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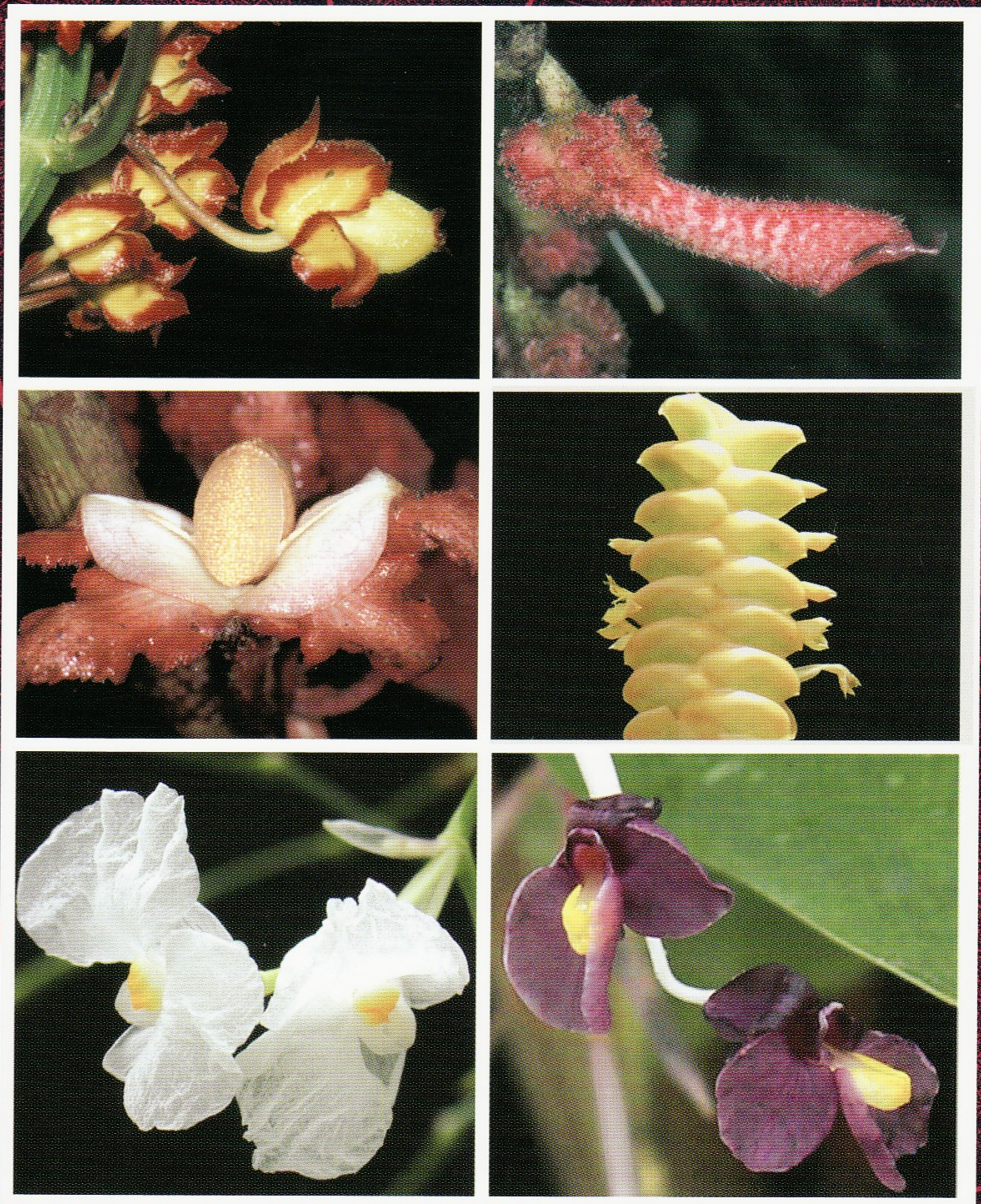
Phylogeny of Marantaceae

Phylogeny of *Usnea* and
Neuropogon (Ascomycota)

Willi Hennig on transforma-
tion series

Potential utility of datasets
for phylogeny reconstruction

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Phylogenetic relationships and generic boundaries in the Episcieae (Gesneriaceae) inferred from nuclear, chloroplast, and morphological data

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Episcieae is the most diverse tribe of Gesneriaceae, with 22 genera and over 700 species, or roughly 21% of all Gesneriaceae. The tribe is restricted to the Neotropics and is characterized by axillary flowers derived from a pair-flowered cyme inflorescence by reduction, a three-trace trilacunar node with split lateral bundles, superior ovaries, and with most members having a haploid chromosome number of $n = 9$ [$n = 8$ in *Codonanthe* and *Nematanthus*]. Most traditionally recognized genera in Episcieae are either known to be non-monophyletic or have not been represented adequately in phylogenetic analyses to test their monophyly. This paper presents phylogenetic analyses utilizing two molecular [the internal transcribed spacer region of 18S-26S nuclear ribosomal DNA (ITS) and the *trnH-psbA* intergenic spacer for 155 species] and one morphological (99 characters for 120 species) datasets, combined in a total evidence analysis. All traditionally recognized genera of Episcieae except for the monotypic genus *Lampadaria* are represented. Of the 21 sampled genera in Episcieae, 16 are represented by the generic type species. The genera *Glossoloma* and *Crantzia* are segregated from the genus *Alloplectus* as traditionally recognized. Other genera that are strongly supported as monophyletic include *Alsobia*, *Columnea* (with the inclusion of *C. dielsii*), *Corytoplectus*, and *Episcia*. *Drymonia* is weakly supported and is shown here to be morphologically diverse and in need of further evaluation. Evolution of fruit structure is examined in the context of the phylogenetic results presented here with two previously unreported features that are here referred to as capsules with tardily dehiscent and non-dehiscent endocarps. Three independent origins of resupinate flowers are inferred for *Glossoloma*, *Nematanthus*, and *Crantzia*. Strongly supported clades have centers of diversity in southeastern Brazil (*Nematanthus*, *Codonanthe*, *Codonanthopsis*, and *Paradrymonia anisophylla*), northern South America (*Alloplectus*, *Drymonia*, *Columnea*, *Neomortonia*), Central America (*Alsobia*, *Oerstedina*, *Rufodorsia*, *Cobananthus*), and two clades with diversity in the Guiana Shield [(*Paradrymonia*, *Nautilocalyx*, *Chrysothemis*) and (*Lembocarpus*, *Cremersia*, *Rhoogeton*)]. *Neomortonia*, a genus of three species, is poorly supported due to conflict among datasets.

KEYWORDS: *Alloplectus*, *Crantzia*, Episcieae, Gesneriaceae, *Glossoloma*, ITS, *trnH-psbA*.

INTRODUCTION

The Neotropical Gesneriaceae comprises two subfamilies, all Gesnerioideae and part of Coronantheroideae (Burt & Wiehler, 1995). Coronantheroideae contains nine genera and 20 species and extends from Chile to the South Pacific Islands and Australia (Wiehler, 1983; Weber, 2004). Gesnerioideae contains five tribes, 56 genera, and over 1800 species and represents nearly half the worldwide diversity of Gesneriaceae (Wiehler, 1983). The Episcieae is a member of Gesnerioideae and is the most diverse tribe in the family with 22 genera and an estimated 784 species, or roughly 21% of all Gesneriaceae. Episcieae is one of the least studied groups in Gesneriaceae and generic boundaries remain poorly

defined, partly because of an overly simplistic use of fruit and flower structure in delimiting taxa. Currently, very few of the traditionally recognized genera are defined by morphological synapomorphies.

The monophyly of most genera in Episcieae has not yet been tested adequately. Recent studies have focused on assessing relationships of major groups of Gesneriaceae such as tribes and subfamilies (Smith, 2000b; Zimmer & al., 2002; Smith & al., 2004; Roalson & al., 2005), but generic-level relationships and delimitation remain in much the same state of confusion today as they were in the 19th century. Generic boundaries for Neotropical Gesneriaceae have been provided by Hanstein (1854, 1865), Fritsch (1893–1894), and Wiehler (1983). The difference between Hanstein's classification of 1854 and

1865 exemplifies the challenge of generic circumscription in Gesneriaceae. Hanstein initially recognized 66 genera (Hanstein, 1854) and then concluded approximately one decade later that 35 genera were sufficient to accommodate the same number of species (Hanstein, 1865). While reducing the number of genera, he added ranks such as subgenus and section. Even after Hanstein's revised classification (1865), many of his tribes included sections of dubious taxa that he could not classify satisfactorily.

Of the 22 genera in Episcieae, *Columnnea* L. is the only genus that has been consistently shown to be monophyletic using morphological and molecular data (Smith, 1994; Smith & Sytsma, 1994a, b, c). A lack of monophyly for large genera (> 20 spp.) in Episcieae has been suggested for *Alloplectus* Mart. (Clark & Zimmer, 2003), *Codonanthe* (Mart.) Hanst. (Clark & Zimmer, 2003), *Drymonia* Mart. (Smith, 2000b; Clark & Zimmer, 2003), *Episcia* Mart. (Smith & al., 1997), *Nematanthus* Schrad. (Clark & Zimmer, 2003), and *Paradrymonia* Hanst. (Smith & Carroll, 1997; Smith, 2000b; Clark & Zimmer, 2003). *Nautilocalyx* Hanst. has been represented by one species in previous analyses, which makes it the only remaining large episcoid genus that has not been tested adequately. *Nautilocalyx*, estimated to be a genus of 70–80 species (Burt & Wiehler, 1995; Weber, 2004), is represented by seven species in this analysis.

The challenge of generic circumscription in Neotropical Gesneriaceae is best summarized by Burt's (1956) statement, "There is probably no group of flowering plants whose generic classification is more in need of revision than the American Gesneriaceae". The goal of this paper is to address this historically confusing group, which was described by Hemsley (1903) as follows: "The genera of the Gesneriaceae have been so diversely defined and limited by different botanists at different periods that it is difficult to understand what really constitutes a genus in the natural order".

Five primary questions are addressed in this project: (1) Are species of traditionally recognized genera nesting with the generic type species? Of the 22 currently recognized genera, the generic type species of 16 were included in the analysis. (2) Are the molecular markers from plastid regions used in earlier studies useful for addressing generic relationships within Episcieae? An evaluation of commonly used plastid regions from previous molecular analyses was carried out in the course of assessing phylogenetically informative characters in the Episcieae. (3) Can the relatively low resolution and low clade support from a previous ITS study (Clark & Zimmer, 2003) be improved with the addition of a chloroplast marker and morphological data? We felt that a more robust phylogenetic hypothesis and interpretation of morphological evolution is necessary for future studies

of Episcieae. (4) What are the morphological synapomorphies for major clades? A morphological cladistic analysis was conducted to test phylogenetic hypotheses and to evaluate morphological features for traditional genera. (5) Are currently recognized genera monophyletic? Traditional classification is compared and contrasted with phylogenetic relationships. Suggestions are made for the circumscription of genera that will be used for monographic studies and major clades of multiple genera are recognized.

MATERIALS AND METHODS

Taxon sampling and outgroup selection. —

One hundred-fifty five species (Appendix 1) were sequenced for the internal transcribed spacer (ITS) region of 18S-26S nuclear ribosomal DNA (nrDNA) and the *trnH-psbA* intergenic spacer (hereafter called *trnH-psbA*) of the chloroplast genome (cpDNA). A morphological character matrix of 99 characters (Appendix 2) was coded for 120 of the 155 sequenced species (Appendix 3). Most species were photographed in the field and determinations were verified with herbarium voucher specimens, photographs, and the literature. The study of type specimens was necessary for the identification of many *Glossoloma* Hanst. and *Alloplectus* species and was carried out in conjunction with monographic revisions of these two genera (Clark, 2005; Clark, in prep.). All taxa except for *Columnnea paramicola* (Wiehler) L.P. Kvist & L.E. Skog, and *Paradrymonia pedunculata* L.E. Skog have fertile voucher specimens archived at the Smithsonian Institution's U.S. National Herbarium (US), Marie Selby Botanical Gardens (SEL), or the Institut de Recherche pour le Developpement (CAY); see Appendix 1.

Preliminary results from this project and a previous molecular phylogeny based on ITS (Clark & Zimmer, 2003) showed traditionally recognized species of *Alloplectus* to nest in six different clades in the tribe Episcieae. Therefore, the ingroup for the analyses presented here has been expanded to include 153 samples representing 21 of the 22 genera in the tribe Episcieae, plus two outgroup species from the tribe Sinningieae [*Sinningia incarnata* (Aubl.) D.L. Denham and *S. cooperi* (Paxt.) Wiehler]. Also included are the type species for the five segregate sections of *Columnnea*, which have been occasionally treated as distinct genera (Wiehler, 1983; Burt & Wiehler, 1995). The monotypic genus *Lampadaria* Fueillet & L.E. Skog, which is only known from the type locality in French Guiana, was the only genus of Episcieae that is not represented in the analysis. Large genera were sampled heavily (Appendix 1). This study was conducted in conjunction with monographic

revisions of two clades that had traditionally been classified as *Alloplectus* (Clark, 2005; Clark, in prep.). The morphological diversity of this formerly polyphyletic genus provided numerous characters for descriptive taxonomy. Sampling included 25 of the 27 species of *Glossoloma*, four of the five species of *Alloplectus*, and three of the four species of *Crantzia* Scop. Only four species of traditionally recognized *Alloplectus* were not included in this analysis (*Alloplectus inflatus* J.L. Clark & L.E. Skog, *Crantzia* [= *Alloplectus*] *spectabilis* (Wiehler ex L.E. Skog & Steyermark) J.L. Clark, *Glossoloma* [= *Alloplectus*] *cucullatum* (C.V. Morton) J.L. Clark, and *Glossoloma* [= *Alloplectus*] *bicolor* (Kunth) J.L. Clark) because of insufficient material for coding morphological characters and/or lack of tissue samples for molecular sequencing. *Columnnea* contains 200 species (Kvist & Skog, 1993; Smith, 1994) and *Drymonia* about 140 species (Burt & Wiehler, 1995). Previous studies support *Columnnea* monophyly (Smith, 1994; Smith & Sytsma, 1994a, b, c). However, it was densely sampled because some authors have placed its species in five separate genera (Burt & Wiehler, 1995 contra Kvist & Skog, 1993; Smith, 1994; Smith & Sytsma, 1994a, b, c) and because of its great morphological diversity. The sample of *Columnnea* species represented the wide range of morphological variation and geographic distribution present in the genus.

Whenever possible, generic type species were sampled. Of the 21 genera in this analysis, 16 included the generic type species (indicated by asterisks in Appendix 2). Outgroups were *Sinningia incarnata* and *Sinningia cooperi*. Although these species are traditionally included in the tribe Gloxinieae (Burt & Wiehler, 1995), recent molecular phylogenetic analyses using cpDNA *trnL-F/trnE-T* spacer regions and the nrDNA ITS spacer region suggest that *Sinningia* Nees belongs to a clade that is sister to a strongly supported monophyletic Episcieae (Zimmer & al., 2002; Perret & al., 2003). Only *Sinningia* species were easily alignable for ITS regions, whereas other taxa from Gloxinieae [e.g., *Heppiella ulmifolia* (Kunth) Hanst.] or Beslerieae [e.g., *Besleria aggregata* (Mart.) Hanst.] were difficult to align.

DNA extraction, amplification, and sequencing. — Most genomic DNAs were isolated from silica-dried leaf material collected in the field. Other samples were obtained from live plants grown at the Smithsonian's National Museum of Natural History Botany Research Greenhouses (Suitland, Maryland) or the Marie Selby Botanical Gardens (Sarasota, Florida). Most of the samples included in the analysis were collected in the field by the first author throughout five years of intensive fieldwork in the Neotropics. Leaf samples were ground using a ThermSavant FastPrep FP120 cell disrupter (Qbiogene, Carlsbad, CA). DNA was iso-

lated using the Qiagen DNeasy™ DNA isolation kit (Qiagen, Valencia, CA).

Templates of the nrDNA internal transcribed spacer region (ITS) were prepared using the primers ITS5HP (Suh & al., 1993) and ITS4 (White & al., 1990). Additionally, the reverse and forward of the internal primers ITS2 and ITS3 (White & al., 1990) were used to obtain double stranded DNA sequence of the entire ITS region. Templates from the intergenic spacer region (*trnH-psbA*) were prepared using the primers *trnH^{GUG}* (Tate & Simpson, 2003) and *psbA* (Sang & al., 1997).

Evaluation of chloroplast DNA regions *trnL-F* intron & spacer, *rps16* intron, *rpl16* intron, and *trnS-G* spacer, was based on subsets of six divergent species from *Alloplectus*, *Columnnea*, *Glossoloma*, and *Paradrymonia*. Sequence variability and potential grouping information for each dataset were evaluated. The primary criterion used for evaluating each potential plastid region was the number of potentially parsimony informative characters (i.e., substitutions and indels). Also evaluated for each DNA region was the range of pairwise divergence, constant characters, mean GC content, transition/transversion ratio, and parsimony uninformative substitutions. If there was insufficient grouping information in the initial six-taxon subset, then the region was not used. Of the five plastid regions evaluated, only the *trnH-psbA* intergenic spacer showed potential for addressing Episcieae phylogeny. Polymerase chain reaction (PCR) amplifications followed the procedures described by Baldwin & al. (1995) utilizing Taq DNA polymerase (Promega, Madison, WI). To reduce within-strand base pairing that can result in interference with Taq polymerase activity, we found it essential to use 5% DMSO and 5% BSA in PCR reactions for ITS. The PCR products were electrophoresed using a 1.0% agarose gel in 1x TBE (pH 8.3) buffer, stained with ethidium bromide to confirm a single product, and purified using PEG 8000 (polyethylene glycol) in 2.5 M NaCl under the conditions described in Johnson & Soltis (1995). Direct cycle sequencing of purified template DNAs followed the manufacturer's specifications, using the ABI Prism® BigDye™ Terminator Cycle Sequencing Ready Reaction Kit (PE Biosystems, Foster City, CA). Cycle sequencing was carried out with the two initial PCR primers and the internal primers, ITS3 and ITS2 (White & al., 1990). Sequencing was performed using an Applied Biosystems Model 377 Automated DNA Sequencing System (PE Biosystems).

DNA chromatograms were proofed, edited, and contigs were assembled using Sequencher 3.0 (Gene Codes Corporation, Ann Arbor, MI). The sequences were truncated to include only ITS1, 5.8S, and ITS2 regions. Identification of the ends of ITS1 and ITS2 were determined by comparisons with other Gesneriaceae sequences (Zimmer & al., 2002). Sequences have been

deposited in GenBank (Appendix 1).

Alignment. — All sequences were aligned manually in the multiple sequence editor program SeAl version 2.0a11 (Rambaut, 2002). Because the sequences were not highly divergent, it was possible to make minor adjustments minimizing overlapping gaps. This approach allowed for single-site and multiple-site gaps to be treated with equal weight (Simmons & Ochoterena, 2000). Regions that were not easily aligned were excluded from the analyses. Tree searches were carried out with gaps as missing data in the alignment, but indels of constant length were incorporated in the final data matrix as separate presence/absence characters.

Morphological dataset. — The morphological matrix includes 99 characters (30 vegetative and 69 reproductive) for 120 of the 155 species sequenced. Characters and character states are described in Appendix 2. The character matrix for the 120 species is provided in Appendix 3. Characters were primarily scored by examination of live material in the field, live material grown in cultivation, herbarium specimens, and from the literature (Skog, 1976; Wiehler, 1976, 1983; Dodson & Gentry, 1978; Beaufort-Murphy, 1983). Characters from previously published morphological analyses of Gesneriaceae (Boggan, 1991; Smith, 1996; Roalson & al., 2002, 2005) were assessed and modified as needed for this analysis. Chromosome information was obtained from Skog (1984) and Oliver & Skog (1985).

Herbarium material was examined using a Leica MZ7.5 microscope. Many flowers were field preserved in Copenhagen mixture (85% ethanol + glycerin) and stored in vials. When pickled material was not available for study, flowers from herbarium collections were rehydrated in Pohl's solution (Pohl, 1965). Other than chromosome number, nearly all characters scored from the literature were also confirmed by direct observation. One exception was *Cremersia platula* Feuillet & L.E. Skog, for which most reproductive characters were scored from the literature because only two collections containing sparse material of this species are known to exist. Several characters are unknown for some species because they are not described in the literature and herbarium/live material was insufficient for their scoring (e.g., fruit and seed characters; Appendices 2, 3). As recommended by Yeates (1992), characters that were uninformative autapomorphies are included in Appendix 2 to provide information for possible future phylogenetic studies of *Episcieae*. All characters were unordered (Fitch, 1971). An effort was made to use reductive binary coding to minimize the number of multistate characters (Strong & Lipscomb, 1999). For some suites of characters (e.g., fruit structure) alternative character definitions that combined several characters into single multistate characters were tested but found to be inferior. Winclada (Nixon,

2002) and MacClade (Maddison & Maddison, 2000) were used for building the data matrices and optimizing characters.

Mechanism of floral inversion. — The mechanism of floral inversions was studied in *Glossoloma*. Field observations of mature and immature flower orientation were observed and photographed. Serial cross sections employing standard paraffin technique were used to verify the absence or presence of a twist in the vascular structure. Pedicels were soaked in bleach, rinsed, dehydrated with an ethanol series, embedded in paraffin and sectioned on an American Optical rotary microtome and stained with safranin-fast green (Berlyn & Miksche, 1976). Additionally, whole pedicels were cleared and stained with safranin and fast green and then mounted on slides.

Phylogenetic analyses. — The parsimony analysis was performed to completion using a two stage heuristic search in PAUP* 4.0b10 (Swofford, 2002). The first stage of the analysis was done using the following settings: 1000 random addition cycles, holding 10 trees at each step; tree bisection-reconnection (TBR) branch swapping with no more than 10 trees saved for each rep; MULTREES option not in effect. The second stage of the analysis was performed on all trees in memory with the same settings, but with the MULTREES option in effect. Other searches were conducted, but did not find shorter trees using the settings above with the following changes: 10 random addition cycles limited to 1000 trees of equal length for each of the replicates; 1000 random addition cycles limited to 100 trees of equal length for each of the replicates.

Additional tree searches were done using the parsimony ratchet analysis with NONA (Goloboff, 1999) and Winclada (Nixon, 2002). Ten separate tree searches were conducted using the following settings: 200 iterations per search, one tree held for each iteration, 132 characters sampled (10% of the total), and amb=poly- (only considers unambiguous support). The total evidence analysis was swapped to completion, but analyses of individual datasets were limited to 100,000 trees. Multiple ratchet searches were performed in WinClada as suggested by Nixon (1999) since the ratchet option can sometimes get stuck on suboptimal "islands" and it is therefore better to perform more separate searches with fewer iterations than one larger search with more iterations.

Clade robustness was evaluated in PAUP* using the bootstrap (Felsenstein, 1985). The bootstrap analysis used 1000 heuristic bootstrap replicates with the following settings: 10 random addition cycles; tree bisection-reconnection (TBR) branch swapping with no more than 10 trees saved for each replicate.

The parsimony analyses and clade support were evaluated for each individual dataset, a combined molec-

ular dataset, and in a total evidence analysis (ITS, *trnH-psbA*, and morphology). Conflict between datasets was evaluated by comparing incongruence of strongly supported clades from individual datasets (e.g., ITS vs. *trnH-psbA*; ITS vs. morphology; and *trnH-psbA* vs. morphology).

RESULTS

Sequence alignment. — Table 1 provides a summary of the two molecular datasets utilized in this study. The two *trnH-psbA* sequencing primers produced overlapping fragments that collectively covered the entire intergenic spacer along both strands. The aligned *trnH-psbA* data matrix was 530 bp long with 289 variable sites (55%). The length of the unaligned complete sequences varied from 205 to 363 bp. The aligned data matrix (excluding ambiguous regions) contained six parsimony informative indels ranging from 5–11 bp in length, and 19 non-informative indels (i.e., autapomorphies), which were not used in the analysis. Excluded from the analysis were 120 ambiguously aligned sites. The number of parsimony informative characters (excluding the ambiguously aligned sites) is 76 (14%). The mean pairwise divergence for the entire *trnH-psbA* region was 6.1% (Table 1). A homoplastic 31 bp inversion near the 3' end of *trnH-psbA* was included in the analysis by manually reversing the region and then coding the complement for the 32 species for which it was present.

The four ITS sequencing primers produced overlapping fragments that collectively covered the entire spacer and 5.8S rDNA regions. The aligned ITS data matrix was 670 bp long with 384 variable sites (57%), of which 296 (44%) were parsimony informative. The length of the unaligned complete sequences varied from 614–629 bp. The aligned data matrix contained fourteen informative indels ranging from 1–7 bp in length, and 23 non-informative indels (i.e., autapomorphies), which were not used in the analysis. There were no ambiguously aligned sites excluded from the analysis. The mean pairwise divergence for the ITS region was 8.3% (Table 1).

Parsimony analysis of sequence data. — Parsimony analysis of the ITS data was restricted to

100,000 most-parsimonious trees [length = 1988 steps, CI (consistency index) = 0.33, RI (retention index) = 0.69, RC (rescaled consistency index) = 0.23]. The strict consensus of these trees, which includes 155 taxa, is mostly congruent with previous results from a dataset of 72 taxa (Clark & Zimmer, 2003) in the sister group relationship between *Glossoloma* and *Alloplectus*. ITS results for this study are not shown because of the lack of strongly supported differences between the ITS results in Clark & Zimmer (2003) and the results obtained here. Parsimony analysis of the *trnH-psbA* data was restricted to 100,000 most-parsimonious trees (length = 400 steps, CI = 0.63, RI = 0.81, RC = 0.51). The strict consensus of these trees is poorly resolved (103 nodes collapsed in strict consensus tree) with a majority of *Alloplectus*, *Drymonia*, and *Columnnea* unresolved (results not shown). Parsimony analysis of the combined *trnH-psbA* and ITS datasets was restricted to 100,000 most parsimonious trees (length = 2470 steps, CI = 0.36, RI = 0.70, RC = 0.35). Support for the monophyly of *Columnnea* (bs = 86%) and *Glossoloma* (bs = 77%) increases slightly with the combined molecular datasets as compared to ITS alone (*Glossoloma*, bs = 63%; *Columnnea*, bs = 75%).

Parsimony analysis of morphological data. — Parsimony analysis of the morphological data was restricted to 100,000 most-parsimonious trees (length = 1064 steps, CI = 0.12, RI = 0.55, RC = 0.06). The strict consensus of these trees is poorly resolved (results not shown). The total amount of missing data (unobserved and inapplicable characters) was 12%. The only genera that were resolved in the morphological analysis were *Columnnea*, *Episcia*, and *Corytoplectus* Oerst.

Combined analysis of cpDNA, nrDNA, and morphology. — Parsimony analysis of the combined data resulted in 4,360 most-parsimonious trees (length = 3639 steps, CI = 0.27, RI = 0.63, RC = 0.17). A summary of major clades from the strict consensus tree of the total evidence analysis of the three datasets is presented in Fig. 1. One of the most parsimonious cladograms is shown in Figs. 2–5 with the unambiguous characters optimized on the branches. *Columnnea*, *Neomortonia* Wiehler, and *Alloplectus* form a clade (Figs. 1, 5). The *Alloplectus* clade has a bootstrap value of 100% (Figs. 1, 5). The monophyly of *Columnnea* [with the inclusion of

Table 1. Characteristics of cpDNA and nrDNA-ITS. Values in parentheses are for the ingroup only (i.e., Episcieae). L = length; AL = alignment length; GC = Mean GC content; PW = Mean pair-wise divergence; Tr/Tv = Transitions/transversions; Ambig. = Ambiguous regions excluded; PUS = parsimony uninformative substitutions; PIS = parsimony informative substitutions; Indel = number of unambiguous indels; CI = Consistency index; RI = Retention index; RC = Rescaled consistency index; TL = tree length.

Region	Taxa	L (bp)	AL (sites)	GC (%)	PW (%)	Tr/Tv	Ambig. (bp)	PUS	PIS*	Indel*	CI	RI	RC	TL
<i>trnH-psbA</i> spacer	155	207–363	530	31.4	6.10 (6.00)	0.49 (0.49)	130	92	76	6	0.63	0.81	0.51	351
ITS	155	614–629	670	58.3	8.29 (8.08)	2.14 (2.14)	0	89	297	14	0.33	0.69	0.23	1988

* Potentially informative characters.

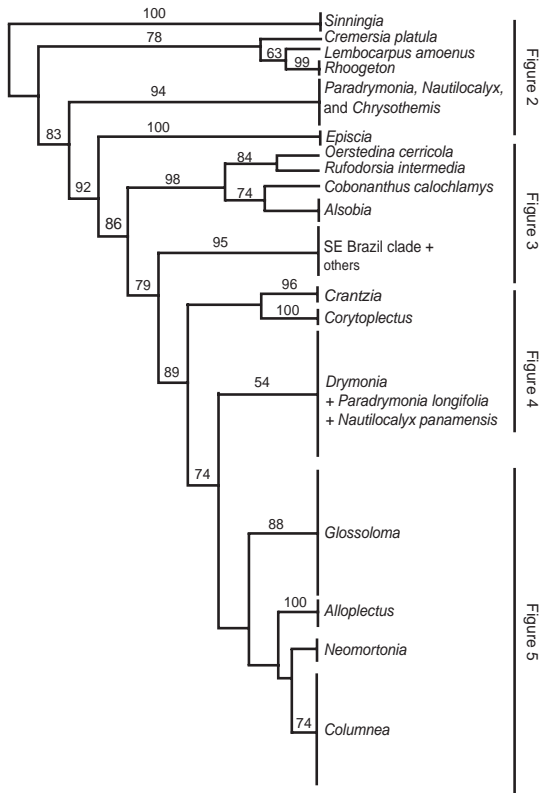


Fig. 1. Summary of the strict consensus tree from total evidence analysis of three datasets (nrDNA ITS, cpDNA *trnH-psbA*, and morphology). The strict consensus tree is from 4,360 most-parsimonious trees of 3639 steps. Numbers above branches are bootstrap percentages where branch support is greater than 50%.

Columnnea dielsii Mansf. = *Alloplectus dielsii* (Mansf.) Wiehler] has a bootstrap value of 74% (Figs. 1, 5). The *Glossoloma* clade has a bootstrap value of 88% (Figs. 1, 5), but the sister taxa relationships between *Glossoloma*, *Neomortonia*, *Alloplectus*, and *Drymonia* are not strongly supported (Figs. 1, 5). Other well-supported monophyletic genera are *Corytoplectus* (bs = 100%), *Episcia* (bs = 100%), *Crantzia* (bs = 96%), and *Rhoogeton* Leeuwenb. (bs = 100%). Strongly supported clades from individual datasets did not conflict with each other. Incongruence between datasets was restricted to clades that were not well-supported. As a result of the lack of conflict between datasets and the lack of resolution of individual datasets, only the results of the total evidence analyses are shown here.

The combination of all three datasets provided significantly more resolution over the analysis of any individual dataset. Thus, a combined analysis for the three datasets presented here is considered to be the most appropriate representation of phylogenetic signal based on lack of apparent data conflict and the inherent benefits of a total evidence approach (Kluge, 1989; Bruneau & al., 1995; Nixon & Carpenter, 1996; Graham & al., 1998).

DISCUSSION

Homoplastic inversion in *trnH-psbA*. — A 31-basepair inversion the *trnH-psbA* intergenic spacer is present in 32 species throughout the Episcieae. The inversion has a CI = 0.03 and an RI = 0.03. This inversion was found to be a single-taxon autapomorphy in 27 of the 32 species where it was present and it occurred in every major clade of this analysis. So that this region could be included in the phylogenetic analysis, the inverted sequence regions were re-inverted and then the complement of the sequence was inserted in the dataset. Small homoplastic inversions have been shown to occur frequently in non-coding plastid regions associated with putative hairpin secondary structures in *rpl16* (Kelchner & Wendel, 1996; Kelchner, 2000) and have been reported for the *trnH-psbA* region (Sang & al., 1997; Tate & Simpson, 2003).

Comparison with other studies of Episcieae phylogeny. — Other phylogenetic studies of Episcieae have had limited taxon sampling or were based on genes or regions with insufficient variability (e.g., *ndhF*, *trnL-F*). Studies that included limited taxon sampling of Episcieae include eight species sampled in Smith & al. (2004); five species sampled in Smith & al. (1997); 25 species sampled in Smith & Atkinson (1998); and 12 species sampled in Smith (Smith & al., 1997). Zimmer & al. (2002) included 13 species from 12 different genera of Episcieae in a large-scale phylogenetic analysis of the Gesnerioideae based on ITS, *trnL-F*, and *trnE-T*. The monophyly of Episcieae was well supported (bs = 81%) and within Episcieae the *Chrysothemis* Decne., *Nautilocalyx*, and *Paradyrmonia* clade was well-supported (bs = 80%) and a clade of *Codonanthe* (Mart.) Hanst. and *Nematanthus* was strongly supported (bs = 100%). Strongly supported clades from Zimmer & al. (2002) are congruent with the present study.

Smith & Carroll (1997) analyzed 27 species from 15 different genera of Episcieae based on *ndhF* sequence data. Smith (2000b) later expanded the study to include 40 species from 16 different genera and added ITS as an additional molecular marker. Strongly supported clades are congruent with results presented here, where the following bootstrap values are from Smith (2000b): a clade of *Nautilocalyx* (1 sp.) and *Chrysothemis* (1 sp.) was strongly supported (bs = 97%); *Alsobia punctata* (Lindl.) Hanst. and *Cobonanthus calochlamys* (Donn.Sm.) Wiehler (bs = 89%); and *Codonanthe elegans* Wiehler and *Codonanthopsis* Mansf. (bs = 100%). Incongruence between this study and Smith (2000b) and Smith & Carroll (1997) is primarily restricted to weakly supported clades (e.g., the placement of *Rhoogeton* as sister to *Nematanthus* instead of being one of the first branching members of the tribe as presented here).

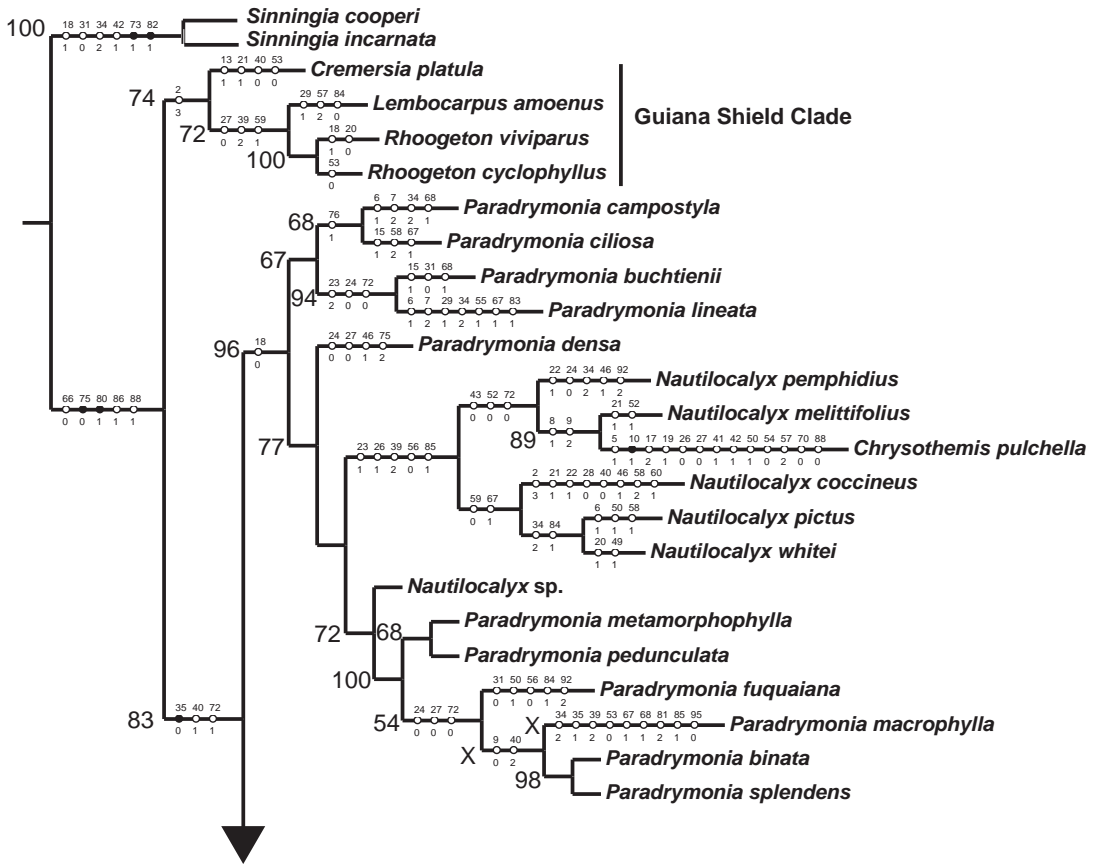


Figure 3

Figs. 2. One of 4,360 most parsimonious cladograms with unambiguous characters optimized on the branches. Character numbers are above the branches and character state numbers are below the branches. Nodes that collapse in the strict consensus tree are indicated ("X") at the base of the branch. Species traditionally recognized as "Alloplectus" are indicated by an ("**"). Bootstrap values (= 50%) for nodes present in the strict consensus tree are given at the base of the branch. (continued on Figs. 3–5)

The study presented here represents the most extensive taxon sampling to date focusing on Episcieae. The 155 included species are from diverse geographic localities and represent exhaustive sampling where episcoid diversity is high: Ecuador/Colombia (70 spp.), Panama/Costa Rica (31 spp.), SE Brazil (11 spp.), northern Central America (8 spp.), Venezuela (7 spp.), Peru (3 spp.), Bolivia (8 spp.), the Caribbean (3 spp.), and the Guiana Shield (13 spp.). Three species are represented by cultivated material from unknown localities. The generic type species missing from this analysis are *Codonanthe gracilis* (Mart.) Hanst., *Columnnea scandens* L., *Corytoplectus capitatus* (Hook.) Wiehler, *Episcia reptans* Mart., *Nautilocalyx bracteatus* (Planch.) Sprague, and *Rufodorsia major* Wiehler.

Generic boundaries in the Episcieae. — The ITS data weakly supported a sister group relationship between *Alloplectus* and *Glossoloma*, which is congruent with Clark & Zimmer (2003). These two clades include

the majority of the diversity of what was traditionally recognized as *Alloplectus*. In contrast to the ITS analysis, the sister group relationship between *Alloplectus* and *Glossoloma* is not found in the combined analysis, rather *Glossoloma* is sister to a clade that includes *Alloplectus*, *Columnnea*, and *Neomortonia* (Figs. 1, 5). The relationship of the two *Neomortonia* species as sister taxa is not supported (< 50% bs). The ITS dataset keeps the two *Neomortonia* species apart (Clark & Zimmer, 2003), but in the combined analysis they form a clade based on morphological characters (Figs. 1, 5). The monophyly of *Glossoloma*, *Columnnea* (with the addition of one species previously treated as *Alloplectus*), and *Alloplectus* is weakly supported. *Glossoloma* and *Alloplectus* could be treated as congeners following traditional classification, as ITS data support them as sister groups (Fig. 1 in Clark & Zimmer, 2003). However, we argue that they should be treated as distinct genera because their recognition is practical since they are morphologically distinct with

Figure 2

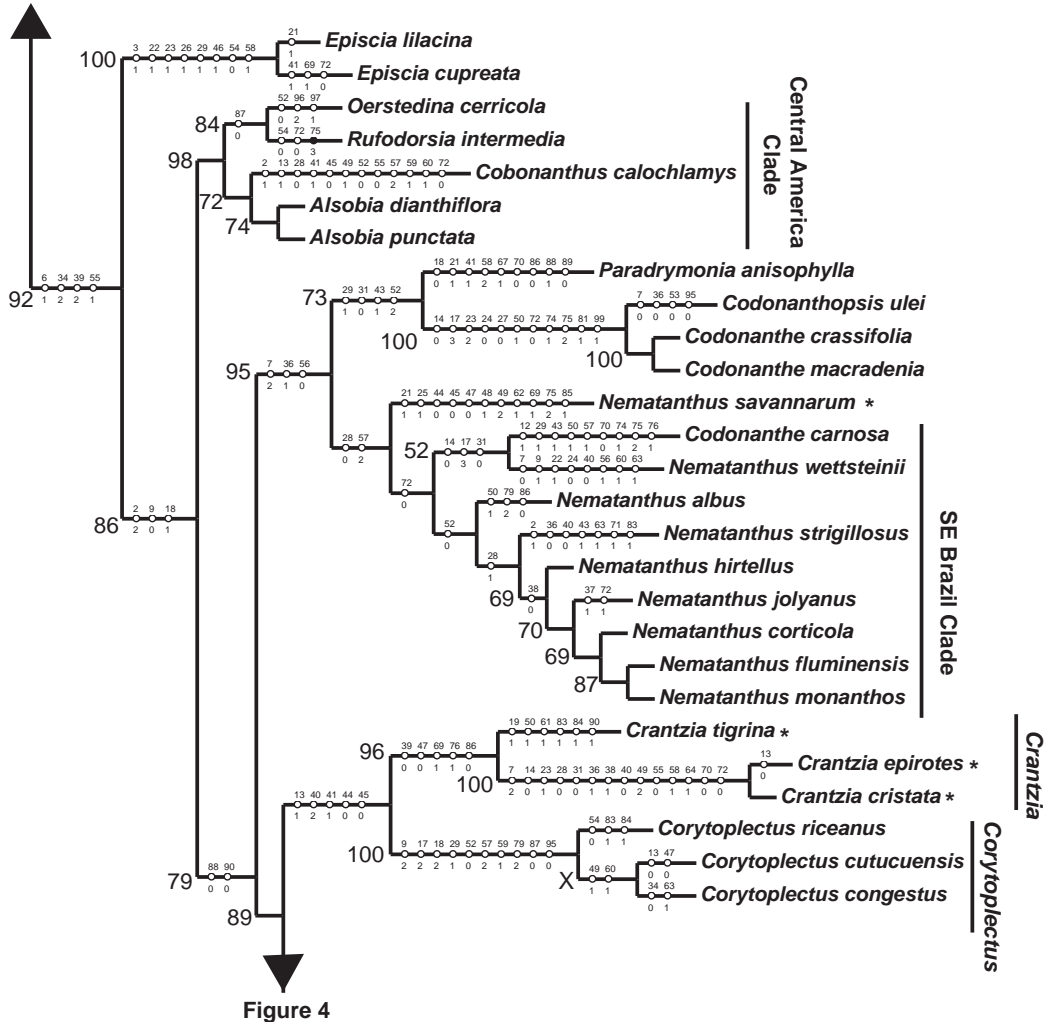


Figure 4

Figs. 3. One of 4,360 most parsimonious cladograms with unambiguous characters optimized on the branches. For further explanations see Fig. 2.

well defined morphological synapomorphies. Traditionally recognized genera that are strongly supported as monophyletic (not counting the monotypic *Cobananthus* Wiehler, *Cremersia* Feuillet & L.E. Skog, *Lembocarpus* Leeuwenb, and *Lampadaria*) are *Columnea*, *Corytoplectus*, *Alsobia*, and *Episcia*. Several genera, including *Nautilocalyx*, *Chrysothemis*, *Paradrymonia*, *Rhoogeton*, and *Codonanthe* are insufficiently sampled in this analysis to assess monophyly and need further evaluation. The separation of the genera *Alsobia* and *Episcia* is well supported. The broad view of *Columnea* as one monophyletic genus instead of five genera is supported. An expanded circumscription of *Drymonia* is presented here that includes a clade of species traditionally recognized as *Alloplectus* (species marked with “*” in Figs. 4, 5) and the inclusion of *Paradrymonia longifolia* (Poepp.) Wiehler and *Nautilocalyx panamensis* (Seem.)

Seem. (Fig. 4). **Generic recognition of *Glossoloma*, *Crantzia*, and *Alloplectus*.** — One of the primary reasons behind conducting this analysis was the need for phylogenetic guidance in preparing a monographic revision of the genus *Alloplectus*, which was suspected to be non-monophyletic. Species traditionally placed in *Alloplectus* are here shown to belong to *Alloplectus* (5 spp.), *Glossoloma* (27 spp.), and *Crantzia* (4 spp.), with other discordant members nesting in *Drymonia* (5 spp.), *Columnea* (1 sp.), and *Nematanthus* (1 sp.). The revised generic circumscription of *Alloplectus* that has been adopted based on these analyses comprises a group of five species, including *Alloplectus hispidus* (Kunth) Mart., the conserved type for the genus (Feuillet & Skog, 1990). Numerous hypotheses have been proposed for the sister group relationship of “*Alloplectus*” (Smith & Sytsma,

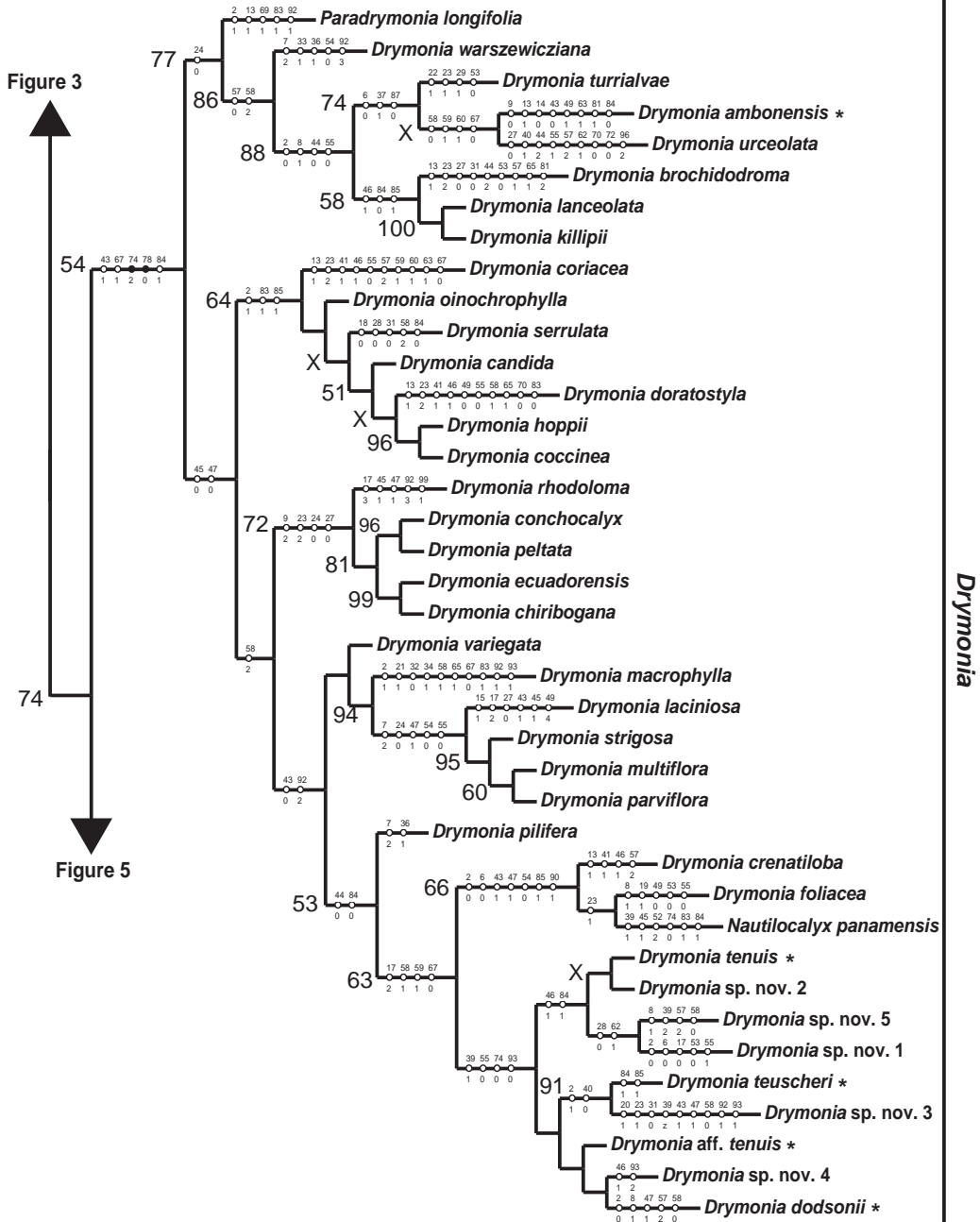


Fig. 4. One of 4,360 most parsimonious cladograms with unambiguous characters optimized on the branches. For further explanations see Fig. 2.

1994a, b, c; Smith, 1996, 2000a, b, c; Smith & Carroll, 1997; Smith & al., 1997, 2004; Smith & Atkinson, 1998; Zimmer & al., 2002), but only one included *A. hispidus* (Clark & Zimmer, 2003). Most of the previous phylogenetic studies utilized species from what is treated here as the genus *Glossoloma*, which has been regarded as a synonym of *Alloplectus* since Hanstein (1865). This study shows that *Glossoloma* is a distinct clade from *Alloplectus* with well defined morphological characteris-

tics.

Most characters traditionally used to define *Alloplectus*, such as a fleshy bivalved dehiscent capsule, a pendent inflorescence of a reduced pair-flowered cyme, and a haploid chromosome number of $n = 9$, are plesiomorphic characters that are shared with other genera such as *Drymonia* and *Paradyrmonia* (Fig. 3). Other characters previously used to define *Alloplectus*, such as a tubular or pouched corolla tube, are convergent with

Figure 4

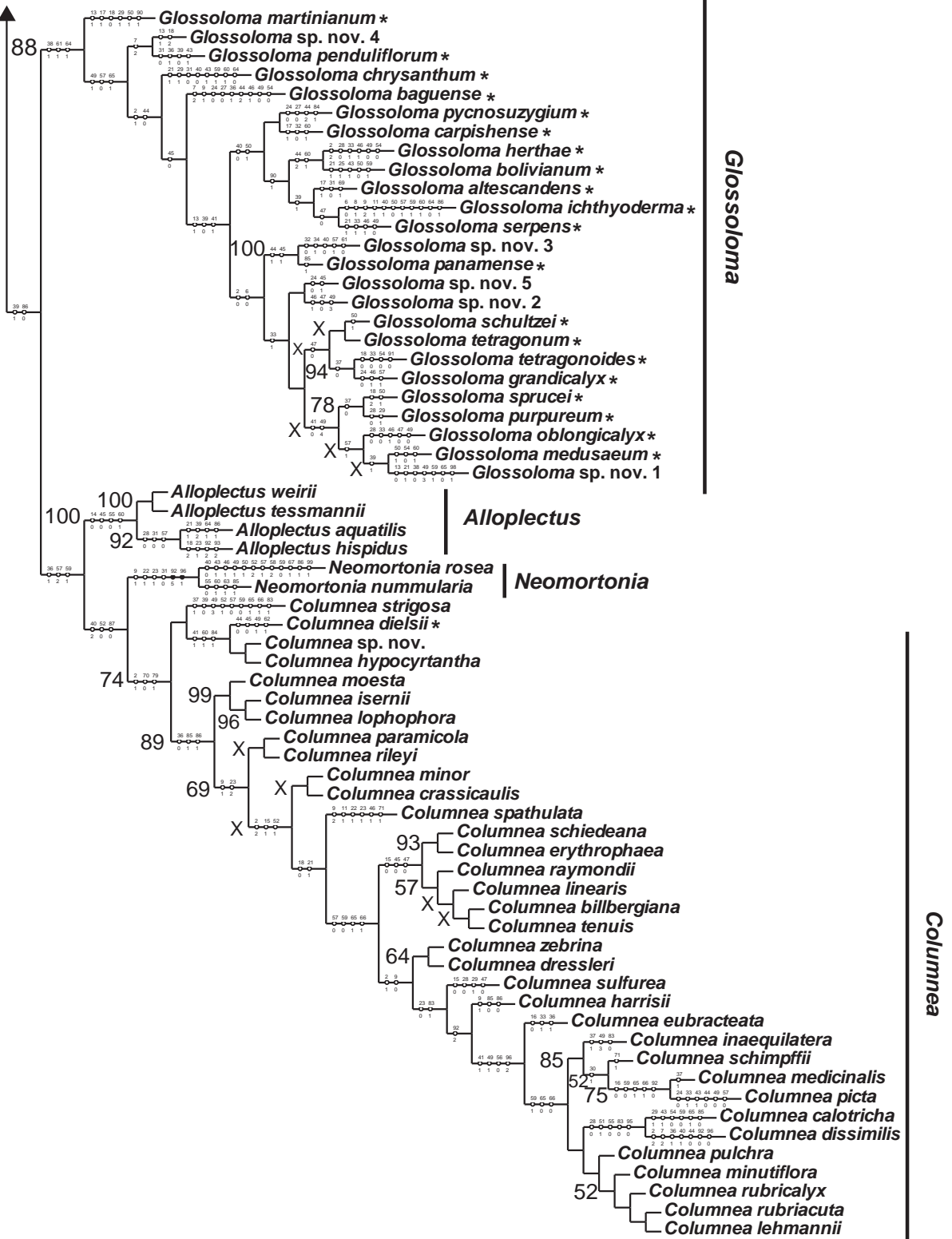


Fig. 5. One of 4,360 most parsimonious cladograms with unambiguous characters optimized on the branches. For further explanations see Fig. 2.

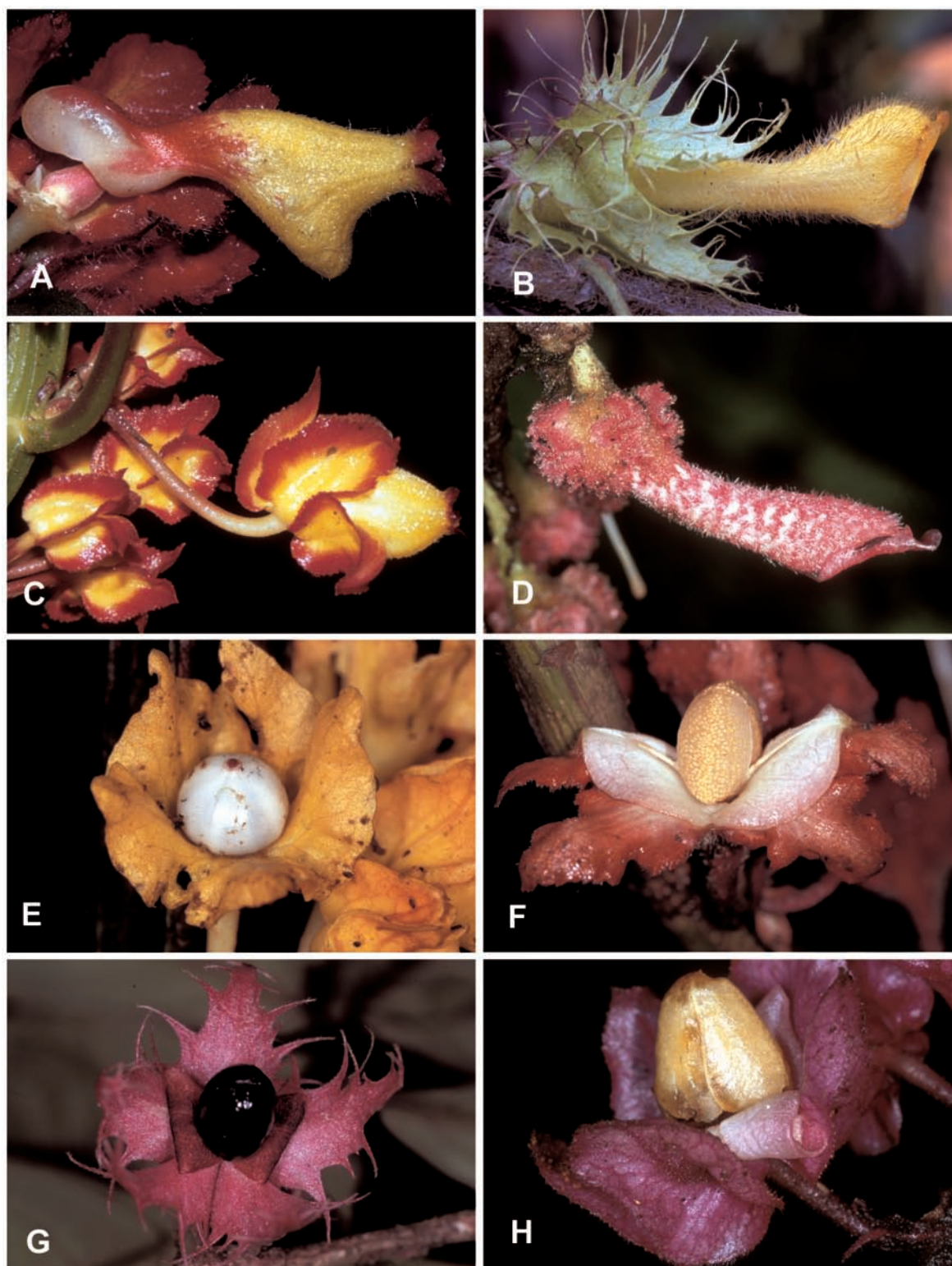


Fig. 6. Variation in flowers and fruits in Episcieae. A, *Drymonia teuscheri* showing non-resupinate flowers with central distended pouch (character 63); B, *Glossoloma purpureum* showing resupinate flower with distal pouch present (character 61); C, *Drymonia* sp. nov. showing non-resupinate flower with central non-distended pouch (character 62); D, *Glossoloma* sp. nov. showing resupinate flower with distal pouch absent (character 61); E, *Drymonia ambonensis* showing berry fruit (character 87); F, *Glossoloma* sp. nov. showing fleshy capsule (character 87); G, *Drymonia multiflora* showing non-dehiscent endocarp; H, *Drymonia* sp. nov. showing tardily-dehiscent endocarp. Note adhering layer covering seeds.

Nematanthus. To a certain extent, *Alloplectus* was defined by what it lacked. For example, species with poricidal anther dehiscence were treated as *Drymonia*, species with translucent berries were treated as *Corytoplectus*, species with non-translucent berries were treated as *Columnnea*, and species with stolons were treated as *Alsobia* or *Episcia*. Thus, *Alloplectus* had become a collection of species that lacked unifying synapomorphies.

Unambiguous morphological synapomorphies that unite the five species recognized here as *Alloplectus* are: secondary leaf venation that is inconspicuous when dry (character 14), ovate calyx lobes (character 45), glabrous internal corolla surface (character 55), and apically constricted corollas (character 60; Fig. 6A). Other characters of *Alloplectus* that are useful for distinguishing it from *Glossoloma* are the subwoody perennial epiphytic habit, non-resupinate flowers, and profusely branched stems.

Unambiguous morphological synapomorphies that unite the 27 species recognized here as *Glossoloma* are: resupinate flowers (character 38; Figs. 6B, D), pouched region near the corolla apex that is not apically constricted (character 61; Figs. 6B, D), and tubular corollas appearing laterally compressed (character 64). Most species of *Glossoloma* are unbranched terrestrial subshrubs in contrast to the branched, primarily epiphytic genera *Drymonia*, *Columnnea*, and *Alloplectus*.

Alloplectus, *Crantzia*, and *Glossoloma* have geographically distinct centers of diversity. The five species of *Alloplectus* range from Costa Rica to Peru and are most abundant in the southern Andes of Colombia. The four species of *Crantzia* are from the Lesser Antilles, coastal Venezuela, and the Guiana Shield. *Glossoloma* extends from southern Mexico to Panama, northwestern South America, and south to Bolivia. It ranges in elevation from sea level in the Chocó forests of northwestern South America to 3500 meters in the Andean cloud forests of Colombia and Ecuador. The center of diversity, with 15 species of *Glossoloma*, is the western lowland forests in Ecuador and Colombia.

Implications for circumscription of *Drymonia*. — *Drymonia* is one of the largest genera of Neotropical Gesneriaceae with an estimated 140 species (Burt & Wiehler, 1995). The primary generic characters that Martius (1829) used for circumscribing *Drymonia* are a leafy calyx and large corolla, but these features are also found in many other episcoid genera. The morphological synapomorphy that distinguishes *Drymonia* from most other Gesneriaceae is poricidal anther dehiscence, first described by Moore (1955) and further elaborated by Wiehler (1983). This feature was not noted nor illustrated in the original description of the genus by Martius (1829). Wiehler (1983) noted that poricidal anthers are not present on *Martius 3014*, the lectotype of *D. cal-*

carata Mart. (= *D. serrulata* (Jacq.) Mart. and the type species of *Drymonia*). However, the lectotype at M represents a specimen with more mature flowers with anthers in a later longitudinal stage of dehiscence, rather than the early pore stage of dehiscence.

Wiehler (1983) described the anthers in *Drymonia* as being “salt-shaker-like”. In bud, the anthers are grouped coherently around the style, with their pore-like thecae facing inward. As the anthers mature, they become connate along the length of the thecal margins and at their upper end. The individual thecae open by a short basal pore. Just before anthesis, the curvature and the differential length of the filament pairs cause the anthers to invert by rotating 180°. At this late stage, the strategically placed anthers are able to pour or “shake” their powdery pollen grains onto visitors. Steiner (1975) noted on *Drymonia serrulata* (Jacq.) Mart. that oil, exuded from gland-tipped trichomes inside the corolla, promotes the adhesion of pollen grains to the body of *Epicharis* bees (Anthophoridae). It was also noted that it takes between five to eight visits to empty the pollen grains from the anthers by birds, bats, or Euglossine bees (Wiehler, 1983).

Based on personal observations from fieldwork and cultivated collections, it is easier to document poricidal anthers on species that have campanulate corollas (e.g., *Drymonia serrulata*) than on species with urceolate (e.g., *D. urceolata* Wiehler) or hypocryroid corollas [e.g., *D. coriacea* (Oerst. ex Hanst.) Wiehler] because, in the latter two, the pore stage appears to be short-lived. The difficulty in detecting the short-lived pore stage is probably why some of the non-campanulate flowered species were not transferred to *Drymonia* by earlier Gesneriaceae systematists. For example, throughout a one-year period, hundreds of flowers of the urceolate (i.e., non-campanulate) *Drymonia urceolata* were photographed, collected, and observed, but the presence of poricidal anthers was only documented on one flower during an early stage of anthesis (Clark, pers. obs.).

The placement of several non-resupinate former “*Alloplectus*” species in *Drymonia* is weakly supported (bs = 63%; species marked with “*” in Fig. 4). One species that nests within this group is the poorly known *D. crenatiloba* (Mansf.) Wiehler from the eastern slopes of the Andes. The generic placement of this species was uncertain before this analysis. Although it was originally described by Mansfeld (1938) in *Alloplectus*, Wiehler (1981) transferred it to *Drymonia* because of the presence of poricidal anther dehiscence. However, based on flower dissections from collections of *D. crenatiloba* at US, all were observed to have longitudinal dehiscence, although this feature has not yet been verified with living material. Determining whether poricidal anther dehiscence is present can be difficult because, as the anthers age, they often open fully, developing longitudinal slits.

Therefore, it is possible that the observed longitudinal slits are from a later stage in anthesis that has already matured past a younger “pore” stage. Two features that help differentiate this clade from other *Drymonia* species are the non-campanulate corollas and presence of capsules with tardily dehiscent endocarps (see fruit structure below). The results presented here imply that pores have been lost in at least one lineage in the *Drymonia* clade (Fig. 4).

Circumscription of *Nematanthus*, *Codonanthe*, and *Codonanthopsis*. — The *Nematanthus*, *Codonanthe*, *Codonanthopsis* clade is well supported in this study (bs = 95%; Figs. 1, 3), congruent with a previous phylogenetic analysis (Clark & Zimmer, 2003). This clade has strong support, yet it has no morphological features that unite these taxa. The single non-molecular synapomorphy that defines this clade is a haploid chromosome number of $n = 8$ with a reversal to $n = 9$ for *Codonanthopsis* (character 1). All other Episcieae groups for which chromosome counts are available have a haploid chromosome number of $n = 9$ (Smith, 2000b; Zimmer & al., 2002), including the type species for *Codonanthopsis* (*C. ulei* Mansf. chromosome count in Oliver & Skog, 1985). Wiehler (1978a) also reported a haploid chromosome count of $n = 9$ for *Codonanthopsis dissimulata* (H.E. Moore) Wiehler, but this species is not included in the present analysis and its phylogenetic placement has never been tested.

Chautems (1988) and Moore (1973) used the presence of resupinate flowers as a character for differentiating groups of species in *Nematanthus*. In his monographic revision of the genus Chautems further divided the resupinate flowered *Nematanthus* species into those that had pendent resupinate flowers with long pedicels (2–20 cm), and those that have non-pendent resupinate flowers. Chautems (1988) recognized nine species of *Nematanthus* that are non-pendent resupinate, seven that are pendent and resupinate, and ten that are not resupinate. Species from each of Chautems’ categories were used in this analysis. A fourth flower type that was not included in Chautems’ revision, but is included in this analysis, is large campanulate white flowers that are non-resupinate (e.g., *Nematanthus albus* Chautems). Results from this study suggest that presence of resupinate flowers in *Nematanthus* is a synapomorphy for a clade within the genus to the exclusion of the non-resupinate species, which are poorly resolved (Fig. 3; character 38).

The clade comprised of *Nematanthus*, *Codonanthe*, *Codonanthopsis*, and *Paradrymonia anisophylla* Feuillet & L.E. Skog is morphologically diverse and has one of the widest biogeographic distributions for Episcieae, extending from southeastern Brazil to the Guiana Shield, the Andes, and northern Central America (Fig. 3). Furthermore, the Caribbean species, *Codonanthe carib-*

aea Urb. would most likely nest within this clade, but it is a poorly collected species and is not included here. There are ca. 20 collections of this species from the islands of Trinidad and Tobago, but only two collections exist from the type locality in Guadeloupe. One of these collections is the type specimen for *Codonanthe caribaea* (A. Duss 3776) made in 1893 and a second collection by J. Jérémie in 1974. It is noteworthy that *Codonanthe* is shown here not to be monophyletic. The species *Codonanthe carnosa* (Gardner) Hanst. is not resolved with other members of *Codonanthe*. In contrast, the Central American *Codonanthe* plus *Paradrymonia anisophylla* and *Codonanthopsis ulei* form a clade to the exclusion of the Brazilian species (*C. carnosa*). The non-monophyly of *Codonanthe* should be addressed in future analyses with expanded taxon sampling.

The traditionally recognized members of *Nematanthus* are restricted to southern and southeastern Brazil. The inclusion of *N. savannarum* (C.V. Morton) J.L. Clark, which was recently transferred from *Alloplectus* to *Nematanthus* (Clark, 2005) expands the current geographic range of the genus. Morton (1962) also described *Columnnea steyermarkii* C.V. Morton, which is recognized to be a taxonomic synonym of *Nematanthus savannarum* (Clark, 2005). The phylogenetic placement of *Nematanthus savannarum* as sister to the rest of *Nematanthus* (Fig. 3) is not supported. Despite creating a disjunct distribution for traditional *Nematanthus* to include the species from the Guiana Shield, its placement would be more unconventional in *Codonanthe* or *Codonanthopsis*. This poorly known species from the Guiana Shield will need to be further evaluated, but based on the results presented here it is best included as a member of *Nematanthus*. Generic boundaries for members of the *Nematanthus*, *Codonanthe*, *Codonanthopsis*, and *Paradrymonia anisophylla* clade require further evaluation. A sample size of three species for the geographically diverse genus *Codonanthe* (20+ spp. total) is insufficient to warrant a revised circumscription. It has not been possible to obtain material to sequence the type species of *Codonanthe* (*C. gracilis*, from the Rio de Janeiro area of Brazil).

Circumscription of *Paradrymonia*, *Nautilocalyx*, and *Chrysothemis*. — The *Paradrymonia*, *Nautilocalyx*, *Chrysothemis* clade is strongly supported in this study (bs = 96%; Figs. 1, 2) as well as in other analyses (Zimmer & al., 2002; Clark & Zimmer, 2003). Features that define the *Paradrymonia*, *Nautilocalyx*, *Chrysothemis* clade are non-lignified capsular fruits that open slightly to 45 degrees. Most other members of the Episcieae have fleshy berries or fleshy capsules (Figs. 6F, H).

This analysis includes the type species for *Chrysothemis* [*C. pulchella* (Donn ex Sims) Decne.] and *Para-*

drymonia [*P. ciliosa* (Mansf.) Wiehler], but the type species for *Nautilocalyx* (*N. bracteatus*) is not included. Further evaluation of generic boundaries must include a more extensive taxon sampling and the type species of *Nautilocalyx* before generic boundaries are redefined.

Neomortonia. — *Neomortonia* has been shown to be polyphyletic in previous analyses (Smith & Carroll, 1997; Smith, 2000b; Zimmer & al., 2002; Clark & Zimmer, 2003). The weakly supported grouping of the two *Neomortonia* species in this analysis (Fig. 5) is suspect and monophyly of this genus needs to be further tested. *Neomortonia* contains three species that range from southern Mexico to Ecuador (Wiehler, 1975, 1978b). The flowers of the two species included in this study [*N. nummularia* (Hanst.) Wiehler, *N. rosea* Wiehler] are quite different; *N. nummularia* has a bright red ornithophilous corolla with a ventral pouch and a constricted throat, whereas *N. rosea* has a white infundibular, euglossophilous corolla with a wide limb. The two *Neomortonia* species differ from all other gesneriads by their unique orange berries that are somewhat laterally compressed. Other evidence that Wiehler (1978b) cited for the recognition of the close relationship between these two species is that they are both epiphytes with similar growth habit in montane forests being thin-stemmed and pendent. Both species have a haploid chromosome count of $n = 9$ (Rogers, 1954; Wiehler, 1972).

Circumscription of *Alsobia*, *Episcia*, *Oerstedina*, *Rufodorsia*, and *Cobananthus*. — *Alsobia* and *Episcia* are sometimes treated as one genus, *Episcia* (Skog, 1979). Results from this study are congruent with other analyses (Smith, 2000b; Clark & Zimmer, 2003) strongly supporting the monophyly of *Episcia* (bs = 100%; Fig. 2) as distinct from *Alsobia*. Thus, both *Episcia* and *Alsobia* should be recognized. It is difficult to compare these results with Zimmer & al. (2002) because *Cobananthus*, *Rufodorsia*, and *Oerstedina* Wiehler were not included in their analyses.

Oerstedina and *Rufodorsia* are strongly supported (bs = 84%) as sister genera (Fig. 2), congruent with the only other analysis that had included *Rufodorsia* (Smith, 2000b). *Rufodorsia* and *Oerstedina* share the unambiguous morphological synapomorphy of a baccate fruit (character 87). Wiehler (1977) differentiated *Oerstedina* from *Rufodorsia* by its larger corollas that lack red coloration on the dorsal surface and pointed berries.

Flower resupination. — The discovery of resupinate flowers in *Glossoloma* provides a significant morphological synapomorphy for the genus. Flower resupination in many members of the Gesneriaceae was discussed by Clark & Zimmer (2003) in the context of a preliminary ITS phylogeny. To our knowledge, the first mention of resupination in the literature for Gesneriaceae was for the genus *Nematanthus* by Moore (1973) and a

recent revision of *Nematanthus* by Chautems (1988). Resupination was also documented in *Sinningia sellowii* (Mart.) Wiehler and *Sinningia sulcata* (Rusby) Wiehler (Boggan, 1991). Although not mentioned in the literature, resupinate flowers can be seen in photos of live plants of *Capanea grandiflora* (Kunth) Decne. ex Planch. (front cover of *The Gloxinian* 36, no. 5, 1986) and *Capanea affinis* Fritsch (Smithsonian Institution's Gesneriaceae Photo File).

Flower resupination has been well documented and studied in Orchidaceae (e.g., Darwin, 1892; Ames, 1938; Dressler, 1981; Nyman & al., 1984; Ernst & Arditti, 1994; Van der Pijl & Dodson, 1996), but remains relatively unstudied in other groups. Other groups that are defined phylogenetically by flower resupination are the Diclipterinae (Acanthaceae; McDade & al., 2000), *Heliconia* subgenus *Stenochlamys* (Heliconiaceae; Anderson, 1985), and the Lobeliaceae (Lammers, 1992).

Flower orientation is often difficult to evaluate from photos and even more difficult to evaluate from herbarium specimens because there is no obvious twist in the pedicels and specimens may be pressed with flowers in unnatural orientations. Most flowers of *Glossoloma* are held nearly horizontal, making the flower orientation relatively easy to evaluate, but a few are pendent, which makes it difficult to differentiate the ventral and dorsal surfaces of the corolla tube. For this reason, fieldwork was essential for accurately determining flower orientation in this study.

The result of floral resupination is usually a 180° rotation that gives the flower an inverted orientation. The mechanism of resupination can be attributed to the twisting or turning of the ovary and/or pedicel (Nyman & al., 1984), or a change in the position of initiation of floral organs. The mechanism of resupination in *Glossoloma* is hypothesized to occur in early development (i.e., change in position of initiation of floral organs) and is not due to any twisting of structures. Field observations of immature flowers indicate that floral orientation is reversed before the immature flower opens. Anatomical work carried out on pedicel cross sections did not reveal a twist in the vascular structure. Additionally, no twisting was evident in pedicels that were cleared and stained then mounted on slides. Thus, the vascular tissue from both of these anatomical procedures did not indicate a twist in the pedicel (J.L. Clark, pers. obs.).

All outgroup taxa and most members of the tribe Episcieae are non-resupinate. Therefore, it is inferred that non-resupinate flowers are ancestral for Episcieae. The results from this analysis suggest that resupinate flowers evolved a minimum of three times in *Glossoloma*, *Crantzia* [*C. cristata* (L.) Scop. + *C. epirotes* (Leeuwenb.) J.L. Clark], and within *Nematanthus* (Figs. 3, 5; character 38) The alternative

and less parsimonious explanation is that resupinate flowers are symplesiomorphic and that non-resupinate flowers resulted from losses in at least seven lineages.

Fruit structure in Episcieae. — Fruit morphology in Gesneriaceae was surveyed by Ivanina (1965, 1967) and Weber (2004) and additional information on Neotropical Gesneriaceae was provided by Wiehler (1983). Otherwise, fruit features in Neotropical Gesneriaceae remain poorly documented. The evaluation and interpretation of homologies in fruit structure in the Neotropical Gesneriaceae is challenging. Most classifications of Gesneriaceae are based on flower morphology (Hanstein, 1854, 1856, 1859, 1865; Oersted, 1861; Kuntze, 1891; Fritsch, 1893–1894), but Wiehler (1983) emphasized fruit morphology because he considered fruit structure to be more conservative than flowers, due to the apparent rapid coevolution found between flowers and pollinators.

Fruits of Episcieae have been traditionally defined as either dry capsules, fleshy capsules, or berries. A majority of the Episcieae have fleshy fruits, but assessing dehiscence is challenging because of the difficulties in working with dried herbarium collections. Fruiting specimens in the herbarium are rare and fruits are also rarely found on specimens in the field because they tend not to last long. Pressed specimens of fleshy fruits are difficult to interpret because important features are destroyed in the process of drying. As a consequence fruit morphology of the Episcieae has been oversimplified in the literature.

Field observations from this study have documented two undescribed fruit types in Episcieae, referred to here as capsules with tardily dehiscent endocarps (Fig. 6H) and non-dehiscent endocarps (Fig. 6G), which occur within two respective clades of *Drymonia*. In addition, field observations in combination with the phylogenetic results presented here document the presence of berries in a clade nesting within *Drymonia* and a species nesting in *Paradrymonia*, genera that were hypothesized to contain only capsules (Skog, 1979; Wiehler, 1983; Weber, 2004).

The most common fruit type in Episcieae is a fleshy, loculicidally dehiscent bivalved capsule in which the valves curve back and become separated from the placentae, which form a central cone covered by a glistening mass of funiculi and seeds. Wiehler (1983) called this fruit type a “display capsule” because of the strikingly colored cone-shaped central structure. It was hypothesized by Wiehler that this type of display fruit offers an outstanding visual target for dispersal by birds, bats, and possibly monkeys (Wiehler, 1983).

A special type of display capsule that has not been described in the literature appears to be a synapomorphy for *Drymonia crenatiloba* and the “*Alloplectus*” species

now in *Drymonia* (species marked with “*” in Figs. 4, 5). We refer to these fruits as capsules with tardily dehiscent endocarps (Fig. 6G). This fruit is similar to the display capsules described above with one major difference: the endocarp remains attached and surrounds the placentae and mass of funiculi and seeds. The endocarp eventually becomes dehiscent at a later stage, but becomes detached from the outer layers of the fruit wall when they reflex. Fieldwork and the documentation of fruits from photographic images of living material were essential for the verification of tardily dehiscent endocarps because it is difficult to validate the presence of this feature from herbarium specimens.

Another variation on the fleshy capsule of *Drymonia* was observed in *D. multiflora* (Oerst. ex Hanst.) Wiehler and *D. parviflora* Hanst. in Panama. In these species, the capsule-like fruit dehisces and exposes an indehiscent inner wall that is fleshy and berry-like (Fig. 6G). The outer layer (exocarp) is dehiscent and the inner layer (endocarp) is non-dehiscent. It differs from the tardily dehiscent endocarp fruits by lacking an endocarp suture and by a more contrasting and glistening endocarp layer. Other species with this type of fruit structure are *Drymonia folsomii* L.E. Skog and an undescribed species from Costa Rica (R. Kriebel, pers. comm.).

Indehiscent fruits in Neotropical Gesneriaceae are rare. Outside of the Episcieae, indehiscent fleshy fruits (= berries) are only known to exist in the Neotropical genus *Besleria* L. (tribe Beslerieae). The difference between the berries in some episcioid genera and the berries of *Besleria* is that the episcioid genera have fleshy funicular tissue, whereas in *Besleria* the fleshy tissue is formed from enlarged placental tissue. Within Episcieae, berries have been reported in *Columnnea*, *Corytoplectus*, *Rufodorsia*, *Neomortonia*, *Oestredina* and *Codonanthe*. Thus, in this analysis indehiscent fleshy fruits are optimized as having five independent origins (Figs. 3–5). The berries in *Paradrymonia metamorphophylla* (Donn. Sm.) Wiehler and a clade in *Drymonia* represent previously undocumented independent origins of berries. The discovery of a berry clade in *Drymonia* is surprising, because descriptions from floras had reported that these species have capsules (Skog, 1978, 1979; Wiehler, 1983). The fruit type of *Drymonia turrialvae* Hanst. was reported as a capsule (Skog, 1979). The circumscription of this species includes populations from Central America, Ecuador, and Colombia. It is likely that the populations from Colombia and Ecuador with capsular fruits represent a different species from Central American populations with berries. Berries for this species were discovered during a recent expedition to Panama and have been observed in populations from Costa Rica (R. Kriebel, pers. comm.). The fruits of *Drymonia ambonensis* (L.E. Skog) J.L. Clark were

reported in the original description of the species as, “broadly globose, white, glabrous, weakly dehiscent in two valves.” More likely, the separated valves reported by Skog (1978, 1979) is an artifact of the berry being pressed as an herbarium collection. The presence of berries for this taxon was documented in numerous populations during a recent collecting expedition in Panama (Clark, pers. obs.). Annotated collections of this species by Hans Wiehler suggested that it belonged to *Corytoplectus*, a genus with berries. Only immature fruits of *Drymonia urceolata* have been documented, and these appear to be indehiscent.

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Appendix 1. Species scored for morphological cladistic analysis and specimens sequenced in molecular phylogenetic study of Episcieae (Gesneriaceae) with voucher specimen, institution and GenBank accession number. Cultivated material is indicated and when available the wild origin of the collection is cited. In cases where the wild origin of a sample is unknown, then a general range of the species is provided. All other samples represent field collections in the wild. Unvouchered samples taken from live material growing at the U.S. Botany Research Greenhouses (USBRG) are designated by their accession number. GenBank accession numbers are for ITS followed by *trnH-psbA*. “Yes” and “No” indicate whether the specimen was used in scoring the morphological data; * indicates generic type species.

Alloplectus aquatilis C.V. Morton, *J.L. Clark 6875* (US), Venezuela, DQ211110, DQ211217, YES; *Alloplectus hispidus* (Kunth) Mart. *, *J.L. Clark 7720* (US), Ecuador, DQ211111, DQ211219, YES; *Alloplectus tessmannii* Mansf., *J.L. Clark 8210* (US), Peru, DQ211108, DQ211213, NO; *Alloplectus weirii* (Kuntze) Wiehler, *J.L. Clark 5788* (US), Ecuador, AF543233, DQ211192, YES. *Alsobia dianthiflora* (H.E. Moore & R.G. Wilson) Wiehler, *John Hall s.n.* (SEL), Cultivated (Costa Rica), DQ211160, DQ211303, NO; *Alsobia punctata* (Lindl.) Hanst. *, *J.L. Clark 8851* (US), Cultivated (Mexico), DQ211159, DQ211302, YES. *Chrysothemis pulchella* (Donn ex Sims) Decne. *, *J.L. Clark 8864* (US), Cultivated (South and Central America), AY047085, DQ211344, YES. *Cobananthus calochlamys* (Donn.Sm.) Wiehler *, *J.L. Clark 5613* (US), Cultivated (Guatemala), AF543273, DQ211304, YES. *Codonanthe carnosa* (Gardner) Hanst., *J.L. Clark 6268* (US), Cultivated (Brazil), AF543271, DQ211296, YES; *Codonanthe crassifolia* (Focke) C.V. Morton, *J.L. Clark 8633* (US), Panama, DQ211156, DQ211297, NO; *Codonanthe macradenia* Donn.Sm., *J.L. Clark 8632* (US), Panama, DQ211157, DQ211298, YES. *Codonanthopsis ulei* Mansf. *, *J.L. Clark 8868* (US), Cultivated (Brazil), DQ211167, DQ211314, YES. *Columnnea billbergiana* Beurl., *J.L. Clark 8630* (US), Panama, DQ211115, DQ211226, NO; *Columnnea calotricha* Donn.Sm., *J.L. Clark 6279* (US), Cultivated (French Guiana), AF543237, DQ211236, YES; *Columnnea crassicaulis* (Wiehler) L.P. Kvist & L.E. Skog, *J.L. Clark 8859* (US), Cultivated (Ecuador and Colombia), DQ211121, DQ211240, NO; *Columnnea dielsii* Mansf., *J.L. Clark 5813* (US), Ecuador, AF543250, DQ211245, YES; *Columnnea dissimilis* C.V. Morton, *J.L. Clark 8629* (US), Panama, DQ211124, DQ211246, YES; *Columnnea dressleri* Wiehler, *J.L. Clark 8559* (US), Panama, DQ211117, DQ211230, NO; *Columnnea erythrophaea* Decne. ex Houll., *J.L. Clark 6273* (US), Cultivated (Mexico), AF543246, DQ211244, YES; *Columnnea eubracteata* Mansf., *J.L. Clark 4582* (US), Ecuador, AF543249, DQ211232, YES; *Columnnea harrisii* (Urb.) Britton ex C.V. Morton, *J.L. Clark 6278* (US), Cultivated (Jamaica), AF543248, DQ211239, YES; *Columnnea hypocyrtantha* (Wiehler) J.F. Sm. & L.E. Skog, *J.L. Clark 6741* (US), Bolivia, DQ211119, DQ211237, NO; *Columnnea inaequilatera* Poepp., *J.L. Clark 5004* (US), Ecuador, AF543234, DQ211249, YES; *Columnnea isernii* Cuatrec., *J.L. Clark 6253* (US), Ecuador, AF543247, DQ211220, YES; *Columnnea lehmannii* C.V. Morton, *J.L. Clark 4960* (US), Ecuador, AF543238, DQ211247, NO; *Columnnea linearis* Oerst., *J.L. Clark 6274* (US), Cultivated (Costa Rica), AF543240, DQ211243, YES; *Columnnea lophophora* Mansf., *J.L. Clark 7888* (US), Ecuador, DQ211116, DQ211229, NO; *Columnnea medicinalis* (Wiehler) L.E. Skog & L.P. Kvist, *J.L. Clark 4482* (US), Ecuador, AF543235, DQ211231, YES; *Columnnea minor* (Hook.) Hanst., *J.L. Clark 2934* (US), Ecuador, AF543243, DQ211235, YES; *Columnnea minutiflora* L.P. Kvist & L.E. Skog, *J.L. Clark 7092* (US), Ecuador, DQ211122, DQ211241, NO; *Columnnea moesta* Poepp., *J.L. Clark 6690* (US), Bolivia, DQ211123, DQ211242, NO; *Columnnea paramicola* (Wiehler) L.P. Kvist & L.E. Skog, *USBRG 1994-529*, Cultivated (Ecuador and Colombia), DQ211113, DQ211224, NO; *Columnnea picta* H. Karst., *J.L. Clark 4513* (US), Ecuador, AF543245, DQ211248, YES; *Columnnea pulchra* (Wiehler) L.E. Skog, *J.L. Clark 6265* (US), Panama, DQ211114, DQ211225, NO; *Columnnea raymondii* C.V. Morton, *J.L. Clark 6281* (US), Cultivated (Costa Rica), DQ211125, DQ211251, NO; *Columnnea rileyi* (Wiehler) J.F. Smith, *J.L. Clark 6263* (US), Ecuador, AF543239, DQ211250, YES; *Columnnea rubriacuta* (Wiehler) L.P. Kvist & L.E. Skog, *J.L. Clark 4975* (US), Ecuador, AF543242, DQ211234, YES; *Columnnea rubricalyx* L.P. Kvist & L.E. Skog, *J.L. Clark 7095* (US), Ecuador, DQ211135, DQ211270, NO; *Columnnea schiedeana* Schlechtend., *J.L. Clark 6272* (US), Mexico, DQ211112, DQ211222, NO; *Columnnea schimpffii* Mansf., *J.L. Clark 6280* (US), Ecuador, AF543236, DQ211228, YES; *Columnnea spathulata* Mansf., *J.L. Clark 7958* (US) for *trnH-psbA*; L.E. Skog 7820 (US) for ITS, Ecuador, AY047092, DQ211227, YES; *Columnnea strigosa* Benth., *J.L. Clark 4480* (US), Ecuador, AF543251, DQ211221, YES; *Columnnea sulfurea* Donn.Sm., *J.L. Clark 6275* (US), Cultivated (Central America), AF543241, DQ211268, YES; *Columnnea tenuis* Klotzsch ex Oerst., *J.L. Clark 8595* (US), Panama, DQ211120, DQ211238, NO; *Columnnea zebrina* Raymond, *J.L. Clark 6277* (US), Panama, AF543244, DQ211223, YES; *Columnnea sp. nov.*, *J.L. Clark 8188* (US), Peru, DQ211118, DQ211233, NO. *Corytoplectus congestus* (Lind. ex Hanst.) Wiehler, *J.L. Clark 6868* (US), Venezuela, DQ211162, DQ211306, YES; *Corytoplectus cutucuensis* Wiehler, *J.L. Clark 6267* (US), Ecuador, DQ211161, DQ211305, YES; *Corytoplectus riceanus* (Rusby) Wiehler, *J.L. Clark 6704* (US), Bolivia, DQ211177, DQ211329, YES. *Crantzia cristata* (L.) Scop. *, *J.L. Clark 6546* (US), Martinique, DQ211154, DQ211294, YES; *Crantzia epirotes* (Leeuwenb.) J.L. Clark, *D. Clarke 10172* (US), Guyana, DQ211153, DQ211293, YES; *Crantzia tigrina* (H.Karst.) J.L. Clark, *J.L. Clark 6892* (US), Venezuela, DQ211155, DQ211295, YES. *Cremersia platula* Feuillet & L.E. Skog *, *J.J. de Granville 14868* (CAY), French Guiana, DQ211152, DQ211292, YES. *Drymonia ambonensis* (L.E. Skog) J.L. Clark, *J.L. Clark 8600* (US), Panama, DQ211134, DQ211269, YES; *Drymonia brochidodroma* Wiehler, *J.L. Clark 7360* (US), Ecuador, DQ211166, DQ211313, YES; *Drymonia candida* Hanst., *J.L. Clark 8341* (US), Ecuador, DQ211131, DQ211265, NO; *Drymonia chiribogana* Wiehler, *J.L. Clark 7358* (US), Ecuador, DQ211149, DQ211288, NO; *Drymonia coccinea* (Aubl.) Wiehler, *J.L. Clark 6492* (US), Ecuador, DQ211132, DQ211266, NO; *Drymonia coriacea* (Oerst. ex Hanst.) Wiehler, *J.L. Clark 6590* (US), Cultivated (Ecuador), DQ211129, DQ211263, YES; *Drymonia conchocalyx* Hanst., *J.L. Clark 6276* (US), Costa Rica, AF543261, DQ211275, YES; *Drymonia crenatiloba* (Mansf.) Wiehler, *J.L. Clark 5462* (US), Ecuador, AF543259, DQ211273, YES; *Drymonia dodsonii* (Wiehler) J.L. Clark, *J.L. Clark 6205* (US), Ecuador, AF543256, DQ211261, YES; *Drymonia doratostyla* (Leeuwenb.) Wiehler, *J.L. Clark 6783* (US), Bolivia, DQ211144, DQ211281, YES; *Drymonia ecuadorensis* Wiehler, *J.L. Clark 6185* (US), Ecuador, DQ211147, DQ211286, NO; *Drymonia foliacea* (Rusby) Wiehler, *J.L. Clark 6808* (US), Bolivia, DQ211138, DQ211274, YES; *Drymonia hoppii* (Mansf.) Wiehler, *J.L. Clark 5036* (US), Ecuador, AF543263, DQ211252, YES; *Drymonia killipii* Wiehler, *J.L. Clark 7521* (US), Ecuador, DQ211136, DQ211271, NO; *Drymonia laciniosa* Wiehler, *J.L. Clark 8794* (US), Ecuador, DQ211126, DQ211253, YES; *Drymonia lanceolata* (Hanst.) C.V. Morton, *J.L. Clark 8553* (US), Panama, DQ211139, DQ211276, YES; *Drymonia macrophylla* (Oerst.) H.E. Moore, *J.L. Clark 4776* (US), Ecuador, AF543262, DQ211284, YES; *Drymonia multiflora* (Oerst. ex Hanst.) Wiehler, *J.L. Clark 8586* (US), Panama, DQ211128, DQ211255, YES; *Drymonia oinochrophylla* (Donn.Sm.) D. Gibson, *J.L. Clark 6282* (US), Cultivated (Central America), DQ211145, DQ211282, NO; *Drymonia parviflora* Hanst., *J.L. Clark 8676* (US), Panama, DQ211148, DQ211287, NO; *Drymonia peltata* (Oliver) H.E. Moore, *J.L. Clark 6286* (US), Cultivated (Costa Rica),

Appendix 1. continued.

DQ211140, DQ211277, NO; *Drymonia pilifera* Wiehler, *J.L. Clark* 8568 (US), Panama, DQ211137, DQ211272, YES; *Drymonia rhodoloma* Wiehler, *J.L. Clark* 4843 (US), Ecuador, AF543260, DQ211283, YES; *Drymonia serrulata* (Jacq.) Mart. *, *J.L. Clark* 8843 (US), Cultivated (Central and South America), DQ211133, DQ211267, YES; *Drymonia strigosa* (Oerst.) Wiehler, *J.L. Clark* 8854 (US), Cultivated (Mexico), DQ211143, DQ211280, NO; *Drymonia tenuis* (Benth.) J.L. Clark, *J.L. Clark* 4597 (US), Ecuador, AF543258, DQ211257, YES; *Drymonia aff. tenuis* (Benth.) J.L. Clark, *J.L. Clark* 4586 (US), Ecuador, AF543254, DQ211256, NO; *Drymonia teuschleri* (Raymond) J.L. Clark, *J.L. Clark* 5911 (US), Ecuador, AF543252, DQ211262, YES; *Drymonia turrialvae* Hanst., *J.L. Clark* 8552 (US), Panama, DQ211141, DQ211278, YES; *Drymonia urceolata* Wiehler, *J.L. Clark* 5225 (US), Ecuador, AF543265, DQ211289, YES; *Drymonia variegata* Uribe, *J.L. Clark* 8570 (US), Panama, DQ211146, DQ211285, NO; *Drymonia warszewicziana* Hanst., *J.L. Clark* 8614 (US), Panama, DQ211127, DQ211254, YES; *Drymonia sp. nov. 1*, *J.L. Clark* 6863 (US), Venezuela, DQ211142, DQ211279, YES; *Drymonia sp. nov. 2*, *J.L. Clark* 8366 (US), Ecuador, DQ211130, DQ211264, NO; *Drymonia sp. nov. 3*, *J.L. Clark* 5736 (US), Ecuador, AF543253, DQ211260, YES; *Drymonia sp. nov. 4*, *J.L. Clark* 4592 (US), Ecuador, AF543255, DQ211258, YES; *Drymonia sp. nov. 5*, *J.L. Clark* 5713 (US), Ecuador, AF543257, DQ211259, YES. *Episcia cupreata* (Hook.) Hanst., *J.L. Clark* 8844 (US), Cultivated (Colombia), DQ211165, DQ211312, YES; *Episcia lilacina* Hanst., *J.L. Clark* 8881 (US) for *trnH-psbA*; *L.E. Skog* 8132 (US) for ITS, Costa Rica, AY047091, DQ211309, YES. *Glossoloma altescandens* (Mansf.) J.L. Clark, *J.L. Clark* 5847 (US), Ecuador, AF543229, DQ211196, YES; *Glossoloma baguense* (L.E. Skog) J.L. Clark, *J.L. Clark* 5448 (US), Ecuador, AF543226, DQ211194, YES; *Glossoloma bolivianum* (Britton ex Rusby) J.L. Clark, *J.L. Clark* 6726 (US), Bolivia, DQ211106, DQ211211, YES; *Glossoloma carpishense* (J.L. Clark & I. Salinas) J.L. Clark, *J.L. Clark* 8247 (US), Peru, DQ211107, DQ211212, YES; *Glossoloma chrysanthum* (Planch. & Lind.) J.L. Clark, *J.L. Clark* 6872 (US), Venezuela, DQ211103, DQ211203, YES; *Glossoloma grandicalyx* (J.L. Clark & L.E. Skog) J.L. Clark, *J.L. Clark* 5449 (US), Ecuador, AF543218, DQ211205, YES; *Glossoloma herthae* (Mansf.) J.L. Clark, *J.L. Clark* 4598 (US), Ecuador, AF543230, DQ211204, YES; *Glossoloma ichthyoderma* (Hanst.) J.L. Clark, *J.L. Clark* 5626 (US), Ecuador, AF543231, DQ211214, YES; *Glossoloma martinianum* (J.F. Smith) J.L. Clark, *J.L. Clark* 5793 (US), Ecuador, AF543228, DQ211209, YES; *Glossoloma medusaeum* (L.E. Skog) J.L. Clark, *J.L. Clark* 4973 (US), Ecuador, AF543223, DQ211200, YES; *Glossoloma oblongicalyx* (J.L. Clark & L.E. Skog) J.L. Clark, *J.L. Clark* 4489 (US), Ecuador, AF543215, DQ211190, YES; *Glossoloma panamense* (C.V. Morton) J.L. Clark, *J.L. Clark* 8612 (US), Panama, DQ211102, DQ211202, YES; *Glossoloma penduliflorum* (M. Freiberg) J.L. Clark, *J.L. Clark* 6122 (US), Ecuador, AF543224, DQ211215, YES; *Glossoloma purpureum* (L.P. Kvist & L.E. Skog) J.L. Clark, *J.L. Clark* 6100 (US), Ecuador, AF543222, DQ211208, YES; *Glossoloma pycnosuzygium* (Donn.Sm.) J.L. Clark 6861 (US), Venezuela, DQ211101, DQ211199, YES; *Glossoloma schultzei* (Mansf.) J.L. Clark, *J.L. Clark* 6039 (US), Ecuador, AF543219, DQ211195, YES; *Glossoloma serpens* (J.L. Clark & L.E. Skog) J.L. Clark, *J.L. Clark* 5904 (US), Ecuador, DQ211109, DQ211216, YES; *Glossoloma sprucei* (Kuntze) J.L. Clark, *J.L. Clark* 6093 (US), Ecuador, AF543221, DQ211206, YES; *Glossoloma tetragonoides* (Mansf.) J.L. Clark, *J.L. Clark* 5033 (US), Ecuador, AF543217, DQ211201, YES; *Glossoloma tetragonum* Hanst. *, *J.L. Clark* 8547 (US), Panama, DQ211104, DQ211207, YES; *Glossoloma sp. 1*, *J.L. Clark* 6020 (US), Ecuador, AF543225, DQ211218, YES; *Glossoloma sp. 2*, *J.L. Clark* 7562 (US), Ecuador, DQ211105, DQ211210, YES; *Glossoloma sp. 3*, *J.L. Clark* 8557 (US), Panama, DQ211100, DQ211198, YES; *Glossoloma sp. 4*, *J.L. Clark* 7510 (US), Ecuador, DQ211098, DQ211193, YES; *Glossoloma sp. 5*, *J.L. Clark* 5961 (US), Ecuador, AF543227, DQ211191, YES. *Lembocarpus amoenus* Leeuwenb. *, *J.L. Clark* 8841 (US), Cultivated (French Guiana), DQ211172, DQ211323, YES. *Nautilocalyx coccineus* Feuillet & L.E. Skog, *D. Clarke* 10295 (US), Guyana, DQ211185, DQ211338, YES; *Nautilocalyx melittifolius* (L.) Wiehler, *J.L. Clark* 6540 (US), Martinique, AY047086, DQ211326, YES; *Nautilocalyx panamensis* (Seem.) Seem., *J.L. Clark* 8625 (US), Panama, DQ211175, DQ211327, YES; *Nautilocalyx pemphidius* L.E. Skog, *D. Bell* 324 (US), Venezuela, DQ211176, DQ211328, YES; *Nautilocalyx pictus* (W. Hook.) Sprague, *D. Clarke* 9974 (US), Guyana, DQ211188, DQ211342, YES; *Nautilocalyx whitei* Rusby, *J.L. Clark* 6793 (US), Bolivia, DQ211189, DQ211343, YES; *Nautilocalyx sp.*, *J.L. Clark* 8268 (US), Ecuador, DQ211187, DQ211341, NO. *Nematanthus albus* Chautems, *J.L. Clark* 6266 (US), Cultivated (Brazil), AF543270, DQ211318, YES; *Nematanthus corticola* Schrad. *, *J.L. Clark* 6271 (US), Cultivated (Brazil), AF543268, DQ211316, YES; *Nematanthus fluminensis* (Vell.) Fritsch, *J.L. Clark* 8853 (US), Cultivated (Brazil), DQ211168, DQ211319, NO; *Nematanthus hirtellus* (Schott) Wiehler, *J.L. Clark* 9445 (US), Cultivated (Brazil), DQ211170, DQ211321, NO; *Nematanthus jolyanus* (Handro) Chautems, *J.L. Clark* 6270 (US), Cultivated (Brazil), AF543269, DQ211315, YES; *Nematanthus monanthos* (Vell.) Chautems, *J.L. Clark* 8852 (US), Cultivated (Brazil), DQ211171, DQ211322, NO; *Nematanthus savannarum* (C.V. Morton) J.L. Clark, *K. Redden* 1339 (US), Guyana, DQ211158, DQ211301, YES; *Nematanthus strigillosus* (Mart.) H.E. Moore, *J.L. Clark* 8850 (US), Cultivated (Brazil), DQ211169, DQ211320, YES; *Nematanthus wettsteinii* (Fritsch) H.E. Moore, *J.L. Clark* 6285 (US), Cultivated (Brazil), AF543272, DQ211317, YES. *Neomortonia nummularia* (Hanst.) Wiehler, *J.L. Clark* 6248 (US), Ecuador, AF543266, DQ211308, YES; *Neomortonia rosea* Wiehler *, *J.L. Clark* 7582 (US), Ecuador, DQ211099, DQ211197, YES. *Oerstedina cerricola* Wiehler *, *J.L. Clark* 8700 (US), Panama, DQ211150, DQ211290, YES. *Paradrymonia anisophylla* Feuillet & L.E. Skog, *D. Clarke* 10413 (US), Guyana, DQ211181, DQ211334, YES; *Paradrymonia binata* Wiehler, *J.L. Clark* 8848 (US), Ecuador, AY047087, DQ211307, YES; *Paradrymonia buchtienii* (Mansf.) Wiehler, *J.L. Clark* 6791 (US), Bolivia, DQ211183, DQ211336, YES; *Paradrymonia campostyla* (Leeuwenb.) Wiehler, *J.L. Clark* 8855 (US), Cultivated (French Guiana), DQ211180, DQ211333, YES; *Paradrymonia ciliosa* (Mansf.) Wiehler *, *D. Clarke* 10239 (US), Guyana, DQ211182, DQ211335, YES; *Paradrymonia densa* (C.H. Wright) Wiehler, *K. Redden* 1060 (US), Guyana, DQ211184, DQ211337, YES; *Paradrymonia fuquaiana* Wiehler, *J.L. Clark* 5409 (US), Ecuador, AF543274, DQ211331, YES; *Paradrymonia lineata* (C.V. Morton) Wiehler, *J.L. Clark* 8649 (US), Panama, DQ211186, DQ211339, YES; *Paradrymonia longifolia* (Poep.) Wiehler, *J.L. Clark* 6262 (US), Ecuador, AF543264, DQ211340, YES; *Paradrymonia macrophylla* Wiehler, *J.L. Clark* 8545 (US), Panama, DQ211174, DQ211325, YES; *Paradrymonia metamorphophylla* (Donn.Sm.) Wiehler, *J.L. Clark* 6028 (US), Ecuador, DQ211178, DQ211330, YES; *Paradrymonia pedunculata* L.E. Skog, *USBRG* 1994-184, Unknown (Costa Rica & Panama), DQ211179, DQ211332, NO; *Paradrymonia splendens* M.Freiberg, *J.L. Clark* 7351 (US), Ecuador, DQ211173, DQ211324, NO. *Rhoogeton cyclophyllus* Leeuwenb. *, *D. Clarke* 10350 (US), Guyana, DQ211163, DQ211310, YES; *Rhoogeton viviparus* Leeuwenb., *D. Clarke* 9255 (US), Guyana, DQ211164, DQ211311, YES. *Rufodorsia intermedia* Wiehler, *J.L. Clark* 8555 (US), Panama, DQ211151, DQ211291, YES.

Outgroup: *Sinningia cooperi* (Paxt.) Wiehler, *J.L. Clark* 8857 (US), Cultivated (Brazil), DQ211097, DQ211299, YES; *Sinningia incarnata* (Aubl.) D.L. Denham, *J.L. Clark* 8849 (US), Cultivated (Colombia), AY047083, DQ211300, YES.

Appendix 2. Descriptions of characters used in morphological phylogenetic analyses. Species were scored almost exclusively from observations of live material in cultivation, live material in the field, and herbarium specimens. Chromosome information was obtained from Skog (1984) and Oliver and Skog (1985).

1. Chromosome number: (0) $n = 8$, (1) $n = 9$, (2) $n = 13$. This character was scored from literature (Skog, 1984; Oliver & Skog, 1985). **2. Plant location:** (0) terrestrial, (1) facultative epiphyte, (2) obligate epiphyte, (3) epilithophyte. **3. Stolons:** (0) absent, (1) present. **4. Stolon number:** (0) one per node, (1) two per node. **5. Tubers:** (0) absent, (1) present. **6. Stem branching:** (0) unbranched, (1) rarely to frequently branched. **7. Stem posture:** (0) erect, (1) arching (i.e., dorsiventral), (2) pendent to scandent. Epiphytes with horizontal stems were scored as erect. **8. Stem cross section:** (0) terete to subquadrangular, (1) quadrangular. **9. Stem texture:** (0) woody to subwoody, (1) herbaceous, (2) succulent to pachycaul. **10. Stem sap:** (0) absent, (1) present. **11. Stem surface:** (0) smooth, (1) scaly or flaky. **12. Leaf glands:** (0) absent, (1) present. The presence of abaxial leaf glands is associated with ant-nest epiphytes in many species of *Codonanthe* (Kleinfeldt, 1978). **13. Basal petiole enations:** (0) absent, (1) present. It is important to evaluate the absence/presence of these glands on newer leaf growth at the junction of the leaf blade base and petiole apex. **14. Secondary leaf venation:** (0) inconspicuous when dry, (1) visible when dry. This character was scored on dry leaves only because many fresh leaves with conspicuous venation have inconspicuous venation when dry. **15. Anisophylly:** (0) leaves equal or subequal in a pair, (1) anisophyllous. **16. Leaf petiolation:** (0) sessile or petioles barely evident, (1) petiolate. **17. Leaf texture:** (0) soft/membranous, (1) stiff/leathery/coriaceous, (2) papyraceous, (3) succulent. **18. Leaf blade shape:** (0) broadest above the middle, (1) broadest at the middle, (2) broadest below the middle. **19. Blade base cuneate:** (0) absent, (1) present. **20. Blade base cordate:** (0) absent, (1) present. **21. Blade base shape:** (0) symmetrical, (1) oblique. **22. Blade apex shape:** (0) acute to acuminate, (1) rounded to obtuse. **23. Blade margin contour:** (0) serrate-dentate, (1) crenate, (2) entire. **24. Blade adaxial indument:** (0) glabrous, (1) pubescent. **25. Blade adaxial indument distribution:** (0) uniformly pubescent, (1) more pubescent on venation. **26. Blade bullations:** (0) absent, (1) present. **27. Blade abaxial indument:** (0) glabrous, (1) pubescent. **28. Blade abaxial indument distribution:** (0) uniformly pubescent, (1) more pubescent on venation. **29. Blade abaxial coloration:** (0) green, (1) red. **30. Translucent red zone on leaf:** (0) absent, (1) present. This is common in many members of *Columnnea* and is usually located near the leaf apex. **31. Floral bracts:** (0) absent, (1) present. **32. Floral bract size:** (0) small to inconspicuous, (2) large and obscuring base of corolla. **33. Floral bract margin:** (0) entire, (1) serrate. **34. Inflorescence structure:** (0) determinate (e.g., cymose), (1) indeterminate (e.g., raceme-like), (2) individual axillary flowers. **35. Determinate inflorescence form:** (0) pseudo-umbellate, (1) cymose. This character is only applicable to taxa with a determinate or cymose-like inflorescence. **36. Number of axillary flowers per node:** (0) more than one, (1) solitary. This character is only applicable to taxa with individual axillary flowers. **37. Pedicel glands:** (0) absent, (1) present. **38. Flower resupination:** (0) absent, (1) present. **39. Flower position/posture:** (0) pendent, (1) horizontal, (2) erect. This is different from corolla orientation relative to calyx and is evaluated by the position of the pedicel in relation to the stem axis. **40. Corolla tube orientation relative to calyx:** (0) perpendicular, (1) oblique, (2) erect. **41. Calyx color:** (0) greenish to yellow, (1) red. **42. Calyx lobe connation:** (0) nearly free, (1) mostly connate. **43. Calyx lobe relative size:** (0) nearly equal, (1) dorsal smaller. **44. Calyx lobe arrangement:** (0) conduplicate, (1) valvate, (2) imbricate. **45. Calyx lobe shape:** (0) ovate, (1) lanceolate. **46. Calyx lobe apex shape:** (0) acuminate to acute, (1) rounded to obtuse. **47. Calyx lobe base:** (0) cordate, (1) truncate. **48. Basal calyx lobe outgrowths:** (0) absent, (1) present. **49. Calyx lobe margin contour:** (0) entire, (1) serrate, (2) dentate, (3) lacinate (i.e., margins with elongated single serrations), (4) fimbriate (i.e., margins with doubly serrate elongate serrate margins). **50. Corolla tube interior spotting:** (0) absent, (1) present. **51. Corolla tube external appendages:** (0) absent, (1) present. These appendages are located between the petal lobes and are most common in *Columnnea* section *Ortholoma*. **52. Corolla base:** (0) unmodified, (1) gibbous, (2) spurred. **53. Corolla tube external indument:** (0) glabrous, (1) pubescent. **54. Corolla tube external indument distribution:** (0) distally pubescent, (1) uniformly pubescent. **55. Corolla internal indument:** (0) glabrous, (1) pubescent. **56. Corolla internal indument type:** (0) simple, (1) glandular. **57. Corolla lobe spreading:** (0) reflexed, (1) spreading, (2) erect. **58. Corolla lobe margin:** (0) entire, (1) serrate, (2) fimbriate. **59. Corolla limb symmetry:** (0) bilateral, (1) sub-regular. **60. Corolla throat constriction:** (0) absent, (1) present. **61. Distal pouch:** (0) absent, (1) present. **62. Central non-distended pouch:** (0) absent, (1) present. **63. Central distended pouch:** (0) absent, (1) present. **64. Corolla throat lateral compression:** (0) absent, (1) present. **65. Corolla mouth:** (0) transverse, (1) oblique. **66. Corolla dorsal lobe fusion - hood:** (0) absent, (1) present. **67. Corolla ventral lobe extension - landing platform:** (0) absent, (1) present. **68. Corolla tube angulation:** (0) absent, (1) present. The corolla tube appears angled or bent in some species of *Nautilocalyx* and *Paradrymonia*. **69. Staminode:** (0) absent, (1) present. **70. Stamen insertion:** (0) inserted at corolla base, (1) adnate to corolla above base. **71. Filament indument:** (0) glabrous, (1) pubescent. **72. Filament curtain:** (0) absent, (1) present. See Manktelow (2000) for a detailed description of filament curtains in Acanthaceae. **73. Stamen pro-jection:** (0) included, (1) exerted. **74. Anther dehiscence:** (0) longitudinal, (1) central pore, (2) basal porical, (3) pores developing into slits. **75. Anther coherence:** (0) all lateral, (1) all apical, (2) didynamous. **76. Broad anther connectives:** (0) absent, (1) present. This character was emphasized for distinguishing *Codonanthe* from other episcioid genera (Wiehler, 1983, p. 192). **77. Anther ciliations:** (0) absent, (1) present. This character is common on some species of *Paradrymonia* (e.g., *P. buchtienii*) where trichomes are present on the sagittate region of the anther cells. **78. Pollen:** (0) powdery, (1) sticky. **79. Nectary disc:** (0) single gland with one to several lobes, (1) 3–5 separate glands, (2) 2 separate glands (i.e., dorsal and posterior). **80. Ovary:** (0) half inferior, (1) superior. **81. Ovary indument:** (0) pilose, (1) puberulent, (2) glabrous. **82. Style projection:** (0) included, (1) exerted. **83. Style glandular trichomes:** (0) absent, (1) present. **84. Style pilose trichomes:** (0) absent, (1) present. **85. Stigma - bilobed:** (0) absent (i.e., stomatomorphic to capitate), (1) present. **86. Fruit posture:** (0) pendent, (1) erect. **87. Fruit type:** (0) berry, (1) capsule. **88. Capsule type:** (0) fleshy, (1) dry. **89. Capsule shape:** (0) globose, (1) cone. **90. Angle of dehiscence:** (0) valves spreading broadly (i.e., 180°), (1) opening slightly (i.e., 45°). **91. Seed attachment:** (0) seeds retained to placenta wall and not adhering to each other, (1) seeds adhere to each other in central mass (Fig. 6F). **92. Fruit color:** (0) white, (1) yellow, (2) red-purple, (3) green, (4) brown, (5) orange. **93. Capsule inner layer - display capsules:** (0) white, (1) yellow, (2) red-purple, (3) orange, (4) brown, (5) green. Scoring of the inner layer of the reflexed valve wall was based on field observations and photographic images. The “display” capsule is thought to be a visual target to attract seed/fruit disperser (Wiehler, 1983). **94. Endocarp layer:** (0) fused to exocarp, (1) separate from exocarp. **95. Fruit-outside indument:** (0) glabrous, (1) pubescent. **96. Berry fruit shape:** (0) globose, (1) cone, (2) ovoid to pointed. **97. Berry - translucence:** (0) absent, (1) present. **98. Seed shape:** (0) fusiform or ellipsoid (i.e., longer than broad), (1) globose (i.e., about as broad as long). **99. Seed gelatinous aril:** (0) absent, (1) present.

Appendix 3. Morphological data matrix of 99 characters for Episceiae (118 species) and Sinningieae (2 species). “?” = missing data, “-” = inapplicable. All species names are listed with authorship in Appendix 1. Character states and descriptions are listed in Appendix 2.

	000000001	111111112	222222223	333333334	444444445	555555556	666666667	777777778	888888889	999999999
	123456789	123456789	123456789	123456789	123456789	123456789	123456789	123456789	123456789	123456789
<i>Alloplectus altescandens</i>	?10-010000	0011011100	0001001100	0-2-01110	1000001011	0111110000	1001000011	0100000101	0000000000	0000000000
<i>Alloplectus aquatilis</i>	?20-012000	0000010100	1001001000	0-2-10021	0001001030	01110-0011	?001000001	0100000101	0000011010	10001--00
<i>Alloplectus hispidus</i>	120-012000	0010011200	0011001000	0-2-10011	0001001010	01110-0011	?001000001	0100000101	0001001010	12201--00
<i>Alloplectus weirii</i>	?20-012000	0010011100	0001001100	1112-10011	1000001040	01110-2011	?010000001	0100000101	0001001010	?0001--00
<i>Alsobia punctata</i>	1210010000	0001010200	0011001100	1102-00020	0001101001	0110111200	0000001001	0100000101	0011011111	13501--00
<i>Chrysothemis pulchella</i>	100-100121	0001012110	0011000-?0	11000-0022	1101-0-001	0010102010	0000000000	0000000101	0000111011	10001--00
<i>Cobananthus calochlamys</i>	110-010000	0011010100	0001001000	1102-00022	1001001010	00110-2011	0000000001	0000000101	0000011111	14401--00
<i>Codonanthe carmosa</i>	020-012000	0100013100	0021001010	0-2-10011	0011101001	0111010000	0000000000	0001210101	0000011010	03301--01
<i>Codonanthe macradenia</i>	020-012000	0100013100	0020-00-10	0-2-10011	0011101001	0211101000	0000000001	0001210101	1001111010	02201--01
<i>Codonanthopsis ulei</i>	120-010000	0000113000	0020-00-10	0-2-10011	0011101001	020-0-10000	0000000001	0001200101	1000011010	1?200--01
<i>Columnea calotricha</i>	?10-011000	0001110000	1001001010	1102-00022	1011101000	11100-2000	0000100000	0000000101	0000010--	-2--02000
<i>Columnea dielsii</i>	?10-010000	0001010200	0001001100	1102-10012	1000001010	00110-2011	0100000000	0100000111	0001001011	0?01--00
<i>Columnea dissimilis</i>	120-012000	0001110000	1001001000	11?2-10011	10001010?0	11110-2010	000000000?	0?00000101	0000110--	-0--00000
<i>Columnea erythrophaea</i>	?20-012010	0001010000	1020-01100	1102-10002	1001000000	0111110000	0000110000	0100000101	0000100--	-0-00000
<i>Columnea eubratteata</i>	?10-011000	0001010000	10010011?0	1012-10022	1001101010	0111100000	0000110000	0100000101	0010110--	-2--12000
<i>Columnea harrisii</i>	110-011010	0001110000	1001001100	1102-00012	0001101000	0111110000	0000110000	0100000101	00111000--	-2--?0000
<i>Columnea hypocyrtantha</i>	-20-010000	0001010100	10010011?0	0-2-10011	1011101000	0-11?2011	0010000000	0100000-11	-001-1--	-----
<i>Columnea inaequilatera</i>	?10-011000	0001110000	1001001100	1102-01012	?001101030	0111101010	0000000000	0100000101	0001110--	-2--12000
<i>Columnea isernii</i>	?10-000000	1011010100	1001001110	11?2-00012	0001011100	0011112010	0100000000	0100000111	0000110--	-?-12000
<i>Columnea linearis</i>	120-010010	1001003100	0020-00-00	1102-00012	?0000000000	0111100000	0000110000	0100000101	0001110--	-0-00000
<i>Columnea medicinalis</i>	?10-011000	0001100000	1001001101	1002-01022	?001101010	0111101000	0000110000	0100000101	0010110--	-0--12000
<i>Columnea minor</i>	120-012010	0001101000	0021001100	1102-00012	1001101040	1111112010	0000000000	0100000101	0010110--	-2--10000
<i>Columnea picta</i>	110-011000	0001100000	1000-01101	1012-00022	0010101000	0111110000	0000110000	0100000101	0010110--	-0-12000
<i>Columnea rileyi</i>	?10-010010	0001010100	0021001000	1102-00022	0001101000	00111?2010	0000000000	0100000111	0000110--	-0--00000
<i>Columnea rubricata</i>	?10-011000	0001110000	1001001101	1002-00022	1001101010	0111102010	0000000000	0100000101	0010110--	-2--12000
<i>Columnea schimpffii</i>	?10-011000	0001110000	1001001101	1002-00012	1001101010	0111111010	0000000000	1100000101	0011110--	-2--12000
<i>Columnea spathulata</i>	?20-011020	1001110000	11110011?0	1102-00012	?0011110000	0111112010	0000000000	1100000111	0001110--	-0--00000
<i>Columnea strogosa</i>	110-012000	0001010200	00010011?0	1102-11002	0001?1030	0111100000	0000110000	0100000111	0010000--	-2--10000
<i>Columnea sulfurea</i>	?10-011000	0001010000	1001001010	1102-00012	0001100000	0111110000	0000110000	0100000101	0010110--	-0-10000
<i>Columnea zebrina</i>	110-011000	0001110000	1020-01101	1102-00012	0000101010	0111100000	0000110000	0100000101	0001110--	-0--10000
<i>Corytoplectus congestus</i>	100-000020	0011012200	0001001110	10000-0022	1000001010	0011112011	00100000?1	1100000121	0000010--	----001?0
<i>Corytoplectus cutucuenensis</i>	?00-000020	0001012200	0001001110	1-?2-00022	1000000010	0011112011	0000000001	1100000121	0000110--	----001?0
<i>Corytoplectus riceanus</i>	?00-000020	0011012200	0001001110	1-02-00022	1000001000	00101112010	0000000001	1100000121	0011110--	----00110
<i>Crantzia cristata</i>	120-012000	0010010100	0011001000	0-2-10100	1000000020	01110-1100	0001000010	0000010101	0000010101	11101--00
<i>Crantzia epirotes</i>	120-012000	0000010100	0011001000	0-2-10100	1000000020	01110-1100	0001000010	0000010101	0000001010	11101--00
<i>Crantzia tigrina</i>	?00-000000	0011010110	0001001100	1102-00002	1000000001	0111111000	1000000011	1100001010	0011001011	?1101--00
<i>Cremersia platula</i>	?30-000010	0011010201	1001001100	11001-0010	0011101000	020-0-1000	0000100011	0000000101	00010111?0	?-??-??-??
<i>Drymonia ambonensis</i>	?00-000100	0010010000	0000-010?0	1101--1020	00000001010	01110-0011	0010000001	0102000-01	1000010--	-0-00000
<i>Drymonia brochidodroma</i>	?00-010120	0011010?00	0020-00-?0	0-2-00010	0012010000	010-0-1200	0000101001	0102?00001	2000111010	10200--00
<i>Drymonia conchoclyx</i>	?10-012020	0011010100	0020-00-00	0-2-01001	1012000001	010-100200	0001001001	0102000001	0001001011	00?01--00
<i>Drymonia corticea</i>	?10-010000	0011010100	00210011?0	1102-00020	1012010010	01110-2011	0010000001	0102000001	001111101?	??-??-??-??

Appendix 3. (continued.)

	000000001	111111112	222222223	333333334	444444445	555555556	666666667	777777778	888888889	999999999
	123456789	123456789	123456789	123456789	123456789	123456789	123456789	123456789	123456789	123456789
<i>Drymonia crenatiloba</i>	?00-000010	0011012200	0001001100	1012-00021	1010011010	01110102111	0000000001	0102000?01	0000111011	12211--00
<i>Drymonia dodsonii</i>	?00-000120	0001012200	0001001000	1112-00011	1000001010	01110-2011	0010000001	0100000101	0000001010	12011--00
<i>Drymonia doratostyla</i>	?10-012000	0011010100	00210011?0	1002-00011	1012011000	01110-1100	0001101000	0102000?01	000110101?	????1--00
<i>Drymonia foliacea</i>	?00-000120	0001012110	00110011?0	1002-00021	?012001100?	010-0-?P1?	000?P0?00?	0?02000?01	00001?P???	?????--??
<i>Drymonia hoppii</i>	?20-012010	0001010100	0001001100	1002-10002	0010001010	01110-1000	0001001001	0102000010	0011001010	10001--00
<i>Drymonia lactinosa</i>	?20-012000	0001112000	0000-00-00	11?2-00011	0011101040	011100-1200	0000001001	0102000001	0001001010	12201--00
<i>Drymonia lanceolata</i>	?00-010120	0001010000	0001001100	1102-00001	0010110000	01110-0201	0000001001	0102000001	0000101010	????1--00
<i>Drymonia macrophylla</i>	?10-010000	0001010100	10010011?0	1011--0011	0001000030	0111111100	0000100001	0102000001	0011001010	11101--00
<i>Drymonia multiflora</i>	?20-012000	0001010200	0000-01100	0--2-00001	1001001030	01100-1200	0000001001	0102000?01	0000001010	12210--00
<i>Drymonia pilifera</i>	?20-012000	0001010?00	00010011?0	11?2-10021	0001101000	0111111200	0000001001	0102000?01	0000011010	12201--00
<i>Drymonia rhodoloma</i>	?20-010020	0001013200	0020-00-00	1102-00020	0011101000	0111111200	0000001001	0102000001	0001011010	13501--01
<i>Drymonia serrulata</i>	110-012000	0001010000	00010010?0	0--2-10020	0010000010	0111111200	0000001001	0102000001	0010111010	1?201--00
<i>Dodsonii tenuis</i>	?20-012010	0001012100	0001001100	0--2-00012	0000010010	01110-1111	0010000001	0100000101	1001101010	100?1--00
<i>Drymonia teuscheri</i>	110-010010	0001012100	10010011?0	1112-00010	1000000010	01110-1111	0010000001	0100000101	0001101010	12011--00
<i>Drymonia turrihvae</i>	?00-000120	0001010200	0110-01110	1001--1020	1010000000	010-0-0200	0000001001	0102000001	0001010--	-2--00000
<i>Drymonia urceolata</i>	?00-000120	0001010200	0000-00-00	1002-01021	1012101000	0111102011	0100000000	0002000001	0001010--	-2--12000
<i>Drymonia warszewicziana</i>	?20-012010	0001010100	0000-01000	1112-10020	0011101000	0111010200	0000001001	0102000001	0001011010	13201--00
<i>Drymonia</i> sp. nov. 1	?00-000000	0001010100	1001001000	1102-00011	0000010010	010-101111	01000000??	?????????1	?????1100?	1?P11--00
<i>Drymonia</i> sp. nov. 3	?10-010010	0001012201	10110011?0	0--2-00020	0010001010	01110-1011	0010000001	0100000?01	00000010-0	11111--00
<i>Drymonia</i> sp. nov. 4	?20-000000	0001012000	10010010?0	1102-00011	1000010010	01110-1111	0010000001	0100000?01	00?P010-0	12211--00
<i>Drymonia</i> sp. nov. 5	?20-010100	0001012200	10010010?0	1102-00021	?000010010	01110-2011	0100000001	0000000?01	00110?P???	?????--??
<i>Episcia cupreata</i>	1011010010	0001010200	0111011110	1102-00021	1011111001	0210111100	0000100010	0000000?01	0000001111	14401--00
<i>Episcia lilacina</i>	1011010010	0001010200	1111011110	11?2-00021	0011111001	0210111100	000010000?	0100000101	0000001111	14401--00
<i>Glossoloma boguense</i>	?10-012010	0001010100	0000-00-00	1102-11111	0002011000	0111110000	1001100001	0100000101	0000001010	10001--00
<i>Glossoloma bolivianum</i>	?10-010000	0011010100	1001101100	1102-01100	1012001010	0111111000	1001100001	0100000101	0000001010	10001--00
<i>Glossoloma carpishense</i>	?10-010000	0011011100	0001001000	1002-01100	1000001011	0111110001	1001100001	0100000101	0000001010	00001--00
<i>Glossoloma chrysanthum</i>	?10-010000	0001010100	1001001110	0--2-01110	0011010101	0111110011	1000100001	0100000101	0000001010	10001--00
<i>Glossoloma grandicalyx</i>	?00-000000	0011010100	0000-01110	1112-00101	1000010010	0111111000	1001100001	0100000101	0000001010	10001--00
<i>Glossoloma herthae</i>	?20-010000	0011010100	00010010?0	1112-01100	1002011001	0110110001	1001100001	0100000101	0000001011	10001--00
<i>Glossoloma ichthyoderma</i>	110-000120	1011010100	00010011?0	1102-01111	?000000010	0111111011	?000000001	0100000101	000001011	10001--00
<i>Glossoloma maritimum</i>	?20-010000	0011011000	0001001110	1102-00111	0001101001	0111111000	1001000001	0100000101	0000001011	10001--00
<i>Glossoloma medusaeum</i>	?00-000000	0011010100	00010011?0	1112-01111	?000001041	0110111001	1001100001	0100000101	0000001011	10001--00
<i>Glossoloma oblongicalyx</i>	?00-000000	0011010100	00010010?0	1102-01101	?000010000	0111111000	1001100001	0100000101	000000101?	?0000--00
<i>Glossoloma panamense</i>	?00-000000	0011010100	00010011?0	1102-01101	1001101010	0111110000	1001100001	0100000101	0000101010	10001--00
<i>Glossoloma penduliflorum</i>	?20-012000	0001010100	0001001100	0--2-10101	0011101010	0111110000	1001100001	0100000101	000000101?	?0001--00
<i>Glossoloma purpureum</i>	?00-000000	0011010100	0001001010	1112-00101	0000001040	0111110000	1001100001	0100000101	0000001010	10001--00
<i>Glossoloma pycnosuzygium</i>	?10-010000	0011010100	00-0-00-00	1102-01100	?002001011	0111110000	1001100001	0100000101	000100101?	?0001--00
<i>Glossoloma schultzei</i>	?00-000000	0011010100	0001001100	1112-01101	1000000011	0111110000	1001100001	0100000101	0000001010	10001--00
<i>Glossoloma serpens</i>	?10-010000	0011010100	10010011?0	1112-01110	1000010001	0111110000	1001100001	0100000101	000000101?	?0001--??
<i>Glossoloma sprucei</i>	?00-000000	0011010200	0001001100	1112-00101	?000001041	0111110000	1001100001	0100000101	0000001010	10001--00
<i>Glossoloma tetragonoides</i>	100-000000	0011010000	00010011?0	1102-00101	?000000010	0110110000	1001100001	0100000101	0000001010	00001--00
<i>Glossoloma tetragonum</i>	100-000000	0011010100	00010011?0	1112-01101	1000000010	0111110000	1001100001	0100000101	0000001010	?0001--00

Appendix 3. (continued.)

<i>Glossoloma</i> sp. nov. 1	000000001	111111112	222222223	333333334	444444445	555555556	666666667	777777778	888888889	999999999
<i>Glossoloma</i> sp. nov. 2	?00-00000	001101010	000100100	1112-01011	000001030	0111111010	1001000001	0100000101	000001011	10000--10
<i>Glossoloma</i> sp. nov. 3	?00-00000	001101010	000100100	1112-01101	-000010030	01111110000	1001100001	0100000101	0000001010	10001--00
<i>Glossoloma</i> sp. nov. 4	?20-01200	001101020	000100100	1001-1100	1001101010	01111110000	0001100001	0100000101	0000001010	10001--00
<i>Glossoloma</i> sp. nov. 5	?00-00000	001101010	0000-01-00	1112-01101	?001101010	01111110000	1001100001	0100000101	00000?101?	??P01--00
<i>Lembocarpus amoenus</i>	?30-1-----	-001010201	0111000-10	11001-0022	0001101000	01111-2010	0000000010	0000000101	1000111110	0-501--00
<i>Nautilocalyx coccineus</i>	?30-000010	0001010000	1111011010	11?01-0020	0011111000	0211101201	000000100?	0100000101	000011111?	?P?P1--10
<i>Nautilocalyx melittifolius</i>	100-000120	0001010200	1011011010	11000-0021	0001101001	0111101201	0000000001	0000000101	0000111111	1?P01--?0
<i>Nautilocalyx panamensis</i>	100-000020	0001012200	0011001100	1102-00011	0011101010	0210111010	0000000001	0000000101	0011111111	1?P01--10
<i>Nautilocalyx pemphidius</i>	?00-000010	00010100?0	0110-111?0	1102-00022	0001111000	00110-1010	0000000001	0000000?01	0000111111	12201--10
<i>Nautilocalyx pictus</i>	?00-010010	0001010000	00110111?0	1102-00021	0011101001	02110-1100	0000001001	0100000121	0001111111	1?P01--?0
<i>Nautilocalyx whitei</i>	?00-000010	0001010001	00110111?0	?P?2-00021	0011101010	02110-1000	000000100?	0?00000?1?	?0011?P?P?	?P?P?--?P?
<i>Nematanthus albus</i>	?20-012000	0001010100	0001001000	1102-10011	0001101001	0111102000	0000000001	0000000121	0000001010	00001--00
<i>Nematanthus corticola</i>	?20-012000	0001010000	0020-00-00	0--2-10101	1001101010	01110-0000	1001100001	0000000101	0001001010	0?P?P--?0
<i>Nematanthus folyanus</i>	?20-010010	0011010000	0020-01100	1102-11111	0001101000	00110-2011	1000000001	0100000101	000001101?	?P?P?--?P?
<i>Nematanthus savannarum</i>	?20-012000	0001010100	1001101000	11?2-10021	0000000120	0111102010	0100000011	0100200101	000111010	?0001--00
<i>Nematanthus strigillosus</i>	010-010010	0001010100	0021001100	1102-00020	0011101000	0011112011	0100000001	1000000101	000101010	?P?P?--?P?
<i>Nematanthus weitstemii</i>	020-010010	0000013100	0120-01000	0--2-10020	0001101000	0111112011	0010000001	0000000101	000000101?	?P?P?--?P?
<i>Neomortonia nummularia</i>	120-012010	0001010100	0111001100	0--2-10012	0001101000	00110-2011	0010000001	0100000101	000001101?	?P?P?--?P?
<i>Neomortonia rosea</i>	120-012010	0001010100	0111001100	0--2-10010	0011111011	0211101200	0000001001	0100000101	000010-00	-5--11000
<i>Oerstedina cerricola</i>	?20-010000	0001010100	00010011?0	1102-00021	0001101001	0011111000	0000100001	0100000101	000010-00	-5--11001
<i>Paradrymonia anisophylla</i>	?20-012000	0001110000	1001001110	0?P2-10011	1011101000	02110-1200	0000001000	0100000?01	000000110?	??P?1--00
<i>Paradrymonia binata</i>	?10-000000	0001110010	0000-00-10	11000-0012	1001001030	00110-2011	0010000001	0000000101	001000111?	?P?P1--?P?
<i>Paradrymonia buchtienii</i>	?00-000010	0001110010	0020-01100	0?P00-0011	0011101000	02110-1010	0000000101	0000001?01	0001011101	?4001--00
<i>Paradrymonia campestyla</i>	?20-012010	0001010000	0001001100	1102-00011	0011101000	02110-1010	0000000100	0100011?01	00010?110?	04401--00
<i>Paradrymonia ciliosa</i>	?10-000010	0001110010	000?P01?00	11000-0011	0011101000	02110-1200	0000000100?	0?00011?01	00?P?1110?	?4401--00
<i>Paradrymonia densa</i>	?00-000010	0001010000	0000-00-10	11000-0011	1011111000	02110-1010	000000000?	0100200?01	00000?P?P?	?P?P?--?0?
<i>Paradrymonia fiquatana</i>	?00-000010	0001110010	0020-00-10	01000-0011	1011101001	0211010101	0000000001	0000000?01	0011011101	?2?01--00
<i>Paradrymonia lineata</i>	110-012010	0001010010	0020-01110	1102-00011	0011101000	0211111000	0000001001	0000000?01	0011011101	?P?01--00
<i>Paradrymonia longifolia</i>	?10-010000	0011010100	0000-010?0	1102-00020	0011101000	0111101000	0000001011	0102000?01	00110110-?	?1?01--00
<i>Paradrymonia macrophylla</i>	?10-000000	0001110010	0020-00-?0	1102100022	1011101030	0210-111010	0000001101	0?00000?01	2010111101	?0?P?0--00
<i>Paradrymonia metamorphophylla</i>	?10-012010	0001010201	0111000-00	11001-0022	0001101000	010-0-1010	0000000010	0000000101	00010?P?P?	?-?P?--?P?
<i>Rhoogeton cyclophyllus</i>	?30-1-----	-001010201	0111000-00	11001-0022	0001101000	0110-1010	0000000010	0000000101	00010?P?P?	?-?P?--?P?
<i>Rhoogeton viviparus</i>	?30-1-----	-001010100	0001000-00	11001-0022	0001101000	0110-1010	0000000010	0000000101	10011?P?P?	?-?P?--?P?
<i>Rufodorsia intermedia</i>	120-01?000	0001010100	0001001100	1102-00021	0001101001	0110111000	0000100001	0000300?01	0000010-00	-0-10000
<i>Sinningia cooperi</i>	200-100010	0001010201	0001001100	11001-0012	0001101000	00110-1000	0000110000	0000100120	00010012--	-----?0
<i>Sinningia incarnata</i>	200-100010	0001010100	0001001100	0102-00012	0101-0-000	01110-1000	0000110010	0010100100	01010012--	-----?0