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## A Cladistic Analysis of the Tribe Episcieae (Gesneriaceae) Based on *ndhF* Sequences: Origin of Morphological Characters

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**ABSTRACT.** The neotropical members of Gesneriaceae are characterized by numerous characters that appear to be adaptations to life in the wet tropics. Among these are epiphytism, anisophylly, hummingbird-pollination, and bird-dispersal of seeds. Many of these characters have diversified to a broad extent in the single tribe Episcieae. This analysis investigates the phylogenetic relationships among genera of Episcieae and also examines the evolutionary origin of several characters found within this tribe such as fruit characters, epiphytism, chromosome numbers, and tubers. All genera of the tribe were included in the analysis except the Guyana endemic *Rhoogeton* and the Central American *Oerstedina*. Larger genera such as *Columnnea* and *Episcia* were represented by several species with attempts to include members of the different sections of these genera. *Columnnea* appears to be a monophyletic group but its relationship to *Drymonia* and *Alloplectus* is not resolved. The latter genera may need to be included in *Columnnea* to make it strictly monophyletic. *Neomortonia* is polyphyletic with one species in the *Columnnea* clade and another with *Episcia*. The anomalous position of some *Paradrymonia* indicate a more thorough analysis of this genus is necessary to resolve phylogenetic relationships.

Comparative studies of morphological characters can be greatly facilitated through a well-supported phylogenetic analysis of the taxa being examined (Donoghue and Ackerly 1996). This approach has been used with success for different plant groups (Donoghue 1989; Sytsma et al. 1991; Baum et al. 1994; Givnish et al. 1996) although less attention has been paid to tropical groups (Chase and Palmer 1989; Smith and Sytsma 1994b; Givnish et al. 1996). Tropical plants, particularly herbaceous groups, possess numerous adaptations to living in lowland wet, montane cloud, and seasonally dry tropical forests. Among these adaptations are epiphytism and suites of vegetative and reproductive characters that co-occur with the epiphytic habit (Ackerman 1986), modification of stems into tubers to survive dry periods, and modification of leaves for increased light-capture efficiency (Givnish 1984).

One tropical plant family that exhibits a broad diversity of morphological characters is Gesneriaceae. Gesneriaceae comprise approximately 2,500–3,500 species in 120–135 genera, distributed primarily in the tropics with a few temperate species in Europe, China and Japan (Heywood 1978; A. Weber, pers. comm.). The majority of species in Gesneriaceae are herbaceous perennials, but others are annuals, shrubs, lianas, or trees. Many species (20%) are epiphytic, and Gesneriaceae rank among the top ten plant families in terms of absolute numbers of epiphytic taxa (Madison 1977; Kress 1986). Leaves are opposite in the majority of the

subfamily but anisophylly, leading to an apparent alternate arrangement following abscission of the smaller leaf, is common. The family is divided into subfamilies with Gesnerioideae found almost exclusively in the neotropics (Burt and Wiehler 1995; Smith et al. 1997b). Gesnerioideae are divided further into six tribes and 60 genera (Burt and Wiehler 1995; Smith et al. 1997b).

Episcieae are one of the largest tribes in Gesnerioideae and comprise 16 genera (Table 1). The tribe is a well-supported monophyletic group on the basis of molecular data (Smith et al. 1997b). Morphologically it is distinct among other Gesnerioideae by its nodal anatomy (Wiehler 1983) a character not used in a cladistic analysis of morphology (Smith 1996). Episcieae are characterized by a three-trace trilacunar node with split lateral bundles, superior ovaries, and most members have chromosome counts of  $x = 9$  ( $x = 8$  in *Codonanthe* (Mart.) Hanst. and *Nematanthus* Schrader). This combination of character states is unknown among other neotropical members of the family.

Episcieae are represented by some of the more diverse morphological characters within Gesneriaceae. Whereas most Gesneriaceae are characterized by capsular fruits, many Episcieae are berry-fruited. Episcieae also contain the only members of the family with a fruit type intermediate between a berry and capsule. This fruit has been called a display fruit (Wiehler 1983) and is distinguished by

TABLE 1. Species sequenced in this study with Genbank submission numbers and voucher specimens. SI—Smithsonian Institution living collection accession numbers. Letters in parentheses indicate herbarium where vouchers are deposited.

Species	Voucher	Genbank number
<i>Alloplectus panamensis</i> C. V. Morton	SI 93–060	AFO13685
<i>Alloplectus</i> sp.	Smith 3418 (SRP)	AFO13686
<i>Alsobia dianthiflora</i> (H. E. Moore & R. G. Wilson) Wiehler	SI 94–258	AFO13687
<i>A. punctata</i> (Lindl.) Wiehler	Smith 3600 (SRP)	AFO13688
<i>Alsobia</i> sp.	SI 94–005	AFO13689
<i>Alsobia</i> sp.	Smith 3599 (SRP)	AFO13690
<i>Chrysothemis friedrichsthaliana</i> (Hanst.) H. E. Moore	SI 94–335	AFO13691
<i>Cobananthus calochlamys</i> (J. D. Sm.) Wiehler	SI 94–421	AFO13692
<i>Codonanthe elegans</i> Wiehler	Smith et al. 1997a	U62178
<i>Codonanthis peruviana</i> Wiehler	Turley s.n. (SRP)	AFO13693
<i>Columnea ambigua</i> (Urban) Morley	Smith 3701 (SRP)	AFO13694
<i>C. mira</i> Morley	Smith 2450 (WIS)	AFO13695
<i>C. oblongifolia</i> Rusby	Smith 1721 (WIS)	AFO13696
<i>C. sanguinea</i> (Pers.) Hanst.	Smith 3369 (SRP)	AFO13697
<i>C. schiedeana</i> Schlecht.	Smith et al. 1997a	U62164
<i>Corytoplectus speciosus</i> (Poepp.) Wiehler	SI 94–268	AFO13698
<i>Drymonia urceolata</i> Wiehler	Smith 3416 (SRP)	AFO13699
<i>Episcia fimbriata</i> Fritsch	SI 95–005	AFO13700
<i>E. sphalera</i> Leeuw.	SI 94–043	AFO13701
<i>Nautilocalyx adenosiphon</i> (Leeuw.) Wiehler	SI 93–017	AFO13702
<i>Nematanthus hirsutus</i> (Mart.) Wiehler	Olmstead & Reeves 1995	L36404
<i>Neomortonia nummularia</i> (Hanst.) Wiehler	SI 94–469	AFO13703
<i>N. rosea</i> Wiehler	SI 94–230	AFO13704
<i>Paradrymonia aurea</i> Wiehler	SI 94–474	AFO13705
<i>P. densa</i> (C. H. Wright) Wiehler	Stewart s.n. (SRP)	AFO13706
<i>P. fuquaiana</i> Wiehler	SI 93–027	AFO13707
<i>Rufodorsia major</i> Wiehler	SI 94–575	AFO13708
<b>Outgroups</b>		
<b>Cyrtandroideae</b>		
<i>Aeschynanthus micranthus</i> C. B. Clarke	Smith et al. 1997a	U62169
<i>Agalmyla parasitica</i> (Lam.) Kuntze	Smith et al. 1997a	U62171
<i>Anna mollifolia</i> (W. T. Wang) W. T. Wang & K. Y. Pan	Smith et al. 1997a	U62188
<i>Boea hygroskopica</i> F. Muell.	Smith et al. 1997a	U62205
<i>Chirita sinensis</i> Lindl.	Smith et al. 1997a	U62189
<i>Cyrtandra hawaiiensis</i> C. B. Clarke	Smith et al. 1997a	U62172
<i>C. umbellifera</i> Merr.	Smith et al. 1997a	U62165
<i>Cyrtandromoea acuminata</i> Benth. & Hook.	Smith et al. 1997a	U62173
<i>Didissandra frutescens</i> Clarke	Smith et al. 1997a	U62190
<i>Didymocarpus albomarginata</i> Hemsl.	Smith et al. 1997a	U62207
<i>Hemiboea henryi</i> C. B. Clarke	Smith et al. 1997a	U62180
<i>Lysionotus pauciflorus</i> Maxim.	Smith et al. 1997a	U62182
<i>Monophyllaea hirticalyx</i> Franch.	Smith et al. 1997a	U62168
<i>Opithandra primuloides</i> (Miq.) B. L. Burtt	Smith et al. 1997a	U62183
<i>Ornithoboea wildeana</i> Craib.	Smith et al. 1997a	U62166
<i>Paraboea rufescens</i> (Franch.) Burtt	Smith et al. 1997a	U62206
<i>Petrosmea flaccida</i> Craib	Smith et al. 1997a	U62184
<i>Primulina tabacum</i> Hance	Smith et al. 1997a	U62167
<i>Ramonda myconi</i> (L.) Rchb.	Smith et al. 1997a	U62185
<i>Rhynchoslossum notonianum</i> (Wall.) B. L. Burtt	Smith et al. 1997a	U62179
<i>Saintpaulia rupicola</i> B. L. Burtt	Smith et al. 1997a	U62176
<i>Streptocarpus holstii</i> Engl.	Olmstead & Reeves 1995	L36415
<i>S. saxorum</i> Engl.	Smith et al. 1997a	U62170
<i>Titanotrichum oldhamii</i> (Hemsl.) Soler.	Smith et al. 1997a	U62187
<b>Gesnerioideae: Beslerieae</b>		

TABLE 1. Continued

Species	Voucher	Genbank number
<i>Besleria affinis</i> Morton	Smith et al. 1997a	U62162
<i>Gasteranthus corallinus</i> (Fritsch) Wiehler	Smith et al. 1997a	U62163
<b>Gesnerioideae: Coronanthereae</b>		
<i>Asteranthera ovata</i> (Cav.) Hanst.	Smith et al. 1997a	U62204
<i>Fieldia australis</i> Cunn.	Smith et al. 1997a	U62196
<i>Mitriaria coccinea</i> Cav.	Smith et al. 1997a	U62193
<i>Negria rhabdothamnoides</i> F. Muell.	Smith et al. 1997a	U62195
<i>Sarmienta repens</i> R. & P.	Smith et al. 1997a	U62194
<b>Gesnerioideae: Gesnerieae</b>		
<i>Gesneria christii</i> Urban	Smith et al. 1997a	U62191
<i>G. pedicellaris</i> Alain	Smith et al. 1997a	U62192
<i>Rytidophyllum auriculatum</i> Hook.	Smith et al. 1997a	U62199
<i>R. tomentosum</i> (L.) Mart.	Smith et al. 1997a	U62200
<i>Sanango racemosum</i> (R. & P.) Barringer	Smith et al. 1997b	U62144
<b>Gesnerioideae: Gloxinieae</b>		
<i>Achimenes skinneri</i> Lindl.	Smith et al. 1997a	U62177
<i>Diastema racemiferum</i> Benth.	Smith et al. 1997a	U62156
<i>Gloxinia sylvatica</i> (H. B. K.) Kunth	Smith et al. 1997a	U62157
<i>Koellikeria erinoides</i> (DC.) Mansf.	Dunn s.n. (SRP)	AFO13709
<i>Kohleria spicata</i> (Kunth) Oerst.	Smith et al. 1997a	U62181
<i>Monopyle macrocarpa</i> Benth.	Smith et al. 1997a	U62197
<i>Niphaea oblonga</i> Lindl.	Smith et al. 1997a	U62160
<i>Solenophora obliqua</i> D. L. Denham & D. N. Gibson	Smith et al. 1997a	U62202
<b>Gesnerioideae: Napeantheae</b>		
<i>Napeanthus costaricensis</i> Wiehler	Smith et al. 1997a	U62198
<i>N. macrostoma</i> Leeuwenberg	Smith et al. 1997a	U62161
<b>Gesnerioideae: Sinningieae</b>		
<i>Paliavana prasinata</i> (Ker-Gawl.) Fritsch	Smith et al. 1997a	U62174
<i>Sinningia (Lietzia) brasiliensis</i> (Regel & Schmidt) Wiehler	Smith et al. 1997a	U62175
<i>S. cooperi</i> (Paxt.) Wiehler	Smith et al. 1997a	U62201
<i>S. richii</i> Clayb.	Smith et al. 1997a	U62186
<i>Vanhouttea lanata</i> Fritsch	Smith et al. 1997a	U62203

the dehiscence of the fleshy fruit walls to reveal a brightly colored interior pericarp that contrasts with the dull, often purple-black mass of seeds and funiculi (Wiehler 1983). It is the goal of this study to construct a well-supported cladogram for genera within the Episcieae as a means of examining the origins of the morphological characters discussed above.

Additionally, this study attempts to examine several of the questions regarding generic delimitations within this tribe. Several taxa have been termed "waste-basket" genera, implying that their species have been placed there due to an overly simplistic classification system (Wiehler 1983). Among these are *Episcia* Mart., *Columnnea* L., and *Alloplectus* Mart. (Wiehler 1983). In his earlier revision of this tribe, Wiehler (1983) described several new genera and rearranged the position of many species among those already described. One group that received a major rearrangement was the

*Columnnea* alliance. Initially comprising three genera, Wiehler (1973, 1983) split this group into eight, most being divided from *Columnnea* s.l. This split has remained controversial and more thorough examinations of these species on the basis of morphology (Kvist and Skog 1994; Smith 1994; Smith and Sytsma 1994a) and chloroplast DNA (cpDNA) restriction site analysis (Smith and Sytsma 1994b, 1994c) indicated that *Columnnea* s.l. was best retained as a single genus and that the other genera were not monophyletic. As a means of investigating this question further, these larger genera have been represented by several species each in the present analysis.

The source of data for this analysis is the cpDNA gene *ndhF* which in tobacco encodes a protein of 740 amino acids presumed to be a subunit of an NADH dehydrogenase (Sugiura 1992). The use of *ndhF* sequences for systematic studies has provided a far greater number of characters to resolve

relationships than studies using *rbcL* (Olmstead and Sweere 1994; Clark et al. 1995; Olmstead and Reeves 1995; Scotland et al. 1995; Smith et al. 1997a, 1997b) The larger number of variable characters makes *ndhF* sequences ideal for taxonomic groups that have not been resolved well using *rbcL* data, such as members of Asteridae and Lamiales s.l. (Olmstead et al. 1992, 1993; Chase et al. 1993).

#### MATERIALS AND METHODS

The gene sequences used in this analysis were generated by thermal cycle sequencing (Innis et al. 1988) of previously amplified *ndhF* regions. The *ndhF* gene was amplified in two overlapping sections (positions 1–1,350, and 972–2,044) from genomic DNA isolated from fresh, frozen, or silica gel dried material (Smith et al. 1992). Amplification and sequencing procedures followed that of Smith et al. (1997b) used for other members of Gesneriaceae.

This analysis focused on the relationships within Episcieae, therefore every attempt was made to gather all genera within the tribe and several species within some of the larger genera. The only members of Episcieae excluded from this analysis are the rare Guyana endemic *Rhoogeton* Leeuwenberg and the Central American *Oerstedina* H. Wiehler. Two to five species each were used to represent the larger or potentially non-monophyletic genera (*Columnea*, *Episcia*, *Alloplectus*, and *Paradrymonia* Hanst.). Two of the three species of *Neomortonia* Wiehler were included in this analysis to test the monophyly of this small, but morphologically diverse, genus. The species used in the analysis, voucher information, and Genbank accession numbers are included in Table 1. The data matrix contains 0.82% missing cells based on total sequence alignments.

Outgroups were selected to root the tree based on recent morphological and molecular analyses of tribal relationships within Gesneriaceae (Smith 1996; Smith et al. 1997b). The most appropriate outgroups for Episcieae were genera representing the other tribes of Gesnerioideae. However, to verify first that the tribe was monophyletic, an initial analysis was performed with 24 representatives (22 genera) of the Old World subfamily Cyrtandroideae as outgroups. Only after all Episcieae included in the analysis were determined to be monophyletic based on *ndhF* sequence data, were members of tribes Beslerieae, Napeantheae and Coronanthereae used as outgroups in a smaller

analysis that included only Gesnerioideae to minimize parsimony.

**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. To search for islands of equally parsimonious trees (Maddison 1991), the search strategy of Olmstead and Palmer (1994) was implemented searching for 1,000 trees each in five subsequent analyses with the nearest neighbor interchange (NNI) search option in effect and mulpars "off." 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." This strategy was used in the full analysis with genera of Cyrtandroideae designated as outgroups. The same strategy was used with only tribes Napeantheae, Beslerieae, and Coronanthereae designated as outgroups, and when using the constraints option of PAUP to test for various monophyletic groups.

Branch support analysis was performed to examine trees that were six or fewer steps longer than the most-parsimonious trees (Bremer 1988, 1994; Donoghue et al. 1992). This type of analysis provides an indication of the robustness of the data by determining which clades persist in a consensus tree as parsimony is relaxed. To minimize computer time and obtain maximal amount of information regarding branch support, a further reduced data set was used for branch support analysis. Only Episcieae were used with members of Gesnerieae (both species of *Rytidophyllum* Mart. excluded) Sinningieae, and Gloxinieae designated as outgroups. Branch support analysis was performed by saving all trees up to six steps longer than the most-parsimonious trees and then examining subsets of trees one to six steps longer with the filter option of PAUP.

Bootstrap analysis (Felsenstein 1985) was performed using 100 replicates with TBR and mulpars "off."

The monophyly of taxa not obtained in the most-parsimonious trees was examined by using the constraints option of PAUP. The constraints option also was used to examine the position of *Koellikeria* Post & Kuntze in Gloxinieae in the full analysis with Cyrtandroideae as outgroup, the monophyly of *Episcia* (including *Alsobia* Hanst.), *Neomortonia*, *Paradrymonia*, berry-fruited genera, and epiphytic genera. Only monophyly of the

designated groups was constrained with no structure designated within the separate groups.

## RESULTS

The full analysis, using members of Cyrtandroideae as outgroup resulted in six most-parsimonious trees of 5,413 steps each, consistency index (CI) = 0.25, retention index (RI) = 0.40. The strict consensus of these trees is presented in Fig. 1. All members of Episcieae used in this analysis form a monophyletic group. *Koellikeria* (Gloxinieae) is the sister to Episcieae in this analysis (see discussion). Since Episcieae were monophyletic, a reduced analysis was justified in including only members of Beslerieae, Napeantheae, and Coronanthereae as outgroups to minimize homoplasy in the data (Fig. 1). This smaller analysis resulted in 10 most-parsimonious trees of 2,910 steps each (CI = 0.30, RI = 0.38). *Koellikeria* is in its traditional tribe, Gloxinieae, in this analysis. The strict consensus of these trees is presented in Fig. 2.

In the analysis, which excluded Beslerieae, Napeantheae, and Coronanthereae, to determine branch support, the topology within Episcieae was identical to the tree that included members of these three tribes as outgroups. Episcieae were monophyletic and strongly supported on the basis of branch support. The sister to Episcieae in this reduced analysis is Gloxinieae (Fig. 2). In the full analysis (Fig. 1) the sister to Episcieae was a single member of Gloxinieae, *Koellikeria*.

The *Columnnea* alliance appears as a single clade which includes *Alloplectus*, *Drymonia* Mart., *Corytoplectus* Oerst., and *Neomortonia rosea* (Fig. 2). However, the relationships among five of these genera are unresolved in the strict consensus. Within this group, *Corytoplectus* and *Columnnea ambigua* form a clade with a branch support of two (Fig. 2).

*Alsobia*, previously removed from *Episcia* (Wiehler 1978), is clearly distinct from that genus, but not monophyletic in this analysis (Fig. 2). *Episcia* sensu Wiehler is a paraphyletic genus in this analysis, containing *Neomortonia nummularia* (Fig. 2).

*Paradrymonia* is polyphyletic in this analysis. However, this is due to the separate position of *Paradrymonia densa* which was purposefully included in the analysis due to its discrepant morphology compared to other members of the genus.

Results of the constraints analyses are presented in Table 2.

Figure 2 was used as the cladogram to map character evolution of fruit type, epiphytism, tubers, and chromosome number. Parsimony was used to plot the character state changes onto the figure by hand. These character transformations are presented in Fig. 3.

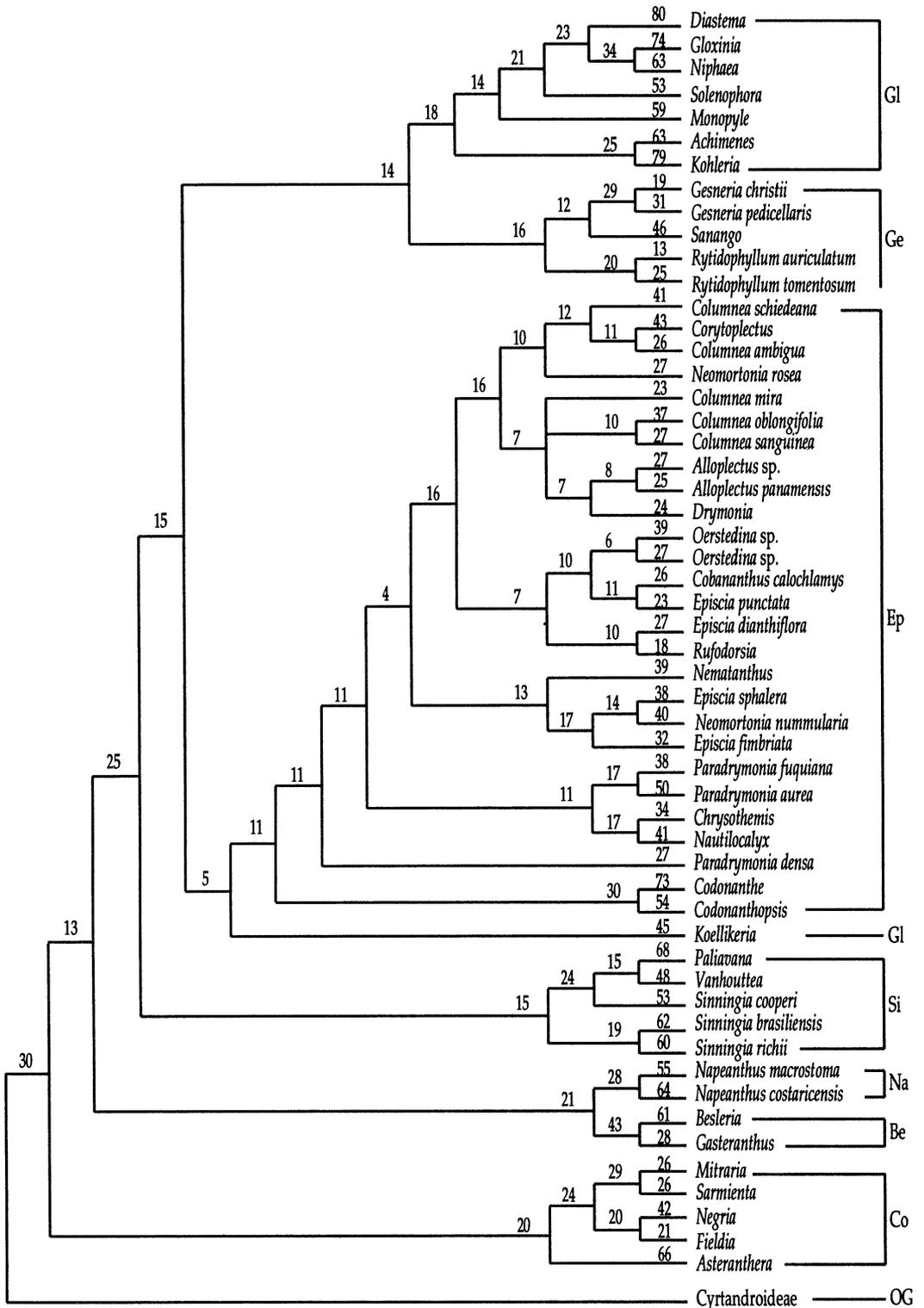
## DISCUSSION

The full cladistic analysis of all genera of Episcieae except *Rhoogeton* and *Oerstedina* identified a monophyletic tribe (Fig. 1). One unusual aspect of this cladogram is the appearance of *Koellikeria* as the sister to Episcieae (Fig. 1). This position of *Koellikeria* is likely to be anomalous due to sampling density. A smaller analysis of Episcieae that excluded Cyrtandroideae results in a more traditional placement of this genus (Fig. 2), and an analysis that includes all genera of Gloxinieae except *Lembocarpus* Leeuw. and *Goyazia* Taubert, results in a paraphyletic Gloxinieae, but *Koellikeria* is with the majority of the genera in this tribe (Smith, unpubl. results).

The reduced analysis of these data that includes only members of the New World subfamily Gesnerioideae also results in a monophyletic Episcieae that is well-supported with a branch support value of six (Fig. 2). Unlike the full analysis, all tribes within Gesnerioideae also are monophyletic with *Koellikeria* in Gloxinieae, and Gloxinieae as sister to Episcieae.

**Taxonomic Anomalies.** The position of *Koellikeria* as sister to Episcieae in the full analysis is likely to be anomalous rather than reflecting its true phylogenetic position. However, in the original description for the genus *Rufodorsia* Wiehler, Wiehler (1975) commented that the corollas of *Rufodorsia* matched those of *Koellikeria* in size, shape, and color; these being the only two genera in Gesnerioideae to possess a short corolla with a red back. The reduced analysis that uses only members of Gesnerioideae, and an unpublished analysis of Gloxinieae (Smith, unpubl. results), both indicate that *Koellikeria* is best retained within Gloxinieae and that the similarity of the flowers between *Koellikeria* and *Rufodorsia* can be explained as convergence.

**Episcia Complex.** *Episcia* has been viewed as a "waste-basket" genus by Wiehler (1978, 1983) with many diverse morphological features. In his treatment of *Episcia*, Wiehler (1978) erected several generic names to encompass the diversity within this morphologically heterogeneous taxon (*Rufodor-*



*sia*, *Oerstedina*, *Nautilocalyx* Lind. ex Hanst., *Neomortonia*, *Alsobia*, and *Paradrymonia*). Support for a division of *Episcia* is strong; 32 additional steps beyond the most-parsimonious trees are necessary to create a monophyletic *Episcia* s.l. (Table 2).

*Episcia* sensu Wiehler, is paraphyletic in this analysis and includes *Neomortonia nummularia*. The support for the relationships among these three species is weak (Fig. 2) and may be the result of limited sampling within *Episcia*. *Neomortonia* was erected to encompass two species that did not fit fully into the generic delimitations of Wiehler (1983) in his revision of New World Gesneriaceae. The genus originally encompassed two species, *N. rosea*, a thin-stemmed, epiphytic, trailing plant with pink funnellform corollas that have a large, rotate, fringed limb, and *N. nummularia*, a terrestrial, trailing plant with red to orange, inflated corollas and a short limb. A third species, *N. alba* Wiehler, was described later and is morphologically similar to *N. rosea* with the exception of having white corollas. Both *N. rosea* and *N. nummularia* are strikingly different morphologically, however, Wiehler (1983) placed them both in a single genus on the basis of a "laterally somewhat compressed" bright orange berry, absence of stolons, and common chromosome number (Wiehler 1983). The latter two character states are symplesiomorphic for Episcieae.

It is apparent from this analysis that *Neomortonia* is not a monophyletic genus. Twenty steps beyond the most-parsimonious trees are necessary to make both species of *Neomortonia* included here monophyletic. *Neomortonia nummularia* perhaps is best viewed as a species of *Episcia* and *N. rosea* may best be viewed as a species of *Columnnea*. The placement of *N. rosea* within *Columnnea* does not have the same morphological support as does the placement of *N. nummularia* in *Episcia*. The large rotate limb of *N. rosea* is unique within *Columnnea* although the latter does comprise several thin-stemmed epiphytic trailing herbs. This analysis does not place *N. rosea* closely to any species of *Columnnea* and instead places it in a polytomy of *Columnnea* species along with *Drymonia* and *Alloplectus* (Fig. 2).

Although it is clear that *N. rosea* belongs to this alliance, its exact generic delimitation can not be resolved by these data.

The separation of *Alsobia* species from *Episcia* is supported in this analysis. The lack of monophyly for *Alsobia* may reflect the poor taxonomy of this genus despite recent revisions (Wiehler 1978, 1983). A more inclusive single genus may be more appropriate that would encompass *Cobananthus* Wiehler and *Rufodorsia*. Alternatively, it is possible that the inclusion of more species in these latter genera, or the inclusion of supplemental molecular data that is more capable of resolving relationships among closely related species (such as ITS, Baldwin et al. 1995), may result in three monophyletic genera.

The separation of both *Nautilocalyx* and *Paradrymonia* from *Episcia* due to their lack of stolons (Wiehler 1978) is justified on the basis of this analysis as is the separation of *Nautilocalyx* from *Paradrymonia* on the basis of erect versus creeping stems, respectively (Wiehler 1978). However, *Paradrymonia* is polyphyletic. Both *P. fuquaiana* and *P. aurea* are in a single clade, but *P. densa* is removed from this clade and is sister to the majority of Episcieae excluding other species of *Paradrymonia*, *Nautilocalyx*, *Chrysothemis* Decne, *Codonanthe*, and *Codonanthopsis* Mansf. (Fig. 2). The decision to include *P. densa* in this analysis was based entirely on its generically unique characters of long-creeping stem and petiolate leaves and potentially uncertain placement within *Paradrymonia*. One potential explanation for this position of *P. densa* is sampling artifact. If additional species, more closely related to *P. densa*, were included in an analysis, it could draw it into one of the genera in this analysis, including *Paradrymonia*. Alternatively, it is possible that *P. densa* is best treated as a new genus within Episcieae since eight additional steps beyond the most-parsimonious trees are necessary to make *Paradrymonia* monophyletic (Table 2). Regardless, *Paradrymonia* as a whole needs further examination both through morphological and molecular means.

**The *Columnnea* Complex.** Perhaps the most controversial generic question within Episcieae is

FIG. 1. Strict consensus of six trees 5,413 steps each of genera of the Gesnerioideae, CI = 0.25, RI = 0.40. These trees were rooted using 24 members of the Cyrtandroideae sensu Burt & Wiehler (1995) as designated outgroups (species not shown in this figure). For a complete list of species used to root the tree, refer to Table 1. Numbers above clades are branch lengths using the acctran option of PAUP. Abbreviations for tribes are as follows: Be - Beslerieae, Co - Coronanthereae, Ep - Episcieae, Ge - Gesnerieae, Gl - Gloxinieae, Na - Napeantheae, Si - Sinningieae, OG - outgroup. See text for the anomalous position of *Koellikeria*.

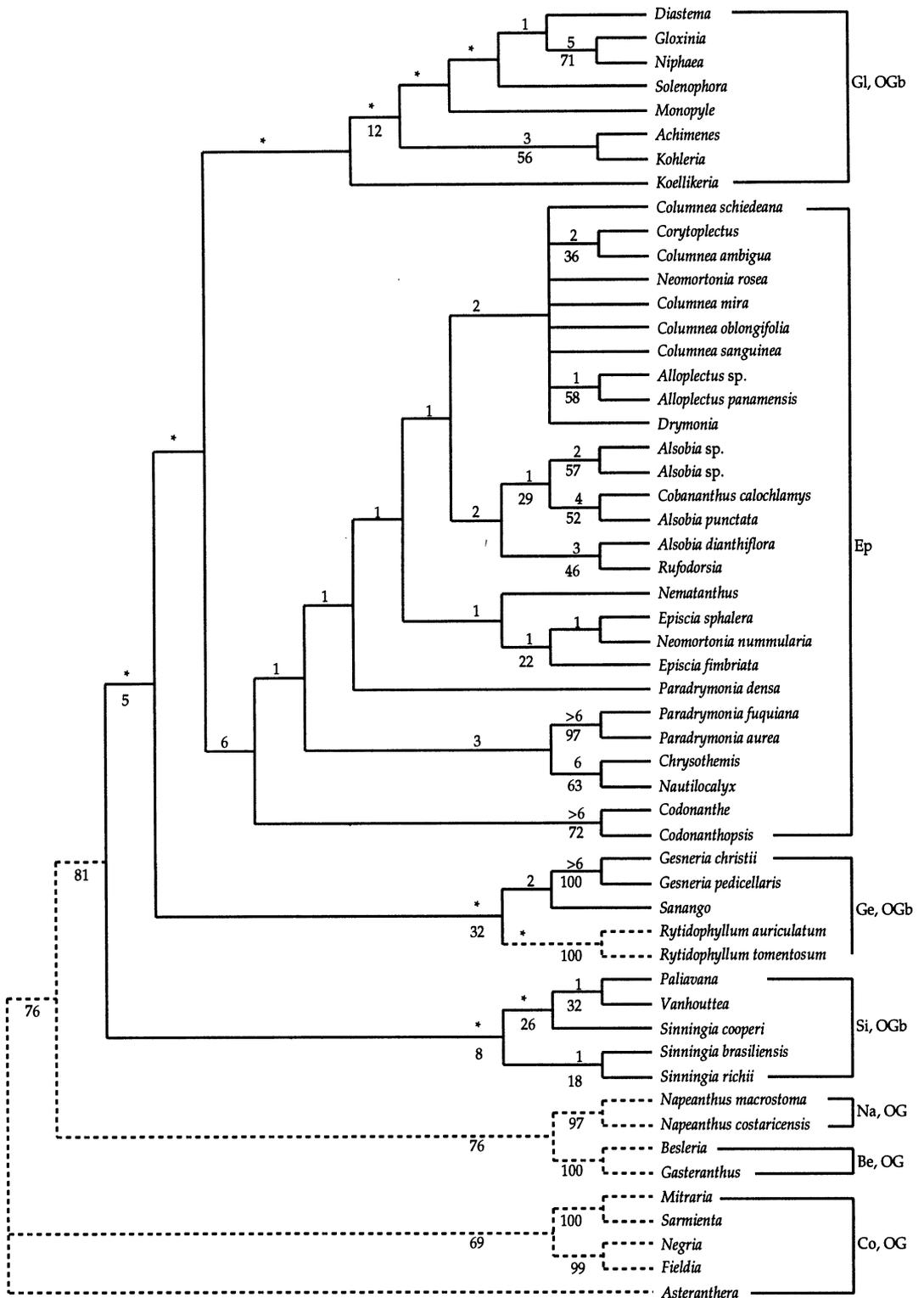


TABLE 2. Number of steps beyond the six most-parsimonious trees of 5,413 steps required to constrain monophyly of various taxa.

Group	Number of extra steps
<i>Koellikeria</i> in Gloxinieae, Cyrtandroidae as outgroup	10
<i>Episcia</i>	32
<i>Paradrymonia</i>	8
<i>Neomortonia</i>	20
berry-fruited genera	22
epiphytic genera	32

that of *Columnnea* sensu Wiehler (1973, 1983). In an attempt to reduce the impact of floral characters on generic delimitations within Gesneriaceae, Wiehler (1973, 1983) divided *Columnnea* into four segregate genera, *Columnnea* s. str., *Dalbergaria* Tuss., *Trichantha* Hook., and *Pentadenia* (Planch.) Hanst. Additionally, a fifth genus, *Bucinellina* Wiehler, was described to encompass the variation found in two newly described species. Morley (1974, 1976) strongly disagreed with the division of *Columnnea* and proposed instead a revised sectional treatment within *Columnnea* to encompass its variation. Subsequent analyses (Kvist and Skog 1993; Smith 1994; Smith and Sytsma 1994a, b, c) have examined this issue and resolved that the species are best retained as a single genus. Despite these analyses, Wiehler (1995) has retained the generic treatment outlined in Wiehler (1973, 1983).

As a means of further examining this generic division, this analysis included representatives from five of the six currently delimited sections of *Columnnea* (Kvist and Skog 1993; Smith 1994). Section *Bucinellina* was not included since material was not available. This analysis places all members of *Columnnea* in a single clade. However, the relationships of the different representative species are not resolved (Fig. 2). Likewise the relationships among species of *Columnnea*, *Alloplectus*, and *Drymonia* are not resolved by this analysis (Fig. 2). These

data do not provide substantial evidence for either a monophyletic *Columnnea* or the genera proposed by Wiehler (1983). It is apparent that the *ndhF* gene is at the limits of its utility at this taxonomic level, and an additional source of data (e.g., ITS) will be necessary to resolve this issue.

The small genus *Corytoplectus* Wiehler originally was described as *Alloplectus* and raised to generic status on the basis of inflorescence structure and fruit color (black or transparent) (Wiehler 1973, 1983). Although *Corytoplectus* has been accepted as a distinct genus from *Columnnea*, this analysis indicates that it is best viewed as a species of *Columnnea*.

#### Evolution Of Morphological Characters.

**FRUIT TYPE.** Three fruit types are known from Episcieae. The majority of genera have capsules common to Gesneriaceae, but some genera have berries, a fruit type known outside of Episcieae only in the genus *Besleria* (Plum.) L. and members of the Coronanthereae. Unique to Episcieae is the "display fruit" (Wiehler 1983). The display fruit is a fleshy dehiscent fruit. The interior of the pericarp is brightly colored, either red, pink, white or yellow, and contrasts with the mass of seeds it reveals when split open, usually black or blue-black. Presumably this provides a strong visual cue to aid in bird dispersal of the seeds (Wiehler 1983).

Berries appear a minimum of four times in the evolution of Episcieae, *Columnnea/Corytoplectus/Neomortonia rosea*, *Rufodorsia*, *Codonanthe*, and *Neomortonia nummularia* (Fig. 3). Each of these clades is well separated from each other and constraining all berry-fruited taxa as monophyletic results in 22 additional steps beyond the most-parsimonious trees. Therefore, the multiple origins of berries in this tribe is likely to be real and not an artifact of the analysis (Fig. 3).

Display fruits are found in a minimum of three instances, *Codonanthopsis/Codonanthe*, *Nematanthus*, and *Alloplectus/Drymonia* (Fig. 3). Since the relationship among genera in the *Columnnea* clade is not

FIG. 2. Strict consensus of 10 trees of 2,910 steps each of genera of the Gesnerioideae with tribes Beslerieae, Napeantheae, and Coronanthereae as designated outgroups (OG), CI = 0.31, RI = 0.38. Numbers above clades represent branch support values, numbers below clades represent bootstrap values. To minimize computer time, branch support was analyzed using a smaller data set that excluded the Beslerieae, Napeantheae, and Coronanthereae (and *Rytidophyllum* from the Gesnerieae to minimize sampling) and used Sinningieae, Gesnerieae, and Gloxinieae as outgroups (OGb). Taxa that were not used in the branch support analysis are indicated with dashed lines in the cladogram. Clades that did not appear in the shortest of these trees are marked with an asterisk. Abbreviations for tribes are as follows: Be - Beslerieae, Co - Coronanthereae, Ep - Episcieae, Ge - Gesnerieae, Gl - Gloxinieae, Na - Napeantheae, Si - Sinningieae, OG - outgroup, OGb - outgroups for branch support analysis.

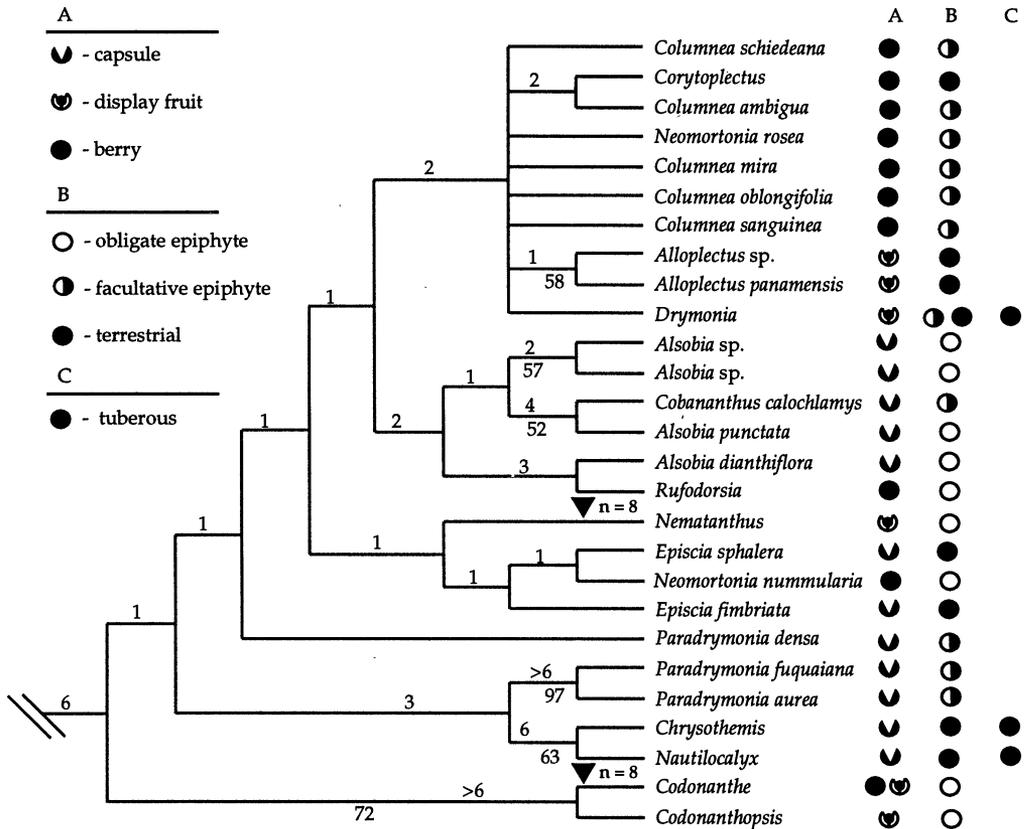


FIG. 3. Strict consensus of genera of the Episcieae used in this analysis as in Fig. 2 but showing only the members of the Episcieae to demonstrate evolution of fruit types (column A), epiphytism (column B), tubers (column C), and chromosome numbers (genera with  $n = 8$  are marked on cladogram, all others are  $n = 9$ ).

fully resolved, it is possible that this fruit has had a fourth origin, but it is more likely to be a synapomorphy for *Alloplectus* and *Drymonia*. Regardless of the number of times it occurs, the display fruit is always found in clades with berry-fruited taxa although one clade with berry-fruited taxa does not possess display fruits (Fig. 3). Two scenarios can be envisioned. Either the display fruit may be an intermediate type between capsules and berries as is suggested by its intermediacy of fleshiness and dehiscence or, it is possible that the display fruit is derived from ancestors with berries and that the ability to dehisce is a reversal. Either possibility can be inferred from the current trees, however, the latter is more likely because berries are found elsewhere in the cladogram without display fruits whereas display fruits are found only in conjunction with berries.

**EPIPHYTISM.** Episcieae contain the majority of epiphytic species within Gesnerioideae, although

epiphytism is largely limited to a few of the larger genera. Epiphytism here is considered a complex character, being the suite of characters that permit plants to grow on trunks and branches of other plants. Since most other genera in the subfamily are terrestrial (including all possible sister groups to the Episcieae), the terrestrial condition is presumed to be ancestral for the Gesnerioideae. Based on the cladograms generated in this analysis, the most parsimonious explanation for the origin of epiphytism (including facultative epiphytes, which are counted as epiphytes) is a single gain at the base of the tribe with five to six reversals to the terrestrial condition (Fig. 3). The terrestrial habit found in species of both *Drymonia* and *Alloplectus* also may serve as an additional synapomorphy to unite these genera and thus would represent one rather than two reversals to the terrestrial condition. Terrestrial species of *Columnnea* also have been described but are not included in this analysis. All other scenarios

of gains and losses require at least one additional step.

**TUBERS.** The tuberous condition is present among several species of Gesneriaceae presumably as an adaptation for surviving seasonally dry habitats (Wiehler 1983). Tubers are known from four genera of Episcieae, *Drymonia*, *Chrysothemis*, *Nautilocalyx* (Fig. 3), and *Rhoogeton* (not included in the analysis). Tubers also are known outside Episcieae in species of Sinningieae and *Lembocarpus* in Gloxinieae (not included in this analysis). The cladogram from this analysis indicates that tubers have evolved at least twice within Episcieae (Fig. 3) and up to four times within Gesnerioideae (Fig. 1). The inclusion of both *Rhoogeton* (Episcieae) and *Lembocarpus* (Gloxinieae) could alter this scenario. Both of these genera have reduced vegetative bodies and have superficial similarities, suggesting that their current classification in separate tribes (Burt and Wiehler 1995) may be inappropriate.

**CHROMOSOME NUMBER.** Episcieae are unique among Gesnerioideae in having a base number of nine. This number serves as an additional synapomorphy for the tribe. However, two genera have counts of  $n = 8$ ; these are *Nematanthus* and *Codonanthe*. Based on the cladogram from this analysis, the count of  $n = 8$  has evolved twice within Gesneriaceae since these two genera are widely separated (Fig. 3). The close sister group relationship of *Codonanthe* to *Codonanthopsis* has been suggested previously and the two genera have been combined (Moore 1973). The close affinity between *Codonanthe* and *Codonanthopsis* ( $n = 9$ ) with branch support of greater than six steps and bootstrap values at 72%, implies that the count of  $n = 8$  in *Codonanthe* must have arisen as an aneuploid reduction from *Codonanthopsis*.

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## ANNOUNCEMENT

The Award Committee of the Lawrence Memorial Fund invites nominations for the 1998 Lawrence Memorial Award. Honoring the memory of Dr. George H. M. Lawrence, founding Director of the Hunt Institute for Botanical Documentation, the Award (\$1,000) is given biennially to support travel for doctoral dissertation research in systematic botany or horticulture, or the history of the plant sciences, including literature and exploration.

Major professors are urged to nominate outstanding doctoral students who have achieved official candidacy for their degrees and will be conducting pertinent dissertation research that would benefit significantly from travel enabled by the Award. The

Committee will not entertain direct applications. A student who wishes to be considered should arrange for nomination by his/her major professor; this may take the form of a letter which covers supporting materials prepared by the nominee.

Supporting materials should describe briefly but clearly the candidate's program of research and how it would be significantly enhanced by travel that the Award would support. Letters of nomination and supporting materials, including seconding letters, should be received by the Committee no later than 1 May 1998 and should be directed to: Dr. R. W. Kiger, Hunt Institute, Carnegie Mellon University, 5000 Forbes Avenue, Pittsburgh, PA 15213-3890 USA. Tel. (412) 268-2434.