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Phylogenetic signal common to three data sets: combining data which initially appear heterogeneous

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Abstract. This study makes use of three sources of data, morphology and two chloroplast DNA sequences, *ndh*F and *rbc*L, to resolve relationships in Gesneriaceae. Cladograms from each of the three data sets separately are not topologically congruent. Statistical indices suggest that each data set is congruent with the *ndh*F data although *rbc*L and morphology are themselves incongruent. Consensus methods provide no resolution of taxonomic relationships when trees from the different data sets are combined. Combining data sets generally results in cladograms that are more fully resolved than each of the data sets analyzed separately and support for the clades increases based on higher decay index and bootstrap values. These results indicate that there is a phylogenetic signal common to each of the data sets, however, the noise (errors due to homoplasy, mis-scoring, etc.) unique to each data source masks this signal. In combining the data, the evidence for the common evolutionary history in each data set overcomes the noise and is apparent in the resulting trees.

Key words: Gesneriaceae, congruence, morphology, *ndh*F, *rbc*L, phylogeny.

The search for a true phylogeny may remain forever an elusive goal for systematists, however, means of assessing cladograms with greater confidence are continually appearing (Faith 1991, Hillis and Huelsenbeck 1992, Källersjö et al. 1992, Huelsenbeck and Hillis 1993, Bremer 1994, Donoghue 1994, Farris et al. 1994b, Mason-Gamer and Kellogg 1996, Ballard et al. 1998, Day et al. 1998, Wiens 1998, Johnson and Soltis 1998). With the advent of molecular techniques and the expansion of these techniques to numerous genes, it is possible for systematists to determine the robustness of the data they are working with, and to construct cladograms from different, independent data sets in the search for congruent cladograms (Donoghue 1994). Congruence among disparate data sets provides greater confidence that the data reflect a common evolutionary history (Donoghue 1994, Miyamoto and Fitch 1995, Brower et al. 1996). The underlying principle of comparing cladograms from different data sets is that it is highly unlikely independent sources of data each will have followed a common evolutionary history different from the evolutionary history of the organisms themselves (Doyle 1992, Miyamoto and Fitch 1995).

Discrepancies between data sets provide a different scenario (Bull et al. 1993, Poe 1996, Mason-Gamer and Kellogg 1996, Wiens 1998). Initial responses to discrepancies are that one of the data sets is likely to be incorrect due to misinterpretation of homology, differential rates of evolution, or events that occurred in the history of the organisms that are not

incorporated into standard cladistic analyses such as hybridization or lineage sorting (Neigel and Avise 1986, Sytsma 1990, Brower et al. 1996). Homoplasy (Sanderson and Donoghue 1996), concerted convergence (where similar environments may select for similar traits in different evolutionary lineages; Givnish and Sytsma 1997a), or horizontal transfer (Soltis et al. 1991) can all result in incongruent data sets.

Although the above examples are frequently cited as potential sources of discrepancy between data sets, they are not the only contributing factors. Other factors may be more subtle such as taxon or data sampling density (Sanderson 1989, Sanderson and Donoghue 1989, Poe 1996, Wendel and Doyle 1998) which can create incongruent trees simply due to limited data. In such cases discrepancies may result from minor topological disparities due to low levels of character support and will not reflect evolutionary differences in the sources of data or the organisms themselves (soft incongruence: Seelanen et al. 1997). Other sources of discrepancy that are not reflective of different organismal history may result from inappropriate gene choice (Wendel and Doyle 1998) or sequencing error (Wendel and Doyle 1998). These factors can result in trees with different topologies, although the data themselves may not be inherently discrepant. In such cases noise (a combination of any or all of the sources of discrepancy listed above in addition to errors in scoring data) within the data set may obscure the organismal phylogeny and be misleading. Therefore it is important to examine the data directly in cases where discrepancies occur to first determine if such factors may be involved before proceeding to search for more basic biological explanations for discrepancy.

In this paper the phylogenetic relationships of the tribes of the Gesneriaceae are examined with three data sets; morphology, *ndh*F sequences, and *rbc*L sequences. The *Gesneriaceae* is comprised of approximately 2500–3700 species in 120–147 genera, distributed primarily in the tropics with a few temperate species in Europe, China and Japan (Heywood 1978, Burtt and Wiehler 1995). The majority of species in the Gesneriaceae are herbaceous perennials, but the family also includes annuals, shrubs, lianas, and trees. Many species (20%) are epiphytic, and the Gesneriaceae ranks among the top ten plant families in terms of absolute numbers of epiphytic taxa (Madison 1977, Kress 1986).

The Gesneriaceae is a member of the Lamiales (APG 1998) and is distinguished from other families in the order by the combination of five-lobed corollas, parietal placentation, and presence of endosperm in most taxa (Cronquist 1981). Classifications of the Gesneriaceae traditionally recognize two subfamilies (Gesnerioideae and Cyrtandroideae) (Bentham 1876; Burtt 1962, 1977; Fritsch 1893–1894; Smith 1996; Smith et al. 1997a) which have been divided further into 9–17 tribes (Bentham 1876; Burtt 1962, 1977; Fritsch 1893–1894; Ivanina 1965; Wiehler 1983; Burtt and Wiehler 1995).

There have been several cladistic analyses performed within the Gesneriaceae (Kvist 1990; Crisci et al. 1991; Boggan 1991; Smith and Sytsma 1994a, b, c; Smith 1996; Smith et al. 1997a, b; Möller and Cronk 1997; Smith and Carroll 1997; Smith et al. 1998; Smith and Atkinson 1998), but few (Smith 1996, Smith et al. 1997a) performed at the tribal level. A comparison of these cladistic analyses is desirable to provide more confidence in the relationships. This paper re-analyzes two previous studies (Smith 1996; Smith et al. 1997a) using only the taxa in common to all three data sets and compares these results with a third data set, *rbc*L sequences.

Numerous methods exist for the analysis of different data sets. The first approach, often referred to as 'total evidence' suggests that any phylogenetic analysis should be based on all evidence that is available in combination (Kluge 1989). A second approach is to analyze the data sets separately and to examine the resulting trees for congruence (Miyamoto and Fitch 1995). The advantage to this latter

method is that data from different partitions (e.g. genes) are likely to be more independent from each other than to data from within each partition. Thus, each analysis is an independent estimate of relationships and clades that are common to each tree may provide some of the strongest evidence that a particular clade is a reflection of organismal history (Swofford 1991, Donoghue 1994). Among the most widely utilized means of analyzing multiple data sets is the conditional combination approach (Sytsma 1990, Bull et al. 1993, Smith and Sytsma 1994c, Bremer 1996, Poe 1996, Pennington 1996, Mason-Gamer and Kellogg 1996, Huelsenbeck et al. 1996, Johnson and Soltis 1998, Wiens 1998). In this latter approach, partitions are kept separate until they can be tested for homogeneity after which, if they are congruent, they are combined.

This paper largely follows the conditional combination approach by first examining each data set separately to determine the relationships each source of data provides as well as examining each data set for its robustness in terms of support for clades by utilizing bootstrap (Felsenstein 1985) and decay (Bremer 1994, 1988; Donoghue et al. 1992) indices. The trees from the separate analysis of each of the data sets are compared using consensus methods (Adams 1972, Nelson 1979, Bremer 1990). The data sets are then compared to calculate congruency using the partition homogeneity test (Farris et al. 1994b) of PAUP version 4.0d65 using each data set pairwise and all three together. Lastly the data are combined (Miyamoto 1981, Kluge 1989, Eernisse and Kluge 1993, Brower et al. 1996) to construct a cladogram based on total evidence.

Materials and methods

The gene sequences used in this analysis were generated by thermal cycle sequencing (Innis et al. 1988) of previously amplified *ndh*F or *rbc*L regions. The *ndh*F gene was amplified in two overlapping sections (positions 1-1350, and 972-2044) from genomic DNA isolated from fresh, frozen, or silica gel dried material (Smith et al. 1992). The *rbc*L gene was amplified in a single section following the procedures and primers used in Smith et al. (1993). Amplification of *ndh*F and sequencing procedures for both genes followed that of Smith et al. (1997a) used for other members of the Gesneriaceae. Sequencing primers for the *rbc*L gene were the same as those used in Smith et al. (1993). Morphological data were based on the reduced taxon sampling from Smith (1996).

The focus of this analysis was to compare tribal relationships within the *Gesneriaceae* using different data sets, but with identical sampling. Two to six genera per tribe were used in all analyses, the exceptions being the smaller tribes Napeantheae (one genus) and Cyrtandreae (three genera) for which a single genus was used. The species used in the analysis and Genbank accession numbers are included in Table 1. Morphological data are presented elsewhere (Smith 1996).

Because relationships of families in Lamiales are not yet well-established, three families from Lamiales were used as outgroups: Acanthaceae, Bignoniaceae, and Scrophulariaceae. These were selected because data are available for morphological characters used in this analysis and they are close to Gesneriaceae in larger analyses based on molecular data (Olmstead et al. 1992, Chase et al. 1993, Olmstead and Reeves 1995). These outgroup taxa are included to root cladograms from the analysis, not to estimate relationships of *Gesneriaceae* to other families.

Phylogenetic analysis. Phylogenetic divergence was reconstructed using PAUP version 3.1.1 (Swofford 1993) to implement parsimony (Farris 1970, Farris et al. 1970, Swofford and Maddison 1987). In this analysis, trees were generated using the general heuristic option, saving minimal trees only, with the collapse zero-length branches, and ignore uninformative characters options in effect. The search strategy of Olmstead and Palmer (1994) was implemented searching for 1000 trees each in five subsequent analyses with the nearest neighbor interchange (NNI) search option in effect and mulpars "off" to search for multiple islands of trees (Maddison 1991). Each of the results from the five NNI searches was used as the starting tree(s) for a search with tree bisection reconnection (TBR) and mulpars "on".

Branch support analysis was performed to examine trees that were five or fewer steps longer than the most-parsimonious tree(s) (Bremer 1988, 1994; Donoghue et al. 1992) by saving all trees five

Table 1. Species sequenced in this study with Genbank submission numbers for *ndh*F and *rbc*L. Voucher information for the species used in this analysis is presented in Smith et al. (1997a). Outgroup sequences are from Olmstead and Reeves (1995) and Chase et al. (1993)

Species	Genbank Number *ndh*F	Genbank Number *rbc*L
Achimenes skinneri Lindl.	U62177	AF170221
Aeschynanthus micranthus C. B. Clarke	U62169	AF170222
Agalmyla parasitica (Lam.) Kuntze	U62171	AF170223
Alloplectus meridensis Klotszch	U62158	AF170224
Asteranthera ovata (Cav.) Hanst.	U62204	AF170225
Besleria affinis Morton	U62162	AF170226
Codonanthe elegans Wiehler	U62178	AF170227
Columnea schiedeana Schlecht.	U62164	AF170228
Cyrtandra umbellifera Merr.	U62165	AF170229
Diastema racemiferum Benth.	U62156	AF170230
Didymocarpus albomarginata Hemsl.	U62207	AF170231
Drymonia stenophylla (J. D. Smith) H. E. Moore	U62159	AF170232
Gasteranthus corallinus (Fritsch) Wiehler	U62163	AF170233
Gesneria pedicellaris Alain	U62192	AF170234
Gloxinia sylvatica (H.B.K.) Kunth	U62157	AF170235
Kohleria spicata (Kunth) Oerst.	U62181	AF170236
Monophyllaea hirticalyx Franch.	U62168	AF170237
Monopyle macrocarpa Benth.	U62197	AF170238
Napeanthus macrostoma Leeuw.	U62161	AF170239
Negria rhabdothamnoides F. Muell.	U62195	AF170240
Ornithoboea wildeana Craib.	U62166	AF170241
Paliavana prasinata (Ker-Gawl.) Fritsch	U62174	AF170242
Ramonda myconi (L.) Rchb.	U62185	AF170243
Rhynchoglossum notonianum (Wall.) B. L. Burtt	U62179	AF170244
Rytidophyllum tomentosum (L.) Mart.	U62200	AF170245
Saintpaulia rupicola B. L. Burtt	U62176	AF170246
Sinningia brasiliensis (Regel & Schmidt) Wiehler	U62175	AF170247
Sinningia cooperi (Paxt.) Wiehler	U62201	AF170248
Solenophora obliqua D.L.Denham & D.N.Gibson	U62202	AF170249
Streptocarpus saxorum Engl.	U62170	AF170250
Outgroups		
Barleria prionitis L.	U12653	L01886
Paulownia tomentosa Steud.	L36406	L36447
Tabebuia heterophylla (A. de Candolle) Britton	L36416	L36451

steps longer than the most-parsimonious tree(s) and then examining subsets of trees one to five steps longer with the filter option of PAUP. Clades that persisted in a strict consensus of all trees five steps longer than the most-parsimonious trees were tested using the constraints option of PAUP to find the shortest tree that did not contain that clade. Bootstrap analysis (Felsenstein 1985) was performed using 1000 replicates.

Trees from all three data sets analyzed separately were combined to create consensus trees. Strict (Nelson 1979), semi-strict (Bremer 1990) and Adams (Adams 1972) consensus methods were used to produce trees from the analyses performed separately.

Average values for bootstrap and decay (Källersjö et al. 1992) were calculated by first summing the values for ingroup clades found in the strict consensus of the most-parsimonious trees (Figs. 1–7) and then dividing by 29, the maximum number of fully resolved nodes for an ingroup of 30 taxa.

The partition homogeneity test (Farris et al. 1994b) was examined by partitioning the data into *rbc*L, morphology and *ndh*F. The test utilized 1000 replicates with the NNI search option and mulpars "off" using PAUP 4.0d65.

Results

The cladistic analysis of the three separate data sets resulted in varying degrees of resolution for the genera examined in this analysis. The number of characters analyzed, number of trees, number of resolved nodes, number of steps, consistency index (CI), retention index (RI), average decay values and average bootstrap values for each of the data sets examined separately and in all combinations are presented in Table 2. Strict consensus trees, showing decay and bootstrap values for the results of each analysis are presented in Figs. 1–7.

In general, as more data are added, the average decay values and average bootstrap values increase (Table 2). CI and RI remained approximately equal.

A visual comparison of all trees analyzed separately results in only the monophyly of the tribe Beslerieae (*Besleria* and *Gasteranthus*) consistent among all data (Figs. 1–3). The combination of each of the data sets pairwise and all three combined results in a unique cladogram for each analysis with aspects from each of the data sets analyzed separately (Figs. 4–7). In no instance does a single data set completely overwhelm the results of any other (based on the unique relationships apparent in each combination of data) despite the highly discrepant number of characters analyzed in each data set separately (Table 2).

Consensus trees resulted in poor, or unusual resolution. Strict (Nelson 1979) and semi-strict (Bremer 1990) consensus resulted in only the monophyly of the Gesneriaceae (as defined by the outgroup designation) and the tribe Beslerieae. Adams consensus (Adams 1972) provides little additional resolution to that obtained from morphological data, but

Table 2. Values for each of the data sets examined singly, pairwise and all combined. Average values for bootstrap and decay were calculated by first summing the values for ingroup clades found in the strict consensus of the most-parsimonious trees (Figs. 1–7) and then dividing by 29, the maximum number of resolved ingroup nodes

Data	Char.	Trees	Nodes	Steps	CI	RI	Boot.	Decay
Morphology	41	72	21	135	0.49	0.65	16.1	0.83
*rbc*L	149	15	13	579	0.36	0.43	18.2	1.14
*ndh*F	573	9	13	2910	0.36	0.35	22.7	1.45
*rbc*L & morphology	190	27	17	790	0.38	0.43	26.6	1.59
*ndh*F & morphology	614	4	24	3071	0.36	0.36	32.0	2.93
*ndh*F & *rbc*L	722	1	28	3582	0.35	0.35	37.8	4.86
All	763	3	25	3743	0.36	0.36	39.0	4.86

Char. number of characters, *CI* consistency index, *RI* retention index, *Boot.* bootstrap.

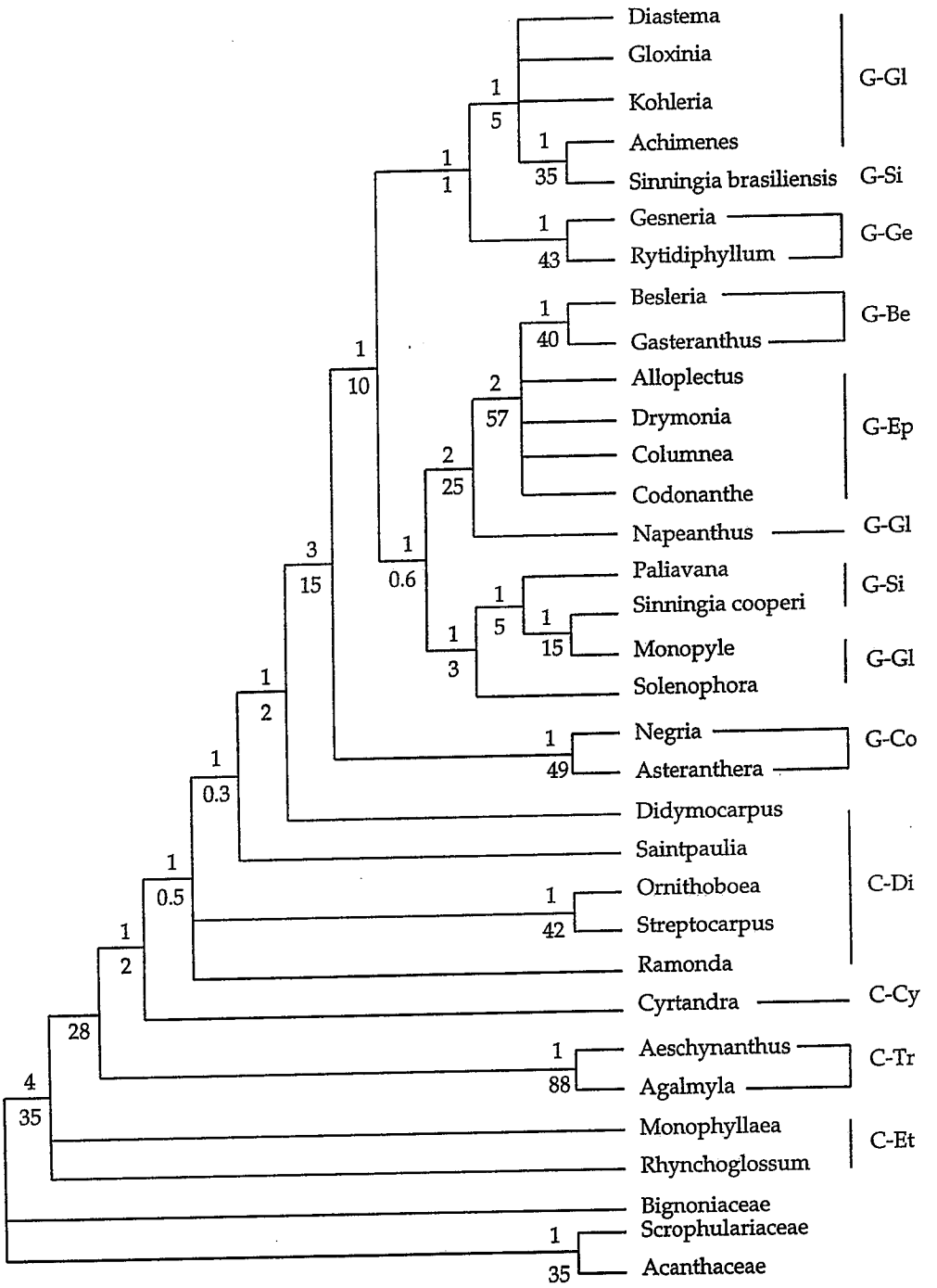

Fig. 1. Strict consensus of 72 most-parsimonious trees from morphological data (CI = 0.49, RI = 0.65). Values above branches indicate decay values, those below are bootstrap values. Nodes without bootstrap values were not present in the bootstrap consensus tree. Abbreviations for subfamilies and tribes are as follows: *C* Cyrtandroideae, *G* Gesnerioideae, *Be* Beslerieae, *Co* Coronanthereae, *Cy* Cyrtandreae, *Di* Didymocarpeae, *Ep* Episcieae, *Et* Epithematae, *Ge* Gesnerieae, *Gl* Gloxinieae, *Na* Napeantheae, *Si* Sinningieae, *Tr* Trichosporeae

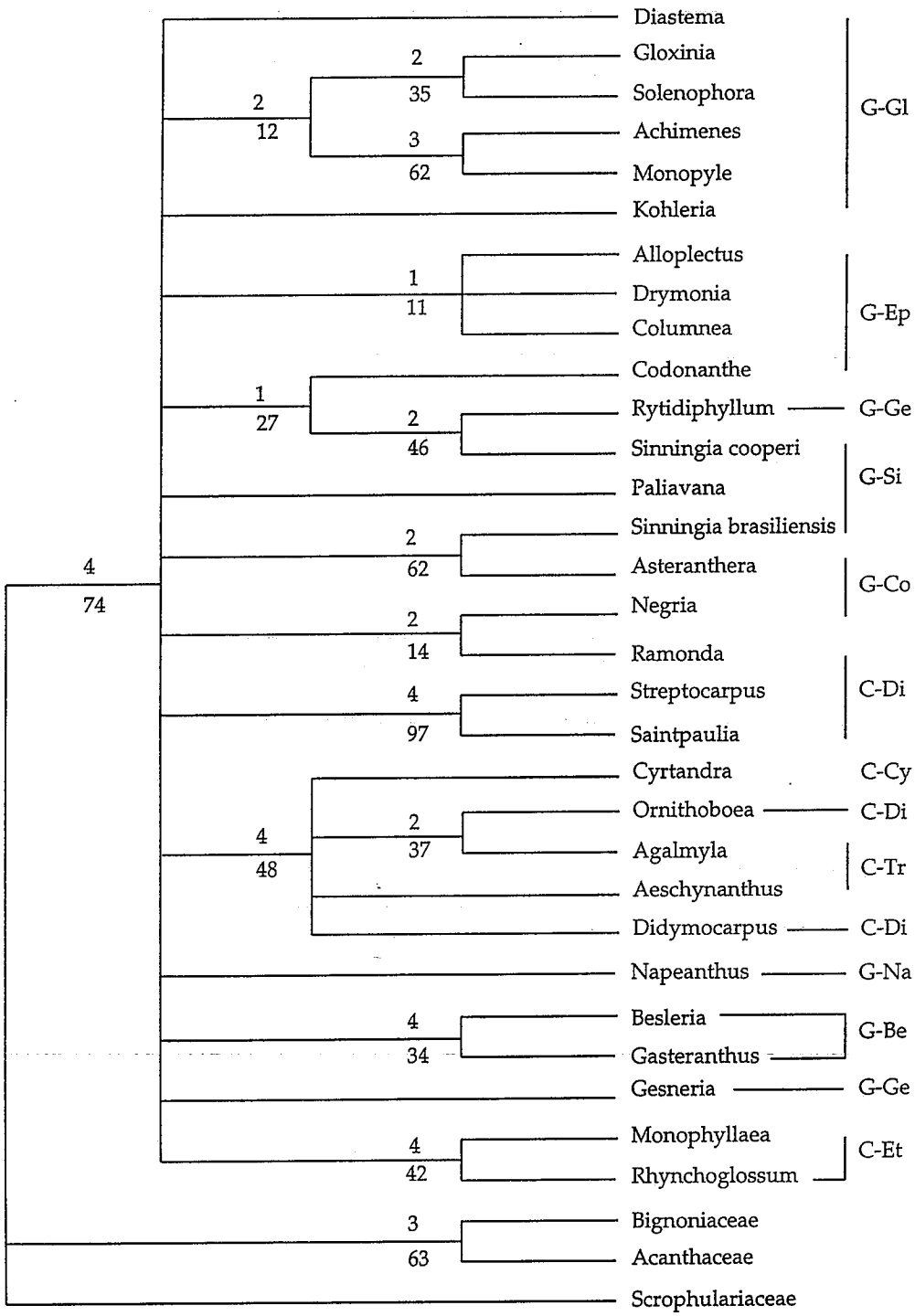

Fig. 2. Strict consensus of 15 most-parsimonious trees from *rbc*L data (CI = 0.36, RI = 0.43). Values above branches indicate decay values, those below are bootstrap values. Nodes without bootstrap values were not present in the bootstrap consensus tree. Abbreviations for subfamilies and tribes follow Fig. 1

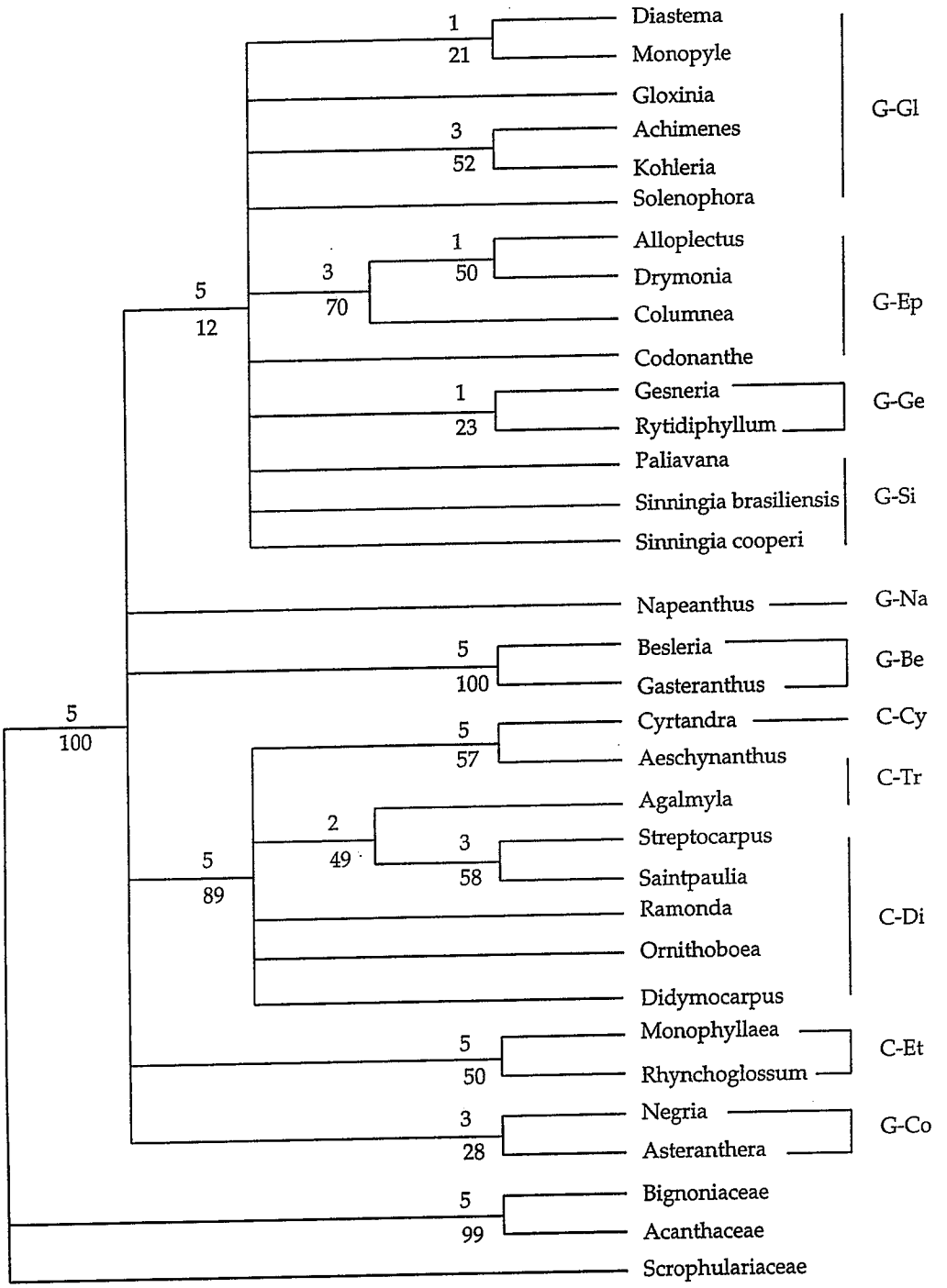

Fig. 3. Strict consensus of nine most-parsimonious trees from *ndh*F data (CI = 0.36, RI = 0.35). Values above branches indicate decay values, those below are bootstrap values. Nodes without bootstrap values were not present in the bootstrap consensus tree. Abbreviations for subfamilies and tribes follow Fig. 1

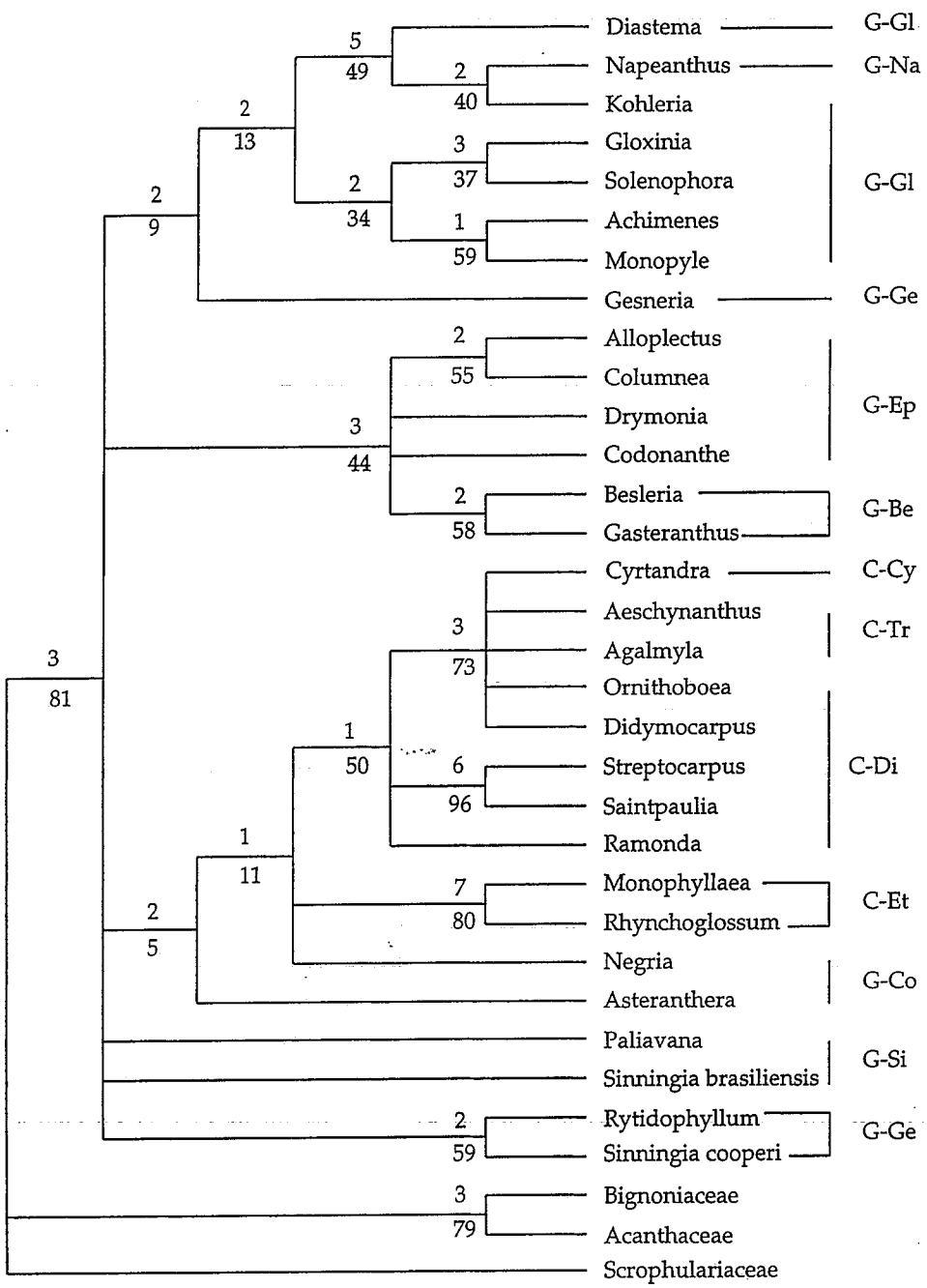

Fig. 4. Strict consensus of 27 most-parsimonious trees from the combined morphological and *rbc*L data sets (CI = 0.38, RI = 0.43). Values above branches indicate decay values, those below are bootstrap values. Nodes without bootstrap values were not present in the bootstrap consensus tree. Abbreviations for subfamilies and tribes follow Fig. 1

does retain the unusual relationships seen in the *rbc*L data alone such as the *Sinningia brasiliensis*/*Asteranthera* and *Ramonda*/*Negria* clades (see discussion).

The results of the partition homogeneity test are; *ndh*F, *rbc*L and morphology: 0.008, *ndh*F and morphology: 0.692, *rbc*L and morphology: 0.002, *ndh*F and *rbc*L: 0.183.

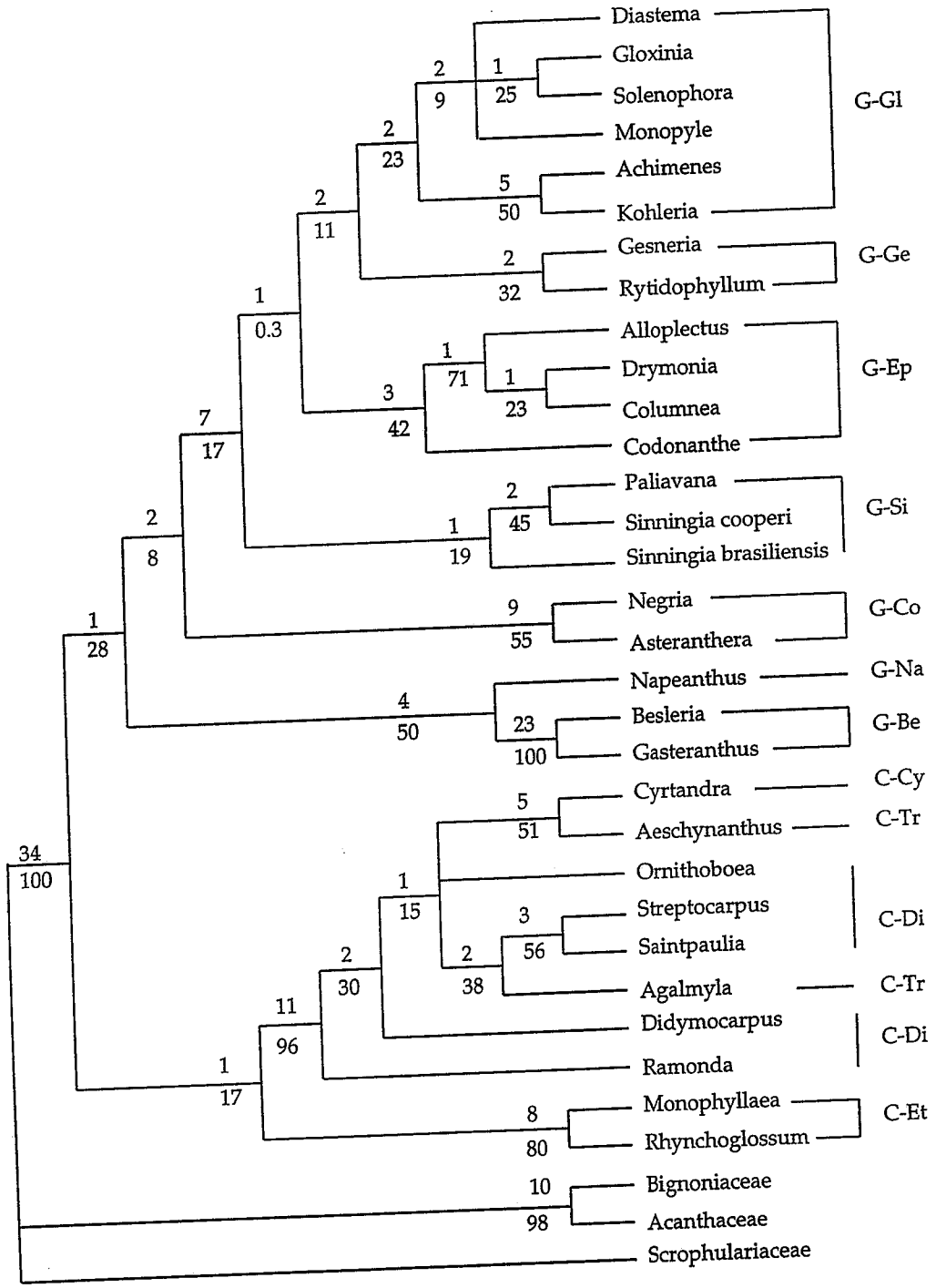

Fig. 5. Strict consensus of four most-parsimonious trees from combined morphological and *ndh*F data sets (CI = 0.36, RI = 0.36). Values above branches indicate decay values, those below are bootstrap values. Nodes without bootstrap values were not present in the bootstrap consensus tree. Abbreviations for subfamilies and tribes follow Fig. 1

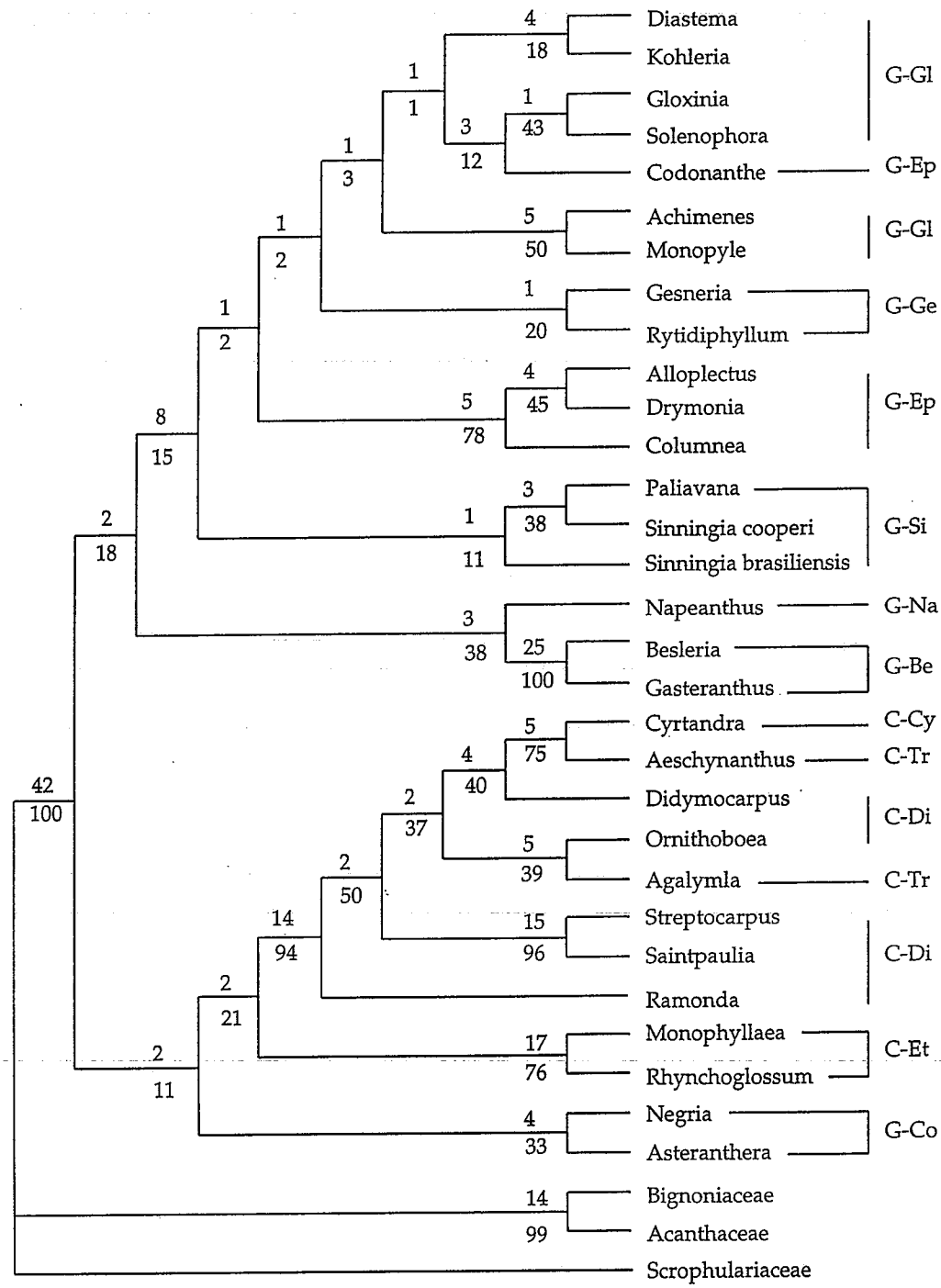

Fig. 6. Single most-parsimonious tree from combined *rbc*L and *ndh*F data sets (CI = 0.35, RI = 0.35). Values above branches indicate decay values, those below are bootstrap values. Nodes without bootstrap values were not present in the bootstrap consensus tree. Abbreviations for subfamilies and tribes follow Fig. 1

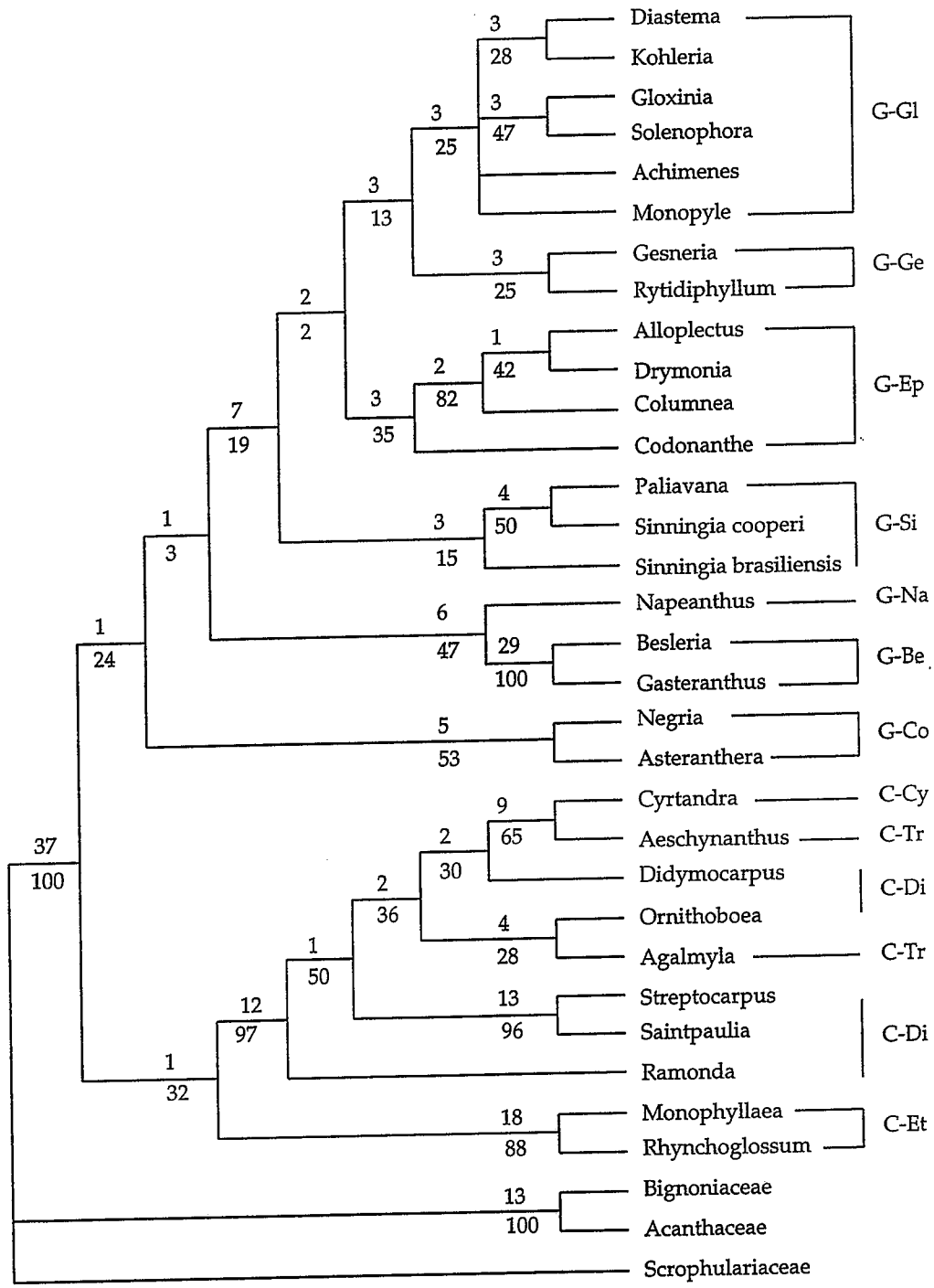

Fig. 7. Strict consensus of three most-parsimonious trees from combined morphological, *rbc*L and *ndh*F data sets (CI = 0.36, RI = 0.36). Values above branches indicate decay values, those below are bootstrap values. Nodes without bootstrap values were not present in the bootstrap consensus tree. Abbreviations for subfamilies and tribes follow Fig. 1.

Discussion

Each data set analyzed separately, in pairwise combination, and all data combined, resulted in strict consensus trees with only the monophyly of the tribe Beslerieae consistent among all analyses (Figs. 1–7). This initial lack of congruence may be misleading in implying that the data are in conflict with each other. The partition homogeneity test indicated a significant degree of incongruence at the $p = 0.05$ level when all three data sets were compared ($p = 0.008$). However, only *rbc*L and morphology were significantly incongruent when compared pairwise ($p = 0.002$) and both *rbc*L and morphology were not significantly incongruent to *ndh*F ($p = 0.183$ and 0.692, respectively). This mutual congruence with one data set implies that there may be congruent phylogenetic signal in all data sets, but noise overwhelms this signal in each data set singly.

Compared. Although arguments exist for combining data in a total evidence approach (Miyamoto 1981, Kluge 1989), the primary reason for not comparing data sets analyzed separately to determine sources of incongruency is detecting false positives if discrepancies are rare (Huelsenbeck et al. 1996). When each of the separate data sets is analyzed singly the results are poor resolution, and support is weak for the relationships found within the trees based on average bootstrap (16.1–22.7) and decay values (0.83–1.45). These values are low regardless of the source of data or number of characters (Table 2). Very few clades in the trees from the data sets analyzed separately have strong support, indicating that the majority of the topological discrepancies are due to soft incongruence (Seelanen et al. 1997).

In the *rbc*L data set, much of the resolution that is present is counter to previous classifications and analyses that comprise greater taxon sampling. Among these are the presence of *Codonanthe*, *Rytidophyllum*, and *Sinningia* in a single clade (Fig. 2). Although all of these genera are traditionally placed in the subfamily Gesnerioideae (Burtt and Wiehler 1995, Wiehler 1983, Ivanina 1965, Fritsch 1893–4, Smith et al. 1997a), they are generally regarded as being in three different tribes (Burtt and Wiehler 1995, Wiehler 1983) each of which has support from cladistic analyses of morphology and *ndh*F sequences with a greater taxon sampling than was used in this study (Smith 1996, Smith et al. 1997a). Likewise, the sister relationship of *Ramonda* (Cyrtandroideae: Didymocarpeae) and *Negria* (Gesnerioideae: Coronanthereae) is highly unlikely on the basis of their traditional placement in separate, well-supported subfamilies (Wiehler 1983, Burtt and Wiehler 1995, Smith 1996, Smith et al. 1997a). However, neither of these clades is strongly supported with only 27 and 14% bootstrap support, respectively. The low level of support for these clades from the *rbc*L data implies that there is low phylogenetic signal for these clades in the *rbc*L data set (soft incongruence: Seelanen et al. 1997).

By restricting comparisons of clades that have 50% bootstrap support or greater, a similarity between the *ndh*F trees and the trees from the other two data sets begins to become apparent. For example *Streptocarpus* and *Saintpaulia* are both sister genera in the *ndh*F and *rbc*L analyses with 58 and 97% bootstrap support respectively (Figs. 2 and 3). Although these genera are not supported as a monophyletic clade in the morphological analysis, their position in the morphology trees is not strongly supported with either bootstrap or decay values (Fig. 1). Likewise the monophyly of *Monophyllaea* and *Rhynchoglossum* is supported with 50% bootstrap value with *ndh*F (Fig. 3), and 42% with *rbc*L (Fig. 2). Although they are not monophyletic, the same two genera are unresolved as sisters to the remainder of the Gesneriaceae in the morphological analysis (Fig. 1). Very few clades within the morphological analysis have support greater than 50%, but one of these, the clade that contains Beslerieae and Episcieae (Fig. 1) is at least partially similar to the *Alloplectus, Drymonia, Columnea* clade found in the *ndh*F trees (Fig. 3) although the latter lacks Beslerieae and *Codonanthe*.

In contrast some true discrepancies (hard incongruence: Seelanen et al. 1997) seem to be apparent among the different topologies. For instance, the tribe Trichosporeae (represented by *Aeschynanthus* and *Agalmyla*) is the most strongly supported clade in the morphology trees with a bootstrap value of 88% (Fig. 1). In the *ndh*F trees, *Aeschynanthus* and *Cyrtandra* are sister with a 57% bootstrap value and *Agalmyla* is sister to *Streptocarpus*/*Saintpaulia* with a 49% bootstrap value (Fig. 3). Likewise differences exist between the *ndh*F and *rbc*L data sets. *Achimenes* and *Monopyle* are sister to each other with 62% bootstrap and decay of 3 with *rbc*L (Fig. 2), yet *Achimenes* is sister to *Kohleria* with a bootstrap of 52% and decay of 3 with *ndh*F (Fig. 3).

Other clades with greater than 50% bootstrap value in any of the trees from the data sets analyzed separately that are discrepant in trees from a different data set have only weak, or no support (Figs. 1–3). Thus, although some discrepancies do seem apparent, the majority are most likely due to a lack of resolution among the data than to any true discrepancy between data sets themselves.

Conflict. The most likely explanation for the discrepancy among the topologies produced from each of the data sets is differential rates of evolution. The *rbc*L sequences traditionally are viewed as highly conserved and substitutions have a high rate of incidence at third position codons. In their study of Polemoniaceae, Steele and Vilgalys (1994) found most variation in *rbc*L at third position codons. In a comparison of tobacco and rice *rbc*L genes, 79% of the differences are at third position codons (Wendel and Doyle 1998). Thus multiple substitutions are more likely in the *rbc*L gene and potentially much of the variation found at the level of analysis in this study could be homoplasy. Sequences from *rbc*L previously have been cited as producing excessive noise such that inter-familial relationships among the Zingiberales were not well-resolved although the monophyly of each of the families was comparatively well-supported (Smith et al. 1993). This gene also has resulted in only poor resolution among genera in more recently evolved orders and subclasses of plants such as the Lamiales to which the Gesneriaceae belongs (Olmstead et al. 1993). Therefore it is not surprising to find poor resolution of relationships within the Gesneriaceae using the *rbc*L sequences, nor to find the resolution that exists to be in conflict with morphological data, especially since most of the conflict is between clades that are only weakly supported. It is likely that the noise in the *rbc*L data also is preventing resolution of relationships among the Gesneriaceae in this data set and is the source of discrepancy, especially between the two molecular data sets.

The characters selected for the morphological data set reflected evolution at the generic, tribal, and subfamilial level within the Gesneriaceae (Smith 1996). Numerous characters were excluded from the analysis that did not fit the appropriate level of analysis for the tribes of the Gesneriaceae; these characters were either too conserved or too variable within a particular genus (Smith 1996). The incongruency between morphology and *rbc*L sequences is likely a reflection on the rate of evolution of the two types of characters and the low ratio of phylogenetic signal to homoplasy present in the *rbc*L data.

An additional source of inter-data set conflict that is frequently cited is a single or few discrepant taxa (Poe 1996, Mason-Gamer and Kellogg 1996). Rodrigo et al. (1993) recommended pruning potentially problematic taxa (those that caused discrepancies between data sets) from the data and re-analyzing to determine if congruence was met. This method has proven to be effective in several instances (Poe 1996, Mason-Gamer and Kellogg 1996) however requires that problematic taxa can be readily identified. Although the placement of one or few taxa can greatly disrupt phylogenetic relationships in some cases, this does not appear to be the case in the present study since the only level of congruence among all data sets is the single tribe Beslerieae and the position of all other genera are in conflict, unresolved, or in weakly supported clades

among the three data sets analyzed independently. Trying to identify one or a few of these genera as problematic would require either random guessing, or systematic removal of all individual and combinations of taxa, a task that is overwhelming and potentially futile.

Consensus. Consensus methods provide a means of comparing data directly across several independent analyses, but are frequently inadequate to resolve relationships (Barrett et al. 1991, Smith and Sytsma 1994c). Consensus methods for the data sets in this study have likewise proven to be inadequate. Both strict (Nelson 1979) and semi-strict (Bremer 1990) result in trees that are completely unresolved with the exception of the monophyly of the tribe Beslerieae. Adams consensus (Adams 1972) provides some resolution among the different clades although some of the more unusual relationships seen from the *rbc*L data set are retained. The absence of the more widely accepted relationships of these taxa, which are seen in the morphology and *ndh*F data sets analyzed separately in previous studies (Smith 1996, Smith et al. 1997a) implies that they are only weakly supported with these data sets and the strength of the unusual relationships with *rbc*L is transmitted in the consensus tree. With such low levels of resolution or unacceptable resolution, none of these consensus methods are adequate to find congruent phylogenetic signal among these three data sets.

Congruence. The partition homogeneity test implies that both morphology and *rbc*L sequences are congruent with the *ndh*F sequences and that morphology and *rbc*L sequences are incongruent with each other. The partition homogeneity test indicated significant incongruency when all three data sets were examined together ($p = 0.008$), but incongruency was only significant between morphology and *rbc*L when compared pairwise ($p = 0.002$).

A common explanation for incongruency when using cpDNA is hybridization and chloroplast capture (Soltis et al. 1991, Rieseberg and Brunsfeld 1992). While these processes are often satisfactory to explain unusual and discrepant relationships in phylogenies, they are less justified in this case. For one, the level of analysis is tribal and in order for chloroplast capture to have occurred, it would imply an event in the long past for these organisms. This can not be eliminated simply at face value, but the discrepancies seen between the *rbc*L trees and the morphological trees are between different subfamilies which are distributed in either the Old or New World tropics. In order for chloroplast capture to explain these anomalies an early hybridization event would be necessary and would be expected to have an effect on a greater portion of the taxa than these results have.

A more convincing argument against chloroplast capture is the fact that *ndh*F is another cpDNA gene and the *ndh*F sequences are apparently congruent to both *rbc*L sequences and morphology ($p = 0.183$ and 0.692, respectively). If chloroplast capture had occurred, both would be incongruent with the morphological data. It is clear by a reconnaissance of the strict consensus trees from these data sets that they do not result in the same phylogenetic relationships (Figs. 2 and 3). Thus the discrepancy between morphology and *rbc*L must be from another source such as differential rates of evolution discussed above.

The congruence between the morphological and *ndh*F data, as well as between the sequences of the two genes implies that there is some degree of phylogenetic signal common to all three data sets. This signal is either obscured or lost in each data set independently because of high levels of noise in each data set. This is particularly true for the *rbc*L data. Since *rbc*L sequences are more conserved than *ndh*F (Olmstead and Sweere 1994) and the characters selected for the morphological data (Smith 1996), there are likely to be fewer phylogenetically informative characters in the *rbc*L data. However, the level of noise may be high enough to obscure the signal due to multiple substitutions at third position sites. If a signal is common to all data sets, the combination of the data should cause this signal to emerge since

it will be additive in its support, but the random noise will persist in being random and have no greater effect on the combined data than on each of the data sets analyzed separately.

Combined. The pairwise combined data sets generally result in trees with greater resolution and the resolved clades are more strongly supported on the basis of average bootstrap and decay values (Table 2). Despite the fact that morphological and *rbc*L data were found to be incongruent ($p = 0.002$), the combination of these two data sets results in a tree that is more resolved than either of the two molecular data sets analyzed singly (17 vs. 13 nodes; Table 2) and has a higher average bootstrap value (26.6) and a higher average decay value (1.59) than that for either of these data sets analyzed singly (Table 2). In addition, many of the nonsensical relationships that were seen with some of the data sets analyzed separately (*rbc*L) are no longer present in the strict consensus of these trees (Fig. 4). These results imply that there is a phylogenetic signal common to all data sets, but that the noise is obscuring this signal when each data set is analyzed separately. In studies where the data were determined to be incongruent through various tests, combining data sets resulted in a drop, rather than increase in bootstrap values (Mason-Gamer and Kellogg 1996). When data are combined in the present study, the phylogenetic signal becomes strong enough to overwhelm the noise and a well-resolved, well-supported cladogram results (Fig. 7). Similar results have been seen with analyses of greater taxon sampling. In these examples the addition of data sets resulted in fewer trees with greater resolution, analyses that ran to completion, and in a shorter time than when each data set was analyzed separately (Chase et al. 1997; Soltis et al. 1997, 1998). Thus, total evidence produces a cladogram that can be viewed with greater confidence than any of the separate smaller data sets, implying that combining data is most likely to provide the best approximation of phylogenetic history (Lavin 1993; Kim and Jansen 1994; Smith and Sytsma 1994c; Brower et al. 1996; Poe 1996; Pennington 1996; Bremer 1996; Givnish and Sytsma 1997a, b; Munro and Linder 1998; Rodman et al. 1998; Seelanen et al. 1998; Soltis et al. 1998) unless a specific discrepancy can be identified (Mason-Gamer and Kellogg 1996, Lutzoni 1997, Graham et al. 1998, Wiens 1998).

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