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Evolution in the Andean Epiphytic Genus *Columnnea* (Gesneriaceae). I. Morphological Variation

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ABSTRACT. A cladistic analysis was performed on morphological data from seven of the nine species of *Columnnea* section *Pentadenia* and sixteen of the eighteen species of section *Stygnanthe* (Gesneriaceae). A nested, global outgroup analysis was performed by including representatives of three other sections of *Columnnea* and two species each of the closely related genera *Alloplectus* and *Drymonia*. Twenty characters were scored as binary, and thirteen were scored as multi-state. All characters scored were qualitative. Because of the high levels of homoplasy in the Gesneriaceae, simple characters were not found to be useful and more complex characters comprising several simple characters were necessary to provide resolution. The data were analyzed using Wagner parsimony, resulting in eight most parsimonious trees. In general, the phylogeny was congruent with current classification schemes and phylogenies derived from molecular data and combined molecular and morphological data. However, several phylogenetic relationships that result from the analysis of morphological data are suspect based on other data. The monophyly of *Alloplectus* is not supported solely with morphological data, although other data support its monophyly. Inferences regarding the biogeographic history and evolution of *Columnnea* sections *Pentadenia* and *Stygnanthe* indicate a southern Andean origin for the genus *Columnnea* with a subsequent migration and radiation northward.

Morphological variation has been useful for systematic analysis and classification for centuries. Only recently, especially within the last 5–10 years, have macromolecular methods been available for phylogenetic analysis (Atchison et al. 1976; Cattolico 1985; Chase et al. 1993; Clegg and Zurawski 1992; Crawford 1990; Downie and Palmer 1992; Hamby and Zimmer 1992; Palmer et al. 1988). Despite the many advantages of cladistic analyses based on molecular data (Crawford 1990; Palmer et al. 1988), a cladistic analysis of morphological variation still provides useful answers to evolutionary questions (Boufford et al. 1990; Crisci and Berry 1990; Donoghue and Sanderson 1992; Hillis 1987; Hoch et al. 1993; Kron and Judd 1990; Moritz and Hillis 1990; Rodman 1991; de Sá and Hillis 1990; Sytsma 1990).

In a group of species where relationships are unclear, cladistic analyses of morphological data can potentially resolve questions of monophyly, evolution, and classification. The neotropical genus *Columnnea* L. (Gesneriaceae) is such a problematic group. *Columnnea* contains over 200 species distributed from southern Mexico to Bolivia (Kvist and Skog 1993; Smith 1994). Plants are primarily epiphytic and range from lowland

rain forests to sub-paramo forests. Morphological variation in *Columnnea* is diverse, and has a pattern of distribution that makes construction of classifications difficult. No single character state accurately defines sections or species in *Columnnea*. As a result, numerous and overlapping characters must be used when defining taxonomic groups within the genus (i.e., groups are polythetic).

Corollas are tubular, generally red or yellow, and hummingbird pollinated (Jones and Rich 1972; Morley 1966, 1971, 1973a; Stearn 1969; Wiehler 1983). Although the basic floral structure is similar among species, there is wide variation in size, degree of zygomorphy, and color patterning throughout the genus. *Columnnea* is equally diverse vegetatively. Leaves are opposite, but in many species one leaf of a pair continues to expand while the other remains small and stipule-like (anisophylly) (Sánchez-Burgos and Dengler 1988), or sometimes abscises to give the appearance of alternate leaves. There is wide variation in leaf shape and color patterns that may act as additional signals for pollinators (Jones and Rich 1972; Wiehler 1983). Habit is also diverse, ranging from small herbaceous creepers, to shrubby herbs, and scandent shrubs.

The current infrageneric classification recognizes six sections, *Columnnea* L., *Collandra* (Lem.) Hanst., *Bucinellina* (Wiehler) Kvist & L. Skog, *Ortholoma* Benth., *Pentadenia* (Planch.) Benth., and *Stygnanthe* Hanst. (Kvist and Skog 1993). Previously, however, as many as nine sections with various subsections have been proposed (Bentham 1876; Fritsch 1894; Hanstein 1865; Morley 1976; Oersted 1858). Wiehler (1973, 1983) considered the morphological variation within *Columnnea* sensu lato great enough to warrant the recognition of five segregate genera. The current classification of Kvist and Skog (1993) largely follows the system of Wiehler (1973, 1983) except the genera are reduced to sections, and Wiehler's (1973) genus *Pentadenia* Hanst. is divided into sections *Pentadenia* and *Stygnanthe*.

The range in morphological variation has made infrageneric classification schemes difficult and frequently arbitrary. For example, section *Collandra* is essentially defined by the presence of anisophyllous leaves. However, anisophyly exists in three of the other five sections as well as numerous other genera in the family. The difficulty is determining strict homology between these characters, and determining whether these characters are synapomorphic or symplesiomorphic. Additionally, many characters superficially appear to be homologous, but upon more detailed examination prove to be the result of convergent evolution and are therefore analogous.

Much of the confusion at the infrageneric level in the taxonomy of *Columnnea* can be attributed to the lack of cladistic analysis. Therefore, to begin determining relationships within *Columnnea*, this study presents a cladistic analysis of the species constituting sections *Pentadenia* and *Stygnanthe*. These two sections are monophyletic on the basis of several characters each. Section *Stygnanthe* is characterized by small, relatively inconspicuous corollas that are only slightly swollen, many flowers per inflorescence, and short pedicels, whereas section *Pentadenia* is characterized by large, strongly ventricose, showy corollas, few flowers per inflorescence, long pedicels, and a robust herbaceous habit. These two sections will serve to anchor further cladistic analyses within *Columnnea*. Both sections are hypothesized to be basal within the genus because of characteristics shared with other neotropical Gesneriaceae. The nectary of sections *Pentadenia* and *Stygnanthe* is

a five-parted gland, the same form found in the genus *Alloplectus* Mart. The remaining four sections of *Columnnea* are characterized by a two-lobed dorsal gland. Thus, the two-lobed gland is likely to be a synapomorphy that separates the remainder of *Columnnea* from sections *Pentadenia* and *Stygnanthe*.

This morphologically based cladistic analysis provides a basis for understanding the classification, biogeography, and evolution of the species involved.

MATERIALS AND METHODS

Species Examined. Two of the smaller sections of *Columnnea*, *Pentadenia* and *Stygnanthe* were examined (Table 1). These two sections contain nine and eighteen species, respectively (Smith 1994), and form monophyletic groups as discussed above (Kvist and Skog 1993; Smith 1994). Four species, *C. antiocana* (Wiehler) J. F. Smith, *C. atahualpae* J. F. Smith & L. Skog, *C. poortmannii* (Wiehler) Kvist & L. Skog, and *C. xiphoidea* J. F. Smith & L. Skog were not included in this analysis because of insufficient material. Very few collections are available for these four species, and the collections that are available did not adequately represent the characters examined in this analysis. It was decided that the numerous characters that would have to be scored as missing would affect the analysis more than the elimination of these four species.

It is unlikely, although unknown, whether the omission of these four species would have an effect on the topology of the tree. Species were randomly eliminated from the data set and major rearrangements did not occur until seven species were eliminated (unpubl. data). Additionally, there is congruence between the trees from independent analyses of morphological and molecular data for species that are in common despite different species used in the two analyses (Smith and Sytsma 1994), thus implying that the elimination of some taxa may not have a major impact on the topology of the tree.

Columnnea spathulata, *C. nervosa*, and *C. strigosa* are highly polymorphic species that have had several names applied to them. To test the monophyly of these species and possible infraspecific relationships, *C. spathulata* was treated as its three segregate species, *C. spathulata* (spa), *C. microsepala* (Morton) Kvist & L. Skog (mic), and *C. zapotalana* (Wiehler) L. Skog (zap). *Col-*

TABLE 1. Species used in the cladistic analysis of morphological characters.

OUTGROUPS	
<i>Drymonia serrulata</i>	(Jacq.) Mart.
<i>D. stenophylla</i>	(J. D. Smith) H. E. Moore
INGROUPS	
<i>Alloplectus peruvianus</i>	(Zahlb.) Kvist & L. Skog
<i>A. meridensis</i>	Klotzch
<i>Columnea</i> section <i>Columnea</i>	
<i>C. schiedeana</i>	Schlecht.
<i>Columnea</i> section <i>Collandra</i>	
<i>C. densibracteata</i>	Kvist & L. Skog
<i>Columnea</i> section <i>Ortholoma</i>	
<i>C. mira</i>	Morley
<i>Columnea</i> section <i>Pentadenia</i>	
<i>C. isernii</i>	Cuatr.
<i>C. lophophora</i>	Mansf.
<i>C. hypocyrtantha</i>	(Wiehler) J. F. Smith & L. Skog
<i>C. nervosa</i>	(Kl. ex Oerst.) Hanst.
<i>C. oblongifolia</i>	Rusby
<i>C. strigosa</i>	Benth.
<i>C. trollii</i>	Mansf.
<i>Columnea</i> section <i>Stygnanthe</i>	
<i>C. ambigua</i>	(Urb.) Morley
<i>C. angustata</i>	(Wiehler) L. Skog
<i>C. byrsina</i>	(Wiehler) Kvist & L. Skog
<i>C. colombiana</i>	(Wiehler) Kvist & L. Skog
<i>C. crassicaulis</i>	(Wiehler) Kvist & L. Skog
<i>C. manabiana</i>	(Wiehler) J. F. Smith & L. Skog
<i>C. fritschii</i>	(Rusby) J. F. Smith
<i>C. inconspicua</i>	Kvist & L. Skog
<i>C. lavandulacea</i>	Kvist & L. Skog
<i>C. riley</i>	(Wiehler) J. F. Smith
<i>C. moesta</i>	Poepp.
<i>C. orientandina</i>	(Wiehler) Kvist & L. Skog
<i>C. ovatifolia</i>	Kvist & L. Skog
<i>C. spathulata</i>	Mansf.
<i>C. suffruticosa</i>	J. F. Smith & L. Skog
<i>C. ultraviolacea</i>	J. F. Smith & L. Skog

umnea strigosa was also analyzed using two morphological variants to represent *C. strigosa* s. str. (stri), and *C. kucyniakii* Raymond (kuc). *Columnea nervosa* includes two very disjunct populations, one in Ecuador, and the other in Mexico and Central America. These populations were analyzed as discrete taxa to test the monophyly of this species.

In addition to the species of section *Pentadenia* and *Stygnanthe*, representatives from three of the remaining four sections of *Columnea*; *Collandra* (~80 species), *Columnea* (~70 species), and *Ortholoma* (~35 species) were examined to determine their relationship to sections *Penta-*

denia and *Stygnanthe* (Table 1). Material representing the fourth section, *Bucinellina*, was not available for analysis. It is likely that section *Bucinellina* is a part of section *Ortholoma* and its absence would have no adverse effect on the analysis (unpubl. data).

Two species of *Alloplectus* (Table 1) were used as potential outgroups, but because of past taxonomic confusion with *Columnea* (Gibson 1972; Morley 1974; Morton 1953; Stearn 1969; Wiehler 1973, 1983), *Drymonia stenophylla* and *D. serrulata* were used as global outgroups (Maddison et al. 1984). The genus *Drymonia* Mart. is clearly a close relative of *Columnea* and *Alloplectus* based on its habit, corolla form, and nodal anatomy (Wiehler 1983). Only the two species of *Drymonia* were designated as global outgroups, thus allowing the data and parsimony to determine the relationships between and among sections *Pentadenia* and *Stygnanthe* and all other taxa in the analysis (Maddison et al. 1984).

Herbarium material (see Smith 1991 for complete list) was screened for morphological variation. Field work provided material of some poorly collected species and allowed compilation of morphological characters from living specimens.

Characters. Three general principles guided the selection of characters for this analysis: 1) characters must be arguably homologous; 2) there must be variation within the group in order to discriminate among clades, and 3) there must be a minimum of intraspecific variation. A total of 33 characters met these requirements.

Columnea, like other genera in the Gesneriaceae, is morphologically heterogeneous, and the patterns of variation are very complex. For example, multicellular trichomes can be found on the adaxial leaf surfaces of most species of *Columnea* section *Stygnanthe*, as well as in numerous other genera throughout the family. This character appears phylogenetically uninformative because of its widespread presence. If scored simply as presence or absence of multicellular trichomes, this feature provides no resolution within the cladogram (unpubl. data). However, the presence of multicellular trichomes can be informative if used in combination with their density and distribution pattern.

Therefore, to maximize the number of informative characters available for a cladistic analysis in *Columnea*, it was sometimes necessary to

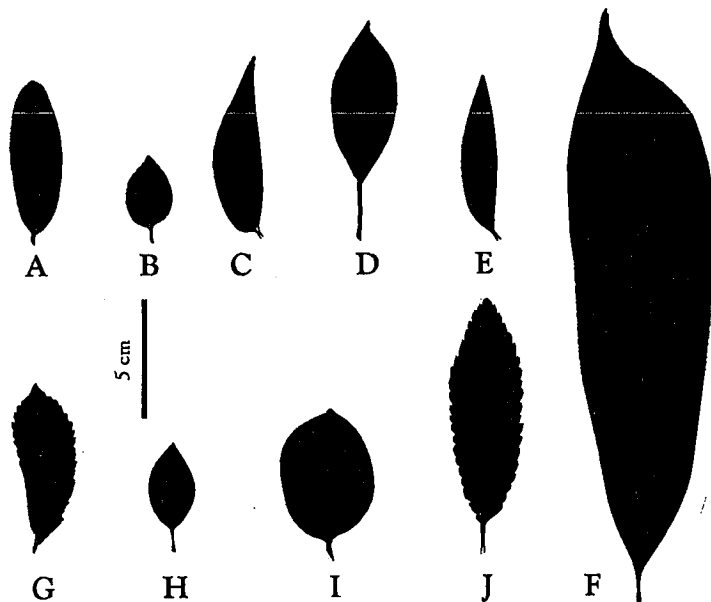


FIG. 1. Outlines of representative leaf shapes for the character states used in the cladistic analysis. A. blunt obovate (*Columnea orientandina*). B. small orbicular-ovate (*C. colombiana*). C. lanceolate (*C. inconspicua*). D. elliptic-ovate (*C. trollii*). E. narrow elliptic (*C. schiedeana*). F. large obovate (*C. densibracteata*). G. small obovate (*C. mira*). H. small ovate (*C. angustata*). I. large orbicular-ovate (*C. crassicaulis*). J. long elliptic (*C. spathulata*).

combine many simple characters into fewer complex ones. The simpler characters were uninformative in a cladistic analysis because of high amounts of homoplasy. Trichome types, densities, and distributions on the adaxial leaf surface may be shared by thousands of species in the family and are therefore symplesiomorphies. However, if the type, density, and distribution of trichomes are combined as a complex character, they may be more informative as synapomorphies, because any particular combination of type, density, and distribution of trichomes may have arisen only once.

To ensure that all material was at the same developmental stage, data were collected only from areas below nodes with flowers at anthesis, unless specifically a character of younger stages. Pickled floral material was available for many of the species and was used as the primary source of information for internal floral characters. These data were also supplemented by living and herbarium material. Characters pertaining to habit were largely gathered as a result of field observations and supplemented with herbarium label data.

Characters were limited to qualitative char-

acters, largely because of the facility of managing these characters in a cladistic fashion. Twenty characters were scored as binary, and 13 as multi-state, for a total of 33 characters. These characters will generate a tree of 73 steps provided no homoplasy exists in the data. Seven characters were scored as complexes of simpler characters. Complex characters are described and illustrated below (Figs. 1-3).

All characters were scored as unordered. Polymorphic multi-state characters were specified as polymorphic for the specific states found in that species. The characters and character states were scored as follows. See Appendix 1 for the complete data matrix.

1. FLOWER NUMBER. Although this is a quantitative character, it can be divided into three discrete categories which were scored as: (0) one flower per axil; (1) two-three flowers per axil; (2) more than four flowers per axil. There is a possibility that additional categories may exist between states 1 and 2, and that the scoring here may be conservative. However, this is unlikely, and not apparent from taxa examined in this group.

2. LIMB LOBE SIZE. The free lobes of the co-

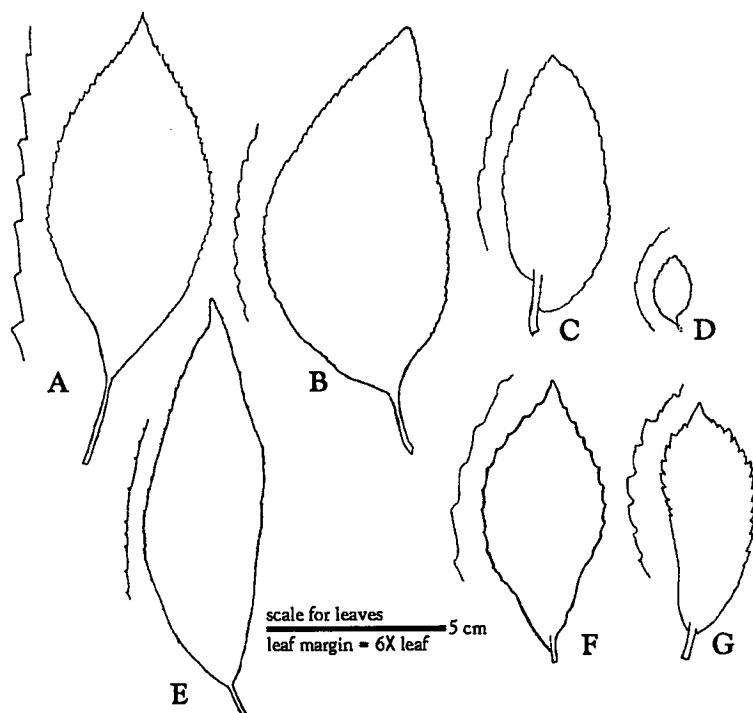


FIG. 2. Representative leaf margins for character states used in the analysis. Entire margins are not illustrated. A. serrate (*Columnea nervosa*). B. serrulate-crenate (*C. isernii*). C. crenate (*C. spathulata*). D. serrate with widely spaced teeth (*C. suffruticosa*). E. serrulate with widely spaced teeth (*C. oblongifolia*). F. sinuate (*Drymonia serrulata*). G. denticulate (*C. mira*).

rolla were scored as: (0) all equivalent in size; (1) enlargement of some of the petals. The homology of the petal enlargement is assumed on the basis of position.

3. LIMB LOBE FUSION. The two dorsal lobes were scored as: (0) free; (1) fused. The argument for homology in this character is the same as that of character 2.

4. CALYX LOBE POSITION. Calyx lobes were scored as: (0) all lobes erect and equal in size; (1) one lobe reflexed and unequal. This is treated as a single character because reflexed calyx lobes are always reduced in size from the remaining calyx lobes.

5. ANTHOR SHAPE. Anthers were scored as: (0) square; (1) rectangular.

6. ANTHOR ARRANGEMENT. Anthers were scored as: (0) connate at the apices; (1) connate along the length of the dehiscent side of the thecae as in *Drymonia* (Wiehler 1983).

7. STAMEN EXSERTION. Stamens were scored as: (0) included; (1) exserted from the mouth of

the corolla at anthesis. Only corollas in which the stage of anthers could be fully assessed were scored.

8. STYLE PUBESCENCE. Style pubescence was scored as: (0) glabrous; (1) with glandular trichomes; (2) with simple trichomes. Species with both glandular and simple trichomes were scored as polymorphic for these two character states.

9. OVARY PUBESCENCE. Ovaries were scored as: (0) glabrous; (1) pubescent.

10. COROLLA TUBE EXTERIOR PUBESCENCE. The corolla tube exterior pubescence was divided into seven character states. These were scored as: (0) sparsely hirsute; (1) lanate; (2) villos; (3) sericeous; (4) hirsute; (5) glabrous; (6) puberulent.

11. COROLLA LIMB PUBESCENCE. In some species, the limb pubescence is denser than the pubescence on the remaining part of the corolla, or present only on the limb. Limb pubescence was scored as: (0) similar to rest of

corolla in density; (1) denser than the rest of the corolla.

12. **COROLLA INTERIOR PUBESCENCE.** The interior surfaces of many corollas possess trichomes that are either glandular or simple. The pubescence on the interior surface of the corolla was scored as: (0) glabrous; (1) glandular; (2) simple. Species with both glandular and simple trichomes were scored as polymorphic.

13. **PEDICEL PUBESCENCE.** Pedicel pubescence was divided into six character states. These were scored as: (0) villous; (1) sericeous; (2) appressed hirsute; (3) hirsute; (4) tomentose; (5) sparsely hirsute.

14. **PEDICEL GLANDS.** In many species of *Columnnea*, the pedicels possess small dark glands just below the calyx. These glands of unknown function are frequently hidden in dense pubescence and are occasionally more prominent in fruit. They were scored as: (0) absent; (1) present.

15. **FRUIT SHAPE.** Mature fruits were scored as: (0) globose; (1) ovate.

16. **FRUIT COLOR.** Mature fruits were scored as: (0) white; (1) colored. This character was predominantly scored from fresh material and field collected material, but data were supplemented from label data and published species descriptions when available.

17. **FRUIT DEHISCENCE.** *Columnnea* is separated from *Alloplectus* by its indehiscent berry fruit. Both *Alloplectus* and *Drymonia* possess fleshy dehiscent "display" fruits (Wiehler 1983). This character was scored as: (0) indehiscent; (1) dehiscent.

18. **BRACT.** Floral bracts were scored as: (0) small to inconspicuous; (1) obscuring the base of the corolla.

19. **FLORAL BRACT MARGINS.** The margins of the floral bracts were considerably less variable than the leaves and were scored as: (0) entire; (1) toothed.

20. **LEAF ARRANGEMENT.** Most species of Gesneriaceae have opposite leaves, but some species of *Columnnea* examined in this study bear leaves in whorls of four. This character was scored as: (0) opposite leaves; (1) leaves in whorls of four.

21. **LEAF SHAPE.** Leaf shape was divided into 10 states. Size differences were taken into consideration for this character. The leaf shapes were scored as shown in Fig. 1: (0) blunt-obo-

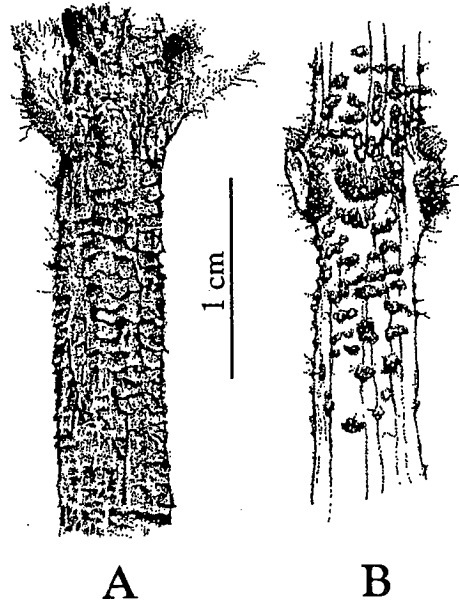


FIG. 3. Epidermis of lower stems seen in species used in this analysis. Smooth epidermis is not illustrated. A. scaly (*Columnnea oblongifolia*). B. flaky (*Alloplectus meridensis*).

vate; (1) small orbicular-ovate; (2) lanceolate; (3) elliptic-ovate; (4) narrow elliptic; (5) large ovate; (6) small obovate; (7) small ovate; (8) large orbicular-ovate; (9) long elliptic.

22. **PETIOLE.** Leaves were scored as: (0) sessile or nearly so (most petioles less than 8 mm); (1) distinctly petiolate (most petioles more than 10 mm). This character could be considered quantitative. However, the distinction between petiolate and sessile or nearly so is clear in the species examined. The distinction between sessile and nearly sessile is variable within species, and was therefore kept as a single character state.

23. **LEAF BASE.** This character was scored as: (0) acute; (1) oblique.

24. **LEAF MARGINS.** Leaf margins were divided into eight character states and are illustrated in Fig. 2. They were scored as: (0) serrate; (1) serrulate-crenate; (2) crenate; (3) serrate with widely spaced teeth; (4) serrulate with widely spaced teeth; (5) sinuate; (6) denticulate; (7) entire (small teeth are visible under 15 \times enlargement).

25. **LEAF MARGIN PUBESCENCE.** The leaves of many species have ciliate margins. Ciliate or

glabrous margins were scored separately from other margin characters because this is an epidermal character and not a leaf morphology character (Metcalfe 1979). This character was scored as: (0) glabrous; (1) ciliate.

26. ADAXIAL LEAF PUBESCENCE. The character was divided on the basis of pattern, density, and type of pubescence on the adaxial leaf surface. Pubescence color was not included because this is frequently a factor of exposure to different light intensities (pers. obs.). The character was scored as: (0) strigose; (1) sericeous; (2) glabrous to nearly so; (3) hirsute.

27. ABAXIAL MIDRIB PUBESCENCE. The midrib pubescence was scored as: (0) glabrous; (1) simple unicellular trichomes; (2) multicellular trichomes. In some instances, species were scored as polymorphic for states 1 and 2.

28. ABAXIAL LEAF PUBESCENCE. This character excludes pubescence on the midribs and was divided into seven character states on the basis of side-by-side comparisons of herbarium material. This character was scored as: (0) sparsely sericeous; (1) glabrous; (2) sericeous; (3) hirsute; (4) strigillose; (5) puberulent; (6) lanate. This character is not correlated with the preceding character in *Columnnea*. Only seven out of thirty-four taxa were scored the same for both characters.

29. LEAF SCARS. In several species, the leaf scar is raised from the surface of the stem. This character was scored as: (0) flush with the stem surface; (1) raised from the stem surface.

30. STEM PUBESCENCE. Stem pubescence was scored from the apical internodes because pubescence is frequently lost on older stem surfaces. The pubescence was scored as: (0) glabrous; (1) simple unicellular trichomes; (2) multicellular uniseriate trichomes. Species with both uni- and multicellular trichomes were scored as polymorphic for these two character states.

31. LOWER STEM SURFACE. The lower stem of *Columnnea* species has a distinctively different appearance from the apex depending on how the young epidermal tissue expands with the growing stem. It is frequently glabrous at this stage, and the manner in which the epidermis breaks is uniform within a species. The lower stem epidermis was scored as: (0) smooth; (1) scaly; (2) flaky (Fig. 3).

32. LOWER STEM CROSS SECTION. The lower

stem can be differentiated as: (0) terete; (1) quadrangular.

33. HABIT. Habit was divided into six character states and took into consideration leaf orientation. The habits were scored as: (0) herb with horizontal planar leaf orientation; (1) creeping herb; (2) shrub (erect or scandent); (3) robust herb; (4) vine; (5) small herb. Some species, in which the habit was difficult to define as a single category or occasionally had populations representative of different categories, were scored as polymorphic.

Characters Excluded in Analysis. Additional characters were examined, but not used in this cladistic analysis because they: 1) are autapomorphic; 2) are polymorphic within a species; 3) exhibit patterns of distribution in *Columnnea* and related genera indicating numerous, independent origins; 4) are possibly not homologous; 5) are highly correlated with other characters, or 6) require an excessive number of states to score adequately. Thus, we have maintained a conservative approach to character selection. The characters that were excluded are as follows.

COROLLA SHAPE. Corolla shape would have required over 10 different character states to be coded properly, many of which would have involved arbitrary dividing lines based on size. It was therefore decided to omit the character.

COROLLA COLOR. Corolla color is variable within a species, and may also be correlated with environmental variables such as light intensity or selection by pollinators. The amount of variation within a species was especially prominent in species that have limbs or limb lobes differing in color from the main corolla body. In many species with red corollas there is a green limb. However, in some accessions the amount of green is reduced, lacking, or more yellow than green. It is clear that many genetic and environmental factors control this character, and, because it was beyond the scope of this study to determine the homology of the controlling factors, the character was excluded.

STIGMA. Species of *Columnnea* have either bilobed or stomatomorphic stigmas. For most species this character is constant, but in several it is both bilobed and stomatomorphic. The apparent constancy of the character seen in other species may well reflect inadequate sampling.

CALYX LOBE SHAPE. Calyx lobe shape was

found to be highly variable within the genus and therefore unlikely to be phylogenetically informative. Over 10 character states would have been necessary to score calyx lobe shape adequately.

PEDICEL LENGTH. This quantitative character was difficult to separate into discrete character states, despite the extreme differences seen between some species. In addition, pedicel length can be quite variable within a species (e.g., *Columnnea strigosa*).

FRUIT PUBESCENCE. This character was found to be correlated with ovary pubescence.

ANISOPHYLLY. This character, although of importance in determining generic and infrageneric classifications (Bentham 1876; Fritsch 1894; Hanstein 1865; Kvist and Skog 1993; Morley 1976; Wiehler 1973, 1983), was eliminated from the cladistic analysis on the assumption that it is the result of strong selective pressures and has repeatedly arisen in disparate groups, thus limiting its phylogenetic utility (Givnish 1984; Morley 1973a, 1973b). The scattered appearance of this character throughout *Columnnea*, Gesneriaceae (*Drymonia*, *Paradrymonia* Hanst., *Monopyle* Moritz ex Benth., *Streptocarpus* Lindl.), and other families (Melastomataceae), is sufficient evidence for its exclusion.

LEAF COLORATION. The leaf coloration patterns that are very distinctive within the genus were found to be variable within a species, and possibly are directly correlated with the amount of light received by the plant (pers. obs.). The same arguments apply for calyx and floral bract color.

ADVENTITIOUS ROOTS. In collecting material for propagation and continued maintenance of cultures, it became obvious that some species were easier to propagate vegetatively than others. This is somewhat correlated to habit because the smaller herbaceous plants propagate more easily than the herbaceous shrubs. Attempts were made to define this character on the basis of adventitious roots but nearly every species had at least one specimen with some adventitious roots and many species with numerous adventitious roots had specimens that lacked them.

Phylogenetic Analysis. Phylogenetic divergence was reconstructed using Swofford's (1993) computer program PAUP version 3.1.1 to implement Wagner parsimony (Farris 1970;

Farris et al. 1970; Swofford and Maddison 1987). This program allows parallelisms and reversals (homoplasy), permits the use of unordered multi-state characters (13 multi-state characters were used in this analysis), and provides an option for missing data. In this analysis, trees were generated using the general heuristic option saving minimal trees only with the collapse zero-length branches in effect. Because of the large number of taxa in this analysis, the branch and bound and exhaustive search options would have consumed an excessive amount of computer time. Therefore the trees presented here are best approximations and not exact solutions. The manner in which the program reconstructs phylogenetic sequences is sensitive to the order of taxa presentation in the data matrix (Maddison 1991). It is therefore important to repeat the analysis several times with a different order of taxa for each replicate. To do this, the random search option was used to examine 500 replicates.

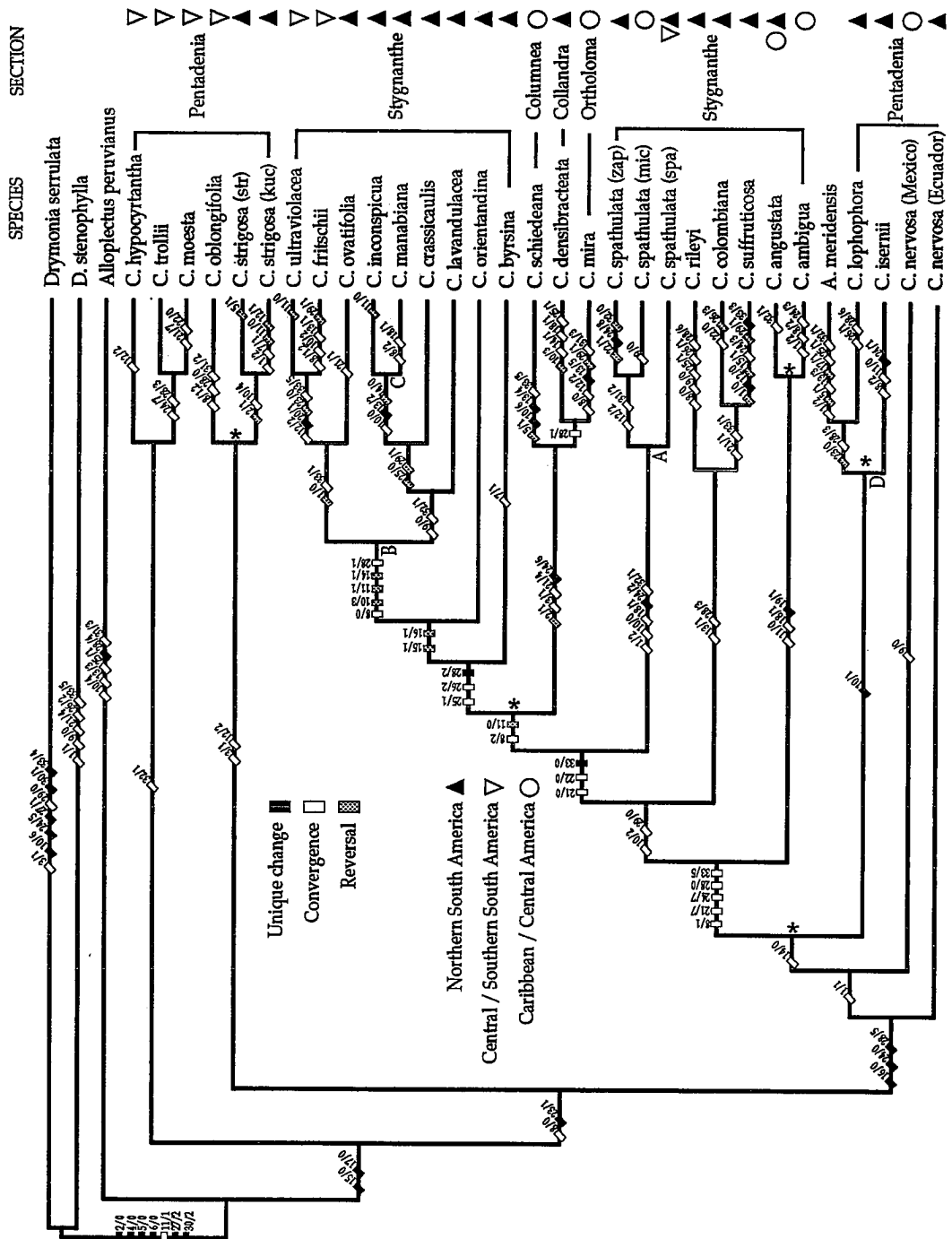
A decay analysis was performed to examine trees that were one or fewer steps longer than the most parsimonious tree (Bremer 1988; Donoghue et al. 1992). This type of analysis provides an indication of the robustness of the data by determining which clades persist in a consensus tree as parsimony is relaxed.

The two species of *Drymonia* were designated as the outgroup in all analyses. The designation of only these two species as outgroup allowed for a global outgroup analysis to determine the relationships of *Columnnea* sections *Pentadenia* and *Stygnanthe* among themselves and to the other taxa in the analysis (Maddison et al. 1984).

Character state changes were plotted onto trees based on the acctran option. The acctran option tends to place character state changes at the base of the tree, whereas the deltran option tends to place character state changes toward the terminal clades. Because the deltran option can sometimes drastically alter their distribution, character state changes were also plotted with the deltran option and compared.

RESULTS

The cladistic analysis produced eight most parsimonious trees of 170 steps each, with a consistency index of 0.44 and retention index of 0.63. No additional trees were found with



500 random searches. One of the eight most parsimonious trees is shown in Fig. 4 with the character state change distribution according to the acctran option. Clades that collapse in a strict consensus of the eight most parsimonious trees are designated with asterisks. It should be emphasized that this tree was arbitrarily chosen to demonstrate the distribution of morphological character state changes and does not reflect any bias on the authors' part towards a particular topology.

The decay analysis resulted in 608 trees of 171 steps or fewer. The consensus of these 608 trees is unresolved with the exception of clades A, B, and C of Fig. 4 with no resolution in clades A or B. Because nearly all resolution was lost with trees one or fewer steps longer, trees two or more steps longer were not examined.

Comparison of character state change distributions between the acctran and deltran options showed only minor differences. In no clade does a difference between the options cause a strongly supported clade to be weakly supported or vice versa. The greatest difference between the two options is the number of autapomorphies attributed to *Drymonia serrulata*. With the acctran option, seven character state changes are attributed to *D. serrulata*, whereas in deltran there are only three. With the deltran option the character state changes are instead placed at the basal nodes of the tree and increase the state changes at the node above the two *Drymonia* species from seven to nine.

DISCUSSION

The strict consensus tree for *Columnnea* sections *Pentadenia* and *Stygnanthe* is well resolved with the exception of four polytomies (see asterisks in Fig. 4). Most of the clades are well supported with two to six character state changes. Only three clades are supported by a

single state change, the clade immediately sister to the Ecuadorian populations of *C. nervosa*, the clade sister to the Central American populations of *C. nervosa*, and clade D. Seventy percent of the character state changes are convergences. Because of this, and because several nodes are supported by few characters, much resolution is lost within the consensus tree of all trees one or fewer steps longer than the most-parsimonious tree.

Comparison to Traditional Classification. The strict consensus tree (see asterisks in Fig. 4) is largely congruent with the current taxonomy of the species with a few exceptions. These exceptions include the placement of the two species of *Alloplectus* (distinguished from *Columnnea* on the basis of fleshy dehiscent fruits), which are not allied as sister species in this analysis (Fig. 4). Both species share several morphological characters that might be expected to unite them in a single clade, such as pubescent ovaries, dehiscent fruits, elliptic-ovate and petiolate leaves that are sparsely sericeous on the adaxial surface, raised leaf scars, and shrubby habit. However, the two *Alloplectus* species branch independently in the cladogram, despite the inclusion of these characters in the analysis. Upon examination of the tree (Fig. 4), it is apparent that all of these character states are homoplastic, many of them shared with the two species of *Drymonia*. These character states are therefore likely symplesiomorphies and thus do not unite these species in a cladistic analysis.

Similarly, the two species of *Alloplectus* are not allied as sister species in a molecular tree (Smith and Sytsma 1994). However, when the two data sets are combined the *Alloplectus* species are allied as sister species in a clade sister to all *Columnnea* species (Smith and Sytsma, in manuscript).

Sectional divisions are weakly supported as monophyletic groups as a result of this cladistic

←

FIG. 4. One of eight most parsimonious trees, length 170, consistency index 0.44, retention index 0.63. Nodes that collapse in a strict consensus of the eight trees are marked with an asterisk. Character state changes are plotted onto the cladogram using the acctran option of PAUP, with characters numbered as in the text. Character state changes were divided into three types, unique, convergent, and reversal of character state to immediate ancestral state. Reversals that are also convergent are marked only as reversals. Numerals after the slash indicate character state changes for that clade. Geographic distribution of species is denoted by symbols into three biogeographic regions: Central/Southern South America, including southern Peru and Bolivia; Northern South America, including Peru, Ecuador, Colombia, and Andean region of Venezuela; Caribbean/Central America, including Mexico and the Coastal Range of Venezuela. Species that occur in more than one region are marked as such.

analysis. *Pentadenia* is a basal paraphyletic clade and the species in this section all branch fairly early in the cladogram (Fig. 4). Section *Stygnanthe* is polyphyletic because *C. moesta* groups within section *Pentadenia*. Excluding *C. moesta* (see below), section *Stygnanthe* is a paraphyletic assemblage because three other sections (sects. *Columnnea*, *Collandra*, *Ortholoma*) are imbedded within this clade (Fig. 4). Taken alone these data might suggest that section *Stygnanthe* should be divided into at least three sections. However, because the data only weakly support this division, we do not propose any realignments of sectional divisions within *Columnnea*. In addition, data from other analyses indicate that splitting section *Stygnanthe* may not be necessary (Smith and Sytsma 1994).

COLUMNNEA MOESTA. *Columnnea moesta* is a species of section *Stygnanthe*, but is imbedded in a clade with species of section *Pentadenia* in the trees based on morphological data (e.g., Fig. 4). However, in trees based on chloroplast DNA restriction site variation, *C. moesta* is clearly the sister species of *C. ultravioleacea* within section *Stygnanthe*. This discrepancy between the two data sets indicates a potential hybrid origin for *C. moesta*. However, examinations of restriction site variation for nuclear ribosomal DNA, morphological variation, and biogeography do not indicate a hybrid pattern for this species (Smith and Sytsma 1994; Smith 1991). The unusual placement of *C. moesta* in the analysis of morphological data may be due either to the presence of symplesiomorphic characters retained in this species or to rapid convergent evolution of morphological characters.

INTRASPECIFIC POLYMORPHISM. Morphological or geographical variants were treated as independent taxa for three species, *Columnnea spathulata*, *C. strigosa*, and *C. nervosa*. Of these, only *C. nervosa* was paraphyletic in the resulting cladograms (e.g., Fig. 4). Surprisingly, the two geographical variants of *C. nervosa* used in the analysis are more homogeneous morphologically than morphological variants used for *C. strigosa* and *C. spathulata*. The branch above Ecuadorian populations of *C. nervosa* (Fig. 4) is defined by a change in flower number per axil from one to two or three. This character has a high level of homoplasy, its consistency index being 0.25. Therefore, the separation of these two taxa is weak in the cladistic analysis. There are also several characters such as calyx lobe

shape and pedicel length (characters that are complex within *Columnnea* as a whole, and thus not used in the cladistic analysis) that unite these taxa as a single species. Therefore, elevation of these geographical variants to species level is probably not warranted.

The variants of *Columnnea spathulata* are all closely related and supported as a monophyletic group by six character state changes (crenate teeth, more than four flowers per inflorescence, sparsely hirsute corolla, long elliptic leaves, bracts obscuring the corolla, quadrangular stems). The variants representing *C. zapotalana* (zap), and *C. microsepala* (mic) are separated from *C. spathulata* (spa) by the presence of a flaky rather than smooth lower stem, and simple as well as glandular trichomes on the corolla interior (Fig. 4). Both of these character states are homoplastic and therefore unlikely to support maintenance of either *C. microsepala* or *C. zapotalana* as separate species.

Columnnea kuczyniakii is a validly published name for a morphological variant of *C. strigosa* and is readily distinguished from *C. strigosa* s. str. in the field and herbarium. The leaves of this taxon are much larger than those of *C. strigosa* and the corollas are narrower and shorter, with smaller lobes, and with purple spots at the sinuses of the lobes. In addition, *C. strigosa* typically has only one or two flowers per axil, and *C. strigosa* (kuc) usually has more than four. Despite these morphological differences, the two morphological variants occur in the same clade, united by hirsute corollas with large unequal lobes (Fig. 4). Both of these characters are homoplastic. The large unequal lobes are convergent with those of species representing other sections of *Columnnea*, and hirsute corollas are shared with *Alloplectus peruvianus*. In part, some of the characters that distinguish the two taxa were not included in the analysis because they were too complicated to score reliably or were variable within the species. However, it is unlikely that these characters would have placed *C. strigosa* (kuc) elsewhere, and more probably would have appeared as additional autapomorphies for this taxon with the four autapomorphies already present in Fig. 4 (more than four flowers per inflorescence, pubescence of the corolla limb similar to the remainder of the corolla, presence of glandular trichomes on corolla interior, and exerted stamens). Despite the obvious differences between these two taxa, they are united

by corolla pubescence and limb lobe size. Although there are specimens that can be identified as either *C. strigosa* (stri) or *C. strigosa* (kuc), there are many intermediate specimens. A few collections also possess a mixture of character states of *C. strigosa* (kuc) and *C. strigosa* (stri). This continuum of variation makes infraspecific division impractical.

Comparison to Molecular and Combined Analyses. The consensus tree derived from morphological data (see asterisks in Fig. 4) is similar in many ways to the consensus tree derived from cpDNA (Smith and Sytsma 1994), as well as to the tree derived from a combination of morphology and molecules (Smith and Sytsma, in manuscript). The morphological tree differs mostly in the exact position of some of the basal clades, although the relative locations of the taxa are similar throughout all three analyses.

Biogeography. The cladistic analysis of the five *Columnnea* sections examined here indicates an origin of *Columnnea* in the middle-southern Andean area (Berry 1982; Molau 1988; Pennell 1945). The species that branch at the base of the cladogram are southern Peruvian or Bolivian species (*C. trollii*, *C. hypocyrtantha*, *C. oblongifolia*), and those that branch toward the tips of the cladogram are mostly from Ecuador and Colombia (Fig. 4).

A model for the biogeographic history of *Columnnea* would include an origin in either southern Peru or Bolivia followed by a northward dispersal with centers of radiation in Ecuador (section *Stygnanthe*), Panama/Colombia (section *Collandra*), and Central America/Caribbean (section *Columnnea*). There are several anomalies in this model, such as the presence of *C. nervosa*, a Central American species, at the base of most of the Ecuadorian species in the cladogram (Fig. 4), and the presence of the Bolivian species *C. ultraviolacea* and *C. fritschii* in the terminal clades of the phylogeny (Fig. 4). These anomalies are largely explained by bird dispersal.

This biogeographic model is similar to that proposed for another Andean genus, *Fuchsia* L. (Onagraceae; Berry 1982). *Fuchsia* was also proposed to have a southern Andean origin, followed by a northward progression and centers of radiation in the northern Andes and Central America. There are also parallel anomalies in the biogeographic hypotheses for *Fuchsia* and *Columnnea*. Similar to the situation of *C. nervosa*

in *Columnnea*, the Central American section *Jimenezia* Breedlove, Berry & Raven of *Fuchsia* is near the base of the cladogram for *Fuchsia* (Sytsma and Smith 1988). The appearance of a basally located clade in Central America was hypothesized as a long distance dispersal event early in the radiation of *Fuchsia* section *Fuchsia* (Berry 1982). Because both *Fuchsia* and *Columnnea* comprise berry-fruited species, a similar hypothesis of long distance dispersal may explain the anomalous distributions of *C. nervosa*, *C. ultraviolacea*, and *C. fritschii* in *Columnnea*.

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LITERATURE CITED

- ATCHISON, B. A., P. R. WHITFIELD, and W. BOTTOMLEY. 1976. Comparison of chloroplast DNA's by specific fragmentation with *EcoRI* endonuclease. *Molecular and General Genetics* 148: 263-269.
- BENTHAM, G. 1876. Gesneriaceae. Pp. 990-1025 in *Genera Plantarum*, vol. 2, eds. G. Bentham and J. D. Hooker. London: Reeve and Co.
- BERRY, P. E. 1982. The systematics and evolution of *Fuchsia* section *Fuchsia* (Onagraceae). *Annals of the Missouri Botanical Garden* 69:1-198.
- BREMER, K. 1988. The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. *Evolution* 42: 795-803.
- BOUFFORD, D. E., J. V. CRISCI, H. TOBE, and P. C. HOCH. 1990. A cladistic analysis of *Circaea* (Onagraceae). *Cladistics* 6: 171-182.
- CATTOLICO, R. A. 1985. Chloroplast biosystematics: Chloroplast DNA as a molecular probe. *Bio-Systems* 18: 299-306.
- CHASE, M. W., D. E. SOLTIS, R. G. OLMSTEAD, D. MORGAN, D. H. LES, B. D. MISHLER, M. R. DUVAL, R. A. PRICE, H. G. HILLS, Y.-L. QUI, K. A. KRON, J. H. RETTIG, E. CONTI, J. D. PALMER, J. R. MANHART, K. J. SYTSMA, H. J. MICHAELS, W. J. KRESS, K. G. KAROL, W. D. CLARK, M. HEDRÉN, B. S. GAUT, R. K. JANSEN, K.-J. KIM, C. F. WIMPEE, J. F. SMITH, G. R. FURNIER, S. H. STRAUSS, Q.-Y. XIANG, G. M. PLUNKETT, P. S. SOLTIS, S. M. SWENSEN, S. E. WIL-

- LIAMS, P. A. GADEK, C. J. QUINN, L. E. EGUIARTE, E. GOLENBERG, G. H. LEARN, S. W. GRAHAM, S. C. H. BARRETT, S. DAYANANDAN, and V. A. ALBERT. 1993. Phylogenetics of seed plants: An analysis of nucleotide sequences from the plastid gene *rbcl*. *Annals of the Missouri Botanical Garden* 80: 528–580.
- CLEGG, M. T. and G. ZURAWSKI. 1992. Chloroplast DNA and the study of plant phylogeny: present status and future prospects. Pp. 1–13 in *Molecular systematics of plants*, eds. P. S. Soltis, D. E. Soltis, and J. J. Doyle. New York: Chapman and Hall.
- CRAWFORD, D. J. 1990. *Plant molecular systematics*. New York: John Wiley and Sons.
- CRISCI, J. V. and P. E. BERRY. 1990. A phylogenetic reevaluation of the old world species of *Fuchsia* (Onagraceae). *Annals of the Missouri Botanical Garden* 77: 517–522.
- DONOGHUE, M. J. and M. J. SANDERSON. 1992. The suitability of molecular and morphological evidence in reconstructing plant phylogeny. Pp. 340–368 in *Molecular systematics of plants*, eds. P. S. Soltis, D. E. Soltis, and J. J. Doyle. New York: Chapman and Hall.
- , R. G. OLMSTEAD, J. F. SMITH, and J. D. PALMER. 1992. Phylogenetic relationships of Dipsacales based on *rbcl* sequences. *Annals of the Missouri Botanical Garden* 79: 333–345.
- DOWNIE, S. R. and J. D. PALMER. 1992. Use of chloroplast DNA rearrangements in reconstructing plant phylogeny. Pp. 14–35 in *Molecular systematics of plants*, eds. P. S. Soltis, D. E. Soltis, and J. J. Doyle. New York: Chapman and Hall.
- FARRIS, S. J. 1970. Methods for computing Wagner trees. *Systematic Zoology* 19: 83–92.
- , A. G. KLUGE, and M. J. ECKARDT. 1970. A numerical approach to phylogenetic systematics. *Systematic Zoology* 19: 172–191.
- FRITSCH, K. 1894. Gesneriaceae. Pp. 133–185 in *Die Natürlichen Pflanzenfamilien*, part 4, section 3b, eds. A. Engler and K. Prantl. Leipzig: Verlag Engelmann.
- GIBSON, D. N. 1972. Studies in American plants IV. *Phytologia* 23: 334–342.
- GIVNISH, T. J. 1984. Leaf and canopy adaptations in tropical forests. Pp. 51–84 in *Physiological ecology of plants of the wet tropics*, eds. E. Medina, H. A. Mooney and C. Vazquez-Yanes. The Hague: Dr. W. Junk Publishers.
- HAMBY, R. K. and E. A. ZIMMER. 1992. Ribosomal RNA as a phylogenetic tool in plant systematics. Pp. 50–91 in *Molecular systematics of plants*, eds. P. S. Soltis, D. E. Soltis, and J. J. Doyle. New York: Chapman and Hall.
- HANSTEIN, J. 1865. Die Gesneriaceen des Königl. Herbariums und der Garten zu Berlin, nebst Beobachtungen über die Familie im Ganzen, II, 3. *Linnaea* 34: 225–462.
- HILLIS, D. M. 1987. Molecular versus morphological approaches to systematics. *Annual Review of Ecology and Systematics* 18: 23–42.
- HOCH, P. C., J. V. CRISCI, H. TOBE, and P. E. BERRY. 1993. A cladistic analysis of the plant family Onagraceae. *Systematic Botany* 18: 31–47.
- JONES, C. E. and P. V. RICH. 1972. Ornithophily and extrafloral color patterns in *Columnnea florida* Morton (Gesneriaceae). *Bulletin of the Southern California Academy of Science* 7: 113–116.
- KRON, K. A. and W. S. JUDD. 1991. Phylogenetic relationships within the Rhodoreae (Ericaceae) with specific comments on the placement of *Ledum*. *Systematic Botany* 15: 57–68.
- KVIST, L. P. and L. E. SKOG. 1993. The genus *Columnnea* in Ecuador. *Allertonia* 6: 327–400.
- MADDISON, D. R. 1991. The discovery and importance of multiple islands of most-parsimonious trees. *Systematic Zoology* 40: 315–328.
- MADDISON, W. P., M. J. DONOGHUE, and D. R. MADDISON. 1984. Outgroup analysis and parsimony. *Systematic Zoology* 33: 83–103.
- METCALFE, C. R. 1979. The leaf: General topography and ontogeny of the tissues. Pp. 63–76 in *Anatomy of the dicotyledons 2nd edition. Vol I: Systematic anatomy of the leaf and stem*, eds. C. R. Metcalfe and L. Chalk. New York: Oxford University Press.
- MOLAU, U. 1988. Scrophulariaceae—Part I. Calceolarieae. *Flora Neotropica Monograph* 47. New York: The New York Botanical Garden.
- MORITZ, C. and D. M. HILLIS. 1990. Molecular systematics: Context and controversies. Pp. 1–12 in *Molecular systematics*, eds. D. M. Hillis and C. Moritz. Sunderland, Massachusetts: Sinauer Associates, Inc.
- MORLEY, B. D. 1966. *Columnnea* and aspects of its evolution. *Science Notes and News, Jamaica* 2: 13–14.
- . 1971. A hybrid swarm between two hummingbird-pollinated species of *Columnnea* (Gesneriaceae) in Jamaica. *Journal of the Linnean Society, Botany* 64: 81–96.
- . 1973a. Ecological factors of importance to *Columnnea* taxonomy. Pp. 265–281 in *Taxonomy and ecology*, ed. V. Heywood. New York: Academic Press.
- . 1973b. Materials for a treatment of *Columnnea* in Panama. *Annals of the Missouri Botanical Garden* 60: 449–460.
- . 1974. A revision of the Caribbean species in the genera *Columnnea* L. and *Alloplectus* Mart. (Gesneriaceae). *Proceedings of the Royal Irish Academy* 74B: 411–438.
- . 1976. A key, typification, and synonymy of the sections in the genus *Columnnea* L. *Contributions from the National Botanical Garden Glasnevin* 1: 1–11.
- MORTON, C. V. 1953. Gesneriaceae. Pp. 520–534 in

- Contributions to the flora of Venezuela*, ed. J. A. Steyermark. Fieldiana, Botany 28: 520-534.
- OERSTED, A. S. 1858. Centralamericas Gesneraceer, et systematisk, plantegeografisk Bidrag til Centralamericas Flora. Det Kongelige Danske Videnskabernes Selskabet Skrifter, Raekke 5, 5: 77-152.
- PALMER, J. D., R. K. JANSEN, H. J. MICHAELS, M. W. CHASE, and J. R. MANHART. 1988. Chloroplast DNA and plant phylogeny. *Annals of the Missouri Botanical Garden* 75: 1180-1206.
- PENNELL, F. W. 1945. The genus *Calceolaria* in south-eastern Peru. *Proceedings of the National Academy of Sciences, U.S.A.* 97: 137-177.
- RODMAN, J. E. 1991. A taxonomic analysis of glucosinolate-producing plants, part 2: Cladistics. *Systematic Botany* 16: 619-629.
- DE SÁ, R. O. and D. M. HILLIS. 1990. Phylogenetic relationships of the pipid frogs *Xenopus* and *Silurana*: An integration of ribosomal DNA and morphology. *Molecular Biology and Evolution* 7: 365-376.
- SÁNCHEZ-BURGOS, A. A. and N. G. DENGLER. 1988. Leaf development in isophyllous and facultatively anisophyllous species of *Pentadenia* (Gesneriaceae). *American Journal of Botany* 75: 1472-1484.
- SMITH J. F. 1991. A revision and study in evolution of *Columnea* sections *Pentadenia* and *Stygnanthe* (Gesneriaceae). Ph.D. dissertation, University of Wisconsin, Madison.
- . 1994. Systematics of *Columnea* sections *Pentadenia* and *Stygnanthe* (Gesneriaceae). *Systematic Botany Monographs* 19: 317-336.
- and K. J. SYTSMA. 1994. Evolution in *Columnea* Part II: Chloroplast DNA variation. *Systematic Botany* (in press).
- STEARNS, W. T. 1969. The Jamaican species of *Columnea* and *Alloplectus* (Gesneriaceae). *Bulletin of the British Museum (Natural History) Botany* 4: 179-236.
- SWOFFORD, D. 1993. *PAUP phylogenetic analysis using parsimony*, version 3.1.1. Champaign: Illinois Natural History Survey.
- and W. P. MADDISON. 1987. Reconstructing ancestral character states under Wagner parsimony. *Mathematical Biosciences* 87: 199-229.
- SYTSMA, K. J. 1990. DNA and morphology: Inference of plant phylogeny. *Trends in Ecology and Evolution* 5: 104-110.
- and J. F. SMITH. 1988. DNA and morphology: Comparisons in the Onagraceae. *Annals of the Missouri Botanical Garden* 75: 1217-1237.
- WIEHLER, H. 1973. One hundred transfers from *Alloplectus* and *Columnea*. *Phytologia* 27: 309-329.
- . 1983. A synopsis of the neotropical Gesneriaceae. *Selbyana* 6: 1-219.

APPENDIX 1. Matrix of coding assignments for the 34 taxa of *Drymonia*, *Alloplectus*, and *Columnnea* (Table 1) and the 33 characters used in this analysis (unknown states were coded as ?, { } indicate the character was polymorphic for that taxon). The different populations of *C. nervosa* are designated as Ecuador or C. A. for Central America.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
<i>D. serrulata</i>	0	1	1	1	1	1	0	1	1	6	0	1	0	1
<i>D. stenophylla</i>	1	1	0	1	1	1	0	?	0	?	?	?	0	?
<i>A. meridensis</i>	2	0	0	0	1	0	0	0	1	1	1	1	3	0
<i>A. peruvianus</i>	0	0	0	0	0	0	0	1	1	4	1	{12}	3	1
<i>C. schiedeana</i>	1	1	1	0	1	0	0	{12}	1	5	0	{12}	4	0
<i>C. densibracteata</i>	1	1	1	0	0	0	0	{12}	1	3	0	1	0	1
<i>C. mira</i>	1	1	1	0	0	0	0	0	1	2	0	2	5	0
<i>C. isernii</i>	1	0	0	0	0	0	0	2	{01}	1	0	{12}	0	0
<i>C. lophophora</i>	1	0	0	0	0	0	0	0	1	1	1	1	0	0
<i>C. hypocyrtantha</i>	0	0	0	0	0	0	0	1	1	3	1	2	0	1
<i>C. nervosa</i> (Ecuador)	0	0	0	0	0	0	0	0	1	3	{01}	1	0	1
<i>C. nervosa</i> (C. A.)	1	0	0	0	0	0	0	0	0	3	{01}	1	0	1
<i>C. oblongifolia</i>	0	0	1	0	0	0	0	{12}	1	3	1	2	0	1
<i>C. strigosa</i> (str)	0	1	1	0	1	0	0	0	1	4	1	2	0	1
<i>C. strigosa</i> (kuc)	2	1	1	0	0	0	1	0	1	4	0	1	0	1
<i>C. trollii</i>	0	0	0	0	0	0	0	1	1	3	1	1	0	1
<i>C. ambigua</i>	2	0	0	0	0	0	0	2	1	3	0	1	0	0
<i>C. angustata</i>	1	0	0	0	0	0	0	1	1	3	0	1	0	{01}
<i>C. byrsina</i>	1	0	0	0	0	0	1	{12}	1	2	0	{12}	0	0
<i>C. colombiana</i>	1	0	0	0	0	0	0	{12}	1	2	1	1	1	0
<i>C. crassicaulis</i>	1	0	0	0	0	0	0	0	0	3	1	1	0	1
<i>C. manabiana</i>	1	0	0	0	0	0	0	2	0	0	1	1	2	0
<i>C. fritschii</i>	0	0	0	0	0	0	0	{12}	1	2	1	{12}	1	1
<i>C. inconspicua</i>	1	0	0	0	0	0	0	0	0	0	0	1	2	0
<i>C. lavandulacea</i>	1	0	0	0	0	0	0	0	0	3	1	1	0	1
<i>C. rileyi</i>	1	0	0	0	0	0	0	0	0	2	1	1	1	0
<i>C. moesta</i>	0	0	0	0	0	0	0	1	1	3	1	1	0	1
<i>C. orientandina</i>	1	0	0	0	0	0	0	2	1	2	0	1	0	0
<i>C. ovatifolia</i>	0	0	0	0	0	0	0	0	1	3	1	1	0	1
<i>C. spathulata</i> (zap)	2	0	0	0	0	0	0	{12}	1	0	{01}	2	0	0
<i>C. spathulata</i> (mic)	2	0	0	0	0	0	0	1	0	0	1	2	0	0
<i>C. spathulata</i> (spa)	2	0	0	0	0	0	0	{12}	1	0	{01}	1	0	0
<i>C. suffruticosa</i>	0	0	0	0	0	0	0	1	1	2	{01}	0	1	0
<i>C. ultraviolacea</i>	0	0	0	0	?	0	0	0	1	3	0	2	0	1

APPENDIX 1. Extended.

1 5	1 6	1 7	1 8	1 9	2 0	2 1	2 2	2 3	2 4	2 5	2 6	2 7	2 8	2 9	3 0	3 1	3 2	3 3
1	?	1	0	0	0	3	1	0	5	0	0	1	1	0	1	0	0	4
1	?	1	0	0	0	4	1	0	4	0	2	0	1	1	0	0	0	5
?	?	1	0	0	0	3	1	0	0	1	0	2	3	1	2	0	1	2
1	1	1	0	0	0	3	1	0	4	1	0	2	4	1	2	3	0	2
0	0	0	0	0	0	4	0	1	6	0	0	2	0	0	2	0	0	5
?	?	0	1	0	0	5	0	1	6	1	0	2	1	0	2	0	0	0
?	?	0	0	0	0	6	0	1	6	0	0	2	1	1	2	3	0	0
0	0	0	0	0	0	3	1	1	1	0	0	2	5	1	2	0	0	2
?	?	0	0	0	0	3	1	0	0	0	1	2	6	1	2	0	0	2
0	1	0	0	0	0	3	1	0	4	0	0	2	1	1	2	0	1	2
0	?	0	0	0	0	3	1	1	0	0	0	2	5	1	{12}	0	0	2
0	0	0	0	0	0	3	1	1	0	0	0	2	5	1	2	0	0	2
0	1	0	0	0	0	3	1	1	4	0	0	2	0	1	2	2	0	2
0	1	0	0	0	0	3	1	{01}	4	0	0	{12}	1	1	2	0	0	{24}
0	{01}	0	0	0	0	3	1	1	4	0	0	{12}	1	1	2	0	0	2
0	1	0	0	0	0	3	1	0	7	0	0	2	3	1	2	0	1	2
0	0	0	{01}	1	0	7	1	1	3	0	0	2	0	1	2	0	0	5
0	0	0	1	{01}	0	7	1	{01}	7	0	0	{12}	0	1	2	0	1	{05}
0	0	0	0	0	0	0	0	1	7	1	2	2	2	0	2	0	0	0
0	0	0	0	0	0	1	0	1	7	0	3	2	3	0	2	0	0	1
1	?	0	0	0	0	8	0	1	7	0	2	{12}	1	1	{12}	0	1	0
?	?	0	1	0	0	2	0	1	7	0	2	2	1	1	2	0	1	0
?	?	0	0	0	1	7	0	0	7	1	2	2	1	1	2	0	0	5
1	1	0	0	0	0	2	0	1	7	0	2	2	1	1	2	0	1	0
1	1	0	0	0	0	7	0	{01}	7	1	2	{12}	1	0	{12}	0	1	0
0	0	0	0	0	0	7	1	1	7	1	1	2	6	0	2	0	0	5
0	1	0	0	0	0	7	0	0	7	0	0	2	3	1	2	0	1	{25}
1	1	0	0	0	0	0	0	1	7	1	2	2	2	0	2	0	0	0
1	1	0	0	0	0	1	0	1	7	1	2	2	1	0	2	0	0	1
0	0	0	{01}	0	0	9	1	1	8	0	0	{12}	0	0	2	2	0	0
0	0	0	1	0	0	9	0	1	2	0	0	2	0	0	2	2	1	0
0	{01}	0	1	0	0	9	0	1	2	0	0	2	0	0	2	0	1	0
1	0	0	0	0	0	1	1	1	3	0	0	2	3	1	2	0	0	3
1	1	0	0	0	1	7	0	0	7	1	2	2	1	0	2	0	0	5