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THE GENUS COLUMNEA (GESNERIACEAE) IN ECUADOR

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ABSTRACT

A survey of the Ecuadorian species of *Columnea* with a key to the 57 accepted species is presented, and their distribution is discussed. Eighteen species are newly described: *Columnea albiflora, C. capillosa, C. cinerea, C. densibracteata, C. fililoba, C. fimbricalyx, C. fuscihirta, C. gigantifolia, C. inconspicua, C. laevis, C. lavandulacea, C. leucerinea, C. longinervosa, C. minutiflora, C. ovatifolia, C. purpurimarginata, C. rubribracteata,* and *C. rubricalyx.* The segregate genera *Pentadenia, Dalbergaria,* and *Trichantha* and the small genus *Bucinellina* are included in *Columnea,* requiring three new names (*C. elongatifolia* for *Trichantha angustifolia, C. flexiflora* for *Trichantha dodsonii,* and *C. tenella* for *Trichantha gracilis*), and ten new combinations. In addition, *Alloplectus microsepalus* is transferred to *Columnea.* Five species are lectotypified and seven species are neotypified. These were for the most part described by Mansfeld based on material at Berlin and later destroyed. Nineteen *Columnea* species are known only from Ecuador, 32 Ecuadorian species also occur in Colombia, 11 occur in Peru, five in all three countries, and four in Panama, as well. *Columnea microsepala* and *C. matudae* have remarkable disjunctions, the first between coastal Ecuador and coastal Venezuela and the latter between southern Ecuador and southern Mexico. In Ecuador, 42 and 22 species occur west and east of the Andes mountains, respectively, and seven species occur on both sides. Nineteen species are only known from a single Ecuadorian province, but only five of these are endemic to Ecuador. The largest diversity exists in the most humid part of Ecuador—the northwestern provinces of Carchi and Esmeraldas.

INTRODUCTION

The distribution of Gesneriaceae and of the genus *Columnea* in Ecuador is primarily related to the country's geography. Ecuador is among the smallest (ca. 270,000 km^2) of the South American countries, but because of the varied topography and climate its flora is exceedingly rich. The north-to-south-running Andes mountains divide Ecuador into three natural regions: the eastern Amazonian lowland, the Andean highland, and the western Pacific lowland (FIGURE 1). On the coastal plain the annual precipitation ranges from less than 200 mm on the Salinas Peninsula in the southwest to more than 5000 mm in the north near Colombia. The vegetation changes from semi-desert through zones of savanna, deciduous forests, semi-deciduous forests, and lowland rain forests (Harling, 1979). Throughout the Amazonian lowland the annual precipitation exceeds 2000 mm, and the vegetation is lowland rain forest. Gentry (1977) subdivided the lowland rain forests into moist, wet, and pluvial evergreen forests. In Ecuador wet forests (precipitation between 3000 and 5000 mm) occur along the foothills of the eastern

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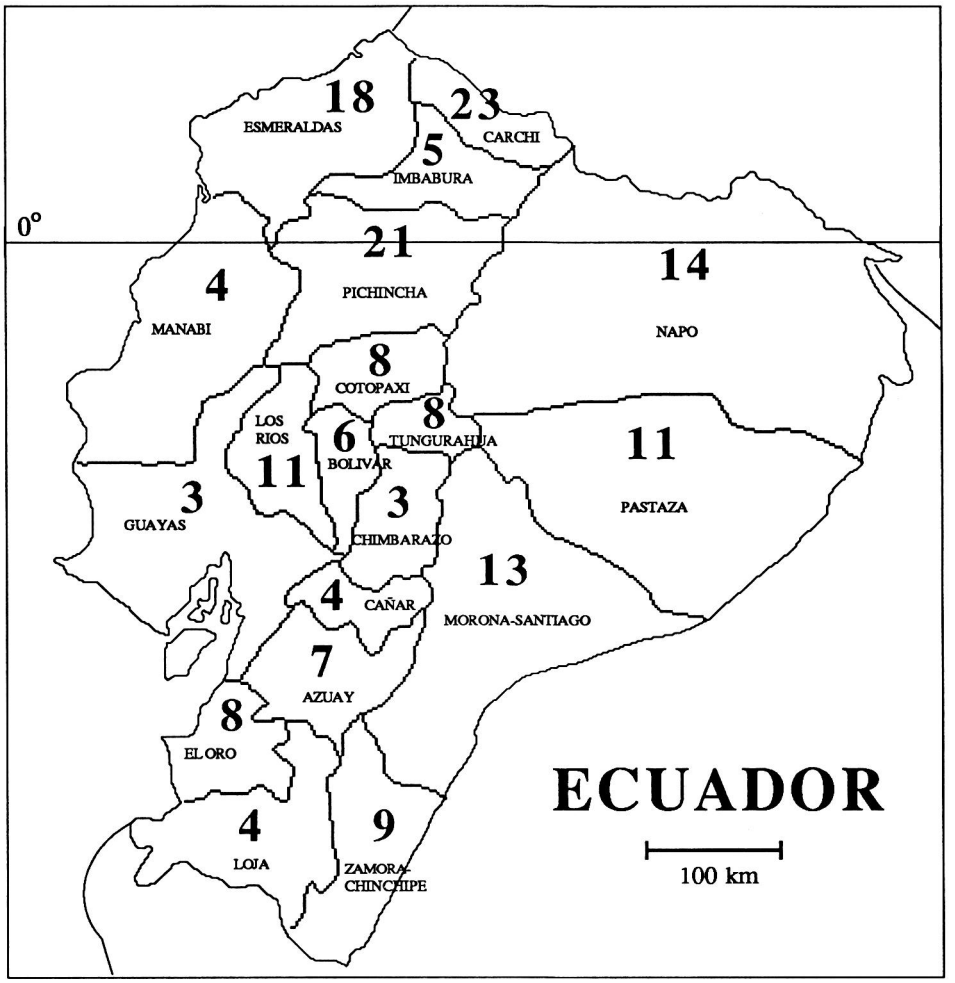

FIGURE 1. The provinces of Ecuador and the number of *Columnea* species known from each province.

Andean slopes and in the north along the western Andean slopes. Pluvial forests (precipitation exceeding 5000 mm) barely reach northwestern Ecuador. Furthermore, mostly very humid montane forests cover both the eastern and western slopes of the Andes mountains. In this work the zones between 700 and 1500 meters, between 1500 and 2500 meters, and above 2500 meters are referred to as lower montane forests, montane forests, and cloud forests, respectively.

The Gesneriaceae comprises 30 genera and more than 200 species in Ecuador. *Columnea,* with more than 200 species ranging from Mexico south to Bolivia and east to Amapá in Brazil, is the largest genus in Ecuador as well as in the neotropics as a whole. In this work 57 species are recognized from Ecuador. Skog (1979) recognized 50 Panamanian species; the number of species in Colombia is unknown but may be considerably larger than in Panama or Ecuador. At least 15 species

occur in Peru. The diversity of *Columnea* rises with increasing humidity and is highest in wet forests, pluvial forests, and the lower montane forests.

TAXONOMIC HISTORY

Columnea Linnaeus (1753) has been treated by most workers as one genus, e.g., Hanstein (1865), Bentham (1876), Fritsch (1894), Morton (1971a), Morley (1976), and Skog (1979). Several sections or subgenera were usually distinguished (TABLE 1), and these were to a great extent based on corolla features. Some early workers, e.g., Hanstein (1854), and Oersted (1858) divided *Columnea* into several genera, and recently Wiehler (1973, 1983) recognized the separate genera *Pentadenia* (Hanstein, 1854), *Dalbergaria* (Tussac, 1811–13), *Ortholoma* (Hanstein, 1854), and *Columnea* sensu stricto. However, Wiehler (1975a) soon transferred the species he had previously referred to *Ortholoma* to *Trichantha,* since this latter genus described by Hooker (1844) had priority. Altogether Wiehler (1973, 1975a, 1981) transferred 71 species of *Columnea* sensu lato to *Pentadenia, Dalbergaria,* and *Trichantha,* and later (1975b, 1977, 1978, 1981, 1984) an additional 28 species were newly described in these genera. A few of these new species have been transferred to *Columnea* by Beaufort-Murphy (1983), Morley (1975), Skog (Oliver & Skog, 1981), and Skog (1979, 1984). Wiehler (1977) created the small genus *Bucinella,* which he referred to the "alliance of columneoid genera" (the generic name was found to be illegitimate and replaced with *Bucinellina* in 1981). In the current work the five "columneoid genera" are fused into *Columnea* sensu lato, and six sections are recognized. The only part of *Columnea* sensu lato that has been recently revised is *Trichantha* by Morton (1963). He later (Morton, 1971b) reduced it to *Columnea* section *Ortholoma.*

DELIMITATION OF COLUMNEA

Under this heading the delimitation of *Columnea* sensu lato is discussed, while the genera segregated by some workers are discussed below (see Discussion of Sections). *Columnea* belongs to the subfamily Gesnerioideae and the tribe Episcieae. The latter is well-delimited and was accepted both by Fritsch (1894) and by Wiehler (1983). Within Episcieae, *Columnea* is mainly set apart by having berries, rather than a capsular fruit. Four other genera, each represented by a few species in Ecuador, have berries: *Codonanthe* and *Codonanthopsis* differ by having anthers that dehisce by pores rather than by longitudinal slits and by having eight rather than nine chromosome pairs (Skog, 1984); *Neomortonia* differs by having urceolate or broadly funnelform corollas different from the cylindric or ventricose corollas of *Columnea;* and *Corytoplectus* always is terrestrial while species of *Columnea* are mostly epiphytic. Nonetheless, *Corytoplectus* is weakly delimited from *Columnea.* The nectary types that characterize the former genus, according to Wiehler (1973), also occur in *Columnea* section *Stygnanthe* (FIGURE 2). In addition, most *Corytoplectus* specimens have pedunculate inflorescences while those of *Columnea* are always epedunculate. Finally, the berries of *Corytoplectus*

TABLE 1. TAXONOMIC HISTORY OF COLUMNEA. THE GENERA, SUBGENERA AND SECTIONS ACCEPTED BY HANSTEIN (1854), OERSTED (1858), HANSTEIN (1865), BENTHAM (1876), FRITSCH (1894), MORTON (1971), WIEHLER (1973), MORLEY (1976), WIEHLER (1983), AND IN THE CURRENT WORK

Taxon	Rank	Type (and current name)	H(1854)	O(58)
Columnea L. (1753)	Genus	*C. scandens* L.	Genus	Genus
Dalbergaria Tussac (1811–13)	Genus	*D. phoenicea* Tussac = *C. sanguinea* (Pers.) J. Hanst.	—	—
Vireya Raf. (1814)**	Genus	*V. sanguinolenta* Raf. = *C. sanguinea* (Pers.) J. Hanst.	—	—
Eusynetra Raf. (1837)**	Genus	*E. bicolor* Raf. = *C. hirsuta* Sw.	—	—
Glycanthes Raf. (1838)**	Genus	*G. scandens* (L.) Raf. = *C. scandens* L.	—	—
Trichantha Hook. (1844)	Genus	*T. minor* Hook. = *C. minor* (Hook.) J. Hanst.	—	—
Ortholoma Benth. (1846)	Sect.	*C. acuminata* Benth. = *C. anisophylla* DC.	Genus	Genus
Collandra Lem. (1847)**	Genus	*C. pilosa* (Lem.) Lem. = *C. aureonitens* Hook.	Genus	—
Pentadenia (Planch.) J. Hanst. (1854)	Genus	*P. aurantiaca* Decne. ex Planch. = *C. strigosa* Benth.	Genus	Genus
Pterygoloma J. Hanst. (1854)	Genus	*P. repens* (Hook.) J. Hanst. = *C. repens* (Hook.) J. Hanst.	Genus	—
Stenanthus Oerst. ex J. Hanst. (1854)	Genus	*S. heterophyllus* Oerst. ex J. Hanst. = *C. grata* C. Morton	Genus	Genus
Stygnanthe J. Hanst. (1854)	Genus	*S. moesta* (Poepp.) J. Hanst. = *C. moesta* Poepp.	Genus	—
Cryptocolumnea J. Hanst. (1865)	Sect.	*Columnea praetexta* J. Hanst.	—	—
Systolostoma Benth. (1876)	Sect.	*Columnea peruviana* Zahlb. = *Alloplectus peruvianus* (Zahlb.) Kvist & L. Skog	—	—
Bucinellina Wiehl. (1981)**	Genus	*B. nariniana* (Wiehl.) Wiehl. = *C. nariniana* (Wiehl.) Kvist & L. Skog	—	—

* Indication of sections to which the type species of the synonymized genera, subgenera, and sections is referred in this work.

** Rafinesque-Schmaltz (1814, 1837, 1838); Lemaire (1847); Wiehler (1981).

*** Wiehler (1973, 1975) accepted *Ortholoma* and *Trichantha,* respectively.

**** The type species of *Stygnanthe, S. moesta,* was treated among the dubious taxa as *Columnea moesta.*

are black or translucent with black seeds, differing from the white, yellow, red, or bluish berries of *Columnea.*

Alloplectus and *Columnea* can be easily distinguished by their bivalved, fleshy capsules and berry fruits, respectively. Unfortunately, this feature rarely appears or is obscure on herbarium sheets. Although the fruit character is currently the only consistent way to set the two genera apart, the following additional features may help: species of *Alloplectus* never have strongly anisophyllous leaves, and *Alloplectus* frequently has urceolate corollas while those of *Columnea* are cylindric or ventricose. Two species that occur in Ecuador, *Alloplectus weirii* and *A. dielsii,* were originally described in *Columnea* by Kuntze (1891) and Mansfeld (1937), and transferred to *Alloplectus* by Wiehler (1973, 1981, respectively). However, the latter species is a synonym of *Columnea peruviana* (Zahlbrückner, 1892), and the combination *Alloplectus peruvianus* appears in this work (see Excluded

TABLE 1. (continued)

H(65)	B(76)	F(94)	M(1971)	W(73)	M(76)	W(83)	K&S(92)*
Subge.	Sect.	Sect.	Sect.	Genus	Sect.	Genus	Sect.
—	—	—	—	Genus	—	Genus	(*Collandra*)
—	—	—	—	—	—	—	(*Collandra*)
—	—	—	—	—	—	—	(*Columnea*)
—	—	—	—	—	—	—	(*Columnea*)
—	Genus	Genus	—	Genus***	—	Genus	(*Ortholoma*)
Subge.	Sect.	Sect.	Sect.	***	Sect.	—	Sect.
Subge.	Sect.	Sect.	Sect.	—	Sect.	—	Sect.
Subge.	Sect.	Sect.	Sect.	Genus	Sect.	Genus	Sect.
Subge.	—	Sect.	—	—	Sect.	—	(*Ortholoma*)
Subge.	—	Sect.	Sect.	—	—	—	(*Ortholoma*)
****	Sect.	Sect.	Sect.	—	—	—	Sect.
Subge.	Sect.	Sect.	Sect.	—	—	—	(*Collandra*)
—	Sect.	Sect.	—	—	—	—	(*Alloplectus*)
—	—	—	—	—	—	Genus	Sect.

Species). Two additional undescribed Ecuadorian species were initially considered to belong to *Columnea* section *Ortholoma,* but were later recognized as belonging to *Alloplectus.*

DISCUSSION OF SECTIONS

The subdivision of *Columnea* sensu lato into sections or into segregate genera has for the last two decades caused much controversy (Morley, 1973b, 1975, 1976; Wiehler, 1973, 1983). The sections recognized by Morley (1976) are obviously artificial since they mainly are based on the length of the free corolla lobes. Consequently, species that have corollas with similar shapes but of different sizes may be referred to different sections. In addition, pollinator interactions may exert high selection pressures on corolla features making these evolutionarily plastic. Wiehler (1973) reduced the emphasis on corolla characters and accentuated somewhat more conservative features, e.g., fruits, nectaries, plant habit, and hybridization data. According to Wiehler (1973), hybrids among the segregate genera are 100% sterile, but few of these experimental hybridization data have

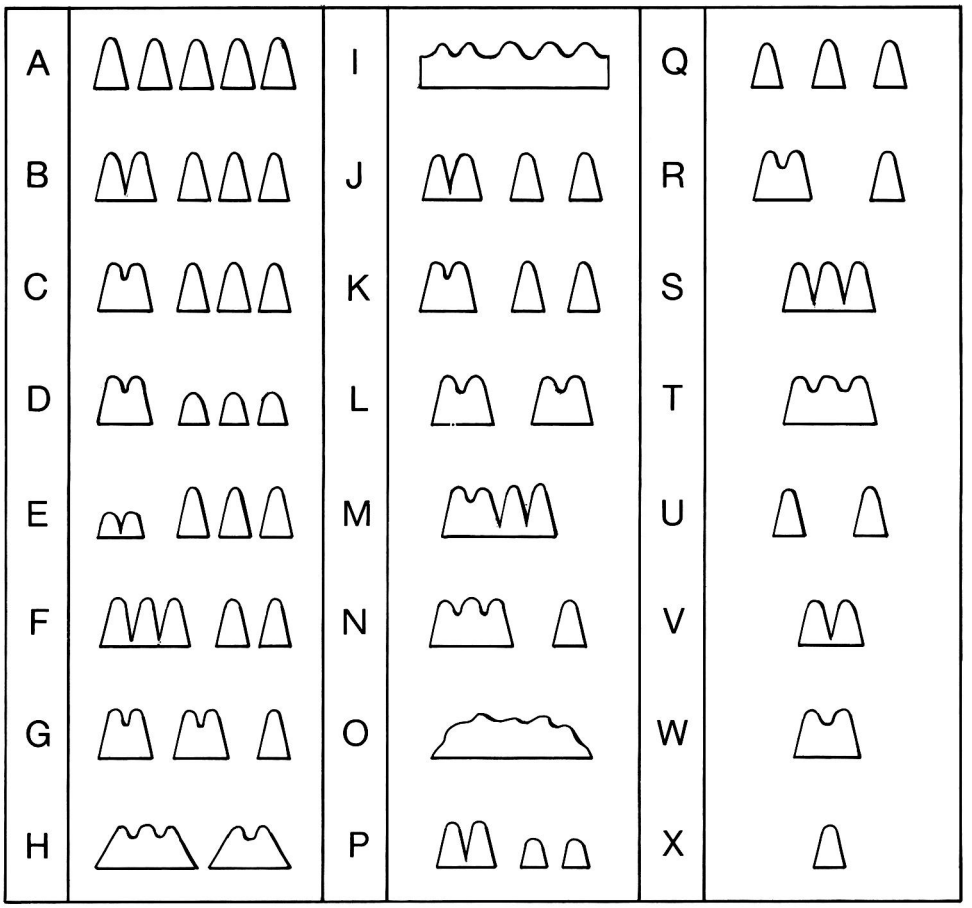

FIGURE 2. Nectary variation in *Columnea*. The most common type is W, which predominates in sections *Bucinellina, Collandra, Columnea,* and *Ortholoma*. Most species of sections *Pentadenia* and *Stygnanthe* have nectary types A and C, but numerous intermediate conditions occur. The illustrations are based on specimens of the following species: A, *C. matudae*; B, *C. colombiana*; C, *C. crassicaulis*; D, *C. strigosa*; E, *C. angustata*; F, *C. angustata*; G, *C. byrsina*; H, *C. ovatifolia*; I, *C. strigosa*; J, *C. strigosa*; K, *C. inconspicua*; L, *C. lavandulacea*; M, *C. strigosa*; N, *C. longinervosa*; O, *C. strigosa*; P, *C. strigosa*; Q, *C. angustata*; R, *C. inconspicua*; S, *C. strigosa*; T, *C. capillosa*; U, *C. albiflora*; V, *C. minutiflora*; W, *C. minor*; X, *C. strigosa*.

been published. Morley (1976) wrote that Wiehler ignored hybridization data published by Sherk & Lee (1967) demonstrating that *Dalbergaria, Pentadenia, Trichantha,* and *Columnea* sensu stricto are weakly interfertile (and thus should be treated as sections). However, commercial *Columnea* growers (pers. comm.) relate that the different segregate genera for the most part are mutually sterile. The Wiehler classification was supported by the palynological study of Williams (1978), and preliminary studies of chloroplast DNA indicate that six species referred to *Pentadenia* (section *Stygnanthe*) are more closely related to each other than to an outgroup including representatives of *Dalbergaria* (section *Collandra*), *Trichantha* (section *Ortholoma*), and *Columnea* sensu stricto (Smith, pers. comm.).

TABLE 2. IMPORTANT FEATURES OF THE SIX ACCEPTED SECTIONS OF COLUMNEA

Character	Section					
	Bucinellina	*Collandra*	*Columnea*	*Ortholoma*	*Pentadenia*	*Stygnanthe*
Plants terrestrial	Never	Often	Never	Never	Occasionally	Occasionally
Shoots "Fern frond"-like	Never	Always	Never	Rarely	Never	Rarely
Leaves strongly unequal	Never	Always	Occasionally	Mostly	Never	Mostly
Leaf apex contrasting red	Never	Usually	Never	Never	Never	Occasionally
Bracts conspicuous	Never	Usually	Never	Never	Never	Occasionally
Calxy lobes unequal	Never	Often	Never	Often	Never	Never
Limb bilabiate	Never	Often	Always	Occasionally	Always	Never
Throat glandular-hairy	Always	Always	Always	Always	Never	Always
Nectary gland number	1	1 (2)	1	1 (2)	1, 2, 3, 4, 5	2, 3, 4, 5 (1)
Ovary glabrous	Never	Never	Never (?)	Rarely	Never	Often
Stigma bilobed	Never	Never	Rarely	Rarely	Never	Often
Berry shape	Flat	Ovoid (Globose)	Globose	Globose (Ovoid)	Globose	Globose (Ovoid)
Pollen shape	Oblate	Spheroidal	Prolate	Spheroidal	Suboblate	Spheroidal

On the other hand, all groups in *Columnea* sensu lato have similar seeds (Beaufort-Murphy, 1983), and a study of phenolic compounds indicated a uniform distribution of these substances throughout the group (Kvist & Pedersen, 1986).

We consider the groups recognized by Wiehler (1973) as more natural than the previous subdivisions based mostly on corolla features. However, the genera Wiehler recognizes are weakly delimited, and to give them sectional rank is more suitable in our opinion. Actually, a recent palynological study by Fritze & Williams (1988) indicates that it may be adequate to treat the genera of Wiehler as sections. The important characteristics of the individual sections appear in TABLE 2, and it appears that few attributes set them consistently apart. Thus, we have not attempted to prepare a key to the sections of *Columnea.* The sections recognized in this work (*Bucinellina, Collandra, Columnea, Ortholoma, Pentadenia,* and *Stygnanthe*) are, to a large extent, identical to the genera of Wiehler (1973). At the sectional level the names *Collandra* and *Ortholoma* have priority over *Dalbergaria* and *Trichantha,* respectively (TABLE 1). The main change is that section *Stygnanthe* has been split off from section *Pentadenia.* Additional work is necessary before a fully satisfying, well-documented sectional classification of *Columnea* sensu lato is possible. The individual sections are briefly discussed below.

A: Section *Bucinellina* (Ecuador: 1 species). The genus *Bucinellina* (2 species) belongs in *Columnea* in our broader concept of the genus. The section is set apart by having a flattened depressed berry (Wiehler, 1977), by having distinctive pollen (TABLE 2; Williams, 1978; Fritze & Williams, 1988), and by having an unusual limb with two dorsal patent lobes and three lateral and ventral reflexed lobes.

B: Section *Collandra* (Ecuador: 23 species). According to Wiehler (1973, 1983),

species of *Dalbergaria* (section *Collandra*) are easily set apart by having shoots with subsessile leaves in close-set, imbricate, distichous pairs, of which one is stipule-like and the other large and oblanceolate. All species of section *Collandra* certainly have these characteristics, but a few species in sections *Ortholoma* and *Stygnanthe* are similar (TABLE 2), e.g., *Columnea tenensis* (*Ortholoma*), which is difficult to distinguish vegetatively from *C. inaequilatera* (*Collandra*). According to Wiehler, another distinguishing attribute is the presence of ovoid berries in contrast to globose berries in the other sections, but a few species in section *Collandra* have globose berries, e.g., *C. capillosa* and *C. cinerea,* and some species in the sections *Ortholoma* and *Stygnanthe* have ovoid berries. In spite of such problems, the section *Collandra* appears to constitute a close-knit, natural group set apart by having shoots with a "fern-frond habit" and by some or all of the following features: ovoid berries, lower leaf surfaces with a red apex, and conspicuous bracts.

Section *Collandra* is the most speciose in Ecuador and also includes the most frequently collected species. This may reflect the fact that *Collandra* species are mostly large-leaved, understory epiphytes or even terrestrial, while members of the other sections are mainly smaller-leaved, canopy epiphytes. Morley (1973a) suggested that this difference reflects the fact that species with large leaves are prone to desiccation. Dorsiventral, large-leaved shoots apparently are an adaptation to low understory light intensities. Few species of section *Collandra* thrive in exposed habitats where the limiting factor is water rather than light. The diversity center of section *Collandra* is western Colombia and adjacent Ecuador.

C: Section *Columnea* (Ecuador: 2 species). *Columnea* sensu stricto may be the most natural and well-delimited group within *Columnea* sensu lato (TABLE 1). The pollen is distinctive (Williams, 1978; Fritze & Williams, 1988), and the corollas are always bilabiate with a gradually expanding (never ventricose) tube, a reflexed lower lip (ventral lobe), and a patent upper lip (the lateral and dorsal lobes). The diversity center is Central America, but two species reach northwestern Ecuador. These are apparently always epiphytic (as are possibly all members of the section).

D: Section *Ortholoma* (Ecuador: 15 species). No characters unite all (or even most) of the species included in section *Ortholoma* (TABLE 2), and the section may be a mixture of two or more groups not fitting the other better defined sections. An additional problem is the delimitation of *Columnea* section *Ortholoma* from the genus *Alloplectus* in the absence of mature fruits (see Delimitation of *Columnea*). Species of section *Ortholoma* apparently always are epiphytic and mostly rare. The diversity center is Colombia.

All Ecuadorian species of section *Ortholoma* can be separated into two apparently natural subgroups. One of these is characterized by having corollas with a densely sericeous, villous or lanate indumentum (the corolla color actually is the color of the indumentum). This group includes seven Ecuadorian species: *Columnea dissimilis, C. fimbricalyx, C. herthae, C. laevis, C. lehmannii, C. minutiflora,* and *C. rubricalyx,* all restricted to northwestern Ecuador, western Colombia, and Panama. The second group has corollas with a sparser indumentum (the corolla color is the color of the tube itself). In addition, several other attributes are frequent

in the second group but absent from the first, e.g., presence of appendages at the sinuses of the corolla, conspicuously brown-hispid stems, ventricose corollas, and isophyllous leaves. This latter group is distributed both in eastern and western Ecuador and includes the type species of both *Trichantha* (*C. minor*) and *Ortholoma* (*C. acuminata* = *C. anisophylla*) (TABLE 1). The former is the most common Ecuadorian species of section *Ortholoma,* while the latter is the most widely distributed species.

E: Section *Pentadenia* (Ecuador: 1 species). Wiehler (1973) treated *Stygnanthe* as a synonym of *Pentadenia* based on the presence of four or five rather than one nectary gland. Sections *Pentadenia* and *Stygnanthe* are primarily set apart by having bilabiate corollas and corollas with subequal lobes, respectively. Section *Pentadenia* at present only includes *Columnea strigosa.* This is the most common and variable of all *Columnea* species occurring in Ecuador.

Section *Pentadenia* (*Columnea strigosa*) differs from apparently all other Ecuadorian *Columnea* species by having corollas with an eglandular throat. The scanning electron micrographs shown by Fritze & Williams (1988) demonstrate that the pollen also is distinctive and very different from that of section *Stygnanthe.* In addition, the up to 20 cm long pedicels of *C. strigosa* contrast with the maximally five cm long pedicels of all other species. However, some *C. strigosa* specimens have pedicels shorter than five cm (TABLE 4). The variation in the nectary of *Columnea strigosa* (FIGURE 2A, B, D, I, J, K, M, O, P, S, W, X) matches the variation of this character in the entire genus (and the tribe Episcieae as a whole).

F: Section *Stygnanthe* (Ecuador: 15 species). According to Wiehler (1973, 1983) the genus *Pentadenia* (sections *Pentadenia* and *Stygnanthe*) is set apart by having four or five free nectary glands rather than a single bilobed gland as found in the other genera (FIGURE 2A, C, W). However, we found much variation, including some intermediate nectary types characterizing species such as *Columnea inconspicua* (FIGURE 2K, R) and *C. lavandulacea* (FIGURE 2L). The nectary elaboration varies in *C. angustata* (FIGURE 2A, B, E, F, Q) and *C. byrsina* (FIGURE 2B, G), but most species consistently have the same nectary type (either that shown in FIGURE 2A or that in 2B). *Columnea poortmannii* is here referred to section *Stygnanthe* despite its nectary being a single bilobed gland (FIGURE 2W). This rare species is obviously a close relative of (and possibly derived from) the more common Peruvian species *C. trollii* (Mansfeld, 1934). In the latter species the nectary was found to vary from three single-lobed and one bilobed gland to a single bilobed gland, and some specimens are intermediate, having a bilobed gland of normal size and three diminutive single-lobed glands (FIGURE 2B, D, W). The leaf pairs are isophyllous in some species, but mostly anisophyllous in other species. The shoot development of *C. orientandina* has recently been studied (Sánchez-Burgos & Dengler, 1988; Morgan & Dengler, 1988). The species was considered to be facultatively anisophyllous. However, in natural habitats nearly all specimens are strongly anisophyllous and have dorsiventral shoots similar to those species in section *Collandra.*

The larger-leaved species in section *Stygnanthe* are frequently terrestrial, while the smaller-leaved species are epiphytic climbers or sometimes epipetric. Section

Stygnanthe species are mostly rare, and only *C. angustata* is common. The diversity center apparently is Ecuador.

POPULAR NAMES AND USES

Many species in section *Collandra* have popular names and folk uses in Ecuador and in Colombia, while the representatives of the rarer (or less commonly collected) sections apparently are little known and rarely used. The primary use is for treatment of snakebite. The ethnobotany and the local names of *Columnea* are discussed by Kvist (1989), and the uses of *Columnea* as well as other Gesneriaceae among Amerindian tribes in northwestern Ecuador are discussed by Holm-Nielsen et al. (1983), Kvist (1986), and Kvist & Holm-Nielsen (1987).

DISTRIBUTION OF ECUADORIAN SPECIES

New World Gesneriaceae often include one or a few species distributed throughout most of the range of the genus and a larger number of local endemics, e.g., *Cremosperma* (Kvist & Skog, 1988b), *Heppiella* (Kvist, 1990), *Kohleria* (Kvist & Skog, in press), and *Reldia* (Kvist & Skog, 1989). In contrast, no *Columnea* species apparently occur throughout most of the range of the genus. The most widely distributed species is probably *C. sanguinea,* which is rare in Ecuador. A third (19 of 57) of the Ecuadorian species are only known from this country, 32 species also occur in Colombia, and 11 in Peru (in addition, *C. laevis* and *C. matudae* have been collected in the immediate vicinity of the Colombian and Peruvian borders, respectively). Five species, *Columnea anisophylla, C. ericae, C. guttata, C. strigosa,* and *C. inaequilatera,* occur from Colombia to Peru (and in the case of the latter species to Bolivia). Four Ecuadorian species, *C. angustata, C. anisophylla, C. dissimilis,* and *C. kalbreyeriana,* are known from Panama, and the two former of these species range to Costa Rica. Skog (1979) found that 31 of 50 Panamanian species were endemic to Panama.

Columnea matudae has an interesting disjunct distribution between southern Ecuador and southern Mexico. Another species of section *Stygnanthe, C. microsepala,* occurs in the deciduous forests of western Ecuador and northern Venezuela. In both these species, the Ecuadorian populations are far more variable than those from Mexico and Venezuela, respectively. This and the fact that the diversity center of section *Stygnanthe* is Ecuador support the idea that *C. matudae* and *C. microsepala* have dispersed from Ecuador to Mexico and Venezuela, respectively. The likely dispersal-vector is migrating birds feeding on the plants' berries. A few other species have interesting although less striking disjunct ranges: *Columnea ciliata* (section *Ortholoma*) is known from the western Andean slopes in Ecuador and from the eastern Andean slopes in central Peru, *Columnea orientandina* is known from southeastern Ecuador and central Peru, and *C. dissimilis* (*Ortholoma*) from northwestern Ecuador (and adjacent Colombia) and Panama.

Ten Ecuadorian *Columnea* species apparently have disjunct distributions between northwestern Ecuador and northwestern Colombia (primarily the Depart-

ments of Antioquia, Chocó, and Valle). However, some of these disjunctions may be artifactual, as the Department of Nariño in particular is much more poorly collected than the Departments of Antioquia and Valle to the north and Ecuador to the south.

In Ecuador, 42 and 22 species are known west and east of the Andes mountains while seven occur on both sides. These latter seven species mainly occur in the montane and high montane forests (TABLE 3). That relatively few *Columnea* species have succeeded in dispersing across the Andes mountains is somewhat surprising considering their apparently bird-dispersed berries and the striking disjunct distributions of some species best explained by long-distance dispersal.

The altitudinal and geographical ranges of the six sections vary in Ecuador (TABLE 3). Section *Bucinellina* is a rare group found in low montane forests of northwestern Ecuador and western Colombia. Section *Collandra* may be most richly represented in the low montane forests but is also common in lowland and montane forests. Only *C. fuscihirta,* a montane forest species, occurs both in eastern and western Ecuador. However, closely related species pairs such as *C. schimpffii–C. guttata* and *C. densibracteata–C. albiflora* apparently speciated from populations separated by the Andes mountains. In Ecuador, section *Columnea* is known only from the northwestern lowlands, indicating that the diversity center of this group is far to the north in Panama and Costa Rica. However, the section may also occur in eastern Ecuador since the widespread *C. oerstediana* occurs in the Peruvian Amazon region. Section *Ortholoma* is best represented in the lower montane forests of western Ecuador. One complex of seven closely related species is actually restricted to this part of Ecuador (see Discussion of Sections). The single species in section *Pentadenia* (*C. strigosa*) is the only common *Columnea* in Ecuadorian cloud forests and also occurs in both Andean cordilleras. Section *Stygnanthe* is mostly a group of the western montane forests. Only *C. orientandina* and apparently the rare *C. poortmannii* are restricted to the eastern Andean slopes. The former species is close to the variable *C. microsepala* of western Ecuador and may have developed from this latter species after dispersal to the eastern slopes. The latter species may have evolved from the Peruvian *C. trollii* (see Discussion of Sections). Section *Stygnanthe* includes five of the seven Ecuadorian *Columnea* species that occur both on the eastern and western slopes: *C. angustata, C. byrsina, C. inconspicua, C. lavandulacea,* and *C. leucerinea.* This is partly due to the fact that species of section *Stygnanthe* mostly occur at higher elevations than other sections, making the mountains a lower barrier for dispersal. However, the strikingly disjunct distributions of *C. matudae* and *C. microsepala* indicate that species in section *Stygnanthe* may be especially successful in establishing viable populations following long-distance dispersal. Section *Stygnanthe* may have developed on the western Andean slopes in Ecuador and Colombia and then spread from there to the eastern Andean slopes, Central America, and Venezuela.

Most species of *Columnea* are known from one or two of the altitudinal zones recognized in this work (TABLE 3), but common species are often known from three, although most collections usually come from one (or two) zones. No species appear to be entirely limited to a narrow altitudinal zone, but they are usually only common in one zone to which they are adapted. All species are probably

TABLE 3. THE ALTITUDINAL DISTRIBUTION OF COLUMNEA IN WESTERN AND EASTERN ECUADOR, THE ELEVATIONS FROM WHICH THE INDIVIDUAL SPECIES ARE KNOWN (+), AND AN INDICATION (*) WHEN THE NUMBER OF COLLECTIONS FROM A PARTICULAR ALTITUDINAL ZONE EXCEEDS 10. IN ADDITION, THE NUMBER OF ECUADORIAN PROVINCES FROM WHERE EACH SPECIES IS KNOWN, AND THEIR OCCURRENCE (+) OR APPARENT ABSENCE (−) FROM THE NEIGHBORING COUNTRIES OF COLOMBIA AND PERU. RF: Lowland rain forest (0–700 m); LMF: Lower montane forest (700–1500 m); MF: Montane forest (1500–2500 m); CF: Cloud forest (above 2500 m); N: Number of Ecuadorian provinces from which the species is known; C: Presence in Colombia; P: Presence in Peru

	Distribution										
	West				East						
Section and Species	RF	LMF	MF	CF	CF	MF	LMF	RF	N	C	P
A. Section *Bucinellina*											
1. *C. nariniana*	−	+	−	−	−	−	−	−	1	+	−
B. Section *Collandra*											
2. *C. albiflora*	−	−	−	−	−	*	−	−	2	−	−
3. *C. asteroloma*	+	−	−	−	−	−	−	−	1	−	−
4. *C. capillosa*	−	−	−	−	−	+	*	−	3	−	−
5. *C. cinerea*	−	+	+	−	−	−	−	−	4	−	−
6. *C. densibracteata*	+	*	*	+	−	−	−	−	7	+	−
7. *C. eburnea*	*	*	−	−	−	−	−	−	5	+	−
8. *C. ericae*	−	−	−	−	−	+	*	*	4	+	+
9. *C. eubracteata*	−	−	+	*	−	−	−	−	3	−	−
10. *C. fililoba*	−	+	−	−	−	−	−	−	1	+	−
11. *C. fuscihirta*	−	−	+	−	−	+	−	−	2	+	−
12. *C. gigantifolia*	−	+	−	−	−	−	−	−	1	+	−
13. *C. guttata*	−	−	−	−	−	+	*	−	5	+	+
14. *C. inaequilatera*	−	−	−	−	−	+	*	+	5	+	+
15. *C. kalbreyeriana*	−	+	−	−	−	−	−	−	1	+	−
16. *C. longinervosa*	−	+	−	−	−	−	−	−	1	+	−
17. *C. picta*	*	*	+	−	−	−	−	−	10	+	−
18. *C. purpurimarginata*	+	−	−	−	−	−	−	−	1	+	−
19. *C. rubriacuta*	*	+	−	−	−	−	−	−	5	+	−
20. *C. rubribracteata*	+	−	−	−	−	−	−	−	1	−	−
21. *C. sanguinea*	−	−	−	−	−	−	−	+	1	+	−
22. *C. schimpffii*	*	+	−	−	−	−	−	−	6	−	−
23. *C. tessmannii*	−	−	−	−	−	+	−	−	3	−	+
24. *C. villosissima*	−	−	−	−	−	+	*	*	4	−	+
C. Section *Columnea*											
25. *C. bilabiata*	+	−	−	−	−	−	−	−	1	+	−
26. *C. kienastiana*	*	+	−	−	−	−	−	−	4	+	−
D. Section Ortholoma											
27. *C. anisophylla*	−	−	−	−	−	−	+	−	2	+	+
28. *C. brenneri*	−	−	−	−	−	−	+	−	3	−	−
29. *C. ciliata*	+	+	+	−	−	−	−	−	4	−	+
30. *C. dissimilis*	+	+	−	−	−	−	−	−	3	+	−
31. *C. elongatifolia*	−	−	−	−	−	−	+	+	2	−	−
32. *C. fimbricalyx*	−	+	−	−	−	−	−	−	1	+	−
33. *C. flexiflora*	−	−	−	−	−	+	−	−	1	−	−
34. *C. herthae*	+	−	−	−	−	−	−	−	3	+	−
35. *C. laevis*	−	+	−	−	−	−	−	−	1	−	−
36. *C. lehmannii*	−	+	−	−	−	−	−	−	1	+	−
37. *C. minor*	+	*	+	−	−	−	−	−	7	+	−
38. *C. minutiflora*	−	+	−	−	−	−	−	−	1	+	−
39. *C. rubricalyx*	+	+	−	−	−	−	−	−	2	+	−
40. *C. tenella*	−	+	−	−	−	−	−	−	1	+	−
41. *C. tenensis*	−	−	−	−	−	−	−	+	2	−	−

TABLE 3. (continued)

Section and Species	Distribution										
	West				East						
	RF	LMF	MF	CF	CF	MF	LMF	RF	N	C	P
E. Section Pentadenia											
42. *C. strigosa*	−	+	*	*	*	+	−	−	13	+	+
F. Section Stygnanthe											
43. *C. angustata*	*	+	−	−	−	−	*	−	9	+	−
44. *C. byrsina*	+	*	+	−	−	+	−	−	3	+	−
45. *C. colombiana*	+	−	−	−	−	−	−	−	1	+	−
46. *C. crassicaulis*	−	−	+	−	−	−	−	−	2	+	−
47. *C. inconspicua*	−	+	+	−	−	+	−	−	4	−	+
48. *C. isernii*	−	+	−	−	−	−	−	−	2	−	−
49. *C. lavandulacea*	−	−	+	−	−	+	−	−	2	−	−
50. *C. leucerinea*	−	−	+	−	−	+	−	−	2	−	−
51. *C. lophophora*	−	−	+	−	−	−	−	−	1	−	−
52. *C. matudae*	−	+	+	+	−	−	−	−	2	−	−
53. *C. microsepala*	*	+	−	−	−	−	−	−	8	−	+
54. *C. orientandina*	−	−	−	−	−	+	+	−	2	−	+
55. *C. ovatifolia*	−	−	+	−	−	−	−	−	2	−	−
56. *C. poortmannii*	−	−	−	−	−	+	−	−	1	−	−
57. *C. spathulata*	+	+	−	−	−	−	−	−	5	+	−

dispersed above and/or below the zone they are adapted to, but only few and small populations became established there.

ENDANGERED SPECIES

In Ecuador, the largest number of *Columnea* species (and other Gesneriaceae) exists along the western foothills of the Andes in the area between Lita (bordering the provinces Imbabura and Esmeraldas) and San Marcos in the province of Carchi close to the Colombian border (FIGURE 1). This is due to both the high precipitation in this area and to the fact that the largest diversity of the genus exists in adjacent western Colombia and northward to Panama. In eastern Ecuador, the richest areas are the very humid front ranges Sierra de Cutucú in Morona-Santiago, the region with the volcanoes Reventador and Sumaco in Napo,

TABLE 4. THE VARIATION OF SOME FEATURES BETWEEN CLIMBING AND PREDOMINANTLY TERRRESTRIAL POPULATIONS OF COLUMNEA STRIGOSA IN THE PROVINCE OF PICHINCHA IN WESTERN ECUADOR. IN THE ADJACENT PROVINCES COTOPAXI AND CHIMBARAZO MOST PLANTS HAVE INTERMEDIATE FEATURES

Character	Climbing	Terrestrial
Leaf arrangement	Never apically congested	Apically congested
Nectary	1 gland	4 glands
Flowers per node	1–2	4–10
Pedicel length	Exceeding 5 cm	Less than 3 cm
Calyx lobe length	Exceeding 2 cm	Less than 1.2 cm
Corolla length	5–7 cm	3–5 cm

and possibly the botanically unexplored Sierra de Cóndor in Zamora-Chinchipe (and adjacent Peru).

Nineteen *Columnea* species are only known from a single Ecuadorian province each. However, many of these barely reach northwestern Ecuador and have a wider distribution in western Colombia, and only five of these 19 species are endemic to Ecuador. Two of these, *C. lophophora* and *C. poortmannii,* have not been collected during the last half century and may be extinct due to habitat destruction. The continued survival of *Columnea asteroloma* is questionable, since nearly all lowland forests in the provinces of Los Ríos and Pichincha have been converted to farmland. Two species only known from a single province, *C. flexiflora* and *C. laevis,* probably are not currently endangered. The former species occurs in the Sierra de Cutucú where much montane forest remains, and the latter survives along the still largely forested northwestern foothills of the Andes (and probably in adjacent Colombia). However, the survival of these species and probably the majority of all Ecuadorian Gesneriaceae may soon be at risk. In eastern Ecuador, the zone of heaviest deforestation is between 500 and 1000 meters, exactly the elevation where *Columnea* and other Gesneriaceae are most common. In western Ecuador, the destiny of the low montane and pluvial forests of Carchi and adjacent parts of Imbabura and Esmeraldas is crucial, since this is the Ecuadorian region with the most Gesneriaceae.

TAXONOMIC TREATMENT

Columnea L. Sp. Pl. 638. 1753. TYPE: *C. scandens* L.

Achimenes P. Br. Civ. nat. hist. Jamaica 270, *pl. 30.* 1756, non Pers. Syn. Pl. **2:** 164. 1806. TYPE: *A. major, herbacea, subhirsuta oblique assurgens* P. Br. = *Columnea fawcettii* (Urb.) C. Morton

Dalbergaria Tussac Fl. Antill. **1:** 141, *pl. 19.* 1811–13. TYPE: *D. phoenicea* Tussac = *Columnea sanguinea* (Pers.) J. Hanst.

Vireya Raf. in Specchio Sci. **1:** 194. 1814. TYPE: *V. sanguinolenta* Raf. = *Columnea sanguinea* (Pers.) J. Hanst.

Eusynetra Raf. Fl. Tellur. **2:** 57. 1837. TYPE: *E. bicolor* Raf. = *Columnea hirsuta* Sw.

Glycanthes Raf. Sylva Tellur. 83. 1838. TYPE: *G. scandens* (L.) Raf. = *Columnea scandens* L.

Trichantha Hook. in Icon. Pl. **3:** *pl. 666.* 1844. TYPE: *T. minor* Hook. = *Columnea minor* (Hook.) J. Hanst.

Collandra Lem. in Fl. Serres Jard. Eur. **3:** *pl. 223.* 1847. TYPE: *C. pilosa* Lem. = *Columnea aureonitens* Hook.

Ortholoma (Benth.) J. Hanst. in Linnaea **26:** 184, 209. 1854. LECTOTYPE: *O. acuminatum* (Benth.) J. Hanst. = *Columnea acuminata* Benth.

Pentadenia (Planch.) J. Hanst. in Linnaea **26:** 187, 211. 1854. TYPE: *P. aurantiaca* (Decne. ex Planch.) J. Hanst. = *Columnea aurantiaca* Decne. ex Planch.

Pterygoloma J. Hanst. in Linnaea **26:** 188, 211. 1854. TYPE: *P. repens* (Hook.) J. Hanst. = *Columnea repens* (Hook.) J. Hanst.

Stenanthus Oerst. ex J. Hanst. in Linnaea **26:** 184, 209. 1854. TYPE: *S. heterophyllus* Oerst. ex J. Hanst. = *Columnea grata* C. Morton

Stygnanthe J. Hanst. in Linnaea **26:** 185, 209. 1854. TYPE: *S. moesta* (Poepp.) J. Hanst. = *Columnea moesta* Poepp.

× *Colbergaria* Wiehl. in Selbyana **1:** 408. 1976.

× *Coltrichantha* Wiehl. in Selbyana **1:** 408. 1976.

× *Coltadenia* Wiehl. in Selbyana **1:** 409. 1976.

× *Daltrichantha* Wiehl. in Selbyana **1:** 409. 1976.

× *Daltadenia* Wiehl. in Selbyana **1:** 409. 1976.

× *Trichadenia* Wiehl. in Selbyana **1:** 409. 1976 (nom. illeg., later homonym of *Trichadenia* Thwaites (Flacourtiaceae)).

Bucinella Wiehl. in Selbyana **2:** 91. 1977 (nom. illeg., later homonym of *Bucinella* A. Fuc. (fossil alga). TYPE: *Bucinella nariniana* Wiehl. = *Columnea nariniana* (Wiehl.) Kvist & L. Skog

Bucinellina Wiehl. in Selbyana **5:** 381. 1981. TYPE: *Bucinellina nariniana* (Wiehl.) Wiehl. = *Columnea nariniana* (Wiehl.) Kvist & L. Skog

× *Tricanthenia* Wiehl. in Selbyana **6:** 116. 1983.

Herbs or shrubs, usually epiphytic, less commonly epipetric or terrestrial, shoots often conspicuously dorsiventral. Leaves opposite, base oblique, isophyllous or anisophyllous, the smaller leaf in a pair often strongly reduced and caducous, lower leaf surfaces often with a conspicuous pattern of red or purple toward the apex and/or along the margin and veins, rarely with translucent and red "windows" on the blade. Inflorescences in leaf axils, in anisophyllous species usually in the axils of the larger leaf in each pair, epedunculate, of 1–10 flowers, bracts usually present but often scale-like, less commonly large and sometimes hiding the calyces, frequently with conspicuous colors. Calyx lobes 5, free nearly to the base, equal or subequal, margin entire or dissected; corolla sympetalous, basally often dorsally gibbous, tube frequently ventricose, outside often red, less commonly yellow, rarely greenish or cream, inside usually glandular hairy in throat, limb subequal and bilabiate, lobes 5 (or 4 due to the fusion of two dorsal ones), usually rotundate; stamens 4, a minute staminode is occasionally present, filaments usually basally fused and adnate to corolla tube, glabrous or pubescent, anthers often coherent, included, subincluded, or exserted; nectary often of 1 bilobed gland, less commonly of 4 or 5 free glands, rarely of 2 or 3 glands; ovary glabrous or sericeous, style glabrous or pilose, stigma usually stomatomorphic, occasionally bilobed. Fruit a berry, frequently globose, less commonly ovoid; seeds narrowly elliptic or elliptic, transversely striate, often ca. 1 mm long. Chromosome number $2n = 18$.

KEY TO THE SPECIES OF COLUMNEA IN ECUADOR

Leaves equal or subequal in pairs.
- Limb bilabiate; pedicels 0.2–20 cm long.
  - Corolla yellow, 4.5–7 cm long, ventricose, maximum diam. exceeding 8 mm, eglandular in throat; pedicels 1.5–20 cm long; in montane forests, eastern and western Andean slopes, common and variable. ..... 42. *C. strigosa*
  - Corolla red, 3.5–4.5 cm long, not ventricose, maximum diam. not exceeding 6 mm; pedicels 0.2–2.5 mm long.
    - Leaves narrowly lanceolate, 4–10 cm long; calyx lobes basally dissected; in lowland forests, western Andean slopes of Esmeraldas and western Colombia. ..... 25. *C. bilabiata*
    - Leaves ovate, 1–3 cm long; calyx lobes entire; in lowland forests, western Andean slopes (Esmeraldas, Los Ríos, Pichincha) and western Colombia. ..... 26. *C. kienastiana*
- Limb subregular; pedicels 0.2–4 cm long.
  - Leaves narrowly lanceolate to elliptic, the length of the blade at least twice the width, up to 3 cm wide.
    - Stems with 3–5 mm long erect trichomes; corolla limb 5–35 mm wide and often with appendages between the lobes.
      - Calyx lobes linear; corolla yellow, limb 5–7 mm wide, with appendages between the lobes; in eastern lower montane forests in Napo and Pastaza. ..... 31. *C. elongatifolia*
      - Calyx lobes spathulate to oblanceolate; corolla red, limb 30–35 mm wide, without appendages between the lobes; in montane forests, eastern Andean slopes in Morona-Santiago. ..... 33. *C. flexiflora*
    - Stems with 0.5–3 mm long appressed trichomes or glabrescent; corolla limb 3–9 mm wide and never with appendages between the lobes.
      - Calyx white-lanate outside; corolla villous, 14–21 mm long, lavender; in montane forests, eastern Andean slopes in Napo and western slopes in Pichincha. ... 50. *C. leucerinea*
      - Calyx pilose to sericeous outside; corolla sericeous, 16–30 mm long, cream, yellow or red.
        - Corolla pale yellow to cream, 16–21 mm long; nectary of 2 glands; in montane forests on

eastern and western Andean slopes (Azuay, Cotopaxi, Morona-Santiago, and Pichincha) and northern Peru. ..... 47. *C. inconspicua*

Corolla red, occasionally yellow, 22–30 mm long; nectary of 3–5 glands; in lowland forests on eastern and western slopes (El Oro, Esmeraldas, Los Ríos, Manabí, Morona-Santiago, Napo, Pastaza, Pichincha, and Tungurahua), as well as to Costa Rica, Panama, and northwestern Colombia. ..... 43. *C. angustata*

Leaves elliptic to ovate, the length of blade less than twice the width, up to 10 cm wide.

Calyx lobes basally dissected; stems sericeous; ovary sericeous; nectary of 4 or 5 glands.

Leaves up to 3 cm long, never apically congested; shoots often pendent; in lowland forests, in northwestern Ecuador (Esmeraldas) and western Colombia. ... 45. *C. colombiana*

Leaves up to 20 cm long, often apically congested; shoots never pendent.

Corolla 2–3 cm long, villous outside, tube and limb uniformly colored; in lower montane forests of the southwest (Bolívar(?), Cañar, and Loja) and northwestern Peru. ..... 48. *C. isernii*

Corolla 3.5–5 cm long, sericeous outside, tube and limb with contrasting colors; in low montane and montane forests in El Oro and Loja, as well as Mexico, Guatemala(?), and Peru(?). ..... 52. *C. matudae*

Calyx lobes entire or subentire (rarely with a few apical teeth); stems sericeous or villous; ovary sericeous or glabrous; nectary of 1, 2, 4, or 5 glands.

Stems and leaves nearly glabrous; leaves and flowers never apically congested.

Leaves 4–7 cm long; corolla yellow; nectary of 4 glands; ovary glabrous; in montane forests of the northwest (Carchi and Pichincha), as well as southwestern Colombia. ..... 46. *C. crassicaulis*

Leaves 1.5–2.5 cm long; corolla red; nectary of 2 glands; ovary sericeous; in montane forests of the northwest (Carchi and Pichincha). ..... 55. *C. ovatifolia*

Stems and leaves pubescent; leaves and flowers often apically congested.

Corolla 2.5–3 cm long, limb with appendages between the lobes; bracts inconspicuous; in lower montane forests on eastern Andean slopes (Morona-Santiago, Pastaza, and Zamora-Chinchipe). ..... 28. *C. brenneri*

Corolla 3–5 cm long, limb without appendages between the lobes; bracts often conspicuous, up to 2 cm long, ovate.

Tube of corolla cylindric; bracts up to 2 cm long, ovate; nectary of 5 glands; ovary sericeous; in montane forests on western Andean slopes (Chimborazo). ..... 51. *C. lophophora*

Tube of corolla ventricose; bracts inconspicuous; nectary of 1 bilobed gland; ovary glabrous; in montane forests of the southeast in Zamora-Chinchipe (and Loja?). ..... 56. *C. poortmannii*

Leaves unequal in pairs with the length of the smaller leaf usually reduced to less than half the length of the larger leaf.

Blades cordate to ovate, the larger leaf in a pair 1.5–3 cm long and the smaller 0.8–1.5 cm long; corolla 2–2.5 cm long; in lower montane forests of the northwest (Carchi) and in southwestern Colombia. ..... 1. *C. nariniana*

Blades ovate, lanceolate or oblanceolate, the larger leaf in a pair 4–60 cm long and the smaller mostly inconspicuous; corolla 0.7–6 cm long.

Nectary of 2–5 glands (if two glands, then these are located opposite each other); bracts scale-like; calyx lobes subequal, lanceolate, or spathulate, margin entire; corolla cylindric, 1.6–2.2 cm long, outside with appressed trichomes, limb subregular, throat up to 4 mm wide; stems glabrescent; leaves up to 15 cm long; pedicels up to 5 mm long.

Lower leaf surface purple with green along margin and veins; calyx lobes spathulate; in lowland and lower montane forests on western Andean slopes (Bolívar, Cotopaxi, Esmeraldas, Los Ríos, and Pichincha) and in northwestern Colombia. ..... 57. *C. spathulata*

Lower leaf surface uniformly green (or reddish) but occasionally green with red apex; calyx lobes lanceolate.

Leaves ovate to elliptic, the smaller leaf in a pair not strongly reduced and scale-like; corolla lavender with purple markings on lobes; ovary glabrous; in montane forests, eastern and western slopes in Morona-Santiago and Pichincha. ..... 49. *C. lavandulacea*

Leaves elliptic, lanceolate or oblanceolate, the smaller leaf in a pair strongly reduced and scale-like; corolla red, yellow, or cream; ovary glabrous or sericeous.

Stamens exserted; corolla red with yellow apex; leaves up to 8 cm long and 2.5 cm wide, lower surface never with red apex; bracts scale-like; ovary sericeous; mainly in lower montane forests on both eastern and western slopes (Carchi, Napo, and Pichincha), and in western Colombia. ..... 44. *C. byrsina*

Stamens included or subincluded (rarely exserted, but then in combination with yellow corolla); corolla red, yellow, or cream; leaves up to 14 cm long and 5 cm wide, lower surface frequently with red apex; bracts occasionally up to 2 cm long; ovary sericeous or glabrous.

Ovary glabrous; corolla pale yellow to cream; bracts scale-like; nectary of 2 glands; mainly in montane forests on eastern and western slopes (Azuay, Cotopaxi, Morona-Santiago, and Pichincha), and northern Peru. ..... 47. *C. inconspicua*

Ovary sericeous; corolla yellow or red; bracts occasionally up to 2 cm long; nectary of 4 or 5 glands.

Corolla not glandular-hairy outside, yellow or red; bracts up to 2 cm long; leaves up to 14 cm long, lower surface frequently with red apex; mainly in lowland forests, widely distributed in western Ecuador (Azuay, Bolívar, El Oro, Esmeraldas, Guayas, Loja, Los Ríos, Manabí, and Pichincha), Venezuela, and northwestern Peru. ..... 53. *C. microsepala*

Corolla glandular-hairy outside, yellow; bracts scale-like; leaves up to 8 cm long, lower surface always with red apex; in montane and lower montane forests on eastern slopes (Morona-Santiago and Pastaza), and in central Peru. ..... 54. *C. orientandina*

Nectary of 1 bilobed gland (rarely 2 but close together); bracts often conspicuous; calyx lobes subequal or unequal, lanceolate, spathulate, ovate, rotundate, orbiculate, or reniform, margin entire or dissected; corolla cylindric or ventricose, 0.7–6 cm long, outside with appressed or erect trichomes, limb subregular or bilabiate, throat up to 15 mm wide; stems glabrescent or with persistent indumentum; leaves up to 60 cm long; pedicels up to 40 mm long.

Leaf pairs each with a persistent, conspicuous, red, ovate to lanceolate bract ca. 2 cm long; the larger leaf in each pair obovate, ca. 12 cm long, lower surface entirely green; calyx lobes subequal, basally dissected, 15–20 cm long; in lowland forests of Esmeraldas. ..... 20. *C. rubribracteata*

Leaf pairs with buds, flowers, or fruits only bearing bracts; the larger leaf in each pair obovate, ovate, lanceolate, or oblanceolate, 4–60 cm long, lower surface often with red patterns; calyx lobes subequal or unequal, dissected or entire, 3–45 mm long.

Larger leaf in each pair ovate, obovate, elliptic, lanceolate, or oblanceolate, 4–20 cm long (oblanceolate leaves only exceed 12 cm long in *C. tenensis,* but this species has corolla limbs with appendages between the lobes); shoots not always plane and horizontal; lower leaf surface either green, red, or purple but never with a conspicuous, contrasting pattern of green and red; bracts reduced and scale-like, never hiding the calyces; corolla 7–55 mm long, limb frequently with an appendage between the lobes, each lobe 2–5 mm long; berries usually globose.

Calyx lobes pectinate, the individual lobes difficult to discern; corolla 25–40 mm long.

Corolla densely villous, 25–28 mm long, limb without appendages between the lobes; flowers nearly sessile; in lower montane forests of northwestern Ecuador (Carchi) and southwestern Colombia. ..... 32. *C. fimbricalyx*

Corolla pilose, 35–40 mm long, limb with appendages 2–4 mm long between the lobes; flowers usually pedicellate; mainly in lower montane forests on western Andean slopes (Azuay, Carchi, Cotopaxi, El Oro, Esmeraldas, Los Ríos, and Pichincha), and in western Colombia. ..... 37. *C. minor*

Calyx lobes entire or with dissected margin, the individual lobes easily discernible; corolla 7–55 mm long.

Pedicels 0–8 mm long; corolla length 7–17 mm; calyx red.

Corolla pilose or glabrescent outside (its color is the color of the epidermis), white with bluish limb; calyx lobes subequal, elliptic to lanceolate; pedicels 4–6 mm long; stem villous; in lower montane forests of northwestern Ecuador (Carchi) and northwestern Colombia. ..... 40. *C. tenella*

Corolla with a densely villous, sericeous, or lanate indumentum outside (its color is the color of the indumentum), white, cream, yellow, or reddish; calyx lobes unequal, lanceolate, obovate, rotundate, orbiculate, or reniform; pedicels 0–8 mm long; stems villous or glabrous.

Upper leaf surfaces and stems nearly glabrous; flowers solitary or several congested in leaf axils; calyx lobes subentire.

Flowers several, congested in leaf axils; the broadest calyx lobe 4–8 mm wide; corolla 9–11 mm long; ovary glabrous; in submontane forests of northwestern Ecuador (Carchi). ..... 35. *C. laevis*

Flowers solitary in leaf axils; the broadest calyx lobe 16–23 mm wide; corolla 13–

17 mm long (in Ecuador); ovary sericeous; in lower montane forests of northwestern Ecuador (Carchi) and Pacific Colombia. ..... 39. *C. rubricalyx*

Upper leaf surfaces appressed pilose, and stems villous; several flowers congested in leaf axils; calyx lobes subentire or incised.

Calyx lobes 8–15 mm long, ovate, dentate; corolla 12–15 mm long; pedicels 2–8 mm long; in lowland forests of western Ecuador (Esmeraldas, Los Ríos, and Pichincha) and southwestern Colombia. ..... 34. *C. herthae*

Calyx lobes 3–6 mm long, lanceolate, margin lobed to pectinate; corolla 7–10 mm long; pedicels 0–3 mm long; in lower montane forests of northwestern Ecuador (Carchi). ..... 38. *C. minutiflora*

Pedicels 8–60 mm long; corolla length 25–55 mm; calyx red or green.

Corolla with a densely villous or lanate indumentum outside (its color is the color of the indumentum), limb lacking appendages between the lobes; calyx lobes ovate or rotundate.

Calyx lobes dissected especially basally; in lowland and lower montane forests, western Andean slopes (Esmeraldas, Imbabura, and Pichincha), Panama, and southwestern Colombia. ..... 30. *C. dissimilis*

Calyx lobes subentire; in lower montane forests of northwestern Ecuador (Carchi). ..... 36. *C. lehmannii*

Corolla pilose or glabrescent outside (its color is the color of the corolla epidermis), limb often with appendages between the lobes; calyx lobes lanceolate.

Upper surface of leaves glabrous apart from the hispid margin, blades elliptic to oblanceolate, 10–15 cm long; stems hispid, trichomes 4–6 mm long, yellow-brown; calyx lobes subentire; corolla lacking purple longitudinal stripes; mainly in lower montane forests on western Andean slopes (Carchi, Esmeraldas, Imbabura, and Pichincha) and in central Peru. ..... 29. *C. ciliata*

Upper surface of leaves appressed pilose, blades lanceolate, oblanceolate, or elliptic, 5–20 cm long; stems villous, trichomes 2–5 mm long, green, yellow, or purple; calyx lobes subentire or dissected; corolla often with purple longitudinal stripes.

Corolla red, limb lacking appendages between the lobes; the width of leaves rarely exceeding 2.5 cm; in lower montane forests of southeastern Ecuador (Morona-Santiago and Zamora-Chinchipe), also from Costa Rica to Peru. ..... 27. *C. anisophylla*

Corolla yellow with purple stripes, limb with appendages between the lobes; the width of leaves usually exceeding 2.5 cm.

Calyx lobes with entire margins; corolla 30–40 mm long; length of leaves rarely exceeding 12 cm; in lower montane forests on eastern slopes (Morona-Santiago, Pastaza, and Zamora-Chinchipe). ..... 28. *C. brenneri*

Calyx lobes with incised margins; corolla 45–55 mm long; length of leaves usually exceeding 12 cm; in lowland forests of northeastern Ecuador (Napo and Pastaza). ..... 41. *C. tenensis*

Larger leaf in each pair oblanceolate, 15–60 cm long; shoots always plane and horizontal (extremely dorsiventral); lower leaf surface often green with contrasting red areas, especially towards the apex and along the margin; bracts often conspicuous and hiding the calyces; corolla 17–60 mm long, limb never with appendages between the lobes; berries usually ovoid.

Calyx lobes incised, laciniate, or pectinate, densely villous or sericeous; bracts rarely conspicuous, never hiding the calyx; corolla never bilabiate; length of pedicels not exceeding 1 cm.

Corolla lobes 25–30 mm long; calyx lobes pectinate, the individual lobes difficult to discern; leaves with 1–2 translucent, red "windows" located along the midrib with the distance from the base of the lamina to the spots ca. ¾ of its length; in lower montane forests of northwestern Ecuador (Carchi) and southwestern Colombia. ..... 10. *C. fililoba*

Corolla lobes 1–7 mm long; calyx lobes incised or laciniate, the individual lobes discernable; leaves lacking translucent, red "windows", but lower surface frequently green with red areas especially apically and along the margin.

Length of corolla 3.5–5 cm, mostly red; lower leaf surface rarely with contrasting red apex; mainly in lower montane forests on eastern Andean slopes (Morona-Santiago, Napo, Pastaza, Tungurahua, and Zamora-Chinchipe), and also from Colombia to Bolivia. ..... 14. *C. inaequilatera*

Length of corolla 2.5–3.5 cm, mostly yellow; lower leaf surface often with contrasting red apex.
Diameter of corolla in throat 2–4 mm; lower leaf surface with no contrasting red apex; in lowland forests in Napo, but also widespread in northern South America and West Indies. ..... 21. *C. sanguinea*
Diameter of corolla in throat 6–9 mm; lower leaf surface usually with contrasting red apex.
Inflorescences and stems brown-hispid; montane forests of eastern and western Andean slopes (Carchi, Tungurahua, and Zamora-Chinchipe) and in western Colombia. ..... 11. *C. fuscihirta*
Inflorescences and stems yellow- or green-villous; mainly in lowland and lower montane forests of eastern Ecuador (Morona-Santiago, Napo, Pastaza, and Tungurahua) and northeastern Peru. ..... 24. *C. villosissima*

Calyx lobes lanceolate or ovate with entire or serrate margins (occasionally incised, but then mostly hidden by ovate bracts), densely villous, sericeous, or sparsely pilose; calyx often hidden by conspicuous ovate bracts; corolla often bilabiate; length of pedicels often exceeding 1 cm.
Leaves with a contrasting 4–8 mm wide margin all the way around; pedicels 1.5–2.5 cm long; calyx lobes 8–11 mm long, with glandular trichomes; stamens exserted; corolla never bilabiate; bracts reduced and scale-like; in lowland forests of northwestern Ecuador (Esmeraldas) and western Colombia. ..... 18. *C. purpurimarginata*
Leaves rarely with contrasting red or purple margin all the way around (and if so, the contrasting is much wider towards the apex); pedicels 0–5 cm long; calyx lobes 10–40 mm long, rarely with glandular trichomes; stamens included, subincluded, or exserted (but only exserted in combination with bilabiate corollas); corolla often bilabiate; bracts often conspicuous.
Secondary veins of leaves of 5–6 pairs, the width of the blade not exceeding 3 cm, the length of the blade at least 5 times the width; in lower montane forests of northwestern Ecuador (Carchi) and western Colombia. ..... 16. *C. longinervosa*
Secondary veins of leaves of 8–15 pairs, the width of the blade usually exceeding 3 cm, the length of the blade 2.5–4.5 times the width.
Calyx lobes ovate and subequal, pale green, not hidden by bracts; corolla white, limb subregular, 10–12 mm wide; in lowland and lower montane forests on western slopes in Ecuador (Carchi, Cotopaxi, Esmeraldas, Imbabura, and Pichincha) and western Colombia. ..... 7. *C. eburnea*
Calyx lobes mostly lanceolate, and if ovate usually unequal, mostly green or red, often hidden by bracts; corolla yellow or red (rarely white, but then with bilabiate limb), limb subregular or bilabiate, 4–40 mm wide.
Leaves with 1–2 translucent red "windows" located along the midrib with the distance from the base of the lamina to the spots ca. ¾ of its length; calyx lobes ovate; limb bilabiate; in lower montane forests of northwestern Ecuador (Carchi), as well as northwestern Colombia and Panama. ..... 15. *C. kalbreyeriana*
Leaves with no translucent red "windows", but lower surface frequently green with red areas apically and along the margin; calyx lobes ovate or lanceolate; limb bilabiate or subregular.
Calyx lobes unequal, the largest ovate to lanceolate, at least 7 mm wide, often purple along the midrib, bracts not hiding the calyx; limb bilabiate; leaves up to 60 × 15 cm.
Largest leaves exceeding 28 × 10 cm; flowers nearly sessile; in lower montane forests of northwestern Ecuador (Carchi) and western Colombia. ..... 12. *C. gigantifolia*
Largest leaves not exceeding 28 × 10 cm; flowers pedicellate; mainly in lowland and lower montane forests of the western Andean slopes in Ecuador (Cañar, Carchi, Cotopaxi, El Oro, Esmeraldas, Guayas, Imbabura, Los Ríos, Manabí, and Pichincha) and western Colombia. ..... 17. *C. picta*
Calyx lobes equal, lanceolate, at least 2 mm wide, rarely purple along the midrib, bracts often hiding the calyx; limb bilabiate or subregular; leaves up to 40 × 10 cm.
Pedicels 1–5 cm long; limb bilabiate; bracts lanceolate to linear, rarely ovate;

mainly in lowland and lower montane forests of eastern Andean slopes in Ecuador (Morona-Santiago, Napo, Pastaza, and Tungurahua), southeastern Colombia, and eastern Peru. ..... 8. *C. ericae*

Pedicels 0–1 cm long; limb subregular or bilabiate (always in combination with ovate bracts that hide the calyces); bracts mostly ovate.

Limb bilabiate, outside sericeous; individual inflorescences "fusing together" due to overlapping ovate bracts that hide pedicels and calyces.

Corolla limb with contrasting red or purple margins; inflorescences with 2 bracts; lower leaf surface green with contrasting red apex; mainly in lower montane and montane forests of western Andean slopes in Ecuador (Azuay, Cañar, Carchi, Cotopaxi, Esmeraldas, Los Ríos, and Pichincha) and southwestern Colombia. 6. *C. densibracteata*

Corolla limb not with contrasting red or purple margins; inflorescences with 3–8 bracts; lower leaf surface usually uniformly green, red, or purple.

Lower leaf surface only sparsely pilose, mostly green; corolla cream, white, or pale yellow; in montane forests of the eastern Andean slopes in Napo and Zamora-Chinchipe. ..... 2. *C. albiflora*

Lower leaf surface sericeous, mostly with a purplish sheen; corolla bright yellow; in montane forests of the eastern Andean slopes (Morona-Santiago, Pastaza, and Zamora-Chinchipe) and in northern Peru. ..... 23. *C. tessmannii*

Limb subregular, outside sericeous or villous; individual inflorescences occasionally "fusing together" due to overlapping bracts.

Maximum diameter of corolla 10–15 mm, limb with contrasting red coloration; ovate bracts conspicuously wine-red, 4–7 cm long; lower surface of leaves usually violet or purplish but often green toward the apex; stigma always with contrasting purple coloration, in montane forests of western Ecuador (Azuay, El Oro, and Pichincha). ..... 9. *C. eubracteata*

Maximum diameter of corolla 4–7 mm, limb rarely with contrasting red coloration; ovate bracts red, green, or yellow-green, 1–6 cm long; apical part of leaves usually with contrasting red coloration; stigma rarely purple.

Corolla limb 10–12 mm wide with lobes 6–8 mm long; in lowland forest of western Ecuador (Los Ríos and Pichincha(?)). ..... 3. *C. asteroloma*

Corolla limb 4–9 mm wide with lobes 2–5 mm long.

Lower leaf surface uniformly colored apart from a 0.5–1.5 mm wide red margin; corolla 1.7–2.2 cm long; margins of calyx lobes with 3–5 teeth; in lower montane and montane forests of the eastern Andean slopes (Napo and Pastaza). ..... 4. *C. capillosa*

Lower leaf surface always with a contrasting red apical part; corolla 2.2–5.5 cm long; margin of calyx lobes entire.

Length of ovate bracts usually exceeding 3.5 cm, inflorescences mostly "fusing together" due to these overlapping bracts; stems, bracts, calyces, and corolla gray-villous; lower leaf surfaces with contrasting red coloration both apically and along the margins; corolla 3.2–4.2 cm long; in lower montane and montane forests on western Andean slopes (Azuay, Bolívar, Carchi, and Pichincha). ..... 5. *C. cinerea*

Length of ovate bracts usually not exceeding 2.5 cm, inflorescences mostly not "fusing together"; stems especially and corollas occasionally villous; lower leaf surfaces usually only with a contrasting red apex; corolla 2.2–5.5 cm long.

Calyx lobes unequal; corolla 2.2–3 cm long; stems and corollas villous; in deciduous lowland forests of southwestern Ecuador (Bolívar, Cotopaxi, El Oro, Guayas, Los Ríos, and Manabí). ..... 22. *C. schimpffii*

Calyx lobes subequal; corolla 3–5.5 cm long; stems and corollas occasionally villous (mostly in eastern Ecuador).

Corolla sericeous or villous, limb 5–9 mm wide, lobes 3–4 mm long; bracts red or green, occasionally hiding the calyces; in lower montane and montane forests of the eastern Andean slopes (Morona-Santiago, Napo, Pastaza, Tungurahua, and Zamora-Chinchipe). . . 13. *C. guttata*

Corolla sericeous, limb 3–5 mm wide, lobes 1–2 mm long; bracts ovate, conspicuously red and always partly hiding the calyces; in lowland and lower montane forests of western Ecuador (Carchi, Esmeraldas, El Oro, Los Ríos, and Pichincha). . . . . 19. *C. rubriacuta*

THE ECUADORIAN SPECIES OF COLUMNEA

The species are arranged alphabetically within the sections *Bucinellina, Collandra, Columnea, Ortholoma, Pentadenia,* and *Stygnanthe.* At least one collection of each species is cited from each Ecuadorian province. However, all collections of newly described species, including those from other countries, are cited (except in the case of the most common newly described species, *Columnea densibracteata*). Also, all collections are cited for species of which fewer than 10 Ecuadorian collections are known. Synonyms described from non-Ecuadorian material have been included where possible, but only when the material has been studied.

Types of several species that were in the Berlin herbarium (B) are now not extant due to the destruction caused by bombing in 1943. The loss of these type specimens has been confirmed by two visits to Berlin and extensive discussion (most recently in September, 1990) with Paul Hiepko, curator at the Berlin herbarium. Where duplicates of the types are known, lectotypes have been chosen. If no duplicates of the types have been located, neotypes have been selected.

A. Section **Bucinellina** (Wiehl.) Kvist & L. Skog, stat. nov.

Bucinella Wiehl. in Selbyana **2:** 91. 1977 (nom. illeg.). TYPE: *Bucinella nariniana* Wiehl. = *Columnea nariniana* (Wiehl.) Kvist & L. Skog.

Bucinellina Wiehl. in Selbyana **5:** 381. 1981. TYPE: *Bucinellina nariniana* (Wiehl.) Wiehl. = *Columnea nariniana* (Wiehl.) Kvist & L. Skog.

1. **Columnea nariniana** (Wiehl.) Kvist & L. Skog, comb. nov. *Bucinella nariniana* Wiehl. in Selbyana **2:** 91. 1977. *Bucinellina nariniana* Wiehl., Selbyana **5:** 381. 1981. TYPE: COLOMBIA: NARIÑO: *Wiehler & Williams 72201* (SEL, HOLOTYPE).

OTHER COLLECTION: ECUADOR: CARCHI: San Marcos, 600 m, *Kvist et al. 48815* (AAU).

DISTRIBUTION: Extreme northwestern Ecuador and adjacent Colombia (Nariño).

DISTINGUISHING FEATURES: The shoots are slender and often pendent, the leaf pairs are unequal with the smaller leaf in a pair being reduced by about 50% (0.8–1.5 cm long rather than 2–2.5 cm), the calyx is red and the lobes are ovate to oblanceolate, up to 8 mm long, the yellow subventricose corolla is ca. 2 cm long, the limb has 2 patent dorsal lobes and 3 reflexed lateral and ventral lobes, and the berry is flattened and depressed rather than globose or ovoid.

NOTES: The reduction of the genus *Bucinellina* to the section *Bucinellina* is discussed above (see Discussion of Sections).

In addition to *Bucinella nariniana,* Wiehler described *Bucinella paramicola* (in

Selbyana **2:** 91. 1977) and then transferred the species to *Bucinellina* as *Bucinellina paramicola* (in Selbyana **5:** 381. 1981). This latter species is so far only known from the Department of Nariño in adjacent Colombia, but is here transferred to *Columnea*: **Columnea paramicola** (Wiehl.) Kvist & L. Skog, comb. nov.

B. Section **Collandra** (Lem.) Benth.

Columnea L. section *Collandra* (Lem.) Benth. Gen. Pl. **2:** 1009. 1876.
Collandra Lem. in Fl. Serres Jard. Eur. **3:** 11, *pl. 223.* 1847. TYPE: *Collandra pilosa* Lem. = *Columnea aureonitens* Hook.
Columnea L. subgenus *Collandra* (Lem.) J. Hanst. in Linnaea **34:** 383. 1865.

2. **Columnea albiflora** Kvist & L. Skog, sp. nov. TYPE: ECUADOR: NAPO: Baeza–Tena road, above Jondachi, southern slope of Cordillera de Guacamayos, montane rain forest, 1700 m, 7 Feb. 1980, *Harling & Andersson 16363* (US, HOLOTYPE; GB, ISOTYPE).

Differt a *Columnea densibracteata* Kvist & L. Skog corollis limbis non purpureis tubisque cremeis vel flavidis, a *C. tessmannii* Mansf. foliis magnis indumentis inconspicuis non dense sericeis.

Shrubs, terrestrial or less commonly epiphytic, to 2 m tall, shoots strongly dorsiventral. Stems glabrescent to pilose near apex, diam. to 12 mm, internodes 1–3 cm long. Leaves strongly anisophyllous, nearly sessile; the larger leaf in a pair oblanceolate to falcate, 15–45 × 4–10 cm, apex acute to acuminate, base rounded, upper surface bright green, pubescent, lower surface pilose, pale yellow-green, usually uniformly colored, occasionally reddish apically and along margin but colors not markedly contrasting, margin weakly serrate, veins ca. 15 per side, orange, red, or yellow; the blade of the smaller leaf in each pair lanceolate, 2–5 cm long. Inflorescences in axils of the larger leaf in each pair, of 1–5 flowers; bracts 3–8, the largest bract ovate to elliptic with acuminate apex, cream to pale green with conspicuous rose or pink midrib, 3–8 × 1.5–3.5 cm, hiding the smaller, usually lanceolate bracts, calyces, and most of corolla tubes; pedicels short, occasionally to 2.5 cm long, with glands below floral tube; calyx lobes subequal to unequal, lanceolate, pilose, light green, 2.2–3.5 cm long, 2–6 mm wide at base, margin subentire; corolla subventricose, 5–7 cm long, basally gibbous dorsally, diam. 4–6 mm at base, widened medially or just above to 11–17 mm, diam. 7–13 mm at throat, tube 3.5–4.5 cm long, outside white, sericeous, inside pilose, lower lip (ventral lobe) reflexed, ovate, 0.8–1.3 cm long, inside white with 2 purple lines stretching from base of lip ca. 8 mm down in tube, upper lip (lateral and dorsal lobes) patent, 1.5–2.5 cm long, white, glandular-hairy; filaments 5–6 cm long, white-pilose, connate for ca. 5 mm at base, anthers exserted, white, ca. 2 × 2 mm; nectary of 1 bilobed or irregularly lobed gland, rarely of two free glands, 1.5–2.5 mm high; ovary sericeous, style 5.5–6.5 cm long, glandular-hairy, white, stigma stomatomorphic, purple. Berries ovoid, ca. 2 cm long, diam. ca. 1.2 cm, pink, pilose; seeds ellipsoid, ca. 1.2 × 0.5 mm.

OTHER COLLECTIONS: ECUADOR: NAPO: Baeza–Lago Agrio, km 18, Puente Sardinas Grandes, 1675 m, *Balslev & Madsen 10557* (AAU, NY); Cosanga, 1900 m, *Boeke & McElroy 428* (SEL, US); Lago Agrio–Baeza road, km 33, *Croat 58728* (MO); Cosanga, 1850 m, *Harling & Andersson 16190* (US); Union of Río Borja and Río Quijos, 1750 m, *Holm-Nielsen et al. 26128* (AAU), 1770 m, *Holm-Nielsen et al. 26209* (AAU); 5 km NW of Borja, 1950 m, *Holm-Nielsen et al. 26432* (AAU), 1950 m, *Holm-Nielsen et al. 26463* (AAU, QCA, US); Río Borja, 1760 m, *Holm-Nielsen et al. 26577* (AAU); Slopes of Guagra Urcu, above Río Bretania, 2000–2200 m, *Holm-Nielsen et al. 26828* (AAU); Cosanga, 2125 m, *Kirkbride & Chamba R. 4197* (MO), 1920 m, *Kirkbride & Chamba R. 4286* (NY); 30 km E of Baeza, 2100 m, *Plowman 3922* (S). ZAMORA-CHINCHIPE: Between Valladolid and Achupallas, 2000–2500 m, *Steyermark 54742a* (F, US).

DISTRIBUTION: The montane forests of the eastern Andean slopes in Ecuador. This species is only known from a relatively small area of the Napo province, except for the solitary, apparently isolated collection from Zamora-Chinchipe near the Peruvian border.

DISTINGUISHING FEATURES: The most similar species are *Columnea densibracteata* and *C. tessmannii. Columnea albiflora* differs from the former species by having corollas in which the limb and the tube have the same cream or pale yellow color rather than having the limb with a contrasting purple margin, by having inflorescences with three to eight rather than two bracts, and by having uniformly colored lower leaf surfaces rather than having a contrasting red apical quarter part of the blade. *Columnea albiflora* differs from *C. tessmannii* by having cream to pale yellow instead of bright yellow corollas, an inconspicuous indumentum instead of a dense sericeous indumentum, and usually larger leaves.

NOTES: One specimen (*Kirkbride & Chamba R. 4286*) was found to have a nectary of two free glands that were not particularly closely adjacent (FIGURE 2U). Among the species referred to section *Collandra,* two free glands have otherwise been seen only once in *C. longinervosa.*

3. **Columnea asteroloma** (Wiehl.) L. Skog in Taxon **30:** 506. 1981. *Dalbergaria asteroloma* Wiehl. in Selbyana **2:** 70, *pl. 20B.* 1977. TYPE: Cultivated material originally from Ecuador, Prov. Los Ríos, Montañas de Ila, *Wiehler 77109* (SEL, HOLOTYPE).

OTHER COLLECTIONS: ECUADOR: Los Ríos; Montañas de Ila, road from Patricia Pilar to 24 de Mayo, 540 m, *Dodson 6100* (SEL), 600 m, *Dodson & Gentry 10329* (MO, SEL); Centinella ridge area, 12 km E of Patricia Pilar, 400 m, *Hansen et al. 7768* (SEL).

DISTRIBUTION: Western Ecuador. *Columnea asteroloma* is among the rarest of the *Columnea* species in Ecuador, being restricted to a small area bordering the provinces of Los Ríos and Pichincha. This species is probably threatened by extinction, as little forest remains in this region (see Endangered Species).

DISTINGUISHING FEATURES: Several features of *Columnea asteroloma* appear intermediate between *C. eburnea* and the species complex including *C. schimpffii* and *C. rubriacuta.* The lanceolate instead of ovate calyx lobes and the yellow instead of white corollas set *C. asteroloma* apart from the first species, while the much wider limb (10–12 mm wide instead of 4–8 mm) and the longer corolla lobes (ca. 8 mm long instead of ca. 2 mm) set it apart from the latter group of species. The corolla of *C. asteroloma* is 4–5 cm long, and the leaves always have red areas towards the apex and along the margin.

NOTES: Because of its intermediate morphology, the extremely rare and local *C. asteroloma* may actually be a natural hybrid between *C. eburnea* and *C. schimpffii* or *C. rubriacuta.*

4. **Columnea capillosa** Kvist & L. Skog, sp. nov. TYPE: ECUADOR: PASTAZA: Mera, 1100 m, 22 Apr. 1969, *Lugo S. 1158* (GB, HOLOTYPE; SEL, ISOTYPE). FIGURE 3.

Differt a *Columnea cinerea* Kvist & L. Skog foliis pagina inferioribus aeque viridibus (praeter margines perangustos purpureos) corollis brevioribus ca. 2 cm

FIGURE 3. *Columnea capillosa* Kvist & L. Skog. A, habit; B, portion of upper leaf surface; C, bracts; D, flower without corolla, showing glands at base of calyx lobes; E, corolla; F, corolla opened; G, flower opened to expose nectary. (A–E, *Lugo 1158,* GB; F–G, *Lugo 2492,* SEL.)

longis flavisque lobis calycum dense villosis marginibus dissectis limbis subaequalis.

Epiphytic herbs or shrubs, occasionally terrestrial, up to 2 m tall, shoots strongly dorsiventral. Stems villous, diam. to 8 mm, trichomes yellow-brown, internodes 1–5 cm long. Leaves strongly anisophyllus, nearly sessile, the larger leaf in a pair oblanceolate, 12–25 × 3–7 cm, apex acuminate, base cuneate, upper surface dull

green, strigose, lower surface pubescent, yellow-green, often with a very narrow red margin but only rarely with a contrasting red apical part, margin weakly serrate, veins 10–12 per side; the blade of the smaller leaf in each pair lanceolate, 1–3 cm long. Inflorescences in axils of the larger leaf of each pair, of 2–5 flowers each with 1–5 mm long pedicels; bracts up to 10, densely congested, the 2 largest bracts ovate with acuminate apex and remotely serrate margin, 2.5–3.5 cm long, deep red or wine-red, smaller bracts 0.5–1.5 cm long, the larger of these ovate and the smaller lanceolate. Floral tube with glands outside at apex. Calyx lobes subequal, lanceolate, violet or reddish, 12–20 mm long, 2–5 mm wide, densely villous with trichomes to 3 mm long, margin dissected, but the indumentum obscures the presence of the 3–5 teeth 1–3 mm long; corolla cylindric, often subventricose, basally and dorsally gibbous, 1.7–2.2 cm long, diam. 3–4 mm at base, widened medially to 5–7 mm, then to 4–6 mm at throat, outside yellow, sericeous to villous, inside pilose, basally glabrous, sparsely glandular-hairy in throat, limb subequal, lobes 1–1.5 mm long and 1.5–2 mm wide at base, yellow with 4 red spots extending from lower 3 lobes into throat; filaments 13–17 mm long, glabrous, connate for 4–5 mm at base, anthers included, coherent, ca. 1.5 × 1.5 mm; nectary a 3-lobed dorsal gland, 1–2 mm high; ovary villous, style 10–13 mm long, basally glabrous to apically pilose, stigma stomatomorphic. Berries globose, ca. 10 × 8 mm; seeds ellipsoid, ca. 1 × 0.5 mm.

OTHER COLLECTIONS: ECUADOR: NAPO: Path Cotapino–Río Bueno, 400 m, *Harling et al. 7157* (GB). PASTAZA: Puyo–Tena road, km 14, 1160 m, *Croat 49671* (MO, US); Puyo–Macas road, km 19, 1200 m, *Croat 50537* (MO, US); Puyo–Macas road, 3 km SE of Veracruz, 900 m, *Harling & Andersson 16810* (GB); Puyo–Arajuno road, 1–5 km SW of Diez de Agosto, 900 m, *Harling & Andersson 16884* (GB); Veracruz (Indillama)–Canelos road, km 11, *Lugo S. 60* (SEL); Veracruz, *Lugo S. 1081* (GB, SEL); 8 km E of Veracruz, *Lugo S. 1106* (GB, SEL), *Lugo S. 1107* (GB); Between Nalpi and Canelos, *Lugo S. 1510* (GB, SEL); Vicinity of Canelos, Río Pacayacu, *Lugo S. 1602* (GB, SEL); Vicinity of Canelos, Puerto Ubilla, *Lugo S. 1702* (GB, SEL); 15–20 km NE of Puyo, Colonia 24 de Mayo, *Lugo S. 2492* (SEL); 5 km E of Puerto Sarayacu, Shiguacocha, *Lugo S. 3862* (GB, SEL); 12 km E of Puyo, Cabeceras along Río Bobonaza, *Lugo S. 4616* (GB); 8 km from Puyo, village of Río Chico, 1000 m, *Shemluck 266* (F). TUNGURAHUA: 5 km W of Baños, 2300 m, *Dodson & Thien 981* (US).

DISTRIBUTION: Endemic to the eastern slopes of the Andes in Ecuador. Apparently, this species is common in parts of the province Pastaza, but has elsewhere only been collected once in the adjacent provinces of Napo and Tungurahua.

DISTINGUISHING FEATURES: The following combination of features sets *Columnea capillosa* apart from related species such as *C. cinerea* (see this latter species): (1) the corolla is ca. 2 cm long and yellow; (2) the densely villous calyx lobes have a dissected margin with 3–5 "teeth"; and (3) the lower leaf surface is uniformly colored (apart from a very narrow red margin).

NOTES: The berries are globose rather than ovoid as is usual in section *Collandra*.

5. **Columnea cinerea** Kvist & L. Skog, sp. nov. TYPE: ECUADOR: PICHINCHA: Along Río Guayllabamba, Nuevo Azuay, rain forest, 22 July 1980, 1000 m, *Holm-Nielsen, Jaramillo & Coello 24587* (AAU, HOLOTYPE; US, ISOTYPE).

Differt a *Columnea capillosa* Kvist & L. Skog foliis pagina inferioribus apicibus et marginibus rubris ad purpureos corollis longioribus ca. 4 cm longis villosis.

Epiphytic herbs or shrubs, occasionally terrestrial, to 1.5 m tall, shoots strongly dorsiventral. Stems grayish-villous, diam. to 8 mm, internodes 1–3 (–10) cm long. Leaves strongly anisophyllous, pubescent, nearly sessile; the larger leaf in a pair oblanceolate, 15–35 × 3–10 cm, apex acute to acuminate, base acute, lower surface green but with red apical part and usually with red margin, weakly serrate, veins 10–12 per side, often red; the blade of the smaller leaf in a pair lanceolate, 2–4

cm long. Inflorescences often densely congested, in axils of the larger leaf in each pair, of 3–6 nearly sessile flowers; bracts to 8, ovate, red or yellow-green, outside sericeous to villous, inside nearly glabrous, margin serrate, the largest to 4 cm long and 3 cm wide and concealing the smaller ones 1–3 cm long. Calyx lobes subequal, lanceolate, 12–20 mm long, 2–4 mm wide, green, often red apically, outside grayish-villous, inside nearly glabrous, margin serrate; corolla cylindric, often subventricose, basally dorsally gibbous, 3.2–4.2 cm long, diam. 3–5 mm at base, widened to 5–9 mm, then to 4–6 mm in throat, outside pale green, pale yellow or cream, villous especially apically, inside pilose, throat glandular-hairy, limb subequal, lobes brownish-yellow inside, 1.5–2.5 × 2–3 mm; filaments 25–35 mm long, glabrous, connate for ca. 4 mm at base, anthers included, ca. 1.5 × 1.5 mm; nectary a 3-lobed dorsal gland, ca. 1.5 mm high; ovary sericeous, style 25–35 mm long, pilose, stigma stomatomorphic. Berry globose, ca. 10 × 8 mm; seeds ellipsoid to narrowly ellipsoid, ca. 1 × 0.4 mm.

OTHER COLLECTIONS: ECUADOR: AZUAY: Chacanceo, slopes toward Río Putucay, Loma de La Plata, 1450 m, *Steyermark 52664* (F, US). BOLÍVAR: Between Guayllanac and hacienda "Rose Mercedes", *Acosta Solís 5298* (F). CARCHI: Maldonado–Tulcan road, km 12, 2230 m, *Gentry & Shupp 26651* (MO); Above Maldonado, *Luer et al. 3390* (SEL). PICHINCHA: 11 km W of Tandápi, Río Chictoa (tributary of Río Pilatón), 1350–1550 m, *Gentry et al. 12114* (MO, US); Santo Domingo–Quito road, Tandápi (Corneja Astarga), 1100 m, *Harling et al. 9156* (GB, SEL); Pacto–Nuevo Azuay road, 5 km N of La Esperanza, 1300 m, *Holm-Nielsen et al. 24546* (AAU); Chillogallo–Santo Domingo road, below Chiriboga, 1600 m, *Holm-Nielsen et al. 24838* (AAU); Aloag–Santo Domingo road, Tandápi, 1500 m, *Sparre 13886* (S); Tandápi, 1500 m, *Wiehler & Masterson 7968* (SEL).

DISTRIBUTION: This species is restricted to montane forests on the western slopes of the Andes in Ecuador.

DISTINGUISHING FEATURES: The combination of gray-villous stems, bracts, calyces, and corollas, lower leaf surfaces with red to purple parts both apically and along the margin, and the ca. 4 cm long villous corollas with subequal limbs and small lobes set *Columnea cinerea* apart. The closest relatives apparently are *C. guttata, C. rubriacuta,* and *C. schimpffii,* but none of these species has the conspicuous indument of *C. cinerea,* and their inflorescences do not "fuse together" due to overlapping bracts. Another relative may be *C. capillosa* from the eastern Andean slopes, but this latter species differs by having uniformly colored lower leaf surfaces (apart from a very narrow purple margin) and by having much shorter corollas ca. 2 cm long. A similarity between these two species is that both *C. capillosa* and *C. cinerea* have globose berries—an unusual feature in section *Collandra.*

NOTES: The nectary is three-lobed rather than a bilobed dorsal gland (FIGURE 2S, W).

6. **Columnea densibracteata** Kvist & L. Skog, sp. nov. TYPE: ECUADOR: AZUAY: Chacanceo–Molleturo road, between Río Blanco and Río Norcay, dense rich jungle, 4 June 1943, 1520 m, *Steyermark 52826* (US, HOLOTYPE; F, ISOTYPE). FIGURE 4.

Differt a *Columnea albiflora* Kvist & L. Skog et *C. tessmannii* Mansf. limbis corollarum marginibus rubris vel purpureis foliis pagina inferioribus apicibus rubris.

Herbs or shrubs, terrestrial or epiphytic, shoots strongly dorsiventral, to 3 m long. Stems glabrescent to sericeous near apex, diam. to 10 mm, internodes 1–1.5 (–7) cm long. Leaves strongly anisophyllous, nearly sessile, pubescent; the larger leaf in a pair oblanceolate to falcate, 10–25 (–35) × 3–10 cm, apex acute

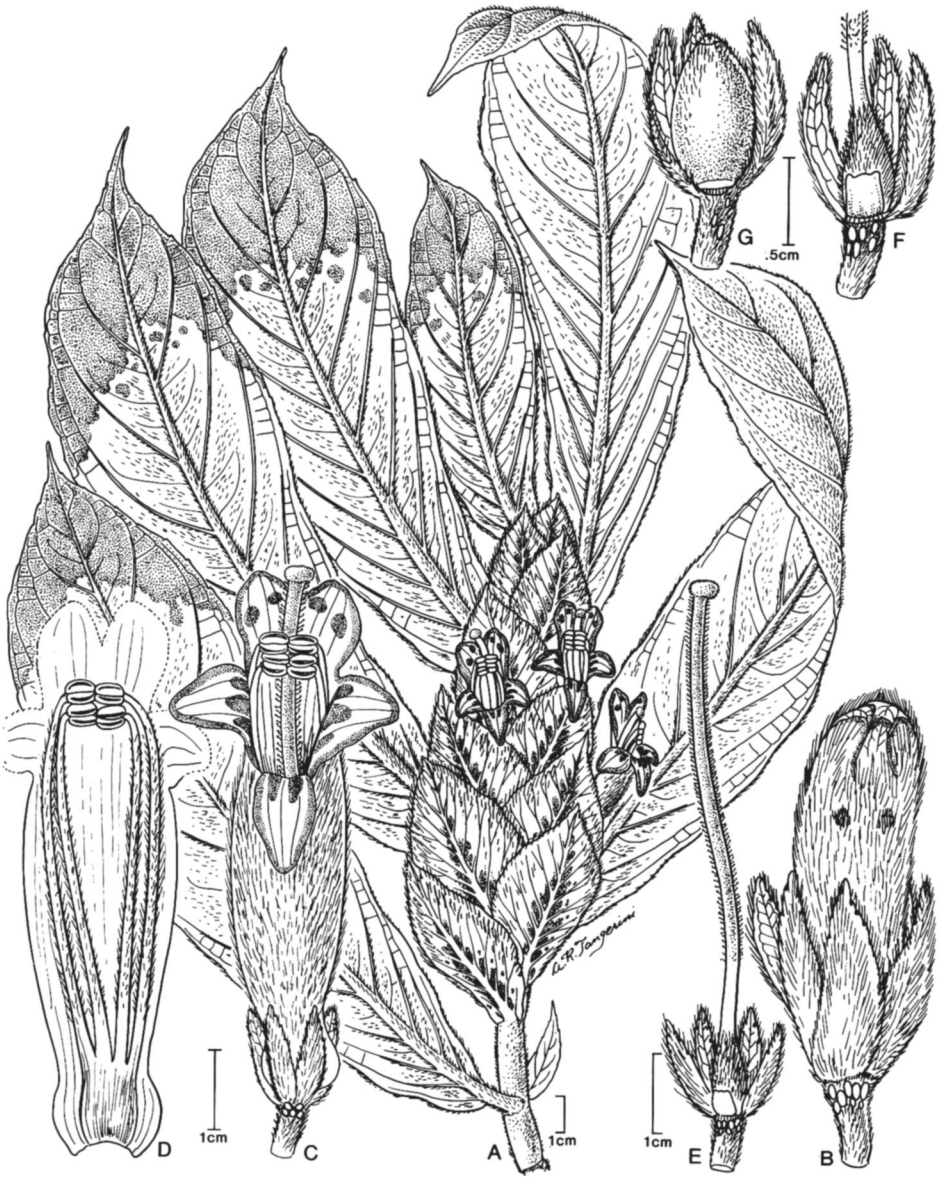

FIGURE 4. *Columnea densibracteata* Kvist & L. Skog. A, habit; B, unopened flower showing glands on floral tube; C, flower; D, corolla opened to show attachment of stamens; E, flower without corolla to expose nectary and pistil; F, nectary; G, fruit. (A, *Steyermark 52826,* US; B–G, *Dodson & Gentry 10225,* MO, *Harling 545,* S, *Luer et al. 3388,* SEL.)

to acuminate, base acute, upper surface dull green, lower surface lighter green or less commonly entirely reddish or purple, the apical quarter with contrasting red or purple, margin weakly serrate, veins 10–13 per side; the blade of the smaller leaf in a pair lanceolate, to 4 cm long. Inflorescences densely congested in axils of the larger leaf in each pair, of 1–4 flowers; bracts 2, conspicuous and hiding

the calyces and most of each corolla tube, yellow or pale green, often partly purple, the largest ovate, 4–7 × 3–5 cm, the smaller lanceolate, 2–4 × 1–2 cm; pedicels to 1 cm long. Floral tube with red glands; calyx lobes subequal, lanceolate, 0.8–2.8 cm long, green to violet, sericeous especially outside, margin weakly serrate; corolla subventricose, basally dorsally gibbous, 4.5–6.5 cm long, diam. 3–5 mm at base, widened medially to 7–13 mm, then to 6–11 mm in throat, outside yellow, apically sericeous, inside nearly glabrous, limb bilabiate, margin red or purple, lower lip (ventral lobe) ovate, reflexed, 8–12 mm long, with 2 purple dots at base, upper lip (lateral and dorsal lobes) 14–34 mm long, inside glandular-hairy, free parts of individual lobes 4–7 mm long, with purple dots basally, dorsal lobes connate; filaments 4–5 cm long, pilose, connate for ca. 5 mm at base, anthers exserted, coherent, ca. 2 × 2 mm; nectary a dorsal gland, bilobed, trilobed or irregularly lobed, ca. 1.5 mm high; ovary pilose, style 4.5–5.5 cm long, pilose, stigma purple, stomatomorphic. Berry ovoid, ca. 10 × 5 mm; seeds ellipsoid, ca. 0.7 × 0.3 mm.

REPRESENTATIVE COLLECTIONS: COLOMBIA: CAUCA: Near Argelia, Quebrada La Laguna, 2000 m, *Core 1264* (US). NARIÑO: Railroad line to Tumaco, La Guayacana, 80 m, *Vogel 9* (US). ECUADOR: CAÑAR: Guayaquil–Cuenca road, 10 km E of Cochan, 1980 m, *Gentry et al. 30821* (MO (2), SEL, US). CARCHI: Tulcán–Maldonado road, 10 km SE of Maldonado, 2200–2400 m, *Harling & Andersson 12300* (GB, SEL); above Maldonado, 2000 m, *Luer et al. 3388* (SEL). COTOPAXI: Quevedo–Latacunga road, 3 km E of El Palmar, *Dodson & Gentry 10225* (MO, SEL). ESMERALDAS: Parroquia de Concepción, Playa Rica, 105 m, *Mexía 8412* (BH, F, GB, NY). LOS RÍOS: Samama, Hacienda Clementina, 700 m, *Harling 545* (S). PICHINCHA: New Quito–Santo Domingo road, 1700 m, *Kvist & Barfod 49087* (AAU, US).

DISTRIBUTION: Southwestern Colombia and western Ecuador. This species is relatively common in the montane forests of Ecuador, but only the two cited collections are known from Colombia.

DISTINGUISHING FEATURES: Only three species occurring in Ecuador have the combination of conspicuously bilabiate corollas and large, densely congested bracts hiding the calyces. *Columnea densibracteata* differs from the other two species, *C. albiflora* and *C. tessmannii,* by having flowers in which the margin of the limb has a contrasting red or purple color, by having inflorescences with only two bracts, and by having lower leaf surfaces with a contrasting red apical part. In addition, both of these latter species occur on the eastern slopes of the Andes rather than on the western slopes. A similar sympatric species is *C. eubracteata,* but the corolla of the latter species is not bilabiate (see *C. eubracteata*). *Columnea densibracteata* is among the most sturdy and fruticose species in the genus.

NOTES: *Columnea densibracteata* is by far the most common of the species newly described in this work. Mansfeld (1937) described *C. eubracteata* from a type at Berlin (later destroyed). His description strongly indicates that *C. eubracteata* was based on material of a related but much rarer species, i.e., his plant had villous stems, all the corolla lobes were patent, and the apex of the lower leaf surface was not contrasting red (see *C. eubracteata*).

The flowers of *Columnea densibracteata* are apparently usually yellow in Pichincha but cream in Carchi. However, in both areas the limb always has a red margin.

7. **Columnea eburnea** (Wiehl.) Kvist & L. Skog, comb. nov. *Dalbergaria eburnea* Wiehl. in Selbyana **5:** 378, *pl. 1A.* 1981. TYPE: ECUADOR: PICHINCHA: Old Quito–Santo Domingo road, below Chiriboga, *Wiehler & Masterson 79108* (SEL, HOLOTYPE).

REPRESENTATIVE ECUADORIAN COLLECTIONS: CARCHI: Between Chical and Pailon, 1000 m, *Kvist et al. 48657* (AAU, MO, QCA, QCNE, SEL, US). COTOPAXI: Quevedo–Latacunga road, 3 km E of El Palmar, 800 m, *Dodson & Gentry 10226* (MO, SEL). ESMERALDAS: Río Cayapa, environs of Zapallo Grande, 150 m, *Kvist & Asanza 40870* (AAU). IMBABURA: Lita, 500 m, *Maas & Cobb 4718* (US). PICHINCHA: Aloag–Tandápi–Santo Domingo road, 600 m, *Jaramillo 43* (AAU, NY, QCA).

DISTRIBUTION: Western Colombia (Chocó, Nariño, Valle) and northwestern Ecuador.

DISTINGUISHING FEATURES: The combination of 3–4 cm long white or translucent corollas, 10–12 mm wide limbs, ca. 5 mm long corolla lobes, and 1.5–2 cm long ovate and usually yellow-green calyx lobes (and often bracts of similar shape and color) distinguishes *Columnea eburnea.*

8. **Columnea ericae** Mansf. in Repert. Spec. Nov. Regni Veg. **36:** 123. 1934. *Dalbergaria ericae* Wiehl. in Phytologia **27:** 317. 1973. TYPE: ECUADOR: NAPO: Tena, *Heinrichs 323* (B, HOLOTYPE, no long extant); ECUADOR: NAPO: Río Aguarico, the small tributary Río Wai Si Ayá, 300 m, *Brandbyge, Asanza, Kelly, & Bryan 32643* (AAU, NEOTYPE, here designated; US, ISONEOTYPE).

Columnea archidonae Cuatr. in Anales Ci. Univ. Madrid **4:** 245 (reprint p. 42). 1935. *Dalbergaria archidonae* Wiehl. in Phytologia **27:** 316. 1973. TYPE: ECUADOR: NAPO or PASTAZA: *Isern 497* (MA, LECTOTYPE, here designated; *Isern 188* (F, MA) was also cited as a SYNTYPE by Cuatrecasas).

REPRESENTATIVE ECUADORIAN COLLECTIONS: MORONA-SANTIAGO: N of Macas on border to Parque Nacional Sangai, 1200 m, *Kvist 60428* (AAU). NAPO: 10 km E of Santa Barbara, Sibundoy, 2400 m, *Kvist et al. 60248* (AAU). PASTAZA: Vicinity of Puyo, 750–1000 m, *Skutch 4418* (F, MO, NY, US). TUNGURAHUA: Río Margarjitas, 1225 m, *Penland & Summers 137* (F, US).

DISTRIBUTION: Southeastern Colombia (Amazonas, Caquetá, Huila, Putumayo, and Vaupés), eastern Ecuador, and Peru (Loreto, Pasco, San Martín, and Ucayali).

DISTINGUISHING FEATURES: The combination of leaves with strigose upper surfaces, narrowly lanceolate bracts 1–2 cm long, 1–5 cm long pedicels, subequal, lanceolate to linear 1.5–3 cm long calyx lobes, and 4.5–6.5 cm long conspicuously bilabiate yellow corollas distinguishes typical *Columnea ericae* specimens. In addition, numerous specimens having features intermediate between *C. ericae* and *C. guttata* are referred to the former species. These latter plants usually have nearly glabrous upper leaf surfaces, nearly sessile flowers, and frequently possess conspicuous, lanceolate or ovate bracts. However, their corollas are strongly bilabiate and similar to those of typical *C. ericae* specimens, and based on this latter attribute such plants are here referred to *C. ericae.* The abundance of intermediate specimens in Ecuador probably is due to extensive hybridization and introgression between *C. ericae* and *C. guttata.*

NOTES: *Columnea ericae* has a broad altitudinal distribution, and *C. archidonae,* here reduced to synonymy, was described by Cuatrecasas (1935) based on material from higher elevations than the material on which *C. ericae* was based. In montane forests the leaves are considerably smaller, but the flowers are similar except that the filaments usually are basally connate for ca. 10 mm in plants from the lowland forests but only for ca. 5 mm in plants from montane forests.

9. **Columnea eubracteata** Mansf. in Biblioth. Bot. **116:** 146. 1937. *Dalbergaria eubracteata* Wiehl. in Phytologia **27:** 317. 1973. TYPE: ECUADOR: PICHINCHA: Saloya, 2500 m, *Diels 820* (B, HOLOTYPE, no longer extant); ECUADOR: CARCHI: Tulcan, Olivos, dense virgin forest, 3200–3500 m, 10–13 July 1935, *Mexía 7463* (US, NEOTYPE, here designated; AAU, US, ISONEOTYPES).

OTHER COLLECTIONS: ECUADOR: AZUAY: Chacanceo–Molleturo road, between Río Blanco and Río Norcay, 1520 m, *Steyermark 52824* (US). EL ORO: Cordillera de Dumarí, W and SW of Sambotambo, 1900 m, *Steyermark 54184* (F(2), US). PICHINCHA: Quito–Santo Domingo road, 10–15 km from Tandápi, 2100 m, *Eriksen 59357* (AAU); Santo Domingo–Quito road, Tandápi (Corneja Astargo), 2000 m, *Harling et al. 9351* (GB). Province unknown: Canchacoto, 2000 m, *André 3651* (F).

DISTRIBUTION: This species is a rare but widely distributed endemic of the higher montane forests on the western slopes of the Ecuadorian Andes.

DISTINGUISHING FEATURES: Both sides of the leaves are sericeous, the lower surface is usually violet or purplish but often green toward the apex (in contrast to all other species with a red-green color pattern), the 4–6 cm long ovate bracts are conspicuously red and densely congested, the 5–7 cm long yellow corollas are subventricose and have an unequal limb with patent, purple lobes (but never with a reflexed ventral lobe), and the stigma is large and conspicuously purple. *Columnea eubracteata* is often terrestrial.

The most similar species is *Columnea tessmannii* from the eastern Andean slopes, but this species has conspicuously bilabiate corollas without a contrasting purple margin of the limb. The most similar sympatric species is *C. densibracteata,* which also has a conspicuously bilabiate corolla with a reflexed ventral lobe, but differs by having lower leaf surfaces with a red or purple apical part.

NOTES: According to the label, the neotype selected was collected by Mexía above 3200 meters elevation. This is an exceptionally high elevation for the genus *Columnea,* and all other collections of *C. eubracteata* come from elevations between 1500 and 2500 meters. Mexía possibly gave an erroneous elevation 1000 meters too high.

10. **Columnea fililoba** Kvist & L. Skog, sp. nov. TYPE: ECUADOR: CARCHI: San Marcos, humid low montane forest, 700 m, 28 Nov. 1983, *Kvist, Barfod, & Nissen 48997* (AAU, HOLOTYPE; QCA, QCNE, US, ISOTYPES). FIGURE 5.

Differt a *Columnea incredibilis* Kvist & L. Skog corollis flavis parvis gracilis lobis corollarum brevioribus hirsutis.

Terrestrial herbs, to 50 cm tall, shoots strongly dorsiventral. Stems pilose, diam. to 5 mm, internodes 1–3 (–6) cm long. Leaves strongly anisophyllous; the blade of the larger leaf in each pair oblanceolate, 10–25 × 3–6 cm, apex acuminate, base cuneate, upper surface dull green, glabrous, lower surface light green, pilose, occasionally with a red flush, with 1 conspicuous translucent red spot on each side close to the primary vein, the distance from the base of the lamina to the spots ca. ¾ of its length, veins 6–8 per side, petiole 0.5–1.5 cm long; the blade of the smaller leaf in a pair elliptic, to 8 mm long. Inflorescences in axils of the larger leaf of each pair, of 1–3 nearly sessile flowers; bracts 3–4, scale-like, 5–13 mm long. Calyx lobes subequal, 2.5–4.5 cm long, pectinate, yellow-green, hispid, trichomes 2–5 mm long, unbranched, of 6–8 translucent cells; corolla ventricose, basally and dorsally gibbous, 20–24 mm long (apart from corolla lobes), diam. 3–5 mm at base, widened to 6–9 mm, diam. 5–7 mm in throat, outside yellow, sericeous, inside puberulent, limb subequal, lobes filiform, 25–30 mm long, hispid; filaments 18–22 mm long, connate for ca. 5 mm at base, adnate to base of corolla tube for ca. 2 mm, anthers subincluded, coherent, ca. 2 × 1.5 mm; nectary a bilobed dorsal gland, 1–1.5 mm high; ovary sparsely pilose, style 13–17 mm long, glabrous, stigma stomatomorphic. Berry subglobose, ca. 10 × 8 mm, sparsely pilose; seeds narrowly ellipsoid, ca. 1.1 × 0.4 mm.

OTHER COLLECTIONS: COLOMBIA: NARIÑO: Between Buenavista and Barbacoas, slopes to Río

FIGURE 5. *Columnea fililoba* Kvist & L. Skog. A, habit; B, calyx lobes and bracts; C, calyx lobe; D, portion of calyx lobe with trichomes; E, corolla; F, pistil and corolla opened to show attachment of stamens; G, pistil; H, young fruit. (All *Kvist 41641,* AAU, and *Kvist 49877,* AAU.)

Telembí, 200–840 m, *García-Barriga 13192* (US). ECUADOR: CARCHI: San Marcos, 700 m, *Barfod 41641* (AAU), *Øllgaard et al. 57335* (AAU, QCA, US), *Øllgaard et al. 57434* (AAU).

DISTRIBUTION: *Columnea fililoba* is restricted to the lower montane forests on the western Andean slopes in northwestern Ecuador and adjacent Colombia.

DISTINGUISHING FEATURES: *Columnea fililoba* is a very unusual species set apart by its long, narrow corolla lobes and pectinate calyx lobes. Apart from the rare *C. kalbreyeriana* it is the only Ecuadorian *Columnea* with red translucent dots located near the primary vein of the lamina. The only close relatives are two western Colombian species, *C. incredibilis* (Kvist & Skog, 1988a) and an undescribed species, from the Departments of Cauca and Valle, respectively. *Columnea incredibilis* differs by having red corollas with a longer and wider tube and by having longer corolla lobes that are sericeous rather than hirsute. The species from Valle differs from *C. fililoba* by having much shorter corolla lobes and lanceolate rather than pectinate calyx lobes.

NOTES: *Columnea fililoba* is tentatively placed in the section *Collandra* based on the dorsiventral "fern-frond habit" of the shoots and the existence of translucent red areas on the lamina. The former feature characterizes the section *Collandra,* and the latter feature is found in several species of this section (especially in the Colombian Chocó region and Panama). However, the presence of globose rather than the usual ovoid berries of section *Collandra* makes this placement questionable. In addition, it is unclear if the corolla lobes represent an extreme extension of the lobes themselves or if they are derived from the corolla appendages located at the sinuses of the limb as in some species of section *Ortholoma.* If the latter is the case, then *C. fililoba* belongs in section *Ortholoma* rather than section *Collandra* (Kvist & Skog, 1988a).

The translucent areas of the leaves apparently serve to attract pollinating hummingbirds (Jones & Rich, 1972). The function, if any, of the filiform corolla lobes is so far unknown.

11. **Columnea fuscihirta** Kvist & L. Skog, sp. nov. TYPE: ECUADOR: CARCHI: 12 km W of Maldonado, Río Blanco drainage above Chical (tributary of Río San Juan), mostly mature forest, 1300–1500 m, 25 Sept. 1979, *Gentry & Schupp 26590* (AAU, HOLOTYPE; MO, ISOTYPE). FIGURE 6.

Differt a *Columnea florida* C. Morton, *C. pectinata* C. Morton et *C. purpurata* J. Hanst. indumentis hispidis infuscatis.

Epiphytes, shoots to 1 m long, strongly dorsiventral. Stems hispid with trichomes to 5 mm long, diam. to 10 mm, internodes 1–4 (–8) cm long. Leaves strongly anisophyllous, the larger leaf in a pair oblanceolate, rarely obovate, 12–23 × 3–9 cm, apex acute to acuminate, base cuneate, both surfaces pubescent to hispid, often with red apical part, margin subentire, veins ca. 10 per side; the smaller leaf in a pair lanceolate, rarely ovate, 1–6 cm long. Inflorescences in axils of the larger leaf in each pair, of 1–5 nearly sessile flowers, bracts lanceolate, scale-like, to 8 mm long. Calyx lobes usually laciniate, 8–16 mm long, densely hispid to villous, yellow to pale green; corolla cylindric, basally and dorsally gibbous, 3–3.5 cm long, diam. 4–6 mm at base and 6–9 mm at throat, outside yellow, villous, inside glandular-hairy in throat, limb subequal, lobes 0.5–1.5 mm long and 1.5–2.5 mm wide at base; filaments pilose, 30–35 mm long, connate 3–5 mm basally, anthers subincluded, coherent, ca. 1.5 × 1.2 mm; nectary of 1 bilobed, trilobed or irregularly lobed dorsal gland, ca. 1.5 mm high; ovary villous, style 25–30 mm long, glabrous, stigma stomatomorphic. Fruit and seeds not seen.

OTHER COLLECTIONS: COLOMBIA: CAUCA: Moscopán region, Río San José valley, Aguabonito, 2280 m, *Cuatrecasas 23496* (US); Above Palmira, hills of Miraflores, 1200–1600 m, *Pittier 894* (US). VALLE: 17 km from Cali, 2000 m, *Dryander 1965* (US); Río Cali valley, close to Peñas Blancas, *Figueiras*

FIGURE 6. *Columnea fuscihirta* Kvist & L. Skog. A, habit; B, flower with corolla removed; C, portion of calyx lobe to show trichomes; D, flower; E, corolla opened to show stamens; F, ovary and nectary. (All from *Gentry & Schupp 26590,* AAU, *Madison 3871,* SEL, and *Madison et al. 4656,* SEL.)

8386 (US); Cali–Buenaventura road, km 18, side road to Dapa, 1900–2100 m, *Giraldo 24* (MO); La Cumbre, 1700–2200 m, *Killip 11407* (US); W of Cali, San Antonio (near summit of Western Cordillera), 1900–2350 m, *Killip & Hernando García 33905* (US); La Cumbre, 2000–2200 m, *Pennell & Killip 5792* (US). Precise locality unknown: *Triana 220* (US(2)). ECUADOR: CARCHI: Tulcán–Maldonado road, km 71, Maldonado Valley, 2150 m, *Holm-Nielsen et al. 6017* (AAU); Vicinity of Maldonado, 1600–1900 m, *Madison 3871* (SEL); Environs of Chical, 12 km W of Maldonado on Río San Juan, 1200 m, *Madison et al. 4656* (SEL). TUNGURAHUA: Baños–Puyo road, 2000 m, *Barfod & Thomsen 49012* (AAU). ZAMORA-CHINCHIPE: Tambo, along Río Valladolid, 2000 m, *Steyermark 54676* (F, US).

DISTRIBUTION: The western Andean slopes of Colombia and northwestern Ecuador, and the eastern Andean slopes of southeastern Ecuador.

DISTINGUISHING FEATURES: The combination of brown-hispid stems, leaves, and inflorescences, and laciniate calyx lobes set *Columnea fuscihirta* apart.

The most closely related Ecuadorian species is *Columnea villosissima,* but the indumentum of this species is yellow-green villous rather than brown-hispid. In addition, *C. fuscihirta* has affinities with the Panamanian species *C. florida* C. Morton (1937), *C. pectinata* C. Morton (1942), and *C. purpurata* Hanstein (1865) (the latter also occurs in adjacent Colombia), but none of these species has the brown-hispid indumentum of *C. fuscihirta.* In addition, *C. florida* differs by having leaves with translucent red "windows", *C. pectinata* differs by having smaller corollas with a sparse indumentum, and *C. purpurata* differs by having larger, intensely red calyx lobes and smaller corollas.

NOTES: In western Colombia there may exist one or two additional related, undescribed species, or else *Columnea fuscihirta* is more variable than circumscribed in this description.

12. **Columnea gigantifolia** Kvist & L. Skog, sp. nov. TYPE: COLOMBIA: NARIÑO: Junín–Barbacoas road, 2–10 km N of Junín, 950 m, 26 July 1986, *Gentry, Benavides, Castillo, & Ramírez 55259* (US, HOLOTYPE; MO, ISOTYPE).

Differt a *Columnea picta* H. Karst. foliis magnissimis floribus fere sessilibus.

Epiphytic or terrestrial climbing shrub, shoots strongly dorsiventral. Stems glabrescent to pubescent near apex, diam. to 8 mm, internodes 2–6 cm long. Leaves strongly anisophyllous, sessile; the larger leaf in a pair obovate to oblanceolate or falcate, 25–60 × 8–15 cm, apex acute to acuminate, base acute to rounded, upper surface green with red apex, glabrescent, lower surface pilose, lighter green or purple but always with purple apical part, margin subentire, veins 15–20 per side; the blade of the smaller leaf in a pair lanceolate, to 3 cm long, caducous. Inflorescences in axils of the larger leaf in each pair, of 2–3 nearly sessile flowers; bracts 1–3, the largest ovate to lanceolate, 1–5 cm long, the smaller ones lanceolate. Calyx lobes unequal, up to 4 cm long, the largest ovate, the smaller lanceolate, glabrescent; corolla basally dorsally gibbous, yellow, 4.5–6.5 cm long, diam. 2–4 mm at base and 5–9 mm at throat, outside sericeous, inside pilose, limb bilabiate, yellow, lower lip (ventral lobe) reflexed, ovate to lanceolate, 10–18 mm long, with 2 purple lines extending from base into throat, upper lip (lateral and dorsal lobes) patent, 1.4–2.8 cm long, inside glandular-hairy, 2 purple lines extending from each lateral lobe down into throat, free part of lobes ca. 5 mm long; filaments 5–6 cm long, pilose, anthers exserted; nectary a 3-lobed dorsal gland, ca. 1.5 mm high; ovary sericeous, style 5.5–6.5 cm long, glandular-hairy, stigma stomatomorphic. Fruit and seeds not seen.

OTHER COLLECTIONS: COLOMBIA: CAUCA: El Tambo, La Costa, 1000 m, *Sneidern 490* (S), 800 m, *Sneidern 768* (S), 1300 m, *Sneidern 835* (S), 1000 m, *Sneidern 836* (S). NARIÑO: Junín-Barbacoas road, km 2–10, 950 m, *Gentry et al. 55348* (MO). VALLE: Western slopes of Western Cordillera, Río Digua valley, 900–1180 m, *Cuatrecasas 14914* (F, US). ECUADOR: CARCHI: San Marcos–Tobar Donoso trail, 660 m, *Barfod 41587* (AAU, QCA, SEL, US); trail between Gualpi Bajo and San Marcos, 1000 m, *Øllgaard et al. 57565* (AAU, QCA).

DISTRIBUTION: Lower montane forests of the Andes in northwestern Ecuador and western Colombia.

DISTINGUISHING FEATURES: This species is a close relative of *Columnea picta* and is primarily set apart by the huge size of its leaves. In addition, the flowers

of *C. gigantifolia* are nearly sessile, while those of *C. picta* are usually pedicellate.

NOTES: Material from Colombia was selected as the type since both Ecuadorian collections are sterile.

The nectary is three-lobed rather than the bilobed gland typical of section *Collandra* (FIGURE 2S, W).

13. **Columnea guttata** Poepp. in Poepp. & Endl., Nov. Gen. et Sp. Pl. **3:** 1. 1840. *Dalbergaria guttata* Wiehl. in Phytologia **27:** 317. 1973. TYPE: PERU: *Poeppig D1481* (W, HOLOTYPE).

Dalbergaria puyana Wiehl. in Selbyana **2:** 104, *pl. 30C.* 1977. TYPE: Cultivated material originally from Ecuador, Prov. Napo, Puyo, *Wiehler 77117* (SEL, HOLOTYPE).

Dalbergaria madisonii Wiehl. in Selbyana **5:** 90, *pl. 4C.* 1978. TYPE: Cultivated material originally from Ecuador, Prov. Morona-Santiago, Cordillera de Cutucú, 25 km SW of Logroño, *Wiehler 79133* "*77133*" (SEL, HOLOTYPE).

REPRESENTATIVE ECUADORIAN COLLECTIONS: MORONA-SANTIAGO: Cordillera de Cutucú, western slopes, trail from Logroño to Yaupi, 1830 m, *Madison et al. 3354* (SEL). NAPO: Puyo, 750–1000 m, *Skutch 4467* (F, MO, NY, US). PASTAZA: 4 km N of Mera, 1200 m, *Øllgaard & Balslev 9185* (AAU). TUNGURAHUA: Confluence of Río Mapoto with Río Pastaza, 1225 m, *Penland & Summers 199* (US). ZAMORA-CHINCHIPE: 3 km E of Paquisha, 1100 m, *Harling & Andersson 23976* (GB, US).

DISTRIBUTION: Eastern Peru (Amazonas, Cuzco, Huánuco, San Martín, and Ucayali), eastern Ecuador, and adjacent Colombia (Putumayo).

DISTINGUISHING FEATURES: The upper leaf surface is appressed pilose to glabrescent, the lower surface has a contrasting red leaf tip, the up to 3 cm long bracts are ovate to lanceolate, the flowers are nearly sessile, the ca. 2 cm long calyx lobes are subequal and have a subentire margin, and the 3–4 cm long yellow corollas have a subequal limb. The most closely related Ecuadorian species is the allopatric *Columnea rubriacuta* from western Ecuador (see this species).

NOTES: *Columnea guttata* and *C. ericae* apparently hybridize in the wild, but the intermediate plants are here referred to the latter species because their limbs are conspicuously bilabiate (see *C. ericae*). The features of *C. guttata* are more stable in Peru than in Ecuador. This may reflect that hybridization with *C. ericae* is rarer in Peru, primarily because this latter species is rare there.

The two species *Dalbergaria madisonii* and *D. puyana* were both described based on material from Ecuador, but their types are very similar to *C. guttata* specimens from Peru.

14. **Columnea inaequilatera** Poepp. in Poepp. & Endl., Nov. Gen. et Sp. Pl. **3:** 1. 1840. *Dalbergaria inaequilatera* Wiehl. in Phytologia **27:** 318. 1973. TYPE: PERU: *Poeppig s.n.* (W, HOLOTYPE).

Columnea ascendens Rusby in Mem. Torrey Bot. Cl. **4:** 239. 1895. *Pentadenia ascendens* Wiehl. in Phytologia **27:** 314. 1973. TYPE: BOLIVIA: Songo: *Bang 853* (NY, HOLOTYPE; BM, E, F, GH, K, MO, NY, PH, US, W, ISOTYPES).

Columnea inaequilatera var. *rhonhofiae* Mansf. in Notizbl. Bot. Gart. Berlin-Dahlem **14:** 37. 1938. TYPE: ECUADOR: PASTAZA: *Schultze-Rhonhof 1839* (B, HOLOTYPE, no longer extant).

REPRESENTATIVE ECUADORIAN COLLECTIONS: MORONA-SANTIAGO: Limón–La Unión road, km 6, 1300 m, *Harling & Andersson 24484* (GB, US). NAPO: Baeza–Tena road, km 40, 1900 m, *Holm-Nielsen 16259* (AAU). PASTAZA: Puyo–Tena road, km 18, 1100 m, *Øllgaard & Balslev 9211* (AAU, MO, NY, SEL). TUNGURAHUA: Pastaza valley, 3 km S of Río Negro, 1400 m, *Kvist 60322* (AAU, COL, M, NY, QCA, QCNE, US). ZAMORA-CHINCHIPE: Valladolid–Río Palanda road, km 7, 1500 m, *Harling & Andersson 21329* (GB, US).

DISTRIBUTION: *Columnea inaequilatera* is a common species on the eastern

Andean slopes from Bolivia northward through Peru, Ecuador, and to southern Colombia (Putumayo).

DISTINGUISHING FEATURES: The combination of large, strongly anisophyllous leaves with a uniformly colored lower surface, the absence of conspicuous bracts, the subequal 12–22 mm long, villous, reddish calyx lobes with a dissected to often laciniate margin, and the 3.5–5 cm long usually red corollas with a subequal to weakly bilobed limb set *Columnea inaequilatera* apart. However, some specimens are difficult to distinguish from *C. villosissima.* Such plants may have lower leaf surfaces with a contrasting red part near the tip and/or smaller yellow corollas. There is possibly some hybridization between *C. inaequilatera* and *C. villosissima.*

NOTES: *Columnea inaequilatera* is usually referred to section *Collandra.* However, there is a striking similarity to *C. tenensis* in section *Ortholoma.* This latter species differs mainly in having conspicuous appendages located at the sinuses of the corolla limb, a feature restricted to section *Ortholoma.*

15. **Columnea kalbreyeriana** Masters in Gard. Chron. n.s., **17:** 44, 216, *pl. 32.* 18 February 1882. *Dalbergaria kalbreyeriana* Wiehl. in Phytologia **27:** 318. 1973. TYPE: COLOMBIA: ANTIOQUIA: Forests of Cinegetas, *Kalbreyer 1808* (K, NEOTYPE, here designated).

Columnea kalbreyeri Hook. f. in Bot. Mag. **108:** *pl. 6633.* 1 July 1882 (nom. illeg., included *C. kalbreyeriana* Masters in synonymy). TYPE: Cultivated material originally collected in the forests of Cinegetas, Dept. Antioquia, Colombia by Kalbreyer (K, HOLOTYPE; K, ISOTYPE).

Columnea citrina C. Morton in Ann. Missouri Bot. Gard. **29:** 44. 1942. TYPE: PANAMA: PANAMÁ: *Allen 2404* (US, HOLOTYPE; US, ISOTYPE).

Columnea conferta C. Morton in Ann. Missouri Bot. Gard. **29:** 44. 1942. TYPE: PANAMA: DARIÉN: *Terry & Terry 1554* (F, HOLOTYPE; A, ISOTYPE).

ECUADORIAN COLLECTIONS: ESMERALDAS: Along Ibarra–San Lorenzo railroad, environs of Lita, 575 m, *Madison et al. 5219* (SEL), *Madison et al. 5231* (SEL).

DISTRIBUTION: Panama, northwestern Colombia (Antioquia, Chocó), and northwestern Ecuador.

DISTINGUISHING FEATURES: The upper leaf surface is glabrous and the lower only sparsely pilose, the blade has two translucent red spots (one at each side of the primary vein) placed about ¾ of the distance from the base, the inflorescences are supported by ovate to lanceolate, 2–4 cm long bracts, the ovate calyx lobes are 1.5–2.5 cm long, and the yellow 4.5–5.5 cm long corollas are strongly bilabiate.

NOTES: The description above mainly fits one of the two Ecuadorian collections (*Madison 5231*). The other collection (*Madison 5219*), a poor specimen without flowers or buds coming from the same locality, has less obvious translucent dots, smaller bracts, and red rather than light green calyces. This specimen looks similar to some collections of *Columnea consanguinea* (Hanstein, 1865) from southern Panama and adjacent Colombia.

The holotype specimen from cultivation, if any exists, of *Columnea kalbreyeriana,* has not been traced and although the description and illustration could serve to typify the name, the illustration does not show the corolla. We have selected the field collection made by Kalbreyer to represent the species. *Columnea kalbreyeri* described and illustrated by J. D. Hooker, only a few months after the publication by Masters, is an illegitimate renaming, because the protologue in-

cludes the citation of Masters' name and publication. One could perhaps argue that Masters did not intend to validate the name in Gardener's Chronicle, for he wrote that the species would later be more amply described in the Botanical Magazine. However, his description in Gardener's Chronicle fulfilled the requirements for valid publication.

16. **Columnea longinervosa** Kvist & L. Skog, sp. nov. TYPE: COLOMBIA: CHOCÓ: Upper Río Atrato, Tutunendo–El Carmen road, km 120–235, 800–1200 m, 29 Apr. 1979, *Forero, Jaramillo, Bernal, León, & Pulido 6100* (US, HOLOTYPE; MO, ISOTYPE). FIGURE 7.

Differt a *Columnea eburnea* (Wiehl.) Kvist & L. Skog a corollis flavis indumentis sparsim.

Climbing epiphyte, shoots strongly dorsiventral. Stems pubescent to sericeous near apex, internodes 1.5–2 cm long. Leaves strongly anisophyllous, nearly sessile, pubescent; the larger leaf in a pair lanceolate to oblanceolate, 9–17 × 1.5–3 cm, apex acuminate, base rounded, upper surface dark green, lower surface lighter green with apical half red to purple or almost entirely red to purple, veins 5–6 per side, conspicuous, individual veins extending nearly from base to apex of blade, impressed above and prominent below; the smaller leaf in a pair to 2 cm long, ovate. Inflorescences in axils of the larger leaf in each pair, of 1–2 flowers; pedicels to 5 mm long, sericeous, bracts 2–3, the largest ovate, 2–3 × 1–2 cm, light green, the smaller ones scale-like, up to 5 mm long. Calyx lobes subequal to unequal, lanceolate, 12–20 mm long, 2–5 mm wide at base, cream or pale green, glabrous inside, sericeous outside; corolla dorsally gibbous, cylindric to narrowly funnelform, 3–3.5 cm long, diam. 3–5 mm at base and 7–9 mm at the throat, outside yellow, sericeous, inside yellow with 2–4 red lines extending from sinuses into tube, each intersected by an earlike appendage, glabrous to glandular-hairy in throat; limb subequal, 13–21 mm wide, yellow, lobes 5–7 mm long and 3–5 mm wide at base, dorsal lobes partly connate; filaments sparsely pilose, 20–25 mm long, basally connate for 3–5 mm, anthers subincluded, ca. 1.5 × 1.5 mm, connate; nectary of one 3–4-lobed gland and occasionally with an additional unlobed gland, ca. 1.5 mm high; ovary sericeous, style 20–25 mm long, glabrous or with sparse glandular trichomes on upper ½ to ⅔, stigma subincluded, stomatomorphic. Berry ovoid, ca. 15 × 8 mm; seeds not seen.

OTHER COLLECTIONS: COLOMBIA: CHOCÓ: Municipio de San José del Palmar, Río Torito valley (tributary to Río Hábita), 730–830 m, *Forero et al. 6500* (US); 850–1000 m, *Forero et al. 7206* (US). VALLE: Old Cali–Buenaventura road, 18 km below Queremal, 1100–1200 m, *Folsom & Escobar 10452* (AAU, US(2)); Old Cali–Buenaventura road, km 52, 400 m, *Londoño & Kvist 187* (AAU, COL, QCA, TULV, US). ECUADOR: CARCHI: San Marcos, 660 m, *Barfod 41507* (AAU).

DISTRIBUTION: The species apparently is restricted to the humid lower montane and pluvial forests of western Colombia and extreme northwestern Ecuador.

DISTINGUISHING FEATURES: *Columnea longinervosa* is easily recognized by having narrowly lanceolate to oblanceolate leaves that are at least five times as long as wide and have only 5–6 conspicuous veins per side. In addition, the entire apical half or more of the lower leaf surface usually is red or purple, each inflorescence is supported by one conspicuous, ovate, light green bract, and the yellow corollas have a large unequal, but not bilabiate, limb.

The nearest relative of *Columnea longinervosa* is possibly *C. eburnea.* In the latter species the corolla shape is similar to that of *C. longinervosa,* but the color

FIGURE 7. *Columnea longinervosa* Kvist & L. Skog. A, habit; B, node showing unequal leaves; C, flower; D, corolla opened to show stamens and appendages; E, flower with corolla and 2 calyx lobes removed to show pistil and nectary; F, ovary and nectary; G, young fruit. (All from *Forero et al. 6100,* US.)

is white or cream rather than yellow. In addition, *C. eburnea* has a much denser indumentum than *C. longinervosa* and has the typical oblanceolate leaves of section *Collandra.*

NOTES: The nectary types observed in *C. longinervosa* (FIGURE 2N, T) differ from the usual bilobed glands of section *Collandra.*

17. **Columnea picta** Karst., Fl. Columb. **2:** 105, *pl. 154.* 1865. TYPE: COLOMBIA: QUINDIO: *Karsten s.n.* (W, HOLOTYPE). *Dalbergaria picta* Wiehl. in Phytologia **27:** 318. 1973.

REPRESENTATIVE ECUADORIAN COLLECTIONS: CAÑAR: Azogues–El Triumfo road, 5 km W of La Delicia, 600 m, *Croat 50884* (US). CARCHI: W of Maldonado, Chical, 1200 m, *Kvist et al. 48637* (AAU). COTOPAXI: Tenefuerste, Río Pilalo, *Dodson & Gentry 12215* (SEL). EL ORO: Between Buenaventura and Garganta de Piñas, Moro, *Steyermark 54240* (US). ESMERALDAS: Río Cayapa, environs of Zapallo Grande, 150 m, *Kvist & Asanza 40871* (AAU). GUAYAS: Manglar Alta, 100-300 m, *Haught 3100* (US). IMBABURA: Above García Moreno, 1700 m, *Drew E-541* (US). LOS RÍOS: Río Palenque Science Center 220 m, *Løjtnant & Molau 15789* (AAU). MANABÍ: Río Ayampe, 600 m, *Haught 3139* (US). PICHINCHA: Santo Domingo–Puerto Limón road, km 23, 100 m, *Kvist & Holm-Nielsen 40230* (AAU).

DISTRIBUTION: Western Colombia (Antioquia, Chocó, Nariño, Risaralda, and Valle) and western Ecuador.

DISTINGUISHING FEATURES: The upper leaf surface is nearly glabrous, the lower surface has a red apex and/or veins, the bracts are ovate (2–4 × 1–2 cm), the pedicels are 0.5–2.5 cm long, the calyx lobes are unequal with the largest lobe being 1.5–3 cm long and ovate, and the smaller lanceolate (occasionally only four lobes are present and the fifth is completely reduced), the lobes are often purple along the midrib, the yellow corolla is 3.5–4.5 cm long, the limb is conspicuously bilabiate, and the lips are yellow with purple dots/stripes.

18. **Columnea purpurimarginata** Kvist & L. Skog, sp. nov. TYPE: ECUADOR: ESMERALDAS: Ibarra–San Lorenzo railroad, environs of Lita, wet submontane forest, 575 m, June 1978, *Madison, Plowman, Kennedy, & Besse 5000* (SEL, HOLOTYPE). FIGURE 8.

Differt a *Columnea pulcherrima* C. Morton et *C. rubrocincta* C. Morton lobis calycum serratis et pedicellis sparsim hirtis glandulosis.

Epiphytic herb, shoots strongly dorsiventral. Stems villous, diam. to 8 mm, internodes 1–4 cm long. Leaves strongly anisophyllous, nearly sessile; the larger leaf in a pair oblanceolate, 12–24 × 3.5–7.5 cm, apex acuminate, base rounded, upper surface dull green, strigose or hispid, with 4–8 mm wide purple margin, lower surface yellow-green but also with a purple margin, pilose, margin weakly serrate, veins 10–12 per side; the smaller leaf in a pair scale-like and caducous. Inflorescences in axils of the larger leaf in each pair, of 1–3 flowers; pedicels 1.5–2.5 cm long, sparsely glandular-hairy; bracts scale-like, to 2 mm long. Calyx lobes subequal, ovate to lanceolate, 8–11 mm long, 2–3 mm wide at base, pale green, sparsely glandular-hairy outside, glabrous inside, margin serrate; corolla cylindric, basally dorsally gibbous, 3.8–4.2 cm long, diam. 2–3 mm at base and 6–8 mm at the throat, outside yellow, sparsely glandular-hairy, inside glabrous, limb subequal, lobes 2–2.5 mm long and 1.5–2.5 mm wide at base, each dark maroon with yellow margin; filaments glabrous, 40–45 mm long, basally connate for ca. 5 mm, anthers exserted, connate, ca. 2.5 × 2 mm; nectary of an unlobed dorsal gland, ca. 2 mm high; ovary glabrous, style 40–45 mm long, glabrous, stigma exserted, stomatomorphic. Berry ovoid, ca. 8 mm × 5 mm; seeds narrowly ellipsoid to ellipsoid, transversely striate, brown.

OTHER COLLECTIONS: COLOMBIA: CAUCA: Río Timbiqui, Coteje, 100–500 m, *Lehmann 8889* (F). ECUADOR: ESMERALDAS: Río Cayapa, environs of Zapallo Grande, 100 m, *Kvist et al. 48085* (AAU).

DISTRIBUTION: Northwestern Ecuador (Esmeraldas) and western Colombia (Cauca and Chocó).

DISTINGUISHING FEATURES: *Columnea purpurimarginata* is easily recognized by a conspicuous purple or red 4–8 mm wide margin visible on both leaf surfaces. In addition, the species is characterized by having reduced bracts, 8–11 mm long

FIGURE 8. *Columnea purpurimarginata* Kvist & L. Skog. A, habit; B, portion of lower leaf surface; C, flower with corolla removed to show ovary and nectary; D, flower; E, flower with corolla opened to show stamens and pistil. (All from *Madison et al. 5000,* SEL.)

glandular-hairy calyx lobes, and exserted anthers and stigma. Among Ecuadorian species, the combination of a subequal limb and exserted stamens is otherwise only known from *C. byrsina* in section *Stygnanthe.*

NOTES: *Columnea purpurimarginata* has no close Ecuadorian relatives, but it has affinities with *C. pulcherrima* and *C. rubrocincta,* both described by Morton (1945) from the Colombian department of Antioquia. Both these species have exserted stamens, but differ by having villous rather than sparsely glandular-hairy pedicels and calyces. In addition, *C. pulcherrima* has 2–4 cm long dissected rather than serrate calyx lobes, and *C. rubrocincta* has obovate leaves with a uniformly purple lower surface. Other species belonging to the same complex are *C. cruenta* B. Morley (1973b), *C. perpulchra* C. Morton (1942), *C. silvarum* C. Morton (1942), and *C. vittata* (Wiehl.) Skog (1979). The latter species was originally described in *Dalbergaria* by Wiehler (1977).

The single nectary gland is not bilobed as usually seen in section *Collandra* (FIGURE 2W, X).

19. **Columnea rubriacuta** (Wiehl.) Kvist & L. Skog, comb. nov. *Dalbergaria rubriacuta* Wiehl. in Selbyana **2:** 72, *pl. 20D.* 1977. TYPE: ECUADOR: LOS RÍOS: Río Palenque Science Center, *Wiehler & Dodson 7102* (SEL, HOLOTYPE).

REPRESENTATIVE ECUADORIAN COLLECTIONS: CARCHI: San Marcos, 600 m, *Kvist et al. 48738* (AAU). ESMERALDAS: Río Cayapa, environs of Zapallo Grande, 100 m, *Kvist & Asanza 40359* (AAU). EL ORO: New Piñas–Machala road, km 10, 900 m, *Dodson & Perry 8442* (SEL). LOS RÍOS: Río Palenque Biological Station, 180 m, *Dodson & Gentry 6454* (SEL, US). PICHINCHA: Santo Domingo–Puerto Limón road, km 23, Colorado community "Congoma Grande", 100 m, *Kvist & Holm-Nielsen 40074* (AAU).

DISTRIBUTION: Northwestern Ecuador and adjacent Colombia.

DISTINGUISHING FEATURES: The indumentum in *Columnea rubriacuta* is not conspicuous, the lower leaf surfaces always have a red apical part and often a red margin or may be entirely purple, the inflorescences are supported by two conspicuous, 3–6 cm long, ovate bracts and several smaller bracts surrounding the three to five flowers, the 1.5–2.5 cm long calyx lobes are lanceolate to linear, the corollas are 3.5–4.5 cm long, narrowly cylindric with a diameter less than 5 mm, and the lobes are patent.

In western Ecuador, two other species along with *Columnea rubriacuta* belong to a complex within section *Collandra* characterized by their cylindric flowers and small, subregular limbs. One of these, *C. schimpffii,* has shorter 2.2–3 cm long corollas and occurs in deciduous forests rather than lowland rain forest. The other species, *C. cinerea,* has gray-villous indumentum, overlapping bracts, and occurs in montane forests. A closely related rain forest species from eastern Ecuador is *C. guttata,* and a complete revision of *Columnea* over its complete range may show that *C. rubriacuta* should be included within the circumscription of *C. guttata.*

NOTES: Plants similar to *Columnea rubriacuta,* but often with considerably longer corollas and larger leaves, are widespread in western Colombia. *Columnea rubriacuta* either is a very variable species in this region or these plants belong to some undescribed close relatives. *Columnea consanguinea* Hanstein (1865) and *C. crassa* C. Morton (1942), both from Panama and adjacent Colombia, may have affinities with *C. rubriacuta,* but they have shorter corollas and leaves with one or two translucent, red "windows".

20. **Columnea rubribracteata** Kvist & L. Skog, sp. nov. TYPE: ECUADOR: ESMERALDAS: Río Cayapa, environs of Zapallo Grande, disturbed rain forest, 50 m, *Kvist et al. 48087* (AAU, HOLOTYPE; QCA, QCNE, US, ISOTYPES).

Species foliis aeque viridibus et bracteis rubris lanceolatis conspicuis in discrepantia a congeneribus diversa.

Epiphytic herbs. Stems pilose to villous near apex, diam. to 4 mm, internodes 1–3 cm long. Leaves strongly anisophyllous, pilose, membranaceous; the blade of the larger leaf in each pair oblanceolate, 8–13 × 3–5 cm, apex acuminate, base acute, margin serrate, veins 8–9 per side, petiole 1–5 mm long, villous; the blade of the smaller leaf in each pair linear to lanceolate, to 2 cm long, caducous, sessile. Inflorescences of 1 (–2) epedunculate flowers in the axils of the larger leaf of each pair; bracts 1, ovate to lanceolate, 2–3 cm long, conspicuously red, persistent, pilose; pedicels 5–15 mm long, villous; calyx lobes subequal, lanceolate with basally dissected margin, 15–20 mm long, yellow with red apex, villous; no fully developed corollas but only buds seen, corolla apparently yellow with 2–4 red stripes, limb apparently subequal, inside especially basally pilose; filaments basally connate, anthers ca. 1.2 × 1 mm; nectary a bilobed gland; ovary and stigma sericeous to pilose. Fruits and seeds not seen.

OTHER COLLECTIONS: ECUADOR: ESMERALDAS: Río Cayapa, Zapallo Grande, 50 m, *Kvist et al. 48420* (AAU).

DISTRIBUTION: Apparently a rare endemic of the Cayapa river system in the Esmeraldas province of northwestern Ecuador.

DISTINGUISHING FEATURES: The contrast between the uniformly green leaves and the conspicuously red, lanceolate bracts each subtending a flower sets *Columnea rubribracteata* apart from all other species.

NOTES: Based on the presence of conspicuous bracts, *Columnea rubribracteata* is tentatively referred to the section *Collandra.* However, neither fully developed corollas nor berries have been seen, and another possibility is placement in section *Ortholoma.* However, in this latter section the bracts are usually scale-like.

21. **Columnea sanguinea** (Pers.) J. Hanst. in Linnaea **34:** 384. 1865. *Besleria sanguinea* Pers. Syn. Pl. **2:** 165. 1807. *Alloplectus sanguineus* G. Don Gen. Syst. **4:** 655. 1837. *Hematophyla villosa* Raf. Sylva Tell. 71. 1838 (Based on *Besleria sanguinea* Pers.). *Dalbergaria sanguinea* Steud. Nom. Bot. (ed. 2) **1:** 479. 1840. *Collandra sanguinea* Griseb. in Mem. Amer. Acad. Arts, n.s. **8:** 526. 1863. TYPE: HISPANIOLA: *Turpin* (P(?), not seen).

Dalbergaria phoenicea Tussac Fl. Ant. **1:** 141, *pl. 19.* 1808. *Collandra phoenicea* G. Don ex Loud. Enc. Sup. **2:** 1402. 1855. TYPE: HISPANIOLA: *Tussac* (not seen).

Vireya sanguinolenta Raf. in Specchio Sci. **1:** 194. 1814. TYPE: SANTO DOMINGO (not seen).

Collandra picta Klotzsch & J. Hanst. in Allg. Gartenzeitung **22:** 162. 1854, not Lem. TYPE: Described from cultivated plants (not seen).

Columnea sanguinea var. *cubensis* Urb. Symb. Ant. **2:** 539. 1901. *Columnea cubensis* Britton in Torreya **5:** 215. 1906. *Alloplectus cubensis* Stearn in Bull. Brit. Mus. (Nat. Hist.) Bot. **4**(5): 189. 1969. TYPE: CUBA: ORIENTE: *Wright 357* (GOET?, HOLOTYPE not seen; BM, GH, K, MO, P, PH, UC, ISOTYPES).

ECUADORIAN COLLECTIONS: NAPO: Río Napo, Añangu, 300 m, *Korning & Thomsen 47056* (AAU (2)).

DISTRIBUTION: Widespread in northern South America and the West Indies.

DISTINGUISHING FEATURES: The single Ecuadorian collection (like collections from the adjacent Colombian Amazon) has pubescent leaves with a uniformly yellow-green lower surface, the inflorescences are supported by 2–3 cm long lan-

ceolate bracts, the 1.5–2 cm long laciniate calyx lobes are densely villous, and the 2.5–3 cm long corollas are yellow and sericeous.

22. **Columnea schimpffii** Mansf. in Repert. Spec. Nov. Regni Veg. **36:** 122. 1934. *Dalbergaria schimpffii* Wiehl. in Phytologia **27:** 315. 1973. TYPE: ECUADOR: CHIMBARAZO: Naranjapata, *Schimpff 483* (G, LECTOTYPE, here designated; MO, ISOLECTOTYPE; HOLOTYPE at B no longer extant).

REPRESENTATIVE ECUADORIAN COLLECTIONS: BOLÍVAR: Tablas de Telimbela, 500–1000 m, *Acosta Solís 6952* (F). COTOPAXI: Muraspungo to Corazón, km 9, 840 m, *Dodson et al. 9208* (SEL). EL ORO: Piñas–Santa Rosa road, above El Placer, 800–1000 m, *Harling et al. 15553* (SEL). GUAYAS: Cerro Cimalón, Hacienda Vainillo, 250 m, *Haught 2895* (F, NY, US). LOS RÍOS: 40 km E of Babahoya, surroundings of Montalva, 150 m, *Holm-Nielsen et al. 2707* (AAU, MO, NY). MANABÍ: Río Ayambe, 500 m, *Haught 3120* (AAU, US(2)).

DISTRIBUTION: Southwestern Ecuador. The species apparently occurs mainly in deciduous forests.

DISTINGUISHING FEATURES: *Columnea schimpffii* is similar to *C. guttata* and *C. rubriacuta,* but differs by having obovate rather than oblanceolate leaves, villous instead of sericeous stems, unequal instead of subequal calyx lobes, and yellow corollas 2.2–3 rather than 3–5.5 cm long. In addition, their occurrence in different habitats—*C. guttata* and *C. rubriacuta* in rain forests and *C. schimpffii* in deciduous forests—serves to maintain the separation of the species.

In addition to *Columnea schimpffii* in drier forests in the southwest and *C. rubriacuta* in permanently humid forests in the northwest, *C. cinerea,* a third species in section *Collandra* having corollas with small, subequal limbs, is found in western Ecuador. This latter species occurs in the montane forests on the eastern Andean slopes and differs especially from *C. schimpffii* by having much larger bracts.

NOTES: The name *Columnea schimpffii* has hitherto been applied in herbaria to a different species occurring on the eastern Andean slopes. The correct name for these plants is *C. villosissima* (q.v.). A type photo at F apparently of the holotype at B (no longer extant) shows that *C. schimpffii* was based on material collected in southwestern Ecuador (an extant isotype at MO is poor, having no flowers).

23. **Columnea tessmannii** Mansf. in Repert. Spec. Nov. Regni Veg. **36:** 123. 1934. *Dalbergaria tessmannii* Wiehl. in Phytologia **27:** 319. 1973. TYPE: PERU: AMAZONAS: Upper Río Marañón, mouth of Río Santiago, *Tessmann 4252* (B, HOLOTYPE, no longer extant); PERU: AMAZONAS: Along Río Marañón, near Teniente Pinglo, just above Pongo de Manseriche, 250–300 m, 4–7 Oct. 1962, *Wurdack 2108* (US, NEOTYPE, here designated; AAU, F, US, isoneotypes).

REPRESENTATIVE ECUADORIAN COLLECTIONS: MORONA-SANTIAGO: Macas–Sucua road, km 10, *Kvist 60453* (AAU, QCA, QCNE, US). PASTAZA: Puyopungu, *Lugo S. 4815* (GB, SEL). ZAMORA-CHINCHIPE: Between Valladolid and Achupallas, 2000–2500 m, *Steyermark 54742* (F).

DISTRIBUTION: In montane forests on the eastern slopes of the Andes in northern Peru (Amazonas) and Ecuador.

DISTINGUISHING FEATURES: The leaves of *Columnea tessmannii* are somewhat rugose, sericeous, and usually have a violet or purple sheen, the lower surface never has a contrasting red apex, the inflorescences are densely congested with conspicuous, ovate, green or purple bracts hiding the calyces and most of the

corolla tubes, the ca. 2 cm long calyx lobes are subequal and lanceolate, and the 4–6 cm long bilabiate corollas are yellow with 2–4 red stripes.

The closest relatives of *Columnea tessmannii* are *C. albiflora* and *C. densibracteata* (see these species). All three species are characterized by conspicuous, densely congested bracts and large, bilabiate flowers. Another similar species is *C. eubracteata,* but in this species the corolla lobes are patent and have a contrasting purple margin.

NOTES: *Columnea tessmannii* mainly occurs in montane forests. However, both the original type collection and the neotype selected here come from lowland rain forest along the Río Marañón near the border of the Peruvian departments of Amazonas and Loreto.

24. **Columnea villosissima** Mansf. in Repert. Spec. Nov. Regni Veg. **36:** 121. 1934. *Dalbergaria villosissima* Wiehl. in Phytologia **27:** 319. 1973. TYPE: PERU: *Tessmann 4964* (B, HOLOTYPE, no longer extant); ECUADOR: NAPO: Tena, *Heinrichs 329* (NY, NEOTYPE; M, ISONEOTYPE; designated here but cited by Mansfeld).

REPRESENTATIVE ECUADORIAN COLLECTIONS: MORONA-SANTIAGO: N of Macas on border to Parque Nacional Sangai, 1200 m, *Kvist 40426* (AAU, QCA, QCNE, US). NAPO: Mishuallí, 500 m, *Holm-Nielsen 19341* (AAU, US). PASTAZA: Río Bobanaza, 35 km SE of Sarayacu, Teresa Mama, *Lugo S. 5651* (AAU, NY, US). TUNGURAHUA: Río Negro, 1200 m, *Harling & Andersson 17265* (US).

DISTRIBUTION: Northeastern Peru (Amazonas, Loreto, and San Martín) and eastern Ecuador.

DISTINGUISHING FEATURES: The lower leaf surface has a reddish apical part, the calyx is densely villous and the 1.2–2 cm long lobes are laciniate, and the 2.5–3.2 cm long yellow, yellow-white or rarely red corolla is villous outside. The most similar species are *Columnea inaequilatera* and *C. fuscihirta.* The former species has uniformly colored lower leaf surfaces and 3–5 cm long red corollas (see *C. inaequilatera*), and the latter has a brown-hispid indumentum.

NOTES: Specimens of *Columnea villosissima* have generally been misidentified as *C. schimpffii* ever since Mansfeld (1934) described both species. This common error may be partly due to the fact that the holotypes were destroyed at Berlin and partly because they were supposed to be synonyms of equal priority for a species distributed on the eastern Andean slopes (while true *C. schimpffii* is actually from the western slopes).

C. Section **Columnea** L.

Columnea L. Sp. Pl. 638. 1753. TYPE: *Columnea scandens* L.

25. **Columnea bilabiata** Seem. Bot. Voy. Herald 186. 1854. TYPE: COLOMBIA: *Seemann 1057* (BM, HOLOTYPE; K, ISOTYPE).

Columnea silvatica C. Morton in J. Washington Acad. Sci. **35:** 130. 1945. TYPE: COLOMBIA: ANTIOQUIA: *Metcalf & Cuatrecasas 30178* (US, HOLOTYPE; UC, ISOTYPE).

ECUADORIAN COLLECTIONS: ESMERALDAS: San Miguel, 200 m, *Holm-Nielsen et al. 25343* (AAU). *Holm-Nielsen et al. 25408* (AAU), *Holm-Nielsen et al. 25415* (AAU), Río Cayapa, Zapallo Grande, 100 m, *Kvist 40519* (AAU), *Kvist 40600* (AAU), *Kvist & Azanza 40816* (AAU), *Kvist et al. 48416* (AAU), *Kvist et al. 49045* (AAU).

DISTRIBUTION: Western Colombia (Antioquia, Cauca, Chocó, Nariño, and Valle) and northwestern Ecuador. *Columnea bilabiata* is locally common along Río Cayapa in the province of Esmeraldas.

DISTINGUISHING FEATURES: The lanceolate, 4–8 cm long leaves are isophyllous, the lanceolate, ca. 1.5 cm long calyx lobes are basally conspicuously dissected, and the ca. 4 cm long red corollas are bilabiate with a reflexed lower lip (ventral lobe). The nearest relative may be *Columnea billbergiana* (Beurling, 1854) from Panama, but that species has ovate or elliptic leaves and calyx lobes with subentire margins.

26. **Columnea kienastiana** Regel in Trudy Glavn. Bot. Sada (Acta Horti Petrop.) **8:** 274. 1883. TYPE: COLOMBIA: *Pfau s.n.* (LE?, HOLOTYPE, not seen).

Columnea dodsonii Wiehl. in Selbyana **2:** 70, *pl. 20A.* 1977. TYPE: Cultivated material originally from Ecuador, Prov. Manabí, Santo Domingo–Chone road, km 15, *Wiehler 77108* (SEL, HOLOTYPE; SEL, US, ISOTYPES).

REPRESENTATIVE ECUADORIAN COLLECTIONS: ESMERALDAS: Cayapa river system, Río Camarones, 200 m, *Kvist et al. 48037* (AAU). LOS RÍOS: Río Palenque Biological Station, 185 m, *Dodson 5144* (AAU, SEL). PICHINCHA: 6 km WNW of P. Vicente Maldonado, 800 m, *Harling & Andersson 23331* (GB).

DISTRIBUTION: Northwestern Colombia (Cauca, Chocó, and Valle) and western Ecuador.

DISTINGUISHING FEATURES: The ovate, 1.5–2.5 cm long leaves are isophyllous, the ovate, 1–1.5 cm long calyx lobes have subentire margins, and the ca. 4 cm long, bilabiate red corollas have a reflexed lower lip (ventral lobe).

NOTES: Plants of this species tend to have ovate leaves in Ecuador and lanceolate leaves in Colombia. In addition, the calyx lobes are nearly entire in Ecuador, while a few small basal teeth are present in Colombian plants. However, neither of these features are consistent, and *Columnea dodsonii,* described by Wiehler based on Ecuadorian material, is here reduced to a synonym of *C. kienastiana.* The apparent disjunct ranges of the Ecuadorian and Colombian populations may be due to the lack of exploration of the adjacent Colombian department of Nariño (see Distribution of Ecuadorian Species).

D. Section **Ortholoma** Benth.

Columnea L. section *Ortholoma* Benth. Pl. Hartw. 231. 1846. LECTOTYPE: *Columnea acuminata* Benth. = *Columnea anisophylla* DC., selected by Morton & Denham in Taxon **21:** 676. 1972.
Ortholoma (Benth.) J. Hanst. in Linnaea **26:** 209. 1854.

27. **Columnea anisophylla** DC. Prodr. **7:** 542. 1829. *Ortholoma anisophyllum* Wiehl. in Phytologia **27:** 320. 1973. *Trichantha anisophylla* Wiehl. in Selbyana **1:** 34. 1975. TYPE: PERU: *Poeppig 1080* (G-DC, HOLOTYPE; BM, F, P, W, ISOTYPES).

Nematanthus heterophyllus Poepp. in Poepp & Endl., Nov. Gen. Sp. Pl. **3:** 4, *pl. 203.* 1840 (nom. illeg.). TYPE: PERU: HUANUCO: Pampayacu, *Poeppig 1080* (W, HOLOTYPE; BM, F, G-DC, P, W, ISOTYPES).
Columnea acuminata Benth. Pl. Hartw. 231. 1846. *Ortholoma acuminatum* J. Hanst. in Linnaea **26:** 209. 1854. *Trichantha acuminata* Wiehl. in Selbyana **5:** 384. 1981. TYPE: COLOMBIA: CAUCA: "Popayan", *Hartweg 1261* (K, HOLOTYPE; BM, CGE, E, G, K, NY, P, W, ISOTYPES).
Ortholoma vestitum Klotzsch ex Oerst. Centralamer. Gesner. 51. 1858. TYPE: COSTA RICA or PANAMA: "Veragua", *Warszewicz 21* (K, L, P, ISOTYPES).
Ortholoma warszewiczianum Klotzsch ex Oerst. Centralamer. Gesner. 51. 1858. *Columnea warszewicziana* J. Hanst. in Linnaea **34:** 392. 1865. TYPE: COSTA RICA or PANAMA: "Veragua", *Warszewicz 30* (GH, K, L, P, W, ISOTYPES).
Columnea sanmartensis Rusby Descr. S. Amer. Pl. 127. 1920. TYPE: COLOMBIA: Santa Marta, *Smith 1394* (NY, HOLOTYPE; F, K, MO, ISOTYPES).

ECUADORIAN COLLECTIONS: MORONA-SANTIAGO: Sevilla de Oro–Mendez trail, Río Negro and Río

Chupianza valley, 1100–1500 m, *Camp 814* (US). ZAMORA-CHINCHIPE: Road La Saque–Yacuambi, N of Chapintza, 1100 m, *Harling & Andersson 23869* (US).

DISTRIBUTION: Costa Rica to Peru. *Columnea anisophylla* is fairly common in parts of Peru and Colombia, but it is rare in Ecuador and apparently restricted to the southeastern slopes of the Andes.

DISTINGUISHING FEATURES: In Ecuador the red, ventricose corollas of *Columnea anisophylla* are similar to those of *C. ciliata* (in Peru this species has cream corollas, however), but the latter species differs by having ovate rather than lanceolate leaves and by having glabrous rather than pubescent upper leaf surfaces. *Alloplectus peruvianus* (see excluded species) also has similar corollas, but has isophyllous, often ovate or elliptic leaves and a bivalved, fleshly capsule rather than a berry fruit. However, this latter feature is rarely seen, which may explain why *A. peruvianus* originally was described as a species of *Columnea.*

28. **Columnea brenneri** (Wiehl.) B. Morley in Garden (London) **100**(9): 438. 1975. *Trichantha brenneri* Wiehl. in Selbyana **1**: 40. 1975. TYPE: Cultivated material originally from Ecuador, Prov. Napo, Tena, *Wiehler 72335* (US, HOLOTYPE, NOT SEEN; SEL, ISOTYPE).

OTHER COLLECTIONS: ECUADOR: MORONA-SANTIAGO: Loja–Gualaquiza road, km 140, Pachicutza, 950 m, *Holm-Nielsen et al. 4440* (AAU); Close to Macas, E of Río Upano and the village Sevilla Don Bosco, 1000 m, *Kvist 60447* (AAU); Cordillera de Cutucú, 25 km SE of Logroño, 900 m, *Madison & Coleman 2577* (SEL); Cordillera de Cutucú, trial from Logroño to Yaupi, 1200 m, *Madison et al. 3191* (SEL), 1300 m, *Madison et al. 3299* (SEL). PASTAZA: Mera, 1100 m, *Harling et al. 10043* (SEL). ZAMORA-CHINCHIPE: Zamora–Gualaquiza road, 29 km N of Yangzatza, 890 m, *Croat 50766* (US).

DISTRIBUTION: The lower montane forests of eastern Ecuador.

DISTINGUISHING FEATURES: The species most similar to *Columnea brenneri* are *C. elongatifolia* and *C. tenensis.* The former species differs from *C. brenneri* by having isophyllous rather than anisophyllous leaves and much longer, linear, 2–4 cm long calyx lobes rather than lanceolate lobes up to 1.5 cm long. The latter species differs from *C. brenneri* by having dissected rather than entire calyx lobes and corollas ca. 4.5 cm long rather than 3 cm long.

NOTES: According to Wiehler (1975b) the holotype of *Columnea brenneri* is at US. However, the specimen has not yet been received at US nor has it been located at SEL.

29. **Columnea ciliata** (Wiehl.) Kvist & L. Skog, comb. nov. *Trichantha ciliata* Wiehl. in Selbyana **2**: 129. 1977. TYPE: ECUADOR: PICHINCHA: Alluriquin–Chiriboga road, *Madison 4065* (SEL, HOLOTYPE).

OTHER COLLECTIONS: ECUADOR: CARCHI: 12 km W of Maldonado, environs of Chical, 1200 m, *Madison et al. 4452* (SEL). ESMERALDAS: Environs of Lita, 575 m, *Madison et al. 5235* (SEL). IMBABURA: W of Otovalo, Selva Alegre region, above Río Pamplona, near San Pablo, 2000 m, *Drew E34* (US). PICHINCHA: Quito–Santo Domingo road, km 96, Hacienda San Luis, *Ortiz 16* (MO); Old Quito–Chiriboga–Santo Domingo road, 3 km from Río Pilatón, 1000 m, *Harling & Andersson 23056* (GB). PERU: PASCO: Pichis trail, San Nicolas, 1100 m, *Killip & Smith 25962* (NY, US).

DISTRIBUTION: Montane forests of central Peru (Pasco) and western Ecuador.

DISTINGUISHING FEATURES: Several species of section *Ortholoma* have stems with a conspicuous yellow-brown, hispid indumentum, but this feature is especially striking in *Columnea ciliata.* However, more distinctive are the elliptic to obovate leaves with their glabrous, dull green upper surface and sparsely pubescent, purple lower surface and hispid margins. The ventricose corollas vary from red to pale yellow in Ecuador and are cream-colored in Peru.

30. **Columnea dissimilis** C. Morton in Ann. Missouri Bot. Gard. **29:** 47. 1942. *Ortholoma dissimile* Wiehl. in Phytologia **27:** 321. 1973. *Trichantha dissimilis* Wiehl. in Selbyana **1:** 34. 1975. TYPE: PANAMA: COCLÉ: *Allen 2483* (US, HOLOTYPE; F, GH, MO, NY, ISOTYPES).

Columnea translucens Raym. in Bot. Not. **114:** 350, *fig. 4–5.* 1961. TYPE: Described from cultivated material originally collected in Panama, *Raymond s.n.* (MTJB, HOLOTYPE).

OTHER COLLECTIONS: ECUADOR: ESMERALDAS: Río Cayapa, close to Zapallo Grande, 50 m, *Kvist et al. 48178* (AAU); Road buildings 5 km W of Lita, toward San Lorenzo, 700 m, *Lawesson et al. 43988* (AAU). IMBABURA: Lita, 540 m, *Acosta-Solís 12587* (F). PICHINCHA: Quito–Puerto Quito road, km 113, Río Salenche, Reserva Forestal ENDESA, 800 m, *Arguello & Betancourt 358* (QCA), 680 m, *Jaramillo 7577* (QCA). COLOMBIA: CAUCA: Gorgona Island, *Cheeseman(?) 552* (US).

DISTRIBUTION: Frequent in Panama but rare in southwestern Colombia and northwestern Ecuador.

DISTINGUISHING FEATURES: The larger lanceolate to oblanceolate leaf of each pair is ca. 8 cm long and the smaller ovate to elliptic leaf is 1–3 cm long, both surfaces are green and sparsely pilose, the ovate calyx lobes are ca. 2 cm long, and the pink, cylindric and densely villous corollas are ca. 3 cm long. The most similar Ecuadorian species is *Columnea lehmannii,* but that species differs from *C. dissimilis* by having reddish rather than green leaves, calyx lobes with rounded rather than acute apices, and sericeous rather than sparsely pilose ovaries. Another related species is *C. pulchra* also from Panama, but this species always has the smaller leaf of each pair reduced to a caducous scale, and the indumentum of the corollas is more sparse.

NOTES: *Columnea dissimilis* previously was only known from numerous collections from Panama. The few Ecuadorian and Colombian collections apparently differ from Panamanian specimens by having the corollas more narrow in the tube and throat and by having sparsely pilose rather than sericeous ovaries. For lack of better material (only a single fully developed corolla has been seen from Ecuadorian/Colombian material), the collections are here referred to *C. dissimilis,* but alternatively they may belong to a distinct species closely related to *C. dissimilis.*

31. **Columnea elongatifolia** Kvist & L. Skog, nom. nov. *Trichantha angustifolia* Wiehl. in Selbyana **7:** 336. 1984, not *Columnea angustifolia* (DC.) O. Kuntze = *Nematanthus dichrus* (Spreng.) Wiehl. TYPE: Cultivated material originally from Ecuador, Prov. Pastaza, Puyo, *Wiehler 80202* (SEL, HOLOTYPE).

OTHER COLLECTIONS: ECUADOR: NAPO: New Cotundo–Coca road, km 2, 1130 m, *Dodson et al. 15062* (US); Tena, 6 km along Río Pano, 600 m, *Holm-Nielsen & Jeppesen 664* (AAU).

DISTRIBUTION: Apparently restricted to the Napo and Pastaza provinces in the Ecuadorian Amazon region.

DISTINGUISHING FEATURES: The combination of lanceolate isophyllous leaves, linear, 2–3.5 cm long calyx lobes, and yellow and purple-striated corollas with limb appendages at the sinuses between the lobes readily distinguishes *Columnea elongatifolia.*

32. **Columnea fimbricalyx** Kvist & L. Skog, sp. nov. TYPE: ECUADOR: CARCHI: Trail between San Marcos and Gualpi Bajo, at ridge with mist forest, 1000 m, 25 Nov. 1983, *Kvist, Barfod, & Nissen 48971* (AAU, HOLOTYPE; QCA, QCNE, SEL, US, ISOTYPES). FIGURE 9.

FIGURE 9. *Columnea fimbricalyx* Kvist & L. Skog. A, habit; B, node showing strongly unequal leaves; C, calyx lobe; D, flower; E, corolla opened to show stamens; F, pistil; G, ovary and nectary. (All from *Kvist et al. 48977,* AAU.)

Differt a *Columnea rosea* C. Morton corollis limbus non appendicibus conspicuibus, et foliis pagina inferioribus aeque viridis, pagina superioribus glabris, lobis calycum marginibus pectinatis profundioribus.

Epiphytic herbs, shoots to 50 cm long. Stems glabrous to villous near apex, diam. to 3 mm; internodes 1.2–2.5 cm long. Leaves strongly anisophyllous; the blade of the larger leaf in a pair oblanceolate, 6–10 × 1–3 cm, apex acuminate,

base cuneate, margin weakly serrate, upper surface dull green, glabrous, lower surface lighter green, sparsely pilose, veins 5–6 per side; the blade of the smaller leaf in a pair linear, 8–15 mm long, caducous. Inflorescences of single flowers in axils of the larger leaf of each pair; pedicels 1–3 mm long, hirsute; bracts ca. 3, scale-like, 2–4 mm long. Calyx lobes subequal, 8–15 mm long, pectinate nearly from the base with no evident apex, pink, villous, trichomes 2–3 mm long, of ca. 6 uniseriate cells; corolla cylindric, 25–28 mm long, diam. 2–4 mm, outside densely villous, trichomes white with red apex, inside glabrous, limb subequal, lobes 2–2.5 mm long and 1.5–2 mm wide at base; filaments 20–25 mm long, connate for 3–4 mm at base, glabrous, anthers located in throat adpressed to corolla lobes, ca. 2 × 2 mm; nectary a bilobed dorsal gland; ovary sericeous; style 20–22 mm long, glabrous, stigma bilobed. Fruits and seeds not seen.

OTHER COLLECTIONS: COLOMBIA: NARIÑO: Municipio de Altaquer, between Junín and Buenavista, 700 m, *Mora 4275* (COL); Between Tumaco and El Diviso, Guayacana, 100 m, *Vogel 33* (US). ECUADOR: CARCHI: Trail above Tobar Donosa to Río Guape, 300–500 m, *Hoover 1165* (MO), *1167* (MO); San Marcos, 600 m, *Kvist et al. 48923* (AAU).

DISTRIBUTION: Pacific Ecuador and Colombia.

DISTINGUISHING FEATURES: *Columnea fimbricalyx, C. minor, C. fililoba,* and *C. fuscihirta* are the only Ecuadorian species that have deeply pectinate calyces. *Columnea minor* differs by having 1–3 cm rather than 1–3 mm long pedicels, sparsely pilose corollas rather than densely villous corollas, and by the presence of appendages at the sinuses of the limb. The latter two species belong to section *Collandra.* Both have leaves longer than 10 cm, and both usually have contrasting red patterns on the lower leaf surface (see *C. fililoba* and *C. fuscihirta*).

NOTES: *Columnea fimbricalyx* may be most closely related to *C. rosea* (Morton, 1963) from the Colombian department of Chocó. However, the corolla lacks the conspicuous appendages of the latter species. In addition, *C. rosea* usually has reddish lower leaf surfaces, hispid upper surfaces, and its calyx lobes are not as deeply pectinate. Several apparently related Colombian species still are undescribed.

33. **Columnea flexiflora** Kvist & L. Skog, nom. nov. *Trichantha dodsonii* Wiehl. in Selbyana **7:** 338. 1984, not *Columnea dodsonii* Wiehl. in Selbyana **2:** 70. 1977. TYPE: Cultivated material originally from Ecuador, Prov. Morona-Santiago, *Wiehler 80201* (SEL, HOLOTYPE).

OTHER COLLECTIONS: ECUADOR: MORONA-SANTIAGO: Cordillera de Cutucú, toward Itzintza, 1600–1900 m, Nov.–Dec. 1944, *Camp 1367* (NY, US); Near Río Calagras, 1600 m, *Dodson et al. 10564* (SEL).

DISTRIBUTION: An apparently rare endemic of the montane forests of southeastern Ecuador.

DISTINGUISHING FEATURES: The large, red flowers with a broad, bent corolla limb set *Columnea flexiflora* apart from all other species. This species can be vegetatively separated from all species except *C. elongatifolia* (see that species) by having isophyllous, lanceolate leaves covered only with a sparse indumentum.

NOTES: The type collection, *Wiehler 80201* at SEL, consists only of a few fragments.

34. **Columnea herthae** Mansf. in Repert. Spec. Nov. Regni Veg. **41:** 146. 1936. *Ortholoma herthae* Wiehl. in Phytologia **27:** 321. 1973. *Trichantha herthae* Wiehl. in Selbyana **1:** 34. 1975. TYPE: ECUADOR: PICHINCHA(?): San Carlos de Los Colorados, *Schultze-Rhonhof 1939* (B, HOLOTYPE, no longer extant);

ECUADOR: Los Ríos (on border with PICHINCHA): 12 km E of Patricia Pilar, Montañas de Ila, Centinella, 600 m, 10 July 1979, *Løjtnant & Molau 15808* (AAU, NEOTYPE, here designated).

REPRESENTATIVE ECUADORIAN COLLECTIONS: ESMERALDAS: Parroquia Concepción, Playa Rica, 105 m, *Mexía 8410a* (US). LOS RÍOS: Patricia Pilar–24 de Mayo road, km 12, Montañas de Ila, 540 m, *Dodson 6112* (SEL). PICHINCHA: Santo Domingo–Quevedo road, km 7, *Wiehler & Dodson 7113* (SEL).

DISTRIBUTION: Western Ecuador and adjacent Colombia (Nariño).

DISTINGUISHING FEATURES: The closest Ecuadorian relative is *Columnea lehmannii,* but this species differs by having corollas 3–4 cm rather than 1.2–1.5 cm long. Another very similar species is *C. parviflora* (Morton, 1945) of western Colombia and Panama, but this latter species has smaller corollas 6–8 mm long. Morton (1945) described the ovary of *C. herthae* as glabrous in contrast to sericeous to pilose in *C. parviflora,* but we found the ovaries of *C. herthae* to be pilose. Both species occur in the Dept. Nariño of southwestern Colombia, and *C. parviflora* may also occur in Ecuador.

35. **Columnea laevis** Kvist & L. Skog, sp. nov. TYPE: ECUADOR: CARCHI: San Marcos, 700 m, 3–11 Feb. 1985, *Øllgaard, Korning, & Thomsen 57367* (AAU, HOLOTYPE; COL, G, GB, MO, NY, QCA, QCNE, SEL, US, ISOTYPES). FIGURE 10.

Differt a *Columnea rubricalyx* Kvist & L. Skog floribus parvis 1–4 congestis, calycis parvis flavis vel flavo-brunneis, foliis ovariisque glabris.

Epiphytic herbs, shoots to 60 cm long, all parts of plants except corolla nearly glabrous. Stem diam. to 3 mm; internodes 1–2 cm long. Leaves strongly anisophyllous, coriaceous; the blade of the larger leaf in a pair obovate to oblanceolate, 4–6.5 × 1–1.7 cm, apex acute, base cuneate, upper surface dark green, lower surface violet to purple, veins ca. 4 per side; petiole 6–12 mm long; the blade of the smaller leaf in a pair linear, 5–15 mm long, caducous. Inflorescences in axils of the larger leaf of each pair, of 1–4 congested, nearly sessile flowers; bracts 2–3, violet-purple, orbicular, the largest to 9 × 8 mm, the smaller lanceolate, to 7 mm long, in addition with 0–3 linear bracts, to 5 mm long. Calyx lobes unequal, ca. 8 mm long, yellow to yellow-brown, the dorsal lobe lanceolate to linear, to 2 mm wide, the lateral lobes and the one ventral lobe obovate, to 4 mm wide, the other ventral lobe orbiculate, to 8 mm wide; corolla cylindric, 9–11 mm long, diam. 1–1.5 mm at base and 2–3 mm in throat, outside densely lanate, white, inside glabrous with a few glandular trichomes in the throat, limb subequal, lobes 1–1.5 mm long and 1–1.5 mm wide at base, the trichomes extend beyond the lobes for ca. 1 mm; filaments glabrous, 8–10 mm long, connate for ca. 1 mm at base, anthers subincluded, ca. 1 × 0.8 mm; nectary a bilobed dorsal gland, 0.5–0.8 mm high; ovary glabrous, style 7–9 mm long, glabrous, stigma stomatomorphic. Berry globose, diam. 4–5 mm, yellow; seeds narrowly ellipsoid, ca. 1.2 × 0.4 mm.

OTHER COLLECTIONS: ECUADOR: CARCHI: San Marcos, *Kvist et al. 48682* (AAU), *Kvist et al. 48794* (AAU, QCA, QCNE, US); 45 km W of Maldonado along path to Tobar Donosa, 800 m, *Madison & Besse 7246* (SEL, US).

DISTRIBUTION: Only known from a small area in northwestern Ecuador close to the Colombian border growing in very humid lower montane forest. The species undoubtedly also occurs in adjacent Colombia.

DISTINGUISHING FEATURES: All parts of *Columnea laevis* (except the white lanate corollas) are nearly glabrous. This unusual feature, combined with strongly anisophyllous, rather succulent, obovate to oblanceolate leaves and tiny densely con-

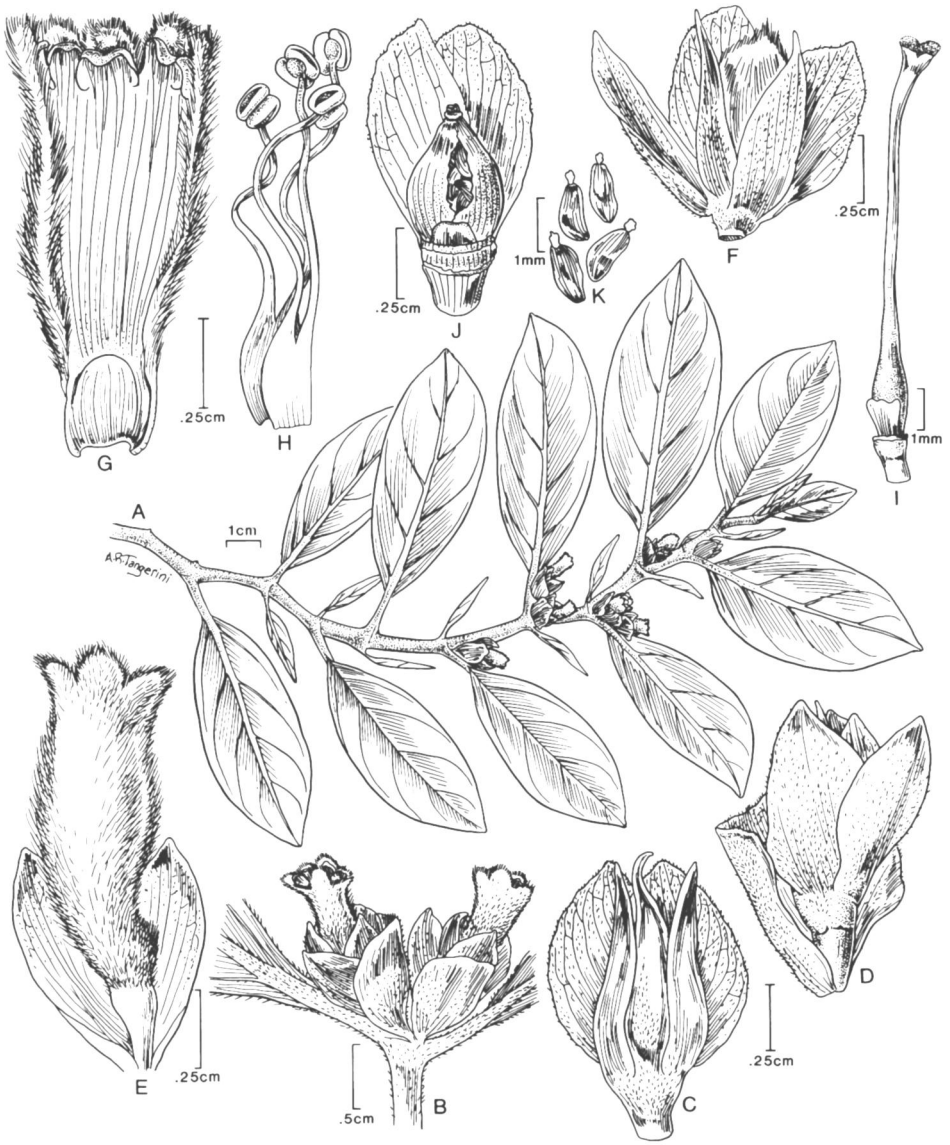

FIGURE 10. *Columnea laevis* Kvist & L. Skog. A, habit; B, node with two axillary flowers; C, minor bracts (see description); D, major bracts; E, flower; F, young fruit; G, corolla opened; H, stamens; I, pistil and nectary; J, dehiscing fruit; K, seeds. (All *Øllgaard et al. 57367,* AAU, and *Kvist et al. 48794,* AAU.)

gested flowers, makes *C. laevis* easily distinguishable. The glabrous condition of the ovaries of *C. laevis* is a rare feature in section *Ortholoma.* This species' closest relative may be *C. rubricalyx,* which differs by having solitary flowers in the leaf axils, an enlarged red calyx, sparsely pilose leaves, and sericeous ovaries.

NOTES: The white indumentum of the corolla appears to close the narrow throat, suggesting the species may be self-pollinating. The labels of two collections (*Mad-*

ison & Besse 7246 and *Øllgaard et al. 57357*) relate that the specimens were ant garden epiphytes. Among New World Gesneriaceae this phenomenon otherwise characterizes the genera *Codonanthe* (Mart.) J. Hanst. and *Codonanthopsis* Mansf. The shape of the leaves of *Columnea laevis* changes when dried: Live material has obovate leaves (confirmed from photos), while those of dried material are oblanceolate. However, when soaked and boiled the leaves regain their original shape.

36. **Columnea lehmannii** Mansf. in Repert. Spec. Nov. Regni Veg. **41:** 146. 1936. *Ortholoma lehmannii* Wiehl. in Phytologia **27:** 322. 1973. *Trichantha lehmannii* Wiehl. in Selbyana **1:** 35. 1975. TYPE: COLOMBIA: *Lehmann 6063* (K, LECTOTYPE, designated here; B, HOLOTYPE, no longer extant).

ECUADORIAN COLLECTIONS: CARCHI: San Marcos, 700 m, *Kvist et al. 48983* (AAU).

DISTRIBUTION: Western Colombia (Cauca, Chocó, and Valle) and northwestern Ecuador.

DISTINGUISHING FEATURES: *Columnea lehmannii* is a close relative of *C. herthae* and *C. parviflora* of western Ecuador and Colombia, respectively, but is distinguished by having much longer corollas (3–4 cm long compared to 0.5–1.5 cm). Another similar species is *C. dissimilis,* which has villous rather than sericeous corollas and green rather than reddish leaves.

NOTES: The Ecuadorian collection has some isophyllous leaf pairs. However, this feature is rare in the Colombian populations of *Columnea lehmannii.*

37. **Columnea minor** (Hook.) J. Hanst. in Linnaea **34:** 387. 1865. *Trichantha minor* Hook. in Icon. Pl. **7:** *pl. 666.* 1844. *Ortholoma minor* Wiehl. in Phytologia **27:** 322. 1973. TYPE: COLOMBIA: *Lobb 175* (K, HOLOTYPE).

Trichantha major Hook. in Icon. Pl. **7:** *pl. 607.* 1844. *Columnea major* J. Hanst. in Linnaea **34:** 388. 1865. TYPE: COLOMBIA: *Lobb 117* (K, HOLOTYPE).

Trichantha bullata C. Morton in Contr. U.S. Natl. Herb. **38:** 16. 1963. *Columnea bullata* C. Morton in Phytologia **22:** 224. 1971. TYPE: COLOMBIA: CAUCA: *Killip 7928* (US, HOLOTYPE; NY, ISOTYPE).

Trichantha teuscheri C. Morton in Contr. U.S. Natl. Herb. **38:** 21. 1963. *Columnea teuscheri* H. E. Moore in Baileya **13:** 16. 1965. TYPE: Cultivated material originally from Ecuador, Prov. Guayas (?), Cuenca–Guayaquil road, *Raymond 2135-56* (US, HOLOTYPE).

Trichantha elegans J. Rose ex C. Morton in Contr. U.S. Natl. Herb. **38:** 23. 1963. *Columnea elegans* C. Morton in Phytologia **22:** 224. 1971. TYPE: ECUADOR: PICHINCHA: Quito–Santo Domingo road, *Haught 3215* (US, HOLOTYPE; NY, ISOTYPE).

REPRESENTATIVE ECUADORIAN COLLECTIONS: AZUAY: Chacanceo–Molleturo road, between Río Blanco and Río Norcay, 1520 m, *Steyermark 52820* (US). CARCHI: San Marcos, 650 m, *Kvist et al. 48740* (AAU). COTOPAXI: Quevedo–Latacunga road, km 46, 600 m, *Holm-Nielsen et al. 2849* (AAU). EL ORO: W of Piñas, 1000 m, *Luer et al. 5557* (SEL). ESMERALDAS: Environs of Lita, 600 m, *Madison et al. 5245* (SEL). LOS RÍOS: E Patricia Pilar–Flor de Mayo road, km 12, Montañas de Ila, La Centinella, 600 m, *Dodson & Dodson 6757* (SEL). PICHINCHA: NE slopes of Pichincha, *Padilla 147* (AAU).

DISTRIBUTION: Western Colombia (Antioquia, Cauca, Nariño, and Valle) and western Ecuador. *Columnea minor* is the most common species of section *Ortholoma* in Ecuador.

DISTINGUISHING FEATURES: The combination of villous pedicels and calyces, pedicellate flowers, deeply pectinate red calyx lobes, and 3.5–4 cm long subventricose, only sparsely pilose corollas with 2–4 mm long appendages located at the sinuses of the lobes, sets *Columnea minor* apart from all other Ecuadorian species of the genus. The only other species with pectinate calyx lobes are *C. fililoba, C. fimbricalyx,* and *C. fuscihirta* (see these species for differences).

NOTES: The leaves of *Columnea minor* vary from lanceolate to ovate, and the corolla also shows much color variation. The limb and the appendages at the sinuses are usually lighter colored than the tube.

38. **Columnea minutiflora** Kvist & L. Skog, sp. nov. TYPE: ECUADOR: CARCHI: 12 km W of Maldonado, Chical, wet montane forest along Río San Juan, 1200 m, 29 May 1978, *Madison, Plowman, Kennedy, & Besse 4755* (AAU, HOLOTYPE; F, SEL, ISOTYPES).

Differt a *Columnea herthae* Mansf., *C. lehmannii* Mansf. et *C. parviflora* C. Morton calycibus dense villosis lobis dissectis foliis pagina superioribus hispidis.

Epiphytic herbs, climbing, shoots to 80 cm long. Stems red, villous, diam. to 5 mm; internodes 1–5 cm long. Leaves strongly anisophyllous, somewhat coriaceous; the blade of the larger leaf in a pair ovate to elliptic, rarely lanceolate, 2–8 × 1–4 cm, apex and base acute, margin weakly serrate, upper surface dull green, hispid, lower surface rose or purple, pubescent to hispid, veins 3–5 per side, petiole 2–7 mm long, villous; the blade of the smaller leaf in a pair ovate to lanceolate, 2–15 × 1–10 mm, sessile, often caducous. Inflorescences in axils of the larger leaf in each pair, of (1–) 3–5 (–7) densely congested epedunculate flowers; bracts 2–3, lanceolate, 2–7 mm long; pedicels 0.5–2 (–5) mm long, villous. Calyx lobes red, subequal, lanceolate with lobed to pectinate margin, 3–6 mm long and 0.5–1.5 mm wide at base, outside and margin covered with red trichomes, inside glabrous; corolla cylindric, 7–10 mm long, diam. ca. 2 mm, outside villous, white with apically red or yellow trichomes, inside glabrous, limb subequal, lobes ca. 1.8 mm long and 1.5 mm wide at base; filaments 8–10 mm long, connate for ca. 2 mm at base, glabrous, anthers subincluded, ca. 0.7 × 0.7 mm, coherent; nectary of 2 free but adjacent dorsal glands, both ca. 0.8 mm high; ovary strigose, style 8–10 mm long, glabrous, stigma bilobed. Berry globose, diam. ca. 5 mm, sericeous, white; seeds ellipsoid, ca. 1 × 0.3 mm.

OTHER COLLECTIONS: COLOMBIA: NARIÑO: Road between Barbacoas and Junín, 1050 m, *Mora 2308* (US). ECUADOR: CARCHI: San Marcos, 700 m, *Kvist et al. 48655* (AAU, QCA, SEL, US), *Kvist et al. 48937* (AAU), *Kvist et al. 48970* (AAU).

DISTRIBUTION: Only known from the lower montane forests of the Pacific Andean slopes close to the border between Ecuador and Colombia.

DISTINGUISHING FEATURES: The Ecuadorian species most closely related to *Columnea minutiflora* are *C. herthae* and *C. lehmannii,* but both have longer corollas (ca. 1.5 and 3 cm long, respectively, rather than 0.8 cm). The corollas of *C. parviflora* (Morton, 1945) from Panama and Pacific Colombia south to the Department of Nariño are as small as those of *C. minutiflora.* The three above-mentioned related species all differ from *C. minutiflora* by having calyx lobes with entire rather than dissected margins, usually pilose rather than densely villous calyces, and usually pubescent or appressed pilose rather than hispid upper leaf surfaces.

NOTES: *Columnea minutiflora* is unusual in having two free although closely adjacent nectary glands (FIGURE 2V). A nectary of more than one (often bilobed or trilobed) gland (FIGURE 2T, W, X) is rare in species belonging to section *Ortholoma* (and also in sections *Collandra* and *Columnea*). The related *C. parviflora* (Morton, 1945) of western Colombia occasionally also has two free nectary glands.

39. **Columnea rubricalyx** Kvist & L. Skog, sp. nov. TYPE: ECUADOR: CARCHI: San Marcos, 700 m, 3–11 Feb. 1985, *Øllgaard, Korning, & Thomsen 57259* (AAU, HOLOTYPE; QCA, ISOTYPE). FIGURE 11.

Differt a *C. laevis* Kvist & L. Skog inflorescentiis unifloribus corollis 1.3–2.1 cm longis ovariis glabris.

Epiphytic climbing herbs, occasionally terrestrial, shoots to 1 m long. Stems glabrous to sericeous near apex, diam. to 5 mm, internodes 1.5–5 cm long. Leaves opposite, strongly anisophyllous, somewhat coriaceous; the blade of the larger leaf in a pair elliptic to lanceolate, 4–10 × 1.2–3.5 cm, apex acute to acuminate, base acute, margin entire, upper surface dull green, sparsely appressed pilose, lower surface reddish, lamina sparsely pilose, veins 3–4 per side, prominent, sericeous, petiole 4–8 mm long; the blade of the smaller leaf in a pair lanceolate to linear, sessile, 5–15 mm long, caducous. Inflorescences of solitary, nearly sessile flowers in axils of the larger leaf of each pair; bracts 1–3, lanceolate, to 5 mm long; pedicels 0.5–3 mm long, sericeous. Calyx lobes red, unequal, outside appressed pilose, basally sericeous, inside glabrous, dorsal lobe lanceolate, 0.9–1.3 cm × 0.2—0.4 cm, lateral lobes and the one ventral lobe rotundate, 1.1–1.6 cm × 1.1–1.8 cm, the other ventral lobe reniform, 1.1–1.5 cm × 1.6–2.3 cm; corolla cylindric, 13–21 mm long, diam. 2–4 mm, outside lanate, yellow, inside glabrous to sparsely glandular-hairy in throat, limb subequal, lobes 2–3 mm long and 1.5–2.5 mm wide at base, indumentum exceeding lobes by ca. 0.5 mm; filaments 10–16 mm long, connate for 2–3 mm at base, glabrous, anthers subincluded, ca. 1.2 × 1.2 mm, coherent; nectary a single or bilobed dorsal gland, 1.2–1.8 mm high; ovary sericeous, style 10–15 mm long, glabrous, stigma stomatomorphic. Fruit a globose berry, diam. ca. 5 mm; seeds narrowly ellipsoid, ca. 0.9 × 0.3 mm.

OTHER COLLECTIONS: COLOMBIA: CAUCA: Chuare, *Haught 5370* (AAU, BH, US). CHOCÓ: Río Azul, confluence with Río Calima, *Hugh-Jones 146* (US). NARIÑO: Barbacoas, Río Telembi, 200–840 m, *García-Barriga 13138* (COL, US); Municipio de Tumaco, 300 m, *Mora 4211* (COL). VALLE: Pacific coast, Río Cajambre, Barco, 5–80 m, *Cuatrecasas 17253* (F, US); Río Azul, confluence with Río Calima, *Hugh-Jones 146* (US). ECUADOR: ESMERALDAS: Quito–San Lorenzo railroad, km 319, Ventanas, 100 m, *Jätiva & Epling 799* (S, UC). CARCHI: San Marcos, 700 m, *Barfod 41466* (AAU, QCA, US), *Kvist et al. 48741* (AAU), *Øllgaard et al. 57322* (AAU); above Tobar Donosa to Río Guape, 300–500 m, *Hoover 1129* (MO), *1275* (MO).

DISTRIBUTION: Pacific Colombia and adjacent Ecuador.

DISTINGUISHING FEATURES: The sparse indumentum, red or violet lower leaf surfaces, sessile, solitary flowers, wide, red, unequal calyx lobes, and lanate corollas 1.3–2.1 cm long characterize *Columnea rubricalyx.* Its closest relative apparently is *C. laevis,* which has an even sparser indumentum, corollas only 7–10 mm long, glabrous rather than sericeous ovaries, and inflorescences with several densely congested flowers. Other related species are *C. herthae, C. lehmannii,* and *C. parviflora* (Morton, 1945) from Colombia, but these all differ from *C. rubricalyx* in having inflorescences with several, usually pedicellate, flowers, and the stems, leaves, and inflorescences have a more conspicuous indumentum.

NOTES: Colombian plants often have longer corollas than the Ecuadorian ones (ca. 19 mm long instead of ca. 14 mm), but are otherwise similar.

40. **Columnea tenella** Kvist & L. Skog, nom. nov. *Trichantha gracilis* Wiehl. in Selbyana **7:** 339. 1984, not *Columnea gracilis* (Mart.) O. Kuntze = *Codonanthe gracilis* (Mart.) J. Hanst. TYPE: COLOMBIA: *White s.n.* (K, HOLOTYPE).

ECUADORIAN COLLECTIONS: CARCHI: San Marcos, very humid low montane forests, 700 m, *Barfod 41447* (AAU), *Barfod 41577* (AAU, COL, QCA, SEL, US), *Hoover 1069* (MO), *Øllgaard et al. 57280* (AAU, QCA, US), *Madison & Besse 7011* (SEL, US), *Thompson et al. 791* (CM, US).

FIGURE 11. *Columnea rubricalyx* Kvist & L. Skog. A, habit; B, bract and calyx lobes; C, flower; D, corolla; E, opened corolla; F, stamens; G, pistil and nectary; H, young fruit; I, mature fruit; J, seeds. (A, *Haught 5370,* US; B–C, *García-Barriga 13138,* US; D–J *Hugh-Jones 146,* US.)

DISTRIBUTION: Northwestern Colombia (Antioquia, Chocó, Valle) and northwestern Ecuador.

DISTINGUISHING FEATURES: *Columnea tenella* is a distinct species set apart by its slender shoots, strongly anisophyllous leaves ca. 6 cm long, inflorescences of 2–4 flowers with pedicels ca. 5 mm long, ovate to oblanceolate, ca. 8 mm long

red calyx lobes, and cylindric, ca. 1.2 cm long corollas that have a cream or yellow-red tube with contrasting violet or purplish lobes. The most closely related species may be *C. brenneri,* but this latter species has ca. 3 cm long corollas and lanceolate calyx lobes. Another apparently related species is *C. calotricha* (Smith, 1905) from Central America, Venezuela, and the Guianas, but it has subequal leaves.

NOTES: The Ecuadorian collections of *Columnea tenella* differ from the type collection from the Dept. Antioquia in Colombia by having corollas ca. 12 mm rather than 17 mm long. In addition, the berries are yellow in Ecuador, while those of the type were described as being white.

41. **Columnea tenensis** (Wiehl.) B. Morley in Garden (London) **100**(9): 438. 1975. *Trichantha tenensis* Wiehl. in Selbyana **1**: 39, *fig. 2.* 1975b. TYPE: Cultivated material originally from Ecuador, Prov. Napo, 4 km S of Tena, *Wiehler 7318* (US, HOLOTYPE; SEL(2), ISOTYPES).

OTHER COLLECTIONS: ECUADOR: NAPO: San Miguel–Lago Agrio, 350 m, *Besse et al. 1546* (SEL); Río Cuyabeno, 2–6 km upstream from Puerto Bolívar, 300 m, *Brandbyge et al. 33722* (AAU(2)), 300 m, *Brandbyge et al. 33788* (AAU, US); Lagunas de Cuyabeno, 300 m, *Brandbyge et al. 33985* (AAU, US); 4 km S of Tena, *Wiehler 7321* (SEL). PASTAZA: Veracruz (Indillama), *Lugo S. 35* (SEL); 5 km E of Puerte Sarayacu, Shiguacocha, *Lugo S. 3859* (SEL).

DISTRIBUTION: Eastern Ecuador.

DISTINGUISHING FEATURES: *Columnea tenensis* is vegetatively similar to *C. inaequilatera* in section *Collandra* but is reproductively distinguished by having 5–6 cm long yellow and purple-striped corollas with ca. 5 mm long appendages at the sinuses between the lobes. The most closely related species possibly are *C. brenneri* and *C. elongatifolia,* but both differ from *C. tenensis* by having entire rather than dissected calyx lobe margins. In addition, *C. brenneri* has ca. 3 cm long corollas, and *C. elongatifolia* has leaves linear to narrowly lanceolate rather than obovate to oblanceolate.

E. Section **Pentadenia** (Planch.) Benth.

Columnea L. section *Pentadenia* (Planch.) Benth. in Benth. & Hook. f., Gen. Pl. **2**(2): 1010. 1876. *Pentadenia* (Planch.) J. Hanst. in Linnaea **26**: 186–197, 211. 1854.

Columnea L. subgenus *Pentadenia* Planch. in Fl. Serres Jard. Eur. **6**: 45, *pl. 552.* 1854. TYPE: *Columnea aurantiaca* Decne. ex Planch. = *Columnea strigosa* (Benth.) J. Hanst.

42. **Columnea strigosa** Benth. Pl. Hartw. 232. 1846. *Pentadenia strigosa* J. Hanst. in Linnaea **26**: 211. 1854. TYPE: ECUADOR: TUNGURAHUA: Mt. Tungurahua, *Hartweg 1262* (K, HOLOTYPE; BM, CGE, E, G, K, NY, P, W, ISOTYPES).

Columnea campanulata Benth. Pl. Hartw. 232. 1846. TYPE: COLOMBIA: CUNDINAMARCA: Bogotá, *Hartweg s.n.* (K, HOLOTYPE).

Columnea macrantha Benth. Pl. Hartw. 232. 1846. TYPE: ECUADOR: PICHINCHA: The Andes near Quito, *Hartweg s.n.* (K, HOLOTYPE).

Columnea aurantiaca Decne. ex Planch. in Fl. Serres Jard. Eur. **6**: 45, *pl. 552.* 1850–1851. *Pentadenia aurantiaca* J. Hanst. in Linnaea **26**: 211. 1854. TYPE: VENEZUELA: MERIDA: *Linden 1454* (MPU, HOLOTYPE; BM, G, GH, K, P, W, ISOTYPES).

Columnea pichinchensis J. Hanst. in Linnaea **34**: 398. 1865. TYPE: ECUADOR: PICHINCHA: Quito, *Jameson 667* (LE, HOLOTYPE; BM, K, NY, P, US, W, ISOTYPES).

Columnea campanulata var. *longipedunculata* Cuatr. in Trab. Mus. Nac. Ci. Nat., Ser. Bot. **33**: 121. 1936. TYPE: COLOMBIA: TOLIMA: Ibague, *Cuatrecasas 2431* (MA, HOLOTYPE).

Columnea kucyniakii Raym. in Svensk Bot. Tidskr. **58**: 185. 1964. TYPE: Cultivated material grown from seeds collected in Ecuador, Prov. Azuay (?), *Raymond s.n.* (MTJB, HOLOTYPE).

REPRESENTATIVE ECUADORIAN COLLECTIONS: AZUAY: Molleturo–Cuenca road, km 6, El Chorro, *Harling & Andersson 22861* (GB, US). BOLÍVAR: Simiatug, Hacienda Talahua, *Penland & Summers*

572 (US). CAÑAR: Between Rivera and Pindilig, 2800 m, *Holm-Nielsen et al. 29241* (AAU). CARCHI: Tulcán–Maldonado road, km 53, Maldonado Valley, 3200 m, *Holm-Nielsen et al. 5593* (AAU). CHIMBARAZO: Riobamba–Baños road, 4 km N of Puela, *Lugo S. 757* (SEL). COTOPAXI: Pilaló, 2895 m, *Boeke 563* (AAU, SEL, US). IMBABURA: Above Apuela, Intag valley, 2600 m, *Holm-Nielsen & Jaramillo 23320* (AAU). LOJA: Alamor–Cazaderos road, W of El Limo, 1400 m, *Harling & Andersson 22285* (GB, US). MORONA-SANTIAGO: Gualaceo–General La Plaza Gutiérrez (Límones) road, 2500 m, *Kvist 60414* (AAU, QCA, QCNE, US). NAPO: Santa Barbara–Sibundoy road, 2600 m, *Kvist et al. 60266* (AAU, QCA). PICHINCHA: Old Quito–Santo Domingo road, 3–16 km W of Chiriboga, *Luteyn et al. 8803* (AAU, US). TUNGURAHUA: Cordillera de Llanganates, valley of Río Sangarinas, 3150 m, *Asplund 9784* (US). ZAMORA-CHINCHIPE: Above Valladolid on road to Yangana, 2700 m, *Harling & Andersson 21440* (GB, US).

DISTRIBUTION: The high montane forests of northwestern Venezuela, Colombia (where the species is common and widespread), Ecuador, and northern Peru (Amazonas, Cajamarca). *Columnea strigosa* is the most frequently collected species in Ecuador and the only one common above 2200 meters.

DISTINGUISHING FEATURES: *Columnea strigosa* usually is a distinctive, stout, climbing epiphyte, set apart by having isophyllous, ovate to lanceolate leaves and long-pedicellate, bilabiate, 4.5–7 cm long yellow corollas that have an eglandular throat. However, *C. strigosa* is very variable, and in the western cordillera some mostly terrestrial populations have smaller corollas, shorter pedicels, and often shoots with apically congested leaves and flowers. Their bilabiate flowers set them apart from *C. lophophora* and *C. matudae* in section *Stygnanthe* which have a similar habit. In addition, terrestrial *C. strigosa* plants often have only a single nectary gland, rather than several glands as found in section *Stygnanthe* (see notes below).

NOTES: The nectary varies more in *Columnea strigosa* than in any other species of *Columnea* (or any other Gesneriaceae). Most specimens possess four or five free nectary glands as is typical in section *Stygnanthe* (FIGURE 2A, C). However, some plants have nectaries reduced to one bilobed, dorsal gland similar to that found in the sections *Collandra, Ortholoma,* and *Columnea* (FIGURE 2W). In addition, several intermediate nectary types occur in *C. strigosa* (FIGURE 2D, I, J, K, M, O, P, S, X).

The features which distinguish the above-mentioned terrestrial populations of the western cordillera from typical climbing plants appear in TABLE 4. In some regions, e.g., the province of Pichincha, most plants can easily be referred to either the terrestrial or the climbing form (the former has often been referred to the synonymous species *Columnea pichinchensis* and *C. kucyniakii*). However, in the adjacent provinces of Cotopaxi and Chimbarazo, most specimens have combinations of features which make it difficult to refer them to either of the two forms. In particular, several intermediate nectary types (or even a single, bilobed gland) occur in otherwise typical climbing plants. The terrestrial form may be a formerly distinct species that is currently "fusing" with the more widespread climbing form due to extensive hybridization. This phenomenon is also known in the genus *Kohleria* (Kvist & Skog, in press).

F. Section **Stygnanthe** (J. Hanst.) Benth.

Columnea L. section *Stygnanthe* (J. Hanst.) Benth. in Benth. & Hook. f., Gen. Pl. **2:** 1010. 1876. *Stygnanthe* J. Hanst. in Linnaea **26:** 185, 209. 1854. TYPE: *Stygnanthe moesta* (Poepp.) J. Hanst. = *Columnea moesta* Poepp.

43. **Columnea angustata** (Wiehl.) L. Skog in Ann. Missouri Bot. Gard. **65:** 844.

1979 ('1978'). *Pentadenia angustata* Wiehl. in Selbyana **2:** 118. 1977. TYPE: COLOMBIA: VALLE: *Wiehler et al. 7276* (SEL, HOLOTYPE).

Columnea sericea Mansf. in Biblioth. Bot. **116:** 145. 1937 (nom. illeg.). *Pentadenia sericea* Wiehl. in Phytologia **27:** 315. 1973. TYPE: ECUADOR: TUNGURAHUA: Río Negro, *Diels 878* (B, HOLOTYPE, no longer extant); ECUADOR: CHIMBARAZO: Naranjapata, Río Chanchan, 1933, *Schimpff 523* (M, NEOTYPE, here selected; MO, TRT, ISONEOTYPES).

Pentadenia ecuadorana Wiehl. in Selbyana **2:** 82. 1977. *Columnea ecuadorana* L. Skog in Taxon **33:** 126. 1984. TYPE: ECUADOR: PASTAZA: Puyo, *Wiehler et al. 7163* (SEL, HOLOTYPE).

REPRESENTATIVE ECUADORIAN COLLECTIONS: EL ORO: New Piñas–Santa Rosa road, km 11, 850 m, *Dodson et al. 9067* (SEL). ESMERALDAS: Cayapa river system, Río Bolborde, 100 m, *Kvist et al. 48293* (AAU). LOS RÍOS: 40 km E of Babahoya, Montalva, 150 m, *Holm-Nielsen et al. 2628* (AAU). MANABÍ: Mt. Montecristi, 475 m, *Dodson & Thien 1736* (US). MORONA-SANTIAGO: Cordillera de Cutucú, trail from Logroño to Yaupi, 1200 m, *Madison et al. 3192* (SEL). NAPO: Tena, *Padilla 8* (AAU). PASTAZA: S of Puyo, Madre Tierra, 1030 m, *Kvist 60325* (AAU, QCA, QCNE, US). PICHINCHA: Santo Domingo, Colorado Community "Cóngoma Grande", 100 m, *Kvist & Barfod 49106* (AAU). TUNGURAHUA: Río Negro, 1250 m, *Asplund 8554* (US).

DISTRIBUTION: Costa Rica, Panama, northwestern Colombia (Antioquia, Chocó, and Valle), and west and east of the Andes mountains in Ecuador.

DISTINGUISHING FEATURES: *Columnea angustata* is set apart by having isophyllous, elliptic to lanceolate, 4–8 cm long leaves with sericeous lower and glabrous upper surfaces and by having uniformly colored, cylindric corollas that are 2.2–3 cm long and usually red, but occasionally yellow and pink. The nectary mostly consists of five free glands (FIGURE 2A), but there is considerable variation (FIGURE 2B, E, F, Q). The nearest relative is *C. leucerinea* (q.v.).

NOTES: Wiehler (1977) described plants from Colombia and Ecuador as *Columnea angustata* and *C. ecuadorana,* respectively. However, the Colombian and Ecuadorian populations are here considered as conspecific, since only minor and apparently inconsistent differences distinguish them. In Colombia (and Central America) the corolla is apparently always yellow, but this feature also occurs in Ecuador, and the average lengths of corollas and leaves are greater in Colombia. The two names have equal priority, but *C. angustata* was preserved, as the epithet "ecuadorana" is of low information content in a genus with 57 Ecuadorian species. The ranges of the Ecuadorian and the Colombian–Central American populations may be disjunct, since no collections are yet known from the southwestern Colombian departments of Nariño and Cauca. Ten species show similar apparently disjunct distributions (see Distribution of Ecuadorian Species).

Although species of *Columnea* usually disappear when forest is converted to farmland, *C. angustata* is an exception. This species commonly grows in isolated trees left in deforested areas, e.g., in the region around Puyo in eastern Ecuador and around Santo Domingo in western Ecuador (Kvist, pers. obs.).

44. **Columnea byrsina** (Wiehl.) Kvist & L. Skog, comb. nov. *Pentadenia byrsina* Wiehl. in Selbyana **2:** 119. 1977. TYPE: Cultivated material grown from seeds collected in Ecuador, Prov. Napo, near Baeza, *Wiehler 77122* (SEL, HOLOTYPE).

REPRESENTATIVE ECUADORIAN COLLECTIONS: CARCHI: Between Chical and Pailon, 1100 m, *Kvist et al. 48658* (AAU). NAPO: Baeza–Lago Agrio road, km 18, *Balslev & Madsen 10575* (AAU, SEL(2)). PICHINCHA: 33 km NE of Alluriquin, Chiriboga, 2000 m, *Sauleda et al. 4011* (SEL).

DISTRIBUTION: Western Colombia (Antioquia, Nariño, and Valle) and the western and eastern Andean slopes of northern Ecuador.

DISTINGUISHING FEATURES: *Columnea byrsina* differs from other species in sec-

tion *Stygnanthe* by having exserted stamens (although a single collection referred to *C. orientandina* also has this attribute—see this latter species). In addition, the anisophyllous, coriaceous leaves and the red corolla with a yellow apex identify *C. byrsina.* The nectary usually consists of four glands with one of them being bilobed (FIGURE 2C), but a few specimens from Carchi have three glands, two of them bilobed (FIGURE 2G).

45. **Columnea colombiana** (Wiehl.) Kvist & L. Skog, comb. nov. *Pentadenia colombiana* Wiehl. in Selbyana **2:** 120. 1977. TYPE: COLOMBIA: VALLE: *Wiehler et al. 72130* (SEL, HOLOTYPE).

ECUADORIAN COLLECTIONS: ESMERALDAS: Río Cayapa, Zapallo Grande, *Kvist et al. 48268* (AAU, QCA, QCNE, US).

DISTRIBUTION: Colombia (Antioquia, Valle) and northwestern Ecuador.

DISTINGUISHING FEATURES: *Columnea colombiana* is a slender epiphyte recognized by having frequently pendent shoots, 1.5–3 cm long ovate, isophyllous leaves, basally dissected, lanceolate calyx lobes, ca. 2.5 cm long, and cylindric lavender corollas with a green limb and four or five nectary glands (FIGURE 2B, C).

46. **Columnea crassicaulis** (Wiehl.) Kvist & L. Skog, comb. nov. *Pentadenia crassicaulis* Wiehl. in Selbyana **2:** 122. 1977. TYPE: COLOMBIA: NARIÑO: *Wiehler & Williams 72185* (SEL, HOLOTYPE).

ECUADORIAN COLLECTIONS: CARCHI: Maldonado, 1500 m, *Harling & Andersson 12391* (SEL). PICHINCHA: Between Nanegalito and Gualea, 1500 m, *Dodson et al. 6983* (SEL); Nono–Tandayapa road, 1700–2000 m, *Dressler 4926* (SEL); Nono–Mindo road, 1500 m, *Luer et al. 4717* (SEL).

DISTRIBUTION: Southwestern Colombia (Nariño) and northwestern Ecuador.

DISTINGUISHING FEATURES: The combination of 4–9 cm long, isophyllous, ovate, nearly glabrous, reddish leaves and 4–5.5 cm long cylindric, somewhat ventricose, yellow corollas, and glabrous ovaries and styles identifies *Columnea crassicaulis.* The nectary consists of one bilobed and three unlobed glands (FIGURE 2C).

NOTES: A similar species is *Columnea moesta* (Poeppig, 1840) described from Huanuco on the eastern slopes of the Peruvian Andes. The main difference is that *C. crassicaulis* has shorter, lanceolate calyx lobes compared to the linear lobes of *C. moesta.*

47. **Columnea inconspicua** Kvist & L. Skog, sp. nov. TYPE: ECUADOR: PICHINCHA: Tandápi (confluence between Río Tandápi with Río Pilatón), subtropical rain and gallery forest, 1500 m, 27 July 1967, *Sparre 17761* (s, HOLOTYPE).

Differt a *Columnea lavandulacea* Kvist & L. Skog corollis parvis flavidis, a *C. microsepala* (C. Morton) Kvist & L. Skog et *C. orientandina* (Wiehl.) Kvist & L. Skog ovariis glabris glandulis nectarifluis 2.

Epiphytic, usually climbing. Stems glabrescent to sericeous near apex, frequently branching, diam. to 10 mm; internodes 1–3 cm long. Leaves mostly anisophyllous but frequently isophyllous; the blade of the larger leaf in a pair lanceolate to oblanceolate, less commonly obovate, 2.5–7 × 0.8–2 cm, apex acuminate, base cuneate to acute, margin often undulate, both surfaces sparsely strigose, below occasionally with red apex, veins 3–6 per side, sericeous below, petiole 0.5–2.5 mm long; blade of smaller leaf in a pair up to 15 mm long, often lanceolate.

Inflorescences in axils of the larger leaf in each pair, of 1–5 flowers; pedicels 2–6 mm long, sericeous; bracts apparently lacking. Calyx lobes equal, green to purple, linear, 8–11 mm long, 1–1.5 mm wide at base, outside sericeous, inside glabrous; corolla cylindric and subventricose, 16–22 mm long, diam. 1–2 mm at base, widened to 3–5 mm, diam. 2–4 mm at throat, pale yellow to cream, without any markings, outside pilose to sericeous and usually glandular-hairy, inside basally glabrous or sparsely pilose and apically glandular-hairy, limb subequal, lobes 1–1.5 mm long, 1.5–2 mm wide at base; filaments 13–18 mm long, adnate to corolla tube for ca. 2 mm at base, basally pilose to apically glabrous, anthers subincluded, ca. 0.7 × 0.7 mm; nectary of 2 (or 3) free, usually opposite glands (1 bilobed and 1 (or 2) unlobed); ovary glabrous, style 16–20 mm long, glabrous, stigma stomatomorphic. Berry ovoid, ca. 6 × 3 mm; seeds narrowly ellipsoid, ca. 1 × 0.3 mm.

OTHER COLLECTIONS: ECUADOR: AZUAY: Road between Chacanceo and Molleturo, between Río Blanco and Río Norcay, 1520 m, *Steyermark 52825* (US). COTOPAXI: El Corazón–Facundo Vela trail, km 2, 1350 m, *Harling & Andersson 19225* (GB, US). MORONA-SANTIAGO: Cordillera de Cutucú, western slopes, trail from Logroño to Yaupi, 1830 m, *Madison et al. 3370* (SEL). PICHINCHA: New Quito–Santo Domingo road, 2 km W of Tandápi, 1400 m, *Dodson & Gentry 9592* (SEL); Nanegalito–Pacto road, Tulipe, 1550 m, *Holm-Nielsen et al. 24499* (AAU). PERU: AMAZONAS: Serrania de Bagua, 12–18 km E of La Peca, 1800–1950 m, *Gentry et al. 22920* (MO, US).

DISTRIBUTION: The Andean slopes in Ecuador (both east and west) and in Peru (only east).

DISTINGUISHING FEATURES: *Columnea inconspicua* has no conspicuous features, but it is set apart by the combination of small, pale yellow to cream corollas, glabrous ovaries, and nectaries of two or three glands with one of these being bilobed (FIGURE 2K, R). The closest relative may be *C. lavandulacea,* which has similar although rarely strongly anisophyllous leaves and glabrous ovaries, but differs in having lavender corollas with a yellow and purple limb and two bilobed nectary glands (FIGURE 2L). Another vegetatively similar species is *C. byrsina,* which differs by its red corollas with a yellow limb and exserted stamens and a nectary of four (rarely three) glands (FIGURE 2C, G). Two species with superficially similar flowers are *C. microsepala* of western and *C. orientandina* of eastern Ecuador, but both have sericeous ovaries and four or five nectary glands (FIGURE 2A, C).

NOTES: The leaf pairs are mostly strongly anisophyllous, but in *Columnea inconspicua* this feature is more variable than in any other species in section *Stygnanthe.* Many shoots have some interspersed equal leaf pairs, and occasionally most or all leaf pairs have equal leaves.

48. **Columnea isernii** Cuatr. in Anales Ci. Univ. Madrid **4:** 247 (reprint p. 44). 1935. *Pentadenia isernii* Wiehl. in Phytologia **27:** 315. 1973. TYPE: ECUADOR: BOLÍVAR(?): *Isern 502* (MA, HOLOTYPE).

OTHER COLLECTIONS: ECUADOR: CAÑAR: km 110 from Duran, 1300 m, *Dodson & Thien 2095* (WIS). LOJA: Alamor road at crossing with Río Alamor, 1250 m, *Harling & Andersson 22199* (GB, US); Alamor–Cazaderos road, just W of El Limo, 1400 m, *Harling & Andersson 22301* (GB). PERU: TUMBES: Bosque Nacional de Tumbes, close to Campo Verde, 600–800 m, *Simpson & Schunke V. 382* (F, US).

DISTRIBUTION: Deciduous forests of southwestern Ecuador and adjacent Peru.

DISTINGUISHING FEATURES: The shoots of *Columnea isernii* have apically congested leaves and flowers—a feature shared with *C. lophophora* and frequently with *C. matudae.* The shorter, 2–3 cm long, villous, yellow-green and purple-striped corollas distinguish *C. isernii* from these latter two closely related species.

The nectary usually consists of five free glands, but two of these are occasionally fused (FIGURE 2A, C).

Columnea isernii is similar to the terrestrial genus *Corytoplectus* Oersted (1858) but differs by usually being epiphytic, by having dissected instead of entire calyx lobe margins, white instead of translucent berries with black seeds, and by lacking pedunculate inflorescences.

NOTES: *Columnea isernii, C. lophophora,* and *C. matudae* are all distributed in southeastern Ecuador (but only *C. isernii* is known from adjacent Peru). This region has a seasonal climate, and the plants apparently lose their leaves during the dry season and sprout and flower by the beginning of the wet season.

49. **Columnea lavandulacea** Kvist & L. Skog, sp. nov. TYPE: ECUADOR: PICHINCHA: Quito–Santo Domingo de Los Colorados road, montane forests and rocky slopes, 1800 m, 11 Dec. 1983, *Kvist & Barfod 49066* (AAU, HOLOTYPE). FIGURE 12.

Differt a *Columnea ovatifolia* Kvist & L. Skog foliis ovatis vel obovatis anisophyllis corollis brevis (2.1–2.6 cm longis) ovariis glabris, a *C. inconspicua* Kvist & L. Skog tubis corollarum exterioribus lavandulaceis.

Epiphytic or epipetric herbs, usually climbing, shoots up to 1 m long. Stems glabrescent to sericeous near apex, diam. to 5 mm, lavender, branching from older shoots; internodes 1.5–4 cm long. Leaves anisophyllous; the blade of the larger leaf in a pair ovate to obovate, 2.5–4.5 × 1–2 cm, apex acuminate, base cuneate to acute, margin undulate, ciliate, often red, upper surface deep green, glabrous, lower surface lighter green, margin red, lamina sparsely pilose, veins and margin sericeous, petiole 0.5–2 mm long, sericeous; the blade of the smaller leaf in a pair 1–2.5 × 0.6–1 cm, otherwise similar. Inflorescences in axils of the larger leaf of each pair, of 1–2 (–4) flowers; pedicels 3–6 mm long, lavender, sericeous; bracts 1–2, scale-like, 1–2 mm long, caducous. Calyx lobes equal, dull rose, linear, 12–15 mm long and ca. 2 mm wide at base, outside appressed pilose, inside glabrous; corolla cylindric and subventricose, 21–26 mm long, diam. 2–3 mm at base, widened to 4–5 mm, diam. 3–4 mm at throat, tube outside lavender and appressed pilose, inside usually pilose and apically glandular-hairy, limb subequal, yellow, pilose, lobes ca. 1.5 mm long and 2.5 mm wide at base, each with 1 deep purple dot outside; filaments 19–25 mm long, adnate to corolla tube for 3–4 mm, basally pilose to apically glabrous, anthers subincluded, ca. 1 × 0.8 mm; nectary of two bilobed glands (1 dorsal and 1 lateral); ovary ca. 2.5 mm high, glabrous, style 20–25 mm long, glabrous, stigma bilobed. Berry ovoid, ca. 7 mm long, diam. ca. 3.5 mm, pale lavender-blue, glabrous; seeds narrowly ellipsoid, ca. 1.2 × 0.4 mm.

OTHER COLLECTIONS: ECUADOR: MORONA-SANTIAGO: 10 km SE of San Juan Bosco, 1570 m, *Gentry et al. 30858* (SEL); Crossroad between Limón and Indanza, Plan del Milagro, 1600–1700 m, *Harling & Andersson 24524* (GB, US). PICHINCHA: Mindo, *André K1479* (NY); Along Río Saloya, 1800–2400 m, *Steyermark 52572* (MO, US); old Quito–Nono–Mindo Road, 9 km S of Tandayapa towards Mindo, 2460 m, *Luteyn 8830* (NY).

DISTRIBUTION: The species occurs on the eastern and the western slopes of the Andes in Ecuador, but is apparently very local.

DISTINGUISHING FEATURES: Species of *Columnea* usually have either isophyllous leaf pairs or strongly anisophyllous pairs with the reduced leaf being bract-like. *Columnea lavandulacea* is intermediate as the smaller leaf in each pair is reduced to only about the half the length of the larger one and is of a similar shape. In addition, the lavender corolla with yellow limb and one deep purple dot on each

FIGURE 12. *Columnea lavandulacea* Kvist & L. Skog. A, habit; B, leaf apex; C, calyx lobes; D, flower; E, corolla; F, corolla opened to show stamens; G, flower with corolla and some calyx lobes removed to show pistil and nectary; H, anthers; I, anthers reverse. (A, *Kvist & Barfod 49066,* AAU; B–I, *Harling & Andersson 25424,* GB, US.)

lobe sets *C. lavandulacea* apart from all species except the related *C. ovatifolia.* The latter species has similar, although less conspicuous and persistent, corolla colors, but it differs in having isophyllous, ovate leaves, considerably longer corollas (4–4.8 cm long in contrast to 2.1–2.6 cm), and sericeous rather than glabrous

ovaries. There is possibly a close affinity with *C. inconspicua,* but, among other attributes, this latter species is set apart by having pale yellow or cream corollas (see *C. inconspicua*). *Columnea lavandulacea* (FIGURE 2L), *C. ovatifolia* (FIGURE 2H), and *C. inconspicua* (FIGURE 2K, R) all have different nectary elaborations.

50. **Columnea leucerinea** Kvist & L. Skog, sp. nov. TYPE: ECUADOR: NAPO: Lago Agrio–Baeza road, km 145, Río Aya Cachi, farmland with disturbed forest remnants, 1800 m, 8 Jan. 1987, *Kvist, Bergmann, & Pedersen 60377* (AAU, HOLOTYPE; COL, MO, NY, QCA, QCNE, US, ISOTYPES). FIGURE 13.

Differt a *Columnea angustata* (Wiehl.) L. Skog foliorum caulium calycumque indumentis dense albis corollarum lobis calycum spathulatis trichomatibus erectis 2–4 mm longis ovariis glabris.

Epiphytic or occasionally terrestrial herbs, shoots 40–70 (–100) cm long, branching from the base. Stems glabrescent to lanate near apex, diam. to 6 mm; internodes 1.5–3.5 cm long. Leaves isophyllous in pairs, blades lanceolate, 4–8 × 1–2.5 cm, apex acuminate, base acute, margin subentire, ciliate, upper surface dull green, puberulent, lower surface sericeous to lanate, trichomes white, but bordeaux-red along margins, veins 4–5 per side, petioles 5–15 mm long, lanate. Inflorescences of 1–4 flowers; pedicels 4–15 mm long, white-lanate; bracts 3–5, linear, 3–8 mm long, caducous. Calyx lobes equal, spathulate to oblanceolate, 7–10 mm long and 1–1.5 mm wide at base, upwards often widened to 1.5–2.5 mm, maroon, outside lanate, inside glandular-hairy; corolla cylindric and usually ventricose, 14–21 mm long, diam. 2–3 mm at base, widened to 3–5 mm, diam. 1.5–2.5 mm at throat, outside orange-red, villous, trichomes bordeaux-red, 2–4 mm long, of ca. 8 uniseriate cells, inside yellow, glabrous, limb subequal, lobes ca. 1.5 mm long and 1.2 mm wide at base, orange to yellow with a dark dot inside; filaments 12–15 mm long, connate for 4–6 mm at base, adnate to base of corolla tube for 1.5–2 mm, glabrous or sparsely pilose, anthers included, ca. 1.2 × 1 mm; nectary of 5 separate glands, each 0.4–0.6 mm high; ovary glabrous, style 11–13 mm long, glabrous, stigma stomatomorphic. Berry globose, diam. ca. 5 mm, glabrous, light brown; seeds 100–200, narrowly ellipsoid, ca. 1 × 0.3 mm.

OTHER COLLECTIONS: ECUADOR: NAPO: Río Quijos, 1650 m, *Harling 3863* (GB); Union of Río Borja and Río Quijos, 1760 m, *Holm-Nielsen et al. 26106* (AAU, COL, MO, QCA, SEL, US), *Holm-Nielsen et al. 26229* (AAU, MO, QCA, US); Creek 3–4 km NW of Borja, 1875 m, *Holm-Nielsen et al. 26298* (AAU, US), *Holm-Nielsen et al. 26357* (AAU, QCA, US); Río Panteor SW of Borja, 1900 m, *Holm-Nielsen et al. 26744* (AAU, QCA, SEL, US). PICHINCHA: Road Nanagalito–Pacto, Tulipe, 1550 m, *Holm-Nielsen et al. 24500* (AAU); Tandápi, 1500 m, *Sparre 14002* (S).

DISTRIBUTION: *Columnea leucerinea* occurs on the western and the eastern slopes of the Andes in Ecuador, but is local and only known from elevations between 1500 and 2000 meters.

DISTINGUISHING FEATURES: *Columnea leucerinea* is related to *C. angustata,* but the dense white indumentum of the leaves, stems and calyces, the spathulate calyx lobes, the 2–4 mm long erect trichomes of the corollas, and the glabrous instead of sericeous ovaries set it apart. In addition, *C. leucerinea* and *C. angustata* occur above and below 1200 meters, respectively.

51. **Columnea lophophora** Mansf. in Biblioth. Bot. **116:** 145. 1937. *Pentadenia lophophora* Wiehl. in Phytologia **27:** 315. 1973. TYPE: ECUADOR: CHIMBARAZO: Above Huigra, Río Chanchan, *Diels 1177* (B, HOLOTYPE, no longer extant); ECUADOR: CHIMBARAZO: close to Huigra, mostly on Hacienda de

FIGURE 13. *Columnea leucerinea* Kvist & L. Skog. A, habit; B, calyx lobes; C, flower; D, corolla opened to show stamens; E, flower with corolla removed to show pistil and nectary; F, stigma; G, mature fruit; H, seeds. (A–B, D–H, *Holm-Nielsen et al. 26229,* AAU; C, *Kvist et al. 60377,* AAU.)

Licay, 1700–1900 m, 21 Aug. 1918, *Rose & Rose 22281* (US, NEOTYPE, here designated; NY, ISONEOTYPE).

OTHER COLLECTIONS: ECUADOR: CHIMBARAZO: Close to Huigra, Hacienda de Licay, *Rose et al. 23880* (US). Precise locality unknown: *Spruce 5529* (NY).

DISTRIBUTION: Western Ecuador, but apparently local and possibly extinct.

DISTINGUISHING FEATURES: The few known collections of *Columnea lophophora* have naked stems with an apical cluster of tender leaves, flowers, and bracts. *Columnea lophophora* differs from *C. isernii* and *C. matudae,* in both of which a similar apical arrangement is often seen, by always having inflorescences with conspicuous ovate bracts and subentire calyx lobe margins. In addition, *C. isernii* has 2–3 cm long corollas and *C. lophophora* 3–4 cm long corollas, and *C. matudae* has ventricose rather than the cylindric corollas of *C. lophophora.*

NOTES: Mansfeld (1937) probably correctly suggested that *Columnea lophophora* is strongly seasonal. The few known collections were made during the months August to October in the late dry season. At this stage of growth, the tender leaves are small and apically congested, but the naked stems below possess 5–10 cm long internodes. This indicates that the shoots elongate during the wet season while the leaves attain their so far unknown mature size.

52. **Columnea matudae** (Wiehl.) Kvist & L. Skog, comb. nov. *Pentadenia matudae* Wiehl. in Selbyana **2:** 122. 1977. TYPE: MEXICO: CHIAPAS: Rodillo, *Matuda 1626* (US, HOLOTYPE; F, GH, K, MEXU, US, ISOTYPES).

ECUADORIAN COLLECTIONS: EL ORO: Above Piñas, close to Ayapampa, *Rose & Rose 23461* (NY, US); Tributary to Río Luis and Piedra Grande, 10 km NE of Curtincapa, 1600–1900 m, *Steyermark 53840* (F, US); Between Sambotambo and Portovelo, 1000–1800 m, *Steyermark 54228* (F). LOJA: 16 km N of Macarí, 1300 m, *Harling et al. 15313* (GB, SEL); Between Utuana and Colaisaca, 2700 m, *Harling et al. 20703* (GB, US); Celica–Alamor road, km 8, 2000 m, *Harling & Andersson 22156* (GB, US); km 3, 2200 m, *Harling & Andersson 22169* (GB), *22176* (GB, US). Province unknown: Palandra, *André 4638* (NY(2)).

DISTRIBUTION: Southern Mexico (Chiapas), probably adjacent Guatemala, southern Ecuador, and probably adjacent Peru (the species has been collected within less than 10 km from the borders of Guatemala and Peru).

DISTINGUISHING FEATURES: The species often has large (up to 20 cm long) ovate leaves, which frequently are apically congested. The 3.5–6 cm long corolla is red with a green limb, the 12–22 mm long calyx lobes are basally dissected, the ovary is sericeous, the style glabrous, and the nectary consists of four or five free glands (FIGURE 2A, C).

NOTES: The Mexican and Ecuadorian populations are considered conspecific although there are some minor differences in quantitative rather than in qualitative features. For example, the corolla length is about 3 cm in Mexico, but usually exceeds 3.5 cm (and occasionally attains 6 cm) in Ecuador, the calyx lobe length is 10–15 mm in Mexico and 15–25 mm in Ecuador, and its width is 1–2 mm and 2–4 mm, respectively.

53. **Columnea microsepala** (C. Morton) Kvist & L. Skog, comb. nov. *Alloplectus microsepalus* C. Morton in Fieldiana: Bot. **28:** 523. 1953. *Pentadenia microsepala* Wiehl. in Phytologia **27:** 375. 1973. TYPE: VENEZUELA: MONAGAS: *Steyermark 61905* (F, HOLOTYPE; US, ISOTYPE).

Pentadenia zapotalana Wiehl. in Selbyana **2:** 85, *pl. 26B.* 1977. *Columnea zapotalana* L. Skog in Taxon **33:** 126. 1984. TYPE: ECUADOR: LOS RÍOS: 20 km S of Quevedo, *Wiehler et al. 71312* (SEL, HOLOTYPE).

REPRESENTATIVE ECUADORIAN COLLECTIONS: AZUAY: Road Pasaje–Santa Isabel–Girón, Río Jubones valley, 600–1600 m, *Harling & Andersson 14460* (SEL). BOLÍVAR: Atio de Telimbela, 1500 m, *Acosta-Solís 6885* (F). EL ORO: Piñas–Santa Rosa road, 460 m, *Dodson et al. 8891* (MO, SEL). ESMERALDAS:

Río Cayapa, Santa María, 50 m, *Kvist et al. 48024* (AAU). GUAYAS: 3 km E of Olón, 75–190 m, *Dodson & Thien 1674* (US). LOJA: W of Loja, 1600 m, *Espinosa 1218* (US). LOS RÍOS: Hacienda Clementina, 30 m, *Harling 1674* (S). MANABÍ: N of Pajan, Naranja, 500 m, *Haught 3408* (AAU, US(2)). PICHINCHA: 35 km N of Santo Domingo de Los Colorados, Río Blanco bridge, 250 m, *Gentry 9625* (US).

DISTRIBUTION: Venezuela (widespread along the coast), extreme northwestern Peru (Tumbes), and western Ecuador. The species apparently is found mainly in semideciduous and deciduous forests and, along with *Columnea angustata,* is the most common species of section *Stygnanthe.*

DISTINGUISHING FEATURES: *Columnea microsepala* has dorsiventral shoots with strongly anisophyllous leaves that often are apically red below as in section *Collandra.* However, the species always has the nectary of four free glands typical of section *Stygnanthe* (FIGURE 2C). The flowers are densely congested and subtended by ovate to lanceolate bracts up to 2 cm long, the ca. 2 cm long calyx lobes are usually lanceolate, and the cylindric corollas are 1.8–2.5 cm long.

NOTES: *Columnea microsepala* is the most variable Ecuadorian species in section *Stygnanthe.* In the drier southern and western parts of its range (Peru, El Oro, and Manabí) the corollas are usually red and smaller than the yellow corollas found in the more humid northern parts of its range (Los Ríos, Pichincha, and Esmeraldas). The lower leaf surfaces vary from uniformly green or reddish to a pattern of green with a red apex.

There are no consistent differences between the Ecuadorian and Venezuelan populations; the latter tend to have a denser indumentum, but some Ecuadorian plants are extremely similar to those from Venezuela. Consequently, *Columnea microsepala* has a remarkable, disjunct distribution.

54. **Columnea orientandina** (Wiehl.) Kvist & L. Skog, comb. nov. *Pentadenia orientandina* Wiehl. in Selbyana **2:** 123. 1977. TYPE: Cultivated material originally from Ecuador, Prov. Morona-Santiago, Cordillera de Cutucú, *Wiehler 77123* (SEL, HOLOTYPE; US, ISOTYPE).

OTHER COLLECTIONS: ECUADOR: MORONA-SANTIAGO: Macas, Hotel El Valle garden, 1000 m, *Kvist 60424* (AAU, QCA, US); 10 km N of Macas, on border to Parque Nacional Sangai, 1200 m, *Kvist 60439* (AAU, QCA, QCNE, US); Cordillera de Cutucú, 25 km SE of Logroño, 1000 m, *Madison & Coleman 2537* (SEL); Cordillera de Cutucú, trail from Logroño to Yaupi, 1500 m, *Madison et al. 3420* (SEL). PASTAZA: Puyo–Tena road, close to Santa Clara, 1050 m, *Kvist et al. 60352* (AAU, NY, QCA, QCNE, US). PERU: PASCO: Pichis Trail, San Nicolas, 1100 m, *Killip & Smith 26059* (NY).

DISTRIBUTION: Central Peru and southeastern Ecuador.

DISTINGUISHING FEATURES: The Andes mountains separate *Columnea orientandina* from its closest relative, *C. microsepala.* Besides the differences pointed out in the key, the latter is a stouter plant.

Columnea orientandina has a habit similar to the species of section *Collandra,* and the red tips of the lower leaf surfaces add to this similarity. However, the only 4–8 cm long leaves of *C. orientandina* usually suffice to distinguish it from species of section *Collandra* where the length of the leaves nearly always exceeds 10 cm. In addition, the ca. 2 cm long narrow corollas and the presence of four or five nectary glands distinguish *C. orientandina* (FIGURE 2A, C).

NOTES: The collection from Pastaza (*Kvist et al. 60352*) differs by having conspicuously exserted stamens, an attribute otherwise only known from *Columnea byrsina* in the section *Stygnanthe.* However, other features of this collection are in accordance with *C. orientandina* rather than *C. byrsina.* This particular specimen may be a hybrid between these two species or a new, closely related species.

FIGURE 14. *Columnea ovatifolia* Kvist & L. Skog. A, habit; B, node showing glands at leaf base; C, calyx; D, flower; E, corolla opened to show stamens; F, flower with corolla and 2 calyx lobes removed to show pistil and nectary. (All *Harling & Andersson 12316,* GB, and *Luteyn et al. 8830,* NY.)

55. **Columnea ovatifolia** Kvist & L. Skog, sp. nov. TYPE: ECUADOR: CARCHI: Road Tulcan–Maldonado, 10 km SE of Maldonado, Campamento Machines, montane rain forest, 2200–2400 m, 28 Nov. 1974, *Harling & Andersson 12316* (GB, HOLOTYPE; SEL, ISOTYPE). FIGURE 14.

Differt a *Columnea lavandulacea* Kvist & L. Skog foliis ovatis isophyllis 1.5–2.5 cm longis corollis rubris 4–5 cm longis.

Epiphytic herbs, shoots to 50 cm long. Stems glabrescent to sericeous near apex with violet trichomes consisting of 5–10 uniseriate cells, stem diam. to 4 mm. Leaves isophyllous in pairs and somewhat coriaceous, blades ovate, 1.5–2.5 × 1–1.6 cm, apex acute to obtuse, base rounded, margin ciliate, upper surface dull green, often with violet blotches, glabrous, lower surface lighter green, sparsely pilose except veins and margin violet-sericeous, veins 3–4 per side, petioles 1–3 mm long. Inflorescences of single flowers in leaf axils (but never in opposite axils); pedicels 3–5 mm long, sericeous; bracts 1 per axil, scale-like, ca. 1.5 mm long, caducous. Calyx lobes equal, linear, 11–15 mm long and 2–3 mm wide at base, green, flushed with red, outside sparsely pilose, inside glabrous; corolla ventricose, 4–4.8 cm long, diam. 2.5–3.5 mm at base, widened to 5–7 mm, diam. 3–4 mm at throat, tube outside pink to red, sericeous mainly apically, inside glabrous to glandular-hairy in throat, limb subequal, lobes 1.5–2 mm long and 1.5–2.5 mm wide at base; filaments 32–42 mm long, basally adnate to corolla tube for 5–7 mm, anthers subincluded, ca. 2 × 2 mm; nectary of 2 glands (1 bilobed and 1 three-lobed or irregularly lobed); ovary 3–5 mm high, densely pilose, style 30–38 mm long, glabrous or sparsely pilose, stigma bilobed. Fruit and seeds not seen.

OTHER COLLECTIONS: ECUADOR: PICHINCHA: Old Quito–Nono–Mindo road, 9 km S of Tandayapa towards Mindo, 2460 m, *Luteyn et al. 8830* (NY). Province unknown: Río Salenté, 2250 m, *André 3705* (F).

DISTRIBUTION: The species is known only from the montane forests on the western slopes of the Ecuadorian Andes.

DISTINGUISHING FEATURES: The combination of 1.5–2.5 cm long ovate isophyllous leaves and 4–5 cm long red corollas sets *Columnea ovatifolia* apart from all other species of *Columnea.* In addition, the nectary morphology is unique (FIGURE 2H). *Columnea ovatifolia* has a close affinity to *C. lavandulacea* (q.v.).

56. **Columnea poortmannii** (Wiehl.) Kvist & L. Skog, comb. nov. *Trichantha poortmannii* Wiehl. in Selbyana **7**: 340. 1984. TYPE: ECUADOR: LOJA (ZAMORA-CHINCHIPE?): Cordillera de Zamora, *Poortmann 265* (P, HOLOTYPE; P, ISOTYPE).

OTHER COLLECTIONS: ECUADOR: ZAMORA-CHINCHIPE: SE of Loja, Zamora, Huaico, 2300 m, *Espinosa 2259* (US).

DISTRIBUTION: Apparently a rare and local endemic of a small area bordering the provinces of Loja and Zamora-Chinchipe in southern Ecuador. The species has not been collected in 40 years and may now be extinct.

DISTINGUISHING FEATURES: The combination of subequal, ovate leaves, lanceolate, ca. 2 cm long calyx lobes, ventricose, ca. 5 cm long red corollas with a green limb, and glabrous ovaries sets *Columnea poortmannii* apart from all other species of *Columnea.*

NOTES: *Columnea poortmannii* was originally described in the genus *Trichantha* (here the section *Ortholoma*) based on the presence of a bilobed dorsal nectary gland (FIGURE 2W). The single subsequent collection has the same nectary morphology. However, several other features common in section *Stygnanthe,* but rare in *Ortholoma,* characterize *C. poortmannii*: e.g., apically congested leaves and flowers, distinctly bicolored corolla tubes, and glabrous ovaries. The apparently most closely related species is the Peruvian *C. trollii* (Mansfeld, 1934), which Wiehler (1973) referred to the genus *Pentadenia* (in our concept of section *Stygnanthe*). The nectary of that species varies from four free glands to a single dorsal

bilobed gland (FIGURE 2C, D, W). Consequently, *C. poortmannii* is referred to section *Stygnanthe* despite the nectary being atypical in this group.

57. **Columnea spathulata** Mansf. in Notizbl. Bot. Gard. Berlin-Dahlem **14**(121): 37. 1938. *Pentadenia spathulata* Wiehl. in Phytologia **27:** 315. 1973. TYPE: ECUADOR: PICHINCHA: Santo Domingo de Los Colorados, *Schultze-Rhonhof 1876* (B, HOLOTYPE, no longer extant); ECUADOR: PICHINCHA: Santo Domingo de Los Colorados, Centinella, Montañas de Ila, 12 km from Patricia Pilar, virgin rain forest, 575 m, 10 July 1979, *Løjtnant & Molau 15811* (AAU, NEOTYPE, here designated).

SELECTED ECUADORIAN COLLECTIONS: BOLÍVAR: Babahoyo–Guaranda road, just above Balzapamba, 1500 m, *Holm-Nielsen et al. 23003* (AAU). COTOPAXI: Quevedo–Latacunga road, 700 m, *Holm-Nielsen et al. 2972* (AAU). ESMERALDAS: Río Cayapa, Zapallo Grande, *Kvist et al. 48344* (AAU, QCA, US). LOS RÍOS: 13 km E of Patricia Pilar, Centinella ridge area, *Hansen et al. 7774* (SEL). PICHINCHA: 5 km S of Santo Domingo, Hacienda San Fernando, *Hansen et al. 7850* (AAU, SEL).

DISTRIBUTION: Northwestern Colombia (Chocó) and western Ecuador.

DISTINGUISHING FEATURES: The shoots of *Columnea spathulata, C. orientandina,* and *C. microsepala* have the dorsiventral habit characterizing section *Collandra.* However, mainly because of the presence of four or five nectary glands, the three species are here referred to section *Stygnanthe* (FIGURE 2A, B, C). In addition, the smaller leaves and flowers also help to set them apart from the section *Collandra.* The purple lower leaf surfaces often have a green margin and/or veins, and the spathulate calyx lobes also distinguish *C. spathulata* from *C. orientandina* and *C. microsepala.*

EXCLUDED SPECIES

The following species occur in Ecuador and were either described as species of *Columnea* or were later transferred to the genus, where they are incorrectly placed:

Columnea dielsii Mansf. in Biblioth. Bot. **116:** 145. 1937. = **Alloplectus peruvianus** (Zahlb.) Kvist & L. Skog, comb. nov., based on *Columnea peruviana* Zahlb. in Ann. K.K. Naturhist. Hofmus. **7:** 8. 1892.

Columnea eriantha (Benth.) J. Hanst. in Linnaea **34:** 442. 1865. = **Kohleria villosa** (Fritsch) Wiehl. var. **anisophylla** (Fritsch) Kvist & L. Skog, stat. nov., based on *Diastema anisophyllum* Fritsch in Bot. Jahrb. Syst. **50:** 408. 1914.

Columnea lindenii O. Kuntze in Rev. Gen. Pl. **2:** 471. 1891. = *Alloplectus weirii* (O. Kuntze) Wiehl. in Phytologia **27:** 327. 1973.

Columnea peruviana Zahlb. in Ann. K.K. Naturhist. Hofmus. **7:** 8. 1892. = **Alloplectus peruvianus** (Zahlb.) Kvist & L. Skog, comb. nov.

Columnea sprucei O. Kuntze in Rev. Gen. Pl. **2:** 471. 1892. = *Alloplectus sprucei* (O. Kuntze) Wiehl. in Phytologia **27:** 327. 1973.

Columnea weirii O. Kuntze in Rev. Gen. Pl. **2:** 471. 1891. = *Alloplectus weirii* (O. Kuntze) Wiehl. in Phytologia **27:** 327. 1973.

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LITERATURE CITED

BEAUFORT-MURPHY, H. T. 1983. The seed surface morphology of the Gesneriaceae utilizing the scanning electron microscope and a new system for diagnosing seed morphology. Selbyana **6**(1–4): 220–422.

BENTHAM, G. 1876. Gesneriaceae. *In:* Bentham, G., & J. D. Hooker. Genera Plantarum **2**(2): 990–1025. Reeve & Co., London.

BEURLING, P. J. 1854. XLI. Gesneriaceae. Kongl. Svenska Vetensk. Acad. Handl. **1854:** 135–136.

CUATRECASAS, J. 1935. Plantae Isernianae, 1. Anal. Ci. Univ. Madrid **4:** 235–259 (reprint 42–56).

FRITSCH, K. 1893–1894. Gesneriaceae. *In:* Engler, A., & K. Prantl. Die Natürlichen Pflanzenfamilien. **4**(3b): 133–185. Verlag Engelmann, Leipzig.

FRITZE, K. J., & N. H. WILLIAMS. 1988. The taxonomic significance of pollen morphology in the *Columnea* alliance (Gesneriaceae: Gesnerioideae). Ann. Missouri Bot. Gard. **75:** 168–191.

GENTRY, A. H. 1977. Endangered plant species and habitats of Ecuador and Amazonian Peru. *In:* Prance, G. T., & T. Elias (eds.). Extinction is Forever, pp. 136–149. The New York Botanical Garden, New York.

HANSTEIN, J. 1854. Die Gesneraceen des Königlichen Herbariums und der Gärten zu Berlin, nebst Beobachtungen über die Familie im Ganzen. I. Abschnitt. Linnaea **26:** 145–216.

———. 1865. Die Gesneraceen des Königlichen Herbariums und der Gärten zu Berlin, nebst Beobachtungen über die Familie im Ganzen. II. Abschnitt, Drittes Stück. Linnaea **34:** 225–462.

HARLING, G. 1979. The vegetation types of Ecuador—A brief survey. *In:* Larsen, K., & L. B. Holm-Nielsen (eds.). Tropical Botany, pp. 165–174. Academic Press, New York.

HOLM-NIELSEN, L. B., L. P. KVIST, & M. AGUAVIL. 1983. Los investigaciones etnobotánicas entre los Colorados y los Cayapas. Misc. Antrop. Ecuadorana **3:** 89–116.

HOOKER, W. J. 1844. *Trichantha minor* Hook. Icon. Pl. **3:** *pl. 666.*

JONES, C. E., & P. V. RICH. 1972. Ornithophily and extrafloral color patterns in *Columnea florida* Morton (Gesneriaceae). Bull. S. California Acad. Sci. **71:** 113–116.

KUNTZE, C. E. O. 1891. Revisio Generum Plantarum. **2:** 375–1011. A. Felix, Leipzig.

KVIST, L. P. 1986. Gesneriads and snakebite. Gloxinian **36**(1): 8–13.

———. 1989. Popular names and medicinal uses of *Columnea* (Gesneriaceae). Gloxinian **39**(2): 21–25.

———. 1990. Revision of *Heppiella.* Syst. Bot. **15:** 610–625.

———, & L. B. HOLM-NIELSEN. 1987. Ethnobotanical aspects of lowland Ecuador. Opera Bot. **92:** 83–107.

———, & J. A. PEDERSEN. 1986. Distribution and taxonomic implications of some phenolics in the family Gesneriaceae determined by EPR spectroscopy. Biochem. Syst. Ecol. **14**(4): 385–405.

———, & L. E. SKOG. 1988a. *Columnea incredibilis* and *Cremosperma filicifolium*—Two remarkable new Gesneriaceae from western Ecuador. Nord. J. Bot. **8**(3): 253–257.

———, & ———. 1988b. The Genus *Cremosperma* (Gesneriaceae) in Ecuador. Nord. J. Bot. **8**(3): 259–269.

———, & ———. 1989. Revision of *Reldia* (Gesneriaceae). Nord. J. Bot. **8**(6): 601–611.

———, & ———. Revision of *Kohleria* (Gesneriaceae). Smithsonian Contr. Bot. **79** (in press).

LEMAIRE, C. 1847. *Columnea pilosa.* Columnée poilue. Fl. Serres Jard. Eur. **3:** *pl. 223.*

LINNAEUS, C. 1753. Species Plantarum. 1200 pp. Impensis Laurentii Salvii, Stockholm.

MANSFELD, R. 1934. VIII. Gesneriaceae Novae Andinae. I. Repert. Spec. Nov. Regni Veg. **36:** 120–124.

———. 1937. Gesneriaceae. *In:* Diels, F. L. E. Beiträge zur Kenntnis der Vegetation und Flora von Ecuador, pp. 144–147. E. Schweizerbart, Stuttgart.

MORGAN, M. T., & N. G. DENGLER. 1988. Vascular architecture in isophyllous and facultatively anisophyllous species of *Pentadenia* (Gesneriaceae). Amer. J. Bot. **75**: 1485–1494.

MORLEY, B. D. 1973a. Ecological factors of importance to *Columnea* taxonomy. *In:* Heywood, V. (ed.). Taxonomy and Ecology, pp. 265–281. Academic Press, New York.

———. 1973b. Materials for a treatment of *Columnea* in Panama. Ann. Missouri Bot. Gard. **60**: 449–460.

———. 1975. *Columnea purpureovittata,* a new species in cultivation. Garden (London) **100**(9): 438.

———. 1976. A key, typification and synonymy of the sections in the genus *Columnea* L. Contr. Natl. Bot. Gard. Glasnevin **1**(1): 1–11.

MORTON, C. V. 1937. New species of Costa Rican plants. J. Washington Acad. Sci. **27**: 304–312.

———. 1942. New Gesneriaceae from Panama. Ann. Missouri Bot. Gard. **29**: 35–58.

———. 1945. Seven new species of Gesneriaceae from Peru and Colombia. J. Washington Acad. Sci. **35**: 126–131.

———. 1963. A revision of *Trichantha* (Gesneriaceae). Contr. U.S. Natl. Herb. **38**(1): 1–27.

———. 1971a. The genus *Columnea* (Gesneriaceae) in Panama. Phytologia **21**: 165–195.

———. 1971b. A reduction of *Trichantha* to *Columnea* (Gesneriaceae). Phytologia **22**: 223–224.

OERSTED, A. S. 1858. Centralamericas Gesneraceer, et systematisk, plantegeografisk Bidrag til Centralamerikas Flora. 78 pp., 11 plates. F.S. Muhle, Copenhagen. Preprinted from Kongel. Danske Vidensk. Selsk. Skrift., Raekke 5, **5**: 77–152.

OLIVER, R. E., & L. E. SKOG. 1981. Gesneriaceae. *In:* Löve, A. Chromosome Number Reports LXXI. Taxon **30**(2): 506.

POEPPIG, E. F. 1840. *In:* Poeppig, E. F., & S. Endlicher. Nova Genera ac Species Plantarum 3, parts 1–2. 91 pp. F. Hofmeister, Leipzig.

RAFINESQUE-SCHMALTZ, C. S. 1814. 18. G. *Vireya.* Specchio Sci. **1**: 194.

———. 1837. 201. *Eusynetra. In:* Flora Telluriana **2**: 57. Philadelphia.

———. 1838. *Glycanthes, Aponoa. In:* Sylva Telluriana, pp. 83–84. Philadelphia.

SÁNCHEZ-BURGOS, A. A., & N. G. DENGLER. 1988. Leaf development in isophyllous and facultatively anisophyllous species of *Pentadenia* (Gesneriaceae). Amer. J. Bot. **75**: 1472–1484.

SHERK, L. E., & R. E. LEE. 1967. Interspecific hybridization in the genus *Columnea* (Gesneriaceae). Baileya **15**: 89–96.

SKOG, L. E. 1979. Family 175, Gesneriaceae. *In:* Woodson, R. E., Jr., & R. W. Schery (eds.). Flora of Panama, Part IX. Ann. Missouri Bot. Gard. **65**(3[1978]): 783–996.

———. 1984. A review of chromosome numbers in the Gesneriaceae. Selbyana **7**: 252–273.

SMITH, J. D. 1905. Undescribed plants from Guatemala and other Central American republics XXXII. Bot. Gaz. (Crawfordsville) **40**(1): 1–11.

TUSSAC, F. R. 1811–1813. *Dalbergaria phoenicea. In:* Flore des Antilles **1**: 141, *pl. 19.* Paris.

WIEHLER, H. 1973. One hundred transfers from *Alloplectus* and *Columnea* (Gesneriaceae). Phytologia **27**(5): 309–330.

———. 1975a. Name changes in neotropical Gesneriaceae. Selbyana **1**(1): 32–36.

———. 1975b. Three new species of *Trichantha* from eastern Ecuador and Peru. Selbyana **1**(1): 36–44.

———. 1977. New genera and species of Gesneriaceae from the neotropics. Selbyana **2**(1): 67–132.

———. 1978. Miscellaneous transfers and new species of neotropical Gesneriaceae. Selbyana **5**(1): 61–93.

———. 1981. New species and name changes in neotropical Gesneriaceae. Selbyana **5**(3–4): 378–384.

———. 1983. A synopsis of the neotropical Gesneriaceae. Selbyana **6**(1–4): 1–219.

———. 1984. Miscellaneous new species in the Gesneriaceae. Selbyana **7**(2–4): 328–347.

WILLIAMS, N. H. 1978. Pollen structure and systematics of the neotropical Gesneriaceae. Selbyana **2**(2–3): 310–322.

ZAHLBRÜCKNER, A. 1892. Novitiae Peruvianae. Ann. K.K. Naturhist. Hofmus. **7**: 1–10.

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