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Tribal Relationships Within Gesneriaceae: a Cladistic Analysis of Morphological Data

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ABSTRACT. This paper investigates cladistic relationships among tribes of Gesneriaceae using morphological data. Forty-four characters were scored across 34 genera selected as exemplar taxa to represent current and previous classification systems. The analysis resulted in 4,840 most-parsimonious trees of 364 steps each. In all trees, Klugieae are identified as sister to the remainder of the family which consists of a paraphyletic Cyrtandroideae, and monophyletic Gesnerioideae. The placement of Coronanthereae in Cyrtandroideae is not supported by this analysis whereas its placement in Gesnerioideae or as a separate monophyletic subfamily is supported. Beyond these changes, current tribal classification systems for the family are largely congruent with the results of this analysis. Exceptions are that Gloxinieae were found to comprise two clades, and monophyly for Didymocarpeae was not supported. Earlier classification systems, besides current ones, are found to be highly inadequate to reflect cladistic relationships within the family.

Gesneriaceae are a family of approximately 2,500 to 3,500 species in 120 to 130 genera, distributed primarily in the tropics with a few temperate species in Europe and Japan (Heywood 1978; A. Weber, pers. comm.). The majority of species in Gesneriaceae are herbaceous perennials, but there are also annuals, shrubs, lianas, and trees. Many species (20%) are epiphytic, and Gesneriaceae ranks among the top ten plant families in terms of absolute numbers of epiphytic taxa (Madison 1977; Kress 1986). Given the diverse habits of Gesneriaceae, it is not surprising that there is a wide array of morphological variation within the family. Corolla tubes may be long and prominent as in *Columnnea*, or short as in *Saintpaulia*. Leaves are opposite in the majority of the family, but anisophylly, leading to an alternate arrangement when the smaller leaf abscises, is common. Many of the morphologically diverse features of Gesneriaceae have been hypothesized to be adaptations to the epiphytic habit (Givnish 1984; Ackerman 1986).

Gesneriaceae are a member of Lamiales s.l., a provisional name based on recent molecular investigations (Olmstead and Reeves 1995), and are distinguished from other families in the order by a combination of five-lobed corollas, parietal placentation, and presence of endosperm in most taxa (Cronquist 1981). However, because these characters vary within some Gesneriaceae, there has been considerable confusion regarding the placement of some genera. For example, members with axile placentation readily can be classified as Scrophulariaceae, and those genera lacking endosperm are potentially classified with Acanthaceae or Bignonia-

ceae. The lack of non-homoplastic synapomorphies for Gesneriaceae raises the question of monophyly. Recent investigations of related families in Lamiales s.l. have demonstrated monophyly (Acanthaceae: Scotland et al. 1995; Bignoniaceae: R. Olmstead, pers. comm.) as well as polyphyly (Scrophulariaceae: Olmstead and Reeves 1995). None of these studies sampled densely within Gesneriaceae and the question of monophyly therefore remains unanswered.

There have been relatively few cladistic analyses of Gesneriaceae (Kvist 1990; Crisci et al. 1991; Boggan 1991; Smith and Sytsma 1994a, b, c), and none have been at the tribal level. A cladistic analysis is desirable to resolve relationships and to improve classifications by circumscribing monophyletic tribes and subfamilies.

Most classifications of Gesneriaceae recognize two subfamilies (Gesnerioideae and Cyrtandroideae) (Bentham 1876; Fritsch 1893–1894; Burt 1962, 1977), but others have included an additional subfamily (Episcioideae, Ivanina 1965; Coronanthereoideae, Wiehler 1983). The division of the family is largely based on uniform (Gesnerioideae) or uneven (Cyrtandroideae) enlargement of cotyledons after germination (Burt 1962). Another character that has been useful in separating subfamilies is presence (Gesnerioideae) or absence (Cyrtandroideae) of endosperm in the seed. In addition, Gesnerioideae have a neotropical distribution and most species have inferior ovaries, whereas Cyrtandroideae are primarily paleotropical and have superior ovaries. However, geo-

TABLE 1. Genera of subfamily Gesnerioideae sensu Burtt and Wiehler (1995) included in this analysis and their classification at the subfamily and tribal level following Wiehler (1983), Ivanina (1965) and Fritsch (1893–1894). NT = not treated. Subfamilial names are italicized to distinguish them more readily from tribal names.

Genus	Wiehler	Ivanina	Fritsch
	<i>Gesnerioideae</i>	<i>Gesnerioideae</i>	<i>Gesnerioideae</i>
<i>Achimenes</i> Pers.	Gloxinieae	Gloxinieae	Gloxinieae
<i>Gloxinia</i> Regel	Gloxinieae	Gloxinieae	Gloxinieae
<i>Monophyle</i> Moritz ex Benth.	Gloxinieae	Gloxinieae	Bellonieae
<i>Kohleria</i> Regel	Gloxinieae	Kohlerieae	Kohlerieae
<i>Diastema</i> Benth.	Gloxinieae	Kohlerieae	Kohlerieae
<i>Sinningia</i> Nees	Gloxinieae	Kohlerieae	Sinningieae
<i>Paliavana</i> Vand.	Gloxinieae	Rechsteinerieae	Sinningieae
<i>Lietzia</i> Regel	Gloxinieae	Rechsteinerieae	Sinningieae
<i>Solenophora</i> Benth.	Gloxinieae	Solenophoreae	Solenophoreae
<i>Gesneria</i> L.	Gesnerieae	Gesnerieae	Gesnerieae
<i>Rytidophyllum</i> Mart.	= <i>Gesneria</i>	Gesnerieae	Gesnerieae
		<i>Episcioideae</i>	<i>Cyrtandroideae</i>
<i>Columnea</i> L.	Episcieae	Columnneae	Columnneae-Columnneae
<i>Codonanthe</i> (Mart.) Hanst.	Episcieae	Columnneae	Columnneae-Codonantheae
<i>Alloplectus</i> Mart.	Episcieae	Episcieae	Columnneae-Columnneae
<i>Drymonia</i> Mart.	Episcieae	Episcieae	Columnneae-Columnneae
<i>Besleria</i> L.	Beslerieae	Episcieae	Beslerieae
<i>Gasteranthus</i> Benth.	Beslerieae	NT	NT
<i>Anetanthus</i> Hiern. ex Benth.	Beslerieae	NT	Anetantheae
<i>Napeanthus</i> G. Gardner	Napeantheae	Episcieae	Klugieae
	<i>Coronantheroideae</i>	<i>Cyrtandroideae</i>	
<i>Asteranthera</i> Kl. ex Hanst.	Coronanthereae	Mitrarieae	Mitrarieae
<i>Rhabdothamnus</i> Cunn.	Coronanthereae	Coronanthereae	Coronanthereae

graphic distribution and ovary position are polymorphic within subfamilies.

The two subfamilies have been further divided into 9–17 tribes (Bentham 1876; Fritsch 1893–1894; Burtt 1962, 1977; Ivanina 1965; Wiehler 1983; Burtt and Wiehler 1995). The classification schemes differ due to the characters emphasized. This paper presents a cladistic analysis based on numerous morphological characters considered in concert rather than singly, such that phylogenetic relationships among taxa may be more clearly resolved and a more stable classification scheme proposed. This is the first study to examine the family as a whole since Ivanina (1965), and the first since Fritsch (1893–1894) to examine the family using more than a single structure.

METHODS

Choice of Taxa. Genera have been selected to represent most recent classifications (Tables 1 and 2). Thirty-four genera, two to ten per tribe, were selected using three criteria: 1) genera that were well studied morphologically were selected to minimize missing data; 2) genera were selected to

represent previously and currently recognized tribes such that these earlier hypotheses could be evaluated, and 3) genera that were readily available in cultivation were selected. In the majority of cases it was possible to select genera that met all three criteria. The genera selected comprise 23 to 28% of the genera in the family.

For genera used in this analysis, I assumed monophyly and scored each genus for the full range of character states present among species (see polymorphic characters below). The absence of cladistic analyses at the genus level makes it impossible to identify less inclusive (and thus less polymorphic) monophyletic groups within each genus. I also decided that the range of character states for some genera was too broad to use a single exemplar species. Although sampling one species per genus would have greatly reduced polymorphism in the data set, haphazard sampling may have resulted in errors in the analysis. Because the focus of this study was to identify monophyletic tribes and discover their inter-relationships, potential paraphyly or polyphyly of genera should not impact the analysis although relationships within tribes may not be meaningful.

TABLE 2. Genera of subfamily Cyrtandroideae sensu Burt and Wiehler (1995) included in this analysis and their classification at the subfamily and tribal level following Burt (1962, 1977), Ivanina (1965) and Fritsch (1893-1894).

Genus	Burt	Ivanina	Fritsch
<i>Ramonda</i> L. C. Richard	Didymocarpeae	Ramondeae	Ramondeae
<i>Saintpaulia</i> Wendl.	Didymocarpeae	Saintpaulieae	Ramondeae
<i>Conandron</i> Sieb. & Zucc.	Didymocarpeae	Didymocarpeae-Conandrinae	Didymocarpeae-Conandrinae
<i>Championia</i> C. B. Clarke	Didymocarpeae	Didymocarpeae-Leptoboieinae	Championieae
<i>Oreocharis</i> Benth.	Didymocarpeae	Didymocarpeae-Roettlerinae	Didymocarpeae-Oreocharinae
<i>Didymocarpus</i> Wallich	Didymocarpeae	Didymocarpeae-Roettlerinae	Didymocarpeae-Roettlerinae
<i>Streptocarpus</i> Lindley	Didymocarpeae	Didymocarpeae-Streptocarpinae	Streptocarpeae
<i>Ornithobea</i> Parish ex C. B. Clarke	Didymocarpeae	Didymocarpeae-Streptocarpinae	Streptocarpeae
<i>Aeschynanthus</i> Jack	Trichosporeae	Trichosporeae	Trichosporeae
<i>Agalmyla</i> Blume	Trichosporeae	Trichosporeae	Trichosporeae
<i>Cyrtandra</i> Forster & Forster	Cyrtandreae	Cyrtandreae	Cyrtandreae
<i>Rhynchoglossum</i> Blume	Klugieae	Klugieae	Klugieae
<i>Monophyllaea</i> Endlicher	Klugieae	Klugieae	Beslerieae

For one genus, *Sinningia*, it was possible to identify a less inclusive monophyletic clade based on a previous cladistic analysis (Boggan 1991). Section *Corytholoma* Benth. includes the genus *Lietzia* [recently combined into *Sinningia* (Wiehler and Chautems 1995)] and sect. *Corytholoma* was either sister to the remainder of *Sinningia* or sister to a clade that contained *Vanhouttea* Lemaire, *Paliavana*, and section *Sinningia* (Boggan 1991). Because sect. *Corytholoma* could potentially be the sister to the remainder of *Sinningia*, and was closely related to another genus included in this analysis (*Paliavana*), it was selected to represent *Sinningia*.

Outgroup Selection. A cladogram of tribes within Gesneriaceae must be rooted by determining primitive character states within the family. The best method for doing this is outgroup comparison (Donoghue and Cantino 1984; Maddison et al. 1984). Because relationships of families in Lamiales s.l. are not yet well-established, three families from Lamiales s.l. were used as outgroups: Acanthaceae, Bignoniaceae, and Scrophulariaceae. These were selected because data are available for 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). Each family was scored as a composite taxon, using data available for as many taxa as possible. Every attempt was made to use all available data to describe fully variation within outgroup families. Limited data for some characters precludes comprehensive treatment. Further, although recent molecular studies have demonstrated that Scrophulariaceae are a polyphyletic group, comprised of at least three

distinct lineages (Olmstead and Reeves 1995), the family in this study is scored as monophyletic. Although a better choice may be to select one clade, or use all three independently, data are not presently available for all of the characters used in this analysis. It should be noted that this study in no way attempts to determine relationships among families of Lamiales s. l.; these outgroup taxa are included to root cladograms from the analysis, not to estimate relationships of Gesneriaceae to other families.

Characters. The majority of characters and character states for this analysis came from the literature. Because many investigations of morphology in Gesneriaceae are preliminary or are yet-to-be-published, I am deeply indebted to those individuals who examined the data set and provided me with up-to-date or corrected information (see acknowledgments). Seventy-two characters were investigated and 44 of these were used in this analysis. Potentially useful characters had to be discarded because data were available for only a few genera. Arbitrarily, I used only characters for which 90% of the sampled taxa could be scored. Four exceptions were made to this rule; these are cotyledon expansion, endosperm, pollen size, and pollen shape. These four characters have been used to separate the two subfamilies of Gesneriaceae (Burt 1962; Luegmayer 1993), but have not been investigated thoroughly for all genera. In order to determine the effect of missing data on the results of this analysis, each of these four characters was eliminated separately, and in all possible combinations (Davis et al. 1993). The data matrix, including these four characters, includes 5% missing data.

Characters used in this analysis are described below. Many of the characters are readily coded as binary. However, patterns of morphological variation found in terminal taxa necessitate the use of some multi-state characters. This has worked successfully to provide resolution in previous analyses within Gesneriaceae (Smith and Sytsma 1994b), and with other groups and taxonomic levels (Rodman 1991; Sanderson 1991; Hufford and Dickson 1992; Hoot et al. 1994; Potter and Doyle 1994; Rothwell and Serbet 1994; Weller et al. 1995). Characters that were excessively polymorphic (arbitrarily designated as over 75% of the taxa) were excluded from the analysis.

Weighting and ordering of morphological characters is a topic of debate (Neff 1986; Wheeler 1986, 1990; Mickevich and Weller 1990; Mickevich and Lipscomb 1991; Barriel and Tassy 1993; Scotland and Williams 1993). I treated all characters as unordered because there is insufficient basis for ordering schemes. Weighting characters in a cladistic analysis requires a biological explanation. No such justification was possible in this analysis, so all characters were weighted equally.

Scoring of the following characters involved an extensive survey of the literature on Gesneriaceae as well as unpublished data (see acknowledgments). Some of the literature surveyed was comparative (e.g., seed characters, Beaufort-Murphy 1983) and these synoptic works are cited with the relevant character. Information regarding characters provided in treatments of taxa at various levels was taken from the taxonomic literature as follows: the family as a whole (Bentham 1876; Fritsch 1893-1894; Burt 1970), Cyrtandroideae (Burt 1962, 1971, 1977; Wang et al. 1992), Gesnerioideae (Skog 1978; Wiehler 1983), Coronanthereae (Allan 1961), Trichosporeae (Rosser and Burt 1969), *Anetanthus* (Howard 1975; Skog 1982), *Besleria* (Morton 1939), *Codonanthe* (Moore 1973), *Columnea* (Smith 1991, 1994; Kvist and Skog 1993), *Cyrtandra* (Burt 1990; Wagner et al. 1990), *Didissandra* C. B. Clarke (Burt 1976; Kiew and Weber 1988), *Didymocarpus* (Kiew and Weber 1988), *Gesneria* (Skog 1976), *Lietzia* (Boggan 1991; Wiehler and Chautems 1995), *Monophyllaea* (Burt 1978), *Oreocharis* (Burt 1956), *Ornithoboea* (Burt 1958a), *Paliavana* (Boggan 1991), *Saintpaulia* (Burt 1958b, 1964), *Sinningia* (Boggan 1991; Chautems 1991, 1993), *Streptocarpus* (Hilliard and Burt 1971; Jong and Burt 1975). Data for outgroup taxa were obtained from Dahlgren (1975), Thorne (1976, 1983, 1992), Heywood (1978), Takhtajan (1980), and Cronquist (1981).

1. HABIT. The growth forms of Gesneriaceae include (0) terrestrial herb, (1) epiphytic herb, (2) shrub, (3) tree, or (4) vine.

2. STEM MODIFICATION. The stems of Gesneriaceae may be (0) not modified, or modified into a (1) scaly rhizome, (2) rhizome, or (3) tuber.

3. SECRETORY CANALS. Secretory canals in the stems were scored as (0) absent or (1) present (Metcalf and Chalk 1983).

4. MEDULLARY RAYS. Medullary rays in the stem were scored as (0) absent, (1) narrow, (2) broad (Metcalf and Chalk 1983).

5. FORKED HAIRS. Forked hairs on leaves were scored as (0) absent or (1) present.

6. LEAF TYPE. (0) simple or (1) compound.

7. LEAF POSITION. (0) cauline, (1) basal, or (2) absent (cotyledon becoming foliaceous).

8. LEAF SCLEREIDS. (0) absent or (1) present (Bokhari and Burt 1970).

9. STOMATA TYPE. Stomata on leaves were scored as (0) anisocytic, (1) anomocytic, (2) diacytic, (3) paracytic, or (4) helicocytic. Wiehler's (1983) treatment of neotropical Gesneriaceae was the primary source of data for this character and his illustrations and terminology were used to score taxa not included in his study. Supplemental information came from Herat and Theobald (1979) and generic descriptions.

10. INFLORESCENCE BRACTS. Bracts subtending the inflorescence were scored as (0) absent or (1) present.

11. PEDUNCLES. Inflorescences were scored as (0) epedunculate or (1) pedunculate.

12. COROLLA TUBE. (0) not ventricose or (1) ventricose.

13. COROLLA BASE. The base of the corolla was scored as (0) neither gibbous nor spurred or (1) gibbous or spurred. Various authors use the terms gibbous and spurred for a character state hypothesized to be homologous based on my examination of herbarium material.

14. COROLLA LIMB. (0) regular or (1) bilabiate.

15. FERTILE STAMEN NUMBER. Fertile stamens were scored as (0) five, (1) four, or (2) two. In this analysis, all genera with two fertile stamens retained the antero-lateral (distal) pair.

16. STAMEN LENGTH. Stamens were scored as (0) equal in length, or (1) didynamous. There is obviously some degree of correlation between this character and fertile stamen number (character 15) in that taxa with two fertile stamens are likely to have stamens equal in length. However, because only seven of the 34 taxa investigated in this study

have two fertile stamens, and only four have exclusively two fertile stamens, I decided that the utility of including this character outweighed the potential problems and scored taxa with two fertile stamens as equal in length.

17. STAMEN ATTACHMENT. The level of the corolla tube at which the stamens are attached is here treated as: (0) base, (1) middle, (2) above middle but in central third of corolla tube, (3) below mouth but in upper third of corolla tube, or (4) at mouth.

18. ANTHER SHAPE. Anthers were described as (0) oblong, (1) quadrate, (2) orbicular, (3) sagittate, (4) reniform, or (5) *Didymocarpus*-like (i.e., with widely divergent thecae and a thickened connective; illustrated in Burt 1971).

19. ANTHER COHERENCE. (0) free or (1) coherent.

20. ANTHER DEHISCENCE. Anthers were scored as dehiscing (0) longitudinally or (1) by apical pores.

21. POLLEN SHAPE. (0) prolate, (1) prolate-spheroidal, (2) oblate-spheroidal, (3) oblate, or (4) spheroidal (Williams 1978; Argue 1986; Fritze and Williams 1988; Bove 1993; Luegmayer 1993; Scotland 1993). All authors of pollen studies cited here used Erdtman (1969) for pollen shape terminology.

22. POLLEN SIZE. Pollen was categorized as (0) small, 9 to 24 μm in diameter or (1) large, 26 to 51 μm in diameter (Williams 1978; Argue 1986; Fritze and Williams 1988; Bove 1993; Luegmayer 1993; Scotland 1993). Although this character is clearly a quantitative trait, the only distinct gap between sizes is as recognized above.

23. NECTARY TYPE. The various nectary types within the family were divided into the following character states: (0) absent, (1) unlobed, unthickened ring, (2) ring thickened dorsally, (3) dorsal lobes only, (4) lobed ring, or (5) five lobed. The primary source of data for this character was Wiehler (1983). Supplemental data for the Cyrtandroideae came from generic descriptions.

24. NECTARY FUSION. The nectary was scored as (0) free from the ovary wall or (1) fused to the ovary wall (Wiehler 1983).

25. OVARY POSITION. Ovaries were scored as (0) superior, (1) semi-inferior or (2) inferior.

26. STYLE. The style may (0) taper gradually from the ovary or (1) narrow abruptly immediately above the ovary.

27. CARPEL STRUCTURE. Carpels were scored as (0) paracarpous, (1) hemiparacarpous, or (2) syncarpous (Ivanina 1965).

28. PLACENTA. The placenta was scored as (0) undivided or (1) divided at base.

29. OVULE ATTACHMENT. Ovules are attached to (0) outer surface of the placenta (facing the wall of the fruit), (1) both outer and inner (facing the medial line of the fruit) surfaces, or (2) tips (Ivanina 1965).

30. FRUIT TYPE. (0) dry or (1) fleshy.

31. FRUIT DEHISCENCE. Because Gesneriaceae have several genera with fleshy dehiscent fruit, this character is independent of the previous one. Fruits were scored as (0) indehiscent, (1) loculicidally dehiscent, (2) septicidally dehiscent, (3) irregularly dehiscent.

32. VALVE SHAPE. The fruit valves were scored as (0) straight or (1) twisted.

33. ENDOSPERM. (0) absent or (1) present.

Characters 34, and 36 to 43 are from the survey of seed surface characters presented by Beaufort-Murphy (1983).

34. SEED SHAPE. For the genera used in this analysis, seeds can be grouped as three different shapes: (0) elliptic, (1) circular, or (2) reniform. In her study, Beaufort-Murphy (1983) utilized only the two-dimensional aspect of the seeds and did not consider their three-dimensional shape.

35. SEED APPENDAGE. Appendages attached to the seeds were either (0) absent or (1) present as hairs or a hair-like process at each end (Burt 1962). This character differs from number 36 in the distinct type and position of the appendage.

36. SEED SURFACE MODIFICATION. Several Gesneriaceae possess variously modified seeds and are scored here as: (0) no modification, (1) carinate, or (2) alate.

37. SEED TIP. The chalazal or basal tip of the seed can be described as (0) acute, (1) arillate, (2) coronate/filiform, (3) obtuse, or (4) truncate/premorse.

38. CELLS OF THE SEED COAT: ORIENTATION. Orientation describes the arrangement of the cells in relation to each other and to the central long axis of the seed. The cells of the seed coat are oriented (0) in straight rows, (1) in spiral rows, or (2) irregularly.

39. CELLS OF THE SEED COAT: SHAPE. The cells of the seed coat are (0) polygonate, (1) lobed/parted, or (2) irregular in shape.

40. CELLS OF THE SEED COAT: ANTICLINAL WALLS.

The anticlinal walls of cells ("edges" in Beaufort-Murphy 1983) of the seed coats can be described as (0) elevated, (1) depressed, or (2) irregular.

41. CELLS OF THE SEED COAT: FUSION. The anticlinal walls of adjacent cells of the seed coat can be (0) discrete, (1) fused, or (2) composite (both discrete

and fused sections). Beaufort-Murphy (1983) refers to this character as the "crest".

42. CELLS OF THE SEED COAT: PERICLINAL WALLS.

The periclinal walls ("face" in Beaufort-Murphy 1983) of the cells of the seed coat can be described as (0) elevated or (1) depressed.

43. CELLS OF THE SEED COAT: ANTICLINAL WALLS, ULTRASTRUCTURAL CHARACTERS. The anticlinal walls of the cells of the seed coat (character 40) are ornamented. These ornamentations are described as (0) papillate, (1) auriculate, (2) undulate, (3) verrucate, (4) striate, (5) rough, or (6) smooth.

44. COTYLEDON EXPANSION. Most information for this character came from Hill (1938), Burt (1962) and Haines and Lye (1979). However, data have been supplemented with unpublished observations (J. Smith, pers. obs.) of seed germination as well as species descriptions in the generic treatments listed above. The character was scored as (0) equal enlargement or (1) unequal enlargement.

Polymorphic Characters. Thirty-three of the 44 characters were polymorphic for at least one taxon (including outgroups). Such characters are frequently omitted from cladistic analyses. In this analysis any character was eliminated for which 75% of the taxa were scored as polymorphic. Recent empirical investigations of polymorphic characters in phylogenetic analyses indicate that, contrary to common opinion, polymorphic characters can provide phylogenetic signal (Wiens 1995). Wiens' (1995) general conclusion was that scoring polymorphic characters based on the frequency of each state within a taxon was most likely to yield the best overall result. Polymorphic characters were not scored as frequency data for Gesneriaceae because data are missing for numerous species. Wiens (1995) also concluded that scoring characters as simply polymorphic resulted in the least resolution, but did not conflict with any of the other analyses. Therefore, based on the available information and the apparently conservative results, I selected the latter method for this analysis.

Characters Excluded from this Analysis. Numerous potentially useful characters had to be excluded from this analysis. For many, data were missing for many or most of the genera selected for investigation [e. g., petiole anatomy, nodal anatomy, stomatal distribution (Wiehler 1983), anthocyanins, flavones, chalcones, aurones (Harborne 1966, 1967)]. In other instances (dihydrophenolics), the genera used in this analysis are extremely polymorphic (Kvist and Pederson 1986). Lastly, chromosome number was excluded because the wide variation

within the family would require more than ten character states to score adequately ($n = 8-15, 17, 19, 21, 27, 30+$) (Rogers 1954; Eberle 1956; Fussell 1958; Lee 1962, 1964, 1966, 1967; Lee and Grear 1963; Ratter 1963, 1975; Ratter and Prentice 1964, 1967; Morley 1967, 1972; Davidse 1970, 1981; Wiehler 1983; Goldblatt 1984; Oliver and Skog 1984; Skog 1984).

Phylogenetic Analysis. Phylogenetic relationships were reconstructed using Swofford's (1993) computer program PAUP version 3.1.1 to implement parsimony (Farris 1970; Farris et al. 1970; Swofford and Maddison 1987). Trees were generated using the heuristic option, saving shortest trees only, with the "collapse zero-length branches," and "ignore uninformative characters" options in effect. The heuristic option is not guaranteed to find all shortest trees as it is sensitive to taxon order sequence. To search for multiple islands, the search strategy of Olmstead and Palmer (1994) was implemented: I searched for 1,000 trees each in five subsequent analyses with the NNI search option in effect and mulpars "off." The trees from each of these five analyses were used as the starting trees for searches with the TBR swapping option and mulpars "on." The same search strategy was used for the subsequent analyses to test the effect of removing characters.

Branch support (decay) was determined by examining trees that were one step longer than the most-parsimonious trees (Bremer 1988, 1994; Donoghue et al. 1992). Additional decay values were determined using the constraint option of PAUP to find the shortest trees that did not include the constrained grouping.

The cost (in terms of reduced parsimony) of forcing certain traditional taxonomic groups to be monophyletic was examined by using the constraints option of PAUP.

RESULTS

Of the 44 morphological characters used in this analysis, two were autapomorphic [leaf sclereids (8) and leaf type (6)] resulting in a minimum length of 86 steps. The cladistic analysis produced 4840 most-parsimonious trees of 364 steps each (C. I. = 0.44, R. I. = 0.62). One of the 4,840 trees was chosen arbitrarily and is shown in Fig. 1. Clades not present in the strict consensus of all trees are represented by dashed lines in Fig. 1.

The strict consensus of 4840 most-parsimonious trees is relatively well resolved, particularly within

Gesnerioideae (Fig. 1). The most notable lack of resolution lies within subfamily Cyrtandroideae. Only a few clades throughout the tree are strongly supported as indicated by the number of character state changes supporting the clade and decay values: Gesnerioideae including Coronanthereae, Episcieae/Beslerieae (excluding *Anetanthus*), *Lietzia* and *Achimenes*, *Ramonda/Championia/Conandron*, and Trichosporeae.

Monophyly of Gesnerioideae (including Coronanthereae) is based on cotyledon expansion (44), endosperm (33), pollen size (22) and pollen shape (21). An additional character, orientation of the cells of the seed coat (38), also supports this group but is homoplastic in *Conandron* (Cyrtandroideae) which also has cells in spiral rows. Nonetheless, this one character (38) was sufficient to define the monophyly of Gesnerioideae even when three of the other characters were excluded from the analysis, the one exception being cotyledon expansion (44) which, when removed from the analysis, resulted in a non-monophyletic Gesnerioideae.

Cyrtandroideae are not monophyletic in this analysis. When members of Cyrtandroideae were constrained to be monophyletic, the results were several trees requiring one more step than the most-parsimonious trees (Table 3). With this constraint in place there is little resolution in a strict consensus of all trees. The only resolved clades are Coronanthereae and Episcieae/Beslerieae (excluding *Anetanthus*) (tree not shown). Because Cyrtandroideae is monophyletic in trees only one step longer than the most parsimonious, it is possible that this subfamily is a monophyletic group and that additional characters may provide support for both a monophyletic Gesnerioideae and Cyrtandroideae.

Alternatively, it is possible that some members of Cyrtandroideae may best be removed from this subfamily (e.g., Klugieae). Constraining Cyrtandroideae (excluding Klugieae) to monophyly requires no additional steps. This indicates that at least one of the 4,840 most-parsimonious trees has a monophyletic Cyrtandroideae excluding Klugieae.

The sequential removal (Davis et al. 1993) of endosperm (33), pollen size (22) and pollen shape (21), independently and in combination, resulted in no changes at the subfamilial level. However, when cotyledon expansion (44) was removed from the analysis, support for a monophyletic Gesnerioideae was lost.

Enforced monophyly of tribes that were not monophyletic in the original analysis resulted in trees that were one to three steps longer than the

most-parsimonious trees (Table 3). Only the enforced monophyly of Klugieae, and Cyrtandroideae excluding Klugieae required no additional steps beyond the most-parsimonious trees; at least one of the shortest trees showed these relationships.

DISCUSSION

Despite the weak support for many of the clades in this analysis, the resulting cladograms provide an initial framework for further cladistic investigations within the family and highlight areas of morphological research needing further investigation. Additionally, when some characters not used in this analysis are mapped onto these trees, some of the clades can be viewed with more confidence.

The monophyly of Gesneriaceae was assumed in this analysis; further investigations utilizing a broader spectrum of outgroup taxa, including the several clades identified within Scrophulariaceae (Olmstead and Reeves 1995), will be necessary to demonstrate that the family is monophyletic. Gesneriaceae have been investigated with molecular techniques, and a broader sampling of outgroup taxa confirms its monophyly (Smith et al. 1997).

Subfamilial Groupings. The separation of Gesneriaceae into two subfamilies (including Coronanthereae in Gesnerioideae) has become well accepted since the discovery of unequal cotyledon enlargement in Cyrtandroideae (versus equal in Gesnerioideae) (Burt 1962). This character is problematic in that it has not been examined for all members of Gesneriaceae, including many taxa used in this analysis. The elimination of this character resulted in loss of resolution of the subfamilies and of several additional clades (marked in Fig. 1) in a strict consensus of the 11,060 trees produced. Additional studies may indicate that anisocotyly is a synapomorphy for a monophyletic Cyrtandroideae. Although anisocotyly is confined to members of Cyrtandroideae in Gesneriaceae it has been identified in eight angiosperm families including such diverse groups as Piperaceae, Primulaceae, Nyctaginaceae, and Apiaceae (Hill 1938; Haines and Lye 1979).

In contrast to the impact of excluding character 44, removal of other characters for which there were many missing data [endosperm (33), pollen size (22), and pollen shape (21)] did not change the monophyletic status of Gesnerioideae. This is undoubtedly due to the lower incidence of missing data for cotyledon expansion (30%) compared to endosperm and pollen shape (49% missing data), and pollen size (57%). Endosperm (33) and pollen

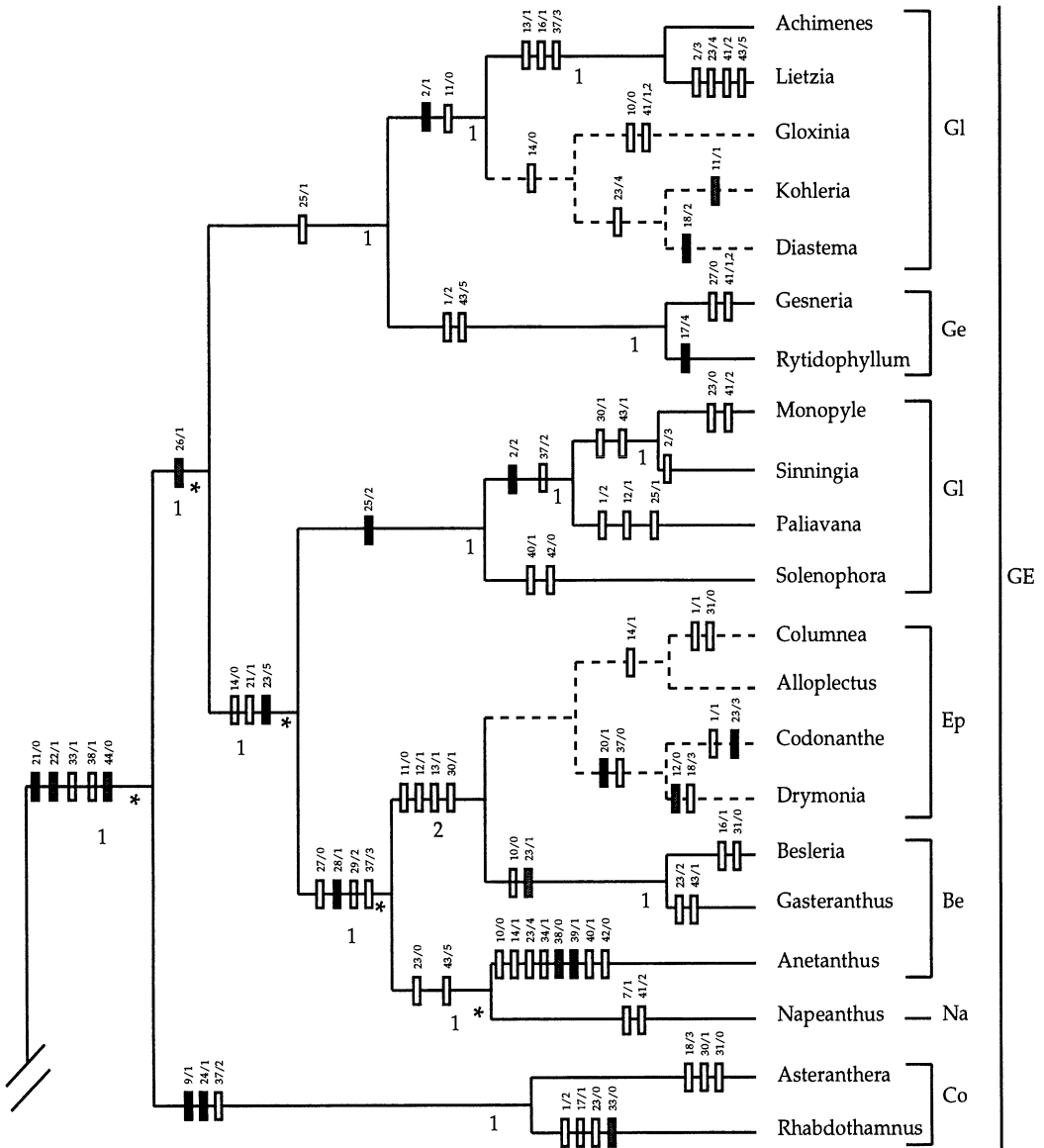
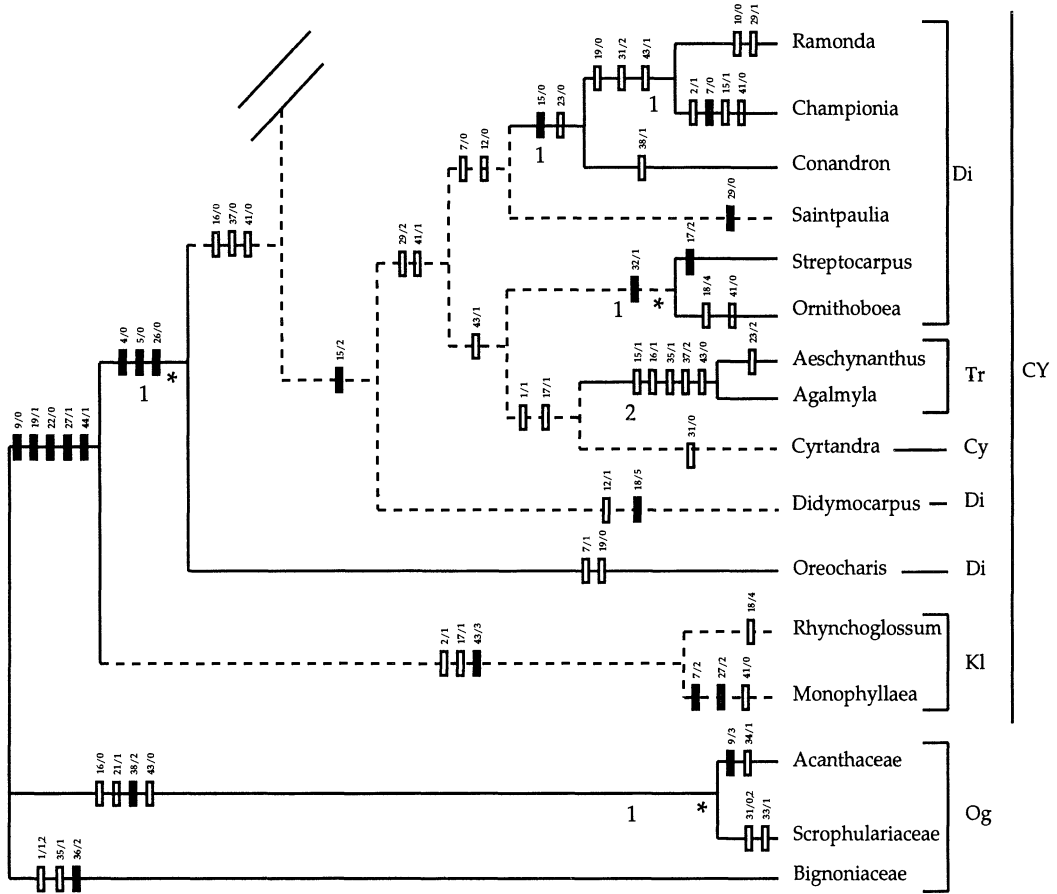


FIG. 1. One of the 4,840 most-parsimonious trees of 364 steps each. 1a shows Gesnerioideae, 1b Gesneriaceae and outgroups less Gesnerioideae. Character state changes are marked and numbered individually as in the text; numbers after the slash are character states. Black boxes indicate unique changes, white boxes are parallel changes, and gray boxes are reversals. Character transitions were plotted using the acctran option. Dashed lines indicate branches that are not found in the strict consensus of all 4,840 trees. Numbers below the clade are decay values (DI). Clades with no values have DI of 1. The tribes and subfamilies are abbreviated as follows: CY = Cyrtandroideae, GE = Gesnerioideae, Be = Beslerieae, Co = Coronanthereae, Cy = Cyrtandreae, Di = Didymocarpeae, Ep = Episcieae, Ge = Gesnerieae, Gl = Gloxinieae, Kl = Klugieae, Na = Napeantheae, Og = Outgroups, Tr = Trichosporeae. Asterisks denote clades that collapse in the strict consensus of trees when cotyledon expansion (44) is removed from the analysis (see text).



size (22) are completely congruent with the strict consensus tree from this analysis (Fig. 1), suggesting that Gesnerioideae may be characterized by the presence of endosperm and large pollen, and

TABLE 3. Results of analyses constraining certain groups to be monophyletic. The number of additional steps is the difference between the length of the shortest trees and those in which the indicated group is constrained to be monophyletic. The indicated groups are sensu Burt and Wiehler (1995).

Group	Number of additional steps
Gloxinieae	1
Gloxinieae, including Gesnerieae	3
<i>Paliavana, Sinningia, Lietzia</i>	2
Beslerieae	2
Klugieae	0
Cyrtandroideae	1
Cyrtandroideae, excluding Klugieae	0

Cyrtandroideae by absence of endosperm and small pollen.

Comparison to Traditional Taxonomy.

GESNERIOIDEAE. The primary conflict between this analysis and the most recent classification (Burt and Wiehler 1995) is polyphyly of Gloxinieae. Only one additional step is necessary to make Gloxinieae a monophyletic group that excludes Gesnerieae (Table 3). A monophyletic Gloxinieae that includes Gesnerieae, however, requires three additional steps (Table 3) indicating that Gesnerieae probably should be retained as a tribe separate from Gloxinieae (Wiehler 1983; Burt and Wiehler 1995).

Another conflict with recent classification schemes is the presence of *Anetanthus* (Beslerieae) with Napeantheae. Its placement there is the result of two homoplastic synapomorphies, lack of a nectary (23) and rough anticlinal walls of the cells of the

seed coat (43) (Fig. 1). It is possible that because Napeantheae is represented by a single genus, long branch attraction (Felsenstein 1978) results in placement of *Anetanthus* with Napeantheae (note numerous autapomorphies on branch to *Anetanthus*, Fig. 1). Wiehler (1983) erected Napeantheae because he found that *Napeanthus* did not fit into previous classifications nor into any of his newly circumscribed tribes. *Napeanthus* was excluded from Gloxinieae by Wiehler (1983) based on absence of several characters such as an inferior ovary (25) and hemiparacarpous carpel (27) that characterize Gloxinieae. It is possible that some members of Beslerieae may be better placed in Napeantheae. Examination of recent collections of *Resia* H. E. Moore (Beslerieae), indicates that many diagnostic characters of Napeantheae such as lack of bracts (10) may be present in poorly-studied members of Beslerieae (Skog 1995; Skog and de Jesus 1996). Placement of *Anetanthus* in Napeantheae thus may not be anomalous. Further examination of other poorly understood members of Beslerieae may result in further realignment of these two tribes. A monophyletic Beslerieae requires two additional steps beyond the most-parsimonious trees (Table 3).

Among the recent classification schemes proposed for Gesnerioideae, Burt's and Wiehler's (1995) is closest to the results obtained in this study. Separation of Wiehler's (1983) Gloxinieae into Bellonieae, Kohlerieae, Rechsteinerieae, and Solenophoreae (Ivanina 1965) (Table 1) is not supported by this cladistic analysis. Likewise Fritsch's (1893–1894) recognition of Bellonieae, Sinningieae, and Solenophoreae all of which were consolidated into Gloxinieae by Wiehler (1983) (Table 1) is not supported (Fig. 1). Ivanina's (1965) elevation of Episcioideae into a separate subfamily is not supported, but the strict consensus tree (Fig. 1) does emphasize the relatedness of the tribes she included in her Episcioideae: Episcieae, Napeantheae, and Beslerieae. On the other hand, Fritsch's (1893–1894) placement of *Napeanthus* in Klugieae (Cyrtandroideae) (Table 1) is inappropriate.

Monophyly of a group including *Paliavana*, *Lietzia*, and *Sinningia* has been proposed by Boggan (1991) who suggested all were members of *Sinningia* based on a cladistic analysis of species of *Sinningia* and several related genera. A minimum of two additional steps is required to move *Lietzia* into a clade with *Sinningia* and *Paliavana* (Table 3). The discrepant position of *Lietzia* between this analysis (Fig. 1) and Boggan's (1991) is likely the result of

taxon sampling. Boggan (1991) did not include *Solenophora* or *Monopyle*, nor did he sample from *Achimenes*, the sister genus to *Lietzia* in this analysis (Fig. 1). However, he did include *Kohleria*, *Diastema* (both included in this analysis), *Parakohleria* H. Wiehler, *Pearcea* Regel, and *Vanhouttea* (not included in this analysis). It is possible that the inclusion of Boggan's (1991) taxa in this analysis may have resulted in a monophyletic *Sinningia*/*Paliavana*/*Lietzia* clade or that the inclusion of *Solenophora*, *Monopyle*, and *Achimenes* may have separated *Lietzia* from *Sinningia* and *Paliavana* in Boggan's (1991) analysis. Alternatively, dense sampling within *Sinningia* but not within *Paliavana* (Boggan 1991) may have created long branch attraction that resulted in the placement of *Paliavana* and *Lietzia* within *Sinningia* (Felsenstein 1978).

CYRTANDROIDEAE. Burt's (1962, 1977) and Burt and Wiehler's (1995) classification of Cyrtandroideae is closer to this cladistic analysis than previous classification schemes (Fritsch 1893–1894; Ivanina 1965). Trichosporeae are supported as a monophyletic clade by five characters: four fertile stamens (15), didynamous stamens (16), presence of seed appendages (35; unique within Gesneriaceae, but shared with Bignoniaceae), coronate/filiform seed apices (37), and papillate edges of the cells of the seed coat (43). Cyrtandreae are represented only by *Cyrtandra* and nothing can be said regarding the monophyly of this small tribe.

Klugieae are monophyletic in at least one of the 4,840 most-parsimonious trees (Fig. 1). The two genera are united by three synapomorphies: presence of secretory canals (3), stamens attached to the middle of the corolla (17), and verrucate anticlinal walls of the cells of the seed coat (43). The latter character is unique to Klugieae. The only genus outside Klugieae that was scored as having secretory canals (3) is *Championia* (Herat and Theobald 1979). If the secretory canals of Klugieae are not homologous with those of *Championia*, this character would provide a unique synapomorphy supporting the tribe. Therefore, Klugieae should be considered as a monophyletic group, and one that may be sister to the remainder of the family.

Didymocarpeae are a large heterogeneous tribe that includes the majority of genera in Cyrtandroideae. In this analysis, it is a paraphyletic assemblage that also includes Cyrtandreae and Trichosporeae (Fig. 1). However, because of the lack of resolution within Didymocarpeae, earlier classifications can not be dismissed (Table 2). Further morphological investigations are underway (B. L.

Burt, pers. comm.) and a cladistic analysis focused on this group will be valuable towards understanding its phylogenetic relationships.

CORONANTHEREAE. Coronanthereae have been considered a tribe of Gesnerioideae (Fritsch 1893–1894), a tribe of Cyrtandroideae (Ivanina 1965) and a separate subfamily, Coronantheroideae (Wiehler 1983) (Table 1). These taxa, distributed in the south Pacific and southern South America, are supported by two non-homoplastic character transitions (Fig. 1). Monophyly of the group is supported by one of the few non-homoplastic, non-polymorphic character transitions in this analysis, fusion of the nectary to the ovary wall (24) (Fig. 1). Whereas the monophyly of Coronanthereae is well supported by this analysis, its status could potentially be congruent with any of the previous classifications (Fritsch 1893–1894; Ivanina 1965; Wiehler 1983) although placement in Cyrtandroideae would render this subfamily paraphyletic.

Distribution of Excluded Characters.

CHROMOSOME NUMBERS. Chromosome numbers were excluded from the analysis because of the numerous character states necessary to code them. High numbers of chromosomes ($x = 30+$) are unique to Coronanthereae and would serve as an additional character for the monophyly of this tribe. $x = 14$ characterizes Gesnerieae and, if chromosome numbers were included in the analysis, may have removed Gesnerieae from Gloxinieae (see above). Homoplastic counts include $x = 9$, which characterizes most Episcieae ($x = 8$ in *Codonanthe* and *Nematanthus* Schrader), and provides support for the monophyly of this tribe, although this character state is homoplastic with some *Didymocarpus* species. Two taxa included in this analysis share a count of $x = 10$, *Solenophora* (Gesnerioideae) and *Oreocharis* (Cyrtandroideae), most likely the result of convergence.

NODAL ANATOMY. Unfortunately only the subfamily Gesnerioideae has been sampled thoroughly for nodal anatomy (Wiehler 1983) and the lack of data for Cyrtandroideae necessitated exclusion of this character. Episcieae (Fig. 1) are characterized by a three-trace trilacunar node that is unique among Gesnerioideae, although this character state is known from members of Cyrtandroideae (Wiehler 1983). This may add further support for a monophyletic Episcieae. Examination of the nodal anatomy of Cyrtandroideae should be a priority for further investigation given its probable phylogenetic utility in Gesnerioideae.

CHEMICAL CONSTITUENTS. Leaf anthocyanins, although sampled haphazardly among the family (Harborne 1966, 1967) may serve to characterize the subfamilies. The presence of columnin in Gesnerioideae and absence in Cyrtandroideae (Harborne 1966, 1967) is another potential synapomorphy for Gesnerioideae. However, data are available for the presence of columnin in only five Gesnerioideae included in this analysis (*Achimenes*, *Kohleria*, *Sinningia*, *Columnnea*, *Alloplectus*). A broader survey for columnin, especially in Coronanthereae, would be extremely valuable.

Dihydrophenolics (Kvist and Pederson 1986) are highly polymorphic for the genera sampled in this study. However, the distribution of some chemical constituents is congruent with the resulting trees. Dihydrophenolics are not found in Klugieae and Napeantheae (Kvist and Pederson 1986). The presence of dihydrophenolics in the majority of Gesneriaceae (except Napeantheae) may serve as a synapomorphy to separate the remainder of the family from Klugieae. Although the lack of these compounds in both Napeantheae and Klugieae is likely to be homoplastic, it is interesting that Fritsch (1893–1894) placed *Napeanthus* in Klugieae.

Despite polymorphism and homoplasmy, a cladistic analysis of morphological characters provides partial resolution among tribes of Gesneriaceae that is largely congruent with traditional classification systems (Burt 1962; Wiehler 1983; Wang et al. 1992; Burt and Wiehler 1995). Further investigation of the distribution of some of the characters examined in this study, as well as others that had to be excluded, is warranted. In particular more complete data on cotyledon expansion (44), endosperm (33), pollen shape (21) and pollen size (22) would be valuable to determine if the character state distributions predicted from this analysis are upheld. Likewise, additional investigations of nodal anatomy (Cyrtandroideae) and chemical constituents may provide better definition of monophyletic groups.

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APPENDIX 1. Data matrix used in this cladistic analysis. See Tables 1 and 2 for more information on included taxa. Taxa are listed in order as in Tables 1 and 2. Characters are listed in order as presented in the text. Brackets denote polymorphic characters. Missing data are designated as ?.

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Achim.	0	1	0	0	0	0	0	0	{01}	1	{01}	0	1	{01}	1	1	0	{01}	1	0	?	?
Gloxinia	0	{12}	0	0	0	0	0	0	0	0	0	{01}	0	0	1	0	0	0	1	0	{01}	1
Monopyle	0	{12}	0	0	0	0	0	0	{01}	1	1	0	0	0	1	0	0	0	1	0	?	?
Kohleria	{02}	{12}	0	0	0	0	0	0	0	1	1	0	0	{01}	1	0	0	0	1	0	{01}	1
Diastema	0	1	0	0	0	0	0	0	{01}	1	0	0	0	0	1	0	0	2	1	0	?	?
Sinningia	{02}	3	0	0	0	{01}	0	0	1	{01}	{01}	0	{01}	1	0	0	0	1	0	1	1	1
Paliavana	2	2	0	0	0	0	0	0	0	1	{01}	1	0	0	1	0	0	0	1	0	?	?
Lietzia	0	3	0	0	0	0	0	0	0	1	0	0	1	1	1	1	0	0	1	0	?	?
Solenoph.	{023}	0	0	0	0	0	0	0	{01}	1	1	0	0	0	1	0	0	0	1	0	?	?
Gesneria	{23}	0	0	0	0	0	0	0	{0234}	1	1	0	0	1	1	0	0	0	1	0	0	1
Rytidoph.	{23}	0	0	0	0	0	0	0	0	1	1	0	0	1	1	0	4	0	1	0	0	1
Columnnea	1	0	0	0	0	0	0	0	0	1	0	{01}	1	1	1	0	0	{01}	1	0	{0-3}	1
Codonan.	1	0	0	0	0	0	0	0	0	1	{01}	1	1	0	1	0	0	0	1	1	?	1
Allopl.	0	0	0	0	0	0	0	0	0	1	0	1	{01}	1	1	0	0	0	1	0	?	?
Drymonia	{024}	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	3	1	1	?	1
Besleria	{02}	0	0	0	0	0	0	0	{01}	0	{01}	{01}	1	0	1	1	{01}	0	1	0	?	?
Gasteran.	{02}	0	0	0	0	0	0	0	0	0	{01}	1	1	{01}	1	0	0	0	1	0	?	1
Anethanth.	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	1	0	?	?
Napeanth.	0	0	0	0	0	0	1	0	0	1	1	0	0	0	1	0	0	{02}	{01}	0	?	1
Asteran.	0	0	0	0	0	0	0	1	1	1	0	0	1	1	0	0	3	1	0	?	?	?
Rhabdath.	2	0	0	0	0	0	0	1	0	{01}	1	0	0	1	1	0	1	0	1	0	?	?
Ramonda	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	?	?
Saintp.	0	0	0	0	0	0	{01}	0	0	1	1	0	0	{01}	2	0	0	0	1	0	?	?
Conandron	0	0	0	0	0	0	1	0	?	1	1	0	0	0	0	0	0	0	1	0	?	?
Champion.	{02}	{02}	1	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	?	?
Oreochar.	0	0	0	0	0	0	1	0	?	1	1	0	0	1	1	1	0	0	0	?	?	{12}
Didymoc.	0	0	0	0	0	0	0	0	0	1	1	1	0	1	2	0	{014}	5	1	0	2	0
Streptoc.	{01}	0	0	0	0	0	{012}	0	0	1	1	{01}	0	1	2	0	2	0	1	0	2	0
Ornitho.	0	0	0	0	0	0	0	?	?	1	1	0	0	1	2	0	0	4	1	0	2	0
Aeschyn.	1	0	0	0	0	0	0	0	0	1	{01}	0	0	1	1	1	{01}	{01}	1	0	2	0
Agalmyla	{01}	0	0	0	0	0	0	0	0	1	{01}	0	0	1	{12}	1	1	0	1	0	?	?
Cyrtandra	{0-3}	0	0	0	0	0	{01}	1	{01}	1	1	{01}	0	{01}	2	0	{13}	{01}	1	0	2	0
Rhynchochl.	0	0	1	1	1	0	0	?	?	1	1	0	0	1	{12}	{01}	{12}	4	1	0	2	0
Monophyll.	0	0	1	1	1	0	2	0	?	1	1	0	0	1	1	1	1	{02}	1	0	2	0
Bignon.	{1-4}	0	0	{12}	1	{01}	0	0	{23}	1	1	0	0	1	{12}	1	0	0	0	0	{024}	1
Acanth.	{02}	0	0	{12}	1	0	0	0	3	1	{01}	0	0	1	{12}	0	{012}	{03}	0	0	{14}	1
Scrophul.	{023}	0	0	1	1	0	0	2	?	{01}	1	0	{01}	1	{012}	0	0	0	0	0	{12}	?

APPENDIX 1. Continued

Taxon	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	
Achim.	1	0	1	1	1	0	1	0	1	0	?	0	0	0	{03}	1	0	0	0	1	6	0	
Gloxinia	{12}	0	{12}	1	1	0	1	0	1	0	1	0	0	0	{02}	1	0	0	{12}	1	{256}	?	
Monophyle	0	0	2	1	1	0	1	1	1	0	?	{01}	0	0	2	1	0	0	2	1	{12}	?	
Kohleria	4	0	1	1	1	0	1	{01}	1	0	?	0	0	0	0	2	1	0	0	0	1	{26}	?
Diastema	4	0	1	1	1	0	1	0	1	0	?	0	0	0	{03}	1	0	0	0	1	{256}	?	
Sinningia	5	0	{12}	1	1	0	1	1	1	0	1	0	0	0	{02}	1	0	0	0	1	{126}	0	
Paliavana	5	0	1	1	1	0	1	0	1	0	?	0	0	0	{12}	1	0	0	0	1	6	0	
Lietzia	4	0	1	1	1	0	1	0	1	0	?	0	0	0	3	1	0	0	2	1	5	0	
Solenoph.	{35}	0	2	1	1	?	?	0	1	0	?	0	0	0	0	1	0	1	?	0	6	?	
Gesneria	1	0	1	1	0	0	1	0	1	0	1	0	0	0	{03}	1	0	0	{12}	1	{56}	0	
Rytidoph.	1	0	{12}	1	1	0	1	0	1	0	1	0	0	0	0	1	0	0	0	1	5	0	
Columnnea	5	0	0	1	0	1	2	1	0	0	1	0	0	0	{03}	1	0	0	0	1	6	0	
Codonan.	3	0	0	1	0	1	2	1	{13}	0	1	0	0	0	{013}	1	0	0	0	1	6	0	
Allopl.	5	0	0	1	0	1	{12}	1	1	0	1	0	0	0	{03}	1	0	0	0	1	{26}	0	
Drymonia	5	0	0	1	0	1	{12}	1	1	0	1	0	0	0	{04}	1	0	0	0	1	6	0	
Besleria	1	0	0	1	0	1	{12}	1	0	0	1	0	0	0	{23}	1	0	0	0	1	{26}	?	
Gasteran.	2	0	0	1	0	1	{12}	1	1	0	?	{01}	0	0	{023}	1	0	0	{01}	1	1	?	
Anetanth.	4	0	0	1	0	1	{12}	0	{12}	0	?	1	0	0	{03}	0	1	1	0	0	5	?	
Napeanth.	0	0	0	1	0	1	{12}	0	1	0	?	0	0	0	3	1	0	0	2	1	5	?	
Asteran.	1	1	0	0	1	0	1	1	0	0	1	0	0	0	2	1	0	0	0	1	{26}	0	
Rhabdoth.	0	1	0	0	1	0	1	0	{12}	0	0	0	0	0	?	1	{02}	0	0	1	{126}	0	
Ramonda	0	0	0	0	1	0	1	0	2	0	?	0	0	0	0	0	0	0	1	1	{15}	1	
Saintp.	1	0	0	0	1	0	0	0	{13}	0	?	0	0	0	{03}	0	0	0	1	1	{46}	1	
Conandron	0	0	0	0	1	0	2	0	1	0	?	0	0	0	{03}	1	{02}	{02}	{01}	1	{06}	1	
Champion.	0	0	0	0	1	0	2	0	2	0	?	0	0	0	{03}	0	0	0	0	1	{15}	?	
Oreochar.	0	0	0	1	0	1	0	1	0	?	0	0	0	3	0	0	0	1	1	6	1		
Didymoc.	{12}	0	0	0	1	0	1	0	1	0	0	0	0	0	{03}	0	0	0	0	1	{136}	1	
Streptoc.	1	0	0	0	1	0	2	0	1	1	0	0	0	0	{03}	0	0	{02}	1	1	{35}	1	
Ornitho.	{01}	0	0	0	1	0	2	0	1	1	?	0	0	0	0	0	0	0	0	1	{56}	1	
Aeschyn.	2	0	0	0	1	0	2	0	1	0	0	0	1	0	2	0	0	0	1	1	{05}	1	
Agalmyla	1	0	0	0	1	0	2	0	1	0	0	0	1	0	2	{01}	{02}	0	1	1	{01}	?	
Cyrtandra	{12}	0	0	{01}	1	0	{12}	{01}	0	0	0	0	0	0	{03}	{02}	{02}	{012}	{012}	{01}	{157}	1	
Rhynchogl.	1	0	0	1	1	0	1	0	1	0	?	0	0	0	{03}	{01}	0	0	1	1	{36}	1	
Monophyll.	{12}	0	0	1	2	0	1	0	{123}	0	?	0	0	0	3	0	0	0	0	1	{35}	1	
Bignon.	1	0	0	1	2	0	?	0	{012}	0	0	0	1	2	3	0	0	0	?	1	6	0	
Acanth.	1	0	0	1	2	0	?	0	1	0	0	1	0	?	?	?	?	?	?	?	?	0	
Scrophul.	1	0	0	1	{12}	0	?	{01}	{02}	0	1	{02}	0	{02}	{03}	2	0	{02}	{12}	1	{0145}	0	