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## Paraphyly of Section *Stygnanthe* (*Columnnea*, Gesneriaceae) and a Revision of the Species of Section *Angustiflorae*, a New Section Inferred from ITS and Chloroplast DNA Data

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**Abstract**—Morphological data have produced conflicting results when analyzing evolutionary relationships within Gesneriaceae due to convergence of morphological characters. *Columnnea*, the largest Neotropical genus in Gesneriaceae subfamily Gesnerioideae, has had a convoluted taxonomic history due to this convergence. Previously, the 200+ species of *Columnnea* were placed in 14 genera, with up to nine sections in the genus; most recently classifying the species in a single genus with five sections. Phylogenetic analyses presented here included 129 accessions representing 90 species for five chloroplast gene regions (*trnQ-rps16* spacer, *rpl32-trnL<sub>UAG</sub>* spacer, *rps16* intron, *trnS-G* spacer, and *trnH-psbA* spacer) and nuclear ribosomal ITS to build a well-supported topology that can test the previously proposed subgeneric classifications. Our goal was to test the monophyly of section *Stygnanthe*, one of the five sections that encompasses 18 species based on floral morphology. Fifteen species of *Stygnanthe* and four species that had not been classified in *Stygnanthe* but shared similar floral morphologies were included in the molecular phylogenetic analyses. Analyses indicate that the 19 species with a similar floral morphology belong in four separate clades including a newly proposed section, *Columnnea* section *Angustiflorae*. Of the remaining three species with similar morphologies that were not sampled, only one is proposed to be a member of section *Angustiflorae*, none are members of clade *Stygnanthe*, but are likely to belong in other clades.

**Keywords**—cpDNA, molecular phylogenetics.

Gesneriaceae is one of the many angiosperm families in need of molecular systematic revision. With over 3,500 species distributed pantropically, the family is divided into two subfamilies: the almost exclusively Paleotropical Cyrtandroideae and nearly exclusively Neotropical Gesnerioideae (Weber 2004). Within subfamily Gesnerioideae, tribe Episcieae is easily delimited by a three-trace trilacunar node with split lateral bundles, generally superior ovaries, and chromosome counts of  $x = 8$  or 9 (Wiehler 1983). *Columnnea* L. is the largest genus within tribe Episcieae with over 200 species and is differentiated from all other congeners by the presence of a fleshy indehiscent berry.

As the largest genus in Gesnerioideae, *Columnnea* has had a convoluted taxonomic history that is summarized in Table 1. Alternate classification systems differ due to emphases on various characters (floral, vegetative, and nectaries) and not knowing which character states are truly homologous. Previous classification systems predominately relied on floral characters (Table 1; Hanstein 1854, 1865; Oersted 1858; Fritsch 1894; Morton 1971; Morley 1974, 1976) until Wiehler (1973, 1975, 1983) questioned their utility. Wiehler (1973, 1983) proposed a reclassification of Gesneriaceae based on vegetative or nectary characters. Wiehler initially outlined sparse details (1973) and then greatly elaborated (1983) a classification where he deemphasized the shape of the flower because he considered corolla characters to be a reflection of pollinator selection activity rather than ancestral relationships.

Misinterpretation of homology among morphological characters has been prevalent within Gesneriaceae despite Wiehler's (1973, 1983) attempt to reorganize the family using characters that were intended to reflect ancestor descendent relationships. Studies of groups within both Cyrtandroideae using molecular data (Möller and Cronk 1997; Smith 1996; Smith et al. 1997, 1998; Mayer et al. 2003; Li and Wang 2007; Möller et al. 2009; Wang et al. 2010, 2011) as well as Gesnerioideae (Clark and Zimmer 2003; Smith et al. 2004a, b; Roalson et al. 2005a, b, 2008; Clark et al. 2006, 2012; Woo

et al. 2011) have uncovered para- and polyphyletic taxa including sections within *Columnnea* (Smith et al. 2013).

Smith and Sytsma (1994b, c) conducted the first molecular phylogenetic analyses of *Columnnea* testing Kvist and Skog's (1993) sections *Pentadenia* (Planch.) Hanst. and *Stygnanthe* J. Hanst. (Table 1). Since Smith and Sytsma (1994b, c), species of *Columnnea* have been sampled in numerous DNA sequence-based phylogenetic analyses (Smith and Carroll 1997; Smith 2000; Zimmer et al. 2002; Clark and Zimmer 2003; Clark et al. 2012) and have been recovered as either a monophyletic genus or unresolved (Smith and Carroll 1997) among other closely related genera. None of these studies have provided sufficient phylogenetic resolution or support to test the subgeneric classification of *Columnnea* (Smith and Carroll 1997; Smith 2000; Zimmer et al. 2002; Clark and Zimmer 2003; Clark et al. 2012).

Section *Stygnanthe* sensu Smith (1994) has not been shown to be monophyletic based on molecular phylogenetic analyses. Smith (1994) placed 18 species in *Stygnanthe* characterized as sublignose (rarely succulent) epiphytes with anisophyllous to slightly anisophyllous leaves, inflorescences of 1–12 flowers per axil, a calyx loosely clasping the corolla, and relatively small tubular corollas with radially to subradially symmetric limbs, ranging in size from 1.4–5.2 cm in length that are slightly ventricose medially and constricted basally (Smith 1994; Figs. 1, 2).

Molecular phylogenetic analyses have begun to resolve subgeneric relationships within *Columnnea* (Smith et al. 2013). The primary objective of the present study was to build on the study of Smith et al. (2013) to examine the relationships among species within *Columnnea* to test the monophyly of section *Stygnanthe* sensu Smith (1994). Phylogenetic analyses were conducted using five chloroplast DNA (cpDNA) gene regions (*trnQ-rps16* and *rpl32-trnL<sub>UAG</sub>* spacers: both from Shaw et al. 2007; *rps16* intron: Oxelman et al. 1997; *trnS-G* spacer: Hamilton 1999; and *trnH-psbA* spacer: Clark et al. 2006), along with nuclear ribosomal ITS1 and ITS2,

TABLE 1. Taxonomic history of *Columnnea*. A history of the classification of the species of *Columnnea* by various authors as adapted from Kvist and Skog (1993). The table includes the number of genera, sections, and subgenera classified by each author and the date of the classification system. Names in bold indicate where species of section *Angustiflorae* have been placed in the past. Letters represent clades as referred to by Smith et al. (2013) and Schulte (2012).

Author	Year	Genera		Section		Subgenera	
		Total number	Names	Total number	Names	Total number	Names
Hanstein	1854	7	<i>Columnnea</i> <i>Ortholoma</i> <i>Collandra</i> <i>Pentadenia</i> <i>Pterygoloma</i> <i>Stenanthus</i> <i>Stygnanthe</i>	-	-	-	-
Oersted	1858	4	<i>Columnnea</i> <i>Ortholoma</i> <i>Pentadenia</i> <i>Stenanthus</i>	-	-	-	-
Hanstein	1865	2	<i>Columnnea</i> <i>Stygnanthe</i>	-	-	7	<i>Columnnea</i> <i>Ortholoma</i> <i>Collandra</i> <i>Pentadenia</i> <i>Pterygoloma</i> <i>Stenanthus</i> <i>Cryptocolumnea</i>
Bentham	1876	2	<i>Columnnea</i> <i>Trichantha</i>	7	<i>Columnnea</i> <i>Ortholoma</i> <i>Collandra</i> <i>Pentadenia</i> <i>Cryptocolumnea</i> <i>Systolostoma</i> <i>Bucinellina</i>	-	-
Fritsch	1894	2	<i>Columnnea</i> <i>Trichantha</i>	9	<i>Columnnea</i> <i>Ortholoma</i> <i>Collandra</i> <i>Pentadenia</i> <i>Pterygoloma</i> <i>Stenanthus</i> <i>Stygnanthe</i> <i>Cryptocolumnea</i> <i>Systolostoma</i>	-	-
Morton	1971	1	<i>Columnnea</i>	7	<i>Columnnea</i> <i>Ortholoma</i> <i>Collandra</i> <i>Pentadenia</i> <i>Stenanthus</i> <i>Stygnanthe</i> <i>Cryptocolumnea</i>	-	-
Wiehler	1973	4	<i>Columnnea</i> <i>Dalbergaria</i> <i>Ortholoma</i> <i>Pentadenia</i>	-	-	-	-
Wiehler	1975	5	<i>Columnnea</i> <i>Dalbergaria</i> <i>Pentadenia</i> <i>Trichantha</i>	-	-	-	-
Morley	1976	1	<i>Columnnea</i>	5	<i>Columnnea</i> <i>Ortholoma</i> <i>Collandra</i> <i>Pentadenia</i> <i>Pterygoloma</i>	-	-
Wiehler	1983	5	<i>Columnnea</i> <i>Pentadenia</i> <i>Collandra</i> <i>Trichantha</i> <i>Bucinellina</i>	-	-	-	-
Kvist & Skog	1993	1	<i>Columnnea</i>	6	<i>Columnnea</i> <i>Ortholoma</i> <i>Collandra</i> <i>Pentadenia</i> <i>Stygnanthe</i> <i>Bucinellina</i>	-	-
Smith	1994	1	<i>Columnnea</i>	5	<i>Columnnea</i> <i>Ortholoma</i> <i>Collandra</i> <i>Pentadenia</i> <i>Stygnanthe</i>	-	-
Smith et al.	2013	1	<i>Columnnea</i>	7	Clade A–G	-	-
Schulte	2012	1	<i>Columnnea</i>	7	<i>Stygnanthe</i> <i>Angustiflorae</i> Clades A, C–F	-	-

hereafter referred to as ITS; Baldwin et al. 1995). Gene regions were chosen because they have resolved subgeneric clades within *Columnnea* (Smith et al. 2013).

This study included 40 accessions representing 15 of the 18 species of *Stygnanthe* sensu Smith (1994), 55 species outside of *Stygnanthe*, and 19 outgroup species for a total of 89 species (129 accessions). In addition, species that were not previously placed in *Stygnanthe* by Smith (1994), but share a similar tubular corolla with radially to subradially symmetric limbs were sampled. These include *C. ulei* Mansf., *C. domingensis* (Urb.) B. D. Morley, *C. moorei* C. V. Morton, and *C. grisebachiana* Kuntze, because these species were overlooked in earlier treatments of the section (Smith 1994).

#### MATERIALS AND METHODS

**DNA Extraction, Amplification, and Alignment**—A complete list of samples, voucher specimens, and GenBank numbers are included in Appendix 1. The ingroup included 129 accessions of *Columnnea* and outgroup genera representing 90 species. These represent multiple individuals from each of Wiehler's (1983) segregate genera (Table 1) and the sections of Kvist and Skog (1993; Table 1), with the exception that only one of the two species of *Bucinellina* was included (*C. paramicola*). Outgroup samples included species of *Alloplectus*, *Corytoplectus*, *Crantzia*, *Drymonia*, *Glossoloma*, *Neomortonia*, and *Pachycaulos* (Appendix 1) chosen based on a study of Episcieae (Clark et al. 2012).

DNA was extracted from silica-dried leaf material using Qiagen DNeasy plant mini kits (Valencia, California) according to the manufac-

turer's instructions. Five cpDNA gene regions, *trnQ-rps16* spacer (Shaw et al. 2007), *rpl32-trnL<sub>UAG</sub>* spacer (Shaw et al. 2007), *rps16* intron (Oxelman et al. 1997), *trnS-G* spacer (Hamilton 1999), and *trnH-psbA* (Clark et al. 2006) and the nuclear ribosomal ITS (Baldwin et al. 1995) were amplified for all accessions (Appendix 1). Only herbarium leaf material was available for *Columnnea xiphoidea* making it difficult to amplify the selected DNA regions. Therefore, only two gene regions, *rpl32-trnL<sub>UAG</sub>* spacer and ITS, were amplified for *C. xiphoidea* following the same procedure as the silica-dried leaf material.

All double-stranded DNA was amplified via PCR following the methods of Smith et al. (1997). Sequences were obtained either through the methods described in Smith et al. (2004a), or through Genewiz (Plainfield, New Jersey) with chromatograms viewed and sequences edited and aligned by hand in PhyDE (Müller et al. 2005).

Each gene region had missing data at the beginning and end in the full alignment. Areas of missing data and ambiguous alignments were excluded from phylogenetic analyses. Additionally, the alignment produced regions of ambiguity due to single bp insertions or microsatellite repeats which can be unambiguously aligned; however, the homology of these regions is uncertain. To test the impact of single bp insertions and microsatellite repeats, we ran additional phylogenetic analyses with the repeats included and compared the consistency indices of analyses with and without repeats.

The alignments also resulted in gaps to account for insertion or deletion (indel) events. The inclusion of indel events can be of phylogenetic significance (Simmons and Ochoterena 2000). Each indel event was scored as present or absent for all accessions. An additional data partition was then added to the end of the concatenated data set representing the score for each indel event and analyzed with maximum parsimony (MP).

**Test of Incongruence**—The partition homogeneity test (Farris et al. 1994) was performed as implemented in PAUP\* v4.0 b10 (Swofford

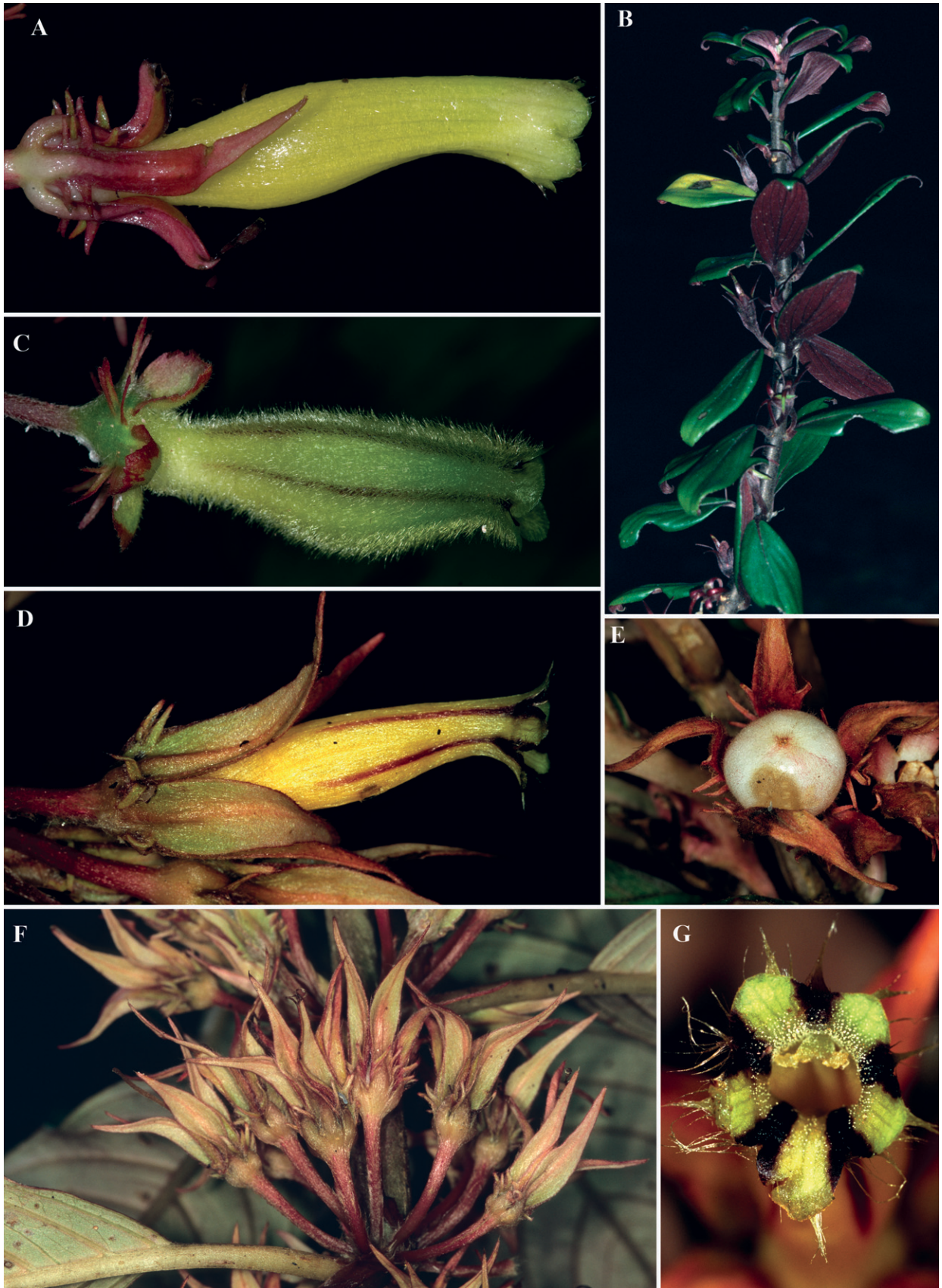


FIG. 1. *Columnnea* section *Stygnanthe*. A. Lateral view of *Columnnea athahualpae* showing basal serrations on calyx lobes. B. Erect habit showing whorled leaves of *Columnnea ultravioleacea*. C. Lateral view of *Columnnea isernii* showing basal serrations on calyx lobes. D. Lateral view of *Columnnea* sp. nov. E. White globose fruit of *Columnnea* sp. nov. F. Reduced pair-flowered cyme inflorescence appearing as a fascicle of axillary flowers in *Columnnea* sp. nov. G. Front view of *Columnnea* sp. nov. showing striations on corolla lobes. (Photos by John L. Clark; A. J. L. Clark et al. 8000; B. J. L. Clark et al. 6603; C. J. L. Clark et al. 10640; D–G J. L. Clark et al. 8898).



FIG. 2. *Columnnea* section *Angustiflorae*. A, C. Lateral views of *Columnnea katzensteiniae* showing basal constriction of corolla and translucent spotting at base of corolla lobes. B. Habit of *C. katzensteiniae* showing isophyllous leaves. D. Lateral view of *C. angustata*. E. Globose white fruit of *C. spathulata*. F. Lateral view of *Columnnea ovatifolia*. G. Front view of *C. ovatifolia* showing inner spotting at base of corolla lobes. (Photos by John L. Clark; A. J. L. Clark et al. 8915; B. J. L. Clark et al. 12240; C. J. L. Clark et al. 7625; D. J. L. Clark et al. 9609; E. J. L. Clark et al. 11025; F, G. J. L. Clark et al. 8461).

2002) with 10,000 bootstrap replicates (using a heuristic search, simple addition, and no branch swapping). Because cpDNA is a single non-recombining unit, the cpDNA gene regions were treated as a single partition. The ITS region was also treated as a separate gene partition. As an additional measure of congruence among partitions, bootstrap analyses were performed on each partition separately to assess areas of conflicting resolution and to determine if any conflict was strongly supported (Seelanen et al. 1997).

**Phylogenetic Analyses**—Phylogenetic trees were estimated using MP, maximum likelihood (ML), and Bayesian inference (BI) for data sets with and without single bp insertions and microsatellite repeats. Maximum parsimony analyses were performed using PRAP2 (Müller 2007) in conjunction with PAUP\* v4.0 b10 (Swofford 2002). Bootstrap support (BS) for nodes (Felsenstein 1985) was estimated with 1,000 heuristic replicates using PRAP2 (Müller 2007). Descriptive statistics reflecting the amount of phylogenetic signal in the parsimony analysis were given by the consistency index (CI; Kluge and Farris 1969), retention index (RI; Farris 1989), and the resulting rescaled consistency index (RC; Farris 1989).

Maximum likelihood and BI analyses were performed using optimal substitution models suggested by Modeltest 3.6 (Posada and Crandall 1998). The Akaike information criterion (AIC), which allows non-nested models to be evaluated, was used as a selection criterion (Posada and Buckley 2004) for the cpDNA and ITS partitions separately and as a concatenated data set.

Two separate BI analyses were completed using MrBayes 3.1.1 (Huelsenbeck and Ronquist 2003). The first BI analysis, referred to as the one model analysis, was performed using a single model for all data (cpDNA and ITS). The second BI analysis, referred to as the partition model analysis, was performed with a separate model for each of the two data partitions.

All BI analyses were run with four chains (three heated, one cold), for ten million generations. The convergence and effective sample size (ESS) of each replicate were checked using Tracer v. 1.5 (Rambaut and Drummond 2007), and a burnin of 50,000 generations was discarded prior to sampling the posterior distribution for both BI analyses. Bayesian inference analyses were repeated twice to ensure that parameter estimates converged to similar values. The separate runs were compared using the online version of AWTY (Nylander et al. 2008) as a means to determine if the separate chains approximated the same target distribution. The ML analysis was completed using GARLI v0.96 (Zwickl 2006) with 100 bootstrap replicates using a single model across the data.

The markers for *Columnnea xiphoidea* were analyzed separately because only two regions amplified successfully from the herbarium material. The sequences for *rpl32-trnL<sub>UAG</sub>* spacer and ITS for the 129 accessions were analyzed with the same two regions from *C. xiphoidea*. The gene regions were analyzed as a single concatenated data set composed only of these two regions using MP in PAUP\* v4.0 b10 (Swofford 2002). Likewise, we only obtained ITS, *rps16* intron, and *rpl32-trnL<sub>UAG</sub>* spacer for *C. grisebachiana*, therefore only these three regions were used to test the placement of this species.

To test whether *C. ulei* could be rejected as sister to the remaining accessions of *C. angustata*, a Shimodaira-Hasegawa (SH) test (Shimodaira and Hasegawa 1999; Goldman et al. 2000) was conducted. This test used a tree that constrained the placement of *C. ulei* as sister to the remaining accessions, but retained the topology of the remainder of the tree as recovered from BI analyses.

**Geographic Distributions and Climate Data**—To create distribution maps for each species, a total of 509 herbarium collection records were georeferenced for specimens with recorded locations known to the nearest minute using specimens cited in Smith (1994) and those listed as additional specimens examined for each species in this publication. Latitude and longitude coordinates were converted to decimal degrees and species distributions were plotted using ArcMap version 10.0 (ESRI, Redlands, California).

Climate data for each georeferenced herbarium collection were extracted using the nineteen available bioclim layers (Hijmans et al. 2005) at 30s Arc (~one km) accuracy. Bioclimatic variables were derived from the monthly temperature and rainfall values (Hijmans et al. 2005). ArcMap v.10.0 was used to combine each of the bioclim layers with a 500 m buffer zone around all data points and climate information was collected for all herbarium collection records (Schulte 2012). The results were averaged across all accessions and we report annual temperature, annual temperature range, and precipitation for each species in the Taxonomic Treatment.

## RESULTS

**DNA Amplification and Sequence Alignment**—Amplifications were successful for all individuals with some exceptions for each DNA gene region (Appendix 1). Regions with ambiguous alignment where homology could not be accurately determined were excluded from the analyses. Phylogenetic analyses with ambiguities excluded and single bp insertions and microsatellite repeats included had a total of 4,708 base pairs. When single base pair insertions and microsatellite repeats were removed there were a total of 4,129 base pairs included in the phylogenetic analyses (All base pairs removed based on the alignment in Appendix S1: 1–114, 425–428, 488, 508, 624–625, 735, 917–918, 964, 968–971, 1052–1160, 1164, 1170, 1469–1472, 1536–1540, 1609–1616, 1868–1875, 1902–1904, 1910, 1969, 1994, 2041–2042, 2332, 2343, 2352, 2491–2528, 2732–2736, 2907–2908, 2972, 2990, 3323–3370, 3398–3401, 3501, 3526–3530, 3535, 3618–3647, 3723–3724, 3847–3854, 3901–3902, 3908, 4004–4114, 4202, 4206–4240, 4389–4556). Of the 4,129 bp, 2,898 were constant and 716 were uninformative leaving 515 (12.5%) as phylogenetically informative. An inversion in the *trnH-psbA* spacer was detected in both accessions of *Columnnea lophophora*, *C. moesta* (J. L. Clark 6690), *C. eburnea*, *C. picta*, and *C. schimpffii*. The inversion was reversed and complemented for all individuals prior to analyses and coded as a separate presence/absence character.

**Test of Incongruence**—The result of the partition homogeneity test ( $p = 0.01$ ) indicated significant differences between partitions. However, as has been reported on many occasions, this test often indicates incongruence when none exists (Reeves et al. 2001; Yoder et al. 2001) and as a result comparing support for partitions may be a better indicator of incongruence (Seelanen et al. 1997). All regions for all accessions were in complete topological congruence or received  $BS < 50$  for the individual analyses (results not shown). Therefore, a combined analysis of all DNA regions was performed and is the basis for all results and discussion with the exception of *C. xiphoidea* and *C. grisebachiana* for which only *rpl32-trnL<sub>UAG</sub>* spacer and ITS sequences were available.

**Single bp Insertions and Microsatellite Repeats**—Phylogenetic analyses with single bp insertions and microsatellite repeats included showed a loss of resolution. Overall, BS was approximately the same in analyses with and without repeats, although there was a decrease in the CI from analyses with repeats included compared to the MP analysis with repeats excluded (single bp insertions and microsatellite repeats included: CI = 0.4533; excluded: CI = 0.4717). A lower CI is an indication of homoplasy among the data. There was also a loss of resolution in the analyses with repeats included (Fig. S1), where Clade G was not recovered as monophyletic, whereas it was when the repeats were excluded from analyses (Fig. 3A, B). The reduced resolution and lower CI value in the analysis with single bp insertions and microsatellite repeats implies that the repeats are homoplastic, at least in part. Because including repeats resulted in a lower CI value and resolution, analyses excluding single bp insertions and microsatellite repeats will be presented hereafter in the text.

**Phylogenetic Analyses**—Maximum parsimony analysis resulted in 232 trees of 2,262 steps (CI = 0.4717; RI = 0.7318; RC = 0.4807) for the concatenated data set. Scoring indels resulted in minimal topological differences and no changes

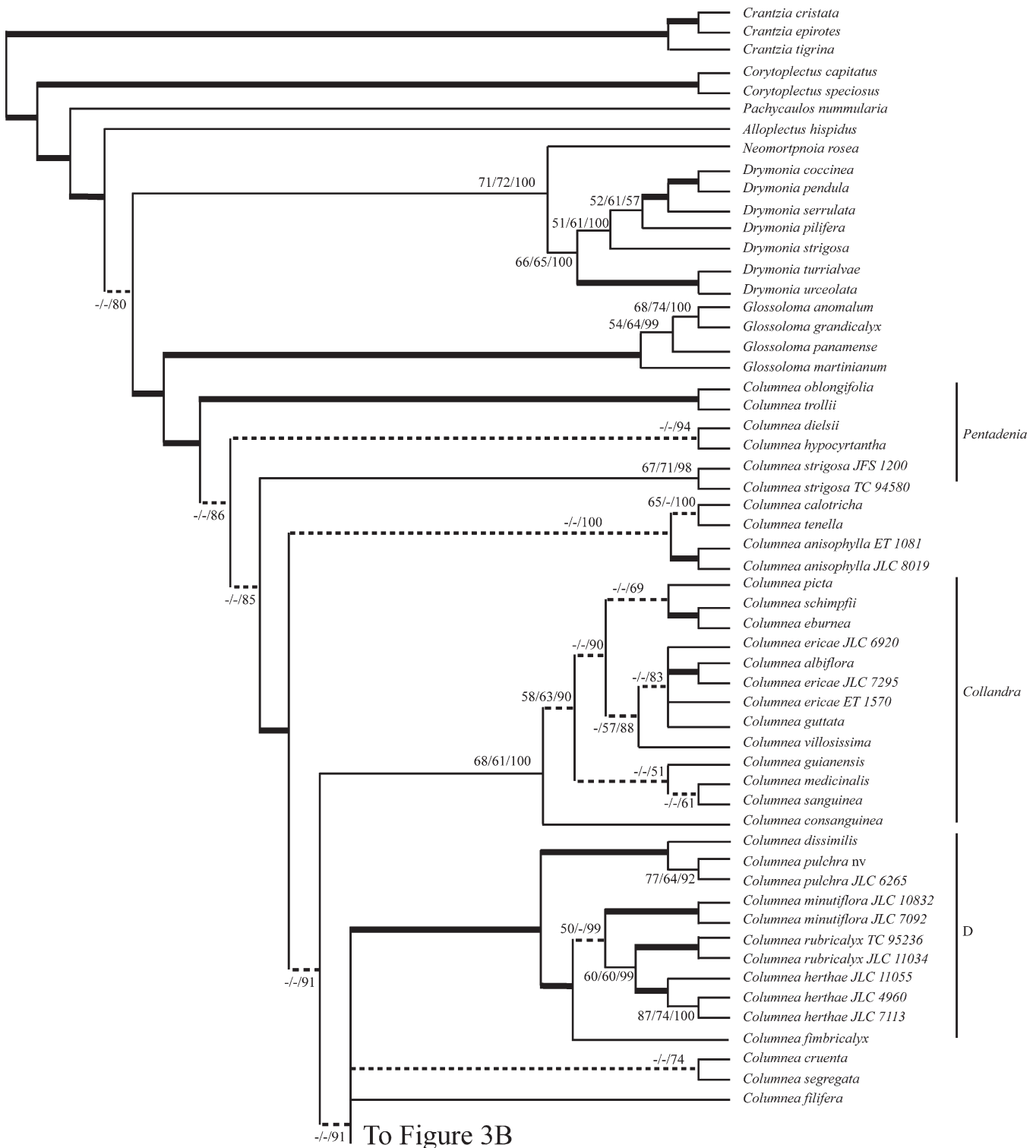


FIG. 3A. Consensus tree from a Bayesian analysis using a partitioned model. Numbers above branches represent maximum parsimony bootstrap (MPBS)/ maximum likelihood bootstrap (MLBS)/Bayesian inference posterior probabilities (BPP). Bold branches are strongly supported in all three analyses (MPBS/MLBS > 75; BPP > 95). Letters represent clades identified by Smith et al. (2013) and Schulte (2012). Dashed lines represent branches that collapse in either MP or ML analyses. Accessions in bold represent species that have a radially to subradially symmetric tubular corolla. Species placed in boxes were previously placed in section *Stygnanthe* sensu Smith (1994). nv- indicates no voucher.

in support resulting in BS > 75 that were not already present in the MP analysis without indel event scores (results not shown). The GTR +  $\Gamma$  + I model was chosen for both the cpDNA partition and the concatenated data set. The GTR + I model was chosen for ITS. We report the 50%

majority-rule consensus tree sampled from the posterior probability (PP) distribution for each of the BI analyses separately (individual results not shown). The AWTY (Nylander et al. 2008) output indicated that the separate chains approximated the same target distribution for both the BI one model

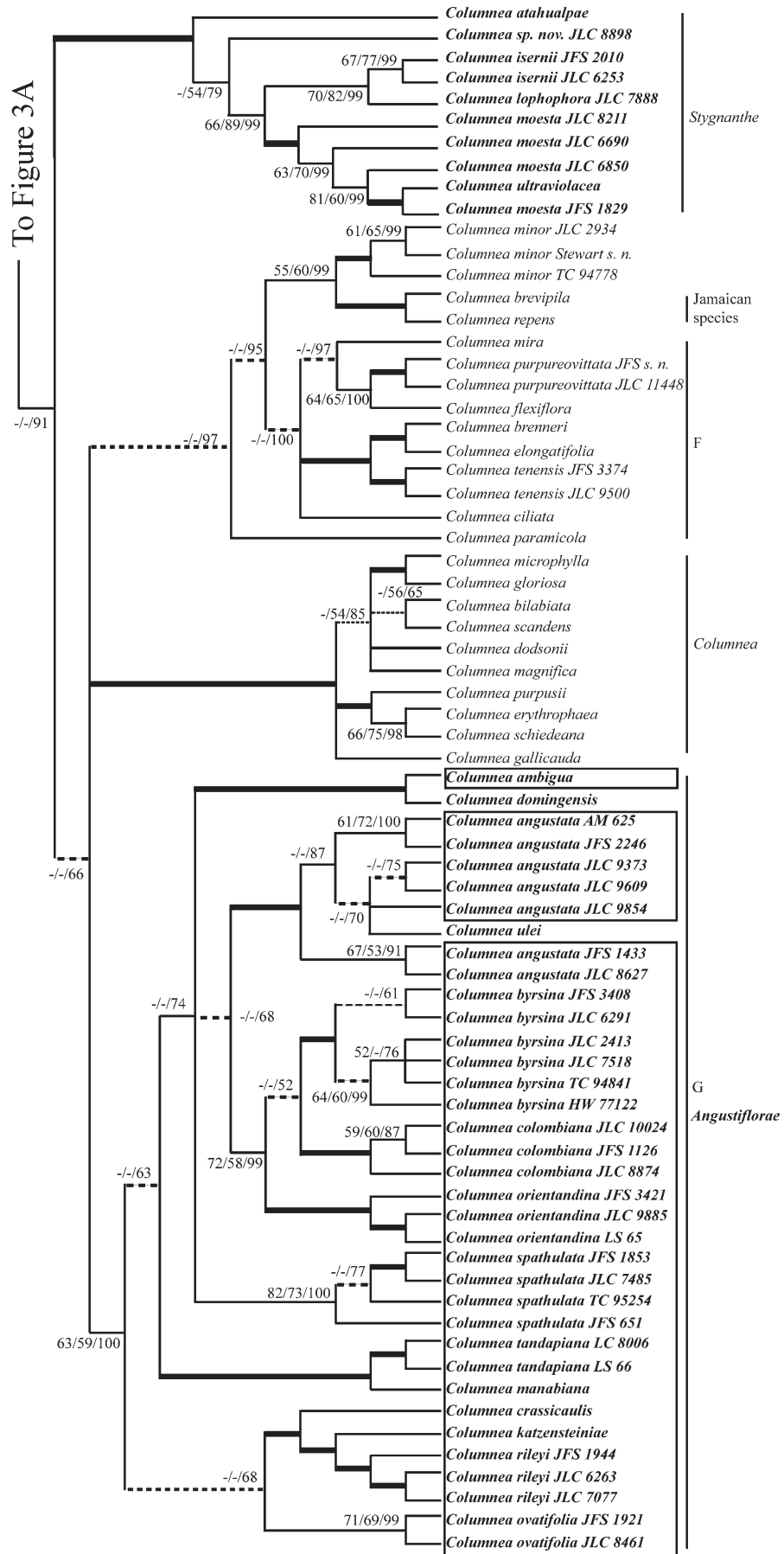


FIG. 3B. Continuation of Fig. 3A - see caption for Fig. 3A.



and partition model analyses (Schulte 2012) and Tracer (Rambaut and Drummond 2007) indicated that ESS for each run were over 4,000. The GTR +  $\Gamma$  + I model for the ML analysis resulted in one tree ( $-\ln L = 21,120.46019$ ; individual results not shown).

All analyses produced trees with congruent topologies that had varying amounts of resolution. The BI partition model produced the most resolved topology (Fig. 3). The two separate BI runs (for both one and partition models) resulted in similar trees with minimal change in PP between nodes. There were no nodes with PP > 95 in the BI one model consensus tree (individual results not shown) that were not present in the BI partition model analysis (Fig. 3). Therefore, a tree presenting the combined results of the MP, ML, and BI partition model is presented in Fig. 3. Support for clades is represented by MPBS, MLBS, or Bayesian PP (BPP) from the partition model and is reported as MPBS/MLBS/BPP hereafter in the text.

**Sections within *Columnnea***—In all analyses, *Columnnea* was recovered as a well-supported monophyletic group (Fig. 3; 96/95/100) with *Glossoloma* supported as sister (Fig. 3; 85/87/100). Smith et al. (2013) identified seven clades. This study shows support for the same seven clades within *Columnnea* (Fig. 3). The present analyses show strong support based on all analyses for the monophyly of clade *Stygnanthe* (Fig. 3; 84/81/100). There was also strong BPP support for the monophyly of section *Angustiflorae* (Fig. 3; 63/59/100).

**Monophyly of Section *Stygnanthe***—The 15 sampled species of section *Stygnanthe* sensu Smith (1994) were recovered in two separate clades. Twelve of the 15 species were recovered as a monophyletic group (section *Angustiflorae*; Fig. 3; 63/59/100), along with previously unsampled species, *Columnnea domingensis* and *C. ulei*. All three of the remaining species sampled from *Stygnanthe* sensu Smith (1994), *C. moesta*, *C. ultraviolacea*, and *C. xiphoidea* were supported as part of clade *Stygnanthe* (Figs. 3, S2). In all analyses *C. moesta* and *C. ultraviolacea* were strongly supported as part of this clade (Fig. 3; 84/81/100). In a separate two gene MP analysis, *C. xiphoidea* was supported as sister to *C. moesta* (Fig. S2; MPBS = 99) and therefore belongs within clade *Stygnanthe* (Fig. S2).

*Columnnea moorei* and *C. grisebachiana* were thought to potentially belong in section *Angustiflorae* because they share a similar corolla morphology to the species in *Stygnanthe* sensu Smith (1994). This study tested the phylogenetic placement of both species with molecular data, which had not previously been done. In the MP majority rule consensus of the ITS partition, *C. moorei* was resolved as sister to the Jamaican species *C. brevipila* and *C. repens* (Fig. 3) in 94% of the trees (results not shown). In the MP strict consensus tree of the cpDNA partition, *C. moorei* was resolved as part of section *Columnnea* of Fig. 3 (results not shown). The placement of *C. moorei* in two separate clades implies a hybrid origin; however, the placement of *C. moorei* in either of these clades receives MPBS < 50 (results not shown) and will require further investigation. The type specimen for *C. moorei* was based on cultivated material and all other material currently in cultivation is assumed to have been propagated from that collection (including the material sampled here). It is possible that hybridization has occurred after being brought into cultivation. Regardless, *C. moorei* is not placed within section *Angustiflorae*. *Columnnea grisebachiana*

was analyzed with three DNA regions separately, and found to be strongly supported in a monophyletic group (Fig. S2, MPBS = 98) with the other endemic Jamaican species *C. brevipila* and *C. repens* (Fig. 3). Neither species are within section *Angustiflorae* or *Stygnanthe*.

**Monophyly of Species**—There is little support for relationships within each of the clades, although species with multiple accessions were recovered as monophyletic with strong support with two exceptions, *Columnnea moesta* and *C. angustata* (see below). Monophyletic species groups indicate that species delimited based on morphological characters are in agreement with their molecular genetic history. The *C. moesta* subclade (Fig. 3; Clade B; 97/99/100) included four accessions of *C. moesta*, but also included the only accession of *C. ultraviolacea* (Fig. 3; 81/90/99). However, these species are not the focus of this study and, thus, will not be discussed further. Seven species with multiple accessions in *Angustiflorae* were recovered as monophyletic: *C. byrsina* (Fig. 3; 100/100/100), *C. colombiana* (80/75/100), *C. orientandina* (100/100/100), *C. spathulata* (82/73/100), *C. rileyi* (99/100/100), *C. ovatifolia* (71/69/99), and *C. tandapiana* (100/100/100). Four species were sampled with only a single accession and therefore their monophyly could not be tested. The one SH test conducted here tested whether *C. ulei* could be rejected as sister to the remaining accessions of the species. The results could not reject this hypothesis compared to the topology that was recovered ( $p = 0.126$ ). Therefore, it is possible that *C. ulei* and *C. angustata* are reciprocally monophyletic, but not supported as such by the current data and analyses.

## DISCUSSION

**Section *Stygnanthe***—Smith (1994) included 18 species in his section *Stygnanthe* based on morphology. Multiple accessions representing 15 of the 18 species of *Stygnanthe* (indicated in boxes on Fig. 3) were sampled. Molecular evidence placed these species into two different clades, *Stygnanthe* and *Angustiflorae* (Fig. 3) indicating that section *Stygnanthe* (Smith 1994) does not represent a monophyletic group.

Phylogenetic analyses provide support for *Columnnea moesta* (Fig. 3; 97/98/99) and *C. ultraviolacea* (Fig. 3; 81/90/100) in clade *Stygnanthe* with at least three other species (Fig. 3; 84/81/100): *C. atahualpae*, *C. lophophora*, and *C. isernii*. Maximum parsimony analysis of *C. xiphoidea* ITS and *rpl32-trnL<sub>UAG</sub>* sequences show support for *C. xiphoidea* as sister to *C. moesta*/*C. ultraviolacea* (Fig. S2; MPBS = 99) providing evidence that it also belongs in clade *Stygnanthe* (Fig. 3). Although the clade contains only three of the species from *Stygnanthe* sensu Smith (1994), this clade will be recognized as clade *Stygnanthe* because it includes *C. moesta*, the type species for the section.

Morphological similarities can be found among the species of clade *Stygnanthe* lending further support to the separation of this clade from the remaining 12 species of section *Angustiflorae*: most of the six species of *Stygnanthe* sampled here are characterized by basal serrations on the calyx lobes (Fig. 1). This trait is present in section *Angustiflorae* only in *C. colombiana*. The exceptions to the presence of basal serrations in clade *Stygnanthe* are *C. moesta* and *C. ultraviolacea*. These latter two species, along with *C. isernii* and *C. lophophora* have a dense sericeous or pilose pubescence that obscures the color of the corolla and covers the

corolla lobes, a characteristic not present in *Angustiflorae* (Fig. 2). Although the range in corolla tube length between *Stygnanthe* and *Angustiflorae* overlap, the corolla tubes of *Stygnanthe* are generally longer and larger (1.8–6.0 vs. 1.0–5.2 cm in *Angustiflorae*). Furthermore, the corolla lobe lengths of clade *Stygnanthe* tend to be nearly equal to those of *Angustiflorae* (1.5–3.5 vs 1.0–3.0 mm in *Angustiflorae*), but again the ranges have a nearly complete overlap. However, the corolla lobes of *Stygnanthe* are proportionally smaller than those of *Angustiflorae* with respect to the length of the corolla tube, thus the ratio of tube to lobe length in *Angustiflorae* is 2.9–6.8 and 8.3–18.0 in clade *Stygnanthe*. These are close, but a tube/lobe length ratio below seven can be used to define section *Angustiflorae* and one that is greater than eight can be used to identify members of clade *Stygnanthe*.

**Section *Angustiflorae***—The remaining 12 species sampled from *Stygnanthe* sensu Smith (1994) formed a monophyletic group (Fig. 3; 63/59/100) that is here recognized as section *Angustiflorae* (Fig. 2). Section *Angustiflorae* have corollas that are slightly ventricose and constricted at the base with a calyx loosely clasping the corolla (Fig. 2). Species of *Angustiflorae* have a shorter corolla length with proportionally longer and larger corolla lobes than species of clade *Stygnanthe* (Fig. 2) as discussed above. Many species in *Angustiflorae* can also be distinguished from *Stygnanthe* by the corolla pubescence. Species in *Stygnanthe* have a dense pubescence that obscures the corolla that often makes it difficult to differentiate between the color of the corolla and the color of the trichomes (Fig. 1C). In contrast, the species in *Angustiflorae* have a sparsely pilose pubescence where the corolla color is readily observable and not obscured by trichomes (Fig. 2). This combination of traits separates the species of section *Angustiflorae* from most of the other species in *Columnnea*.

Two species that had previously been unsampled were also included in these analyses and are clearly members of section *Angustiflorae*, *C. domingensis* and *C. ulei* (Fig. 3). *Columnnea domingensis*, a species endemic to Hispaniola, and *C. ulei*, an endemic to Brazil, were previously classified as a species of *Trichantha* (Wiehler 1973). *Columnnea domingensis* was strongly supported as sister to *C. ambigua*, which is endemic to Puerto Rico (Fig. 3; 92/80/100), and *C. ulei* made *C. angustata* paraphyletic, but without support.

Two other species that share a similar corolla morphology to species of *Angustiflora* were also sampled for the first time in molecular analyses and were phylogenetically outside of the clade, *Columnnea moorei* and *C. grisebachiana* (Fig. S2). *Columnnea moorei* is known from fewer than ten collections from Central Panama (Colón and Panamá) but is common in cultivation. The preliminary data here imply a hybrid origin for the species since ITS and cpDNA place it in distinctly different clades, albeit further analyses are warranted and *C. moorei* will be the focus of a future study. It is also possible that the *C. moorei* accession in cultivation has been hybridized since its introduction into cultivation, but until further samples from the wild can be sampled, this remains untested.

More challenging is the placement of *Columnnea grisebachiana*. This endemic Jamaican species has a bright red slightly ventricose corolla, a lobe to tube length proportion of 2.9–6.8, and dense pubescence, characters that are all similar to members of section *Angustiflorae*. Only its distribution in

Jamaica can be used as a diagnostic character to place it outside of *Angustiflorae* at the present as no species of section *Angustiflorae* is known from Jamaica. Future investigations may uncover micromorphological characters that can be used to distinguish this species from other members of *Angustiflorae*. One other Jamaican endemic species of *Columnnea* shares this corolla morphology and remains unsampled, *C. pubescens*. We assume for the present that the shared corolla traits between members of section *Angustiflorae* and these two Jamaican endemics are the result of convergent evolution as indicated by the phylogenetic placement of *C. grisebachiana* (Fig. S2). Although currently unsampled in our molecular results, we predict that *C. pubescens* is likely to be more closely related to *C. grisebachiana* than to section *Angustiflorae* and in that case, biogeographic distribution is more informative than morphology in defining sections.

#### TAXONOMIC TREATMENT

**Columnnea section *Angustiflorae*** L. J. Schulte and J. F. Smith—TYPE SPECIES: *Pentadenia angustata* Wiehler (*Columnnea angustata* (Wiehler) L. E. Skog).

Small herbs, suffrutescent, epipetric, epiphytic, vining or terrestrial. Stems succulent to sublignose, frequently branching at base, ascending, creeping, spreading, or pendant to 3.0 m long, 1.5–15.0 mm in diameter, sometimes with a zigzag appearance, terete, green sometimes suffused with purple, tawny, maroon to red-brown, or tan, quadrangular when dried, apically smooth and glabrous to flaking basally, sometimes hirsute with a few multicellular transparent or red trichomes, sometimes dark purple, distally glabrescent, glabrate, appressed pilose, pubescent, hirsute, or sericeous, sometimes lanate or villous with uniseriate or multicellular transparent or red trichomes; with numerous adventitious, (sometimes conspicuous) roots; internodes 0.4–9.5 cm long, sometimes swollen; nodes flush with stem; leaf scars raised or flush with stem. Leaves opposite, isophyllous to strongly anisophyllous, sometimes dorsiventrally arranged; larger laminas 0.65–16.2 cm long, 0.4–6.0 cm wide, orbicular, oblong, ovate, elliptic, lanceolate, sometimes slightly falcate, obovate, or oblanceolate, apex acute, long-acuminate, obtuse, sometimes blunt and rounded, base cuneate or rounded, oblique to strongly oblique, adaxially dull green, yellow-green, dark green, sometimes purple, suffused with pink, or with violet spots, glabrous, strigillose, strigose, slightly appressed pilose, pilose, slightly hirsute to hirsute, sometimes tomentose to villous with uniseriate or multicellular red or transparent trichomes, abaxially green, reddish, pale green, sometimes suffused with red-purple mottling or entirely colored, rose-red, pink-purple, rarely with a red apex, glabrate, sparsely pilose, rarely appressed, sericeous, long sericeous, lanate, strigose, or hirsute, sometimes short tomentose with red or transparent unicellular transparent trichomes, veins glabrous, appressed pilose, lanate, strigose, appressed sericeous, sericeous, slightly hirsute to lanate, sometimes denser on veins with red or transparent uniseriate or multicellular trichomes, lateral veins 3–12, margin entire, subentire, crenulate, crenate, serrulate, slightly undulate, undulate to ciliate with red to violet or transparent uniseriate trichomes; smaller laminas 0.55–4.2 cm rarely to 6.0 mm long, 0.2–2.4 cm wide, linear, lanceolate, ovate, or elliptic, sometimes absent, otherwise like larger laminas; petioles

0.0–3.1 cm, green, sparsely pilose, sometimes appressed, sericeous to hirsute with red or transparent unicellular to multicellular trichomes. Inflorescence a reduced pair-flowered cyme that appears as axillary clusters of 1–12 flowers per leaf axil, commonly in axil of larger leaf, rarely in both axils; floral bracts 1–3, 2–19 mm long, 0.4–9 mm wide, conspicuous or caducous, linear, lanceolate, or ovate, apex acute to acuminate, green or pink-red, sometimes suffused with red or with red tips, villous, pilose, lanate, sericeous, sparsely hirsute, or hirsute with red or transparent uniseriate to multicellular trichomes, margin entire. Pedicels 0.1–21 mm long, erect, maroon-red or green, sometimes lavender, pilose, villous, hirsute, sericeous with red or transparent uniseriate to multicellular trichomes, eglandular or rarely with long round to oval purple glands near calyx 0.5–0.7 mm. Calyx loosely clasping corolla, rarely with slightly recurved tips; lobes equal to subequal 0.6–1.8 cm long, 0.1–0.6 mm wide, linear, lanceolate, oblanceolate, sometimes subulate, spatulate, narrowly elliptic, or ovate, apex acute to acuminate, rarely long acuminate or obtuse, green, purple, pink-red, or maroon sometimes flushed with pink-rose, purple, or with red or purple tips and teeth, exterior sparsely pilose, sometimes appressed, lanate, strigose, hirsute, villous, sericeous, rarely less densely sericeous toward apex with transparent uniseriate trichomes, interior glabrate or nearly glabrous, slightly pilose, sparsely hirsute, or glandular-pubescent with multicellular transparent trichomes, margins entire, subentire, serrate, coarsely toothed, or lacinate, rarely dissected at base of lobe to minutely denticulate in fruit. Corolla 1.0–5.2 cm long, 1.5–10.0 mm at widest point, 1.5–6.0 mm at constriction before limb, 1.0–3.0 mm wide at constriction before base, tubular, slightly ventricose on lower surface, rarely proximally and ventrally with two small invaginations of corolla tube, cream, lemon-yellow, orange, red, violet, exterior glabrate, puberulent, pubescent, sometimes appressed pilose, long-sericeous, long-hirsute, or long-glandular, more densely so towards limb with red or transparent sometimes lavender-purple uniseriate to multicellular trichomes, rarely trichomes on limb transparent with red base, interior glabrous to villous, slightly hirsute, slightly pilose, or slightly pubescent at base with glandular trichomes dorsally and distally; limb 6.5–8.5 mm in diameter, pale yellow to green; lobes equal to subequal, sometimes inconspicuous, 1.0–3.0 mm long, 1.0–4.0 mm wide, lemon-yellow to green, semiorbicular, sometimes with darker red to orange-yellow or dark purple spots on interior surface. Filaments connate at base 2.0–10.0 mm, adnate to base of corolla 1.0–5.0 mm, white-yellow, red, proximally pilose, slightly pubescent becoming glabrous distally; anthers 0.5–2.5 mm long, 0.5–2.5 mm wide, rectangular, quadrate, or subquadrate, usually included in corolla tube, rarely exerted up to 9.0 mm beyond opening of corolla. Ovary 0.8–5.0 mm long, green, conical, nearly glabrous or glabrate becoming pilose, pubescent, or sericeous at apex with uniseriate red or transparent trichomes; style white-yellow or red, proximally glabrous, sparsely pilose becoming minutely pilose, pilose, or slightly pubescent distally with glandular, short multicellular trichomes distally; stigma stomatomorphic or bilobed, white-yellow, green or red, smooth, papillate, usually included in corolla tube, rarely exerted to 0.7 mm beyond opening of corolla. Nectary variable, with 5 free glands or with 2 dorsal glands

connate and 3 free or ventrally connate glands. Fruit a berry 5.0–12.0 mm long, 3.5–7.0 mm wide, 1.0–12.0 mm in diameter, ovate, ovoid, or globose, glabrate, slightly pilose, or pubescent, white to pink-red, pale lavender-purple, or blue, sometimes dark in color when dried; seeds 0.8–1.6 mm long, 0.3 mm wide, fusiform, oblong, or falcate, twisted, red-purple to light-brown or brown-yellow, striate.

**Etymology**—The name of the section is derived from the narrow corolla tube.

**Diagnostic Characters**—The species of *Angustiflorae* can be distinguished by their small corollas that range in size from 1.0–5.2 cm in length and from 0.15–1.0 cm in width at the widest point with a corolla tube to lobe ratio under 7. A few other species within Clade D (Fig. 3A) also have small corollas including *C. minutiflora* and *C. parviflora*. However, the species of Clade D (Fig. 3A) can be distinguished from the species of *Angustiflorae* by broad calyx lobes that are folded in a conduplicate manner. Conduplicate folding is a term used when each lobe is appressed to an adjacent lobe and folded lengthwise with the margin curved inward. In contrast, the calyx lobes of *Angustiflorae* are completely separate and narrow (Fig. 2). *Columnnea grisebachiana* and *C. pubescens* also have small corollas similar to those of *Angustiflorae*; however, they have a different geographic distribution. These two species are endemic to the island of Jamaica, while the species of *Angustiflorae* range from Mexico to Bolivia and east into Brazil. They are also found on the islands of Puerto Rico and Hispaniola in the Caribbean, but do not spread further west into Jamaica (Figs. 4–8). Other species with

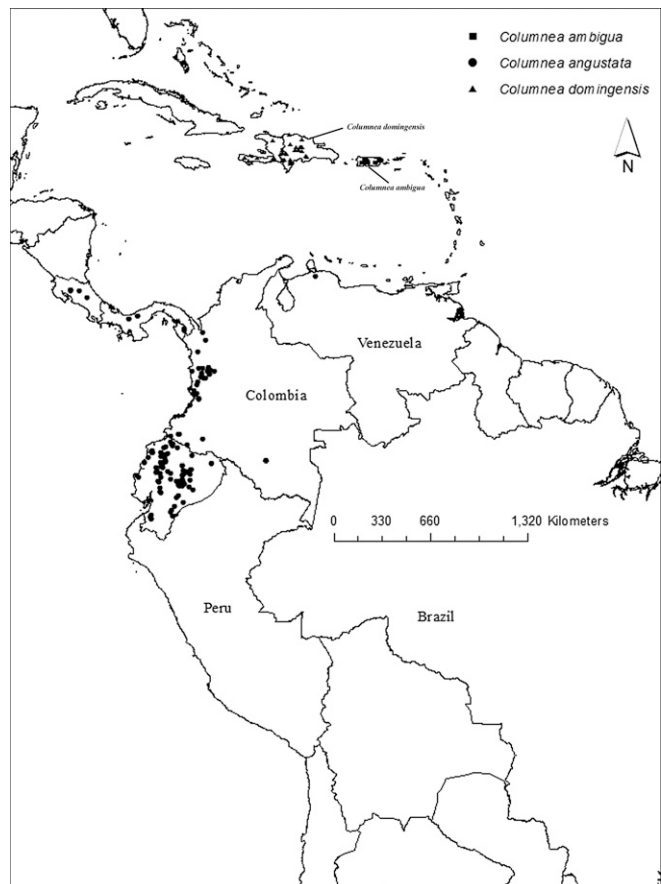


FIG. 4. Distribution of *Columnnea ambigua*, *C. angustata*, and *C. domingensis*.

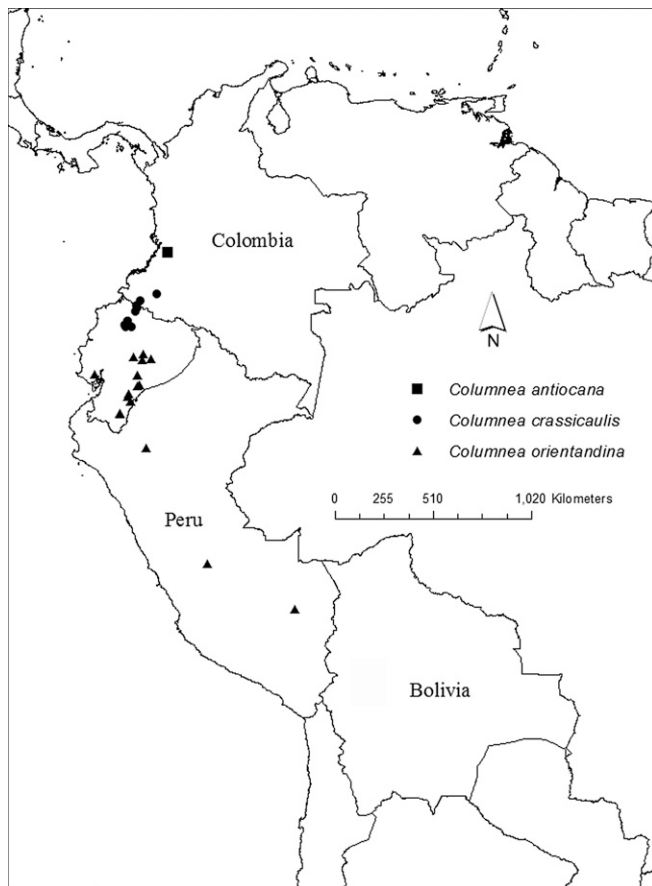


FIG. 5. Distribution of *Columnea antiocana*, *C. crassicaulis*, and *C. orientandina*.

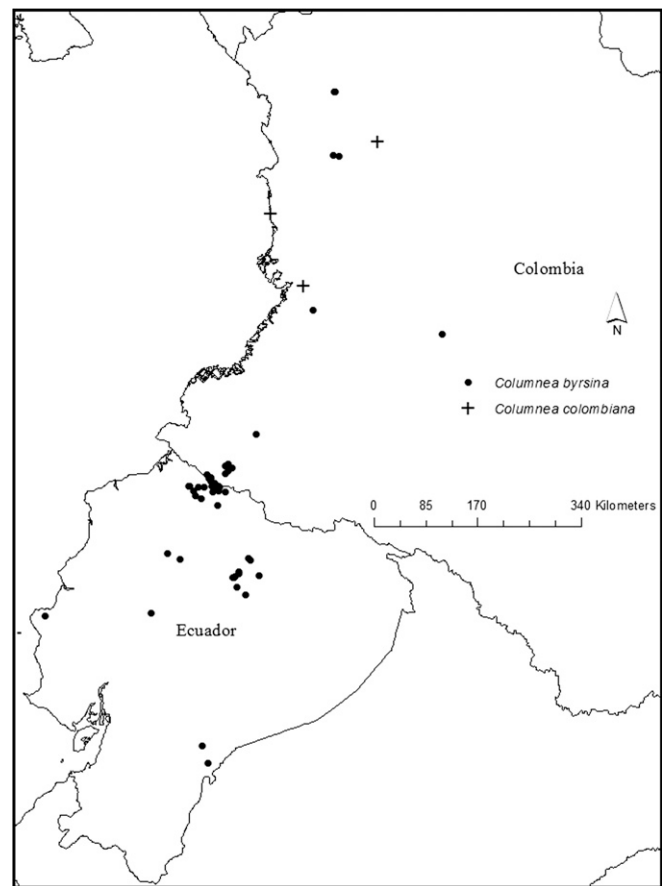


FIG. 6. Distribution of *Columnea byrsina*, and *C. colombiana*.

similar corolla morphologies, *C. moesta*, *C. ultravioletacea*, and *C. xiphoidea*, belong to clade *Stygnanthe* (Fig. 3). Most species of clade *Stygnanthe* also have a denser pubescence that obscures the corolla (Fig. 1C) and have a corolla tube to lobe ratio over 8.

**Note**—Specimens examined to compose distribution maps include all specimens examined by Smith (1994) that are not listed here, and additional specimens listed below for each species. Descriptions of the species have not altered significantly from Smith (1994) and are therefore not reproduced here, the exceptions being *C. domingensis* and *C. ullei* that had not previously been considered members of this clade.

1. COLUMNEA AMBIGUA (Urban) Morley, Proc. Roy. Irish Acad. 74B(24): 423. 1974. *Alloplectus ambiguus* Urban, Symb. Antill. 1: 408. 1899. *Alloplectus ambiguus* var. *chlorosepalus* Urban, Symb. Antill. 1: 408. 1899, nom. superfl. *Crantzia ambigua* (Urban) Britton, Britton and Wilson, Sci. Surv. P. R. and V. I. 6: 204. 1925. *Ortholoma ambiguum* (Urban) Wiehler, Phytologia 27: 320. 1973. *Trichantha ambigua* (Urban) Wiehler, Selbyana 1(1): 34. 1975.—TYPE: PUERTO RICO. Sierra de Luquillo, May 1883 Eggers 1303 (lectotype, designated by Smith 1994: US).

*Alloplectus ambiguus* var. *erythrosepalus* Urban, Symb. Antill. 1: 408. 1899.—TYPE: PUERTO RICO. Sierra de Luquillo, May 1883 Eggers 1302 (lectotype, designated by Morton, Contr. U. S. Nat. Herb. 29: 19, 1944: US).

*Columnea ambigua* is endemic to Puerto Rico and most closely related to *C. domingensis* (Fig. 3). *Columnea ambigua* can be readily distinguished from *C. domingensis* by relatively larger laminae; more flowers per inflorescence; and its coarsely toothed calyx lobes (Smith 1994).

**Phenology**—Flowering occurs from March to October.

**Distribution**—The species is endemic to Puerto Rico found between 350–1,075 m (Fig. 4).

**Climate**—The annual mean temperature for *Columnea ambigua* is 21.27° with an annual average range of 12.91° between warmest and coldest days, and average precipitation of 2,576. mm.

**Additional Specimens Examined**—PUERTO RICO. Alto de La Bandera, near Adjuntas, Britton & Shafer 20016 (US); Caribbean National Forest, Pico del Este Road, Boom 7972 (US); Carite Forest Reserve: Cerro La Santa, along secondary road off of road 184, Acevedo-Rodriguez 7923 (US); Eastern slope of the Luquillo Mountains, Heller 4617 (US); El Yunque, Caribbean National Forest, along El Toro Park trail, Acevedo-Rodriguez 7108 (US); El Yunque, Sargent 8137 (MO); Rt. 187, Jct. 195, D'Arcy 1860 (MO); Monte Jayuya, Reserva Forestal Toro Negro, 6 km west of Divisoria, Thompson 9995 (US); Mt. Britton, Luquillo Insular Forest, along trail, Schubert & Winters 393 (US); Mt. Jayuya, forest, Sargent 3170 (US, MO); Rt 191, km 18, D'Arcy 1859 (MO); Mt. Mandios, near Jayuya, Britton & Cowell 931 (US); Municipio Río Grande, El Verde Research Station, route 186 at the Río Sonadora, wet montane forest, Taylor & Gereau 11857 (MO); Taylor 11679 (MO); Naguabo, Bo. Río Blanco, Caribbean National Forest, along closed portion of Rt. 191 from gate at Río Caboy to landslide area, wet mountain forest, Axelrod & Chavez 2958 (MO); Pico del Este, Caribbean National Forest, along highway 930, Boom 6925 (US); Pico del Oeste, Luquillo Mtns., Wagner 1750 (MO); Reserva Forestal Carite, Boom 9861 (US); Sierra Naguabo, Sintenis 1301 (MO); Sierra de Naguabo, Quebrada Grande to Chuchilla Firme, Shafer 3594 (US); Trail to Cerro La Santa,

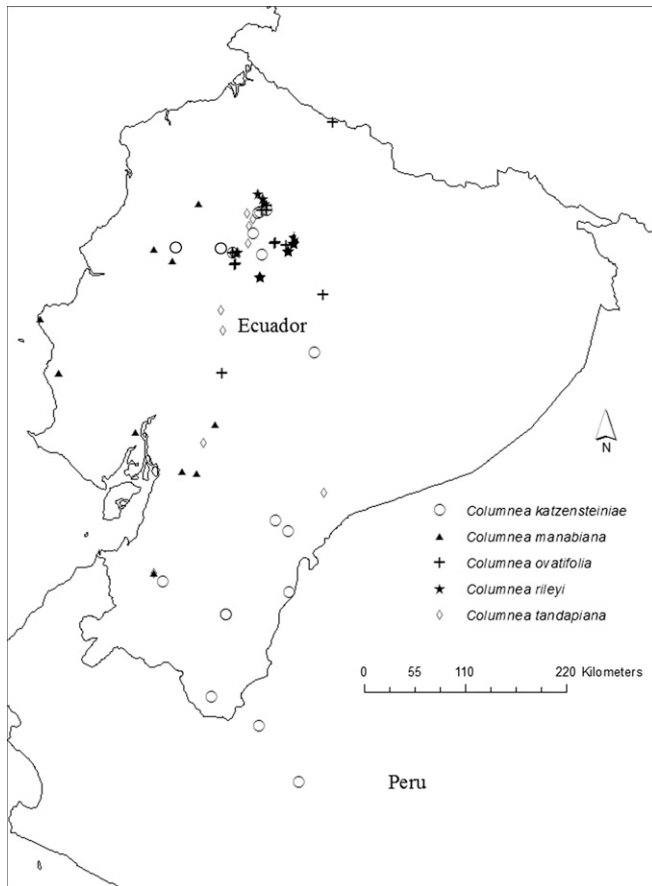


FIG. 7. Distribution of *Columnnea katzensteiniae*, *C. manabiana*, *C. ovatifolia*, *C. rileyi*, and *C. tandapiana*.

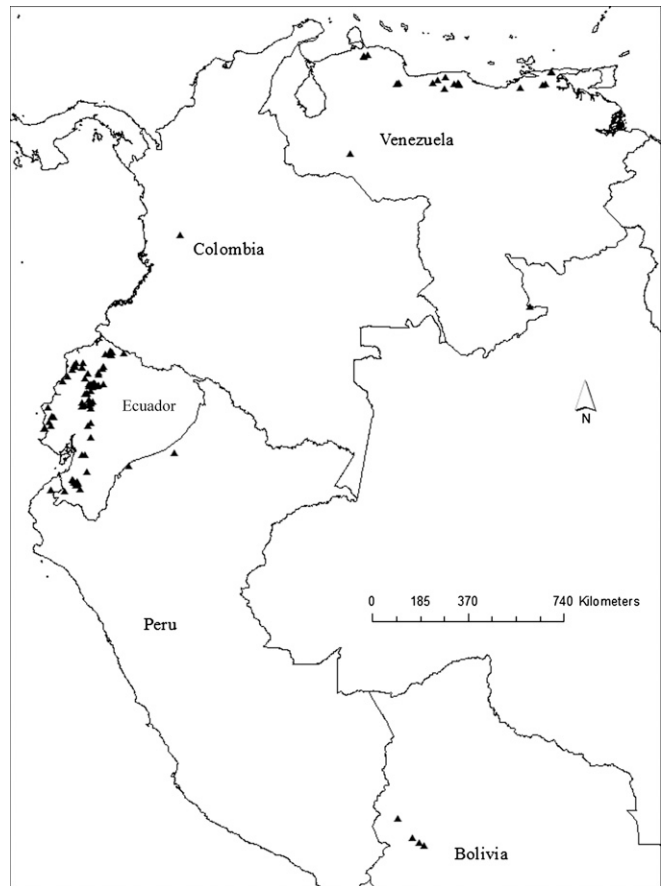


FIG. 8. Distribution of *Columnnea spathulata*.

Carite Forest, Howard 16828 (US); Villalba, Toro Negro Forest, road 149 close to Maravilla, Acevedo Rodriguez & Alvarez 002987 (MO).

2. *COLUMNNEA ANGUSTATA* (Wiehler) L. E. Skog, Ann. Missouri Bot. Gard. 65: 85. 1979 ["1978"]. *Pentadenia angustata* Wiehler, Selbyana 2: 118. 1977.—TYPE: COLOMBIA. Valle del Cauca: 8 km past La Elsa, old rd from Cali to Buenaventura, 30 Apr. 1972, Wiehler et al. 7276 (holotype: SEL).

*Columnnea sericea* Mansfield, Biblioth. Bot. 116: 145. 1937, non *Columnnea sericea* (Hanstein) Kuntze, 1891. *Pentadenia sericea* (Mansfield) Wiehler, Phytologia 27: 315. 1973.— TYPE: ECUADOR. Tungurahua: Río Negro, Diels 878 (holotype: B, destroyed). NEOTYPE: ECUADOR. Chimborazo: Naranjapata, Río Chanchan, 1933, Schimpff 523 (neotype, designated by Kvist and Skog 1993: M; isoneotypes: MO, TRT, GH).

*Pentadenia ecuadorana* Wiehler, Selbyana 2: 82. 1977. *Columnnea ecuadorana* (Wiehler) L. E. Skog, Taxon 33: 126. 1984.— TYPE: ECUADOR. Pastaza: Puyo, 30 July 1971 Wiehler et al. 7163 (holotype: SEL).

*Columnnea angustata* is widely distributed across most of the range of section *Angustiflorae*. It is morphologically variable, but can be readily distinguished from other species by a relatively small, yellow, orange, or red corolla in combination with leaves that are slightly but not strongly anisophyllous (Smith 1994).

**Phenology**—Flowering occurs from March to October in Central America, December to June (one collection in August) in Colombia, and continuously in Ecuador.

**Distribution**—The species is known from Costa Rica to Ecuador and into Venezuela in wet montane forests between 0–1,950 m (Fig. 4).

**Climate**—The annual mean temperature for *Columnnea angustata* is 22.41° with an annual average range of 10.78° between warmest and coldest days, and average precipitation of 3,439 mm.

**Additional Specimens Examined**—COLOMBIA. Municipio de Mistrato, en la via San Antonio de Chami y Mistrato, F. Alonso 10235 (US); Antioquia: in wet and dense forest between Guapa River and Leon River, E. R. Landa et al. 123 (US, COL); Chocó: Bicordo River, tributary of the San Juan River, E. Forero et al. 4646 (US, MO, COL); Carretera Quibdo-Medellin, M. Amaya & L. P. Kvist 434 (US); Lloro 50 km south of Quibdo at junction of Río Atrata and Río Andagueda, W. A. Archer 2053 (SEL); Mpio. de Novita, en pección de Curundo, right margin of Ingard River, S. Diaz 3419 (COL); Mpio. de Nuqui, Corregimiento de Coqui, Por el bosque que rodea la quebrada Trapiche, M. Amaya & L. P. Kvist 402 (US); Mpio. de Nuqui, Corregimiento de Coqui, M. Amaya & L. P. Kvist 412 (US); Near hwy 5–8 km E of Playa de Oro (E of Tado), disturbed forest above pasture, A. Juncosa 2504 (US); Nuqui-Panguí. Playa la Olimpica, A. Gomez et al. 499 (SEL); on the Panamericana road (in construction) between the San Pablo River and the Pato River, E. Forero et al. 5528 (COL, MO); Río Atrato, Yuto, rocky margins of the river above Yuto, J. Cuatrecasas & M. Llano 24150 (US); Putumayo: Mpio. Mocoa, corregimiento de San Antonio, vereda Alto Campucana, finca La Mariposa, J. B. Dataneur et al. 5183 (US); Risaralda: Mun. Pueblo Rico, Corr. Santa Cecilia, F. Gonzalez 2331 (US); Santuario, Borde de carretera de Santuario a Pueblo Rico, M. Amaya & J. F. Smith 534 (US); Valle del Cauca: Bajo Calima, road to Juanchaco Palmeras, A. Gentry et al. 48327 (MO); Mpio. Buenaventura, forest

exploitation in the concesión of Carton de Colombia, *J. van Rooden* 540 (US, COL); old road to Buenaventura from Cali, 65 km from inception, 83 km from Cali, *J. P. Folsom & L. Escobar* 10477 (US); Río Maya upriver from Puerto Merizalda, *A. Gentry & A. Juncosa* 40668 (COL, MO).

COSTA RICA. Jungles near Cariblanco, *M. H. Stone* 1168 (US); Alajuela: Reserva Biológica Monteverde, Río Penas Blancas, *W. Haber & E. Bello* 6878 (MO); Reserva Biológica Monteverde, Río Penas Blancas, Finca de Jesus Rojas, *E. Bello* 1548 (MO); Reserva Biológica Monteverde, Valle del Río Penas Blancas, Quebrada Celeste, *W. Haber & E. Bello* 7069 (MO).

ECUADOR. Road from Quito to Puerto Quito, km 104, then nw on side road toward Pachical, *M. Whitten et al.* 91276 (SEL); Bolívar: along road from Guaranda to Balsapamba, *H. Wiehler* 34 (SEL), *H. Wiehler* 95145 (US); Hcda. Changuil, en potrero, bosque muy humido tropical, nubiado, suelos fértiles, *X. Cornejo & C. Bonifaz* 4533 (US); Carchi: 5 km above Lita (Colonia) along open road & by small creeks, *H. Wiehler & GRF Study Group* 9050 (SEL); Cotopaxi: km 5 to km 15 above La Mana, *H. Wiehler & GRF Study Group* 9751 (SEL); El Oro: Hcda. Daucay, bosque humedo premontano, bosque nublado estacional, *X. Cornejo & C. Bonifaz* 323 (US); road from Pinas to Sta. Rosa km 19, *C. H. Dodson & A. Gentry* 8916 (SEL); 10 km W of Pinas along new road from Pinas-Machala, *C. H. Dodson et al.* 8448 (SEL), *C. H. Dodson et al.* 8447 (SEL); Esmeraldas: area of Río Barbosa (near Lita), *H. Wiehler* 9567 (US); between Lita & Alto Tambo, 5 km from Lita, Río Chuchubi, *H. Wiehler* 29 (SEL), *H. Wiehler* 9024 (US); Bilsa Biological Station, Rana Roja trail, wet primary and secondary forest, roadsides, *P. Mendoza-T. et al.* 555 (US, MO); Eloy Alfaro, Reserva Ecológica Cotacachi-Cayapas, Charco Vicente, Río San Miguel, bosque humedo tropical, bosque primario, *M. Tirado et al.* 482 (US, SEL); Eloy Alfaro, Reserva Ecológica Cotacachi Cayapas, Río Santiago, Angostura, bosque muy humedo tropical, bosque primario, sobre colina, *M. Tirado et al.* 1131 (US, MO); km 5–18 on road Lita to Alto Tambo, *C. H. Dodson et al.* 16856 (SEL); Lita-Sana Lorenzo road, 10–20 km NW of Lita, *A. Gentry et al.* 70070 (US); 1 km W of Santa Isabel, toward Bilsa Biological Station, along logging road, in *Pouteria* tree in cacao plantation, *P. Mendoza-T. et al.* 599 (US); Quininde, Bilsa Biological Station, Mache Mountains, 35 km W of Quininde, 5 km W of Santa Isabel, premontane wet forest, Monkey Bone trail, *J. L. Clark & B. Adnepos* 50 (US, SEL); Quininde, Bilsa Biological Reserve, Montañas de Mache, 35 km W of Quininde, 5 km W of Sanata Isabela, premontane wet forest, primary and disturbed forest along Dogala trail, *N. Pitman & M. Bass* 998 (US), *N. Pitman & M. Bass* 874 (US); Quininde, Community Chorrera Grande, 15 km SW of Cube (via pircuta), premontane wet forest, *J. L. Clark et al.* 2835 (US); Quininde, noreste de Las Golondrinas, Cooperativa 3 de septiembre en sect San Isidro, cerca Río Jordan, *W. Palacios* 11501 (SEL), *W. Palacios* 11496 (SEL); Quininde, Reserva Ecológica Mache-Chindul, Bilsa Biological Station, 35 km W of Quininde, Permanent plot #3, *J. L. Clark* 4747 (US); Quininde, Reserva Ecológica Mache-Chindul, Comunidad Cana Bravel, Cabaceras del Río Viche, estero Sabaleta, tropical wet forest, sunny clearing near rice plantation, *J. L. Clark* 4689 (US); Quininde, Reserva Ecológica Mache-Chindul, 35 km W of Quininde, The Bilsa Biological Station, Cordillera Mache-Chindul, collections made along main road between Sta. Isabel and Station, *J. L. Clark* 9609 (US, SEL); Reserva Cotacachi-Cayapas, al pie de Río Bravo, en lugar abierto, bosque muy humedo tropical, primario, *X. Cornejo & C. Bonifaz* 6234 (US); San Lorenzo Canton, Carretera Lita-Alto Tambo-La Punta, bosque muy humedo tropical, bosque primario, *E. Gudino & R. Moran* 1294 (US); 35 km W of Quininde, *J. L. Clark et al.* 8776 (US); Imbabura: Ibarra, *J. L. Clark et al.* 7484 (US); Imbabura, Cotacachi, Parroquia García Moreno, Cordillera de Toisán, Cerro de la Plata, Bosque Protector Los Cedros, *J. L. Clark et al.* 7380 (US); Los Ríos: Río Palenque Science Center, Km 56 on the Quevedo-St. Domingo rd., *J. B. Watson* 331 (SEL); Río Wajia, on second hill beyond Río Palenque past bridge by Dodson's house, on bank by river, *H. Wiehler* 7129 (SEL); Manabí: Canton Jipijapa, Parroquia Jipijapa, Cerro Montecristi (ca. 1 km W of the town of Montecristi); *J. L. Clark et al.* 6193 (US); Canton Pedernales, Cerro Pata de Pajaro, 10 km E of Pedernales, finca of the family Aroyo, fog/cloud forest, wet forest, *J. L. Clark et al.* 2635 (US); Jama Canton, Cordillera de Jama (costal range), Cerro Nueve, 15 km E of Jama, N of Río Jama, remnant wet forest with frequent fog, below microwave tower, *D. Neill* 11579 (US); just below entering cloud forest on Mt. Montecriste, *C. H. Dodson & L. B. Thien* 1736 (SEL); Morona Santiago: along road from Milagro & Limón - then toward Mendez, *H. Wiehler & GRF Study Group* 97137 (SEL); Canton Limón Indanza, Parroquia Chiviza, road from Limón (Gral Leonidas Plaza Gutiérrez) to Santa Susana de Chiviza, *J. L. Clark et al.* 5982 (US); Macas, along new road, west into the Andes, first 17 km westward, then ca. 12 km south on side road, *H. Wiehler & GRF Study Group* 8801 (SEL); Palora, Parroquia San Vicente de Tarqui, vegetación alterada camino al Río

Yushin, *J. Caranqui et al.* 821 (US); San Juan Bosco, road between San Juan Bosco and El Pangui, 27 km S of San Juan Bosco, *J. L. Clark* 9915 (US); San Juan Bosco, road between San Juan Bosco and the village of Santiago de Panantza (following Río Panantza), *J. L. Clark* 9854 (US, SEL); Sucua, along road to Los Tanques de Aguas, ca. 12 km out of town, *H. Wiehler & GRF Study Group* 8885 (SEL); Napo: along road from Hollin to Loreto, past km 45, *H. Wiehler* 9594 (SEL); along road from Napo to Puyo on way to Hacienda Dos Ríos below Evangelical Mission, Tena, *H. Wiehler* 71124 (SEL); Archidona, Parroquia Catundo, buffer zone of Parque Nacional Sumaco Napo Galeras, comunidad Mushullakta, *J. L. Clark et al.* 7220 (US); *J. L. Clark & N. Harris* 7232 (US); Archidona Canton, Reserva Ecológica Antisana, Comunidad Shamato, entrada por km 21-Shamato, Camino Sardinias-Shamato, premontane/montane wet forest, *J. L. Clark et al.* 5233 (US); Baeza to Lago Agrio, about 25 km from Baeza, *H. Wiehler & GRF Study Group* 86169 (US, SEL); Hollin to Loreto, past km 45, *H. Wiehler* 95118 (SEL); Río Jatunyacu (Shandia), *A. Hirtz* 9609 (SEL); Tena, road Baeza-Río Hollin, *A. Hirtz & X. Hirtz* 4468 (SEL); Tena to Baeza, *H. Wiehler & GRF Study Group* 86224 (SEL); Tena to Pano and Río Janinyacu, on tree in field in front of Hotel Auca, *H. Wiehler & GRF Study Group* 93203 (SEL); Tena to Río Pano, *H. Wiehler & GRF Study Group* 93219 (SEL), *H. Wiehler & GRF Study Group* 93220 (SEL); 25 km from Baeza, *H. Wiehler* 3351 (SEL); Pastaza: along rock road to Tarabita and the portage over the Río Pastaza, ca. 3 km from the turnoff from main Puyo-Mera road, *T. B. Croat* 49680 (US); between km 104 on Quito-Esmeraldas Road and Pachijal, along wet roadside banks, terrestrial, *P. Mendoza-T. et al.* 515 (US); between Puerto Quito and Pedro Vincente Maldonado, in creek area, *H. Wiehler* 90111 (US); between Reserva Río Guaycuyacu and Guayabillas, wet montane forest, on trees at forest edge, *P. Mendoza-T. et al.* 546 (US); Canton Puyo, Parroquia Fatima, secondary forest along border of Escobar Finca (ca., 2 km N of Puyo near turn off toward Ahuano), *J. L. Clark et al.* 9368 (US); cloud forest along ridge near La Centinella at km 12, road from Patricia Pilar to Flor de mayo, *G. L. Webster* 22927 (US); "Gesneriad woods," 2 km NE outside Puyo at Río Grande, *H. Wiehler & D. Masterson* 79208 (SEL); Hacienda San Antonio de Baron von Humboldt, 2 km to the NE of Mera, *D. Neill et al.* 5790 (US); Hotel Germania, Mera, *J. L. Clark & M. Mailloux* 7834 (US); Pastaza Canton, Puyo, Sector Tarqui, bosque pluvial premontano, *G. Tipaz et al.* 408 (US); Puyo-Puerto Napo road, 14–18 km N of Puyo, heavily cut-over forest, now pasture with remnant trees, *J. L. Luteyn & M. Lebron-Luteyn* 5820 (NY, SEL); Shell, bosque muy humedo subtropical, *X. Cornejo & C. Bonifaz* 1408 (US); Shell-Mera rainforest, 2 km N of Shell-Mera, *L. Holm-Nielsen & S. Jeppesen* 469 (OV, S); Simon Bolívar, *J. L. Clark & J. Katzenstein* 8322 (US); south of Mera, *J. L. Clark et al.* 7797 (US); Teresa Mama on the Río Bobonaza c. 35 km SE of Sarayacu, *H. Lugo S.* 5702 (US, GB); 3 km S of Puyo close to the Pastaza river and the border to the province of Morona-Santiago, slopes close to the village Madre Tierra, farmland and forest remnants mixed with banana plantations, *L. P. Koist* 60325 (US); Veracruz (Indillama), *H. Lugo S.* 34 (US); Pichincha: golf course and pastures of Hotel Tinalandia, *H. Wiehler* 7997 (SEL); Montañas de Ila, *H. Wiehler & GRF Study Group* 9081 (US, SEL); Montañas de Ila; sub-cloud forest, exposure toward the Pacific, *H. Wiehler & GRF Study Group* 9098 (SEL); Quito, Río Guaycuyacu, *J. L. Clark* 8270 (US); Quito Canton, Reserva Río Guaycuyacu, near confluence of Río Guaycuyacu and Río Guayabamba, *J. L. Clark et al.* 4959 (US); road off road to Puerto Quito at Maldonado, km 116 to Cecilia, *A. Hirtz* 4473 (SEL); Santo Domingo de los Colorados, Tinalandia resort, *R. W. Dunn* 95–04–136 (US); Sto. Domingo de los Colorados, bosque humedo premontano, *X. Cornejo & S. Laegaard* 2038 (US); trek from Lloa to Mindo, forest between Hacienda Pacay and main bridge to Mindo (south side of Río Cinto), *J. L. Clark* 4520 (US); Puyo: epiphyte on trees surrounding Hotel Turingia, *H. Wiehler* 1176 (US); Puyo-Tena road, *J. L. Clark et al.* 9373 (US); Veracruz, *J. L. Clark & J. Katzenstein* 9302 (US); Tungurahua/Pastaza: along road from Baños to Puyo, 2 km below Río Topo, *H. Wiehler* 79140 (SEL); Tungurahua: Canton Baños, Parroquia Río Negro, locality near Río Topo, wet montane forest, *J. L. Clark & V. Duran* 6024 (US); road Baños to Puyo, 5 km past Baños near Río Blanco, *H. Wiehler & GRF Study Group* 8665 (SEL); Tungurahua, Baños, *J. L. Clark & J. Katzenstein* 8397 (US); Valley of Pastaza River, between Baños and Cashurco, 8 hr east of Baños, *A. S. Hitchcock* 21769 (MO); Zamora-Chinchipe, in the vicinity of the mining camp at the Río Tundaime, pastures along Río Quimi with small patches of disturbed forest, *H. Van der Werff et al.* 19260 (US, MO).

PANAMA. Coclé: La Pintada, Corregimiento, El Ariño, Omar Torrijos National Park, 6–10 km NNW from El Cope, main trail from abandoned sawmill to the Comunidad La Rice, *J. L. Clark* 8627 (US); near Aserradero El Cope, ca 8 km N of El Cope, Atlantic slope, *R. L. Dressler* 5642

(SEL); Darien: Distrito de Santa Fe, Alrededores del Río Primer brazo de Ulaha, *C. Galames et al.* 3171 (US); south of Cerro Pirre, *J. A. Duke* 15614 (US).

VENEZUELA. Distrito Petit: Falcón, Falcón, *W. Meier & G. Forbes* 12856 (US).

3. *COLUMNEA ANTIOCANA* (Wiehler) J. F. Smith, *Pentadenia antiocana* Wiehler, *Selbyana* 7: 335. pl. 2D. 1984.—TYPE: COLOMBIA. Antioquia: *Jewise s. n.* (holotype: K).

*Columnnea antiocana* is most likely related to *C. katzensteiniae*, *C. rileyi*, *C. crassicaulis*, and *C. ovatifolia*. These species share a similar leaf shape and vesture. They are also the only species with darker colored spots on the interior surfaces of the lobes of the corollas in section *Angustiflorae*. *Columnnea antiocana* can be distinguished from other species by the presence of corolla lobe spots on the entire margins of its calyx lobes and its more ovate, acute to acuminate laminas (Smith 1994).

**Phenology**—Full phenology is unknown because only a single collection from February is available.

**Distribution**—The species is endemic to Colombia (Antioquia) at ca. 2,000 m (Fig. 5).

**Climate**—The annual mean temperature for *Columnnea antiocana* is 19.5° with an annual average range of 12.1° between warmest and coldest days, and average precipitation of 1,644 mm. It should be emphasized here that these data are based on a single georeferenced collection.

4. *COLUMNEA BYRSINA* (Wiehler) L. P. Kvist and L. E. Skog, *Allertonia* 6: 384. 1993. *Pentadenia byrsina* Wiehler, *Selbyana* 2: 119. 1977.—TYPE: [ECUADOR.] Cultivated material grown from seeds collected near Baeza, Napo (*Dressler et al. s. n.*), 17 July 1977, *Wiehler* 77122 (holotype: SEL).

*Columnnea byrsina* is most closely related to *Columnnea orientandina* both molecularly and morphologically (Smith and Sytsma 1994a; Schulte 2012). Both *C. byrsina* and *C. orientandina* have dorsiventral shoots and share the presence of tubular corollas with subradial limbs. The flowers are located beneath the larger leaf of a pair. In full sun the flowers are extended and exposed to the open; in low light or shade they are tightly appressed to the lower leaf surface (Smith and Sytsma 1994a, b, c). *Columnnea byrsina* is readily distinguished from other species by strongly anisophyllous leaves, acute to acuminate blades, and bright red corollas with exerted stamens and styles. It is also the only species of *Columnnea* known to have a variable fruit shape. The berries are generally globose, but several collections from near Baeza, Napo, Ecuador, have ovoid berries (Smith 1994).

**Phenology**—Flowering occurs continuously.

**Distribution**—The species is known from Central Colombia to Ecuador in wet forests between 650–4,000 m (Fig. 6).

**Climate**—The annual mean temperature for *Columnnea byrsina* is 19.24° with an annual average range of 11.53° between warmest and coldest days, and average precipitation of 2,440 mm.

**Additional Specimens Examined**—COLOMBIA. Antioquia: Mpio. de Frontino, km 14 of road Nutibara-Murri, disturbed wet/very wet montane vegetation, roadside, *J. L. Zarucchi et al.* 5670 (US); Nariño: Finca La Planada, near Chucunes, *S. Libenson et al.* 30577 (MO); La Planada, Salazar finca 7 km above Ricaurte, *A. Gentry* 34996 (COL, US, MO); La Planada Reserve, 7 km from Chucunes, *A. Gentry et al.* 60328 (US); La Planada Biological Reserve, ca. 7 km S of Chucunez, along trail to Pialapi to Quebrada La Calledita, disturbed premontane forest and open potreros, *J. L. Luteyn et al.* 13912 (US); trail from El Mirador up to open field, *J. F. Smith & M. Galeano* 1457 (WIS);

Reserva Natural La Planada, municipio de Ricaurte, *C. Restrepo & G. Ramirez* 563 (US); Ricaurte, *K. von Sneidern* 10.IV.1941 (OV); Ricaurte, Chucunes, The Planada Natural Reserve, the bank towards the way that you see the Administration of the Mirador, *X. Londono* 240 (US); Valle del Cauca: Querebral, on tree near river, *P. J. M. Maas & T. Plowman* 1838 (OV).

ECUADOR. Carchi: Canton Espejo, Parroquia Guatal, Mirador de las Golondrinas (Fundación Golondrinas), trail from El Corazon toward La Cortader (2 km NE of refugio), *J. L. Clark et al.* 8460 (US); Canton Mira, Parroquia Jijon y Camano, unfinished road from El Carmen toward Chical, Agua Amarilla, *J. L. Clark & E. Folleco* 8539 (US); Canton Tulcán, Parroquia Chical, collection made along path from the village of Chical towards an area known locally as "Crystal," walked along Río Blanca via the Cordillera Guilchan (ca. 6–8 km SW of Chical), *J. L. Clark et al.* 6343 (SEL, US); Canton Tulcán, Parroquia Chical, collection made along path from the village of Quinyal toward an area known locally as "Gualpi" (near the boarder of the Reserva Awa), *J. L. Clark & O. Mejia* 6291 (SEL, US, MO); Chical, pasture and edge of pasture, *S. A. Thompson & J. A. Rawlins* 719 (US); environs of Chical, 12 km below Maldonado on the Río San Juan, *M. T. Madison et al.* 4451 (SEL, F); environs of Maldonado, *M. T. Madison et al.* 4419 (SEL); Carchi, vic. of Maldonado, *M. T. Madison* 3873 (SEL); Espejo, bosque Protector Mirador de Golondrinas, collections made between the village, Las Juntas and la Cabana del Corazon, lower montane wet forest, *J. L. Clark et al.* 2413 (US, MO); from Maldonado to Chical and return, *H. Wiehler* 93110 (SEL, US, MO); Mira, El Carmen. Cerro Golondrinas, bosque Montaña, bosque primario en colinas, *M. Tirado et al.* 1230 (US, MO); trail from Rafael Quindí's Finca back toward Untal to stream, approx. 0.5 km from finca, *W. S. Hoover & S. Wormley* 1577 (MO); Tulcán Canton, Parroquia Tobar Donoso, Reserva Indígena Awa, Centro El Baboso, bosque primario, bosque muy humedo premontano, *G. Tipaz et al.* 1914 (SEL, MO); Tulcán Canton, Reserva Indígena Awa, Comunidad El Baboso, 12 km al norte de Lita, bosque pluvial premontano, bosque primario, *D. Rubio et al.* 2203 (MO); Tulcán Canton, Reserva Indígena Awa, Comunidad Gualpi Alto, parroquia Chical, Bosque pluvial Montano Bajo, *D. Rubio et al.* 1692 (MO); vic. of Chical *L. Besse et al.* 887 (SEL); vic. of Chical, west of Maldonado on trail to Peñas Blancas, *A. Gentry & G. Shupp* 26406 (SEL, MO); Cotopaxi: Canton Pujili, Reserva Ecológica Los Ilinizas, Sector II (Sector Sur), sector Chuspitambo, al occidente de Choasilli, Cordillera Occidental, vertiente occidental, *P. Silverstone-Sopkin et al.* 9967 (MO); Esmeraldas: Alto Tambo, *A. Hirtz & J. Kent* 4556 (SEL); Esmeraldas, Canton San Lorenzo, Parroquia Alto Tambo, Comunidad El Cristal, 8–10 km S of San Lorenzo-Ibarra highway, *J. L. Clark et al.* 7539 (US); km 12, Cristal, Lita-(La Merced de) Buenos Aires, edge of Cotacachi Cayapas Reserva Ecológica, *C. H. Dodson* 17604 (US, MO); Imbabura: Canton Ibarra, Parroquia Lita, Comunidad San Francisco, next to Río Verde (13 air-km S of Lita), *J. L. Clark et al.* 7518 (US); Manabí: Montecristi, Cerro Montecristi, Carretera Manta-Jipijapa, entrada por Montecristi o El Chorrillo, bosque seco premontano, *T. Nuñez et al.* 356 (MO); Morona-Santiago: Canton Limón-Indanza, Cordillera del Condor, trail from camp #1 to camp #2 towards crest of Cordillera del Condor (ca. 10–15 km S/SE of the Comunidad Warints), *J. L. Clark & L. Jost* 6992 (US); Canton Limón Indanza, Parroquia Chiviaza, road from Limón (Gral Leonidas Plaza Gutierrez) to Santa Susana de Chiviaza, *J. L. Clark et al.* 5969 (US); Napo: along road from Baeza to Lago Agria about 42 km from Baeza, *H. Wiehler* 79298 (SEL); Napo, forest north of Baeza, *A. Hirtz* 4496 (SEL); Canton El Chaco, margen derecha del Río Quijos, Finca "La Ave Brava" de Segundo Pacheco, bosque pluvial Premontano, bosque primario, sobre suelos saturados, *W. Palacios* 5410 (SEL, MO); cloud forest 44–45 km by road N of Tena, *G. L. Webster* 23237 (US); cloud forest north of Baeza, *C. Luer et al.* 4496 (SEL), *C. Luer et al.* 3177 (SEL); km 20 Baeza-Tena, *L. Besse et al.* 2329 (SEL); road Baeza-Lago Agrio, 18 km from Baeza, *H. Balslev & E. Madsen* 10575 (MO, OV, COL, SEL, F); road Baeza-Lago Agrio, km 14, *B. B. Klitgaard et al.* 606 (US); Pichincha: Montañas de Ila, sub-cloud forest, exposure towards the Pacific, *H. Wiehler* 9095 (SEL, US); Quito Canton, trek from Lloa to Míndo, following south side of Río Cinto, disturbed, sunny roadside with remnant forest of steep/vertical sections, growing along stream, *J. L. Clark* 4502 (US); Sucumbios: Cosanga area-10 km to Río Aliso, between Río Aliso and Río Cosanga 6 km, then south of Cosanga about 5 km, *H. Wiehler* 98156 (SEL, US).

5. *COLUMNEA COLOMBIANA* (Wiehler) L. P. Kvist and L. E. Skog, *Allertonia* 6: 385. 1993. *Pentadenia colombiana* Wiehler, *Selbyana* 2: 120. 1977.—TYPE: COLOMBIA. Valle del

Cauca: along Río Dagua, old rd Cali-Buenaventura, near Buenaventura, 1 May 1972, *Wiehler et al.* 72130 (holotype: SEL).

*Columnnea colombiana* is closely related to *C. angustata*, *C. byrsina*, and *C. orientandina* based on molecular analyses (Fig. 3); however, the exact placement is unknown. Cladistic analysis of morphology placed *C. colombiana* with *C. rileyi* and *C. suffruticosa* (Smith and Sytsma 1994a). Chloroplast restriction site DNA analysis placed it as a sister to *C. bryrsina* and *C. orientandina* (Smith and Sytsma 1994b, c), while other molecular phylogenetic analyses placed *C. colombiana* as sister to *C. angustata* (Schulte 2012). The slightly anisophyllous, ovate to orbicular leaves, thin pendent stems, red corollas with green limb, and dissected calyx lobes distinguish *C. colombiana* from other species (Smith 1994).

**Phenology**—Flowering occurs from May to August, possibly longer.

**Distribution**—The species is known from Colombia in wet forests from sea level to 800 m (Fig. 6).

**Climate**—The annual mean temperature for *Columnnea colombiana* is 25.39° with an annual average range of 10.12° between warmest and coldest days, and average precipitation of 4,508 mm.

**Additional Specimens Examined**—COLOMBIA. Chocó: Boca Pepe, Pacific coast of Chocó, downstream of Porto Maluk Río Baudo, tree growing on edge of riverbank, *J. W. White & R. H. Warner* 74 (COL, MO); El Valle: Sabaletas, km. 29 on highway from Buenaventura to Cali, *E. P. Killip & J. Cuatrecasas* 38847 (US).

6. COLUMNEA CRASSICAULIS (Wiehler) L. P. Kvist and L. E. Skog, *Allertonia* 6: 385. 1993. *Pentadenia crassicaulis* Wiehler, *Selbyana* 2: 122. 1977.—TYPE: COLOMBIA. Nariño, near Ricaurte at km 79 on road to Tuquerres to Tumaco, along Río Guabo, 9 May 1972 *Wiehler and Williams* 72185 (holotype: SEL).

*Columnnea crassicaulis* is most closely related to *C. katzensteiniae*, *C. rileyi*, and *C. ovatifolia* based on molecular analyses (Fig. 3). These species are all morphologically similar based on the presence of darker colored spots on the interior surface of the corolla lobes. A thickened stem, ovate to orbicular leaves, and long yellow corollas with a long constriction at the base distinguishes *C. crassicaulis* from other species of *Columnnea* (Smith 1994).

**Phenology**—Flowering occurs continuously.

**Distribution**—The species is known from southern Colombia to northern Ecuador in wet forests between 1,200–2,300 m (Fig. 5).

**Climate**—The annual mean temperature for *Columnnea crassicaulis* is 18.52° with an annual average range of 12.21° between warmest and coldest days, and average precipitation of 1,832 mm.

**Additional Specimens Examined**—COLOMBIA. Nariño: Mpio. de Mallama, Piedrancha, orilla izquierda del Río Guisa, *B. R. Ramirez P. & A. L. Joja* B. 5.718 (US).

ECUADOR. Carchi: road to Chical, back to Maldonado and toward Tulcán and return to Maldonado, along Río San Juan, *H. Wiehler* 93128 (SEL, US); Cotopaxi: Nanegalito, *H. Wiehler & GRF Study Group* 97172 (SEL); Imbabura: Otavalo via Quiroga, Apuela, Vacas Galindo to the mines of Selva Alegre and back to Otavalo, total of 139 km, *H. Wiehler & GRF Study Group* 93164 (SEL); road from Gualupe to Buenos Aires off road from Ibarra to Lita at km 32, *C. H. Dodson et al.* 16779 (SEL); Selva Alegre, *A. Hirtz* 4500 (SEL); Pichincha: along road near Nanegal, in pasture land or small forest remnants, *H. Van der Werff et al.* 12307 (SEL, US).

7. COLUMNEA DOMINGENSIS (Urban) B. Morley. *Proc. Royal Irish Acad.* 74: 424. 1974. *Alloplectus domingensis* Urban

*Symb. Antill.* 2: 357. 1901. *Trichantha domingensis* (Urban) *Wiehler*.—TYPE: SANTO DOMINGO. Río Jimenes, May 1887 *Eggers* 2314 (holotype: K!; isotype: HBG).

*Alloplectus domingensis* Urban var. *microphylla* Morton. *Contr. U. S. Nat. Herb.* 29: 19. 1944.—TYPE: HAITI. Summit of Morne Delcour, Montagnes de la Hotte, Aug. 1927 *W. J. Eyerdam* 351 (holotype: US!; isotypes: GH!, NY!).

Epiphytic vining herb, stems to 50 cm long, to 3.5 mm diameter, red-brown to tan, proximally nearly glabrous with a few multicellular transparent trichomes, distally appressed pilose with multicellular red or transparent trichomes; internodes 0.9–4.0 cm long; leaf scars raised or flush with the surface. Leaves opposite, subequal to anisophyllous, larger lamina of a pair 6.5–60.0 mm long, 4.0–28.0 mm wide, ovate to oblanceolate, apex acute to blunt and rounded, base oblique or cuneate, lateral veins 2–3 per side, adaxially green, sparsely appressed pilose with multicellular and unicellular transparent trichomes, adaxially pale green to reddish, sparsely appressed pilose with unicellular transparent trichomes, veins glabrous to appressed pilose with multicellular red trichomes; margin crenate to crenulate; petioles 0.0–22.0 mm long, sparsely pilose with appressed multicellular transparent trichomes. Smaller lamina of a pair 5.5–22.0 mm long, 2.0–13.0 mm wide, ovate, apex acute to blunt and rounded, base oblique or cuneate, lateral veins 2–3 per side, adaxially green, sparsely appressed pilose with multicellular and unicellular transparent trichomes, adaxially pale green to reddish, sparsely appressed pilose with unicellular transparent trichomes, veins glabrous to appressed pilose with multicellular red trichomes; margin crenate to crenulate; petioles 0.0–4.0 mm long, sparsely pilose with appressed multicellular transparent trichomes. Inflorescences of 1 flower per leaf axil; bracts 2.0–5.5 mm long, 0.4–1.0 mm wide, linear, apex acute, red, pilose with multicellular red trichomes. Pedicels 8.0–21.0 mm long, red, pilose with multicellular red trichomes. Calyx clasping corolla, lobes 7.5–17.0 mm long, 1.5–3.0 mm wide without lobes, lanceolate (without lobes), apex acute, interior nearly glabrous, exterior sparsely pilose with multicellular transparent trichomes, red, margins lacinate. Corolla 1.7–2.6 cm long, 5.5–7.0 mm at widest point, 3.0–5.0 mm at constriction before limb, 2.0 mm wide at constriction before gibbous base, tubular, slightly ventricose, yellow, exterior sparsely pilose with long multicellular transparent trichomes, interior glabrous; limb 6.5–8.5 mm in diameter, lobes semi-orbicular, 2.0–2.5 mm long, 2.0–3.0 mm wide, yellow. Filaments connate 3.5 mm, adnate to corolla 2.0 mm, glabrous; anthers 1.0 mm long, 1.4 mm wide, rectangular, included in corolla tube. Ovary 2.5–3.0 mm long, conical, nearly glabrous; style yellow, pilose with short multicellular trichomes distally, glabrous proximally; stigma bilobed, papillate, included in corolla tube. Nectary two dorsal glands. Fruit an ovate to globose berry 5.0–7.0 mm long, 3.5–7.0 mm wide, nearly glabrous, red to purple. Seeds 1.0 mm long, red-brown, twisted striate.

**Phenology**—Flowering occurs all year. Fruiting specimens are known from February, June, August, and November, presumably all year.

**Distribution**—This species is endemic to Hispaniola, from 0–1,725 m (Fig. 4).

**Climate**—The annual mean temperature for *Columnnea domingensis* is 19.50° with an annual average range of 15.69°



between warmest and coldest days, and average precipitation of 1,514 mm.

**Additional Specimens Examined**—DOMINICAN REPUBLIC. *T. Zanoni* & *R. Garcia* 30462 (NY); Jarabacoa, Cienaga de Manabao, along Tablones river, mostly second growth forest, *B. A. H. Liogier* 12066 (US); near Jarabacoa, *De J. Jimenez* 3033 (US); Barahona: Constanza, *H. von Turckhelm* 3375 (NY); Constanza, on old track [sic] in wet woods La Descubierta, *A. H. Liogier* 18055 (NY, F); Cordillera Central, Santiago Rodriguez, National Park, between Monte Llano & Los Descansaderos, *T. Zanoni* & *R. Garcia* 41853 (NY); Monteada Nueva, forested hillslopes SE of Polo, *R. A. Howard* & *E. S. Howard* 8556 (US); Monteada Nueva, near Polo *W. S. Judd* et al. 1078 (AAH, AAU); Monteada Nueva, 6.3 km from Cruce de El Puerto-Monteado-Nueva, 3.4 km E of Cortico, *A. Gentry* & *M. Mejia* 50693 (MO); Mt. Laho, trail from La Cueva to Pla cer Bonita, *R. A. Howard* 12291 (US); Paradis, *P. Fuertes* 329 (US, MO); Sierra de Baoruco, 4 km arriba el pueblecito rural de "Entrada de Corico" en el camino a El Gajo (sitio tradicional de Botánicos, bajo el nombre "Monteada Nueva;" un bosque latifoliado y nublado con *Magnolia pallescens* y *M. hamori*), *T. Zanoni* et al. 18876 (US, MO); Sierra de Baoruco, Loma "Pie Pol" (Pie de Palo en el mapa) de La Guasara de Barahona, bosque latifoliado y humedo, con *Magnolia hamori*, *Obolonia zanonii*, *T. Zanoni* et al. 38670 (US, MO); Sierra de Bahoruco (extremo oriental), más arriba de la Finca Habib, Loma Pie de Pol (Pie Pol), al final de la carretera de La Guasara (de Barahona), bosque latifoliado, humedo sobre el firme de la loma, muchas plantas epifíticas, *T. Zanoni* et al. 41040 (US); vicinity of Paradis, *W. L. Abbott* 1610 (US); vicinity of Paradis, *W. L. Abbott* 1583 (US); vicinity of Constanza, *W. L. Abbott* 6 (US); Estrella: en la ladera del norte de la Loma El Hoyazo, entre el Puesto Militar Aniseto Martinez y el Puesto Militar "km. 204" en la Carretera Internacional, bosque latifoliado, en su limite bajo donde cambia a bosque de *Pinus*, *T. Zanoni* et al. 39798 (US). Independencia: Munic. La Descubierta, Parque Nacional Sierra de Neiba, *L. Halm* 445 et al. (SRP); plants collected above Aguacate toward Los Arroyos, *T. E. Talpey* 73 (BH); Sierra de Baoruco, 38 km Sur de Duverge, *T. Zanoni* & *J. Pimentel* 26542 (NY); La Vega: Cordillera Central, en las orillas del Arroyo La Sal, approx. 1 km arriba (este) del poblado rural de La Sal, bosque latifoliado y secundario, con cafetales, entre Loma La Sal Y Loma La Golondrina, *T. Zanoni* et al. 19975 (US, MO); Cordillera Central, Parque Nacional J. A. Bermudez, en el sendero entre la caseta de parques Nacionales en lost Tablones (de La Cienaga de Manabao y Loma Alto de La Cotorr), bosque latifoliado y humedo, a veces con *Pinus occidentalis*, *T. Zanoni* et al. 39209 (US, MO); Los Tablones, ca. 2 miles W of La Cienega, *G. J. Gastony* et al. 244 (US); Pedernales: 4 km NE of Los Arroyos, edges of remnant cloud forest, *S. A. Thompson* et al. 7592 (US); in dark forest of Sierra de Neiba, *A. H. Liogier* & *P. Liogier* 22699 (NY); in sylvia ad Río Jimenoa, *Eggers* 2314 (KEW); Puerto Plata: in elfin forest, Cordillera de Yaroa, on limestone ridge, facing the Yaroa valley, *A. H. Liogier* 11206 (NY, GH); San Cristobal: Los Cacaos, Colonia Ranfis, ravines among coffee plantations, *B. A. H. Liogier* 11624 (US); Santiago: SW spur of Monte Pallo, in forest, *E. L. Ekman* 12898 (US).

HAITI. Camp No. 2, Mt. Maleuvre, *G. V. Nash* & *N. Taylor* 1154 (US); Peli on Ville, *E. L. Ekman* 1129 (US); Grand'anse: Riviere Glace, cloud forest, *J. T. Curtis* & *E. C. Leonard* 45 (WIS); Summit of Mount Dilcorer, Montagnes de la Hotte, *W. J. Everdam* 351 (NY, US, GH); Nord: Vicinity of Marmelade, thicket on mountain slope east of road, *E. C. Leonard* 8359 (US); Ouest: collected along path 3/4 of way from Furcy toward M. La Visite, *T. E. Talpey* 46 (BH); cultivated, *Talpey* no. 46, seed collected along path from Furcy to Morne La Visite, grown in the Hortorium Conservatory, Cornell Univ. *M. H. Stone* 1136 (US); Gonave Island, *W. J. Everdam* 280 (US); Massif de la Selle, *L. H. Bailey* 199 (US); Massif de la Selle, Parc National Morne la Visite, vicinity of lower cascade of Riviere Blanche about 2 km SW of Park Headquarters, S of Morne la Visite, *W. S. Judd* & *J. D. Skeepey Jr* 4436 (GH); Massif de la Selle, sud'est 8 km north of Seguin in the carretera Furcy and Petionville, *T. Zanoni* & *M. Mejia* 24559 (NY); near Petite Source, Morves des Commissaires, *L. R. Holdridge* 955 (US); vicinity of Furcy, *E. C. Leonard* 4630 (US); vicinity of Mission, Fonds Varettes, *E. C. Leonard* 3802 (US); Sud: Morne de la Hotte in dechiv, Sept-orient in sylvia moutanis, *E. L. Ekman* 79 (S, AAH); Sud-Est: vicinity of Bassin Bleu, *E. C. Leonard* & *G. M. Leonard* 15058 (US).

8. COLUMNEA KATZENSTEINIAE (Wiehler) L. E. Skog and L. P. Kvist, *Novon* 7: 413. 1997 [1998]. *Pentadenia katzensteiniae* "katzensteinii" Wiehler, *Phytologia* 73: 235. 1992.—TYPE: ECUADOR. Morona-Santiago: Cordillera del Boliche,

ca 60 km from Limón, 21 Apr. 1988, *Wiehler* & *GRF Expedition 88128* (holotype: GES; isotypes: F, K, MO, NY, QCA, US).

*Columnea lavandulacea* L. P. Kvist and L. E. Skog, *Allertonia* 6: 387. 1993.—TYPE: ECUADOR. Pichincha: Quito-Santo Domingo rd, 11 Dec 1983, *Kvist* & *Barfod* 49066 (holotype: AAU; photo: AAU).

*Columnea katzensteiniae* is most closely related to *C. rileyi* based on molecular phylogenetic analyses (Fig. 3). Both species, along with *C. crassicaulis* and *C. ovatifolia*, have similar corollas with darker colored lobe spots on the interior surfaces. However, the lavender corollas with purple spots and lavender pubescence distinguish *C. katzensteiniae* from other species of *Columnea* (Smith 1994).

**Phenology**—Flowering occurs continuously.

**Distribution**—This species is known from northern Ecuador into northern Peru in wet forests between 1,400–2,430 m (Fig. 7).

**Climate**—The annual mean temperature for *Columnea katzensteiniae* is 17.43° with an annual average range of 13.00° between warmest and coldest days, and average precipitation of 1,827 mm.

**Additional Specimens Examined**—ECUADOR. Cotopaxi: Canton Sigchos, Parroquia San Francisco de las Pampas, bosque Integral Otonga, *J. L. Clark* & *A. Muñoz* 6129 (SEL, US, MO); Manabí: old road from Santo Domingo to Quito, *R. W. Dunn* 57 (US); Morona-Santiago, Cordillera del Boliche, about 60 km from Limón south to Gualaquiza, *H. Wiehler* & *GRF Expedition 88128* (SEL); Morona-Santiago: Plan del Milagro at cross-road between Limón and Indanza, *G. Harling* & *L. Andersson* 24524 (US); Pastaza: Mera near Río Pastaza, *G. C. G. Argent* & *R. B. Burbidge* 423 (MO); Pichincha: Canton Quito, Reserva Florística-Ecológica "Río Guajalito," km 59 de la carretera antigua Quito-Sto. Domingo de los Colorados, a 3.5 km al NE de la carretera, *J. L. Clark* et al. 7625 (US); road Aloato-Santo Domingo, San Ignacio, *B. Sparre* 14693 (US); route Tandayapa - Nanegalito, *F. Billiet* & *B. Jadin* 6690 (MO); Pichincha, along road from Los Bancos to Mindo, 4 km from western road to Mindo *H. Wiehler* et al. 90145 (SEL, US); Zamora-Chinchipe: area of the Estación Científica San Francisco, road Loja-Zamora, ca. 35 km from Loja, *J. Homeier* 1527 (MO), *J. Homeier* & *E. Brandes* 1218 (MO), *F. A. Werner* 876 (US); Canton Chinchipe, Parroquia Zumba, finca de Sandy Leon, forest near Río Tarrangami, *J. L. Clark* et al. 8915 (US).

PERU. Cajamarca: San Ignacio, Distrito Huarango, Poblado Selva Andina, trocha camino a Paquisha, *J. Perea* & *J. Mateo* 3038 (MO).

9. COLUMNEA MANABIANA (Wiehler) J. F. Smith and L. E. Skog, *Novon* 3: 189. 1993. *Pentadenia manabiana* Wiehler, *Phytologia* 73: 236. 1992.—TYPE: [ECUADOR.], cultivated plants from living material (*C. H. Dodson* & *H. C. Dodson* 6791), collected in Manabí, Ecuador, Km 67 on rd Chone-Santo Domingo, 500 m, 31 Jul 1977, *H. Wiehler* 87102 (holotype: GES; isotypes: B, F, HBG, K, MO, NY, QCA, SEL, U, US).

*Columnea manabiana* is most closely related to *C. tandapiana* (Fig. 3). Both *C. manabiana* and *C. tandapiana* have long, narrow, lanceolate to slightly falcate leaves and small yellow corollas. The two species can be distinguished from one another by the presence of large, conspicuous, ovate floral bracts, which partly obscure the inflorescence on *C. manabiana* (Smith 1994).

**Phenology**—Flowering occurs from October to April.

**Distribution**—This species is endemic to Ecuador (Manabí, El Oro) between 50–1,700 m (Fig. 7).

**Climate**—The annual mean temperature for *Columnea manabiana* is 23.37° with an annual average range of 11.35° between warmest and coldest days, and average precipitation of 1,442 mm.

**Additional Specimens Examined**—ECUADOR. Azuay: Cuenca, Bosque Protector Molleturo Mullopungo, collections made along main road near the village, Mantareal and forest ca. 2 km east, *J. L. Clark et al.* 2487 (US); Bolívar: Hcda. Changuil, Nuevo Mundo, bosque muy humedo tropical, nublado, *X. Cornejo & C. Bonifaz* 4591 (US); Cañar: La Troncal, Manta Real, tropical wet forest, mixture of mature forest, cacao plantation, and cow pasture, *J. L. Clark et al.* 1588 (US, MO); Manabí: Manta, bosque seco tropical, area de bosque comunal, *C. Espinoza* 58 (MO); San Sebastian, Machalilla National Park, ridge-top moist forest, *A. Gentry et al.* 72571 (MO); *A. Gentry et al.* 72578 (MO); Pichincha: ca. 35 km N of Santo Domingo de los Colorados, vicinity of bridge over Río Blanco, *A. Gentry* 9625 (MO).

10. COLUMNEA ORIENTANDINA (Wiehler) L. P. Kvist and L. E. Skog, *Allertonia* 6: 392. 1993. *Pentadenia orientandina* Wiehler, *Selbyana* 2: 123. 1977.—TYPE: [ECUADOR.] cultivated material, grown from cuttings (*Madison & Coleman* 2532, collected in the Cordillera de Cutucu, Morona-Santiago), 20 July 1977, *H. Wiehler* 77123 (holotype: SEL; isotype: US).

A relatively compact habit, laminae with a blunt red apex and a dorsiventral arrangement, and yellow corollas distinguish *C. orientandina* from other species of *Columnnea*. *Columnnea orientandina* is most closely related to *C. byrsina* (Fig. 2) both of which may have bright red corollas and dorsiventrally arranged leaves. The exerted anthers and stigma are also distinguishing characteristics of *C. orientandina*, but they are not always present in pressed specimens (Smith 1994).

**Phenology**—Flowering occurs continuously.

**Distribution**—This species is known from Ecuador (Morona-Santiago) and Peru (Cusco, Pasco, and San Martín), between 1,000–1,500 m (Fig. 5).

**Climate**—The annual mean temperature for *Columnnea orientandina* is 21.52° with an annual average range of 12.61° between warmest and coldest days, and average precipitation of 2,720 mm.

**Additional Specimens Examined**—ECUADOR. Morona-Santiago: collected outside city limits of General Leonidas Plaza Gutiérrez (Limón), *J. L. Clark* 6264 (US); Gualaquiza, Cordillera del Condor, vertiente occidental de la Cordillera del Condor, arriba del valle del Río Quimi, *G. Pabon & J. Cavanqui* 309 (MO); Macas, garden around Hotel el Valle, *L. P. Kvist* 60424 (US, MO); N of Macas, on border to Sangay National Park, *L. P. Kvist* 60439 (US, MO); San Juan Bosco, road between San Juan Bosco and El Pangui, 27 km S of San Juan Bosco, *J. L. Clark* 9924 (US); San Juan Bosco, road between San Juan Bosco and El Pangui, 2–3 km S of San Juan Bosco, *J. L. Clark* 9885 (US); Pastaza: Canton Puyo, Parroquia Veracruz, La Esperanza (Siguin), Finca Salina (de Hilda Perez), km 14 on the Puyo-Macas road, *J. L. Clark & J. Katzenstein* 8294 (US); Pastaza Canton, km 17 del propuesto oleoducto ARCO-Villano-El Triunfo, *W. Palacios* 12088 (MO); Tungurahua: Canton Baños, small path of forest on north side of main highway between Baños and Puyo, 3–5 km east of El Topo, *J. L. Clark & J. Katzenstein* 8282 (US, MO); Zamora-Chinchipec: El Pangui, Cordillera del Condor, Valle del Río Quimi, bosque alterado y potreros, en suelo aluvial del val, *T. Montenegro* 142 (MO); Los Encuentros, Estación Experimental El Padmi (Universidad de Loja), located on the northern outskirts of the town El Padmi, *J. L. Clark* 9949 (US); Zamora Canton, Jamboe Bajo, eastern border of Podocarpus National Park, mature forest near cow pasture, *J. L. Clark et al.* 3203 (US).

PERU. Cusco: Quispicanchis, hills around Río Araza between Pande Azucar and Quince Mil airport, forests 292 km from Cusco, *P. Nuñez V.* 14090 (MO); San Martín: Prov. Rioja, Dist. Pardo Miguel, El Afluente y la Marginal, *I. Sanchez Vega & M. Dillon* 9023 (US).

11. COLUMNEA OVATIFOLIA L. P. Kvist and L. E. Skog, *Allertonia* 6: 393. 1993.—TYPE: ECUADOR. Carchi: rd Tulcán-Maldonado, 10 km SE of Maldonado, Campamento Machines, 28 Nov 1974, *Harling and Andersson* 12316 (holotype: GB; isotype: SEL).

*Columnnea ovatifolia* is most closely related to *C. crassicaulis*, *C. katzensteiniae*, and *C. rileyi* (Fig. 3). All four of these species, along with *C. antiocana* have dark spots on the interior surface of the corolla lobes. *Columnnea ovatifolia* can be distinguished from these species and other species of *Columnnea* by its smaller leaves, pink-purple corolla, and thinner stem (Smith 1994).

**Phenology**—Flowering occurs from January to May.

**Distribution**—This species is known from northern Ecuador in cloud forests between 1,900–2,800 m (Fig. 7).

**Climate**—The annual mean temperature for *Columnnea ovatifolia* is 14.37° with an annual average range of 12.75° between warmest and coldest days, and average precipitation of 1,586 mm.

**Additional Specimens Examined**—ECUADOR. Carchi: Canton Espejo, Parroquia Guatal, Mirador de las Golondrinas (Fundacion Golondrinas), trail from El Corazon toward La Cortadera (2 km NE of refugio), *J. L. Clark & E. Folleco* 8461 (US); Cotopaxi: Canton Sigchos, bosque al lado izquierdo de via Sigchos-Las Pampas, *J. Ramos et al.* 7188 (US, MO); Canton Sigchos, orillas del Río Los Illinizas, dentro del bosque, *J. Ramos et al.* 6025 (US); Canton Sigchos, Parroquia San Francisco de las Pampas, bosque Integral Otonga, *J. L. Clark & A. Muñoz* 6129 (US); Canton Sigchos, Triunfo Grande, bosque al N de carretera, ca. 2 horas de casa de Galo Roballo, loma La Delicia, *J. Ramos et al.* 7003 (US, MO); Pichincha: Route Tandayapa-Nanegalito, *F. Billiet & B. Jadin* 6687 (MO).

12. COLUMNEA RILEYI (Wiehler) J. F. Smith, *Pentadenia rileyi* Wiehler, *Phytologia* 73: 236. 1992.—TYPE: ECUADOR. Napo: 37 km from Baeza on rd to Lago Agrio, 24 Apr 1986, *H. Wiehler and GRF Expedition* 86243 (holotype: GES; isotypes: F, K, MO, NY, QCA, SEL, U, US).

*Columnnea leucericina* L. P. Kvist and L. E. Skog, *Allertonia* 6: 389. 1993.—TYPE: ECUADOR. Napo: Lago Agrio-Baeza rd, km 145, Río Aya Cachi, 8 Jan 1987, *L. P. Kvist et al.* 60377 (holotype: AAU; isotypes: COL, MO, NY, QCA, QCNE, US).

Phylogenetic analyses place *C. rileyi* as sister to *C. katzensteiniae* (Fig. 3). *Columnnea rileyi* has a dense white pubescence covering the entire plant body, which distinguishes it from other species of *Columnnea*. *Columnnea lophophora* has a similar pubescence; however, the small orange-yellow corolla of *C. rileyi* easily separates these two species (Smith 1994).

**Phenology**—Flowering occurs continuously.

**Distribution**—This species is known from northern and western Ecuador in wet forests between 1,200–2,000 m (Fig. 7).

**Climate**—The annual mean temperature for *Columnnea rileyi* is 18.42° with an annual average range of 12.16° between warmest and coldest days, and average precipitation of 2,591 mm.

**Additional Specimens Examined**—ECUADOR. Cotopaxi: Canton Sigchos, Parroquia San Francisco de las Pampas, collections made along trail near entrance of Bosque Integral Otonga, *J. L. Clark & A. Muñoz* 6099 (US, MO); Canton Sigchos, Parroquia San Francisco de las Pampas, propiedad de Cesar Tapia, *J. L. Clark et al.* 6180 (US); Nanegalito area, *H. Wiehler* 97176 (US); Napo: along road between main Baeza-Lago Agrio Hwy. and village of Gonzalo Diaz de Pineda on road to Parque Nacional Sumaco Napo Galeras, Sector Gonzales Diaz de Pineda, 0.6 km from main highway, between main highway and bridge over Río Quijos, *T. B. Croat & L. Hamnon* 93495 (US); along road from Baeza to El Chaco, vic. Río Sardinas Grande, along Río Quijos, disturbed area along swampy pasture, 6 km NNE of San Francisco Borja, *T. B. Croat et al.* 87690 (US); Río Panteor SW of Borja, montane forest and rocky outcrops, *L. Holm-Nielsen et al.* 26744 (US); union of Río Borja and Río Quijos, E bank, wet riverside forest, never inundated, *L. Holm-Nielsen et al.* 26229 (US); Pichincha: Canton Quito, Parroquia Nanegalito, Finca Kayalami, south of Cartegena, 2–3 air-km SE of Nanegalito, *J. L. Clark et al.* 7077 (US, MO).

13. *COLUMNNEA SPATHULATA* Mansfeld, Notizbl. Gard. Berlin-Dahlem 14(121): 37. 1938. *Pentadenia spathulata* (Mansfeld) Wiehler, Phytologia 27: 315. 1973.—TYPE: ECUADOR. Pinchincha: Santo Domingo de los Colorados, *Schultze-Rhnhof 1876* (holotype: B, destroyed). NEOTYPE—ECUADOR. Pichincha: Santo Domingo de los Colorados, Centinella, Montanas de Ila, 12 km from Patricia Pilar, 575 m, 10 Jul 1979. *Lojtnant and Molau 15811* (neotype, designated by Kvist and Skog 1993: AAU; isoneotype: US).

*Alloplectus microsepalus* C. V. Morton, Fieldiana, Bot. 28: 523. 1953. *Pentadenia microsepala* (C. V. Morton) Wiehler, Phytologia 27: 375. 1973. *Columnnea microsepala* (C. V. Morton) L. P. Kvist and L. E. Skog, Allertonia 6: 391. 1993.—TYPE: VENEZUELA. Monagas: Cerro de la Cueva de Dona Anita, S of and bordering valley of Caripe, 1,100–1,200 m, 7 Apr 1945, *J. A. Steyermark 61905* (holotype: F; isotype: US).

*Pentadenia zapotalana* Wiehler, Selbyana 2: 85, pl 26B. 1977. *Columnnea zapotalana* (Wiehler) L. E. Skog, Taxon 33: 126. 1984.—TYPE: ECUADOR. Los Ríos: 20 km S of Quevedo, *H. Wiehler et al. 71312* (holotype: SEL; isotype: US).

Similar to *C. angustata*, *C. spathulata* is a widely distributed species covering most of the range of section *Angustiflorae*. The specimens of *C. spathulata* have variable morphological characteristics including leaf coloration, corolla color, and the number of flowers per axil, most likely as a result of selection in a wide range of habitats that span its distribution. *Columnnea spathulata* can be distinguished by strongly anisophyllous leaves in combination with a crenate laminar margin and a dense inflorescence (Smith 1994).

**Phenology**—Flowering and fruiting occurs continuously throughout most of its range, but is restricted to July to April in Venezuela.

**Distribution**—This species occurs from Venezuela to Bolivia in cloud forest, wet forest, and in disturbed areas, such as *Citrus* plantations between 40–2,800 m (Fig. 8).

**Climate**—The annual mean temperature for *Columnnea spathulata* is 22.23° with an annual average range of 11.50° between warmest and coldest days, and average precipitation of 1,927 mm.

**Additional Specimens Examined**—BOLIVIA. La Paz: Nor Yungas, Coroico, valle del Río Huarinilla, +/- 3 km abajo de Chairo, Yucupi, L. S. G. Beck 21427 (US).

ECUADOR. Azuay: Cuenca, road from Cuenca to Guayaquil (via Molleturo/El Cajas), San Jose de Molleturo, trail from road leading South through small patches of primary forest, *J. L. Clark 9823* (US); Río Patul, collection made along path from El Cajas to Manta Real following Río Patul (2–3 d trek), *J. L. Clark et al. 6256* (US); Bolívar: Hcda. Changuil, en potrero, bosque muy humedo tropical, nublado, *X. Cornejo & C. Bonifaz 4532* (US); Carchi: Espejo, Bosque Protector Mirador de Golondrinas, collections made between the village, Las Juntas, and la Cabana del Corazon, lower montane wet forest, *J. L. Clark et al. 2420* (US); 5 km above Lita (Colonia) along open road & by small creeks, *H. Wiehler 9042* (SEL, US); Cotopaxi: km 5 to km 15 above La Mana, *H. Wiehler 9775* (SEL, US); foothills above Valencia near cane mill, *M. E. Mathias & D. Taylor 5180* (US); 3 km E of El Palmar on road Quevedo-Latacunga, *C. H. Dodson & A. Gentry 10242* (SEL); El Oro: along road from Loja to Santa Rosa ca. 20 km past Pinas, below cloud forest at edge of road cut, *H. Wiehler 8649* (SEL, US); along the new road west of Pinas, *C. Luer et al. 5555* (SEL); Canton Pinas, Parroquia Moromoro, Reserva Ecológica Buenaventura, remnant patch of forest S of "Entrada la Virgin," *J. L. Clark et al. 7958* (SEL, US), *J. L. Clark et al. 7957* (SEL, US); road Loja-Santa Rosa, ca. 20 km past Pinas, *H. Wiehler & GRF Expedition 8648* (SEL); 10 km west of Pinas along new road from Pinas - Machala, *C. H. Dodson et al.*

*8463* (SEL); Zaruma, Cerro El Calvario, bosque transicional seco-humedo montano, *C. Bonifaz & X. Cornejo 3678* (US); Esmeraldas: along road from Lita, *H. Wiehler 9074* (SEL, US); Bilsa Biological Station, N and NE border cut in NE part, then to Cube River tributary, then Invader Trail to Dogala Trail, *P. Mendoza-T. et al. 591* (US); Canton San Lorenzo, Parroquia Alto Tambo, Comunidad El Cristal, 8–10 km S of San Lorenzo-Ibarra highway, *J. L. Clark et al. 7532* (US); environs of Lita, on the Ibarra-San Lorenzo, *M. T. Madison et al. 4991* (SEL); Canton San Lorenzo, Parroquia Alto Tambo, small patch of forest between Lita and Alto Tambo, *J. L. Clark et al. 7482* (SEL, US); Canton Quininde, Bilsa Biological Reserve, Reserva Ecológica Mache-Chindul, 35 km W of Quininde, *J. L. Clark et al. 8777* (US); Canton Quininde, Bilsa Biological Reserve, Reserva Ecológica Mache-Chindul, 35 km W of Quininde, trail from SW border of reserve to Don Bolívar's home (trail connecting the road toward Piedrita and the road toward Mono), *J. L. Clark et al. 8827* (US); 1 km W of Santa Isabel, toward Bilsa Biological Station, along logging road, *P. Mendoza-T. et al. 598* (US); Quininde Canton, Bilsa Biological Station, Reserva Ecológica Mache-Chindul, 35 km W of Quininde, permanent plot #3, *J. L. Clark 4644* (US); Quininde Canton, Reserva Ecológica Mache-Chindul, Comunidad Cana Bravel, Cabaceras del Río Viche, estero Sabaleta, *J. L. Clark 4711* (US); Quininde, Community Piedrita, 10 km SW of Cube (via pircuta), *J. L. Clark et al. 2823* (US); Quininde, Fundación Paraiso de Papagayos, Centro de Rescate de Aves y Mamíferos, km 2 via Esmeraldas, *J. L. Clark et al. 2793* (US); Quininde, Reserva Ecológica Mache-Chindul, 35 km W of Quininde, The Bilsa Biological Station, Cordillera Mache-Chindul, Sendero Café to Río Cube and then to Río Piscina to vivero near main Bilsa cabin, *J. L. Clark 9768* (US); Guayas: Cord. Chongon-Colonche, Bosque Protector Loma Alta, *X. Cornejo & C. Bonifaz 5716* (US); Cord. Chongon-Colonche, Bosque Protector Loma Alta, *X. Cornejo & C. Bonifaz 6650* (US); La Crucita, Cuenca Río Ayampe, bosque transicional seco-humedo tropical, *X. Cornejo & C. Bonifaz 939* (US); Imbabura: along road from Ibarra to Lita, 5 km W of Lita, *H. Wiehler 9503* (SEL, US); Canton Cotacachi, Parroquia Garcia Moreno, Cordillera de Toisan, Cerro de la Plata, Bosque Protector Los Cedros, main trail from the comunidad El Chontal to Los Cedros, *J. L. Clark et al. 7368* (SEL, US); Canton Ibarra, Parroquia Lita, Comunidad San Francisco, next to Río Verde (13 air-km S of Lita), *J. L. Clark et al. 7530* (SEL, US), *J. L. Clark et al. 7485* (SEL, US); Los Ríos: Centinela Ridge area, 12.5 km E of Patricia Pilar, *B. Hansen et al. 7774* (SEL); Centinela ridge, ca. 20 km E of Patricio Pilar, cultivated land with scattered thickets, *H. Van der Werff et al. 12386* (US); mature forest across Río Palenque from biological station following road along river after crossing Río Bimbo and Río Waija, *A. Gentry & C. H. Dodson 18027* (MO); 9 km E of (11 km by road from) Patricia Pilar (1 km to the E of Escuela Centrinelas, a minute settlement) 58 km ENE of Quevedo, on Pan-Am highway to Santo Domingo de los Colorados, *H. H. Iltis & M. G. Iltis 59* (WIS); Manabí: Barbasmonte, Cuenca Río Ayampe, bosque transicional-humedo, *X. Cornejo & C. Bonifaz 1011* (US); Canton Pedernales, Cerro Pata de Pajaro, 10 km E of Pedernales, finca of the family Aroyo, *J. L. Clark et al. 2700* (US); Jama, 28 km S of Pedernales (as the crow flies), 3.5 km SW of the town Camarones, remnant tropical fog forest, off trail NW of Pertextaxto Gutierrez's house, *T. Delinks 504* (US); Manta, bosque seco tropical, area de bosque comunal, *C. Espinoza 58* (US); Naranja, north of Pajan, *O. Huaght 3408* (US); Pedernales Canton, Reserva Ecológica Mache-Chindul, Comunidad Ambache (via marginal de la costa-Chindul), *J. L. Clark et al. 4143* (US); Morona-Santiago: Canton Tiwintza, Parroquia Santiago, Cordillera Winchinkiaim Naint #19, south of Centro Shuar Kusumas, ridge and border between Ecuador and Peru, *J. L. Clark et al. 9268* (US); Pichincha: along old road between new Santo Domingo-Quito road and Chiriboga, *P. Mendoza-T. et al. 615* (US); along Río Toachi, below Tinalandia, on both sides of river, *H. Wiehler 7972* (SEL, US); along road from Quevedo to Latacunga, along western slope, *H. Wiehler 79133* (SEL, US); along trail between Guayabillas and Pachijal, ca. 1 km from Pachijal, *P. Mendoza-T. et al. 549* (US); between km 104 on Quito-Esmeraldas Road and Pachijal, *P. Mendoza-T. et al. 530* (US); between Puerto Quito and Pedro Vicente Maldonado, in creek area, *H. Wiehler 90112* (SEL, US); bridge over Río Chiguilpe near junction with Río Baba, 7 km from junction of entrance and road from Sto Domingo to Quevedo at km 7, *C. H. Dodson 5944* (SEL); Canton Santo Domingo, Parroquia Allurquin, La Union del Toachi, cow pasture with remnant patches of primary forest, *J. L. Clark & A. Muñoz 6098* (US); 5 km S of Santo Domingo at Hacienda San Fernando, *B. Hansen et al. 7850* (SEL); Montañas de Ila, sub-cloud forest, exposure toward the Pacific, *H. Wiehler 9082* (SEL, US); Santo Domingo de los Colorados, *A. Gilli 116* (W); *F. Fagerlind & G. Wibom 1657* (OV, S); Santo Domingo de los Colorados, Tinalandia resort, *R. W. Dunn 95-04-135* (US); 35 km N

of Santo Domingo de los Colorados, vicinity of bridge over Río Blanco, *A. Gentry* 9625 (US); 7 km S of Santo Domingo, along Río Chiguilpe *H. Wiehler* 79365 (SEL, US); Zamora-Chinchi: Chiguango, about 70 km west of Loja, *R. Espinosa* 1216 (SEL).

VENEZUELA. Aragua: Rancho Grande, Paraiso trail, *H. Wiehler* 72378 (SEL, US); Miranda, limite Municipio Baruta/Municipio El Hatillo, Cerro El Volcan, sureste de Caracas, entre Baruta y El Hatillo, a lo largo de la carretera que sigue hacia las antenas, arbustales y herbazales secundarios, *W. Meier* 12912 (US); Miranda: Distrito Urdaneta, Cordillera de la Costa, Serranía del Interior, Macizo del Golfo Triste, subida al macizo entre la Quebrada La Providencia y la Fila Las Yaguas, bosque, *W. Meier & S. Nehlin* 10188 (US); Monagas: bosque siempre verde, Quebrada Pajal, 3 km al E de escuela rural El Aguacate, 11.2 km al E del puente sobre el Río Colorado, Cuenca del Río Caripe, al E de Caripe, via Las Margaritas, *F. A. Michelangeli & M. Alfor* 613 (US); Distrito Caripe, Cordillera de la Costa, 10 km al este de Caripe (distancia aerea), Quebrada Grande, propiedad de Rolf Struppek, bosque nublado, *W. Meier & R. Struppek* 13461 (US); Distrito Caripe, Parque Nacional Guacharo, Cordillera de la Costa, 12.5 km al noroeste de Caripe (distancia aerea), Alto El Silencio, vertiente norte, conucos alternado con remanentes de bosque, *W. Meier & R. Struppek* 10464 (US); Municipio Caripe, parroquia Teresen, sector Quebrada Grande, Cordillera de la Costa, 10 km al este de Caripe (distancia aerea), parte oriental de la propiedad de Rolf Struppek, zona de cultivos, *W. Meier & R. Struppek* 10868 (US). Sucre: Distrito Benitez, Peninsula de Paria, al sureste de Carupano, Cerro La Cerbatana, antiguo camino desde carretera Maturincito-refugio hacia el caserío San Juan: bosque nublado, *W. Meier et al.* 14354 (US); limite Distritos Arismendi/Bermudez/Benitez Peninsula de Paria, al sureste de Carupano, al noreste de Maturincito, Cerro Cerbatana: bosque nublado perturbado, *W. Meier & P. Molina* 6790 (US); limite Distritos Bermudez/Benitez, Peninsula de Paria, al sureste de Carupano, Cerro La Cerbatana, carretera Maturincito-refugio: montana al este de Maturincito con estación sismica de FUNVISIS, remnente de bosque nublado al sur de carretera, *W. Meier & C. Mentel* 11860 (US); Yaracuy: Cumbre Gamelatal, 4.3–11 km N of Salom on road from Salom to Candelaria, *S. Mori et al.* 14658 (US); Distrito Nirgua, Serranía Santa Maria-Cerro La Chapa, 6 km al norte de Nirgua, en selva nublada on *Iriartea fusca*, *W. Meier & M. Roeser* 1006 (US); Distrito Nirgua y Distrito San Felipe, Serranía Santa Maria-Cerro La Chapa, en la cumbre al este de la pica Nirgua-Las Marias, en selva nublado con *Iriartea fusca*, *W. Meier* 3231 (US); Distrito Nirgua/Distrito San Felipe Serranía Santa Maria, al norte de Nirgua, Cerro La Chapa, bosque nublado en la cumbre con *Dictyocaryum fuscum* como palma emergente y areas intervenidas, *W. Meier et al.* 8467 (US); limites Distrito Nirgua-Distrito San Felipe Cerro La Chapa, ca. 5 km al norte de Nirgua, fila de la montaña al este de la pica Nirgua-Las Maria, pastos de ganado, *W. Meier et al.* 7790 (US).

14. *COLUMNEA TANDAPIANA* (Wiehler) L. E. Skog and L. P. Kvist, *Novon* 7: 414. 1997[1998]. *Pentadenia tandapiana* Wiehler, *Phytologia* 73: 238. 1992.—TYPE: ECUADOR. Pichincha: 7 km from San Miguel de los Bancos on road to Mindo, 30 Apr. 1990, *H. Wiehler & GRF Expedition 90133* (holotype: GES, isotypes: QCA, US).

*Columnea inconspicua* L. P. Kvist and L. E. Skog, *Allertonia* 6: 385. 1993.—TYPE: ECUADOR. Pichincha: Tandapi, confluence between Río Tandapi with Río Pilaton, 1,500 m, 27 Jul 1967, *Sparre* 17761 (holotype: S).

*Columnea tandapiana* is most closely related to *C. manabiana* (Fig. 3). The two species share character states of lanceolate and slightly falcate leaves, small inconspicuous pale yellow corollas, and narrow calyx lobes. However, *C. tandapiana* can be distinguished from *C. manabiana* by caducous floral bracts (Smith 1994).

**Phenology**—Flowering occurs continuously.

**Distribution**—This species is endemic to Ecuador in wet forests between 1,200–1,950 m (Fig. 7).

**Climate**—The annual mean temperature for *Columnea tandapiana* is 18.46° with an annual average range of 11.58° between warmest and coldest days, and average precipitation of 2,333 mm.

**Additional Specimens Examined**—Ecuador. Azuay: dense, rich jungle between Río Blanco and Río Norcay on road between Chacanceo and Molleturo, *J. A. Steyermark* 52825 (US); Cotopaxi: Canton Pujili, Reserva Ecológica Los Ilinizas, Sector II (Sector Sur), sector Chuspitambo, al occidente de Choasilli, Cordillera Occidental, vertiente occidental, bosque nublado primario y arboles aislados en potrero, *P. Silverstone-Sopkin et al.* 9967 (US); Canton Sigchos, Parroquia San Francisco de las Pampas, Bosque Integral Otonga, *J. L. Clark & A. Muñoz* 6106 (SEL, US); *J. L. Clark et al.* 6168 (US); Canton Sigchos, Parroquia San Francisco de las Pampas, propiedad de Cesar Tapia, *J. L. Clark et al.* 6181 (US); Nanegalito area, *H. Wiehler* 97171 (SEL, US); trail from El Corazon to Facundo Vela, 1–3 km S of El Corazon, remnants of montane rain forest and secondary scrub, *G. Harling & L. Andersson* 19225 (US); El Oro: Canton Pinas, buffer zone/border region of Reserva Ecológica Buenaventura, 11 km (air-km) north of the “Entrada la Virgen” on road toward Viron, *J. L. Clark* 8006 (SEL, US); Morona-Santiago: Cordillera de Cutucu, western slopes, along a trail from Logrono to Yaupi, *M. Madison et al.* 3370 (SEL); Pichincha: along road near Nanegal, in pasture land or small forest remnants, *H. Van der Werff et al.* 12298 (US, MO); Canton Quito, Parroquia Nanegalito, Finca Kayalami, south of Cartegena, 2–3 air-km SE of Nanegalito, *J. L. Clark et al.* 7076 (US, MO); 7 km from San Miguel de los Bancos on road to Mindo, on tree in meadow along roadside, *H. Wiehler & GRF Expedition 90133* (SEL); Tandapi forest, on south side of Río Pilaton, after crossing bridge, *H. Wiehler & D. Masterson* 7954 (SEL, US).

15. *COLUMNEA ULEI* Mansf., *Fedde Repert.* 38: 26. 1935. *Trichantha ulei* (Mansf.) Wiehler, *Selbyana* 1:35. 1975.—TYPE: BRAZIL. Ceará, Oct. 1910, *E. Ule* 9109 (holotype: B, destroyed, lectotype, here designated: US; isotypes: G, K, L).

Epiphytic herb, stems to 30 cm, up to 7.5 mm diameter, red-brown, proximally glabrous, distally appressed pilose with multicellular transparent trichomes; internodes 0.3–3.1 cm long; leaf scars raised. Leaves opposite, clustered at stem apex, subequal, lamina 1.9–6.0 cm long, 8.5–22.0 mm wide, elliptic, apex blunt to acute, base cuneate, lateral veins 2 per side, adaxially green, appressed pilose with short multicellular transparent trichomes, abaxially green, appressed pilose with multicellular transparent trichomes, denser on veins, margin entire; petioles 3.0–6.0 mm long, appressed pilose with multicellular transparent trichomes. Inflorescence of 1–2 flowers per axil of leaf; bracts 4.0 mm long, 1.0 mm wide, linear, apex acute, green, pilose with multicellular yellow trichomes. Pedicels 3.0–12.0 mm long, green, appressed pilose with multicellular transparent trichomes. Calyx loosely clasping corolla, lobes 7.5–13.0 mm long, 1.2–3.0 mm wide, lanceolate, apex acute, interior appressed pilose with multicellular transparent trichomes, exterior pilose with multicellular transparent trichomes, exterior green, apex red on interior; margin entire with a few teeth at base. Corolla 2.8–3.7 mm long, 3.5–5.0 mm wide at widest point, 4.0–4.5 mm before limb, 1.5–1.8 mm wide at constriction before gibbous base, tubular, slightly ventricose, red, exterior pilose with multicellular red trichomes, interior glabrous at base with stalked glandular trichomes on distal half; limb 4.5–9.0 mm in diameter, lobes semi-orbicular, upper lobes more or less galeate, 1.5–2.5 mm long, 1.5–2.0 mm wide, red. Filaments connate 3.5 mm and adnate to corolla 0.3 mm, glabrous, with a few short trichomes at base, anthers 1.0 mm long, 1.0 mm wide, quadrangular, included in corolla tube to just exceeding corolla opening. Ovary 3.5 mm long, conical, pilose with multicellular transparent trichomes, style red, glabrous, with a few short multicellular red and glandular stalked trichomes on distal fourth, stigma bilobed, papillate included in corolla tube. Nectary a dorsal double gland. Fruit a globose berry, 8.0–9.0 mm long, 8.0 mm wide, pilose

with short multicellular transparent trichomes, possibly red. Seeds not seen.

**Phenology**—Flowering specimens seen from October, fruits seen in September.

**Distribution**—This species is a rare endemic from Brazil.

*Columnea ulei* is morphologically nearly identical to *C. angustata*. The phylogenetic analysis strongly supports a close relationship between the two species, but has poor support for relationships among the individuals sampled in this analysis. These results still leave open the possibility that *C. angustata* and *C. ulei* are sister species, or possibly conspecific. However, given that the SH tests cannot reject a sister relationship of *C. ulei* from the remaining accessions indicates that the molecular data are weak and that *C. angustata* could still be monophyletic exclusive of *C. ulei*. Morphologically the accessions are similar and few accessions have been available for study, indicating that future studies may uncover more morphological characters. One photo of a live plant from Brazil (Souza and Lorenzi 2012) shows that the restriction toward the limb (Fig. 2) is not as pronounced, although this restriction was observed in two pressed specimens. Lastly, the placement of *C. ulei* within *C. angustata* creates a wide disjunction within a species. Such disjunctions are rare in Gesneriaceae. Therefore we are keeping these two species distinct at present until further data can provide more support for the synonymization of *C. ulei* into *C. angustata*.

**Additional Specimens Examined**—BRAZIL. Ceará, Baturité, Pico Alto, 19.II.200 (HPL 2978), *H. Lorenzi* 3160 (note, material from this voucher was grown at the Botanical Garden in Geneva and the material used in the molecular study was from the cultivated specimen, vouchered as *A. Chautems & M. Perret* 10109 [G]).

**Unsampled Species**—Although this study includes increased taxon sampling, there are still some species of *Stygnanthe* sensu Smith (1994) that need to be analyzed using molecular data to determine their placement within *Columnea*. Smith (1994) had placed three other species, *C. antiocana*, *C. fritschii*, and *C. suffruticosa*, in section *Stygnanthe*. Due to difficulties in obtaining DNA from herbarium specimens and the rarity of these species in the field, we were unable to obtain complete DNA sequence data for these three species although material of *C. suffruticosa* arrived while an earlier version of this manuscript was in review, allowing us to generate at least some of the sequences used in this paper to place it in a clade. Although no previous subgeneric classification system in *Columnea* based on morphology matches the phylogenetic results recovered here and in Smith et al. (2013), we are now better able to evaluate which characters and character states represent evolutionary homology, and we can now use morphology to make predictions regarding the classification of these unsampled species.

Based on morphological characters, *Columnea antiocana* is most likely a member of section *Angustiflorae*. *Columnea antiocana* has similar morphological features to *C. katzensteiniae*,

*C. rileyi*, *C. crassicaulis*, and *C. ovatifolia*, including a similar ovate to lanceolate or elliptic leaf shape with an oblique base and the presence of darker colored lobe spots on the interior surface of the corolla that are transparent on the exterior surface (Fig. 1A). Smith (1994), erroneously reported the lobe spots described above as as limited to the exterior surface in *C. katzensteiniae* (1994; as *C. lavandulacea*), which are actually on the interior surface and transparent on the exterior surface (Fig. 1A). The presence of dark spotting on the corolla lobes is not a unique morphological character since such spots are also known in *C. moesta*, *C. ultraviolacea*, *C. fritschii*, and *C. xiphoidea*. These latter four species are all evolutionarily divergent from species of section *Angustiflorae*, but had been considered members of section *Stygnanthe* along with the species currently ascribed to *Angustiflorae* by Smith (1994) in large part because of the presence of the corolla lobe spots. However, the other features of the corolla, such as proportionally larger corolla lobe to tube length and sparse vesture suggest the placement of *C. antiocana* within *Angustiflorae* and the lobe spots would place it specifically among the *C. crassicaulis/C. rileyi* clade. *Columnea suffruticosa* also has darker lobe spots on the interior surface of the corolla as well as proportionally larger corolla lobe to tube length and sparse vesture, which would suggest it is closely related to the same species as *C. antiocana*. However, Smith and Sytsma's (1994a) phylogenetic study placed *C. suffruticosa* with *C. colombiana* based on morphological characters not taking into account the presence of interior corolla lobe spots. In either case, sequences of ITS and *rps16* intron from *C. suffruticosa* place this species in clade D (Fig. 3; unpublished results) apart from either clade *Stygnanthe* or section *Angustiflorae*.

The morphological characters of *Columnea fritschii* suggest that it belongs in clade *Stygnanthe* as sister to *C. ultraviolacea*. *Columnea fritschii* and *C. ultraviolacea* are the only species of *Columnea* that have whorled leaves (Smith 1994). Both species are only known from a small area in Bolivia, where they occur within the same mountain range. Likewise, they are among the four species in clade *Stygnanthe* to have corolla lobe spots on the interior surface and a dense vesture on the exterior of the corolla tube, along with *C. moesta* and *C. ultraviolacea*. A cladistic analysis based on morphological characters (Smith and Sytsma 1994a) suggests the same relationship.

Another undescribed species of *Columnea* may be placed within clade *Stygnanthe* based on morphological characters. *Columnea* sp. nov. (*R. Ferreyra* 351) is only known from a single collection in Peru that is deposited at MO. This specimen is a sublignose, terrestrial herb with opposite, slightly anisophyllous leaves, and limb spots on the interior surface of the corolla. The species has a dense pilose corolla distinguishing it from species of *Angustiflorae* (Fig. 1) and suggesting that it belongs in clade *Stygnanthe*.

#### KEY TO THE SPECIES OF SECTION *ANGUSTIFLORAE*

1. Leaves lanceolate or oblanceolate and strongly anisophyllous ..... 2
2. Corolla bright red with lemon-yellow limb ..... *C. brysiina*
2. Corolla yellow to cream, orange, or red, but always with limb of same color ..... 3
3. Leaf margin crenate to crenulate ..... 4
4. Calyx lobe margin entire; plants of Central or South America ..... *C. spathulata*
4. Calyx lobe margin lacinate; plants of Hispaniola ..... *C. domingensis*
3. Leaf margin entire to undulate ..... 5

5. Leaf apex obtuse ..... *C. orientandina*
5. Leaf apex acute to acuminate ..... 6
6. Floral bracts large (1.0–2.0 cm long) ..... *C. manabiana*
6. Floral bracts small (0.5 cm long) ..... *C. tandapiana*
1. Leaf shape otherwise and slightly to not anisophyllous ..... 7
7. Leaves, stem, and calyx covered with dense white indumentum ..... *C. rileyi*
7. Leaves, stem, and calyx pubescent or glabrescent, but not dense and white ..... 8
8. Calyx lobe margin serrate, coarsely toothed, serrate to dissected at base, or lacinate ..... 9
9. Corolla red-purple with yellow-green limb ..... *C. colombiana*
9. Corolla red, orange or yellow, but with limb of same color ..... 10
10. Calyx lobe margin coarsely toothed; plants of Puerto Rico ..... *C. ambigua*
10. Calyx lobe margin serrate at base to lacinate ..... 11
11. Calyx lobe margin lacinate; plants of Hispaniola ..... *C. domingensis*
11. Calyx lobe margin serrate at base; plants of Central and South America ..... 12
12. Plants from Brazil ..... *C. ulei*
12. Plants not from Brazil ..... *C. angustata*
8. Calyx lobe margin entire ..... 13
13. Corolla red with red limb ..... *C. antiocana*
13. Corolla yellow, red, pink to red-violet, lavender, but always with contrasting limb color ..... 14
14. Corolla lemon-yellow with green limbs ..... *C. crassicaulis*
14. Corolla red, pink to red-violet or lavender with contrasting limb color ..... 15
15. Corolla less than 3.0 cm long ..... *C. katzensteinae*
15. Corolla greater than 4.0 cm long ..... *C. ovatifolia*

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APPENDIX 1. Species, voucher specimens, and GenBank accession numbers for all accessions included in phylogenetic analyses. Accessions newly sequenced for this study are in bold. Data are presented in the order of species, voucher, herbarium, locality, and GenBank numbers for: rpl32-trnL<sub>UAG</sub> spacer, trnQ-rps16 intron, rps16 intron, trnS-G spacer, trnH-psbA spacer, and ITS.

*Alloplectus hispidus* (Kunth.) Mart. ECUADOR. J. L. Clark 7720 (US), KF005812, KF006030, KF005921, JQ953700, DQ211219, DQ211111.

*Columnea albiflora* L. P. Kvist & L. E. Skog. ECUADOR. J. L. Clark and J. Rea 8015 (UNA), KF005813, KF006031, KF005922, KF006135, KF005640, KF005725. *C. ambigua* (Urb.) B. D. Morley. cultivated, originally PUERTO RICO. J. Smith 3701 (SRP), KF005814, KF006032, KF005923, JQ953713, KF005641, JQ953789. *C. angustata* (Wiehler) L. E. Skog. COLOMBIA. Amaya M. and J. Smith 625 (COL), KF554345, KF554365, KF554385, KF554404, KF554304, KF554324. *C. angustata* (Wiehler) L. E. Skog. COLOMBIA. J. Smith 1433 (WIS), KF005815, KF006033, KF005924, KF006136, KF005642, KF005726; PANAMA. J. L. Clark 8627 (UNA), KF005816, KF006034, KF005925, KF006137, NA, KF005727. *C. angustata* (Wiehler) L. E. Skog. ECUADOR. J. L. Clark et al. 9373 (US), KF554346, KF554366, KF554386, KF554406, KF554305, KF554325. *C. angustata* (Wiehler) L. E. Skog. ECUADOR. J. L. Clark et al. 9609 (UNA), KF554347, KF554367, KF554387, KF554407, KF554306, KF554326. *C. angustata* (Wiehler) L. E. Skog. ECUADOR. J. L. Clark et al. 9854 (UNA), KF554348, KF554368, KF554388, KF554408, KF554307, KF554327. *C. angustata* (Wiehler) L. E. Skog. cultivated at SEL, J. Smith 2246 (WIS), KF554349, KF554369, KF554389, KF554409, KF554308, KF554328. *C. anisophylla* DC. PANAMA. E. J. Tepe 1081 (SRP), KF005817, KF006035, KF005927, KF006138, KF005643, KF005729. *C. anisophylla* DC. ECUADOR. J. L. Clark and J. Rea 8019 (UNA), KF005819, KF006037, KF005926, KF006141, KF005646, KF005728. *C. atahualpae* J. F. Smith & L. E. Skog. ECUADOR. J. L. Clark et al. 8000 (UNA), KF005821, KF006038, KF005930, KF006142, KF005647, KF005732. *C. bilabiata* Seem. ECUADOR. J. L. Clark et al. 11157 (UNA), KF005822, KF006039, KF005931, KF006143, KF005648, KF005733. *C. bremeri* (Wiehler) B. D. Morley. ECUADOR. J. L. Clark and M. Mailloux 7842 (UNA), KF005824, KF006041, KF005933, KF006145, KF005650, KF005735. *C. brevipila* Urb. cultivated, originally from JAMAICA. J. F. Smith 10058 (SRP), KF005825, KF006042, KF005934, KF006146, KF005651, KF005736. *C. byrsina* (Wiehler) L. P. Kvist & L. E. Skog. ECUADOR. J. F. Smith 3408 (SRP), KF005826, KF006043, KF005935, JQ953714, KF005652, KF005737. *C. byrsina* (Wiehler) L. P. Kvist & L. E. Skog. ECUADOR. J. L. Clark and O. Meija 6291 (UNA), KF005827, KF006044, KF005936, KF006148, KF005653, KF005738. *C. byrsina*

- (Wiehler) L. P. Kvist & L. E. Skog. ECUADOR. *J. L. Clark* 2413 (US), KF554350, KF554370, KF554390, KF554410, KF554309, KF554329.
- C. byrsina* (Wiehler) L. P. Kvist & L. E. Skog. ECUADOR. *J. L. Clark et al.* 7518 (US), KF554351, KF554372, KF554391, KF554411, KF554310, KF554330. *C. byrsina* (Wiehler) L. P. Kvist & L. E. Skog. cultivated at SEL, *H. Wiehler* 7712 (SEL), KF554353, KF554373, KF554393, KF554413, KF554312, KF554332. *C. byrsina* (Wiehler) L. P. Kvist & L. E. Skog. ECUADOR. *T. Croat* 94841 (MO), KF554352, KF554372, KF554392, KF554412, KF554311, KF554331. *C. calotricha* Donn. Sm. FRENCH GUIANA. *J. F. Smith et al.* 4117 (SRP), KF005828, KF006045, KF005937, KF006149, KF005654, KF005739. *C. ciliata* (Wiehler) L. P. Kvist & L. E. Skog. ECUADOR. *J. L. Clark et al.* 7508 (UNA), KF005829, KF006046, KF005938, KF006150, NA, KF005740. *C. colombiana* (Wiehler) L. P. Kvist & L. E. Skog. cultivated, *J. L. Clark et al.* (UNA), KF005831, KF006048, KF005940, KF006151, KF005656, KF005742. *C. colombiana* (Wiehler) L. P. Kvist & L. E. Skog. cultivated, *J. L. Clark* 8874 (US), KF554354, KF554374, KF554394, KF554415, KF554313, KF554333. *C. colombiana* (Wiehler) L. P. Kvist & L. E. Skog. cultivated at SEL, *J. F. Smith* 1126 (WIS), KF005832, KF006049, KF005941, KF006153, KF005657, KF005743. *C. consanguinea* Hanst. PANAMA. *E. J. Tepe* 1082 (SRP), KF005833, KF006050, KF005942, KF006154, KF005658, KF005744. *C. crassicaulis* (Wiehler) L. P. Kvist & L. E. Skog. cultivated, *J. L. Clark* 8859 (US), KF005834, KF006051, KF005943, KF006155, KF005659, KF005745. *C. cruenta* B. D. Morley. cultivated, originally from PANAMA. *J. F. Smith* 8606 (SRP), KF005835, KF006052, KF005944, KF006156, KF005660, KF005746. *C. dielsii* Mansf. ECUADOR. *J. F. Smith* 1989 (WIS), KF005836, KF006053, KF005945, KF006157, KF005661, KF005747. *C. dissimilis* C. V. Morton. PANAMA. *E. J. Tepe* 1070 (SRP), KF005837, KF006054, KF005946, KF006158, KF005662, KF005748. *C. dodsonii* Wiehler. cultivated, *B. Stewart s. n.* (SRP), KF005838, KF006055, KF005947, KF006159, KF005663, KF005749. *C. domingensis* (Urb.) B. D. Morley. DOMINICAN REPUBLIC. *L. Hahn* 445 (SRP), KF005839, KF006056, KF005948, JQ953715, KF005664, JQ953790. *C. eburnea* (Wiehler) L. P. Kvist & L. E. Skog. ECUADOR. *J. L. Clark et al.* 6353 (UNA), KF005840, KF006057, KF005949, KF006160, KF005665, KF005750. *C. elongatifolia* L. P. Kvist & L. E. Skog. cultivated, originally from ECUADOR. *J. L. Clark et al.* 10015 (UNA), KF005841, KF006058, KF005950, KF006161, KF005666, KF005751. *C. ericae* Mansf. ECUADOR. *J. L. Clark et al.* 6920 (UNA), KF005842, KF006059, KF005951, KF006162, KF005667, KF005752. *C. ericae* Mansf. ECUADOR. *E. J. Tepe* 1570 (UNA), KF005818, NA, KF005928, KF006139, KF005644, KF005730. *C. erythrophaea* Decne. Ex Houlet. cultivated, *J. F. Smith* 3727 (SRP), KF005843, KF006060, KF005952, KF006163, KF005668, AF543246. *C. filifera* (Wiehler) L. P. Kvist & L. E. Skog. ECUADOR. *J. L. Clark et al.* 7140 (UNA), KF005844, KF006061, KF005954, KF006165, KF005669, KF005753. *C. fimbriatylax* L. P. Kvist & L. E. Skog. ECUADOR. *J. L. Clark et al.* 7395 (UNA), KF005845, KF006062, KF005955, KF006166, KF005670, KF005754. *C. flexiflora* L. P. Kvist & L. E. Skog. ECUADOR. *J. L. Clark and L. Jost* 6968 (UNA), KF005846, KF006063, KF005956, KF006167, KF005671, KF005755. *C. gallicauda* Wiehler. cultivated, *J. L. Clark* 6283 (UNA), KF005847, KF006064, KF005957, KF006168, KF005672, KF005756. *C. gloriosa* Sprague. ECUADOR. *J. L. Clark et al.* 9921 (UNA), KF005848, KF006065, KF005958, KF006169, KF005673, KF005757. *C. guianensis* C. V. Morton. GUYANA. *J. F. Smith* 3711 (SRP), KF005849, KF006066, KF005959, JQ953718, KF005674, JQ953791. *C. guttata* Poepp. ECUADOR. *J. L. Clark and L. Jost* 6974 (UNA), KF005850, KF006067, KF005960, KF006170, KF005675, KF005759. *C. herthae* Mansf. ECUADOR. *J. L. Clark* 4960 (UNA), KF005852, KF006070, KF005961, KF006172, KF005676, KF005760; ECUADOR. *J. L. Clark* 7113 (UNA), KF005853, KF006069, KF005963, KF006173, KF005677, KF005761; ECUADOR. *J. L. Clark et al.* 11055 (UNA), KF005851, KF006068, KF005962, KF006171, KF554314, NA. *C. hypocyrtantha* (Wiehler) J. F. Smith & L. E. Skog. BOLIVIA. *J. L. Clark et al.* *E. Rodriguez* 6741 (US), KF005854, KF006071, KF005964, KF006174, KF005679, KF005762. *C. isernii* Cuatrec. ECUADOR. *J. F. Smith* 2010 (WIS), KF005856, KF006073, KF005966, KF006176, KF005681, KF005764; ECUADOR. *J. L. Clark et al.* 6253 (UNA), KF005857, KF006074, KF005967, KF006177, DQ211220, AF543247. *C. katzensteiniae* (Wiehler) L. P. Kvist & L. E. Skog. ECUADOR. *J. L. Clark et al.* 7625 (UNA), KF005858, KF006075, KF005968, KF006178, KF005683, KF005766. *C. lophophora* Mansf. ECUADOR. *J. L. Clark et al.* 7888 (US), KF005860, KF006076, KF005969, KF006179, KF005684, KF005767. *C. magnifica* Klotzsch ex. Oerst. cultivated, *J. F. Smith* 8602 (SRP), KF005861, KF006078, KF005971, KF006181, KF005685, KF005769. *C. manabiana* (Wiehler) J. F. Sm. & L. E. Skog. cultivated at SEL, *Dodson and Dodson* 6791 (SEL), KF554360, KF554380, KF554400, KF554421, KF554320, KF554339. *C. medicinalis* (Wiehler) L. E. Skog & L. P. Kvist. ECUADOR. *J. F. Smith* 1972 (WIS), KF005862, KF006079, KF005972, KF006164, KF005686, KF005770. *C. microphylla* Klotzsch & Hanst. cultivated, *J. L. Clark* 6261 (UNA), KF005863, KF006080, KF005973, KF006182, KF005687, KF005771; cultivated, *B. Stewart s. n.* (SRP), KF005865, KF006082, KF005974, KF006184, KF005689, KF005773; ECUADOR. *J. L. Clark* 2934 (SRP), KF005864, KF006081, KF554396, KF006183, KF005688, KF005772; ECUADOR. *T. Croat* 94778 (MO), KF005866, KF006084, KF005975, KF006185, KF005690, KF005774. *C. minutiflora* L. P. Kvist & L. E. Skog. ECUADOR. *J. L. Clark et al.* 10832 (UNA), KF005867, KF006085, KF005976, KF006186, KF005691, KF005775; ECUADOR. *J. L. Clark et al.* 7092 (US), KF005868, KF006086, KF005977, KF006187, KF005692, KF005776. *C. mira* B. D. Morley. cultivated, originally from PANAMA. *J. F. Smith* 2450 (WIS), KF005869, KF006087, KF005978, KF006188, KF005693, KF005777. *C. moesta* Poepp. BOLIVIA. *J. F. Smith* 1829 (WIS), KF005870, KF006084, KF005979, KF006189, KF005694, KF005778; BOLIVIA. *J. L. Clark and M. Zeballos* 6850 (UNA), KF005872, KF006089, KF005981, KF006191, KF005695, KF005779; BOLIVIA. *J. L. Clark and D. Barrientos* 6690 (US), KF005871, KF006088, KF005980, KF006190, DQ211224, DQ211123; PERU. *J. L. Clark et al.* 8211 (UNA), KF005873, KF006091, KF005982, KF006192, KF005696, KF005780. *C. oblongifolia* Rusby. BOLIVIA. *J. F. Smith* 1721 (WIS), KF005874, KF006092, KF005983, KF006193, KF005697, KF005781. *C. orientandina* Mansf. ECUADOR. *J. F. Smith* 3421 (SRP), KF005875, KF006093, KF005984, KF006194, KF005698, KF005782; ECUADOR. *J. L. Clark et al.* 9885 (UNA), KF005876, KF006094, KF005985, KF006195, KF005699, KF005783. *C. orientandina* Mansf. cultivated, *L. Schulte* 65 (SRP), KF554356, KF554375, NA, KF554417, KF554316, KF554334. *C. ovatifolia* L. P. Kvist & L. E. Skog. ECUADOR. *J. F. Smith* 1921 (WIS), KF005877, KF006091, KF005986, KF006196, KF005700, KF005784. *C. ovatifolia* L. P. Kvist & L. E. Skog. ECUADOR. *J. L. Clark* 8461 (US), KF554357, KF554376, KF554397, KF554418, KF554317, KF554335. *C. paramicola* (Wiehler) L. P. Kvist & L. E. Skog. cultivated, no voucher USBRG94529 (NA), KF005878, KF006095, KF005987, JQ954064, DQ211224, DQ211113. *C. picta* H. Karst. ECUADOR. *T. Croat* 94956 (MO), KF005879, KF006096, KF005988, KF006197, KF005701, KF005785. *C. pulchra* (Wiehler) L. E. Skog. cultivated, no voucher, -, KF005881, KF006097, KF005989, KF006199, KF005702, KF005787; cultivated, *J. L. Clark* 6265 (US), KF005880, NA, KF005990, KF006198, DQ211225, KF005786. *C. purpureovittata* (Wiehler) B. D. Morley. PERU. *J. L. Clark et al.* 11448 (UNA), KF005882, KF006098, KF005991, KF006200, KF005703, KF005788; cultivated, *J. F. Smith s. n.* (SRP), KF005855, KF006072, KF005965, KF006175, KF005680, KF005763. *C. purpusii* Standl. MEXICO. *A. Rincon et al.* 2302 (XAL), KF005883, KF006099, KF005992, JQ953719, KF005704, JQ953792. *C. repens* (Hook.) Hanst. cultivated, originally from JAMAICA. *J. F. Smith* 8605 (SRP), KF005884, KF006100, KF005993, KF006201, KF005705, KF005790. *C. rileyi* (Wiehler) J. F. Smith. ECUADOR. *J. F. Smith* 1944 (WIS), KF005885, KF006101, KF005994, KF006202, KF005706, KF005791; ECUADOR. *J. L. Clark* 6263 (US), KF005886, KF006102, KF005995, KF006203, DQ211250, AF543239. *C. rileyi* (Wiehler) J. F. Smith. ECUADOR. *J. L. Clark* 7077 (US), KF554358, KF554377, KF554398, KF554419, KF554318, KF554336. *C. rubricalyx* L. P. Kvist & L. E. Skog. ECUADOR. *J. L. Clark et al.* 11034 (UNA), KF005887, KF006103, KF005997, KF006204, KF005707, KF005792; ECUADOR. *T. Croat* 95236 (MO), KF005888, KF006104, KF005996, KF006205, KF005708, KF005793. *C. sanguinea* (Pers.) Hanst. cultivated, *J. F. Smith* 636 (WIS), KF005889, KF006105, KF005998, KF006206, KF005709, KF005794. *C. scandens* L. MARTINIQUE. *J. L. Clark and S. G. Clark* 6541 (UNA), KF005890, KF006106, KF005999, KF006207, KF005711, KF005795. *C. schiedeana* Schltdl. cultivated, originally from MEXICO. *J. F. Smith* 288 (WIS), KF005891, KF006107, KF006000, KF006208, KF005712, KF005796. *C. schimpffii* Mansf. cultivated, originally from ECUADOR. *J. F. Smith* 8605 (SRP), KF005892, KF006109, KF006001, KF006209, KF005713, KF005797. *C. segregata* (B. D. Morley) Wiehler. cultivated, *J. L. Clark et al.* 10029 (UNA), KF554378, KF006108, KF006002, KF006210, KF005714, KF554337. *C. sp. nov.* ECUADOR. *J. L. Clark et al.* 7295 (UNA), KF005820, KF006036, KF005929, KF006140, KF005645, KF005731. *C. sp. nov.* ECUADOR. *J. L. Clark et al.* 8898 (UNA), KF005859, KF006077, KF005970, KF006180, KF005684, KF005768. *C. spathulata* Mansf. ECUADOR. *J. F. Smith* 1853 (WIS), KF005893, KF006110, KF006003, KF006211, KF005715, KF005798; ECUADOR. *J. L. Clark et al.* 7485 (UNA), KF005894, KF006111, KF006004, KF006212, KF005716, KF005799. *C. spathulata* Mansf. ECUADOR. *T. Croat* 95254 (MO), KF554359, KF554379, KF554399, KF554420, KF554319, KF554338. *C. spathulata* Mansf. cultivated at SEL, *J. F. Smith* 651 (WIS), KF554361, KF554381, KF554401, KF554422, KF554321, KF554340. *C. strigosa* Benth. VENEZUELA. *J. F. Smith* 1200 (WIS), KF005895, KF006112, KF006005, KF006214, KF005717, KF005800; ECUADOR. *T. Croat* 94580 (MO), KF005896, KF006113, KF006006, KF006213, KF005718, KF005801. *C. tandapiana* (Wiehler) L. E. Skog & L. P. Kvist. cultivated, *L. Schulte* 66 (SRP), KF554362, KF554382, KF554402, KF554423, KF554322, KF554344.



*C. tandapiana* (Wiehler) L.E. Skog & L.P. Kvist. ECUADOR. J. L. Clark et al. 8006 (US), KF554355, KF554384, KF554395, KF554416, KF554315, KF554343. *C. tenella* L. P. Kvist & L. E. Skog. COLOMBIA. M. Amaya M. and J. F. Smith 603 (COL), KF005897, KF006114, KF006007, KF006215, KF005719, KF005802. *C. tenensis* Wiehler. ECUADOR. J. L. Clark et al. 9500 (UNA), KF005899, KF006116, KF006009, KF006217, KF005721, KF005803; ECUADOR. J. F. Smith 3374 (SRP), KF005898, KF006115, KF006008, KF006216, KF005720, KF005804. *C. trollii* Mansf. BOLIVIA. J. F. Smith 1723 (WIS), KF005899, KF006117, KF006010, KF006218, KF005722, KF005805. *C. ulei* (Wiehler) L. E. Skog. BRAZIL. A. Chautems and M. Perret 10109 (G), KF554363, KF554383, KF554403, KF554424, KF554323, KF554341. *C. ultravioletacea* J. F. Smith & L. E. Skog. BOLIVIA. J. L. Clark and V. Velaz 6603 (UNA), KF005900, KF006118, KF006011, KF006219, KF005723, KF005806. *C. villosissima* Mansf. ECUADOR. E. J. Tepe 1628 (SRP), KF005901, KF006119, KF006012, KF006220, KF005724, KF005807. *C. xiphoidea* J. F. Sm. & L. E. Skog. PERU. Allard 21300 (US), KF554364, NA, NA, NA, NA, KF554342.

*Corytoplectus capitatus* (Hook.) Wiehler. ECUADOR. T. Croat 94581 (MO), KF005902, KF006120, KF006013, JQ953698, NA, JQ953798. *Corytoplectus speciosus* (Poepp.) Wiehler. cultivated, no voucher, SI 94-268, -, KF005903, KF006117, KF006010, JQ953699, NA, JQ95379.

*Crantzia cristata* (L.) Scopoli. MARTINIQUE. J. L. Clark 6346 (US), KF005809, KF006027, KF005918, KF006134, DQ211294, DQ211154. *Crantzia epirotes* (Leeuwenb.) J. L. Clark. GUYANA. D. Clarke 10172 (US), KF005810, KF006028, KF005919, JQ953702, DQ211293, DQ211153. *Crantzia tigrina* (Karsten.) J. L. Clark. VENEZUELA. J. L. Clark 6892 (US), KF005811, KF006029, KF005920, JQ953703, DQ211295, DQ211155.

*Drymonia coccinea* (Aubl.) Wiehler. ECUADOR. J. F. Smith 3373 (SRP), KF005905, KF006121, KF006014, JQ953704, DQ211266, DQ211132. *Drymonia pendula* (Poepp.) Wiehler. ECUADOR. J. F. Smith 3384 (SRP), KF005906, KF006122, KF006015, KF006221, NA, NA. *Drymonia pilifera* Wiehler. PANAMA. E. J. Tepe 1065 (SRP), KF005907, KF006123, KF006016, KF006222, DQ211272, DQ211137. *Drymonia serrulata* (Jacq.) Mart. FRENCH GUIANA. J. F. Smith 4202 (SRP), KF005908, KF006124, KF006017, JQ953705, DQ211267, DQ211133. *Drymonia strigosa* (Oerst.) Wiehler. MEXICO. A. Rincon 2301 (XAL), KF005909, KF006125, KF006018, JQ953706, DQ211280, DQ211143. *Drymonia turrialvae* Hanst. Panama E. J. Tepe 1063 (SRP), KF005910, KF006126, KF006019, KF006223, DQ211278, DQ211141. *Drymonia urceolata* Wiehler. ECUADOR. J. F. Smith 3416 (SRP), KF005911, KF006127, KF006020, JQ953707, DQ211289, AF543265.

*Glossoloma anomalum* J. L. Clark ECUADOR. J. F. Smith 3418 (SRP), KF005912, KF006128, KF006021, KF006224, NA, AF543225. *Glossoloma grandicalyx* (J. L. Clark & L. E. Skog) J. L. Clark. ECUADOR. J. F. Smith 3417 (SRP), KF005913, KF006129, KF006024, JQ953708, DQ211205, AF543218. *Glossoloma martinianum* (J. F. Smith) J. L. Clark. ECUADOR. J. L. Clark 6101 (US), KF005914, KF006130, KF006022, JQ953709, DQ211209, AF543228. *Glossoloma panamense* (C. V. Morton) J. L. Clark. cultivated, L. E. Skog et al. 7641 (US), KF005915, KF006131, KF006023, JQ953710, DQ211202, DQ211102.

*Neomortonia rosea* Wiehler. cultivated, no voucher, SI 94-230, -, KF005917, KF006133, KF006026, JQ953712, DQ211197, DQ211099.

*Pachycaulos nummularium* (Hanst.) J. L. Clark and J. F. Smith. cultivated, J. F. Smith 3944 (SRP), KF005916, KF006132, KF006025, JQ953711, DQ211308, AF543266.