida</i> Schultes s.	Hunt 1993; Faden, unpubl. data
Undescribed Genus (Faden, in prep.)	Faden, unpubl. data

port for each node, 100 bootstrap replicates were conducted. Due to the high number of trees produced, a maximum of 5000 trees per replicate was saved.

As a measure of which characters are more phylogenetically informative and which are more homoplasious (with respect to the topologies of the trees produced), as well as to arrive at a more stable topology, the characters were re-weighted *a posteriori* (using the "REWEIGHT CHARACTERS" command

in PAUP) based on their fit to the trees produced in the unordered analysis. The multi-step analysis described above was then repeated using the re-weighted characters. This process was repeated until the same set of most parsimonious trees was produced in two consecutive runs. PAUP allows the character to be re-weighted based on consistency index (CI), retention index (RI), or rescaled consistency index (RC). The maximal value of each of these indices was used in three separate analyses.

In addition to the unordered analysis, an analysis was performed in which three character transformations were ordered (fruit locule number [Character 35] and seed number per locule [Characters 37 and 38]). The same procedure described above was used in this analysis to find multiple islands of most parsimonious trees.

For purposes of character state mapping, one of the most parsimonious trees was arbitrarily selected for illustration. However, due to the lack of resolution of several clades in the strict consensus tree, distributions were examined on all of the most parsimonious trees.

RESULTS

Unordered Analysis. In the unordered analysis, 154 equally most parsimonious trees were produced, with a length (excluding autapomorphies) of 239 steps and a consistency index (CI) of 0.43 (length = 272 and CI = 0.44 when autapomorphies are included). Figure 1 illustrates the tree chosen for character state reconstructions.

Cartonema is sister to the rest of Commelinaceae. The remaining genera form four lineages (Fig. 1): *Callisia*, which is sister to the remaining genera; *Weldenia*; and two largely unresolved clades. Within the clade that is sister to *Anthericopsis*, 15 genera (*Bufoerestia*, *Floscopa*, *Pseudoparis*, *Tricarpelema*, *Polyspatha*, *Aneilema*, *Commelina*, *Rhopalephora*, *Dictyospermum*, *Palisota*, *Tinantia*, *Cochliostema*, *Aetheolirion*, *Geogenanthus*, and an undescribed genus) form a clade that is supported by two characters, antesealous staminal filament lengths (Character 26), and the presence of a zygomorphic androecium (Character 31; note: *Floscopa* produces an asymmetric androecium). For ease of reference, this clade will be referred to as the "zygomorphic clade." The remaining genera (*Murdannia*, *Gibasis*, *Elasis*, *Thyrsanthemum*, *Gibasoides*, *Matudanthus*, *Coleotrype*, *Porandra*, *Amisotolype*, *Cyanotis*, *Belosynapsis*, *Triceratella*, *Streptolirion*, *Spatholirion*, *Sauvallea*, *Tradescantia*, and *Tripogandra*) form a large clade that is supported by the presence of bearded antesealous staminal filaments (Characters 22, 23). For ease of reference, this clade will be referred to as "Clade 1."

A posteriori Re-weighting. Each of the re-weighted analyses (CI-, RI-, and RC-based; Table 3) produced topologies that were similar to the unordered tree. The RI-based analysis produced 45 equally most parsimonious trees (not shown) that were a subset of the 154 trees found in the un-

ordered analysis. The CI- and RC-based analyses produced identical sets of 15 equally most parsimonious trees (not shown) that differed from the unordered topology in the lineages sister to the zygomorphic clade. In the unordered tree (Fig. 1), the zygomorphic clade has a sister group consisting of *Stanfieldiella*, *Polliia*, *Siderasis*, and *Dichorisandra*. The CI- and RI-based analyses produced a set of nested relationships from the more basal *Siderasis* to, sequentially, *Polliia*, *Stanfieldiella*, *Anthericopsis*, *Dischorisandra*, and the zygomorphic clade.

Ordered Character Analysis. When assumptions about the sequence of evolutionary steps in characters 35, 37, and 38 were incorporated, 115 equally most parsimonious trees were produced (not shown). This topology is nearly identical to the unordered topology, except that it showed greater resolution in the zygomorphic clade. The undescribed genus and *Cochliostema* were united in one clade and *Polyspatha*, *Aneilema*, and *Commelina* formed an unresolved clade.

DISCUSSION

The discordant classifications that have been proposed for the Commelinaceae reflect the high degree of uncertainty in homology among morphological characters in the family. Likewise, the low CI values for many characters in this study (Table 3) demonstrate a high amount of homoplasy in the family. The cladistic analysis presented here, although supporting particular elements of some previous classifications, does not agree closely with any one of them. The zygomorphic clade (Fig. 1) includes all but three genera (*Polliia*, *Stanfieldiella*, and *Murdannia*) of Faden and Hunt's (1991) tribe Commelineae. However, several members of Tradescantieae are also included in this clade. Likewise, few elements of Brenan's (1966) classification are supported. Of the 15 informal "groups" put forward by Brenan, one, "Group VI" (= subtribe Cyanotinae), is monophyletic here. Relatively narrow circumscriptions of several of Brenan's groups (i.e., the inclusion of only one or two genera per group) make a direct comparison of relationships among those genera difficult. Pichon's (1946) classification included ten tribes, five of which contain only a single genus. Of the remaining five tribes, not one is supported by this analysis. The large number of taxonomic groups with only a single genus in Pichon's and Brenan's systems, as well as lack of statistical support for most clades in this analysis, suggest that there is a high degree of uncertainty in

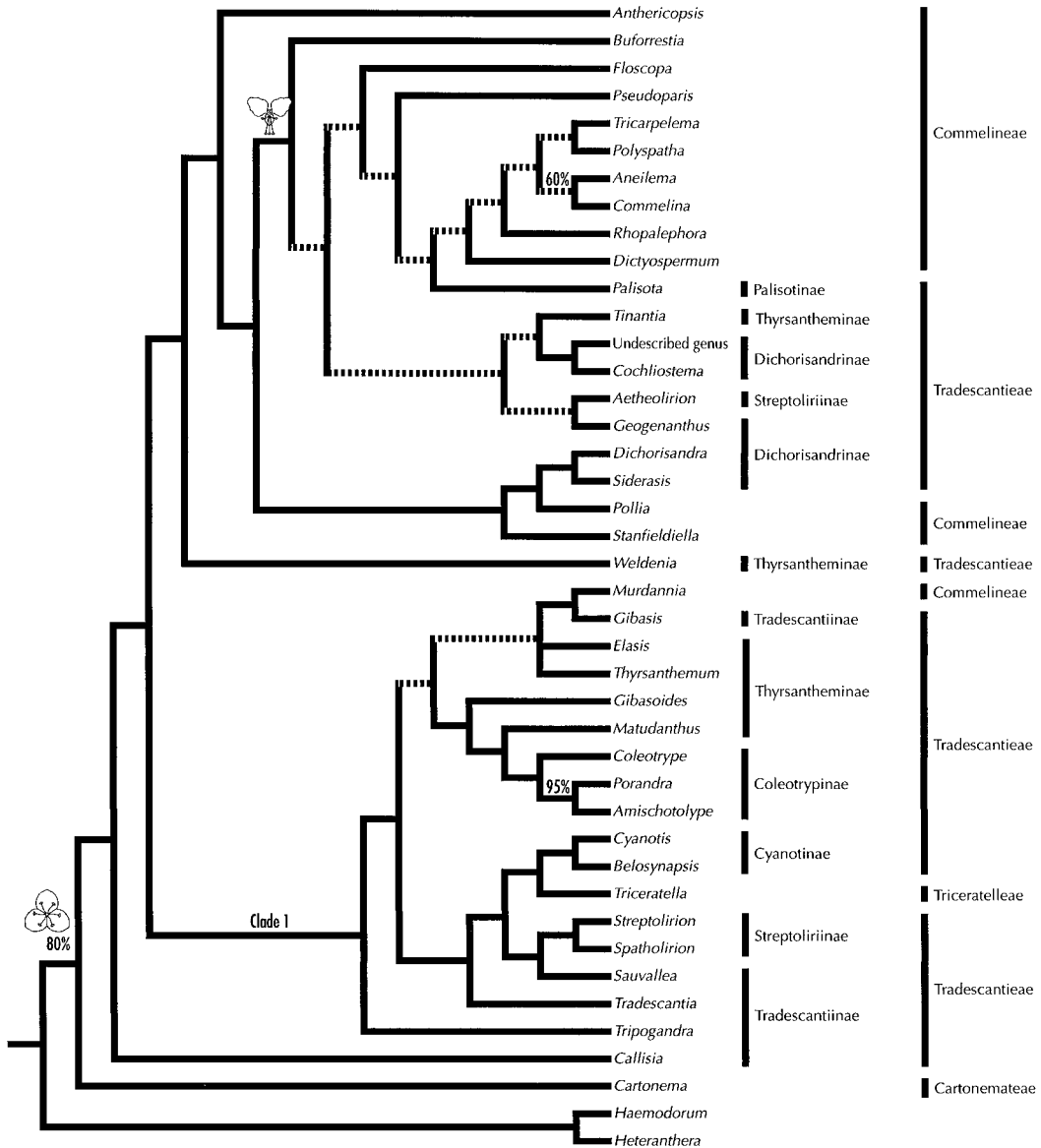


FIG. 1. A representative of the 154 equally most parsimonious trees found in the unordered analysis of 47 morphological characters in Commelinaceae using *Haemodorum* and *Heteranthera* as outgroups. Dashed lines represent branches that collapse in the strict consensus of most parsimonious trees. Bootstrap values greater than 50% are shown above branches. Subtribal and tribal affinities are shown to right of generic names. "Clade 1" and the "zygomorphic clade" discussed in the text are indicated.

assessing homology of structures among genera of Commelinaceae.

Basal Lineages in the Commelinaceae. Each analysis divided the Commelinaceae into several main lineages, with *Cartonema* sister to the rest of the family and *Callisia* sister to everything except

Cartonema. *Callisia* is a member of subtribe Tradescantiinae, a well defined group based on features of the inflorescence (cincinni contracted, fused in bifacial pairs; Faden and Hunt 1991). The New World distribution of this entire subtribe, as well as its putatively recent origin (Faden and

TABLE 3. Character statistics from each analysis. CI = consistency index; RI = retention index; RC = rescaled consistency index; W_{CI} = character weight after re-scaling according to the CI; W_{RI} = character weight after rescaling according to the RI; W_{RC} = character weight after re-scaling according to the RC.

Character	States	Steps	CI	RI	RC	Weight		
						W_{CI}	W_{RI}	W_{RC}
1	01	3	.333	.500	.167	333	286	167
2	01234	13	.308	.308	.095	307	357	94
3	01	9	.111	.429	.048	100	400	36
4	012	6	.333	.556	.185	286	500	127
5	01	2	.500	0.00	0.00	500	0	0
6	012	7	.286	.444	.127	286	500	127
7	01	5	.200	.636	.127	200	583	127
8	01	4	.250	.400	.100	250	286	100
9	012	7	.286	.375	.107	286	375	107
10	01	3	.333	.600	.200	333	800	200
11	01	4	.250	0.00	0.00	250	0	0
12	01	5	.200	.429	.086	200	375	86
13	01	3	.333	.333	.111	333	667	111
14	01	2	.500	.500	.250	500	333	250
15	01	2	.500	.500	.250	500	333	250
16	01	3	.333	.500	.167	333	500	167
17	01	1	1.00	—	—	1000	1000	1000
18	01	1	1.00	1.00	1.00	500	1000	417
19	01	2	.500	.500	.250	1000	1000	1000
20	01	3	.333	.333	.111	333	333	111
21	01	3	.333	.778	.259	250	778	167
22	01	3	.333	.882	.294	500	889	471
23	01	3	.333	.882	.294	500	889	471
24	01	1	1.00	1.00	1.00	1000	1000	1000
25	01	3	.333	.889	.296	250	842	208
26	012	2	1.00	1.00	1.00	1000	1000	1000
27	012	2	1.00	1.00	1.00	1000	1000	1000
28	012	7	.286	.167	.048	333	333	111
29	012	9	.222	.222	.049	222	333	49
30	01	2	.500	0.00	0.00	500	0	0
31	012	5	.400	.812	.325	500	813	438
32	012	3	.667	0.00	0.00	667	0	0
33	01	7	.143	0.00	0.00	143	0	0
34	012	3	.333	.667	.222	333	667	222
35	012	4	.500	.333	.167	500	333	167
36	01	6	.167	.444	.074	125	444	28
37	0123	7	.286	.737	.211	286	609	211
38	0123	8	.250	.667	.167	250	545	167
39	0123	11	.273	.500	.136	273	421	136
40	01	6	.167	.500	.083	200	455	120
41	01	2	.500	.500	.250	500	500	250
42	01	5	.200	.750	.150	167	750	115
43	0123	9	.333	.667	.222	375	722	271
44	01	3	.333	.600	.200	333	800	200
45	01	2	.500	.667	.333	500	667	333
46	012	2	1.00	1.00	1.00	1000	1000	1000
47	01	1	1.00	1.00	1.00	1000	1000	1000

Hunt 1991) shed doubt on the basal position of *Callisia*.

The position of *Cartonema* sister to the rest of the family is consistent with other data, particularly *rbcl* sequences (Evans 1995; Evans et al., in prep.). On the basis of various morphological characters (e.g., actinomorphic flowers with six fertile stamens, the absence of raphide canals), *Cartonema* has been postulated to be one of the more primitive members of the family (Pichon 1946; Hutchinson 1959; Brenan 1966; Faden and Hunt 1991).

Relationships in the Tradescantieae. With the exceptions of *Murdannia* (tribe Commelineae) and *Triceratella* (subfamily Cartonemateae), Clade 1 consists exclusively of members of Tradescantieae (Fig. 1). Several members of the tribe, however, are placed in other parts of the tree. As discussed above, *Callisia*, for example, is basal to all other genera except *Cartonema*. Likewise, eight genera are placed either sister to the zygomorphic clade (*Dichorisandra* and *Siderasis*) or within it (*Palisota*, *Tinantia*, undescribed genus, *Cochliostema*, *Aetheolirion*, and *Geogenanthus*). The position of *Dichorisandra* and *Siderasis* as the sister group of *Pollia* (tribe Commelineae) is supported by the presence of biseriate seeds (Character 36). This character, however, is highly variable within the family. Within the zygomorphic clade and its sister clade, biseriate seed arrangement has arisen a minimum of three times (Fig. 2). This character is even more variable in other most parsimonious trees, some of which force *Aetheolirion* and *Geogenanthus* to gain biseriate seeds independently. Likewise, relative filament length within the antepetalous staminal whorl (Character 27) is the single character that supports the clade containing *Aetheolirion*, *Cochliostema*, *Geogenanthus*, *Tinantia*, and the undescribed genus as the sister group of the zygomorphic clade. This character too is variable within the zygomorphic clade (not shown).

The taxonomic placement of the genus *Triceratella* has been problematic. When *Triceratella* was originally described, a loose affinity with *Stanfieldiella* was suggested (Brenan 1961). Tomlinson (1964)

used anatomical characters to suggest that the genus may form a link between *Cartonema*, which he placed in a separate family, and the Commelineaceae. He indicated that it might be treated as a separate subfamily of Commelinaceae. Faden and Hunt (1991) placed *Triceratella* and *Cartonema* in a subfamily within the Commelinaceae, with each genus in a separate tribe.

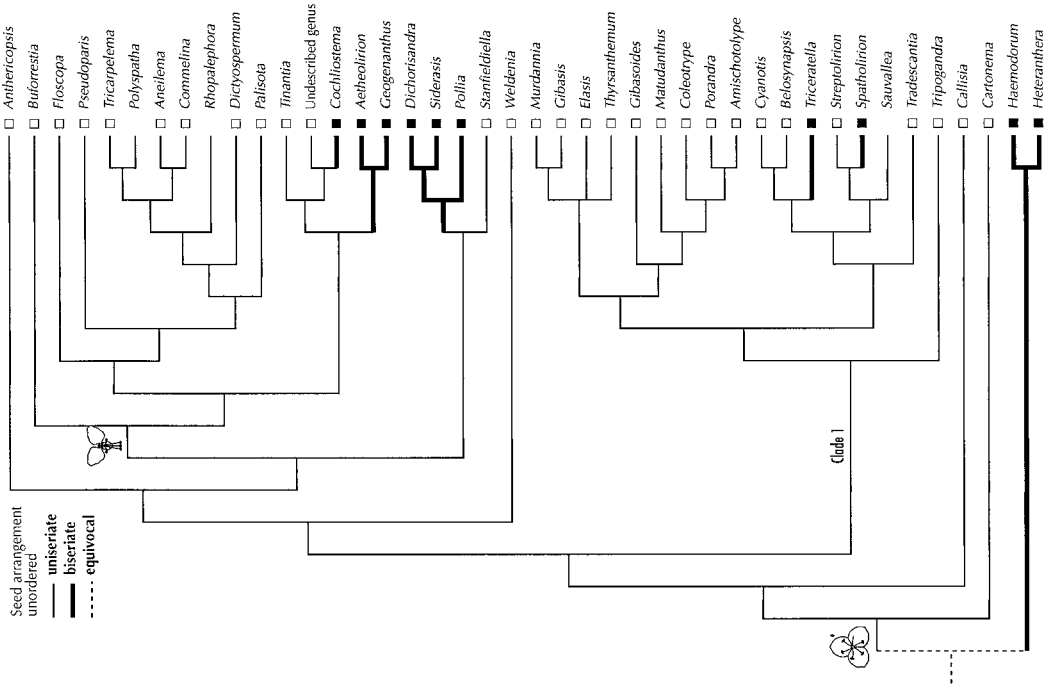
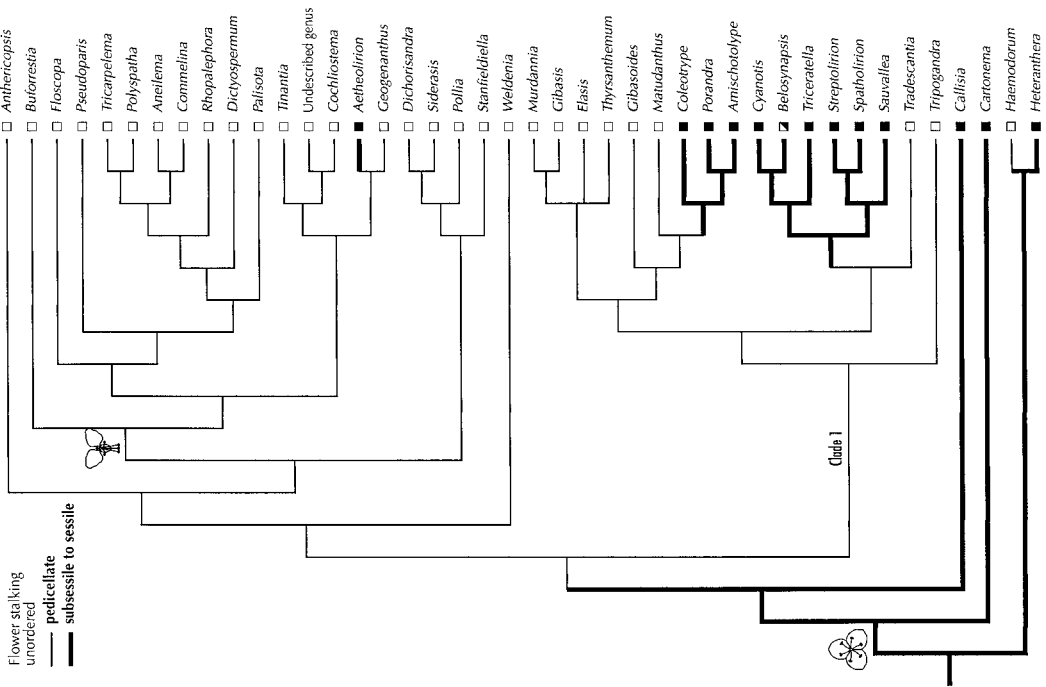
The morphological data presented here place *Triceratella* as a sister group of subtribe Cyanotinae (*Cyanotis* and *Belosynapsis*), nested well within the Tradescantieae. The clade containing *Belosynapsis*, *Cyanotis*, *Sauvallea*, *Spatholirion*, *Streptolirion*, and *Triceratella* is supported by a single character (sessile flowers). The presence of sessile flowers is labile within Commelinaceae, having been lost once and gained at least three times (Fig. 2). Although a relationship between *Triceratella* and the Streptolirinae has some support, it needs further study. Until less homoplasious characters are found to support such a relationship, it will remain suspect.

Of the seven subtribes circumscribed by Faden and Hunt (1991), only two, Coleotrypininae and Cyanotinae, are supported as monophyletic in this study. The remaining subtribes are polyphyletic and largely unresolved. Two genera in subtribe Thyrsantheminae (*Thyrsanthemum* and *Elasis*) contribute to a polytomy in Clade 1. Thyrsantheminae, as defined by Faden and Hunt (1991), is based largely upon the absence of characters or the presence of putatively primitive characters, and may be an unnatural assemblage (R. Faden, unpubl. data). Recent molecular data also suggest that this subtribe is polyphyletic (Evans et al., in prep.), and the lack of resolution and weak support in this analysis illustrate the difficulty in finding taxonomic characters that will unambiguously unite these taxa with other genera.

Relationships in the Commelineae. Ten of the thirteen genera in tribe Commelineae were placed within the zygomorphic clade (Fig. 1). Of the three remaining Commelineae genera, two (*Pollia* and *Stanfieldiella*) are part of the sister group of the zygomorphic clade; *Murdannia* is nested within Clade

→

FIG. 2. Distribution of characters on the representative tree (see Fig. 1) from the unordered analysis of 47 morphological characters in Commelinaceae. Left: Seed arrangement. Biseriate seed arrangement has arisen at least three times within the zygomorphic clade and its sister clade. One additional step is required in some other equally most parsimonious trees due to shifts in position of *Aetheolirion* and *Geogenanthus*. Right: Pedicel. The presence of pedicellate flowers is homoplasious within Commelinaceae. The distribution of this character is not altered in any other most parsimonious trees.



1. The only synapomorphy that supports the zygomorphic clade is the presence of a zygomorphic androecium (Character 31), a character that is variable within the family as a whole. However, all members of this clade, except *Palisota*, share a common stomatal type consisting of six cells, with small terminal subsidiary cells (Figs. 3 and 4). Although this stomatal type is restricted to genera belonging to the tribe Commelineae, it is not a synapomorphy for the zygomorphic group, as it is also found in *Pollia*, *Anthericopsis*, and *Murdannia*. This anatomical character is in agreement with a molecular phylogeny for Commelinaceae (Evans 1995; Evans et al. 2000), and the distribution of stomatal types here raises questions regarding the placement of *Murdannia* within Clade 1, and calls for a re-evaluation of the homology of the filament bearding between *Murdannia* and the other genera in that clade.

Although the unordered analysis produced a highly unresolved zygomorphic clade, the re-weighting analyses each yielded a smaller clade within the zygomorphic group containing *Polyspatha*, *Aneilema*, *Rhopalephora*, *Commelina*, *Dictyospermum*, and *Tricarpelema*. This clade is supported by a reduction in seed number in each locule (*Tricarpelema* is polymorphic for this character). As relationships in the tribe Commelineae have been difficult to evaluate due to a lack of informative characters (Faden and Hunt 1991), the formation of distinct clades based on fruit characteristics may provide some insight as to where such characters may be found.

A Comparison of Different Methods of Parsimony Analysis. Several different methods of character weighting and ordering were explored with this data set, and the question arises as to which one(s) are the best approximation of the true history of the family. The unordered analysis contains the fewest *a priori* assumptions about character evolution, as it incorporates few assumptions about character weight or direction of transformation. The absence of additional assumptions, however, imposes a penalty in terms of the potential loss of phylogenetic information. For example, the number of locules in the fruit (Character 35) may represent a series, in which fruits with three unequal locules (e.g., one locule is reduced) are intermediate between fruits with three locules and fruits with two locules. By coding such characters as ordered, hypotheses about evolutionary trends may be incorporated in estimates of phylogenetic relationships.

In addition to ordering, characters were also re-

weighted on the basis of three different measures of their internal consistency (CI, RI, and RC). Each of these re-weighting schemes starts with the unordered topology, and then re-evaluates the fit of the characters to that topology. The CI, a measure of the fit of the characters to the tree, is derived as the ratio of the number of state changes for a character in the data to the number of state changes for the character on the hypothesized tree (Kluge and Farris 1969). A potential problem with the consistency index, however, is that it only measures how well a character fits onto a particular topology; it does not evaluate how well that character actually supports the topology (i.e., if it is synapomorphic for any clade). Farris (1989) developed the retention index (RI) and rescaled consistency index (RC) in an attempt to incorporate the internal consistency of each character with respect to the worst and best possible fit to a tree. The RI and RC both incorporate the minimum number of steps a character must undergo on any tree, as well as the actual amount of synapomorphies on the hypothesized tree.

By using these values as bases for re-weighting characters, slightly different properties of the characters are being selected. When CI is used, for example, each character is re-weighted according to the number of steps it undergoes when mapped onto the tree. However, this scheme does not take into account whether the character supports any of the clades in the tree. Incorporating RI and RC, however, does take this into account. A good example of the differences in these measures can be seen with Character #5 (number of flowers per cincinnus). This character has a CI of 0.5 (Table 3). However, it does not unite any clades (Fig. 4), so it lends no support to the topology. Because it does not support a clade, it has an RI and RC value of zero (Table 3). Therefore, the CI re-weighting scheme assigned a relatively high weight to that character whereas the RI and RC decreased its weight.

While each of the re-weighting schemes produced phylogenies similar to the unordered phylogeny (RC- and CI-based analyses produced a subset of the unordered trees), they all showed greater resolution than the unordered analysis. Whereas the unweighted analysis produced a nearly completely unresolved zygomorphic clade, each of the re-weighting analyses produced a highly resolved zygomorphic clade. The re-weighting analyses differed from each other mainly in the relationships of the sister taxa to the zygomorphic clade. These differences reflect biases toward different charac-

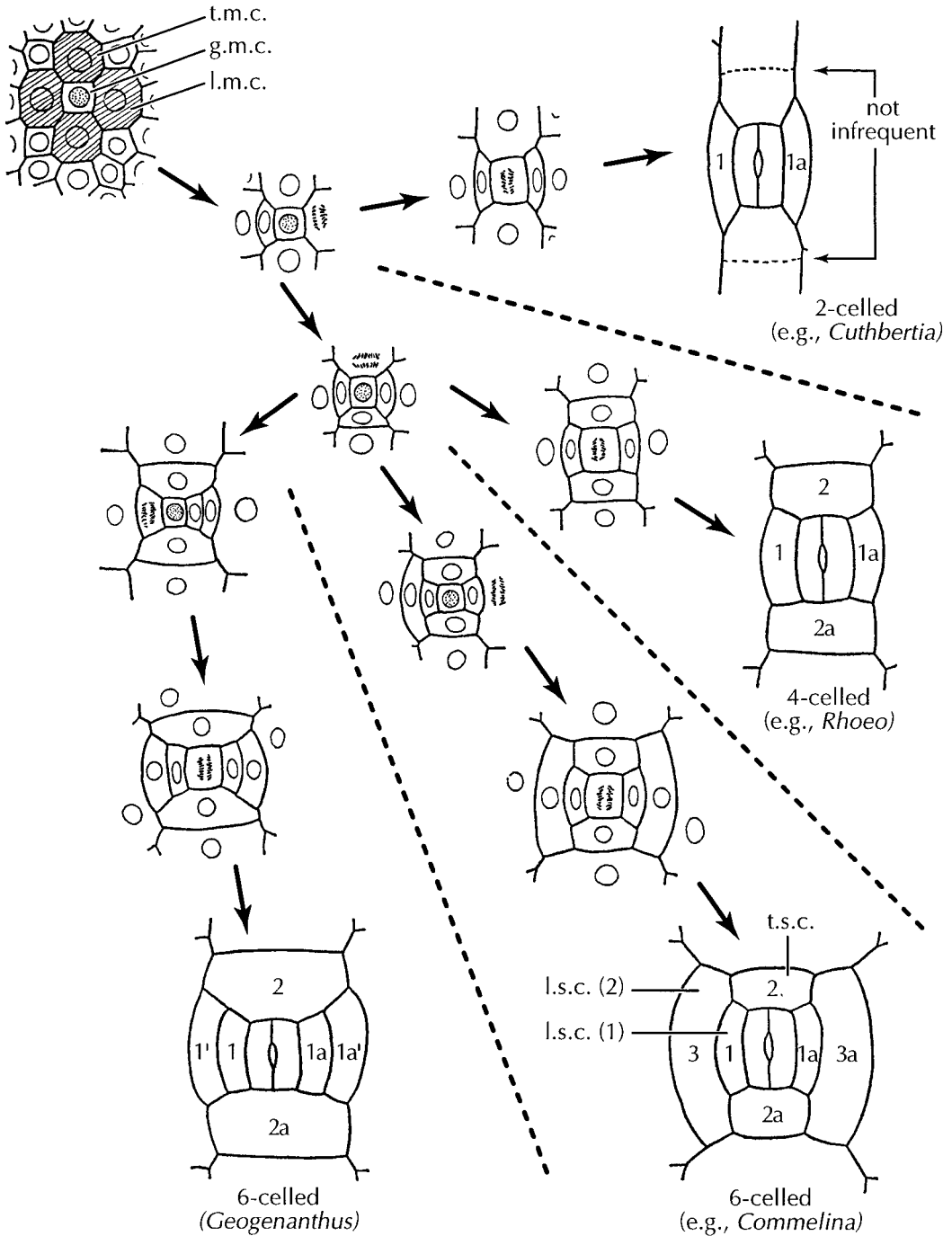
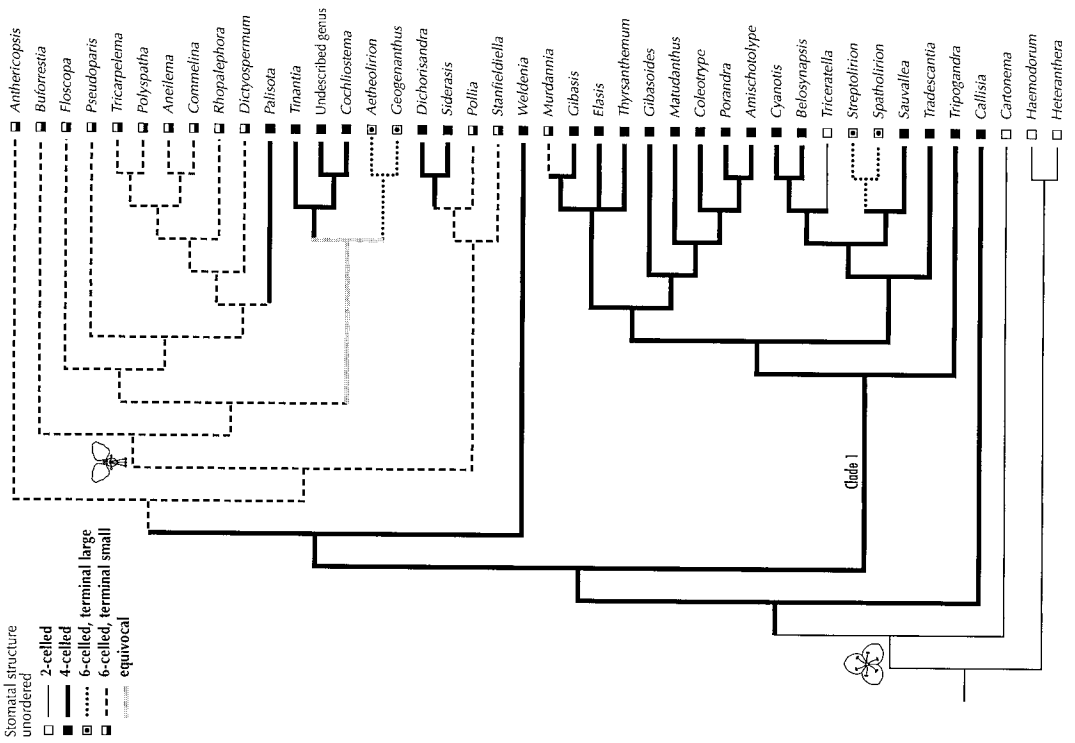
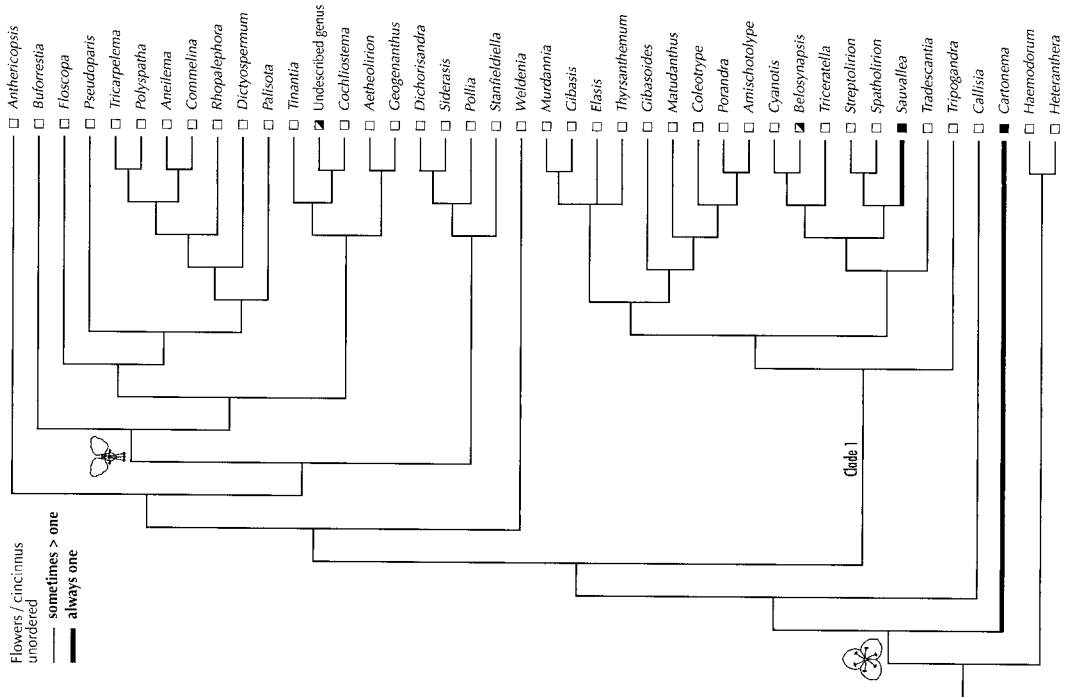


FIG. 3. Diagrams depicting developmental pathways for the four stomatal types found in the Commelinaceae: stomata with two subsidiary cells, four subsidiary cells, and two types with six subsidiary cells. Abbreviations: t.m.c., terminal subsidiary cell mother cell; g.m.c., guard cell mother cell; l.m.c., lateral subsidiary cell mother cell; t.s.c., terminal subsidiary cell; l.s.c. (1), innermost lateral subsidiary cell; l.s.c. (2), outermost lateral subsidiary cell (from Tomlinson 1966).



ters, depending on how well they support the initial (unordered) phylogeny (e.g., Character 5, number of flowers per cincinnus, as discussed above).

It is unclear which of these values (CI, RI, or RC) will provide a more accurate reflection of the suitability of each character in reconstructing phylogeny, but they do provide information about which characters are more homoplasious and/or more informative with respect to a particular data set and topology. It is evident that the number of flowers per cincinnus, for example, does not contribute to the phylogenetic interpretation provided by the rest of the data. Furthermore, if the data set as a whole is misleading, then re-weighting the characters *a posteriori* may reinforce the incorrect parts of the phylogeny and reduce the support for some more accurate areas.

The Commelinaceae are quite diverse morphologically, and, as has been demonstrated in this study, many of the morphological characters in the family are highly homoplasious (e.g., characters relating to pollination). Many classifications of the family have been based in large part on these homoplasious characters, thereby creating unnatural assemblages (an obvious example of this is Brenan's [1966] "Group I", a diverse and artificial group united mainly by inflorescence characters and a dehiscent fruit). Although relatively few anatomical characters have been examined in great enough detail for a comprehensive anatomy-based cladistic analysis, anatomical characters (e.g., stomatal characters; Fig. 3) appear to hold great promise for evaluating relationships at the tribal and, possibly, subtribal levels.

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FIG. 4. Distribution of characters on representative tree (see Fig. 1) from the unordered analysis of 47 morphological characters in Commelinaceae. Left: Stomatal structure. This anatomical character may be useful for higher level relationships within the family. Although it is homoplasious here, its distribution is congruent with recent molecular data (Evans 1995, in prep.). Note that the four-celled stomatal type is one step shorter in equally most parsimonious trees that unite *Palisota* with the clade containing *Cochlostema*, *Tinantia*, and the undescribed genus. The number of steps for the other stomatal types is not altered in other equally most parsimonious trees. Right: Number of flowers per cincinnus. Although this character possesses a relatively high consistency index (CI = 0.75), it does not unite any clades and thus has a retention index of zero. The distribution of this character is not altered in any other most parsimonious trees.

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APPENDIX 1

Description and rationale for characters and coding used in this analysis. A brief justification for the rationale behind the ordering scheme for characters 35 (fruit locule number), 37 (seed number per dorsal locule), and 38 (seed number per ventral locule) is included. Although the characters were not polarized a priori, they were scored so that those states that have traditionally been believed to be primitive in the family (based on observed trends in monocots as a whole) were given a state of “0”, and those states that have been considered more derived were scored as “1” or higher.

CHARACTER 1. INFLORESCENCE PEDUNCLE DEVELOPMENT. The inflorescence may be pedunculate or sessile to subsessile. The inflorescences of *Haemodorum* and *Heteranthera* are pedunculate. This character is divided into two states: 0 = inflorescence peduncle well developed; 1 = inflorescence peduncle absent or nearly so.

CHARACTER 2. CINCINNUS BRACT DEVELOPMENT. The bract of the cincinnus may be large, small or lacking. If present, it may be persistent or cauducous. In *Commelina*, the cincinnus bract encloses the inflorescence and is spathe-like. In all three genera of the subtribe *Streptoliriinae sensu Faden and Hunt* (*Streptolirion*, *Spatholirion*, and *Aetheolirion*), bracts may be large and foliaceous, small, or lacking. In *Stanfieldiella* and *Floscopa*, a clear gradation from large foliaceous bracts at the lower region of the inflorescence, to small bracts at the distal regions often can be found within a single inflorescence.

The development of the cincinnus bract is variable in the outgroups. The bracts in *Haemodorum* are small and cauducous or absent, and in *Heteranthera* they are large and foliaceous.

This character is divided into four different char-

acter states: 0 = cincinnus bracts small and persistent; 1 = cincinnus bracts small and cauducous or absent; 2 = cincinnus bracts all large and foliaceous or spathaceous; 3 = some cincinnus bracts large and foliaceous and some small or lacking; 4 = cincinnus bracts grading from large and foliaceous at the proximal region of the inflorescence to small or lacking at the distal regions.

As it is difficult to make any reliable assumptions regarding the order of transformation of this character, it is left unordered in the second analysis.

CHARACTER 3. CINCINNUS PEDUNCLE DEVELOPMENT. The individual cincinni may be either pedunculate or sessile (or nearly so). In some genera (see Character 7) the cincinnus is reduced to a single flower, making it problematic to distinguish between the cincinnus peduncle and the flower pedicel (Character 7). In these cases, it is possible to distinguish between the two structures by their positional relationship to the floral bracteole (see Character 4). When a floral bracteole is present, any stalk that is proximal to the bracteole (i.e., between the bracteole and the main axis) is considered to be the cincinnus peduncle, while any stalk that is distal to the bracteole is interpreted as the flower pedicel.

The cincinni of *Haemodorum* and *Heteranthera* are distinctly pedunculate.

This character is divided into two states: 0 = cincinnus peduncle well developed; 1 = cincinnus peduncle absent or nearly so.

CHARACTER 4. BRACTEOLE DEVELOPMENT. Each flower in the cincinnus may be opposed by a small bracteole. Most commonly, the bracteole is persistent and not perfoliate, but in two genera, *Aneilema* and *Rhopalephora*, as well as in some *Murdannia* species, it is usually perfoliate. Several genera (*Palisota*, *Streptolirion*, *Spatholirion*, *Siderasis*, *Cochlostema*, *Sauvallea*, *Murdannia*, *Tricarpelema*, *Dictyospermum*, and *Commelina*) contain species in which the bracteole is cauducous or absent. The bracteole is absent in *Heteranthera* and persistent, not perfoliate in *Haemodorum*.

This character is divided into three states: 0 = bracteole persistent, not perfoliate; 1 = bracteole persistent, perfoliate; 2 = bracteole cauducous or absent.

No clearly ordered series is apparent for this character, so it is left unordered in the second analysis.

CHARACTER 5. NUMBER OF FLOWERS PER CINCINNUS. The basic unit of the inflorescence in the Commelinaceae is the helicoid cyme, or cin-

cinnus, implying the presence of more than one flower per primary inflorescence. *Belosynapsis*, Undescribed Genus, *Sauvallea*, *Murdannia*, and *Aneilema*, as well as *Cartonema*, each contain species interpreted here as having cincinni that, through reduction, consist of a single flower.

Several flowers per cincinnus are found in the inflorescences of *Haemodorum* and *Heteranthera*.

This character is divided into two states: 0 = sometimes more than one flower per cincinnus; 1 = always only one flower per cincinnus.

CHARACTER 6. FLOWER TYPES PRESENT. While Commelinaceae typically have perfect flowers, two different types of andromonoecy have arisen within the family. In seven genera (*Palisota*, *Tinantia*, *Tricarpelema*, *Polyspatha*, *Aneilema*, *Rhopalephora*, and some species of *Dichorisandra*), perfect and staminate flowers may be found in random positions on the same plant. Members of the subtribe *Streptoliriinae*, as well as *Pseudoparis* and *Commelina*, possess both perfect and staminate flowers that are largely separate from one another. *Haemodorum* and *Heteranthera* produce only perfect flowers.

This character is divided into three states: 0 = flowers all perfect; 1 = flowers perfect and staminate, distribution random; 2 = flowers perfect and staminate, types largely separate.

It may be a safe assumption that the perfect flower type is primitive in the family, but there is no way to discern which type of andromonoecy is more derived than the other, or whether they both arose independently from the perfect flower state. Therefore this character is left unordered in the second analysis.

CHARACTER 7. PEDICEL PRESENCE/ABSENCE. Flowers in the Commelinaceae may be either pedicellate or sessile to subsessile (see Character 3 for a discussion about the identification of the flower pedicel and the cincinnus peduncle in one-flowered cincinni). All of the genera in the tribe Commelineae possess pedicellate flowers, whereas approximately half of the genera in the Tradescantieae, as well as the genus *Triceratella*, have sessile or subsessile flowers. The flowers in *Haemodorum* are pedicellate and in *Heteranthera* are sessile.

This character is divided into two states: 0 = flowers pedicellate; 1 = flowers sessile or nearly so.

CHARACTER 8. SEPAL COLOR. In most genera, members of the outer perianth whorl are distinctly sepal-like, although they may be slightly colored. The sepals of *Palisota* and the three genera of the subtribe *Streptoliriinae* are petal-like and colored the same as the petals. This state is also found

in some species of *Porandra* and *Amischotolype*, and has arisen (almost certainly independently) in *Pollia* as well. Both outgroup genera produce tepals, so the "sepals" were scored as petal-like.

This character is divided into two states: 0 = outer perianth whorl distinctly sepal-like (although sometimes colored); 1 = outer perianth whorl similar to the petals.

CHARACTER 9. SEPAL (OUTER PERIANTH WHORL) WIDTH. While sepal width has not been used as a taxonomic character in much of the family, it has been useful in defining the subtribe Streptoliriinae. In most genera in the family, the sepals are narrower than the inner (or lateral) petals. In the Streptoliriinae, as well as in some species of *Callisia* and *Floscopa*, the sepals are noticeably wider than the inner petals. Additionally, several genera possess sepals that are nearly equal in width to the inner petals. Both outgroups produce tepals, so the "petals" and "sepals" were scored as equal in width.

This character is divided into three states: 0 = sepals narrower than the inner petals; 1 = sepals equal in width to the inner petals; 2 = sepals wider than the inner petals.

CHARACTER 10. PETAL SIZE AND FORM. The corolla in the Commelinaceae is composed of three petals and may be either actinomorphic or zygomorphic. The zygomorphic state is expressed through one or both of the following features: 1) enlargement or reduction in size of the outer petal (the terms "inner" and "outer" are meant to represent the positions of the petals in the bud, where the outer petal is the single petal that slightly envelops the two lateral, or inner petals [Fig. 5]; they do not necessarily correspond to the position of the petals relative to the main axis of the inflorescence, as the flower may sometimes be rotated 60 degrees; Faden 1975); or 2) shape of the outer petal (the outer petal may be saccate and/or strongly reflexed in the zygomorphic corollas). A zygomorphic corolla is found primarily in some genera of the tribe Commelineae (*Floscopa*, *Buforesstia*, *Tricarpelema* [in some species], *Polyspatha*, *Aneilema*, *Rhopalephora*, and *Commelina*). Strongly zygomorphic flowers are rare in tribe Tradescantieae but occasionally occur (e.g., *Tinantia anomala* [Torrey] C. B. Clarke). It should be noted, however, that several genera in the tribe Tradescantieae (e.g., *Cochliostema*) express a slight tendency toward zygomorphic corollas (the outer petal is subequal to the inner petals), particularly in flowers that are oriented horizontally instead of vertically. Because zygomorphy in these genera is

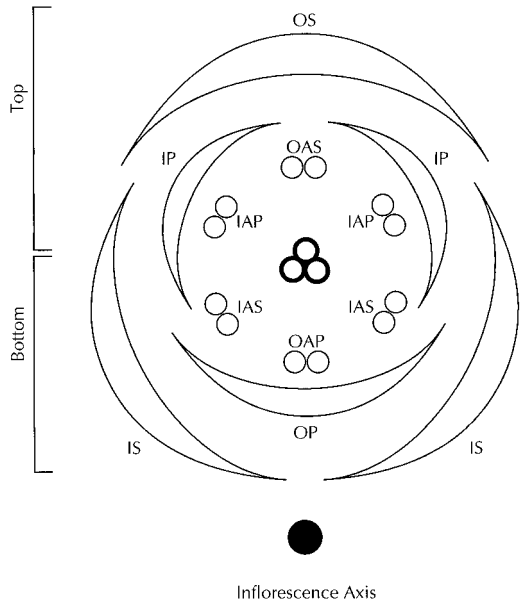


FIG. 5. Floral diagram illustrating the relative position of each floral unit in the Commelinaceae. OS = outer sepal; IS = inner sepal; OP = outer petal; IP = inner petal; OAS = outer antepetalous stamen; IAS = inner antepetalous stamen; OAP = outer antepetalous stamen; IAP = inner antepetalous stamen. The "outer" and "inner" positions refer to the relative location of each structure in the developing bud.

slight (particularly when compared to the strongly zygomorphic corollas found in the Commelineae), or is due primarily to the androecium, these genera are treated here as having actinomorphic corollas. The tepals in *Haemodorum* and *Heteranthera* are all equal.

This character is divided into two states: 0 = petals all equal or subequal (corolla mostly actinomorphic); 1 = one petal strongly differentiated from the other two (corolla zygomorphic).

CHARACTER 11. PETAL FUSION. The petals may be either free or fused, as in *Cyanotis*, *Coleotrype*, *Weldenia*, and some species of *Tradescantia*. The degree of fusion is variable, ranging from the relatively short corolla tubes in *Cyanotis* to the long corolla tube in *Weldenia*.

The tepals in *Haemodorum* are distinct and in *Heteranthera* are connate. Because of the uncertainty of homology between petal connation and tepal connation, this character was scored as "unknown" in *Heteranthera*. This character is divided into two states: 0 = petals distinct; 1 = petals at least basally connate.

CHARACTER 12. PETAL FORM. The shape of the petals is variable in that some species have distinctly clawed petals and others do not. Because the outer petal may evolve independently of the two inner petals, it is possible to have a situation in which two of the petals are clawed and the third is not (Faden 1991). The petals in *Haemodorum* and *Heteranthera* are not clawed.

This character is divided into two states: 0 = petals not clawed; 1 = at least one petal clawed.

CHARACTER 13. PETAL FRINGING. Although the petal margin is usually not fringed in the Commelinaceae, fringed margins are found in three genera within the subtribe Dichorisandrinae (*Geogenanthus*, Undescribed Genus, and *Cochliostema*). The petals are not fringed in either outgroup genus.

This character is divided into two states: 0 = petal margins entire; 1 = petal margins fringed.

Characters 14 through 33 represent the androecial characters. Because these characters comprise such a large proportion of the those used in this study, and because of the complex evolutionary trends found in the androecium, it is necessary to first discuss the manner in which these characters were distinguished from each other before describing each one in detail.

The simplest type of androecium in the Commelinaceae is composed of two whorls of three stamens each, all equal and fertile (Fig. 5). Stamens of the outer whorl are antesealous, and those of the inner whorl are antepetalous. Within each whorl, one stamen may evolve independently of the other two. In order to accurately score the stamens, the androecium was divided into four different components. Each whorl was divided into two units, a single outer stamen, and two inner stamens. The terms "outer" and "inner" here do not refer to the location of the stamens relative to the axis of the inflorescence, but rather to the sepal or petal in front of which they are attached. For example, the outer antesealous stamen (the outer stamen of the outer whorl) is the stamen that is attached in front of the single sepal that slightly encloses the other two sepals in bud. Likewise, the inner antesealous stamens arise in front of the two inner sepals in the bud. The same convention is used for the antepetalous stamens. Although it may appear unnecessarily complex, this system for naming the members of the androecium accomplishes two purposes: 1) it divides the androecium into individually evolving units (as opposed to artificially treating each whorl, or the entire androecium, as a single

character); and 2) it allows for the consistent recognition of homologous stamens, regardless of the orientation of the flower to the main axis of the inflorescence (in some genera, the entire flower is rotated 60 degrees).

CHARACTERS 14–17. STAMEN PRESENCE/ABSENCE. As was noted above, the basic (and putatively primitive) form of the androecium in monocots is the presence of two whorls of three stamens each. One, two, or all three stamens may be absent or vestigial in either whorl. For example, the outer antesealous stamen (OAS) is absent in *Dictyospermum*, as well as some species of *Palisota*, *Dichorisandra*, *Floscopa*, *Murdannia*, *Pollia*, *Aneilema*, and *Rhopalephora*. Both outgroup genera lack the antesealous whorl of stamens.

Each evolutionary component in the androecium is scored for its presence or absence: Character 14—outer antesealous stamen; Character 15—inner antesealous stamens; Character 16—outer antepetalous stamen; Character 17—inner antepetalous stamens. Each of these characters is divided into two states: 0 = stamen(s) present; 1 = stamen(s) absent.

CHARACTERS 18–21. STAMEN FERTILITY. The stamens may be either fertile or sterile. While most of the sterile stamens produce no pollen, a few species possess antherodes (staminode anthers) that produce sterile pollen (e.g., the antepetalous stamen in *Tripogandra grandiflora* (Donnell-Smith) Woodson [Lee 1961], the outer antepetalous stamen in *Aneilema hockii* DeWild. [Faden 1991], and the inner antepetalous stamens in *Palisota* [Faden 1983b, 1988]). It should be noted that although the sterile anthers that produce no pollen (or in which no anther is produced) and those that do produce sterile pollen were both scored the same (i.e., "sterile"), the homology of these different types of sterility is suspect. The presence of anthers that produce sterile pollen is rare, however, and is almost certainly autapomorphic for those taxa that express it. If a particular stamen or whorl is absent or vestigial in a genus (see Characters 14–17), then stamen fertility is not applicable, and it was scored as "?". The antesealous whorl of stamens is absent, and the antepetalous whorl is fertile in *Haemodorum* and *Heteranthera*.

Each unit of the androecium, then, is scored for staminal fertility: Character 18—outer antesealous stamen; Character 19—inner antesealous stamens; Character 20—outer antepetalous stamen; and Character 21—inner antepetalous stamens. These characters are divided into two states: 0 = stamen(s) fertile; 1 = stamen(s) sterile.

CHARACTERS 22–25. STAMINAL FILAMENT BEARDING. The filaments may be either glabrous or bearded, often with distinctly moniliform hairs. Although several different types and degrees of bearding may be found (even when comparing different filaments from the same flower), information is lacking regarding homology of the different hair types. Therefore, the plants are scored on the simple basis of the presence or absence of any type of hairs.

The stamen filaments of *Haemodorum* and *Heteranthera* are all glabrous.

Each unit of the androecium is scored for the presence/absence of staminal hairs: Character 22—outer antesepalous filament; Character 23—inner antesepalous filaments; Character 24—outer antepetalous filament; and Character 25—inner antepetalous filaments. These characters are divided into two states: 0 = staminal filament(s) glabrous; 1 = staminal filament(s) bearded.

CHARACTERS 26–27. RELATIVE FILAMENT LENGTH WITHIN A WHORL. A considerable amount of variation in staminal length is found in the Commelinaceae, particularly within the tribe Commelineae. While absolute filament lengths are not informative due to variation in overall flower size within the family, relative length among staminal filaments is directly comparable, even among flowers of varying sizes. The length of each filament relative to the others was determined (both within a whorl and between whorls; see also Characters 28–29) by first comparing the length of the outer filament with the inner filaments in the same whorl, and then comparing each outer filament with the two inner filaments of the other whorl (Characters 28–29). Thus, all of the length variation may be included without any unnecessary redundancy in the character coding.

The antepetalous stamens are equal in *Haemodorum* and *Heteranthera*.

The filament length comparisons within a whorl are scored as follows: Character 26—relative filament length in the antesepalous whorl; and Character 27—relative filament length in the antepetalous whorl. These characters are divided into three states: 0 = filaments equal; 1 = outer filament longer, inner filaments shorter; 2 = outer filament shorter, inner filaments longer.

There is no obvious evolutionary sequence among these character states, so they are left unordered in the second analysis.

CHARACTERS 28–29. RELATIVE FILAMENT LENGTH BETWEEN WHORLS. In comparing the

filaments between whorls, it is useful to distinguish between a “top” (sometimes called “posterior” or “posticous” in horizontal flowers) and a “bottom” (or “anterior” or “anticous”) of the flower (see Fig. 5). The “top” was earlier defined as the half of the flower containing the outer antesepalous and inner antepetalous stamens, while the “bottom” of the flower contains the remaining three. Because the outgroup genera lack the antesepalous whorl, these characters were not applicable, and were scored as “?”.

Relative filament length between whorls, then, is scored as two characters: Character 28—relative length of outer antesepalous (OAS) and inner antepetalous (IAP) filaments (“top”); and Character 29—relative length of inner antesepalous (IAS) and outer antepetalous (OAP) filaments (“bottom”). They are divided into three states: 0 = filaments equal; 1 = antesepalous filament(s) longer, antepetalous filament(s) shorter; 2 = antesepalous filament(s) shorter, antepetalous filament(s) longer.

There is no obvious evolutionary sequence among these character states, so they are left unordered in the second analysis.

CHARACTER 30. FILAMENT ADNATION TO THE COROLLA. Epipetalous filaments are found in *Coleotrype* and *Weldenia*, as well as some species of *Tradescantia*. The filaments of *Haemodorum* are epipetalous and those of *Heteranthera* are free. This character is divided into two states: 0 = filaments free; 1 = filaments epipetalous.

CHARACTER 31. ANDROECIAL SYMMETRY. While the androecial characters above provide a fairly complete description of the variation found either within a single stamen (or pair of stamens when considering the lateral ones) or between different individual components of the androecium, they do not completely describe the arrangement of the androecium as a whole. As was mentioned earlier, the putatively primitive state for the androecium in the Commelinaceae is a radially symmetrical arrangement of six fertile stamens. Almost half of the genera, however, possess species with a zygomorphic (bilaterally symmetrical) androecium. Additionally, the androecium in *Cochliostema* and many species of *Murdannia* is neither actinomorphic nor perfectly zygomorphic, but asymmetric because one or more of the stamens curve to one side of the flower. In many *Murdannia* species, the stamens show a mirror-image symmetry between flowers, similar to enantiostyly, but due to the curvature of the stamens instead of the style (Faden, unpubl. data). Although the homology of the asymmetrical

androecia in these genera is suspect, it cannot be assumed that they arose independently, particularly for a family in which such heavy emphasis has been placed on androecial characters. The androecium is actinomorphic in both outgroup genera. This character is divided into three states: 0 = androecium actinomorphic at anthesis; 1 = androecium zygomorphic (bilaterally symmetrical) at anthesis; 2 = androecium asymmetrical at anthesis.

CHARACTER 32. ANTHOR DEHISCENCE. Anther dehiscence in the Commelinaceae is almost always through longitudinal slits. *Porandra*, *Dichorisanthra*, and some species of *Coleotrype* exhibit poricidal anther dehiscence through terminal pores or slits. In *Cyanotis* anthers, dehiscence occurs basally. Both outgroup genera exhibit terminal longitudinal anther dehiscence. This character is divided into three states: 0 = anther dehiscence longitudinal; 1 = anther dehiscence poricidal, by terminal pores or slits; 2 = anther dehiscence poricidal basally.

There is no obvious evolutionary sequence among these character states, so this character is left unordered in the second analysis.

CHARACTER 33. ANTHOR CONNECTIVE WIDTH. The width of the connective relative to the anther sacs is variable in the Commelinaceae. In most genera, the connective is narrower than the anther sacs. Nine genera, however, possess species with broad connectives. Both outgroup genera have narrow connectives. This character is divided into two states: 0 = connective narrower than the anther sacs; 1 = connective broader than the anther sacs.

CHARACTER 34. STYLE CURVATURE. The single style in a flower may be central in the flower, or it may have a distinct curve to one side. The three genera in subtribe Coleotrypinae (*Coleotrype*, *Porandra*, and *Amischotolype*), as well as *Gibasoides*, *Tinantia*, and some species of *Aneilema* and *Commelina* have curved styles. Additionally, some species of *Murdannia* exhibit enantiostyly, in which the direction of curvature of the style is predictable (i.e., there are "left" and "right handed" flowers; Faden, unpubl. data). The style in *Haemodorum* is regularly curved (enantiostylous) and in *Heteranthera* is straight. This character is divided into three states: 0 = style always central; 1 = style irregularly curved; 2 = style regularly curved (enantiostylous).

CHARACTER 35. FRUIT LOCULE NUMBER. The fruit in the Commelinaceae is typically a loculicidal capsule (with the two notable exceptions of *Palisota*, which produces a berry, and *Pollia*, which produces an indehiscent, berry-like, crustaceous fruit). Various degrees of zygomorphy are found in

the fruits, which may have three equal locules (radially symmetrical), reduction in size of one locule, forming three unequal locules (in *Siderasis*, *Rhopalephora*, and some species of *Coleotrype*, *Aneilema*, and *Commelina*), or even the complete loss of one or two locules (in *Floscopa* and *Polyspatha*, as well as some species of *Callisia*, *Aneilema*, and *Commelina*). Although it might be argued that there may be a correlation between the degree of zygomorphy of other parts of the flower (i.e., the corolla or the androecium) with the number of locules in the fruit (thereby making this character redundant), it should be noted that flowers of some genera are radially symmetrical for one part of the flower and zygomorphic for another. For example, both the corolla and the androecium in *Siderasis* are regular, while the fruit is composed of two larger and one smaller locules, and *Palisota* has a zygomorphic androecium and a berry composed of three equal locules. It is apparent that the evolution of the zygomorphic state may occur independently within different parts of the flower.

The fruits of both outgroup genera contain three equal locules.

This fruit character is divided into three different states: 0 = fruit consisting of three equal locules; 1 = fruit consisting of three unequal (to two) locules; 2 = fruit consisting of two (or occasionally one) locules. Because the states in this character form a continuous series, they were ordered in the second analysis as follows: 0 ↔ 1 ↔ 2.

CHARACTER 36. SEED ARRANGEMENT. About one third of the genera contain species with biseriate seed arrangement, while the remaining genera have uniseriate seed arrangement.

Haemodorum and *Heteranthera* have biseriate seed arrangement.

This character is divided into two states: 0 = seed arrangement uniseriate; 1 = seed arrangement biseriate.

CHARACTERS 37–38. SEED NUMBER PER LOCULE. The locule facing the outer sepal (dorsal locule) evolves independently of the locules facing the inner sepals (ventral locules). In *Aneilema*, for example, the dorsal locule, when developed, always contains fewer seeds than each ventral locule. The fruit of *Dictyospermum*, in contrast, always contains a single seed in each of the three locules. Additionally, some genera produce fruits with the putatively primitive state of more than two seeds in each locule (e.g., *Cochlostema* and *Weldenia*). Finally, some fruits contain all three locules, but one or two of them do not produce seeds.

The fruits in *Haemodorum* consist of three locules, each of which produces two seeds. The fruits of *Heteranthera* consist of three locules, each of which produces numerous seeds.

The number of seeds per locule, then, is treated as two independent characters: Character 37—seed number per dorsal locule; Character 38—seed number per ventral locule. These characters are divided into four different states: 0 = more than two seeds/locule; 1 = two seeds/locule; 2 = one seed/locule; 3 = zero seeds/locule (if the locule is entirely absent, then it is scored as “unknown”).

Because the states in this character form a continuous series, they are ordered in the second analysis as follows: 0 ↔ 1 ↔ 2 ↔ 3 (note that these numbers indicate the *character state*, not the actual number of seeds/locule).

CHARACTER 39. EMBRYOTEGA POSITION. All the seeds in the Commelinaceae possess a small embryotega, or operculum, a cap-like structure over the embryo. The embryotega may be dorsal, semi-dorsal, semi-lateral, lateral, or terminal according to the genus. The outgroups do not produce an embryotega, so they are scored as unknown.

This character is divided into four states: 0 = embryotega dorsal; 1 = embryotega semi-dorsal to semi-lateral; 2 = embryotega lateral; 3 = embryotega terminal. Although it is easy to envision a transformation series in which the position of the embryotega has moved around the seed (e.g., starting from the dorsal position and moving through semi-dorsal and semi-lateral to the lateral), there are no intermediates between the terminal position and any of the others. Without further developmental information to document the order of transformation, this character is left unordered in the second analysis.

CHARACTER 40. HILUM SHAPE. The funicular scar is most commonly linear, but it is punctiform in *Cartonema*, *Triceratella*, *Palisota*, *Belosynapsis*, *Weldenia*, *Callisia*, and *Polliia*, as well as a few scattered species of other genera. *Haemodorum* produces a punctiform hilum, and information was unavailable for *Heteranthera*, so it is treated as unknown. This character is divided into two states: 0 = hilum punctiform to elliptic; 1 = hilum oblong to linear.

CHARACTER 41. ARIL. The genus *Dichorisan-dra*, as well as some species of *Amischotolype* and *Porandra* produce arillate seeds. Depending on which species are chosen to represent *Amischotolype* and *Porandra*, this character could appear autapo-

morphic for *Dichorisan-dra*. Note, however, that *Amischotolype hispida* (the species used in this analysis) does produce arillate seeds. Both outgroup genera produce exarillate seeds. This character is divided into two states: 0 = seeds exarillate; 1 = seeds arillate.

CHARACTER 42. PTYXIS. Ptyxis refers to the folding of the leaves in bud. In the Commelinaceae, the developing leaf is typically in one of two positions as it emerges from the bud: its margins may be rolled into two distinct curls on the upper surface, scroll-like (involute) or they may be rolled into a single curl (convolute; or “supervolute” in Dahlgren and Clifford 1982). Occasionally they are simply folded (conduplicate). Ptyxis in *Haemodorum* is convolute, and information is unavailable for *Heteranthera*, so it is scored as unknown. This character is divided into two states: 0 = ptyxis convolute or conduplicate; 1 = ptyxis involute.

CHARACTER 43. STOMATAL STRUCTURE. While most classifications for the Commelinaceae have relied heavily upon traditional macro-morphological characters, attempts to incorporate anatomical characters have shown promise (e.g., Pichon 1946; Tomlinson 1966, 1969; Faden and Inman 1996). However, genus-specific data for most anatomical characters are not readily available. This study incorporates four different anatomical characters (Characters 43–46).

Of the different types of anatomical data that have been studied, the most useful is stomatal structure. Four distinct types of stomata have been described in the Commelinaceae (Fig. 3; Tomlinson 1966, 1969), the simplest of which have only two subsidiary cells positioned laterally (found in *Triceratella*, some *Cartonema* species, and both outgroup genera). Most members of the tribe Tradescantieae have four-celled stomata, with two lateral and two terminal subsidiary cells. The stomata of *Streptolirion*, *Spatholirion*, and *Aetheolirion* (subtribe Streptoliriinae), as well as *Geogenanthus*, are six-celled, with four lateral and two terminal subsidiary cells. In these three genera, the terminal cells are relatively large, extending to the outer edge of the lateral cells. Finally, members of the tribe Commelineae possess stomata with four lateral and two terminal subsidiary cells, but the terminal cells are smaller, not extending to the outer edge of the outermost lateral cells. Stomata in *Haemodorum* and *Heteranthera* are two-celled. This character is divided into four states: 0 = stomata two-celled; 1 = stomata four-celled; 2 = stomata six-celled, termi-

nal cells large; 3 = stomata six-celled, terminal cells small.

Although Tomlinson (1966) presents information on the development of each of these stomatal types (Fig. 3), he also mentions that the sequence of cell divisions is variable. Until more about the development of the stomatal apparatus is understood, it is difficult to make a priori hypotheses regarding the order of character state transformations, so this character is unordered in the second analysis.

CHARACTER 44. HOOK HAIRS. Tomlinson (1966) described two main categories of hairs for the Commelinaceae: "microhairs", which show limited variability in structure, and "macrohairs", which are quite diverse. He recognized eight different types of macro-hairs, ranging from single-celled papillae to multicellular uniseriate hairs. One particular type of macro-hair which has been examined more closely by one of the authors (R. Faden, unpubl. data) is the "hook hair". These two-celled, hook shaped hairs have been observed on the leaves of *Polyspatha*, *Dictyospermum*, *Pollia*, *Rhopalephora*, *Aneilema*, and some species of *Commelina*, and are notably absent in the rest of the family (Tomlinson 1966; R. Faden, unpubl. data). Hook hairs are absent in both outgroup genera. This character is divided into two states: 0 = hook hairs absent; 1 = hook hairs present.

CHARACTER 45. GLANDULAR MICROHAIRS. Three-celled glandular microhairs (or simply "microhairs" in Tomlinson 1966) are present on the leaves of every genus in the Commelinaceae except *Cartonema* and *Triceratella*. The distribution of these hairs on the leaf, stem, and flower is quite variable, and Tomlinson has suggested that their distribution might be useful for diagnosing genera. As an example, he points out that few or no microhairs are found on the adaxial leaf surface

in *Murdannia*, but they are abundant in *Aneilema*. Due to the difficulty of collecting data on hair distribution, as well as assessing homology on such data, however, this character is simply scored for its presence or absence.

Glandular hairs are present in some Haemodoraceae and some Pontederiaceae (Simpson 1990), but they are largely restricted to the outer surfaces of flowers and inflorescence branches. As the homology of these hairs with the vegetative glandular microhairs is suspect, both outgroup genera were scored as lacking glandular microhairs.

This character is divided into two states: 0 = glandular microhairs absent; 1 = glandular microhairs present.

CHARACTER 46. RAPHIDE CANALS. Raphide canals are present in all genera of Commelinaceae except *Cartonema*. Indeed, the absence of raphide canals has been one of the most compelling arguments for the separation of *Cartonema* into its own family (Pichon 1946; Hutchinson 1959; Tomlinson 1966). Of the remaining genera, only in *Triceratella* are the raphide canals located next to the veins, instead of being evenly distributed throughout the leaf blade.

Raphide canals are absent in *Haemodorum* and *Heteranthera*.

This character is divided into three states: 0 = raphide canals absent; 1 = raphide canals present next to the veins; 2 = raphide canals present, not exclusively next to the veins.

CHARACTER 47. CLOSED LEAF SHEATH. All members of the Commelinaceae possess distinct closed sheathing leaf bases (Cronquist 1981; Dahlgren et al. 1985). Although both outgroup genera possess a sheathing leaf base, it is open. This character was divided into two states: 0 = closed sheathing leaf bases absent; 1 = closed sheathing leaf bases present.

